Original Research

Paddock Size Mediates the Heterogeneity of Grazing Impacts on Vegetation ☆

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A B S T R A C T

Domestic herbivores' effect on vegetation is spatially heterogeneous, being one of the major causes of forage resources degradation. It has been proposed that paddock size controls grazing impact's heterogeneity because as size decreases, herbivores' utilization is spatially more even. However, this has not been critically evaluated in commercial-scale paddocks isolating paddock size effects from other factors influencing the interaction between herbivores and vegetation. Here we assessed how paddock size mediates the heterogeneity of continuous sheep grazing effects on vegetation, at constant stocking rate in Patagonian steppes. We selected three small (ca. 110 ha) and three large (ca. 1 100 ha) paddocks dominated by the same plant community. All paddocks contained a single watering point and presented similar shape. Total and specific plant cover, vegetation patchiness, population size distribution of dominant grass species, plant morphology, and sheep feces density were estimated at increasing distances from watering points. Relationships between vegetation variables and distance from the watering point were in most cases asymptotic exponential, although responses generally differed between small and large paddocks. In small paddocks, vegetation variables mostly reached a plateau at a short distance from the watering point (~200 m). Instead, in large paddocks, the changes in vegetation variables were larger and more gradual, and reached a plateau at much greater distances (~2 000 m). Vegetation heterogeneity throughout the paddock was lower in small than large paddocks. Our findings suggest that paddock size mediates the spatial pattern of grazing effects on vegetation. Reducing paddock size decreases grazing impacts spatial heterogeneity, which makes plant-animal interactions more predictable and might improve forage utilization efficiency.

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Introduction

Herbivores' selectivity controls forage resources use heterogeneity (Prache et al., 1998). Thus, animal distribution is heterogeneous at different spatial scales, being grazing pressure heavy in some localized areas while other areas receive light or no utilization (Senft et al., 1987; Coughenour, 1991; Bailey et al., 1996; Bailey, 2004; Teague et al., 2004). In arid and semiarid rangeland ecosystems, this heterogeneous impact of selective grazing is exacerbated and has been identified as one of the major causes of forage resources degradation (Senft et al., 1985; Schlesinger et al., 1990; Golluscio et al., 2005; Teague et al., 2013; Norton et al., 2013). However, research experiments often assume a homogeneous forage distribution and utilization, ignoring uneven grazing impacts (Norton, 1998; Laca, 2009).

The spatial distribution of herbivores is mainly controlled by distance to water, spatial variation in vegetation structure (i.e., vegetation types, cover, floristic composition, forage quantity and quality), topography, and animal interactions (Coughenour, 1991; Bailey et al., 1996; Adler et al., 2001; Provenza, 2003; Briske et al., 2008). Many management actions focus on reducing the heterogeneous grazing impacts by promoting uniform animal distribution. The most common are manipulations of livestock type, stocking rate, grazing and rest periods, paddock structure (i.e., size and shape), herding and supply sites of water and supplements (Briske and Heitschmidt, 1991; Adler et al., 2001; Adler and Hall, 2005; Laca, 2009; Bailey and Brown, 2011). However, the impacts of some of these actions, such as the nonlinear effects of herd size or paddock size (potential grazing area), are still misunderstood (Laca, 2009). Paddock size is one of the leading factors that must be empirically evaluated because of its ecological importance (Laca, 2009) and economic cost of paddock size changes (Aguiar and Román, 2007). Decreasing paddock size has been proposed to counteract the undesired effects of uneven grazing (Bailey and Brown, 2011). In

smaller paddocks, animals would be evenly distributed and grazing impacts would be more homogeneous (Hart et al., 1993; Norton, 1998; Barnes et al., 2008; Laca, 2009; Brown and Kothmann, 2009). Nonetheless, this assertion has not been critically studied by isolating paddock size effects from other factors influencing the interaction between herbivores and vegetation in commercial scale paddocks.

Few studies have evaluated how paddock size affects vegetation utilization (Norton et al., 2013), although they have generally studied different grazing systems (Norton, 1998; Barnes et al., 2008). This approach makes it difficult to separate paddock size effect from impacts associated with grazing pressure, rest periods, or animal behavior under different systems. One study separately evaluated different paddock sizes (24 vs. 207 ha) and showed that spatial utilization was more homogeneous in the small paddock than the large one (Hart et al., 1993). However, this work did not have replicates for paddock size treatments. Even the large paddock was smaller than those commonly found on farms (Barnes et al., 2008) and presented an unusual shape. Single-paddock treatment reduces the robustness of inferences. In another study, increasing paddock size reduced the proportion of the area that animals effectively explored (Hunt et al., 2007). Nevertheless, spatial grazing impact on vegetation is not necessarily linear with explored areas, due to the existence of other hierarchical controls of herbivore diet selection (Laca, 2009).

In most rangeland ecosystems, water is one of the major limiting factors for animals. Thus, watering points exert significant control over spatial distribution and impacts of grazing (Andrew, 1988). In general, domestic grazing causes great effects on vegetation and soil in areas close to watering points, which are defined as piospheres (Andrew, 1988). Numerous studies have evaluated domestic grazing impacts around piospheres and different vegetation response patterns as functions of increasing distance from watering points have been described (e.g., Bisigato and Bertiller, 1997; James et al., 1999; Heshmatti et al., 2002; Adler and Hall, 2005; Todd, 2006; Fensham et al., 2010). It has been stressed that these different response patterns may be mediated by the size of management units (Heshmatti et al., 2002), highlighting the importance of empirically studying the isolated effects of paddock size on piospheres (Heshmatti et al., 2002; Barnes et al., 2008).

The objective of this study was to evaluate how paddock size mediates the heterogeneity of domestic livestock effects on vegetation at constant stocking rate and grazing periods. Specifically, we estimated vegetation heterogeneity within paddocks of different sizes, among areas located at increasing distance from watering points. Vegetation response variables were total plant cover, vegetation patchiness, species abundance, and population plant-size distribution of dominant grass species (forage and nonforage species) and their plant morphology. The study was carried out in continuously grazed commercial paddocks, containing a single watering point. The hypothesis states that as the paddock size increases, forage utilization and grazing impact on vegetation within a paddock are more heterogeneous. This occurs because the highly selected patches near watering points receive higher grazing pressure in large paddocks, resulting from a greater animal concentration (as they tend to move in herds). On the contrary, distant patches are avoided because of the difficulty for herbivores to explore the entire area. Contrastingly, in smaller paddocks, herbivores explore the whole area and, therefore, use the available forage more evenly. In rangelands where intensive grazing promotes species replacement and nonpreferred species dominance, it is predicted that the boundary of heavy use around watering points (piosphere size) increases as the abundance of preferred plants decreases. This effect would be higher in large paddocks, where local grazing pressure in the piosphere is more significant than in small paddocks. It is also predicted that population size distribution of dominant grass species and vegetation patch structure are more uniform throughout the whole paddock (i.e., as distance to watering points increases) in small management units than larger ones.

