

Small-scale Environmental Heterogeneity and Spatiotemporal Dynamics of Seedling Establishment in a Semiarid Degraded Ecosystem

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ABSTRACT

In semiarid environments, surface soil properties play a major role in ecosystem dynamics through their influence on processes such as runoff, infiltration, seed germination, and seedling establishment. Surface soil properties usually show a high degree of spatial heterogeneity in semiarid areas, but direct tests to evaluate the consequences of this heterogeneity on seedling establishment are limited. Using a combination of spatial analysis by distance indices (SADIE) and principal components analysis (PCA), we quantified the spatiotemporal patterns of seedling survival of a Mediterranean native shrub (*Pistacia lentiscus*) during the first 3 years after planting on a semiarid degraded site in southeastern Spain. We used a variation partitioning method to identify environmental variables associated with seedling survival patterns. Three years after planting, only 36% of the seedlings survived. During the first summer, one-third of the seedlings died, with secondary major mortality in the 3rd summer after

planting. The spatial pattern of survival became strongly clumped by the end of the first summer, with clearly defined patches (areas of high survival) and gaps (areas of low survival). The intensity of this pattern increased after subsequent high-mortality periods. Of the 14 environmental variables evaluated, the ones most strongly coupled to seedling survival were bare soil cover, sand content, and soil compaction. These findings contribute to our understanding of the linkages between the spatial heterogeneity of abiotic factors and the response of plant populations in semiarid degraded ecosystems and can be used to optimize restoration practices in these areas.

Key words: logistic regression; principal components analyses (PCA); *Pistacia lentiscus*; spatial analysis by distance indices (SADIE); semiarid ecosystems; surface soil properties; soil heterogeneity; restoration; variation partitioning.

INTRODUCTION

Soils are highly variable over both space and time, and their heterogeneity has strong consequences for community structure and ecosystem-level processes (Tilman 1988; Huber-Sannwald and Jackson

2001). Soil heterogeneity is especially important in semiarid ecosystems throughout the world, where vegetation is often arranged as a two-phase mosaic of vegetated patches on a bare ground matrix (Valentin and others 1999). In these environments, runoff generated in the bare ground areas is spatially redistributed toward vegetated patches, which act as a sink for water, sediments, and nutrients (Tongway and Ludwig 1994; Ludwig and Tongway 1995). The concentration of rainwater in vegetated

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sinks allows for an increase in ecosystem productivity (Noy-Meir 1973), which is further enhanced by self-reinforcing processes that lead to the formation of "resource islands" beneath the canopy of plants (Reynolds and others 1999). These islands also increase diversity and act as focal points for plant interactions and seedling establishment (Aguilar and Sala 1999).

When semiarid ecosystems are degraded, the rate of resource capture is greatly reduced, and vegetation structure, as well as ecosystem function, may be lost at mid- or long-term time intervals (Ludwig and others 1999, 2000). Under these conditions, the spatial heterogeneity of soil resources may be a key element in the regeneration of vegetation after disturbance (Whisenant 1999). In semiarid environments, the germination and subsequent establishment of plants is mainly controlled by soil water availability (Veenendal and others 1996; Grantz and others 1998). Water availability shows a strong degree of heterogeneity due to large spatial and temporal variations in rainfall patterns (Le Houérou and others 1988) and to the complex spatial redistribution of rainwater on the soil surface (Tongway and Ludwig 1994; Seghieri and others 1997). The redistribution of rainwater is strongly influenced by soil surface properties, such as compaction, physical crusts, and rock fragments, which play a prevailing role in runoff and infiltration dynamics (Valentin and Bresson 1992; Valentin 1994; Poesen and Lavee 1994). Other soil properties, such as the percentage of organic matter and the sand content, are also of major relevance for soil water-holding capacity (Ward and Robinson 1990). Thus, the spatial pattern of surface soil properties, which is often quite complex (Bromley and others 1997; Seguiéri and others 1997; Maestre and Cortina 2002), is critical for seedling establishment in semiarid degraded areas with very low vegetation cover. Furthermore, it also has strong implications for the restoration and management of those areas. Attempts to restore degraded semiarid ecosystems with plantings of woody species along regular grids have often been ineffective (Noble and Ludwig 2001). Instead of uniform plantings, the restoration of these areas should focus on the introduction of vegetation that follows the natural vegetation patterns, with the aim of recovering previous landscape processes (Ludwig and others 1999). Such restoration efforts can be further improved by incorporating knowledge of the spatial pattern of those soil properties that have the greatest effect on seedling establishment.

Despite the important body of knowledge acquired in the last decades on the response of plants

to soil heterogeneity, studies that characterize the small-scale spatial pattern of seedling establishment and attempt to identify the factors responsible for such patterns in semiarid areas are lacking. To improve our understanding of the linkages between environmental heterogeneity and the development and sustainability of vegetation in semiarid degraded ecosystems, it is important to identify the causes of spatial variation in seedling survival. Their identification would also help in designing effective restoration strategies. To this end, we have quantitatively characterized the spatiotemporal patterns of seedling survival over a 3-year period following the experimental planting of a native shrub, *Pistacia lentiscus* L., and related this variation to some relevant environmental factors at a hillslope scale in a degraded area in southeastern Spain. We hypothesized that the spatial distribution of these elements would define the spatial pattern of seedling survival in semiarid degraded areas. Thus, the main objectives of this study were (a) to quantify the spatial pattern of seedling survival, (b) to describe the temporal dynamics of this pattern during the first 3 years after planting, and (c) to identify the environmental properties most strongly related to seedling success. To achieve these objectives, we used a combination of spatial analysis by distance indices (SADIE) (Perry 1998; Perry and others 1999), with principal components analysis (PCA), and logistic regression coupled with a variation partitioning method.

