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Biotic and abiotic changes along a cyclic succession driven by shrubs in semiarid steppes from Patagonia

Pablo A. Cipriotti · Martín R. Aguiar

Abstract
Aim We studied the legacy effects of shrubs during the downgrade phase of high–cover patches. Specifically, are woody species able to modify environmental attributes at patch level to such an extent as to alter the colonization once they have vacated their original position?
Methods We monitored five environmental variables along an experimental four-stage downgrading gradient of high–cover patches during two years in cold- and warm-seasons, individual plant growth during three years, as well as the floristic composition of patches along the same gradient after 13 years.
Results The downgrade of high–cover patches reduces the aboveground protection due to the increase in wind speed (400–500%) and evaporation rate (43–160%) associated with shrub death and senescence. In addition, high–cover patches increase the total soil nitrogen (400–600%) and reduce the infiltration rate (44–73%) on the top layer. Leaf length and flower culms of grass tussocks were lower in bare soil patches (7.5 cm and 3) compared to whatever degradation stage of high–cover patches (9–10 cm and 18–32). Floristic composition after 13 years reveals that grass species occupied the patch stages differentially, with a disjunctive pattern among species within the *Poa* and *Pappostipa* genus.
Conclusions Legacy effects prompted by shrubs through changes in soil properties at the horizontal plane can conditioned the patch dynamics. The ability of different plant species to cope with the spatial heterogeneity at the horizontal plane should be included as a new criterion to define plant strategies from arid ecosystems according to the gap–phase dynamics and mosaic maintenance.

Keywords Colonization · Gap-phase dynamics · Grass-shrub coexistence · Legacy effects · Patch dynamics · Plant strategies · Two–phase mosaics

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Introduction

Watt ([1947](#)) proposed that plant communities are organised as an array of different vegetation patches linked by a common working dynamic. Several plant community types (e.g., grasslands, woodlands, forests, savannas) include internal cyclical dynamics in which the colonization of bare ground patches "upgrade" to a fully vegetated patch. In time, vegetated patches can

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"downgrade" to bare ground again closing the loop of the gap-phase dynamics (Watt 1947; Pickett and White 1985; Meyer et al. 2007). In most arid and semi-arid ecosystems the vegetation is organized as two–phase mosaics with high–cover vegetation patches interspersed in a matrix of low or null plant cover (Noy Meir 1981; Fuentes et al. 1984; Couteron and Kokou 1997; Aguiar and Sala 1999). In general, vegetation mosaics are described by two discrete stages as the minimum number of patch stages to represent both phases. But, the occurrence of transient stages between the two extremes is also important to a thorough description of spatial organization and vegetation dynamics (Meyer et al. 2007; Moustakas et al. 2009). The spatial organisation of vegetation mosaics has been identified as a key attribute of the structure and functioning of arid ecosystems because it can affect diversity, productivity, water dynamics, carbon and nutrients cycling (Ludwig and Tongway 1995; Segoli et al. 2008). In addition, population processes such as seed dispersal, seedling recruitment and biotic interactions are conditioned by the particular spatial arrangement of local plant populations or individuals (Montaña 1992; Aguiar and Sala 1994).

The most frequent mechanism proposed to explain the maintenance of two–phase mosaics is a positive feedback between vegetation and resources through the lateral water redistribution (run–off and run–on) (Galle et al. 1999; Ludwig et al. 1999; Dunkerley 2002). Specifically, areas of low or no plant cover, with sealed or crusted soils located on gentle slopes, and under the influence of intense rainfall events which promote water run–off to areas of high plant cover with high infiltration rates that act as barriers to the lateral water redistribution (Dunkerley and Brown 1999; Imeson and Prinsen 2005; Mills et al. 2009). Indeed, long term and complex dynamics of two–phase mosaics were described mostly by using different modelling approaches (Klausmeier 1999; Rietkerk et al. 2004).

Alternative mechanisms of mosaic maintenance point to the role of the balance of biotic interactions among plants (competition and facilitation) in conjunction with seed dispersal as the main drivers of the vegetation patch dynamics in arid ecosystems (Aguiar and Sala 1999; Olff et al. 1999; Pueyo et al. 2008; Moustakas et al. 2013). During the upgrading to high–cover patches, the net balance between competition and facilitation is expected to be positive in a biological sense (i.e. facilitation dominates over competition), while during the downgrading of high–cover patches, this situation is reversed and in turn, the net balance of plant-plant interactions becomes negative (i.e. competition dominates over facilitation). These processes have been mostly tested by modelling approaches (Couteron and Lejeune 2001; Dickie et al. 2005), and field experiments have been able to disentangle the role of this balance on the spatial patterns and patch dynamics of vegetation mosaics (Schenk and Mahall 2002; Barbier et al. 2008).

Moreover, in the two proposed mechanisms employed to explain the maintenance of vegetation mosaics, woody plants play a central role during the upgrade phase of high–cover patches. They change the hydrological properties (e.g., increasing infiltration), trap seeds, ameliorate microclimate conditions and promote nutrient enrichment (Zhang et al. 2011; Giladi et al. 2013; Daryanto et al. 2012; Navarro-Cano et al. 2015). Thus, they facilitate the recruitment of new individuals into their neighbourhood. However, a key condition to maintain the vegetation mosaic and the cyclic succession is that after the shrub death (the beginning of downgrade phase of high–cover patches), the vacated patch should be able to reinitiate a similar upgrading dynamics. This issue is crucial to understand patch dynamics in a spatial domain, but we cannot be entirely sure if this in fact really happens because woody long-lived species are able to modify the soil properties, accumulate seeds differentially below their canopy, or even maintain the patch occupied with their remains (e.g., debris, litter, or logs) for a long time after death (Bergelson 1990; Facelli and Facelli 1993; Daryanto et al. 2012; Monger et al. 2015). Hence, after dying, woody species are able to leave a kind of fingerprint inside the degraded high–cover patches associated with the chemistry of litter or debris, changes in chemical and physical soil properties and the seed bank. These legacy effects can drive the future colonization of degraded patches and the dynamics of the whole plant community in the long term (Facelli and Brock 2000; Meyer et al. 2009; Monger et al. 2015), as well to control the ecosystem functioning (Carrera et al. 2003; Sala et al. 2012a; Reichmann et al. 2013).

