



Scale-dependent determinants of plant species richness in a semi-arid fragmented agro-ecosystem

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Keywords

Habitat fragmentation; Hierarchical partitioning of variance; Multi-grain sampling; Scale-dependence; Species density; Uniform sampling.

Nomenclature

Feinbrun-Dothan & Danin (1991)

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Abstract

Aims: (1) Understanding how the relationship between species richness and its determinants depends on the interaction between scales at which the response and explanatory variables are measured. (2) Quantifying the relative contributions of local, intermediate and large-scale determinants of species richness in a fragmented agro-ecosystem. (3) Testing the hypothesis that the relative contribution of these determinants varies with the grain size at which species richness is measured.

Location: A fragmented agro-ecosystem in the Southern Judea Lowland, Israel, within a desert–Mediterranean transition zone.

Methods: Plant species richness was estimated using hierarchical nested sampling in 81 plots, positioned in 38 natural vegetation patches within an agricultural matrix (mainly wheat fields) among three land units along a sharp precipitation gradient. Explanatory variables included position along that gradient, patch area, patch isolation, habitat heterogeneity and overall plant density. We used general linear models and hierarchical partitioning of variance to test and quantify the effect of each explanatory variable on species richness at four grain sizes (0.0625, 1, 25 and 225 m²).

Results: Species richness was mainly affected by position along a precipitation gradient and overall plant density, and to a lesser extent by habitat heterogeneity. It was also significantly affected by patch area and patch isolation, but only for small grain sizes. The contribution of each explanatory variable to explained variance in species richness varied with grain size, i.e. scale-dependent. The influence of geographic position and habitat heterogeneity on species richness increased with grain size, while the influence of plant density decreased with grain size.

Main conclusions: Species richness is determined by the combined effect of several scale-dependent determinants. Ability to detect an effect and effect size of each determinant varies with the scale (grain size) at which it is measured. The combination of a multi-factorial approach and multi-scale sampling reveals that conclusions drawn from studies that ignore these dimensions are restricted and potentially misleading.

Introduction

The number of species in any given area is determined by various processes operating over a wide range of spatial and temporal scales (Shmida & Wilson 1985; Hillebrand & Blenckner 2002; Ricklefs 2004). For example, climate, biogeographic history and long-term evolutionary processes determine large-scale regional species pools (Currie et al. 2004; Pärtel et al. 2007; Harrison & Cornell 2008), whereas habitat diversity, disturbance regime and inter-

specific interactions mainly affect local species richness (Grime 1973; Grace 1999; Michalet et al. 2006). However, the fact that species richness is often correlated across scales (e.g. local–regional relationships) indicates that factors affecting it at any given scale may also have an apparent effect at other scales (Zobel 1997; Harrison & Cornell 2008). In insular environments (e.g. archipelagos, fragmented landscapes), species richness patterns are also affected by processes of extinction and colonization

(MacArthur & Wilson 1967). The island biogeography theory (MacArthur & Wilson 1967) has been repeatedly tested in fragmented landscapes with a focus on the effects of patch area and patch isolation on species richness patterns observed at a whole-patch scale. Patch-level species richness is expected to increase with patch area because larger patches hold a wider variety of habitat types, have more individuals which can more closely represent regional species richness and support larger populations which are less prone to extinction (Rosenzweig 1995; Rosenzweig & Ziv 1999; Scheiner 2003; Turner & Tjørve 2005). Patch isolation is expected to decrease patch-level species richness as it reduces the probabilities of colonization and re-colonization of patches by species. These 'island biogeography' effects, which control variation in patch-level species richness, may also leave a similar signature on among-island variation in local species richness (Kelly et al. 1989; Holt 1992, 1993; Hill et al. 1994; Hoyle 2004; Harrison et al. 2006; Helm et al. 2006). Here we refer to local species richness as the number of species within a standardized area (species density).

In this study, we test the effects, and partition the contribution, of various scale-dependent determinants of local plant species richness in habitat patches within a fragmented agro-ecosystem in southern Israel. Furthermore, we test whether the effects of each of these determinants (position along a precipitation gradient, patch area, patch isolation, habitat heterogeneity and plant density) and their contribution to the explained variance in local species richness are scale-dependent in a predictable manner. We acknowledge that scale dependence may take several meanings depending on the exact definition of scale and its components (extent, focus and grain, *sensu* Scheiner et al. 2000). Our current investigation involves testing whether the relationship between local species richness and its determinants varies with the grain size at which local species richness is measured. The shape and significance of observed relationships between species richness and its hypothesized determinants (e.g. productivity, altitude) may vary with other components of scale (Mittelbach et al. 2001; Belmaker & Jetz 2011).

Local species richness is positively correlated with regional species richness, and the strength of this correlation is expected to increase with the grain size used for measuring local species richness (Caley & Schluter 1997; Hillebrand & Blenckner 2002; He et al. 2005; Harrison & Cornell 2008). This grain dependency of local-regional richness patterns is usually attributed to the effect of inter-specific interactions (mostly competition), which mainly limit local species richness at small grain size (Caley & Schluter 1997; Hillebrand & Blenckner 2002; He et al. 2005; Harrison & Cornell 2008). In fragmented landscapes, local species richness is sampled from, and is

positively correlated with, the patch-level species richness (Stiles & Scheiner 2010). Therefore, local species richness is expected to be affected by determinants of patch-level species richness, i.e. it will increase with patch area and decrease with patch isolation. These relationships are expected to weaken at smaller grain sizes, where other factors limit local species richness.

In general, species richness is expected to increase with an increase in habitat heterogeneity, as a heterogeneous environment provides a wider niche space than a homogeneous one (Tilman 1982). However, recent theoretical and empirical studies have shown that the relationship between habitat heterogeneity and species richness may be positive, unimodal or even negative, and that this relationship may vary with scale (Kadmon & Allouche 2007; Lundholm 2009; Tamme et al. 2010). In particular, it has been argued that an increase in habitat heterogeneity is associated with higher probabilities of local extinctions of habitat specialists, thus reducing species richness. As local extinctions are more likely to occur at smaller grain sizes, the negative effect of heterogeneity on richness is mainly expected to operate at small grain sizes, where it may even offset the positive effect that is based on a niche space consideration. Therefore, we predicted that overall, the positive effect of habitat heterogeneity on species richness will increase with grain size.

Functions that describe the accumulation of species in a sample or a community with the addition of individuals are always positive. They are usually steep at first and decelerate until they approach an asymptote that marks the total number of species (Gotelli & Colwell 2001). Since the number of individuals in a sample or a community (community/sample size) is the product of area and density, for a standardized area, species richness is expected to increase with overall density. Due to the decelerating nature of this relationship, the effect of overall density is expected to be less pronounced as community size increases; i.e. the effect weakens with an increase in grain size (Oksanen 1996; Pärtel & Zobel 1999).

