

RESEARCH ARTICLE

Degradation influences equilibrium and non-equilibrium dynamics in rangelands: implications in resilience and stability

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Funding information Instituto Nacional de Tecnología Agropecuaria; Ministerio de Ciencia y Tecnología de la Nación Argentina

Co-ordinating Editor: Lauchlan Fraser

Abstract

Question: Plant communities are structured by both equilibrium and non-equilibrium dynamics, which interact at different spatiotemporal 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: Graminous–subshrubby steppes of northern Patagonia, Argentina.

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 anticipate climatically favorable and unfavorable periods.

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KEYWORDS

alternative states, amplitude, elasticity, grazing, malleability, rainfall events, resistance, states and transitions model, thresholds

1 | 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 the 1990s. This model is based in the equilibrium paradigm (Briske et al., 2003, 2017), and asserts that vegetation dynamics are mainly driven by internal regulation processes through *negative feedback mechanisms* (e.g. intra- and interspecific interactions such as herbivory and competition; see the explanation of feedback mechanisms in [Appendix S3](#)) (Wu & Loucks, 1995; Briske et al., 2003, 2005; Derry & Boone, 2010; Briske, 2017). 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 & Boone, 2010). However, new advances in the 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 spatiotemporal 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 not in balance 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 & Sala, 1992; Noy-Meir, 1995; Fernández-Gimenez & Allen-Diaz, 1999). Then, 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 & Venable, 1996; Ludwig et al., 1999). Stochastic rain events can modulate the dynamics of plant communities (Noy-Meir, 1973; Westoby, 1979; Westoby et al., 1989; Chesson et al., 2004) at distinct scales (Schwinning & Sala, 2004).

The occurrence and intensity of rainfall events can affect internal regulation processes via biogeochemical cycles at the ecosystem scale and biological interactions and recruitment processes (Guterman, 1993) at the community scale (Noy-Meir, 1973; Gebauer & Ehleringer, 2000; Novoplansky & Goldberg, 2001; Chesson et al., 2004), and may even trigger recovery processes, plant succession (Schwinning & Sala, 2004) or degradation. External factors usually drive vegetation dynamics in arid and semi-arid ecosystems (Fuhlendorf et al., 2001; Briske et al., 2003; Bestelmeyer et al., 2004). These types of ecosystems are characterized by high spatiotemporal variability, mainly in climate (Romero et al., 1998; Ramos & Martínez-Casasnovas, 2006). However, the consequences of climate uncertainty in the functioning of plant communities have rarely been 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 & 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. In this framework, for the same reference ecosystem (i.e. same *ecological site*, see [Appendix S6](#)), 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, and 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 intraspecific 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 to be more stable and thus, to persist or remain in their 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 understanding how degradation affects the response capacity of ecosystems to environmental drivers (Chesson et al., 2004; Gillespie & 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 such 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.

2 | MATERIALS AND METHODS

2.1 | 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 ± 82.5 mm, and more than 70% of the precipitation falls during autumn and winter (Bustos & Rochi, 1993; Bustos, 2006). In this area, stochastic high rainfall events are common (Golluscio et al., 1998; Oesterheld et al., 2001; Schwinning & Ehleringer, 2001; Schwinning & Sala, 2004; Appendix S1). 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, Appendix S1). 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 the Western Patagonian District. Species nomenclature follows Flora Argentina (<https://floraargentina.edu.ar/>).

2.2 | 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 States I and II in state and transition models developed for the area (López et al., 2013; López & Cavallero, 2017). The vegetation of the sectors in the reference state is graminous–shrubby steppe

of *Poa ligularis* and *Mulinum spinosum*. These sectors have been excluded from sheep grazing since 1975 (i.e. >30 years without livestock grazing). Plant cover is greater than 60%, dominated by *Poa 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 *Mulinum spinosum*, *Senecio* spp. and *Pappostipa speciosa*, generated by an interaction between high grazing pressure (i.e. 0.6–0.7 sheep ha⁻¹ year⁻¹) for more than 25 years and recurrent droughts. Specifically, plant cover is near 40%, with 20% *Pappostipa speciosa*, and 1.5% *Poa 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 for the effects of a slight slope (<3%) in the landscape, we used a Completely Randomized Block Design (Steel & 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 × 25 m enclosures in October 2005 (adjacent to the reference state), one enclosure in each block ($n = 4$ enclosures in the degraded state). Within each block and state, we delimited two 2 m × 2 m subplots and irrigation treatments (with irrigation, hereafter “I”; and without irrigation, hereafter “NI”) that were randomly assigned to each subplot ($n = 4$ 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 subplot. The dimensions of the main plots were 25 m × 25 m, and of subplots they were 2 m × 2 m. In each subplot we assessed: (i) the density of emerged seedlings of perennial species and their survival; (ii) grass and shrub growth; and (iii) plant cover (at the beginning and at the end of the experiment).

2.3 | Sampling procedure

2.3.1 | Perennial species recruitment

During four years (2006–2009) 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 subplot. Recording seedling density in distinct seasons allows its association with different demographic processes such 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°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.

2.3.2 | Plant growth

2.3.2.1 | Grasses

In September 2005, 2006 and 2007, we selected two individuals of *Poa ligularis* and two of *Pappostipa 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 on the eastern edge and another on 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 lengths of the longest leaf of each tiller were summed to obtain a single value for each marked tiller. To calculate these variables, the initial number of tillers and leaves, and initial leaf lengths recorded in September were subtracted from the final values recorded in April of the subsequent year. To be able to compare between subplots having distinct cover of each grass species, we estimated relative tiller production per subplot. Thus, tiller production was relativized by species cover in each state:

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

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*).

2.3.2.2 | Shrubs

In each subplot we selected one individual of *Mulinum spinosum* and another of *Senecio 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, 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 from the distal portion of each branch. To estimate bud production, we counted the number of secondary branches arising from the marked branch. Finally, in *Mulinum 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).

2.3.3 | Plant cover

To assess whether the community response to simulated high summer rainfall events can be recorded at a subplot scale (i.e. at a scale broader than the 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 m × 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.

2.3.4 | 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:

$$RI_{St} = (NI_{RRi} - I_{RRi}) \times \frac{1}{(NI_{RRi})}$$

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 (NI_{RR}) plots and irrigated plots (I_{RR}) 25 days after the last irrigation of each year i (i.e., this is the first sampling carried out 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, as they imply a great change in response to external factors (Appendix S6).

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:

$$EI_{St} = \sum_k^m \left[(NI_{RRi} - I_{RRi}) \times \frac{1}{(NI_{RRi})} \right]$$

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 and irrigated plots in year i (2006 or 2007). This index was calculated for each state (St: reference state or degraded state) separately. The smaller the monthly difference between non-irrigated plots and irrigated plots, the higher the speed of recovery to the reference values (NI_{RR}). 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 did not return, or returned slowly, to its initial or original levels after the occurrence of a disturbance or a favorable 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 and Suding, 2009). Malleability index (MI) was calculated as follows:

$$MI_{St} = (I_{RRf} - NI_{RRi}) \times \frac{1}{(NI_{RRi})}$$

This index was calculated for each state separately (St: reference state or degraded state) for a given variable (seedling density and species cover) as the difference of irrigated plots (I_{RRf}) and

non-irrigated plots (NI_{RRi}) 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 and initial values, the higher the index will be, 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 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 Appendix S6), whereas a greater malleability indicates a lower resilience of that state due to a lower ability to recover pre-disturbance levels. The main adaptation of three resilience proxies 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 the 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 preceding the rainfall simulations and at the end of the study in October 2009).

2.3.5 | 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 between 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 from the historical maximum (Bustos, 2006). According to these data, we added a maximum of 70 mm of water per year, by simulating several events not larger than 10 mm each (Coronato & Bertiller, 1996; Golluscio et al., 1998; Oesterheld et al., 2001; Schwinning & Ehleringer, 2001; Schwinning & 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 subplots 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 subplot. To avoid the “edge effect” on soil humidity that could be caused by the dry microenvironment surrounding each subplot, we also irrigated a 1-m buffer belt around each subplot. Thus, we irrigated a total area of 4 m × 4 m, that included the 2 m × 2 m subplot at the center. We checked that each subplot received the same amount of water (i.e. homogeneously distributed in space) by

placing four beakers at the vertices of each subplot. 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 the frequency and intensity of precipitation. 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 subplots 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 the 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 subplots received a total of 111.4 mm (i.e. simulated + natural rainfall, see Table 1).

2.4 | 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 versus degraded state), irrigation, with two levels (I versus 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. Degradation state and irrigation with their 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 subplots. The response variables considered in this model were: total density of seedlings of main perennial species emerged and surviving, 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: *Poa ligularis* versus *Pappostipa speciosa*), and their 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 subplot were included as response variables. Because these variables were recorded in subsamples (i.e. four tillers within each plant, and two plants within each subplot), raw data were averaged to include a single value for each subplot 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 in the statistical software SAS (SAS Institute Inc., 1999, Cary, NC, USA; 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 power x^2 . Significance level used in all analyses was $\alpha = 0.05$. Significant interactions were evaluated using Bonferroni tests.