Vegetation in the occidental Patagonian steppes is spatially organised as a two–phase spot mosaic comprising mostly individual shrubs that are surrounded by a dense ring of perennial grasses as high–cover patches and scattered grass tussocks in a matrix of bare ground as low–cover patches (Soriano et al. 1994; Cipriotti and Aguiar 2005). Soriano et al. (1994) proposed that both mosaic phases are linked by a cyclic succession based on the balance of biotic interactions between shrubs and

grasses. During early stages of high–cover patches the net balance would be positive (i.e. facilitation > competition) promoting the growth into the mature stage, while at mature stage the net balance turn negative (i.e. competition > facilitation) and high–cover patches downgrade. Despite the current understanding about the role of shrub facilitation, nutrient enrichment, and seed dispersal as a means of explaining the occurrence of high–cover patches (Aguiar and Sala 1994, 1997; Armas et al. 2008), there remains limited knowledge about the long term community dynamics in the spatial domain of vegetation mosaics, particularly after the death of woody species and the consequent degradation phase of high–cover patches (Cipriotti and Aguiar 2015). In this work we are particularly interested in testing the legacy effects of high–cover patches. Our main question is: Are woody species able to modify environmental attributes at patch level to such an extent as to alter the colonization once they have vacated their original position? In addition, which plant species colonized bare ground areas previously occupied by shrubs? Are the same species that colonized bare ground areas unoccupied by shrubs? Our hypothesis is that woody species modify the soil beneath their canopy, in such a way that they constraint the re-colonization by grass species. Particularly, we predict that patches originally occupied by woody plants reduce the grass colonization, especially of those species reproducing by seeds. To test this hypothesis we conducted a field experiment that manipulates mature high–cover patches to reproduce a degradation gradient, and also followed natural shrub debris and bare soil patches for more than ten years in the grass-shrub Patagonian steppes. We measured five environmental variables (soil water content at two depths, wind speed at two heights, evaporation rate, infiltration rate, and nitrogen content as nitrates and ammonia) during two years in warm and cold season along the degradation gradient of high–cover patches. In addition, we surveyed the individual plant growth and flowering at short term (1–3 years) and after 13 years the floristic composition of high–cover patches along the same degradation gradient to identify the main colonizer species.

Materials and methods

Study site

The study site is located at the Río Mayo INTA Experimental Station in South Central Patagonia,

Chubut Province, Argentina (45° 41′ S, 70° 16′ W; 500 m a.s.l). Mean annual precipitation is 153 mm (1960–present) and ranges between 47 and 245 mm. More than 70% of the precipitation falls during the autumn and winter season, from March to August (Jobbágy et al. 1995). The mean annual temperature is 8.1 °C and the mean monthly temperature ranges from 2 °C in July to 14 °C in January. The landscape is typically flat and soils are coarse textured (sandy), with cobbles and pebbles making up 50% of the soil mass. The vegetation is co–dominated by tussock perennial grasses (*Pappostipa speciosa* Trin. Et Rupr., *P. humilis* Vahl., and *Poa ligularis* Nees ap. Steud.) and shrubs (*Mulinum spinosum* (Cav.) Pers., *Senecio filaginoides* AD, and *Adesmia volckmanni* Philippi.), which cover 28% and 12% of the ground, respectively (Fernández-Alduncin et al. 1991). *M. spinosum* and *S. filaginoides* species cover ca. 4–6% each one, while *A. volckmanni* generally did not overpass 2% (Golluscio et al. 1982). The three shrub species presented secondary metabolites compounds in their foliar tissues, but with significant differences in concentration especially from oils and phenols (*S. filaginoides* > *M. spinosum* > *A. volckmanni*) (Cavagnaro et al. 2003). The vegetation is spatially organized as a two–phase mosaic where high–cover vegetation patches (shrubs and grasses) occur within a matrix of low–cover scattered grass tussocks on bare ground (Cipriotti and Aguiar 2005).

Field experiment

The experiment followed a completely randomized design to test the effects of pre-defined stages of high–cover patches along the downgrade phase of the cyclic succession proposed by Soriano et al. (1994). Four different stages were represented by a gradient from mature high–cover to bare soil patches. In May 2001, we delimited a ½-ha experimental area inside an excluded grazing paddock enclosing approximately 1500 mature vegetation patches formed only by adult shrubs. Therein, we randomly selected ten patches of bare soil (BS), twenty mature high–cover patches formed by a living adult shrub (diameter of 0.8–1 m) with a dense grass ring, and ten old degraded high–cover patches formed by shrub debris or remains (SR) with a similar diameter to living shrubs. Thereafter, ten of twenty mature patches were randomly selected to stay intact (LS), and the other ten with a killed shrub and an

untouched complete grass ring to represent a recent dead condition (DS). In DS treatment, we cut the main stem or multiple stems (2–3) below the ground level (5–15 cm), and then we fixed the dead crown of shrub in their original position with wires and spikes. To avoid shrub species–specific effects, all high–cover patches selected were represented by a single *Mulinum spinosum* plant, a dominant and key shrub species in this vegetation community (Cipriotti and Aguiar 2012). Environmental variables were surveyed during two consecutive years shortly after the beginning of the experiment (May 2001–November 2003), while floristic composition was recorded previous to the treatment randomization and after thirteen years (March 2014. See details below).

Environmental measurements

We monitored five abiotic variables across patch stages for each experimental unit (i.e. vegetation patch) or a random sub-sampling according to the abiotic variable as we detailed below. We measured the following possible drivers during cold and warm seasons: soil water content at two depths (0–5 cm and 0–20 cm), wind speed at two heights (0.10 and 100 cm), evaporation rate at ground level (2 cm), and soil nitrogen content at the top soil layer (nitrates and ammonia). The surface infiltration rate was evaluated only during warm season (late spring) at two different soil water contents, because we did not expect changes across seasons more than that related to the soil humidity (see details below).

