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Differential effects of goat browsing on herbaceous plant community in a two-phase mosaic

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Abstract The impact of herbivores on herbaceous plant communities is usually attributed to direct consumption of plants. We hypothesized that goats affect herbaceous plants both directly (consumption by foraging) and indirectly, by changing environmental conditions through modification of woody plant structure. We assessed the effects of goats browsing on environmental conditions, landscape structure, and herbaceous plants to link the direct and indirect effects of goats on herbaceous communities. Our model system was the Mediterranean woodland in Mt. Carmel, Israel. This is a two-phase mosaic landscape, composed of herbaceous (open) and woody patches. We delineated 10 plots of 1000 m^2, goats were introduced to five plots and five plots remained without goats. We monitored plant species richness and composition in two adjacent patch types (woody and open) in each plot. For each patch type, in all plots, we collected data on environmental conditions. We analyzed landscape structure using landscape metrics derived from a high-resolution vegetation map. We found that goats modified the structure of woody plants and hence the landscape mosaic. This alteration was associated with changes in environmental conditions, with more light penetration and higher temperatures. The impact of goats on the herbaceous plant community depended on patch type. In open patches, goats affected the herbaceous community mostly by direct consumption, whereas in woody patches they affected the herbaceous community mainly by modification of abiotic conditions. Our results stress the importance of considering landscape and patch structure in analyzing the effect of herbivory on plant communities.

Keywords Environmental conditions · Ecosystem engineers · Grazing · Mediterranean woodland · Patchiness · Species richness

Nomenclature: Feinbrun-Dothan and *Danin* (1998)

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Introduction

The impact of herbivores on herbaceous plant communities is often attributed to trophic relationships between herbivores and plants. However, herbivores affect herbaceous plant communities not only by direct consumption, but also indirectly, through modulation

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of the ecosystem and the landscape (Hobbs 1996). Herbivores may alter the structure of the landscape and the physical attributes of the ecosystem by activities such as soil trampling or modifying shrub canopy through browsing. Thus, they can indirectly affect herbaceous plant communities by causing biotic or abiotic changes and modulating the availability of resources to other species; such herbivores function as ecosystem engineers (Jones et al. 1994; Oren et al. 2007).

Foraging by domestic animals has a principal role in molding Mediterranean woodlands (Naveh and Whittaker 1980). Small ruminants, mainly sheep and goats, have been foraging the Mediterranean region for more than 7000 years (Blondel 2006) and can be considered as an integral part of the agro-natural system (Perevolotsky and Seligman 1998). Therefore, it is important to understand the different impacts of herbivores on the structure and function of the landscape.

In Mediterranean woodlands, goats are browsers, feeding mainly on foliage of woody plants (Bartolome et al. 1998). Therefore, hereafter we refer to the impact of goats on vegetation as “browsing,” even though goats may also consume herbaceous vegetation and function as grazers (Kababya et al. 1998). Foliage consumption modifies the canopy structure of woody plants and consequently affects microclimate conditions and soil nutrients (Suominen et al. 1999). At a larger scale, by controlling woody plant size, shape, and spatial distribution, herbivores have a significant impact on landscape structure (Cierjacks and Hensen 2004; Kefi et al. 2007). As landscape structure affects material and nutrient flow and distribution (Pickett and Cadenasso 1995; Turner 1989), its modification by goats may affect the distribution of resources in the system. In addition, through soil trampling and compaction, herbivores change the physical properties of soils and reduce water percolation and soil water content (Mwendera and Saleem 1997; Proffitt et al. 1993). Herbivores also affect soil chemical processes such as carbon and nitrogen mineralization, by changing the quantity and quality of litter deposited on the soil and by excretion of fecal pellets and urine (Jaramillo and Detling 1992; Pastor et al. 1993). Modification of ecosystem processes and characteristics by goats affects the availability of resources for plants and thus may alter plant species composition (Farris et al. 2010).

