

# Cushion Shrubs Encroach Subhumid Rangelands: Fertility Islands in Fragile Soils Along a Grazing Gradient in Patagonia

Braian Vogel (✉ [braian.vogel@conicet.gov.ar](mailto:braian.vogel@conicet.gov.ar))

Consejo Nacional de Investigaciones Científicas y Técnicas <https://orcid.org/0000-0002-3136-0813>

**César Mario Rostagno**

• Instituto Patagónico para el Estudio de los Ecosistemas Continentales (IPEEC-CENPAT- CONICET),  
Bvard. Brown s/n, 9120 Puerto Madryn, Chubut, Argentina

**Marcos Antilef**

• Centro de Estudios Ambientales Integrados, Facultad de Ingeniería, Universidad Nacional de la Patagonia San Juan Bosco (UNPSJB), Ruta 259 Km 16.4, 9200 Esquel, Chubut, Argentina

**Ludmila La Manna**

• Centro de Estudios Ambientales Integrados, Facultad de Ingeniería, Universidad Nacional de la Patagonia San Juan Bosco (UNPSJB), Ruta 259 Km 16.4, 9200 Esquel, Chubut, Argentina

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## Research Article

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# Abstract

## *Purpose*

This work assesses changes in soil and vegetation structure associated with grazing intensity (GI) in subhumid grasslands. We conducted the study in the Subandean district of Patagonia, Argentina. Non-degraded Subandean grass steppes have extremely erodible volcanic soils and are valuable grazing ranges. However, nowadays vast portions exhibit a heterogeneous cover that is mostly of cushion shrubs, with big eroded soil patches.

## *Methods*

We selected four study sites along a GI gradient and one grazed-excluded site. Soils, vegetation cover and patches structure were characterised. We took soil samples beneath grass and shrub patches and their interpatches and in undisturbed spots.

## *Results*

Soils in undisturbed spots had the highest chemical fertility. Soils in grazing areas showed high heterogeneity associated with plant life-form and GI. Results also showed that medium and fine sand particles remobilised from bare soil to vegetated patches. Total nitrogen and organic matter increased in the same direction. Grass cover decreased as GI increases, while shrubs cover and total richness increased, until a collapse at the highest intensity. Relative cover of cushion shrubs and bare soil grow steadily with GI.

## *Conclusions*

The fertility island effect was associated with cushion shrubs. Grazing caused cushion shrub encroachment regardless of its intensity. Notwithstanding this, the same disturbance -grazing- which promoted cushions prevalence also favoured the collapse of fertile islands when reached to maximum intensity. Ecosystem services provision from a range management standpoint decreased. However, the increases in richness under moderate GI could represent an enhancement in system functionality.

# Introduction

Rangelands across the world are under increasing pressure by a growing demand for livestock products, land competition with agriculture and urbanisation, cultural and social drivers, and climate change (Godde et al. 2018). Large modifications in soil and vegetation are expected, especially in drylands (Oliva et al. 2020). Shrub encroachment in grasslands is a global concern since this shift in density and cover of native shrubs represents losses from a livestock production standpoint (Beeskow et al. 1995; D'Odorico et al. 2012) though Eldridge and Soliveres (2014) consider that shrub traits may influence encroachment outcomes. Other studies highlight some benefits in ecosystem services though not denying a probable forage provision decrease (Maestre et al. 2016).

Cushion-forming shrubs are widespread in harsh environments and interact strongly with other species (Cavieres and Badano 2009). Their ground-contacted canopy has a positive influence on soil nutrients stock (Chen et al. 2015; Eldridge et al. 2011; Zhao and An 2021) and have high windblown-sediment trapping ability (Li et al. 2007; Zhang et al. 2011). Nurse effects developed under shrub patches are key to retrieve herbs cover of denuded soil spaces (Kröpfl et al. 2013).

The mechanism of sediment redistribution and trapping accompanying shrub encroachment leads to the development of fertility islands (Ridolfi et al. 2008). Thus, the system develops high heterogeneity in the spatial configuration of vegetation, resources, and soil properties (Ding and Eldridge 2021; Mihoč et al. 2016; Schlesinger et al. 1990). Nutrient cycling became restricted to sink spaces beneath canopies, and source interpatches become poorer (Reynolds et al. 1999; Videla et al. 2008). Environmental factors and plant species influence these processes (Ding and Eldridge 2021). Canopy traits are a key island–driver agent being in the focus of renewed interest in fertility islands studies (Hao et al. 2016; Mihoč et al. 2016; Zhao and An 2021).

The formation of islands is linked to accelerated aeolian and water soil erosion, which reinforces the contrast between sink vegetation patches and barren source interpatches (Chartier and Rostagno 2006; Parizek et al. 2002). This resource depletion leads to a decrease in plant-suitability and productivity of these spaces (Lal 2001; Wang et al. 2018). Size-differential particle redistribution magnifies the soil heterogeneity effect created by erosion (Navas et al. 2017; Paruelo and Golluscio 1993; Romero Ovalle et al. 2021). Erosion effects are also soil type dependent. Volcanic soils are an extreme example of vulnerability to these processes, with losses of highly erodible microaggregates containing silt, clay and organic colloids (La Manna et al. 2021).

Grazing activities establish positive feedback with system heterogenization, contributing to resource islands formation (Allington and Valone 2014) and degradation (Cai et al. 2020). Grazing promotes floristic changes in rangelands, with a reduction in the cover of perennial grasses and replacement of mesophytic with xerophytic species (Cesa and Paruelo 2011; Eldridge et al. 2011; Golluscio and Mercau 1995). Higher heterogeneity or disturbance levels frequently promote increments in exotics, forbs, and annual species (Anchorena and Cingolani 2002; Cesa and Paruelo 2011; Lyseng et al. 2018). High grazing intensities increments barren soil area and favour shrubs establishment (Gaitán et al. 2018; Paruelo et al. 2008).

Overall, grazing effects on vegetation vary with grazing livestock type (Tóth et al. 2018), climate, soils, and use history (Díaz et al. 2007; Gao and Carmel 2020; Lezama et al. 2014; Milchunas and Lauenroth 1993). Effects of grazing over rangelands plant diversity are contradictory, with studies reporting decreases (Paruelo et al. 2004), increases (Gao and Carmel 2020) and no changes (Howard et al. 2012). Some authors warned the relative lack of attention that more humid grasslands had received could mask dramatic diversity changes at these rangelands (Bertiller and Bisigato 1998).

Rangelands in the forest-steppe ecotone of western Argentinian Patagonia have long-known management problematic issues. Surveys and reports from the beginning of the 20th century, describe

the high human and grazing pressure over these ecotonal rangelands. Extensive areas, even forest areas, were burnt-cleared to promote grass growth, with subsequent overgrazing resulting in species replacement and shrub encroachment (Roig 1998; Rothkugel 1916; Willis 1914). Despite not being as extensively studied as central and eastern rangelands (Anchorena and Cingolani 2002; León and Facelli 1981), recent information about these western areas does not describe a better situation than mentioned first reports (La Manna et al. 2019).

Soils in the western Argentinian Patagonia Andean region originated mainly from volcanic ashes (La Manna et al. 2020). Because of restricted precipitation in the subhumid transitional area (ecotone) between the forest and the steppe, these volcanic soils are highly erodible (La Manna et al. 2016). Their potential and actual erosion rates are even higher than those soils in the more arid, eastern steppes (La Manna et al. 2019). Vegetation cover loss of these soils might result in organic matter decrease and a further increase in soil erodibility (La Manna et al. 2018).

Nowadays vast portions of the rangeland area appear as degraded shrub steppes, showing high spatial heterogeneity with large denuded soil patches, perennial vegetation patches mostly represented by cushion shrubs and scarce grasses tussocks. Also, there are scattered scrub patches of tall shrubs with tree specimens, possibly a post-fire succession of originally spotted woodlands (Anchorena and Cingolani 2002). Progressive and accelerating land degradation processes originated a non-stop loss of functional and structural attributes (Irisarri et al. 1995; La Manna et al. 2018; León and Aguiar 1985). It may cause irreversible damage to the capacity of these rangelands to provide ecosystem services, forage productivity included (Rusch et al. 2016). It is necessary to deepen the knowledge about these especially valuable grasslands (León et al. 1998) and make efforts to comprehend how this degradation processes proceeds and can be stopped and eventually reverted.

This work aimed to identify changes in soil properties associated with vegetation type, soil cover and historical grazing intensity, and to describe the vegetation composition and rangeland structure and its changes along a gradient of historical grazing intensity. We had two hypotheses. First, that shrub patches behave as fertility islands and that in consequence the soil beneath shrub patches would exhibit better conditions than all other soils from rangelands. This island effect would lead to more heterogeneity between soil from shrub patches and their corresponding barren interpatches than of soils from grass patches with their own interpatches. Second, we predicted that higher historical grazing intensity would reflect in greater shrub, annual, exotic and forb cover and higher bare soil percentage, while it would reduce grass cover.

## Methods

### Study area

The study area is located in the Percy river basin, in proximities of Esquel city (Chubut Province, Argentina). The area belongs to the Subandean district of the Patagonia phytogeographic province. Climate is cold-temperate, with mean annual precipitation ranging from 300 to 770 mm, concentrated in

the colder months (April to September) and diminishing from west to east in a strong gradient determined by the orographic shadow of the Andes mountain range (Cesa and Paruelo 2011). Following this gradient, the moisture regime ranges from subhumid to semi-arid (Verón and Paruelo 2010). The semipermanent anticyclone of the Pacific Ocean determines the prevalence of strong winds from the west in spring and summer (Anchorena and Cingolani 2002; Paruelo et al. 1998a).

Grass steppe is the dominant physiognomic units of the Subandean district, with *Festuca pallescens* (St.-Yves) Parodi predominating at higher altitudes and *Pappostipa speciosa* (Trin. & Rupr.) Romasch [= *Stipa speciosa* Trin. & Rupr. **var. major (Speg.) Parodi**] in lower altitudinal ranges (Del Valle et al. 1995). Glacial frontal and side moraines configured a complex landscape, with hills alternated with lowlands (Andrada de Palomera 2002). Soils developed from volcanic ashes in a moisture dependant gradient, from Andisols to Mollisols (Irisarri et al. 1995; La Manna et al. 2020). Variations in landscape morphology and soils determine an intricate mosaic pattern where grass steppe coexists with scrub thickets and meadows developed in azonal environments (Del Valle et al. 1995). There are also incursions, throughout irregular boundaries, of species from subantarctic forests and occidental district from west and east respectively (León et al. 1998).

