



# Woody vegetation patch types affect herbaceous species richness and composition in a Mediterranean ecosystem

L. Blank<sup>1,2</sup> and Y. Carmel<sup>1</sup>

<sup>1</sup> Faculty of Civil and Environmental Engineering, Technion – Israel Institute of Technology, Haifa 32000, Israel

<sup>2</sup> Present address: Institute of Evolution and Department of Evolutionary and Environmental Biology, Faculty of Sciences, University of Haifa, Haifa 31905, Israel. Corresponding author; Fax: 972-4-822-8898; E-mail: liorblank@gmail.com

**Keywords:** Community structure, Randomization tests, Redundancy analysis, Vegetation mosaic, Weighted preference index.

**Abstract:** Ecology seeks to study the factors affecting the distribution of species. In terms of their effects on species richness and composition, woody plants can be considered as dominant factors which extensively affect their environment, changing the distribution of resources in space and time. In structurally rich and diverse plant communities, such as Mediterranean ecosystems, the specific species that form the woody patch can be important. The specific woody species patch type may impose a set of abiotic conditions, which in turn would result in specific traits of the given herbaceous community under that patch. Evidence revealed in this study suggests that the general notion of a two-patch type (woody and non-woody) system for describing ecosystems is simplistic, and may be misleading. We found that patterns of herbaceous species richness and composition are related to specific woody species patch type. We found that herbaceous species richness under each patch type coincided with respective differences in solar radiation reaching the sub-canopy. Accounting for specific patch characteristics may largely enhance our understanding of plant community structure.

**Abbreviations:** GLMM—Generalized Linear Mixed Model, PAR—Photosynthetic Active Radiation, PT—Patch Type, RDA—Redundancy Analysis.

**Nomenclature:** Feinbrun-Dothan et al. (1998).

## 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 et al. 1991). On a local scale (referring to small, relatively homogeneous patches of habitat), 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 on 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). 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 (Tielbörger and Kadmon 1997, Holzapfel et al. 2006, Madrigal-Gonzalez et al. 2010). 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 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. The influence of woody vegetation 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 and Archer 1997).

Ecosystems are often described as composed of two-patch types, woody and non-woody patches, implicitly as-

suming that herbaceous species would be equally distributed between the different woody patch types (hereafter PTs). 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 Houerou 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, Noy-Meir et al. 1989, 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 et al. 2002). We believe that in such heterogeneous ecosystems, a plausible approach would be to account for the specific nature of the patch, particularly its dominant woody species, which is a field almost untouched. Woody species obviously differ in their morphology (canopy size and density, and canopy height above ground) and phenology. Studies showed differences between woody species in soil preferences (Davies et al. 1998, Franklin 1998, Clark et al. 1999), leaf orientation (Gratani and Bombelli 2000), water content (Sternberg and Shoshany 2001), organic matter deposition (Charley and West 1975), nutrient mineralization of leaf litter (Charley and West 1975) and nutrient soil enrichment (Barth and Klemmedson 1978, Wezel et al. 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 under that patch. In this study we focus on the effect of woody cover morphology on light penetrating the sub-canopy. Understory light is determined by several overstory characteristics, particularly height and density of woody plants. For example, shrubs are different from trees as their canopy is adjacent to the ground. In addition, some PTs have denser canopy (in our study for example *Phillyrea latifolia*) while others have thinner canopy (for example *Calicotome villosa*). Sub-canopy solar radiation affects several environmental properties, such as leaf temperature, soil temperature and evaporation, and plant evapotranspiration (Martens et al. 2000). Some processes, such as seedling establishment, germination, facilitation, and growth, were shown to be affected by microclimate (Floyd 1983, Padien and Lajtha 1992, Martens et al. 1997). Thus, we hypothesize that the differences in herbaceous species richness between these PTs are to some extent the outcome of the specific physical properties of each PT.

Here, we employ a set of quantitative analyses in order to evaluate the role of specific woody species Patch Types 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), in an area of 4.5 km<sup>2</sup> surrounded by human settlements and agricultural fields (Fig. 1a). The area is a plateau with an elevation of 120 m a.s.l. The area receives approximately 600 mm rainfall annually. The vegetation is mostly eastern Mediterranean scrubland, consisting of structurally rich and diverse plant communities. It is highly heterogeneous at a broad range of spatial scales, starting from a grain size as small as a few meters. The fine-grained mosaic is characterized by woody patches of different heights and sizes, herbaceous clearings, exposed rocks and bare ground.

The area is dominated by dwarf shrubs (*Sarcopoterium spinosum*), low summer deciduous shrubs (*Calicotome villosa*), evergreen medium shrubs (*Pistacia lentiscus*) and tall evergreen shrubs (*Phillyrea latifolia*). The vegetation types are batha (dwarf shrubs of up to 0.5 m and herbs), garrigue (a higher stage of shrubs, 1-2 m high, and small trees), and scrub forest ('maquis', of medium-sized trees up to 12 m). 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), with 373 plant species recorded in the park area in a recent survey (Blank L., unpublished data).

