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Root proliferation strategies and exploration of soil patchiness in arid communities

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Abstract Soil patchiness is a key feature of arid rangelands. As root proliferation contributes to soil exploration and resource uptake, it is ecologically relevant to understand how species respond to soil heterogeneity and coexist. Campbell *et al.*'s influential 1991 hypothesis proposes that dominant species deploy root systems (scale) that maximize soil volume explored. Instead, subordinate species show accurate root systems that exclusively proliferate in nutrient-rich patches (precision). After many experiments under controlled conditions, the generality of this hypothesis has been questioned but a field perspective is necessary to increase realism in the conceptual framework. We worked with a guild of perennial graminoid species inside a grazing exclosure in an arid Patagonian steppe, a model system for ecological studies in arid rangelands for four decades. We buried root traps in bare ground patches with sieved soil, with or without a pulse of nitrogen addition, to measure specific root biomass and precision at 6 and 18 months after burial. We also estimated scale (root density) in naturally established plants, and root decomposition in litter bags. Several species grew in root traps. Dominant species showed the highest root biomass (in both harvests) and scale. Subordinate species grew more frequently with nitrogen addition and showed lower biomass and scale. Similar total root biomass was found with and without nitrogen addition. Species differed in root decomposition, but correcting species biomass by decomposition did not change our conclusions. We did not find a relation between scale and precision, indicating that Campbell's hypothesis is probably not supported in this Patagonian steppe. Soil resource acquisition differences probably do not utterly explain the coexistence of dominant and subordinate species because the steppe is also affected by large herbivore grazing. We propose that root proliferation in this steppe is the result of the interaction between individual density in the community and specific root growth rates.

Key words: graminoids, nutrient heterogeneity, precision, scale, species coexistence.

INTRODUCTION

Soil is spatially heterogeneous regarding concentration of nutrients and water at different temporal and spatial scales (Farley & Fitter 1999). This is particularly true in arid and semiarid rangelands where plants strongly affect soil nutrients and water availability (Burke *et al.* 1998). Grazing, the common disturbance of rangelands, increases this heterogeneity because small disturbances kill individual plants. Killing frequency is high enough to significantly affect the structure of the community (Coffin & Laueroth 1988). Additionally, herbivore faeces and urination further increase patchiness of essential nutrients (Morton & Baird 1990). Because soil patchiness is a crucial feature of rangelands, it is ecologically relevant to understand how plant roots respond to soil heterogeneity. The term 'foraging' has been proposed to describe the process by which root systems grow in soil and uptake nutrients (Bray 1954). An early study by Campbell *et al.* (1991) compared root proliferation of different herbaceous species from mesic-temperate grasslands and described two extreme strategies. One set of species presents an especially broad scale and their roots did not preferentially proliferate in nutrient-rich patches. Instead, the other set of species presents high precision and proliferated in nutrient rich patches, preferentially. Campbell *et al.* (1991) proposed an influential hypothesis that addressed specific variations in root foraging to explain community organisation. It states that there is a trade-off between scale and precision of root foraging strategies which promotes species coexistence. On the one hand, dominant species generally deploy root systems (scale), maximize the volume of soil explored and capture a large portion of soil resources. Instead, on the other hand, rare or subordinate species show accurate root systems that exclusively proliferate in nutrient rich patches (precision).

Empirical support to Campbell *et al.*'s hypothesis has been ambiguous. It has been reported that scale

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and precision are strongly correlated, both positively (Farley & Fitter 1999; Rajaniemi & Reynolds 2004) and negatively (Campbell *et al.* 1991; Wijesinghe *et al.* 2001). Other studies indicate no correlation (Einsmann *et al.* 1999; Bliss *et al.* 2002; Grime & Mackey 2002). Contrasting outcomes may result from different experimental conditions, methods for assessing the two strategies and/or the number of species included in each study (Kembel *et al.* 2008). Because scientific hypotheses depend on context conditions, scale-precision merits further exploration (Grime 2007). For example, most of the works that studied this hypothesis were performed under highly controlled conditions (pot experiments) and for a relatively short period of weeks or months (Kembel *et al.* 2008). In this way it was possible to control patchiness in resource availability and estimate species root growth, harvest and identification. We found that reviews report no studies that address root proliferation in arid communities and few studied the response of a natural and multispecies community over long periods (>1 year) (Bliss *et al.* 2002). We propose that field studies in heterogeneous habitats such as arid communities will allow a better evaluation of the importance of this distinctive ecological aspect (i.e. root proliferation strategy in resource mosaic) with implications for plant species coexistence (García-Palacios *et al.* 2011). However, working under natural conditions represents a gain in realism at the expense of accuracy.