3 | RESULTS

3.1 | Perennial species recruitment

Seedling emergence of perennial species significantly increased in response to irrigation (Figure 1a,c; $p \leq 0.05$). Overall, forage grass species (mainly *Pappostipa speciosa*, *Bromus setifolius* and *Hordeum comosum*) accounted for more than 80% of all seedling counts, whereas shrub species (mainly *Mulinum spinosum* and *Senecio filaginoides*) accounted for less than 5% of seedling counts (Appendix S4). The response pattern of the grass species was similar to the general pattern of all perennial species (Figure 1; Appendix S4). The density of seedlings emerged in 2006 was, on average, two times greater in irrigated subplots than in those not irrigated (Figure 1a; $p \leq 0.05$). We recorded the same pattern for seedlings

| | | December | January | February | March | Total |
|--------------------|-------------|----------|---------|----------|-------|-------|
| Historical average | | 6.8 | 4.5 | 13.3 | 17.4 | 42 |
| Summer 2005–2006 | Rainfall | 22.6 | 17.4 | 55.2 | 5.6 | 100.8 |
| | Irrigations | 5.0 | 10.0 | 0.0 | 30.0 | 45.0 |
| Summer 2006–2007 | Rainfall | 11.8 | 4.6 | 4.0 | 21.0 | 41.4 |
| | Irrigations | 10.0 | 10.0 | 20.0 | 30.0 | 70.0 |

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

emerged in 2007, with mean density being 5.6 times greater in irrigated than in non-irrigated subplots (Figure 1c; $p \leq 0.05$).

At the end of the experiment, seedling survival depended on irrigation and on rangeland degradation state (Figure 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 subplots of degraded state than in non-irrigated subplots of both states (see April 2009 in Figure 1a; $p < 0.05$). However, survival percentage was greatest in non-irrigated plots of the reference state, followed by irrigated plots of the degraded state, being lowest in

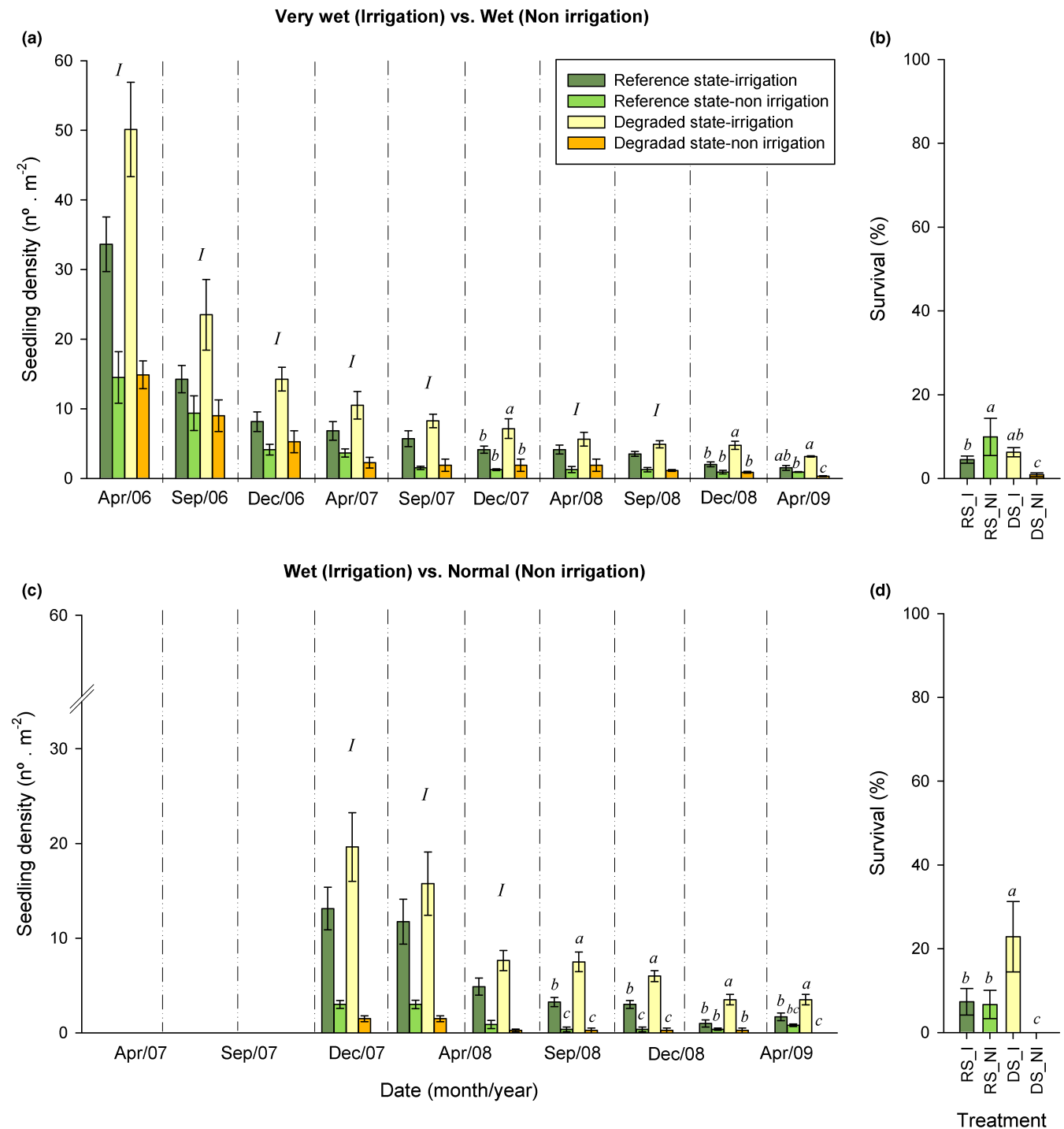


FIGURE 1 Mean density (\pm SE) of seedlings of perennial species emerged in April 2006 (a) and 2007 (c) and mean density of surviving seedlings (\pm SE) during the subsequent years until April 2009. Mean survival percentage (\pm SE) of seedlings of perennial species at the end of the study for the cohorts 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 the irrigation factor in each month are shown by the letter "I", whereas significant interactions for state and irrigation factors are shown with lowercase letters, based on Bonferroni tests ($p \leq 0.05$). Statistical analyses were done for each month separately

non-irrigated plots of the degraded state (Figure 1b). Two years after emergence in 2007, the density of surviving seedlings was, at least, 4.8 times greater in irrigated plots of the degraded state than in the other treatments (see April 2009 in Figure 1c; $p < 0.05$). Survival percentage showed the same pattern, being highest in irrigated plots of the degraded state and null in non-irrigated plots of the degraded state (Figure 1d; $p < 0.05$).

3.2 | Plant growth

3.2.1 | Grasses

The influence of irrigation on grass growth depended mainly on the species, but in some cases on rangeland degradation state (Figures 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, *Poa ligularis* showed a greater response to higher water availability than *Pappostipa speciosa* (Figure 2). In contrast, when considering the cover of each species at subplot level, the degradation state became more important in modulating the response to irrigation (Figure 3). Thus, at subplot level, the response to irrigation was highest in *Poa ligularis* individuals growing in the reference state (Figure 3).

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

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

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

ligularis than in *Pappostipa speciosa*, independently of degradation state and irrigation (Figure 2i).

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

3.2.2 | Shrubs

Seasonal growth depended on degradation state and irrigation for both shrub species (Figure 4a-c). Specifically, irrigation only promoted seasonal growth in the degraded state. This pattern was recorded during the three years of the study in *Mulinum spinosum*, whereas during 2006 and 2007 it was found in *Senecio filaginoides*. In 2008, seasonal growth of *Senecio filaginoides* was similar between treatments (Figure 4a-c).

Bud production showed different patterns between years in both shrub species (Figure 4d-f). In 2006, bud production of *Mulinum spinosum* depended on degradation state and irrigation. Specifically, individuals in the degraded state produced 69% more buds than those in the reference state without irrigation ($p < 0.05$; Figure 4d). In contrast, bud production of *Senecio filaginoides* was similar among treatments (Figure 4d). In 2007, irrigation promoted bud production in *Mulinum spinosum*, in subplots with irrigation being twice that in those without it ($p < 0.05$; Figure 4e). During the same year, bud production in *Senecio filaginoides* in irrigated subplots of both states was at least twice that in non-irrigated subplots of the degraded state ($p < 0.05$; Figure 4e). Finally, in 2008 bud production was similar among treatments for both species (Figure 4f).

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

3.3 | Resilience assessment

3.3.1 | Perennial species recruitment

Resistance, elasticity and malleability of the cohort 2006 were similar between states (Figure 5). However, for the cohort 2007, the reference state had significantly greater resistance and elasticity to simulated high summer rainfall events than the degraded state

