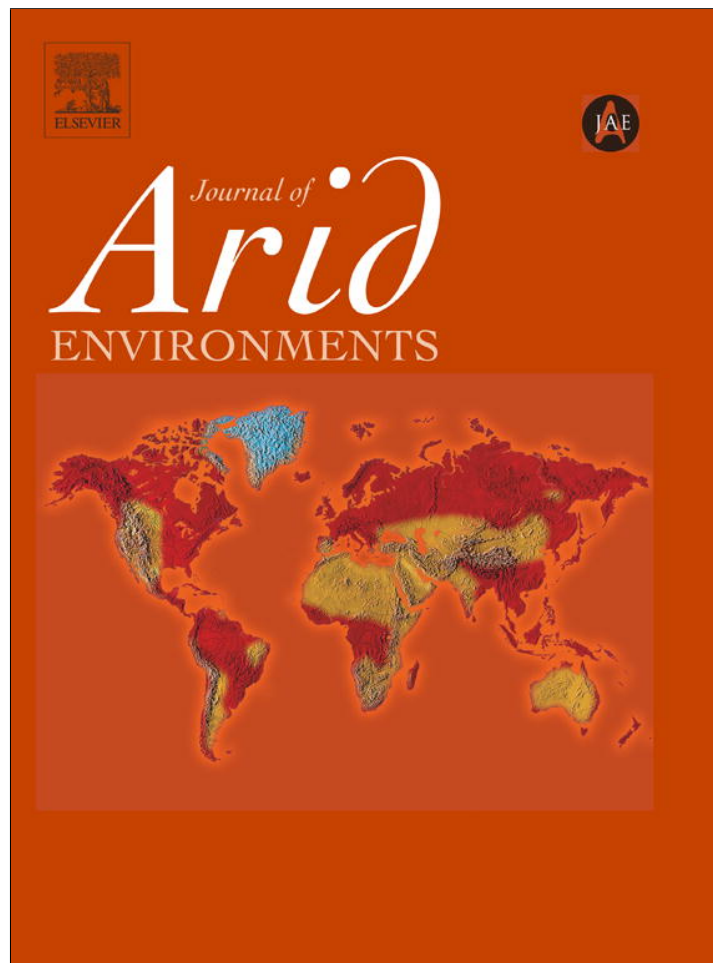


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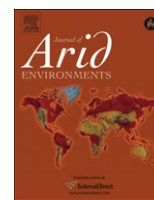
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Short communication

Biological soil crusts affect small-scale spatial patterns of inorganic N in a semiarid Mediterranean grassland

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ABSTRACT

The influence of biological soil crusts (BSCs) on the small-scale spatial distribution of inorganic nitrogen (N) in drylands is largely unknown, despite their known impact and importance on the N cycle in these environments. We evaluated how perennial plants and BSCs affected small-scale spatial patterns of soil inorganic N (ammonium and nitrate) availability in a semiarid grassland from Spain. The data were analyzed by using geostatistical methods. The range of semivariograms for ammonium and nitrate, and the coefficient of variation of nitrate, were lower in BSC-dominated microsites than in plant-dominated microsites. Our results suggest that BSCs modulate the small-scale spatial pattern of inorganic N, producing more homogeneous conditions for spatial distribution of inorganic N forms than microsites provided by plants. These results may have important repercussions for the foraging strategies and ability of plant roots to uptake N.

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1. Introduction

Nitrogen (N) is, after water, the most important factor limiting plant growth and net primary production in soil ecosystems (Robertson and Groffman, 2007). The small-scale spatial heterogeneity in the availability of soil N is a ubiquitous feature of natural ecosystems (Gallardo et al., 2006; Schlesinger et al., 1996), and can influence plant performance and ecosystem processes at multiple organization levels (Hutchings et al., 2000). The spatial pattern of inorganic N is largely affected by isolated plant patches in drylands (Halvorson et al., 1994; Jackson and Caldwell, 1993), which establish islands of fertility (Gallardo et al., 2006; Garner and Steinberger, 1989). Biological soil crust (BSC) communities, dominated by algae, mosses, liverworts, fungi, bacteria and lichens, live in the uppermost millimeters of the soil surface of drylands worldwide (Belnap and Lange, 2003). Their influence on the spatial inorganic N distribution in semiarid ecosystems is largely unknown, although BSCs influence N cycling processes such as N fixation (Belnap and Lange, 2003), nitrification (Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2010), and gaseous N loss

(Barger et al., 2005). We analyzed the small-scale spatial patterns of inorganic N availability in plant- and BSC-dominated microsites in a semiarid grassland from Spain dominated by the tussock grass *Stipa tenacissima* L. These ecosystems, which have sparse plant coverage, are one of the most widespread semiarid ecosystems in the Mediterranean Basin (Le Houérou, 2001). Biological soil crusts frequently occupy the open spaces located between *Stipa* canopies and play multiple functional roles in these grasslands (Maestre et al., 2011).