In order to estimate the implication of diversity of foraging strategies for the organisation of plant communities, it is necessary to make the transition from individual plant level to community level and to extend the duration of experiments. We decided to use specific root biomass as a proxy of root proliferation under field conditions in root traps. In this condition, roots of several species could proliferate in response to nutrient availability. Because extending study timeline includes growth, mortality and decomposition of roots, we also assessed field decomposition. In this way we can estimate residence times of roots in the soil for a better estimation of root proliferation differences. In order to study root proliferation in an arid community and to assess species under Campbell *et al.*'s hypothesis framework, we worked with a guild of perennial graminoids that dominate the Patagonian steppe. This study site has been used as a model system for studying the ecology of arid rangelands (e.g. Aguiar & Sala 1999; Adler *et al.* 2004; Cipriotti & Aguiar 2005; Graff *et al.* 2007). Previous studies allowed taxonomic identification of roots of species growing under field conditions by their morphology with 95% accuracy (Leva *et al.* 2009; Reyes & Aguiar 2017). As nitrogen is a critical resource for xeric plants (Austin 2011), we evaluated root growth with soil without roots and with or without nitrogen fertilisation to create a heterogeneous microsite. We expect that species with high plant density that dominate the community have maximum scale, while subordinate species show the highest precision.

METHODS

Study site and grass species

All studies were conducted in a semi-arid Patagonian steppe ecosystem (Chubut, Argentina 45°25′S, 70°20′W). The climate is cold semi-arid, with intense summer drought. In June and July average temperatures are the lowest of the year (between 2 and 3°C mean day temperature). In August and September temperature starts to increase (between 5 and 7°C), reaching values of 16°C in January. Mean annual precipitation is 131 ± 40 mm (mean ± SD) and mostly occurring during winter and early spring (May-September). Plant cover (<50%) and species richness (<50 species) are low. The livestock exclosure, where we established our studies, is dominated by five perennial grasses, since shrubs only cover 18% of total surface (Oñatibia & Aguiar 2016). Herbaceous dicots comprise <0.5% of total cover. Grasses have most of their roots in the upper soil layer (30 cm). Thus, 54% of their root biomass occupies the first 10 cm of the profile. Grass roots develop horizontally, while shrubs mainly explore deeper soil layers (Sala *et al.* 1989).

The grass community includes eight perennial-graminoid species, the five most abundant are: *Poa ligularis* Nees ex Steud; *Pappostipa speciosa* (Trin. & Rupr.) Romasch; *Pappostipa humilis* (Cav.) Romasch; *Bromus pictus* J. Presl (*Poaceae* species) and *Carex* sp. (Cyperaceae), and other three with <3% frequency in the field: *Bromus setifolius* J. Presl (Hook. f.) Skottsb; *Festuca argentina* (Speg.) Parodi and *Hordeum comosum* J. Presl (all *Poaceae* species). Leva *et al.* (2009) built a taxonomic key to identify species using major features of roots harvested in the field that showed systematic variation (e.g. diameter, colour, hairiness), and also calculated the relative growth rates of the species in the grass community. The highest to the lowest (average ± SE) include: *B. setifolius* (2.93 ± 0.11 100 day^{-1}); *B. pictus* (2.67 ± 0.22 100 day^{-1}); *P. ligularis* (1.58 ± 0.35 100 day^{-1}); *Carex* sp. (0.80 ± 0.11 100 day^{-1}); *H. comosum* (0.77 ± 0.33 100 day^{-1}); *P. speciosa* (2.67 ± 0.22 100 day^{-1}); *P. humilis* (2.67 ± 0.22 100 day^{-1}) and *F. argentina* (2.67 ± 0.22 100 day^{-1}). Reyes and Aguiar (2017) tested the taxonomic key and obtained a specific biomass recovery rate on blind samples of 95%. This way of identifying species allowed us to obtain specific root biomass, whereas it is not possible with molecular identification techniques (Cahill & McNickle 2011). We worked in a grazing exclosure with a perennial graminoid guild that included *P. ligularis* (individual density: 7.0 ± 0.2 ind m^{-2}, average ± SE, Oñatibia 2013) and *P. speciosa* (3.5 ± 0.2 ind m^{-2}) as dominant species, *P. humilis* (2.8 ± 0.2 ind m^{-2}) as intermediate, and *B. pictus* (1.2 ± 0.1 ind m^{-2}) and *Carex* sp. (0.5 ± 0.1 ind m^{-2}) as subordinate species.

