

Does habitat structure matter? Spatially explicit population modelling of an Iberian gypsum endemic

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Received: 24 April 2008 / Accepted: 14 December 2008 / Published online: 4 February 2009
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Abstract Habitat heterogeneity may influence plant demography because conditions for survival, growth, and reproduction vary within a species' range. We assessed the role of microhabitat spatial structure on the demography of *Helianthemum squamatum*, a shrubby gypsum specialist endemic to the Iberian Peninsula. We evaluated the demographic effect of microhabitat spatial variation using an approach that combined cellular automata with matrix population models, and included environmental and demographic stochasticity. We collected data on seed bank (2003–2005), seedling emergence (2003–2006), and adult survivorship (2004–2007) for *H. squamatum* in two independent blocks with different grazing intensity in Belinchón (Cuenca, Spain). We built spatial scenarios for each block based on field data of cover and spatial pattern of four microhabitats: lichenic crust, litter, *H. squamatum*, and shrub. Seedling survivorship was affected by year, block, and microhabitat, with individuals emerging under conspecifics having the highest survival rate and on litter

the lowest in both blocks, whereas the effect of crust and other shrubs differed across blocks. Our models indicated population increase in the block with low grazing, but population decline in the block with intense grazing. We hypothesize that higher pressure of livestock grazing and trampling leads to a shift in relative microhabitat suitability for crust and shrub. This potential effect of grazing on spatial demographic variation opens interesting questions for future research. We emphasize the importance of considering microhabitat spatial structure when evaluating management and conservation strategies.

Keywords Autocorrelation · Cellular automata · Demography · Grazing · *Helianthemum squamatum* · Microhabitat heterogeneity

Introduction

Environmental heterogeneity strongly influences individual performance in plant species at a variety of spatial scales (Czárán and Bartha 1989; Law et al. 2001; Hutchings et al. 2000, 2003). Conditions for survival, growth and reproduction vary spatially within a plant species' range (Poff 1997). For instance, emergence and seedling survival, which will determine the structure and dynamics of most plant populations (Harper 1977; Kitajima and Fenner 2000), usually varies among microhabitats (Fenner and Kitajima 1999). In fact, spatial discordance among plant regeneration stages such as dispersal, germination, early survival, and net recruitment seems to be the norm (Jordano and Herrera 1995; Schupp 1995). As a consequence, most recent papers on plant regeneration take all critical stages and environmental heterogeneity at several spatial and temporal scales into account (e.g., Rey and

Electronic supplementary material The online version of this article (doi:10.1007/s10144-008-0135-z) contains supplementary material, which is available to authorized users.

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Alcántara 2000; Traveset et al. 2003). Thus, predictions of population persistence require understanding of not only environmental patterns, but also how plants respond to different forms and scales of heterogeneity along ontogeny (Kolasa and Rollo 1991).

Neighboring plants, conspecifics or not, may control focal plant performance through a wide range of interactions, ranging from facilitation to competition, which shift along ontogeny (Fowler 1986; Callaway 1997; Miriti et al. 1998, 2001; Miriti 2006). Furthermore, the direction and strength of these interactions are modulated by environmental heterogeneity at contrasting scales (Caldwell and Pearcy 1994; but see Forseth et al. 2001). However, microhabitat variation has been rarely incorporated into population dynamic analysis even though the spatial patterning of microhabitats may profoundly affect plant persistence (Tiélborger and Kadmon 2000).

Probably one of the reasons why this vast knowledge is not scaled-up to the population level is due to the fact that current quantitative models do not consider environmental heterogeneity (Menges 2000). Although population models can incorporate spatial aspects in many ways (Akçakaya 2000), spatially-explicit modeling of plant population viability is rare. Menges (2000) reported that only 2 of 95 plant population viability analyses included some spatial information and only from a metapopulation perspective.

We developed a spatially explicit demographic model based on a cellular automaton in which both environmental and demographic stochasticities are considered to increase the spatial resolution of a simple demographic model and, consequently, to make current viability models more realistic. Cellular automata model dynamics in a spatially-structured system in a discrete fashion using a regular lattice of cells and rules that define changes in each cell and interactions among cells (Silvertown et al. 1992; Balzter et al. 1998; Rhode 2005). In our case, changes within each lattice cell are simulated using matrix demographic models in which critical life stages such as emergence and seedling survival are affected by microhabitat cover. Connecting rules among the lattice cells are determined by a spatial function of seed dispersal. We used this model to evaluate the effect of microhabitat heterogeneity on population growth of *Helianthemum squamatum* (L.) Dum. Cours (Cistaceae), a shrubby gypsum specialist endemic to central Spain. This species is a good model system because small-scale heterogeneity affects several of its life stages (Escudero et al. 1999, 2005) and because of its short life span (Caballero 2006). We hypothesize that microhabitat structure strongly affects population growth of *H. squamatum* and that changes in microhabitat structure will determine the viability and persistence of its populations.

Materials and methods

Study species and site

Helianthemum squamatum is one of the most frequent gypsophytes of the Iberian Peninsula. It is an erect dwarf chamaephyte growing in gypsum outcrops at lower elevations (40–900 m). Its fruits are capsules (average length 3 mm) containing small seeds (average diameter 1.3 mm) with a mucilage coating that favors their adhesion onto the soil. The seeds possess no special mechanism for dispersal, although ants and down-slope run-off may affect seed distribution (A. Escudero, personal observation). Seeds can emerge within the next year or persist, forming a persistent seed bank (Caballero et al. 2003, 2005). Emergence is favored by low temperatures (Escudero et al. 1997), which mainly occur in winter and early spring. Survival of *H. squamatum* seedlings is affected by several factors including soil microhabitat characteristics (Escudero et al. 1999; Romão and Escudero 2005), inter- and intra-specific competition (Escudero et al. 2005), and allelopathic inhibition (Escudero et al. 2000).

This study was carried out in Belinchón (Cuenca province, 40°3'20"N, 3°3'31"W, 720 m a.s.l.). Climate is upper semi-arid mesomediterranean (Rivas-Martínez and Loidi 1999), with a mean annual temperature of 14°C and very unpredictable rainfall (a yearly average of 435 mm, but with an extreme summer drought; only 5.6% of rainfall occurs during July and August). The soils are classified as Calcic Gypsisols, developed over gypsum parental rocks (Monturiol and Alcalá del Olmo 1990). Our study community was dominated by dwarf gypsum specialist chamaephytes: mainly *H. squamatum* and *Lepidium subulatum* L., but also other narrow endemics such as *Teucrium pumilum* L. and *Thymus lacaitae* Pau, and some wide generalists like *H. hirtum* (L.) Miller. A diverse annual community (Olano et al. 2005) and lichen-dominated biological soil crust (Martínez et al. 2006) were interspersed with patches of shrubby species (10% median shrub cover per 0.25 m², 85% maximum cover).

Field sampling

We collected microhabitat-specific demographic data on *H. squamatum* seeds, seedlings, and adults in two 20 × 20 m areas, hereafter block A and block B, in a gypsum vegetation area. Blocks were 300 m apart. Each block was divided into 100 (2 × 2 m) cells. We obtained demographic data for two dry years (383 and 219 mm of annual precipitation for 2003 and 2005, respectively) and one wet year (542 mm for 2004). Our study years encompassed from the lower 10th annual precipitation percentile in 2005 to the upper 80th percentile in 2004 for a 30-year data set

(Instituto Nacional de Meteorología, Spain). The greatest heat wave registered in Europe in the last 150 years occurred in the summer of 2003 (Schär and Jendritzky 2004). There is relatively intense, but heterogeneous in space and time, grazing by sheep, especially in block A.