2. Methods

This study was conducted in the Aranjuez experimental station, in the center of Spain (40°02'N – 3°32'W; 590 m a.s.l.). The climate is Mediterranean semiarid, with an average annual rainfall and temperature of 349 mm and 15 °C, respectively. Perennial plant coverage is lower than 40%, and is dominated by isolated individuals of *Stipa* and the N-fixing shrub *Retama sphaerocarpa* L. Open areas between plant patches contain a well-developed BSC community dominated by lichens such as *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt, and *Toninia sedifolia* (Scop.) Timdal (see Castillo-Monroy et al., 2010 for a full species checklist). The soil is classified as Xeric Haplogypsid (USDA, 2003), and has a fine texture

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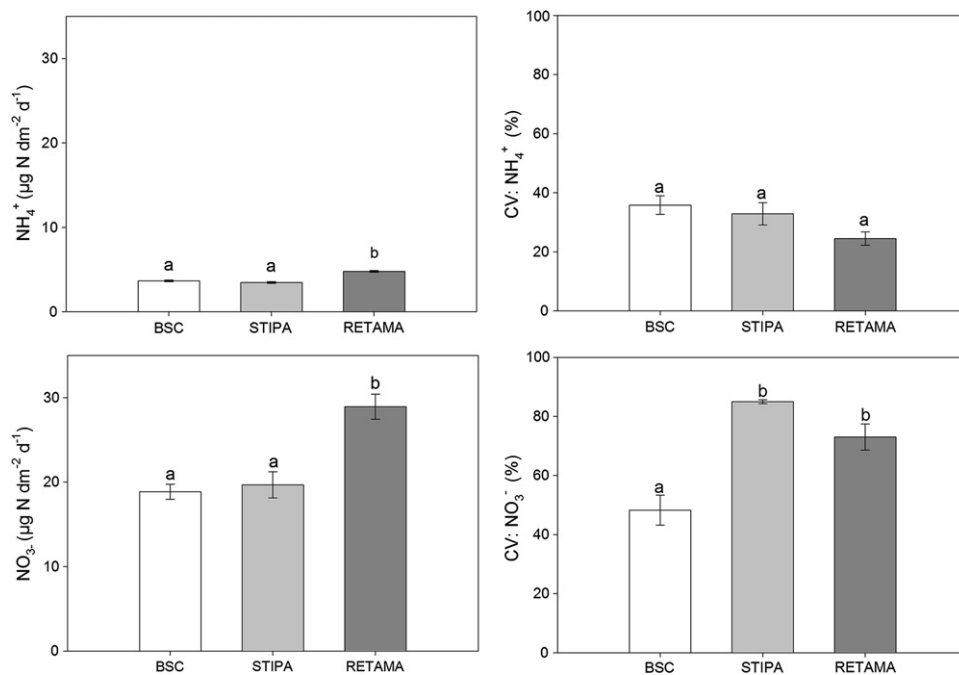


Fig. 1. Concentration ($\mu\text{g dm}^{-2} \text{d}^{-1}$) and coefficient of variation (CV, in %) of ammonium (NH_4^+) and nitrate (NO_3^-) for biological soil crust (BSC), *Stipa tenacissima* (STIPA) and *Retama sphaerocarpa* (RETAMA) microsites. Data are means \pm SE ($n = 70, 80$ and 160 for the BSC, STIPA and RETAMA microsites, respectively). Different letters indicate significant differences between microsites ($p < 0.05$) in the concentration (post-hoc tests after one-way ANOVA) and CV (post-hoc tests after PERMANOVA analysis) of NH_4^+ and NO_3^- .