Multi-grain sampling has been used to test the grain-dependent response of species richness to various factors, such as biomass, disturbance regime, climatic variables and habitat heterogeneity (Anderson et al. 2007; Lundholm 2009). However, to the best of our knowledge, this sampling and data analysis approach has not been applied to studies that considered landscape-scale processes. Here, we use a hierarchical multi-grain design to sample plant species richness in habitat islands of natural vegetation within an agricultural landscape in the Southern Judea Lowland (SJL) of Israel.

We evaluate the relative contributions of local, intermediate and large-scale determinants of plant species richness using a hierarchical partitioning of the variance

(Gromping 2006). Our main goal is to test the hypothesis that the relative contributions of several potential determinants – (a) position along a sharp precipitation gradient, (b) patch area, (c) patch isolation, (d) habitat heterogeneity, and (e) plant density – to variation in plant species richness will vary with the grain size. Specifically, we predict that plant species richness will increase along the precipitation gradient with an expected increase in regional species pool. The correlation between regional and local species richness is expected to increase with grain size. We expect species richness to increase with patch area and decrease with patch isolation, and that these correlations will be most apparent at larger grain sizes. We also predict that species richness will increase with habitat heterogeneity, especially as grain size increases. Finally, we expect species richness to increase with plant density, and that this effect will be most apparent at small grain sizes. Although simultaneous consideration of several determinants often explains significantly more of the variation in species richness than a single factor approach, demonstrating scale dependency

of the relationships between local species richness and its determinants rarely includes more than a single determinant (Grace 1999; Turner & Tjørve 2005; Harrison et al. 2006). By partitioning the explained variance in local species richness we show how the relationship between species richness and its determinants depends on the interaction between the scales at which the hypothesized determinants operate and the grain at which species richness is measured.

Methods

Study area

The study area (31°24'00"-31°40'50"N, 34°48'30"-34°50'30"E) is located in the Southern Judea Lowland (SJL), Israel, which represents a sharp transition zone between Mediterranean and desert ecosystems (Fig. 1). The climate is a typical semi-arid, with short mild winters and long, dry and hot summers. Average annual temperature is 19°C (12°C in January and 26°C in August) throughout the study area. Average annual precipitation

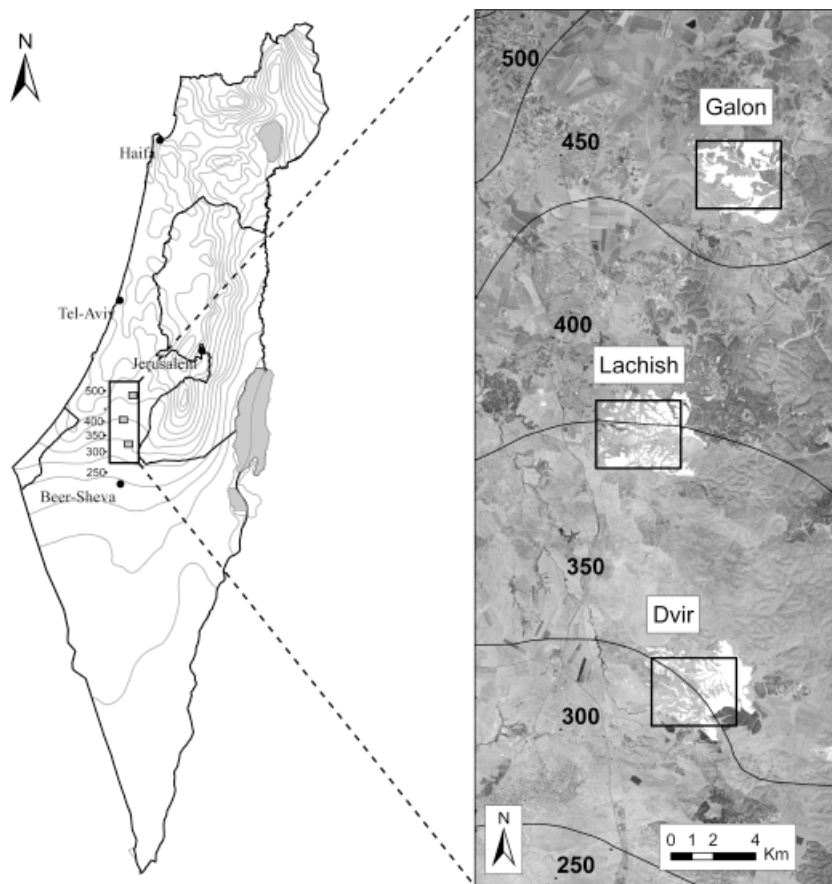


Fig. 1. The Southern Judea Lowland – the left panel presents the general location of the study area. The right panel depicts the positions of the three land units along the precipitation gradient within the study area. Contour lines represent average annual precipitation (mm).

Table 1. List of the 30 most common species in the sampling plots in the Southern Judean Lowland, Israel. Species names are given with their life cycle, life form and incidence in the whole study (SJL) and in each of the three land units (Dvir, Lachish and Galon). The total number of plots in the study and in each unit is given (in brackets) in the column description.

