



Short Communication

Quantitative assessment of shrub–grass mosaic development in grazed shrublands: An example in the Patagonian Monte (Argentina)

G.E. Pazos*, J.O. Ares, M.B. Bertiller

Centro Nacional Patagónico (CONICET), Boulevard Brown 2915, U9120ACD Puerto Madryn, Chubut, Argentina

ARTICLE INFO

Article history:

Received 28 May 2009

Received in revised form

28 September 2009

Accepted 24 December 2009

Available online 29 January 2010

Keywords:

Autocorrelation

Grazing

Indicators

Spatial pattern

Two-phase mosaic

ABSTRACT

Grazing alters the spatial structure of shrubs and perennial grasses in desert shrub communities. The resulting spatial distribution of shrub–grass patches constitutes a sensitive indicator of the integrated result of grazing impacts on them. While several procedures were developed to estimate the size of shrub clumps, metrics of the geometry of the interacting grass matrix received less attention. In this study, we conceptualised the spatial structure of shrub–grass patches as consisting of two components: a grass crown of ill-defined outer borders (the ‘grass component’) encircling a shrub clump (the ‘shrub component’). We fitted exponential functions to autocorrelograms of spatially explicit shrub–grass cover data surveyed at different locations of the Patagonian Monte (Argentina) differing in livestock grazing pressure. After that, we derived two metrics from the function parameters that quantitatively estimate the size of both the shrub and the grass components of shrub–grass patches. The patterns of variation of these metrics are consistent with field measurements and observations previously reported for the studied areas, indicating that they are sensitive indicators of the state of development of the shrub–grass mosaic under different grazing pressures. These results suggest that its applicability to similar semi-arid shrublands deserves further attention.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

In semi-arid shrublands, the vegetation is spatially patterned as a two-phase mosaic composed by discrete shrub clumps distributed on a matrix of herbaceous plants and bare soil (Aguar and Sala, 1999). The spatial dynamics of ecosystem processes such as water and nutrient cycling and plant establishment is linked to this spatial patterning of vegetation. This is mainly due to differences in soil infiltration capacity and plant density between both phases that determine different capacities of resource capture and retention (Bhark and Small, 2003; Ludwig et al., 2005). This results in a tight coupling between the spatial heterogeneity of soil resources and that of vegetation (Schlesinger et al., 1996), so that the size of both phases of the mosaic is an important feature determining the dynamics of these ecosystems. Particularly, changes in the size and cover of the perennial-grass matrix are relevant to the detection of early stages of land degradation and desertification processes

induced by grazing (Bertiller et al., 2002a; Bestelmeyer et al., 2006; Chartier and Rostagno, 2006). While many indices and approaches useful to estimate the shrub-clump size have been reported in the literature (Gustafson, 1998; Fortin and Dale, 2005), the assessment of the size of the grass matrix received less attention.

Many studies in arid shrublands reported spatial dependence of perennial grasses on the shrub phase (e.g. Moro et al., 1997; Montaña et al., 2001; Bisigato and Bertiller, 2004; Cipriotti and Aguiar, 2005). Shrub clumps generate heterogeneity of microenvironmental conditions for the establishment of perennial grasses, leading to different patterns of association between both functional groups that mainly depend on the morpho-functional attributes of the grass species, their dispersal ability, the size of the shrub clumps, and the grazing pressure (Moro et al., 1997; Fernández et al., 2002; Maestre and Cortina, 2005; Pazos et al., 2007; Pazos and Bertiller, 2008). In general, the establishment of perennial grasses is more frequent in the neighbourhood of shrub clumps due to higher resource availability, ameliorated microclimatic conditions, and higher seed trapping in these microsites than in open inter-shrub spaces (Aguar and Sala, 1997; Flores and Jurado, 2003; Bisigato and Bertiller, 2004; Pazos and Bertiller, 2008). However, subtle differences in substrate characteristics between neighbouring soil microsites determine different probabilities of establishment for perennial grasses growing scattered across the inter-shrub

* Corresponding author. Unidad de Investigación Ecología Terrestre, Centro Nacional Patagónico (CONICET), Boulevard Brown 2915, U9120ACD Puerto Madryn, Chubut, Argentina. Tel.: +54 2965 451024; fax: +54 2965 451543.

