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שימוש מסחרי בחומר הכלול בחיבור זה אסור בהחלט.

# Multiscale analysis of species distribution pattern

Research Thesis

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Lior Blank

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## **Abstract**

Understanding the factors regulating the distribution of species is one of the greatest challenges of ecology. Studies of species distribution patterns and of correlations between species and environmental factors overlooked woody vegetation as an important determinant of species distribution. Organisms can affect their immediate environment, and do so in proportion to the scale and nature of their activity. In terms of their effects on species composition and richness, woody plants can be considered as dominant factors which extensively affect their environment, changing resource distribution in space and time. In this study I investigated the role of woody vegetation in affecting the distribution of herbaceous species.

There is an increasing recognition that different types of ecological processes are important drivers at different scales. Studies conducted at a single spatial scale as the basic sampling unit may overlook species–environment relationships that operate at finer or coarser scales. Multi-scaled studies can provide important insights for conservation management. In order to study biodiversity at multiple scales, I planned a hierarchically nested sampling design that is balanced across scales. Using this sampling scheme we recorded vascular plants at the spring of 2007. In order to assess the relationships between herbaceous species diversity and various environmental variables, I also conducted an extensive soil sampling and using remote sensing I characterized the spatial pattern of the woody vegetation. Using advanced statistical methods I was able to address the following questions:

The first research question focused on evaluating the role of fine scale effect of specific woody species patch types in determining herbaceous species distribution, community properties and the relative frequency of various functional groups. Most studies that explored the effects of woody vegetation on herbaceous species richness and composition viewed the ecological system as composed of two elements: woody patches and open patches. We believe that in a heterogeneous ecosystem such as the Mediterranean ecosystem, a more plausible approach would be to account for the specific nature of the patch, particularly its dominant woody species, which is a field almost untouched.

The second research question explored the effects of scale on the functioning of communities, and attempted to identify the environmental factors most highly correlated with species richness and composition at different scales.

The third research question dealt with understanding how the spatial configuration and landscape heterogeneity affect species richness at different scales. It is important to know whether the processes that determine community structure are in different to the scale of observation, and if not, how and under what circumstances the dominant processes change with scale.

My finding revealed that viewing ecological systems as composed of woody and non-woody patches is rather simplistic. I believe that in heterogeneous ecosystems such as Mediterranean ecosystems, accounting for specific woody species patch may largely enhance our understanding of plant community structure. In addition, I found that woody vegetation is an important element in controlling the spatial distribution of herbaceous species across scales. Additionally, I present evidence for scale-dependence in the

relations between woody vegetation and herbaceous species richness. I propose a mechanism that may explain most of these observed scale-dependent responses.

Together, the three components of this work enhance our understanding of the study of species distribution and its scale dependence.

## **Symbols and abbreviations**

PT- Patch Type

SE- Standard Error

DEM- Digital Elevation Model

PLAND- Percent of Land Cover

NP- Number of Patches

AREA SD- Standard Deviation of patch Area

LiDAR- Light Detection and Ranging

WPI- Weighted Preference Index

S - Total number of PTs,

$p_i$  - Number of samples at patch type  $i$

P - Total number of samples

$n_{ij}$  - Number of samples containing species  $j$  in patch type  $i$

$N_j$  - Total number of samples in which species  $j$  occurred

CCA- Canonical Correspondence Analysis

RDA- Redundancy Analysis

GAM- Generalized Additive Models

## **Introduction**

### **Background**

The last two decades have experienced unprecedented loss of species and their habitats due to environmental changes (Ehrlich 1991, Wilson 1992). Recent studies have increased our awareness that the loss of biodiversity is a threat to ecosystem processes that maintain and control life support systems (Johnson et al. 1996, Bengtsson et al. 1997, Chapin et al. 1997, Daily 1997, Hooper and Vitousek 1997, Schlapfer and Schmid 1999, Schwartz et al. 2000). Therefore, there is a concern over the future of biodiversity. Understanding the forces that govern the spatial variation in species diversity is of a practical interest in the conservation of natural ecosystems. These challenges can be approached through landscape ecological research that provides conceptual framework and set of techniques for studying and explaining patterns of biodiversity at multiple spatial scales.

### **Hierarchy theory**

There is a growing awareness that ecological systems are scaled in space and time (Wiens 1989). Scaled structure has been noted in marine (Steele 1978), freshwater (Carpenter and Kitchell 1987), and terrestrial ecosystems (Delcourt 1983). Hierarchical structure is a fundamental property of biological systems that can be traced back to the first observations that organisms are composed of cells. This intuitive structure is equally applicable to communities and ecosystems (Allen and Starr 1980, Neill et al. 1986). Hierarchical structuring simply means that, at a given level of resolution, a biological system is composed of interacting components (lower-level entities) and is itself a component of a larger system (higher level entity).



It has been suggested that due to scale dependence, patterns of species richness in small plots cannot be scaled up to entire landscapes, and vice versa (Wagner and Edwards 2001, Waldhardt et al. 2004). Studies that focus on one spatial scale as the basic sampling unit in studies of species richness and composition in Mediterranean landscapes may overlook species–environment relationships that operate at finer or coarser scales (Best and Stauffer 1986). In order to maintain biodiversity, it is not only crucial to document species–environment relationships in as many community types as possible (Hobson et al. 2000), but also to examine these associations at multiple spatial scales, since species often respond hierarchically to habitat factors (Kotliar and Wiens 1990, Levin 1992, Cushman and McGarigal 2004). Multi-scaled studies can provide important insights for conservation management.

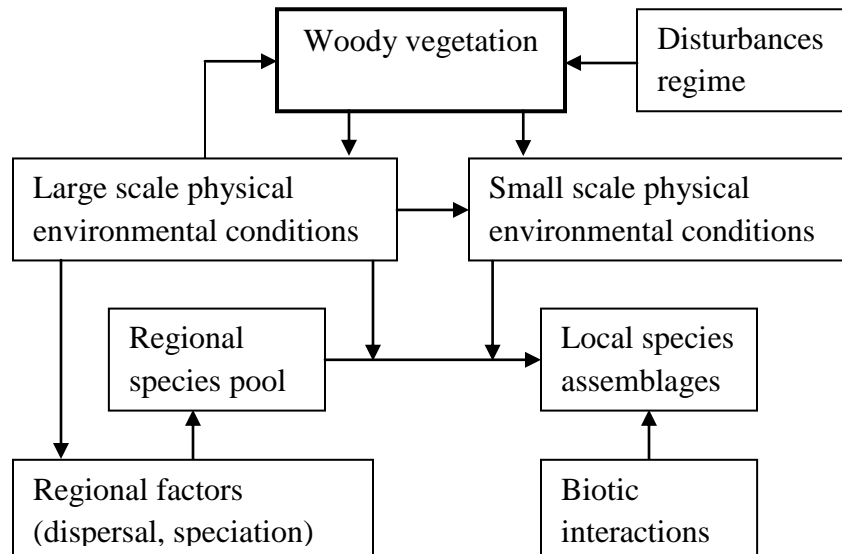
### **Woody vegetation role in environmental modulation**

All plants and animals modulate the landscape to some extent. Relatively few studies have dealt with the impact of certain species on the environment and the consequential effect on the distribution of other species (Shachak et al. 2008). Organisms can affect their immediate environment, and do so in proportion to the scale and nature of their activity. However, in terms of their effects on species richness and composition, woody plants can be considered as dominant factors which extensively affect their environment, changing resource distribution in space and time (House et al. 2003). Environmental modifications caused by trees and shrubs have been widely investigated in arid and semiarid systems (Haworth and Mcpherson 1995, Tielborger and Kadmon 1997, Holzapfel et al. 2006). The effects of woody vegetation on herbaceous species can occur

via amelioration of harsh environmental conditions, alteration of substrate characteristics, or increased resource availability (Belsky and Canham 1994, Callaway 1995).

Experimental manipulations suggest that factors related to soil fertility (Belsky 1994) and amelioration of radiant energy regimes (Parker and Muller 1982) show a range of interactions that influence herbaceous production. Woody vegetation influence on grasses may result also from rainfall interception, litter accumulation, shading, root competition, alteration of soil moisture and enhancing pools of soil nutrients. These effects depend on factors such as leaf area, canopy architecture and rooting patterns of the woody vegetation (Padien and Lajtha 1992, Schlesinger et al. 1996, Scholes 1997).

According to our framework, regional environmental conditions (such as rainfall, soil, topography) influence the spatial distribution and structure of woody vegetation (Figure 1). Woody vegetation in turn affects both large scale environmental conditions (such as climate and long distance dispersal) and small scale conditions (such as distribution of water and light, biomass and litter accumulation and resource availability (Jones 1997)). These processes create and organize niches in the ecological system space and by that constitute an important element in controlling species distribution.



**Figure 1-** The conceptual model describing the role of woody vegetation in the ecosystem.

One of the aims of this study is to expand our understanding of the role of woody vegetation in determining local species richness and composition, a relatively unexplored field. I focused on three issues: the role of woody species patch type, the importance of woody vegetation at different scales and the nature of the relationship between woody vegetation and herbaceous species richness.

### **Woody species patch type**

Mediterranean ecosystems, commonly referred to as vegetation mosaics, are highly heterogeneous at a broad range of spatial scales, starting from a grain size as small as a few meters (Naveh 1975, Di Castri 1983, Noy-Meir et al. 1989, Pausas 1999, Shoshany 2000, Bar Massada et al. 2008). In such vegetation mosaic, the effects of a specific woody patch on its associated herbaceous communities can be important. The

specific woody species patch type may impose a set of abiotic conditions, which in turn would result in specific herbaceous community under that patch.

### **Scale and species distribution**

There is an increasing recognition that different types of ecological processes are important drivers at different scales (Allen et al. 1984). The choice of scale can affect the results and the comparison between similar studies (Hamer and Hill 2000, Magura et al. 2000, Scheiner et al. 2000, Rahbek 2005). Studies conducted at a single spatial scale as the basic sampling unit may overlook species–environment relationships that operate at finer or coarser scales (Best and Stauffer 1986). Multi-scaled studies can provide important insights for conservation management.

Ecological space is multidimensional. Numerous environmental factors affect species distribution. However, the contribution of each individual factor is likely to be small. This is why we need to focus on variables that exert integrative affect on species. Such factors are woody vegetation, soil and topography. The effects of topography and soil on community composition have been studied before. Yet, a thorough analysis of the respective roles of topography and soil at multiple scales is lacking. Furthermore, these studies typically overlooked woody vegetation as an important determinant of species distribution (Jones et al. 1994, Shachak et al. 2008).

## **The relationship between woody vegetation and herbaceous species richness**

The nature of the relationship between woody vegetation and herbaceous species richness is still debated. Some studies found this relationship to be negative linear whereas other studies found hump-shaped relationship. Much of the incongruity about this relationship may be the result of differences in the scale of observation. In order to assess the role of woody vegetation we explored two aspects of woody vegetation: woody cover and landscape heterogeneity. Since the effects of woody vegetation on its environment are extensive, changes in its overall cover are expected to affect herbaceous species distribution. Changes in heterogeneity may imply changes in habitat diversity and influence the diversity of organisms such as plants, insects, birds and mammals (Bock and Bock 1984, Dennis et al. 1998, Dufour et al. 2006). Activities of many organisms depend on the structure of their immediate environment, and thus are expected to be affected by changes in the spatial heterogeneity of their landscape. Many studies have focused exclusively on a single aspect of environmental heterogeneity (Clough et al. 2005, Gratwicke and Speight 2005). Relatively small number of studies have related to the spatial pattern of environmental heterogeneity.

## Research questions

This thesis concerns the environmental factors affecting herbaceous species distribution focusing mainly on woody. Specifically, the main objectives were:

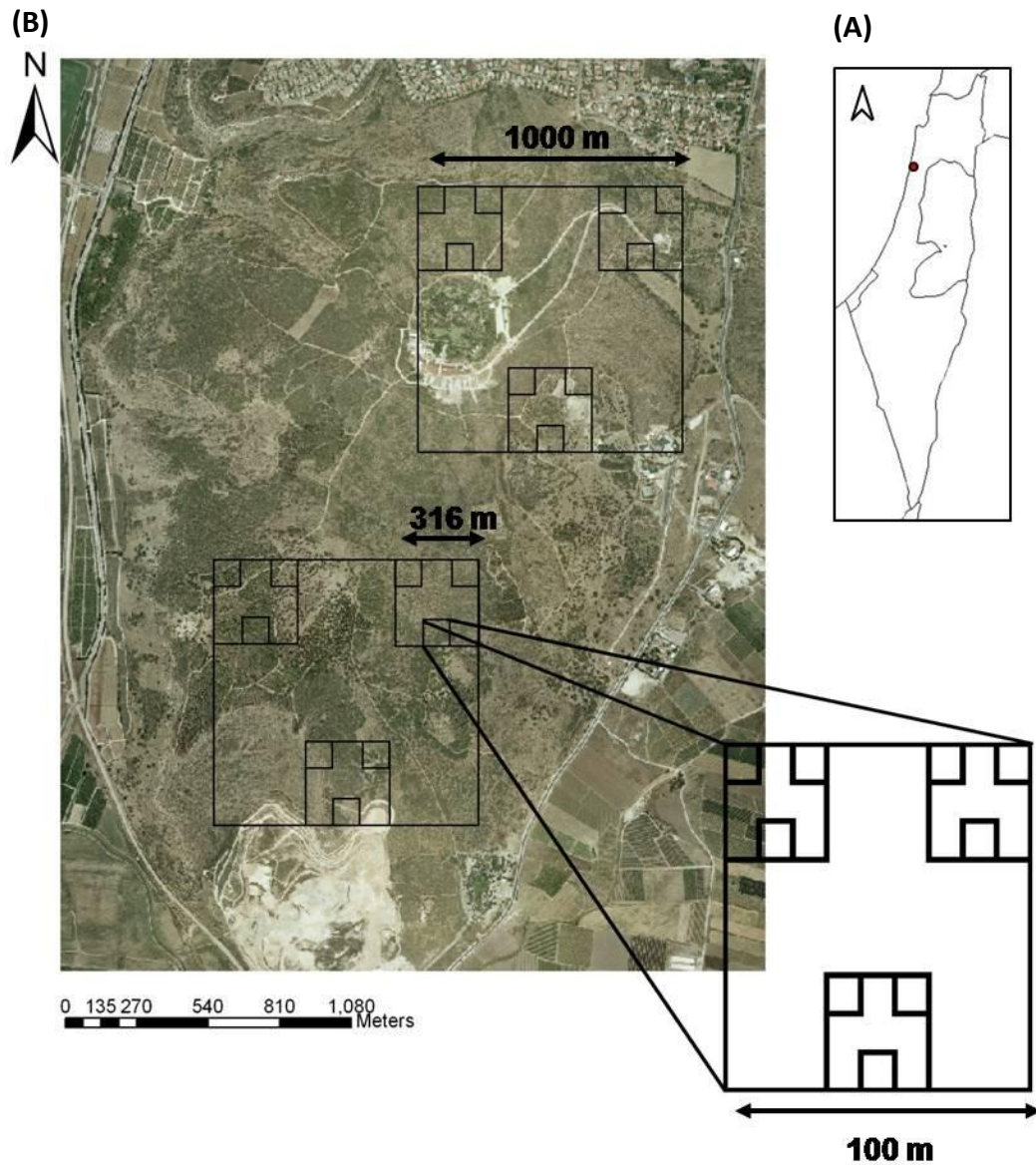
- (1) To quantify the fine scale effects of woody species patch type on herbaceous species richness and composition.
- (2) To study the effects of different environmental factors on herbaceous species richness and composition at various spatial scales and between groups of herbaceous species.
- (3) To understand how the spatial configuration and size of habitat patches affect herbaceous species richness at different scale.

## Methodology

### Study site

The study was conducted in Ramat Hanadiv Nature Park, located at the southern tip of Mt. Carmel in northern Israel (32°30' N, 34°57' E), in an area of 4.5 km<sup>2</sup> surrounded by human settlements and agricultural fields (Figure 2). The area is a plateau with an elevation of 120 m a.s.l. The soil is mainly Xerochreps, developed on hard limestone or dolomite (Kaplan 1989). The climate is eastern Mediterranean, characterized by relatively cool, wet winters and hot, dry summers. The area receives approximately 600 mm rainfall annually, mainly between November and March. The vegetation is mostly eastern Mediterranean scrubland, dominated by dwarf shrubs (*Sarcopoterium*

*spinosum*), low summer deciduous shrubs (*Calicotome villosa*), evergreen medium shrubs (*Pistacia lentiscus*) and tall evergreen shrubs (*Phillyrea latifolia*). Additionally, several scattered planted forest groves exist in the area, consisting mostly of conifer plantations (mainly *Pinus halepensis*, *Pinus brutia*, and *Cupressus sempervirens*). The area has a very rich herbaceous flora (Hadar et al. 1999).



**Figure 2:** (A) Location of the study area in Israel. Circle indicates Ramat Hanadiv Nature Park. (B) Aerial photo of Ramat Hanadiv study site and the hierarchical sampling scheme used in this study. The figure shows the scale ranging from  $10^6 \text{ m}^2$  through  $10^2 \text{ m}^2$ . The scales  $10 \text{ m}^2$ ,  $1 \text{ m}^2$  and  $0.04 \text{ m}^2$  are not shown.



## Field sampling

In the spring of 2007 vascular plant species were recorded in 4374 quadrats of 20 × 20 cm. Plant species were identified by a team of botanists. About 10% of the individuals could not be identified to the species level, mainly due to their early phenological stage, and were excluded from further analysis. A composite list of the plant species was compiled, and the species were classified into three functional groups: geophytes, annuals and perennials. The full database is available at <http://envgis.technion.ac.il/>.

In order to study herbaceous species distribution at multiple scales, we used a hierarchically nested sampling design that is balanced across scales (Figure 1). This means that when going up from lower units to upper units, the change in scale is constantly and equally incremented. Each sampling unit was composed of three sub-units of the next lower level. The exact geographic coordinates of each 10 m<sup>2</sup> square were verified using real time kinematic GPS, which allows location of points with a precision of 1–2 cm. This design allowed us to study species distribution at three different spatial scales (also referred to as ‘grain size’): fine scale (486 all plots of 10 m<sup>2</sup>), medium scale (162 medium plots of 100 m<sup>2</sup>), and coarse scale (54 main plots of 1000 m<sup>2</sup>).

Data was aggregated to enable analysis at three different scales, as follows: Local species richness was calculated as the total number of species observed in each 10 m<sup>2</sup> in nine quadrats. Species richness in each 100 m<sup>2</sup> was calculated as the total number of species observed in 27 quadrats, and species richness in each 1000 m<sup>2</sup> was calculated as the total number of species observed in 81 quadrats. These three scales are termed hereafter fine, medium, and coarse scales, respectively.

# **Chapter 1- Woody vegetation patch types affect herbaceous species richness and composition**

## **Introduction**

One central objective of ecology is to study the factors affecting the distribution of biodiversity in space and time (Shmida and Wilson 1985, Lubchenco 1991). At a local-scale (refers to small, relatively homogeneous patches), aspects of the physical or biological environment affect the persistence of populations within patches.

Hypotheses often predict that local communities are assembled according to relatively deterministic rules and that species composition should therefore be closely related to aspects of the local environment. Experiments conducted at local scales demonstrate that biological interactions (e.g. competition, predation) and abiotic environmental factors (e.g. climate, topography, soil) constrain the ability of species to arrive at, and persist in, a particular habitat, and thus regulate species diversity and composition (Zobel 1997, Karlson and Cornell 1998, Lawton 1999). Relatively few studies have dealt with the impact of certain species on the environment and the consequential effect on the distribution of other species (Shachak et al. 2008). Organisms can affect their immediate environment, and do so in proportion to the scale and nature of their activity. However, in terms of their effects on species richness and composition, woody plants can be considered as dominant factors which extensively affect their environment, changing resource distribution in space and time (House et al. 2003). Environmental modifications caused by trees and shrubs have been widely investigated in arid and semiarid systems (Haworth and Mcpherson 1995, Tielborger and Kadmon 1997, Holzapfel et al. 2006). The effects of woody vegetation on herbaceous species can occur

via amelioration of harsh environmental conditions, alteration of substrate characteristics, or increased resource availability (Belsky and Canham 1994, Callaway 1995). For example, increased herbaceous production beneath tree canopies in a Kenyan savanna was associated with lower soil temperatures, lower plant water stress, and greater soil organic matter concentrations, mineralizable N, and microbial biomass compared to those away from tree canopies (Belsky et al. 1989, Weltzin and Coughenour 1990). Experimental manipulations suggest that factors related to soil fertility (Belsky 1994) and amelioration of radiant energy regimes (Parker and Muller 1982) show a range of interactions that influence herbaceous production. Woody vegetation influence on grasses may result also from rainfall interception, litter accumulation, shading, root competition, alteration of soil moisture and enhancing pools of soil nutrients (C, N, P, and cations), or a combination of these factors. These effects depend on leaf area, canopy architecture and rooting patterns of the woody vegetation (Padien and Lajtha 1992, Schlesinger et al. 1996, Scholes 1997).

