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Woody species as landscape modulators: their effect on the herbaceous plants in a Mediterranean maquis

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Abstract "Landscape modulators" are ecosystem engineers that have an impact on community structure by creating patches in the landscape mosaic. Our aim was to study the effect of evergreen-trees, as landscape modulators, on herbaceous plants in a Mediterranean maquis system in northern Israel. We examined the effects of canopy removal and cattle grazing on species richness, plant functional types, and rare plant species in two patch-types: (1) woody—under tree canopy (or the location of a removed canopy); (2) herbaceous—in open areas with no tree canopy. Patch-type and tree removal affected species richness and plant functional types. The extreme negative effect of the woody patch-type on species richness disappeared soon after the removal of the landscape modulator canopy. We conclude that the dominant effect of the evergreen woody landscape modulators can be regulated by canopy removal and grazing for maintaining patch-type and landscape diversities, and consequent high species richness in Mediterranean ecosystems, which is a main goal of global nature conservation policy.

Keywords Evergreen-trees · Grazing · Israel · Landscape mosaic · Patch-type · Plant functional types · Species richness

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Introduction

Dense multi-stemmed, evergreen, sclerophyllous low trees are the dominant life forms constructing the Mediterranean 'maquis' vegetation in Mediterranean type ecosystems worldwide (di Castri et al. 1981; Archibold 1995). Natural selection under Mediterranean climate shaped the Mediterranean vegetation, but its evolution has also been affected by intensive human activities since prehistoric times (Naveh 1990). The first evidence of hominoid control of fire in the Middle East is found at the Gesher Benot Ya'akov (northern Israel) prehistoric site 790,000 years ago (Goren-Inbar et al. 2004); this is a milestone, marking the beginning of large-scale human impacts on nature. Later (ca. 10,000 years ago), after the beginning of early agriculture, grazing, and tree clearing significantly increased man's effect on nature (Naveh 1990). In historical periods when the agricultural population in Israel was dense, the proportion of agricultural areas was high, while that covered by natural vegetation was low; but as in the western Mediterranean when wars and epidemics decreased human population, the natural maquis recovered over wider areas (Barbero et al. 1990). Nowadays, dense and well-developed maquis covers the upper Galilee in northern Israel. Until 1948, traditional agriculture intensively exploited this area, similar to the current situation across the Lebanese border. However, the semi-humid Mediterranean climate enhanced natural regeneration after the severe disturbance. From 1964 to 1992, the tree-cover increased from 2% to 41%, while during the same period the herbaceous vegetation cover decreased from 56% to 24% (Carmel and Kadmon 1999).

The Mediterranean basin is a global biodiversity hotspot; the number of endemic plant species in this area is ca. 13,000, the third in richness after the tropical South American Andes and the Sundaland in southeast Asia (Myers et al. 2000). In the Mediterranean basin, Israel has high species richness and endemism rate (Shmida 1984; Médail and Quézel 1999). Heliophilous herbaceous plant species account for most plant diversity in Israel (Naveh and Whittaker 1980; Sternberg et al. 2000); therefore, the natural regeneration and the expansion of the woody maquis (Carmel and Kadmon 1999) should have a negative effect on plant species diversity.

Furthermore, the natural regeneration process has already led to severe decrease in flowering and subsequent population size of some rare species such as *Paeonia mascula* (Ne'eman 2003), *Lilium candidum* (Oz and Dafni 1991), and probably other species that cannot reproduce in heavy or semi-shaded habitats. Loss of species and decrease in species diversity may affect stability and threaten the existence and the functioning of ecosystems (Balvanera et al. 2006). This emphasizes the importance of predicting the impact of natural factors and management regimes on biodiversity.

While the effect of the environment on organisms has received much scientific attention, research on organisms' impact on their environment has broadened only recently. Organisms that modify habitats by changing the availability of resources for other organisms are "Ecosystem engineers". Autogenic engineers (e.g., corals or trees) change their environment via their own physical structure, while allogenic engineers (e.g., beavers or moles) modify their environment by changing the physical structure of other living or non-living materials in the system (Jones et al. 1994). "Landscape modulators" are "ecosystem engineers" that have an impact on community structure by creating patches in the landscape mosaic, in which the availability of resources and distribution of organisms differ from that of the background area (Shachak et al. 2008). Patchiness of the landscape created by landscape modulators induces ecological processes that affect biodiversity in general and species diversity in particular (Shachak et al. 2008). Trees are autogenic landscape modulators that create landscape patchiness by their own presence and physical structure, which create local changes in the availability of some main resources such as light, water, and soil organic matter content, thereby affecting the presence of other species (Shachak et al. 2008).

The model of Shachak et al. (2008) predicts that woody-landscape modulators affect local species richness by filtering from the regional species pool to the local assemblage. It predicts that traditional human activities (tree cutting and grazing) affect local species richness mainly through their effect on the landscape modulators (Shachak et al. 2008). The overall effect of the woody vegetation as landscape modulators on the herbaceous vegetation depends on the balance between their positive and their negative effects (Jones et al. 1997), which depends on environmental conditions. A positive effect is expected in arid areas, where woody landscape modulators improve seed trapping, nutrient, moisture, and protection from browsing or trampling (Flores and Jurado 2003); a negative effect is expected in the more humid areas of the Mediterranean climatic zone in Israel as a result of their heavy shade (Holzapfel et al. 2006; Shachak et al. 2008).

