

Are Ecosystem Composition, Structure, and Functional Status Related to Restoration Success? A Test from Semiarid Mediterranean Steppes

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Abstract

Theoretical models emphasize the importance of considering the composition, structure, and functioning of an ecosystem when restoring it. However, there is a lack of empirical studies evaluating how these ecosystem attributes are linked, if any, to the success of restoration actions. We conducted experimental plantings of the native late-successional shrub *Pistacia lentiscus* in 10 semiarid steppes located in southeast Spain and related seedling survival rates to measures of ecosystem structure and composition and to surrogates of ecosystem functioning. Seedling survival widely differed among the studied steppes and 17 months after planting ranged from 0 to 89%. Mortality occurred mostly during the first summer in the field, coinciding with a strong drought lasting 3 months. Survival was lower in the steppes located at the highest altitudes

and with the highest values of total plant cover, species richness, shrub cover, and functionality. Seedling survival was mainly controlled by abiotic conditions and showed a negative relationship with some of the surrogates of ecosystem functioning evaluated. Our results suggest, but cannot confirm, that the functional status of the ecosystem may not limit the early stages of establishment of *P. lentiscus* in semiarid steppes and that abiotic conditions play an overriding role in this process. If true, its introduction in these areas would not necessarily need a previous phase of recovery of ecosystem functions like nutrient cycling and infiltration.

Key words: ecosystem functioning, *Pistacia lentiscus*, plant–plant interactions, seedling survival, semiarid steppes *Stipa tenacissima*.

Introduction

The need of a firm ecological basis to restore degraded ecosystems (Clewett & Rieger 1997) has derived in the development of theoretical models to describe how ecosystem structure and functioning recover after disturbances (Hobbs & Norton 1996; Whisenant 1999). These emphasize the importance that both nonlinear trajectories and thresholds have in this process and highlight the need to take into account the composition, structure, and functioning of ecosystems when restoring them (Hobbs & Harris 2001). Considering these ecosystem attributes may be of great help to define restoration goals, to prioritize economical investments, and to select the target ecosystem functions and components to recover with the restoration of a given area (Tongway & Hindley 2000; Hobbs 2002).

In parallel to the building of a relevant theoretical foundation, important advances have been made in the

development of methodologies to evaluate the functional status of ecosystems, especially in arid and semiarid areas (Tongway & Hindley 1995; Herrick et al. 2005). Vegetation in these ecosystems is often arranged as a set of discrete plant patches inserted on a bare ground matrix, and their functioning is largely based on the capture and retention of the water, sediments, and nutrients moving from the bare ground areas to isolated plant patches during rainfall events (Valentin et al. 1999). The patterns of redistribution and capture of runoff are strongly influenced by soil surface properties like compaction, physical crusts, and rock fragments and by patch attributes like size, width, and spatial distribution (Whitford 2002). Thus, methods developed to monitor ecosystem functioning in these areas heavily rely on the assessment of patch attributes and the condition of the soil surface (Tongway & Hindley 1995; Herrick et al. 2005).

Despite the advances in both the theoretical and the monitoring fields, there is a clear lack of studies evaluating the relationships between the structural and/or functional attributes of a degraded ecosystem and the success of the management measures taken to restore it (Lindig-Cisneros et al. 2003). Such studies are of great interest to evaluate how changes to ecosystem functioning may impair restoration, to assess current theoretical models, and to establish appropriate management and restoration programs (Whisenant 1999; Hobbs 2002). In this study we explored the relationships between ecosystem attributes

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(abiotic features, structure, composition, and functional status) and restoration success in steppes dominated by the tussock grass (*Stipa tenacissima* L.). *Stipa*-dominated steppes are widespread in the semiarid areas of the Mediterranean Basin and derive from the degradation of open shrublands and woodlands by human activities carried out over centuries (Le Houérou 2001). Remnants of native, late-successional, sprouting shrubs like *Pistacia lentiscus* L. and Kermes oak (*Quercus coccifera* L.) play key functional and structural roles in semiarid *S. tenacissima* steppes. They enhance ecosystem functioning (Maestre & Cortina 2004a), are a major determinant of plant diversity (Maestre 2004; Maestre & Cortina 2005), provide resilience against disturbances (Trabaud 1991), and supply shelter and food for wild and game animals (López & Moro 1997). Increasing shrub cover and density in degraded *S. tenacissima* steppes through direct planting is often a target objective when restoring them (Maestre et al. 2001). Thus, seedling survival can be used as a good estimator of the success of restoration activities. The main objective of this study was to evaluate if differences in abiotic factors and ecosystem attributes (structure, composition, and functional status) correlate with restoration success in semiarid degraded steppes.