### Field sampling

The data set we are using in this study is based on extensive survey of vascular plant species conducted in Ramat Hanadiv in the spring of 2007. The data were collected by a hierarchically nested sampling design using 4,374 quadrats of 20 cm × 20 cm (Fig. 1). This sampling design was balanced across scales. This means that when ascending from lower to upper units, the change in scale is continually incremental. Each sampling unit comprised three sub-units of the next lower level. For example, three sampling units of 20 cm × 20 cm were nested within one sampling unit of 1 m<sup>2</sup> and three sampling units of 1 m<sup>2</sup> were nested within one sampling unit of 10 m<sup>2</sup>. Overall, this sampling scheme was nested within two 1 km<sup>2</sup> squares (Fig. 1). The spatial structure of the sampling design was completely independent of the spatial structure of the woody patches. The minimal distance between sampling units in the lowest scale was 80 cm. The distance of the sampling units from the patch trunk varied and the number of units in a single patch ranged from one to three. The woody PTs were distributed all over the study area. We planned and used this scheme to explore various hypotheses at different scales. Thus, the number of sampling units for each woody PT is different (Table 1). Although a straightforward decision would be to use the same number of units for all PTs, we decided to use all the available data, since it included a large number of rare species and we did not want to lose this information, particularly since the ques-

tions we asked concerned affinity of herbaceous species to woody PTs.

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. 2,039 quadrats were mixed, meaning that they were located at the edge of the canopy, thus consisting of less than full woody vegetation cover or consisting more than one woody species. 2,335 of the quadrats were recorded in homogeneous patches (covered either by a single woody species or with no woody cover at all). Samples with woody species that were sampled in less than 100 quadrats were excluded. Thus, 2,188 of the quadrats were used in the analyses of the present study. The remaining six woody species corresponded to six distinct PTs. These woody species PTs were: *Phillyrea latifolia*, *Pinus* spp. (including *Pinus pinea*, *Pinus halepensis*, *Pinus brutia* and *Pinus canariensis*), *Pistacia lentiscus*, *Cupressus* spp. (including *Cupressus sempervirens* and *Cupressus arizonica*), *Calicotome villosa* and *Sarcopoterium spinosum*. The 7<sup>th</sup> PT was termed 'open' and included patches with no woody cover at all.

**Solar radiation measurements.** In order to quantify the differences in sub-canopy solar radiation between the six woody PTs we measured Photosynthetic Active Radiation (PAR) reaching the sub-canopy each hour from 7:20 am to 15:20 pm on a clear day, using an AccuPAR PAR/LAI Cep-

tometer, Model LP-80 (Decagon Devices). Each PT was represented by three individuals. Sampled shrub and tree individuals did not receive shading from adjacent woody vegetation. Each individual PT was measured at three sub-canopy locations. Each measurement inside the canopy was preceded by an above-canopy measurement. PAR reaching the sub-canopy was calculated as the difference between the PAR above-canopy and the averaged sub-canopy PAR. Changes in sub-canopy PAR were plotted along the day and the cumulative PAR (total PAR reaching the sub-canopy during the day) was calculated using the area under the curve for each PT.

### Data analysis

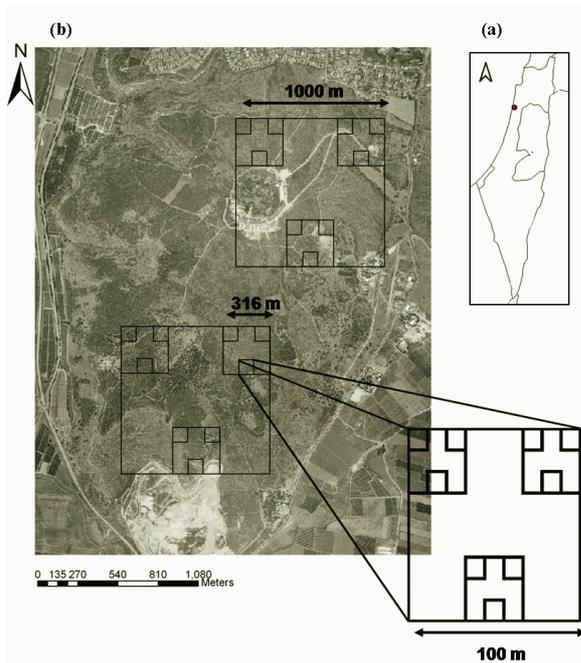
The variability in species richness between PTs was analyzed using generalized linear mixed models (GLMM). We used Poisson error distribution and sampling units location as random factor in the lme4 package implemented in R (Bates 2007). The use of GLMM allowed us to account for non-independent errors that could occur because of hierarchically nested designs by including location as random factors. Tukey's test for multiple comparisons was applied using the glht (general linear hypothesis testing) function in R (multcomp library).

