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A novel approach to assess livestock management effects on biodiversity of drylands

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ABSTRACT

In drylands livestock grazing is the main production activity, but overgrazing due to mismanagement is a major cause of biodiversity loss. Continuous grazing around water sources generates a radial gradient of grazing intensity called the piosphere. The ecological sustainability of this system is questionable and alternative management needs to be evaluated. We apply simple indicators of species response to grazing gradients, and we propose a novel methodological approach to compare community response to grazing gradients (double reciprocal analysis). We assessed degradation gradients of biodiversity under different management strategies in semiarid rangelands of the Monte desert (Argentina) by analyzing changes in vegetation, ants and small mammal richness and diversity, and variation due to seasonality. At the species level, we determined the trend in abundance of each species along the gradient, and the potential cross-taxa surrogacy. At the community level, the new methodological consists of assessing the magnitude of biodiversity degradation along different piospheres by comparing the slopes of linear functions obtained by the double reciprocal analysis. We found that most species showed a decreasing trend along the gradient under continuous grazing; while under rotational grazing fewer species showed a decreasing trend, and a neutral trend (no change in the abundance along the gradient of grazing intensity) was the most common. We found that vegetation cannot be used as a surrogacy taxon of animal response. Moreover, weak cross-taxa surrogacy was found only for animal assemblages during the wet season. The double reciprocal analysis allowed for comparison of multi-taxa response under different seasons and management types. By its application, we found that constrains in precipitation interacted with disturbance by increasing the negative effect of grazing on vegetation, but not on animal assemblages. Continuous grazing causes biodiversity loss in all situations. Rotational grazing prevents the occurrence of vegetation degradation and maintains higher levels of animal diversity, acting as an opportunity for biodiversity conservation under current scenarios of land use extensification. Our approach highlights the importance of considering multi-taxa and intrinsic variability in the analysis, and should be of value to managers concerned with biodiversity conservation.

1. Introduction

Drylands occupy around 41% of world's land surface and are home to over two billion people who depend on the natural resources of these systems for their livelihoods (MEA, 2005; Reynolds et al., 2007). One of most common mode of livelihood is livestock production, which supports over 600 million smallholder farmers in the developing world (Thornton, 2010). As a major component of food security, livestock production – which is one of the fastest-growing agricultural subsectors in developing countries (Thornton, 2010) – is also one of the key drivers of land degradation (Pelletier and Tyedmers, 2010). Biodiversity loss associated with land degradation deserves special attention as it is widely recognized that this can decrease ecosystem functioning and services (Hooper et al., 2012; Maestre et al., 2012). Thus, rangeland management strategies that promote biodiversity conservation are urgently needed.

There is a strong dependence between livestock production and water availability. Hence, providing point water sources, e.g., water trough at a borehole, is a widespread practice in drylands. This

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practice generates a piosphere or pattern of grazing-induced changes in biotic and abiotic factors that radiate outward from the concentrator or watering point (Lange, 1969). Piosphere analysis is a quantitative measure of the degree of radial attenuation that exposure to livestock has on ecosystem structure and function (Landsberg et al., 2003; Washington-Allen et al., 2004; Sasaki et al., 2011 Wesuls et al., 2013). A variety of vegetation patterns associated with piospheres in arid and semiarid rangelands have been reported, the nature of which are a function of numerous ecological factors, including competitive relationships, soil types, species life history (Landsberg et al., 2003; Sasaki et al., 2009), as well as stocking rates and other management strategies (Pringle and Landsberg, 2004). With increasing distance from water points, researchers have found increases in species diversity (Sasaki et al., 2009), plant cover (Brooks et al., 2006), plant vertical structure (Macchi and Grau, 2012), abundance of perennial grasses and forbs (Gonnet et al., 2003), palatable grasses and non-tolerant species (Landsberg et al., 2003), but a decrease in the cover of annual forbs (Sasaki et al., 2011). Although such changes in vegetation undoubtedly affect animal communities by modifications of habitat structure and food availability (James et al., 1999), surprisingly few studies have examined non-livestock animal responses. Saba et al. (1995) found that the piosphere effect on mammals depended mainly on changes in vegetation structure, while Hoffmann and James (2011) reported that ants were sensitive to natural variability in soil and vegetation structure (although some grazing effects were also present). Macchi and Grau (2012) found an inverse relationship between the abundance of several bird guilds and distance from the water hole, which they suggest may be due to higher resource availability (water, insects, open space, etc.) nearest the water source, although restricted species showed an opposite response.

In the rangelands of the Central Monte desert (Argentina), there are two main livestock management strategies: (i) the dominant one involves continuous, year-long grazing (hereafter, continuous), and (ii) a rest-rotation approach that invokes the use of recovery periods for paddocks depending upon range conditions (hereafter, rotational). Guevara et al. (2009) describe an experimental adaptive management approach (AMA) that involves 12 months of rest and 4 months of intense grazing and argue that it has economic advantages with regard to cattle production. However, the long-term sustainability of this AMA is under debate due to the potential negative effects that short-term periods of intense grazing pressure has on the semiarid rangelands of the Monte. Similar results have been reported in rangeland assessment in general, where the effectiveness of AMA-type strategies remain equivocal (Teague et al., 2011).