E-mail addresses: gpazos@cenpat.edu.ar (G.E. Pazos), joares@cenpat.edu.ar (J.O. Ares), bertil@cenpat.edu.ar (M.B. Bertiller).

spaces (Fowler, 1988; Bertiller et al., 2002b). These factors determine the distribution of grasses around shrub clumps and the external boundaries of grass patches are generally not clearly delimited (Couteron and Lejeune, 2001; Bisigato et al., 2002). Under these circumstances, the direct field measurement of its size is a subjective task involving an arbitrary definition of the limit between the grass matrix and the surrounding bare soil. Objective, statistical-based methods to estimate the size of the grass matrix are necessary and preferable.

Grazing alters the spatial structure of shrub–grass mosaics. Previous work in the Patagonian Monte shrublands (Bisigato et al., 2005; Pazos et al., 2007) showed that dominant species of perennial grasses (*Poa ligularis*, *Nassella tenuis*, and *Jarava speciosa*) occupy microsites increasingly closer to shrub clumps with increasing grazing pressure. In intensely grazed areas the grass matrix retracts to a minimum development restricted to microsites surrounding shrub clumps (Fig. 1). Based on these evidences, we build a conceptual model of the spatial structure of shrub–grass mosaics, develop a method to quantitatively estimate the size of both mosaic phases, and apply it to analyse a spatially explicit field dataset on shrubs and perennial grasses of the Patagonian Monte under different grazing pressures.

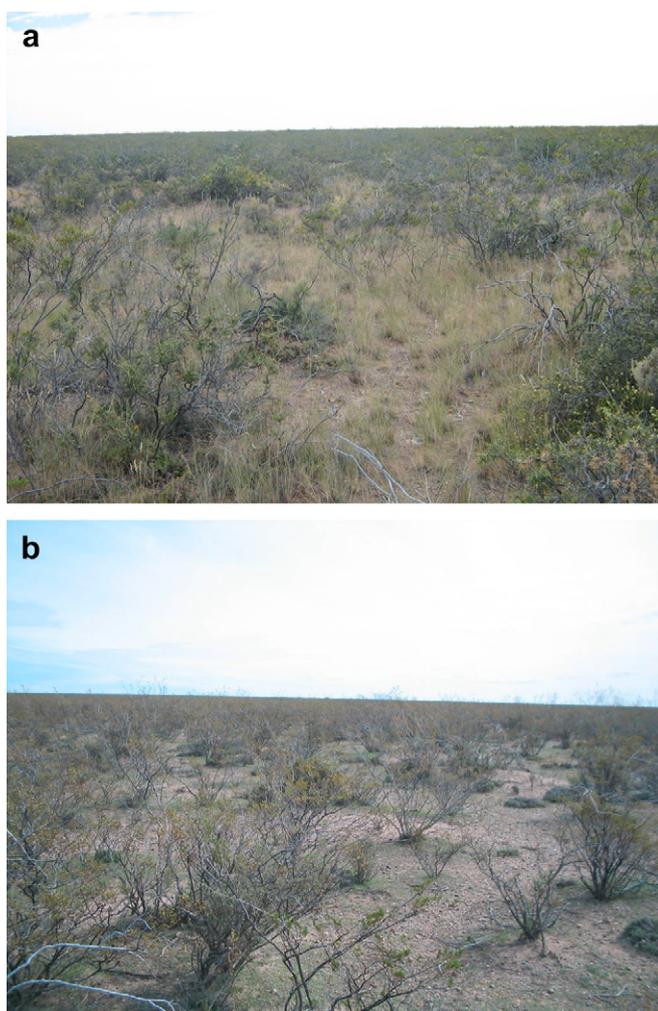


Fig. 1. Structure of the shrub–grass mosaic in the Patagonian Monte shrublands. (a) Area with grazing exclusion for at least 15 years. (b) Area under continuous high grazing pressure.