We measured soil water content at the top and middle layers for each experimental unit using two different methods on two dates in cold (May 2002 and May 2003) and two dates in warm season (Jan 2002 and Jan. 2003). Gravimetric soil water content in the top layer (0–5 cm) was estimated for the same soil samples collected for nitrogen analyses (see below). Soil water estimations for the middle layer were performed with the time domain reflectometry (TDR) technique (Reeves and Smith 1992) (Tektronix 1502C equipment, Oregon, USA, 1999) and TDR probes 20 cm in length in each vegetation patch. All measures were then expressed as gravimetric soil water content (g/100 g dried soil) by considering the soil bulk density of finer fraction for top soil layer and the average of fine and coarse fractions for the middle soil layer (Paruelo et al. 1988).

Wind speed at two different heights for each vegetation patch was recorded in the afternoon (2–6 p.m.) by using Kestrel© 2000 anemometers (Nielsen-Kellerman Co., Boothwyn, USA, 2001). We set the anemometers in a random sub-sample of experimental units ($n = 4$–6) across all patch stages. We used the average wind speed during five minutes intervals on two dates in cold (May 2002 and May 2003) and four dates in warm season (Nov 2001, Jan. 2002, Nov 2002 and Jan. 2003). We measured evaporation rate with Piche's evaporimeters (Soriano and Sala 1986). We set the evaporimeters in a random sub-sample of experimental units ($n = 4$–6) across all patch stages with an initial known water content at 7–8 a.m. and measured the remaining water in the afternoon (5–6 p.m.). We calculated the evaporation rate as a ratio of evaporated water to time, standardized by the evaporating area on two dates in cold (May 2002 and May 2003) and four dates in warm season (Nov 2001, Jan. 2002, Nov 2002, Jan. 2003). We also measured the soil surface infiltration rate under dry (ca. $\psi < -5.9$ MPa) and saturated soil conditions (ca. $\psi = -0.03$ MPa) by the double ring method (Robertson et al. 1999) in a new sub–sample of experimental units ($n = 5$) across two vegetation patches: bare soil in the low–cover patches (BS) and below shrubs in mature high–cover patches (LS). We set the stainless double ring on the soil ground for each patch and recorded the time needed to infiltrate a certain water volume applied in the double ring. In the same way, we calculated the infiltration rate as a ratio of the volume of water infiltrated to time, standardized by the central ring area. Infiltration measures were taken on one date in warm season (Nov'03).

Inorganic soil nitrogen content such as ammonium and nitrate was measured for each experimental unit. Soil samples were extracted with a steel soil corer at 5 cm depth on two dates in cold season (May 2002 and May 2003) and two dates in warm season (Jan 2002 and Jan. 2003). In mature high–cover (LS) or degraded patches (DS or SR) soil samples were taken from below shrubs, but in low–cover patches soil samples were taken in bare soil areas (BS). Soil samples were transferred into plastic bags for transport from the field to the laboratory. We sieved fresh soil samples through a 2 mm mesh, and extracted a sub-sample of 10 g of soil in 50 ml 2 N KCl in order to determine inorganic nitrogen (N–NH_4 and N–NO_3) on the same day of extraction. Soil nitrogen concentrations were corrected for soil water content (Robertson et al. 1999) by placing a sub-

sample of soil in a drying oven at 105 °C for 48 h for the determination of gravimetric soil water content. Nitrogen concentrations were converted to mass of N per unit of soil mass using bulk density for the fine soil fraction (Paruelo et al. 1988). Soil extracts were analysed using an Alpkem autoanalyzer (O–I Co., College Station, Texas, USA, 2001), which uses a colorimetric analysis of inorganic nitrogen in liquid extracts.

Plant measures and floristic composition

We estimated individual plant growth during three years (2001–03). We measured the length of fully expanded leaves (4–6 leaves per tussock) for a random subset of tussock grasses of *Pappostipa humilis* (n = 3) established in the patches at the end of growing season (January 2003). *P. humilis* species was chosen because was one of the three co-dominant perennial grass tussocks and the perennial grass species less affected by grazing (Golluscio et al. 1982). In addition, we counted the total flower culms per grass tussock in the same year at seed dispersal stage (20th January 2003), assuring the end of flowering season for this species according to previous phenological studies in the same area (Golluscio et al. 2005). On other hand, we recorded the plant composition for each vegetation patch previous to the treatment application [May 2001, for a subsample of mature high–cover (LS), dead shrubs (DS) and shrub remains (SR) patches; n = 18], and 13 years after for all patches (March 2014). To record plant composition across different vegetation stages, we identified each perennial plant located in the grass-ring and at the centre of high–cover patches for all patches. To conduct the plant measures and to survey the plant composition in bare soil patches, we performed the same sampling scheme by placing a steel ring at the centre of low–cover patch with the same diameter of high–cover patches (ca. 1 m). Thereafter, density for each species was calculated as the number of individuals or ramets per square meter according to the approximated circle area of the sampled patch and the modular structure of plant species considered.

Statistical analysis

Soil water and nitrogen content were analysed using one–way ANOVA models for repeated measures design (because we measured the same experimental units over the time) to test the main effects across different patch stages, separately for each season (warm or cold season). The other environmental variables (i.e. wind speed, evaporation and infiltration rate) were analysed using one–way ANOVA models according to a completely randomized design to test the main effects across different patch stages and dates, separately for each season (cold or warm season). In this case, we did not use a repeated measures design because a different random sub-set of experimental units (i.e. vegetation patches) were measured for each date and season. Hence, we treated dates as a block effect within each season. We performed post–hoc comparisons with Tukey-HSD tests with a significance level of 5%. These statistical analyses were performed with the software Statistica© v9.1.

