





# Vegetation recovery after fire in mountain grasslands of Argentina

**Alejandro LOYDI**<sup>1,2\*</sup>  <http://orcid.org/0000-0002-0306-905X>;  e-mail: [aloydi@cerzos-conicet.gob.ar](mailto:aloydi@cerzos-conicet.gob.ar)

**Flavia A. FUNK**<sup>2,3</sup>  <http://orcid.org/0000-0003-4694-3701>; e-mail: [ffunk@criba.edu.ar](mailto:ffunk@criba.edu.ar)

**Andrés GARCÍA**<sup>1</sup>  <http://orcid.org/0000-0001-6342-241X>; e-mail: [agarcia@cerzos-conicet.gob.ar](mailto:agarcia@cerzos-conicet.gob.ar)

\*Corresponding Author

<sup>1</sup> Renewable Natural Resources Center of the Semi-Arid Zone (CERZOS) – CONICET-UNS, Bahía Blanca, Argentina

<sup>2</sup> Department of Biology, Biochemistry and Pharmacy, South National University, Bahía Blanca, Argentina

<sup>3</sup> Argentine Institute of Oceanography (IADO), CONICET-UNS, Bahía Blanca, Argentina

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**Abstract:** Fire is a natural disturbance occurring every few years in many grasslands ecosystems. However, since European colonization, fire has been highly reduced or even suppressed in Argentinean grasslands, fostering ignitable material accumulation. This has led to occasional catastrophic control-demanding fire events, extended for larger areas. The aims of this work are to study vegetation recovery and change after a non-natural fire event in mountain grasslands. The study area is located in the Ventania mountain system, mid-eastern Argentina. We studied vegetation recovery after fire (January 2014) in two different communities: grass-steppes (grasslands) and shrub-steppes (open low shrublands). We measured vegetation cover, species richness and bare ground percentage in burned and unburned areas 1, 4, 8, 11 and 23 months after fire. Vegetation surveys were also performed at the end of the growing season (December) 11 and 23 months after fire. Data were analyzed using regression analysis, ANOVA and multivariate analysis (NMS, PERMANOVA). Both communities increased their vegetation cover at the same rate, without differences between burned and unburned areas after two years. Species richness was higher in shrublands and their recovery was also

faster than in grasslands. Considering functional composition, besides transient changes during the first year after fire, there were no differences in abundance of different functional vegetation groups two years after fire. At the same time, shrublands showed no differences in species composition, while grasslands had a different species composition in burned and unburned plots. Also, burned grassland showed a higher species richness than unburned grassland. Data shown mountain vegetation in Pampas grassland is adapted to fire, recovering cover and richness rapidly after fire and thus reducing soil erosion risks. Vegetation in mountain Pampas seems to be well adapted to fire, but in grasslands species composition has changed due to fire. Nonetheless, these changes seem to be not permanent since pre-fire species are still present in the area.

**Keywords:** *Amelichloa caudata*; Forbs; Grass; Natural grassland; *Nassella trichotoma*; Piedmont valleys; Shrubs; Sierra de la Ventana; Vegetation functional groups

## Introduction

Fire is a common disturbance in natural

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environments (Waldrop et al. 1992; Tizón et al. 2010). Several ecosystem types have evolved in the presence of fire and species in these environments are adapted to fire occurrence (Bond and Keeley 2005). In many grasslands fire is a natural disturbance that occurs yearly or every few years (Heisler et al. 2003; Medina 2007), being in part responsible for the maintenance of grasslands habitat type, avoiding the establishment of woody species (Chaneton et al. 2012). In ecosystems dominated by herbaceous species, when a fire event occurs and due to a low combustible material (i.e. lack of wood), fire temperature and residence time are usually low (Fidelis et al. 2010), increasing the chances of individuals survival and recolonization after fire. However, frequent fires can reduce or eliminate seedlings of woody species in herbaceous-dominated ecosystems reducing their recruitment (Briggs et al. 2002). For example, Heisler et al. (2003) working in Konza Prairie Biological Station (Kansas, USA) showed that shrub cover is inversely related to fire frequency and C4-grass species can maintain dominance depending on the occurrence of annual burning.

Vegetation in fire prone grassland is usually adapted to the prevailing fire regime (Bond and Keeley 2005). In crown-fire regimes, woody biomass is consumed during fire, while in surface-fire regimes, the herbaceous layer of the vegetation is consumed but not the woody species (Bond and Keeley 2005). In both cases, vegetation traits may determine the response of vegetation to fire, considering that different types of vegetation may respond differently to burning. Pausas et al. (2004) mentioned two main traits related with fire-prone ecosystems species: resprouting ability and propagule persistence. The former is related with longer lived and slower maturing species, like some shrubs and bunch grasses that can resprout after a fire occurrence (Gonzalez et al. 2015). While the latter is more relevant for species with persistent soil seed bank. Species that survive fire as seeds can recolonize the empty space generated after burning (Pausas et al. 2004; Bossuyt and Honnay 2008), since after a fire occurrence vegetation cover is greatly reduced (Frangi et al. 1980; Peláez et al. 2013). This may increase the risk of soil erosion in the system (Fernández et al. 2010; Lira-Caballero et al. 2018). Nonetheless, if vegetation is adapted to fire, its cover will increase shortly after

burning, reducing at the same time erosion risks (Gittins et al. 2011). However, species that rapidly increase their cover after fire may not be the dominant species before burning. It is expected that, if an ecosystem is adapted to fire, vegetation composition may be resilient to fire occurrence and, after some time, the vegetation may show a resemblance to its original state (Cingolani et al. 2005). Nevertheless, right after the fire, several species may increase their abundance transiently before the ecosystem reaches the pre-fire species composition.