About 25% of terrestrial ecosystems are composed of two-phase mosaics with various proportions of woody and herbaceous patches (House et al. 2003). Nevertheless, most studies of foraging impacts on plant communities in two-phase mosaics analyzed the average impact of foraging on species richness over the entire landscape, while ignoring the differences in the responses to foraging among patch types (e.g., Milchunas and Lauenroth 1993). We hypothesize that in systems composed of different patch types, the impacts of browsing on herbaceous plant species vary among patch types. Although goats are mainly browsers, they may also consume herbaceous plants, and the availability of herbaceous vegetation to direct consumption is affected by patch structure. In open patches, herbaceous plants are more exposed to direct consumption, whereas woody patches are relatively safe sites in which herbaceous plants are protected (Milchunas and Noy-Meir 2002). In woody patches, the effect of goats on herbaceous species is mainly an indirect outcome of browsing the foliage of the woody plant, which modifies the environmental conditions in the patch. We suggest that indirect effects of herbivory on herbaceous plants are important, particularly where the dominant herbivores are typical browsers.

In this study, we assessed the effects of goats on a two-phase mosaic ecosystem, composed of herbaceous (open) and woody patches. We examined the impact of goats on herbaceous plants in the woody and open patches separately, to test the hypothesis that the impacts of browsing on herbaceous plant species vary among patch types. We also asked how goats affect landscape structure and how alteration of landscape structure by goats affects the herbaceous plant community. We hypothesized that the introduction of goats will result in an increase in size and number of the open patches, and hence increase herbaceous species richness.

Methods

Study site

The study site is located at the southern tip of Mt. Carmel, in the Ramat Hanadiv Park (32°555754′N, 34°943815′E, 120 m a.s.l.). The average annual precipitation is ~550 mm. The bedrock is dolomite and limestone, and the vegetation form is evergreen Mediterranean Garrigue, with sclerophyllous trees and shrubs and open patches. The dominant woody species is *Phillyrea latifolia* L. (Oleaceae), which constitutes over one-third of the woody cover. *Phillyrea latifolia* is a tall (2–5 m), branched, and dense evergreen shrub, and is common in Mediterranean lowlands (up to 800 m) in Israel (Feinbrun-Dothan and Danin 1998). The study site has a long history of human impact, especially livestock grazing and clear-cutting, but in the last 50 years these activities have been suppressed. However, the area was burned by a wildfire in 1980.

Experimental design

The effects of goats on the vegetative community were examined in a controlled experiment held in a two-phase mosaic. We studied two types of patches: patches dominated by the woody species *P. latifolia* and open patches dominated by herbaceous vegetation.

Ten square plots of 1000 m^2 were established. Five of them were left intact (control plots hereafter), while a herd of approximately 16 goats was introduced into the other five plots (browsed plots hereafter) during two consecutive seasons: April–December 2004 and 2005. Plots were randomly allocated and were mixed and adjacent to each other, to retain similar environmental conditions. Goats were excluded from the plots between the germination and sampling periods (Dec.–Apr.), in order to enable establishment of plant species and their subsequent identification during sampling. In order to obtain similar conditions, we rotated the goats between the plots. In total, each plot has experienced about 3,035 goat foraging hours during the experiment.

Landscape structure analysis

Low-altitude aerial photographs of the 10 experimental plots were taken in July 2006 by the Sky Balloons™ Company, with a digital camera mounted on a helium balloon hovering 110 m above the ground surface (Bar Massada et al. 2008). The resulting images had a spatial resolution of $\sim$3 cm and were classified into three thematic classes: (1) woody vegetation, (2) herbaceous vegetation, and (3) rocks; based on a maximum likelihood supervised classification in ERDAS IMAGINE 8.6 (ERDAS 1999). We used Fragstats 3.3 (McGarigal et al. 2002) to analyze the spatial structure of woody vegetation in the study plots. Four basic landscape metrics were used during the analysis; they quantify landscape structure according to size and spatial distribution of woody patches (Bar Massada et al. 2008). Woody vegetation cover was quantified in terms of the proportion of woody cover (PLAND) and mean patch size (AREA); patch spatial configuration was quantified in terms of patch density (PD); and their spatial structure in terms of edge density (ED). A detailed description of these metrics appears in Bar Massada et al. (2008). To assess the effect of goats on canopy structure, we used light penetration measurements, as described below.