To better understand and predict dryland ecosystem response to livestock disturbance, a variety of piosphere analyses of degradation have been proposed. For example, Landsberg et al. (2003) classified species response curves based on changes in their abundance, Sasaki et al. (2011) posited plant functional groups could be indicators of ecological thresholds, Washington-Allen et al. (2004) developed a GIS-remote sensing technique to help decipher short- from long-term disturbances, and Wesuls et al. (2013) used hierarchical response curves of increasing complexity to analyze changes in plant growth form and life cycles. Another widely used methodology is the identification of surrogate groups (Caro and O'Doherty, 1999), which is based on the assumption of a concordance in the response of species across different taxonomic groups such that some taxa may be correlated with the diversity of other taxa. For example, as vascular plants are a key component of ecosystem structure and function, they may serve as surrogates of non-vascular plants and some animal groups (Kati et al., 2004; Anand et al., 2005). These indicators are useful tools for the analysis of species response but the results are not easy to compare between piospheres, as differences such as higher or lower species richness due to site condition (i.e., different land use history) may cause non-valid statistical comparisons. In this paper we propose and evaluate with a case study a statistical approach which allows for simple but effective comparison of different piospheres with regards of community level richness and diversity. Our analysis involves a simple transformation of the data in order to fit a linear regression and compare the parameters between piospheres (see Section 2).

Thus, the aim of this study was to develop and test a new piosphere analytical approach that allows for valid comparison of different piospheres, and thus useful for rangeland monitoring and management. In our case study we assess how different livestock management strategies (continuous vs. rotational) affect the diversity of vegetation, ants and small mammals in the semiarid rangelands of the temperate Central Monte desert of Argentina. Because of the importance of rainfall, our analysis also considered the role of seasonality in precipitation as a contributing factor that can impact biodiversity. Our piosphere analysis involved the use of two ecological indicators of species level response: (i) trends in species abundance along grazing gradients (e.g., Landsberg et al., 2003) and (ii) the identification of potential surrogate taxa for grazing disturbance assessment. Moreover, we used a novel statistical approach to compare piospheres at the community level. Our analysis is novel in that it takes into account several taxa and the complex dynamics of drylands, where intrinsic factors (seasonality of precipitation) interact with extrinsic factors (grazing intensity as dictated by either continuous or rotational management).

2. Methods

2.1. Study sites

The study was conducted approximately 200 km southeast of Mendoza province, Argentina (33°46′ S, 67°47′ W), between December 2008 and September 2010. The climate is semiarid and markedly seasonal, with cold dry winters and hot wet summers. The mean annual temperature is 12 °C and mean annual precipitation is 342.5 mm (data from the Ñacuñán Reserve weather station; www.cricyt.edu.ar/ladyot/red_iadiza/index.htm). All study sites (of both management strategies) were placed within sand dunes habitat type. The vegetation is an open xerophytic savanna and shrubland where grasses dominate the herbaceous layer.

For continuous management treatments, we selected seven piospheres in different private rangelands ($n = 7$ replicates), where stocking rates varied between 18 and 26 ha/AU, and the areas ranged from 3000 to 6000 ha. Since rotational management is not common, the few sites we found were located in different habitat types and had a wide variety of stocking and resting regimes. Therefore, we selected a single 25-year old experimental rangeland ("El Divisadero") of 5000 ha for our rotation AMA treatment, with a mean stocking rate of 20–25 ha/AU (Guevara et al., 2009). The spatial design involved four paddocks ($n = 4$ replicates) radiating from a central water source. Appendix S1 shows the spatial location of all replicates. In this system, as cattle are rotated each paddock is exposed to four months of intense grazing followed by twelve months of recovery (or rest). The minimum distance of the closest site between piospheres was 300 m, a distance found within the limits of the recommended range to consider sites as different replicates for small mammals (minimum distance suggested between 300 and 500 m; Ojeda *pers. obs.*). Thus, we considered the potential occurrence of spatial autocorrelation for the piosphere analysis selection (see Section 2.3.3 and Appendix S2). It is important to highlight that, due to the wide

variation between AMAs, we decided to focus only on this rotation AMA. This is why the sampling design does not include other rangelands as replicates, but rather replicates of this particular experimental rangeland.

2.2. Sampling sites and data collection

In each piosphere we used a sampling scheme that consisted of a line transect that originated at the water point. Measurements of vegetation, ants and small mammals were taken at 10 sampling sites located at 100, 180, 290, 400, 600, 850, 1200, 1800, 2400 and 3200 m from the water point. At each sampling site we measured vegetation in 10 randomly distributed quadrants of 1 m^2, where the percentage of cover of each vascular plant species was visually estimated. Ants were sampled using four pitfall traps (circle containers of 9 cm diameter) placed in a grid, 40 m apart each and active during three days. Small mammals were sampled using Sherman live traps, placed in a 4×4 grid, 10 m apart each and active during three nights. Captured individuals were marked with a small cut in the ear and released in the same site. Because of the low density of small mammals in the area, we combined data from two consecutive years for the analysis. All sampling was conducted during May–September (the dry season) and November–March (the wet season).

2.3. Data analysis

2.3.1. Species trends in abundance in the piosphere

To quantify the pattern of species abundance associated with each piosphere we used the methodology suggested by Landsberg et al. (2003). Using simple models, we regressed species relative abundance (y) against distance from the water source (x). Landsberg et al. defined five potential trends: increasing if a species increases in abundance closest to the water source, decreasing if its abundance decreases closest to the water source, medial if its abundance is highest at intermediate distances, extremist if it is only present at the closest or furthest distances from the water source, and neutral if it has no discernible pattern along the gradient. We calculated the Akaike Information Criterion (AIC) and the relative weight of each model (ω_i), and selected the model with the best fit based on the lower value of AIC and the higher ω_i between models. Analyses were performed using the MuMin package in R (R Core Team, 2013).