**Weighted preference index (WPI).** Species' distributions in relation to woody species PTs were analyzed using the Weighted Preference Index (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

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

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. A WPI value was calculated for each herbaceous species. Next, we randomized the woody PT between sampling units and calculated WPI again for each herbaceous species separately. We repeated the randomization 500 times and compared the initial WPI value to the 500 values generated by the randomization. If the test statistic was greater than 95% of the random values, then we rejected the null hypothesis at  $p < 0.05$ . 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. Randomizations were performed using a code written in Visual Basic and implemented in Excel.

**Community ordination.** We used multivariate analyses to assess the relative importance of PTs in determining the observed species distributions. We used the program CANOCO version 4.5 (ter Braak and Smilauer 2002) to perform a Redundancy Analysis (RDA) on all the species that had oc-



**Figure 1.** 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  $10^6$  m<sup>2</sup> through  $10^2$  m<sup>2</sup>. The scales 10 m<sup>2</sup>, 1 m<sup>2</sup> and 0.04 m<sup>2</sup> are not shown.

**Table 1.** Mean ( $\pm$ SE) number of herbaceous species in seven PTs for three functional groups, perennials, geophytes and annuals. PTs with different letters are significantly different within each functional group (Tukey's HSD multiple comparison test). N- number of patches.

PT	N	Perennials	Geophytes	Annuals
<i>Phillyrea latifolia</i>	195	0.149 $\pm$ 0.05 a	0.492 $\pm$ 0.02 ab	0.4 $\pm$ 0.07 a
<i>Pinus</i> sp.	128	0.195 $\pm$ 0.04 ab	0.281 $\pm$ 0.03 b	0.563 $\pm$ 0.1 a
<i>Pistacia lentiscus</i>	491	0.314 $\pm$ 0.03 bc	0.625 $\pm$ 0.02 a	1.564 $\pm$ 0.1 b
<i>Sarcopoterium spinosum</i>	127	0.315 $\pm$ 0.05 abc	0.441 $\pm$ 0.04 ab	1.906 $\pm$ 0.2 b
<i>Cupressus</i> sp.	100	0.31 $\pm$ 0.05 abc	0.29 $\pm$ 0.05 b	3.3 $\pm$ 0.27 c
<i>Calicotome villosa</i>	158	0.475 $\pm$ 0.06 c	0.589 $\pm$ 0.05 a	3.766 $\pm$ 0.3 c
Open	989	0.254 $\pm$ 0.02 ab	0.396 $\pm$ 0.01 b	6.048 $\pm$ 0.13 d

**Table 2.** The relationship between herbaceous species richness and PTs using GLMM. The intercept refers to the *Phillyrea latifolia* PT.

	Estimate	SE	z Value	p Value
Intercept	-0.0078	0.086	-0.091	0.928
<i>Pinus</i> sp.	-0.03	0.14	-0.22	0.828
<i>Pistacia lentiscus</i>	0.79	0.093	8.47	<0.001
<i>Sarcopoterium spinosum</i>	0.78	0.11	6.92	<0.001
<i>Cupressus</i> sp.	1.29	0.12	10.44	<0.001
<i>Calicotome villosa</i>	1.35	0.1	13.26	<0.001
Open	1.71	0.088	19.37	<0.001

curred in at least five quadrats. RDA is a direct gradient analysis technique that relates species composition to measured environmental variables (ter Braak and Prentice 1988). We used the RDA canonical ordination, which is more suitable for the analysis of categorical factors than other ordination techniques (Lepš and Šmilauer 2003). We coded PTs as dummy (binary) variables. Monte Carlo permutation tests (n = 499 permutations) were used to evaluate the significance of species–environment relationships.

## Results

A total of 308 herbaceous species were recorded in 2188 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.

### Species richness

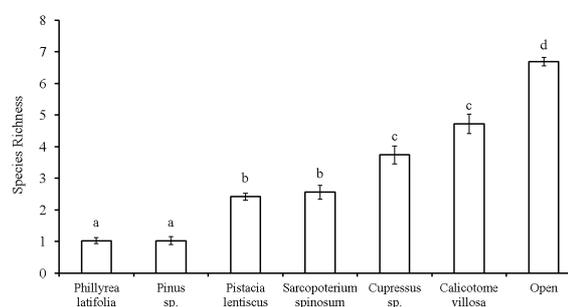
Open patches had significantly more species than woody patches (GLMM analysis,  $Z = -28.69$ ,  $P < 0.0001$ ). Open

patches had, on average, 6.69 species per quadrat, while woody patches had 2.54 species per quadrat.