However, viewing ecological systems as composed of woody and non-woody patches is rather simplistic. This is the case particularly in Mediterranean ecosystems, consisting of structurally rich and diverse plant communities (Naveh and Dan 1973, Le Honerou 1981, Naveh and Kutiel 1986). These landscapes, commonly referred to as vegetation mosaics, are highly heterogeneous at a broad range of spatial scales, starting from a grain size as small as a few meters (Naveh 1975, Di Castri 1983, Noy-Meir et al. 1989, Pausas 1999, Shoshany 2000, Bar Massada et al. 2008). The fine-grained mosaic is characterized by woody patches of different heights and sizes, herbaceous clearings, exposed rocks and bare ground (Perevolotsky 2002). We believe that in such

heterogeneous ecosystems, a more plausible approach would be to account for the specific nature of the patch, which is a field almost untouched. Woody species obviously differ in their morphology and phenology. Studies showed differences between woody species in soil preferences (Davies 1998, Franklin 1998, Clark et al. 1999), leaf orientation (Gratani and Bombelli 2000), water content (Sternberg 2001), organic matter deposition (Charley 1975), nutrient mineralization of leaf litter (Charley 1975) and nutrient soil enrichment (Barth and Klemmedson 1978, Wezel 2000). Thus, the specific woody species patch type may impose a specific set of abiotic conditions, which in turn would result in specific traits of the specific herbaceous community developing under that patch.

Here, we employ a set of quantitative analyses in order to evaluate the role of specific woody species Patch Types (hereafter PT) in determining herbaceous species distribution, community properties (species richness and community composition) and the relative frequency of various functional groups. We selected an area that is relatively homogeneous in terms of climate, soil, topography, and disturbances, thus minimizing the possible effects of these factors on the herbaceous community.

## **Methods**

### **Study site**

The study was conducted at Ramat Hanadiv Nature Park, located at the southern tip of Mt. Carmel in northern Israel (32°30' N, 34°57' E), as described in the methodology section (Figure 2).

## Field sampling

In the spring of 2007, we recorded vascular plant species using 4,374 quadrats of  $20 \times 20$  cm. Species were identified by a team of botanists. About 10% of the herbaceous individuals could not be identified to species level, mainly due to phenological stage, and were excluded from further analysis. 2,335 of the quadrats were recorded in homogenous patches (covered either by a single woody species or with no woody cover at all), and only these quadrats were used in the analyses of the present study. Samples with woody species that were sampled in less than 100 quadrats were excluded. The remaining six woody species corresponded to six distinct patch types (PTs). These woody species PTs were: *Phillyrea latifolia*, *Pinus* sp. (including *Pinus pinea*, *Pinus halepensis*, *Pinus brutia* and *Pinus canariensis*), *Pistacia lentiscus*, *Cupressus* sp. (including *Cupressus sempervirens* and *Cupressus arizonica*), *Calicotome villosa* and *Sarcopoterium spinosum* (Table 1). The 7<sup>th</sup> PT was termed 'open' and includes patches with no woody cover at all.

## Data analysis

In order to test the distribution of herbaceous species in relation to woody species PTs, we used randomization and ordination techniques. We analyzed whether the herbaceous species richness differed between woody species PTs. For this purpose, non-parametric tests were used to analyze whether herbaceous species richness differed (i) between woody and open patches (Mann–Whitney U-test); (ii) between different woody species PTs (Kruskal Wallis test). Mann–Whitney U-tests with a Bonferroni adjustment were used to examine all pair-wise comparisons for significant differences. For all other

analyses P-value of 0.05 was considered significant. SPSS was used for all statistical analysis (version 15.0, SPSS Inc., Chicago, IL).

### Weighted preference index

Herbaceous species' distributions in relation to woody species PTs were analyzed using the Weighted Preference Index, a randomization technique that does not require knowledge of the availability of the various PTs in the environment (Clark et al. 1999, Arrington and Winemiller 2006). For each species, we calculated weighted preference index based on the standard deviation of the proportions among samples, weighted by the number of samples per PT. Weighted preference index for species j is calculated as

$$WPI_j = \sqrt{\left[ \sum_{i=1}^S p_i \left( \frac{n_{ij}}{p_i} - \frac{N_j}{P} \right)^2 / P \right]} \quad (1)$$

where i is a given PT, S is the total number of PTs,  $p_i$  is the number of samples at patch type i, P is the total number of samples,  $n_{ij}$  is the number of samples containing species j in patch type i, and  $N_j$  is the total number of samples in which species j occurred. The weighted preference index is zero for a perfect generalist (i.e., equal frequencies in all PTs) and increases with increasing affinity to certain PTs. For each species, we drew 500 random samples without replacement then compared each species' index to the 95th percentile of the index calculated from the randomly simulated data ( $\alpha=0.05$ ).

## **Community ordination**

We used ordination to assess the relative importance of PTs in determining the observed herbaceous species distributions. Ordination is primarily a research tool for the interpretation of field data on plants and animal assemblages and their environment.

In multivariate analysis, ordination is a method complementary to data clustering, and used mainly in exploratory data analysis (rather than in hypothesis testing). Ordination orders objects (sampling units, species etc.) so that similar objects in the ordination space are near each other and dissimilar objects are farther from each other. These relationships between the objects, on each of several axes, are then characterized numerically and graphically.

Ordination methods can be divided in two main groups: direct and indirect. Direct methods use species and environment data in a single, integrated analysis. Indirect methods use the species data only. Thus, direct ordination uses both the species and environment data to arrange the sites along ordination axes. This method can be further subdivided on the basis of the underlying model they use for the species responses along environmental gradient- linear or nonlinear, with unimodal response model being a case of particular ecological interest). Redundancy analysis (RDA) is a linear method for direct gradient analysis that relates species composition to measured environmental variables (ter Braak and Prentice 1988a). We used the RDA canonic ordination, which is more suitable for the analysis of categorical factors. We coded PTs as dummy (binary) variables.

RDA seeks to find the values of a new variable (denoted here as X) that will represent the best predictor for the values of a given species data. The value of the new

variable for the  $i$ th sample is  $X_i$  and is used to predict the value of the  $k$ th species in the  $i$ th sample based on the following equation:

$$Y_{ik} = b_{0k} + b_{1k} X_i + e_{ik}$$

RDA aims to estimate the values of  $X_i$ , which are the sample scores on the first ordination axis, and the regression coefficient for each species ( $b_{1k}$ ), which are the species score on the first ordination axis. The values of the sample scores are further constrained. They are defined as a linear combination of the explanatory variables:

$$X_i = c_1 z_{i1} + c_2 z_{i2}$$

Where,  $z_1$  and  $z_2$  are two environmental variables. The estimation of the sample and species score is done in a process that starts with arbitrary initial site scores and using several iterative steps calculate new sites scores that are used to calculate new species scores (see detailed description of the process in (Lep and milauer 2003)). The algorithm continues until there is no noticeable change in species and site scores from one iteration to the next. The result is the first axis. Given a data set, an identical solution will result from any set of initial arbitrary numbers. Computation of the second axis is the same as described above except that the linear effects of the first axis are factored out. Third and higher axes are calculated using the same method.

Monte Carlo permutation tests were used to evaluate the significance of species–environment relationships. In this test, an estimate of the distribution of the test statistic under the null hypothesis is obtained in the following way. The null hypothesis states that the response (species data) is independent of the environmental variables. In the next



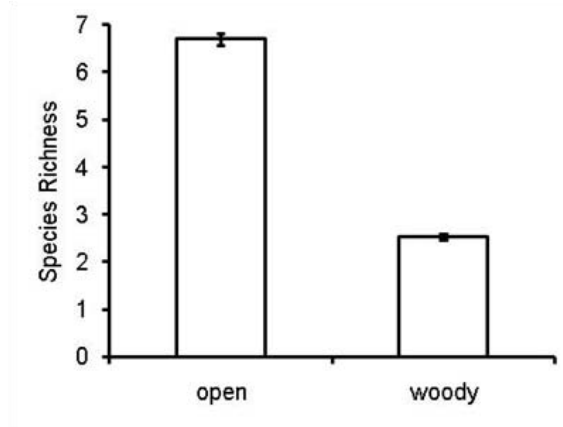
step, the values of the environmental variables are randomly assigned to the individual samples of species composition, a constrained ordination model is constructed and the value of the test statistic is calculated. A total of 499 permutations were performed. We record the value of each permutation. The distribution of these values defines the distribution of this test statistic under the null. The model probability that the 'data-derived' value of the test statistics originates from the null model distribution then represents the probability of a type I error, i.e. the probability of rejecting the correct null hypothesis. We used the program CANOCO version 4.5 (ter Braak and Smilauer 1998) to perform a RDA on all the species that had occurred in at least five quadrats.

## **Results**

A total of 308 herbaceous species were recorded in 2335 quadrats (232 annuals, 46 perennials and 30 geophytes). Of the 308 species, 56 (18.18%) were found in a single quadrat only. *Brachypodium distachyum* was the most common species, appearing in 17.5% of the samples.

### **Herbaceous species richness**

Open patches had significantly more herbaceous species than woody patches (Mann Whitney U test,  $Z=-26.53$ ,  $P<0.001$ , Figure 3). Open patches had, on average, 6.69 herbaceous species per quadrat, while woody patches had 2.54 herbaceous species per quadrat.



**Figure 3:** Herbaceous species richness in open and woody PT. Error bars represents  $\pm$ SE.

Segregating the herbaceous species into the three functional groups, perennials, geophytes, and annuals, and analyzing their occurrence in woody and open PTs revealed that ~30% (for geophytes and annuals) and ~41% (for perennials) of the herbaceous species occurred exclusively either at open or at woody PTs. However, the distribution of these herbaceous species between the two PTs for each of the functional groups was different (Table 1). For geophytes, ~21% occurred exclusively at woody PT compared to only ~9% which occurred exclusively at open PT. An opposite trend was apparent for annuals: ~6% of the herbaceous species occurred exclusively at woody PT compared to ~24% which occurred exclusively at open PT. Equal number of perennials species showed exclusive preference for open and woody PTs (Table 1).

**Table 1:** The percentage of herbaceous species occurring exclusively either at open or woody PTs for three functional groups, perennials, geophytes and annuals.

	open	woody
<b>Perennials</b>	20.48	20.48
<b>Geophytes</b>	9.09	21.21
<b>Annuals</b>	23.45	6.17

Herbaceous species richness in the six woody PTs and in open patches is presented in Table 2. The seven PTs differed significantly in their herbaceous species richness (Kruskal Wallis test,  $\chi^2_{(6)} = 892.4$ ,  $P < 0.001$ ). Using Mann–Whitney U-tests with a Bonferroni adjustment we examined all pair-wise comparisons for significant differences in herbaceous species richness at the seven PTs. *Cupressus* sp. and *Calicotome villosa* were differ significantly from all the other PTs ( $P < 0.001$ ) and had the highest number of herbaceous species compared to all other woody PTs, with an average of 3.74 and 4.72 herbaceous species per quadrat, respectively. *Phillyrea latifolia* and *Pinus* sp. were the patch types with the smallest number of herbaceous species, with only about one herbaceous species on average per quadrat. These two PTs were statistically different from all other PTs. *Pistacia lentiscus* and *Sarcopoterium spinosum* differed significantly from all other PTs and had on average 2.5 herbaceous species per quadrat. Open patches differed significantly from all the six woody PTs.

**Table 2:** Mean ( $\pm$ SE) number of herbaceous species in the quadrats ( $20 \times 20$  cm) in the six woody and the open patch types.

PT	N	Maximum	Mean
<i>Phillyrea latifolia</i>	195	8	$1.03 \pm 0.1$
<i>Pinus</i> sp.	128	7	$1.03 \pm 0.12$
<i>Pistacia lentiscus</i>	491	13	$2.42 \pm 0.11$
<i>Sarcopoterium spinosum</i>	127	10	$2.56 \pm 0.22$
<i>Cupressus</i> sp.	100	12	$3.74 \pm 0.28$
<i>Calicotome villosa</i>	158	15	$4.72 \pm 0.3$
<b>Open</b>	989	30	$6.69 \pm 0.13$

The seven PTs differed significantly in the herbaceous species richness of each of the functional groups (Kruskal Wallis test,  $\chi^2 = .39$ ,  $df = 2$ ,  $p = 0.70$ ,  $\chi^2 = 1000.8$  for non-woody perennials, geophytes and annuals, respectively,  $P < 0.001$ ) (Table 3). Using Mann–Whitney U-tests with a Bonferroni adjustment we examined all pair-wise comparisons for significant differences in the richness of the functional groups at the seven PTs. Perennials had the highest herbaceous species richness under *Calicotome villosa* patches. *Calicotome villosa* differed significantly from *Phillyrea latifolia* (who had the lowest level of herbaceous species richness), *Pinus* sp. and open PTs. Geophytes had the highest level of herbaceous species richness under *Pistacia lentiscus* patches. *Pistacia lentiscus* differed significantly from *Pinus* sp. (who had the lowest level of herbaceous species richness), *Cupressus* sp. and open PTs. Annuals exhibited different pattern with highest richness in open patches and the lowest level of herbaceous species

richness under *Phillyrea latifolia*. Open patches differed significantly from all the six woody PTs and had the highest number of herbaceous species from all other PTs, with an average of 6.69 herbaceous species per quadrat (Table 2).

**Table 3:** Mean ( $\pm$ SE) number of herbaceous species in seven PTs for three functional groups, perennials, geophytes and annuals.

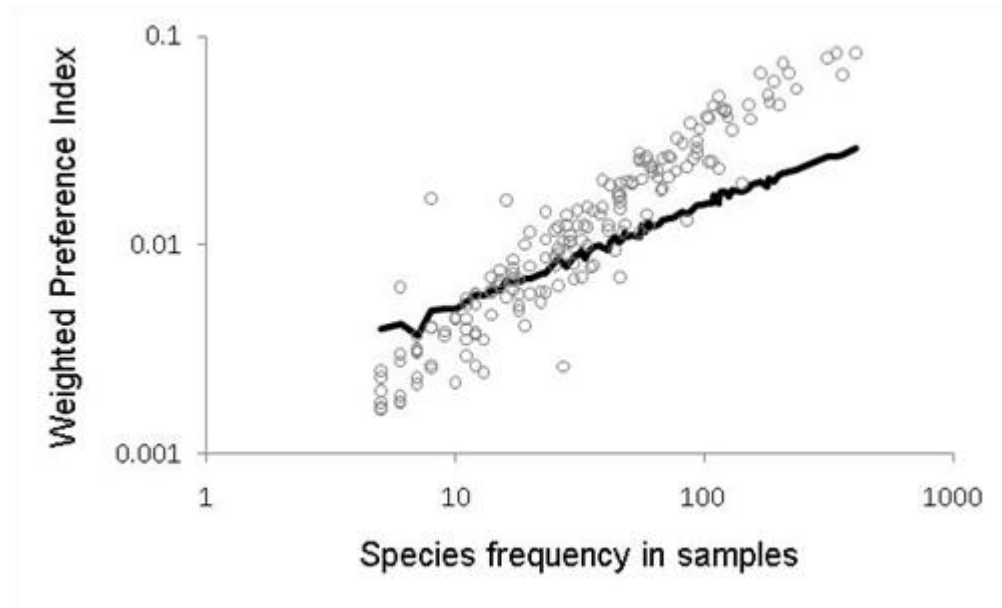
PT	Perennials	Geophytes	Annuals
<i>Phillyrea latifolia</i>	0.149 $\pm$ 0.05	0.492 $\pm$ 0.02	0.4 $\pm$ 0.07
<i>Pinus</i> sp.	0.195 $\pm$ 0.04	0.281 $\pm$ 0.03	0.563 $\pm$ 0.1
<i>Pistacia lentiscus</i>	0.314 $\pm$ 0.03	0.625 $\pm$ 0.02	1.564 $\pm$ 0.1
<i>Sarcopoterium spinosum</i>	0.315 $\pm$ 0.05	0.441 $\pm$ 0.04	1.906 $\pm$ 0.2
<i>Cupressus</i> sp.	0.31 $\pm$ 0.05	0.29 $\pm$ 0.05	3.3 $\pm$ 0.27
<i>Calicotome villosa</i>	0.475 $\pm$ 0.06	0.589 $\pm$ 0.05	3.766 $\pm$ 0.3
Open	0.254 $\pm$ 0.02	0.396 $\pm$ 0.01	6.048 $\pm$ 0.13

#### Herbaceous species distributions in relation to patch type

Out of the 179 herbaceous species that occurred in more than five quadrats, 111 species showed non-random distribution with respect to  $P\alpha$  (Ts. (0.05) Figure 4). The actual occurrences of 20 of these species were at least three times more than the estimated occurrences at least in one of the PTs, however none of these PT was open PT. The occurrences of these species range between eight and 181. Table 4 presents the herbaceous species with the highest observed to expected ratio for each PT. The two woody PTs that had a particularly large number of associated herbaceous species

relatively to the total number of herbaceous species occurring in each one of them were *Cupressus* sp. and *Calicotome villosa* patches. More than a third of the herbaceous species that occurred in each one of them were significantly associated with them.

In an additional analysis of the weighted preference index, we excluded the open patches, and examined the woody patches only. This analysis revealed that out of 116 herbaceous species that occurred in more than five quadrats, 76 species showed non-random distribution with respect to the woody PTs ( $\alpha = 0.05$ ) data not shown. The actual occurrences of 55 of these species were at least three times more than the estimated occurrences at least in one of the PTs.



**Figure 4:** The distribution of herbaceous species, in terms of weighted preference index for woody species PTs. The dash line indicates the 95<sup>th</sup> percentile value from randomization calculation (see Method section for details). Species above the line are significantly ( $p < 0.05$ ) non-randomly distributed in relation to woody species PTs. Species occurring in less than five samples were not included in this analysis.

**Table 4:** Species with the highest observed to expected ratio for each PT. The 'observed'

column refers to the actual occurrences of each species under the specified PT. The 'Expected' column refers to the estimated number of times the selected species occurred under the specified PT, taking into account the relative distribution of this PT.

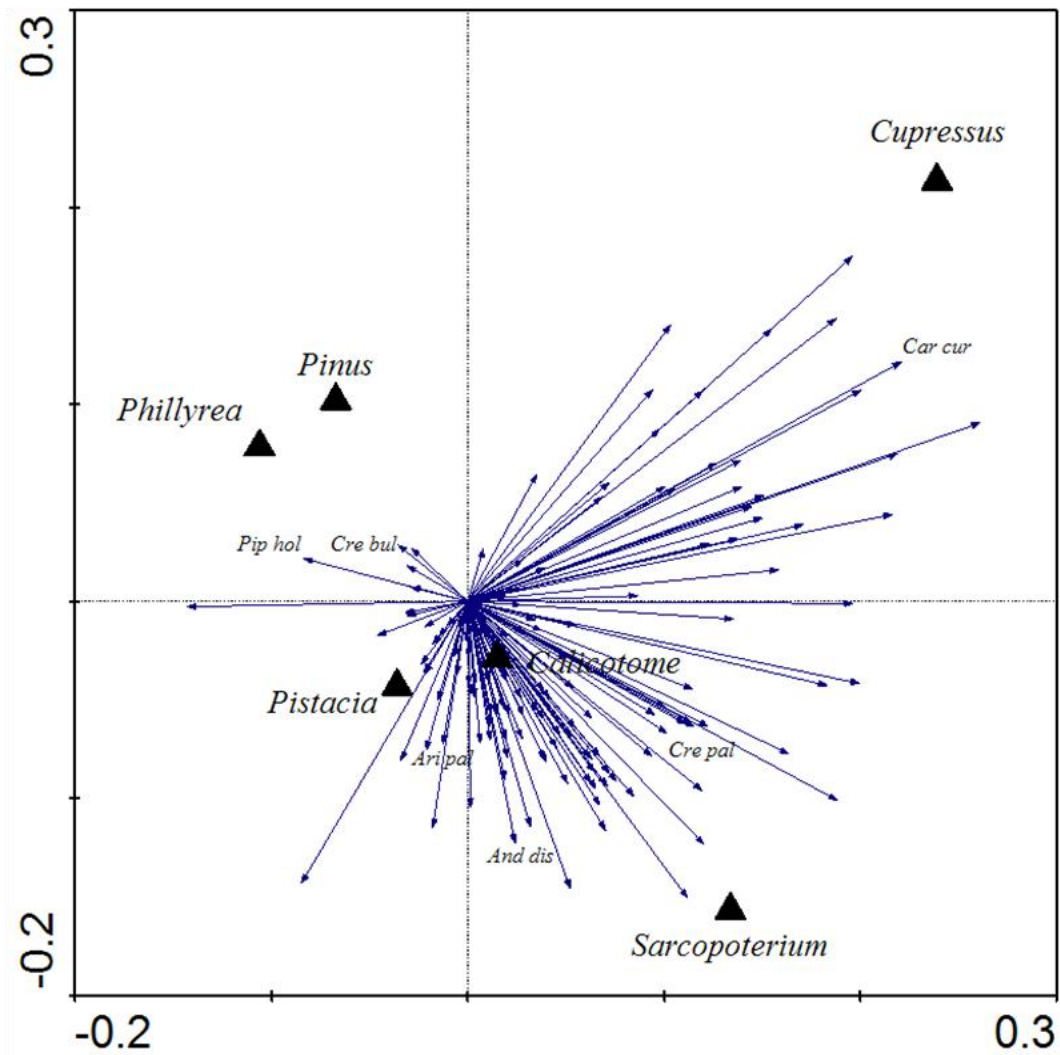
Herbaceous species	PT	Total occurrences	Observed occurrences	Expected occurrences	ratio
<i>Piptatherum holciforme</i>	<i>Phillyrea latifolia</i>	23	10	2.05	4.88
<i>Crepis bulbosa</i>	<i>Pinus</i> sp.	19	6	1.11	5.41
<i>Aristlchia parvifolia</i>	<i>Pistacia lentiscus</i>	28	17	6.28	2.71
<i>Andropogon distachyos</i>	<i>Sarcopoterium spinosum</i>	62	12	3.6	3.33
<i>Carline curetum</i>	<i>Cupressus</i> sp.	55	14	2.51	5.58
<i>Crepis palaestina</i>	<i>Calicotome villosa</i>	45	12	3.25	3.69



### **Multivariate analyses of herbaceous species distribution**

We used RDA to evaluate the value of classifying woody species into six PTs, as opposed to lumping them into one group of woody PT. The explained variance in the RDA model with the six woody species PTs and 'open' patches was 42% larger than the explained variance when using only woody vs. open PTs (data not shown).