2.3.2. Surrogate groups

To identify potential surrogate groups we performed an ordination of the transect data. We used non-metric multidimensional scaling (NMDS) to determine if the sampling sites at different distances from the water source could be grouped based solely on species richness, diversity and abundance. We selected NMDS because unlike most other methods of ordination, there is no assumed statistical distribution for the data (Legendre and Legendre, 2012).

Also, the composition of each assemblage was estimated using NMDS on the Bray–Curtis distance of the relative abundance of each species in each site. Thus, the NMDS score vectors represent gradients in the composition of the assemblage of vegetation, ants and small mammals across the piosphere, with similar score values representing similar compositions in the assemblages analyzed. Next, we performed Pearson correlations between taxonomic groups to assess the degree of cross-taxa congruence. This cross-taxa congruence analysis was done in order to identify if two different taxa have a similar response to the disturbance, and thus be used as surrogate groups. Correlations were performed for species diversity (based on the Shannon–Weiner index H'; Magurran, 2004) and assemblage composition (1st axis of the NMDS ordination). Analyses were performed using the VEGAN package in R (R Core Team, 2013).

2.3.3. Piosphere analysis

We computed species richness (S) and diversity (H') at each of the 10 sampling sites within each piosphere. For vegetation we used the mean value of the 10 samples; for ants, we pooled capture data of the 4 pitfall traps and computed one value per site (following Hoffmann, 2000), abundance was converted to an ordinal scale: 1 = 1 ant; 2 = 2–5 ants; 3 = 6–20 ants; 4 = 21–50 ants; 5 = 51–100 ants; 6 = 101–1000 ants; 7 = >1000 ants); and for small mammals, the abundance of each species was determined by the minimum number alive method (MNA) for the 4×4 trap grid (Tabeni and Ojeda, 2005).

Following a thorough exploration of the resulting data, we found that most S and H' values along the transects displayed a similar pattern: that is, the minimum value of the response variable was always closest to the water source and was increasingly asymptotic with increasing distance away from the source. Hence, we used a simple rectangular hyperbola function to characterize the piosphere patterns:

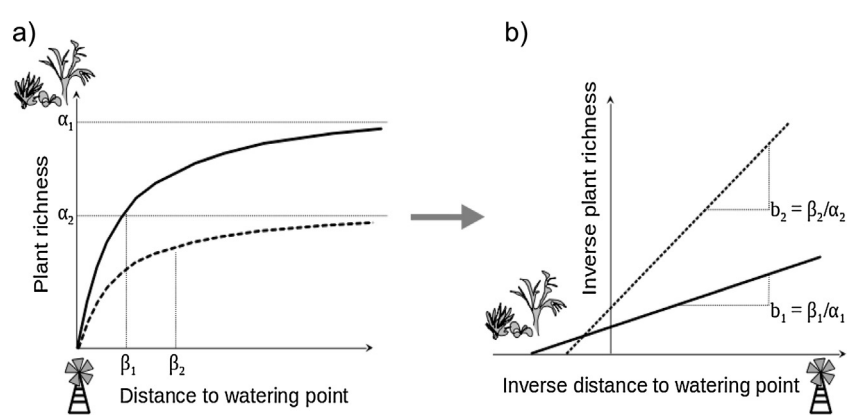

Fig. 1. Schematic representation of the double reciprocal analysis used for the comparison of piospheres. The windmill represents the water source and the plants represent higher species richness. Panel (a) shows the saturation relationship found in almost all the gradients analyzed, where a Michaelis–Menten function was fitted to plant richness of two grazing gradients. The solid line shows one piosphere with lower distance of recovery ($\beta_2 < \beta_1$) but higher maximum richness ($\alpha_1 > \alpha_2$) than the dashed line. Panel (b) shows the same piospheres in plant richness after a double reciprocal transformation of the variables and the fit of a linear function.

$$y = \frac{(a \times x)}{(\beta + x)} \quad (1)$$

where parameter a represents the theoretical maximum value of S or H' (if x is sufficiently large) and parameter β represents the distance along the transect where either S or H' reaches half of its theoretical maximum (Bolker, 2008) (Fig. 1a). While Eq. (1) is conceptionally appealing, estimating the parameters a and β (i.e., via nonlinear least squares) is problematic since a is approached asymptotically and β is a function of $a/2$ (Berges et al., 1994). However, a and β can be accurately estimated if the rectangular hyperbola is transformed with a double reciprocal (a method used in biochemistry to estimate kinetic parameters in enzyme inhibition; Lineweaver and Burk, 1934):

$$\frac{1}{y} = \frac{1}{a} + \frac{\beta}{a} \times \frac{1}{x} \quad (2)$$

$$y = a + b \times x \quad (3)$$

where $1/a$ (Eq. (2)) represents the intercept (parameter a, Eq. (3)) and β/a is the slope (i.e., parameter b, Eq. (3)) (Fig. 1b). This approach enabled us to make a simple but effective comparison of the piospheres, especially via the use the parameter b (Eq. (3)). Higher values of the slope suggest a stronger response between assemblages, seasons and management strategies to the grazing gradient (Fig. 1b).

As the transformation to double reciprocal distorts the structure of the error, we used generalized linear mix models to estimate the parameters (Bolker, 2008). These models showed good Type I error control for spatial autocorrelation in data and – importantly – precise and stable parameter estimates (Dormann et al., 2007; Chamaillé-Jammes et al., 2009)(see Appendix S2 for details). For S we assumed a Poisson distribution and for H' a Gamma distribution. To assess the significance of the models we calculated R^2 value of each relationship as the residual sum of squares divided by the total sum of squares of the model. Analysis were done using R software.