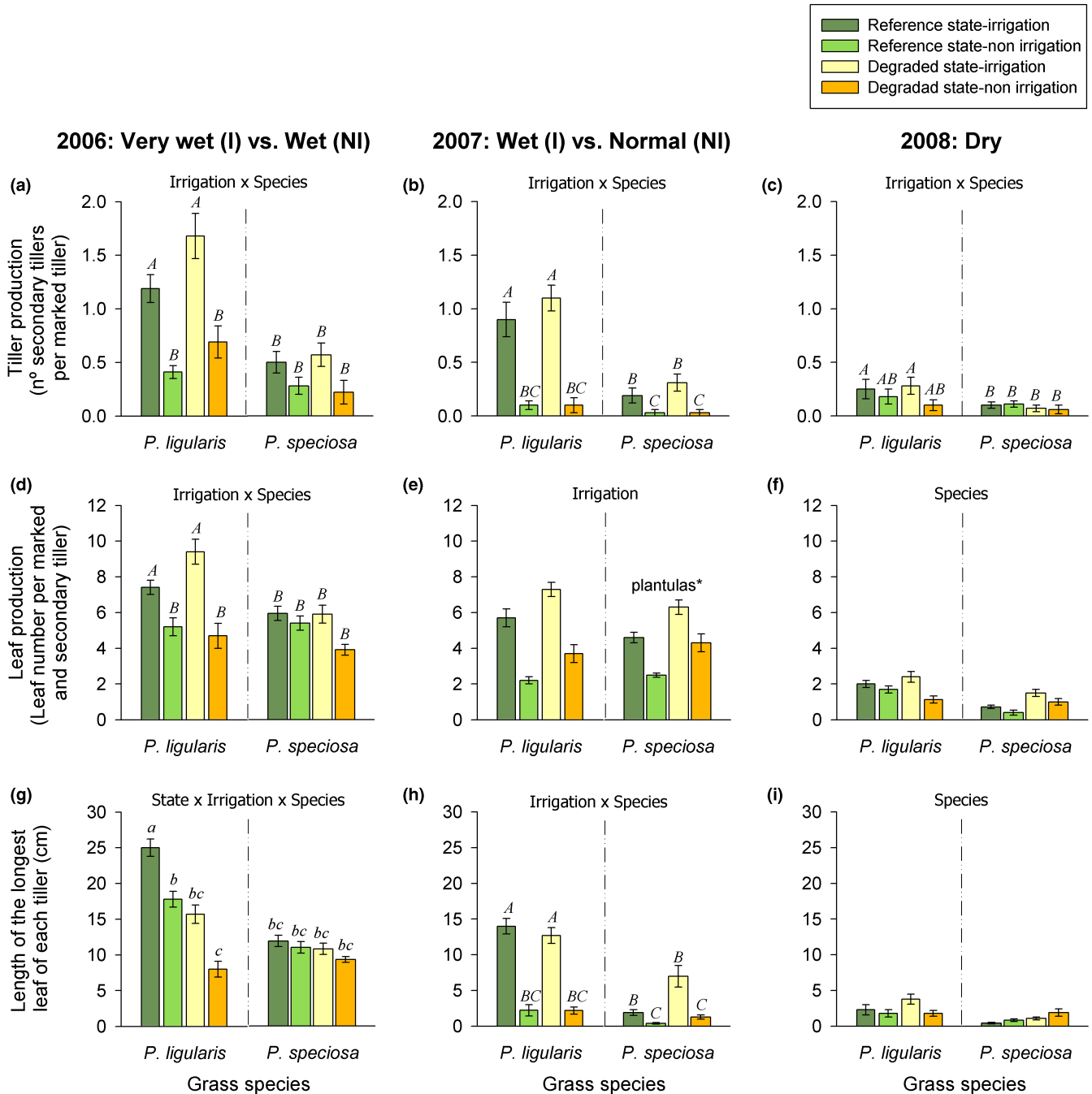


FIGURE 2 Mean (\pm SE) tiller production (a–c), leaf production (d–f), and length of the longest leaf (g–i) of each marked tiller for *Poa ligularis* and *Pappostipa speciosa* during the growing seasons of 2006, 2007 and 2008, in reference and degraded states with and without irrigation. Significant effects (for one factor or its interactions) are indicated on each graph as follows: State, Irrigation and/or Species) are shown at the top of each subgraph based on Bonferroni tests ($p \leq 0.05$). Significance of two-way interactions (irrigation \times species) is shown with uppercase letters; of three-way interactions (state \times irrigation \times species) with lowercase letters

(Figure 5b,c). In contrast, malleability was significantly greater in the degraded than the reference state (Figure 5c).

3.3.2 | Vegetation cover

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

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 (Figure 1) and seasonal shrub growth (Figure 4). In contrast, irrigation promoted grass growth in both states (degraded and reference state), with *Poa ligularis* having the greatest response (Figure 2). Nevertheless,

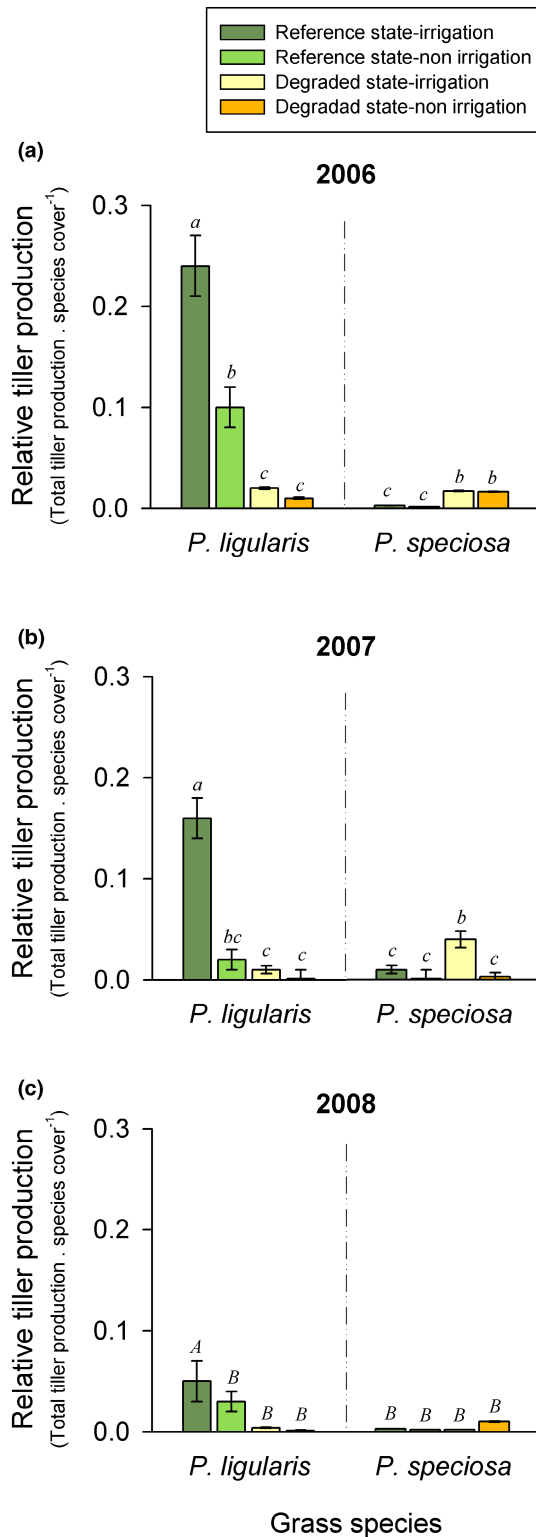


FIGURE 3 Mean (\pm SE) relative tiller production for *Poa ligularis* and *Pappostipa speciosa* during the growing seasons of 2006 (a), 2007 (b) and 2008 (c), in reference and degraded states with and without irrigation. Significance of two-way interactions (State \times Species) based on Bonferroni tests ($p < 0.05$) is shown with uppercase letters, and the three-way interactions (State \times Irrigation \times Species) with lowercase letters.

since the cover by species is different between the alternative states, at community level, the response to irrigation also depended on the state of the ecosystem. The effect of irrigation on grass growth was greater in the reference than in the degraded state (Figure 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 higher 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 (Figures 5–7).

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 (Villagra et al., 2009; Easdale & Rosso, 2010). This pattern highlights that rainfall variability is the rule rather than the exception in arid and semiarid ecosystems (Ramos & 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.

4.1 | Perennial species recruitment

The simulation of high summer rainfall events increased seedling emergence and short-term survival in both states (Figure 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 (Figure 1b, d). In fact, seedling survival was the lowest in the degraded state without irrigation. 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 the absence of irrigation 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, but greater malleability in the degraded than in the reference state in response to abundant summer rainfall events (Figure 5a–c). Consequently, our results indicate that rainfall variability exerted a

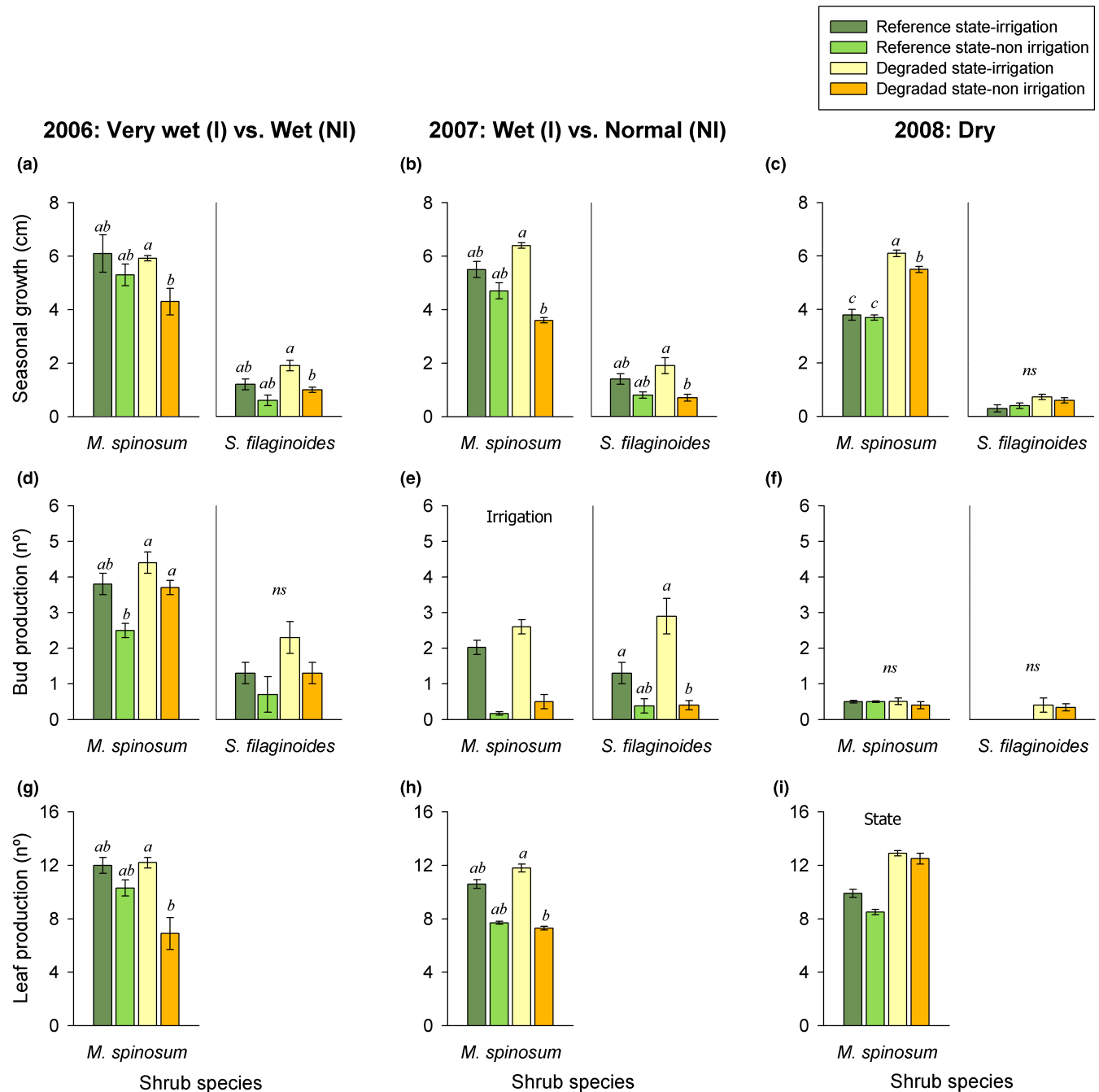


FIGURE 4 Mean (\pm SE) seasonal growth (a–c), bud production (d–f), and leaf production (g–i) in each marked branch for *Mulinum spinosum* and *Senecio filaginoides* during the growing seasons of 2006, 2007 and 2008, in reference and degraded states with (I) and without irrigation (NI). Significant effects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