In an additional analysis, we excluded the open patches, and examined the woody patches only. The canonical ordination analysis (RDA) exploring the distribution of the herbaceous species among the woody species PTs was significant ( $F=5.799$ ,  $P=0.002$ ) (Figure 5). The first two axes explained 84.5% of the explained variance. *Cupressus* sp. was the main component of the first and second axes ( $r=0.347$  and  $r=0.263$ , respectively). The occurrences of only a few herbaceous species were related to *Pinus* sp. and *Phillyrea latifolia* PTs. The herbaceous species relation to woody PTs was consistent with weighted preference index analysis (Table 4 and Figure 5).



**Figure 5:** RDA ordination for herbaceous species with the six woody PTs.

Abbreviations- woody species PTs are identified according to their genus.

Abbreviation of selected species (corresponding to species in table 4)

indicated with the first three letters of their genus and species name

respectively: *Piptatherum holciforme*, *Crepis bulbosa*, *Aristlchia parvifolia*,

*Andropogon distachyos*, *Carline curetum* and *Crepis palaestina*.

## Discussion

Most studies that explored the effects of woody vegetation on species richness and composition viewed the ecological system as composed of two elements: woody patches and open patches (House et al. 2003, Shachak et al. 2008). Some studies focused on the effects of woody cover or biomass on species richness, and most found a unimodal relationship with maximal richness at intermediate level of cover or biomass (Grime 1979, Moore and Keddy 1989, Garcia et al. 1993, Grytnes 2000, Casado et al. 2004). Other studies focused on species composition in addition to richness, and found significant differences in species composition between woody patches and non-woody patches (Ko and Reich 1993, Scholes 1997, Pugnaire and Luque 2001, Holzapfel et al. 2006, Wright et al. 2006, Madrigal et al. 2008).

Based on our results, we argue that the common distinction between 'open' and 'woody,' and the notion that woody vegetation as a whole creates and organizes niches in the ecological space, are too simplistic. We speculate that different conditions imposed by different woody species create distinct niches, and thus different woody species PTs are characterized by different herbaceous richness and composition. Allelopathic effects, where toxic compounds are produced and released by some woody species, were found to be a major factor in regulating plant community composition (Fernandez et al. 2006, Herranz et al. 2006). Other possible explanations of the observed affinities between herbaceous species and woody species PTs may be canopy density, litter volume or nutrient deposition into the soil. In this study we quantify herbaceous species affinities, and assess the differences in herbaceous species richness and composition in six common woody species PTs in an east Mediterranean ecosystem. It is expected, of course, that

factors such as climate, soil, grazing and fire would have a strong impact on local herbaceous species richness and composition; in our study we selected an area that is relatively homogeneous with respect to all these factors, thus elucidating much of the net effect of woody species.

### **Woody species patch type and herbaceous species richness**

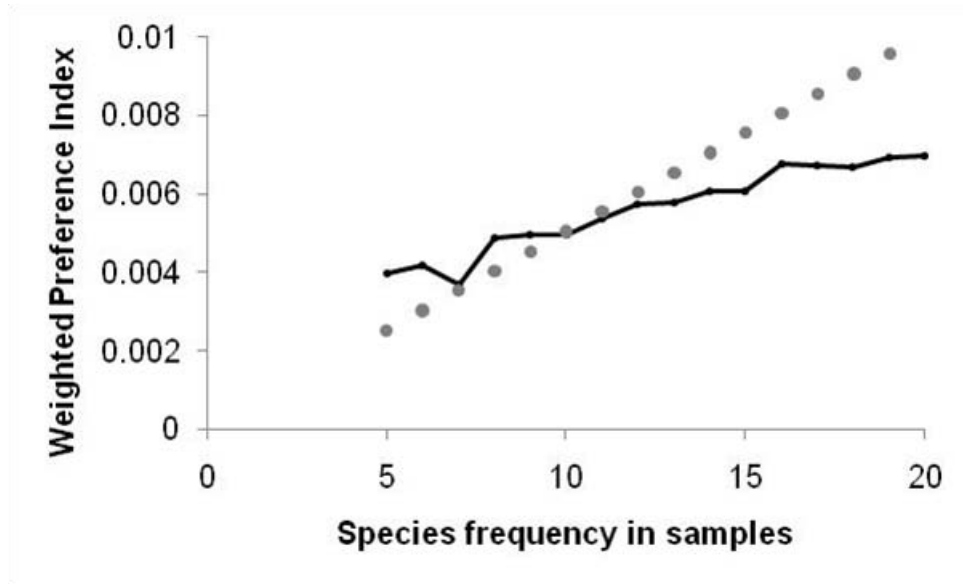
In agreement with Holzapfel et al. (2006) and with Agra and Ne'eman (2009), we found significant difference in herbaceous species richness between woody and open patches, indicating that the abiotic conditions differ between woody and open patches. Yet, by segregating 'woody' patches into six types, we found significant differences in herbaceous species richness. The difference in species richness spans from 4.72 species per quadrat under *Calicotome villosa* patches, to 1 species per quadrat under *Phillyrea latifolia* and *Pinus* sp. patches. These findings suggest that the woody species PTs are different and herbaceous species richness varies among the different woody species PTs.

### **Herbaceous species distribution among woody species patch type**

Woody species PTs differ not only in herbaceous species richness, but also in the distribution of these herbaceous species among PTs. Here, 62% of herbaceous species were non-randomly distributed between the various woody species PTs.

Clark (1999), who developed the weighted preference index method, demonstrated that for a given sample size it is harder to detect significant bias in the more common class types. Thus, herbaceous species that prefer the more dominant PTs and have low abundance are not likely to be classified as biased towards these PTs. For example, open

PT is the most common PT. Species that occurs only in open PT would need to be present in at least 10 open PT patches to be detectable as significantly biased toward this PT (Figure 6). Thus, this method presents a minimum estimate of the number of herbaceous species having a tendency toward certain PTs.



**Figure 6:** The Weighted Preference Index obtained if all individuals at different sample sizes occurred only in open PT (gray dots), and the WPI randomization 95th percentile values (black line).

### Woody species patch type and herbaceous species composition

Local community composition is another indication of the importance of specific woody species PT to the herbaceous species. Direct gradient analysis revealed a significant effect of woody species PTs on local herbaceous assemblages.

Most herbaceous species are associated to four of the six woody PTs: *Cupressus* sp., *Calicotome villosa*, *Sarcopoterium spinosum* and to a lesser extent to *Pistacia*

*lentiscus*. Only a small number of herbaceous species relate to *Pinus* Sp. and *Phillyrea latifolia*. We speculate that the difference between these two groups of PTs is their physical properties, mainly thinner versus denser canopy. The physical structure of the first group is less dense than the second group, and they are thus more similar to open patches in terms of solar radiation, temperature and humidity. Support for this speculation comes from a study that took place in Ramat Hanadiv in 2005 and found that *Phillyrea latifolia*, *Calicotome villosa* and open patches differ significantly in three abiotic variables- light penetration, temperature and soil water content. Other abiotic variables (such as- pH, conductivity,  $\text{NO}_3^-$ , P-olsen and OM) were not significant (O. Gabay, *personal communication*). However, other possible explanations of the observed affinities between herbaceous species and woody species PTs may be allelopathic effects (Fernandez et al. 2006, Herranz et al. 2006), litter volume which is dependent upon the woody species and which can physically condition the germination capacity of the herbaceous species (Charley 1975) or nutrient deposition into the soil (Barth and Klemmedson 1978, Wezel 2000).

Altogether, our results indicate that the differences in plant communities between woody species PTs result from their physical structure, which affects the radiation reaching the sub-canopy area. This, in turn, affects soil temperature and moisture, evaporation rates, and humidity. Other factors, such as organic matter deposition and leaf litter composition were found to be different between woody species (Charley 1975), and may have contributed to the differences between local herbaceous communities.

### **Effect of woody vegetation on herbaceous functional groups**

Plant species can be grouped into different functional groups based on structural and functional similarities (Mueller-Dombois 1974, Lande 1982, de Mera et al. 1999, Lavorel et al. 2007). Plants of the same functional group are expected to exhibit similar responses to environmental conditions and have similar effects on the dominant ecosystem processes (Walker 1992, Noble and Gitay 1996, Pausas and Austin 2001). Our findings showed that many of the annuals prefer non-woody habitats while many geophytes preferred woody habitats. It is possible that annuals are more affected by woody vegetation compared to geophytes, because their little resource reservations do not allow survival in the shade of woody species. On the contrary, non-woody patches represent habitats in which geophytes establish themselves with difficulty, because of the extreme summer drought. In contrast, the cycle of annuals is adapted to these conditions: individuals take advantage of precipitation from winter to spring, and die before or during the summer stress. In addition, our findings show that each functional group responded to the woody species PTs differently. As each functional group is characterized by specific eco-physiology or life-history strategy these group specific response indicate that each specific woody species PT imposes a specific set of abiotic conditions.

### **Conclusion**

This study revealed evidence about the affinities of herbaceous species to specific woody species, which suggests that the general notion of a two-patch types system for describing ecosystem and community structure is simplistic, and may be misleading. We found that patterns of herbaceous species richness and composition are related to specific woody species PT. Herbaceous species richness and community composition in the less

dense woody species are more similar to open patches than to other woody PTs, suggesting that canopy density may be a major mediator of these relationships. Apparently, in mosaics of open and woody vegetation, herbaceous communities are strongly affected by the nature of the specific woody species PT, and are structured at very fine scales. Accounting for specific woody species patch characteristics may largely enhance our understanding of plant community structure.



## **Chapter 2- A multi-scale analysis of herbaceous species richness and composition in Mediterranean ecosystem**

### **Introduction**

The description of species-distribution patterns and the mechanisms explaining these patterns have long been an objective in ecology (Ricklefs 1993, Schulze and Mooney 1993, Rosenzweig 1995, Gaston 2000, Rahbek and Graves 2001, Whittaker et al. 2001). Studies of species distribution patterns and of correlations between species and environment traditionally have been conducted at a single scale of observation; that is, employing one quadrat size and sampling a single extent of area. More recently, the assumption that the description of any system depends on the spatial and temporal scales (Allen et al. 1984, Wiens 1989, Hamer and Hill 2000, Rahbek 2005) has resulted in the incorporation of scale as another aspect in determining the mechanisms explaining species diversity and distribution (Rahbek and Graves 2001, Whittaker et al. 2001, Chase and Leibold 2002, Rahbek 2005, Okland et al. 2006, Coreau and Martin 2007). This understanding stemmed from the recognition that different types of ecological processes are important drivers at different scales (Allen et al. 1984, Willis and Whittaker 2002). For example, (Crawley and Harral 2001) suggested that at small scales ( $1 \text{ m}^2$  or less), ecological interactions are the most important processes controlling plant diversity in a system, but at larger scales, drivers such as topography, management, geology and hydrology are more important because they influence habitat type.

The choice of scale can affect the results and the comparison between similar studies (Hamer and Hill 2000, Magura et al. 2000, Scheiner et al. 2000, Rahbek 2005).

Conducting research at a single scale can lead to inaccurate and even wrong conclusions concerning the relationship between species and their habitats.

Studies conducted at a single spatial scale as the basic sampling unit may overlook species–environment relationships that operate at finer or coarser scales (Best and Stauffer 1986). Thus, in order to maintain biodiversity, it is not only crucial to document species–environment relationships in as many community types as possible (Hobson et al. 2000), but also to examine these associations at multiple spatial scales (Perevolotsky 2005). Multi-scaled studies can provide important insights for conservation management. For example, areas prioritized using regional scale analyses would differ from areas selected by local analyses. In addition, since the impact of different environmental factors is scale dependent, it may be that in order to maintain high species richness we will need to analyze species–environment relationship at different scales and integrate the insights into a single management regime.

Differences between functional groups result from group-specific characteristics. Each functional group represents unique structural and functional traits, and group members have similar adaptations to certain ecological conditions (Lande 1982, de Mera et al. 1999, Lavorel et al. 2007). Thus, it is expected that different functional groups will have different species–environment relationships.

A number of approaches have been used to develop predictive models for species–environment relationships. Common to most of these approaches is the use of topography, soil, and climate as predictors (Oliveirafilho 1994, Stohlgren et al. 1998, Stohlgren et al. 1999, Stohlgren et al. 2000, Hutchings et al. 2003, Davies et al. 2005, Stohlgren et al. 2005) and overlooking woody vegetation as an important determinant of

species distribution (Jones et al. 1994, Shachak et al. 2008). Organisms can affect their immediate environment, and do so in proportion to the scale and nature of their activity. In terms of their effects on species composition and richness, woody plants can be considered as dominant factors which extensively affect their environment, changing resource distribution in space and time (House et al. 2003). We hypothesize that the effects woody vegetation exerts on herbaceous species at fine scales will moderate the effects of environmental variables at these scales where the plants are in physical contact while at large scales, woody vegetation effects will be averaged out and the overall herbaceous species patterns will reflect primarily the broader variations of the physical environment.

Our primary motivation was to quantify the contributions of different predictors of herbaceous species composition and richness at different scales. We address two hypotheses for the studied Mediterranean landscapes, and in a more general ecological context: (1) the most important environmental variable for herbaceous species composition and richness will be different at different scales; (2) the impact of woody vegetation on plants would be expressed chiefly at fine scales ( $10 \text{ m}^2$ ) while topography and soil will be more important at coarse scales ( $1000 \text{ m}^2$ ).

## **Methods**

Study site and field sampling are described in the methodology section (Figure 2).

## Environmental variables

Four subsets of independent variables were used in the analysis; three sets of environmental variables (woody vegetation pattern, topography and soil) and one set of spatial variables (Table 5). We limited the full environmental data set to a maximum of 18 variables in order to maintain the 3:1 sample to variable ratio optimal for multivariate analyses (McGarigal et al. 2000), as the number of samples at the coarse scale was 54.

**Table 5:** The environmental variables included in the analysis.

Class	Variables	Units
<b>Woody vegetation pattern</b>	Woody cover	%
	Number of woody patches	
	Mean vegetation height	meters
<b>Topography</b>	north-south components of aspect (northness)	Degrees from north
	Slope	degrees from the horizon
<b>Soil</b>	Calcium carbonate ( $\text{CaCO}_3$ )	(g[ $\text{CaCO}_3$ ]/g[dry soil])
	Organic matter (OM)	(mg[OM]/g(dry soil))

The spatial dataset consisted of nine variables, therefore we could include up to a total of nine environmental variables in the analysis. In order to assign similar weights to each group of environmental variables, we selected similar number of variables for each group. Soil variables were quantified using an acoustic spectrophotometer (see below), capable of quantifying accurately a large number of samples. Here, we were able to quantify only calcium carbonate ( $\text{CaCO}_3$ ) and organic matter. Two variables were

selected to represent topography. Topography consisted of four variables: elevation, slope, north-south and east-west components of aspect. East-west component had the lowest explained variance for all functional groups at all scales and was excluded from the analysis. Elevation was also excluded from the analysis as it had significantly high correlation with the other two variables. Three variables were selected to represent woody vegetation pattern: percentage of woody cover, number of woody patches and woody vegetation height. These variables were selected based on their potential ecological relevance to plant distribution and because they represent different aspects of woody vegetation. In addition, these variables are easy to interpret and can be used in management (see below). Percentage of woody cover is a measure of how much of the landscape is comprised of woody vegetation. The number of woody patches is a measure of landscape fragmentation. Using these three variables, we were able to characterize the 3D structure of woody vegetation, as oppose to the 2D vegetation description in most of studies of landscape effects on species distribution (e.g. Kie et al. 2002, Kumar et al. 2006). Vertical vegetation stratification was suggested to affect plant species diversity (Kumar et al. 2006). For example, the spatial structure of the canopy in a forest greatly influences understory plant regeneration and succession patterns (Clark et al. 1996, Moeur 1997) and may affect community structure and biodiversity patterns. Sunlight penetration through the canopy is directly related to the three-dimensional spatial pattern of vegetation and influences the interactions between organisms and their physical environments (Stohlgren et al. 2000).

In order to quantify the values of mean vegetation height, northness, slope, CaCO<sub>3</sub> and organic matter at each scale I averaged the values of each variable as follows:

topography variables and vegetation height were calculated as averages of nine points in each 10 m<sup>2</sup>, 27 points in each 100 m<sup>2</sup> and 81 points in each 1000 m<sup>2</sup> (Table 6). Soil variables were averages of three points in each 100 m<sup>2</sup> and nine points in each 1000 m<sup>2</sup>. I used one-way analysis of variance (ANOVA) to test whether the variability between units, in each scale separately, were larger compared to the variability within each unit. The idea behind ANOVA is to divide this total variability into variability between groups and variability within groups. If the variability between groups is large compared to the variability within groups, as determined via a statistical test, we conclude that there are significant differences between groups. The ANOVA procedure produces an F statistic, a value whose probability enables to reject or retain the null hypothesis, i.e., to conclude whether or not the differences in the scores on the dependent variable are statistically significant or due to chance. Using this test I found that for the variables: mean vegetation height, northness, slope, CaCO<sub>3</sub> and organic matter, the variability between units were significantly different from the variability within units, in all the scales (Table 6). This procedure was not applied to woody cover and number of woody patches as the values of these variables was quantified for the entire sampling units area and not the result of averaging.

**Table 6:** Description of the variable values at the different scales. \* P <0.0001

<b>Variables</b>	<b>Range</b>		
	<b>10 m<sup>2</sup></b>	<b>100 m<sup>2</sup></b>	<b>1000 m<sup>2</sup></b>
<b>Woody cover</b>	0.69-100	5.81-99.62	24.89-95.61
<b>Number of woody patches</b>	1-9	1-42	3-270
<b>Mean vegetation height</b>	0.02-11.46*	0.12-9.21*	0.21-6.64*
<b>Northness</b>	2.82-178.6*	15.3-175.04*	25.93-163.94*
<b>Slope</b>	0.73-29.75*	0.96-22.14*	1.53-17.16*
<b>Calcium carbonate</b>		0-48.59*	0-34.32*
<b>Organic matter</b>		0-145.29*	0-134.17*

Significant was calculated using one-way ANOVA.

We tested all the variables for multicollinearity by examining cross-correlations among variables. We also calculated variance inflation factors (VIF; Neter et al. 1996). Neter et al. (1996) suggested that multicollinearity is only severe at VIFs >10. Our variables had a maximum VIF of 5.5. Cross-correlations between the variables were lower than 0.6 except between woody cover and number of patches at the medium and coarse scales (-0.78 and -0.81, respectively). However, both variables were retained in the analysis because they represent different aspects of woody vegetation pattern.

### **Woody vegetation pattern**

A binary map of woody and non-woody vegetation was generated from a digital color orthophoto of the study area. This orthophoto was generated by Ofek™ aerial photography, in the summer of 2007 at a pixel size of 0.25 m (Figure 2). The image was classified into two classes using unsupervised IsoData classification (Campbell 1996). In

the summer, there are only two major spectral classes, woody vegetation and non-woody vegetation. The later included dry herbaceous vegetation, bare soil and rocks. Woody cover and the number of patches were quantified using FRAGSTATS software (McGarigal et al. 2002) from the woody and non-woody vegetation map, for each hierarchical level independently.