Materials and Methods

Study Site Description

The study site corresponds to a grass-shrub steppe located in South Central Patagonia, Chubut province, Argentina. Studied paddocks were inside the Río Mayo INTA Experimental Station (lat 45°24'S, long 70°18"W, see Appendix A). This area has been grazed by sheep for > 100 yr. Grazing management is extensive, in continuously grazed paddocks (Golluscio et al., 1998). Mean monthly temperature varies between 2°C in July and 14°C in January. Average annual precipitation is 154 ± 44 mm, and most rainfall occurs between May and September (Jobbágy et al., 1995). Soils are Calciorthids and present a coarse texture (sandy), with a high content of pebbles of varying diameter (Paruelo et al., 1988). Few dominant perennial grass and shrub species contribute to 96% of total biomass (Oñatibia and Aguiar, 2016), and mean aboveground net primary production is 56 g m^{-2} yr^{-1}, half of which corresponds to grasses and half to shrubs (Jobbágy and Sala, 2000). The dominant grass species are *Pappostipa speciosa* Trin. et Rupr., *Pappostipa humilis* Cav., *Pappostipa major* Speg., *Poa ligularis* Nees ap. Steud, and *Bromus pictus* Hook. The dominant shrub species are *Mulinum spinosum* Cav. Pers, *Adesmia volckmannii* Philippi, and *Senecio filaginoides* De Candolle. Among grasses, *Poa ligularis* and *Bromus pictus* are the most preferred species for sheep. *Pappostipa speciosa* is a species of intermediate preference, and *Pappostipa humilis* and *Pappostipa major* are unpreferred species (Bonvissuto et al., 1983; Oñatibia and Aguiar, 2016).

Data Collection

We selected three small paddocks (between 100 and 120 ha) and three large paddocks (between 1 000 and 1 200 ha) ($n = 3$), located in a 150 km^2 homogeneous plateau dominated by the same grass-shrub community (see Appendix A). All paddocks presented the same soil type and topographic position (Cipriotti and Aguiar, 2005; Golluscio et al., 2009; Oñatibia and Aguiar, 2016). Paddock fences were installed more than 3 decades ago. Thus, we assumed that the community has been receiving the footprint of domestic herbivores grazing inside them. All paddocks have been continuously (yr-round) grazed by sheep at the same moderate stocking rate (~0.2 sheep ha^{-1} yr^{-1}) for several decades (Oñatibia and Aguiar, 2016). The shape of evaluated paddocks was similar to an aureus rectangle. In all cases, paddocks had a single watering point (see paddocks' shape and configuration in Appendix A). Inside each paddock, 50 m — long transects were outlined at 50, 100, 200, 500, and 1 000 m distance from the watering point in small paddocks and 50, 100, 200, 500, 1 000, and 2 000 m in large ones (Fig. 1). The different distances to watering points were selected to detect piosphere patterns (Andrew, 1988).

Along each transect, we estimated total perennial plant cover (foliar), size and number of vegetation patches, interpatch distance, and specific cover of dominant species. These variables reflect medium- and long-term use heterogeneity impacts, and they are useful to study desertification processes in arid and semiarid ecosystems (Rietkerk et al., 2004; Kéfi et al., 2007; Maestre and Escudero, 2009; Oñatibia et al., 2018). We recorded perennial plant cover (the identity of the species or litter) or bare soil every 0.1 m, in 500 consecutive segments. A vegetation patch was defined as every discrete section of at least 0.1 m along each transect covered with perennial vegetation and/or standing dead biomass, separated by at least 0.1 m of bare soil. Along each transect, we also located a plot of 6 m^2 (30 × 0.2 m), where individual plant morphology and the population size distribution of dominant grass species were estimated. We measured specific density, the height of the top green leaves, and the basal diameter (average between the longest and its perpendicular) of each individual, while we visually estimated the standing dead biomass proportion (with an interval scale of 5%). Population size distribution of each species was characterized by

the cumulative relative frequency of plant height. Cumulative curves considered all individuals from the three paddocks of each size. Population structure and individual plant morphology of dominant grasses are key response variables because they determine effective forage availability (Oñatibia, 2013, 2017). As a complementary variable, we counted all sheep fecal pellets into each 6 m² plot as an index of local grazing pressure (Lange and Willcocks, 1978).

Data Analysis

Due to the distribution of values, we performed nonlinear regression analyses between each response variable and distance from watering points. Parameters of different nonlinear models (exponential, potential, and logistic) were estimated. We selected models presenting the best fit (nonlinear least squares) for each relationship, following the minimal adequate model criterion (see Crawley, 2012). Models for small paddocks and large paddocks were separately adjusted and compared with each other through an F test to evaluate if the nonlinear relation between variables and distance from watering points was affected by paddock size. In large paddocks, litter presented a linear response to increasing distance from watering points, which was analyzed through linear regression.

We followed Barnes et al. (2008) and used the mean absolute deviation (metric variance) as the heterogeneity index for each response variable, using the values of different distances from watering points in relation to the average of the paddock. Mean deviations were compared between small and large paddocks through the Levene test.

Finally, cumulative frequency distribution curves of both vegetation patch size and individual plant size (height) of dominant grass species were constructed. We compared them in pairs between small and large paddocks and between each distance from watering point combination, using Kolmogorov-Smirnov tests for nonparametric distributions. Data from the three paddocks of each size were combined for these analyses after corroborating that there were no significant differences in any variable within paddocks with the same size category (Kolmogorov-Smirnov tests). Analyses were conducted using R software (version 3.2.4, functions lm, nls and ks.test).

Results

Plant Cover and Vegetation Patches

Relationships between most vegetation variables and the distance from watering points were asymptotic exponential (increase or decrease until reaching a plateau), and they generally differed with paddock size. Total cover increased to a plateau as the distance from watering points increased in both paddock sizes. However, exponential association models that best explained patterns in each case sharply differed from each other ($F = 13.5$, $P < 0.001$). In small paddocks, the plateau was found at a much shorter distance from watering points (ca. 200 m) than in large paddocks (Fig. 2a). The lowest plant cover (around 45%) was measured close to watering points in large paddocks. In these paddocks, cover gradually increased and reached the plateau at distances > 2 000 m (see Fig. 2a). Heterogeneity index for total plant cover throughout the paddock exhibited marginal differences ($P = 0.08$, Levene test) between small and large paddocks (Table 1).

Responses in the number of patches presented patterns similar to total cover (Fig. 2b). Nonlinear models differed between small and large paddocks ($F = 5.82$; $P = 0.003$). Average patch size did not significantly differ in function of distance from watering points in any paddock size (Fig. 2c). The average distance between patches exponentially decreased as the distance from watering points increased, independently of paddock size (Fig. 2d). Nonlinear models did not differ between small and large paddocks ($F = 2.07$; $P = 0.13$).