Species	Life cycle	Life form	Family	SJL	Dvir	Lachish	Galon
				(81)	(24)	(29)	(28)
<i>Avena sterilis</i>	Annual	Therophyte	Poaceae	1	1	1	1
<i>Anagallis arvensis</i>	Annual	Therophyte	Primulaceae	0.98	0.96	1	0.96
<i>Linum strictum</i>	Annual	Therophyte	Linaceae	0.96	0.96	1	0.93
<i>Urospermum picroides</i>	Annual	Therophyte	Asteraceae	0.94	0.83	1	0.96
<i>Plantago afra</i>	Annual	Therophyte	Plantaginaceae	0.91	0.83	1	0.89
<i>Pallenis spinosa</i>	Annual	Therophyte	Asteraceae	0.91	0.92	1	0.82
<i>Eryngium creticum</i>	Annual	Therophyte	Apiaceae	0.88	0.96	1	0.68
<i>Pterocephalus brevis</i>	Annual	Therophyte	Dipsacaceae	0.88	1	1	0.64
<i>Lotus peregrinus</i>	Annual	Therophyte	Fabaceae	0.84	0.88	0.97	0.68
<i>Torilis tenella</i>	Annual	Therophyte	Apiaceae	0.84	0.92	0.93	0.68
<i>Teucrium capitatum</i>	Perennial	Chamaephyte	Lamiaceae	0.84	0.92	1	0.61
<i>Convolvulus dorycnium</i>	Perennial	Hemicryptophyte	Convolvulaceae	0.81	0.79	0.97	0.68
<i>Biscutella didyma</i>	Annual	Therophyte	Brassicaceae	0.80	0.58	0.93	0.86
<i>Erodium gruinum</i>	Annual	Therophyte	Geraniaceae	0.80	1	0.86	0.57
<i>Stipa capensis</i>	Annual	Therophyte	Poaceae	0.79	1.00	0.97	0.43
<i>Phagnalon rupestre</i>	Perennial	Chamaephyte	Asteraceae	0.78	0.75	0.90	0.68
<i>Asphodelus aestivus</i>	Perennial	Hemicryptophyte	Liliaceae	0.78	0.88	0.97	0.50
<i>Carthamus tenuis</i>	Annual	Therophyte	Asteraceae	0.78	0.96	0.76	0.64
<i>Scilla autumnalis</i>	Annual	Geophyte	Liliaceae	0.75	0.83	0.86	0.57
<i>Filago pyramidata</i>	Annual	Therophyte	Asteraceae	0.73	0.67	0.90	0.61
<i>Medicago coronata</i>	Annual	Therophyte	Fabaceae	0.70	0.54	0.97	0.57
<i>Hymenocarpus circinnatus</i>	Annual	Therophyte	Poaceae	0.70	0.83	0.69	0.61
<i>Hippocrepis unisiliquosa</i>	Annual	Therophyte	Fabaceae	0.70	0.83	0.93	0.36
<i>Gundelia tournefortii</i>	Perennial	Hemicryptophyte	Asteraceae	0.69	0.83	0.90	0.36
<i>Onobrychis squarrosa</i>	Annual	Therophyte	Fabaceae	0.68	0.21	0.93	0.82
<i>Trigonella monspeliaca</i>	Annual	Therophyte	Fabaceae	0.68	0.50	1	0.50
<i>Anemone coronaria</i>	Perennial	Geophyte	Ranunculaceae	0.68	0.96	0.93	0.18
<i>Trifolium dasyurum</i>	Annual	Therophyte	Fabaceae	0.67	0.46	0.93	0.57
<i>Euphorbia chamaepeplis</i>	Annual	Therophyte	Euphorbiaceae	0.67	0.83	0.90	0.29
<i>Erodium malacoides</i>	Annual	Therophyte	Geraniaceae	0.65	0.38	0.59	0.96

(restricted to October–March) exhibits a sharp gradient, ranging from 300 mm in the south to 450 mm in the north along a short stretch of only 30 km (Goldreich 2003). Soil types in the study area vary from Loessial light brown soils in the south to light brown Rendzina and dark brown Grumusols in the north (Dan et al. 1976). The area has experienced grazing by sheep and goats and small-scale agriculture for thousands of years (Naveh & Dan 1973; Ackermann et al. 2008). Intensified agricultural practice over the past 60 years has reshaped the landscape to its current form, which comprises a mosaic of natural vegetation patches within a predominately agricultural matrix (Mazor 2006; Svoray et al. 2007; Yaacobi et al. 2007).

Depending on aspect, grazing regime and soil characteristics, the vegetation in the study area is represented by several types of species dominance and plant structure. The main vegetation types are semi-steppe batha and

grassland with a decreasing shrub cover from north to south and from east to west. The batha is mostly characterized by *Sarcopoterium spinosum*, a dwarf shrub up to 0.5-m high that is dominant in many eastern Mediterranean shrublands. It is often accompanied by other shrubs, such as *Teucrium capitatum*, *Phlomis brachyodon* and *Phagnalon rupestre*. The perennial grasslands are mainly dominated by *Hyparrhenia hirta*, often accompanied by *Hordeum bulbosum* and *Anchusa strigosa*. Another grassland community in our study area is characterized by the annual grasses *Avena sterilis* and *Hordeum spontaneum*. In all of these community types, the herbaceous layer consists of many annuals and geophytes, most notable in the latter is *Asphodelus aestivus*, which is very common in heavily grazed areas. Trees are absent from the landscape, except for very few and isolated individuals of *Rhamnus lycioides* and *Ziziphus spina-christi*, reaching a maximum height of 3–4 m. The total number of

species in the landscape is close to 500 (personal observation). Species with the highest incidence in the sampling plots are listed in Table 1.

We focused our research in three land units – Dvir, Lachish and Galon – positioned along a south–north precipitation gradient (Fig. 1). Average annual rainfall is 291, 376 and 424 mm in Dvir, Lachish and Galon, respectively (average for 1998–2009, measured within 3 km of each land unit, Data from the Ministry of Agriculture, Israel). Each land unit (3.2 km × 4 km) includes 70–170 natural vegetation patches of different sizes, ranging from continuous (> 100 ha) to very small patches (< 100 m²). We used rectified aerial photographs (Ofek 2005, pixel size = 1 m²) to identify all the patches of natural vegetation within each of these land units. We then demarcated their boundaries on a digitized map and stored the information as a

vector-based coverage in a geographical information system (GIS) platform (ArcInfoTM; ESRI). The data were converted to a raster-based layer (grid cells size = 5 × 5 m) and exported to FRAGSTATS[©] (University of Massachusetts, Amherst, MA, US, <http://www.umass.edu/landeco/research/fragstats/fragstats.html>) for the calculation of patch area, distance to nearest neighbour and patch proximity index. Proximity index is a measure of patch isolation, which quantifies the spatial context of a patch in relation to neighbouring patches. For each patch *i*, the proximity index (PI_{*i*}) is given by:

$$PI_i = \sum_{j=1}^n \frac{a_j}{h_{ij}^2}, \tag{1}$$

where *a_j* is the area of patch *j*, *h_{ij}* is the distance (edge-to-edge) between patch *i* and patch *j*, and the summation is done for all *n* patches that are within a certain search radius, *r_s*, of the focal patch *i*. We report the data analysis conducted using a proximity index calculated using *r_s* of 1000 m. Preliminary data analysis conducted using a proximity index with smaller *r_s* (500 m and 100 m) yielded very similar results (proximity indices calculated with several *r_s* are provided in Appendix S3).

Table 2. Results of mixed linear models testing the effects of plant density, patch area, habitat heterogeneity, patch proximity and geographic position (land unit) on species richness at four grain sizes (0.0625 m² (a), 1 m² (b), 25 m² (c) and 225 m² (d)) in the Southern Judea Lowland landscape. Plant density, patch area and patch proximity were all log-transformed prior to any analysis. The coefficients of the continuous explanatory variables (Coef.) are estimated for the full model including all explanatory variables. The likelihood ratio tests (LRT) and the associated Chi-square based *P*-values are based on single-term deletions of each explanatory variable.