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Root proliferation study

We conducted a study with root traps to estimate differences among species on root proliferation. Traps were filled with two types of substrates: a. sieved soil (no roots) (control, C); b. sieved soil with the addition of 4 gN m^{-2} (N+). Nitrogen was added as granulated ammonium nitrate, which has low liberation rate, providing time for the increasing precipitations to dilute N during spring. The amount of N added represents, on average, ten times the annual nitrogen mineralisation of the site (Austin *et al.* 2006). In the same study site, Soriano *et al.* (1987) reported that growth rates of grass species are negligible in winter, increase during spring, reach their highest values in early summer and then, decrease due to summer drought. Therefore, in order to sample the growing season from the beginning, we buried traps in winter (June 2011), until early summer (the first half of a growing season, December 2011) when we performed the first harvest. This allowed us to observe the root community response to soil devoid of roots during spring (increasing precipitations and temperatures). The second and last harvest was conducted 18 months after the burial to estimate the root dynamics after a second growing season (December 2012). Each trap had a label and a coloured wire that emerged from the soil in order to make identification easier when harvesting.

We used commercial hair curlers as root traps. The mesh screen cylinder (4 cm diameter and height 6 cm) had 10 mm^2 perforations all along and around. Traps allowed colonisation by roots of different diameters such as the species studied (Reyes & Aguiar 2017). The study had a blocked factorial design with two factors: substratum (control and N+) and harvest (2011, 2012), with 10 replications for each 4 combinations of these levels (i.e. treatments). We decided to use this number of replications because we did not find significant differences in the variability (coefficient of variation) of root biomass when the number of replications was increased from 10 to 30. These calculations were based on a previous unpublished study (Reyes 2015). Each block with the four treatments occupied an area of 100 m^2. Blocks were inter-dispersed inside a grazing exclosure of 4 ha. Distance among blocks was >30 m. Blocks did not present differences either in vegetation (above-ground neighbourhood) or soil surface characteristics, but the blocks ensured a reduction of the environmental variability of the system. They also facilitated precision index calculations. Root traps were buried to sample the 5–11 cm depth soil layer and were placed in the centre of bare soil patches surrounded by at least three of the five mentioned species. The nearest plant was more than 15 cm away from buried traps. At harvests, we followed the wire up to the upper edge, carefully removed soil up to the trap, and then cut the root with a sharp knife following the outside surface of the trap.

After the harvest, roots were separated from the soil with a sieve of 1.25 mm in the laboratory. The species that appeared inside the traps presented only fine roots (diameter $\leq 0.61 \pm 0.10$ mm, average $\pm$ SE, Leva *et al.* 2009). Then, these roots were identified by their morphological characteristics (Leva *et al.* 2009; Reyes & Aguiar 2017), oven-dried at 70°C for 48 h and weighed. The recovered and identified roots were used to calculate the frequency (presence of species in traps) of dominant and subordinate species in control (C) and N+ traps. We obtained total biomass (by summing up the root biomass of all species in each trap) and specific root biomass (the biomass of each species in each trap). With specific biomass, following Einsmann *et al.* (1999), we calculated precision for all species, as preferential proliferation of roots in nutrient-rich patches (N+) compared with less fertile patches (C, both traps of the same block):

$$\text{Precision} = (\text{specific biomass in N+}) * [(\text{specific biomass in C}) + (\text{specific biomass in N+})]^{-1} \quad (1)$$

In the case of subordinate species, which appeared with low frequency or were absent in traps, we calculated their precision only with blocks where the species were present, so the statistical analysis included only those blocks. Because of the variability of the root biomass, especially of the subordinate species, we also calculated the precision index with the presence-absence of the species which allowed us to evaluate the response to N addition including species with low density. Chi-square analyses were performed to test for differences in root proliferation frequency (presence-absence data).We compared species frequency in both N+ and C traps. The analyses were conducted comparing root biomass and root proliferation frequency between harvests (6 *vs.* 18 months) and between treatments (N+ *vs.* C). If both groups were similar ($P > 0.05$), the species were not accurate in N foraging (low precision). Differences among species were analysed with MANOVA (because the presence of the species in the traps was not independent), including block as an independent factor and using root biomass or precision as dependent variables. Homoscedasticity and normality assumptions were checked. Dependent variables were transformed as $X` = Log\ (X + 1)$ or $X' = X^{1/2}$ when variance homogeneity assumption was not achieved. A non parametric test (Kruskal Wallis) was used when residual distribution was not normal. Tukey's post hoc tests were performed when significant differences were detected.