To examine piosphere patterns between seasons and management strategies we compared parameter b using a likelihood ratio test (Bolker, 2008), which

$$(m_1) y = a + b \times x \quad (4)$$

$$(m_2) y = a + (b_D + b_W) \times x \quad (5)$$

$$(m_3) y = a + (b_C + b_R) \times x \quad (6)$$

The first model (Eq. (4)) represents the null hypothesis that there is no difference in the value of the parameter b; Eq. (5) represents the fit of a function with two different values of the parameter b to test if there is a difference in the slopes of the function between dry (b_D) and wet (b_W) seasons; and the third model (Eq. (6)) evaluates differences in the function between continuous (b_C) and rotational (b_R) grazing.

3. Results

3.1. Trend in abundance and cross-taxa congruence

Under continuous grazing, a total of 43 and 60 plant species were recorded during the dry and wet seasons, respectively. For ants, maximum richness was 19 and 31, respectively (Appendix S3). Small mammal capture success was 3% in the dry and 4% wet seasons, with a maximum of three rodent species (*Eligmodontia typus*,*Eligmodontia moreni* and *Graomys griseoflavus*) captured in both seasons. Regarding species trends along the transect, in the continuous piosphere sites the decreasing trend was the most common, followed by species that were neutral (Table 1).

Under rotational grazing, a total of 49 and 64 plant species were recorded during dry and wet seasons, respectively. Ants showed a maximum richness value of 22 and 33 species, respectively (Appendix S4). The success of small mammals capture was 5.7% in dry season and four species were recorded (*E. typus, E. moreni, G. griseoflavus* and *Akodon molinae*), whereas during wet season the capture success was of 5.4% and a fifth species, the desert marsupial *Thylamys pallidior* was captured. The most frequent species-level trend in abundance in the piosphere was neutral, followed by decreasing and medial (Table 1).

Table 1
Percentage of species based on abundance along the grazing gradient, during dry and wet seasons, and under continuous and rotational grazing. Trends (from Landsberg et al., 2003): decreasing: highest abundance with increasing distances from the water source; increasing: highest abundance nearest source; restricted: only present at distances >1200 m from water source; medial: highest abundance at intermediate distances; and neutral: abundance does not change with the gradient.

		Trends (% of species)				
Dry season		Decreasing	Increasing	Restricted	Medial	Neutral
Continuous	Plants	37.84	13.51	5.41	8.11	35.14
	Ants	52.63	15.79	0	10.53	21.05
	Small mammals	33.33	0	0	0	66.67
Rotational	Plants	30.61	16.33	2.04	10.20	40.82
	Ants	13.64	0	0	31.82	54.55
	Small mammals	33.33	0	0	0	66.67
		Trends (% of species)				
Wet season		Decreasing	Increasing	Restricted	Medial	Neutral
Continuous	Plants	35.59	15.25	10.17	13.56	25.42
	Ants	48.39	9.68	19.35	12.90	9.68
	Small mammals	33.33	0	0	0	66.67
Rotational	Plants	23.53	17.65	7.35	16.18	35.29
	Ants	17.14	5.71	11.43	17.14	48.57
	Small mammals	20	0	40	0	40