The effect of fire on species composition and species turnover is widely known (Abrams and Hulbert 1987; Špačková and Lepš 2004; Alba et al. 2015; Liu et al. 2017). However, there are no global synthesis of the response of vegetation to fire, particularly in those ecosystems where fire has been suppressed for a long time (Bond and Keeley 2005). This is the case for Argentinean mountain grasslands in the Pampa region. This area has been greatly transformed within the last hundred years since the introduction of agriculture and cattle (Loydi et al. 2012). Moreover, in the last 25 years new crops (including GMO crops) and farming techniques (e.g. no-till farming) are displacing cattle raising to relictual grassland areas, leading to overgrazing (Oliva et al. 2019). In this region, fire together with grazing and precipitation are responsible for shaping vegetation communities (Busso 1997; Tizón et al. 2010). However, after European settlement wildfires were highly reduced or even suppressed (Brailovsky and Foguelman 1998; Bilenca and Miñarro 2004). Medina (2007) reported a fire-free interval of ca. 4 years in nearby areas (<300 km) until 1930s. Afterwards fire interval increased with a mean of 7 years and a maximum of 17 years and their extension has reduced, being more confined (few hundred hectares). This lower frequency of fire has led to the occurrence of occasional catastrophic control-demanding fire events extended for larger areas, i.e. thousands of hectares (Irigoin et al. 1996; Marini 2014). Therefore, knowing the response of native vegetation to fire is increasingly important for grassland management (Whelan 2009).

In this study, we sampled vegetation in burned and unburned areas after a large fire during a two year period in Ventania Mountains located in mid-eastern Argentina. We tried to answer the following

questions: (1) How fast do vegetation cover and species richness change after a fire? (2) Are these changes similar for plant communities with different vegetation structure? (3) Does plant community composition change as a response to fire? And (4) Which vegetation groups or species benefit (or are harmed) by fire?

## 1 Materials and Methods

### 1.1 Study area

The study area is located in a privately owned ranch near Villa Serrana La Gruta, Argentina (between 38°02'50"- 38°03'40" S and 62°03'20"- 62°04'30" W). It includes piedmont valleys, with 3% to 11% slopes and occasional rocky outcrops located in the Ventania mountain system, mid-eastern Argentina (elevation ranging from ~450 m to ~1240 m). The topography in the Ventania Mountains ranges from steep mountain slopes at high elevations (hilly system) to gentler slopes at lower levels (piedmont). The nucleus of the hilly system is formed of intensely folded quartzitic rocks resting on a crystalline base in the form of reduced outcrops of granite and quartziferous porphyry. The remainder of the area is covered by late Pleistocene–Holocene loessal sediments (Amiotti et al. 2000). These sediments are 1–2 m thick, rich in calcium carbonates and they exhibit a well-defined contact with the underlying rocks. Soils in the area are classified as lithic hapludols and argidols with a high content of organic matter in the superficial horizons (Cappannini et al. 1971). Climate is temperate and sub-humid (Burgos and Vidal 1951). Average annual air temperature is 14°C and average annual precipitation is 800 mm, concentrated in the spring and late summer. The Ventania system belongs to the southern Pampas. These grasslands have been historically subjected to grazing by native herbivores, principally “guanaco” (*Lama guanicoe*) (Bilenca et al. 2009). Recurrent fires and droughts are other structuring forces in this ecosystem (Barrera and Frangi 1997). Land use and cover in the area had been changing over at least the last 130 years, after the introduction of agriculture and cattle (Bilenca et al. 2009). Since European settlement, native herbivores were replaced by domestic and feral

herbivores (i.e. horses, cattle and sheep). Domestic herbivores biomass is one order of magnitude higher than native herbivores (Oesterheld et al. 1992).

The study area has two different vegetation communities, grass-steppes and shrub-steppes (Oyarzabal et al. 2018), called hereafter grasslands and shrublands. Grasslands (i.e. steppes dominated by perennial grasses) are located in deeper soils (>70 cm) and are covered by tussock grasslands dominated by *Amelichloa caudata* accompanied by other species such as *Nassella trichotoma* and *Bromus* spp. (Frangi and Bottino 1995). Shrublands (i.e. open low shrubland steppes) are located in areas with shallow soil (<40 cm) and are dominated by herbaceous species (e.g. *Nassella trichotoma* and species of the genus *Piptochaetium*) with low abundance (approximately 20% cover) of small shrubs (e.g. *Baccharis salicifolia* and *Discaria americana*). Aboveground annual primary production reaches approximately 500 g m<sup>-2</sup>, although this may vary depending on rainfall (Pérez and Frangi 2000).