### **Vegetation height**

Vegetation height was assessed by Ofek™ aerial photography in 2005 with an OptecA™ (TM2050 LiDAR) Light Detection and Ranging, using the single return method with a horizontal spacing of ~2 m between points. Flight altitude was 1500 m. Following geo-rectification, the vertical accuracy of the LiDAR points was 0.15 m, and the planimetric accuracy was 0.75 m. A digital elevation model of the ground was generated by overlaying the LiDAR image on the orthophoto, and identifying LiDAR hit-points that were located on the ground. A digital elevation model was then generated by extrapolating the data from the points, resulting in a 2 m grid. The DEM value underneath each point was subtracted from the point elevation, in order to convert the values of the LiDAR points from elevation above sea level to height above ground,

### **Soil**

A single soil sample was collected in each 10 m<sup>2</sup> sampling unit, using the sampling design described above (Figure 2). A total of 417 samples were collected. The



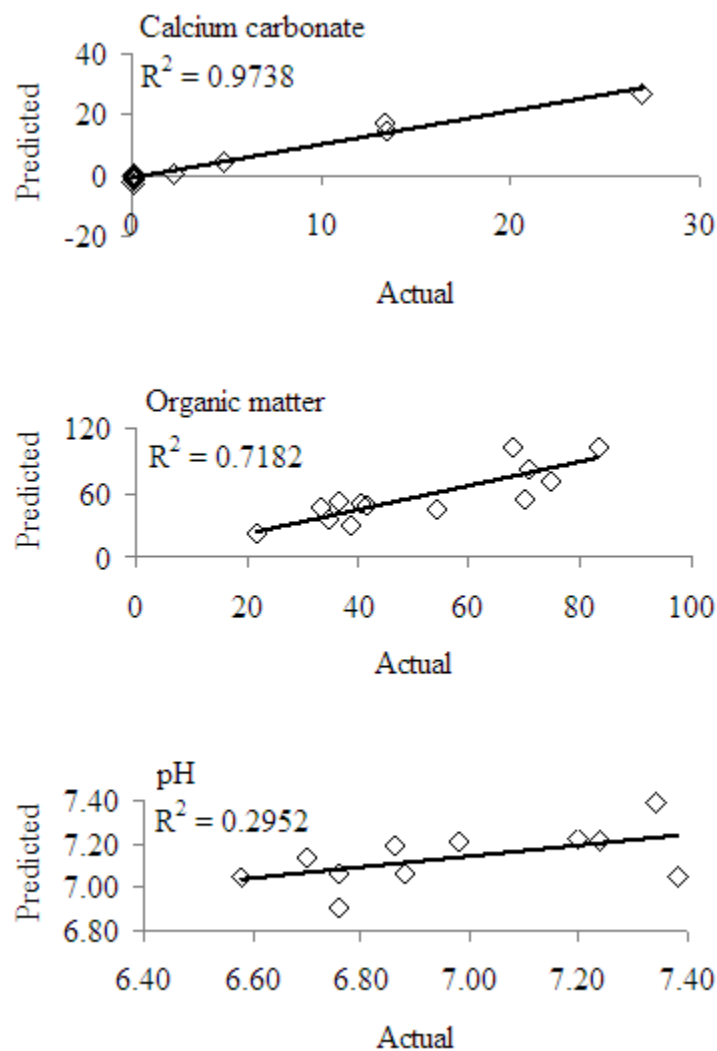
surface litter, if present, was removed, and the top five cm of soil was sampled. Samples were air dried, and passed through a 2 mm sieve, then ground in a three-ball grinder. In order to quantify  $\text{CaCO}_3$ , organic matter and soil pH, we applied a new approach, developed recently in the Soil Chemistry Laboratory at the Technion (Linker 2005a, Du et al. 2007).

The approach is based on Fourier Transform Infrared Measurements, which is a spectral technique that is rapid and relatively inexpensive compared to the conventional methods for soil characterization. Compared to other spectral techniques the major advantage of photoacoustic spectroscopy is that it is suitable for highly absorbing solid samples without any special pre-treatment. Thus, we were able to characterize large area at high resolution.

Fourier Transform Infrared Measurements- Photoacoustic spectra were recorded for all soil samples using a Bruker Vector 22 spectrophotometer equipped with a photoacoustic cell (Graseby Specac Inc.). Fourier transform infrared photoacoustic spectroscopy is based on the absorption of electromagnetic radiation by the sample and non-radiative relaxation that leads to local warming of the sample. Pressure fluctuations are then generated by thermal expansion, which can be detected by a very sensitive microphone.

After placing the sample in the cell holding cup (diameter 1 cm, height 3mm) and purging the cell with helium for 30 seconds, eight successive scans were recorded over the range of  $400\text{-}4000\text{ cm}^{-1}$  and averaged. The scans were performed with a modulation frequency of 2.2 kHz and a resolution of  $8\text{ cm}^{-1}$ .

Quantitative analysis of the spectra was performed using partial least squares. The samples were split randomly into a calibration set containing 75% of the samples and a validation set containing the remaining 25% of the samples that their  $\text{CaCO}_3$ , organic matter and pH concentrations were determined by conventional chemical methods. The root mean square of the determination errors was used to estimate model performance (for detailed description of the method see (Du et al. 2008, Du et al. 2009)). Plotting the predicted versus the actual values of the validation data revealed that  $\text{CaCO}_3$  and organic matter had high  $R^2$  values, while pH had low  $R^2$  and thus was excluded from further analysis (Figure 7).



**Figure 7-** Actual versus predicted (top) calcium carbonate, (middle) organic matter, and (bottom) pH concentrations.

## Topography

Aspect and slope were determined for each sampling plot using high resolution (2 m pixel size) DEM. Aspect is represented by angular data ( $0^{\circ}$ – $360^{\circ}$ ). To convert it to linear scale representing the north-south axis we subtracted all the values higher than 180

from 360. The north-south component of aspect is a variable in the range of  $0^{\circ}$ – $180^{\circ}$ , where north =  $0^{\circ}$ , south =  $180^{\circ}$  and east = west.

### **Spatial variables**

Typically, species distribution is positively autocorrelated, such that nearby points in space tend to be more similar than expected by random chance (Sokal and Oden 1978, Legendre 1993, Lichstein et al. 2002). The presence of spatial autocorrelation within ecological data results in a lack of independence of data points and, consequently, an overestimation of the number of degrees of freedom in an analysis (Legendre 1998, Lichstein et al. 2002). In order to quantify and remove the spatial autocorrelation effects from the analysis we included spatial variables constructed from the geographical coordinates (X, Y) of each plot (Borcard et al. 1992, Legendre 1993, Hobson et al. 2000). First, the X and Y coordinates of the midpoints of the plot were centered on their means (Anderson and Gribble, 1998). Second, we generated a cubic trend surface polynomial with nine variable (X, Y,  $X^2$ ,  $Y^2$ , XY,  $X^3$ ,  $Y^3$ ,  $X^2Y$ , and  $XY^2$ ), which is appropriate for capturing broad-scale spatial trends (Legendre 1998).

### **Data analysis**

Variation in herbaceous species richness was partitioned using Redundancy Analysis (RDA; ter Braak and Prentice 1986). In RDA, a univariate response variable reduces to standard linear multiple regression, and the variance is quantified by sum-of-squares (Birks 1996, ter Braak and Smilauer 2002, Okland et al. 2006) (see methods section in chapter 1). Variation in herbaceous species composition was partitioned using

Canonical Correspondence Analysis (CCA; ter Braak and Prentice 1986). CCA is a direct gradient analysis (see methods section in chapter 1). The statistical model underlying CCA is that a species' abundance or frequency is a unimodal function of position along environmental gradients. CCA is an approximation to Gaussian Regression under a certain set of simplifying assumptions, and is robust to violations of those assumptions (ter Braak and Prentice 1988b). In CCA the total variation is quantified as the total inertia. Variation partitioning was carried out using partial CCA and RDA analyses in order to quantify the variance explained by the environmental variables and by the spatial variables (Borcard et al. 1992).

In the analysis of CCA for herbaceous species composition and RDA for herbaceous species richness, spatial variables were always considered covariables to remove their effects. For each analysis we recorded the statistical significance, as measured by a Monte Carlo unrestricted permutation test with 499 permutations, of all canonical axes (ter Braak and Smilauer 2002).

The significance of each explanatory variable was measured using Monte Carlo permutation test with 499 randomizations. These analyses were conducted with CANOCO version 4.5 (ter Braak and Smilauer 2002). For each analysis, we recorded the sum of canonical eigenvalues and divided it by the total variation in the species data (total inertia) to estimate the proportion of the total explained variance by a set of variables (Greenacre 1984). We calculated the proportion of the total explained variance by each specific variable by dividing its explained variance singly i.e. when that particular variable is used as the only environmental variable )also term 'marg inal contribution'( by the total ine.rtia

## Results

A total of 325 herbaceous species were recorded in 4374 quadrats (243 annuals, 49 perennials and 33 geophytes, Table 7). Fifty herbaceous species (~15 %) were found in a single 20×20 cm quadrat only, and 120 herbaceous species (~37%) were present in less than four quadrats. These species were excluded from further analysis since they were insufficiently sampled. Thus, a total of 205 herbaceous species were included in the analysis. The average number of herbaceous species found in each functional group at each scale is shown in Table 7.

**Table 7:** Mean number of species per quadrat at the three scales.

<b>Total number of species</b>		<b>10 m<sup>2</sup></b>	<b>100 m<sup>2</sup></b>	<b>1000 m<sup>2</sup></b>
<b>geophytes</b>	33	2	3.58	6.03
<b>perennials</b>	49	1.4	3.04	6.05
<b>annuals</b>	243	12.47	24.09	43.64

## Autocorrelation

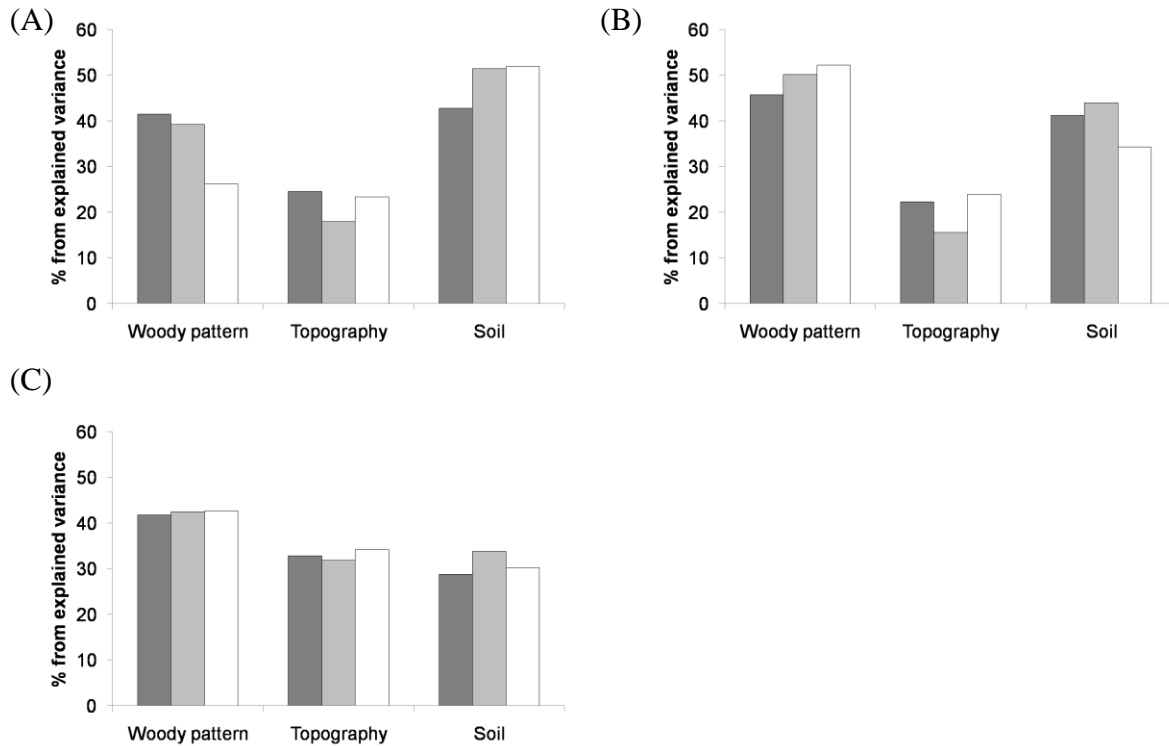
For all functional groups, the proportion of variation explained by space (geographical coordinates) was high and varied between 34 and 50% of the total explained variance (Table 8). The proportion of variation explained by spatial variables was similar for all functional groups, and for all spatial scales.

**Table 8:** The explained variance by spatial variables (geographic coordinates) given as percentages of the total explained variance.

	species composition			species richness		
Scale (m <sup>2</sup> )	10	100	1000	10	100	1000
% spatial variance of total explained variance						
<b>Geophytes</b>	49.5	40.83	41	50	42.3	44.8
<b>Perennials</b>	45.6	42.7	40.7	36.8	35.1	34.5
<b>Annuals</b>	50	43.6	38.8	39.3	37.6	35.9

#### **Herbaceous species composition**

Woody vegetation was the most important group of variables for annuals and perennials accounting for more than 40% of the total explained variance at all three scales (Figure 8). For geophytes, soil was the most important group of variables, accounting for more than 40% of the total explained variance at all three scales. Topography was the second most important group for annuals at fine and coarse scales, accounting for 30% of the explained variance. For geophytes and perennials topography was less important than woody vegetation and soil variables, accounting for about 20% of the explained variance. The percentage of the total variance explained by each group varied very little across spatial scales for perennials and annuals. For geophytes woody vegetation variables provided 41% of the total explained variance at the fine scale but only 26% at the coarse scale. Similarly, soil variables explained 42% at fine scale and 52% at coarse scale (Figure 8).



**Figure 8:** The variance explained by environmental predictors of herbaceous species composition given as percentages of the total explained variance. Dark gray bars represent the scale of 10 m<sup>2</sup>, light gray bars represent the scale of 100m<sup>2</sup> and white bars represent the scale of 1000 m<sup>2</sup>. (a) Geophytes; (b) Perennials; (c) Annuals.

The predictor accounting for the highest explained variance was organic matter for geophytes at all scales. For perennials and annuals this predictor differed between scales (Table 9). CaCO<sub>3</sub> accounted for the highest explained variance for perennials at the fine and medium scales, while at the coarse scale woody cover and vegetation height accounted for the highest explained variance. The variables with the highest explained variance for annuals were woody cover, CaCO<sub>3</sub> and slope, at the fine, medium, and coarse scales, respectively.



**Table 9:** The variance explained by environmental predictors of species composition given as percentages of the total explained variance. \*  $P < 0.05$ .

Scale (m <sup>2</sup> )	Geophytes			Perennials			Annals		
	10	100	1000	10	100	1000	10	100	1000
<b>northness</b>	7.67	5.57	5.28	9.08*	6.25*	7.06*	17.87*	16.50*	15.46*
<b>slope</b>	15.86*	11.15	14.39	12.68	8.87*	15.99*	16.18*	15.52*	19.94*
<b>CaCO<sub>3</sub></b>	16.37*	13.41*	9.11	32.71	31.83	21.44*	18.36*	18.27*	17.93*
<b>organic matter</b>	26.60*	37.11*	42.26*	8.61*	13.23*	13.26*	10.63*	15.32*	12.36
<b>woody cover</b>	23.20*	17.24*	13.27	22.53	25.14	23.58	20.53*	17.87*	14.77*
<b>number of patches</b>	14.83	18.98	11.27	8.76*	16.86	20.86*	6.52	8.84	13.07*
<b>vegetation height</b>	8.95	8.01	6.72	22.22	22.67	25.43	15.45*	13.72*	17.38*

When considering the different predictors comprising the three groups of variables it appears that there is no one prominent variable that explains a large portion of the total explained variance. The common situation was that the different predictors explained approximately the same proportion of the explained variance (Table 9). In

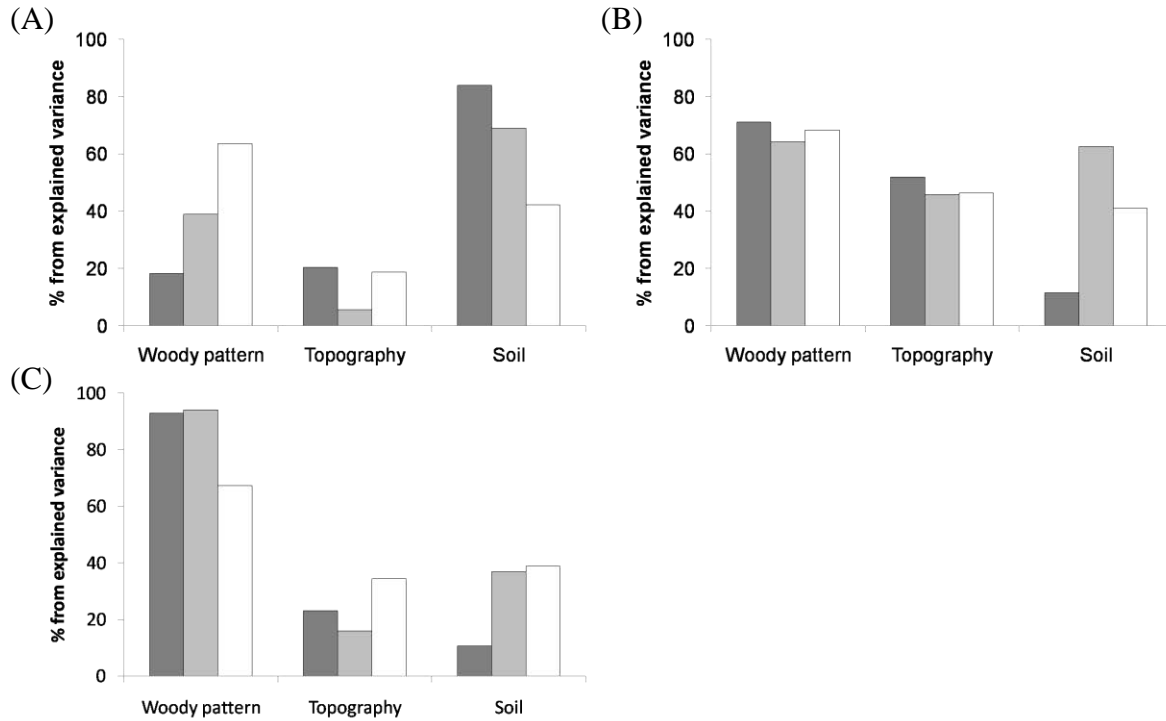
addition, the rank of importance of the different predictors in terms of the proportion of variance explained at each scale for each functional group was relatively constant (Table 9). The only major changes were: for geophytes, slope was ranked the 5<sup>th</sup> predictor at medium scale while at coarse scale it was the 2<sup>nd</sup> predictor. For annuals, slope was the 4<sup>th</sup> predictor at fine and medium scales while at coarse scale it was the 1<sup>st</sup> predictor; woody cover was the 1<sup>st</sup> predictor at fine scale and was ranked only as the 5<sup>th</sup> predictor at coarse scale (Table 9).

When considering only the significant predictors comprising the three groups of variables it appears that these predictors are different at different scales, except for annuals that were represented at all three scales by predictors from all three groups of variables. For geophytes, predictors from all three groups of variables were represented at fine scale, however topography variables were absent at medium and coarse scales. Woody vegetation variables were also absent at coarse scale. For perennials, predictors from all three groups of variables were represented at fine scale. However, topography variables were absent at medium and coarse scales and soil variables were absent at coarse scale.

### **Herbaceous species richness**

Woody vegetation was the prominent group of variables for annuals and perennials at all three scales and for geophytes at the coarse scale accounting for more than one half of the total explained variance (Figure 9). Soil variables were the most important group for geophytes at fine and medium scales, accounting for more than 65% of the total explained variance. Topography variables were the second most important

variables for all functional groups at fine scale accounting for ~20% of the explained variance for annuals and geophytes and ~50% for perennials, but at medium and coarse scales topography was less important than woody vegetation and soil variables.



**Figure 9:** The variance explained by environmental predictors of herbaceous species richness given as percentages of the total explained variance. Dark gray bars represent the scale of 10 m<sup>2</sup>, light gray bars represent the scale of 100m<sup>2</sup> and white bars represent the scale of 1000 m<sup>2</sup>. (a) Geophytes; (b) Perennials; (c) Annuals.

The percentage of the total variance explained by each group of variables varied across spatial scale for all functional groups: for geophytes, woody vegetation variables

provided 63% of the total explained variance at the coarse scale but only 18% at the fine scale. Similarly, soil variables explained 83% at the coarse scale and 42% at the fine scale (Figure 9). Soil was stronger group of variables predictors at the medium scale for perennials accounting for 62% of the total explained variance compared to 11% and 41% at the fine and coarse scales, respectively. Woody vegetation was stronger group of predictors at the fine scale (92%) than at the coarse scale (67%) for annuals while soil was more important group of predictors at the coarse scale (38%) than in the fine scale (10%). Explained variance accounted for by topography did not change much across scale for any of the functional groups.