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 & 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 & 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 *Poa 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

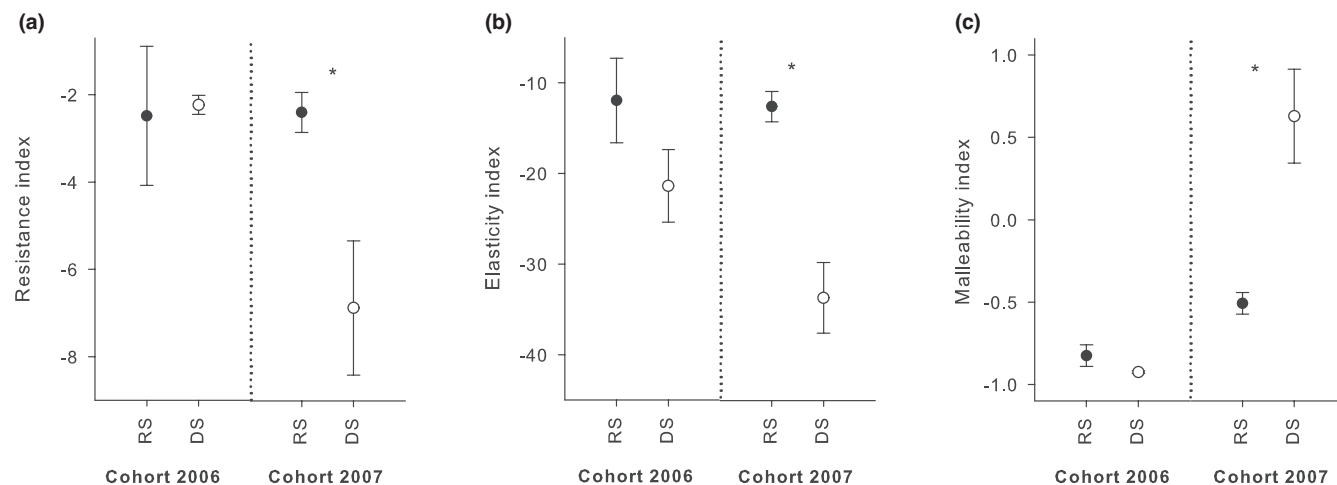


FIGURE 5 Mean (\pm SE) of ecological resilience proxies (adapted from Sheehan, 1984; Washington-Allen et al., 2008; Wang et al., 2014; and Hoekstra et al., 2015) for the reference (RS) and degraded states (DS): resistance index (a), elasticity index (b) and malleability index (c) in response to the simulation of high summer rainfall events, calculated for seedling density of perennial species for cohorts 2006 and 2007; significant differences between states are indicated by an asterisk (*) ($p < 0.05$)

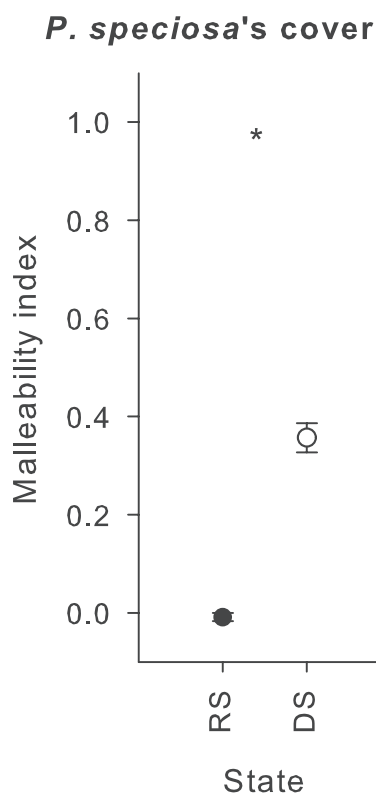


FIGURE 6 Mean (\pm SE) of malleability index calculated for the change in *Pappostipa speciosa* cover in response to the simulation of high summer rainfall events; significant differences between reference (RS) and degraded states (DS) are indicated by an asterisk (*) ($p < 0.05$)

those of other studies that found that competition between adults and seedlings decreased the survival of younger individuals (Aguar & Sala, 1994; Defossé et al., 1997; López & Cavallero, 2017). This fact could explain the greater resistance and elasticity of the reference state in comparison with that recorded in the degraded state

(Figures 4 and 5). In contrast, a low grass cover in the degraded state (i.e. 21.5% *sensu* López et al., 2013) would diminish competition for water between seedlings and adult grass individuals, and thus would increase state malleability in response to abundant summer rainfall events (Figure 5c). 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 (Aguar & Sala, 1994; Greenlee & Callaway, 1996; Holmgren et al., 2001, 2006; Hunt, 2001; Bisigato & Bertiller, 2004). 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 such as seed germination and seedling emergence (López & 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 the reference state; see Appendix S6). 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 & Walkinson, 1981; Aguar & Sala, 1994; Soriano et al., 1994; Baskin & Baskin, 2001; Bisigato & 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).

4.2 | 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 (Figure 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 *Poa ligularis* individuals in both states, whereas *Pappostipa speciosa* showed no response (Figure 2a,d). Therefore, at the individual level, *Poa ligularis* showed a greater capacity than *Pappostipa speciosa* to take advantage of increases in water availability in both states. This result suggests that *Pappostipa speciosa* would be more adapted than *Poa ligularis* to grow in drier conditions (Fernández et al., 2002; Graff et al., 2007; Graff, 2009; López, 2011). Interspecific differences in the response to irrigation could be caused by a net photosynthetic rate in *Pappostipa speciosa* that saturates at lower levels of soil water availability than that of *Poa ligularis* (Graff, 2009). Therefore, *Poa ligularis* and *Pappostipa 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 spatiotemporal 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 *Poa ligularis*, irrigated subplots in the reference state had the greatest relative tiller production (Figure 3a,b). This result was mainly due to differences in species cover between alternative states. In the reference state, *Poa ligularis* covered approximately a 30% of the surface; in the degraded state cover was ~1.5% (López et al., 2013). This large cover differences may have caused differences in relative tiller production at the subplot level between states (Figure 3a,b). In contrast, relative tiller production per subplot in *Pappostipa speciosa* was greater in the degraded than in the reference state; showing no response to irrigation during the wet year (i.e. 2006 growing season; Figure 3a), but increasing relative tiller production in response to irrigation during the normal year (i.e. 2007 growing season; Figure 3b). The greater relative tiller production of *Pappostipa speciosa* in the degraded state could also be caused by cover differences between alternative states. In the reference state, *Pappostipa speciosa* accounted for 7% of surface cover but covers 20% of the 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 (Figure 3a) suggests that the net photosynthetic rate of *Pappostipa speciosa* might saturate with large increases in water availability. Consequently, in concordance with the results found at individual level, *Poa ligularis* would be more efficient

in taking advantage of increases in water availability during wet periods, whereas *Pappostipa speciosa* would be more drought-tolerant (Fernández et al., 2002; Graff et al., 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) (Figure 4a,b,d,g,h). The greater response of shrubs to irrigation in the degraded state could be caused by a lower grass cover in that state (mainly of *Poa 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 *Poa ligularis* and *Pappostipa speciosa*) would decrease water availability for species with deeper roots (like *Mulinum spinosum*) (López & 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 & 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 (Aguar & Sala, 1994; López & 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, *Mulinum spinosum* has deeper roots than *Senecio filaginoides*, which can partially overlap the roots of grasses (López & Cavallero, 2017). Thus, *Mulinum 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 & Huntly, 1997; Chesson et al., 2004) would also explain the differential response to abundant summer rainfall events for *Poa ligularis* and *Pappostipa speciosa* (Fernández et al., 2002; Graff et al., 2007; Graff, 2009). Therefore, the use of soil water resources would be spatially and temporally 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 *Poa ligularis* cover in the reference state in response to irrigation (i.e. since relative tiller production was highest in this treatment, Figure 3). 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 intraspecific competition, which increases in the absence of grazing pressure. Specifically, Gittins (2011) recorded a high tiller mortality in *Poa ligularis* individuals growing in areas with low or null grazing pressure (i.e. with a high plant and *Poa ligularis* cover). The increase in tiller mortality in