Scale study

We estimated species scale in the study site as the density of roots of the guild of perennial graminoids found in a soil volume of 3600 cm^3. We used density of roots based on the sharp decrease of root biomass of three of the dominant grass species based on the distance away from established plants (*Poa ligularis*, *Pappostipa speciosa* and *P. humilis*, following Soriano *et al.* 1987). We carefully excavated soil around single plants. Thirty complete adult plants per species were collected in December. In the laboratory, we separated the roots attached to the plants. Roots of other species were discarded. Differences among species were analysed with one way ANOVA and biomass of species (scale) as dependent variable ($n = 30$). We related scale and precision at 6 and 18 months performing a simple regression for each comparison.

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Decomposition study

We collected plants of the five most abundant species during early summer. Roots attached to the plants were identified in the laboratory and separated in order to fill litter bags (one species per bag) (Leva *et al.* 2009). Following Austin *et al.* (2009), roots with signs of damage and decomposition were discarded. Each litter bag was filled with 0.75 g of selected root mass of *P. ligularis*, *P. speciosa*, *P. humilis*, *B. pictus* or *Carex* sp. species. Litter bags were made of fiberglass mesh of 2 mm^2, and were 12 cm wide and 12 cm long. Litter bags were placed at 5 cm depth under bare soil patches, as were traps in the root proliferation study. Because root proliferation substantially decreases (Soriano *et al.* 1987) and mortality and decomposition probably starts after early summer, we placed litter bags in December 2011. Each litter bag had a wire with a label in order to easily harvest it. Litter bags were harvested in June and December 2012. There were five replications for each harvest.

In each harvest, litter bags were carefully retrieved and placed in labelled paper bags. In the laboratory, the remaining material in litter bags was dried in an oven to stop decomposition (70°C for 48 h). Then, it was cleaned, dried and weighed again to quantify the remaining litter. Extra litter bags were prepared to estimate mass loss during handling and burial. Mass losses in the extra litter bags were averaged by species and subtracted to the initial litter placed in bags in order not to overestimate decomposition. We used one-way ANOVA to compare root decomposition of different species. We performed simple regression using decomposition as predictor of precision and scale. We also estimated specific biomass loss by decomposition in root proliferation study. We summed up to root biomass found in traps (original biomass) the proportion of root mass loss to correct it by decomposition (corrected biomass) and we compared both with ANOVA (Appendix S1). All statistical analyses were conducted with Statistica 7.0 software (Stat Soft Inc., Tulsa, OK, USA).

RESULTS

Root proliferation

All root traps showed root proliferation. Proliferation frequency (estimated as species presence in traps) was different in control (C) or nitrogen addition (N+) traps depending on the species (Table 1). *Poa ligularis*, *P. speciosa* and *P. humilis* showed the same proliferation in C and N+ traps ($P = 0.53$, $P = 0.75$ and $P = 0.50$ respectively). However, *P. ligularis* and *P. speciosa* frequencies were high and similar in both harvests ($P = 0.48$ and $P = 0.75$), but the frequency of *P. humilis* was higher in the first harvest (6 months) than in the second one (18 months, $P < 0.01$). *Bromus pictus* and *Carex* sp. showed low frequency; *B. pictus* roots were more frequently present in N+ than in C traps ($P = 0.02$) in both harvests ($P = 0.65$). *Carex* sp. frequency was different between substrates and harvests (both $P = 0.02$), it was higher in N+ traps than in C traps in the first harvest and it showed the opposite pattern in the second one (Table 1).

Nitrogen addition did not change root biomass. Total root biomass was similar in C and N+ traps ($P = 0.39$), but it was higher in the first harvest (6 months) than in the second one (18 months, $P = 0.03$). There was no interaction between substrate and harvest factors ($P = 0.28$). At 6 and 18 months harvests, there was no effect of substrate ($P = 0.19$ and $P = 0.99$, Fig. 1). In both harvests root biomass was different depending on the species ($P < 0.01$). There was no interaction between substrate and species factors ($P > 0.05$). In C traps, at the first harvest, *P. speciosa* had higher root biomass than *P. humilis, B. pictus* and *Carex* sp.; *P. ligularis* showed intermediate values ($P < 0.01$, Fig. 1a). At the second harvest, *P. speciosa* had the highest root biomass ($P < 0.01$); differences among species decreased because *P. ligularis* biomass was lower than at the first harvest ($P = 0.04$, Fig. 1a). In N+ traps, *P. speciosa* also had the highest root biomass at both harvests (both $P < 0.01$, Fig. 1b). There were no differences between the two harvests ($P > 0.05$). The subordinate species, *B. pictus* and *Carex* sp., had the lowest root biomass, close to nought, in C and N+ substrates at both harvests.