The predictors accounting for highest explained variance differ in different scales for all the functional groups (Table 10). The predictors accounting for highest explained variance for geophytes at the fine scale was  $\text{CaCO}_3$ , at the medium scale it was organic matter and at coarse scale both variables accounted for the highest explained variance. Woody cover accounted for the highest explained variance for perennials at the fine scale while at the medium and coarse scales it was  $\text{CaCO}_3$ . Woody cover accounted for the highest explained variance for annuals at the fine and medium scales, while at the coarse scale it was the number of patches.

**Table 10:** The variance explained by environmental predictors of species richness given as percentages of the total explained variance. \*  $P < 0.05$ .

Scale (m <sup>2</sup> )	Geophytes			Perennials			Annuals		
	10	100	1000	10	100	1000	10	100	1000
<b>northness</b>	7.02	4.58	3.38	7.14	4.44	3.77	6.85*	9.52*	13.82
<b>slope</b>	14.04*	15.27*	9.46	16.67*	13.33*	18.87	19.18*	18.25*	23.04*
<b>CaCO<sub>3</sub></b>	33.33*	25.19*	28.38*	33.33*	36.67*	42.14*	8.22*	8.73*	12.90*
<b>organic matter</b>	26.32*	41.98*	28.38*	2.38	11.11	11.95	8.22*	19.05*	14.29
<b>woody cover</b>	8.77*	8.4	10.14	40.48*	26.67*	25.16*	63.01*	52.38*	30.41*
<b>number of patches</b>	5.26	9.92*	10.14	14.29*	23.33*	25.79*	15.07*	34.92*	35.02*
<b>vegetation height</b>	5.26	4.58	14.19	19.05*	18.89*	20.13	19.18*	17.46*	17.51*

When considering the different predictors comprising the three groups of variables, it appears that the rank of importance of the different predictors in terms of the proportion of explained variance in each scale for each functional group did not change much (Table 10). The only major changes were: for geophytes, slope was the 3<sup>rd</sup> important predictor at fine and medium scales while at coarse scale it was the 6<sup>th</sup>

predictor. Vegetation height was the 7<sup>th</sup> predictor at fine and medium scales while at coarse scale it was the 3<sup>rd</sup> predictor. For perennials, number of patches was the 5<sup>th</sup> predictor at fine scale while at coarse scale it was the 2<sup>nd</sup> predictor. For annuals, number of patches was the 4<sup>th</sup> predictor at fine scale while at coarse scale it was the 1<sup>st</sup> predictor (Table 10).

When considering only the significant predictors comprising the three groups of variables it appears that there is no one prominent variable that explains a large portion of the total explained variable. The more common situation was that the different predictors explained approximately the same proportion of the explained variance (Table 10). The only exception was woody cover that explained 63.01% of the total explained variance for annuals at fine scale. However, the significant predictors are different at different scales (Table 10). For geophytes and perennials, predictors from all three groups of variables were represented at fine and medium scales. Topography variables were absent at coarse scale. For annuals, soil variables were absent at coarse scale.

## **Discussion**

*Do environmental determinants of herbaceous species composition and richness differ between scales?*

The relationships between the environmental variables and herbaceous species composition varied only little across scales except for geophytes. In contrast, the relationships between the environmental variables and herbaceous species richness varied considerably across scales. For geophytes and annuals the impact of both woody

vegetation and soil varied across scales and for perennials only the impact of soil varied across scale.

Although Ramat Hanadiv is a plateau with an elevation ranging from 90-150 m a.s.l., topography was still important. We expect that in areas with higher topographic heterogeneity, the importance of topography would increase.

One possible explanation of the scale-variant pattern is that the processes controlling species composition and species richness are specific at each spatial scale (Wiens 1989, Levin 1992, Wright et al. 1993). Some authors have suggested that the factors responsible for species distribution patterns are scale dependent (González-Mégias et al. 2007), reinforcing the idea of using more than one spatial scale when trying to discern the mechanisms determining species distribution. Many studies that explicitly address the issue of scale do so by comparing local scale (up to tens of square meters) and regional scale (spanning broad geographic scale) (Boyer 2003, Grand and Cushman 2003, Bosch et al. 2004, Coreau and Martin 2007). We showed that the scale dependence between environmental variables and herbaceous species composition and richness is apparent at fine scales even for narrow range of scales ( $10 \text{ m}^2$  -  $1000 \text{ m}^2$ ). We speculate that the scale dependence pattern we observed would be even more obvious when a broader range of scales is studied.

Studies of species distribution patterns and of correlations between species and environment traditionally were conducted at a single scale of observation; that is, employing one quadrat size and sampling one extent of area. However, as we demonstrated in this study, the relationships between the environmental variables and herbaceous species composition and richness varied across spatial scales. Thus, patterns

of species composition and richness at small scale cannot be scaled up to coarser scales, and vice versa (Wagner and Edwards 2001, Waldhardt et al. 2004). These results outline the need to include multiple scales of observation in ecological research.

Interestingly, the most important group of variables was different for different functional groups. Overall, woody vegetation was the prominent group of variables for annual and perennial composition and richness at all three scales, while soil variables were the most important group for geophytes composition and richness (note that soil was represented by only two variables, compared to three variables representing woody vegetation). In addition, the importance of these environmental variables was different at different scales: woody pattern was a stronger predictor at coarse scale for geophyte richness while for annual richness it was a stronger predictor at fine scale. Soil, on the other hand, was a stronger predictor at fine scale for geophyte richness while for annual and perennial richness it was stronger at coarse scale.

When considering the different predictors comprising the three groups of variables it appears that the soil variables,  $\text{CaCO}_3$  and organic matter, were the most important predictors affecting herbaceous species composition for all functional groups at all scales. They appeared as the first or second predictors with the highest percentage of explained variance for the three functional groups and at all scales except for perennials at coarse scale. These two variables were also the most important predictors affecting species richness for geophytes and perennials at all scales. Annual species richness was more affected from woody vegetation variables at all scales. Overall, these results presumably relate to differences in life history between annuals and perennials. Agra and Ne'eman (2009) who studied Mediterranean maquis in northern Israel found that the



proportion of annuals was lower than perennials in woody patches. Woody cover removal resulted in a sharp increase of annuals, but only a moderate increase of perennials. This indicates that most annuals, but only half of the perennials, prefer non-woody habitats. Apparently, annuals are immediately affected by changes in woody vegetation compared to perennials, presumably because their little resource reservations do not allow survival in the shade of woody species, while the ubiquity of their seeds allow rapid regrowth wherever the woody vegetation is removed.

#### *The impact of woody vegetation on plants*

Our initial hypothesis, that the impact of woody vegetation would be expressed chiefly at fine scales, while soil will be more important at coarse scales, was not confirmed. Our hypothesis was confirmed only for geophytes composition and annual species richness. It is possible that in order to identify a change across scales in the relative importance of different environmental variables one needs to study broader ranges of scale.

Woody vegetation was found to affect plant species composition and richness in Mediterranean ecosystems at fine scales (up to tens of square meters) (Casado et al. 2004, Agra and Ne'eman 2009) and at broader scales (thousands of square meters) (Atauri and de Lucio 2001). In this work we showed that woody vegetation affects plant species richness and composition at all the studied scales, and there was no clear trend regarding its overall effects. Mediterranean vegetation mosaics are fine-grained and characterized by woody patches of different heights and sizes, herbaceous clearings, exposed rocks and bare ground (Perevolotsky 2002). Therefore, we expect that the major effect of woody

vegetation would be at fine scale. We speculate that woody vegetation would reveal a decrease in its contribution at much broader scales.

### **Implication for conservation**

Several researchers have acknowledged the need for multi-scaled approaches to conservation planning (Saab 1999, Grand and Cushman 2003, Perevolotsky 2005), but most conservation planning analyses are performed at a single scale. Further, studies that explicitly address the issue of scale in the context of conservation refer mostly to local sampling unit (up to 10 m<sup>2</sup>) and regional scale (spanning broad geographic scale) (Donovan et al. 2000, Poiani 2000, Shriner et al. 2006). The results of the present study demonstrate that conservation efforts need to relate also to scale dependence in species distribution that is present at fine scales.

Two implications of our study maybe relevant for conservation: the first point concerns the selection of areas for conservation. Our results indicate that selection of areas should be done at a multi-scale approach. Areas regarded as being important by coarse scales analyses may not be those regarded as being important by local analyses. For example, the conclusion from analyzing geophyte species richness at the fine scale is that soil is by far the most important aspect of the environment which can lead to selecting area for conservation while neglecting the woody vegetation predictors (Figure 3). However, the woody vegetation is more important than soil at the coarse scale. Conservation efforts should strive for a comprehensive, multi-scale approach. Conserving species at a single scale can miss important linkages, ecological processes, and biodiversity at other scales (Simberloff 1998).

The second point deals with multi-scaled approaches to conservation. High species richness at different spatial scales may be achieved by integrating species-environment relationship at different scales into a single management regime. For example, in Ramat Hanadiv Nature Park, annual species richness at the fine scale may be increased by reducing the area covered by woody plants (Table 5, trends are not shown). However, at the coarse scale annual species richness may be increased by increasing the number of woody patches. These somewhat contradicting results should be integrated in order to establish a management regime that will strive to increase the number of woody patches and at the same time reduce the overall woody cover. It can be done by using different management regimes that will increase fragmentation of the woody cover such as grazing (either by goats or cattle), fire and clear-cutting (Adler 2001, Henkin et al. 2007, Bar Massada et al. 2008).

### **Concluding remarks**

Soil variables were found to be the most important environmental variables, affecting both herbaceous species composition and richness. The effect of woody vegetation on herbaceous species distribution is relatively unexplored. In this study it appears that woody vegetation is an important element in controlling the spatial distribution of herbaceous species across scales. This finding is important for conservation and management of biodiversity since on one hand quantifying the spatial pattern of woody vegetation in small and large areas is feasible using remote sensing methodology while on the other hand, changing its cover and spatial distribution is possible using different management regimes such as grazing, fire and clear cutting

(Adler 2001, Henkin et al. 2007, Bar Massada et al. 2008). In addition, this study shows that the species–environment relationships are scale dependent, and the responses are specific to each functional group. This means that generalization would be very difficult and the extrapolation should be undertaken with caution. In order to study species distribution it is recommended to use multi-scale sampling scheme that enables researcher to reach conclusions at different spatial scale simultaneously.

# **Chapter 3- The role of spatial scale in the relationship between woody cover and landscape heterogeneity versus herbaceous species richness**

## **Introduction**

Understanding the forces that govern the spatiotemporal variation in species diversity is of practical interest in the conservation of natural ecosystems. Relatively few studies have dealt with the impact of certain species on the environment and the consequential effect on the distribution of other species (Jones et al. 1994, Shachak et al. 2008). Organisms can affect their immediate environment, and do so in proportion to the scale and nature of their activity. In terms of their effects on species richness and composition, woody plants can be considered as dominant factors that extensively affect their environment, changing resource distribution over space and time (House et al. 2003). Woody vegetation affects the distribution of water and light, pattern niches through biomass and litter accumulation, and availability of resources (Jones 1997). These processes create and organize niches in the ecological system space, and as such, constitute an important element in controlling species distribution.

In order to assess the role of woody vegetation we explored two of its aspects: woody cover and landscape heterogeneity. Since the effects of woody vegetation on its environment are extensive, changes in its overall cover are expected to affect species distribution. Spatial heterogeneity is an important aspect of woody cover. Landscape heterogeneity is a common term describing the spatial heterogeneity in vegetation at the geographical scales. We used it to describe vegetation structure at fine scale as well. Changes in landscape heterogeneity are important because they may imply changes in

habitat diversity and influence the diversity of organisms such as plants, insects, birds and mammals (Bock and Bock 1984, Dennis et al. 1998, Dufour et al. 2006). Activities of many organisms depend on the structure of their immediate environment, and thus are expected to be affected by changes in the spatial heterogeneity of their landscape.

### **Woody vegetation cover**

The relationship between species richness and woody cover has been at the core of many studies whose results were equivocal: Grytnes (2000) found that even though a unimodal pattern was most common, the response of vascular plant species richness to cover varied in different plots in low alpine zones in west Norway. Gillet et al. (1999) found that the best fit between herbaceous species richness and *Larix decidua* cover was obtained using Gaussian regression in sub-alpine wooded pastures in Switzerland. Casado et al. (2004) found a negative linear relationship between woody plant cover and herbaceous richness in Mediterranean grasslands and shrublands of the Iberian Peninsula. In contrast, researchers who studied the tallgrass prairie vegetation in northeastern Kansas showed that the relationship between species richness and woody cover is highly non-linear with a well-defined threshold, where species richness does not vary beyond a critical point but decays quickly below it (Bascompte and Rodriguez 2001). Thus, the relationship between woody cover and species richness is still not clear.

The factors that condition diversity-cover patterns, consequently, still wait to be discovered. Yet even more so, the causal mechanisms of this relationship must be understood. Several authors have argued that if the percentage of woody vegetation cover is high, an increase in woody cover will reduce species richness due to increased

competition for light (e.g., Newman 1973, Huston and DeAngelis 1994). Shachak et al. (2008) postulated that the overall relationship of species richness with woody cover is either linear positive or hump-shaped: when woody vegetation cover is low, species richness typically increases with increased woody cover, since species of woody habitats join species of non-woody habitats. The overall relationship depends on the ratio between extinction rates of species that prefer non-woody patches to the colonization rate of species preferring woody patches: A linear positive relationship is expected when the colonization rate of species preferring woody patches is higher than the extinction rate of species that prefer non-woody cover, whereas a hump-shaped relationship is expected in the opposite case.

### **Landscape heterogeneity**

Spatial heterogeneity is thought to be a major driver of biological diversity (Wiens 1976, Milne 1991, Huston and DeAngelis 1994). Spatial heterogeneity results from the spatial interactions between a number of biotic and abiotic factors and the differential responses of organisms to these factors (Milne 1991). Spatial heterogeneity of vegetation patterns (i.e., landscape heterogeneity) is a structural property of landscapes that can be defined by the complexity and variability of ecological systems in space (Li and Reynolds 1994). Different components of landscape heterogeneity can be quantified in terms of landscape metrics (Gustafson 1998), which are indices that quantify specific spatial characteristics of patches, classes of patches, or entire landscape mosaics (McGarigal 1995). Landscape metrics have been successfully used to quantify different

aspects of landscape heterogeneity (e.g., Meyer et al. 1998, Kie et al. 2002, Bar Massada et al. 2008).

Species establish in a particular site depending on their ability to reach it and on the presence of suitable habitats. Once established, the persistence of a species at a site depends mainly on inter-species interactions and changes in the environment over time. Therefore, local biodiversity should be influenced by the rates of ecological processes such as immigration, competitive exclusion, and emigration or death. It has been shown that the rates of such processes are affected by the spatial heterogeneity of the environment. For example, competitive exclusion can be delayed indefinitely in spatially structured environments (Tilman and Kareiva 1997, Amarasekare 2003).

Many studies have focused exclusively on a single aspect of environmental heterogeneity (Clough et al. 2005, Gratwicke and Speight 2005). Only a small number of studies have related to the spatial pattern of environmental heterogeneity. Palmer (1992) studied the effect of both environmental variability and its spatial heterogeneity using a simulation experiment, and found that increasing environmental variability or fractal dimension allowed more species to exist per microsite and per landscape. However, increasing the fractal dimension to extremely high values reduces the number of species that coexist at the landscape level. In a similar simulation, Steiner and Kohler (2003) found that landscape level richness increased with decreasing habitat aggregation. Yet, field studies have very rarely considered spatial heterogeneity. Dufour et al. (2006) found that, in a wooded pasture in western Switzerland, plant richness generally increased with increasing environmental variability and decreasing spatial aggregation. Altogether, these results from real systems suggest that species richness generally increases as



environmental heterogeneity increases, while theoretical considerations dictate a reduction in richness for extreme heterogeneity values.

Measuring environmental heterogeneity is not trivial. One difficulty is that ecological space is multidimensional. Numerous environmental factors affect species distribution. However, the contribution of each individual factor is likely to be small. This is why we need to focus on variables that exert an integrative effect on species. Such a factor is woody vegetation, which extensively affects its environment due to its impact on many environmental factors such as light availability (Zobel et al. 1994, Gillet et al. 1999), soil acidity (Augusto et al. 2000) and humidity (Callaway and Walker 1997).

### **The effect of scale**

The scale in which the relationship between environmental heterogeneity and species diversity is studied appears to be one factor that conditions the variation of the patterns (Moore and Keddy 1989, Rosenzweig 1995, Huston 1999, Gross et al. 2000). There is an increasing recognition that different types of ecological processes are important drivers at different scales (Allen et al. 1984, Willis and Whittaker 2002). For example, Crawley and Harral (2001) suggest that at small scales ( $1 \text{ m}^2$  or less), ecological interactions are the most important processes controlling plant diversity in a system, while at larger scales, drivers such as topography, management, geology and hydrology are more important because they influence habitat type.

Although woody cover and spatial heterogeneity should have an effect at all scales, their relative importance may vary between scales, since the underlying ecological drivers vary between scales. The sampling scale affects the information gathered about a

system (He et al. 1994, He and Gaston 2000). A major question is how spatial heterogeneity and sizes of habitat patches affect species richness at different scales. It is important to know whether the processes that determine community structure at different scales are similar, and if not, how and under what circumstances the dominant processes vary with the scale of observation.

It has been suggested that due to scale dependence, patterns of species richness in small plots cannot be scaled up to entire landscapes (Wagner and Edwards 2001, Waldhardt et al. 2004). Studies that focus on one arbitrarily selected spatial scale as the basic sampling unit in studies of Mediterranean landscape species richness may overlook species–environment relationships that operate at finer or coarser scales (Best and Stauffer 1986). To maintain biodiversity, it is not only crucial to document species–environment relationships in as many community types as possible (Hobson et al. 2000), but also to examine these associations at multiple spatial scales. Studies are restricted to a single specific scale, and scales vary from one study to another, thus it remains unclear whether relationships are scale-dependent or whether a single relationship holds across scales. If the mechanisms that determine species richness vary with spatial scale, then so would the shape of the relationship.

In this study we present evidence for scale-dependence in the relations between woody cover and herbaceous species richness for three functional groups of herbaceous species in a Mediterranean ecosystem. In addition, we describe the relationships between landscape heterogeneity and herbaceous species richness for these functional groups at different spatial scales.

## Methods

Study site and field sampling are described in the methodology section (Figure 2).

### Woody vegetation pattern

A digital color orthophoto of the study area was generated by Ofeat<sup>TM</sup>keria 1 photography, in the summer of 2007 at a spatial scale of 0.25 m (Figure 2). The image was classified into two classes using unsupervised IsoData classification (Campbell 1996). In the summer, there are only two major spectral classes, woody vegetation and non-woody vegetation. The latter class includes dry herbaceous vegetation, bare soil and rocks.

The woody vegetation pattern in the woody/non-woody vegetation map was quantified by common landscape indices using FRAGSTATS software (McGarigal et al. 2002), for each hierarchical level independently. Percentage of woody cover reflects the proportional abundance of woody cover for each 10 m<sup>2</sup>, 100 m<sup>2</sup> and 1000 m<sup>2</sup>.

Heterogeneity was quantified using patch size standard deviation. In many ecological applications, second-order statistics, such as the variation in patch size, may convey more useful information than first-order statistics, such as mean patch size. Variability in patch size measures a key aspect of landscape heterogeneity that is not captured by mean patch size and other first-order statistics. Patch size standard deviation is a measure of absolute variation; it is a function of the mean patch size and the difference in patch size among patches. In addition, we also calculated woody patch core area and edge area. Core area is defined as the central portion of a patch that remains after removing a specific perimeter edge zone. The differences in these two areas are the

result of a combination of biotic and abiotic factors that alter environmental conditions along patch edges compared to patch interiors. Studies have shown that there are differences in species diversity between the core and edge areas (Thompson 1993, Wagner et al. 2000). In order to evaluate the change in woody core area and woody edge area between scales we used FRAGSTATS to calculate the total core area of the woody patches at each scale. Woody edge area was calculated by subtracting the total core area from the percentage of woody cover.

### **Statistical analyses**

Generalized additive models (GAMs) are a nonparametric extension of generalized linear models (GLMs). GLMs have been successfully applied in ecological research (e.g. Austin and Cunningham 1981, Austin et al. 1990). The use of GLMs in ecology has several drawbacks compared with the GAM modelling approach; most importantly, most species-environment interactions are likely to be non-linear (Gaston and Williams 1996). Ter Braak and Gremmen (1987) observed that in practice, the correct model to be fitted is rarely known. GAM is preferred to other regression methods (Steck et al. 2007) because it is a nonparametric model and is, therefore, able to handle non-linear relationships between responses and predictive variables. This allows the fitting of statistical models in better agreement with ecological theory (Austin 1999, 2002).

GAMs are data-driven rather than model-driven; that is, the resulting fitted values do not come from an a priori model. The rationale behind fitting a nonparametric model

is that the structure of the data should be examined first, before fitting an a priori determined model.