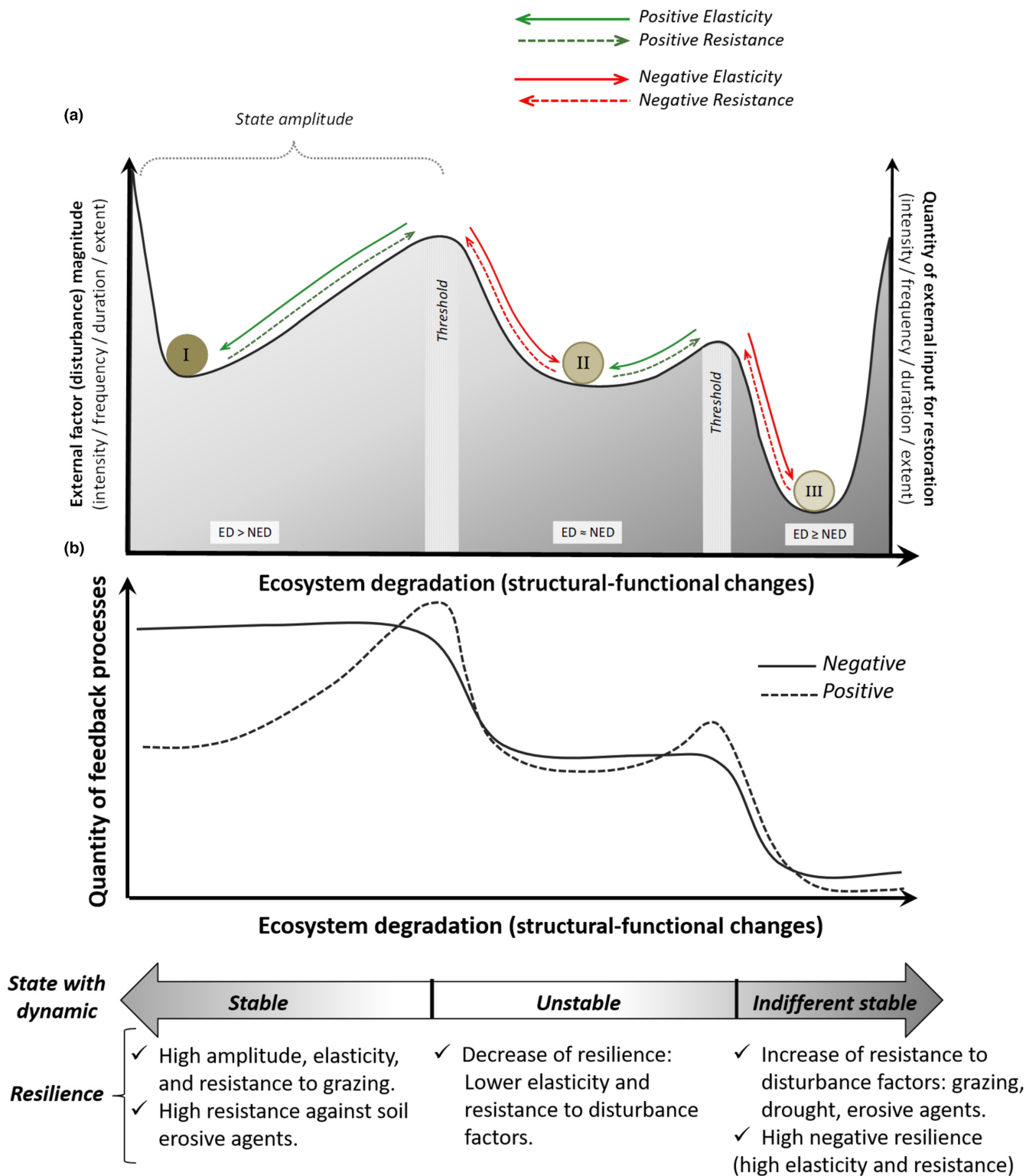
response to decreasing grazing pressure has also been recorded for several forage grasses (Lemaire et al., 2000). Therefore, in the reference state where grazing was excluded during at least 30 years, *Poa ligularis* individuals had a high tiller production which might have been compensated by a high mortality caused by competition not only for resource 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 (Figure 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, *Poa 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 *Pappostipa speciosa*'s cover in response to irrigation in the degraded state. In this case, *Pappostipa speciosa* is the dominant grass species in the degraded state, accounting for 93% of grass cover. In this state, tiller mortality due to resource competition at intra- and interindividual 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 *Pappostipa speciosa*'s cover. Finally, the lack of response for the total plant cover and of species cover (except for *Pappostipa speciosa*) can be associated with the occurrence of a drought during 2008–2009, 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 *Pappostipa speciosa* to a lesser extent than that of *Poa 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; Figures 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

FIGURE 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). States 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's degradation (structural-functional changes) triggered by a disturbance factor (e.g. overgrazing and/or droughts). The y-axis represents the amount of pressure 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 the absence of disturbance (associated with the recovery slope of the 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 speed and amount of degradation (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 y-axis of Figure 7a), and the y-axis represents the amount of feedback processes (negative and positive) in each state. In this example (see panels [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 Appendix S3). 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 in Appendix S6) causing high negative resilience limiting restoration (*sensu* Lake, 2013)



resource availability (i.e. wet or dry periods respectively). This is evidenced by the increase in seedling recruitment (Figure 1), in shrub growth (Figure 4), and in *Pappostipa speciosa*'s relative tiller production (Figure 3a,b) and cover in response to irrigation (Figure 6); as well as in the low seedling emergence (Figure 1a), null seedling survival (Figure 1b), and low grass growth (Figure 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 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 Appendix S6) (Figure 5). These parameters capture different aspects of resilience of alternative states in response to external drivers and/or disturbance factors (Figure 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 continuing to degrade and/or recovering 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).

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) (Figure 7; Appendix S6). 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 2008–2009 drought; Figures 5a), 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* (Figure 5b) due to its ability to recruit new individuals and vegetative growth, even after the 2007–2008 drought (Figures 1–3), and to quickly return to its pre-event values (or “average values”) following disturbance (Figure 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 Figure 7a) to an alternative state. Consequently, state I has a malleability index close to zero and lower

than that of more degraded states (Figures 5c, 6), 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 (Figure 7b; Appendix S3 and Appendix S6) 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 Figure 7a), negative feedback mechanisms prevail over positive feedback mechanisms, maintaining the ecosystem in the alternative state (Briske et al., 2006; Briske, 2017) (Figure 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) (Figure 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 unstable dynamics, and it would have a lower resilience (positive and negative) than the reference state. In our case study, the reduced ecological resilience of the intermediately degraded state II is indicated by reduced *amplitude*, *resistance*, and *elasticity* but greater malleability than the reference state (Figures 5, 6, 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 accelerate erosion; López et al., 2013); and (iii) stochastic weather events, including favorable high summer rainfall events (Figure 5a) or unfavorable droughts (due to the null seedling recruitment and low grass growth in response to the 2007–2008 drought; Figures 1–3; López & Cavallero, 2017). Lower *elasticity* might also be associated with more xeric micro-environmental conditions, which decreased plant recruitment and vegetative growth in non-irrigated subplots (Figures 1–3, 5) (López, 2011; López & Cavallero, 2017). Finally, the greater *malleability* (Figures 5c, 6) is reflected in the 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 lesser

basin depth of state II in [Figure 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. *Poa ligularis*), and the increase in the abundance of drought-resistant and unpalatable species (i.e. *Pappostipa speciosa* f. *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 of state II for two reasons ([Figure 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 & Cavallero, 2017). Second, there is less soil to be eroded because the soil has been already been lost with exposed rock at the surface (see State III in [Figure 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 & Cavallero, 2017), decreasing in turn the state's ability to respond to disturbances (see greater basin depth of State III in [Figure 7](#)). In contrast, the negative resilience of this state ([Figure 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 ([Figure 7a](#)).

To summarize, reference 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 (such 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 & Cavallero, 2017) ([Figure 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 [Figure 7a](#)), the stocking rate should periodically be adjusted based on the rainfall recorded during the growing season, and on threshold indicators of the state (e.g. risk phase with >45% plant cover, and >7% *Poa ligularis* cover, *sensu* López et al., 2013). In states with intermediate degradation, our results suggest that, in the absence of grazing, high summer rainfall events can trigger a positive transition ([Figure 1](#)). This positive transition (associated with episodic windows of recovery) would increase grass cover (i.e. *Pappostipa 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 recovery to the reference state, or if wet periods trigger a transition to a new state dominated by *Pappostipa speciosa* and co-dominated by other species of high forage value, such as *Hordeum comosum*. Therefore, in states with intermediate degradation, grazing should be excluded during wet periods to allow recovery transitions (positive transition, see [Appendix S6](#)), 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, [Figure 7](#)), rehabilitation practices promoting shrub species adapted to arid environments should be implemented (López & 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.

ACKNOWLEDGEMENTS

We thank INTA for providing the structure and logistics for this study, the project PICT-2012-1392 (FonCyT) for financial support; and M. Easdale, G. Siffredi, D. Bran, H. Moraga and M. Aguiar for contributions and conceptual suggestions on field work. We also thank M. Easdale for encouraging us to publish these ideas.

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1.

Appendix S2.

Appendix S3.

Appendix S4.

Appendix S5.

Appendix S6.