Materials and Methods

Study Area

In a previous study, Maestre and Cortina (2004a) characterized the composition, structure, and functional status of 17 *Stipa tenacissima* steppes in southeast Spain. Ten of these sites, capturing a wide range in the abiotic factors and ecosystem attributes found along this gradient, were selected for this study. They spread over an area of 60 × 50 km. The climate is Mediterranean semiarid, with annual precipitation values ranging from 220 to 388 mm and annual temperatures ranging from 16 to 18°C (averages for the 1960–1990 period). All the sites share the same soil (*Haplocalcid*, Soil Survey Staff 2003) and vegetation (open steppe dominated by *S. tenacissima*) types. However, they differ substantially in abiotic features like slope and elevation, as well as in structural/compositional attributes like species richness, species evenness, total cover, and area covered by late-successional sprouting shrubs (Table 1).

Experimental Plantings

Pistacia lentiscus seeds from local provenances—provided by the Regional Government (Banc de Llavors, Generalitat Valenciana, Spain)—were used in this experiment. Seedlings were grown in the open air at the University of Alicante (located 2–60 km away from the experimental sites) for 11 months in 150 mL containers and were watered as needed during this time. Seedlings of homogeneous size were planted on two microsites: “Tussock” and “Open.” The Tussock microsite was located upslope and adjacent

to isolated *S. tenacissima* tussocks of medium size (over 1–1.5 m in width), the Open microsite was located in the intertussock areas devoid of vascular vegetation. Seedlings were planted in late Winter 2003 (17–20 February) by using manually dug 25 × 25 × 25-cm planting holes. At each site, 18 seedlings per microsite and site were randomly planted (one seedling per planting hole) in the area where the soil and vegetation sampling was carried out (see below). The experiment was conducted under natural conditions without any watering or weeding. During the course of the experiment some seedlings were excavated by rabbits (*Oryctolagus cuniculus*), with the final number of seedlings being 13–18 per microsite and site. Seedling survival was measured every 2–4 weeks between February and October 2003 and later in June 2004. Despite being relatively short (17 months), this monitoring period covers a key stage in the establishment of planted shrubs in semiarid Mediterranean areas (Maestre et al. 2001, 2003b), and thus it is suitable to achieve the objectives of this study. Rainfall was measured in all sites by an on-site pluviometer (Hellman type) during the first eight months after planting (February–October 2003), when most of the mortality took place. Pluviometers were sampled in all the sites during the 48 hours following individual rainfall events.

Assessment of Ecosystem Composition, Structure, and Abiotic Features

Within each site, a 30 × 30-m plot starting on the upper edge of the hillslope was set up. Four 30-m-long downslope transects, separated 8 m each and starting in the upper left corner of the plot, were established. In each transect, a continuous record of patch and interpatch zones was collected. According to Tongway and Hindley (1995), a patch is defined as a long-lived feature that is able to collect water, sediments, and nutrients coming from runoff, such as perennial plants and shrub branches contacting soil, that is separated by bare soil surface from the next patch. The following attributes were used to describe the structure of patches at the study sites: total cover (%), total width perpendicular to the transect (m/10 m segments of the transect), and distance between consecutive patches (m). The total area covered by isolated sprouting shrubs and the number of perennial plant species in the 30 × 30-m plot were also measured. The latter was used as a surrogate of species richness. Transects were also used to evaluate perennial plant species evenness (ratio of observed to maximum diversity, Magurran 1988) and spatial pattern by using the line-point sampling method, with a sampling frequency of 50 cm along the 30-m transect. The latter was characterized with the spatial analysis by distance index (SADIE) methodology (see Perry et al. 1999 for details) and the data generated from the evenness survey. SADIE's index of aggregation (I_a) was used to summarize the spatial pattern of perennial vegetation in the transects; it is clumped if $I_a > 1$, random if I_a is close to 1, and regular if $I_a < 1$. An increase in the I_a values suggests an increase in the spatial

Table 1. Variables forming the abiotic and biotic matrices.