During the last several decades, woody vegetation in the Mediterranean basin has been increasing at the expense of herbaceous vegetation and decrease in biodiversity (e.g., Verdú et al. 2000). As a result, several studies documented a positive effect of trimming, partial removal of the woody vegetation, or grazing on herbaceous plant diversity in Mediterranean maquis on a relatively large scale (Hadar et al. 1999; Barbarl et al. 2001; Noy-Meir and Kaplan 2002).

The current research examines, by removal and mild cattle grazing, the effect of the woody-landscape modulator canopy on herbaceous plant species richness, plant functional types, and some Israeli rare herbaceous plant species in two patch-types: (1) woody—under tree canopy (or the location of a removed canopy); (2) herbaceous—in open areas with no tree canopy. Patch-type and tree removal affected species richness and plant functional types. Our specific hypotheses were: (A) herbaceous species richness will be lower in the woody than in the herbaceous patches (Holzapfel et al. 2006); (B) landscape modulators' canopy removal will increase herbaceous species richness (Hadar et al. 1999) mainly in the woody patches; (C) cattle grazing will increase herbaceous species richness (Hadar et al. 1999; Noy-Meir and Kaplan 2002); and (D) landscape modulators' canopy removal and cattle grazing will have differential effects on the presence of plant functional types and individual plant species according to their specific traits (Hadar et al. 1999; Díaz et al. 2007).

A deep and comprehensive understanding of the processes by which landscape modulators affect biodiversity and of the effect of the traditional plant management treatments (tree removal and grazing) on these processes will assist in planning management regimes to increase biodiversity according to the global nature conservation policy.

Materials and methods

The study site

The research site is located on Mt. Tziv'on (35.25°E, 33.15°N), Upper Galilee, Israel; at an average altitude of 850 m. The bedrock is limestone, the soil is terra-rosa and average annual precipitation is 900 mm. The vegetation consists of *Quercus calliprinos* (60% of the trees) and *Pistacia palaestina* association (Zohary 1973), accompanied by *Quercus boissieri* and other deciduous tree species mainly of the Rosaceae, which are frequent in the *Quercus–Pistacia* association in the higher mountains (Waisel et al. 1978). The vegetation forms dense maquis, with patches of herbaceous plants, which are green in winter and spring but dry in summer, separating the woody patches. At the beginning of the experiment (October 2005), the average total vegetation cover was ca. 95%, of which 60% were trees, 15% shrubs, 10% dwarf-shrubs, and 10% herbaceous plants.

Experimental design

Five blocks of 4,000 m^2 were marked and divided into four plots of 1,000 m^2. In November–December 2005, we randomly subjected each plot in each block to one of the following treatments: (1) No tree removal and no grazing (NRNG), (2) no tree removal with grazing and (NRG), (3) tree removal with no grazing (RNG), and (4) tree removal with grazing (RG). In all R plots, we removed all the woody plants to ground level, and all the NG plots were wire-fenced to exclude cattle that regularly graze at moderate intensity (ca. 30 cows per km^{-2}) in summer in the area.

Sampling

In each plot, we located two patch-types: (1) Woody patch—covered with an evergreen tree (*Q. calliprinos*) canopy, or one that was covered with such a tree prior the tree removal treatment. (2) Herbaceous patch—not covered with any woody plant prior to tree removal, but with herbaceous vegetation in winter and spring. The patch-type per plot, which consisted of all patches of the same type (woody or herbaceous) in each plot, was our independent sampling unit. For each patch-type per plot, we randomly sampled 0.04 m^2 quadrats, in which we identified all plant species following Zohary and Feinbrun-Dothan (1966–1986), Feibrun-Dothan and Danin (1991) and Danin (1998).

One of the main issues in the analysis of species richness is estimating the real species richness out of the number of species recorded in the samples while taking sampling effort into account (Gotelli and Colwell 2001). In a preliminary study (spring 2006), we analyzed species accumulation curves of 30 sampling quadrats of 0.04 m^2 for each patch-type per plot using the 'EstimateS' computer software (Colwell 2005). In consequence, we fixed our sampling effort at 30 quadrats of 0.04 m^2 for the herbaceous patch-type per plot and 50 quadrats of 0.04 m^2 for the woody patch-type per plot. All the results presented here are from the second sampling season (spring 2007).

Estimated herbaceous plant species richness

We determined and estimated the herbaceous plant species richness for each patch-type per plot ($N = 40$) by analyzing the species accumulation curves using the 'Species Richness Estimators' tool of the EstimateS computer software (Colwell 2005). When sampling homogeneous habitats, non-parametric methods give more accurate results than others (Brose et al. 2003). Therefore, we determined the estimated herbaceous plant species richness as the asymptote of the average curve between the two most commonly used non-parametric methods: Chao and Jackknife. Using three-way ANOVA, we analyzed the effects of patch-type and the two treatments (removal and grazing) on the estimated herbaceous plant species richness and their interaction. Estimated herbaceous plant species richness data showed normal distribution (Shapiro-Wilk, $P < 0.05$) for all eight patch-types per plot. Species richness depends on the size of the area, so the initial tree-cover in each plot may directly affect the estimated herbaceous plant species richness. To separate this effect from that of our independent variables, we used the initial tree-cover as covariate in the ANOVA model. Since the ANOVA results showed a significant effect of pre-treatment tree-cover on the estimated herbaceous plant species richness, we checked the correlation (Pearson) between the estimated herbaceous plant species richness and the initial tree-cover for each of all eight patch-types per plot. For patch-types per plot, where we detected a significant correlation, we also applied a linear regression analysis.