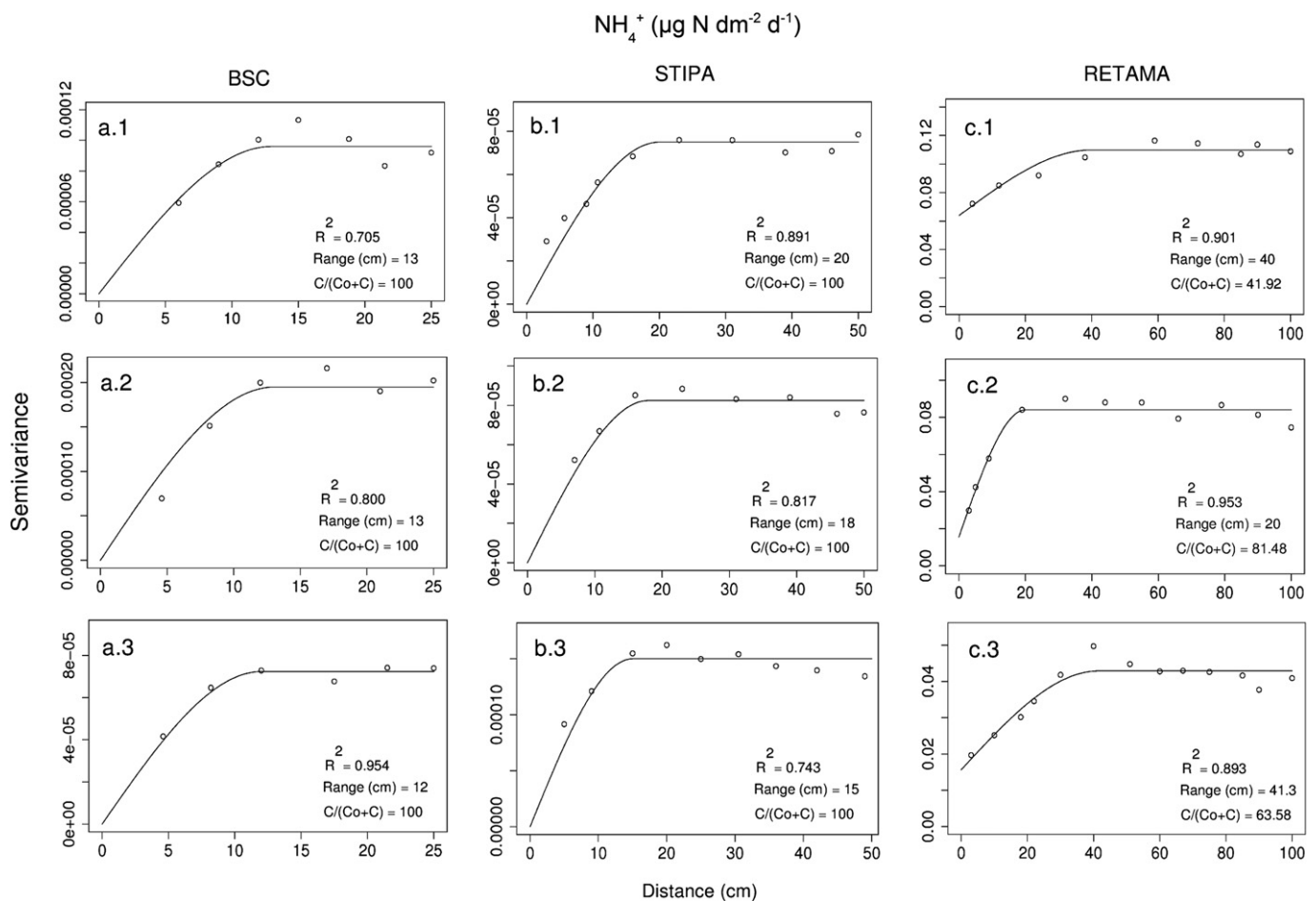


Fig. 2. Semivariograms for ammonium (NH_4^+) under biological soil crusts (BSC), *Stipa tenacissima* (STIPA) and *Retama sphaerocarpa* (RETAMA). The line represents the fitted spherical model. Additional details on each of the models fitted are given in each panel.