Site	ELE ^b	RAI	ASP ^b	SLO ^{a,b}	UTM ^b	SPA ^a	SRI ^b	EVE ^a	ASS ^b	DCP ^{a,b}	WPA ^{a,b}	TCO ^{a,b}
Albatera	355	133	228	24.8 ± 0.6	683000 E, 4235820 N	1.02 ± 0.27	34	0.61 ± 0.02	62.2	0.47 ± 0.02	7.76 ± 0.77	44.6 ± 3.3
Finestrat	212	171	160	22.8 ± 0.6	745052 E, 4271046 N	1.49 ± 0.24	27	0.52 ± 0.03	7.9	0.58 ± 0.05	8.76 ± 0.26	47.1 ± 2.4
Foncalent	63	109	100	23.5 ± 0.3	713572 E, 4246605 N	1.11 ± 0.08	23	0.49 ± 0.06	0	1.71 ± 0.30	1.62 ± 0.36	17.4 ± 3.4
Jijona	240	125	180	24.8 ± 0.3	720312 E, 4263831 N	1.30 ± 0.39	23	0.53 ± 0.02	0	1.42 ± 0.07	2.84 ± 0.51	18.8 ± 2.2
La Nuza	102	134	160	27.8 ± 0.6	730961 E, 4260414 N	1.08 ± 0.19	23	0.55 ± 0.05	0.6	0.77 ± 0.09	7.81 ± 1.46	42.0 ± 4.3
Marquesa	85	156	178	23.8 ± 0.3	727972 E, 4259533 N	1.31 ± 0.38	22	0.49 ± 0.05	4.0	1.04 ± 0.18	7.57 ± 0.82	44.5 ± 3.4
Palomaret	540	139	190	23.5 ± 1.8	703116 E, 4261639 N	1.21 ± 0.29	28	0.56 ± 0.01	17.8	0.66 ± 0.06	7.65 ± 0.79	37.0 ± 2.2
Peñarrubia	769	187	180	22.5 ± 0.3	690160 E, 4273578 N	1.33 ± 0.25	36	0.50 ± 0.02	85.2	0.73 ± 0.07	8.63 ± 0.52	44.6 ± 1.0
Relleu	395	150	125	10.8 ± 0.3	735591 E, 4269506 N	0.99 ± 0.14	33	0.53 ± 0.03	16.5	0.61 ± 0.06	7.85 ± 0.53	47.1 ± 1.5
Ventós	468	102	270	26.3 ± 0.6	707768 E, 4259748 N	1.39 ± 0.29	28	0.51 ± 0.02	10.1	0.54 ± 0.04	8.86 ± 1.23	46.4 ± 3.8

ELE = elevation (meters above sea level), RAI = rainfall accumulated during the first eight months after planting (mm), ASP = aspect (°), SLO = slope (°), UTM = coordinates, SPA = spatial pattern (SADIE's I_a , unitless), SRI = species richness (n), EVE = species evenness (unitless), ASS = area covered by sprouting shrubs (m²), DCP = distance between consecutive patches (m), WPA = width of patches (m/10 m of linear transect), and TCO = total cover of patches (%).

^a Mean ± SE ($n = 4$).

^b Data come from Maestre (2004).

aggregation of vegetation. We performed SADIE analysis separately for each transect by using presence/absence data and 2,340 permutations with the SADIEShell for Windows software, version 1.22 (downloaded from http://www.rothamsted.bbsrc.ac.uk/pie/sadie/SADIE_home_page_1.htm).

The structure and composition of the study sites was characterized by seven variables (Biotic matrix): species richness, species evenness, spatial pattern, cover of patches, width of patches, distance between consecutive patches, and area covered by sprouting shrubs. In addition, the abiotic environment of the study sites was also characterized with six variables (Abiotic matrix): elevation, slope, aspect, UTM coordinates (North and East), and rainfall accumulated during the eight months after planting.

Assessment of Ecosystem Functional Status

To assess the functional status of each site, we focused on three processes that are crucial for the proper functioning of semiarid ecosystems (Whitford 2002): resistance against erosive forces, infiltration, and nutrient cycling. They were estimated by using the landscape function analysis (LFA) methodology, which is based on the use of soil surface indicators (Tongway 1995; Tongway & Hindley 1995). The main output of LFA is given by three quantitative indices (stability, infiltration, and nutrient cycling) that are strongly related to quantitative measures of these ecosystem processes. These relationships have been calibrated in semiarid ecosystems of Australia and show strong linear relationships with variables like soil aggregate stability (stability index), infiltration rate (infiltration index), and total soil nitrogen, total soil carbon, and soil respiration (nutrient cycling index) (Tongway & Hindley 2003). The infiltration index is being calibrated in *S. tenacissima* steppes of Spain, and the data available so far indicate that this index is closely related to direct measurements of infiltration rate in steppes located within our study area (S. Bautista, University of Alicante, personal communication, 2005).

Within each site, six Tussock and Open microsites were randomly selected, and a 0.5 × 0.5-m quadrat was placed

in each of them ($n = 12$ per site). Eleven soil surface indicators (soil cover, litter cover, degree of decomposition of litter, biological crust cover, crust broken-ness, erosion type and severity, deposited materials, soil microtopography, surface resistance to disturbance, soil stability, and soil texture; see Maestre & Cortina 2004a for a detailed description) were visually assessed in these quadrats during the week prior to planting. In this assessment, each soil surface indicator receives a unitless score according to an interval scale. The scores obtained in the field were further combined to obtain the LFA indices with a Microsoft Excel template developed by David Tongway (available from <http://www.cse.csiro.au/research/ras/efa/#manual>; see Tongway & Hindley [1995] for a complete description of score assignment and calculations). Here we present LFA values as percentages (resulting from dividing the value obtained in previous step by the maximum score that can be obtained for a given LFA index): the higher the values obtained, the better the status of the ecosystem for a given function. The three LFA indices (stability, infiltration, and nutrient cycling) constitute our Functional matrix.