Mean herbaceous species richness per quadrate

In addition to analysis of the estimated herbaceous plant species richness at the plot scale (1,000 m^2), we analyzed the mean number of herbaceous species at the smallest scale of 0.04 m^2 quadrate in each patch-type per plot ($N = 40$). The mean herbaceous species richness per quadrate data showed normal distribution (Shapiro-Wilk, $P < 0.05$) for all eight patch-types per plot. As for the estimated herbaceous plant species richness, whenever we found significant correlation between the mean herbaceous species richness per quadrate and the initial tree-cover, we also applied a linear regression analysis.

Plant functional types

Dividing plants into similar functional groups by their traits provides an additional way of estimating biodiversity (Box 1996; Lavorel et al. 1977). The classification of species into plant functional types is based on species biological traits (e.g., morphology, physiology, reproduction, and phenology). For our classification into plant functional types, we used a variation of Raunkiær's (1934) traditional division of plant life forms: tree saplings, climbers, dwarf-shrubs, annual herbs, and perennial herbs. In addition, we analyzed annual Gramineae and perennial Gramineae. We excluded shrubs from the analyses because of their low frequency in the samples. We used the percentage of occurrences of each of the plant functional types in each patch-type per plot ($N = 40$) as the dependent variable for the analyses.

To explore the responses of the various plant functional types relative to the three factors (patch-type, tree removal, and grazing), we used canonic ordination (CANOCO: ter Braak and Smilauer 1998) for the data from all patch-types per plot. This analysis presents both the independent and dependent variables on a single ordination plot, whose axes represent two independent linear combinations that optimally separate the functional types being tested (ter Braak and Smilauer 1998). We used the RDA-type canonic ordination, which is more suitable for the analysis of categorical factors. We also analyzed the effects of the four treatments on each of the functional groups separately. Since the data had non-normal distribution, even after conventional transformations, and plots within each block are not independent, we used the Friedman non-parametric test for repeated measures; this test minimizes the effect of the differences among the blocks.

Rare species

We analyzed the effects of patch-type and treatments on rare herbaceous plant species in Israel [following Feibrun-Dothan and Danin (1991)], which were present in more than ten samples. The rare species included three annual plants: *Alyssum simplex*, *Arabis verna* (Cruciferae), *Galium divaricatum* (Rubiaceae), and three perennial herbaceous plants: *Asperula libanotica* (Rubiaceae), *Crepis reuteriana* (Compositae), and *Brachypodium pinnatum* (Gramineae).

We used the percentage of occurrences for each of the species in each patch-type per plot ($N = 40$) as the dependent variable. Data analyses were similar to those of the plant functional types.

Results

Vegetation cover

In summer 2006, one growing season after the treatments were applied, we measured the cover of the vegetation along the two diagonals in each plot (ca. 90 m). In the intact (NR) plots, the average tree-cover was 64%, shrub cover 17%, dwarf-shrub cover 10%, and 9% of herbaceous vegetation. In the removal (R) plots, tree-cover was first estimated in 2005, prior tree removal, and in summer 2006, we measured the regenerating canopies. In 2006, the average tree-cover was 16%, shrub cover 8%, dwarf-shrub 10%, and 66% of herbaceous vegetation.

Estimated herbaceous plant species richness

The lowest estimated herbaceous plant species richness was in the woody patch-type in the NR plots, with or without grazing (Fig. 1). Patch-type, removal and grazing, and their interaction, significantly affected the estimated herbaceous plant species richness with high percentage of the explained variance (Table 1). The significant interaction between the patch-type and the removal indicated that removal affected the estimated herbaceous plant species richness only in the woody patch (Table 1; Fig. 1). The pre-treatment tree-cover in the plots (as a covariate) had a significant effect on the estimated herbaceous plant species richness (Table 1). Pre-treatment tree-cover was also negatively and significantly correlated (Spearman) with the estimated herbaceous plant species richness in the woody patch in the NRNG plots ($r = -0.881$, $P = 0.049$), and in the herbaceous patch in the RG plots ($r = -0.901$, $P = 0.037$). In contrast, we found a positive (Spearman) correlation between the estimated herbaceous plant species richness and the initial tree-cover in the woody patch in the RNG plots ($r = 0.898$, $P = 0.038$). The significant linear regression (Fig. 2) allows prediction of the estimated herbaceous plant species richness in the patch-types per plot from the pre-treatment tree-cover in any specific plot.

Table 1 Three-way ANOVA testing the effects of patch-type, tree removal, grazing and their interaction on the estimated species richness of herbaceous plants at the plot scale, using pre-treatment tree-cover as covariate

Source	*df*	Mean square	*F*	*P*
Corrected model	8	4412.2	**9.071**	**<0.001**
Intercept	1	16857.5	34.655	**<0.001**
Tree-cover (covariate)	1	2500.9	**5.141**	**0.030**
Grazing	1	739.5	1.520	0.227
Removal	1	10662.8	**21.920**	**<0.001**
Patch-type	1	9241.6	**18.999**	<0.001
Grazing × removal	1	151.5	0.312	0.581
Grazing × patch-type	1	0.400	0.001	0.977
Removal × patch-type	1	12180.1	**25.040**	**<0.001**
Grazing × removal × patch-type	1	44.1	0.091	0.765
Error	31	486.4		
Total	40			
	Adjusted R squared = 0.623			

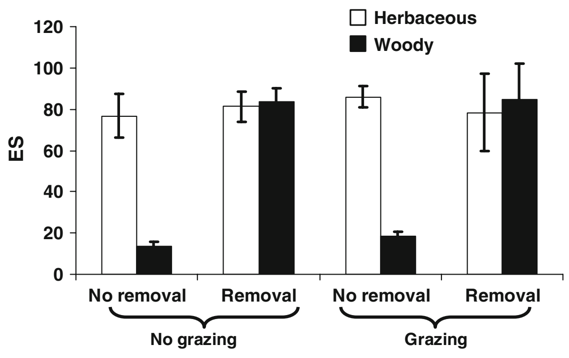

Fig. 1 Average (and SE) estimated herbaceous species richness (ES) in woody and in herbaceous patches under removal, no removal, grazing or no grazing treatments, a year and a half after treatment application. $N = 5$ for each column