	Coef. (mean ± SE)	DF	AIC	LRT	Pr(Chi)
Grain = 0.0625 m ² , R ² = 0.84					
None			215.51		
Plant density	3.85 ± 0.54	1	253.08	39.568	< 0.001
Heterogeneity	1.14 ± 0.58	1	217.32	3.808	0.05
Patch area	0.32 ± 0.48	1	214.01	0.50	0.48
Proximity	0.71 ± 0.25	1	221.41	7.900	0.005
Land unit		2	217.83	6.318	0.04
Grain = 1 m ² , R ² = 0.75					
None			328.70		
Plant density	6.17 ± 1.42	1	344.67	17.9692	< 0.001
Heterogeneity	3.64 ± 1.61	1	332.11	5.41	0.02
Patch area	1.96 ± 1.07	1	330.35	3.6532	0.056
Proximity	0.94 ± 0.55	1	329.71	3.0073	0.083
Land unit		2	337.18	12.4774	0.002
Grain = 25 m ² , R ² = 0.67					
None			405.44		
Plant density	7.39 ± 2.69	1	411.25	7.8023	0.005
Heterogeneity	11.97 ± 3.08	1	418.15	14.7082	0.0001
Patch area	2.38 ± 1.95	1	405.11	1.6664	0.19
Proximity	0.87 ± 1.00	1	404.27	.8319	0.36
Land unit		2	418.48	17.0330	0.0002
Grain = 225 m ² , R ² = 0.66					
None			452.13		
Plant density	3.11 ± 3.96	1	450.72	0.59	0.44
Heterogeneity	14.66 ± 4.35	1	461.74	11.61	0.0006
Patch area	−0.56 ± 3.26	1	450.16	0.032	0.85
Proximity	2.08 ± 1.67	1	451.84	1.71	0.19
Land unit		2	467.29	19.16	< 0.001

Vegetation sampling

We established 81 vegetation sampling plots in 41 patches of natural vegetation (25, 28 and 28 plots in 12, 15 and 14 patches within Dvir, Lachish and Galon, respectively). The number of plots placed within each patch varied correlatively with patch area and ranged between one and five. The sampling design is a hierarchical nested design that was modified after Kalkhan et al. (2007).

Each sampling plot (15 m × 15 m) was divided into nine 5 m × 5 m subplots, three of which were further divided into smaller sampling units (Fig. 2). Two frames

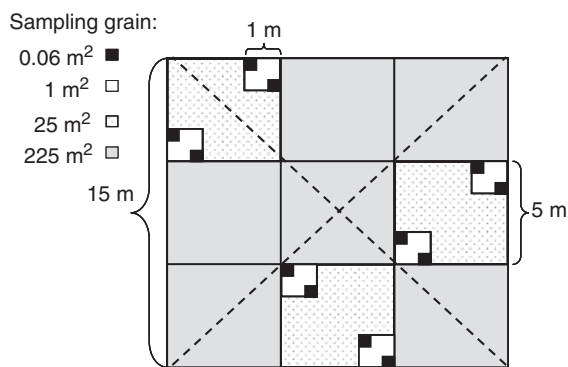


Fig. 2. Vegetation sampling plot. Sampling was conducted in a hierarchical manner, starting by recording any vascular plant species observed at the smallest sampling unit (0.0625 m²) and adding newly observed species to the larger sampling until all plots were surveyed for any species not yet recorded in any of the smaller sampling units.

of 1 m × 1 m were placed in opposite corners within each of those three 5 m × 5 m subplots, and two sampling quadrats (0.25 m × 0.25 m) were placed within each of the 1 m × 1 m frames (Fig. 2). As a result, the grain size ranged over four orders of magnitude that overlap with many studies of similar plant communities (Grace 1999; Drakare et al. 2006). Altogether, each vegetation sampling plot included 12, six, three and one sampling units for grain sizes of 0.0625, 1 and 25 and 225 m², respectively. All vascular plant species within each of the sampling units were recorded during the height of the growing season between early March and early April 2009. Plant density was measured by counting all individuals within each of the smallest sampling units (0.0625 m²). Plant identification and nomenclature followed Feinbrun–Dothan & Danin (1991).

Habitat heterogeneity

Habitat heterogeneity within each of the vegetation sampling plots was evaluated by recording the distribution of different microhabitats along two transects that form the main diagonals of the plot (Fig. 2). Eighty-four consecutive quadrats (0.25 m × 0.25 m) were surveyed along both sides of each diagonal transect, and each quadrat was assigned to one of six microhabitat categories: 'exposed rock', 'herbaceous patch', each of the two most dominant perennials (*Sarcopoterium spinosum* and *Hyparrhenia hirta*), 'small shrub' (other than *S. spinosum*) and 'large bush'. The spatial resolution (0.0625 m²) for depicting different habitat types was chosen according to the minimal size of habitat elements, which was in the order of 0.5 m (e.g. shrub) to a few meters (e.g. exposed rock). The two dominant perennials were used as surrogates for microhabitat category because: (a) their presence has been shown to correlate well with underlying physical and chemical conditions (Litav 1967), and (b) woody perennials in this region significantly modulate the spatial distribution of resources (e.g. water, organic matter, nutrients, shade) and of propagules (Giladi et al. 2007; Segoli et al. 2008). Consequently, they affect the distribution and abundance of herbaceous plants, which form almost 90% of the species within our study area (66% annuals, 14% herbaceous perennials and 8% geophytes). After combining the data from the two diagonal transects, the proportions of the different microhabitats were used to calculate the Shannon index of diversity as a measure of plot-scale habitat heterogeneity. By combining data along shorter segments of the diagonal transects, we also calculated the Shannon index of diversity for smaller sampling units (1 and 25 m²), which correspond to the vegetation sampling grains. We averaged these segment-based heterogeneity indices for each plot and used them to represent grain-specific heterogeneity.