GLMs relate the mean response to the  $\mathbf{x}$  variables via

$$g(y) = \alpha + \sum_{j=1}^p \beta_j x_j$$

GAMs relax this to simply

$$g(y) = \alpha + \sum_{j=1}^p f_j(x_j)$$

where the  $f_j$  are unspecified smooth functions. In practice the  $f_j$  are estimated from the data by using techniques developed for smoothing (Goodall 1990, Hastie and Tibshirani 1990). A smoother is a tool for summarizing the trend of a response measurement  $Y$  as a function of one or more predictor measurements  $X_1, \dots, X_p$ . It produces an estimate of the trend that is less variable than  $Y$  itself. An important property of a smoother is its nonparametric nature: it does not assume a rigid form for the dependence of  $Y$  on  $X_1, \dots, X_p$  (Hastie and Tibshirani 1990). Each variable is smoothed separately, different variables may have different smoothers.

Thus GAMs allow the data to determine the shape of the response curves, rather than being limited by the shapes available in a parametric class. As a result, features such as bimodality and pronounced asymmetry in the data can be easily detected. For this reason GAM modelling provides a better tool for data exploration than GLM modelling.

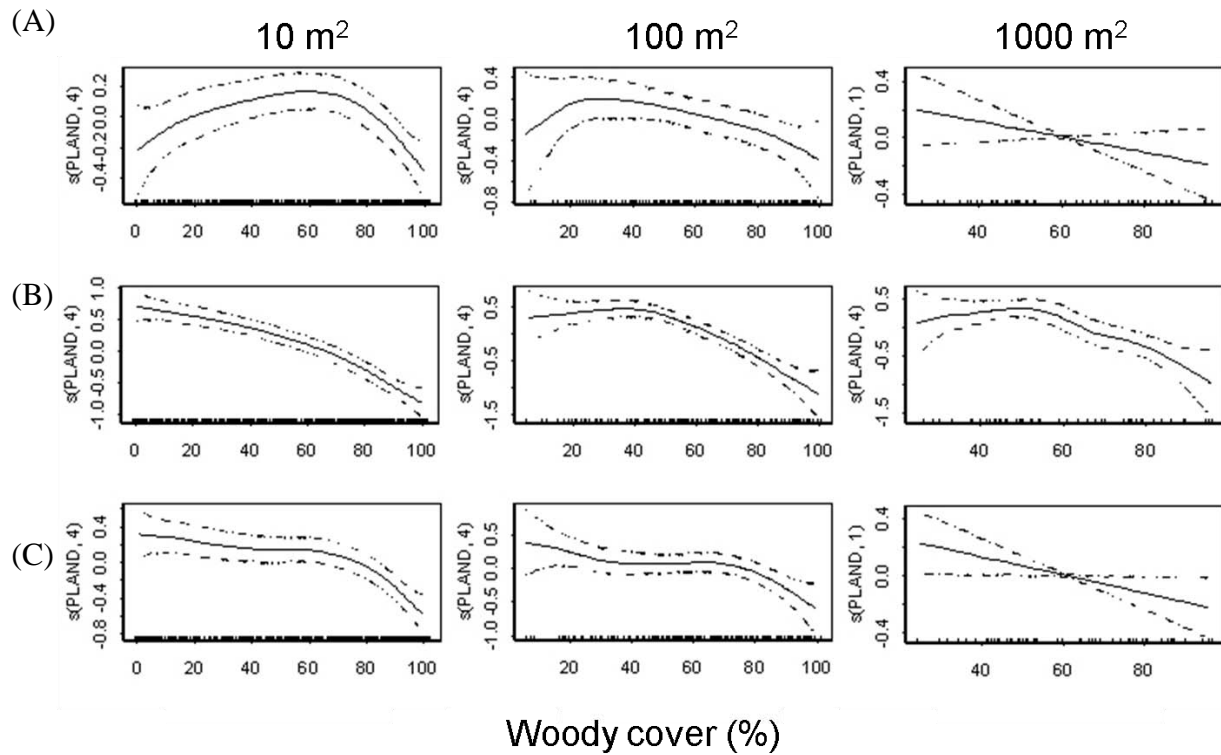
The dependent variable was herbaceous species richness of each functional group. The independent variables were woody cover and the heterogeneity (standard deviation

in patch size). We used a Poisson distribution as implemented in the GRASP library (Lehmann et al. 2002) of S-Plus (Insightful Corp., Seattle, Washington). Poisson distribution is recommended, as species richness is often considered as a form of count data (Crawley 1993). The default smoother degree of freedom was set to 4; to test for linear relationships, the alternative smoother degree of freedom was set to 1. We applied a stepwise regression in order to assess the relationship between the response and predictor. The significance of converting to a linear form was then tested using the Akaike information criterion (Parviainen et al. 2008).

## **Results**

### **Relationship between herbaceous species richness and woody cover**

The shape of the response curves of herbaceous species richness and percentage of woody cover show distinct differences between functional groups, and between the scales for each functional group (Figure 10). The relationship between percentage of woody vegetation cover and herbaceous species richness was hump-shaped for geophytes at 10 m<sup>2</sup> and 100 m<sup>2</sup>. Maximum richness was attained at 60% woody vegetation cover at 10 m<sup>2</sup> and at 30% woody cover at 100 m<sup>2</sup>. At the scale of 1000 m<sup>2</sup> a negative response was observed namely, the number of species decreased as the percentage of woody vegetation cover increased. The relationship between annual species richness and percentage of woody vegetation cover was negative at the scale of 10 m<sup>2</sup> and unimodal at the scale of 1000 m<sup>2</sup> (Figure 10). In general, the number of perennial species decreased as the percentage of woody vegetation cover increased.



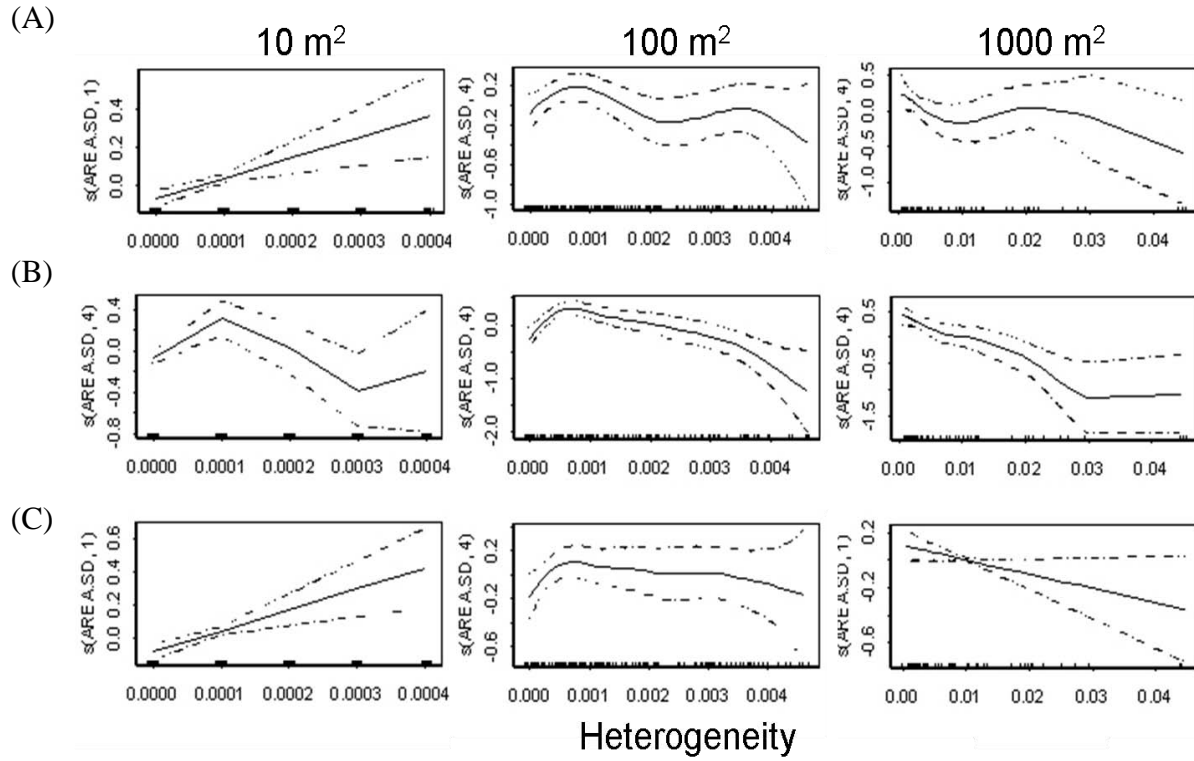
**Figure 10:** Response curves of herbaceous species richness to percentage of woody cover using generalized additive model (center lines). The y-axes are based on partial residuals and indicate the relative influence of the explanatory variable on the prediction. Distance between the lower and upper curves is twice the point specific standard error for each curve or factor level. (A) Geophytes; (B); Annuals (C) Perennials.

### Relationship between herbaceous species richness and landscape heterogeneity

The relations between heterogeneity and herbaceous species richness changed considerably at different scales and among functional groups (Figure 11). At fine scales

the number of species increased as heterogeneity increased for geophytes and perennials whereas a hump-shaped curve was observed for annuals. At broader scales the obvious trend was a decrease in species richness as heterogeneity increased in all functional groups.





**Figure 11:** Response curves of herbaceous species richness to heterogeneity using generalized additive model (center lines). The y-axes are based on partial residuals and indicate the relative influence of the explanatory variable on the prediction. Distance between the lower and upper curves indicates twice the point specific standard error for each curve or factor level. Heterogeneity refers to the standard deviation of woody patch size. (A) Geophytes; (B) Annuals; (C) Perennials.

## **Discussion**

The relationship between pattern and scale is both extremely intriguing and important in ecology (Levin 1992), but remains elusive even when the pattern is restricted to a spatial pattern and the scale is restricted to grain and extent. The multi-scale structure of spatial heterogeneity still remains largely unexplained.

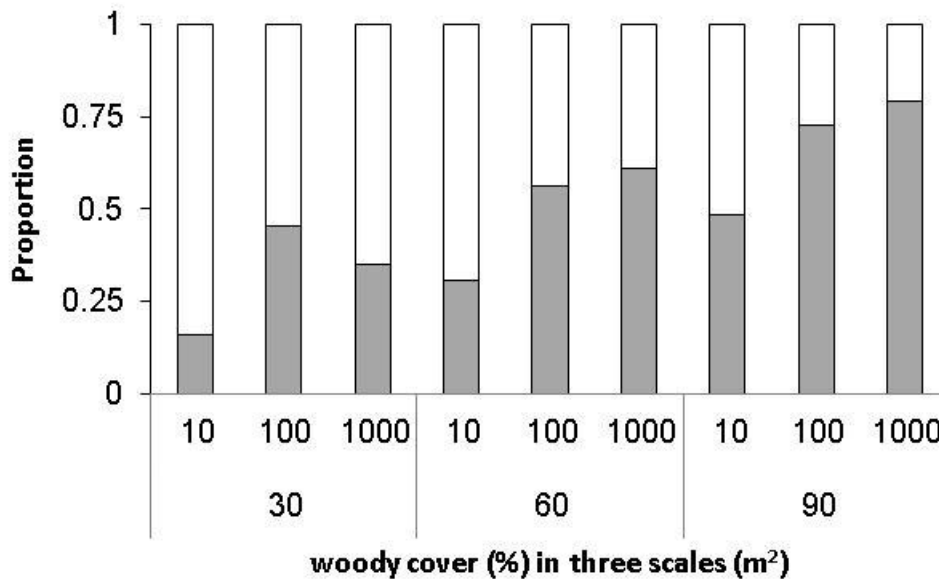
### **Relationship between herbaceous species richness and woody cover**

At 10 m<sup>2</sup>, annual and perennial species richness declined with increased woody cover, while geophytes revealed hump-shaped relationship with woody cover. In contrast, at the scale of 1000 m<sup>2</sup>, geophyte and perennial richness decreased as the percentage of woody cover increased, while the relationship between annual richness and woody cover was hump-shaped. Such scale-dependent responses may be explained within a framework of edge and core of woody patch (Harris 1988, Reese and Ratti 1988, Noss 1991). Many studies have shown that certain species reach their highest abundances at particular habitat edges (Kroodsma 1984, Lynch and Whigham 1984). Such specific preferences may be the outcome of different abiotic and biotic conditions. Woody edges usually have increased solar insolation, and higher daily maximum temperatures than the patch interior (Chen et al. 1999). Shade-intolerant species would, accordingly, favor edges (Ranney et al. 1981).

The major difference between the fine and coarse scales is that at the scale of 10 m<sup>2</sup>, a small percentage of woody cover might be the result of very small patch or even part of a patch, while at the scale of 1000 m<sup>2</sup> a small percentage of woody cover is the result of a whole shrub or tree.

Lord and Norton (1990) highlighted the differences between fine and coarse scale fragments. In fine scale fragments, they noted that there is practically no core, and the entire woody patch is a "edge" patch, in contrast to coarse scale fragments, where woody core areas comprise large proportions of the patch (Figure 12). Therefore, the differences between functional groups could be explained by the proportions of herbaceous species that prefer the woody patch core vs. the woody patch edge, as their habitat. Presumably, many geophyte species as opposed to annual species prefer the edge interface, and a small proportion of species from both groups prefer the woody core areas. These assumptions are supported by the findings of Gabay (2008), who also worked at Ramat Hanadiv Nature Park, and studied the filtering of herbaceous species from the scale of 1000 m<sup>2</sup> into woody and non-woody patches. She found that out of the annual species that were recorded at 1000 m<sup>2</sup>, 4% were found under woody patches and 90% were found in non-woody patches, while about half of the geophytes were found in woody patches and a similar proportion was found in non-woody patches. The increase in woody cover at fine scale had two outcomes: a decrease in non-woody areas and a decrease in total woody edge area (Figure 12). Thus, presumably, the increase in woody cover at fine scale increased geophyte richness up to the point where the number of geophytes preferring non-woody habitats and the number of geophyte species preferring woody edge habitats decreased. On the other hand, annual and perennial richness decreased as woody cover increased, presumably since a large proportion of annuals and perennials prefer non-woody habitats (Table 1). The decrease in perennials was less steep compared to the decrease in annuals and might indicate that perennials may withstand the conditions under shrubs better compared to annuals. This result is consistent with the

work of Agra and Ne'eman (2009) who studied a Mediterranean maquis system in northern Israel. They found that the proportion of annuals was lower than perennials in woody patches. Woody cover removal resulted in a sharp increase of annuals and a moderate increase of perennials, indicating that although both annuals and perennials prefer non-woody habitats, relatively more perennial species may populate woody habitats.



**Figure 12:** The relative partition of woody cover between total woody core area (gray bars) and the woody edge area (white bars) at different percentages of woody cover and at different scales.

At the scale of 1000 m<sup>2</sup>, the increase in woody cover is largely an increase in woody core areas, while the proportion of the total edge interface is low (Figure 12). The result is that for all herbaceous groups, the number of species declines. However, we could not explain the observed increase in annual species richness in low woody cover.

### **Relationship between herbaceous species richness and landscape heterogeneity**

We found that the relationship between herbaceous species richness and heterogeneity depended on the spatial scale at which the pattern was analyzed, which is consistent with other studies (Pearson et al. 1995, Kie et al. 2002, Steffan-Dewenter et al. 2002). Geophyte and perennial richness increased with the increase in heterogeneity at the scale of 10 m<sup>2</sup>, as suggested by Niche Theory (Hutchinson 1957). As environmental variability increases, more habitat types exist, and more species can coexist (Statzner and Moss 2004). On the other hand, annual richness at the same scale declined. Apparently, the increase in spatial heterogeneity of woody vegetation did not affect annuals, given that most annual species prefer non-woody habitats (Agra and Ne'eman 2009). These findings point again to the apparent benefits of woody cover edges for geophytes and perennials. At broader scales all functional groups experienced a decline in richness as heterogeneity increased, probably as a result of an increase in the woody vegetation core areas, as explained above.

Some differences between functional groups result from group-specific characteristics. Each functional group represents unique structural and functional traits, and group members have similar adaptations to certain ecological conditions (Lande 1982, de Mera et al. 1999, Lavorel et al. 2007). Thus, plants of the same functional group are expected to exhibit similar responses to environmental variation and have similar effects on ecosystem processes (Walker 1992, Noble and Gitay 1996, Pausas and Austin 2001). Several authors have pointed out the specificity in the response of particular species across scales (Giller and Gee 1987, Wright et al. 1993, Halaj et al. 2000, Ruggiero and Kitzberger 2004). When analyzing the relationship between species and

environmental factors, it is crucial to consider both the spatial scale of the analysis and the specific characteristics of each functional group.

In conclusion, this study shows that patterns of diversity-heterogeneity relationships are scale-variant, and the responses are specific for each functional group. This means that analyzing the relationship between species richness and environmental factors at only one scale reveals only part of the complex picture and can lead to incomplete or even wrong conclusions.

## Synthesis

The description of species-distribution patterns and the mechanisms explaining these patterns have long been an objective in ecology (Ricklefs 1993, Schulze and Mooney 1993, Rosenzweig 1995, Gaston 2000, Rahbek and Graves 2001, Whittaker et al. 2001). Understanding the forces that govern the spatial variation in species diversity is of a practical interest in the conservation of natural ecosystems.

A number of approaches have been used to develop predictive models for species–environment relationships. Common to most of these approaches is the use of topography, soil, and climate as predictors (Oliveirafilho 1994, Stohlgren et al. 1998, Stohlgren et al. 1999, Stohlgren et al. 2000, Hutchings et al. 2003, Davies et al. 2005, Stohlgren et al. 2005) and overlooking woody vegetation as an important determinant of species distribution and diversity patterns (Jones et al. 1994, Shachak et al. 2008). In these three chapters I study the importance of woody vegetation on the distribution of herbaceous species. The affects of woody vegetation on herbaceous plants is apparent at small scale, as demonstrated in the first chapter, as well as at larger scales, as demonstrated in the second and third chapters. I also found in the three chapters that the three herbaceous functional groups differ in their response to woody vegetation. It appears that overall there is a tendency of geophytes to grow under woody cover, whereas most annuals prefer non-woody habitats. I did not check empirically the mechanism shaping these phenomena.

Another fundamental question in ecology is how the scale of observation influences the description of pattern. Each species experiences the environment at a unique range of scales, and thus responds to environmental variability in its own unique

way. Many of the studies analyzing species distribution at multiple scales focus on identifying the scale that is most relevant for species distribution (Grand and Cushman 2003), typically checking different environmental variables at each scale (Grand and Cushman 2003, Coreau and Martin 2007, Sarr and Hibbs 2007). In contrast, in this study I do not ask which scale is the most relevant, assuming that all scales are relevant to species distribution. My major question is -- which are the most important factors at each scale. Thus, I analyze the same set of variables across scales. The results of this study indicate the importance of multiscale studies where information on the system's behavior is analyzed at several scales simultaneously, and conclusions are made based on integration of multiscale information.

In addition, my results show that the effects of woody vegetation and soil on herbaceous species distribution are scale dependent. The impact of woody vegetation on plants was expressed chiefly at fine scales while soil was more important at coarse scales.

In order to maintain biodiversity, it is important to document species–environment relationships at multiple spatial scales since species respond hierarchically to habitat factors (Kotliar and Wiens 1990, Levin 1992, Cushman and McGarigal 2004). Identification of factors underlying distribution of diversity has been under intense research during the past decade (Gaston 2000). The results of this work show that distribution of diversity is an outcome of various environmental factors and that the relative importance of different environmental variables varies between the different scales of examination and between functional groups.

The results of the three chapters emphasize the importance of examining different groups of herbaceous species in order to acquire a wider perspective of the determinants



of diversity. For example, in the second chapter I show that geophyte species richness is mainly related to soil, whereas annual species richness is affected by woody vegetation.

In the three presented chapters I presented the influence of scale on the relationship between herbaceous species richness and composition and environmental factors, focusing mainly on woody vegetation. In the first chapter we showed a small scale interaction between the woody species PT and herbaceous richness and composition. This affects of the woody species PT stems from the specific traits of woody species, whether it is the canopy shape and density, allelopathic effects or other factor which is species specific. In the second chapter we demonstrated relations between richness and composition and habitat characteristics at higher scales. We found that the relationship between environmental predictors and herbaceous species richness and composition varied across spatial scales and groups of species. At these scales woody vegetation was found to be the most prominent factor for annuals and perennials, for both richness and composition. The importance of woody vegetation decreased as the scale increased for annuals and perennials richness while its importance increases for geophytes richness. In the third chapter, we further demonstrated that the observed relationship between herbaceous woody vegetation and species richness was scale dependent.

## Implication for conservation

The results of the present work have important implications in conservation ecology and community management:

1. Woody species PT is important determinant of herbaceous richness and composition at small scale. Heterogeneous landscape in terms of the woody species comprising it will result with high herbaceous species richness and composition. In addition, as we showed in the first chapter of this work, most herbaceous species appearing in our study had significant tendency to grow under a certain woody species PT. This finding is important especially for conservation of rare and endangered species. For example, *Salvia pinnata* and *Allium schubertii* are two rare species that were found to have significant affinity towards specific PT. *Salvia pinnata* occurred more than twice than expected at open patches whereas *Allium schubertii* occurred only under *Cupressus* sp. PT. These finding can enhance our ability to conserve those species.
2. According to the results presented in the second chapter, selection of areas for conservation should be done in a multiscale approach. Areas regarded as being important by regional analyses may not be those regarded as being such by local analyses.
3. In the second chapter we showed that conservation efforts should strive for a comprehensive, multiscale approach. Conserving species at a single scale can miss important linkages, ecological processes, and biodiversity at other scales (Simberloff 1998). Conservation goals should be met using different management regimes at different spatial scales.