Volcanic ashes originated most soils in the Patagonian Andean region (Irisarri et al. 1995), with non-crystalline minerals giving these soils their distinctive properties (Dahlgren et al. 2004; McDaniel et al. 2012). In the subhumid ecotone between the forest and the steppe, precipitation and silica (Si) concentration quite restricts the formation of non-crystalline minerals (Parfitt et al. 1984). These volcanic soils are highly erodible (La Manna et al. 2016) and have potential and actual erosion rates even higher than those soils in the more arid, eastern steppes (La Manna et al. 2019). It was suggested for these soils that desiccation, due to cover loss, affects non-crystalline materials, leading to soil organic matter decrease and an increase of soil erodibility (La Manna et al. 2018). Intense human pressure over the vulnerable soils of this ecotone may produce strong changes in soil and vegetation.

Non-degraded states of Subandean steppes have high value as grazing ranges, characterised by high homogeneity of perennial grass cover and little shrub cover (Bertiller and Defossé 1993; Bertiller et al. 1995; León et al. 1998; Paruelo and Golluscio 1993). Since the end of the XIX century, the entire area had intense pressure from human origin because of livestock grazing, firewood extraction and wildfires (Aguar et al. 1996; Willis 1914). Current vegetation in large portions of the area is visually dominated by invasive native cushion shrub *Mulinum spinosum* (Cav.) Pers. (León and Aguilar 1985; Roig 1998). This shrub covers almost all landscape positions except meadows and hilltops. Perennial grasses cover which complements the vegetation, consist of scarce, small and coned-shaped tussocks of *F. pallescens*, *Poa ligularis* Nees ex Steud and *P. speciosa*. Barren soil spaces are big and ubiquitous. There are little but relatively big and dense thickets formed mainly by *Discaria articulata* (Phil.) Miers, *Colletia hystrix* Clos, also with *Berberis heterophylla* Juss. Ex Poir. [= *Berberis microphylla* G. Forst.]. There are also sparse specimens of trees like *Maytenus boaria* Molina, *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri and *Nothofagus antartica* (G. Forst.) Oerst.

We defined our potential spectrum of study sites among sheep ranches with the typical productive configuration for this region (Irisarri et al. 1995). Since stocking rates registration is not a common practice in the region, we prioritised for our sites selection the availability of information about historical use. We selected a ranch, Estancia Rio Percy (14000 hectares, 730-1010 metres above sea level -masl-, 42°51' S, 71°23' W), which belongs to the same family since the early XX<sup>th</sup> century. This enabled us to get, through interviews with its owners and its manager, invaluable information orally shared from a generation to the next, and reconstruct the ranch's grazing history. Like many other ranches in this region of Patagonia, it followed the regional pattern of decreasing stocks (Golluscio et al. 1998; INTA 2003). Four paddocks with different mean stocking densities were selected as study sites (PL, CA, AR, PM). We included a 5th site (AN) that was a small paddock (12 hectares) of grass steppe near Esquel city (570 masl, 42°55' S, 71°20' W) which remains ungrazed since 1961. This latter site, possibly disturbed by anthropic activities before its fencing and with probable border effects because of its size, represented the only steppe portion we could locate meeting the criteria of high total and tussocks cover and low shrub density characterising Subandean district non-degraded states (Anchorena and Cingolani 2002; Del Valle et al. 1995; Paruelo et al. 2008). Through Trabucco and Zomer Aridity Index (2018) we verified using QGIS software (QGIS Development Team 2009) that all of our study sites were within the subhumid regime zone of the Subandean district.

### Grazing intensity

We converted stocking densities of a 20-year period (1999-2019) to *Unidad Ganadera Ovina* (UGO), a dry sheep equivalent used in Northern Patagonia which equals to 331 kg yr<sup>-1</sup> (Oliva et al. 2020). Then, we estimated for each paddock the normalised difference vegetation index (NDVI) values for the same time lapse through Landsat TM 5 and Landsat 8 OLI satellite images using QGIS software (QGIS Development Team 2009). We calculated aboveground net primary production (ANPP) for the five plots using the NDVI value for each pixel, through the method adjusted by Paruelo et al. (2004) for Patagonian steppes. We defined grazing intensity (GI) by calculating the proportion of ANPP needed to satisfy herbivores dry matter requirements for each plot for each year (Milchunas and Lauenroth 1993). Finally, we assigned five categories, ranging from less (non-grazed) to more intensity (A-E) based on the average GI for the two decades.

### Field survey

We identified at each paddock sectors of grass-shrub and shrub-steppe. To better capture vegetation heterogeneity after more than a century of sheep livestock grazing in the area, we randomly selected two of them (one of each condition). Following the MARAS method (Oliva et al. 2020) we placed in each selected spot 3 transects of 50 m length (6 in total). We determined, by point-intercept lines, floristic composition, diversity and cover, and soil surface conditions in two transects. Patch-interpatch structure was measured by gap-intercept lines in the third transect. With transects raw data we calculated rangeland structure properties such as the absolute and relative cover of different vegetation traits, vegetation layer superposition, mean length of interpatches and richness (Oliva et al. 2020). Field work

was in late spring and early summer when this western Patagonian rangeland exhibits its maximum productivity (Paruelo et al. 2004).

### Laboratory analysis

We took 19 0-5 cm soil samples in each ranch's paddock. Sixteen samples were associated with vegetation transects. In the grass-shrub sector, 4 samples beneath *F. Palleescens* patches (PATCH\_GRASS) and 4 more samples in the barren soil spaces next to each of those patches (BARE\_GRASS). Within the shrub-steppe, we took 4 samples below shrub patches of *M. spinosum* (PATCH\_SHRUB) and 4 from the barren soil interpatches associated (BARE\_SHRUB). We also took 3 more 0-5 cm samples beneath tall shrubs canopies inside woody thickets (REFERENCE) as reference parameters. These spaces make part of the vegetation mosaic of the area and probably develop from the occurrence of early fires or chopping in *Austrocedrus* forests (Anchorena and Cingolani 2002; Bran 2000). Since they present a very dense stem arrangement with many species having hardened spines which turn them into spaces difficult to reach, we assumed these spots as less livestock-disturbed. To measure the depth of soil horizons and their variations, and the micro-topographic relief of vegetation hummocks, we cut at each grazed paddock two soil trenches (one for grass and one for shrub) (Charley and West 1977). Each spanned from the centre of the hummock beneath the vegetation patch to the centre of the barren soil interpatch. In the ungrazed paddock, we took 3 more 0-5 cm PATCH\_GRASS soil samples beneath dominant tussocks of *P. speciosa* and 3 more BARE\_GRASS samples from associated interpatches. We estimated they were sufficient because of the size and vegetation homogeneity of this plot. No cushion shrubs were present in this area. For each soil sample, both in grazed and ungrazed paddocks, we took an undisturbed sample for bulk density determination.

At the laboratory, all soil samples were air-dried and sieved through 2 mm mesh to separate coarse fragments from fine soil particles (IRAM 1998). We determined particle sizes distribution through laser diffraction with previous organic matter elimination and sonication (Arriaga et al. 2006). Effective porosity was calculated by subtracting field capacity to total porosity (Helalia 1993). The percentage of wind erodible fraction was determined according to Chepil (1953) technique. To estimate non-crystalline clays presence, we determined soil pH in sodium fluoride solution (Fieldes and Perrot 1966). We also determined the soil pH in water (1:2.5 soil/water relation) (IRAM 1999), electrical conductivity (1:2.5) (IRAM-SAGPyA 2006), organic matter (IRAM-SAGPyA 2008), total nitrogen (IRAM-SAGyP 2018) and organic carbon: nitrogen ratio.

### Statistical analysis

To quantify the fertile island effect, we calculated the Relative Interaction Index (RII) (Armas et al. 2004). The RII, originally developed for measuring plant interactions, has been recently applied for assessing fertile island effect through biotic and abiotic properties of soil (Ding and Eldridge 2021; Mihoč et al. 2016; Zhao and An 2021). This index takes values between -1 and +1, is symmetrical around zero, and its absolute value for interactions with opposite sign (i.e., competition and facilitation) is identical. We calculated it for each PATCH sample and its associated BARE as:

$$RII = (X_{PATCH} - X_{BARE}) / (X_{PATCH} + X_{BARE})$$

where  $X_{PATCH}$  is the soil property measured value beneath the vegetation patch, and  $X_{BARE}$  is the value taken by the same property on the paired bare soil interpatch.

We also calculated RII for each REFERENCE sample, quantifying the relative difference with the dominant conditions in its paddock, represented by the mean value of all other samples (PATCH and BARE) taken in the same paddock as:

$$RII = (X_{REFERENCE} - X_{MEAN}) / (X_{REFERENCE} + X_{MEAN})$$

where  $X_{REFERENCE}$  is the measured value for a soil property beneath the canopy of the tall shrub in reference scrub spot, and  $X_{MEAN}$  is the mean of the values taken by the same property in the other samples of the paddock.

We condensed in a unique numerical value the fertility island effect for each PATCH-BARE pair of samples (or REFERENCE-MEAN) at the different vegetation classes assessed. Our motivation was having a measure of heterogeneity or contrast concurrent for all soil properties linked to a particular vegetation cover, instead of having one RII value for each soil variable. With RII values ranging from -1 to +1 (Armas et al. 2004), it was not possible to just averaging the values obtained at (1) or (2), since compensation may mask real heterogeneity between positive and negative RII scores for some or another variable. Hence, after obtaining the RII value for each variable, we transformed it to absolute before averaging all of them and finally getting one RII value for each pair of samples.

To statically evaluate RII differences between the vegetation classes, we performed a univariate analysis of variance (ANOVA). Bonferroni comparison test performed had incomplete block design (Di Rienzo et al. 2011), since the ungrazed site (AN) has no SHRUB or REFERENCE samples.

We analysed soil laboratory results through principal component analysis (PCA) (Hotelling 1933; Rao 1964). We used the package FactoMineR (Lê et al. 2008) for R software (R Core Team 2020). To integrate RII into PCA, we took the values for each PATCH-BARE pair of samples and applied a multiplication factor of -1 to them. Thus, we get an identical RII value reflecting the same effect intensity but with opposite sign (Armas et al. 2004). Then, we assigned the original (positive) RII to the PATCH sample and the negative to the BARE one. We included all soil samples in the analysis and standardised all variables to unit variance (O'Connor 1988). We plotted PCA results with the package factoextra (Kassambara and Mundt 2020) for R software (R Core Team 2020).