On December 30<sup>th</sup> 2013, a fire was accidentally started at Villa Serrana La Gruta and rapidly spread into nearby grassland areas in private ranches and public lands. The fire was active until January 8<sup>th</sup> 2014, affecting 30,458 ha (Marini 2014). The fire brigade established firebreakers to avoid the spread of the fire into the village, but grasslands and shrublands were rapidly burned. The residence time of the fire was low, but due to the high wind speed, the fire changed directions several times, leaving a mix of burn and unburned patches especially in the shrubland communities (Figure 1). After the fire was extinguished, vegetation cover in the burned areas was completely absent.

### 1.2 Sampling design

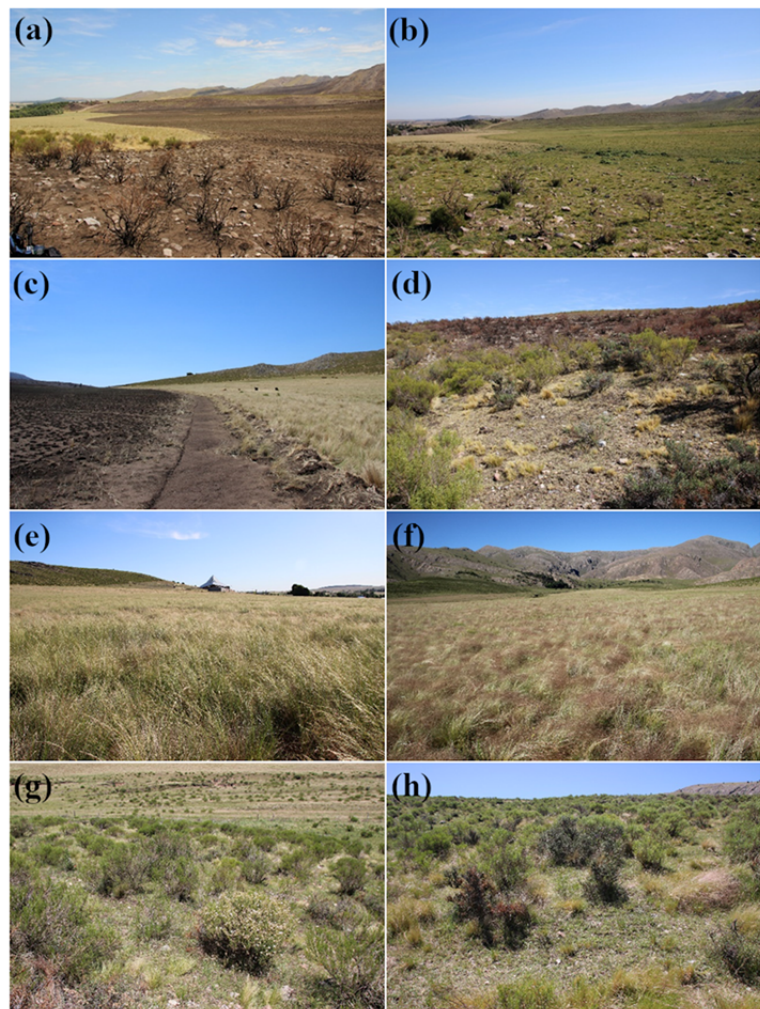
The sampled area comprised 170 ha in piedmont valleys. Before the fire, right after it (January 2014) and throughout the sampling period (January 2014 – December 2015) the area was lightly grazed by cattle at low stocking rates (<0.1 animals ha<sup>-1</sup>). Vegetation was studied in burned and unburned areas 1, 4, 8, 11 and 23 months after fire. We selected four grassland areas and four shrubland areas within the study area.



These areas shared similar orientation and topography and where at least 200 m away from each other. In each area, we selected a burned and an unburned plot (4 m<sup>2</sup>, n=4) where vegetation composition was measured. Burned and unburned plots were located close to each other (<20 m). The unburned treatment in the shrublands was established by selecting naturally burned and unburned patches within each site. On the other hand, in grassland communities, the establishment of fire breakers by the fire department during the fire allowed us to have burned and unburned areas next to each other. In each sampling date, we measured species richness and bare ground percentage. During December 2014 and 2015 (11 and 23 months after fire respectively), we also visually estimated percentage cover of each species using a modification of the Braun-Blanquet dominance scale (van der Maarel 1979). This period was chosen because most of the present species in the study area bloom in spring (Frangi and Bottino 1995) and they reach their peak biomass and cover at the beginning of summer. Therefore, measuring cover in this time of the year will show differences among treatments (i.e. fire) and not differences among seasons. All species were classified into the three dominant functional groups in the area: forbs (herbaceous dicots), grasses (all monocots) and shrubs (all woody species). Botanical nomenclature of all taxa and all additional information (i.e. functional type) follow the criteria used in the catalog of vascular plants of Argentina (Zuloaga and Morrone 2007).