Mean herbaceous species richness per quadrate

Mean herbaceous species richness per quadrate was higher in the herbaceous patch than in the woody patch, and it was relatively higher under tree-removal and lower under grazing. The ANOVA for the effects

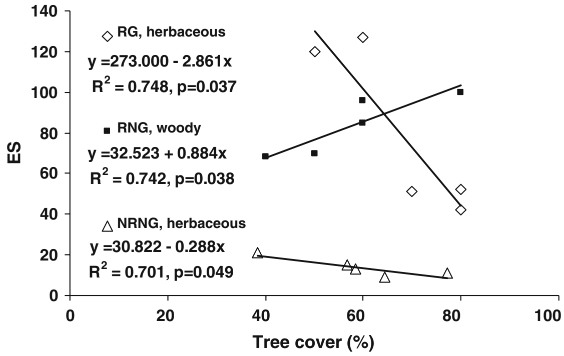

Fig. 2 The relation between the estimated herbaceous species richness (ES) of each patch type per plot and the pre-treatment percentage of tree-cover in the plot. Significant equations of the linear regressions are presented for the herbaceous and woody patch-types under the various treatments: no tree removal with no grazing (NRNG), no tree removal with grazing (NRG), and removal with grazing (RG)

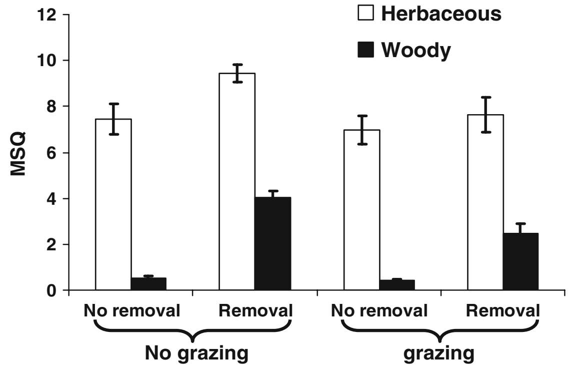

Fig. 3 Average (and SE) of the mean herbaceous species richness per quadrate (MSQ) in woody and in herbaceous patches under removal, no removal, grazing and no grazing treatments in the second growing season after treatment application. $N = 5$ for each column

of patch-type, tree removal, grazing, and of their interaction, and on the mean herbaceous species richness per quadrate was significant, and the percentage of explained variance was high (Table 2). The interaction was significant because the main effect of the tree removal was in the woody patch, while grazing had an effect mainly in the R plots (Table 2; Fig. 3). The pre-treatment tree-cover in the plots (as covariate) had a significant effect on the mean herbaceous species richness per quadrate (Table 2), and it was negatively and significantly correlated (Spearman) with the mean herbaceous species richness per quadrate in the woody patch in the NRNG plots ($r = -0.974$, $P < 0.005$) and in the NRG plots ($r = -0.927$, $P = 0.023$). Pre-treatment tree-cover was also correlated with the mean herbaceous species richness per quadrate in the herbaceous patch in the NRNG plots ($r = -0.940$, $P = 0.018$) and in the RG plots ($r = -0.962$, $P = 0.009$). The significant linear regression (Fig. 4) allows prediction of the mean herbaceous species richness per quadrate

Table 2 Three-way ANOVA testing the effects of Patch-type, tree removal, grazing and their interaction on the species richness of herbaceous plants per quadrate, using pre-treatment tree-cover as covariate

Source	*df*	Mean square	F	*P*
Corrected model	8	54.867	**71.184**	<0.001
Intercept	1	91.764	119.055	**<0.001**
Tree-cover (covariate)	1	13.266	**17.212**	<0.001
Grazing	1	2.505	3.250	0.081
Removal	1	40.143	**52.081**	<0.001
Patch-type	1	363.328	**471.379**	<0.001
Grazing × removal	1	4.973	**6.451**	**0.016**
Grazing × patch-type	1	0.216	0.280	0.600
Removal × patch-type	1	5.237	**6.794**	**0.014**
Grazing × removal × patch-type	1	0.010	0.014	0.908
Error	31	0.771		
Total	40			
	Adjusted R squared = 0.935			

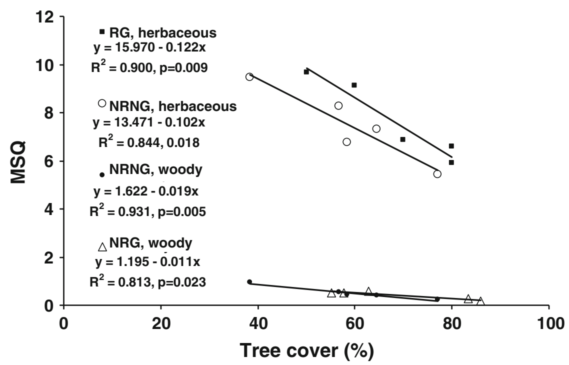

Fig. 4 The relation between the mean herbaceous species richness per quadrate (MSQ) of each patch-type per plot and the pre-treatment percentage of tree-cover in the plot. Significant equations of linear regressions are presented for the herbaceous and woody patch-types under the various treatments: no tree removal with no grazing (NRNG), no removal with grazing, (NRG), tree removal with no grazing (RNG), and removal with grazing (RG)

in all patch types per plot according to the initial pre-treatment tree-cover in any specific plot.