Data analysis and statistics

The total number of species recorded in each sampling plot (plot-scale species richness) and average species richness per plot at each of the smaller grain sizes (i.e. 0.0625, 1 and 25 m²) were treated as the main response variables. Position along the precipitation gradient (i.e. Dvir, Lachish and Galon), patch area, patch proximity, habitat heterogeneity and plant density were treated as explanatory variables. Plot was nested within a patch that was included as a random factor. We used linear mixed effect models (LME) in the nlme package (nlme: linear and nonlinear mixed effects models; R version 3.1-100, R Core Development Team, Vienna, Austria 2006) to test for the effects of the various explanatory variables on species richness at each grain size. The marginal effect of each explanatory factor on species richness was tested by single term deletions followed by a likelihood ratio test (using the dropterm function in the MASS package in R (Venables & Ripley 2002)). We also extracted partial residuals from the LMEs and plotted them against the respective explanatory factor. We used linear models to partition the contributions of each of the explanatory variables to the explained variance in species richness by employing hierarchical variance partitioning. For that purpose, we used the pmvd metric, which was calculated by the relaimpo R package (Gromping 2006). The pmvd metric controls for potential biases in the decomposition of model explained variance whenever explanatory variables are not fully orthogonal. We conducted all of the above-mentioned analyses separately for each grain size using the R statistical platform and the associated packages mentioned above. We used data from all 81 plots for counting species richness at the land unit scale and for the whole study. However, prior to the statistical analyses, we excluded from our data set 21 plots that were either within continuous patches (non-isolated), were recently used as livestock pens (and thus were heavily disturbed and had a high percentage of ruderals), or whose marking posts disappeared before we could complete the measurement of all explanatory variables. Plant density, patch area and patch proximity were all log-transformed prior to all statistical analyses.

Results

Altogether, we observed 428 plant species (256, 318 and 342 in Dvir, Lachish and Galon, respectively). Less than half (192) of the species were recorded in all three land units. Ninety-seven species were recorded in two land units only; of these, 89 species were shared among the central land unit (Lachish) and either the southern (Dvir) or the northern (Galon) land units (Fig. 3). Only eight species were absent from the central land unit only. Most

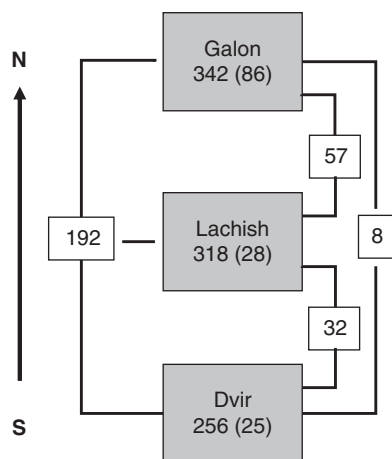


Fig. 3. Plant species richness along a south–north precipitation gradient. The total number of plant species is given for each land unit in addition to the number of species unique to this land unit (in parentheses). The number of plant species shared by all combinations of two or three of the land units is presented in boxes connected to the respective unit.

of the 139 species that were recorded in one land unit only were either rare species or Mediterranean species that were observed in the northernmost land unit (Galon) only (Table 3, Fig. 3). Species richness at the plot scale (225 m²) ranged between 26 and 133 (83.09 ± 17.94, mean ± SD, n = 81). Species richness was 46.03 ± 11.15, 20.70 ± 6.30 and 7.68 ± 3.45 (all mean ± SD, n = 81) at the 25, 1 and 0.0625 m² grain sizes, respectively (Fig. 4).

All of the explanatory variables except patch area had a significant effect on species richness in at least one of the grain sizes. In accordance with our predictions, the coefficients of all the continuous variables that had significant effects on species richness (plant density, habitat heterogeneity and proximity) were always positive (Fig. 5, Table 2). Species richness at all grain sizes increased significantly along the geographic gradient from south (Dvir) to north (Galon) (Fig. 4). Patch area had a positive and marginally significant (P = 0.056) effect on species richness at a grain size of 1 m² (Fig. 5a). Proximity had a positive and significant effect on species richness only at a grain size of 0.0625 m² (Fig. 5b). Habitat heterogeneity had a positive and significant effect on species richness at all scales (Fig. 5c). The effect of plant density on species richness was positive and significant at all the grain sizes except the largest (Fig. 5d).

The relative contribution of the explanatory variables to the explained variance in species richness was dependent upon grain size (Fig. 6). Combined, two of the five determinants that we considered in our analysis (plant density and the position along precipitation gradient) contributed to 80–90% of the explained variance. Plant density explained most of the variance in species richness

Table 3. List of the ten most common plant species that are unique to each of the three land units. The phylogeographic province and incidence of the species within their respective land unit are given. An asterisk with a capital letter indicates that a species has been observed in another land unit, but not within the sampling plots.

	Species	Phylogeographic origin	Incidence
Dvir	<i>Astragalus aleppicus</i>	Irano-Turanian	0.50
*L	<i>Deverra tortuosa</i>	Saharo-Arabian	0.50
	<i>Thymelaea hirsuta</i>	Saharo-Arabian, Mediterranean	0.46
	<i>Malabaila secacul</i>	Irano-Turanian	0.29
	<i>Asparagus stipularis</i>	Saharo-Arabian, Mediterranean	0.21
	<i>Astragalus sanctus</i>	Irano-Turanian	0.21
	<i>Atractylis serratuloides</i>	Saharo-Arabian	0.21
	<i>Carrichtera annua</i>	Saharo-Arabian	0.17
*L	<i>Plantago coronopus</i>	Widespread	0.13
*L	<i>Schismus arabicus</i>	Irano-Turanian, Saharo-Arabian	0.13
	<i>Euphorbia grossheimii</i>	Saharo-Arabian	0.08
Lachish	<i>Pimpinella corymbosa</i>	Irano-Turanian	0.59
*G	<i>Sanguisorba minor</i>	Mediterranean	0.17
*G	<i>Hirschfeldia incana</i>	Mediterranean, Irano-Turanian	0.14
	<i>Scandix iberica</i>	Mediterranean, Irano-Turanian	0.14
	<i>Acanthus syriacus</i>	Mediterranean, Irano-Turanian	0.10
	<i>Astragalus macrocarpus</i>	Mediterranean	0.10
*G	<i>Euphorbia helioscopia</i>	Mediterranean	0.10
	<i>Lathyrus pseudocicera</i>	Mediterranean	0.10
	<i>Lomelosia palaestina</i>	Mediterranean, Irano-Turanian	0.10
*D,G	<i>Majorana syriaca</i>	Mediterranean	0.10
*D	<i>Telmisa microcarpa</i>	Mediterranean	0.10
Galon	*L <i>Trifolium alexandrinum</i>	Mediterranean	0.82
	*L <i>Convolvulus pentapetaloides</i>	Mediterranean	0.73
	<i>Linum corymbulosum</i>	Mediterranean, Irano-Turanian	0.55
	<i>Prosopis farcta</i>	Irano-Turanian	0.55
	<i>Trifolium clypeatum</i>	Mediterranean	0.45
*L	<i>Carduus argentatus</i>	Mediterranean	0.41
*L	<i>Trifolium spumosum</i>	Mediterranean, Irano-Turanian	0.36
	<i>Polygala monspeliaca</i>	Mediterranean	0.32

at the smallest grain size (0.0625 m²) and its contribution to the explained variance declined with an increase in grain size. Geographic position exhibited the opposite trend, contributing to most of the explained variance in species richness at a grain size of 225 m² and less so as grain size decreased. The contribution of habitat heterogeneity to the explained variance in species richness was