Seed bank composition was estimated in September 2003, April 2004, September 2004, and April 2005 for a 0.5×0.5 m plot within each grid cell (100 points per block; see Caballero 2006; Caballero et al. 2008a, b). Nested in 50 cells of each block, we evaluated seedling (newly recruited plants) emergence and plant survivorship and growth in 0.5×0.5 m plots (a total of 12.5 m^2 per block) distributed in a checkerboard pattern [Appendix S1 in the Electronic Supplementary Material (ESM)]. Seedling emergence and survivorship were evaluated from April 2003 to April 2006. Every seedling was marked and its emergence microhabitat recorded and classified into four classes: under *H. squamatum*, under other shrubs (mostly *L. subulatum*, *T. pumilum* and *Thymus lacaite*; see Caballero et al. (2005, 2008a, b for a complete list of species in this habitat), on bare areas with litter, and on bare areas with lichenic surface crust. We tagged all the newly recruited *H. squamatum* that survived the first 6 months within the seedling plots and continued monitoring them every 6 months. We analyzed the association of annual seedling survival with block, microhabitat, and year using logistic regression implemented using the *glm* function of *R* (Crawley 2007; data from 2004 was not included because no seedlings survived, code in Appendix S1). We also included other adult plants within a band 30 cm wide to obtain sufficiently large sample sizes (579 adult plants were monitored in both blocks across the studied period). We recorded annual survival and measured height and canopy length and width of monitored individuals from April 2004 to April 2007.

We estimated the relative percent ground cover of shrubs, litter, lichenic crust, and *H. squamatum* in each seedling plot every spring. In July 2005, we also evaluated these cover variables in four similarly sized (0.25 m^2) cells located one in the left, one in the top, and two in the right to obtain information concerning their spatial structure to determine the initial conditions for our simulations (Fig. 1 and Appendix S1). We used Moran's I correlograms (Legendre and Legendre 1998) to evaluate the extent of spatial autocorrelation of *H. squamatum* cover and for each microhabitat cover at different distances.

Model construction

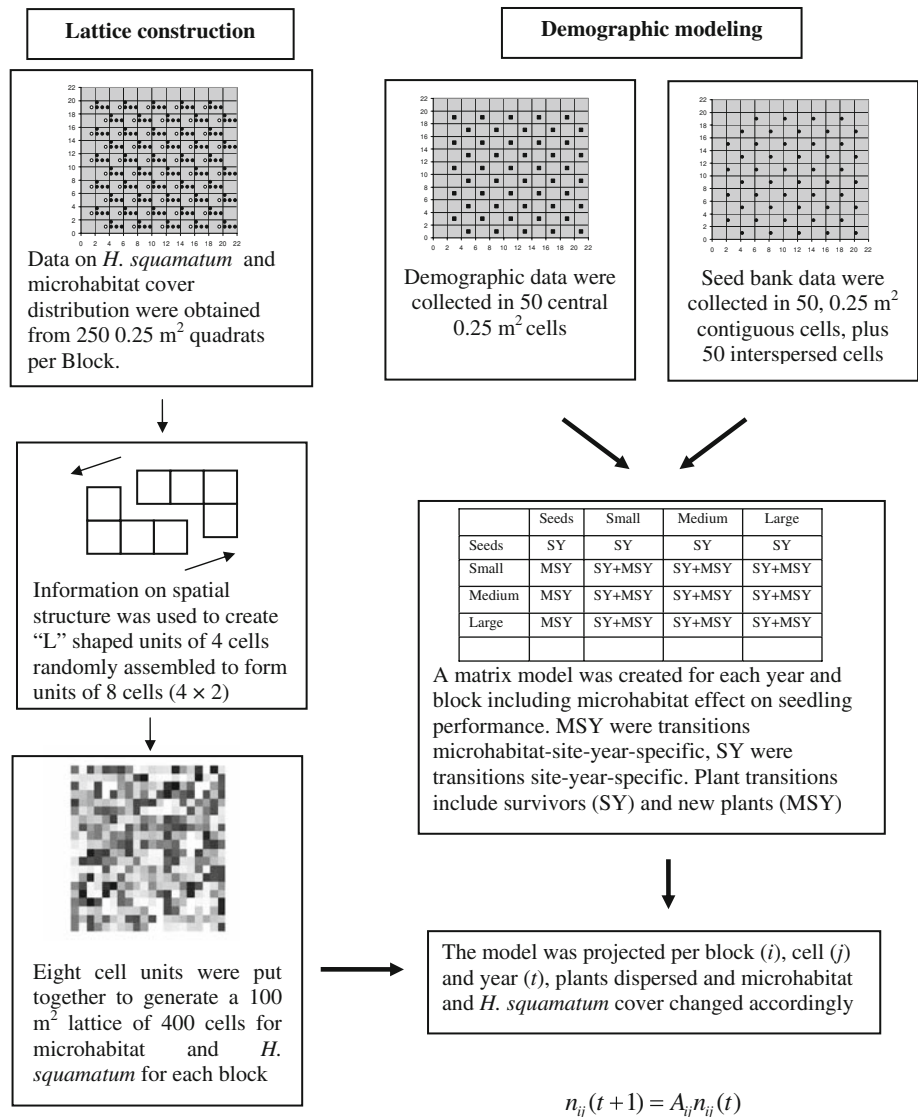
We used Matlab (MathWorks 2007) to build a cellular automaton model of *H. squamatum*. This model describes annual demographic dynamics starting in early March just before the peak of seedling emergence (Escudero et al. 1999)

and before seed production. Calculation of viability is based on a typical demographic matrix selection approach to simulate annual variation in seed, seedling, and adult demography per cell, but also accounts for spatially-explicit microhabitat-dependent seedling emergence and survival. We divided the population into four stages: seeds, and small, medium, and large adult plants. We identified class boundaries of non-seed life stages following Moloney (1986). Maximum diameter was used to classify adults into the three diameter classes (small: <4.5 cm; medium: >4.5 to <8 cm; and large: >8 cm). Connection among cells was simulated based on general observed seed dispersal movements.

We did not attempt to duplicate the demographic or microhabitat spatial structure in the blocks. Instead, we used our sampled data to construct scenarios that evaluated the effect of conditions whose range of variation included the observed values of spatial autocorrelation and microhabitat diversity. We began with scenarios based on the two sampled blocks. The initial population was distributed in a 100-m^2 lattice of 400 (20×20) 0.5×0.5 m cells (hereafter lattice cell) with specific combinations of four substrata microhabitats in each lattice cell (see examples in Fig. 2). We built these initial lattices (independently for each block) using sampled information about the cover of microhabitats and *H. squamatum*. To mimic the observed spatial patterns, we randomly assembled "L" shaped cell units observed in July 2005 to form eight cell units (2×4 cells), and put these units together to form the lattice (Fig. 1; see Appendix S1 in ESM for more details of lattice construction). To allocate demographic data into the assembled plots, we classified all the plots (with and without demographic data) by categories of observed *H. squamatum* cover (1, 2, 3, 4–9, >9), and matched each plot without data with a randomly chosen plot among those in the same *H. squamatum* cover category, but with demographic data.