2. Field sampling and data

The study sites were located within a representative area of the dominant community of *Larrea divaricata* Cav. and *Stipa* spp. of the Patagonian Monte (León et al., 1998). Complete descriptions of climate, soils, floristic composition, and spatial structure of vegetation of the study area can be found in Bisigato and Bertiller (1997) and Ares et al. (2003). We performed field sampling in seven paddocks of ca. 2500 ha each located at four ranglands used for extensive sheep grazing typical of the Patagonian Monte. Five of them, located at San Luis (3) (42°39'S; 65°23'W) and El Milagro (2) (42°43'S, 65°38'W), were submitted to the usual stocking rates for the area (0.17–0.22 sheep ha⁻¹). The other two, located at Gallastegui (1) (42°44'S; 65°07'W) and Laguna Blanca (1) (42°48'S; 65°08'W), had been excluded from grazing during the last 15 years.

We selected two areas of 2 ha each located at 0.5–1 km and at 4–5 km from the permanent watering point within each of the five grazed paddocks, which corresponded to sites with high (H) and low (L) grazing pressure, respectively (Bisigato and Bertiller, 1997; Bertiller et al., 2002a; Pazos et al., 2007). Similarly, we selected one area of 2 ha within each of the paddocks excluded from grazing (EX). All these sites were known to display different spatial patterns of shrub clumps and perennial grasses related to grazing pressure (Bertiller et al., 2002a; Bisigato et al., 2005; Pazos et al., 2007).

At each site, during spring–summer (2003–2005) we delimited four linear transects of 50 m each oriented SW–NE (2) and NW–SE (2) (total: 48 transects) and recorded the intercepted diameter and cover of shrub clumps, and the intercepted diameter of the basal area of bunches of perennial grasses located around shrub clumps. We defined a shrub clump as a discrete cluster of shrub canopies separated from other cluster by at least 5 cm of bare soil, and a grass bunch as a group of tillers isolated from other group by a minimum distance of 5 cm (Pazos et al., 2007). Then, we divided each transect in 500 segments of 10 cm each and calculated the percentage cover of shrubs and perennial grasses at each segment.

3. Conceptual model and data analysis

We conceptualised the spatial patterning of perennial grasses around shrub clumps as forming 'crowns' whose external boundaries depend on the exposure to unprotected microsites and the impact of herbivores (Bisigato and Bertiller, 2004; Bisigato et al., 2005). According to this model, the shrub–grass mosaic is composed by multiple patches consisting of a shrub clump (the 'shrub component') encircled by a crown of perennial grasses (the 'grass component') (Fig. 2a).

We estimated the autocorrelation function of the cover values of both shrub clumps and perennial grasses along transects at 50 increasing lag distances (10–500 cm) (SPSS for Windows Statistical Package, SPSS Inc., Chicago, USA). We then fitted (Peakfit v3.0, Jandel Scientific, CA, USA) the following decreasing function to the shrub autocorrelogram of each transect:

$$y_s = \exp(-x/k_s) \quad (1)$$

where y_s is the estimated autocorrelation coefficient, x is the lag distance, and k_s is the rate of decay of cover autocorrelation at increasing lag distances (Fig. 2b). The k_s metric is an indicator of the diameter of the shrub component, such that steeply decreasing y_s (low k_s) correspond to a predominance of small shrub clumps, and smoothly decreasing y_s (high k_s) to areas with predominant large shrub clumps (Fig. 2a,b) (Tobin, 2004; Uemaa et al., 2008).