Segregating the herbaceous species into the three functional groups, non-woody perennials, geophytes, and annuals, and analyzing their occurrence in woody and open PTs revealed that between 30% (for geophytes and annuals) and 41% (for perennials) of the species appeared exclusively either in woody or in open PTs. However, the distribution of these species between the two PTs for each of the functional groups was different. For geophytes, 21% preferred woody PT compared to only 9% which preferred open PT. An opposite trend was apparent for annuals: 6% preferred woody PT compared to 24% which preferred open PT. The same number of perennial species appeared in each of the two PTs: ~20% preferred woody PT and ~20% preferred open PT.

Species richness in the six woody PTs and in open patches is presented in Figure 2 and the results of the GLMM analysis are presented in Table 2. Using Tukey's multiple comparison tests among PTs, we found four groups of PTs (Figure 2): (a) open, (b) *Calicotome villosa* and *Cupressus* sp., (c) *Sarcopoterium spinosum* and *Pistacia lentiscus* and (d) *Pinus* sp. and *Phillyrea latifolia* patches. Each of these groups differed significantly from all the other PTs ( $P < 0.0001$ ).

Using GLMM, we checked if the seven PTs differed significantly in species richness for each of the functional groups (Table 1). *Pinus* sp. was the only PT whose annual and perennial species richness did not differ significantly from those of other PTs. *Sarcopoterium spinosum*, *Calicotome villosa* and open PTs were the only PTs whose geophyte species richness did not differ significantly from those of other PTs. Using Tukey's multiple comparison tests among PTs, we examined all pair-wise comparisons for significant differences in the richness of the functional groups at the seven PTs (Table 1). The highest species richness of perennials was under *Calicotome villosa* patches, while geophyte richness was highest under *Pistacia lentiscus* patches. Annual richness was highest in open patches. All these results were significant.



**Figure 2.** Mean ( $\pm$ SE) number of herbaceous species in a quadrat in the six woody and the open PTs. Means headed by different letters were significantly different (Tukey's HSD multiple comparison test).

**Table 3.** 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 would have occurred under the specified PT, taking into account the relative distribution of this PT.

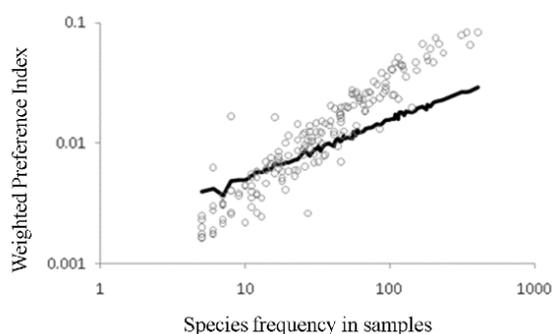
Herbaceous species	PT	Total occurrences	Observed number of occurrences in PT	Expected number of occurrences in PT	Ratio
<i>Piptatherum holciforme</i>	<i>Phillyrea latifolia</i>	23	10	2.05	4.88
<i>Crepis bulbosa</i>	<i>Pinus</i> sp.	19	6	1.11	5.41
<i>Aristochia parvifolia</i>	<i>Pistacia lentiscus</i>	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
<i>Alyssum strigosum</i>	Open	17	17	7.68	2.21

### Species' distributions in relation to patch type

Out of the 179 species that occurred in more than five quadrats, 111 species showed non-random distribution with respect to PTs ( $\alpha < 0.05$ ) (Fig. 3). The observed occurrences of 20 of these species were at least three times more than the expected occurrences at least in one of the PTs, however none of these PTs was open. The incidence of those species ranged from very rare (appeared in 8 plots) to very common (appeared in 181 plots) (Fig. 3). Table 3 presents the species with the highest observed to expected ratio for each PT. The two woody PTs that had a particularly large number of associated 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.

### Multivariate analyses of species distribution

We used the explained variance of each model in the RDA ordinations 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

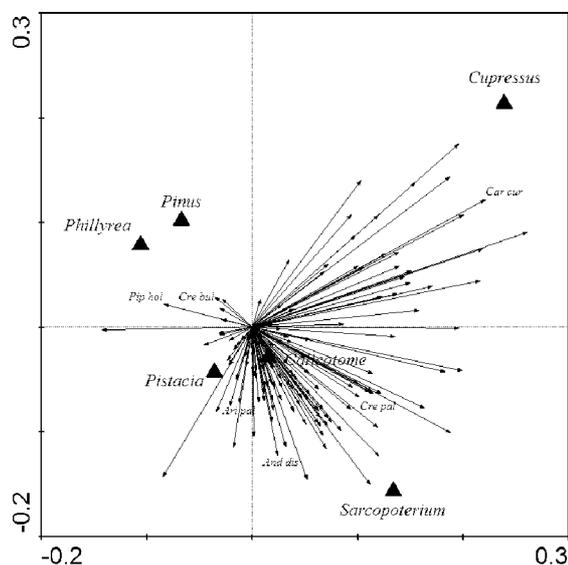


**Figure 3.** The distribution of species, in terms of weighted preference index for woody species PTs. Dashed line indicates the 95<sup>th</sup> percentile value from randomization calculation (see Method section for details). Species above the line are significantly ( $p < 0.05$ ) non-randomly distributed in relation to woody species PTs. Species occurring in less than five samples were not included in this analysis.

was 2.6% while the explained variance when using only woody vs. open PTs was 1.9%. These two canonical ordination analyses were significant ( $F = 9.74$ ,  $P = 0.002$  and  $F = 41.685$ ,  $P = 0.002$ , respectively).