Plant functional types

The canonical ordination analysis (RDA) for the data of all patch-types per plot (Fig. 5) exploring the distribution of the various plant functional types among the woody or herbaceous patch-type and their responses to the removal or grazing treatments was significant ($F = 35.600$, $P = 0.002$). The canonical function of the first (horizontal) ordination axis explained 95.4%, and the functions of the two axes together explained 99.7% of the variance in the relations between species and environment. The first axis was mostly affected by the patch-type ($r = 0.865$) and thus the patch-types are located close to it. Removal was the main component of the second function ($r = 0.629$), and thus it is located close to the vertical axis. Grazing is located next to axes origin and close to the second axis meaning it had only a small effect, and its correlation with the second axis is 0.121 (Fig. 5). The occurrence of the four functional types of herbaceous plants was mostly related to the herbaceous patch. Dwarf-shrubs showed a similar but much weaker trend. Climbers were strongly related to the woody patch, while tree-saplings were associated with the woody patch under the no-removal treatment (Fig. 5).

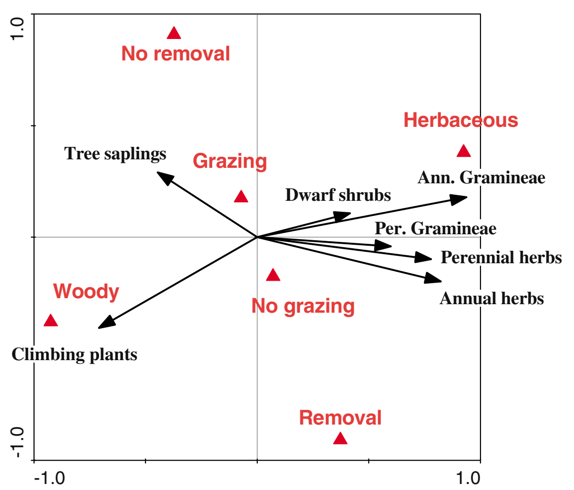

Fig. 5 Location of the plant functional types: annual Graminaeae (Ann. Gramineae), perrenial Graminaeae(Per. Gramineae), annual herbs, perennial herbs, climbing plants, dwarf-shrubs, and tree saplings, marked as vectors on the canonic ordination plane (RDA), relative to the location of the patch-types: woody and herbaceous, and the treatments: grazing, removal (marked as *triangles*)

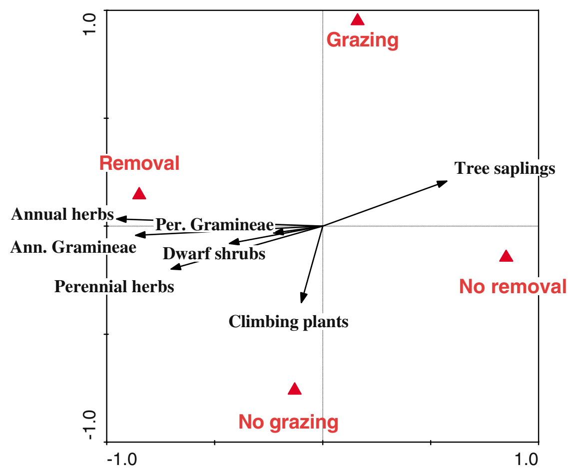

Fig. 6 Location of the plant functional types: annual Graminaeae (Ann. Gramineae), perrenial Graminaeae (Per. Gramineae), annual herbs, perennial herbs, climbing plants, dwarf-shrubs and tree saplings, growing in the woody patch only, marked as vectors on the canonic ordination plane (RDA), relative to the location of the treatments: grazing, no grazing, removal and no removal (marked as *triangles*)

The canonic ordination (RDA) using the plant functional types dataset only for the herbaceous patch was not significant, meaning the treatments did not have a significant effect on the occurrence of plant functional types in the herbaceous patch. In contrast, the same analysis for the plant functional types dataset of only the woody patch (Fig. 6) was highly significant ($F = 30.638$, $P = 0.002$). The canonical function of the first (horizontal) ordination axis explained 99.0% of the variance in the dataset and the functions of the two axes together explained 100.0% of the variance. The main component of the first axis was removal ($r = 0.934$), while grazing was the main component of the second function ($r = 0.629$) (Fig. 6). In the woody patch, the occurrence of the annual herbs and grasses was strongly and positively affected by tree-removal treatment, while that of perennial herbs and to less extent, dwarf-shrubs were also affected by the NG treatment. The occurrence of climbers in the woody patch was associated with the NG treatment, while tree saplings occurred mainly in the NR plots (Fig. 6).