Patch conditions

In order to characterize the effects of goats on environmental conditions in the two-patch system, we monitored abiotic variables in each plot and for each patch type. We monitored the following abiotic variables: light penetration through the canopy, soil moisture, pH, soil conductivity, and contents of NO_3^-, P, and organic material. Fifteen soil samples from a depth of 0–5 cm were collected from each combination of patch type and treatment (open and woody patches, with and without goats) in September 2005. Soil samples were analyzed for N, P, and organic matter contents by the Gilat Field Services Laboratory of the Ministry of Agriculture and Rural Development.

To evaluate the effect of goats on the litter layer in the woody patch, we collected the litter in 20 cm × 20 cm quadrats under *P. latifolia* in all plots. Litter samples were dried for 48 h at 80°C and weighted. We sampled 20 quadrats from each treatment.

Light penetration through *P. latifolia* canopy was recorded in December with a Sunfleck PAR Ceptometer (Decagon Devices, Pullman, WA). The Ceptometer consists of a probe with 40 photosynthetically active radiation sensors located at 1-cm intervals; it measures the fraction of the ground covered by sunflecks (the bright areas under the canopy where direct solar radiation penetrates without attenuation). It is a useful measurement for determining canopy cover density. For each patch type, in each of the plots, we took six measurements. In total, 30 readings were taken for each combination of patch type and treatment.

Soil water content at 0–12 cm depth was determined with time-domain reflectometry (TDR) probes (HydroSense® CS620, Campbell Scientific, Logan, UT) in the winter. Measurements were taken 3 and 11 days after a rain event, to examine the impact of patch type on water penetration and soil water content dynamics. Five measurements were taken for each patch type in each plot, i.e., 25 measurements in each patch type in each treatment. Soil temperature was measured with iButtons instruments (Maxim Integrated Products, Sunnyvale, CA) buried 5 cm below the soil surface, recording every hour during the growing season, from January to April. Three measurements were taken from each combination of patch type and treatment every hour. Here, we present the averaged temperature at 13:00 during February, i.e., the average temperature during 28 days in three different patches of the same combination of patch type and treatment.

Species sampling

We sampled the herbaceous plant community on spring 2006, after two browsing seasons. Herbaceous species were sampled in each patch type separately, according to a stratified random sampling scheme. For each patch type in each plot, we randomly sampled herbaceous plant species in 48 quadrats of 20 × 20 cm and recorded the species within each quadrat. Species richness S_{ij} is the total number of species in patch type i in plot j and S_j is the total number of species in plot j. Species density is the number of species in a sampling quadrat. Species frequency calculated for each patch type in each plot is the proportion of quadrats in which a species is present from the total number of sampled quadrats in each patch type in each plot.

Statistical analysis

We used two-way ANOVA to determine if goats and patch type significantly affected environmental variables. We used Tukey's HSD post hoc tests to analyze the statistical differences between browsed and control plots and in each patch type. This enabled us to determine differences in the response to goats between patch types. For comparing the effects of goats on litter cover under the woody patches, we used t test. Prior to analysis, data were checked for normality and homogeneity of variances. The following data were log transformed to meet ANOVA assumptions: light measurements, average soil temperature at 13:00 during February, and soil moisture 3 days after the rain.

We used two-way ANOVA to test the effect of goats on species richness, species density (the average number of species in 400 cm^2 sampling quadrat), and frequency of specific species in woody and open patch types. To assess the effect of goats on species richness and on landscape metrics, we used a non-parametric test, Wilcoxon Rank Sum, for small number of samples, since we had only five replicates (plots) for each treatment.

In order to test the relationships between landscape structure and species richness, we calculated Spearman rank correlation between richness and each landscape metric in each plot. We assumed that the strength of the correlation might differ in between treatments. We used a permutation test (Crowley 1992) to test the differences in Spearman rank correlation values between treatments. Toward that end, we constructed all 252 possible combinations of selecting 5 of 10 plots and calculated the Spearman rank correlation values for each combination.

The Bray–Curtis similarity coefficient (Bray and Curtis 1957), based on square root transformation of frequency of species within each patch type, was used for constructing similarity matrices. Non-metric multi-dimensional scaling analysis (MDS), a distance-based ordination, was used for presentation of differences in species composition between samples. We used analysis of similarity by permutations (ANOSIM; Clarke 1993) to test significance of differences in species composition between treatments. These analyses were performed using the PRIMER software, version 4.0 (Clarke and Gorley 2001).