We simulated stochastic population dynamics of each block independently (see Matlab program in Appendix S2 in ESM). We used a matrix selection approach to project annual transitions per 0.25 m^2 unit. In every step (simulating annual intervals), our model randomly chose one of the three population matrices for each block (built from data for the intervals: 2004–2005, 2005–2006, 2006–2007; Appendix S3 in ESM) and projected the population numbers for each lattice cell. Transitions among stages were independent of microhabitat for adults, but not seeds. Our model captured cover changes between years induced by population dynamics. We included demographic stochasticity by randomly sampling individual fates using a multinomial probability density function (Caswell 2001; Morris and Doak 2002). We did not find density dependence for individual plant growth [$\ln(\text{cover year}_{i+1}/\text{cover year}_i)$; Fig. 3, $R^2 < 0.05$, $P > 0.1$ in both intervals, $n = 57$ and 72 for 2004–2005 and 2005–2006, respectively] nor

Fig. 1 Flowchart describing *Helianthemum squamatum* model construction. In simulations evaluating microhabitat variation, microhabitat cover was increased or decreased accordingly with the combination of values



for adult survival (logistic regression: $P = 0.753$ for 2004–2005 and $P = 0.997$ for 2005–2006). As a consequence, we did not include density dependence in the model. We conducted 1,000 simulations lasting 10 years for each scenario and block.

Adults produced seeds during summer (June–August). Annual fertility (seeds per lattice cell) was estimated based on a linear regression of the number of newly available seeds (September seed bank minus prior April seed bank) on adult cover by plot ($R^2 = 0.34$, $P < 0.001$, $n = 100$; seeds = $0.101 \times$ adult cover). We did not use direct estimates of fecundity based on seed and inflorescence counts before dispersal and depredation because they were an order of magnitude higher than estimates based on seed bank and seedling counts (Aragón et al. 2007). This loss can be attributed to harvester ants that removed large numbers of newly-produced seeds (A. Escudero, personal observation).

We assumed that all seedlings emerge after the March census, and therefore seedlings were implicit and recruitment was expressed as numbers of new adults. We modeled seedling emergence probability per block as the ratio between seedlings counted in April and seeds present in the previous September seed bank. We used microhabitat-specific seedling recruitment and survival data to estimate *H. squamatum* seedling transitions by microhabitat. During simulations, the emerging seedlings per cell were allocated based on microhabitat cover and emergence probability by microhabitat. Seedling survival was also evaluated in relation to microhabitat.

Since *H. squamatum* has limited dispersal which is affected primarily by gravity and ground slope, we used a dispersal model function in which 40% of newly produced seeds remained within the source cell, 30% dispersed to the immediately lower cell, 12.5% moved right, 12.5% left,

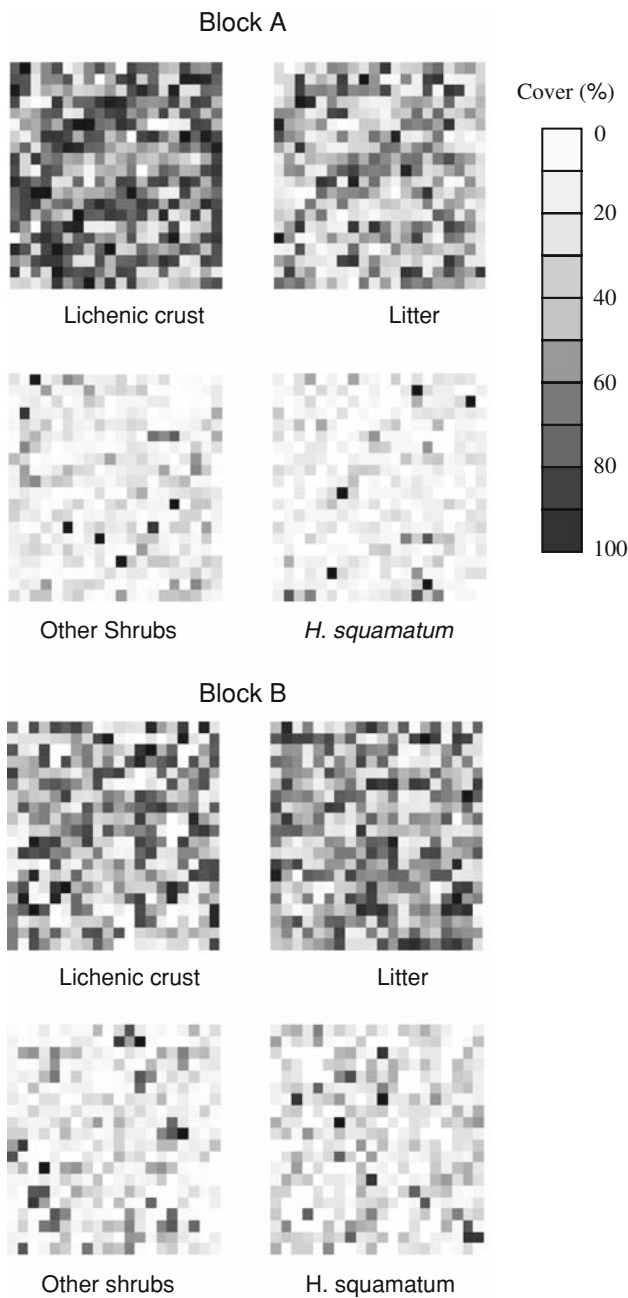


Fig. 2 Examples of simulation scenarios by microhabitat and block. Each lattice was assembled with “L” shaped units (3×2 0.25 m² plots) based on observed plots to preserve spatial structure and demographic information. The shading gradient represents cover variation with darker blocks having higher covers (range 0–100%)

and only 5% to the upper cell (Escudero et al. 1999). We coped with edge effects by wrapping our grid using a torus.

Effects of microhabitat variation on population growth

To evaluate the effect of microhabitat variation on the demographic dynamics we generated 66 spatially-explicit

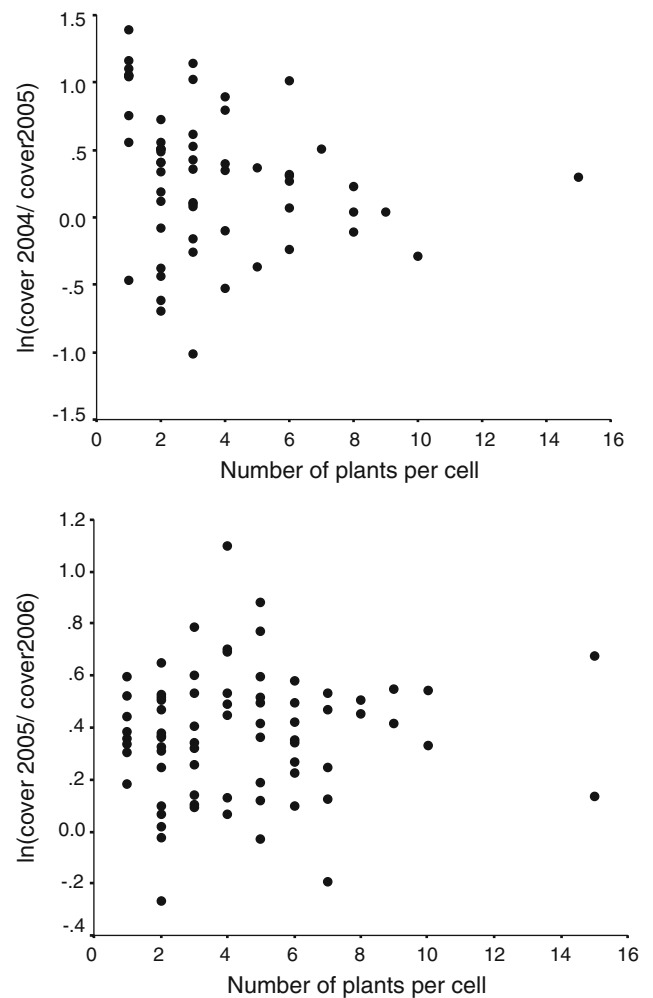


Fig. 3 Individual growth *H. squamatum* versus plant density (blocks pooled) in 2004–2005 and 2005–2006