Patch size frequency distribution did not significantly change between small and large paddocks when comparing accumulated frequency at each distance from watering points ($P > 0.05$ in all cases). However, when comparing patch size distribution including measured patches at all different distances from watering points, large paddocks presented higher frequencies of small and intermediate size patches than small paddocks ($D = 0.123$, $P < 0.001$) (Fig. 3).

Dominant species cover depended on paddock size, distance from watering points, life form, and species preference by herbivores (see Appendix B). Preferred grass species cover (*P. ligularis* and *P. speciosa*) increased nonlinearly until reaching a plateau as the distance from watering points increased. However, only *P. ligularis* exhibited significant differences between small and large paddocks ($F =$
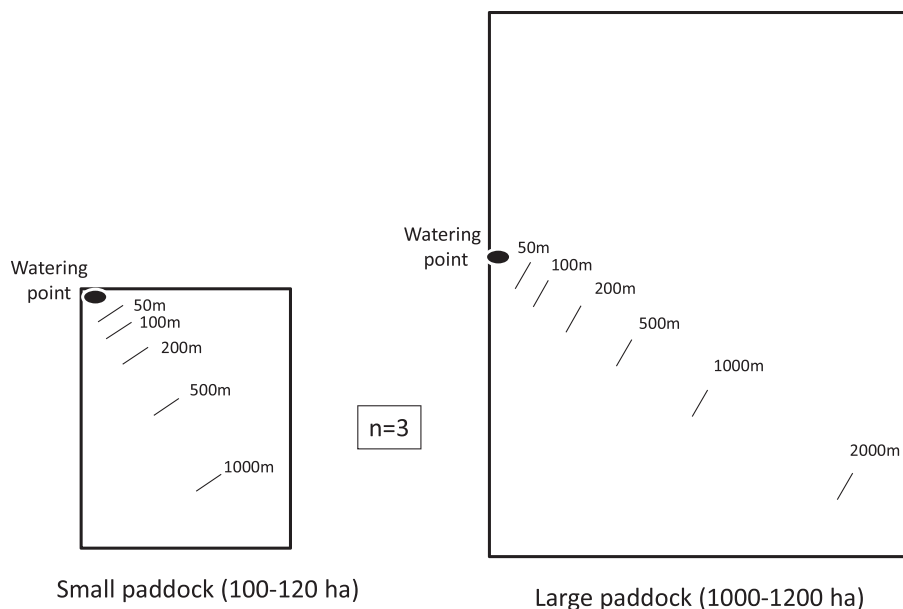

Figure 1. Sample design and location of transects at increasing distance from watering points in small and large paddocks. The figure represents an example of a small and a large paddock, and it is out of scale because it was made just to provide a better understanding of the experiment design. See the map in Appendix A for paddocks' geographic distribution, shape, and configuration.
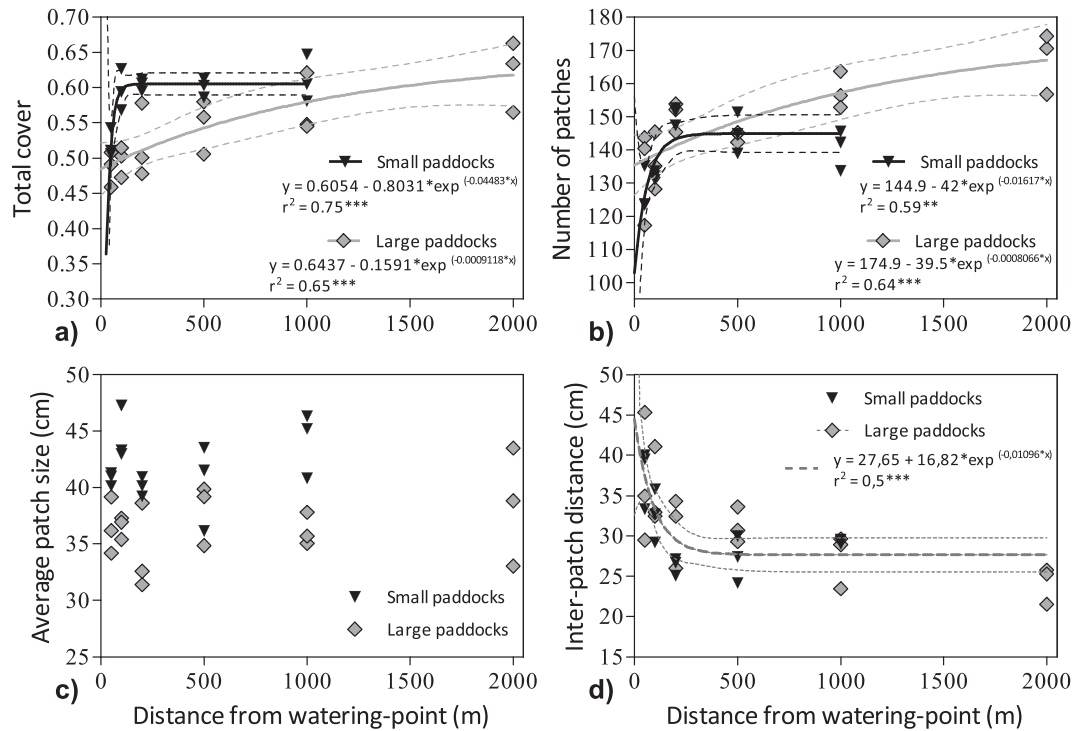
Figure 2. a, Total plant cover, **b,** number of patches along 100 m, **c,** average patch size, and **d,** average interpatch distance as function of distance from watering points in small paddocks *(black triangles)* and large paddocks *(gray rhombus)*. In the response variables of panels **a** and **b**, equations, determination coefficients (r^2), and lines (with confidence intervals) representing the selected models (best fit, nonlinear least squares) are individually shown for each paddock size because they presented significant patterns that differed between each other. In panel **c** there were no significant patterns. In panel **d**, the equation and line of the model that best fits the entire data set *(dashed gray line)* are presented, because small and large paddock models did not differ from each other. *Asterisks* next to determination coefficients (r^2) indicate P values of significant nonlinear model: (*) between 0.05 and 0.01; (**) between 0.01 and 0.001; (***) < 0.001.

12.95; $P < 0.001$), while *P. speciosa* just showed a significant pattern in large paddocks ($P > 0.05$) (see Appendix B, a, b). Cover heterogeneity index for both species did not differ between small and large paddocks ($P > 0.05$; see Table 1). Nonpreferred grass species cover (*P. humilis* and *P. major*) exponentially decreased with the distance from watering points, although each species presented idiosyncratic decline patterns and effect of paddock size. Cover of *P. humilis* showed minimal changes inside small paddocks, while it was markedly affected in large paddocks (see Appendix B, c). Exponential models that best fit in each paddock size sharply differed from each other ($F = 40.45$; $P < 0.001$). Cover of *P. major* similarly decreased in both small and large paddocks (see Appendix B, d), and nonlinear models did not differ from each other ($F = 1.74$; $P = 0.18$). Both nonpreferred grass species presented greater heterogeneity index in large than small paddocks ($P < 0.05$ in both cases; see Table 1).