Statistical Analyses

As the LFA indices were obtained in the same squares and thus cannot be considered to be independent of each other, permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used to analyze overall site and microsite effects on them (both factors were considered fixed). This approach provides a partitioning of multivariate variability in the data according to particular factors on the basis of any distance measure.

Seedling survival data were analyzed in different ways. First, we evaluated the shape of the survival curves by calculating Kaplan–Meier estimates of these curves. Then, we performed a log-rank test to evaluate differences between sites and microsites. In the first case, separate analyses were conducted for each microsite (Tussock and Open), in the second case separate analyses were conducted for each site. In addition to these analyses, differences in

seedling survival between microsites were evaluated at each sampling point using log-linear models.

The relationship between seedling survival and ecosystem attributes (Biotic, Abiotic, and Functional matrices) was analyzed using correlation analyses. Due to the low number of sites as compared to the large number of variables forming these matrices, we reduced their dimensionality. First, we eliminated those variables that were strongly correlated within each matrix. According to these correlations, we removed the area covered by sprouting shrubs, the average distance between consecutive patches and the width of patches from the Biotic matrix, and the stability index from the Functional matrix for further analyses. The dimensionality of the Abiotic and Biotic matrices was further reduced by using principal component analysis (PCA) with a correlation matrix. From each PCA, all the components that had eigenvalues greater than one were retained (Quinn & Keough 2002). After these analyses, we evaluated the correlation between seedling survival and (i) each of the PCA components that had eigenvalues greater than one and (ii) the infiltration and nutrient cycling indices. The significance of correlation analyses was assessed using a permutation test with 10,000 randomizations (Legendre & Legendre 1998). Separate analyses were conducted for data obtained from the Open and Tussock microsites. Significance levels ($\alpha = 0.05$ was used throughout the manuscript) were corrected for multiple testing by using the false-discovery method (Benjamini & Hochberg 1995).

PERMANOVA analyses were conducted with the program PERMANOVA_2factor (<http://www.stat.auckland.ac.nz/~mja/Programs.htm>) using the Euclidean distance and 10,000 permutations (permutation of residuals under a reduced model; Anderson & ter Braak 2003). Correlation analyses were conducted with the program Corr_permute (http://www.bio.umontreal.ca/Casgrain/en/labo/corr_permute.html). The remaining statistical analyses were performed with the software SPSS for Windows 9.0 (SPSS, Inc., Chicago, IL, U.S.A.).

Results

The LFA indices obtained at the different sites are shown in Figure 1. There was a strong microsite effect, with higher values for the three indices in the Tussock microsite in all sites, but its magnitude differed between sites, as suggested by the significant Site \times Microsite interaction found (PERMANOVA; $F_{\text{Site}} = 10.43$, degrees of freedom [df] = 9,100, $p = 0.0001$, $F_{\text{Microsite}} = 559.28$, $df = 1,100$, $p = 0.0001$; $F_{\text{Site} \times \text{Microsite}} = 2.74$, $df = 9,100$, $p = 0.0042$). Despite this interaction, the LFA indices were higher in the Tussock microsite in all sites (Post-hoc analyses not shown; $p < 0.0032$ in all cases).

Seedling survival differed between sites and between microsites and 17 months after planting ranged from 0 to 89% (Fig. 2). Mortality occurred mostly during the first summer in the field, coinciding with a strong drought lasting three months. The shape of the survival curves for both Tussock and Open microsites showed substantial differ-