### 1.3 Statistical analysis

We performed linear regressions to compare changes in bare ground percentage and species richness in time for burned and unburned areas within each community (i.e. grassland and shrubland). Time data was log transformed to meet regression assumptions. We used a dummy



**Figure 1** Study area (a) one month and (b) one year after the fire event. (c) Burned and unburned grasslands separated by firebreakers. (d) Naturally burned and unburned shrubland areas. (e) Unburned and (f) burned grassland 24 months after of the fire event. (g) Unburned and (h) burned shrublands 24 months after of the fire event.

variable to indicate community and make comparisons between regressions slopes and intercepts. We analyzed if slopes and intercept were the same (i.e. the regression curves for both communities are coincidental), if only slopes were the same (i.e. the regression curves of both communities are parallel), or if both slope and intercept were different (i.e. the regression curves are different between communities).

To analyze vegetation structure and composition, we analyzed changes in vegetation group cover one and two years after the fire, using paired t-test for each community. To assess the differences in the species composition according to the different treatments and communities, a

nonmetric dimensional scaling (NMS) and a two-way permutational ANOVA (PERMANOVA) were performed. We performed a NMS one year and two years after the fire separately, to assess changes in composition at different times. The NMS was conducted using the Sørensen-distance measure, a random starting configuration and 250 runs with real data. The final solution determined a 2-dimensional solution using 40 iterations for the first year data and 62 iterations for the second year data. This number of iterations was defined according the instability criterion, when the standard deviation in stress was  $<0.00001$  during at least 10 consecutive iterations (for details see McCune and Grace 2002, pp 125-128). The PERMANOVA was done using Euclidean distance and considering two factors: vegetation community (grassland vs shrubland) and fire occurrence (burned vs unburned). Pair-wise comparisons with Bonferroni correction were performed to detect significant differences among treatments. In each year significant indicator species of the vegetation plots in each year were identified through an Indicator Species Analysis using the defined groups obtained with the PERMANOVA and following the Dufrene and Legendre's method (Dufrene and Legendre 1997). All multivariate analyses were made using PC-ORD (version 6.0, MjM Software, Glenden Beach, OR, US).

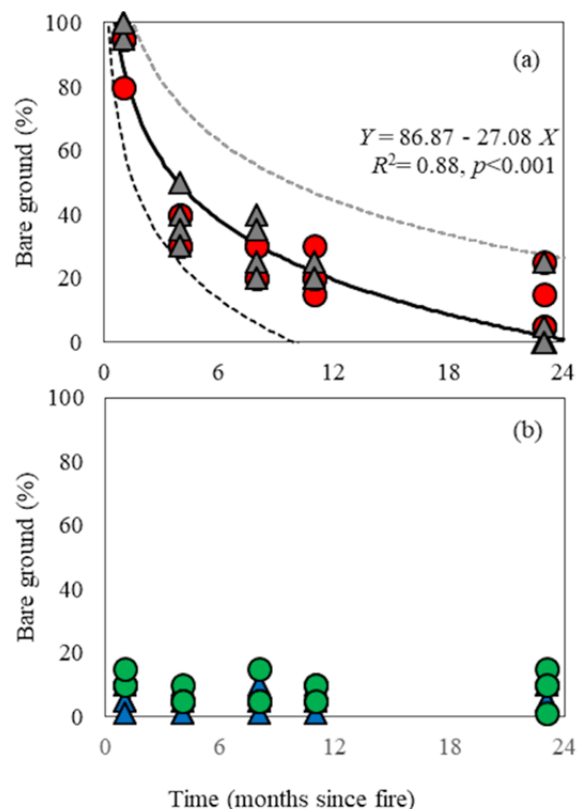
## 2 Results

### 2.1 Vegetation recovery after the fire

In the burned plots, both grassland and shrubland communities showed a large decrease in bare ground percentage and a large recovery of species richness over time. In both cases, this recovery was in a logarithmic fashion, with higher initial speeds. Mean bare ground percentage changed from nearly 90% to ca. 20% only 11 months after fire and  $<2\%$  23 months later (Figure 2a). However, despite differences in vegetation composition, both communities reduced bare ground percentage at the same speed, without showing differences in the parameters estimated in their regression curves ( $F_{1,36} = 1.29$ ,  $p = 0.263$  and  $F_{1,37} = 0.44$ ,  $p = 0.511$ , for the slope and the intercept respectively, Figure 2a). For unburned areas there

was no significant change in bare ground percentage during the same period of time ( $F_{1,18} = 2.48$ ,  $p = 0.133$  and  $F_{1,18} = 0.80$ ,  $p = 0.383$  for grasslands and shrublands, respectively, Figure 2b). Two years after the fire there were no significant differences in bare ground percentage between burned and unburned plots in the grassland areas (i.e.  $7.25\% \pm 5.7\%$  and  $7.5\% \pm 1.4\%$  for burned and unburned plots respectively, paired t-test = 0.04,  $p = 0.972$ ) or in the shrubland areas (i.e.  $9.0\% \pm 2.9\%$  and  $12.5\% \pm 4.8\%$  for burned and unburned plots respectively, paired t-test = 0.82,  $p = 0.471$ ).