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 ( $F = 5.66$ ,  $P = 0.002$ ) (Fig. 4). The explained variance was 2.3% and the first two axes explained 84.3% 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 herbaceous species composition of the six woody PTs can be divided into two groups: the first group includes



**Figure 4.** 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 3) indicated with the first three letters of their genus and species name respectively: *Piptatherum holciforme*, *Crepis bulbosa*, *Aristochia parvifolia*, *Andropogon distachyos*, *Carline curetum* and *Crepis palaestina*.

**Table 4.** Cumulative PAR reaching the sub-canopy for each PT and the corresponding herbaceous species richness.

	Species richness	Cumulative PAR
<i>Phillyrea latifolia</i>	1.03	94.42
<i>Pinus</i> sp.	1.03	102.86
<i>Pistacia lentiscus</i>	2.42	41.93
<i>Sarcopoterium spinosum</i>	2.56	17.48
<i>Cupressus</i> sp.	3.74	267.86
<i>Calicotome villosa</i>	4.72	223.66

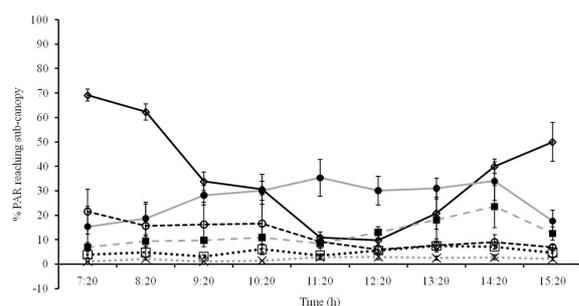
four of the six woody PTs: *Cupressus* sp., *Calicotome villosa*, *Sarcopoterium spinosum* and to a lesser extent also *Pistacia lentiscus*. The second group includes *Pinus* sp. and *Phillyrea latifolia*. Most herbaceous species related to the first group of PTs while only a small number of herbaceous species related to the second group of PTs. 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 3 and Fig. 4).

#### Solar radiation measurements

Changes in sub-canopy PAR along the day for each of the woody PTs are plotted in Fig. 5. Light penetration into the sub-canopy is lower under shrubs than under trees in early morning and late afternoon. In addition, among PTs having relatively constant PAR during the day, *Calicotome villosa* had much higher PAR values than *Phillyrea latifolia*, *Pinus* sp., *Pistacia lentiscus* and *Sarcopoterium spinosum*. The cumulative PAR (total PAR reaching the sub-canopy during the day) for each PT is summarize in Table 4. *Cupressus* sp. and *Calicotome villosa* had the highest cumulative PAR. All other PTs had notably lower cumulative PAR.

#### Discussion

Most studies that explored the effects of woody vegetation on species richness and composition viewed the ecologi-

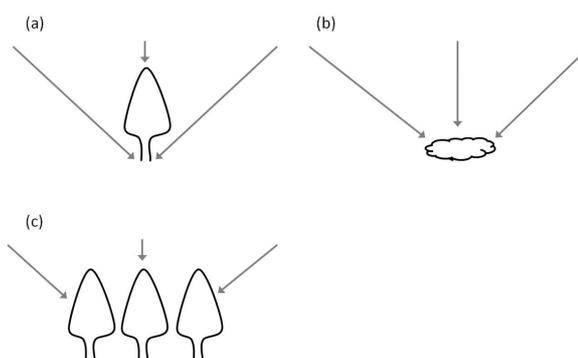
**Figure 5.** Change in the percentage of PAR reaching the sub-canopy during the day for the six PTs: *Cupressus* sp. (◇), *Calicotome villosa* (●), *Pinus* sp. (■), *Phillyrea latifolia* (○), *Pistacia lentiscus* (□) and *Sarcopoterium spinosum* (×). Bars indicate ±SE around the mean.

cal 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 an unimodal relationship with maximal richness at intermediate level of cover or biomass (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 and Archer 1997, Pugnaire 2001, Holzapfel et al. 2006, Wright et al. 2006, Madrigal et al. 2008). In this study, we have not taken into account the different properties of each individual patch. Our goal was to find out if the woody species and its inherent characteristics can explain herbaceous species richness and composition patterns. Indeed, we found clear indications that in this Mediterranean system, a large number of herbaceous species are strongly affiliated with particular woody species at a very fine scale.