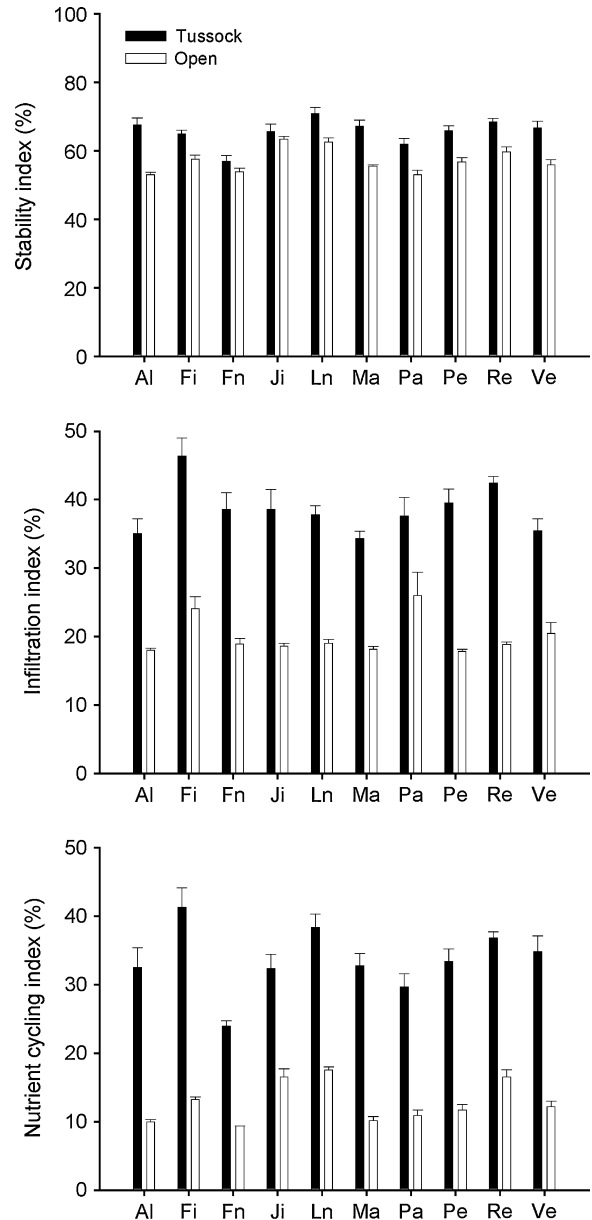


Figure 1. Characterization of Tussock and Open microsites in terms of the landscape function analysis indices. Data represent means \pm SE ($n = 6$). Note different scales in the y-axes. Site abbreviations as follows: Al = Albatera, Fi = Finestrat, Fn = Fontcalent, Ji = Jijona, Ln = La Nuza, Ma = Marquesa, Pa = Palomaret, Pe = Peñarrubia, Re = Rellu, and Ve = Ventós.

ences between sites (Table 2). Significant differences in the shape of the survival curves between microsites were only found at the Peñarrubia site (Log-rank statistic = 5.14, $df = 1$, $p = 0.023$). Log-linear analyses revealed higher survival in Tussock versus Open microsites in four sites (Marquesa, Palomaret, Rellu, and La Nuza) and the opposite pattern in two sites (Fontcalent and Finestrat). Grazing by rabbits (*Oryctolagus cuniculus*) was observed at two study sites (Finestrat and La Nuza) and was probably related to high