To perform an indirect and direct gradient analysis of vegetation data from the transects, we run a constrained or canonical correspondence analysis (CCA) (Ter Braak 1986). We assessed the relation of community structure and floristic changes with rangeland structure attributes and growing grazing

intensity (Ter Braak 1987). We also performed a detrended correspondence analysis (DCA) (Hill and Gauch 1980) to compare axes length, eigenvalues, species and sites ordination with CCA results (Ter Braak and Prentice 2004). RII values for the PATCH-BARE pairs of samples associated with each transect were averaged to allow their inclusion in CAA. Before analysis, we standardised environmental data to zero mean and unit variance (Ter Braak 1987). For both DCA and CCA analysis and CCA plotting, we use the R package Vegan (Oksanen et al. 2020).

We checked multivariate analysis results with Inferential statistics using InfoStat software (Di Rienzo et al. 2011). We performed Hotelling multivariate variance analysis and Lawley-Hotelling a-posteriori comparison of variables means between groups of analysis (Johnson and Wichern 2014). InfoStat software (Di Rienzo et al. 2011) was utilised to draw dot plots and to perform ANOVA over RII mean values.

## Results

### Grazing intensity classes

Table 1 shows the grazing intensity (GI) classes according to average values of proportional ANPP required to satisfy the needs of the herbivore stocking density (SD) assigned at each plot. The assigned class for each paddock, from lower to higher GI, is expressed with letters A to E. It is interesting that for these study sites, GI values followed roughly SD increasing average levels.

### Soil analysis

Table 2 lists soil variables mean and standard deviation by vegetation and cover condition. The mean relative interaction index (RII) and its standard deviation by vegetation class are listed, together with Bonferroni a-posteriori mean comparison test.

Correlations of the 16 soil variables plus RII on the first 3 dimensions of the PCA were analysed. The biplot in figure 1 displays the first two dimensions. **Dimension 1** (27% of variance) had strong positive correlations with silt content (SILT) ( $\cos^2=0.82$ ), very coarse sand (VCS) ( $\cos^2=0.51$ ) and clay content (CLAY) ( $\cos^2=0.50$ ). It had strong negative correlations with medium sand (MS) ( $\cos^2=0.62$ ) and fine sand (FS) ( $\cos^2=0.55$ ). There were moderate positive correlations with soil pH in sodium fluoride (NAF) ( $\cos^2=0.34$ ) and relative interaction index (RII) ( $\cos^2=0.29$ ). Dimension 1 had moderate negative correlations with erodible fraction composed by particles smaller than 0,84 mm (ER) ( $\cos^2=0.30$ ) and effective porosity (EP) ( $\cos^2=0.23$ ). Dimension 1 thus defined a change in soil texture. There were losses of medium-sized particles (MS and FS) from vegetated patches to bare soil spaces, and gains of finer (CLAY and SILT) and coarser (VCS) fractions in the same direction. Dimension 1 also exhibited the contrast between different soil conditions related to shrubs, with covered and uncovered patches displayed distant from each other. Also, RII values followed the increments in finer and coarser particles. Instead, grass-related soil samples were close to each other on this axis. Reference patches differed little with shrub and grasses patches or with grass related small bare soil spaces about soil textural variables.

Lawley-Hotelling and Hotelling tests showed significant differences ( $p < 0.05$ ) between all groups, except grass-related ones (bare soil and patch).

**Dimension 2** (17.3% of variance) was strongly correlated with total nitrogen (N) ( $\cos^2=0.79$ ), and total organic matter (OM) ( $\cos^2=0.70$ ). It had moderate positive correlations with electrical conductivity (EC) ( $\cos^2=0.48$ ) and effective porosity (EP) ( $\cos^2=0.32$ ). Negative correlations were with coarse fragment (CF) ( $\cos^2=0.24$ ). Thus, chemical fertility-related properties (N and OM) defined dimension 2, with an increasing fertility gradient from bare spaces to vegetated patches (and from grasses to shrubs inside this latter group). Unlike dimension 1, reference patches differed clearly from shrub and grass ones at this level. Also, there were increments in effective porosity (EP) from shrub to grass bare soil spaces, and from patches to reference spots. Dimension 2, therefore, differentiates through chemical properties those patches of current vegetation from the scrub/thicket reference spots. As in dimension 1, bare soil spaces associated with shrub patches showed the poorest soil condition. Lawley-Hotelling and Hotelling test showed significant differences ( $p < 0.05$ ) between all groups, except grass-related ones (bare soil and patch).

**Dimension 3** (14% of variance) showed strong negative correlation with very fine sand (VFS) ( $\cos^2=0.74$ ) and moderate positive correlation with coarse sand (CS) ( $\cos^2=0.50$ ). This axis reflected minor changes between groups for these two soil fractions. The non-grazed group (REF) had the highest contents of CS and PATCH\_SHRUB group was richer in VFS. Dimension 4 only captures 8.3% of the variance (data non shown).

Figure 2 shows highly correlated variables in PCA dimensions 1 and 2 against the five soil and vegetation cover groups (REF; BARE\_SHRUB; BARE\_GRASS; PATCH\_SHRUB; PATCH\_GRASS). Textural fractions were grouped on a size basis: clay + silt; fine sand + medium sand (Fig. 2a). Total nitrogen and organic matter were plotted aside (Fig. 2b). Lawley-Hotelling and Hotelling test found significant differences between BARE\_SHRUB, REF, and the group conformed by PATCH\_GRASS, PATCH\_SHRUB and BARE\_GRASS. These 3 groups didn't differentiate between them ( $p > 0.05$ ).

The finest pool of soil particles (CLAY+SILT) had percentage values growing from vegetated spaces to bare ones. All grass-related spaces and shrub patches had similar values, without significant differences between them. Sand particles pool (FS+MS) showed lower values proportionally to higher values of fine particles, in an inverse gradient. The reference group took, for all particle categories, intermediate values between the most degradation-prone soil condition (BARE\_SHRUB) and the others (Fig. 2a).

Mean values for chemical variables (OM and N) decreased from vegetated patches to bare spaces ones, and from grass to shrub inside each soil cover condition (bare and patch). The reference group had the highest levels for these two properties in all cases (Fig. 2b).

The trenches we opened showed the high soil heterogeneity existing in grazed areas, between soil mounds formed under canopies and barren interpatch areas. Barren spaces are depletion zones exposed directly to the biotic and abiotic environment. Superficial soil horizons were thicker beneath canopies,

with a narrowing trend towards the barren space. Grassy areas had more homogeneity between patches and bare spaces than trenches opened in shrub area, where erosion created more contrast (fig. 3)

## Vegetation analysis

The eigenvalues for CCA first two axes were not reduced compared to DCA results (CCA1=0.64; CCA2=0.36); (DCA1=0.62; DCA2=0.33). Also, species and sites position in both ordinations were similar. Hence, variables selected for CCA model (Fig. 4) explained major variation in the community (Ter Braak 1987).

We found some major community composition changes with the indirect gradient analysis performed over CCA. Table 3 shows the best-represented species for each axis branch (negative and positive) together with its life form, cycle and status. The species gradient length for CCA axes was 3.09 standard deviations (sd) for the first, and 2.32 sd for the second. The gradient showed an important community change, but also that some species remain common between sites. We expected a full turnover in species composition in about 4 sd, and a half-change in that composition in about 1 sd (Hill and Gauch 1980).

The first axis showed, on its positive branch, a shrub-grass community with 57% of shrubs and 43% of grasses, all being perennial and native. On the negative side of the axis, half of the species were forbs (52%), with grasses (19%) and shrubs (29%) sharing the other half. Species at this end were 24% annual, while 33% were exotic species. Gradient length for this axis showed that if not a full turnover (sd below 4), there was a major change in composition throughout it. Forbs have a dramatic role in this change since they were absent at one edge and turned into the dominant life form at the other. Most of the forbs were perennial (71%) and native (65%). There was also a shift in the grass community, with 22% being annual and 33% exotic species. All annual grasses were exotic at this axis end.

The second axis had a gradient length of 2.32 sd. From positive to negative scores, forbs kept stable with a participation from 47 to 45%, grasses decreased from 41 to 36%, and shrubs raised from 12 to 18%. At the positive end of the gradient, annuals represented 18% of total species, while at the negative end they represented 27%. Similar to the first axis, there was an important change in exotics from 12% to 55%. This change was best represented by forbs (25 to 80%), with a shift from native to exotic dominance in this group. The abundance of grasses decreased and exotics incremented dramatically within this group (going from 0 to 50%), being annuals half of them. All shrubs were native species.

Thus, the first CCA axis determined a shift from a shrub-grass mixed community to a forbs-dominated one, with some losses in perennial and native species. The second axes showed decay in the participation of grasses and an increment in shrubs in the same direction, with a dramatic increase of forbs and annual grasses in the community.

The direct gradient analysis of CCA showed how the variables selected for the model influenced the ordination. Total grass cover (GRASSES) defined the first axis on the positive scores ( $r^2=0.81$ ). For the negative scores, bare soil percentage (BARE) ( $r^2=0.79$ ), cushion shrubs relative to total shrub cover

(CUSHIONS) ( $r^2=0.60$ ), total shrub cover (SHRUBS) ( $r^2=0.57$ ), historic grazing intensity (GI) ( $r^2=0.66$ ) and total vegetation richness (RICH) ( $r^2=0.45$ ) were determinant. Grass cover trend was inverse of USE and BARE. Forbs relative cover (FORBS) ( $r^2=0.18$ ) and vegetation layers superposition (LAYERS) ( $r^2=0.14$ ) defined the positive scores of axis 2. The negatives scores were defined by barren soil interpatches average length (BIL) ( $r^2=0.81$ ), relative interaction index (RII) ( $r^2=0.61$ ) and annual grasses relative cover (ANNUALS) ( $r^2=0.33$ ). The proportion of the total inertia explained by constraint variables in our CCA model was 0.87. The eigenvalue of the first axis (0.64) implied a stronger gradient than the second (0.36). Our model explained most of the variation since the first residual axis (CA1) had a much smaller eigenvalue (0.07).

Figure 5 shows the mean values of the most informative cover and structure variables and their behaviour with growing GI. Variables were GRASSES, BARE, CUSHIONS, SHRUBS, RICH, and LAYERS. Lawley-Hotelling and Hotelling test showed significant differences between GI categories. The extremes of grazing intensity range (A and E) were significantly different between them and also compared to middle intensities (B, C and D), which didn't differentiate between them ( $p > 0.05$ ).