habitat scenarios varying the initial average relative proportion of substrata: non-*H. squamatum* shrubs, soil crust, and litter cover. Random scenarios explored microhabitat cover variation within three axes in the space defined by [0, 0, 100; 0, 100, 0; and 100, 0, 0] (see Appendix S1 in ESM for the complete series). We allocated crust cover for each lattice cell by sampling a value from a normal distribution with the first value in the set (for example, 20 from the set 20, 30, 50) as the mean and with standard deviation = 1, then we allocated litter cover in a similar fashion but using the second value as the mean (30), and finally we allocated the value that resulted from the subtraction of the sum of these two sampled values from 100 as the value for shrub cover. The total contribution of these three microhabitats was proportionally adjusted to consider the *H. squamatum* cover for the focal cell. Demographic data from the two blocks were independently used in all these scenarios.

Results

Seeds, seedling emergence and survival by microhabitat

There were differences in seed dynamics between years and blocks. The September seed bank density was higher in dry 2003 (block A = 794 seed \times m⁻²; block B = 905 seed \times m⁻²) than in the wet 2004 (block A = 583 seed \times m⁻²; block B = 756 seed \times m⁻²). The number of seeds in the seed bank in April was always lower than in the previous September (2004: block A = 211 seed \times m⁻², block B = 360 seed \times m⁻²; and 2005: block A = 124 seed \times m⁻², block B = 533 seed \times m⁻²). Persistence of seeds in the seed bank from September to April was estimated as the ratio of the numbers in the seed bank at those times, and was higher for block B (2003–2004: block A = 0.2656; block B = 0.3973, 2004–2005: block A = 0.2128; block B = 0.7049). Rate of emergence, estimated as the ratio of the seedling density and the density in the seed bank in September, was similar between blocks but differed between years (2003: block A = 0.0348; block B = 0.0366; 2004: block A = 0.218; block B = 0.197).

Table 1 Proportion of *Helianthemum squamatum* seedlings emerging by habitat and block

Microhabitat	Block A			Block B		
	2003–2004	2004–2005	2005–2006	2003–2004	2004–2005	2005–2006
Crust	0.37	0.41	0.51	0.41	0.26	0.37
Litter	0.46	0.34	0.34	0.39	0.45	0.49
<i>H. squamatum</i>	0.04	0.08	0.03	0.07	0.16	0.03
Other shrubs	0.13	0.17	0.12	0.13	0.13	0.11
Number of seedlings	345	1,593	586	414	1,866	616

Table 2 Global and site average microhabitat specific annual survival of *H. squamatum* seedlings

Microhabitat	Block A			Block B		
	2003–2004	2004–2005	2005–2006	2003–2004	2004–2005	2005–2006
Crust	0.000	0.012	0.013	0.000	0.064	0.026
Litter	0.000	0.013	0.000	0.000	0.014	0.003
<i>H. squamatum</i>	0.000	0.026	0.143	0.000	0.020	0.100
Other shrubs	0.000	0.022	0.000	0.000	0.007	0.000
Overall	0.000	0.013	0.007	0.000	0.027	0.015

Table 3 Lag distance and associated probability (Monte Carlo permutation test) of maximum Moran's I by microhabitat (2004–2005; lag intervals increments by 0.75 m) blocks A and B

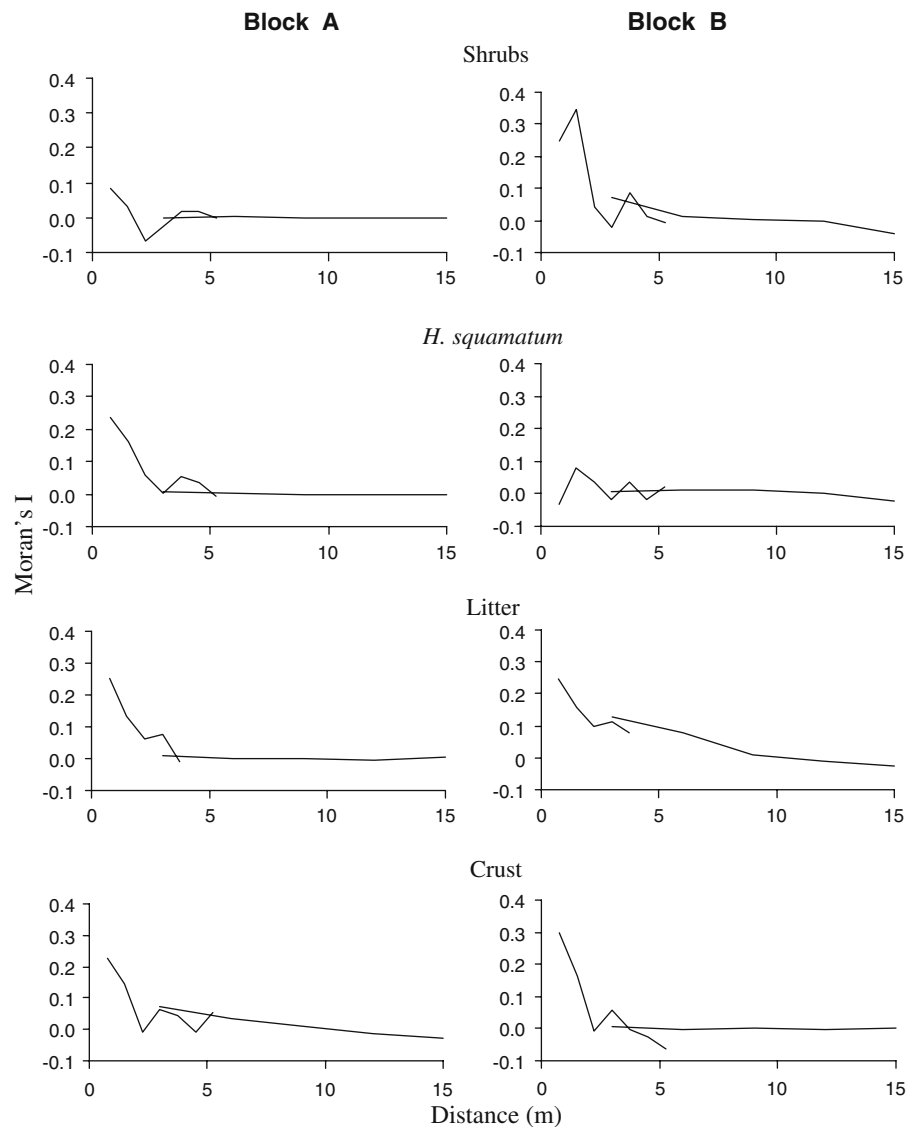
	Block A				Block B			
	Shrubs	<i>H. squ</i>	Litter	Crust	Shrubs	<i>H. squ</i>	Litter	Crust
Moran's I	0.0848	0.239	0.253	0.297	0.344	0.081	0.247	0.227
Lag distance	0–0.75	0–0.75	0–0.75	0–0.75	0.75–1.5	0.75–1.5	0–0.75	0–0.75
<i>P</i>	0.213	0.005	<0.001	<0.001	<0.001	0.236	<0.001	<0.001

A total of 5,420 seedlings emerged and were monitored during the study period. Seedling emergence was low during 2003 ($n = 759$), high during 2004 ($n = 3,459$), and intermediate during 2005 ($n = 1,202$) (Table 1). No seedlings survived after 12 months for 2003, an extremely dry year, but survival reached 2% in 2004 and 1% in 2005. Considering only the last 2 years, we found higher seedling survival in block B, a block by microhabitat interaction with litter and shrub microhabitat, and a marginally significant ($P = 0.058$) interaction between year and *H. squamatum* microhabitat (Table 2 and Appendix S1).