The average length of leaves of grass tussocks was analyzed using one–way ANOVA model according to a completely randomized design to test the main effects across different patch stages and years (as a block effect). The number of flower culms was analyzed by Wald statistic and Chi-square test for generalized models (Poisson distribution and log link function) to test the main effects across different patch stages. On the other hand, plant composition of vegetation patches was first analysed using a MANOVA approach (Wilks statistic) at life form level (i.e. grasses and shrubs), and then at species level where the multiple variables were the density of dominant plant species recorded in the final monitoring (e.g., *Pappostipa speciosa, Pappostipa humilis, Poa ligularis, Senecio filaginoides, Poa lanuginosa*, etc.). After detecting differences among main response variables, we conducted single F-tests by one–way ANOVA models according to a completely randomized design to test the main effects across different patch stages, separately for each shrub or grass species. However, since some species were rare or in very low density across almost all experimental units (e.g. *Hordeum commosum* or *Carex* spp.), we performed one-way ANOVAs only for the common perennial species. In addition, to explore the legacy effects associated with the death of shrubs in mature high-cover patches we conducted constrained correspondence analysis (CCA) based on permutations of the floristic composition for a subsample of shrubs surveyed at the beginning and the end of experiment for both treatments involved dead shrubs (DS and SR). These analyses were performed with the package vegan of R environment (Oksanen et al. 2016).

Results

Environmental measurements

Most of the environmental variables differed across the stages of high–cover patches and seasons. Soil water content changed according to the patch stage, season and soil layer (Fig. 1a, b; Table S1). Soil water content was higher in bare soil patches than in any other stage of high–cover patches, during cold season and at both soil layers (Fig. 1a, b). However, this difference was the largest at the top soil layer (ca. 64%; Fig. 1a), while at the middle soil layer the difference was small (ca. 16.5%; Fig. 1b). During the warm season, soil water content was lower than in the cold season and the differences among patch stages were also smaller (Fig. 1a, b). However, there was a subtle decrease in the soil water content in bare soil patches with respect to the other patch stages at the top soil layer (Fig. 1a), and a reversal response at the middle soil layer (Fig. 1b).
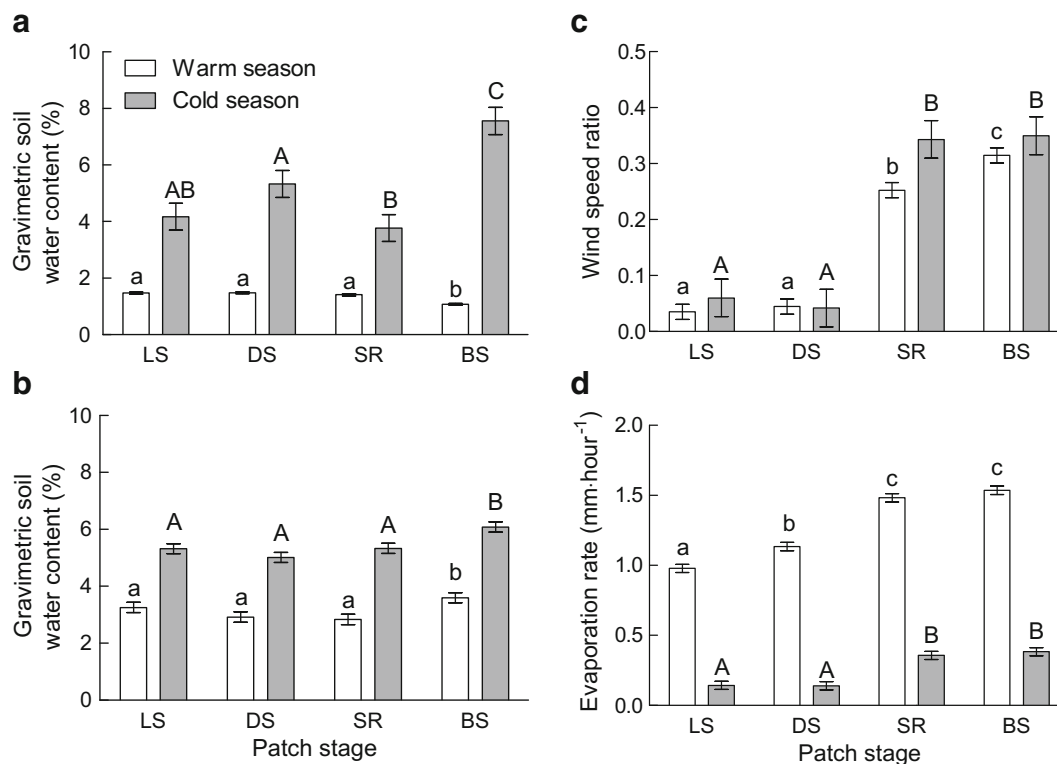
The wind speed ratio (10:100 cm) increased six times in shrub remains or bare soil patches with respect to the intact or recently dead high–cover patches, and this effect was similar across both seasons (Fig. 1c; Table S2). It is important to note, that the absolute wind speed is higher during warm-season (especially at noon. Data not shown), but we evaluated the ratio to test the effect of differences across vegetation patch stages.

Evaporation rate followed a similar pattern to the wind speed ratio, but with marked differences across seasons (Fig. 1d; Table S3). The evaporation rate in shrub remains or bare soil patches increased with respect to the same rate in intact or recently dead high–cover patches by ca. 160% in cold season, and 43% in warm season (Fig. 1d).

The infiltration rate also changed between the two patch stages analyzed (Fig. 2; Table S4). The infiltration rate in bare soil patches was greater than that under shrubs, in both wet (79.2%) and dry (277%) soil conditions (Fig. 2).