Dominant shrub species that are usually browsed (preferred) by sheep (*A. volckmannii* and *M. spinosum*) did not significantly change their cover along watering point gradients in any type of studied paddocks (see Appendix B, e, f). Their heterogeneity index did not vary between small and large paddocks ($P > 0.05$ in both cases; see Table 1). Cover of the nonpreferred shrub species *(S. filaginoides)* decreased nonlinearly as the distance from watering points increased, but neither this declining pattern nor the heterogeneity index differed between paddock sizes ($F = 1.88$; $P = 0.16$) (see Appendix B, g; see Table 1). Litter cover presented contrasting patterns in different paddock sizes. In small ones, litter sharply increased in the nearest distance from the watering point and reached a plateau before 200 m. Contrarily, in large paddocks, litter cover linearly increased, reaching higher values than those in small paddocks in areas most remote from water (see Appendix B, h). Litter cover heterogeneity index was higher in large paddocks ($P = 0.032$; see Table 1).

Population Structure and Individual Plant Morphology of Dominant Grass Species

Patterns of total grass density as a function of distance from watering points were different when comparing small with large paddocks ($F = 6.5$, $P = 0.002$), and response patterns were similar to total plant cover (Fig. 4). Total density heterogeneity index was higher in large paddocks ($P = 0.05$; see Table 1). Specific density responses to increasing distance from watering points were also similar to patterns shown by the specific cover (Fig. 5). Nonlinear models that best explained each grass species response significantly differed between small and large paddocks for *P. ligularis* ($F = 17.67$; $P < 0.001$; see Fig. 5a), *P. speciosa* ($F = 5.1$; $P = 0.006$; see Fig. 5b), and *P. humilis* ($F = 19.85$; $P < 0.001$; see Fig. 5c), while they did not differ for *P. major* ($P > 0.05$; see Fig. 5d). The heterogeneity index for specific density was higher in large paddocks than in small paddocks for *P. ligularis* ($P < 0.001$) and *P. humilis* ($P < 0.001$) species, whereas it did not differ depending on the paddock size for *P. speciosa* ($P = 0.82$) and *P. major* ($P = 0.63$) species (see Table 1).

In general, relationships between individual plant size of dominant grasses and distance from watering points were similar in small and large paddocks, except for *P. ligularis* (preferred species). This species presented different relationships between small and large paddocks in plant height and standing dead proportion ($F = 3.31$; $P = 0.04$ and $F = 3.57$; $P = 0.03$, respectively), with patterns more pronounced in large paddocks (Fig. 6a and b). Population size structure of *P. ligularis* suffered lower changes along the watering point gradient in small paddocks. Inside these paddocks, differences only between size distribution curves at 50 m and the reference distance (500 m) were found. The area closest to watering points presented a higher frequency of small and intermediate size individuals (see Appendix C, a). In contrast, although in large paddocks it was not possible to make statistical comparisons at 50

Table 1
Effect of paddock size on spatial heterogeneity of studied variables: total vegetation cover, specific cover, litter cover, total and specific density of grasses (individuals m^{-2}), and sheep feces density (pellets.m^{-2}). Heterogeneity of each variable was compared between small and large paddocks through Levene test. Significant differences are highlighted in bold type.

Variable	Species	Paddock size	Mean[1]	Heterogeneity[2]	Levene P Value
Total cover		Small	0.59	**0.03**	0.08
		Large	0.54	**0.05**	
Specific cover	*Poa ligularis*	Small	0.13	0.05	0.16
		Large	0.07	0.06	
	Pappostipa speciosa	Small	0.12	0.05	0.22
		Large	0.08	0.03	
	Pappostipa humilis	Small	0.04	**0.01**	**< 0.001**
		Large	0.1	**0.06**	
	Pappostipa major	Small	0.06	**0.03**	**0.029**
		Large	0.08	**0.05**	
	Adesmia volckmannii	Small	0.03	0.01	0.15
		Large	0.03	0.01	
	Mulinum spinosum	Small	0.09	0.02	0.75
		Large	0.08	0.02	
	Senecio filaginoides	Small	0.04	0.04	0.22
		Large	0.03	0.03	
	Litter	Small	0.08	**0.02**	**0.032**
		Large	0.08	**0.03**	
Grass density		Small	13.06	**1.2**	**0.05**
		Large	11.86	**2.15**	
Density	*Poa ligularis*	Small	4.82	**1.19**	**< 0.001**
		Large	3.09	**2.69**	
	Pappostipa speciosa	Small	4.46	1.43	0.82
		Large	2.92	1.52	
	Pappostipa humilis	Small	1.8	**0.63**	**< 0.001**
		Large	3.68	**1.77**	
	Pappostipa major	Small	1.98	0.78	0.63
		Large	2.18	0.88	
	Feces	Small	20.59	**6.84**	**0.014**
		Large	26.18	**17.98**	

[1] Mean is the average value of each variable considering all distances from watering point in each paddock size.
[2] Heterogeneity was estimated through the absolute deviation of the mean (metric variance) of each variable along the different distances from watering points in each paddock size.

and 100 m because there were few individuals (< 10), significant differences were found between 200 m and 500 m and 500 m and 2 000 m size distribution curves. At 200 m from the watering point, the
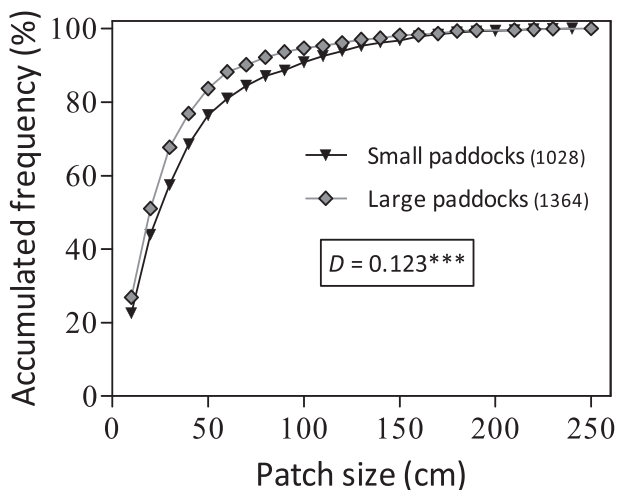