dominated by the presence of gypsum. For the top 10-cm of the soil profile, pH ranges between 7.2 and 7.7; soil C between 1% and 3.2%; and soil N between 0.16% and 0.4%; both extremes corresponding to bare soil and under *Retama* canopies respectively. Three representative microsites were selected from our study site: *Stipa*, *Retama* and bare-ground areas with well-developed BSC communities. Whereas articles focusing on the spatial patterns of soil properties are typically conducted in a single site (i.e. without replication at this level, Maestre and Cortina, 2002; Gallardo et al., 2006), three replicated plots of each microsite were randomly selected in this study. This allowed us to obtain more representative estimates of the spatial patterns evaluated, given the small-scale heterogeneity characterizing BSCs (Castillo-Monroy et al., 2010). At each selected plot, we measured soil inorganic N availability using 2.5 cm × 2.5 cm anionic and cationic exchange membranes (IEMs, Subler et al., 1995). The number and spatial configuration of membranes at each replicated plot on the microsite considered (a minimum of 70 sampling points per microsite were used; see Appendix 1 for details on the spatial sampling design). The minimal distance between points was 5 cm. At each sampling point, anionic and cationic exchange membranes were incubated for 30 days during spring of 2010, the season when higher inorganic N contents are found at the study area (Castillo-Monroy et al., 2010). The membranes were positioned just below the top of the surface horizon with a metal spatula, and the soil around them was compacted together with the BSC to ensure proper contact between the

membranes and the soil. The IEMs technique has minimal soil disturbance compared to traditional destructive methods such as soil extraction and resin bags (Duran et al., 2012). Upon retrieval, the IEMs were individually transported to the lab, air-dried, and cleaned of soil particles. The amount of nitrate (NO₃⁻-N) and ammonium (NH₄⁺-N) in the IEMs was obtained as described in Castillo-Monroy et al. (2010). Data were expressed as μg N dm⁻² resin surface day⁻¹.

To include the effects of spatial autocorrelation of data, the differences between microsites in the amount of NO₃⁻-N and NH₄⁺-N were tested by using a spatially adjusted one-way ANOVA (Griffith, 1978). The coefficients of variation of inorganic N forms were calculated within the different microsites, and statistically compared by using the semi-parametric PERMANOVA technique (Anderson, 2001). The spatial dependence of the samples was analyzed using geostatistical analyses (Robertson, 1987). Semivariograms were calculated for each variable in this study to show the average variance found in comparison to samples taken at an increasing distance from one another, also known as the lag interval. In order to quantify the spatial dependence, we calculated the percentage of total variance (sill; C0 + C) explained by the spatial variance (C). The range indicates the distance, beyond which samples are spatially independent. Variance that exists at a scale smaller than the field sampling is found at 0 lag distance and is known as the nugget variance (C0). All semivariograms were fitted to a spherical model. The statistical analyses were performed with