Fig. 1 Gravimetric soil water content in 0–5 cm **a**, 0–20 cm **b** soil layers, wind speed ratio (10:100 cm) **c** and evaporation rate **d** in warm and cold seasons across four stages of vegetation patches (LS: living shrub, DS: dead shrub, SR: shrub remains, and BS: bare soil). The vertical bars indicate means ± SE. Different letters indicate significant differences ($P < 0.05$) across patch stages within each season (lower-case for warm season and upper-case for cold season) and inside each panel
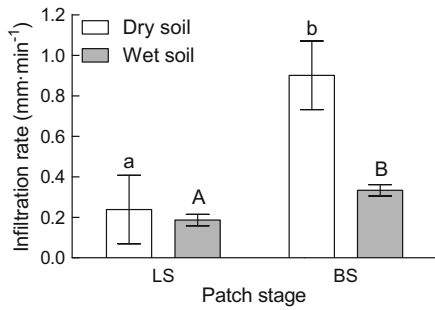
Fig. 2 Infiltration rate for two stages of vegetation patches (LS: living shrub and BS: bare soil) from dry or wet soil initial condition. The vertical bars indicate means ± SE. Different case letters indicate significant differences ($P < 0.05$) between patch stages within each initial water condition (lower-case for dry soil and upper-case for wet soil)

The soil nitrogen concentration at top layer, as ammonia (N–NH₄) and nitrates (N–NO₃), changed among patch stages in warm and cold seasons (Fig. 3a, b; Table S5). Overall, whatever stage of high–cover patches had higher N–NH₄ concentration than bare soil for warm (7–11 vs. 1.2 µg/g) and cold season (7–8 vs. 2.4 µg/g) (Fig. 3a). N–NO₃ concentration in warm

season was similar across stages of high–cover patches (4–5 µg/g), and higher than concentration in bare soil patches (0.5 µg/g; Fig. 3b). But in cold season, the N–NO₃ concentration was the highest under shrub remains (6.4 µg/g) in comparison with mature and recent dead high–cover patches (2–2.5 µg/g), and bare soil (0.77 µg/g; Fig. 3b).

Plant measures and floristic composition

Individual plant measures revealed that length of fully expanded leaves and the number of flower culms in grass tussocks were lower in bare soil patches (Fig. 4; Table S6). However, changes in leaf length among patch stages were minor (9–10 vs. 7.5 cm) in comparison with flower culms (18–32 vs. 3). In addition, the number of flower culms was a 77% higher under shrub remains in comparison to living shrub patches (Fig. 4b; Table S6b).

Life form composition at the end of experiment was different only in grass density across degradation stages of high–cover patches (Fig. 5 inset; Table S7). Contrary to the results on grass density, we were unable to detect significant differences in shrub density, at the life form
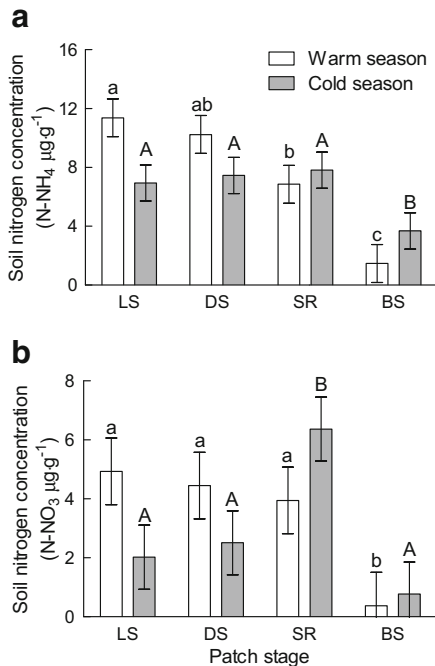

Fig. 3 Inorganic soil nitrogen concentration from ammonia **a** and nitrates **b** in the 0–5 cm soil layer in warm and cold seasons across four stages of vegetation patches (LS: living shrub, DS: dead shrub, SR: shrub remains, and BS: bare soil). The vertical bars indicate means ± SE. Different case letters indicate significant differences ($P < 0.05$) across patch stages within each season (lower-case for warm season and upper-case for cold season)
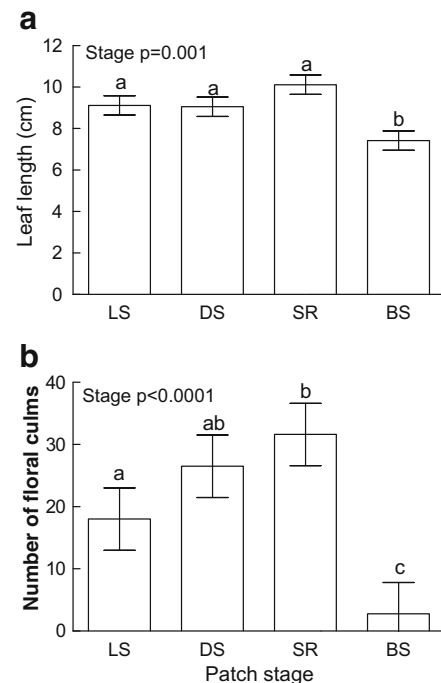

Fig. 4 Leaf length **a** and number of floral culms **b** in grass tussocks across four stages of vegetation patches (LS: living shrub, DS: dead shrub, SR: shrub remains, and BS: bare soil). Different lower-case letters indicate significant differences ($P < 0.05$) across patch stages inside each panel

or species level (Fig. S1; Table S7 and S8). The main differences in grass density have obeyed species-specific changes across patch stages (Table S7 and S8). Particularly, density of one dominant grass species remained quite similar across different vegetation patches (i.e. *Pappostipa speciosa*; Fig. 5a), while other three species presented marked differences (i.e. *Pappostipa humilis*, *Poa ligularis* and *Poa lanuginosa*; Figs. 5b-d; Table S6b-d). Density of *P. humilis* decreased significantly in bare soil patches ($F_{3,36} = 6.62$, $P = 0.001$; Fig. 5b), with a gradual increase in density from the intact living to shrub remains high–cover patches (Fig. 5b). On the contrary, plant density of *Poa ligularis* increased in the bare soil patches, with low and similar densities from high–cover patches ($F_{3,36} = 4.46$, $P = 0.009$; Fig. 5c). On the other hand, density of *Poa lanuginosa* increased significantly in vegetation patches with dead shrub or shrub remains in comparison to patches of bare soil or with intact living shrubs

($F_{3,36} = 11.2$, $P < 0.0001$; Fig. 5d). In addition, constrained correspondence analysis revealed remarkable changes through time on the floristic composition of patch stages conformed by dead shrubs and shrub remains (Fig. 6; Table S9). Time explained 50–60% of total variation in floristic composition, and the first two axes reached 82% of total variation in both patch stages (Table S9). Particularly, floristic responses through time show a replacement of *P. lanuginosa* grass species by dominant tussock grass species after the death of shrub (Fig. 6).