Shrub cover increased from less to more GI, with a final decay in the most intensely-used class (E). Superposition of vegetation layers and total richness followed a similar trend (Fig. 5a). Total grass cover followed an inverse trend compared to shrubs, decreasing with a higher GI. Bare soil and relative cover of cushions were coupled in their trends. Cushions behaved as increaser with increments in grazing intensity levels (Fig. 5b).

## Discussion

### Soil and fertility islands

Through estimations of ANPP, a requirement to calculate GI, we could see the consequences of the grazing history in each paddock. Indeed, aerial biomass production calculated for our sites reflected fairly good the historical use contrasts we identified among plots with the qualitative survey made via interviews. We found that the non-grazed site produced more biomass than all grazed ones and that within them, the most heavily grazed site yielded far less than the others. Overgrazing affects ecosystem structure and functioning (López et al. 2011). ANPP has been proposed as a comprehensive indicator of system functioning through condensing information about energy flow and nutrient cycling (Gaitán et al. 2014). Though the assessment of ecosystem functionality was not an explicit aim of our work, our results concur with the observation of ecosystem malfunctioning at high grazing loads.

Our results evidenced the formation of fertile islands, with a differential expression between the cover categories evaluated. We could identify a significant land use effect on soil properties (Fig. 1 and table 2). Also, it was related to indicators of degraded states in grasslands as shrub cover, large interpatches, and annual grasses (Fig. 4). The effect was linked to shrubs and their surrounding bare soil spaces. Medium sand and fine sand fractions were remobilised preferentially over other fractions. Important chemical variations occurred on organic carbon and total nitrogen, two of the most important variables for soil

fertility characterization. Many rangelands across the world developed fertile islands, with changes in many soil properties and vegetation arrangement (Allington and Valone 2014; Ridolfi et al. 2008). We found that bare soil areas were bigger when associated with shrub patches, compared to those associated with grasses. This resulted in enlarging the bare soil vs. patch contrast and consequently in a bigger island effect detected for shrub encroached sites. The magnitude of the heterogeneity of the resources developed in cushion dominated patches is really important. This becomes clear when comparing our reference spots with the grazed areas (Table 2). Even being the long-term less disturbed conditions, we found that soil heterogeneity between the scrubs and their paddocks was lower (but not significant) than between cushions and their interpatches.

Our quantification of island effect for subhumid Patagonian rangelands through RII agrees with previous studies on Patagonia and in the world (Aguiar and Sala 1999; Bertiller and Bisigato 1998; Gao and Carmel 2020; Okin et al. 2015; Rostagno et al. 1991). Larger barren soil spaces accompanied shrub cover growth. Shrub patches of the cushion plant *M. spinosum* and their associated bare interpatches exhibited more heterogeneity than grasses. Recent studies found an important influence of canopy size on the fertility island effect (Zhao and An 2021). Ding and Eldridge (2021) found a greater effect in shrubs than grasses for both biotic and abiotic variables, also with increments positively related to aridity. Howard et al. (2012) found microclimatic amelioration under shrubs, for nutrients cycling, soil properties and diversity indices. Cushion plants are a common life form in harsh environments across the world (Aubert et al. 2014). Cushions are an important fertile island formation agent since their canopies are good in trapping and maintaining sediments beneath them and in producing facilitative interactions (Cavieres and Badano 2009; Gavini et al. 2019). Mihoč et al. (2016) measured nurse effects along an environmental gradient, finding higher fertility and activity under cushion shrubs than any other life form.

We found that soil particles intervening in remobilisation (FS, MS, CLAY and SILT) took intermediate values in the soil of reference spots, compared to the soil beneath shrub and grass canopies and barren areas (Fig. 2). Plants with different shapes and traits don't behave as sediment traps equally (Cavieres and Badano 2009; Mihoč et al. 2016). Tall shrubs with Y-shaped crowns have less capacity to capture and retain airborne sediments than those with hemispheroidal-canopies (Li et al. 2007). Besides, the larger size of the reference spots and the greater distance from bare soil spaces, in comparison to the other vegetated patches, also reduces the accumulation of material from bare areas (Ravi et al. 2011). We suppose the differential trapping ability together with the greater distance from redistributed particles sources contributed to maintaining less altered particles distribution of our reference spots compared to areas dominated by cushion shrubs and grasses. Our results showed that soil of grass and cushion shrub patches differ to a large degree from reference spots in the particles intervening in remobilisation (Fig. 2). The higher content of organic matter could also mediate this effect (Figs. 1 and 2). The organic matter reduces soil susceptibility to erosion by enhancing the stability of its aggregates, which turns into lesser particle mobilisation (Cambardella and Elliott 1993; La Manna et al. 2018). Thus, because of less particle entrapment and also to fewer losses, we assume that the soil of these spots exhibits a situation closer to the existent before intense disturbance from sheep grazing.

Our results showed preferential remobilisation of soil, with differential effects at deposition patches (sink) and source areas. Sand medium and fine particles were higher in the soil beneath canopies. In source patches (bare soil spaces), we found consequent increments of fine particles (clay and silt) and gravel. In Patagonia, these redistribution effects were found for climatic regimes ranging from arid to subhumid (Kröpfl et al. 2013; Paruelo and Golluscio 1993; Rostagno 1989) and other rangeland systems of the world (Li et al. 2007; Navas et al. 2017; Zhang et al. 2011). Volcanic soils are wind-erosion-prone, particularly in rangelands, because of high proportions of volcanic glass in their sand fraction, strongly vesicular or pumiceous (McDaniel et al. 2012). This turns these particles lighter than sand particles from non-volcanic soils (Nanzoyo and Kanno 2018). Recent water erosion studies in volcanic soils in the same region of Patagonia found remobilisation of coarse and very coarse single sand particles in the rangelands, while erosion processes in afforested areas involved the removal of microaggregates rich in organic matter and silt fractions (La Manna et al. 2021). Based on our results and the spotted vegetation pattern we found at our study sites (Aguiar and Sala 1999), we suppose remobilisation processes taking place are mainly wind-driven. The erodible fraction was lower and gravel content was higher in barren soil spaces related to shrub patches. Thus, soil losses effectively happened with more intensity there, while vegetated patches showed the opposite situation.

The soils we sampled under plant canopies had better chemical properties than those in barren areas. This was an expected finding since many other studies reported it for this region and other rangelands of Patagonia and the world (Aguiar and Sala 1999; Cheng et al. 2004; Hao et al. 2016; Kröpfl et al. 2013; Mihoč et al. 2016; Rostagno et al. 1991). Nitrogen and organic matter are within the most cited chemical properties with increases (Kröpfl et al. 2013; Rostagno 1989; Rostagno and del Valle 1988; Zhao and An 2021). Other studies reported increasing values for electric conductivity and decreasing pH beneath vegetation canopies (Rostagno et al. 1991; Zhao and An 2021). Indeed, a review has reported a general lowering pH value with an increase in shrub dominance (Eldridge et al. 2011). As for textural properties, soil fertility indicators were more heterogeneous for shrubs than for grasses.

The soils of our reference spots (scrub thickets) were far more fertile (OM and N) than the soil of grass and shrub patches. Differential C and N turnover rates due to litter quality can explain these variations. Many studies focused on woody species leaf traits found that deciduous plant litter mineralises faster than evergreens (Carrera et al. 2005; Cornwell et al. 2008; Satti et al. 2003). Evergreens long-lasting tissues usually contain higher levels of secondary compounds in leaves (Bertiller et al. 2005; Carrera and Bertiller 2010; Carrera et al. 2005, 2008; Mazzarino et al. 1998; Saraví Cisneros et al. 2013). Most shrubs, both in our reference spots and in encroached areas, have short-lived foliage. Despite this, the litter quality framework is worth value. Our shrub patches comprised deciduous *M. spinosum* cushions. This shrub has a high concentration of secondary metabolites in leaves (Cavagnaro et al. 2003), seeds (Folgarait and Sala 2002), flowers and fruits (Seoane et al. 2011). Also, it yields a moderate quantity of essential oils (Guerra et al. 2012). However, scrubs species of the reference spots were mainly of *Discaria* and *Colletia* genus, tribe *Colletieae* (*Rhamnaceae*). Their low-strengthen deciduous leaves (De Paz et al. 2013) don't have detectable essential oils (Guerra et al. 2012). These chemical and physical features turn into very different decomposition rates (k). Under similar conditions, *M. spinosum* litter k values ranged

from 0.3 to 0.38 (Araujo and Austin 2015), while  $k$  was as high as 1.17 for *D. articulata* (de Paz et al. 2017). Moreover, sunlight is an important control of litter turnover for environments where vegetation cover is heterogeneous or scarce (Adair et al. 2017; Araujo and Austin 2015; Bosco et al. 2016). It speeds up litter degradation as much as twice through photodegradation and photofacilitation (Berenstecher et al. 2020). The growth habit of *M. spinosum* implies the formation of a compact canopy with structural avoidance of excessive irradiance (Damascos et al. 2008). Conversely, vertical stems of shrubs or trees from tribe *Colletieae* (Tortosa et al. 1996) enables sunlight to reach the basement. We propose that soil fertility under high shrubs reflects the light-enhanced degradation of the high-quality litter produced by these plants.

We didn't find extensive indications of amorphous materials at our study sites. We expected to have these minerals, in the same line of previous assessments for soils with similar moisture regimes in this region (Broquen et al. 2005; La Manna et al. 2020). The sodium fluoride pH test only detected allophane or imogolite consistent values (Irisarri 2000) in one of our study sites (AN) and one of our scrub references samples. Hence, we assumed the non-general current presence of these non-crystalline clays. The hilly landscape of this area determines a wide variety of positions and expositions that enable the coexistence of Andisols and Andic Mollisols (Irisarri et al. 1995). In previous studies on the same sites, we found NaF pH imogolite consistent values in one sub-superficial (25 cm depth) sample (Vogel and La Manna 2018). In our present assessment, we only found imogolite NaF pH values in one of the non-disturbed tall shrub spots and the grassy area excluded from livestock grazing. Except for these scattered spots, our study sites and most of the region had historically high levels of livestock grazing. Such kind of disturbance leads to important losses of vegetation cover, exposing superficial layers to direct climate action. Intense disturbance by human activities can lead to the transformation of non-crystalline clays into halloysite-type minerals because of continuous exposure to desiccation and re-wetting of aggregates (Hernández et al. 2012). Other assessments in the region suggested this transformation (La Manna et al. 2018), which is irreversible and relatively fast (McDaniel et al. 2012). The evaluated sites faced strong erosion processes, as we showed before through the analysis of soil particles redistribution, fertility island effect and soil profiles. If imogolite developed in these volcanic ash-originated soils, its irreversible transformation to halloysite may be possible.