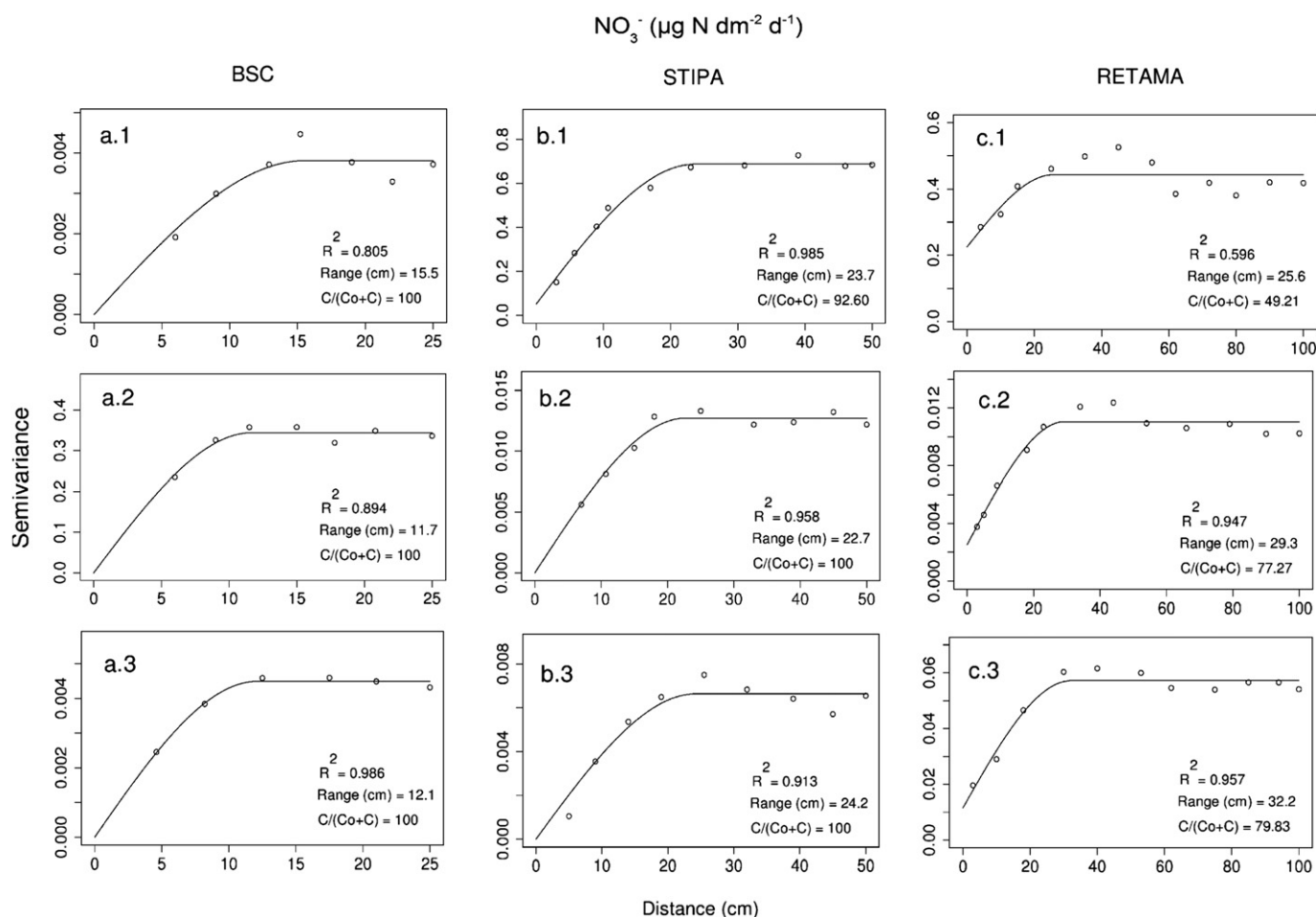


Fig. 3. Semivariograms for nitrate (NO₃⁻) under biological soil crusts (BSC), *Stipa tenacissima* (STIPA) and *Retama sphaerocarpa* (RETAMA). Rest of legend as in Fig. 2.

R 2.7 statistical software (R Development Core Team, 2008). The geostatistical analyses were carried out using the geoR and gstat R modules (Ribeiro and Diggle, 2001).

3. Results and discussion

Ammonium and NO_3^- -N concentrations were the highest under *Retama* canopies (Fig. 1; $p < 0.01$). However, no differences were found between BSC and *Stipa* microsites for any inorganic N form (Fig. 1; $p > 0.05$), suggesting that BSC-dominated microsites can be also an important source of inorganic N for plants and microorganisms. The coefficient of variation (CV) of NH_4^+ -N was similar ($p > 0.05$) for the different microsites: BSC ($35.8 \pm 3.1\%$), *Stipa* ($32.9 \pm 3.8\%$) and *Retama* ($24.5 \pm 2.3\%$), but that of NO_3^- -N was almost two times higher under the canopies of *Stipa* and *Retama* than at BSC microsites (Fig. 1, $p < 0.05$). These results suggest that BSCs provide more homogeneous conditions for the spatial distribution of NO_3^- -N than plant microsites, but similar conditions for NH_4^+ -N. The range of the semivariograms obtained for NH_4^+ -N and NO_3^- -N was lowest in the BSC microsites (Figs. 2 and 3), and highest under *Retama* canopies (Figs. 2 and 3). This fact may have important repercussions for the plant ability to uptake N, as BSCs typically form extensive carpets in open spaces located between plant canopies in ecosystems such as those studied (Maestre et al., 2011). Thus, a root foraging for nutrients may need less length under BSCs (between 11.7 cm and 15.5 cm) than under the canopies of *Stipa* (between 15 cm and 24.2 cm) and *Retama* (between 20 cm and 41.3 cm) to explore all inorganic N variability. In general, the CV of NO_3^- -N was higher than that of NH_4^+ -N under the canopies of both *Stipa* and *Retama* (Fig. 1); this response was not observed at BSC microsites. These results suggest that the conditions for nitrification may be more heterogeneous than those for ammonification at *Stipa* and *Retama* microsites. However, BSCs may homogenize the soil conditions, coupling these N transformation processes in soil.