In the woody patch, the occurrence of all herbaceous plant functional types and dwarf-shrubs was

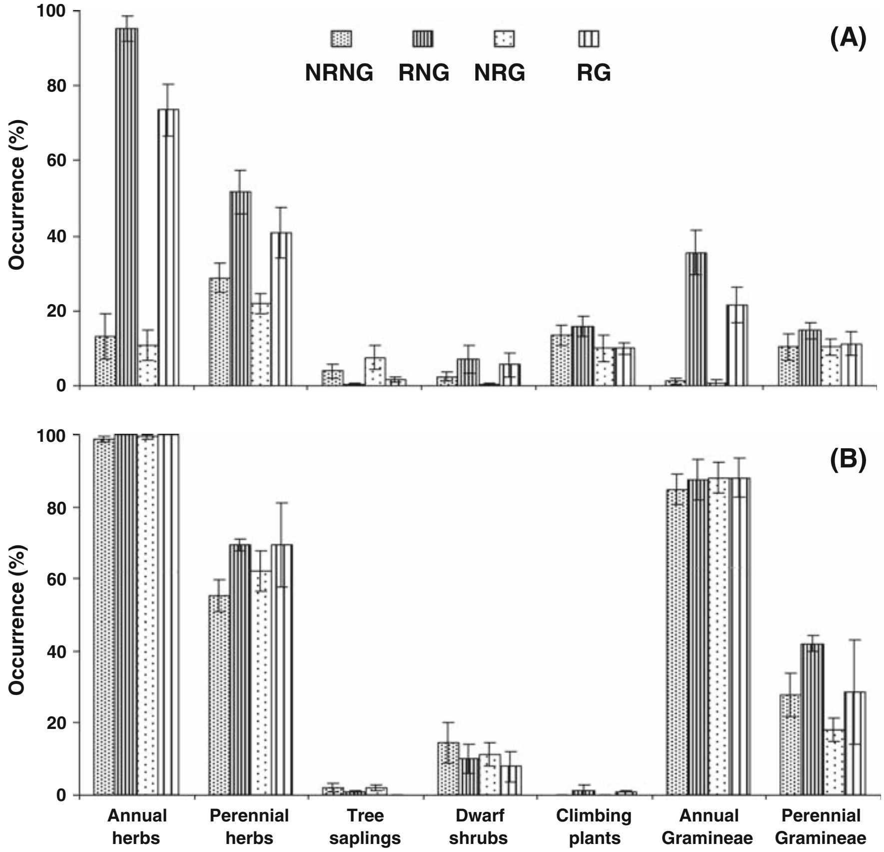

Fig. 7 The average (and SE) occurrence percentage of the plant functional types: Annual herbs, perennial herbs, tree saplings, dwarf-shrubs, climbing plants, annual graminaeae and perennial gramineae, in the various treatment plots: no removal, no grazing (NRGR), removal and no grazing (RNG), grazing, no removal (NRG), grazing and removal (RG), in the woody patch-type (**a**) and in the herbaceous patch-type (**b**). $N = 5$ for each column

higher in RG and RNG plots than in the NRG and NRNG plots (Fig. 7). In woody patch, the effect of the treatments on the occurrence of annual herbs was significant (Friedman, $\chi^2_3 = 13.560$, $P = 0.004$), as it was on perennial herbs ($\chi^2_3 = 9.612$, $P = 0.022$) and annual grasses ($\chi^2_3 = 14.739$, $P = 0.002$). In contrast, in the herbaceous patch, the mean occurrence of perennial grasses was higher in the RNG plots than in the RG plots (Fig. 7), but this difference was not significant (Friedman, $P > 0.05$); likewise, the effects of the treatments on all other plant functional types in the herbaceous patch.

Rare species

The distribution of the rare species (in Israel) was significantly ($F = 2{,}272$, $P = 0.004$) affected by the woody or herbaceous patch-types and by the removal or grazing treatments tested by (RDA) canonical ordination analysis for the full dataset of all patch-types per plot (Fig. 8). The canonical function of the

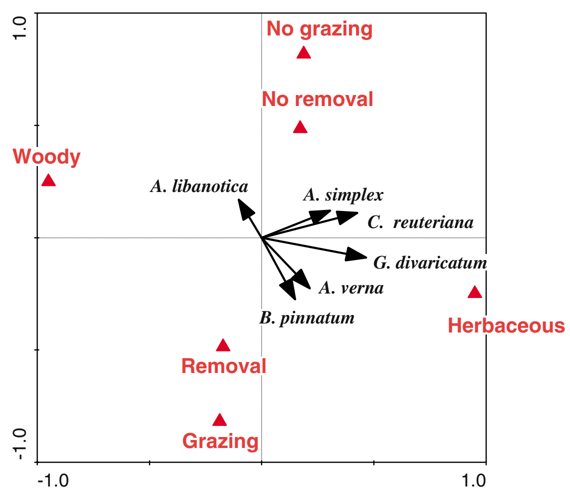

Fig. 8 Location of the rare plant species (in Israel): *Alyssum simplex, Arabis verna*, *Asperula libanotica*, *Brachypodium pinnatum*, *Crepis reuteriana*, and *Galium divaricatum* (marked as *vectors*) on the canonic ordination plane (RDA), relative to the location of the patch-types: woody and herbaceous, and the location of the treatments: grazing, no grazing, removal and no removal (marked as *triangles*)

first (horizontal) ordination axis explained 79.5% of the variance, and the two axes together explained 97.3%. The main components of the first axis, which were located close to it, were the woody or herbaceous patch-types ($r = 0.611$), while removal was the main component of the second axis ($r = 0.295$) (Fig. 8). *A. libanotica* was the only rare species that occurred more in the woody patch, in the no-removal, no-grazing plots (Fig. 8). The other rare species occurred more in the herbaceous patch: *A. verna* and *B. pinnatum* mainly in the tree removal and grazed plots, and *A. simplex* and *C. reuteriana* mainly in the no-removal and no-grazing plots.

In the woody patch, none of the four treatments had a significant effect (Friedman, $P > 0.05$) on any of the six rare species, but the following tendencies could be observed (Fig. 9). *A. simplex* was present only in NRNG plots, *A. verna* only in RG plots, and *B. pinnatum* only in RG and RNG plots. The occurrence of *A. libanotica* was lower in NRNG and RG plots than in RNG plots and absent from NRG plots. *C. reuteriana* was the only rare species present in all treatments' plots, more in RNG than in NRNG plots. *G. divaricatum* was totally absent from the woody patch.