MATERIALS AND METHODS

Study Area and Species Employed

We established a 0.28-ha (100 × 28 m) experimental plot near Crevillente, in southeastern Spain (38°13'N, 0°46'W, 130 m a.s.l.). The climate is semiarid, with a mean annual precipitation of 277 mm (1960–90) and a pronounced dry season from June to September. Mean annual temperature is 20.1°C; mean monthly temperatures range from 12.5°C in January to 28.8°C in July (1960–90). The plot lies on a southwest-facing hillside with a slope of 32%. The soil is a Lithic Calciorthid (Soil Survey Staff 1990) derived from marls and limestone. Natural perennial vegetation is sparse. Total plant cover is less than 30% and is composed mainly of small shrubs, such as *Sideritis leucantha* Cav. and *Thymus vulgaris* L. This area is representative of a semiarid degraded ecosystem in the western Mediterranean.

As the target species we used *P. lentiscus*, an evergreen shrub that is part of the climax vegetation in semiarid coastal areas of the Mediterranean basin

(Tomaselli 1981). It forms tall (up to 1 m in height), dense-leaved shrubs that tend to create a compact, cushion-like canopy. Seedlings of *P. lentiscus* typically develop a dichotomous root system (*sensu* Fitter 1991) that can reach depths up to 30 cm during the 1st year after planting in semiarid conditions (Fonseca 1999).

Seedling Survey

In December 1997, we planted 205 1-year-old seedlings of a local provenance of *P. lentiscus* randomly, resulting in a density of 732 seedlings ha⁻¹. Seedlings were placed in 40 × 40 × 40 cm mechanically dug holes. We did not water or weed the plot. We recorded seedling survival four times during the 1st year (April, June, September, and November 1998), twice in the 2nd year (April and November 1999), and three times in the 3rd year after planting (April, September, and December 2000). In each sampling, we calculated survival as the portion of initial seedlings alive at that time.

Sampling of Environmental Variables

In autumn 2000, we measured the following environmental variables at each planting hole: topography, cover of bare soil, cover of superficial rock fragments, soil compaction, microslope, sand content, soil organic matter, and microcatchment depth. Topography was estimated by measuring the height (above the lowest height of the plot) at the position of each planted seedling by using an electronic total station (model TC1101; Leica, Heerbrugg, Switzerland) in spring 2000. This procedure enabled us to accurately locate and map each seedling. We evaluated the percentage cover of bare soil and surface rock fragments with the point-sampling method, using a 0.5 × 0.5 m quadrat centered on each seedling and a 5 × 5 cm grid (100 points). We evaluated three size classes of rock fragments (Valentin 1994): fine and medium gravel (2–20 mm), coarse gravel (21–75 mm), and cobble (76–250 mm). The position of the rock fragments—that is, whether embedded or lying free on the soil surface—was also recorded. We measured the compaction of the soil surface as penetration resistance by using a portable penetrometer (model 06.06; Eijkelkamp, Giesbeek, The Netherlands) when the soil was dry (gravimetric soil moisture content at 0–5 cm depth = 1.7 ± 0.4% [mean ± SD, n = 5]). We made six measurements per seedling location and averaged the values for subsequent analyses. Microslope was measured in the center of each planting hole with a hand-held clinometer (model Slant-100; Tajima, Japan). It was considered to be

positive when the slope within the planting hole followed the same direction as that of the hillslope and negative when opposite. Sand content (0.05–2 mm) at 0–10-cm depth was estimated by sieving after the removal of soil organic matter (Archer and Marks 1977). We estimated soil organic matter content at the same depth following the loss-on-ignition method, after burning in a furnace at 550°C for 2 h. The depth of the small microcatchment formed in each hole after planting was also recorded with a hand-held ruler.

All the seedlings were initially planted in holes of approximately the same depth, but we also measured hole depth to take into account the small variations inherent in the digging process and any changes in this variable due to settling. We measured hole depth using ground penetrating radar (GPR), (Davis and Annan 1989). In each measured hole, we took measurements at 2.5-cm intervals along a 150-cm transect using a 900-MHz antennae and a pulse Ekko 1442 GPR system (Sensors and Software., Ontario, Canada). From the GPR profiles obtained in the field, we measured hole depth visually on images processed with Ekko Tools 42 software (Sensors and Software). This measurement included the subtraction of the average trace for the whole section of each image, a procedure that reduced noise and enabled the identification of hole boundaries. These images were drawn by hand, and we considered the maximum depth of this profile to be the hole depth for further analyses. Due to sampling constraints, measurements of hole depth were made in 110 randomly selected holes throughout the plot.

Statistical Analyses

We analyzed the spatial pattern of seedling survival using SADIE, a method designed for the spatial analysis of variables measured on ordinal scales that also can handle binary data (for a complete description, see Perry 1998; Perry and others 1999). We used two of the indices produced by SADIE, the index of aggregation, I_a , and the index of clustering, v . The first index provides information on the overall spatial pattern of seedling survival. It is clumped if I_a is greater than one, random if I_a is close to one, and regular if I_a is less than one. The index of clustering (v) measures the degree of clustering of the data into patches (areas of high survival) and gaps (areas of low survival); when contoured in a two-dimensional map, it shows their spatial distribution. Seedlings within patches have values of v (by convention v_j) greater than 1.5, whereas those within gaps have values of v (by convention, v_j) less than -1.5.