We extended this reasoning to the spatial analysis of the two-phase shrub–grass mosaic by fitting an exponential function to the autocorrelograms of perennial-grass covers. According to our

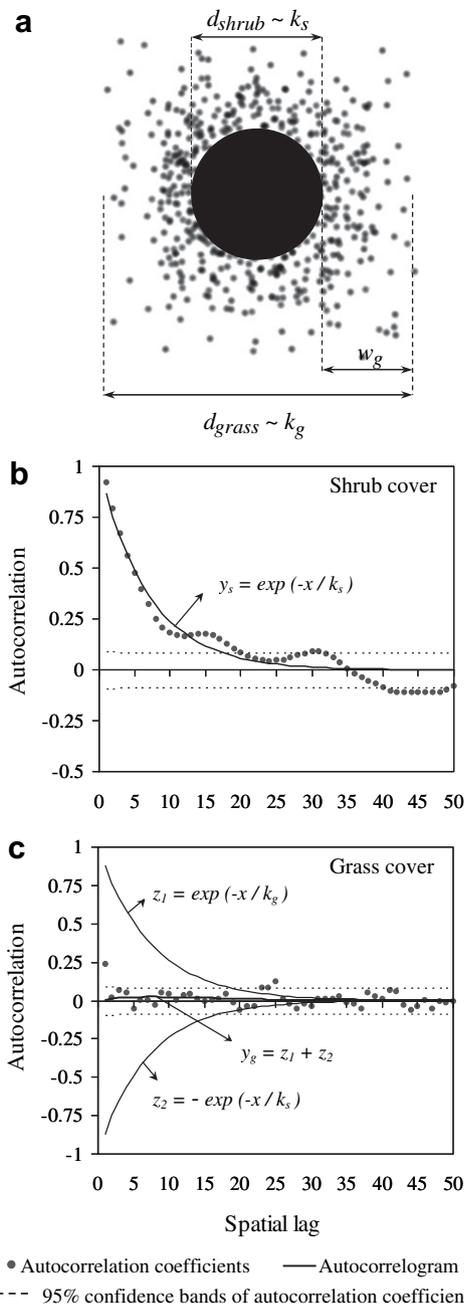


Fig. 2. (a) Components of a shrub–grass patch as conceptualised in this study. Perennial grasses (dots) form crowns around shrub clumps (black circle) (the ‘grass’ and the ‘shrub component’, respectively). The relationships between their external diameters (d_{shrub} , d_{grass}) and the k_s , k_g parameters (see main text, Eqs. (1) and (2)) are indicated. k_s and w_g (Eq. (3)) are indicators of the diameter of the shrub clump and the width of the grass crown, respectively. (b)–(c) Estimation of k_g and w_g parameters: the exponential fit to the autocorrelogram of shrub cover values (b) is used to fit the autocorrelogram of grass cover values by means of a double exponential function (c). The 95% confidence bands correspond to the autocorrelation coefficients.

conceptual model, the internal diameter of the grass crowns would be approximately coincident with the external diameter of shrubs while the external diameter of the grass crowns would be proportionally related to k_g , the rate of decay in a double exponential function describing shrub–grass patches (Fig. 2a,c):

$$y_g = \exp(-x/k_g) - \exp(-x/k_s) \tag{2}$$

where y_g fits the autocorrelation function of the cover of perennial grasses of each transect as in the case of shrub clumps (Eq. (1))

(Fig. 2c). In this way, we calculated the difference between the k_g and k_s parameters for each transect as a measure of the average width of the grass crowns (the size of the grass component) along a transect (Fig. 2a):

$$w_g = k_g - k_s \tag{3}$$

We compared the values of cover and diameter of shrub clumps and grass bunches around them, and k_s and w_g among sites with different grazing pressures through two-way ANOVA using grazing pressure (EX, L, and H) as a fixed factor and the transect number (1–4) as a random one, and used the LSD test to assess the significance of the differences among grazing pressures. Cover and diameter values were previously transformed (cover: arcsine; diameter: logarithmic) as necessary to meet ANOVA assumptions (Sokal and Rohlf, 1997).