Figure 3. Accumulated frequency (%) of patch size (patch size distribution) along different paddock sizes (small: *black symbols* and large: *gray symbols*). The table indicates *D* statistics value and *P* value resulting from Kolmogorov-Smirnov test between the distribution curves: (***) < 0.001. Numbers in brackets show the number of patches represented in each distribution curve.
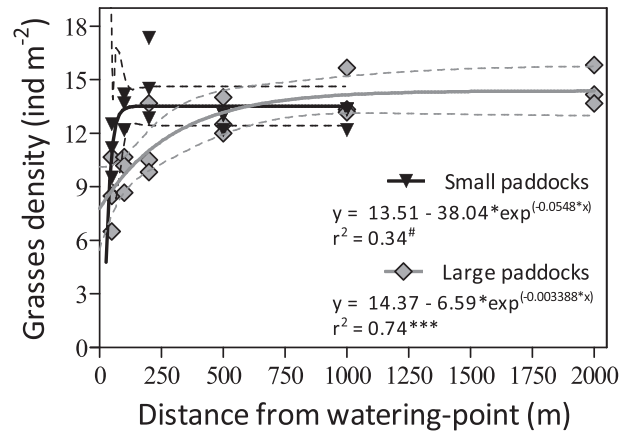

Figure 4. Total dominant grass species density (individuals.m^{-2}) as function of distance from watering points in small paddocks *(black triangles)* and large paddocks *(gray rhombus)*. Equations, determination coefficients (r^2), and lines (with confidence intervals: *dashed lines*) representing the selected models (best fit, nonlinear least squares) are shown for each paddock size (small paddocks: *black line* and large paddocks: *gray line*). Symbols next to determination coefficients (r^2) indicate *P* values of each nonlinear model: (#) between 0.1 and 0.05; (*) between 0.05 and 0.01; (**) between 0.01 and 0.001; (***) < 0.001.

frequency of small and intermediate size individuals increased in comparison with 500 m distribution, while at 2 000 m, the frequency of small plants decreased (see Appendix C, b).

Sheep feces density exponentially decreased with the distance from watering points in both paddock sizes, although the magnitude of these changes depended on paddock size, in agreement with the main vegetation patterns found in this study. In small paddocks, the number of dung pellets found in remote areas from watering points was around one-third of those in the closest areas. In large paddocks, the decline pattern was more pronounced and the number of dung pellets was 10× higher in areas closest to watering points than in remote ones (Fig. 7). Nonlinear models that best explained these patterns were significantly different between small and large paddocks ($F = 6.34$; $P = 0.002$). In turn, feces density heterogeneity index was significantly higher in large paddocks ($P = 0.014$; see Table 1).

Discussion

Our results showed that paddock size controls the spatial pattern of long-term continuous grazing effects on vegetation, measured through the changes produced by sheep grazing pressure in areas at different distances from watering points. Nonlinear and spatially uneven effects were found in all paddocks. However, the magnitude of this heterogeneous impact was higher in large paddocks, where plant cover and structure of dominant grass species presented greater variation along watering point gradients than in small paddocks. These differential impacts corresponded to sheep feces density patterns, which reflect grazing pressure and spatial animal distribution. Our findings support the hypothesis that domestic herbivores tend to be more evenly distributed in small than large paddocks, making their spatial impact on vegetation more homogeneous. As a general effect, the carrying capacity in smaller paddocks would increase because the availability of forage is not limited by the unequal distribution of herbivores, while preferred areas are less degraded (Norton, 1998; Teague et al., 2013).

Plant community and vegetation mosaic responses along watering point gradients were consistent with previous studies using discrete treatments to estimate grazing effects in the same Patagonian rangeland (Cipriotti and Aguiar, 2005; Oñatibia et al., 2015; Oñatibia and Aguiar, 2016). In both kinds of approaches, grazing significantly modified grass species composition and abundance (preferred species decreased
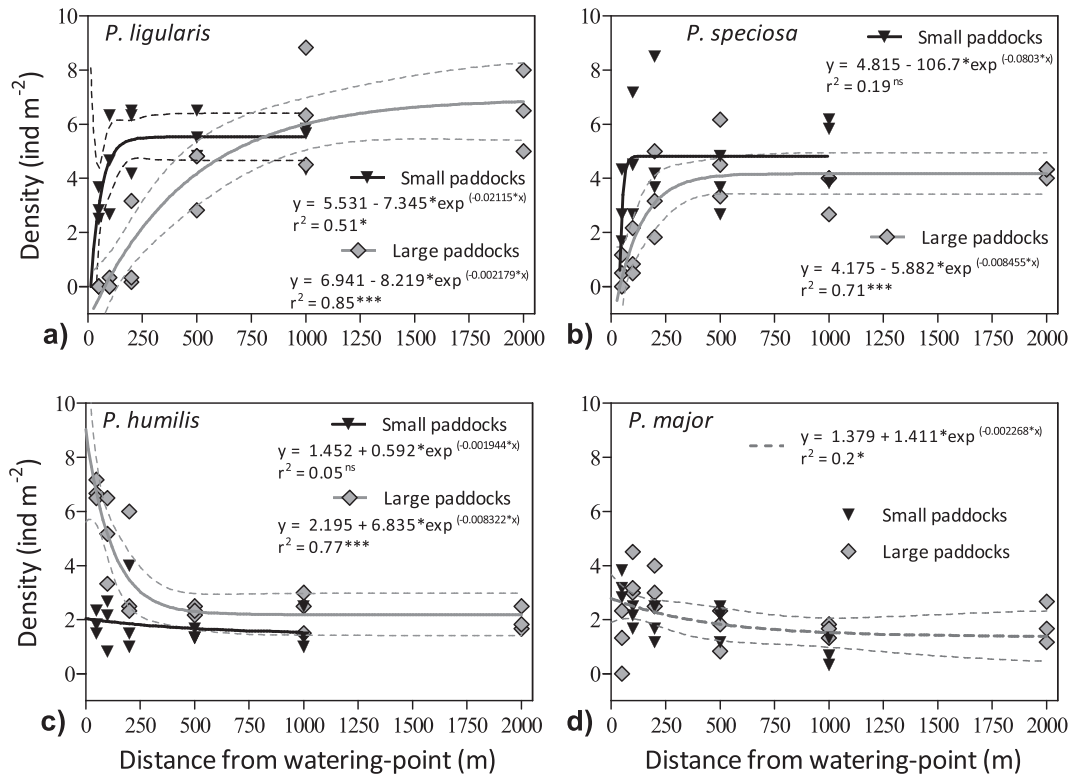
Figure 5. Specific density (individuals.m^{-2}) of dominant grass species **a,** *Poa ligularis,* **b,** *Pappostipa speciosa,* **c,** *Pappostipa humilis,* **d,** *Pappostipa major* as function of distance from watering points in small paddocks *(black triangles)* and large paddocks *(gray rhombus)*. In species in which models significantly differed between small and large paddocks (panels **a**, **b**, and **c**), equations, determination coefficients (r^2), and lines (with confidence intervals: *dashed lines*) representing the selected models (best fit, nonlinear least squares) are shown for each paddock size (small paddocks: *black line* and large paddocks: *gray line*). In the species in which models of small and large paddocks did not differ from each other (*Pappostipa major,* panel **d**), equation and line of the model that best fits the entire data set *(dashed thick line)* are presented. Symbols next to determination coefficients (r^2) indicate *P* values of each nonlinear model: (ns) > 0.1; (#) between 0.1 and 0.05; (*) between 0.05 and 0.01; (**) between 0.01 and 0.001; (***) < 0.001.