## References

- Adler, P. B., Raff, D. A., and Lauenroth, W. K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* **128**:465-479.
- Agra, H. and G. Ne'eman. 2009. Woody species as landscape modulators: Their effect on the herbaceous plants in a Mediterranean maquis. *Plant Ecology* (**In press**).
- Allen, R. F. H., R. V. O'Neill, and T. W. Hoekstra. 1984. Interlevel relations in ecological research and management: Some working principles from hierarchy theory. USDA Forest Service General Tech Report RM-110. Rocky Mountain Forest and Range Experiment Station.
- Allen, T. F. H. and T. B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.
- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* **6**:1109-1122.
- Arrington, D. A. and K. O. Winemiller. 2006. Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. *Journal of the North American Benthological Society* **25**:126-141.
- Atauri, J. A. and J. V. de Lucio. 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landscape Ecology* **16**:147-159.
- Augusto, L., M. P. Turpault, and J. Ranger. 2000. Impact of forest tree species on feldspar weathering rates. *Geoderma* **96**:215-237.
- Austin, M. P. 1999. A silent clash of paradigms: some inconsistencies in community ecology. *Oikos* **86**:170-178.

- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**:101-118.
- Austin, M. P. and R. B. Cunningham. 1981. Observational analysis of environmental gradients. Pages 109-119. Blackwell Scientific Book Distributors.
- Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs* **60**:161-177.
- Bar Massada, A., O. Gabay, A. Perevolotsky, and Y. Carmel. 2008. Quantifying the effect of grazing and shrub-clearing on small scale spatial pattern of vegetation. *Landscape Ecology* **23**:327-339.
- Barth, R. C. and J. O. Klemmedson. 1978. Shrub-induced spatial patterns of dry-matter, nitrogen, and organic-carbon. *Soil Science Society of America Journal* **42**:804-809.
- Bascompte, J. and M. A. Rodriguez. 2001. Habitat patchiness and plant species richness. *Ecology Letters* **4**:417-420.
- Belsky, A. J. 1994. Influences of trees on savanna productivity - tests of shade, nutrients, and tree-grass competition. *Ecology* **75**:922-932.
- Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* **26**:1005-1024.
- Belsky, A. J. and C. D. Canham. 1994. Forest gaps and isolated savanna trees - an application of patch dynamics in 2 ecosystems. *Bioscience* **44**:77-84.

- Bengtsson, J., H. Jones, and H. Setälä. 1997. The value of biodiversity. *Trends in Ecology & Evolution* **12**:334-336.
- Best, L. B. and D. F. Stauffer. 1986. Factors confounding evaluation of bird-habitat relationships. Pages 209–216 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000, modeling habitat relationships of terrestrial vertebrates*. The University of Wisconsin Press, Madison, WI, USA.
- Birks, H. J. B. 1996. Statistical approaches to interpreting diversity patterns in the Norwegian mountain flora. *Ecography* **19**:332-340.
- Bock, C. and J. Bock. 1984. Responses of birds, rodents, and vegetation to livestock enclosure in a semi desert grassland site. *Journal of Range Management* **37**:239–242.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**:1045-1055.
- Bosch, J., L. Boyero, and I. Martinez-Solano. 2004. Spatial scales for the management of amphibian populations. *Biodiversity and Conservation* **13**:409-420.
- Boyero, L. 2003. Multiscale patterns of spatial variation in stream macroinvertebrate communities. *Ecological Research* **18**:365-379.
- Callaway, R. M. 1995. Positive interactions among plants. *The Botanical Review* **61**:306– 349.
- Callaway, R. M. and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology* **78**:1958-1965.
- Campbell, J. B. 1996. *Introduction to remote sensing*. Taylor & Francis, London.

- Carpenter, S. R. and J. F. Kitchell. 1987. The Temporal Scale of Variance in Limnetic Primary Production. *American Naturalist* **129**:417-433.
- Casado, M. A., I. Castro, L. Ramirez-Sanz, M. Costa-Tenorio, J. M. de Miguel, and F. D. Pineda. 2004. Herbaceous plant richness and vegetation cover in Mediterranean grasslands and shrublands. *Plant Ecology* **170**:83-91.
- Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* **277**:500-504.
- Charley, J. L., and West, N.E. 1975. Plant-induced soil chemical patterns in some shrub dominated semi-desert ecosystems of Utah. *Journal of Ecology* **63**:945-963.
- Chase, J. M. and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* **416**:427-430.
- Chen, J. Q., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology - Variations in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience* **49**:288-297.
- Clark, D. B., M. W. Palmer, and D. A. Clark. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* **80**:2662-2675.
- Clough, Y., A. Kruess, D. Kleijn, and T. Tschamntke. 2005. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *Journal of Biogeography* **32**:2007-2014.

- Coreau, A. and J. L. Martin. 2007. Multi-scale study of bird species distribution and of their response to vegetation change: a Mediterranean example. *Landscape Ecology* **22**:747-764.
- Crawley, M. J. 1993. *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Crawley, M. J. and J. E. Hurrell. 2001. Scale dependence in plant biodiversity. *Science* **291**:864-868.
- Cushman, S. A. and K. McGarigal. 2004. Patterns in the species-environment relationship depend on both scale and choice of response variables. *Oikos* **105**:117-124.
- Daily, N. 1997. *Culture's Service: Societal Dependence on Natural Systems*. Island Press, Washington DC.
- Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* **86**:1602-1610.
- Davies, S. J., Palmiotto, P.A., Ashton, P.A., Lee, H.S., and Lafrankie, J.V. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* **86**:662-673.
- de Mera, A. G., M. A. Hagen, and J. A. V. Orellana. 1999. Aerophyte, a new life form in Raunkiaer's classification? *Journal of Vegetation Science* **10**:65-68.
- Delcourt, H. R., Delcourt, P.A. and Webb, T. 1983. Dynamic plant ecology: the spectrum of vegetation change in space and time. *Quat. Sci. Rev.* **1**:153-175.

- Dennis, P., M. R. Young, and I. J. Gordon. 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology* **23**:253-264.
- Di Castri, F. 1983. Mediterranean-type shrublands. *Plant Ecology* **53**:96-96.
- Donovan, T. M., K. E. Freemark, B. A. Maurer, L. Petit, S. K. Robinson, and V. A. Saab. 2000. Setting local and regional objectives for the persistence of bird populations. Pages 53-59 *in* R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, editors. Strategies for bird conservation: the Partners in Flight planning process. Proceedings RMRS-P-16. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.
- Du, C., R. Linker, and A. Shaviv. 2008. Identification of agricultural Mediterranean soils using mid-infrared photoacoustic spectroscopy. *Geoderma* **143**:85-90.
- Du, C. W., R. Linker, and A. Shaviv. 2007. Characterization of soils using photoacoustic mid-infrared spectroscopy. *Applied Spectroscopy* **61**:1063-1067.
- Du, C. W., J. M. Zhou, H. Y. Wang, X. Q. Chen, A. N. Zhu, and J. B. Zhang. 2009. Determination of soil properties using Fourier transform mid-infrared photoacoustic spectroscopy. *Vibrational Spectroscopy* **49**:32-37.
- Dufour, A., F. Gadallah, H. H. Wagner, A. Guisan, and A. Buttler. 2006. Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. *Ecography* **29**:573-584.
- Ehrlich, P. R. a. E. O. W. 1991. Biodiversity studies: science and policy. *Science* **253**:758-762.



- Fernandez, C., B. Lelong, B. Vila, J. P. Mevy, C. Robles, S. Greff, S. Dupouyet, and A. Bousquet-Melou. 2006. Potential allelopathic effect of *Pinus halepensis* in the secondary succession: an experimental approach. *Chemoecology* **16**:97-105.
- Franklin, J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science* **9**:733-748.
- Gabay, O. 2008. Woody plants as landscape modulators in Mediterranean woodland. Ben-Gurion University of the Negev.
- Garcia, L. V., T. Maranon, A. Moreno, and L. Clemente. 1993. Aboveground biomass and species richness in a Mediterranean salt-marsh. *Journal of Vegetation Science* **4**:417-424.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* **405**:220-227.
- Gaston, K. J. and P. H. Williams. 1996. Spatial patterns in taxonomic diversity. Pages 202–229 in K. J. Gaston, editor. *Biodiversity: A Biology of Numbers and Difference*. Blackwell Science Ltd., Oxford.
- Giller, P. S. and J. H. Gee. 1987. The analysis of community organization: the influence of equilibrium, scale and terminology. Pages 519-542 in J. Gee and P. Giller, editors. *Organization of communities. Past and present*. 27th Symp. of the British Ecological Society. Blackwell.
- Gillet, F., B. Murisier, A. Buttler, J. D. Gallandat, and J. M. Gobat. 1999. Influence of tree cover on the diversity of herbaceous communities in subalpine wooded pastures. *Applied Vegetation Science* **2**:47–54.

- González-Megías, A., J. M. Gómez, and F. Sánchez-Piñero. 2007. Diversity-habitat heterogeneity relationship at different spatial and temporal scales. *Ecography* **30**:31-41.
- Goodall, C. 1990. A survey of smoothing techniques. Sage Publications, Newbury Park, CA.
- Grand, J. and S. A. Cushman. 2003. A multi-scale analysis of species-environment relationships: breeding birds in a pitch pine-scrub oak (*Pinus rigida*-*Quercus ilicifolia*) community. *Biological Conservation* **112**:307-317.
- Gratani, L. and A. Bombelli. 2000. Correlation between leaf age and other leaf traits in three Mediterranean maquis shrub species: *Quercus ilex*, *Phillyrea latifolia* and *Cistus incanus*. *Environmental and Experimental Botany* **43**:141-153.
- Gratwicke, B. and M. R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* **66**:650-667.
- Greenacre, M. J. 1984. Theory and applications of correspondence analysis. Academic Press, London.
- Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, London.
- Gross, K. L., M. R. Willig, L. Gough, R. Inouye, and S. B. Cox. 2000. Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos* **89**:417-427.
- Grytnes, J. A. 2000. Fine-scale vascular plant species richness in different Alpine vegetation types: relationships with biomass and cover. *Journal of Vegetation Science* **11**:87-92.

- Gustafson, E. J. 1998. Quantifying landscape spatial pattern: What is the state of the art? *Ecosystems* **1**:143-156.
- Hadar, L., I. Noy-Meir, and A. Perevolotsky. 1999. The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. *Journal of Vegetation Science* **10**:673-682.
- Halaj, J., D. W. Ross, and A. R. Moldenke. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos* **90**:139-152.
- Hamer, K. C. and J. K. Hill. 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology* **14**:1435-1440.
- Harris, L. D. 1988. Edge effects and conservation of biotic diversity. *Conservation Biology* **2**:330-339.
- Hastie, T. J. and R. J. Tibshirani. 1990. *Generalized Additive Models*. Chapman and Hall, London, UK.
- Haworth, K. and G. R. Mcpherson. 1995. Effects of *Quercus-emoryi* trees on precipitation distribution and microclimate in a semiarid savanna. *Journal of Arid Environments* **31**:153-170.
- He, f., P. Legendre, C. Bellehumeur, and J. V. LaFrankie. 1994. Diversity pattern and spatial scale: a study of a tropical rain forest of Malaysia. *Environmental and Ecological Statistics* **1**:265-286.
- He, F. L. and K. J. Gaston. 2000. Occupancy-abundance relationships and sampling scales. *Ecography* **23**:503-511.

- Henkin, Z., L. Hadar, and I. Noy-Meir. 2007. Human-scale structural heterogeneity induced by grazing in a Mediterranean woodland landscape. *Landscape Ecology* **22**:577-587.
- Herranz, J. M., P. Ferrandis, M. A. Copete, E. M. Duro, and A. Zalacain. 2006. Effect of allelopathic compounds produced by *Cistus ladanifer* on germination of 20 Mediterranean taxa. *Plant Ecology* **184**:259-272.
- Hobson, K. A., D. A. Kirk, and A. R. Smith. 2000. A multivariate analysis of breeding bird species of western and central Canadian boreal forests: Stand and spatial effects. *Ecoscience* **7**:267-280.
- Holzapfel, C., K. Tielborger, H. A. Parag, J. Kigel, and M. Sternberg. 2006. Annual plant-shrub interactions along an aridity gradient. *Basic and Applied Ecology* **7**:268-279.
- Hooper, D. U. and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302-1305.
- House, J. I., S. Archer, D. D. Breshears, and R. J. Scholes. 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography* **30**:1763-1777.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* **86**:393-401.
- Huston, M. A. and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. *American Naturalist* **144**:954-977.
- Hutchings, M. J., E. A. John, and D. K. Wijesinghe. 2003. Toward understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* **84**:2322-2334.

- Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. **22**:415-427.
- Johnson, K. H., K. A. Vogt, H. J. Clark, O. J. Schmitz, and D. J. Vogt. 1996. Biodiversity and the productivity and stability of ecosystems. Trends in Ecology & Evolution **11**:372-377.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373-386.
- Jones, C. G., Lawton, J. H., and Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946-1957.
- Kaplan, Y. 1989. The soils of Ramat Hanadiv (in Hebrew). Society of Nature Protection, Tel Aviv, Israel.
- Karlson, R. H. and H. V. Cornell. 1998. Scale-dependent variation in local vs. regional effects on coral species richness. Ecological Monographs **68**:259-274.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. Ecology **83**:530-544.
- Ko, L. J. and P. B. Reich. 1993. Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. American Midland Naturalist **130**:31-42.
- Kotliar, N. B. and J. A. Wiens. 1990. Multiple Scales of Patchiness and Patch Structure - a Hierarchical Framework for the Study of Heterogeneity. Oikos **59**:253-260.
- Kroodsma, R. L. 1984. Ecological factors associated with degree of edge effect in breeding birds. Journal of Wildlife Management **48**:418-425.

- Kumar, S., T. J. Stohlgren, and G. W. Chong. 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* **87**:3186-3199.
- Lande, R. 1982. A quantitative genetic theory of life-history evolution. *Ecology* **63**:607-615.
- Lavorel, S., S. Diaz, J. H. C. Cornelissen, E. Garnier, S. P. Harrison, S. McIntyre, J. G. Pausas, N. Perez-Harguindeguy, C. Roumet, and C. Urcelay. 2007. Plant functional types: are we getting any closer to the holy grail? Pages 171-186 in J. G. Canadell, D. E. Pataki, and L. F. Pitelka, editors. *Terrestrial Ecosystems in a Changing World*. Springer Berlin Heidelberg.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* **84**:177-192.
- Le Honerou, H. N. 1981. Impact of man and his animals on Mediterranean vegetation. Pages 479–521 in F. Di Castri, D. W. Goodall, and R. L. Specht, editors. *Ecosystems of the World, II, Mediterranean Shrublands*. Elsevier Scientific, Amsterdam.
- Legendre, P. 1993. Spatial autocorrelation - trouble or new paradigm. *Ecology* **74**:1659-1673.
- Legendre, P., Legendre, L. 1998. *Numerical ecology*. 2nd English edition edition. Elsevier Science, Amsterdam, The Netherlands.
- Lehmann, A., J. M. Overton, and J. R. Leathwick. 2002. GRASP: generalized regression analysis and spatial prediction. *Ecological Modelling* **157**:189-207.
- Lep , J. and P. milauer. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge Univ Pr.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**:1943-1967.

- Li, H. B. and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* **75**:2446-2455.
- Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* **72**:445-463.
- Linker, R., I. Shmulevich, A. Kenny, and A. Shaviv. . 2005a. Soil identification and chemometrics for direct determination of nitrate in soils using FTIR-ATR midinfrared spectroscopy. *Chemosphere*. **61**:652-658.
- Lord, J. M. and D. A. Norton. 1990. Scale and the spatial concept of fragmentation. *Conservation Biology* **4**:197-262.
- Lubchenco, J. 1991. The sustainable biosphere initiative - an ecological research agenda-a report from the Ecological-Society-of-America. *Ecology* **72**:371-412.
- Lynch, J. E. and D. E. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* **28**:287-324.
- Madrigal, J., J. A. Garcia-Rodriguez, R. Julian, A. Puerto, and B. Fernandez-Santos. 2008. Exploring the influence of shrubs on herbaceous communities in a Mediterranean climatic context of two spatial scales. *Plant Ecology* **195**:225-234.
- Magura, T., B. Tothmeresz, and T. Molnar. 2000. Spatial distribution of carabids along grass-forest transects. *Acta Zoologica Academiae Scientiarum Hungaricae* **46**:1-17.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps, University of Massachusetts, Amherst.

- McGarigal, K., S. A. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife ecology research. Springer, New York.
- McGarigal, K., Marks, B.J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA For. Serv- Gen. Tech. Rep. PNW-GTR-351,, Portland.
- Meyer, J. S., L. L. Irwin, and M. S. Boyce. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. Wildlife Monographs:5-51.
- Milne, B. T. 1991. Heterogeneity as a multiscale characteristic of landscape. Pages 69–84 *in* J. Kolasa and S. T. A. Pickett, editors. Ecological heterogeneity. Springer-Verlag, New York, New York, USA.
- Moore, D. R. J. and P. A. Keddy. 1989. The relationship between species richness and standing crop in wetlands - the importance of scale. *Vegetatio* **79**:99-106.
- Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. Wiley, New York.
- Naveh, Z. 1975. The evolutionary significance of fire in the Mediterranean region. *Vegetatio* **29**:199-208.
- Naveh, Z. and J. Dan. 1973. The human degradation of Mediterranean landscapes in Israel. Pages 370– 390. *in* F. di Castri and H. A. Mooney, editors. Mediterranean Type Ecosystems, Origin and Structurer. Springer-Verlag, New York.
- Naveh, Z. and P. Kutiel. 1986. Changes in the Mediterranean vegetation of Israel in response to human habitation and land use. Pages 259-296 *in* G. M. Woodwell,



- editor. *The Earth in Transition, Patterns and Processes of Biotic Impoverishment*. Cambridge University Press, Cambridge.
- Neter, J., M. , H. Kutner, C. J. Nachtsheim, and W. W. 1996. *Applied linear statistical models: regression, analysis of variance, and experimental designs.*, Chicago, Illinois, USA.
- Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. *Nature* **244**:310-310.
- Noble, I. R. and H. Gitay. 1996. A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science* **7**:329-336.
- Noss, R. F. 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth hammock. *Natural Areas. Natural Areas Journal* **11**:34-47.
- Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* **77**:290–310.
- O'Neill, R. V., L. DeAngelis, B. Waite, and T. A. Hillebrand. 1986. *A hierarchical concept of ecosystems.*, Princeton Univ. Press, Princeton, NJ.
- Okland, R. H., H. Bratli, W. E. Dramstad, A. Edvardsen, G. Engan, W. Fjellstad, E. Heegaard, O. Pedersen, and H. Solstad. 2006. Scale-dependent importance of environment, land use and landscape structure for species richness and composition of SE Norwegian modern agricultural landscapes. *Landscape Ecology* **21**:969-987.
- Oliveira Filho, A. T., E. A. Vilela, D. A. Carvalho, and M. L. Gavilanes,. 1994. Effects of soils and topography on the distribution of tree species in a tropical riverine forest in South-Eastern Brazil. *Journal of Tropical Ecology* **10**:483-508.

- Padien, D. J. and K. Lajtha. 1992. Plant spatial pattern and nutrient distribution in Pinyon-Juniper woodlands along an elevational gradient in northern New-Mexico. *International Journal of Plant Sciences* **153**:425-433.
- Palmer, M. W. 1992. The coexistence of species in fractal landscapes. *American Naturalist* **139**:375-397.
- Parker, V. T. and C. H. Muller. 1982. Vegetational and environmental-changes beneath isolated live Oak trees (*Quercus-agrifolia*) in a California annual grassland. *American Midland Naturalist* **107**:69-81.
- Parviainen, M., M. Luoto, T. Rytteri, and R. K. Heikkinen. 2008. Modelling the occurrence of threatened plant species in taiga landscapes: methodological and ecological perspectives. *Journal of Biogeography* **35**:1888-1905.
- Pausas, J. G. 1999. Mediterranean vegetation dynamics: modelling problems and functional types. *Plant Ecology* **140**:27-39.
- Pausas, J. G. and M. P. Austin. 2001. Patterns of plant species richness in relation to different environments: An appraisal. *Journal of Vegetation Science* **12**:153-166.
- Pearson, S. M., M. G. Turner, L. L. Wallace, and W. H. Romme. 1995. Winter habitat use by large ungulates following fire in northern Yellowstone-National-Park. *Ecological Applications* **5**:744-755.
- Perevolotsky, A. 2005. Integrating landscape ecology in the conservation of Mediterranean ecosystems: The Israeli experience. *Israel Journal of Plant Sciences* **53**:203-213.