In the burned plots, total species richness did not increase at the same rate when comparing both communities, having significantly different slopes ( $F_{1,36} = 86.43$ ,  $p = 0.014$ ). The shrubland areas showed a faster increased in species richness compared to the grassland plots ( $F_{1,36} = 6.73$ ,  $p = 0.013$ , Figure 3a and b). In the unburned areas,



**Figure 2** Bare ground percentage in (a) burned and (b) unburned plots during the study. Red and green circles represent shrublands and grey and blue triangles represent grassland plots. Continuous line represents the logistic regression line and their confidence intervals (dashed line). The equation for the linearized model is shown, in green for unburned shrubland plots and in blue for unburned grassland plots.

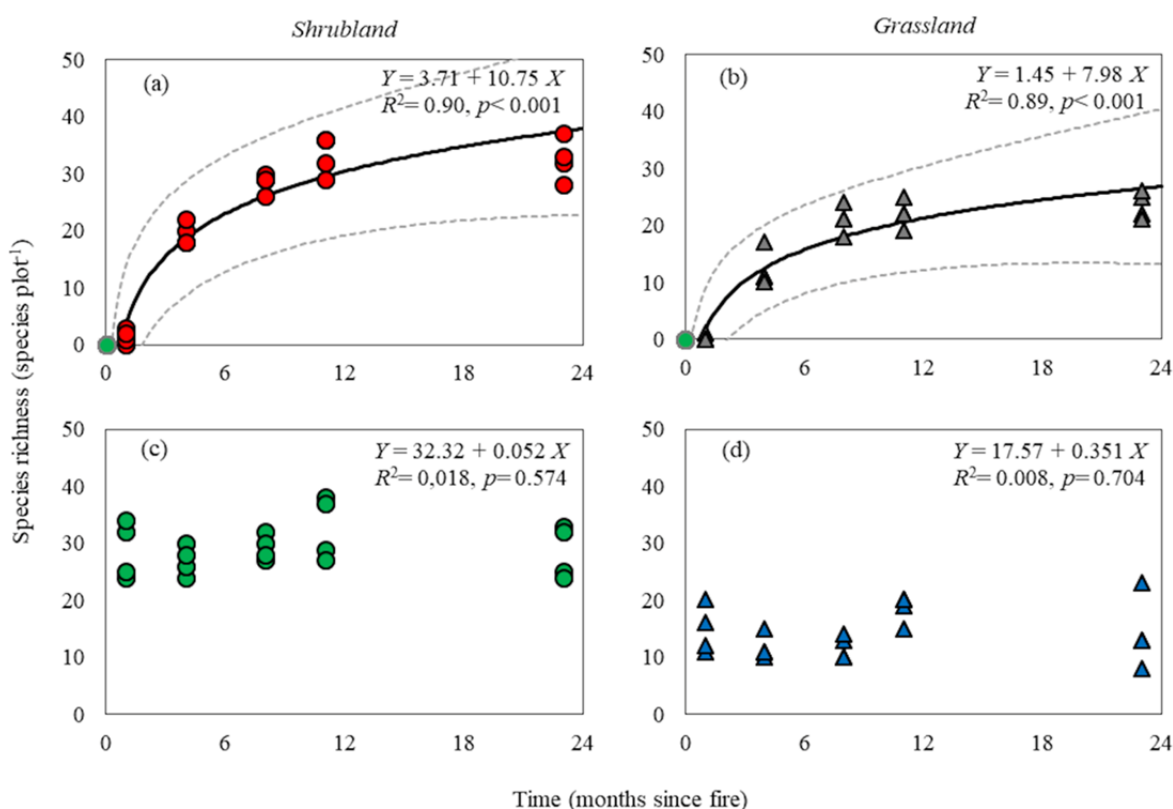
species richness did not vary during the same period of time ( $F_{1,18} = 0.33, p = 0.574$  and  $F_{1,18} = 0.15, p = 0.704$ ; for shrubland and grassland areas, respectively, **Figures 3c and 3d**).

Twenty-three months after the fire, species richness in burned and unburned shrubland plots was similar (i.e.  $32.5 \pm 1.8$  species plot<sup>-1</sup> and  $28.5 \pm 2.3$  species plot<sup>-1</sup> for burned and unburned plots, respectively, paired t-test= 1.92,  $p = 0.150$ ). On the other hand, burned grassland plots showed a higher species richness than unburned grassland plots (i.e.  $23.5 \pm 1.2$  species plot<sup>-1</sup> and  $14.3 \pm 3.15$  species plot<sup>-1</sup> for burned and unburned grassland

plots, respectively, paired t-test=3.81,  $p = 0.03$ ), showing an increase in species richness after the fire.