The precision index for the first harvest did not differ among species ($P = 0.22$, Fig. 2). In the

Table 1. Absolute frequency of species roots in traps with control (C) and N addition (N+) treatments ($n = 10$), in the 6 and the 18 months harvests. Results of Chi-square test and *P*-values are shown for each species, in response to harvests and to substrates

	6 months		18 months		Comparing between harvests		Comparing between treatments	
Species	C	N+	C	N+	Chi-square	*P*-value	Chi-square	*P*-value
Poa ligularis	10	10	8	10	0.50	0.48	0.40	0.53
Pappostipa speciosa	9	10	10	10	0.10	0.75	0.10	0.75
Pappostipa humilis	7	9	1	1	100.00	<0.01	0.44	0.50
Bromus pictus	1	4	1	5	0.20	0.65	5.45	0.02
Carex sp.	1	3	3	1	5.33	0.02	5.33	0.02

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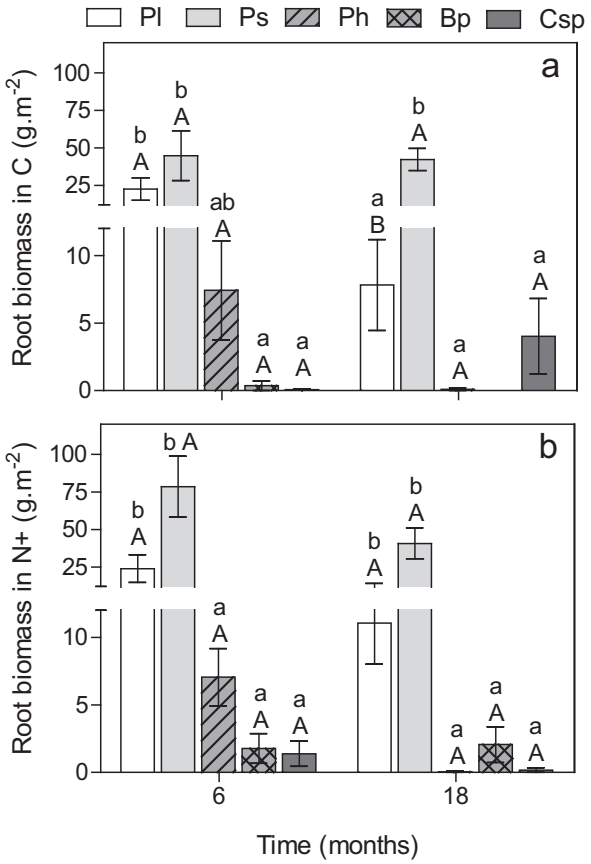

Fig. 1. Specific root biomass proliferated in traps (g m^{-2}) buried in the steppe for 6 and 18 months, under control (a) or N addition condition (b). Species are: Pl, *Poa ligularis*; Ps, *Pappostipa speciosa*; Ph, *Pappostipa humilis*; Bp, *Bromus pictus*; Csp, *Carex* sp. Bars show mean values and vertical lines show standard errors. Lower case letters (a and b) indicate comparisons among species in the same trap harvest. Upper case letters (A and B) indicate differences of one species between harvests ($P < 0.05$).

second harvest, traps showed that *B. pictus* had higher precision than *Carex* sp. whereas the other species showed intermediate values ($P < 0.01$). The precision of each species did not change between harvests ($P > 0.05$).

Scale

Scale was different among species ($P < 0.01$). The scales of *Poa ligularis* and *Carex* sp. were 30% higher than the scale of *P. speciosa*, twice the scale of *P. humilis* and more than three times the scale of *B. pictus* (Fig. 3). The precision of the five species in the study site was not related to their scale, neither at 6 ($r^2 = 0.14$, $P = 0.54$, black points and line, Fig. 4) nor at 18 months ($r^2 = 0.43$, $P = 0.23$, grey points and line, Fig. 4).

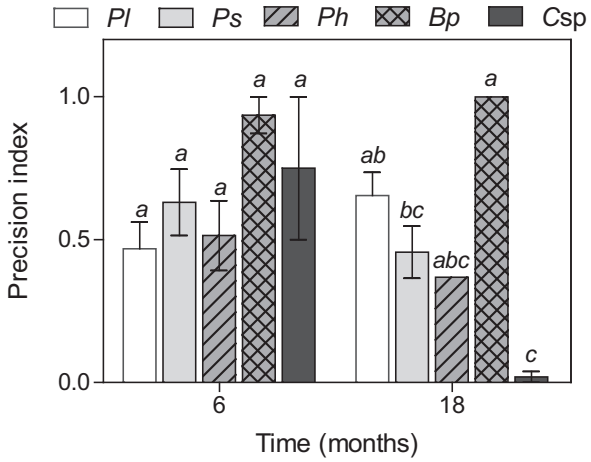

Fig. 2. Precision index for the five species at the two harvests estimated using the traps with and without N addition (Precision = (specific biomass in N+) * [(specific biomass in C) + (specific biomass in N+)]$^{-1}$. Species are: Pl, *Poa ligularis*; Ps, *Pappostipa speciosa*; Ph, *Pappostipa humilis*; Bp, *Bromus pictus*; Csp, *Carex* sp. Bars show mean values and vertical lines show standard errors. The absence of errors in *Ph* and *Bp* bars at 18 months is explained by the lack of variability for the Precision Index in these species. Letters indicate significant differences among species in the same trap harvest.