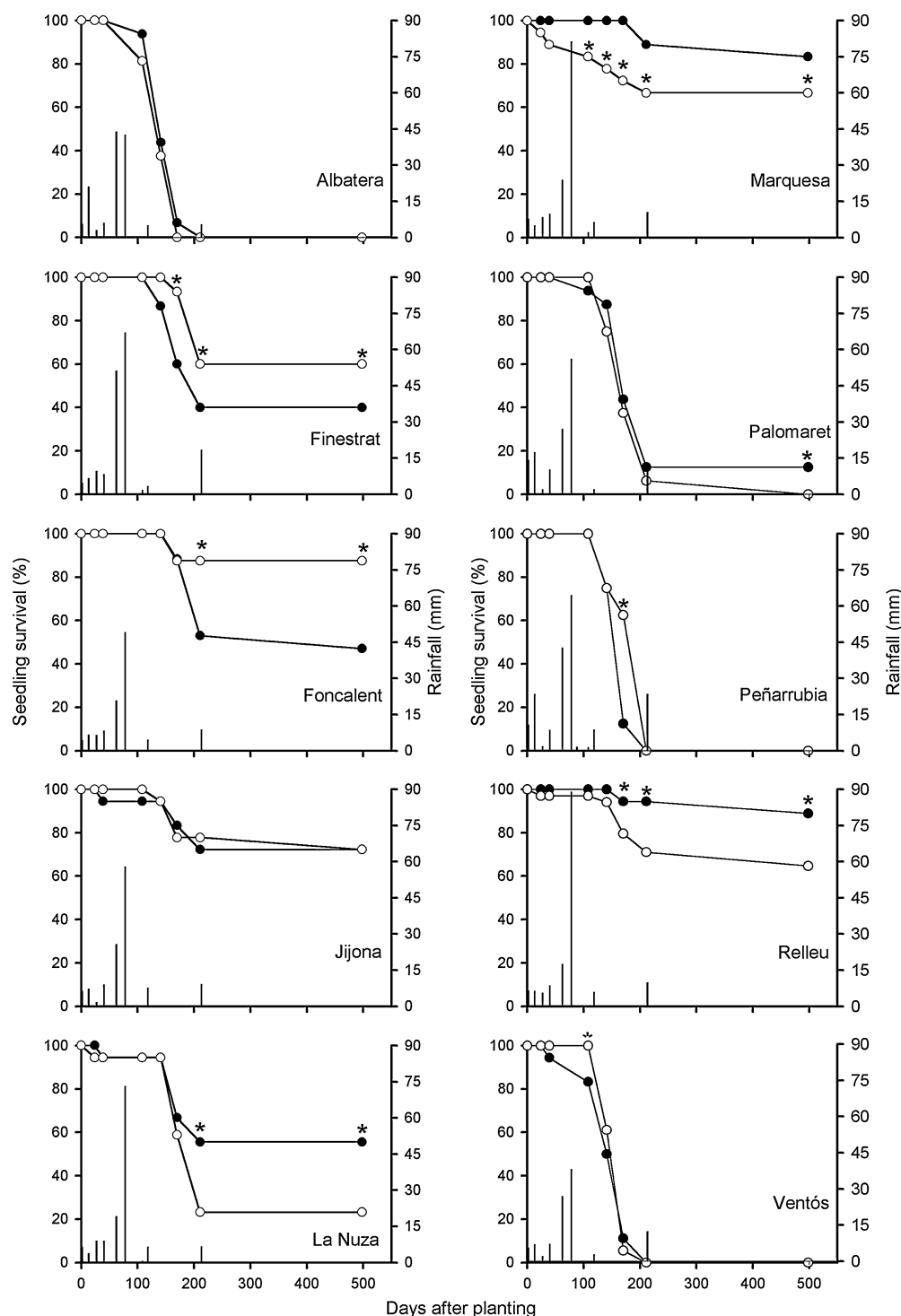


Figure 2. Survival of *Pistacia lentiscus* seedlings planted at Tussock (black circles) and Open (open circles) microsites during the first 500 days after planting. Horizontal bars represent rainfall events, as measured by an on-site pluviometer during the first eight months after planting. Significant differences between microsites (log-linear analysis) are indicated by *. Seedlings were planted on 17–20 February 2003. Initial $n = 13$ –18.

local densities of rabbits in these sites (as suggested by visual observations of individuals and fecal pellets).

Two components of the PCA performed with the Abiotic matrix had eigenvalues greater than one, explaining over 72% of the variance in the data. Rainfall, slope, and

the UTM North coordinate showed the highest correlations with the first component of this PCA (Table 3). The second component of this PCA had the highest correlation with elevation, aspect, and the UTM East coordinate. Only one component had an eigenvalue higher than one for the PCA

Table 2. Pairwise comparisons of the log-rank statistic to evaluate differences between sites in the survival curves obtained in the Tussock and Open microsites.

Microsite	Site	Al	Fi	Ft	Ji	Ln	Ma	Pa	Pe	Re
Tussock	Fi	12.43								
	Ft	24.40	1.42							
	Ji	22.02	3.36	0.86						
	Ln	16.91	0.74	0.06	1.06					
	Ma	33.61	9.84	5.66	1.79	5.45				
	Pa	8.24	2.10	8.88	11.39	5.64	22.02			
	Pe	3.06	8.44	21.18	20.40	13.85	32.97	3.92		
	Re	31.33	7.43	3.60	0.74	3.59	0.24	19.26	30.62	
Open	Ve	0.03	12.63	24.92	24.14	18.16	35.86	7.85	1.99	33.85
	Fi	30.14								
	Ft	23.83	1.96							
	Ji	30.87	0.19	0.97						
	Ln	13.25	6.39	10.72	7.89					
	Ma	14.15	0.02	1.93	0.33	3.42				
	Pa	9.67	19.65	23.45	22.39	3.24	11.46			
	Pe	14.12	14.62	19.01	16.18	0.67	8.42	0.75		
	Re	16.80	0.08	2.11	0.44	3.26	0	12.15	7.99	
	Ve	3.11	27.03	23.94	28.63	9.26	12.63	4.08	8.68	14.84

Values in bold are significant ($\alpha = 0.05$) after adjusting for multiple testing using the false discovery rate method of Benjamini and Hochberg (1995). Al = Albaterra, Fi = Finestrat, Fn = Fontcalent, Ji = Jijona, Ln = La Nuza, Ma = Marquesa, Pa = Palomaret, Pe = Peñarrubia, Re = Rellou, and Ve = Ventós.

performed with the Biotic matrix, which explained over 50% of its total variance. Species richness and total patch cover were the variables most strongly correlated to this axis. The second component of the PCA performed with the Abiotic matrix was the only variable significantly correlated with seedling survival at both the Tussock and Open microsites (Table 4). This variable alone explained 72 and 76% of the variance in seedling survival at the Tussock and Open microsites, respectively. Seedling survival at the Open microsite was also negatively related to the infiltration index.