4. Results

Sites under different grazing pressures showed similar shrub cover and diameter of grass bunches (Table 1, rows 1, 4). Shrub-clump diameter and grass cover around them, however, diminished with increasing grazing pressure (Table 1, rows 2, 3). The k_s and k_g parameters estimated from Eqs. (1) and (2), respectively, were significant at $p < 0.01$ for all the 48 transects. As expected, k_s (Table 1, row 5) diminished in correspondence with shrub diameter, since these constitute similar metrics of a same geometric attribute of the shrub–grass patches. Changes in w_g (Table 1, row 6) were consistent with the overall reduction of grass cover at increasing grazing pressures, although these metrics refer to different attributes of the shrub–grass patches. Appendix shows examples of autocorrelograms of shrub and grass cover values in transects at different grazing pressures and the corresponding estimation of parameters.

5. Discussion

Grazing has various effects upon the shrub–grass patches in the Patagonian Monte. During grazing, shrub clumps are trampled and fragmented (Bisigato and Bertiller, 1997) and after grazing exclusion, shrubs re-grow and coalesce into units larger than the original patch components (Ares et al., 2003). As a result of these, the size of shrub clumps is larger in areas excluded from grazing than during grazing (Bertiller et al., 2002a; Pazos et al., 2007). This is adequately reflected by the k_s metric, pointing out that it is an indicator of the size of the shrub component of shrub–grass patches sensitive to changes promoted by livestock grazing.

Table 1

25th–75th quartile values of cover and diameter of shrub clumps and grass bunches located around them, and mean (± 1 SE) k_s and w_g metrics (Eq. (1) and (3), respectively) per grazing pressure (EX: Exclusion; L: Low grazing pressure; H: High grazing pressure). Different letters indicate significant differences (LSD test; $p < 0.05$) among grazing pressures. For rows 1–4, data analyses were performed on the transformed values (see text).

	EX	L	H
1 Cover of shrub clumps (%)	25.8–47.3 a	31.9–41.0 a	28.9–52.9 a
2 Intercepted diameter of shrub clumps (cm)	100.2–147.9 a	61.9–93.8 b	60.9–104.6 b
3 Grass cover around shrub clumps (%)	2.04–4.11 a	1.70–2.86 a	0.33–0.92 b
4 Intercepted diameter of grass bunches around shrub clumps (cm)	3.98–4.96 a	3.73–5.01 a	2.70–5.00 a
5 k_s	9.87 \pm 1.40 a	5.02 \pm 0.27 b	5.72 \pm 0.55 b
6 w_g	0.44 \pm 0.08 a	0.36 \pm 0.07 ab	0.17 \pm 0.08 b

Characterizing the grass component of shrub–grass patches poses difficulties because its external border diffuses into neighbouring bare soil areas. The w_g metric provides a quantitative estimate of the average width of the grass crown instead of subjective field estimations based on observer's definition of the limit between the grass crown and the surrounding bare soil. The w_g metric gradually decreased with increasing grazing pressure, i.e., the width of the grass crowns around shrub clumps decreases at higher grazing impact and adequately reflects the concentration of perennial grasses under and around shrub clumps at heavy grazing pressure reported by Pazos et al. (2007). The information included in the w_g metric adds the spatial dimension of the integrated impact of grazing on arid lands. This is important in the context of vegetation monitoring systems because w_g could detect grazing-related changes before a significant reduction in grass cover is measured. In the case of the Patagonian Monte, relatively high values of w_g , i.e., relatively wide grass crowns, indicate a recovery of the shrub–grass mosaics following grazing exclusion in the Patagonian Monte. Probably, the release from grazing and the microclimatic amelioration at the interpatch spaces promoted by the large shrub clumps (Bertiller et al., 2000) allows perennial-grass populations to expand to open, unprotected microsites. On the contrary, small values of w_g , i.e., narrow grass crowns, indicate a higher degree of association of perennial grasses with shrub clumps in grazed areas and a less conserved state of the grass component.