Microhabitat spatial heterogeneity between blocks

There was a significant spatial autocorrelation in the cover of crust and litter microhabitats at shorter distances (<0.75 m) for 0.25 m² cells. This pattern was consistent between blocks (Table 3; Fig. 4). *Helianthemum squamatum* cover was also significantly autocorrelated between neighboring cells at the same small scale in block A but not in block B. In contrast, shrub cover was autocorrelated at 0.75–1.5 m in block B, but random in block A. There were no significant autocorrelations at any distance among cells for density of seeds and seedlings of *H. squamatum*.

Fig. 4 Correlogram (Moran's I) per block and microhabitat. Notice the change of interval size due to the two sampled scales (0.25 and 2 m² cells)



Shrub cover per 0.25 m² was negatively correlated with cover of *H. squamatum* in block B ($r = -0.171$, $P = 0.018$, $n = 191$; double absences excluded), but not in block A ($r = 0.118$, $P = 0.104$, $n = 192$). Shrub was also negatively correlated with crust cover in both blocks ($r = -0.396$, $P < 0.001$, $n = 248$; $r = -0.397$, $P < 0.001$, $n = 243$ for blocks A and B, respectively). Litter cover was negatively correlated with crust cover in both blocks ($r = -0.906$, $P < 0.001$, $n = 247$; $r = -0.864$, $P < 0.001$, $n = 243$) whereas shrub cover was not correlated with litter in both blocks ($P > 0.087$). Finally, neither litter nor crust cover were correlated with *H. squamatum* ($P > 0.672$).

Observed *H. squamatum* occupancy in 2005 was higher among plots with low shrub cover in block B (Fig. 5, $G = 47.09$, $df = 1$, $P < 0.001$). Our data did not support any other occupancy differences among cells with

contrasting cover by litter or crust in block B, or any microhabitat in block A (Fig. 5, G tests, $P > 0.133$).

Population dynamics and effect of changes in microhabitat structure

Simulated stochastic lambdas (finite population growth rates) were higher in block B (range 0.950–1.239) than in block A (lambda range 0.791–0.895) for a 10-year period simulation. These results suggest a stable or growing population in block B, but a sharp decrease in population size in block A. We found a significant positive association between simulated final percent of occupied cells and stochastic lambda in both scenarios (Fig. 6). Our simulated data did not demonstrate a relationship between the stochastic lambda and the amount of spatial autocorrelation of

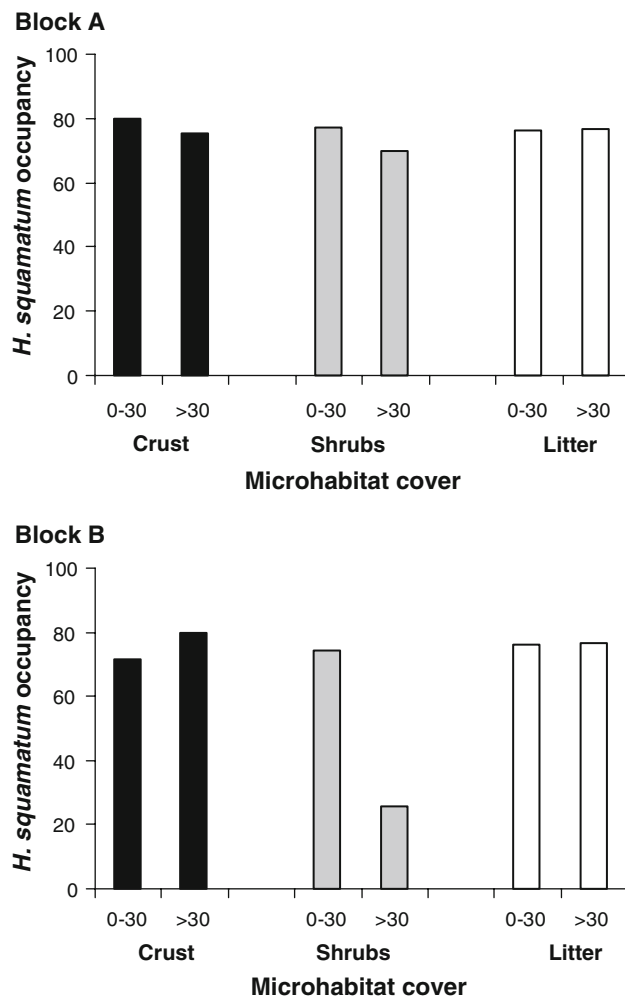


Fig. 5 Observed percent occupied cells by *H. squamatum* by microhabitat and block in 2005. The x-axes are grouped into intervals of 0–30 and >30% microhabitat cover

the microhabitats at small scale (correlation between lambda and Moran I for the first lag was not significant for any microhabitat).

Simulated microhabitat variation affected population dynamics in both blocks. Thus, in Block B, scenarios with a higher proportion of crust and lowest proportion of shrubs were associated with the highest stochastic lambdas (Fig. 7). In contrast, all combinations of scenarios were associated with declining population growth rates in block A. Lower litter cover was associated with the lowest lambdas in both blocks.

Discussion

Our simulations of stochastic lambda indicated that demographic projections varied from stability to sharp decline between populations of *H. squamatum*. This