### 2.2 Vegetation composition after the fire

One year after the fire occurred, vegetation cover of the dominant vegetation groups has changed. In grassland plots, forb cover has significantly increased after the fire, while shrub cover decreased after burning (**Table 1A**). Grass cover also tend to decreased after fire, but this difference was not significant ( $p = 0.091$ ). In the



**Figure 3** Changes in species richness in burned (a and b) and unburned (c and d) plots. Red and green circles represent shrublands and grey and blue triangles represent grassland plots. Continuous line represents the logistic regression line and their confidence intervals (dashed line). The equation for the linearized model is shown.

**Table 1** Percentage mean cover value (mean±S.E.) for each vegetation group and total cover in burned and unburned plots one (A) and two years (B) after fire.  $t_{(4)}$ : paired t- test with 4 degrees of freedom,  $p$ : probability of error.

|                          | Vegetation group | Grassland |          |           |       | Shrubland |          |           |       |
|--------------------------|------------------|-----------|----------|-----------|-------|-----------|----------|-----------|-------|
|                          |                  | Unburned  | Burned   | $t_{(4)}$ | $p$   | Unburned  | Burned   | $t_{(4)}$ | $p$   |
| A - First year sampling  | Forb             | 18.4±2.2  | 43.3±5.1 | 3.49      | 0.040 | 11.1±2.4  | 15.2±2.4 | 1.36      | 0.268 |
|                          | Grass            | 47.2±7.2  | 27.2±6.7 | 2.45      | 0.091 | 77.3±5.0  | 61.1±2.3 | 2.69      | 0.075 |
|                          | Shrub            | 26.9±5.9  | 8.2±3.8  | 3.96      | 0.029 | 6.3±2.7   | 2.5±1.4  | 2.72      | 0.073 |
|                          | Total            | 92.5±1.4  | 78.8±3.1 | 4.37      | 0.022 | 94.8±1.8  | 78.8±1.3 | 7.04      | 0.006 |
| B - Second year sampling | Forb             | 14.9±1.3  | 12.8±3.8 | 0.638     | 0.569 | 8.7±2.2   | 9.3±0.6  | 0.18      | 0.867 |
|                          | Grass            | 58.2±8.2  | 70.5±5.6 | 1.67      | 0.194 | 78.6±3.5  | 68.1±6.0 | 1.99      | 0.141 |
|                          | Shrub            | 17.9±6.4  | 13.0±1.6 | 0.73      | 0.520 | 5.1±2.0   | 6.4±0.8  | 0.50      | 0.653 |
|                          | Total            | 91.0±2.9  | 96.3±1.3 | 1.59      | 0.210 | 92.5±1.4  | 83.8±5.9 | 1.33      | 0.275 |

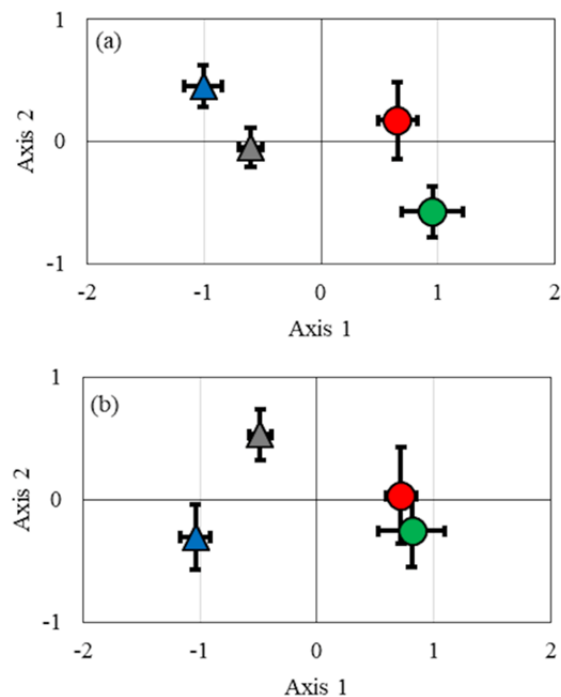


**Table 2** Indicator species of vegetation surveys on burned and unburned plots in shrubland and grassland areas. Vegetation group of each species is indicated: F: forb, G: grass, S: shrub. IV: indicator value. *p*: significance level.