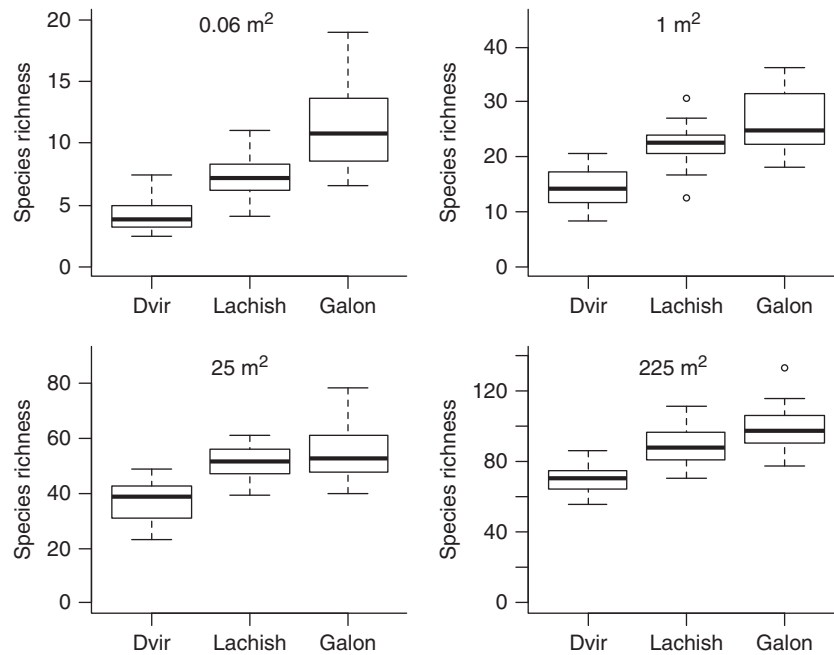


Fig. 4. Species densities at the various grain sizes in the three land units along a precipitation gradient. Average annual precipitation is 291, 376 and 424 mm in Dvir, Lachish and Galon, respectively. The total number of plant species observed in each of the three land units was 256, 318 and 342 in Dvir, Lachish and Galon, respectively.

apparent mainly at the 25 m² and 225 m² grain sizes. The contribution of the other two factors (patch area and proximity) to the explained variance in species richness was minor at all grain sizes. In all of the analyses presented above, we considered habitat heterogeneity as measured for the plot scale only. We also conducted similar analyses where the scale of quantifying habitat heterogeneity was matched to the grain size of vegetation sampling (Appendix S1). Overall, the results of these analyses were very similar to those presented above, with the notable difference that the effect of grain-matched habitat heterogeneity was statistically significant only at the larger grain sizes (25 and 225 m²).

Discussion

Our main goal was to test the effects of various scale-dependent explanatory factors – geographical position along a precipitation gradient, patch area, patch isolation, habitat heterogeneity and plant density – on species richness as measured at several (nested) spatial grains. The results indicate that at the range of scales considered in our study, plant species richness is mainly affected by the position along a precipitation gradient and by plant density. In addition, local species richness is positively correlated with habitat heterogeneity, and to a limited extent is positively correlated with patch area and negatively correlated with patch isolation. Importantly, the contribution of

each of the explanatory factors to the explained variance in species richness varied with grain size.

The position along the precipitation gradient contributed significantly to the explained variance in species richness at all grain sizes, and this contribution increased with grain size. Although the extent of the study area is relatively small (10 km × 30 km), due to its position within a sharp transition zone between desert and Mediterranean ecosystems, it represents a transition in species pools. This transition is well reflected in the pattern of species overlap among the three land units (Fig. 3). The central land unit (Lachish) shared many species with either extreme (Dvir or Galon) compared to only a few species that were absent from the central land unit only. The spatial turnover of species along this transition zone was not symmetrical. The northward gain in Mediterranean species was higher than the loss of desert species, as indicated by a south to north increase in the number of species unique to each land unit. This asymmetry within our study area reflects a clear south-to-north increase in regional species pool, which corresponds to a well-described pattern at a larger extent (e.g. Levin & Shmida 2007). The south-to-north increase in local species richness that we observed at all grain sizes may mirror this gradient-correlated variation in regional species pools (Zobel 1997). Based on both theoretical and empirical studies, we predicted that the strength of the local-regional relationship would increase with grain size (Caley &