Discussion

Most seedling mortality took place during summer drought, a period that acts as a bottleneck for the recruitment of

shrubs in Mediterranean environments (Escudero et al. 1999; Castro et al. 2002). Besides this general pattern, we found important differences in seedling survival rates, and thus in our measure of restoration success, among sites. In addition to these differences, the magnitude and direction of the effect of *Stipa tenacissima* tussocks on the performance of planted *Pistacia lentiscus* seedlings also varied among sites. This suggests that both competitive and facilitative effects co-occur in this interaction, as demonstrated in a previous manipulative study (Maestre et al. 2003a), and that these effects are modulated by biotic and/or abiotic factors acting at spatial scales beyond that of the neighboring interaction. Among them, abiotic stress has been found to affect the net outcome of *S. tenacissima* on *P. lentiscus* in this experiment (Maestre & Cortina 2004b).

Table 3. Pearson correlations (p values) between the variables forming the abiotic and biotic matrices and the components from the principal component analysis (PCA), which had eigenvalues greater than one.

Matrix	Variable	PCA Component	
		1	2
Abiotic	Elevation	0.549 (0.100)	0.795 (0.007)
	Accumulated rainfall	0.813 (0.005)	0.043 (0.903)
	Aspect	-0.256 (0.478)	0.777 (0.002)
	Slope	-0.644 (0.021)	0.301 (0.511)
	UTM North coordinate	0.844 (0.002)	-0.135 (0.720)
	UTM East coordinate	0.230 (0.514)	-0.864 (0.001)
Biotic	Species richness	0.781 (0.008)	—
	Spatial pattern	-0.676 (0.034)	—
	Species evenness	0.584 (0.080)	—
	Total patch cover	0.775 (0.005)	—

p values were obtained using a permutation test with 10,000 permutations. In all cases, $n = 10$.

Table 4. Correlation coefficients (*p* values) between seedling survival and (i) the PCA components derived from the principal component analysis (PCA) of the abiotic and biotic matrices and (ii) the landscape function analysis indices.

Variable	Survival in the Tussock Microsite	Survival in the Open Microsite
Component 1 of the PCA performed with the abiotic matrix	0.134 (0.698)	−0.014 (0.970)
Component 2 of the PCA performed with the abiotic matrix	−0.850 (0.004)	−0.869 (0.004)
Component 1 of the PCA performed with the biotic matrix	−0.283 (0.435)	−0.565 (0.098)
Infiltration index *	−0.281 (0.432)	−0.652 (0.023)
Nutrient cycling index *	−0.185 (0.609)	−0.357 (0.289)

The *p* values were obtained using a permutation test with 10,000 permutations. Values in bold are significant (at $\alpha = 0.05$) after adjusting for multiple testing using the false-discovery rate method of Benjamini and Hochberg (1995). In all cases, $n = 10$.

* Correlations with survival data from the Tussock and Open microsites were performed with the values of the indices obtained at the Tussock and Open microsites, respectively.

Our results suggest that seedling survival at both Tussock and Open microsites was mainly controlled by abiotic conditions and, to a lesser extent, by the functional status of the study sites. This agrees with the overall notion that environmental conditions play an overriding role in the patterns of plant recruitment and establishment in semi-arid areas (Whitford 2002). The correlations observed between survival data and the PCA components provide indirect evidence that altitude and aspect, but not accumulated rainfall, were the abiotic variables that most influenced observed seedling survival rates. This result was unexpected, given the importance of rainfall for the establishment of *P. lentiscus* in semiarid areas (Maestre et al. 2003b). It suggests that other environmental variables that vary with altitude, aspect, and longitude, as well as other aspects of the rainfall regime not taken into account in this study (e.g., size of individual rainfall events), might explain observed survival patterns. In this regard, the potential role of variation in soil properties needs to be highlighted. Despite site selection aimed to minimize differences in soil type and mineralogy among them, unmeasured variations in properties such as soil texture can override other factors due to their importance as a driver of soil water availability (Fernandez-Illescas et al. 2001). Previous studies have found some degree of site-to-site variation in soil texture in our study area (Maestre et al. 2001). Thus, it is possible that such variations may be influencing our results.

It is interesting to point out that the relationships between seedling survival and the variables forming the Biotic, Abiotic, and Functional matrices were in all cases more negative when the seedlings were introduced in the Open microsite. This may be related to improved soil and microclimatic conditions in the vicinity of *S. tenacissima* tussocks as compared with the adjacent bare ground areas (Puigdefábregas et al. 1999; Maestre et al. 2001; Maestre et al. 2003a). Such improvements may ameliorate negative effects of other abiotic and biotic factors on seedling survival. We suggest that the higher mortality found in the Tussock microsite in 2 of the 10 study sites is promoted by increased competition with *S. tenacissima* (Maestre et al. 2003a), rather than by an improvement of environmental conditions in the Open microsite.