We used PCA to evaluate the changes in the spatial pattern of survival over time, using the values of v for the different surveys ($n = 205$). Because v reflects the pertinence of each seedling to either a patch, a gap, or neither of the two, we expected that changes in the spatial pattern or in the degree of clustering over time would be reflected on it. Values of v were not from a normal distribution (Kolmogorov-Smirnoff test, $P < 0.001$) and showed a certain degree of spatial and temporal correlation. However, we performed PCA with Varimax rotation on the raw data, since as both autocorrelation and deviations from normal distribution do not necessarily bias this analysis (Webster 2001). We performed a SADIE analysis separately for each survey by using 2340 permutations with the software described in Perry and others (1999). We used raw survival values (1/0) as the data. Maps of v were produced with SURFER (Golden Software, Golden, CO, USA); PCA was performed with SPSS for Windows 9.0 (SPSS, Chicago, IL, USA).

We used logistic regression to model seedling survival as a function of the measured environmental variables (Hosmer and Lemeshow 1989) and the variation partitioning method of Borcard and others (1992) to evaluate their importance in relation to spatially structured biotic and abiotic factors not considered in this study. This approach provides a partitioning of seedling survival into four fractions of variation: (a) survival explained by environmental variables independent of any spatial structure (fraction a), (b) survival explained by spatially structured environmental variables (fraction b), (c) survival explained by the spatial structure independent of any environmental variables (fraction c), and (d) survival explained by neither environmental nor spatial variables (fraction d). Fraction c may reflect some contagious biological processes that have no environmental component or no relation to the measured environmental variables. To calculate these fractions, we performed the following analyses: (a) a logistic regression of seedling survival constrained by a matrix of environmental variables (X), which extracts fraction $a + b$; (b) a logistic regression of seedling survival constrained by a matrix of spatial variables (W), which extracts fraction $b + c$; and (c) a logistic regression of seedling survival constrained by X and W , which extracts fraction $a + b + c$. For each of these analyses, we used the Nagelkerke R^2 statistic (Nagelkerke 1991) to quantify the proportion of variation that each fraction explains. Individual fractions were obtained as described in Legendre and Legendre (1998).

We ran two sets of analyses, one including data

from all planting holes and all environmental variables except hole depth (whole matrix, 14 variables, $n = 205$), and the other including data from all environmental variables where hole depth was assessed (reduced matrix, 15 variables, $n = 110$). In both cases, W was formed by the geographical coordinates of seedlings completed by adding all terms of a third-degree polynomial of them. Before building the polynomial, we centered geographical coordinates on their means to reduce collinearity problems (Legendre and Legendre 1998). We evaluated the goodness-of-fit of logistic regression models using the chi-square model (Hosmer and Lemeshow 1989). Variables were introduced using a forward stepwise selection; once entered into the model, they were retained if their significance level was at least 0.05 when tested by the conditional statistic. To assess the contribution of individual variables of the environmental matrix, we used the R statistic, which ranges from -1 to 1 . If R is positive, as the variable increases in value so does the likelihood of the event occurring; if negative, the opposite is true. Values of R close to zero indicate that the variable has a small, partial contribution to the model.

Although normality of response variables is not a necessary assumption in logistic regression, we transformed continuous data to meet normality to obtain more stable solutions (Norušis 1997). Transformations were performed accordingly to Legendre and Legendre (1998). Prior to logistic regression analyses, we checked for colinearity between environmental variables. We performed multiple linear regressions separately for each environmental variable, using it as the dependent variable, and the rest as independent variables, using the variance inflation factor (VIF) between the different variables as an indicator for colinearity. The same procedure was followed for the matrix of centered spatial variables. The VIF was in all cases below seven, suggesting the absence of strong colinearity problems (Chatterjee and Price 1991). All regression analyses were performed with SPSS for Windows 9.0.

RESULTS

Spatiotemporal Dynamics of Seedling Survival

Rainfall during the period of study ranged between 142 and 181 mm y^{-1} , 52%–65% of the 30-year average (Figure 1). Drought years are common in this area; more than 56% of years have a below-average rainfall (1960–90) (Pérez 1994). At 3 years after planting, seedling survival was 36% (Figure

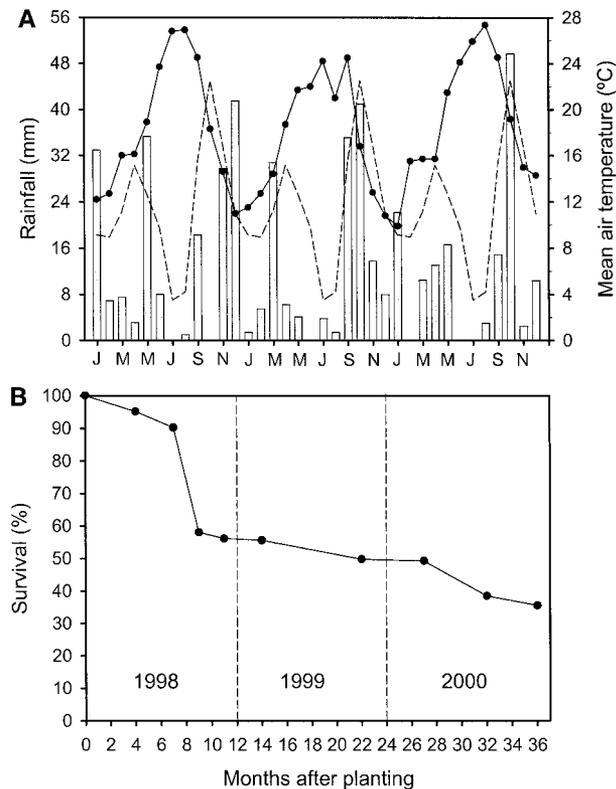


Figure 1. Evolution of main climatic characteristics (monthly rainfall in bars and temperature in black circles, upper graph) and seedling survival (lower graph) during the studied period. Seedlings were planted in late December 1997 ($n = 205$). Dashed line in the upper graph indicates the 30-yr average monthly rainfall. Meteorological data come from the Crevillente meteorological station ($38^{\circ}13'N$, $0^{\circ}46'W$).