while nonpreferred species increased), although neither shrub species nor vegetation mosaic structure considerably changed (Cipriotti and Aguiar, 2005; Oñatibia et al., 2015; Oñatibia and Aguiar, 2016). In large paddocks, on the one hand, community structure in remote areas from watering points (2 000 m) was similar to that found in long-term exclosures (> 30 yr). On the other hand, areas surrounding watering points (even beyond 200 m distance) presented similar characteristics to pastures grazed at high long-term stocking rates (Cipriotti and Aguiar, 2005; Oñatibia et al., 2015; Oñatibia and Aguiar, 2016). In contrast, throughout small paddocks, dominant community maintained structural characteristics similar to those found in pastures grazed at light/moderate stocking rates (except in a reduced area very close to watering points). Grazing at moderate stocking rate has been proposed as the best land use alternative in these environments, maintaining productivity and forage supply (Oñatibia et al., 2015; Oñatibia and Aguiar, 2016). In addition, this management model is more advisable and presents lower ecological risks than that at high stocking rate, especially under great climatic variability (Holechek et al., 1999; Reece et al., 2001; Easdale and Aguiar, 2012). In this sense, reducing paddock size can promote a more homogeneous moderate use in space, maximizing benefits.

The management of domestic herbivores' spatial distribution has been proposed to increase livestock production sustainability (Norton, 1998; Hunt et al., 2007; Bailey and Brown, 2011). In this Patagonian steppe, we showed that reducing paddock size is an adequate tool to improve sheep distribution and their medium- and long-term effects, decreasing the heterogeneity between the most impacted and the most avoided areas (Fuls, 1992; Norton, 1998; Barnes et al., 2008). Due to low productivity and the cost of fencing, in arid and semiarid

rangelands, most paddocks are large and include landscape-scale heterogeneity (Teague and Dowhower, 2003; Laca, 2009; Bailey and Brown, 2011). This complexity highlights the importance of delimiting homogeneous areas to efficiently achieve a more even grazing impact (Bailey and Rittenhouse, 1989; Bailey, 2005). When subdivision does not consider environmental heterogeneity given by stands of different communities within the landscape or topography, the effects of herbivore habitat selection may be exacerbated (Bailey and Brown, 2011; Ormaechea and Peri, 2015).

In general, the whole suite of vegetation attributes evaluated exhibited nonlinear responses along areas close to watering points as already described (e.g., Graetz and Ludwig, 1978; see a review of D'Odorico et al., 2013). However, the distance from watering points has often been used as a surrogate of grazing intensity (Pickup et al., 1998; Ludwig et al., 1999). This approach ignores that grazing impact can be exponentially more severe near watering points than in the rest of the paddock (Manthey and Peper, 2010) or that there may be a unimodal relationship between the distance from water and herbivores' utilization (Adler and Hall, 2005). In turn, paddock size can modify this type of response. In general, management decisions are applied at ranch scale, using information obtained at finer experimental scales (stands close or far from watering points) through extrapolations. However, most procedures to extrapolate information across scales are linear and do not contemplate the complexity of management units described in the present study (Turner et al., 2001; Peters et al., 2004). Cross-scale linear extrapolation in rangelands assumes, for example, that 10 herbivores in 10 ha behave and interact with pasture in the same way as 1 000 herbivores in 1 000 ha, because the animal stocking rate and grazing system do not change (Laca, 2009). The results of this study
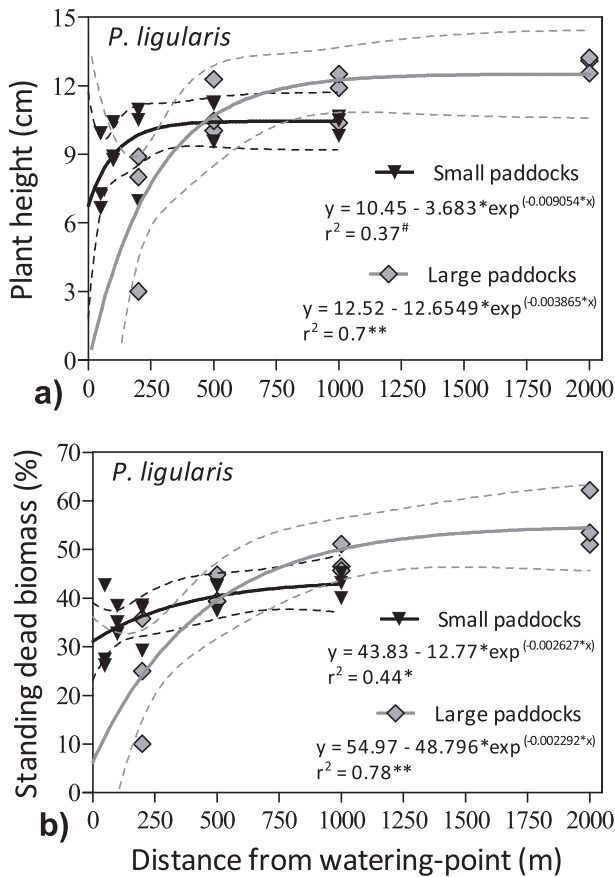
Figure 6. a, Height (cm) and **b,** Plant standing dead biomass (%) of *Poa ligularis* as function of distance from watering points in small paddocks *(black triangles)* and large paddocks *(gray rhombus)*. Equations, determination coefficients (r^2), and lines (with confidence intervals: *dashed lines*) representing the selected models (best fit, nonlinear least squares) for each paddock size are presented (small paddocks: *black line* and large paddocks: *gray line*). Symbols next to determination coefficients (r^2) indicate *P* values of each nonlinear model: (ns) > 0.1; (#) between 0.1 and 0.05; (*) between 0.05 and 0.01; (**) between 0.01 and 0.001; (***) < 0.001.
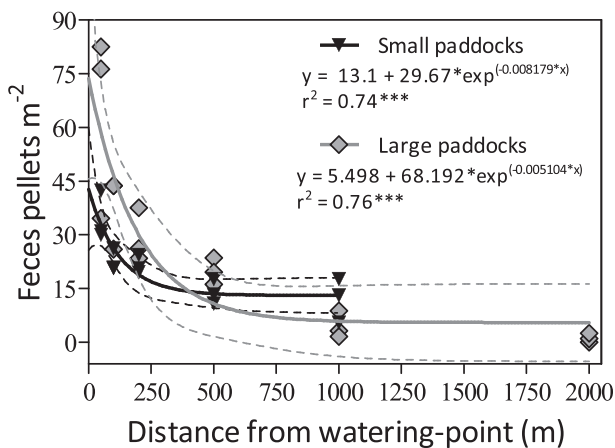

Figure 7. Sheep feces density (pellets m^{-2}) as function of distance from watering points in small paddocks *(black triangles)* and large paddocks *(gray rhombus)*. Equations, determination coefficients (r^2), and lines (with confidence intervals: *dashed lines*) representing the selected models (best fit, nonlinear least squares) for each paddock size are shown (small paddocks: *black line* and large paddocks: *gray line*). Symbols next to determination coefficients (r^2) indicate *P* values of each nonlinear model: (***) < 0.001.

exemplify that cross-scale linearity can present severe limitations for understanding plant-animal interactions, highlighting the need to develop tools that promote incorporating heterogeneity and nonlinear scale changes in ecological interactions (Laca, 2009). Besides, it should be mentioned that the nonlinear sheep effect measured in this study may change depending on the herbivore species. Herbivores perceive and impact on resource heterogeneity at scales relative to their body sizes (Laca et al., 2010). Thus, impact heterogeneity of larger herbivores (e.g., cattle) might differ from that found in the present study.