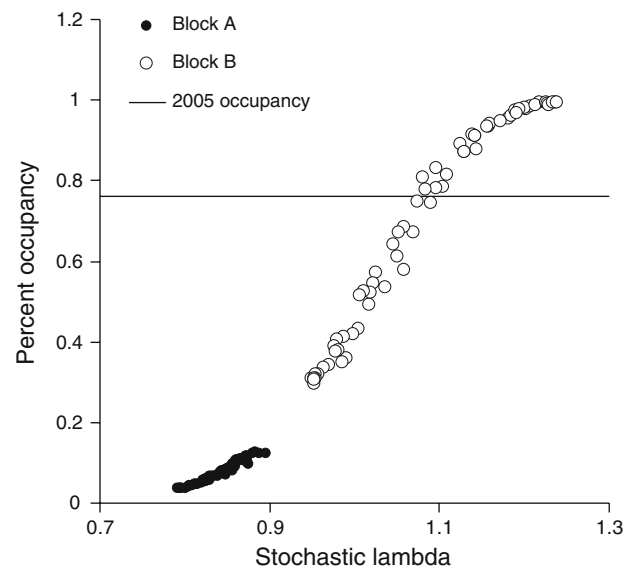
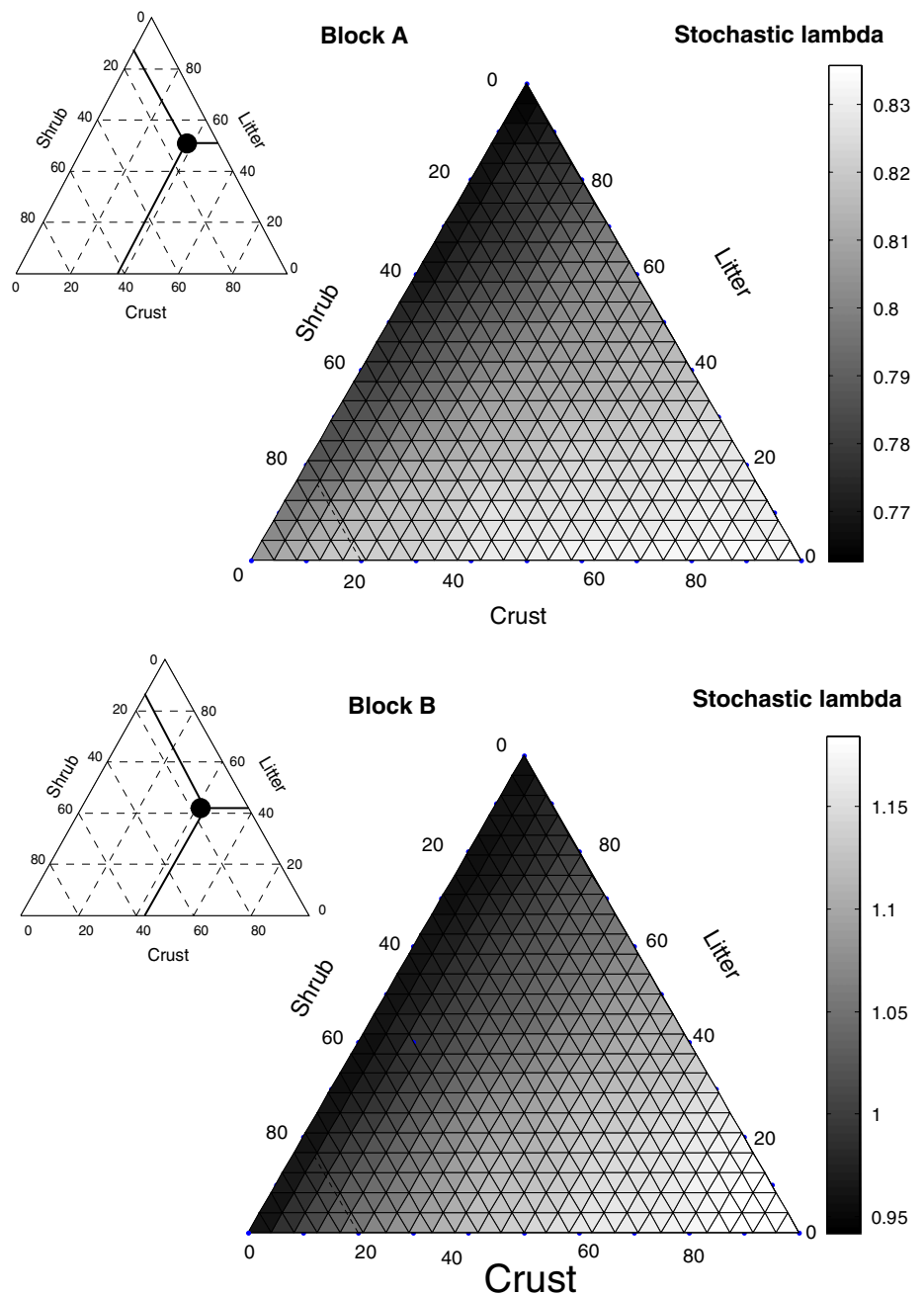


Fig. 6 Average stochastic lambdas versus average percent final occupied cells (after 10 years) of 1,000 simulations per scenario with different shrub, crust, and litter cover using data from Belinchón blocks A and B

demographic variation was mediated by the effect of microhabitat spatial heterogeneity on vital rates, more specifically by the differential response of seedlings to microhabitat heterogeneity and, at a higher scale, by the different response to microhabitats between blocks. Vital rates are profoundly affected by environmental heterogeneity at hierarchical scales, especially in plants in stressful habitats (Czárán and Bartha 1989; Law et al. 2001) and mainly at the seedling stage (Harrington 1991; Kitajima and Fenner 2000). For instance, seed emergence and seedling survival of *H. squamatum* depend on microhabitat characteristics (Escudero et al. 1999). Prior information suggested that *H. squamatum* seedlings can benefit from the proximity of conspecific adults and be negatively affected by the presence of adults from other plant species of the community (Escudero et al. 2005), but our results indicate that such relationships may shift between close (sub)populations. Accordingly, the difference in stochastic lambdas between blocks indicates a change of microhabitat responses between them.

Population dynamics of *H. squamatum* was differentially affected by microhabitat heterogeneity in the two blocks. This species is considered a pioneer that benefits from openings in a dynamic system, having a better seedling performance in bare soil crusted areas (Escudero et al. 2000). Our data and simulations indicated that increasing cover of the lichenic soil surface crust or an equivalent decrease of shrub or litter cover increased population growth in one block (block B). Surprisingly, seedling responses to microhabitat heterogeneity was

Fig. 7 Average stochastic lambdas under scenarios (1,000 simulations per scenario, 10 years) with different shrub, crust, and litter cover simulating data from blocks A (range 0.791–0.895) and B (range 0.950–1.239). *Small triangles* illustrate how to read the triangular chart (Batschelet 1971) using as example the observed cover in 2003 (0.12, 0.37, 0.51 and 0.15, 0.43, 0.42 for shrubs, litter, and crust in Blocks A and B, respectively) and the average baseline (relative habitat as observed; $\lambda = 0.794$ and 1.11, respectively). *Shading* in the plot indicates a descending trend in lambda



substantially different in the other block (block A). In this block, shrub cover increases produced an unexpected increase of the stochastic lambda. This difference in the microhabitat-seedling response between blocks may be related to a differential pressure from grazing which is mainly associated with trampling. Block A constitutes one of the daily paths of a local sheep flock moving to its sheepfold (A. Escudero, personal observation). Under such conditions, shrub patchiness may confer a hypothetical facilitative effect against herbivore consumption and trampling by limiting the grazing and trampling incidence of the sheep flock (Rebollo et al. 2002). Herbivores may

ignore *H. squamatum* seedlings growing in a matrix of other unpalatable species. At the same time, *H. squamatum* growing in this habitat avoid being trampled owing to deterrence caused by perennial shrubs (Baraza et al. 2006). It is also known that grazing mammals vary considerably in their use of habitat at relatively large scales (Rueda et al. 2008), which could explain why the incidence of sheep grazing on these two blocks which are close spatially is so different. At smaller scales, this effect is exacerbated by the feeding behavior of the two main grazers in the community, sheep and rabbits, which results in clustered herbivory-induced deaths (De la Cruz et al. 2008). Such

differential pressure may determine contrasting population fates: local extinction in block A versus stable dynamics in block B. Such changes in the viability of very close (sub)populations are mediated by differential responses of seedlings to microhabitat quality. This degradation is likely linked to an increase in grazing primarily through trampling pressure (Reynolds et al. 2007). Our data are not sufficient to evaluate this hypothesis and it should form the basis for future research.