1). There was a major mortality event in summer 1998 and a secondary mortality event in summer 2000. Rainfall during these summers (27 and 18 mm in 1998 and 2000, respectively) was substantially lower than that during summer 1999 (40 mm), when there was less mortality (Figure 1).

The values of I_a were not significant in April and July 1998, suggesting that mortality during this time occurred randomly (Table 1). After September 1998, there was a deviation from randomness in the spatial pattern of seedling survival, as suggested by values of I_a significantly greater than one. We found a general trend towards a gradual increase of all SADIE indices with time. Maps of v show the distribution and temporal changes of patches (areas of high survival) and gaps (areas of low survival) within the plot (Figure 2). The first major change in the pattern of seedling survival occurred between July and September 1998, when several patches became visible on the eastern side of the plot and a

large gap gradually developed at its center. This pattern remained virtually unchanged for 2 years; only an increase in the size of the main central gap, and in the degree and number of patches at the eastern side of the plot, was noticeable.

The first three axes of PCA accounted for 72%, 9%, and 8%, respectively (89% in total), of the variation in the values of v for the different sampling dates. Within the general increasing trend of the values of v with time, PCA clearly discriminated three main groups in the degree of clustering of seedling survival: April and July 1998, September 1998–April 2000, and September and December 2000 (Figure 3).

Variation Partitioning

Measured environmental variables exhibited substantial variability within the site, as indicated by their standard deviations and coefficients of variation—variables constrained and unconstrained in the range of possible values, respectively (Webster 2001) (Table 2). Hole depth, soil moisture, soil organic matter, and sand content showed moderate variability, with CVs below 35%. Embedded cobble, surface cobble, and surface coarse gravel—variables that are related to larger rock fragments—showed strong variability, as suggested by SDs close to or higher than the mean.

A significant amount of the variation in seedling survival was explained by the matrix of environmental variables (X), the matrix of spatial variables (W), and a combination of both (Tables 3 and 4). Although it was significant for all of the sampling dates, the goodness-of-fit of the models including the environmental variables improved greatly after the 1st summer in the field. The significant relationships between seedling survival and spatial variables observed after the 1st summer in the field confirmed the strong spatial structure suggested by the SADIE analysis. When the whole matrix is considered, environmental variables consistently explained more of the variation in seedling survival (33%–66%) than spatial variables (0–23%) (Table 3). The fraction of variation explained by environmental variables that is independent from any spatial structure (fraction a) was higher than that explained by the spatial structure of the environmental variables (fraction b) throughout the study period (25%–49% versus 0–20%). The variation explained by W that could not be related to the measured environmental variables (fraction c) was very low, below 9% in all cases. Fraction d was relatively high for all the sampling dates, especially before the spatial pattern of seedling survival became clearly defined (April and July 1998) and

Table 1. Summary of SADIE Analysis of Seedling Survival for the Different Surveys

Survey	a	V_j	V_i
April 1998	1.35 (0.127)	-1.23 (0.171)	1.43 (0.092)
July 1998	1.41 (0.102)	-1.23 (0.172)	1.54 (0.055)
September 1998	1.84 (0.016)	-1.63 (0.033)	2.03 (0.005)
November 1998	2.19 (0.003)	-1.91 (0.007)	2.44 (0.001)
April 1999	2.15 (0.005)	-1.90 (0.010)	2.42 (0.001)
November 1999	2.32 (0.001)	-2.07 (0.005)	2.47 (0.002)
April 2000	2.38 (0.002)	-2.10 (0.006)	2.52 (0.002)
September 2000	2.70 (0.001)	-2.37 (0.001)	3.10 (< 0.001)
December 2000	2.69 (0.001)	-2.39 (0.002)	3.12 (0.001)

I_a , index of aggregation; v_j , mean index of clustering for gaps (low-survival areas); and v_i , mean index of clustering for patches (high-survival areas)
P values derived from a randomization test (2340 permutations) are shown in parentheses ($n = 205$).