## Vegetation changes

We found a clear association of higher levels of use intensity with changes in community composition and vegetation structure. One of the most remarkable by its consequences on secondary productivity is the cover reduction of perennial grasses. Previous studies informed this for the sub-Andean district (Aguar et al. 1996; Anchorena and Cingolani 2002; Bertiller and Bisigato 1998; Cesa and Paruelo 2011; Gaitán et al. 2018; Paruelo et al. 2004, 2008) despite evidence of a not universal association (Lezama et al. 2014). Grazing disturbance favour grasslands to shrublands transition (Kröpfl et al. 2013; Ridolfi et al. 2008). Besides a grass cover contraction, we also found an increment in total shrub cover with increases in disturbance (grazing) intensity. The most relevant species (>1% total frequency) found in sites with high grass cover were *Pappostipa speciosa* (Pap.spe) and *Bromus stamineus* (Bro.sta). On the opposite

edge, where grass cover reduced, *Mulinum spinosum* (MUL.spi) and *Festuca pallescens* (Fes.pal) were the most notorious species (Table 3 and fig. 4). Increments in cushion shrubs were more associated with grazing intensity and bare soil than total shrubs, which shows their encroacher trait in disturbed sub-Andean rangelands (León and Aguiar 1985). Grazing is also a major driver of fertility island formation (Cai et al. 2020; Allington and Valone 2014). As discussed before, we found a greater fertility island effect associated with shrub patches and their paired large bare soil interpatches (Fig. 1 and Table 2). Moreover, we also verified a determinant effect related to increments of shrub in community contribution and cover (Fig. 4).

We detected that larger bare interpatches accompanied the increase in total shrub cover (fig. 4). Lin et al. (2010) proposed patch edge as a key indicator of water and sediments trapping efficiency. Larger patches like those formed by shrubs have less edge by area than smaller patches like those of grasses and forbs. Our survey results support this asseveration since grass patches were higher in sand remobilised particles, nitrogen and organic matter than those of shrubs (Fig. 2). Also, the bare interspace between shrubs was bigger (Fig. 4) and more heterogeneous with their corresponding patch than those of grasses (Fig. 1, Table 2). These increased losses in shrub interspace areas together with soil amelioration under both grass and shrub canopies created the island effect we found.

We also found that the percentage of uncovered area incremented with growing disturbance intensity (Fig. 4). Despite not being an effect unrestrictedly detected (Cesa and Paruelo 2011; Eldridge et al. 2011), this response of rangelands to grazing has received consensus both for Patagonia and other ranges (Aguiar et al. 1996; Cheng et al. 2004; Van Auken 2000; Verón and Paruelo 2010). Grazing and trampling by herbivores change the topsoil conditions of interpatches, playing a key role in the fertility island effect (Allington and Valone 2014) and even desertification (Schlesinger et al. 1990). Indeed, sheep grazing habits may magnify these effects of trampling (Tóth et al. 2018). Our results verified the description of the present range status we made in the methods section. There, we emphasised the visually stunning experience of large barren spaces related to the domination of shrubs and high historical disturbance pressure in almost the entire area.

Our assessment detected structural changes, such as increments of forbs and annuals (in cover and proportional contribution to community) (Fig. 4). Literature mentions them as indicators of grazing disturbance for sub-Andean rangelands (Anchorena and Cingolani 2002; Cesa and Paruelo 2011; Paruelo and Golluscio 1993). These changes were both associated with grazing pressure increases but were not much related to each other. Community with forb increments had *Poa ligularis* (POA.lig), *Acaena pinnatifida* (ACA.pin) and *Carex argentina* (CAR.arg) as the most relevant species (>1% total frequency). The most relevant in communities where annuals increased was *Vulpia sp* (VUL.sp) (Table 3 and Fig. 4). When a patch collapse after heavy disturbance, the resources flow to bare spaces promoting recovery processes in rangelands (Kröpfl et al. 2013). Resources are lost if surrounding patches and interpatches cannot catch them efficiently. Following Lin et al. (2010) we assume that having less proportional patch edge, shrub patches trap resources depleted from bare soil with lesser efficiency than grasses. Thereby,

these encroached ranges reached soil conditions limiting vegetation growth. In that situation, some species can take advantage of spatial heterogeneity created by disturbance.

At our study sites, annual species accompanied shrubs cover growth, an effect previously reported for moderate and heavily grazed rangelands (Noy-Meir et al. 1989). Annuals increment usually follows perennials decrease (Milchunas and Lauenroth 1993). These species prevail in bare interpatches because of advantages such as tolerance to harsh environmental conditions, higher seed production, shorter and prostrate canopy, secondary compounds and life cycles suitable to benefit from any benign microclimatic condition (Anchorena and Cingolani 2002; Gao and Carmel 2020; Milton et al. 1994; Noy-Meir et al. 1989). We verified clay increments in superficial soil of bare shrub interpatches (Fig. 2). This causes a xerification effect in Subandean highly eroded soils, diminishing water available for plants uptake (Paruelo and Golluscio 1993). The situation described here is comparable to the shrub-steppe of NW Chubut named state IV, with a very unlikely return to a more productive state because of irreversible soil changes (Paruelo and Golluscio 1993). In such harsh conditions, reinforced by a high content of coarse fragments (Table 2 and fig. 3), we assumed as possible the constitution of niche gaps in the highly eroded big barren interspaces, where only annual grasses could complete an entire life cycle. Annuals are the most successful trait for such levels of resources depletion and spatial heterogeneity.

We found forbs gained participation in cover, being most of them perennial and native. We didn't observe the increment in exotics with grazing intensity reported for other subhumid rangelands (Lyseng et al. 2018). Many forbs share key traits with successful exotic invader plants, like grazing tolerance/avoiding. Forbs are usually smaller than shrubs and grasses, which enables them to explore microhabitats created by disturbing activities such as herbivory, increasing plant richness (Jobbágy et al. 1996). Vegetation cover may become more fragmented because of destructive grazing and trampling (Lin et al. 2010), creating spatial heterogeneity and opening niche gaps, thus encouraging species coexistence (Gao and Carmel 2020). We believe that grazing intensity could lay behind the independent response of forbs to abiotic heterogeneity reported by Jobbágy et al. (1996). We observed vegetation layers superposition together with increasing forbs cover (Fig. 4) in our study sites, variables which are showing the mentioned niche heterogeneity. Indeed, in those sites with less bare soil and shrub cover, and smaller barren spaces, growth several life forms of perennial vegetation other than shrubs, like native forbs (Fig. 4). This situation pairs with grass and grass-shrub steppe of SW Chubut named as states II and III by Bertiller and Defossé (1993). Maintaining current grazing pressure will cause a probable transition to shrub-grass steppes of *M. spinosum* or *Acaena spp.* We consider that grazing management should focus on sites like these since they exhibit less soil heterogeneity and still sustain life forms other than shrubs and annual grasses.

Our results showed that increasing grazing intensity exerted a positive effect on total richness. This effect manifests along all grazing intensities evaluated with exception of the highest, where richness finally declines (Fig 5). While shrubs and grasses responded by replacement in species of one life form by the other, perennial forbs (and secondarily annual grasses and forbs) represented an addition to the community (Fig. 4). Golluscio and Mercau (1995) identified shrubs and cushions as increasers, some

grasses and palatable forbs as decreasers and other grasses and forbs with maximum cover values at mid grazing intensities. Grazing induces changes in interspecific competition, producing a shift in species abundance that otherwise won't succeed because of resistance of non-grazed grasslands to invasion (Lyseng et al. 2018). The effects of grazing on grasslands richness have been controversial, and attempts to generalise them had arrived at different conclusions (Eldridge et al. 2011, 2016; Herrero-Jáuregui and Oesterheld 2018; Howard et al. 2012). For Subandean grasslands, while some authors didn't observe major changes (Anchorena and Cingolani 2002; León and Aguiar 1985) most studies negatively related richness and grazing intensity (Cesa and Paruelo 2011; Golluscio et al. 1982; Lezama et al. 2014; Paruelo et al. 2004). We found a hint for our controversial results in the warning given by Bertiller and Bisigato (1998) about the drastic magnitude of changes in the *more humid* grasslands of Patagonia.

We verified via the Global Aridity Index dataset (Trabucco and Zomer 2018) that most of the Subandean vegetation assessments take place at the eastern semi-arid portion, while western subhumid zones were less surveyed. Milchunas and Lauenroth (1993) reviewed moisture-dependant effects of grazing on diversity, with increases for subhumid rangelands at low-moderate to moderate intensities. They postulated that grazing influences species composition more in subhumid than in arid environments because vegetation removal enhances the intensity of plant interactions. A recent global meta-analysis concluded that grazing increases plant richness, particularly for dry-subhumid or wetter grasslands with an aridity index (AI) > 0.51 (Gao and Carmel 2020). Destructive animal activity (trampling, grazing) over edible and highly competitive species may release resources such as space, light, water and nutrients for those with grazing avoidance strategies. Also, non-destructive activities (urine and dung deposition) may reinforce this vegetation heterogeneity and increase richness over a threshold of moisture limitations for plant growth (AI 0.51) (Gao and Carmel 2020). Grazing produced modest increases in richness in mesic sites of north-American temperate grasslands (Lyseng et al. 2018) with structural and functional convergence with Patagonia (Paruelo et al. 1998b). However, once surpassed a threshold, heavily disturbed sites would present a downslope in the curve of diversity changes (Milchunas and Lauenroth 1993). Effectively, the highest grazing intensities exhibited less richness of all our study sites in our assessment (fig. 5), in line with previous reports for sub-Andean district (Cesa and Paruelo 2011; Golluscio et al. 1982; Lezama et al. 2014; Paruelo et al. 2004). Notwithstanding this, moderate grazing intensities at the subhumid sites we evaluated created niche gaps that favoured the coexistence of grazing tolerant and intolerant plant species and resulted in larger richness mainly because of perennial forbs species addition.