Autocorrelation analysis is a standard statistical tool used in plant spatial pattern analysis (Fortin and Dale, 2005), but the aims and criteria used to extract the information afforded by autocorrelograms had been diverse (Dale, 1999; Tobin, 2004; Fortin and Dale, 2005; Uuemaa et al., 2008). We chose curve fitting because the function parameter estimates describe the complete function and not just one or a few points at certain predefined lags (Fortin and Legendre, 1989; Uuemaa et al., 2008). The choice of a decreasing exponential function seems justified since the shrub–grass autocorrelograms of cover data invariably converge to 0 at high lag distances and a few low lag intervals convey most of the information about the spatial distribution of patches, a characteristic of irregular spatial patterns (Fig. 2b,c; Appendix) (Fortin and Dale, 2005). Further, our choice allowed us to extend the reasoning of exponential fitting to the analysis of the two-phase shrub–grass mosaic, to our knowledge a yet unexplored task in autocorrelation analysis.

In summary, we developed an autocorrelation-based method to simultaneously assess two important geometric attributes of the shrub–grass mosaic in semi-arid shrublands: the diameter of shrub clumps and the width of grass crowns. Both metrics summarize two characteristics of the impact of grazing upon the spatial structure and functioning of the shrub–grass mosaic in rangelands of the Patagonian Monte: the fragmentation of large shrub clumps into smaller units and the increased association of remaining perennial-grass bunches with them. This indicates that they are sensitive indicators of the state of development of the shrub–grass mosaic and the functional integrity of the system. Since a quantitative detection of changes related to environmental degradation is a central task for the sustainable management and conservation of arid and semi-arid ecosystems, the applicability of this method to similar semi-arid shrublands merits further attention.

Acknowledgements

Mr. F. Sarasa and Mr. F. Pérez Sarlangue allowed access to the study sites. This research was supported by Projects PICT 08-06027, PICT 08-20454 BID 1201-1728/OC-AR of the National Agency for

Scientific and Technological Promotion (ANPCyT). G.E.P. was supported by ANPCyT and CONICET research fellowships.

Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jaridenv.2009.12.004.