|           |          | Indicator species of vegetation surveys |      |          |                                  |                                |          |       |  |
|-----------|----------|---|------|----------|----------------------------------|--------------------------------|----------|-------|--|
|           |          | First year after fire                   |      |          |                                  | Second year after fire         |          |       |  |
|           |          | Species                                 | IV   | <i>p</i> | Species                          | IV                             | <i>p</i> |       |  |
| Grassland | Unburned | <i>Amelichloa caudata</i> (G)           | 67.5 | 0.011    | Unburned and Burned              | <i>Amelichloa caudata</i> (G)  | 81.8     | 0.003 |  |
|           |          | <i>Bowlesia incana</i> (F)              | 66.7 | 0.034    |                                  | <i>Bromus unioloides</i> (G)   | 72.2     | 0.020 |  |
|           |          | <i>Sonchus oleraceus</i> (F)            | 75.0 | 0.027    |                                  |                                |          |       |  |
|           | Burned   | <i>Nassella trichotoma</i> (G)          | 55.9 | 0.014    |                                  | <i>Nassella trichotoma</i> (G) | 58.4     | 0.020 |  |
|           |          | <i>Schleranthus annus</i> (F)           | 81.4 | 0.020    |                                  | <i>Schleranthus annus</i> (F)  | 88.9     | 0.004 |  |
| Shrubland | Unburned | <i>Aristida spagazzinii</i> (G)         | 70.4 | 0.017    | <i>Aristida spagazzinii</i> (G)  | 100.0                          | <0.001   |       |  |
|           |          | <i>Baccharis salicifolia</i> (S)        | 87.0 | 0.008    | <i>Baccharis salicifolia</i> (S) | 87.5                           | 0.004    |       |  |
|           |          | <i>Piptochaetium medium</i> (G)         | 85.7 | 0.007    | <i>Bouteloa gracilis</i> (G)     | 75.0                           | 0.011    |       |  |
|           |          | <i>Hedypnois rhagadioloides</i> (F)     | 87.5 | 0.006    | <i>Carex rupicola</i> (G)        | 61.6                           | 0.038    |       |  |
|           | Burned   | <i>Polycarpon tetraphyllum</i> (F)      | 79.5 | 0.014    | <i>Dichondra sericea</i> (F)     | 81.8                           | 0.003    |       |  |
|           |          | <i>Oxalis articulata</i> (F)            | 66.7 | 0.038    | <i>Discaria americana</i> (S)    | 87.5                           | 0.002    |       |  |
|           |          |   |      |          | <i>Oxalis articulata</i> (F)     | 75.0                           | 0.010    |       |  |
|           |          |   |      |          | <i>Rinchosia senna</i> (F)       | 87.5                           | <0.001   |       |  |

shrubland areas, grass and shrub cover tend to decreased after burning, although this difference was not significant ( $p= 0.075$  and  $p= 0.073$  for grasses and shrubs, respectively). As a result, total cover was higher in unburned plots than in burned plot for both community types (Table 1A). Nonetheless, two years after the fire there were no differences in percentage cover between burned and unburned plots for grassland nor shrubland plots, considering total cover or each vegetation group cover (Table 1B).

The NMS-Ordination performed one and two years after the fire had a stress of 9.52 and 11.60 respectively. The ordination plot of the first sampled year after the fire showed a clear separation between both communities (i.e. grasslands vs shrubland) and between burned and unburned plots (Figure 4a). The result of the PERMANOVA showed significant effect of vegetation community ( $F_{(1,12)}= 18.1, p<0.001$ ), fire occurrence ( $F_{(1,12)}= 4.4, p<0.05$ ) and their interaction ( $F_{(1,12)}= 3.9, p<0.05$ ). Post-hoc test defined four significantly different groups and several indicator species were found for each one (Table 2). Burned grassland plots were dominated by a perennial grass (*Nassella trichotoma*) and a non-native annual forb (*Schleranthus annus*). On the contrary, unburned grasslands were characterized by a different perennial grass (*Amelichloa caudata*) and two non-native annual forbs (*Bowlesia incana* and *Sonchus oleraceus*). In the shrublands, burned plots were characterized by two non-native annual forbs (*Hedypnois rhagadioloides* and *Polycarpon tetraphyllum*) and



**Figure 4** NMS Ordination diagram of vegetation surveys (a) one year and (b) two years after fire. Centroids for each group  $\pm$  standard error are shown. Red and green circles represent burned and unburned shrubland plots respectively, while grey and blue triangles represent burned and unburned grassland plots.

a native perennial forb (*Oxalis articulata*), while unburned plots were dominated by two perennial grasses (*Aristida spagazzinii* and *Piptochaetium medium*) and a shrub species (*Baccharis salicifolia*).

Two years after the fire the ordination plot showed a clear separation between burned and

unburned grassland areas, but no separation among shrubland plots. There was a significant effect of both factors in the PERMANOVA ( $F_{(1,12)}=11.1$ ,  $p<0.001$  and  $F_{(1,12)}=4.8$ ,  $p<0.001$ , for vegetation community and fire occurrence, respectively) and their interaction ( $F_{(1,12)}=4.2$ ,  $p<0.001$ ). However, pair-wise comparison tests showed that species composition between burned and unburned shrubland plots was similar ( $p>0.233$ ), while for grassland separation between burned and unburned plots was statistically significant ( $p<0.05$ ). This defined three different groups: burned grasslands, unburned grassland and shrublands (including burned and unburned plots). The indicator species analysis showed that burned grasslands were characterized by the same species as the year before (*N. trichotoma* and *S. annuus*). While the unburned grassland plots were characterized by the same perennial grass as one year after the fire (*A. caudata*) and also an annual grass (*Bromus unioloides*). On the other hand, the shrubland areas were characterized by several perennial species including grasses, shrubs and forbs (see Table 2).