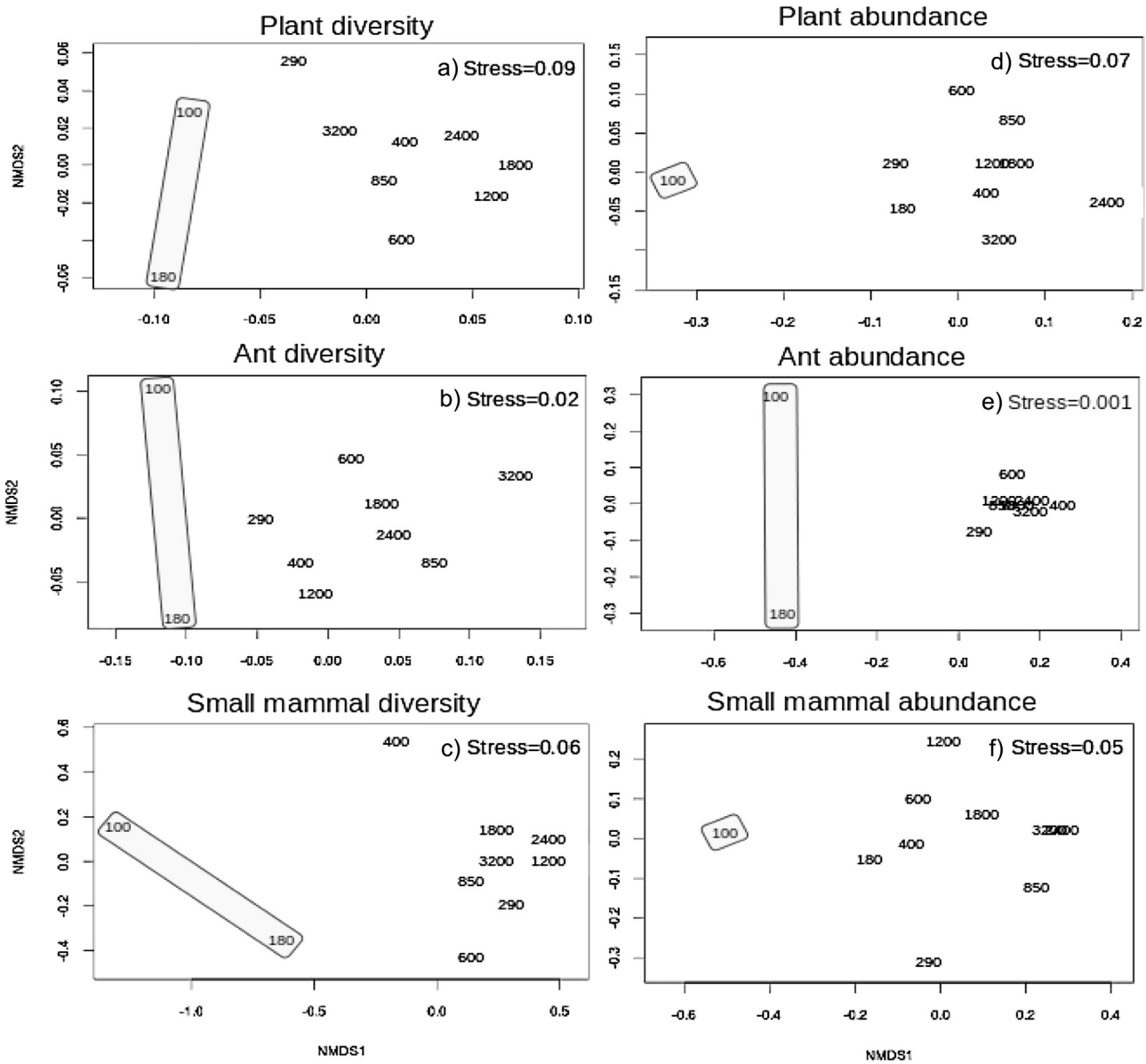

Fig. 2. Nonmetric multidimensional analysis (NMDS) plots of the 10 distances from the water source (100, 180, 290, 400, 600, 850, 1200, 1800, 2400 and 3200 m) based on the diversity (panels a–c) and relative abundance (panels d–f) of taxonomic groups.

When examining similarities and differences between sampling sites with respect to the structure (diversity and relative abundance) of the assemblages, the NMDS results suggested that the 100 m sampling site was unique for most of the taxa, and the 180 m sampling site for 4 out of 6 situations analyzed (Fig. 2). When assessing for cross-taxa congruence, correlations among the three taxa showed different results between seasons and management strategies, and most of the correlations were not significant statistically. The only consistent correlation among both management strategies were ants and small mammal assemblage composition and diversity during the wet season (Table 2). There were some other significant correlations, but not consistent among seasons or management strategies (Table 2).

3.2. Piosphere patterns and seasonality

Plant H' under continuous grazing showed higher slope values during dry season than during wet season, while for plant S there were no significant differences in the slope of the functions

Table 2
Pearson correlation coefficients (P value) among taxonomic groups for the identification of potential surrogate taxa. Information about assemblage composition (1st axis of NMDS *ordination* based on species relative abundance) and species diversity (H') was used for the analysis. Significant correlations ($P < 0.05$) are shown in bold.

Assemblage composition	Continuous		Rotation	
	Dry season	Wet season	Dry season	Wet season
Plants/ants	0.03 (0.87)	0.19 (0.3)	**−0.51 (0.01)**	**−0.36 (0.05)**
Plans/small mammals	−0.04 (0.83)	0.2 (0.29)	−0.4 (0.03)	−0.25 (0.18)
Ants/small mammals	−0.01 (0.96)	**−0.44 (0.01)**	0.22 (0.25)	**0.59 (0.01)**
Diversity	**Continuous**		**Rotation**	
	Dry season	Wet season	Dry season	Wet season
Plants/ants	0.29 (0.12)	0.28 (0.13)	0.12 (0.53)	0.76 (0.69)
Plants/small mammals	0.29 (0.13)	0.14 (0.47)	**0.37 (0.04)**	0.28 (0.13)
Ants/small mammals	0.18 (0.33)	**0.52 (0.01)**	**0.46 (0.01)**	**0.39 (0.03)**

Table 3
Likelihood ratio test between with no differences in the parameter b (m_1) and a model that includes different values of the parameter b for different seasons (dry and wet season = m_2) and for different management strategies (continuous and rotational grazing = m_3). Significant differences between models ($P < 0.05$) are shown in bold.

Seasonality (m_1 vs. m_2)	Deviance	χ^2	P
Plants diversity in continuous grazing	**−631.37**	**32.4**	**<0.001**
Plants richness in continuous grazing	162.12	3.37	0.26
Small mammals diversity in rotational grazing	−255.1	**12.01**	**<0.05**
Management strategy (m_1 vs. m_3)	**Deviance**	**χ^2**	**P**
Ants diversity during wet season	**−444.92**	**26.54**	**<0.001**
Small mammals diversity during wet season	−178.06	5.23	0.03
Ants richness during wet season	291.46	17.13	0.35

between seasons (Table 3). Under rotational grazing, there were no significant relationships in plant S and H' in neither season (Fig. 4). Ant S and H' in the dry season did not vary with distance to water source in either management strategy (Figs. 3 and 4). The diversity of small mammals did not show consistent responses: the slope was not significant during dry season under continuous grazing (Fig. 3), but it was significantly higher under dry than wet season under rotational grazing (Table 3).

3.3. Piosphere patterns and management strategies

Under continuous grazing the number of relationships that showed no significant effect of grazing on biodiversity was lower (3 out of 10) than the number of relationships that showed a significant effect (7 out of 10) (Fig. 3). Vegetation S and H' both presented values of the fit of the function to the data higher than 0.5 (Fig. 3), showing the occurrence of a pronounced degradation pattern. Under rotational grazing, the number of relationships that showed no significant effect of grazing on biodiversity was higher (6 out of 10) than the once that had a significant effect (4 out of 10) (Fig. 4). Notably, there was no piosphere effect in neither vegetation S or H' (Fig. 4). When comparing the slopes between management we found that H' of ants and small mammals had a significantly higher slope value (parameter b) under continuous rather than rotational grazing, while S of ant species showed no significant difference (Table 3).