Inter-annual variability is strong in such Mediterranean ecosystems, and results based on a single year need to be interpreted cautiously. Yet, 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 microhabitats in the ecological system space are too simplistic. We speculate that the different conditions imposed by different woody species create distinct microhabitats, and thus different woody species PTs are characterized by different herbaceous richness and composition.

#### 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 her-

**Figure 6.** Schematic presentations of the effect of the physical properties of the PTs on PAR reaching the sub-canopy. **a:** Large proportion of the PAR will reach the sub-canopy of trees during early morning and around 14:00; **b:** most of the PAR will not reach the sub-canopy of shrub if its canopy is dense and adjacent to the ground and **c:** most of the PAR will be filtered out from the sub-canopy by adjacent trees in dense plantations. Arrows represent solar radiation during the day: early morning, noon and around 14:00.

baceous 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 one herbaceous 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.

#### *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 et al. (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, species preferring the more dominant PTs and are not abundant, 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 have to have been present in at least 10 open PT patches to be detectable as significantly biased toward this PT (see Appendix). Thus, this method presents a minimum estimate of the number of species having a tendency toward certain PTs.

Spatial patterns of sub-canopy light are determined by several overstorey characteristics, particularly spatial pattern, height, and cover of woody plants. For example, shrubs are different from trees as their canopy is adjacent to the ground. Therefore, light penetration into the sub-canopy is lower under shrubs than under trees in early morning and late afternoon. In addition, some PTs have thinner canopy (such as *Calicotome villosa*) while others have denser canopy (such as *Phillyrea latifolia*). This trait also affects the amount of radiation reaching the sub-canopy. Sub-canopy solar radiation affects several environmental properties, such as leaf temperature, soil temperature, soil evaporation and evapotranspiration (Martens et al. 2000). Further, microclimate affects plant processes such as seedling establishment, germination, facilitation, and growth (Floyd 1983, Padien and Lajtha 1992, Martens et al. 1997). Thus, we speculate that the differences in herbaceous species richness between these PTs are to some extent the outcome of the specific physical properties of each PT.

These speculations are supported by the PAR measurements performed in each of the PTs along the day. Summing across an entire day, *Cupressus* sp. and *Calicotome villosa* had the highest cumulative PAR, presumably due to the elevated canopy of the former and the thinner canopy of the later. All other PTs had notably lower cumulative PAR. In the case of *Pinus* sp., the lower cumulative PAR was possibly related to the fact that *Pinus* is the only PT that is confined to patches of dense plantations in our study site. This in turn

affects the cumulative PAR because large proportion of the radiation is filtered out by surrounding trees (Fig. 6). These results correspond well to the herbaceous species richness in these PTs (Table 4). Support for our speculation comes from a study of three PTs in Ramat Hanadiv: *Phillyrea latifolia*, *Calicotome villosa* and open patches (Gabay 2008). These PTs differed significantly in three abiotic variables: light penetration, temperature and water content. Other abiotic variables (such as pH, conductivity,  $\text{NO}_3^-$ , P-olsen and OM) were not significant (Gabay 2008). However, other possible explanations of the observed affinities between herbaceous species and woody species PTs may be allelopathic effects (Fernandez et al. 2006, Hernandez et al. 2006), and litter volume which is dependent upon the woody species and which can physically condition the germination capacity of the herbaceous species (Charley and West 1975) or nutrient deposition into the soil (Barth and Klemmedson 1978, Wezel et al. 2000).

#### *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.

The relations between herbaceous composition and woody species PTs are probably more complex than the relation between PTs and richness. In addition to solar radiation, allelopathic effects were found to be a major factor in regulating plant community composition (Fernandez et al. 2006, Hernandez et al. 2006). Other possible explanations of the observed affinities between herbaceous species and woody species PTs may be litter volume or nutrient deposition into the soil.

#### *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 and Ellenberg 1974, Lande 1982, 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 the functional groups respond to the woody species PTs, but their responses were different, indicating that different abiotic conditions exist under different woody species PTs.

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 than geophytes, because their smaller resource reservations do not allow survival in the shade of woody species. Possibly, non-woody patches represent habi-

tats in which geophytes establish themselves with difficulty because of competitive inhibition of geophytes by their surrounding herbaceous vegetation. For example, Perevolotsky et al. (2011) proposed that the rapid growth of surrounding herbaceous vegetation generates shading that induces elongation of leaf petioles, flower and fruit stems of geophytes. These parts do not contribute to photosynthesis, but possibly decrease reserve accumulation in the bulb. Reproductive success of geophytes is often positively correlated to bulb size (Boeken 1989), and a decrease in corm reserves could potentially impair reproductive success in the following year.

## Conclusions

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. 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 due to its effect on solar radiation reaching the sub-canopy. 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.