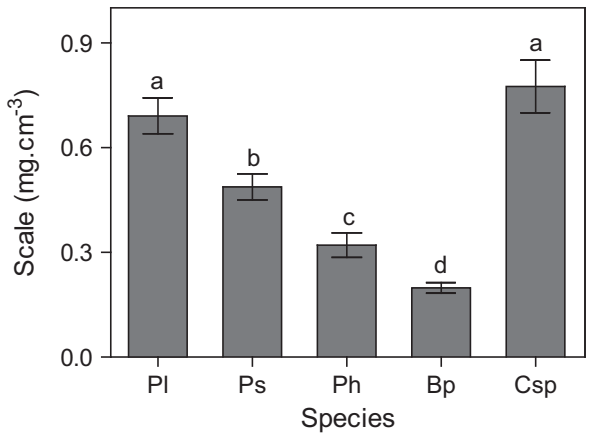

Fig. 3. Scale of root proliferation estimated as the density of roots in a soil volume of 3600 cm^3 under field conditions. Species are: Pl, *Poa ligularis*; Ps, *Pappostipa speciosa*; Ph, *Pappostipa humilis*; Bp, *Bromus pictus*; Csp, *Carex* sp. Letters indicate significant differences among species in the same trap harvest.

Root decomposition

The remaining root litter after 6 months for the five species was on average 88.2 ± 2.1% ($P = 0.07$, Fig. 5). After 12 months *P. speciosa* litter bags had significantly less remaining root litter than *Carex* sp. litter bags ($P < 0.01$; 70.8 ± 9.6% *vs.* 95.8 ± 1.2%), the other species showed intermediate values. *Poa*

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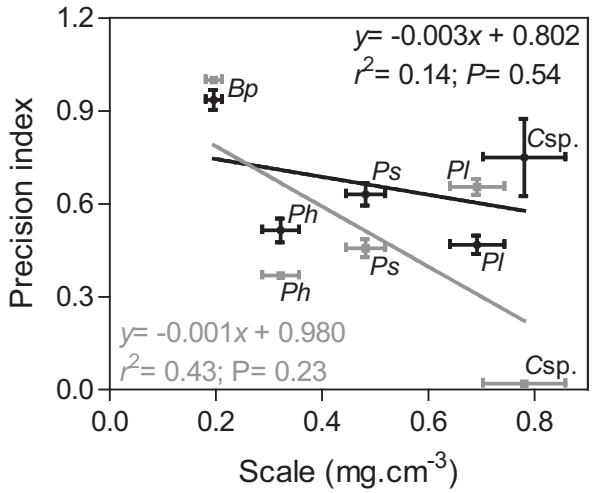

Fig. 4. Relationship between scale and precision (mean values ± SE, $n = 5$) estimated after 6 (black points and lines) and 18 months (grey points and lines). Species are: *Pl*, *Poa ligularis*; *Ps*, *Pappostipa speciosa*; *Ph*, *Pappostipa humilis*; *Bp*, *Bromus pictus*; *C*sp, *Carex* sp.

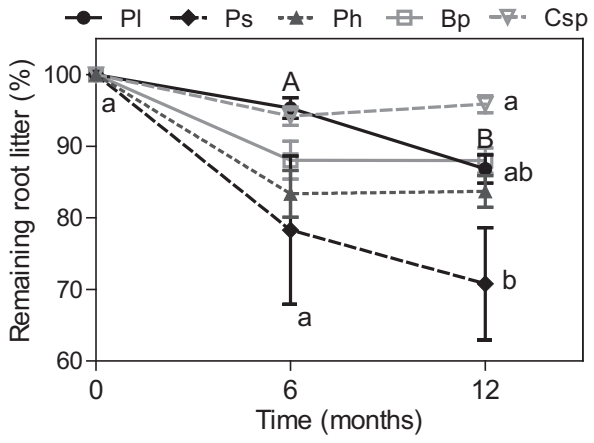

Fig. 5. Proportion of remaining root litter found in litter bags at 6 and 12 months. Litter bags were filled with 0.75 g of roots of: Pl, *Poa ligularis*; Ps, *Pappostipa speciosa*; Ph, *Pappostipa humilis*; Bp, *Bromus pictus*; Csp, *Carex* sp. Lines connecting points were drawn to easily visualize the temporal dynamics of the response variables. Lower case letters (a and b) indicate significant differences among species in the same trap harvest. Capital letters (A and B) in *Poa ligularis* indicates significant differences between harvests, the other species showed no differences (letters not shown).