Discussion

Environmental and individual plant measures show significant changes along the degradation gradient of high–cover patches during the first 2–3 years. On the other hand, results of floristic composition after 13 years also
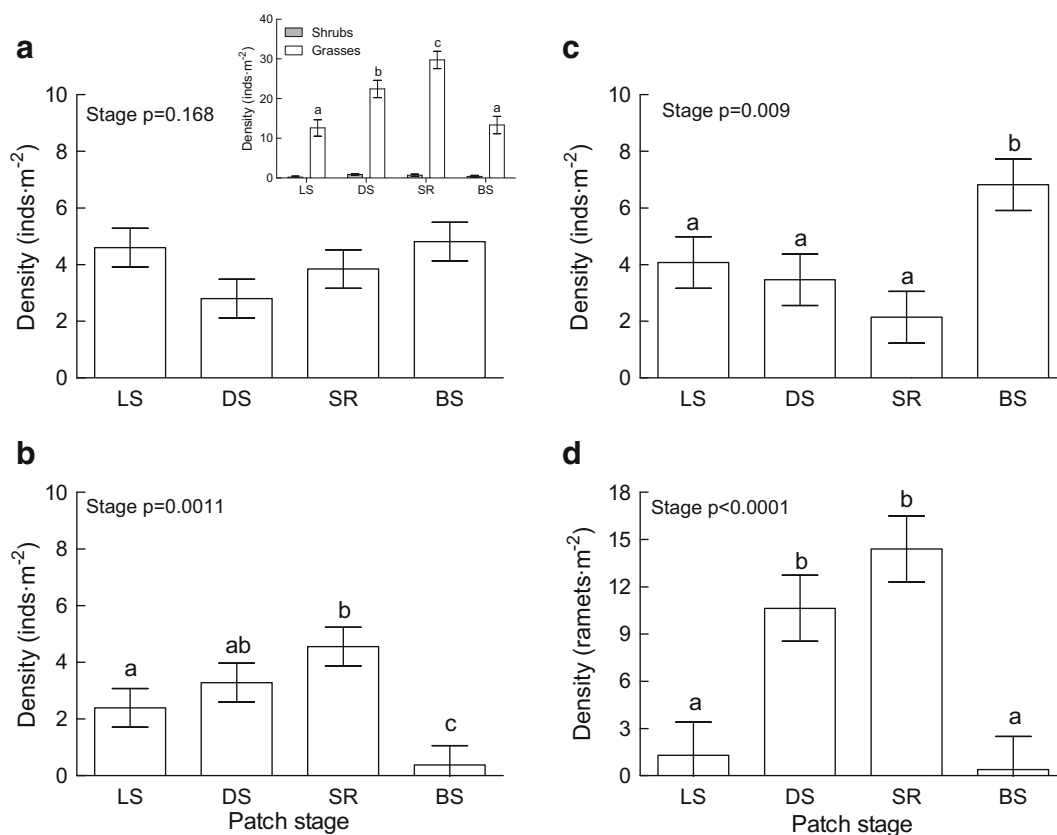

Fig. 5 Density of grasses *Pappostipa speciosa* **a**, *Pappostipa humilis* **b**, *Poa ligularis* **c**, and *Poa lanuginosa* **d** across four stages of vegetation patches (LS: living shrub, DS: dead shrub, SR: shrub remains, and BS: bare soil) at the final survey (2014). The vertical bars indicate means ± SE. Different lower-case letters indicate significant differences ($P < 0.05$) across patch stages inside each panel. Inset: Total density of perennial grasses and shrubs across the same patch stages

Fig. 6 Biplots derived from the CCA analysis indicating the changes in floristic composition along time (0: 2001 vs. 1: 2014) for two stages of vegetation patches with DS: dead shrubs **a** and SR: shrub remains **b**. Ordination plane is determined by the constrained correspondence axis (time) and the first unconstrained correspondence axis. Numbers indicated different patches, names the grass species (Papp: *Pappostipa speciosa* and *P. humilis*; Plig: *Poa ligularis*, Plan: *Poa lanuginosa*; and Bpic: *Bromus pictus*) and ellipses enclosed the different time surveys in the ordinated plain (confidence level = 99%)
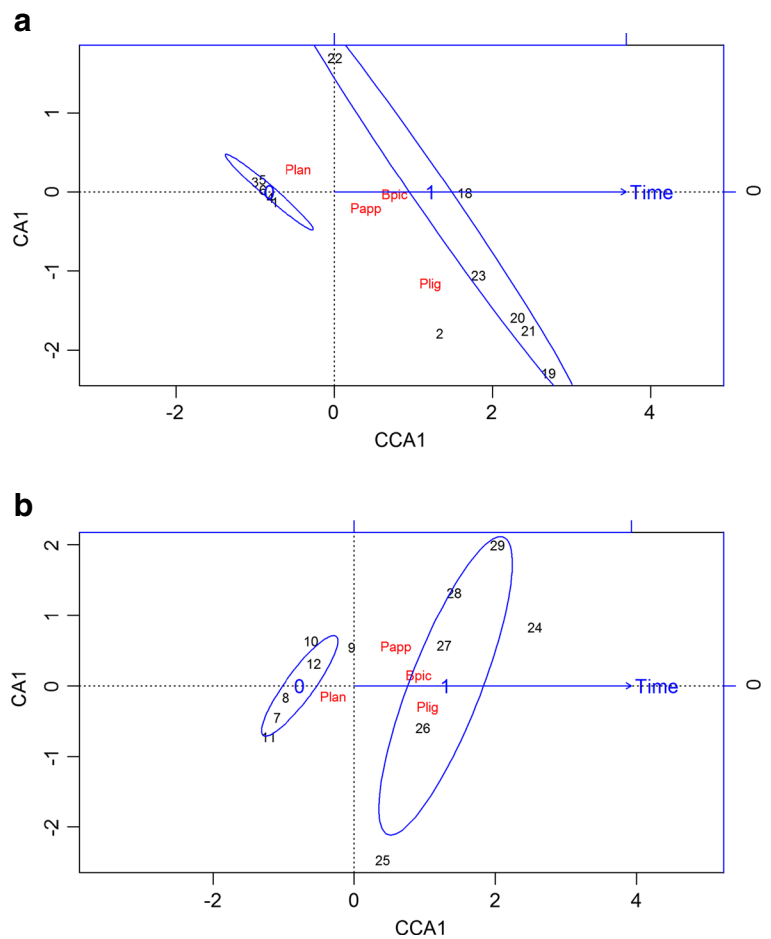
show significant changes along the same degradation gradient of high–cover patches supported by a replacement of grass species after the shrub death. Our results agreed with the hypothesis about legacy effects of shrubs on grass colonization of high–cover patches, because remarkable differences appear in the grass species density across different vegetation patch stages and time, at least for those organized around *M. spinosum* shrubs. However, we were unable to detect differences in woody species because the overall low recruitment of shrubs across all patch stages. Below, we discuss the significant responses along the degradation of high–cover patches for each single variable and then we propose a theoretical framework to understand the role of different plant strategies according to the cyclic succession and the maintenance of vegetation mosaics.