**Acknowledgments:** This study was supported by a grant from the Eshkol Foundation of the Israeli Ministry of Science. We thank the botanists Y. Or, B. Segal, R. Lotan, R. Luria, R. Nukrian and G. Abraham. Special thanks to L. Hadar. We also thank J. Kob, E. Freedman, N. Shmuelov, S. Ellwood-Hofi, M. Givoni, R. Tamari, A. Maymon, A. Spiegel, I. Halperin and D. Lotan for their help in the field work, G. Ne'eman, A. Perevolotsky and R. Kent for their useful advice, and O. Gabay for unpublished data. Special thanks to L. Hadar and Ramat Hanadiv Nature Park for their help.

## References

- Agra, H. and G. Ne'eman. 2009. Woody species as landscape modulators: their effect on the herbaceous plants in a Mediterranean maquis. *Plant Ecol.* 205:165-177.
- 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. *J. N. Am. Benthol. Soc.* 25:126-141.
- 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. *Landsc. Ecol.* 23:327-339.
- Barth, R. C. and J. O. Klemmedson. 1978. Shrub-induced spatial patterns of dry matter, nitrogen, and organic carbon. *Soil Sci. Soc. Am. J.* 42:804-809.
- Bates, D. 2007. lme4: Linear mixed-effects models using S4 classes. *R package version 0.99875-9.*
- 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. *J. Appl. Ecol.* 26:1005-1024.
- Boeken, B. 1989. Life histories of desert geophytes- the demographic consequences of reproductive biomass partitioning patterns. *Oecologia* 80:278-283.
- Callaway, R. M. 1995. Positive interactions among plants. *The Bot. Rev.* 61:306-349.
- 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 Ecol.* 170:83-91.
- Charley, J. L. and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *J. Ecol.* 63:945-963.
- 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.
- Davies, S. J., P. A. Palmiotto, P. S. Ashton, H. S. Lee, and J. V. Lafrankie. 1998. Comparative ecology of 11 sympatric species of Macaranga in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *J. Ecol.* 86:662-673.
- Feinbrun-Dothan, N., A. Danin, and U. Plitmann. 1998. *Analytical flora of Eretz-Israel*. Cana Publishing House, Jerusalem.
- Fernandez, C., B. Lelong, B. Vila, J. P. Mévy, C. Robles, S. Greff, S. Dupouyet, and A. Bousquet-Mélou. 2006. Potential allelopathic effect of *Pinus halepensis* in the secondary succession: an experimental approach. *Chemoecology* 16:97-105.
- Floyd, M. E. 1983. Dioecy in five *Pinus edulis* populations in the southwestern United States. *Am. Midl. Nat.* 110:405-411.
- Franklin, J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *J. Veg. Sci.* 9:733-748.
- Gabay, O. 2008. Woody plants as landscape modulators in Mediterranean woodland. PhD dissertation, Ben-Gurion University of the Negev.
- Garcia, L. V., T. Maranon, A. Moreno, and L. Clemente. 1993. Above-ground biomass and species richness in a Mediterranean salt marsh. *J. Veg. Sci.* 4:417-424.
- 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*. *Environ. Exp. Bot.* 43:141-153.
- Grytnes, J. A. 2000. Fine-scale vascular plant species richness in different alpine vegetation types: relationships with biomass and cover. *J. Veg. Sci.* 11:87-92.
- 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. *J. Veg. Sci.* 10:673-682.
- Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773-785.