Results

The impacts of goats on patch characteristics

Light penetration was significantly affected by the presence of goats ($F_{1,116} = 7.8$, $P = 0.006$) and by patch type ($F_{1,116} = 200.8$, $P < 0.0001$). The interaction between the two factors was not significant ($F_{1,116} = 2.2$, $P = 0.14$), indicating higher light penetration in the presence of goats in both patch types (Fig. 1a). Midday soil temperatures were higher in browsed plots in both patch types (Fig. 1b, c). The two-way ANOVA showed a significant effect of browsing ($F_{1,332} = 83.3$, $P < 0.0001$) and patch type ($F_{1,332} = 6.22$, $P = 0.013$) on average soil temperature at 13:00 during February. The interaction between the two factors was not significant ($F_{1,332} = 0.24$, $P = 0.62$). In addition, in browsed plots, the variations in daytime temperatures were higher in both patch types (Fig. 1b, c).

The increased opening of the shrub canopy by goats affected rainwater penetration into the patch. This effect was different between patch types, and the

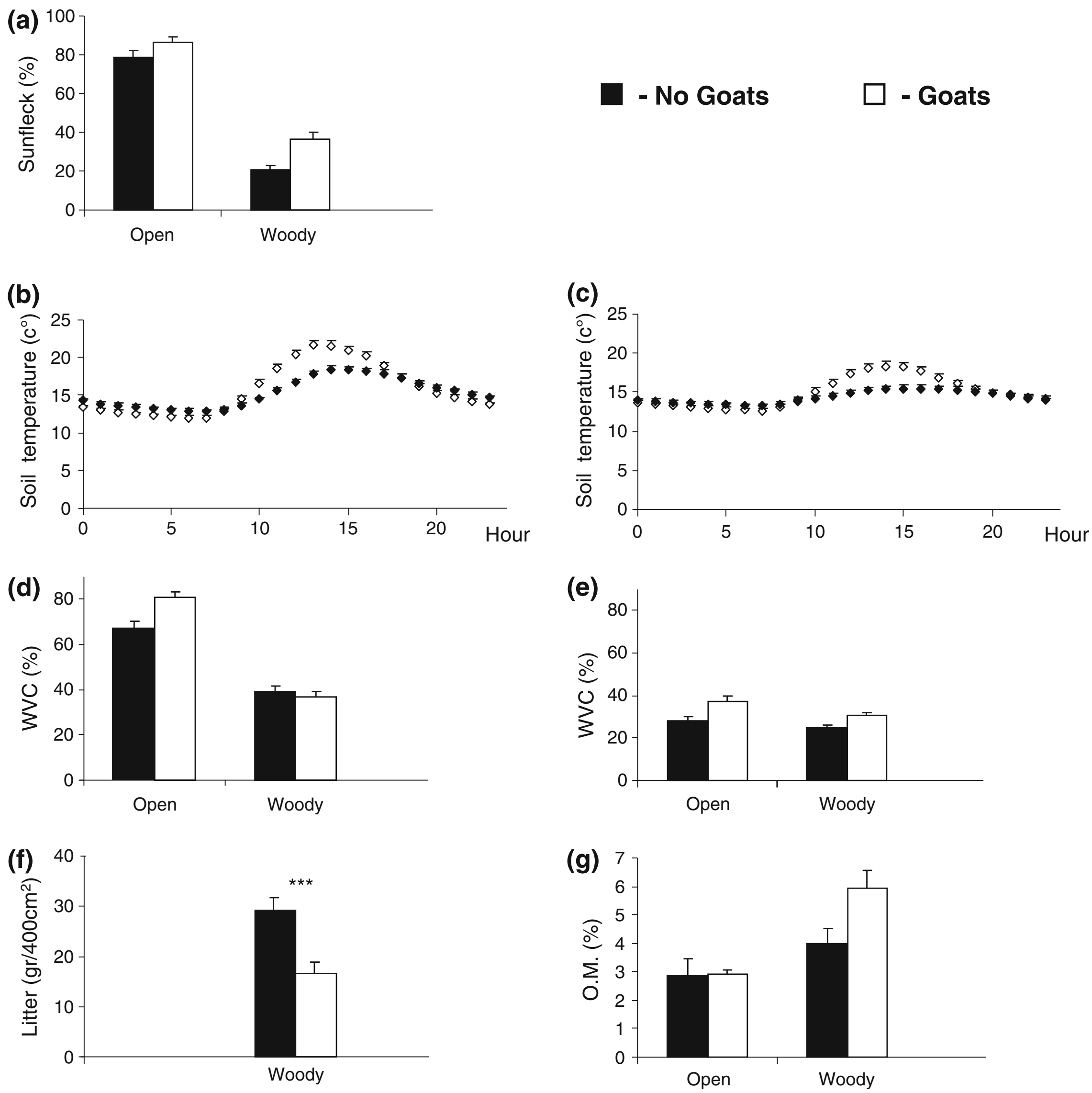

Fig. 1 Abiotic conditions in the various patch types, with and without goats: **a** percentage of sun flecks, $n = 30$; **b** 24 h average (±SE) soil temperature in open patches with goats (*open symbols*) and without goats (*full symbols*) in February, $n = 84$; **c** 24 h average (±SE) soil temperature in woody patches in February, $n = 84$; **d** soil water content (%) 3 days after rain, $n = 25$; **e** soil water content (%) 11 days after rain, $n = 25$; **f** amount of litter in the woody patches, $n = 20$; **g** percentage of soil organic matter, $n = 15$. *Asterisks* indicate statistical significance according to *t* test, *** $P < 0.001$

interaction was significant ($F_{1,96} = 7.12$, $P = 0.009$). Three days after a rain event, soil water content was higher in browsed plots only in the open patches (Fig. 1d). Eleven days after a rain event, soil water content was significantly lower in browsed plots ($F_{1,96} = 5.5$, $P = 0.02$) and was higher in the open patches in comparison to the woody patches ($F_{1,96} = 12.42$, $P < 0.0007$, Fig. 1e). The interaction between the two factors was not significant ($F_{1,96} = 6.86$, $P = 0.4$). The reduction in soil moisture between 3 and 11 days after the rainfall was somewhat lower in browsed plots in the woody patches, but not in the open patches (Fig. 1d, e).