4. Discussion

4.1. The use of simple ecological indicators reveals important information for rangeland management

In drylands an increase in grazing intensity may trigger soil erosion and species extinction processes, causing – sometimes irreversible – biodiversity losses (Cingolani et al., 2005). The use of species trend in abundance in the piosphere as a biodiversity degradation indicator helped to identify species under higher (or lower) local extinction risk (Landsberg et al., 2003), as well as management strategies that may avoid biodiversity loss. In general, our results show that under continuous grazing, a decreasing trend in the abundance was the main response of plant species (Table 1). Similar to other semiarid rangelands, the negative effect of the accumulation of grazing pressure close to the water source leads to the outcome of losers (decreasing trend + restricted) that are the most threatened by local extinction (Landsberg et al., 2003; Macchi and Grau, 2012). While under continuous grazing approximately 45% of the plant species are losers, under rotational grazing this number decreases up to no more than 32% (Table 1). These changes may be explained by a preferential use of vegetation by livestock when the stocking rate expected for 5000 ha is concentrated during a short time period in 1250 ha (Pringle and Landsberg, 2004; Teague et al., 2011).

Ants are expected to respond to grazing disturbance indirectly through changes in vegetation composition and cover (Hoffmann, 2010), but still proposed as good indicators for rangeland management (Hoffmann and James, 2011). Under continuous grazing, species with decreasing trend and restricted species always outnumbered species with increasing, medial and neutral trend. While under rotational grazing, neutral trend was the main response (Table 1), showing that the gradient of grazing intensity of the piosphere is not a structuring factor in ants' abundance when short term exclosures are allowed. As well as ants, small mammals are expected to be indirectly affected by grazing disturbance through changes in resource availability which may affect species abundance (Tabeni and Ojeda, 2005). But our results showed that the main response to the piosphere under both management strategies was a neutral trend in abundance (Table 1). Nevertheless, we found 2 new species in the assemblage during the wet season and under rotational grazing, which were classified as restricted to sites with lower grazing pressure.

We are aware that species identification at the taxonomic level is not easy, but still is an indispensable 'first action' needed for biodiversity monitoring. With this information, assessing the trend in abundance is an easy task. In this sense, the use of species trend in abundance as an indicator of species level response for plants and animals showed that the exclosure of livestock grazing during one wet season applied at El Divisadero AMA helped to prevent biodiversity loss.

The potential occurrence of surrogacy among taxonomic groups may be very helpful to diminish the effort of further monitoring of different management practices and/or restoration programs (Anand et al., 2005). But contrary to what we expected, vegetation diversity and composition were not valid surrogates of ants or small mammals assemblages (Table 2). These findings are in concordance with other studies that found that vegetation is not a good surrogate of insects in more humid ecosystems (Santi et al., 2010; Babin-Fenske and Anand, 2010). We found cross-taxa congruence (i.e., significant correlation coefficients) among animal diversity and composition during wet season, but the correlation value was always lower than 0.6 (Table 2), and thus, considered to be weak. This lack of strong cross-taxa congruence represents a challenge for rangeland managers, with the need of deeply understanding the system in order to choose appropriate indicators of degradation.

4.2. Double reciprocal analysis of piospheres as a novel tool for rangeland assessment

The double reciprocal analysis of the piospheres allowed us to compare the response of the community to seasonality and different management strategies. The double reciprocal analysis standardizes the parameter that represents the distance to the water source at which the community diversifies (β of Eq. (1)) with the maximum values of the response variable (a of Eq. (1)) (Fig. 1). As such, and as used widely in biochemistry analysis, the parameter b of this transformation (Eq. (4)) can be a very useful tool to do valid and effective comparisons of the community response of several taxa. By using the parameter b to compare the response of plants, ants and small mammals under different seasons and management strategies we were able to assess the ecological sustainability of the rest-rotational experimental AMA applied at El Divisadero, in the Central Monte desert.

For vegetation we found that summer precipitation interacts with disturbance by diminishing the negative effect of grazing over diversity. In this sense, under continuous grazing the piosphere effect on vegetation was less intense during wet than dry season, as