- Holzappel, C., K. Tielbörger, H. A. Parag, J. Kigel, and M. Sternberg. 2006. Annual plant–shrub interactions along an aridity gradient. *Basic Appl. Ecol.* 7:268-279.
- House, J. I., S. Archer, D. D. Breshears, and R. J. Scholes. 2003. Conundrums in mixed woody-herbaceous plant systems. *J. of Biogeogr.* 30:1763-1777.
- Karlson, R. H. and H. V. Cornell. 1998. Scale-dependent variation in local vs. regional effects on coral species richness. *Ecol. Monogr.* 68:259-274.
- Ko, L. J. and P. B. Reich. 1993. Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. *Am. Midl. Nat.*:31-42.
- 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 U. C. 2007. Plant functional types: are we getting any closer to the holy grail? In J. G. Canadell, D. E. Pataki, and L. F. Pitelka, (eds.) *Terrestrial Ecosystems in a Changing World*. Springer Berlin, Heidelberg. pp. 171-186.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177-192.
- Le Houerou, H. N. 1981. Impact of man and his animals on Mediterranean vegetation. In F. Di Castri, D.W. Goodall, and R.L. Specht, (eds.) *Ecosystems of the World, II, Mediterranean Shrublands*. Elsevier Scientific, Amsterdam. pp. 479-521
- Lepš, J. and P. Šmilauer. 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press.
- Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, and J. M. Melillo. 1991. The Sustainable Biosphere Initiative: an ecological research agenda: a report from the Ecological Society of America. *Ecology* 72:371-412.
- Madrigal-Gonzalez, J., J. A. Garcia-Rodriguez, A. Puerto-Martin, B. Fernandez-Santos, and P. Alonso-Rojo. 2010. Scale-dependent effects of pines on the herbaceous layer diversity in a semi-arid mediterranean ecosystem. *Community Ecol.* 11:77-83.
- Madrigal, J., J. A. Garcia-Rodriguez, R. Julian, A. Puerto, and B. Fernández-Santos. 2008. Exploring the influence of shrubs on herbaceous communities in a Mediterranean climatic context of two spatial scales. *Plant Ecol.* 195:225-234.
- Martens, S. N., D. D. Breshears, and C. W. Meyer. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. *Ecol. Model.* 126:79-93.
- Martens, S. N., D. D. Breshears, C. W. Meyer, and F. J. Barnes. 1997. Scales of aboveground and below-ground competition in a semi-arid woodland detected from spatial pattern. *J. Veg. Sci.* 8:655-664.
- Mueller-Dombois, D. and H. Ellenberg. 1974. *Aims and Methods of Vegetation Ecology*. Wiley, New York, USA.
- Naveh, Z. 1975. The evolutionary significance of fire in the Mediterranean region. *Plant Ecol.* 29:199-208.
- Naveh, Z. and J. Dan. 1973. The human degradation of Mediterranean landscapes in Israel. In F. di Castri and H. A. Mooney, (eds.) *Mediterranean Type Ecosystems. Origin and Structure*. Springer-Verlag, New York, USA. pp. 370-390.
- Naveh, Z. and P. Kutiel. 1986. Changes in the Mediterranean vegetation of Israel in response to human habitation and land use. In G. M. Woodwell, (eds.) *The Earth in Transition, Patterns and Processes of Biotic Impoverishment*. Cambridge University Press, Cambridge, UK. pp. 259-296.
- Noble, I. R. and H. Gitay. 1996. A functional classification for predicting the dynamics of landscapes. *J. Veg. Sci.* 7:329-336.
- Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing and protection. *J. Ecol.* 77:290-310.
- 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. *Int. J. Plant Sci.* 153:425-433.
- Parker, V. T. and C. H. Muller. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *Am. Midl. Nat.*:69-81.
- Pausas, J. G. and M. P. Austin. 2001. Patterns of plant species richness in relation to different environments: An appraisal. *J. Veg. Sci.* 12:153-166.
- Perevolotsky, A., E. Ettinger, R. Schwartz-Tzachor, and R. Yonatan. 2002. Management of fuel breaks in the Israeli Mediterranean Ecosystem: the case of Ramat Hanadiv Park. *J. Medit. Ecol.* 3:13-22.
- Perevolotsky, A., R. Schwartz-Tzachor, R. Yonathan, and G. Ne'eman. 2011. Geophytes-herbivore interactions: reproduction and population dynamics of *Anemone coronaria* L. *Plant Ecol.* 212:563-571.
- Pugnaire, F. I. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93:42-49.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. 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 interactions in savannas. *Annu. Rev. Ecol. Syst.* 28:517-544.
- 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. *J. Biogeogr.*:1-20.
- Shoshany, M. 2000. Satellite remote sensing of natural Mediterranean vegetation: a review within an ecological context. *Prog. Phys. Geogr.* 24:153-178.
- Sternberg, M. and M. Shoshany. 2001. Aboveground biomass allocation and water content relationships in Mediterranean trees and shrubs in two climatological regions in Israel. *Plant Ecol.* 157:173-181.
- ter Braak, C. J. F. and I. C. Prentice. 1988. A theory of gradient analysis. *Adv. Ecol. Res.* 18:271-313.
- ter Braak, C. J. F. and P. Šmilauer. 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, USA.
- Tielbörger, K. and R. Kadmon. 1997. Relationships between shrubs and annual communities in a sandy desert ecosystem: a three-year study. *Plant Ecol.* 130:191-201.
- Walker, B. H. 1992. Biological diversity and ecological redundancy. *Conserv. Biol.* 6:18-23.
- Weltzin, J. F. and M. B. Coughenour. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *J. Veg. Sci.* 1:325-332.

- Wezel, A., J. L. Rajot, and C. Herbrig. 2000. Influence of shrubs on soil characteristics and their function in Sahelian agro-ecosystems in semi-arid Niger. *J. Arid Environ.* 44:383-398.
- 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. *Ecology* 94:815-824.
- Zobel, M. 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species co-existence? *Trends Ecol. Evol.* 12:266-269.

Received July 26, 2011  
Revised November 20, December 12, 2011  
Accepted March 27, 2012

## Appendix

Relationship between the weighted preference index and species frequency. The file may be downloaded from the web site of the publisher at [www.akademai.com](http://www.akademai.com).