Implications for Ecosystem Restoration

We found that seedling survival was, overall, lower in the steppes located at the highest altitudes and with the highest values of cover, species richness, and functionality, as suggested by the LFA indices. This result, unexpected initially, suggests that the functional status of the ecosystem may not limit establishment of *P. lentiscus* in degraded steppes, at least during its early stages. Our site selection encompassed a wide range of abiotic and biotic conditions and included sites with plant cover below 20%, with reduced functionality and with clear symptoms of degradation (Appendix D). Thus, our results suggest that the restoration of semiarid steppes by planting woody shrubs would not require a previous phase of recovery of ecosystem structure and/or functioning. The results also suggest that early stages in the restoration of *S. tenacissima* steppes are more limited by abiotic conditions than by impaired ecosystem functioning.

Current approaches and models aimed to restore degraded ecosystems emphasize the need to recover ecosystem function in degraded ecosystems prior to the introduction of species (Whisenant 1999; Hobbs 2002). They also highlight the presence of thresholds in ecosystem functioning that may impair the establishment of key structural components of the ecosystem, such as shrubs in *S. tenacissima* steppes (Maestre 2004; Maestre & Cortina 2004a, 2005). Our findings do not support these predictions and suggest that the amount of energy and economic input needed to introduce shrub seedlings in steppes with reduced functionality may not be higher than those needed to restore steppes with better functional status (as measured by the LFA indices). It has been suggested that the restoration of semiarid *S. tenacissima* steppes should follow a two-step approach according to their functional status and structural attributes (Maestre & Cortina 2004a). In steppes showing clear symptoms of impaired functionality, restoration actions should focus on repairing soil stability, infiltration, and nutrient cycling. This can be achieved by using low-cost methods such as the creation of new patches using dead branches (Ludwig & Tongway 1996; Tongway & Ludwig 1996). In steppes with better functional status, restoration actions should focus on the introduction of

late-successional shrubs as a way to improve ecosystem functions, to increase ecosystem resilience against disturbances, and to foster the establishment of other plant and animal species. Our results suggest that the first step may not be fully needed in order to achieve the second and that shrubs can be established in steppes with reduced functionality and with clear symptoms of degradation. However, this does not mean that the recovery of ecosystem structure and functioning is unimportant. Such a recovery is critical to get resilient and self-sustainable ecosystems at the mid- to long term and should be always considered when restoring *S. tenacissima* steppes. Due to the low growth rate of shrubs, to the risks facing shrub plantings in semi-arid areas, and to the negative impacts by animals, planting shrubs alone in very degraded steppes would not always be the best approach to restore them. However, if enough resources are available, these plantings could complement other actions aimed to the self-recovery and maintenance of ecosystem processes in degraded steppes.

Our experimental approach has some limitations that need to be acknowledged. Despite recent experimental work indicating that the infiltration index is a suitable descriptor of infiltration rate under field conditions in *S. tenacissima* steppes, we can only postulate that the stability and nutrient cycling indices are acting as surrogates of these ecosystem functions. We were able to conduct our study in 10 sites due to logistic constraints associated with the high costs of the experimental plantings. This precluded the utilization of statistical procedures to numerically detect the joint direct and indirect influences of ecosystem composition, structure, and functioning on seedling survival and to evaluate their relative importance. In addition, and despite the fact that we covered a key period in the establishment of *P. lentiscus*, our conclusions are based on the survival of seedlings only 17 months after planting. Another weakness of our approach is related to the statistical properties of the LFA indices. When individual indicators are summed to form these indices, reporting and testing means and variance terms is questionable because the statistical properties of such indices are not known. Although we used nonparametric statistical methods to evaluate site-to-site differences in the LFA indices and to correlate them with seedling survival, results from statistical comparisons involving these indices should be interpreted with caution.

Despite its limitations, this study represents one of the first attempts to evaluate the relationship between ecosystem composition, structure, and functioning and the success of restoration actions. Our results provide valuable insights on those factors that limit the early stages of the restoration of degraded semiarid steppes and can be used to guide land managers and restoration practitioners involved in this process. Further experiments using a larger number of sites and sampled over longer periods of time are needed to improve our understanding on the relative importance of ecosystem attributes versus abiotic factors during early stages of restoration. This is crucial to criti-

cally test current conceptual models and to advance the development of ecologically sound approaches for the restoration of degraded ecosystems.

Acknowledgments

We thank J. Huesca, N. Martín, M. D. Puche, C. Espinosa, V. Bortolotti, E. Vega, and V. Pérez for their help during fieldwork, D. Tongway for his help with the use of the LFA methodology, and B. Bestelmeyer, D. Tongway, and two anonymous referees for improving the manuscript with their useful comments. This work was supported by the research project FANCB (REN2001-0424-C02-01/GLO), funded by the Spanish FEDER-MICYT. F.T.M. was supported by FPU and Fulbright (FU2003-0398) fellowships from the Spanish Ministerio de Educación y Ciencia.

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