Many studies have proposed that increasing animal density (for short time periods) and decreasing management units' size (in rotational grazing systems) promote more uniform herbivore use and effect on forage under rotational grazing systems (see Teague et al., 2013). However, in most cases, the increase in animal density co-occurs with the decrease in paddock size (or the reduction of the maximum distance from watering points). This covariation generates mixed (confounded) effects. Here, we showed that grazing treatment effects should be separated from those that can be generated by the difference in paddock sizes (or experimental units), in order to make robust inferences about different grazing systems (Hart et al., 1993; Barnes et al., 2008). Our study provides evidence supporting the idea that the lack of effect between rotational grazing systems and continuous grazing (found in many studies) may be attributed to the fact that they have been carried out generally in very small paddocks. Under these conditions, the potential to detect changes resulting from a more uniform animal distribution and forage use (lower selectivity) is reduced (Norton, 1998; Barnes et al., 2008; Briske et al., 2008; Teague et al., 2013).

Management Implications

Here we demonstrated that paddock size controls the spatial pattern of sheep impacts on Patagonian steppe vegetation. Thus, we infer that changing paddock size is a useful management tool to manipulate the spatial effect of grazing without changing the grazing regime (animal density or grazing seasonality). Reducing paddock size would decrease the extent of the inaccessible area (increasing forage availability), while it would reduce degradation of preferred areas, promoting a more homogeneous moderate utilization (reducing the undergrazed and overgrazed patches syndrome of vegetation mosaic). This management practice can maximize the benefits of moderate grazing on sheep farms (Oñatibia et al., 2015; Chen et al., 2015; Oñatibia and Aguiar, 2016). As paddock size is reduced, the relationship between the average animal stocking rate and animal performance in interaction with vegetation is more predictable (Laca, 2009), increasing the effectiveness of management tools. Notwithstanding, the economic dimension of this management needs to be considered. In Patagonian steppes, where surface water is not frequent, it is necessary to consider both the costs of fencing and watering point creation. In the territory covered by this vegetation type, there are farms of different sizes. Aguiar and Román (2007) found that only large farms (> 15 000 sheep) can afford the investments necessary to reduce paddock size. Nonetheless, medium and small farms (> 4 000 and 1 000 sheep, respectively) need financial subsidies for the establishment of fences and watering points. Rangelands degradation is a complex problem, and management practices in these ecosystems need a comprehensive analysis. Our study addresses some ecological consequences of paddock size, which should be complemented with socioeconomic analyses in order to address complexity and sustainability.

Acknowledgments

Appendix A. Study site location and paddock configuration
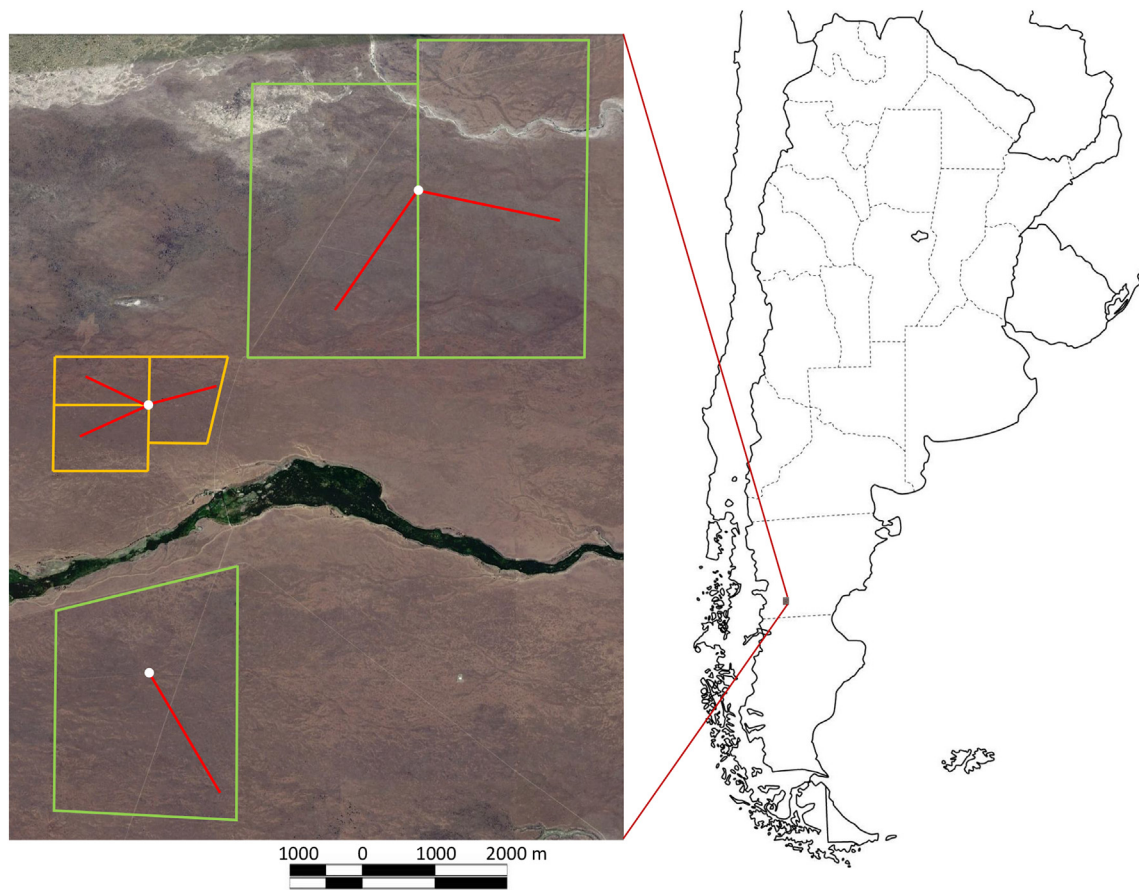
Study site and configuration of the six evaluated paddocks, juxtaposed on a Google Earth image. The three small paddocks are delimited by *yellow lines,* and the three large paddocks are delimited by *green lines. White symbols* represent each watering point, and *red lines* indicate the orientation for which increasing distances from watering points were evaluated in each paddock.