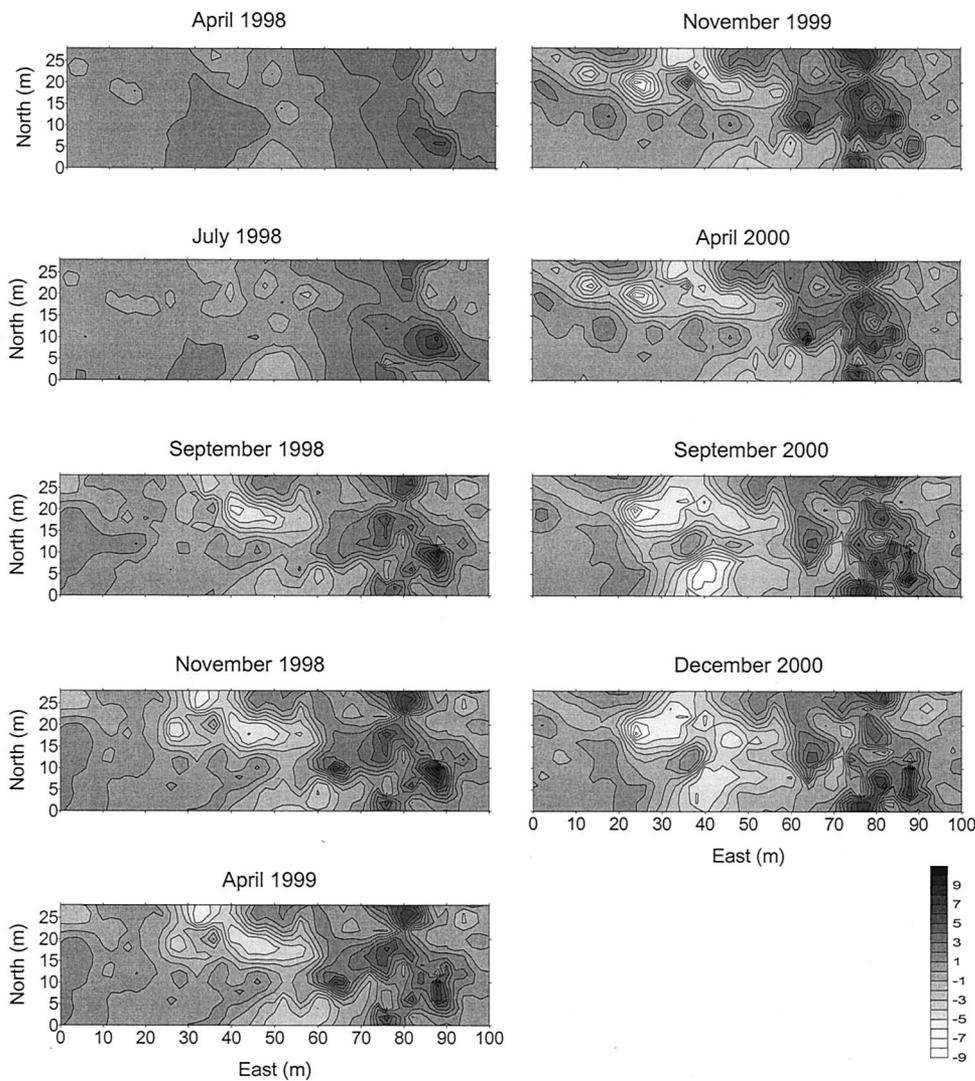


Figure 2. Maps of SADIE index of clustering (v) showing the distribution and evolution of patches (high-survival areas shown in dark shading) and gaps (low-survival areas shown in white) in the 3 years after planting. Scale values are dimensionless.

by the end of the experiment (September and December 2000). The results obtained with the reduced matrix including hole depth showed the

same trend, but in general the amount of variation explained by X and by the combination of X and W (fraction $a + b + c$), was higher than that explained

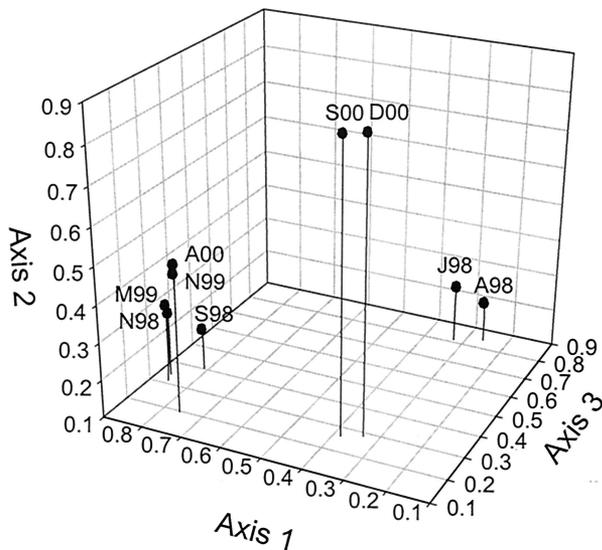


Figure 3. Principal components analysis (PCA) after Varimax rotation of SADIE index of clustering (ν) for the different sampling dates ($n = 205$). A98, April 1998; J98, July 1998; S98, September 1998; N98, November 1998; A99, April 1999; N99, November 1999; A00, April 2000; S00, September 2000; D00, December 2000.

Table 2. Summary of Environmental Variables Sampled during Autumn 2000

Variable	Mean	SD	CV
Bare soil (%)	22.87	14.98	65.50
Surface fine gravel (%)	28.63	9.30	32.48
Surface coarse gravel (%)	9.92	7.90	79.64
Surface cobble (%)	8.07	8.87	109.91
Embedded fine gravel (%)	12.08	5.67	46.94
Embedded coarse gravel (%)	9.60	5.50	57.29
Embedded cobble (%)	8.82	7.26	82.31
Penetration resistance (Kpa)	453.56	265.02	58.43
Sand content (%)	54.36	10.32	18.98
Organic matter (%)	2.68	0.66	24.63
Topography (m)	5.95	2.71	45.55
Microslope ($^{\circ}$)			
Positive ($n = 158$)	5.54	3.46	62.45
Negative ($n = 48$)	-4.06	3.19	78.57
Hole depth ($n = 110$) (cm)	44.63	5.64	12.64
Microcatchment depth (cm)	6.74	2.89	42.88

CV, coefficient of variation (expressed as percentage) ($n = 205$, except when indicated)

with the whole matrix without hole depth (Table 4).

For the whole matrix, bare soil cover and penetration resistance were the only variables that were consistently good predictors of mortality across all sampling dates (Table 5). Surface coarse gravel, soil

organic matter, and microslope were not selected as predictors at any sampling date. Survival before September 1998 was related to topography, bare soil cover, and sand content; in all three cases, the relationship was negative. After this date, the three most important variables influencing seedling survival were bare soil cover, sand content, and penetration resistance. Bare soil cover always showed negative values of R that were higher (in absolute terms) than those of other accompanying variables, except in April 1998, when sand content showed the highest value (in absolute terms) (Table 5). This indicates the relevance of bare soil cover in defining the spatial pattern of seedling survival. The values obtained for sand content and penetration resistance were very similar and always showed a negative relationship with seedling survival. Microcatchment depth showed a positive relationship with seedling survival, as did embedded rock fragments. Superficial rock fragments showed mostly a negative relationship with seedling survival. When selected, microcatchment depth and rock fragment cover showed values of R lower (in absolute terms) than those obtained for penetration resistance. Results for the reduced matrix were similar (Table 6). Hole depth was introduced on four occasions (June 1998, November 1998, April 1999, and November 1999), suggesting that this variable was important for seedling establishment. However, the values of R for this variable were generally lower (in absolute terms) than those obtained for bare soil cover, sand content, and penetration resistance.