How to cite this article: López, D.R., Cavallero, L., Willems, P., Bestelmeyer, B.T. & Brizuela, M.A. (2022) Degradation influences equilibrium and non-equilibrium dynamics in rangelands: Implications in resilience and stability. *Applied Vegetation Science*, 25, e12670. Available from: <https://doi.org/10.1111/avsc.12670>

Appendix S1

Table S1.A. Mean annual rainfall (\pm SD) and wet years, in which rainfall was one standard deviation greater than the historical average. Bustos and Rochi (1993); Bustos (2006); unpublished data recorded by meteorological station of INTA EEA Bariloche field station.

| Year | Mean anual rainfall (\pm SD) | 1980 | 1993 | 1997 | 2006 |
|------------------|------------------------------------|------|------|------|------|
| Rainfall (mm) | 265 (80) | 356 | 485 | 364 | 370 |

Table S1.B. Mean summer rainfall (december-march), and years in which rainfall was one standard deviation greater or smaller than mean summer rainfall. Bustos and Rochi (1993); Bustos (2006); unpublished data recorded by meteorological station of INTA EEA Bariloche field station.

| Summer | Mean summer rainfall (\pm SD) | 1978- 1979 | 1979- 1980 | 1984- 1985 | 1986- 1987 | 1988- 1998 | 1990- 1991 | 1992- 1993 | 2002- 2003 | 2005- 2006 | 2007- 2008 |
|------------------|--|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| Rainfall (mm) | 43,5 (12) | 0 | 74 | 85 | 115 | 9.5 | 10 | 72 | 16 | 100,8 | 14 |

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Appendix S2

Table S2. Mean plant and litter cover (\pm SE) and mean density (\pm SE) of individuals recorded in reference state and degraded state. Significant differences within each variable are indicated by * ($\alpha = 0.05$) (extracted from Supplementary file of López and Cavallero 2017).

| Variables | Reference State | Degraded State |
|--|-----------------|----------------|
| Total plant cover (%) | 58.3 (2.3) | 42.0 (2.2)* |
| Shrubby stratum cover (%) | 12.9 (0.5) | 16.7 (0.7)* |
| ^a <i>Mulinum spinosum</i> | 7.0 (0.3) | 8.2 (0.3) |
| ^a <i>Senecio filaginoides</i> | 3.9 (0.3) | 6.9 (0.3) |
| Grasses stratum cover (%) | 48.3 (2.3) | 23.3 (1.2)* |
| ^b <i>Poa ligularis</i> | 30.5 (1.4) | 1.7 (0.1)* |
| ^c <i>Pappostipa speciosa</i> var. <i>speciosa</i> | 5.8 (0.5) | 17.9 (1.0)* |
| Litter cover (%) | 4.6 (1.0) | 2.2 (0.4) * |
| Shrub density (n°.m ⁻²) | 0.6 (0.02) | 1.2 (0.1)* |
| ^a <i>M. spinosum</i> | 0.3 (0.03) | 0.4 (0.02) |
| ^a <i>S. filaginoides</i> | 0.1 (0.01) | 0.4 (0.07)* |
| Grass density (n°.m ⁻²) | 8.3 (0.5) | 9.4 (0.9) |
| ^b <i>P. ligularis</i> | 4.0 (0.4) | 0.4 (0.03)* |
| ^c <i>P. speciosa</i> var. <i>speciosa</i> | 2.7 (0.3) | 8.3 (0.4)* |

^aMain shrub species (*M. spinosum*: deep-rooted shrub; *S. filaginoides*: shallow-rooted shrub); ^bmain forage species; ^csecondary forage species.

Appendix S3

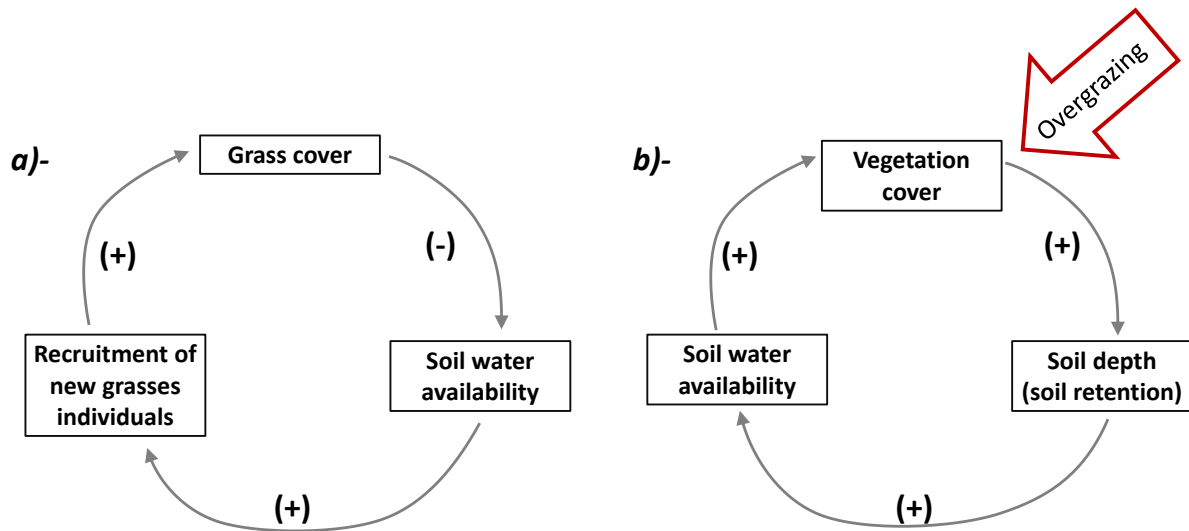


Fig. S3. Schematic representation of negative feedback processes (**a**) and positive feedback processes (**b**) in a rangeland ecosystem. There are two general categories of interactions that modify the response of any system to a change in input or interactions between factors of a system. A positive feedback amplifies the change in input (arrows), pushing the system towards a more pronounced change. A negative feedback counteracts the change in input, tending to maintain the system in its current state. The presence of negative feedbacks is a key to maintain the long-term sustainability of an ecological system in their current state in the face of global change (Chapin F S. & Whiteman G. 1998; Briske et al. 2006). Boxes represent factors or key processes; arrows indicate the direction of the interaction among this factors or processes. The 'plus' sign (+) maintains the sense of the relationship between factors (i.e., boxes); whereas the 'minus' sign (-) changes the sense of the relationship between factors (e.g. when an input in growing sense encounters a minus sign, it turns to a decreasing sense). In (a) a negative feedback loop, which stabilizes the system through a density-dependent process. Specifically, a greater plant cover increases soil water consumption, and thus, soil water availability decreases, decreasing in turn, seedling recruitment (by competitive exclusion). The lower seedling recruitment determines, in the long term, the absence of individuals to replace those who die, decreasing grass cover. The lower grass cover, decreases water consumption, and thus, increases water availability, which in turn, allows an increase in seedling recruitment, ultimately increasing grass cover. In (b) a negative transition (degradation by overgrazing) is exemplified with a positive feedback loop. Specifically, overgrazing decreases the cover of forage species, decreasing in turn, soil cover. A lower soil cover, leaves the soil exposed to further soil loss caused by water and wind erosion, decreasing soil depth, and thus, their ability to store water. The lower ability to store water determines that the system can sustain lower grass cover, increasing the soil exposure to erosive agents.

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Appendix 4

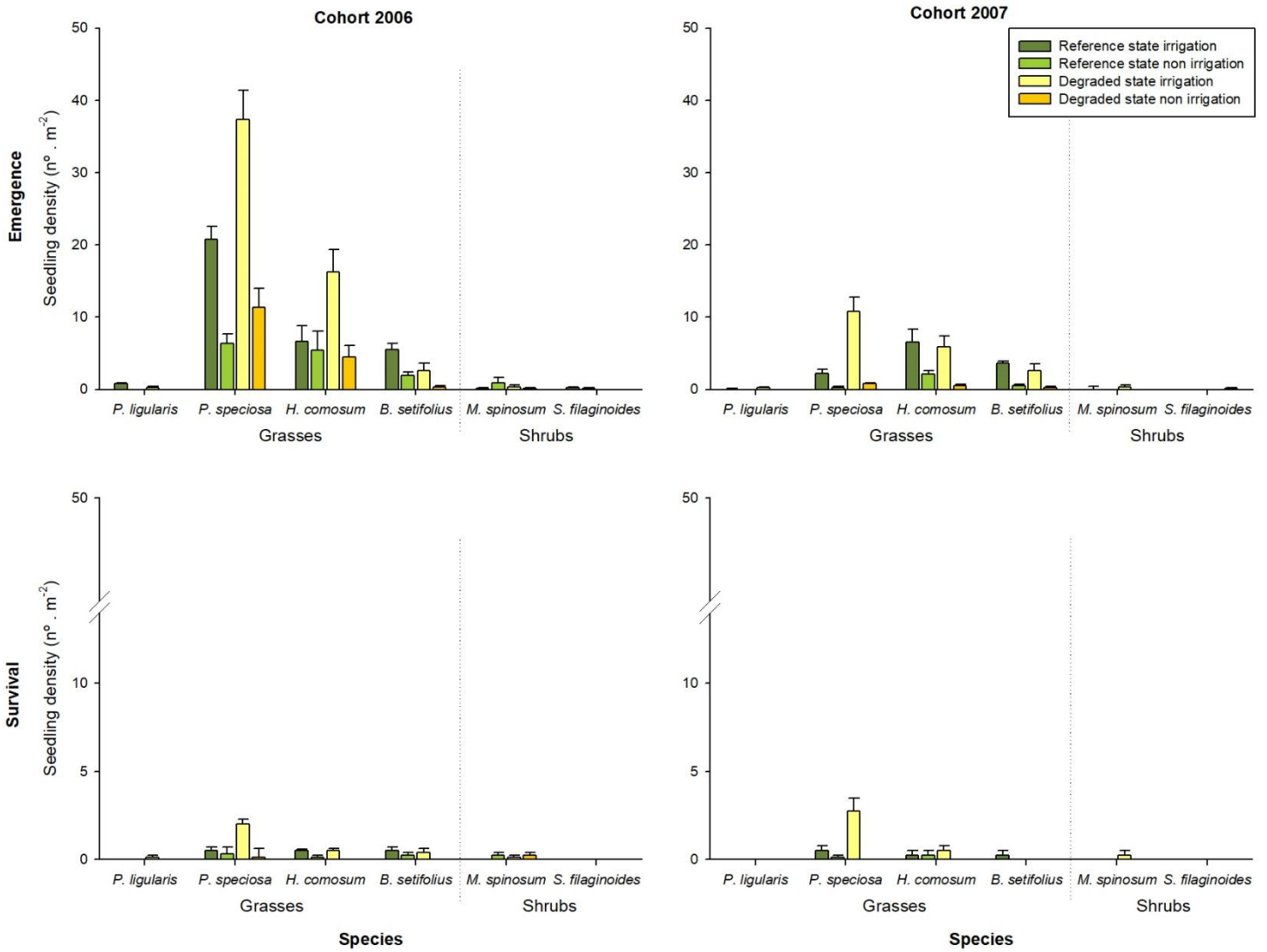


Fig. 2.A4. Mean density (\pm SE) of seedlings emerged of the main grass and shrub species in April 2006 (a) and 2007 (b) and mean density (\pm SE) of surviving seedlings during the subsequent years until April 2009 for the cohorts 2006 (c) and 2007 (d).