References

- Aguiar, M.R., Sala, O.E., 1997. Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* 78, 93–100.
- Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution* 14, 273–277.
- Ares, J., Bertiller, M., Bisigato, A., 2003. Modeling and measurement of structural changes at a landscape scale in dryland areas. *Environmental Modeling and Assessment* 8, 1–13.
- Bertiller, M.B., Ares, J.O., Bisigato, A.J., 2002a. Multiscale indicators of land degradation in the Patagonian Monte, Argentina. *Environmental Management* 30, 704–715.
- Bertiller, M.B., Ares, J.O., Graff, P., Baldi, R., 2000. Sex-related spatial patterns of *Poa ligularis* in relation to shrub occurrence in northern Patagonia. *Journal of Vegetation Science* 11, 9–14.
- Bertiller, M.B., Sain, C.L., Carrera, A.L., 2002b. Effect of fine-scale spatial variation of soil nitrogen on the performance of the sexes of *Poa ligularis* in patchy ecosystems of northern Patagonia. *International Journal of Plant Sciences* 163, 419–425.
- Bestelmeyer, B.T., Trujillo, D.A., Tugel, A.J., Havstad, K.M., 2006. A multi-scale classification of vegetation dynamics in arid lands: what is the right scale for models, monitoring, and restoration? *Journal of Arid Environments* 65, 296–318.
- Bhark, E.W., Small, E.E., 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. *Ecosystems* 6, 185–196.
- Bisigato, A., Ares, J., Bertiller, M., 2002. Assessment of pristine vegetation structure in semiarid shrublands based on spatial explicit modeling. *Phytocoenologia* 32, 581–594.
- Bisigato, A.J., Bertiller, M.B., 1997. Grazing effects on patchy dryland vegetation in northern Patagonia. *Journal of Arid Environments* 36, 639–653.
- Bisigato, A.J., Bertiller, M.B., 2004. Temporal and micro-spatial patterning of seedling establishment. Consequences for patch dynamics in the southern Monte, Argentina. *Plant Ecology* 174, 235–246.
- Bisigato, A.J., Bertiller, M.B., Ares, J.O., Pazos, G.E., 2005. Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. *Ecography* 28, 561–572.
- Chartier, M.P., Rostagno, C.M., 2006. Soil erosion thresholds and alternative states in northeastern Patagonian rangelands. *Rangeland Ecology and Management* 59, 616–624.
- Cipriotti, P.A., Aguiar, M.R., 2005. Effects of grazing on patch structure in a semi-arid two-phase vegetation mosaic. *Journal of Vegetation Science* 16, 57–66.
- Couteron, P., Lejeune, O., 2001. Periodic spotted patterns in semi-arid vegetation explained by a propagation–inhibition model. *Journal of Ecology* 89, 616–628.
- Dale, M.R.T., 1999. *Spatial Pattern Analysis in Plant Ecology*. Cambridge University Press, Cambridge.
- Fernández, R.J., Golluscio, R.A., Bisigato, A.J., Soriano, A., 2002. Gap colonization in the Patagonian semidesert: seed bank and diaspore morphology. *Ecography* 25, 336–344.
- Flores, J., Jurado, E., 2003. Are nurse–protégé interactions more common among plants from arid environments? *Journal of Vegetation Science* 14, 911–916.
- Fortin, M.-J., Dale, M.R.T., 2005. *Spatial Analysis: a Guide for Ecologists*. Cambridge University Press, Cambridge.
- Fortin, M.-J., Legendre, P., 1989. Spatial autocorrelation and sampling design in plant ecology. *Vegetatio* 83, 209–222.
- Fowler, N.L., 1988. What is a safe site? Neighbor, litter, germination date, and patch effects. *Ecology* 69, 947–961.
- Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* 1, 143–156.
- León, R.J.C., Bran, D., Collantes, M., Paruelo, J.M., Soriano, A., 1998. Grandes unidades de vegetación de la Patagonia extra andina. *Ecología Austral* 8, 125–144.
- Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J., Imeson, A.C., 2005. Vegetation patches and runoff–erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* 86, 288–297.
- Maestre, F.T., Cortina, J., 2005. Remnant shrubs in Mediterranean semi-arid steppes: effects of shrub size, abiotic factors and species identity on understorey richness and occurrence. *Acta Oecologica* 27, 161–169.
- Montaña, C., Seghieri, J., Cornet, A., 2001. Vegetation dynamics: recruitment and regeneration in two-phase mosaics. In: Tongway, D., Valentin, C., Seghieri, J. (Eds.), *Banded Vegetation Patterning in Arid and Semi Arid Environments. Ecological Processes and Consequences for Management*. Springer Verlag, New York, pp. 132–145.

- Moro, M.J., Pugnaire, F.I., Haase, P., Puigdefábregas, J., 1997. Mechanisms of interaction between a leguminous shrub and its understorey in a semi-arid environment. *Ecography* 20, 175–184.
- Pazos, G.E., Bertiller, M.B., 2008. Spatial patterns of the germinable soil seed bank of coexisting perennial-grass species in grazed shrublands of the Patagonian Monte. *Plant Ecology* 198, 111–120.
- Pazos, G.E., Bisigato, A.J., Bertiller, M.B., 2007. Abundance and spatial patterning of coexisting perennial grasses in grazed shrublands of the Patagonian Monte. *Journal of Arid Environments* 70, 316–328.
- Schlesinger, W.H., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77, 364–374.
- Sokal, R.R., Rohlf, F.J., 1997. *Biometry*, third ed. W.H. Freeman, New York.
- Tobin, P.C., 2004. Estimation of the spatial autocorrelation function: consequences of sampling dynamic populations in space and time. *Ecography* 27, 767–775.
- Uuemaa, E., Roosaare, J., Kanal, A., Mander, Ü, 2008. Spatial correlograms of soil cover as an indicator of landscape heterogeneity. *Ecological Indicators* 8, 783–794.