DISCUSSION

Spatiotemporal Dynamics of Seedling Survival

In semiarid environments, the establishment of woody seedlings is severely constrained by summer drought (Harrington 1991; Escudero and others 1999, 2000). The survival of planted seedlings is also strongly related to the length of postplanting drought (Alloza and Vallejo 1999). Our results support these observations, since seedling mortality was highest during the 1st summer. However, an intense summer drought during the 3rd summer also caused substantial mortality. The spatial pattern of seedling survival, once defined, was maintained throughout subsequent mortality events—that is, regions with high mortality in 1998 also showed high mortality in 2000, despite the severe drought during the last year. These results show the important role that the small-scale heterogeneity of

Table 3. Results of Logistic Regression Analyses Performed during Variation Partitioning Analysis of the Whole Matrix

Fraction of Variation	Sampling Date									
	Apr 1998	June 1998	Sept 1998	Nov 1998	Apr 1999	Nov 1999	Apr 2000	Sept 2000	Dec 2000	
Env										
χ^2	26.02	35.13	91.07	120.36	102.31	124.57	140.13	90.14	83.80	
df	4	4	4	5	5	4	5	6	5	
<i>P</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
<i>R</i> ²	0.37	0.33	0.48	0.55	0.53	0.61	0.66	0.48	0.46	
Spa										
χ^2	4.57	^a	33.96	37.86	35.93	28.76	30.97	30.78	26.93	
df	1		4	4	4	4	4	3	3	
<i>P</i>	0.032		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
<i>R</i> ²	0.07		0.21	0.23	0.22	0.18	0.19	0.19	0.17	
Env + Spa										
χ^2	26.02	35.13	107.38	121.55	117.59	124.57	140.13	98.13	93.74	
df	4	4	6	7	7	4	5	6	5	
<i>P</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
<i>R</i> ²	0.37	0.33	0.55	0.56	0.58	0.61	0.66	0.52	0.50	

Env, environmental variables (fraction of variation $a + b$); Spa, spatial variables (fraction of variation $b + c$); Env + Spa, environmental and spatial variables (fraction of variation $a + b + c$); χ^2 , model chi-square statistic; *R*², Nagelkerke *R*² statistic, df, degrees of freedom.

^aNone of the spatial monomials was selected during the stepwise procedure.

For these analyses, $n = 205$.

Table 4. Results of Logistic Regression Analyses Performed during Variation Partitioning Analysis of the Reduced Matrix

Fraction of Variation	Sampling Date									
	Apr 1998	June 1998	Sept 1998	Nov 1998	Apr 1999	Nov 1999	Apr 2000	Sept 2000	Dec 2000	
Env										
χ^2	20.12	25.51	53.65	71.68	71.68	85.89	97.79	50.11	50.98	
df	3	3	3	5	5	6	5	3	3	
<i>P</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
<i>R</i> ²	0.48	0.45	0.53	0.65	0.65	0.73	0.74	0.49	0.50	
Spa										
χ^2	^a	^a	33.40	32.73	32.73	11.79	12.58	20.13	29.37	
df			4	4	4	1	1	3	5	
<i>P</i>			< 0.001	< 0.001	< 0.001	0.001	< 0.001	< 0.001	< 0.001	
<i>R</i> ²			0.36	0.35	0.35	0.14	0.15	0.22	0.32	
Env + Spa										
χ^2	20.12	25.51	71.03	78.56	78.76	85.89	97.79	54.33	55.68	
df	3	3	5	6	6	6	5	4	4	
<i>P</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
<i>R</i> ²	0.48	0.45	0.65	0.70	0.70	0.73	0.74	0.52	0.53	

^aNone of the spatial monomials was selected during the stepwise procedure.

For these analyses, $n = 110$.

abiotic factors other than rainfall plays in the vegetation dynamics of semiarid degraded ecosystems.

After the 1st summer, the spatial pattern of survival remained strongly consistent over the succes-

sive surveys. In addition, survival became strongly aggregated with time. This trend contrasts with field observations and simulation studies of even-aged shrub populations in arid and semiarid areas show-

Table 5. Values of the *R* Statistic for Each of the Environmental Variables Selected during Logistic Regression Analyses^a of the Whole Matrix

	Sampling Date									
	Apr 1998	June 1998	Sept 1998	Nov 1998	Apr 1999	Nov 1999	Apr 2000	Sept 2000	Dec 2000	
Bare soil	-0.15	-0.33	-0.37	-0.38	-0.38	-0.34	-0.34	-0.29	-0.34	
Surface fine gravel			-0.13	-0.14	-0.10					
Surface cobble	0.23				-0.09				-0.19	
Embedded fine gravel							0.10	0.09	0.11	
Embedded coarse gravel						0.18	0.19	0.09	0.11	
Embedded cobble								0.14		
Penetration resistance	-0.14	-0.22	-0.22	-0.22	-0.21	-0.23	-0.15	-0.12		
Sand content	-0.31	-0.22	-0.21	-0.23	-0.24	-0.25	-0.25	-0.13	-0.10	
Topography	-0.12									
Microcatchment depth		0.17		0.09	0.09					