## Conclusions

Our results indicates that historical livestock grazing activity caused a vegetation cover loss, which turned into organic matter decrease and a further increase of soil erodibility. The soil heterogeneity was in part created by soil resources remobilisation and magnified by differential erosion. Indeed, it was stressed by greater losses in shrub interspace areas. Bare soil areas were larger and more eroded when associated with shrub patches. In contrast, shrub patches exhibited the biggest island effect. Thus, fertility islands

were associated with indicators of degraded states in grasslands like high shrub cover, large interpatches, and annual grasses cover. This loss of resources turned into limiting conditions for vegetation growth.

Perennial grasses had a sustained cover decrease with a higher intensity of grazing. Grasses and shrubs reacted to grazing by replacement in species of one life form of species from the other. Higher grazing intensities incremented barren soil area and favoured the establishment of shrubs. Grazing provoked cushion shrub increases, even more than shrubs showing their encroacher trait at disturbed sub-Andean rangelands. Cushions increments with grazing intensity were paired with growth of bare soil area. Shrub total cover decay in the most intensely grazed class.

Increasing grazing intensity exerted a positive effect in vegetation richness of these subhumid rangelands. Increments of forbs and annuals were both associated with grazing pressure increases. Livestock grazing also favoured the increment of vegetation and soil resources heterogeneity. Moderate grazing intensities created niche gaps which favoured the coexistence of more plant species and resulted in perennial forbs species addition. Once surpassed an intensity threshold, this effect fades out. Our results confirmed early warnings about the drastic magnitude of changes in humid grasslands of Patagonia.

Regardless of the intensity, livestock grazing favoured shrub encroachment and a decrease in aerial biomass production. There was a loss in system services provision from a range management and conservation point of view. However, richness increases at moderate grazing intensities could represent an enhancement in system functionality. Bare soil increment was part of the shrub encroachment process, which resulted in challenging conditions for plant growth. However, shrub encroachment is aiding to keep within the system some resources depleted from bare spaces. Highest grazing intensities must be avoided, since causes shrub fertile island collapse and the eventual loss of these resources.

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### **Conflicts of interest/Competing interest**

The authors declare that they have no conflict of interest or competing interest

### **Availability of data and material**

Data is available by request to corresponding authors

## Code availability

Not applicable

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## Tables

**Table 1** Study sites (paddocks) with their mean ANPP and its rank for 1999-2019 lapse, and the assigned SD, with resulting GI (mean, rank and class) for the same term

Site	ANPP rank (Kg ha <sup>-1</sup> yr <sup>-1</sup> )	ANPP mean (Kg ha <sup>-1</sup> yr <sup>-1</sup> )	SD mean (UGO ha <sup>-1</sup> )	GI rank	GI mean	GI class
AN	155-1881	943	0	0	0.0	A
PL	314-1328	549	0.2	0-0.3	0.1	B
CA	344-1791	766	0.3	0-0.8	0.2	C
AR	339-1377	618	0.5	0-0.8	0.4	D
PM	51-995	331	1.8	0-2.5	0.9	E

acronyms are ANPP for aboveground net primary productivity, SD for stocking density, UGO for *Unidad Ganadera Ovina*, and GI for grazing intensity

**Table 2** Mean values and standard deviation of relative interaction index (RII) and soil variables grouped by vegetation type and cover condition

	Vegetation									
	Grass				Shrub				Reference	
	Mean	sd			Mean	sd			Mean	sd
RII	0.12a	0.04			0.19b	0.06			0.16b	0.04
	Soil cover									
	Patch		Bare		Patch		Bare		(scrub spot)	
Soil variables	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
OM (%)	4.4	0.9	4.0	0.7	4.3	1.1	3.7	0.4	7.1	2.4
ER (%)	82.4	11.1	85.3	8.9	75.0	14.5	69.6	11.2	83.9	7.8
CF (%)	4.5	3.9	3.6	3.0	3.5	6.1	12.9	10.8	2.9	2.6
NAF	8.2	0.5	8.5	0.6	8.1	0.2	8.5	0.2	8.6	0.5
PH	6.4	0.3	6.4	0.2	6.7	0.4	6.4	0.4	6.2	0.3
EC ( $\mu\text{S m}^{-1}$ )	60.8	19.4	49.9	15.5	105.9	93.9	39.2	8.2	146.5	55.6
N (%)	0.13	0.03	0.12	0.03	0.13	0.03	0.10	0.02	0.23	0.1
CLAY (%)	1.5	0.8	1.5	0.7	1.2	0.9	3.5	1.9	2.0	0.7
SILT (%)	29.2	5.5	30.9	5.8	30.5	3.8	37.2	5.4	34.1	6.0
VFS (%)	16.9	3.4	16.7	2.9	19.2	2.9	17.8	2.3	17.2	2.5
FS (%)	25.1	6.1	23.3	3.9	24.8	2.1	21.1	2.1	21.3	2.8
MS (%)	17.6	4.5	17.4	5.2	15.5	3.1	12.7	3.7	15.0	3.6
CS (%)	9.5	3.9	9.8	2.5	8.6	3.1	7.4	2.7	9.9	3.9
VCS (%)	3.5	2.7	3.8	1.9	4.8	2.6	7.1	3.3	6.1	3.8
EP (%)	38.5	7.5	35.4	5.2	42.3	8.1	27.7	3.0	44.1	6.9
C_N	19.4	3.1	19.3	3.2	19.7	2.7	21.1	2.9	18.2	4.6

variables acronyms are: C\_N (carbon/nitrogen ratio); CF (coarse fragments >2000  $\mu\text{m}$ ); CLAY (clay content 0,1-2  $\mu\text{m}$ ); CS (coarse sand 500-1000  $\mu\text{m}$ ); EC (electrical conductivity); EP (effective porosity); ER (erodible fraction <840  $\mu\text{m}$ ); FS (fine sand 100-250  $\mu\text{m}$ ); MS (medium sand 250-500  $\mu\text{m}$ ); N (total nitrogen); NAF (soil: NaF pH); OM (total organic matter); PH (soil pH in water); SILT (silt content 2-50  $\mu\text{m}$ ); VCS (very coarse sand 1000-2000  $\mu\text{m}$ ); VFS (very fine sand 50-100  $\mu\text{m}$ ). RII (relative interaction index) means and standard deviation are displayed together with results of Bonferroni means comparison test. Means with a common letter are not significantly different ( $p > 0.05$ )



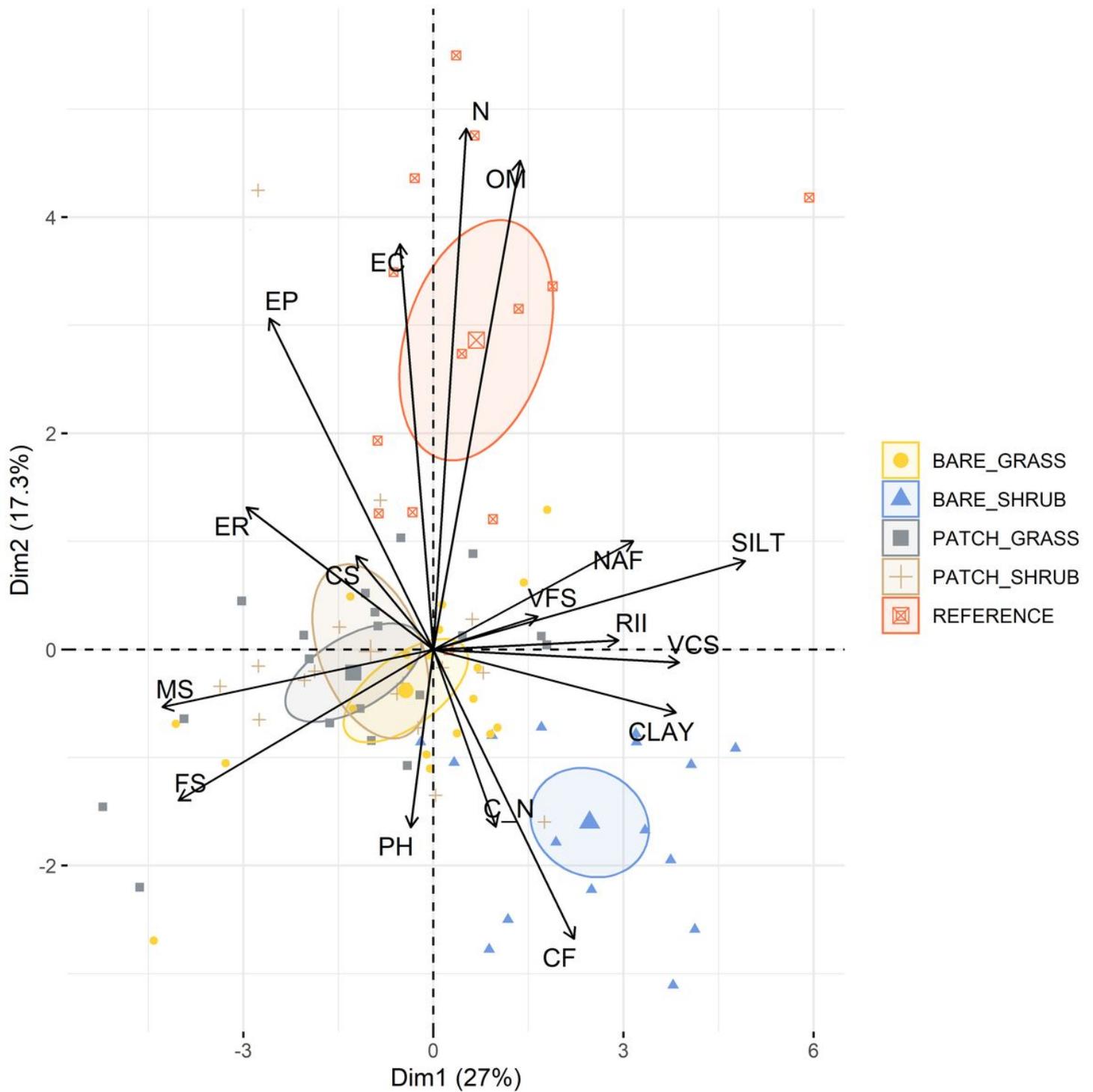
**Table 3** Best represented species in CCA ordination results, with their classification by life cycle, status and life form. Species at each branch are ordered from higher to lower score