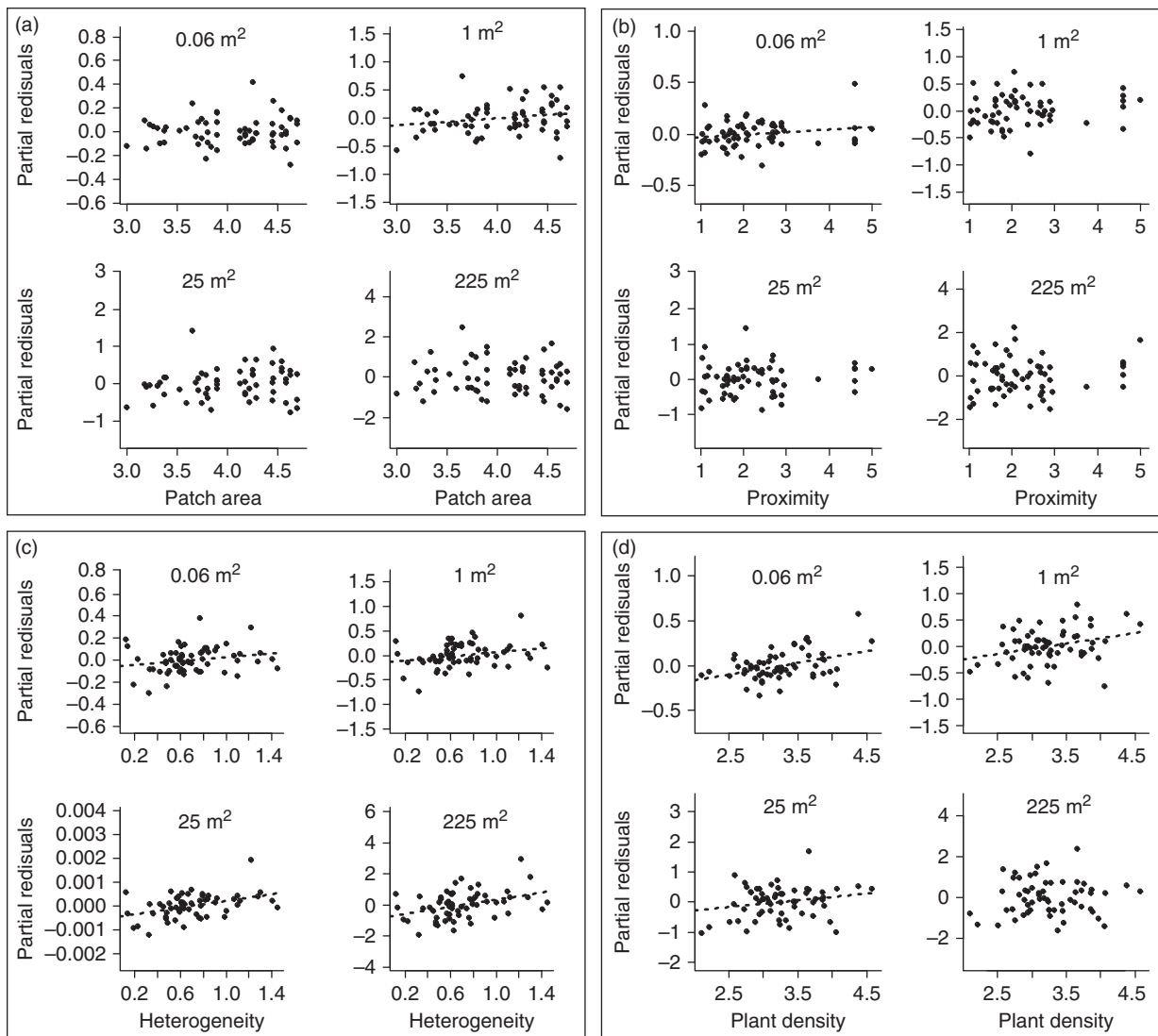


Fig. 5. Partial residual plots for each of the continuous explanatory factors used in our analyses for each of the grain sizes: (a) Patch area (\log_{10} transformed), (b) Patch isolation – \log_{10} transformed proximity index, (c) Microhabitat heterogeneity, Shannon index of diversity calculated with a focus on the 225 m² plot scale, (d) Plant density, total number of individuals within 0.0625 m² averaged per plot and log-transformed. Partial residuals represent the unexplained (residual) variance extracted from a regression model that includes all explanatory factors except one. Regression lines are shown only when the slope of the relationship was found to be significantly different from zero (based on the statistical models reported in Table 2).

Schluter 1997; Hillebrand & Blenckner 2002; He et al. 2005; Harrison & Cornell 2008). Indeed, the observed intensification of the influence of the geographic position on local species richness as grain size increased is in agreement with this prediction.

As predicted, we found a significant and positive effect of patch area on species richness, but this effect was only found for a grain size of 1 m² and its contribution to the overall explained variance was minor. Similarly, the data supported the prediction for a decrease in species richness with an increase in patch isolation, but only at the

smallest grain size (0.0625 m²) with a modest contribution to the explained variance. The lack of overwhelming evidence in our data for effects of patch area and patch isolation on local species richness may result from slow extinction rates following landscape fragmentation and/or high inter-patch colonization rates. The degree of patch isolation in our study system is somewhat lower than that in many other studies considering natural vegetation patches within agricultural landscapes (Krauss et al. 2004; Cousins et al. 2007; Reitalu et al. 2009), but similar to studies in similar Mediterranean shrublands

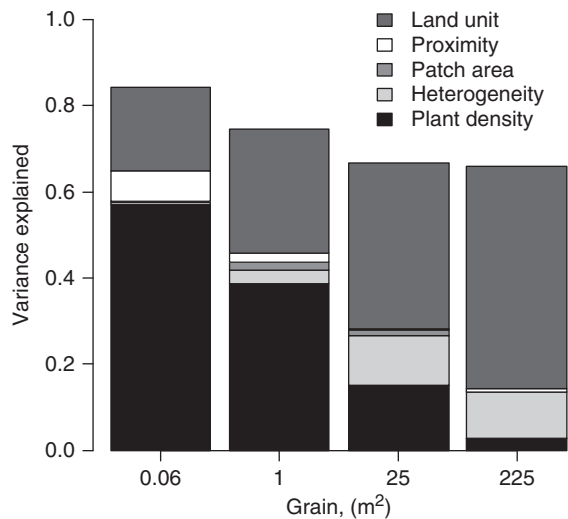


Fig. 6. Contribution of various explanatory variables to the explained variance of species richness at different grain sizes. The height of each column equals the total explained variance (R^2) from a GLM for the respective grain size. The partitioning of the total variance explained ('relative importance') is given by the proportional marginal variance decomposition (PMVD) metric (see text for details and reference).

(Pueyo et al. 2008). A low degree of patch isolation may support high inter-patch colonization rates. Considering the study area and the plant communities that inhabit it, the movement of grazing animals (mainly sheep) and wind are the main dispersal vectors that may augment inter-patch colonization for some species. Yet, most of the plant species in our study system are annuals of short stature that lack any apparent adaptations for long-distance dispersal (Ellner & Shmida 1981; Chambers & Macmahon 1994). For these species, inter-patch dispersal limitation may be substantial. The high plant density (~ 4 million ha^{-1}), and the presence of a long-term seed bank in the plant community, may make patch-level extinction unlikely. These results are in line with a recurrent theme in recent studies of plant communities in fragmented landscapes, i.e. a presumably slow response rate of plant communities to fragmentation effects (Bruun 2000; Lindborg & Eriksson 2004; Adriaens et al. 2006; Helm et al. 2006; Cousins et al. 2007; Öster et al. 2007; Cousins & Eriksson 2008; Pueyo et al. 2008). Therefore, even though positive correlations between local species richness and patch area and patch proximity have strong theoretical support, the detection of such correlations is not trivial, especially when other determinants of local species richness are dominant.