The highest soil water content measured in the bare soil patches at the top and middle layer during cold season agree with previous findings from our study site, reported by Soriano and Sala (1986) as soil water pockets. These water pockets in top soil are important to assure the germination and emergence of seedlings, but these patches had generally fewer seeds in comparison with any other vegetated patches (Aguiar and Sala 1997; Fernández-Alduncin et al. 2002). Modelling of soil water content in Patagonian steppes has also reflected this advantage during the cold season for the bare soil patches (Paruelo and Sala 1995). However, the crucial phase to define plant recruitment in Patagonian steppes is the seedling survival at the end of the growing season (Dec-Feb.; Aguiar et al. 2005; Cipriotti et al. 2008). During this dry period, the differences recorded here in the soil water content among patch stages were minor. However, modelling and field results based on daily time series of soil water content have reported a positive role of high–cover patches on soil water content at top soil layer shortly after the occurrence of rainfall events (Cipriotti et al. 2014).

The woody canopy facilitative effect was more important during the seedlings survival period (Dec-Mar) rather than that of emergence (Apr-Sep), due to the harsh dry atmospheric conditions in summer. The reduction of the wind speed and evaporation rate at canopy level as a result of the shrub crowns, improved the microclimate conditions of high–cover patches in comparison with the bare soil patches. These effects were previously reported for different woody plants in arid ecosystems, where shrub canopies reduced solar radiation, temperature, wind speed, evaporation, water stress, and our results point in the same direction (Vetaas 1992; Breshears et al. 1998). Hence, shrubs can facilitate the recruitment by reducing water losses during a period normally dry and with the highest water atmospheric demand (Paruelo et al. 2000). But these aboveground effects associated with the presence of shrub canopy generally disappear shortly after the shrub death with the senescence and decomposition of the shrub crown.

The infiltration rates measured under the canopy of *Mulinum spinosum* shrubs were significantly lower in comparison with bare soil patches, probably due to the existence of exudates (e.g. resins) able to seal the soil surface, such as was reported for other *Apiaceae* and *Mulinum* species (Chiaramello et al. 2003). Generally, woody species in arid ecosystems increase the water infiltration rates below its canopy by the accumulation of organic matter (Dunkerley and Brown 1999; Eldridge et al. 2015; Navarro-Cano et al. 2015) or by water stem flow (Levia and Germer 2015). Moreover, the increase of infiltration rate promoted by woody species is one key mechanism to support the positive feedback based on lateral movement of water that maintain the two–phase vegetation mosaics and also explain the up slope migration of vegetation bands (Dunkerley and Brown 1999; Imeson and Prinsen 2005; Mills et al. 2009). Surprisingly, we cannot confirm this result from the occidental grass-shrub Patagonian steppes. Our results indicate that patches previously occupied by the dominant shrub *Mulinum spinosum* can act as water sources due to the micro-topography (i.e. shrub hummocks) and the permanence of hydrophobic resin effects on top soil. In this way, one legacy effect of *Mulinum spinosum* shrubs might be that the water run–off from hummocks to the grass ring in degraded high–cover patches. This new hypothesis about the after shrub–death effect can delay the degradation of grass ring in high–cover patches. Despite these results must be confirmed by more measures on infiltration rates and lateral water

movement along year, our results agree with the permanence of positive net balances at degraded stages as it was recently reported (Cipriotti and Aguiar 2015).

Irrespective of the degradation stage of high–cover patches and season, in these patches we measured an increase in the soil nitrogen content such as ammonia and nitrates in the top layer in comparison with bare soil patches. Our findings are consistent with previous results about the micro-site heterogeneity of nutrients and organic matter commonly associated with the occurrence of fertility islands below shrubs from Patagonian steppes (Mazzarino et al. 1998; Austin and Sala 2002; Yahdjian et al. 2006) and other arid ecosystems (Schlesinger et al. 1996; Zhang et al. 2011). High–cover patches across the two different degradation stages increased more than seven times the total inorganic nitrogen content in comparison with bare soil patches in warm-season, and triplicate in cold-season. In addition, the soil nitrogen content such as nitrates in the top layer reached the highest content below shrub debris during the cold season in comparison with mature or recently degraded high–cover patches. This difference in the soil nitrate content among high–cover patch stages could be associated with differences in the decomposable organic matter under shrub debris or to the differential nitrate uptake by shrubs in comparison with grasses (Gherardi et al. 2013).