Axis 1 CCA				Axis 2 CCA			
Species	Cycle	Status	Life form	Species	Cycle	Status	Life form
Positives branch				Positives Branch			
COL.hys	P	N	S	BER.het	P	N	S
PAP.spe	P	N	G	CAR.sub	P	N	G
BRO.sta	P	N	G	HOR.com	P	N	G
SEN.fil	P	N	S	RYT.vir	P	N	G
ADE.obc	P	N	S	HYP.inc	P	N	F
ADE.cam	P	N	S	CER.arv	P	E	F
BRO.set	P	N	G	ARM.mar	P	N	F
Negatives branch				GAL.apa	A	E	F
NAS.acu	P	N	S	NAR.chi	P	N	S
SEN.bra	P	N	S	CAR.arg	P	N	G
POA.pra	P	E	G	ACA.pin	P	N	F
MYO.sco	P	E	F	POA.lig	P	N	G
TRI.pra	P	E	F	CAM.den	A	N	F
CAM.den	A	N	F	CAL.sp	P	N	F
BER.emp	P	N	S	BRO.set	P	N	G
HOL.lan	A	E	G	GAL.ric	A	N	F
GAM.sel	P	N	F	Negatives branch			
MUL.spi	P	N	S	TRI.pra	P	E	F
HOF.tri	P	N	F	POA.pra	P	E	G
PLA.pat	P	N	F	MYO.sco	P	E	F
VUL.sp	A	E	G	BER.emp	P	N	S
ANE.mul	P	N	F	ERO.cic	A	E	F
SEN.ser	P	N	S	TIQ.nut	A	N	F
FES.pal	P	N	G	BRO.sta	P	N	G
ERO.cic	A	E	F	HYP.rad	P	E	F

TIQ.nut	A	N	F	MUL.spi	P	N	S
CAL.sp	P	N	F	VUL.sp	A	E	G
CER.arv	P	E	F	FES.pal	P	N	G
NAR.chi	P	N	S				

Classification acronyms are P for perennial life cycle and A for annual; N for native status and E for Exotic; S for shrub life form, G for grass and grasslike, and F for forb. Species acronyms are: ACA.pin (*Acaena pinnatifida*), ADE.cam (*Adesmia campestris*), ADE.obc (*Adesmia obcordata*), ANE.mul (*Anemone multifida*), ARM.mar (*Armeria maritima ssp andina*), BER.emp (*Berberis empetrifolia*), BER.het (*Berberis heterophylla*), BRO.set (*Bromus setifolius*), BRO.sta (*Bromus stamineus*), CAL.sp (*Calceolaria sp*), CAM.den (*Camissonia dentata*), CAR.arg (*Carex argentina*), CAR.sub (*Carex subantartica*), CER.arv (*Cerastium arvense*), COL.hys (*Colletia hystrix*), ERO.cic (*Erodium cicutarium*), FES.pal (*Festuca pallescens*), GAL.apa (*Galium aparine*), GAL.ric (*Galium richardianum*), GAM.sel (*Gamocarpha selliana*), HOF.tri (*Hoffmannseggia trifoliata*), HOL.lan (*Holcus lanatus*), HOR.com (*Hordeum comosum*), HYP.inc (*Hypochaeris incana*), HYP.rad (*Hypochaeris radicata*), MUL.spi (*Mulinum spinosum*), MYO.sco (*Myosotis scorpioides*), NAR.chi (*Nardophyllum chilotrichioides*), NAS.acu (*Nassauvia aculeata*), PAP.spe (*Pappostipa speciosa*), PLA.pat (*Plantago patagonica*), POA.lig (*Poa ligularis*), POA.pra (*Poa pratensis*), RYT.vir (*Rytidosperma virescens var. patagonica*), SEN.bra (*Senecio bracteolatus*), SEN.fil (*Senecio filaginoides*), SEN.ser (*Senecio sericeo-nitens*), TIQ.nut (*Tiquilia nuttallii*), TRI.pra (*Trifolium pratense*), VUL.sp (*Vulpia sp*)

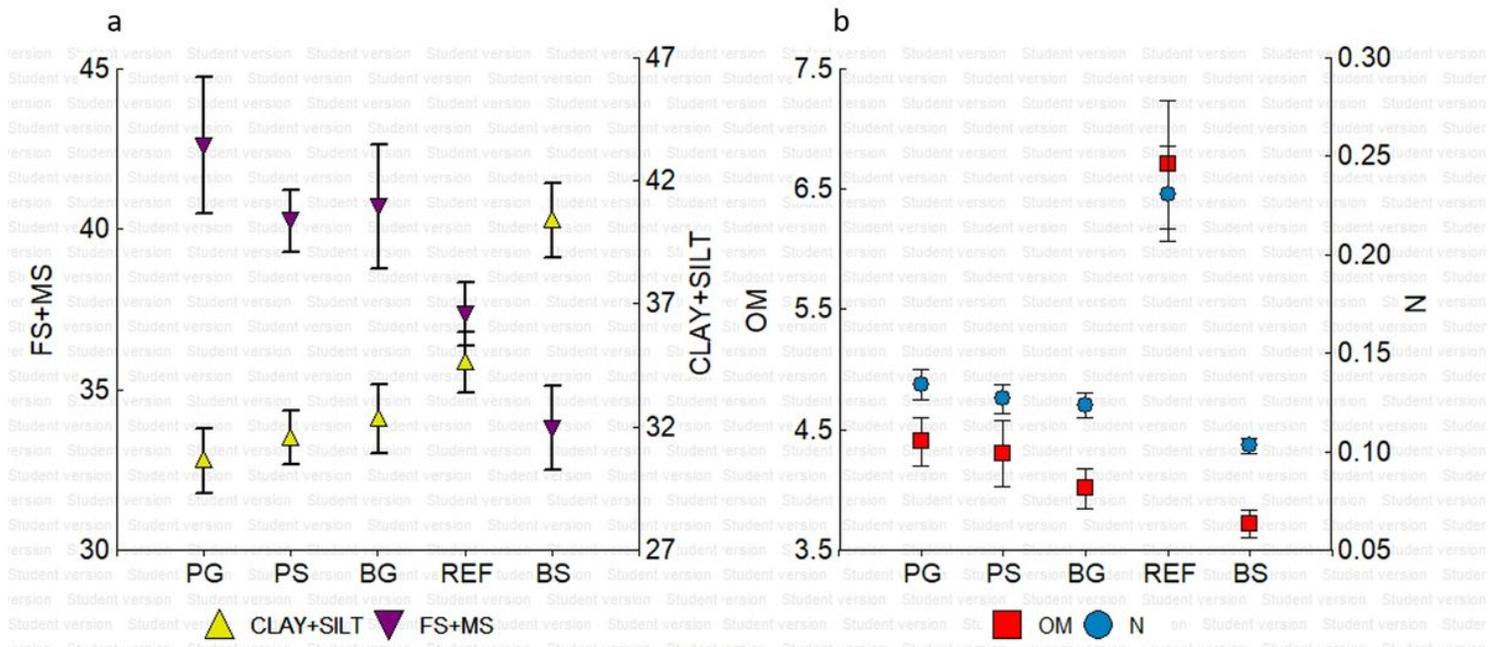
## Figures



**Figure 1**

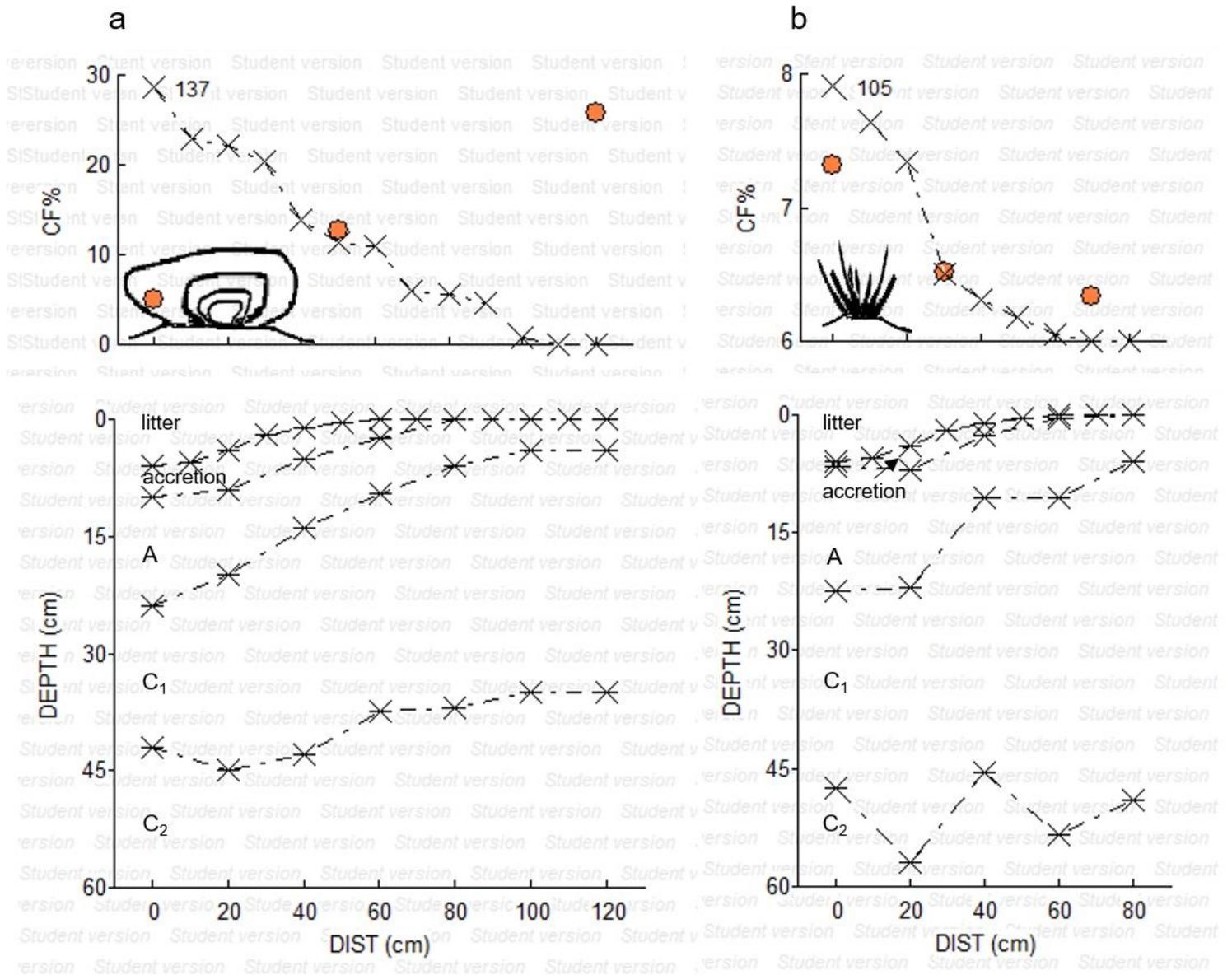
Principal components analysis (PCA) biplot illustrating correlations between the 16 soil variables plus the RII in the first and second principal components, shown as biplot arrows. Dimension 1 explains 27% of the variance and is most strongly correlated with silt (SILT), clay content (CLAY) and very coarse sand (VCS). It is negatively correlated with medium sand (MS), fine sand (FS) and erodible fraction (ER). Dimension 2 explains 17% of the variance and is most strongly correlated with total nitrogen (N), organic matter (OM) and electrical conductivity (EC). Dots give positions of soil samples (n =82) which are shape-

given according to both soil cover condition (bare soil=BARE; soil beneath vegetation=PATCH) and vegetation (GRASS; SHRUB; REFERENCE). Confidence ellipses around each group centroid predict where 95% of spots for each category are expected to occur. All variables acronyms are detailed in table 2