Litter cover under woody patches in browsed plots was lower than under woody patches in control plots ($t = -3.5$, $P = 0.0011$, Fig. 1f). Goats tended to increase soil organic matter content in woody patches, although the difference was not significant ($F_{1,56} = 4$, $P = 0.06$ in two-way ANOVA, Fig. 1g). Goats did not affect pH, soil conductivity, NO_3^-, or P content.

The impacts of goats on the plant community

Two-way ANOVA revealed a significant interaction between patch type and treatment in their effect on total species richness in the plot ($F_{1,16} = 6.7$, $P = 0.02$, Table 2). Species richness in the open patches was lower in browsed plots (75.2 vs. 85.4 in browsed and control plots, respectively, Table 1). In contrast, species richness in the woody patches was higher in browsed plots (39.2 vs. 31.4 in browsed and control plots, respectively, Table 1). Species density (average number of species in 400 cm^2) also had a significant interaction between patch type and treatment ($F_{1,956} = 78.94$, $P < 0.001$, Tables 1, 2).

Table 1 Average (±SE) species richness and species density in herbaceous and woody patches and total per plot (0.1 h)

	Control	Browsed
Average species richness ($n = 5$)		
Plot (total)	108.4 ± 4.68	101.4 ± 2.94
Open	85.4 ± 2.8	75.2 ± 3.3
Woody	31.4 ± 4.9	39.2 ± 2.35
Average species density (per 400 cm^2) ($n = 5$)		
Plot (total)	5.8 ± 0.14	5 ± 0.09
Open	9.4 ± 0.22	6.94 ± 0.17
Woody	3.1 ± 0.09	3.35 ± 0.09

Table 2 Two-way analysis of variance for the significance of the effects of browsing, patch type and their interactions on species richness and density

Source	df	Mean square	*F* ratio	*P* value
Average species richness ($n = 5$)				
Browsing	1	7.2	0.12	0.73
Patch type	1	10125	167.35	<0.001
Browsing × patch	1	405	6.7	0.02
Average species density (per 400 cm^2) ($n = 240$)				
Browsing	1	297.04	52.63	<0.001
Patch type	1	5870.7	1040.2	<0.001
Browsing × patch	1	445.5	78.94	<0.001

Similar to species richness, species density in open patches was higher in the control plots, and species density in woody patches was higher in the browsed plots (Table 1).