### 3 Discussion

In this work we have shown mountain vegetation in Pampas grassland is adapted to fire. Vegetation cover after fire changed rapidly. This is an important feature since soil cover is inversely related with soil erosion (Fernández et al. 2010; Gittins et al. 2011). Moreover, the fast response in both vegetation communities suggest that some species are capable of surviving fire, resprouting or germinating rapidly after burning (Bowman et al. 2016). Fire can reduce competition intensity benefiting re-sprouter species, generating at the same time favorable microsites for the recruitment of new individuals (Keeley and Fotheringham 2000; Franzese et al. 2009). In the study area, although it was not measured, our observations indicate that both processes are taking place during recovery (see Figure 1). Some species, particularly shrubs and bunch grasses, resprout after fire. Other species, that greatly increased their abundance after fire (e.g. *Nassella trichotoma*) or that were only present in the burned plots (e.g. *Hedypnois rhagadioloides*), are probably emerging from the

soil seed bank (A Loydi, pers. obs.). This rapid vegetation cover recovery of the Pampas mountain grassland vegetation reassures that community functionality, and thus provided ecosystem services, will be preserved in the long term (Latterra et al. 2011).

Unburnt grasslands were dominated by bunch grasses that are usually good competitors that can reduce the abundance of other species (Corbin and D'Antonio 2004). This is related, not only with their higher competitive ability (Holmes and Rice 1996), but also with a higher resource availability in these sites, with deeper soils and higher humidity content (Loydi and Distel 2010). These tussock grasses usually outcompete other species by accumulating standing dead biomass, occupying available space. Burning in tussock grassland sites reduced the competition intensity by releasing space that was occupied by the dominant bunch grass species (Frangi et al. 1980). After the fire, other species were able to establish and increase their abundance, changing the species dominance. This way, two years after the fire, vegetation cover recovered fast but species composition did not fully recover. There was a clear change in the dominant species. Unburned areas were dominated by *Amelichloa caudata*, a tall bunch grass species (50-120 cm height), that was replaced by *Nassella trichotoma*, a short bunch grass (20-60 cm height) (Zuloaga et al. 2012). The lack of resilience in term of species composition to fire may be a normal feature for these mountain grasslands. However, it has to be considered that fire in these mountain grasslands had been suppressed for several years (Barrera and Frangi 1997; Medina 2007) and the response we observed may not be the usual if the regular fire regime would be maintain.

On the other hand, shrublands are more resource-limited than grasslands, with shallower soils that can retain less humidity (Loydi and Distel 2010). This resource limitation might be the reason why shrublands have a higher species richness than grasslands (Cornwell and Grubb 2003). Species dominance is less marked in these sites and a higher number of species can coexist (Koerner et al. 2018). Vegetation cover of shrublands also recovered fast following fire. Moreover, the species composition between burned and unburned shrublands was very similar two years after the fire,



which shows a higher resilience to fire than grasslands. This higher resilience of shrublands may be related to their higher plant diversity (i.e. species richness), as higher plant diversity generally leads to a higher resilience to disturbance (Hooper et al. 2005). Having more species may be a reassurance that there are species capable of rapidly responding to fire (i.e. portfolio effect, Figge 2004), being the whole community capable to positively response to fire, for example increasing their vegetation cover. However, vegetation cover recovery was also observed in the grassland areas, at the same rate, indicating that species richness may not fully lead this particular response. More studies are needed to solve this particular issue.

Analyzing changes in vegetation functional groups, as a proxy for functional diversity (Petchey and Gaston 2002), can give information about changes in community structure (Fukami et al. 2005). Fire can have an impact on community structure due to changes in the dominant functional groups, since resprouting or new colonization by different functional groups can lead to different vegetation structure (Pausas et al. 2004). In terms of functional composition, besides transient changes during the first year after fire, we did not detect long-term changes in the dominance of the different functional groups. Barrera and Frangi (1997), in a proposed state and transitions model for the area (Westoby et al. 1989), suggested that the communities with low to no cover of shrubs in the study area are stable and maintained by low grazing intensity. They suggested that fire will have no effect on community structure in the long term and the expected time of recovery

(measure as vegetation abundance) would be around two years (Barrera and Frangi 1997). Nonetheless, the process for species composition change is slower and highly dependent on land management (Cingolani et al. 2005; Koerner et al. 2018) and environmental conditions (e.g. dry and wet years; Morecroft et al. 2004; Evans et al. 2011). Climate, grazing and fire are mentioned as the main factors affecting vegetation dynamics in grasslands (Koerner and Collins 2014). Therefore, knowing the response of vegetation to fire in grazed ecosystems is particularly important to manage these areas trying to maintain cattle production and biodiversity conservation at the same time. More studies have to be done to understand how these factors interact.

#### 4 Conclusion

Plant species in the mountain Pampas seems to be well adapted to fire occurrence, but in areas where competition is stronger (i.e. grasslands), a change in the dominant species, such as the one triggered by fire, can drastically change species composition, but not their structure. Nonetheless, these changes are hardly permanent since pre-fire species are still present in the area.

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