- Perevolotsky, A., Ettinger, E., Schwartz-Tzachor, R., Yonatan, R. 2002. Management of fuel breaks in the Israeli Mediterranean Ecosystem: the case of Ramat Hanadiv Park. *Journal of Mediterranean Ecology* **3**:13-22.
- Poiani, K. A., Richter, B. D., Anderson, M. G. AND Richter, H. E. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *BioScience* **50**:133-146.
- Pugnaire, F. I. and M. T. Luque. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* **93**:42-49.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**:224-239.
- Rahbek, C. and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences of the United States of America* **98**:4534-4539.
- Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67–92 *in* R. L. Burgess and D. M. Sharpe, editors. *Forest Island Dynamics in Man-dominated Landscapes*, Springer-Verlag, New York.
- Reese, K. P. and J. T. Ratti. 1988. Edge effects: a concept under scrutiny. *Transactions of the North American Wildlife and Natural Resource Conference* **53**:127-136.
- Ricklefs, R. E., and Schluter, D. 1993. Species diversity: regional and historical influences. Pages 350–363 *in* R. E. Ricklefs, and Schluter, D., editor. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press.

- Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press.
- Ruggiero, A. and T. Kitzberger. 2004. Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. *Ecography* **27**:401-416.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: A hierarchical analysis. *Ecological Applications* **9**:135-151.
- Sarr, D. A. and D. E. Hibbs. 2007. Multiscale controls on woody plant diversity in western Oregon riparian forests. *Ecological Monographs* **77**:179-201.
- Scheiner, S. M., S. B. Cox, M. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari. 2000. Species richness, species-area curves and Simpson's paradox. *Evolutionary Ecology Research* **2**:791-802.
- Schlapfer, F. and B. Schmid. 1999. Ecosystem effects of biodiversity: A classification of hypotheses and exploration of empirical results. *Ecological Applications* **9**:893-912.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. E. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**:364-374.
- Scholes, R. J., and S.R. Archer,. 1997. Tree-grass interaction in savannas. *Annual Review of Ecology and Systematics* **28**:517-544.
- Schulze, E. D. and H. A. Mooney. 1993. Biodiversity and ecosystem function. Springer-Verlag, New York, NY.

- Schwartz, M. W., C. A. Bringham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**:297-305.
- Shachak, M., B. Boeken, E. Groner, R. Kadmon, Y. Lubin, E. Meron, G. Ne'eman, A. Perevolotsky, Y. Shkedy, and E. D. Ungar. 2008. Woody species as landscape modulators and their effect on biodiversity patterns. *Bioscience* **58**:209-221.
- Shmida, A. and M. V. Wilson. 1985. Biological determinants of species-diversity. *Journal of Biogeography* **12**:1-20.
- Shoshany, M. 2000. Satellite remote sensing of natural Mediterranean vegetation: a review within an ecological context. *Progress in Physical Geography* **24**:153-178.
- Shriner, S. A., K. R. Wilson, and C. H. Flather. 2006. Reserve networks based on richness hotspots and representation vary with scale. *Ecological Applications* **16**:1660-1673.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? *Biological Conservation* **83**:247-257.
- Sokal, R. R. and N. L. Oden. 1978. Spatial autocorrelation in biology .2. Some biological implications and four applications of evolutionary and ecological Interest. *Biological Journal of the Linnean Society* **10**:229-249.
- Statzner, B. and B. Moss. 2004. Linking ecological function, biodiversity and habitat: a mini-review focusing on older ecological literature. *Basic and Applied Ecology* **5**:97-106.

- Steck, C. E., M. Burgi, J. Bolliger, F. Kienast, A. Lehmann, and Y. Gonseth. 2007.  
Conservation of grasshopper diversity in a changing environment. *Biological Conservation* **138**:360-370.
- Steele, J. H. 1978. Spatial pattern in plankton communities. Plenum Press, New York.
- Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tschardtke. 2002.  
Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**:1421-1432.
- Steiner, N. C. and W. Kohler. 2003. Effects of landscape patterns on species richness - A modelling approach. *Agriculture Ecosystems & Environment* **98**:353-361.
- Sternberg, M., and Shoshany, M. 2001. Aboveground biomass allocation and water content relationships in Mediterranean trees and shrubs in two climatological regions in Israel. *Plant Ecology* **157**:171-179.
- Stohlgren, T. J., R. R. Bachand, Y. Onami, and D. Binkley. 1998. Species-environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. *Plant Ecology* **135**:215-228.
- Stohlgren, T. J., D. Barnett, C. Flather, J. Kartesz, and B. Peterjohn. 2005. Plant species invasions along the latitudinal gradient in the United States. *Ecology* **86**:2298-2309.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25-46.

- Stohlgren, T. J., A. J. Owen, and M. Lee. 2000. Monitoring shifts in plant diversity in response to climate change: a method for landscapes. *Biodiversity and Conservation* **9**:65-86.
- Ter Braak, C. J. F. and N. J. M. Gremmen. 1987. Ecological amplitudes of plant species and the internal consistency of Ellenberg's indicator values for moisture. *Plant Ecology* **69**:79-87.
- ter Braak, C. J. F. and I. C. Prentice. 1986. Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**:1167-1179.
- ter Braak, C. J. F. and I. C. Prentice. 1988a. A theory of gradient analysis. *Advances in Ecological Research* **18**:271-313.
- ter Braak, C. J. F. and I. C. Prentice. 1988b. A theory of gradient analysis. *Advances in ecological research* **18**:271-313.
- ter Braak, C. J. F. and P. Smilauer. 1999. CANOCO reference manual and user's guide to CANOCO for windows: software for canonical community ordination. Microcomputer Power, Ithaca, New York.
- ter Braak, C. J. F. and P. Smilauer. 2002. CANOCO reference manual and user's guide to CANOCO for windows: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York.
- Thompson, F. R. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United-States. *Conservation Biology* **7**:325-333.

- Tielborger, K. and R. Kadmon. 1997. Relationships between shrubs and annual communities in a sandy desert ecosystem: A three-year study. *Plant Ecology* **130**:191-201.
- Tilman, D. and P. Kareiva. 1997. *Spatial ecology. The role of space in population dynamics and interspecific interactions*, Princeton Univ. Press.
- Wagner, H. H. and P. J. Edwards. 2001. Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. *Landscape Ecology* **16**:121-131.
- Wagner, H. H., O. Wildi, and K. C. Ewald. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology* **15**:219-227.
- Waldhardt, R., D. Simmering, and A. Otte. 2004. Estimation and prediction of plant species richness in a mosaic landscape. *Landscape Ecology* **19**:211-226.
- Walker, B. H. 1992. Biological diversity and ecological redundancy. *Conservation Biology* **6**:18-23.
- Weltzin, J. F. and M. B. Coughenour. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *Journal of Vegetation Science* **1**:325-334.
- Wezel, A., Rajot, J.L., and Herbrig, C. 2000. Influence of shrubs on soil characteristics and their function in Sahelian agro-ecosystems in semi-arid Niger. *Journal of Arid Environments* **44**:383-398.
- Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* **28**:453-470.



- Wiens, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* **7**:81-120.
- Wiens, J. A. 1989. Spatial Scaling in Ecology. *Functional Ecology* **3**:385-397.
- Willis, K. J. and R. J. Whittaker. 2002. Species diversity - Scale matters. *Science* **295**:1245-1248.
- Wilson, E. O. 1992. *The Diversity of Life*. Harvard University Press, Boston.
- Wright, D. H., D. J. Currie, and B. A. Maurer. 1993. Energy supply and patterns of species richness on local and regional scales. Pages 66–76 *in* R. E. Ricklefs and D. Schluter, editors. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University Chicago Press, Chicago, USA.
- Wright, J. P., C. G. Jones, B. Boeken, and M. Shachak. 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology* **94**:815-824.
- Zobel, k., M. Zobel, and E. Rosen. 1994. An experimental test of diversity maintenance mechanisms by a species removal experiment in a species-rich wooded meadow. *Folia Geobotanica* **29**:449-457.
- Zobel, M. 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends in Ecology & Evolution* **12**:266-269.

הגורמים הקובעים את פיזור המינים בסקאלות מרחביות שונות

ליאור בלנק

הגורמים הקובעים את פיזור המינים בסקאלות מרחביות שונות

לצורך מילוי חלקי של הדרישות לקבלת התואר דוקטור לפילוסופיה

ליאור בלנק

הוגש לסנט הטכניון - מכון טכנולוגי לישראל

אלול תשס"ט      חיפה      ספטמבר 2009

המחקר נעשה בהנחיית פרופסור יוחאי כרמל בפקולטה להנדסה אזרחית וסביבתית

אני מודה לטכניון על התמיכה הכספית הנדיבה

ברצוני להביע את תודתי לפרופ"ח יוחאי כרמל על הנחייתו המקצועית

ברצוני להודות לחברי המעבדה על עזרתם ותמיכתם

תודה לצוות רמת הנדיב על עזרתם בעבודת השדה

תודה מיוחדת לאשתי, יעל, על סבלנותה ותמיכתה לאורך הדרך

## תקציר

סוגיית מגוון המינים זוכה לתשומת לב רבה בשנים האחרונות כתוצאה משיעור הכחדה חסר תקדים. מחקרים מראים שמגוון ביולוגי חיוני לשימור שירותים אקולוגיים שונים כגון: שירותי אספקה (לדוגמה: מים, מזון), שירותי ויסות (שיטפונות, מחלות) (שירותי תרבות) (השראה, נופש ופנאי) (שירותי תמיכה) (יצירת קרקעות, מחזור יסודות). אספקת השירותים האקולוגיים מקורה במערכת מורכבת דינאמית בה מתקיימים יחסי גומלין בין מינים, משאבים ונוף. הבנת התהליכים והגורמים המשפיעים על תפוצת מינים במרחב היא אחד האתגרים המרכזיים במחקר אקולוגי. המחקר הנוגע לפיזור מינים במרחב התמקד בעיקר בהשפעות של גורמים סביבתיים כדוגמת אקלים, טופוגרפיה וקרקע אך התעלם מההשפעות של מינים ביולוגיים מסוימים על סביבתם. התנאים הנוצרים על ידי מינים אלו משפיעים על התפוצה של מינים אחרים. כל האורגניזמים משפיעים על סביבתם במידה זו או אחרת. אך מינים מסוימים משפיעים על המערכת בה הם פועלים במידה משמעותית בהרבה מזו שניתנת לניבוי רק בהסתמך על ממדי האורגניזם או תכונות פיזיות אחרות שלו. בהקשר זה, צומח מעוצה יכול להיחשב כגורם דומיננטי המשפיע בצורה ניכרת על סביבתו. צומח מעוצה משנה את זמינות המשאבים למינים אחרים ע"י שינוי של התנאים הביולוגיים והאביוטיים במערכת. ההשפעות של צומח מעוצה על מינים עשבוניים יכולות ידי להתבטא במיתון השפעות קיצוניות של תנאי הסביבה, שינוי הרכב המינרלים בקרקע, הצטברות נשר עלים, הצללה, העלאת הלחות וכדומה. שינויים אלו יוצרים סביבה שונה לעומת האזורים שאינם מכוסים בצומח מעוצה.

בישראל רוב המערכות האקולוגיות היבשתיות הן מערכות משולבות של צמחים מעוצים ועשבוניים. לכן, על מנת ללמוד על התנהגותם של מערכות מורכבות אלה, המגוון הביולוגי שלהם, השירותים האקולוגיים הניתנים על ידם והדרכים לניהול בר-קיימא של שטחים פתוחים שלהן, יש לברר תחילה את החוקיות ביחסי הגומלין בין צמחים מעוצים לעשבוניים. יש לחקור את יחסי מעוצים-עשבוניים בהקשר של המבנה הנופי שהם יוצרים, והגורמים הקובעים את מגוון המינים המשתתפים בפעילות המערכת.

לפי המודל שאנו מציעים תנאים תהליכים סביבתיים אזוריים) כדוגמת משקעים, קרקע וטופוגרפיה) משפיעים על התפוצה המרחבית והמבנה הנופי של צומח מעוצה. בשלב הבא צומח מעוצה משפיע על תהליכים בסקלה האזורית) כדוגמת משטר רוחות, נדידה והפצה לטווח רחוק) ועל תנאים בסקלה המקומית) כדוגמת חדירות אור, קרינה, הצטברות נשר עלים). השילוב של התהליכים והתנאים הללו מהווה גורם מרכזי שמשפיע על תפוצת המינים במרחב.

תפוצת מינים נחקרה באופן מסורתי בסקלה בודדת, כלומר שימוש ביחידת דיגום בגודל אחד. לאחרונה גברה ההכרה שתאור מערכת אקולוגית תלוי בסקלה המרחבית בו היא נבחנת. הבנה זו נובעת מההכרה שתהליכים אקולוגיים פועלים בסקלות שונות. לכן, מחקרים בהם נעשה שימוש בסקלת דיגום בודדת עשויים להראות רק חלק מהתמונה המורכבת ולתאר רק חלק מהקשר בין המינים לגורמים המשפיעים על סביבתם ואשר פועלים בסקלות גדולות או קטנות יותר. לכן מחקר בסקלות מרובות הינו חשוב בכדי לתאר תמונה שלמה ומורכבת יותר של המערכת האקולוגית ובכך לתרום לשימור המגוון הביולוגי. המטרה הכללית עבודה זו היא לחקור את השפעתם של גורמים סביבתיים שונים על תפוצת מינים עשבוניים בסקלות מרחביות שונות תוך התמקדות בהשפעתו של הצומח המעוצה. לשם כך תכננתי סכמת דיגום היררכית מקוננת. בעזרת סכמת דיגום זו דגמתי צומח עשבוני באביב 2007 בפארק טבע רמת הנדיב. ניתוח הנתונים שנאספו נועד להעריך את הקשר בין עושר והרכב מינים עשבוניים למשתנים סביבתיים שונים) קרקע, טופוגרפיה ודגם מרחבי של הצומח המעוצה).

לשם אפיון הקרקע ערכתי דיגום קרקע של כל אזור המחקר. שני מאפייני קרקע נמדדו - ריכוזי קלציום קרבונט וחומר אורגני. לשם כך השתמשנו בשיטה חדשה בה נמדד ספקטרום פוטו אקוסטי של כל דגימה בתחום האינפרא אדום. ספקטרום זה שימש לכימות הערכים של ריכוז קלציום קרבונט וחומר אורגני בכל דגימה. הדפוס המרחבי של הצומח המעוצה כומת באמצעות יצירת מפה בינארית של כיסוי צומח מעוצה ושטחים פתוחים הכוללים קרקע חשופה, סלעים ואזורים המכוסים בצומח עשבוני. מפה זו יוצרה באמצעות תצלום אוויר של אזור המחקר שעבר תהליך ממוחשב של סיווג לאזורים מעוצים ופתוחים. מפה זו מאפשרת תצוגה דו-מימדית של הדפוס המרחבי של הצומח המעוצה וכימות של משתנים כמו אחוז הכיסוי של הצומח

המעוצה ומספר הכתמים המעוצים במרחב. היות ומימד הגובה של הצומח המעוצה יכול להיות בעל השפעה כימתית את גובה הצמרות של הצומח המעוצה באמצעי חישה מרחוק בשם (Light Detecting and Ranging) LiDAR שהוא מערכת לייזר מוטסת הסורקת שטחים נרחבים ומאפשרת מדידה של גובה התכסית ברזולוציה גבוהה.

המטרות הספציפיות של העבודה הן: 1) הערכת חשיבותו של מין הצומח המעוצה בקביעת תפוצת מינים עשבוניים בסקלה מקומית. 2) בדיקת חשיבותם של משתני סביבה שונים על תפוצת מינים עשבוניים בסקלות שונות. 3) בחינת הקשר שבין המבנה המרחבי וההטרוגניות של הצומח המעוצה ובין עושר מינים עשבוניים בסקלות מרחביות שונות.

בחלק הראשון של העבודה, בחנתי את ההבדלים בעושר והרכב מינים עשבוניים בין שישה כתמים שונים של מינים מעוצים ובנוסף בכתמים פתוחים שאינם מכוסים בצומח מעוצה. רוב המחקרים שבחנו את השפעתו של הצומח המעוצה על עושר והרכב מינים תארו מערכת אקולוגית המורכבת משני מרכיבים: כתמים של צומח מעוצה וכתמים של שטחים פתוחים. התוצאות של עבודה זו מעידות על כך שתאור כזה של מערכת אקולוגית הוא פשטני. עושר המינים שונה באופן מובהק בין הכתמים המעוצים והממצאים מראים שתפוצתם של רוב המינים העשבוניים שנבדקו אינו אקראי בין המינים השונים של המעוצים. למעשה מהתוצאות עולה כי רוב המינים העשבוניים שנבדקו העדיפו לגדול מתחת לכתם או כתמים מעוצים ממין מסוים. כמו כן נמצא שהרכב המינים העשבוניים שונה בין המינים השונים של צומח מעוצה. למעשה, באקוסיסטמה הטרוגנית כמו האקוסיסטמה הים-תיכונית התייחסות למין הכתם המעוצה יכולה להעשיר את הבנתנו לגבי המבנה של החברה העשבונית.

בחלק השני של העבודה בחנתי את השפעתם של גורמי קרקע (ריכוז קלציום קרבונט וחומר אורגני), טופוגרפיה (מפנה ושיפוע) וצומח מעוצה (אחוז כיסוי, מספר כתמים וגובה צומח מעוצה) על תפוצת מינים עשבוניים בסקלות מרחביות שונות. מהתוצאות עולה שקרקע היא הגורם הסביבתי החשוב ביותר המשפיע על תפוצת מינים במרחב. לעומת זאת נמצא במחקר שהשפעת הטופוגרפיה על תפוצת מינים הינה נמוכה. תוצאה

זו נובעת ככל הנראה מהעובדה שאזור המחקר הוא רמה מישורית ששינויי הגובה בה אינם גדולים ולכן טופוגרפיה אינה צפויה להשפיע במידה רבה על המינים באזור זה. עוד נמצא שצומח מעוצה הוא גורם חשוב המשפיע של תפוצה של מינים בסקלות שונות ושהשפעה זו היא תלוית סקלה. כלומר נמצא שבסקלה מקומית השפעת הצומח המעוצה על עושר והרכב מינים עשבוניים גדולה יותר מאשר בסקלה גדולה יותר. בנוסף, מחקר זה מראה שהקשר בין תפוצת מינים לבין המשתנים הסביבתיים משתנה בהתאם לקבוצת המינים הנבדקת. לדוגמא, עושר מינים של גיאופיטים הושפע יותר ממשתני קרקע בעוד עושר מינים של עשבוניים חד שנתיים הושפע יותר ממשתנים של צומח מעוצה.

בחלק השלישי של העבודה נבדק הקשר בין השינוי בכיסוי המעוצה ומידת ההטרוגניות של הנוף לבין עושר מינים. מחקרים שונים מצאו קשרים שונים בין משתנים אלו. תוצאות חלק זה מעידות כי הקשר בין כיסוי מעוצה והטרוגניות לבין עושר מינים הוא תלוי סקלה. בנוסף נמצא שהקשר הזה תלוי בקבוצת המינים הנבדקת. בכך מסבירות תוצאות אלו חלק מאי ההתאמות בין התוצאות של מחקרים קודמים. בחלק זה של העבודה אני מתאר מנגנון שעשוי להסביר את ההבדלים בקשרים המתקבלים בסקלות השונות. מנגנון זה מתבסס על העדפותיהם של מינים עשבוניים שונים לאזור מרכז הכתם המעוצה לעומת מינים עשבוניים שמעדיפים את האזור החיצוני של הכתם המעוצה. במחקרים שונים נמצא שאזורים אלו שונים בתנאים האביוטיים המתקיימים בהם כגון קרינה, לחות וטמפרטורה. המנגנון מתבסס על הממצא, שבסקלות גדולות החלק היחסי שתופס האזור החיצוני ביחס לאזור הפנימי של הכתם הולך וקטן.

לסיכום, מכלול התוצאות של עבודה זו ממחיש את חשיבותו של הצומח המעוצה כגורם משמעותי במערכת האקולוגית המשפיע באופן ניכר על תפוצת מינים עשבוניים במרחב. לתוצאות אלו חשיבות רבה לצורך שימור המגוון הביולוגי וניהול שטחים פתוחים. ניהול זה יכול להתאפשר היות ומחד אפיון הדפוס המרחבי של הצומח המעוצה אפשרי באמצעים של חישה מרחוק ומאידך שינוי הדפוס המרחבי של הצומח המעוצה אפשרי באמצעות רעית עיזים ובקר, כריתה ו/או שריפות מבוקרות. לבסוף, מחקר זה מצביע על כך כי ניהול מחקר בסקלה בודדת עלול להוביל לתוצאות שגויות בנוגע לקשר בין מינים וסביבתם ולפיכך עבודה זו מדגישה את הצורך לחקור מערכות אקולוגיות במגוון של סקלות מרחביות.