^aFraction of variation $a + b$ **Table 6.** Values of the *R* Statistic for Each of the Environmental Variables Selected during Logistic Regression Analyses^a of the Reduced Matrix

	Sampling Date									
	Apr 1998	June 1998	Sept 1998	Nov 1998	Apr 1999	Nov 1999	Apr 2000	Sept 2000	Dec 2000	
Bare soil	-0.33	-0.34	-0.35	-0.32	-0.32	-0.36	-0.31	-0.34	-0.37	
Surface fine gravel						-0.23				
Surface cobble						-0.14			-0.21	
Embedded fine gravel										
Embedded coarse gravel							0.20	0.09		
Embedded cobble				0.15	0.14		0.16	0.17		
Penetration resistance	-0.23		-0.31	-0.29	-0.28	-0.23	-0.30	-0.18	-0.17	
Sand content	-0.34	-0.26	-0.20	-0.17	-0.17	-0.26	-0.21			
Hole depth		0.27		0.12	0.12	0.14				

^aFraction of variation $a + b$

ing an increasingly regular spatial distribution of plant individuals as a consequence of increased intraspecific competition (Schlesinger and Gill 1978; Brisson and Reynolds 1997). Due to the relatively slow growth of *P. lentiscus* in the study area, we did not expect density-dependent mortality during the course of the study. But it is likely that, in the longer term, some individuals could outcompete others, so that a regular distribution would emerge in areas that initially showed a clumped pattern.

Role of Measured Variables on Seedling Establishment

The importance of surface soil properties in the formation of "safe sites" (*sensu* Harper 1977) for

seed establishment and germination in semiarid areas is widely recognized (Eldridge and others 1991; Escudero and others 1999; Montaña and others 2001). However, the direct role played by these properties, as compared with other biotic and abiotic factors, in seedling survival is still poorly understood (Milton 1995; Escudero and others 2000). Our results showed that the spatial dynamics of *P. lentiscus* seedling survival were controlled mainly by a limited set of surface soil properties, including bare soil cover, sand content, and soil compaction. Our findings are in accord with studies showing the importance of surface soil properties for both soil water balance and plant performance in arid and semiarid ecosystems (Valentin 1994; Bromley and

others 1997; Hamerlynck and others 2000) and underscore the important role played by small-scale heterogeneity in these properties in providing "safe sites" for seedling establishment.

Bare soil cover was the variable that most influenced seedling survival in the first few years after planting. Surfaces dominated by bare soil are typically hotter than those shaded by vegetation or protected by litter and rock fragments (Danalatos and others 1995; Facelli and others 1999; Maestre and others 2001). Near-surface soil temperatures strongly affect soil evaporation rates in semiarid environments (Breshears and others 1998), and the increased evaporation fostered by the impact of high temperatures on bare surfaces substantially reduces the amount of soil moisture available to plants (Danalatos and others 1995). Bare surfaces are also more likely to form physical crusts, which are promoted by the repeated percussion of raindrops (Morin and Winkel, 1996). The formation of these crusts reduce soil water availability by limiting water infiltration and increasing runoff (Belnap 2001). Resistance to penetration, which is also negatively related to seedling survival is also associated with the formation of a superficial crust. Our results agree with studies performed in semiarid environments that found negative relationships between physical soil crusts and seedling establishment (Escudero and others 2000).

The sand content of the soil may have opposing effects on seedling establishment in semiarid areas. The higher infiltration characteristic of sandy soils may enable plants to extract water more readily after a rainfall event than they are able to do in fine-textured soils (Hamerlynck and others 2000). Sandy soils are also less prone to crusting than fine-textured soils (Belnap 2001). In addition, lower resistance to root penetration may facilitate root development in sandy soils (Brock 1986). On the other hand, water-holding capacity may decrease with increasing sand content (Ward and Robinson 1990). The negative relationship between sand content and seedling survival found in this study suggests that water storage capacity is more relevant for seedling establishment than the positive factors associated with coarse textures. In semiarid environments, the persistence of extractable soil water may be more relevant for plant establishment than transient periods of high water availability (Veñendal and others 1996; Gaze and others 1998). It is also interesting to emphasize the importance of sand content despite its low CV within the study site; this suggests that even small changes in sand content exert a strong influence on seedling survival.

The positive effect of rock fragments on seedling survival in this study supports the results of other studies that found a positive relationship between rock fragment cover and plant performance in arid and semiarid areas (Kadmon and others 1989; Kosmas and others 1994). Rocks on the soil surface play an important role in the infiltration and evapotranspiration dynamics of semiarid ecosystems (Poesen and Lavee 1994; Danalatos and others 1995). They act as a mulch, reducing soil temperature and evapotranspiration and protecting the soil against compaction, runoff, and desiccation. Our results indicate that the positive effect of rock fragment cover on seedling survival was associated with embedded rock fragments. These results are contrary to the current modeling and empirical evidence suggesting that embedded rock fragments reduce infiltration, whereas free rock fragments have the opposite effect (Poesen and Lavee 1994). Total rock fragment is likely to be relatively constant in time, but the ratio of embedded to surficial rock fragments may have increased slightly between time of planting and time of measurements due to fine-sediment entrapment and crusting.

When included in logistic regression analyses, depth of planting hole had a positive effect on seedling survival. Similar results were obtained by Meredieu and others (1996), who showed that small-scale changes in soil depth influenced the spatial pattern of survival in a 15-year-old red oak (*Quercus rubra*) forest. Early growth of *Pinus radiata* seedlings under Mediterranean conditions is also negatively affected by shallow soils (Cortina 1992). Planting hole depth has recently been shown to be important for seedling establishment in semiarid areas, especially in regions with shallow soils (Vallejo and others 2000). However, few investigators have performed field experiments to test its relevance (Grantz and others 1998). Root growth during the first stages after planting can be crucial to ensure successful establishment (Burdett 1990), and in degraded soils it is frequently confined to the planting hole (Fonseca 1999). Deep holes may accumulate more water than shallow ones, and eventually they may provide a reservoir of available water that lasts for most of the summer.