Plant responses at near term indicate positive effects associated to whatever degradation stage of high–cover patches in comparison to bare soil patches. But particularly significant were the observed differences (ca. 10 times) in the number of flower culms, with the highest mean under shrub remains. A priori we can not discarded that this effect could be associated with a delay in plant phenology from bare soil patches, however our measurements were recorded after the end of flowering season for this species (Golluscio et al. 2005), and well advanced in the drought period (20th January). Therefore, this positive plant response from grass tussocks may result from the soil nitrogen enrichment under degraded high-cover patches rather than the above-ground protection (Armas et al. 2008). On the other hand, field experiments in Patagonia have shown that facilitation of adult shrubs was determinant to grass seedling recruitment in the high-cover patches (Aguiar and Sala 1994). At long term, floristic composition was different among stages along the degradation phase of high–cover patches, and showed also changes along time. Previous results from observational surveys in Patagonia have reported

differences in plant composition between bare soil and mature high–cover patches (Soriano et al. 1994). Our results indicate more details about the occurrence of grass species-specific relationships across patch stages, with disjunctive occupancy patterns of species within *Pappostipa* and *Poa* genus. *Pappostipa humilis* reached the lowest density in bare soil patches, while *Pappostipa speciosa* had similar densities across all patch stages. On the other hand, *Poa ligularis* occurs in high density in bare soil patches, while *Poa lanuginosa* occurs in high density particularly in degraded high–cover patches. These four strategies of occupancy according to the patch stages in the vegetation mosaic can reveal differences in their competitive ability or ecological niche breadth among plant species. In fact, *P. humilis* is probably unable to occupy poor micro-sites in nitrogen. It was previously observed this grass species is usually found in high density near sheep piospheres or associated with legume shrubs (Armas et al. 2008), while *P. speciosa* represented a more generalist species able to colonize both phases of the vegetation mosaic. On the other hand, *Poa ligularis* is probably one of the most highly competitive grass species especially under low nitrogen content (Semmartin et al. 2004; Bertiller et al. 2005), while *Poa lanuginosa* could be displaced by plant competition to degraded patches.

Particularly interesting is the response of *P. lanuginosa*, because it is a non-tussock and subdominant grass species with rhizomes able to colonize degraded patches. During the degradation phase of high–cover patches where a thick litter layer of shrub debris still remains above ground (2–10 cm; Fig. S2), grass recruitment from seeds is strongly restricted (Rotundo and Aguiar 2004, 2005). However the soil under these patches represents a significant nitrogen reservoir from arid ecosystems (Mazzarino et al. 1998; Austin and Sala 2002; Yahdjian et al. 2011), they are dryer than bare soil patches. *Poa lanuginosa* species represents a growth–form with an agamic reproductive strategy able to overcome the recruitment by seed in a litter layer. Indeed, this species develop a rhizomes network across a long distance (1–2 m) joining different patch stages and to grow through a compact layer of shrub litter. Based on our multivariate results through time, it is possible think that patches dominated by *P. lanuginosa* represent an intermediate stage in the downgrading phase, in the middle between shrub remains and bare soil stages in the cyclical succession originally proposed by Soriano et al. (1994).

Short term environmental changes and plant responses, as well as long term floristic compositional changes can be integrated under general theoretical frameworks for explaining spatial mosaic organization and patch dynamics in semi-arid ecosystems. Several authors have proposed that patch dynamics can be controlled by different drivers like water redistribution, biotic interactions, and fire among others (Olff et al. 1999; Moustakas et al. 2013; Blaser et al. 2013). It has been proposed that biotic interaction balance regulates the patch dynamics and the mosaic maintenance in the Patagonian steppes (Soriano et al. 1994). According to this hypothesis, we would have expected negative net balances become significant during mature and degraded stages of high–cover patches (i.e. by promoting poor grass performance). However, previous results indicate that even positive net balances can occur at late stages of high–cover patches as shrub remains on grass seedlings, despite of the aerial protection disappears at this stage (Cipriotti and Aguiar 2015). Similarly, our results point to the occurrence of facilitative legacies after the death of woody plants on grasses through above- (water infiltration) and below-ground (soil nitrogen) processes, conditioning the re-colonization of degraded high–cover patches and rescuing the role of sub-dominant grass species with an agamic reproductive strategy to benefit from the resource patchiness of mosaic. The occurrence of facilitative legacies after shrub death and the appearance of intermediate stages probably delay the downgrading of high–cover patches and increase the cycle length. Our best estimate is about 50–65 years as a minimum for the cycle length, because we assumed the longevity of shrubs is 35–50 years (Fernández et al. 1992; Cipriotti and Aguiar 2012) while the downgrading can take 15 or more years. But, it is important to notice that further research is necessary for getting a full description of the cycle length, as well as the specific environmental drivers involved in the legacy effects here advanced based on floristic composition changes during the time period assessed. It is possible that environmental drivers can also change within this temporal window (2001/03–2014).

Soriano and Sala (1983) suggest different plant functional types and strategies from the Patagonian steppe according to the vertical water and roots distribution along the soil profile. Moreover, Sala et al. (1997) proposed that different life-forms from arid and semiarid ecosystems (i.e., succulents, forbs, grasses, and shrubs) coexist by virtue of separation niches formed according

to the soil depth and residence time of water, basically determined by the soil texture. Other studies suggested a new dimension concerning the coexistence of different plant strategies in semiarid ecosystems according to the nitrogen uptake strategy, mostly based on the vertical roots distribution between grasses and shrubs (Carrera et al. 2003; Rodríguez et al. 2007; February et al. 2011; Sala et al. 2012b). However, this theoretical framework emphasized the importance of the vertical differentiation along the soil profile, but it neglects to take into consideration the role of the spatial organization of vegetation patches in the horizontal plane that is commonly widespread in semiarid vegetation mosaics (Aguiar and Sala 1999). Results on total nitrogen soil content (N-NO$_3$ + N-NH$_4$) across different soil layers reported by Sala et al. (2012b) from Patagonian steppes indicated a 3–4 times ratio between the top (0–5 cm) and bottom soil layers (15–60 cm), while this ratio in the horizontal plane from the top layer was ca. 3–7 times between bare soil and high–cover patches based on our own results. Our results show the importance of including ability of different plant species to cope with the spatial heterogeneity at the horizontal plane as a new criterion to define plant strategies from arid ecosystems according to the gap–phase dynamics and the mosaic maintenance.

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