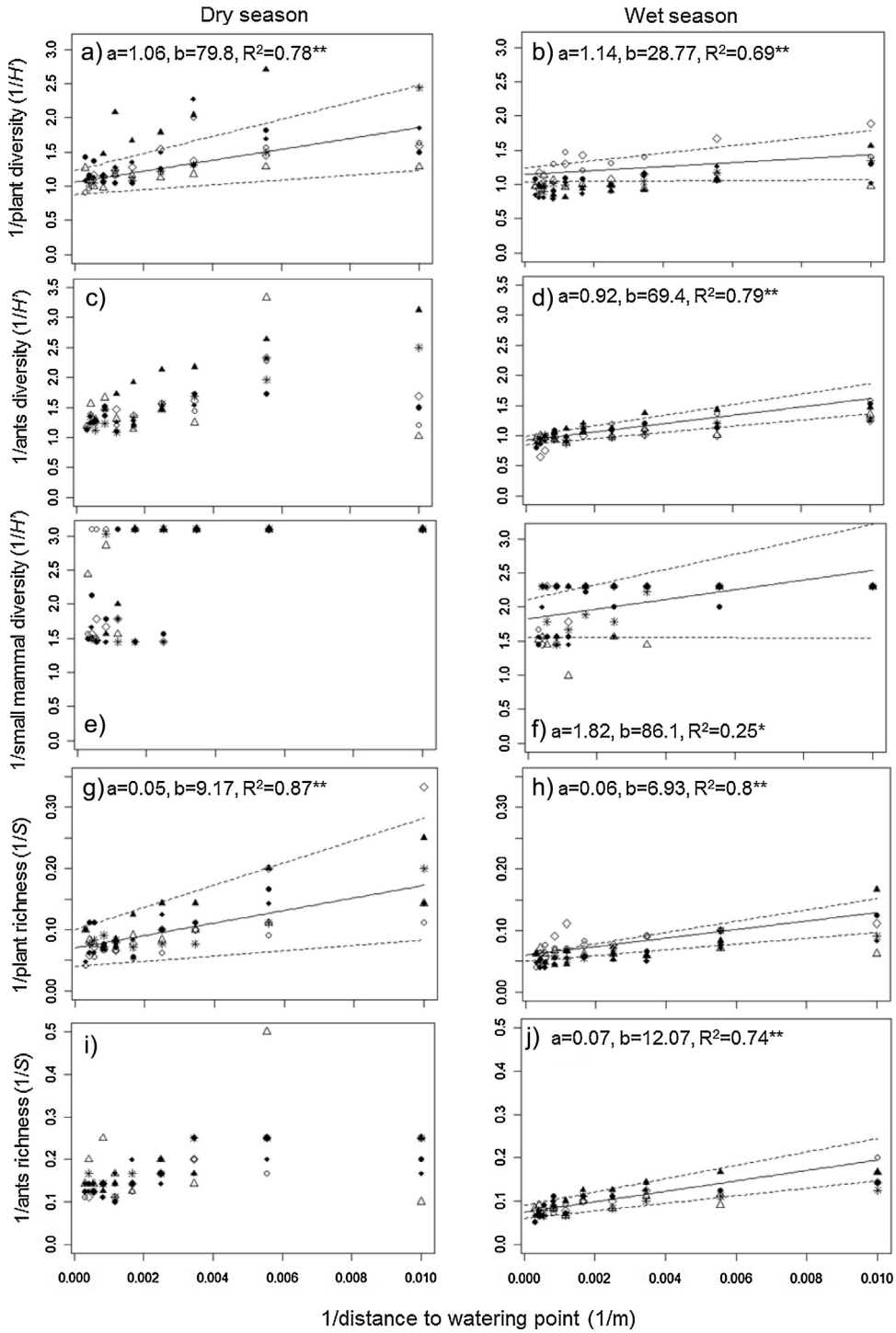

Fig. 3. Continuous grazing. Relationship between the inverse of species diversity ($1/H'$) and richness ($1/S$) and the inverse of the distance to the watering point ($1/m$), during dry and wet seasons. Different symbols indicates different transects ($n = 7$). The parameters of the function (a = intercept, b = slope), goodness of fit (R^2) and statistical significance ($^*P < 0.05$ $^{**}P < 0.01$) of the function are shown.

diversity presented lower values of the parameter b (Fig. 3, panel a and b) (Table 3). Notably, under rotational grazing, neither plant richness nor diversity showed changes in the piosphere, not even during the dry season (Fig. 4, panel a and b, and g and h). Similar results of the positive effect of seasonal precipitation on vegetation together with grazing exclosure were found for semiarid rangelands in the United States, showing the advantages of an adaptive management using multi-paddock grazing (Teague et al., 2011). The use of the double reciprocal analysis helped to identify the positive effect of the rest-rotation grazing AMA applied at El Divisadero, as the grazing exclosure during one wet season contributes to diminish species richness and diversity degradation in areas closer to water source.

The response of animal community to seasonality showed no consistency among assemblages. On the one hand, the response of small mammal diversity to seasonality was different under