A positive relationship between seedling survival and the microcatchment depth of planting holes has been found in other studies in arid and semiarid areas (Whisenant and others 1995). However, the lack of importance of this variable as compared to other soil surface features was initially unexpected because microtopographic discontinuities have often been shown to be effective in capturing water and other resources in arid and semiarid areas

(Boeken and Shachak 1994; Shachak and others 1998 *inter alia*.) This result may be caused by the low depth of the microcatchments formed after planting. But it is also likely that this depth has been reduced and homogenized since planting, reducing its potential to affect seedling performance. Topography had a negative relationship with seedling survival in April 1998. Mortality was low during this period (5%), and the fact that topography was not selected as an explanatory variable on the other sampling dates suggests that it may not be an important factor in determining survival under the conditions of our study.

Among the variables that were not found to be explanatory for seedling survival by logistic regression analyses, soil organic matter is the most remarkable. This variable plays a major role in soil fertility, water storage, and plant development in semiarid areas (Fuller 1991). The organic matter content in our study was higher than that of agricultural soils (1.13%–1.92%) but lower than that of shrublands (5.02%–6.30%) (López-Bermúdez and others 1996) in areas close to the study site. However, it was very similar to that of a shrubland located close to the study site 9 years after vegetation removal (2.77%) (Martinez-Mena and others 2002). The lack of response to organic matter may be a consequence of the low range of variation within the study site (the CV is below 25%), but it may also be due to the fact that this range does not correspond to any threshold level (Aronson and others 1993). It is also likely that soil organic matter is not a limiting factor (*sensu* Tilman 1988) for seedling establishment in this degraded ecosystem.

Variation Partitioning

Our modeling approach explained a substantial amount of the variation in seedling survival—up to 66% of the total variation for some sampling dates. Most of the variation in survival was explained by environmental variables (fractions a + b). Excluding July 1998, 17%–40% of this variation corresponded to that explained by the spatial structure of the environmental variables (fraction b), suggesting a high degree of overlap between the spatial pattern of seedling survival and the pattern of environmental variables. It is interesting to note that very little of the variation was explained by spatial variables independent of environmental variables (fraction c). This finding indicates that contagious biological processes and biotic interactions between the introduced seedlings, or between the seedlings and the natural vegetation, are unimportant for seedling establishment under the conditions in our study. This result is contrary to those of other studies in

semiarid plant communities, where an important part of the total variation in plant distribution patterns was controlled by fraction c (Pan and others 1999; Rubio and Escudero 2000).

The unexplained variation (fraction d) found in this study may be due to a combination of random causes of mortality and other biotic and abiotic factors that were not taken into account but nonetheless influence seedling survival. But it is also likely that morphophysiological differences in the condition of the seedlings at the time of planting could explain some of this variation. Similar high percentages of unexplained variation have been found in other studies using the same modeling approach (Borcard and others 1992; Pan and others 1998; Rubio and Escudero 2000). On the other hand, the highest percentage of unexplained variation was found for the first and the last two sampling dates, which also showed greatest differences between the two groups of the dichotomous dependent variable. This factor could also have influenced the reliability of the results, since logistic regression biases classification into the larger group defined by the dependent variable (Hosmer and Lemeshow 1989).

Ecological Consequences of Small-scale Heterogeneity

There have been only a few experiments so far that addressed the consequences of small-scale soil heterogeneity for plant populations (Casper and Cahill 1996, 1998; Smilauerová 2001). To our knowledge, none of them were conducted under field conditions in semiarid areas. Greenhouse experiments using herbaceous species often found that soil heterogeneity had negligible effects on plant performance at the population level. Fitter and others (2000) argued that this lack of response was due to the adaptiveness of phenotypic plasticity to soil heterogeneity. Although our experimental approach does not allow a direct comparison with these studies, we found that soil heterogeneity had a clear effect on the performance of our experimental even-aged plant population, suggesting that phenotypic plasticity does not compensate for soil heterogeneity under field conditions.

Our results also have implications for the restoration of semiarid degraded areas. Current approaches for restoration in these environments focus on the amelioration of water stress through efficient water management practices (Shachak and others 1998), the creation of favorable microsites for natural plant colonization (Ludwig and Tongway 1996), the improvement soil conditions through organic amendments and mycorrhizae

(Caravaca and others 2002), and the use of existing vegetation to facilitate restoration (Maestre and others 2001). However, exploitation of the small-scale heterogeneity of surface soil properties has been largely ignored in restoration programs. We believe that the identification of environmental factors associated with mortality clumps should be a priority in the restoration of semiarid degraded areas because (a) it may help to develop suitable technology that could attenuate these limitations, and (b) these or associated factors could be used to identify suitable and unsuitable sites for planting. Areas of potentially high mortality could be defined beforehand by performing an analysis of the spatial distribution of these variables closely related to seedling survival. Alternatively, restoration success could be improved by reducing the amount of bare soil cover in the planting hole at the time of planting.

Our findings should serve to expand our understanding of the processes that lead to the ultimate patterns of adult plant populations in semiarid degraded ecosystems. Moreover, they contribute to our knowledge of the linkages among abiotic factors, the heterogeneity of these factors, and the response of plant populations in these areas. Further studies that integrate seed and seedling responses to spatial soil heterogeneity at larger temporal scales are needed to improve our predictions and to further our understanding of these linkages.

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