ligularis was the only species which showed a significant decrease in remaining root litter between the first and the second harvest ($P < 0.01$). The rest of the species had similar remaining root biomass ($P = 0.57$; $P = 0.93$; $P = 0.99$; $P = 0.37$, for *P. speciosa*, *P. humilis*, *B. pictus* and *Carex* sp. respectively). Correcting root biomass of C traps by decomposition did not change the distribution pattern of the studied species over time (Appendix S1). Precision (at 6 and 18 months) of the five species were not related to remaining root biomass ($r^2 = 0.03$, $P = 0.55$ and $r^2 = 0.09$, $P = 0.13$ respectively). Scale also showed no relation with remaining root biomass ($r^2 = 0.03$, $P = 0.02$).

DISCUSSION

Soils of arid ecosystems are particularly heterogeneous in resource distribution due to, among other factors, plant influences (i.e. island of fertility) and small scale disturbance regimes (Coffin & Laueroth 1988; Burke *et al.* 1998; Aguiar & Sala 1999). In the steppe, root proliferation under bare soil patches indicates that neighbour plants (located <15 cm from the trap) tend to grow rapidly (6 months) in unoccupied traps. However, species differed in their root proliferation according to their individual density (measured as number of individuals × m^{-2}, in Oñatibia 2013). Increasing N did not significantly raise biomass accumulation in traps. Dominant species tended to dominate root traps with and without N addition. Differences between dominant and subordinate species decreased after 18 months, indicating that the N pulse did not persist for more than one growing season and that decomposition is acting on the root biomass present in the traps, our variable to estimate proliferation. Subordinate species were less frequent than dominant species but *B. pictus* showed precision since it was more frequent in fertilized traps than in control traps in the two harvests, which probably is related to the high growth rates that this species has (Leva *et al.* 2009). The precision index supported this trend; subordinate species grew more biomass in nutrient-rich traps.

Root proliferation in this Patagonian community presented several interesting patterns. First, we found that after 6 months all traps located under bare ground areas were colonized by two or more species (Table 1). Several recent studies established that roots of different species intermingled in different herbaceous communities (Frank *et al.* 2010; de Kroon *et al.* 2012; Reyes & Aguiar 2017). The intermingling of root species in the traps persisted over time (at least for 18 months) indicating that it was not necessarily just the result of the initial re-growth after root severing when traps were buried. Second, traps indicated that the species that dominate the canopy, *P. ligularis* and *P. speciosa*, were also dominant belowground. Instead, the root biomass of *P. humilis* (a species of intermediate cover dominance) did not differ from the root biomass of the subordinate species. Furthermore, *P. humilis* reduced

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in absolute frequency from 70 to 90% (at 6 months) to 10% (at 18 months). Because we statistically blocked all treatments, we are confident that this pattern is not a result of spatial variability at sampling scale. The subordinate species, *B. pictus* and *Carex* sp., showed low root frequency and low root biomass in all traps. *Bromus pictus* had a consistent pattern of higher frequency in response to N addition traps in both harvests. But *Carex* sp. changed from being more frequent in N+ than in control to show the opposite pattern. Currently, we do not have an explanation for this pattern shown by *Carex* sp.

We found that total root biomass did not differ between traps with and without N addition. This result could indicate that there is a maximum root biomass per soil volume. Other studies proved the relationship between root proliferation and soil volume (Poorter *et al.* 2012). Nevertheless, little is known about the effect of N addition on root biomass at species level in a community setup. In this Patagonian steppe, specific root proliferation estimated by root biomass was not significantly affected by N addition (Fig. 1). Considering that the fertilisation pulse equalled ten times the annual N mineralisation, we are confident that it was a biologically significant increment in resources. This fertilisation treatment may resemble nutrient pulses that are common in grazed rangelands (Coffin & Laueroth 1988; Morton & Baird 1990). However, N is a critical resource for xeric plants provided that there is no water limitation. As it is a mobile nutrient, it needs soil moisture to be absorbed by plants. Such moisture is only available in the study site in the spring season, when water is not limiting. Still, the studied guild of grasses appears to have no response behaviour (*sensu* Cahill & McNickle 2011) and the added N could have been distributed among different sinks during the months before the harvest.