Integration of widely-used PVA techniques within the framework of cellular automata models provides a tool to simulate the effect of spatially realistic factors on plant demography. The consideration of spatially-explicit data in plant population biology has related mainly to metapopulation contexts, where the fate of each metapopulation was based on colonization/extinction/occupancy processes (reviewed by Husband and Barrett 1996). However, such approaches are not able to model what occurs within a (sub)population and more specifically how spatial biotic or abiotic factors may modulate the fate, growth, and reproduction of individuals and, consequently, the whole population. Our model offers a simple and flexible way to account for spatially-explicit processes at the individual scale and an adequate mechanism for scaling up such information to the population level. For instance, our model is able to capture the differential response of seedlings, emergence, and survival, to microhabitat. The effect of such responses and of the cover structure is considered at very small scales (0.25 m² lattice cells). Microhabitat structure could be modified over time to achieve more realistic models. In our case, the *H. squamatum* cover changes over time and allows our model to reflect the high turnover of this plant due to its short lifespan (Caballero 2006). The rules which define connectivity among cells were related to dispersal. Consequently, we could test a wide range of meaningful ecological hypotheses by modifying the dispersal functions (Quintana-Ascencio et al. 2008). For instance, the implications of some dispersal functions, such as atelechory (no dispersal), which is common among desert plants (Ellner and Shmida 1981), versus long distance dispersal on population growth, could be easily explored with our model.

Conclusions

Spatial microhabitat heterogeneity is a potential key factor in plant population dynamics. Thus, its explicit consideration in demographic modeling seems necessary to achieve more realistic models. Plant performance often relies on processes that depend on types and scales of environmental heterogeneity (Kolasa and Rollo 1991). Recognition of the effect of spatial heterogeneity and their

hierarchical linkage across scales has improved understanding of ecological dynamics, particularly for plants, and the ability to design proper management strategies (Wu and Loucks 1995; Law et al. 2001). Our model assessed the demographic consequences of microhabitat variation and spatial structure on vital rates and population dynamics of the gypsum endemic *H. squamatum* and indicated the importance of these processes for proper management and conservation of stress and endangered habitats such as the gypsum Mediterranean steppes. For instance, the effects of processes changing the relative importance of microhabitats can affect the persistence of specialist species like *H. squamatum* in the gypsum ecosystem (González-Bernáldez 1991; Díaz et al. 1994; Dalaka and Sgardelis 2006). Furthermore, degradation processes may modify the response of some key life stages to this microhabitat heterogeneity long before the microhabitat structure itself suffers a significant change. Here, we showed a mechanism of how habitat quality loss, probably one of the most relevant global change drivers (Millennium Ecosystem Assessment 2005), may lead to the local extinction of a specialist shrub of semi-arid environments, even before the general community structure will suffer a significant change.

Acknowledgments Dr. Santiago Pajarón and his family granted access to their property and Dra. S. García Rabasa provided meteorological data. We benefited from the comments of E. Boughton, E. Stephens, J. Fauth, J. M. Iriondo, D. Jenkins, X. Picó, E. Menges, J. Navarra, and two anonymous reviewers. Luis Giménez-Benavides, Arantzazu L. Luzuriaga, Cristina Fernández-Aragón and Joseba collaborated with field work. D. Stephens helped in preparing the figures. P.F.Q.A. was supported in part by the Spanish Ministerio de Educación y Ciencia and Universidad de Valladolid. This work was partially funded by the Spanish Ministerio de Educación y Ciencia (REN2003-03366) and Comunidad de Madrid (REMEDINAL, S-0505/AMB-0335).

References

- Akçakaya HR (2000) Population viability analysis with demography and spatially structured models. *Ecol Bull* 48:23–38
- Aragón CF, Albert MJ, Giménez-Benavides L, Luzuriaga AL, Escudero A (2007) Environmental scales on the reproduction of a gypsophyte: a hierarchical approach. *Ann Bot* 99:519–527. doi:10.1093/aob/mcl280
- Balzer H, Braun PW, Köhler W (1998) Cellular automata models for vegetation dynamics. *Ecol Model* 107:113–125. doi:10.1016/S0304-3800(97)00202-0
- Baraza E, Zamora R, Hódar JA (2006) Conditional outcomes in plant-herbivore interactions: neighbours matter. *Oikos* 113:148–156. doi:10.1111/j.0030-1299.2006.14265.x
- Batschelet E (1971) Introduction to mathematics for life sciences. Springer, New York
- Caballero I (2006) Estructura espacio-temporal de un banco de semillas: Las comunidades gipsícolas del centro de la Península Ibérica. Ph.D. thesis, Universidad del País Vasco, Bilbao, Spain (in Spanish)