Appendix S5

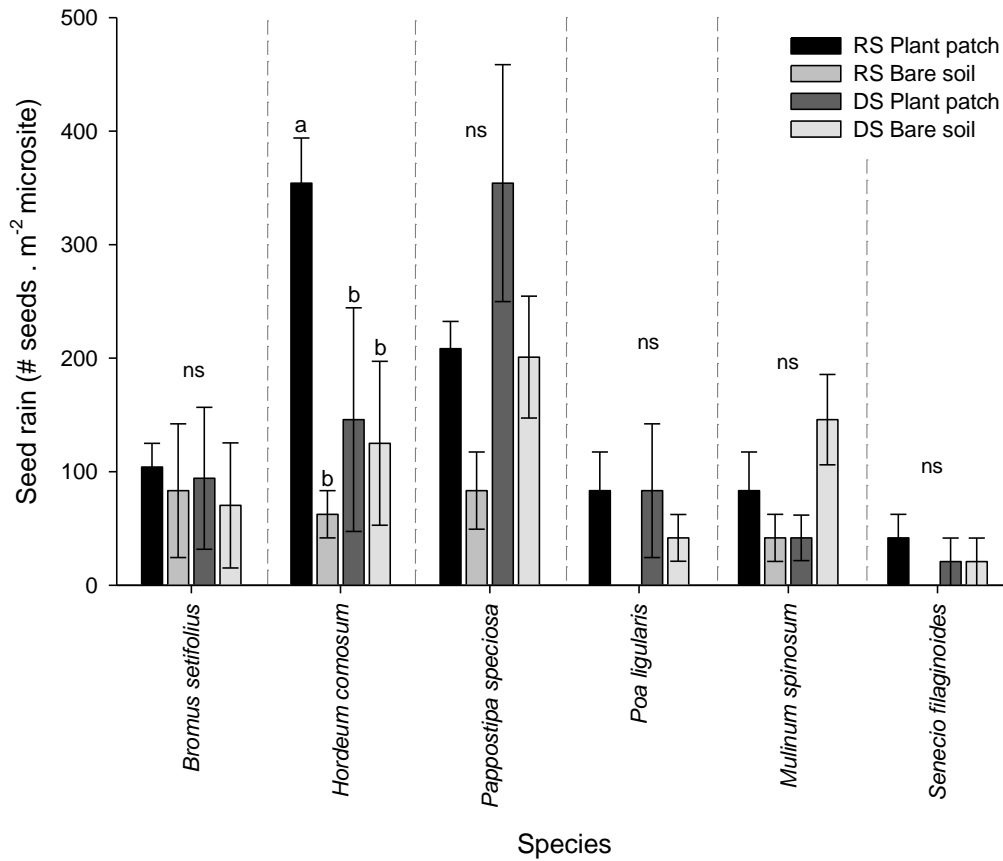


Fig. S5. Seed rain (mean seed number \pm SE) of the main perennial species recorded in distinct microsites (plant patches and bare soil) in two alternative states (reference state and degraded state) of a graminous-subshrubby steppe of northwestern Patagonia (Argentina). Lower case letters indicate significant interaction ($p < 0.05$) among State (RS vs. DS) and Microsite (Plant patch vs. Bare soil). ns: not significant.

Methods: Between November 2008 and April 2009, eight seed traps were installed in each state (RS and DS) in two microsite types (four at the edge of *M. spinosum* patches and four in bare soil). Seed number of the main perennial species was recorded monthly. The seed traps were made of a cylindrical plastic container (12 cm diameter and 15 cm height) opened at the top. A plastic mesh protection (1.5 x 1.5 cm openings) was placed covering the upper part of the cylinder to avoid seed loss by wind drift and post dispersal predation by birds and rodents.

Appendix S6

Glossary

Synthesis of the key concepts on Ecological Sites and the State and Transition Model (STM)

The approach and definitions were adapted from Briske et al. (2008), Bestelmeyer et al. (2017), López (2011), and Peri et al. (2017). The States and Transitions Model allows the integration of key theoretical concepts, such as ecological resilience to the management of natural ecosystems under anthropic use and/or under the influence of environmental drivers.

Ecological Site

Units or landscape elements with similar characteristics of soil, topography, geological formations and climatic regime that differ from other classes in: (1) The growth and composition of potential plant species, under a disturbance regime with reference conditions that are associated with the properties of the soil, the natural dynamics of the plant community and the capacity to provide environmental services. (2) Responses to management, degradation and restoration processes. Classes of the same ecological site are repeated in similar components of land units, within the same ecoregion or another area. Each ecological site has a reference state and a specific model with transition between one or more alternative states.

Ecological resilience

Ecosystem capacity to absorb a disturbance factor and/or reorganize after a disturbance, maintaining structural-functional integrity. This resilience approach assumes that ecosystems can have two or more alternative stable states and those transitions between states occur. These state transitions are associated with changes in key attributes of its structure and self-regulation processes (i.e. with negative feedback mechanisms). Each state has a specific resilience to different disturbance factors. Then, the original resilience of the ecosystem is associated with the ability to maintain and/or recover the structural-functional attributes of the reference state (i.e. ecosystem identity). Resilience can be assessed by the following attributes:

- 1) *Amplitude*: defined by a threshold beyond which the ecosystem significantly decreases or loses its state resilience (i.e., ability to return to the previous or reference state). Thresholds are associated with changes in structural-functional attributes, beyond the limits of ecological resilience, resulting in a transition to an alternative state (see Fig. S3).
- 2) *Resistance*: the system sensitivity to suffer structural-functional changes, or sensitivity to degradation in response to a disturbance factor. A low degradation speed or magnitude means that the ecosystem has a high resistance. Resistance is also associated with the carrying capacity of a state, if the carrying capacity is high, the resistance will be high (e.g. animal units per hectare during a given time period).
- 3) *Elasticity* (or “*engineering resilience*”): speed at which an ecosystem can return to the reference phase or community of the reference state after a disturbance. (or to the potential phases in an alternative state, which it was before a disturbance).

4) *Malleability*: The degree to which a new stable state, generated after recovery or degradation, differs (at structural-functional levels) from the original stable state (*sensu* Westman 1985).

Also, three types of ecological resilience can be described:

a) *Original resilience of ecosystem*: the resilience of the reference state of an ecosystem (López et al. 2013).

b) *Positive resilience*: the resilience of each alternative state against anthropic or environmental disturbance factors (e.g. overgrazing and / or droughts) (Lake 2013).

c) *Negative resilience*: is the resilience of each alternative state against restoration or rehabilitation practices. In other words, it is the ability to persist and/or return to a degraded state and therefore the lack of recovery to a state with better structural-functional levels in response to an external driver or inputs (such as revegetation, fertilization, irrigation) (Lake 2013).

Feedback mechanisms

The dynamics of each state of an ecosystem is regulated by feedback mechanisms. This feedback represents ecological processes that reinforce (i.e. negative) or decrease (i.e. positive) the resilience of ecosystem states. A positive feedback mechanism maintains the sense of the processes that occur in the feedback loop, which reinforces or amplifies the change that this loop generates in the system, pushing the system towards a more pronounced change. A negative feedback counteracts the change in input, tending to maintain the system in its current state. The occurrence of negative feedbacks is key to maintain the long-term stability in each state. Instead, the factors that amplify change (positive feedbacks) can be beneficial (e.g. restoration) or detrimental (e.g. degradation) (see more in Briske et al. 2006; Fig. 7 of main document, Fig. S1 of this Supplementary file).

State

Set of plant communities associated with a temporary dynamic that occurs in a landscape unit with certain properties (i.e., ecological site), ranges of factors and processes at soil level (e.g. seasonal fluctuation of the water phreatic). These factors and processes produce attributes persistent over time with characteristics, and with particular structural and functional dynamics of this state of the ecosystem (Fig. S3).

Reference state

Is the state from which all other states (and phases) of the same ecological site can be identified and derived. Represents a range of structural-functional fluctuation associated with historical or natural variability (i.e. original or pristine state before intensive anthropic use) (e.g., S-I in Fig. S3). This is the state that has the potential to provide the greatest variety or diversity of environmental services, in comparison to the rest of the ecosystem states.

Phases or communities within a state

Different plant communities that can be associated with distinct levels of soil (e.g.. water availability) and climatic variables (e.g., mean annual rainfall) which annually fluctuate but characterize the dynamic of a state. Phase change do not implicate threshold crossing. Phase change also could occur in response anthropic use (e.g. rotational grazing) (e.g., phases I.a and I.b

for state I, Fig. S3.b). Each state is characterized by a specific ecological resilience to different disturbance factors, and the dynamic among phases within a state is associated with engineering resilience (i.e., elasticity).

Reference phase of an ecosystem

Represents the plant community (or potential phase) of the reference state, which is the community with the greatest resilience within that state. This is the plant community that has structural-functional values “further” from the threshold and it is the phase that the system tends to return in absence of disturbance factors. Also, each alternative state can have a potential phase, which is the plant community towards which each state of the ecosystem tends in absence of disturbance factors (e.g., phases of states: S-I, S-II and S-III in Fig. S3.b).