The lack of response of total root biomass to N addition may also be explained by a rapid translocation of absorbed N to above-ground biomass. Additionally, as more than one species colonized N+ traps, nitrogen may have been absorbed by different species reducing the effect in individual species. This could indicate that root biomass is limited by soil volume and species are able to use the increase in nitrogen without increasing root biomass. A recent study explored the hypothesis that in ecosystems limited by soil nutrients, some plant species show a restricted horizontal distribution of their roots (de Parseval *et al.* 2016). They proposed that this particular foraging strategy results from trade-offs between root proliferation (which increases the accessibility of nutrients for the plants) and the local control of nutrient cycling within the soil that the plant occupies. McNickle *et al.* (2016) suggest that species prioritize information about neighbours over nutrients in choosing root growth strategies. This is in agreement with Cahill *et al.* (2010) that plants integrate information about resource and neighbour-based cues in the environment. As we worked under field-realistic conditions, we did not have the no-neighbours condition. We propose that our results were also a consequence of the fact that the guild of perennial grasses includes species with different responses to grazing, the other driver of species coexistence in rangelands (Oñatibia & Aguiar 2016). Pucheta *et al.* (2004) proposed that grazing could enhance root turnover, fine root productivity and belowground net primary production.

There are several influential papers that measure scale-precision correlation with time close or similar to 6 months, but under pot conditions which preclude longer time of experimentation due to soil volume restrictions (Einsmann *et al.* 1999; Wijesinghe *et al.* 2001; Rajaniemi & Reynolds 2004; among others). Our field experiment with traps allowed us to consider the correlation after a growing season, when roots are probably active, and after a longer period allowing the coexistence of active and dead roots, as it happens in natural conditions. Adding the specific decomposition knowledge to the specific root proliferation allows us to make stronger inferences about how the belowground space is occupied and shared by several species. In addition, the presence of slow-decomposing root species has a confounding effect (active and dead roots) in active root biomass. The opposite would happen for species with fast decomposition rates, which are probably active when present.

It has been recommended that future studies on root foraging tackle specifically root plasticity (Kembel *et al.* 2008). Kembel and Cahill (2005) defined plasticity as the ability of plants of a particular species to modify their root morphology in response to soil nutrient heterogeneity. Root plasticity probably plays a major role in this Patagonian plant guild, as proliferation of new roots which appears to be determined by the response of species to different above-ground influences. Wijesinghe *et al.* (2001) proposed that distance between nutrient- rich patches and plant location is a crucial issue to root proliferation studies. But, Bliss *et al.* (2002) suggested that heterogeneity effects on competition are context specific. Therefore, we propose that root proliferation in this steppe is the result of the interaction between individual density in the community (Oñatibia 2013) and specific root growth rates (Leva *et al.* 2009). For example, the species with the highest root growth rates and low individual density (*B. pictus*) was also the most precise species and showed plasticity in response to different above-ground influences. The proliferation of its new roots was completely different under its

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above-ground portion (Reyes & Aguiar 2017) or under bare soil (this study). However, the species with high growth rates but the highest individual density (*P. ligularis*) showed the highest scale and no-plasticity, its proliferation was similar under both conditions and also in control and N+ traps. If individual density of species is defined by grazing and growth rate traits, we propose that plasticity in proliferation of new roots will be defined by the interaction between both types of traits.

Testing the scale-precision hypothesis (Campbell *et al.* 1991) under field-realistic conditions in the Patagonia steppe, a model system of arid rangelands, was our main goal since most of the published studies were under controlled conditions for a short time period. Kembel *et al.* (2008) meta-analysis indicates that the mean duration of studies was 84 days (range 14–180 days). Our root proliferation study lasted 550 days. Nevertheless, we did not find any significant relationship between scale and precision (quantitative analysis), or with decomposition to support the scale-precision hypothesis. However, the qualitative analysis (absolute frequency of species in the root traps) supports the hypothesis. Root foraging strategies were proposed assuming resource competition as the main driver of community functioning. And this hypothesis was mostly tested in pot experiments. Rangelands represent a challenge to this view because grazing, as well as resource competition, are both key drivers. In other words, species coexistence, in this system, could be explained by these two drivers and there is not necessarily a convergence in plant traits that maximize fitness, as Grime (2007) proposed. Our field study supports the notion that realistic analysis will also require the inclusion of wild or domestic grazing as key drivers of plant traits. While such research could be logistically challenging, it also provides an exciting opportunity. For example, repeating our experiment under grazing conditions will determine changes in the guild of species present in the community increasing the abundance of non-grazed species and decreasing abundance of grazed species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Correction of root biomass by root decomposition.

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