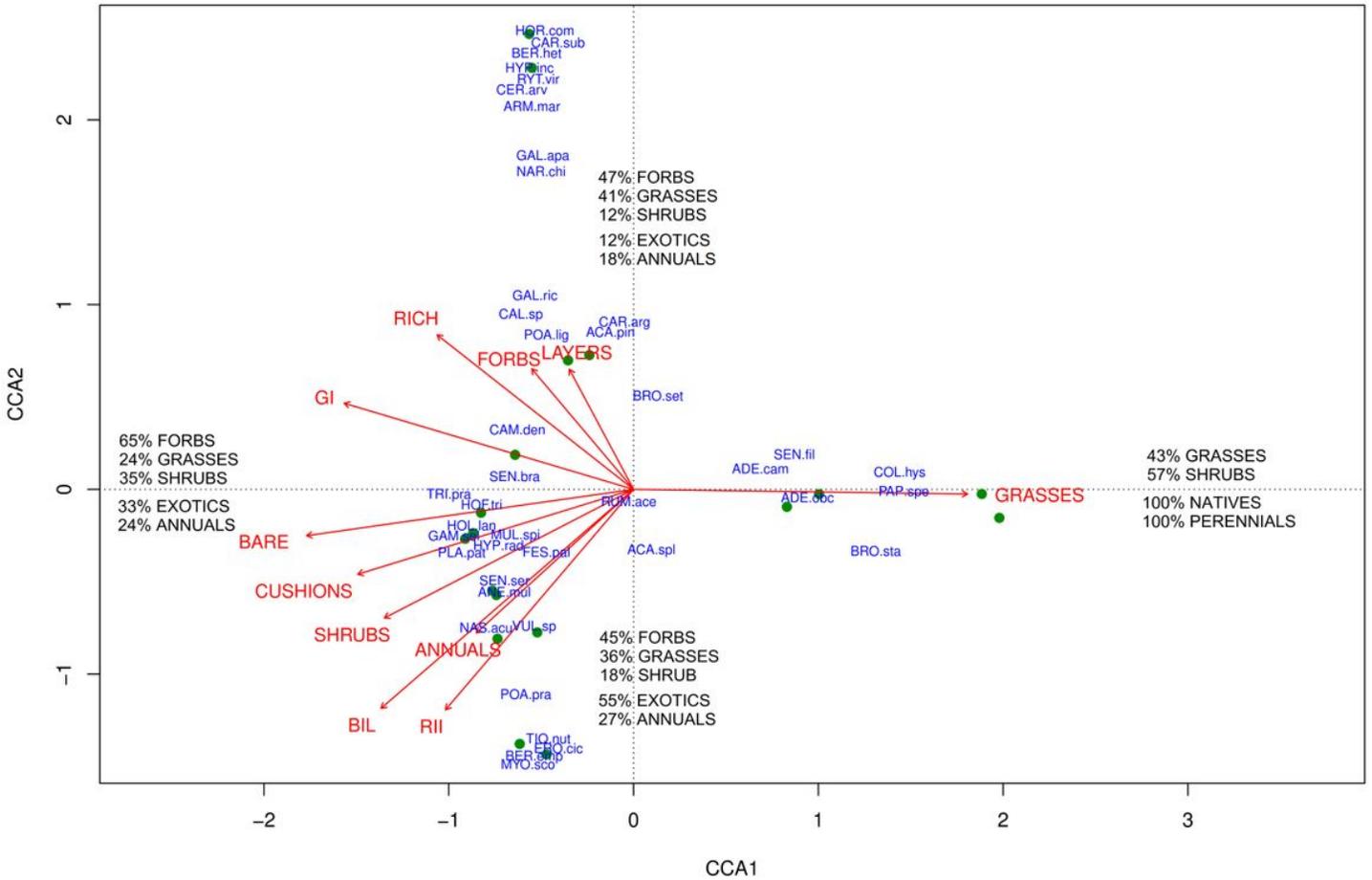
**Figure 2**

Dot plots showing selected soil variables with high correlations on the first two dimensions of PCA. Fig. 2a shows two soil particles pools (CLAY&SILT and FS&MS) related to dimension 1. Fig. 2b shows chemical fertility variables (OM and N) correlated with dimension 2. The X-axis groups are defined by both soil cover condition (bare soil=B; soil beneath vegetation=P) and vegetation: (grass=G; shrub=S; reference=REF). Soil variables acronyms are: CLAY (clay content); MS (medium sand); N (total nitrogen); OM (total organic matter); SILT (silt content). Dots represent mean values for each variable or variable combination. Line bars represent standard errors



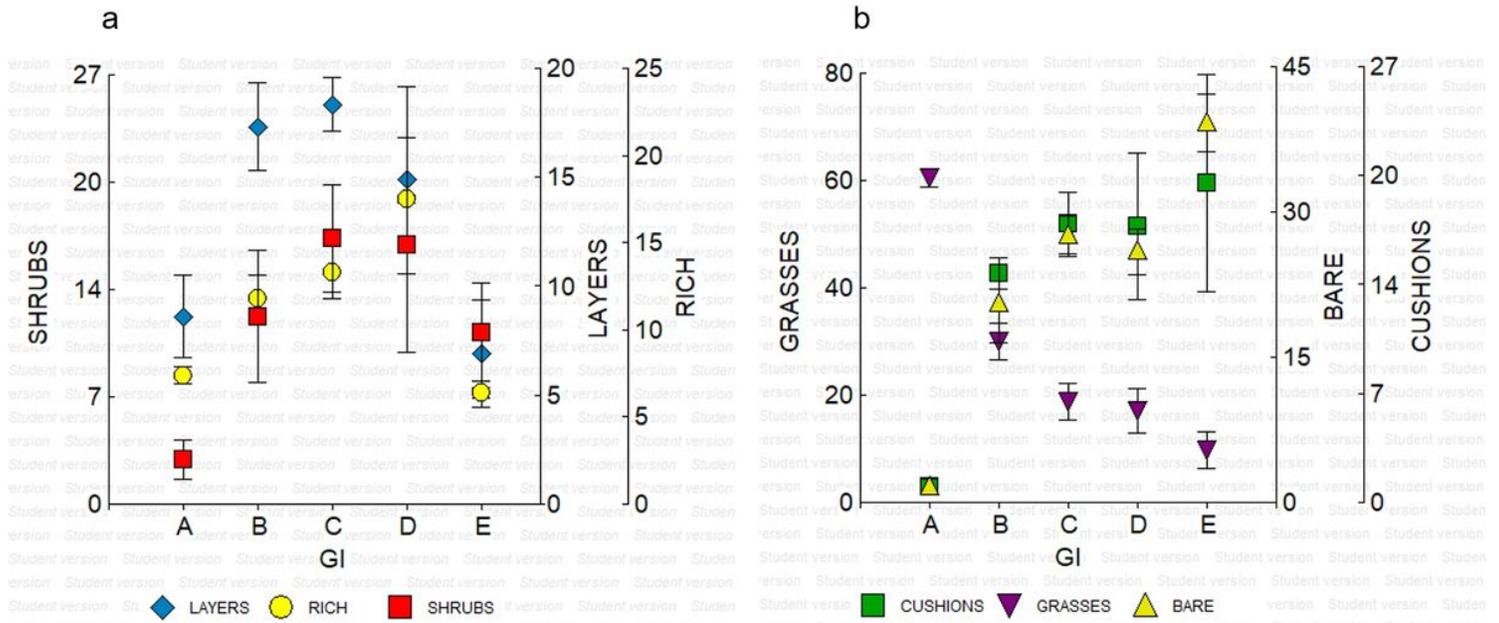
**Figure 3**

Diagrams of soil profile corresponding to a cushion shrub patch (*Mulinum spinosum*) (Fig. 3a) and native perennial palatable grass patch (*Festuca pallescens*) (Fig. 3b). Both patches are shown with their associated interpatch of bare soil space, with X-axis showing the distance (DIST) from the vegetation hummock centre. The upper plots show with a dashed line the micro-topography relief of hummock and interpatch measured at each distance, with the maximum height indicated in mm. The percentage of coarse fragments (CF%) in 0-5 cm soil samples is indicated with circles. The lower plot portion shows the sequence of soil horizons and depth (DEPTH) at each distance from the centre, measured from the soil surface



**Figure 4**

Constrained correspondence analysis (CCA) triplot. Eigenvalues were 0.64 for CCA1 and 0.35 for CCA2. Arrows show the variables included in the model. The proportion of the total inertia explained by the constraining variables in the model was 0.87. Acronyms for variables are GI (historic grazing intensity); BARE (percentage of bare soil); SHRUBS (shrubs and dwarf shrubs total cover); GRASSES (grasses and grasslike total cover); RICH (richness); FORBS (forbs relative cover); LAYERS (percentage of superposition in vegetation); CUSHIONS (cushion shrubs relative to total shrub cover); BIL (bare interpatch spaces average length); RII (relative interaction index); ANNUALS (annual grasses relative cover). Species acronyms are detailed in table 3. Circles represent sampling units. Community composition at each plot quadrant is described in % of life forms, and % of exotics and annual species



**Figure 5**

Dot plot showing mean values of selected cover and structure variables with high correlations on the first two dimensions of CCA, against grazing intensity classes (GI) displayed in X-axis. Fig. 5a shows shrubs total cover (SHRUBS) together with total richness (RICH) and percentage of vegetation layers superposition (LAYERS). Fig. 5b shows grasses total cover (GRASSES) together with bare soil percentage (BARE) and cushion shrubs relative cover (CUSHIONS). Line bars represent standard errors

## Supplementary Files

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