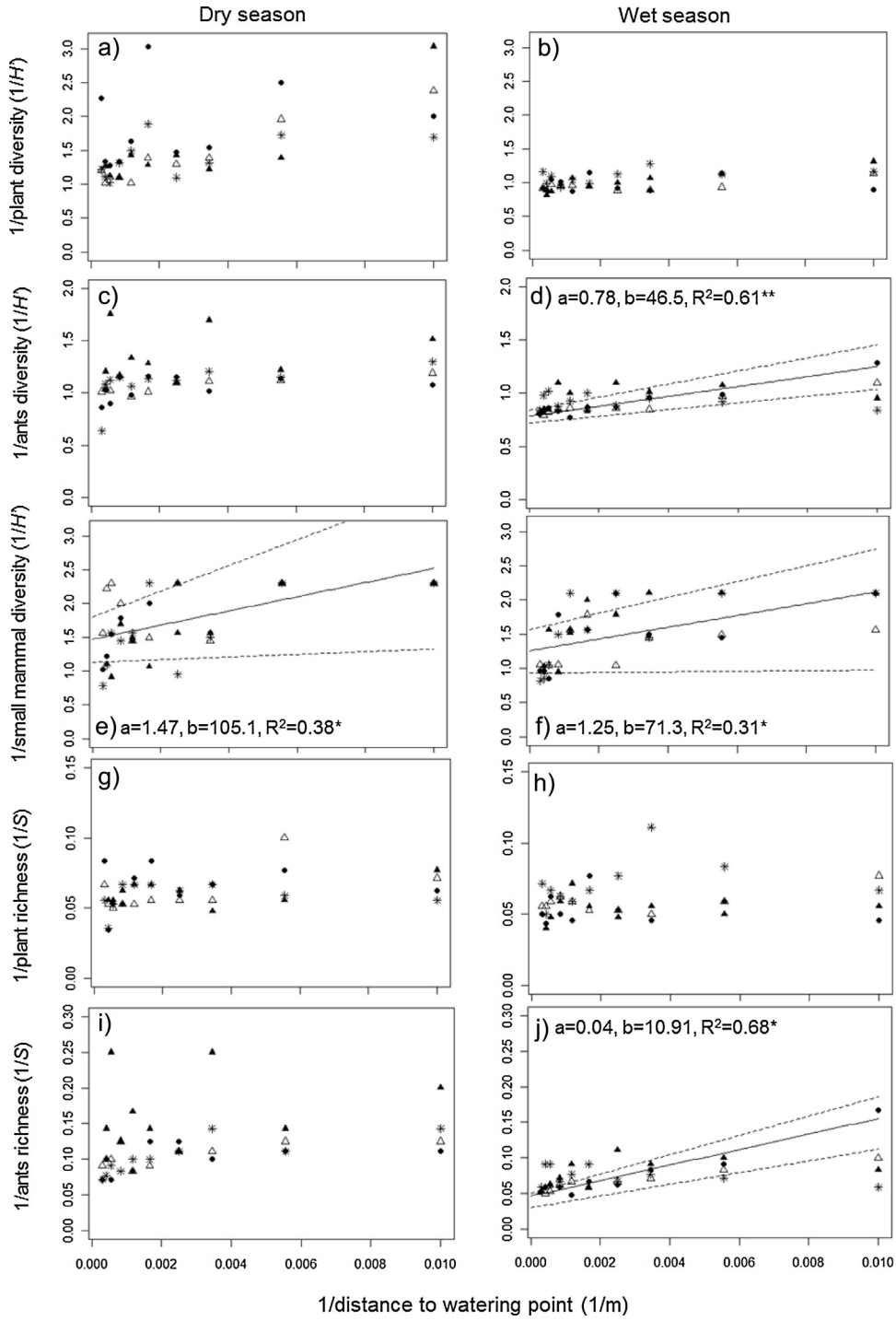

Fig. 4. Rotational grazing. Relationship between the inverse of species diversity ($1/H'$) and richness ($1/S$) and the inverse of the distance to the watering point ($1/m$), during dry and wet seasons. Different symbols indicates different transects ($n = 4$). The parameters of the function (a = intercept, b = slope), goodness of fit (R^2) and statistical significance ($^*P < 0.05$ $^{**}P < 0.01$) of the function are shown.

continuous (Fig. 3e and f) and rotational grazing (Fig. 4e and f). On the other hand, ants showed an opposite response to that of vegetation, where under both management strategies the degradation in the piosphere was more intense (higher value of the parameter b) during the wet season than in the dry season (Figs. 3 and 4, panels c and d, i and j). The lack of response of the ant assemblage to the grazing gradient during the dry season may be explained by a reduction in the activity of ants during non-favorable conditions (dry and cold weather), a well-reported pattern in temperate regions (Hoffmann, 2010).

Moreover, the use of the double reciprocal analysis allowed us to assess that ants and small mammal assemblages showed a varied response to management strategy, perhaps due to the dominant effect of seasonality (Bestelmeyer and Wiens, 1996; Ojeda and Tabeni, 2009). Nevertheless, in assemblages with similar responses to seasonality, the degradation in the piosphere were always more intense under continuous than under rotational management (Table 3). We found an increase in small mammal richness under rotational grazing, as species that are known to prefer more complex habitats (*A. molinae* and *T. pallidior*)

(Ojeda and Tabeni, 2009) were restricted to this AMA. The positive effect of grazing exclosure on mammals of this region had been demonstrated mainly in long-term exclosures (Tabeni and Ojeda, 2005). This is the first study to show that short-time exclosures also helps to diminish the negative effect of livestock grazing on fauna. This conclusion of the effect of different management strategies on animal community could be achieved thanks to the use of the double reciprocal analysis, as the use of the *b* parameter allows for a standardization of the degradation gradient (Fig. 1), and thus, for statistically valid comparisons.

5. Conclusions

For most of the situations analyzed we found a marked gradient of decreasing biodiversity in the piosphere during both seasons. Although other factors such as landscape heterogeneity, other water sources, grazing history and management strategy may modify the influence of the distance to the water source on structuring the grazing pressure, they are rarely included in piosphere analysis (Pringle and Landsberg, 2004). Besides its importance for rangeland management, to our best knowledge this is the first study that examines intra-annual variation in precipitation together with differences in management strategies and the response of several taxonomic groups. This characteristics of the sampling design could be effectively analyzed thanks to the use of simple ecological indicators of species response, and a new methodological approach to assess community response – the double reciprocal analysis – which allows for a valid comparison between piospheres besides differences in the main factors that structures grazing pressure.

By analyzing the trend in abundance of species in the piosphere we were able to detect an elevated percentage of species considered to be losers under continuous grazing, and the potential of rotational grazing to reverse this negative effect. Complemented with this analysis we assessed the potential use of an indicator taxa of species loss. But the cross-taxa congruence analysis showed that vegetation is not a good surrogate group of ants and small mammals besides its importance in food and habitat availability. Moreover, vegetation response was dominated by the management strategy while animal assemblage response was dominated by precipitation regime. This different response highlights the importance of different conservation actions based on the target taxa. Finally, the double reciprocal analysis seems to be a powerful tool for managers as it is easy to calculate and may be used to assess the effect of different management strategies on biodiversity, and even to follow up conservation actions through time. In this sense, the experimental rest-rotational management evaluated in this study showed how AMAs may diminish the conflict between beef production and biodiversity conservation in the Central Monte desert. This is a very important result because livestock production is the main economic activity in drylands world-wide. Thus, research on regional AMA in arid, semiarid and sub-humid lands needs to be encouraged, and the analysis proposed here may be powerful tools to do it.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.10.009.

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