Risk phase

It is the plant community most susceptible to experience a negative transition to an alternative state (i.e. a state with a lower level of structural-functional integrity compared to the reference state). This phase represents the least resilient plant community within a state (i.e. pre-threshold community) and therefore more susceptible to being degraded (e.g., phase I.b of S-I, II.b of S-II and phase II.b of S-III, Fig. S3.b)

Negative (or degradation) transitions

Mechanisms and temporal dynamics by which a state is modified towards a more degraded state (with lower levels of structural-functional integrity compared to the reference state). A negative transition occurs (or is triggered) in response to overuse and/or interaction with environmental factors (e.g. extreme droughts, fire) (Fig. 1b). A transition is defined based on: *(i)* the triggers (natural and/or anthropic disturbances factors) that produce a process of change at a specific moment; *(ii)* the threshold; and *(iii)* the time that lasts the system to cross that threshold.

Triggers

Events, factors, processes and/or drivers that initiate a transition between alternative states. Triggers can be one (or more) disturbance factor(s) (e.g., overgrazing and/or extreme droughts), which cause significant structural-functional changes in the ecosystem. If the change causes degradation, the trigger causes a negative transition (e.g. a change determined by the interaction between extreme drought and forest use). In contrast, if the change causes recovery to a state with a higher level of structural-functional integrity of the system, the trigger causes a positive or restoration transition (e.g. a change triggered by a very wet year in absence of grazing and/or reforestation; restoration of State-III: R-State-III in Fig. S3.b).

Threshold

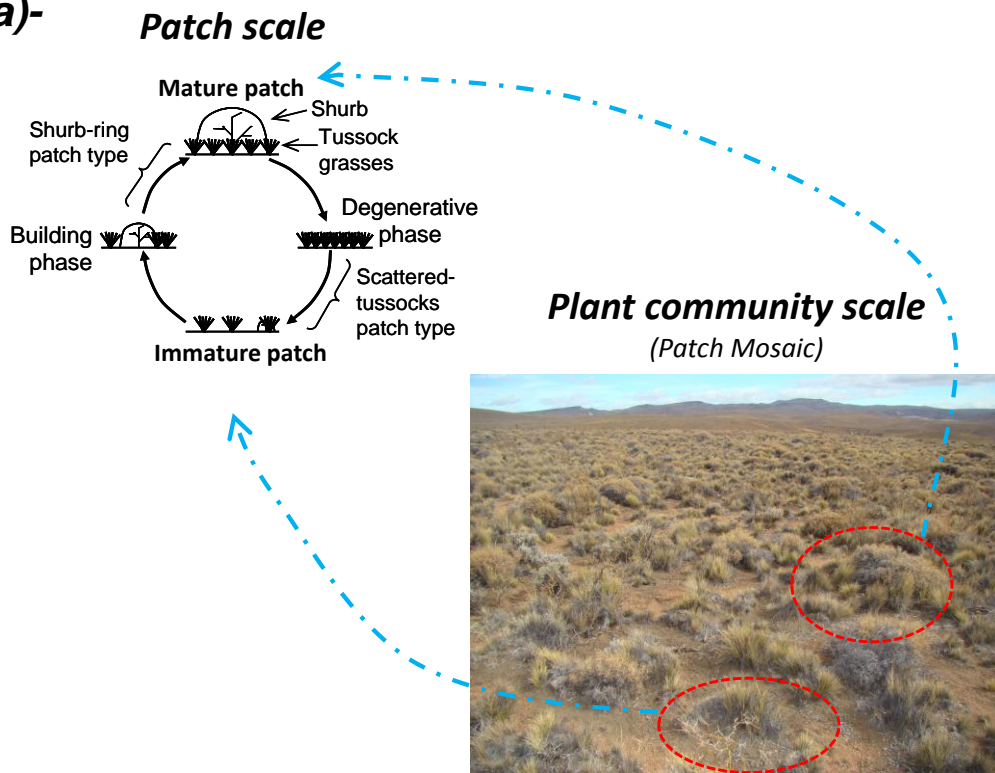
Key abiotic and/or biotic factors and processes that are modified during a negative transition, and that limit (or significantly decrease) the intrinsic recovery capacity (without intervention or external input from the ecosystem) to the previous or reference state. These ecological thresholds are identified (or quantified) by certain values of key indicators. The thresholds represent the structural-functional limits beyond which the ecosystem resilience to the previous (or reference) state has been significantly reduced or lost. If the thresholds are associated with very severe abiotic and/or biotic restrictions (e.g. soil erosion, local extinction of species), the occurrence likelihood of

a positive transition to the reference or previous state is very low (or restoration will require more time and a lot of external input). In states with intermediate degradation (e.g. state-II with intermediate levels of structural-functional integrity) the original resilience (i.e., ability to recover to the reference state) is significantly reduced (i.e. the ecosystem needs intermediate recovery periods, with wet years and with intermediate levels of input in energy/work/matter). Very degraded states have lost the original resilience of the ecosystem and recovery transitions are unlikely and /or require very high levels of external inputs, during very long time periods, to enable ecosystem recovery or rehabilitation (State-III, Fig. S3.b).

Positive transitions

Transitions that trigger recovery processes. Restoration transitions are management practices or interventions (and required times) carried out in a particular degraded state, necessary to recover the structural-functional conditions of a previous state or of the reference state. In addition, there may be rehabilitation transitions aimed to improve the structural-functional conditions of highly degraded states, triggering recovery transitions to novel states. (i.e., increasing structural-functional levels, novel ecosystem *sensu* Hobbs et al. 2009) (Fig. S3.b).

a)-



b)-

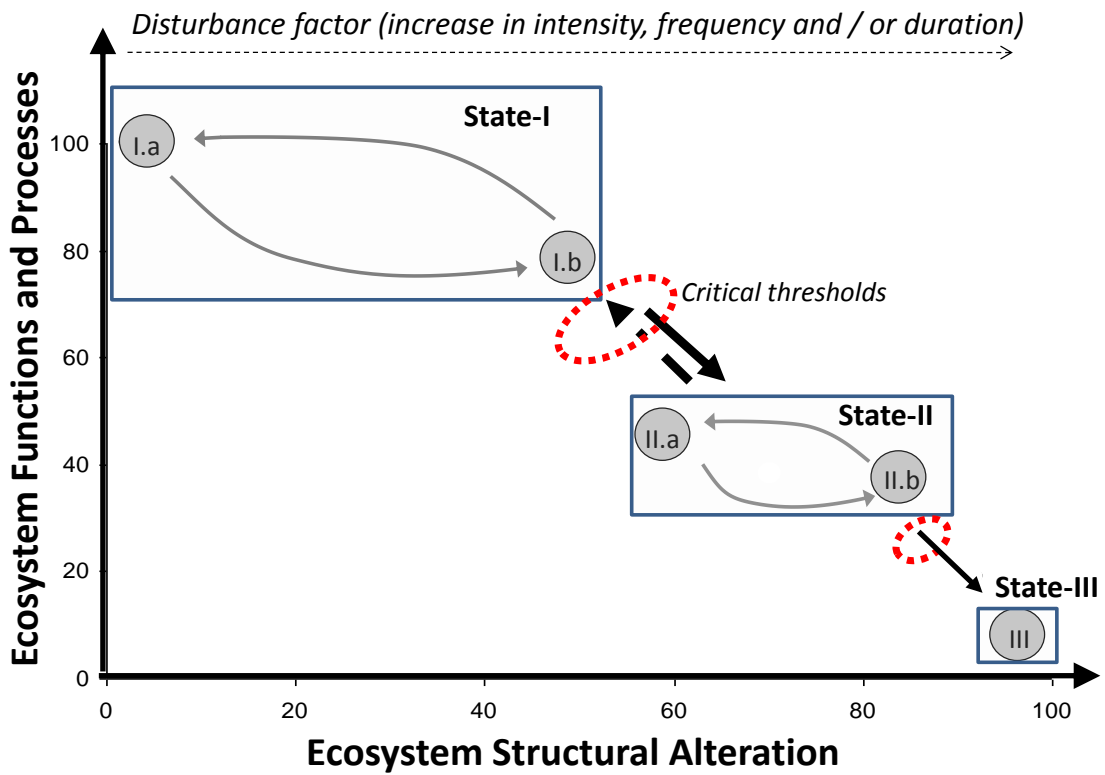


Fig. S6. (a) Schematic representation of the dynamic equilibrium of a state of the study system at patch- and community-scale of the grass-shrubby steppes of *Poa ligularis* and *Mulinum spinosum* (northern Patagonia, Argentina). The dynamics at patch-scale are governed by two types of patches (mature and immature) and two phases (building and degenerative), among which there are natural fluctuations. The pathway from one patch type to another may last different periods, which depend upon internal- (topography and/or species-specific ecophysiological characteristics), or external-factors (cycles of wet-dry years) or the interaction of both. Patch dynamics determines that the ecosystem has spatio-temporal fluctuations in the proportion of patch types that build the mosaic at community-scale. The photograph shows the plant community of a reference phase of a state, where a mosaic with a different proportion of patch types and/or phases can be seen (see more in López et al. 2011). **(b)** Structural-Functional State and Transitions Model for the study system (López et al. 2011). The *x-axis* represents the degradation or alteration of the ecosystem structure and the *y-axis* represents key ecosystem functions and processes. Alternative states are identified by squares and Roman numbers (the higher the number, the more degraded state). Phases within states are represented by gray circles (e.g. phases I.a and I.b for State I). The probability of a transition (degree of irreversibility after crossing a threshold) is reflected by the width and type of arrows: negative transitions (more feasible than positive transitions) are represented by thicker and continuous arrows, whereas positive transitions (more unlikely to occur) by thin and dashed arrows, and positive transitions that are unlikely are represented by dotted arrows. Red dotted circles indicate critical thresholds. The scheme has the assumption that the intensity, frequency and/or duration of disturbance factor(s) increases from the upper left to the lower right. Thus, the effect of the disturbance factor(s) on the ecosystem structure and function is not necessarily linear and continuous (López et al. 2011; Easdale and López 2017).

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