Our results indicate that, BSCs may produce similar or more homogeneous soil conditions than plant canopies for the spatial distribution of both NH_4^+ -N and NO_3^- -N, and thus for N mineralization. These findings may have important implications for plant nutrient uptake. As BSCs form extensive carpets in the open spaces between plant canopies, and inorganic N concentrations in these areas are similar to those found under *Stipa* canopies; the homogeneous spatial structure for soil nutrients may facilitate the acquisition of N by plant roots under developed BSCs.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2013.01.005>.

References

- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.
- Barger, N.N., Belnap, J., Ojima, D.S., Mosier, A., 2005. NO gas loss from biologically crusted soils in Canyonlands National Park, Utah. *Biogeochemistry* 75, 373–391.
- Belnap, J., Lange, O.L., 2003. *Biological Soil Crusts: Structure, Function, and Management*. Springer-Verlag, Berlin.
- Castillo-Monroy, A.P., Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., 2010. Biological soil crusts modulate nitrogen availability in semi-arid ecosystems: insights from a Mediterranean grassland. *Plant and Soil* 333, 21–34.
- Delgado-Baquerizo, M., Castillo-Monroy, A.P., Maestre, F.T., Gallardo, A., 2010. Change in the dominance of N forms within a semi-arid ecosystem. *Soil Biology and Biochemistry* 42, 376–378.
- Durán, J., Delgado-Baquerizo, M., Rodríguez, A., Covelo, F., Gallardo, A., 2012. Ionic Exchange Membranes (IEMs): a Good Indicator of Soil Inorganic N Production. *Soil Biology and Biochemistry*. <http://dx.doi.org/10.1016/j.soilbio.2012.07.016>.
- Gallardo, A., Parama, R., Covelo, F., 2006. Differences between soil ammonium and nitrate spatial pattern in six plant communities. Simulated effect on plant populations. *Plant Soil* 279, 333–346.
- Garner, W., Steinberger, Y., 1989. A proposed mechanism for the formation of “Fertile Islands” in the desert ecosystem. *Journal of Arid Environments* 16, 257–262.
- Griffith, D.A., 1978. A spatially adjusted ANOVA model. *Geographical Analysis* 10, 296–301.
- Halvorson, J.J., Bolton, H., Smith, J.L., Rossi, R.E., 1994. Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. *Great Basin Naturalist* 54, 313–328.
- Hutchings, M.J., John, E.A., Stewart, A.J.A. (Eds.), 2000. *The Ecological Consequences of Environmental Heterogeneity*. Blackwell Science, Cambridge, UK.
- Jackson, R.B., Caldwell, M.M., 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology* 81, 683–692.
- Le Houérou, H.N., 2001. Biogeography of the arid steppe land north of Sahara. *Journal of Arid Environments* 48, 103–128.
- Maestre, F.T., Cortina, J., 2002. Spatial patterns of surface soil properties and vegetation in a Mediterranean semi-arid steppe. *Plant and Soil* 241, 279–291.
- Maestre, F.T., Bowker, M.A., Cantón, Y., Castillo-Monroy, A.P., Cortina, J., Escobar, C., Escudero, A., Lázaro, R., Martínez, I., 2011. Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain. *Journal of Arid Environments* 75, 1282–1291.
- R Development Core Team, 2008. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. URL: <http://www.R-project.org>.
- Ribeiro, P.J., Diggle, P.J., 2001. geoR: a package for geostatistical analysis. *R-NEWS* 1, 15–18.
- Robertson, G.P., 1987. Geostatistics in ecology: interpolating with known variance. *Ecology* 68, 744–748.
- Robertson, G.P., Groffman, P., 2007. Nitrogen transformations. In: Paul, E.A. (Ed.), *Soil Microbiology, Biochemistry, and Ecology*. Springer, New York, USA, pp. 341–364.
- 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.
- Subler, S., Blair, J.M., Edwards, C.A., 1995. Using anion-exchange membranes to measure soil nitrate availability and net nitrification. *Soil Biology and Biochemistry* 27, 911–917.
- USDA, 2003. *Key to Soil Taxonomy*. Handbook 436, ninth ed. Soil Survey Staff, NRCS, Washington, USA, pp 332.