Appendix B. Coverage patterns of dominant species
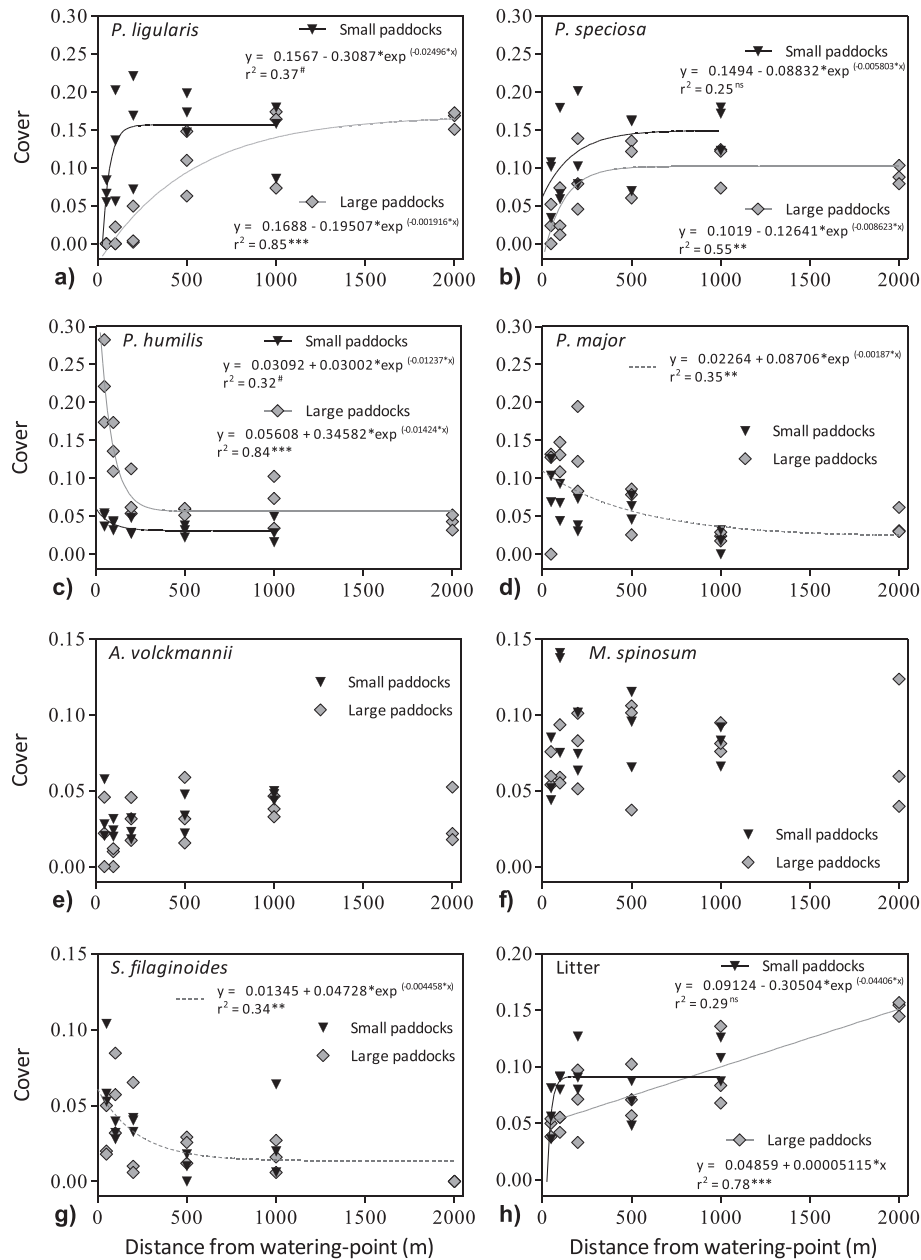
Specific cover of dominant grass species: **a)** *P. ligularis*, **b)** *P. speciosa*, **c)** *P. humilis*, **d)** *P. major*, dominant shrub species: **e)** *A. volckmannii*, **f)** *M. spinosum*, **g)** *S. filaginoides*), and **h)** litter as function of distance from watering point in small paddocks *(black triangles)* and large paddocks *(gray rhombus)*. In species that exhibited significant patterns, equations, determination coefficients (r^2), and lines representing the selected models (best fit, nonlinear least squares) are shown. Equations are presented separately (small paddocks: *black line* and large paddocks: *gray line*) to indicate when models differed between small and large paddocks. When small and large paddock models did not differ, equation and line of the model that best fit the entire data set *(dotted line)* are presented. Equation, line, and coefficient are not shown when patterns were not significant in any paddock size ($P > 0.1$, panels **e** and **f**). Symbols next to determination coefficients (r^2) indicate P values of each nonlinear model: (ns) > 0.1; (#) between 0.1 and 0.05; (*) between 0.05 and 0.01; (**) between 0.01 and 0.001; (***) < 0.001.

Appendix C. Population size distribution of *P. ligularis*
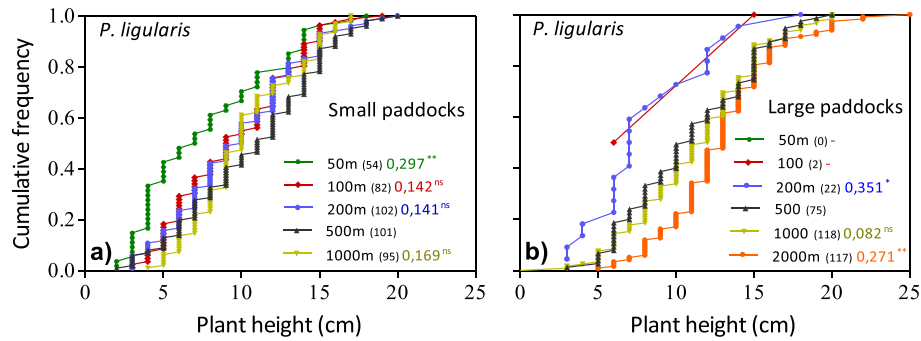
Cumulative relative frequency distribution of plant size of *P. ligularis* at increasing distances from watering points in **a**) small paddocks and **b**) large paddocks. Numbers in color corresponding to each distribution curve represent the *D*-statistics resulting from Kolmogorov-Smirnov tests between the distribution of each different distance (50, 100, 200, 1 000, and 2 000 m) in comparison with the 500-m distribution. This distance was selected as reference distance due to the fact that the distributions at 500 m did not significantly differ between small and large paddocks ($D = 0.066$, $P = 0.9$). *Asterisks* next to *D* statistics indicate *P* values of each comparison: (*) between 0.05 and 0.01; (**) between 0.01 and 0.001; (***) < 0.001; and (ns) not significant. Numbers in brackets show the number of plants represented in each distribution curve.

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