In the herbaceous patch, treatments significantly affected the occurrence of *C. reuteriana* (Friedman, $\chi^2_3 = 8.022$, $P = 0.046$), which was present mainly in NRG and no NRNG plots, less in RNG and still less in RG plots (Fig. 9). We found no significant effects for the other rare species (Friedman, $P > 0.05$), but the following trends could be observed (Fig. 9): *A. simplex* was present mainly in NRNG plots and less in RNG and RG plots. *A. verna* was present mainly in RG plots but less in NRNG and NRG plots. *B. pinnatum* was present mainly in RG plots, less in NRG and NRNG plots, and not at all in RNG plots. *A. libanotica* was present mainly in NRNG plots and less in RNG, RG and NRG plots. *G. divaricatum*, which was absent from the woody patch, was present in the herbaceous patch mainly in NRNG, RNG and NRG, and less in RG plots.

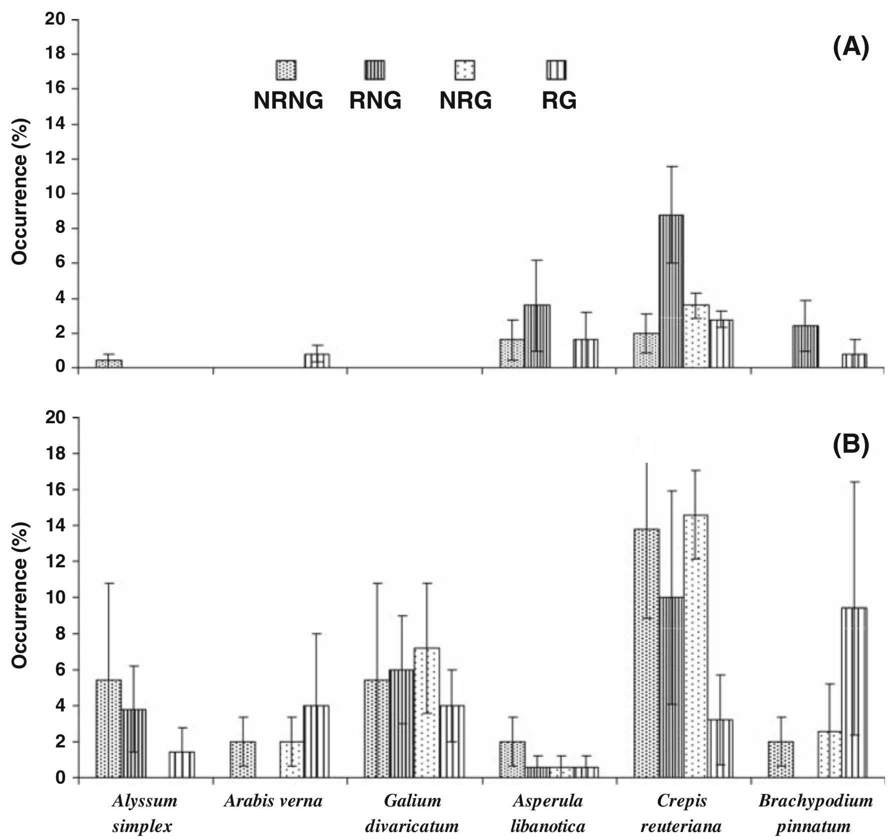

Fig. 9 Average (and SE) percentage occurrence of the rare plant species (in Israel): *Alyssum simplex*, *Arabis verna*, *Asperula libanotica*, *Brachypodium pinnatum*, *Crepis reuteriana*, and *Galium divaricatum*, in the various treatment plots: no removal, no grazing (NRGR), removal and no grazing (RNG), grazing, no removal (NRG), grazing and removal (RG), in the woody patch-type (**a**) and in the herbaceous patch-type (**b**). $N = 5$ for each column

Discussion

Species richness

Our results show for the first time that an extremely short time (a year and a half) was enough for the herbaceous plants to populate the removed wood patches to a similar degree of species richness as in the herbaceous patches. As predicted by our hypotheses (A and B), species richness was higher in the herbaceous than in the woody patch-type, and the removal of landscape modulators' tree canopy significantly affected species richness. However, contrary our hypothesis (C), under the moderate grazing intensity which is typical to maquis areas in the upper Galilee, we found no effect of grazing on the estimated herbaceous plant species richness (Fig. 1; Table 1). The interaction between patch-type and tree removal was the main factor affecting species richness because tree-removal affected species richness only in the woody patch, and patch-type affected species richness only in the unremoved plots (Table 1; Fig. 1). Following tree-removal, numerous new species infiltrated the former woody patches and dramatically increased the estimated herbaceous plant species richness. A similar increase in herbaceous species richness was reported earlier (Hadar et al. 1999; Barbarl et al. 2001; Noy-Meir and Kaplan 2002).

The results demonstrate the crucial role of landscape modulator canopy in modulation of landscape by the woody plant. Pre-treatment tree-cover was a major factor affecting species richness at the plot scale (1,000 m^2) (Table 1), even in the herbaceous patch in grazed and tree removal plots (GR), species richness was negatively related to the pre-treatment tree-cover (Fig. 2). Pre-treatment tree-cover also negative affected species richness at the small quadrate scale (Fig. 4; Table 2). This was because as the tree-cover percentage increased, the total area of the herbaceous patches decreases, and consequently, probably due to the relations between size of the sampled area and species richness. Due to the same reason, species richness in the woody patches in the no grazing with tree removal plots was positively related to the pre-treatment tree-cover (Fig. 2; Table 1). The pre-treatment tree-cover negatively affected species richness at the plot and the square scales in the woody patches in the no removal no grazing plots because of the filtering role of landscape modulator canopies', which directly or indirectly prevented the infiltration of herbaceous species from the regional pool to enter the woody patch (Shachak et al. 2008).