- Caballero I, Olano JM, Loidi J, Escudero A (2003) Seed bank structure along a semi-arid gypsum gradient in Central Spain. *J Arid Environ* 55:287–299. doi:10.1016/S0140-1963(03)00029-6
- Caballero I, Olano JM, Luzuriaga AL, Escudero A (2005) Spatial coherence between seasonal seed banks in a semi-arid gypsum community: density changes but structure does not. *Seed Sci Res* 15:153–160
- Caballero I, Olano JM, Escudero A, Loidi J (2008a) Seed bank spatial structure in semiarid environments: beyond the patch-bare area dichotomy. *Plant Ecol* 195:215–223. doi:10.1007/s11258-007-9316-7
- Caballero I, Olano JM, Loidi J, Escudero A (2008b) A model for small-scale seed bank and standing vegetation connection along time. *Oikos* 117:1788–1795. doi:10.1111/j.1600-0706.2008.17138.x
- Caldwell MM, Pearcy RW (1994) Exploitation of environmental heterogeneity by plants: ecophysiological processes above- and belowground. Academic Press, San Diego
- Callaway RM (1997) Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112:143–149. doi:10.1007/s004420050293
- Caswell H (2001) Matrix population models: construction, analysis and interpretation. Sinauer, Sunderland
- Crawley MJ (2007) The R book. Wiley, Chichester
- Czárán T, Bartha S (1989) The effect of spatial pattern on community dynamics: a comparison of simulated and field data. *Vegetatio* 83:229–239. doi:10.1007/BF00031695
- Dalaka A, Sgardelis S (2006) Life strategies and spatial arrangement of grasses in Mediterranean ecosystem in Greece. *Grass Forage Sci* 61:218–231. doi:10.1111/j.1365-2494.2006.00527.x
- de la Cruz M, Romão RL, Escudero A, Maestre FT (2008) Where do seedlings go? A spatio-temporal analysis of seedling mortality in a semi-arid gypsophyte. *Ecography*. doi:10.1111/j.2008-0906-7590-05299-x
- Díaz S, Acosta A, Cabido M (1994) Community structure in montane grasslands of Central Argentina in relation to land use. *J Veg Sci* 5:483–488
- Ellner S, Shmida A (1981) Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* 51:133–144. doi:10.1007/BF00344663
- Escudero A, Carnes L, Pérez-García F (1997) Seed germination of gypsophytes and gypsosvags in semiarid central Spain. *J Arid Environ* 36:487–497
- Escudero A, Somolinos RC, Olano JM, Rubio A (1999) Factors controlling the establishment of *Helianthemum squamatum* (L.) Dum., an endemic gypsophile of semi-arid Spain. *J Ecol* 87:290–302. doi:10.1046/j.1365-2745.1999.00356.x
- Escudero A, Albert MJ, Pérez-García F (2000) Inhibitory effects of *Artemisia herba-alba* on the germination of the gypsophyte *Helianthemum squamatum*. *Plant Ecol* 148:71–80. doi:10.1023/A:1009848215019
- Escudero A, Romão R, de la Cruz M, Maestre FT (2005) Spatial pattern and neighbor effects on *Helianthemum squamatum* seedlings in a semiarid Mediterranean gypsum community. *J Veg Sci* 16:383–390. doi:10.1658/1100-9233(2005)016[0383:SPANEO]2.0.CO;2
- Fenner M, Kitajima K (1999) Seed and seedling ecology. In: Pugnaire F, Valladares F (eds) Handbook of functional plant ecology. Marcel-Dekker, New York, pp 589–648
- Forseth IN, Wait DA, Caspe BB (2001) Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial. *J Ecol* 89:670–680. doi:10.1046/j.0022-0477.2001.00574.x
- Fowler NL (1986) The role of competition in plant communities in arid and semiarid regions. *Annu Rev Ecol Syst* 17:89–110
- González-Bernáldez F (1991) Ecological consequences of the abandonment of traditional land use in central Spain. *Options Méditerranéennes* 15:23–29
- Harper JL (1977) Population biology of plants. Academic Press, London
- Harrington GN (1991) Effects of soil moisture on shrub seedling survival in a semi-arid-grassland. *Ecology* 72:1138–1149. doi:10.2307/1940611
- Hutchings MJ, Wijesinghe DK, John EA (2000) The effects of heterogeneous nutrient supply on plant performance: a survey of responses, with special reference to clonal herbs. In: Hutchings MJ, John EA, Stewart AJA (eds) The ecological consequences of environmental heterogeneity. Blackwell, Oxford, pp 91–110
- Hutchings MJ, John EA, Wijesinghe DK (2003) Toward understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* 84:2322–2334. doi:10.1890/02-0290
- Husband BC, Barrett SCH (1996) A metapopulation perspective in plant population biology. *J Ecol* 84:461–469
- Jordano P, Herrera CM (1995) Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* 2:230–237
- Kitajima K, Fenner M (2000) Ecology of seedling regeneration. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International, Oxon, pp 331–359
- Kolasa J, Rollo CD (1991) Introduction: the heterogeneity of heterogeneity: a glossary. In: Kolasa J, Pickett STA (eds) Ecological heterogeneity. Springer, New York, pp 1–23
- Law R, Purves DW, Murrell DJ, Dieckmann U (2001) Causes and effects of small-scale spatial structure in plant populations. In: Silvertown J, Antonovics J, Webb NR (eds) Integrating ecology and evolution in a spatial context. Cambridge University Press, Cambridge, pp 21–44
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam
- Martínez I, Escudero A, Maestre FT, de la Cruz A, Guerrero C, Rubio A (2006) Small-scale patterns of abundance of mosses and lichens forming biological soil crusts in two semi-arid gypsum environments. *Aust J Bot* 54:339–348. doi:10.1071/BT05078
- MathWorks (2007) MATLAB: the language of technical computing. Version 7.2. R14. MathWorks, Natick
- Menges ES (2000) Population viability analysis in plants: challenges and opportunities. *Trends Ecol Evol* 15:51–56. doi:10.1016/S0169-5347(99)01763-2
- Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: current state and trends. Island Press, Washington, DC
- Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *J Ecol* 94:973–979. doi:10.1111/j.1365-2745.2006.01138.x
- Miriti MN, Howe HF, Wright SJ (1998) Spatial patterns of mortality in a Colorado Desert plant community. *Plant Ecol* 136:41–51. doi:10.1023/A:1009711311970
- Miriti M, Wright S, Howe HF (2001) The effects of neighbors on the demography of a dominant desert shrub (*Ambrosia dumosa*). *Ecol Monogr* 71:491–509
- Moloney KA (1986) A generalized algorithm for determining category size. *Oecologia* 69:176–180. doi:10.1007/BF00377618
- Monturiol F, Alcalá del Olmo L (1990) Mapa de asociaciones de suelos de la Comunidad de Madrid. Escala 1:200.000. Consejo Superior de Investigaciones Científicas, Madrid (in Spanish)
- Morris WF, Doak DF (2002) Quantitative conservation biology: the theory and practice of population viability analysis. Sinauer, Sunderland
- Olano JM, Caballero I, Loidi J, Escudero A (2005) Prediction of plant cover from seed bank analysis in a semi-arid plant community on

- gypsum. *J Veg Sci* 16:215–222. doi:[10.1658/1100-9233\(2005\)016\[0215:POPCFS\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2005)016[0215:POPCFS]2.0.CO;2)
- Poff NL (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J North Am Benth Soc* 16:391–409
- Quintana-Ascencio PF, Albert MJ, Caballero I, Olano JM, Escudero A (2008) ¿Qué sentido tiene una dispersión poco eficaz? Un modelo demográfico espacialmente explícito de *Helianthemum squamatum*. In: Maestre FT, Escudero A, Bonet A (eds) Introducción al análisis espacial de datos en ecología y ciencias ambientales: métodos y aplicaciones. Universidad Rey Juan Carlos, Mostoles, pp 697–710 (in Spanish)
- Rebollo S, Milchunas DG, Noy Meir I, Chapman PL (2002) The role of a spiny refuge in structuring grazed shortgrass steppe plant communities. *Oikos* 98:53–64. doi:[10.1034/j.1600-0706.2002.980106.x](https://doi.org/10.1034/j.1600-0706.2002.980106.x)
- Rey PJ, Alcántara JM (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *J Ecol* 88:622–633. doi:[10.1046/j.1365-2745.2000.00472.x](https://doi.org/10.1046/j.1365-2745.2000.00472.x)
- Reynolds JF, Smith DMS, Lambin EF, Turner BL, Mortimore M, Batterbury SPJ, Downing TE, Dowlatabadi H, Fernández RJ, Herrick JE, Hubber-Sannwald E, Jiang H, Leemans R, Lynam T, Maestre FT, Ayarza M, Walker B (2007) Global desertification: building a science for dryland development. *Science* 316:847–851. doi:[10.1126/science.1131634](https://doi.org/10.1126/science.1131634)
- Rhode K (2005) Cellular automata and ecology. *Oikos* 110:203–207. doi:[10.1111/j.0030-1299.2005.13965.x](https://doi.org/10.1111/j.0030-1299.2005.13965.x)
- Rivas-Martínez S, Loidi J (1999) Bioclimatology of the Iberian Peninsula. *Itinera Geobot* 13:41–47
- Romão RL, Escudero A (2005) Gypsum physical soil crust and the existence of gypsophytes in semi-arid central Spain. *Plant Ecol* 181:127–137. doi:[10.1007/s11258-005-5321-x](https://doi.org/10.1007/s11258-005-5321-x)
- Rueda M, Rebollo S, Galvez-Bravo L, Escudero A (2008) Habitat use by large and small herbivores in a fluctuating Mediterranean ecosystem: implications of seasonal changes. *J Arid Environ* 72:1698–1708
- Schär C, Jendritzky G (2004) Hot news from summer 2003. *Nature* 432:559–560. doi:[10.1038/432559a](https://doi.org/10.1038/432559a)
- Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am J Bot* 82:399–409
- Silvertown J, Holtier S, Johnson J, Dale P (1992) Cellular automaton models of interspecific competition for space—the effect of pattern on process. *J Ecol* 80:527–534
- Tiëlbörger K, Kadmon R (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81:1544–1553. doi:[10.1890/0012-9658\(2000\)081\[1544:TEVTTB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1544:TEVTTB]2.0.CO;2)
- Traveset A, Gulias J, Riera N, Mus M (2003) Transition probabilities from pollination to establishment in a rare dioecious shrub species (*Rhamnus ludovici-salvatoris*) in two habitats. *J Ecol* 91:427–437. doi:[10.1046/j.1365-2745.2003.00780.x](https://doi.org/10.1046/j.1365-2745.2003.00780.x)
- Wu J, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q Rev Biol* 70:439–466