A more heterogeneous environment is expected to support a higher species number. However, habitat heterogeneity may also have a negative effect on species richness, especially at small scales (Kadmon & Allouche

2007; Lundholm 2009; Tamme et al. 2010). Our results are in agreement with recent ideas regarding the balance between positive and negative effects of habitat heterogeneity on species richness and their scale dependency. We found a positive effect of habitat heterogeneity on local species richness at all grain sizes but the smallest, and the contribution of habitat heterogeneity to the explained variance increased with grain size. Kadmon & Allouche (2007) proposed a mechanism where an increase in habitat heterogeneity (within a given total area) entails smaller areas of each habitat type. These smaller patches support smaller population sizes of habitat specialists, thus increasing the probabilities for local extinction. This argument was made for the case where all habitats are equally represented so that an increase in habitat richness necessarily makes each of them rare. When habitats are not evenly distributed, local extinctions is even more likely in the rare habitats. The combined effects of habitat richness and habitat evenness (two components of habitat heterogeneity) on species richness still await further theoretical and empirical tests.

In our main data analysis, there is a growing mismatch between the scale used to measure habitat heterogeneity (225 m^2) and the scales used to measure species richness as the latter decreases. This directional mismatch may explain the reduced explanatory power of habitat heterogeneity as species richness grain size decreases (Fig. 6). However, the analyses that included grain-matched heterogeneity measures (Appendix S1) do not support this notion. Actually, if anything, grain-matched heterogeneity explained even less of the variation in small-grain species richness than larger-scale heterogeneity.

Plant density had a positive significant effect on species richness at all grain sizes except the largest. As predicted, the contribution of plant density to the explained variance in species richness decreased with grain size. These results agree with other studies where the effect of overall plant density on species richness was mostly apparent at a small grain size (Oksanen 1996; Pärtel & Zobel 1999).

Scale-dependent biodiversity patterns are generated by the combined operation of various scale-dependent processes. However, we cannot always predict *a priori* which is the right scale for detecting the effects of each of the hypothesized processes. The choice of sampling unit size may significantly affect our ability to detect and correctly characterize the relationships between species richness and its determinants. Consequently, the choice of grain size influences the inference that we draw regarding the importance of various determinants and the underlying mechanisms (Braschler et al. 2004; Chalcraft et al. 2004; Anderson et al. 2007; Dengler 2009). This important notion has rarely been addressed in studies testing species

richness patterns in fragmented landscapes (but see Stiles & Scheiner 2010).

When compared across ecosystems, the importance of each determinant of species richness may vary not only with scale, but also with the main vegetation type, land-use history, local conditions and plant traits. Research on the effect of habitat fragmentation on plant communities in the Mediterranean has mostly focused on forests and woodlands (Guirado et al. 2007; De Sanctis et al. 2010; Rosati et al. 2010), whereas only a few studies have explored fragmentation effects on vegetation in the more arid grassland or shrubland communities of the Mediterranean basin (Chust et al. 2006; Pueyo et al. 2008).

Caveats and robustness of the results and conclusions

As with most studies conducted at the landscape (or larger) scale, the spatial configuration of patches was not within our control, although we made an attempt to choose patches that would represent a wide range of patch area and patch isolation. The idiosyncrasies of the landscape we studied dictated some methodological choices, which may have affected some of our results and conclusions. For example, based on the low levels of isolation (nearest neighbour distances was always < 250 m) and the position of many patches along linear chains of isolates or within small clusters, we chose to use a proximity index rather than a nearest neighbour index as a measure of isolation. We repeated the statistical analyses by using different search radii for proximity calculations, and by replacing proximity with nearest neighbour as a measure of isolation. As the results of all of these attempts were almost identical to those presented above, we conclude that our analysis and interpretation are robust to these choices.

The choice of the scale at which habitat heterogeneity was measured had little effect on our results. This may be due to the fact that habitat heterogeneity measures in our study were highly correlated across scales ($r=0.92$, 0.87 and 0.97 between heterogeneity measures at 1–25, 1–225 and 25–225 m², respectively, $n=56$). Such high cross-scale correlations in habitat heterogeneity may not necessarily exist in other study systems. Except for the largest grain size (225 m²), where we used the total number of species, we used the average species richness per plot at each of the smaller grain sizes for all further analyses. By using average values per plot we might have reduced the variance in species richness among plots, especially at smaller grain sizes where each average was based on as many as 12 sampling units. However, species richness measured at the smallest grain size is also expected to be affected by stochastic processes whose effects are averaged out as the grain size increases. By using average values for

each plot we strove to balance these stochastic effects and to avoid pseudo-replication. In fact, the coefficient of variation of species richness among plots actually decreased with grain size, although this decrease was modest (CV = 0.46, 0.31, 0.22 and 0.19 for 0.0625, 1, 25 and 225 m², respectively).

Species–area relationships (SPARs) in insular environments are attributed to sampling effects, habitat heterogeneity effects and island biogeography effects. Uniform sampling (i.e. using standardized sampling units) for testing SPAR-generated mechanisms has been proposed as a method for isolating the island biogeography effects while controlling for both sampling and heterogeneity effects (Kelly et al. 1989; Holt 1992, 1993; Hill et al. 1994; Hoyle 2004; Helm et al. 2006; but see Schoereder et al. 2004). Our study clearly demonstrates that the (frequently arbitrary) choice of a grain size in a single-scale application of the uniform approach significantly affects the conclusions. The application of the uniform approach using a multi-scale hierarchical sampling provides, at a relatively low cost, important insights that could not have been gained using a single-scale sampling. The multi-scale sampling approach points to the scales at which various processes operate and it can guide a refinement of testable hypotheses regarding scale-dependent SPAR-generating mechanisms. Thus, it can be practically used to provide significant and better understanding of heterogeneous landscape communities in the context of scale dependency.

The study region, which has experienced a significant reduction in precipitation over the last decades (Kafle & Bruins 2009), represents an ecotone between the Mediterranean and the desert ecosystems (Kark & van Rensburg 2006). It has been recognized as an important ecological corridor (Pe'er & Safriel 2000) and is part of a biosphere reserve. It hosts a set of unique species that are absent or extremely rare elsewhere (e.g. *Nigella nigellastrum*, *Pimpinella corymbosa*, *Astragalus macrocarpus*, *Centaurea ascalonica*). The success of this important landscape in fulfilling its conservation functions in the face of human development and climate change depends not only on its unique geographical position, but also on its connectivity. Our study provides a first look into the main factors that affect plant distribution within this area. Further studies that will link plant traits, including dispersal modes and their mechanisms, and their interactions with landscape connectivity will improve our understanding of the system and its ability to respond to current and impending threats.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Analysis of determinants plant species richness using grain-specific heterogeneity measurements.

Appendix S2. List of microhabitat types that were used for evaluating habitat heterogeneity in the plant sampling plots.

Appendix S3. A list of patches that were sampled for plant richness including their area, distance to nearest neighbour (NND) and proximity indices calculated with three different search radii: 100 m, 500 m and 1000 m.

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