In the small quadrate scale, patch-type was the main factor that affected species richness (Table 2), and not its interaction with tree removal, as was in the case for species richness at the plot scale. This was probably because one year after tree removal the woody patches had still a low herbaceous plant density that kept species richness lower than in the herbaceous patches at the small scale. The interaction between grazing and tree removal also significantly affected species richness and the quadrate scale but not at the plot scale, because the negative effect of grazing was only in the tree removal plots (Fig. 4). This was probably because the cows preferred to feed on the herbaceous vegetation and young growing fresh foliage of the regenerating trees rather than on the mature foliage of the trees in the no tree removal plots (Perevolotsky and Pollak 2001). Species richness at the quadrate scale, unlike at the plot scale, was lower in the tree removal with grazing than in tree removal with no grazing plots (Figs. 1, 3). This was probably the result of the activity of wild boars, which focused on the herbaceous patches; wild boars turned the soil upside down, thereby decreased the density of the herbaceous plants. This thinning negatively affected the number of species in the small quadrate scale but not in the large plot scale.

Plant functional types

The differential responses of plant functional types to patch-type and treatments confirmed our hypothesis (D). The occurrence of all the herbaceous functional types was lower in the woody than in the herbaceous patch-type, which is in concert with earlier results from similar Mediterranean maquis (Holzapfel et al. 2006). The woody patch also had a negative effect on dwarf-shrubs; as expected, the tree saplings and climbers were found mostly in the woody patch (Fig. 5). The occurrence of herbaceous plants was much higher in the woody patches in the tree-removal plots than in the NR plots (Fig. 7), because landscape modulator canopies directly (physical barrier) or indirectly (sunlight filtering etc.) prevented entering of new species and their establishment in the woody patch. Grazing negatively affected the occurrence of annual herbs in the woody patch only in the tree removal plots, where grazing had a higher impact (Fig 7). We have neither good explanation why tree removal slightly affected the occurrence of the perennial herbs and grasses in the herbaceous patches (Fig. 7), nor do we have an explanation for the positive effect of grazing on the occurrence of tree saplings (Figs. 6, 7).

In one growing season, tree removal caused a dramatic decrease in the occurrence of tree saplings in the woody patch (Fig. 7). The reason is the limited spatial dispersal of seeds of trees (mostly oaks), their short viability, and their consequent absence from soil seed bank. Competition with the large number of herbaceous plants that re-occupied the woody patch soon after tree removal explains the absence of establishment of saplings from nearby trees. Occurrence of the climbers was higher in the woody patch; it was negatively affected by grazing but not by tree removal (Figs. 6, 7). The spatial relation between the climbing plants and the woody patch is due to the dispersal of their seeds by birds eating their juicy fruits (Izhaki et al. 1991). The negative effect of grazing on the climbers is cows' differential food preference; due to their morphology, climbing plants tend to suffer more damage from the grazing cattle (Hadar et al. 1999; Lavorel et al. 1999).

Rare species

As expected (hypothesis D), patch-type and treatments differentially affected the occurrence of rare species, indicating differences in their traits and unique niches. For example, *A. simplex* occurred in herbaceous patch in NRNG plots, *A. libanotica* in the woody patch in RNG plots, and *A. verna* and *B. pinnatum* mainly in the herbaceous patch in the RG plots (Fig. 8, 9). The general common goal of management in nature reserves is keeping or increasing diversity. However, while managing to increase plant diversity, rare plants can be adversely affected. Discovering the responses of the rare plant species to tree removal and grazing provides the land managers with a tool to predict their responses to future management regimes.

Conclusions

The results demonstrate conclusively the dramatic effect of removal of the landscape modulator evergreen trees on herbaceous plant species richness in Mediterranean ecosystems. It supports the hypothesis that the effect of the landscape modulators on the herbaceous vegetation in this system is mediated mainly by the role of the tree canopy as a filter of dispersal units and as a sunlight screener (Shachak et al. 2008), and is not due to root competition (Callaway and Walker 1997) or enriching the ground with organic matter (Muñoz et al.2007).

Since grazing had a significant negative effect on regrowing of the landscape modulators' canopy (Agra 2007), we expect a long-term negative effect of cattle grazing on the size and spatial structure of the woody patches following clear cutting, and a consequent positive effect on herbaceous plant richness. In contrast, we found no evidence of the expected (Perevolotsky and Pollak 2001) difference between grazed and none-grazed plots. Extremely high and continuous grazing pressure is needed to reduce landscape modulator canopy and decrease the area of the woody patch (Gutman et al. 2000). We conclude that traditional cattle grazing can be used as an effective biodiversity management tool, mainly after removal or intensive trimming of landscape modulator tree canopy.

Preservation of woody and herbaceous patches, side-by-side, is essential for maintaining a high herbaceous plant biodiversity. The differential responses of the various plant functional types and the examined rare species to the treatments demonstrate their possible use as management tools for the maintenance of high diversity in general and conservation of some rare species in particular. Intelligent use of various active management tools (Perevolotsky 2005) is needed for maintaining landscape diversity, coexistence of various successional stages of the woody landscape modulators, and patch-types side-by-side for the maintenance of the high biodiversity level in Mediterranean ecosystems, which is a main goal of current nature conservation policy.

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