Only a few species differed significantly in their frequency between treatments. The average frequency of *Urospermum picroides* increased from 0.08 in control plots to 0.18 in browsed plots ($F_{1,16} = 4.96$, $P = 0.04$). *U. picroide* frequency was higher in the open patches ($F_{1,16} = 7.6$, $P = 0.014$), and there was no interaction between the two factors ($F_{1,16} = 0.29$, $P = 0.6$). The species *Crucinella macrostachya* and *Plantago cretica* had significant interactions between treatment and patch type ($F_{1,16} = 11.97$, $P = 0.003$ for *C. macrostachya* and $F_{1,16} = 4.96$, $P = 0.04$ for *P. cretica*). Both species showed a significant lower average frequency in browsed plots (0.2 and 0.06 for *C. macrostachya* and 0.18 and 0.04 for *P. cretica*, in control and browsed plots, respectively). The species *Anagallis arvensis* presented different responses to goat foraging in different patch types. The interaction between patch type and treatment was significant ($F_{1,16} = 21.54$, $P = 0.0003$), and its frequency decreased in open patches (from to 0.38 to 0.23) and increased in woody patches (from 0.008 to 0.15). The frequencies of many other species decreased after the introduction of goats. These trends were not significant, but contributed to the reduction in species richness and density under the presence of goats.

In addition to the effects on species richness and density, we also examined species composition. Species composition in the woody patches was significantly different between treatments (Table 3). Differences in species composition between patch

Table 3 Significance of differences in species composition between treatments, in the whole plot and in open and woody patch type separately

	ANOSIM statistic (*P* value)
Differences in species composition ($n = 5$)	
Plot	0.252 (0.071)
Open	0.24 (0.063)
Woody	0.412 (0.024)

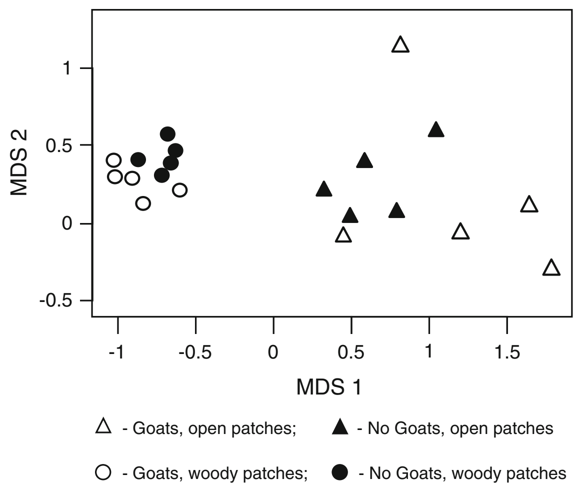

Fig. 2 Multi-dimensional scaling diagram, a distance-based ordination presenting species similarity between patch types in plots with and without goats. Distances between symbols represent Bray–Curtis dissimilarities in species composition. $n = 5$ for each combination of treatment and patch type

types and treatments are presented in an MDS diagram in Fig. 2; distances between symbols represent dissimilarities in species composition according to the Bray–Curtis index. Each symbol in the MDS represents species composition in a patch type in a plot. Proximity between two symbols indicates high similarity in species composition between two patch types in a plot. The diagram shows clustering by patch type. Species composition in open patches differed from that of woody patches. In addition, two groups of woody patches could be distinguished: browsed and control.

Effects of goats on landscape structure and the link to plant community

The consumption of woody plants by goats changed the structure and configuration of the shrubs. This effect was expressed in the shape and size of patches as well as in their numbers: the average size of a woody patch and the total extent of woody cover were significantly lower, while the density of patches was higher in browsed plots (Table 4). In addition, the shape of the browsed patches became more compact and their edge became more twisted.

Table 4 Average (±SE) landscape metrics in browsed and control plots ($n = 5$)

	Control	Browsed	*P*
PLAND	74.85 ± 5.03	56.97 ± 2.49	0.016
AREA	6.47 ± 1.62	1.81 ± 0.24	0.021
PD	153.24 ± 41.27	299.41 ± 30.62	0.076
ED	13703.61 ± 1389.44	21326.61 ± 1472.3	0.016

PLAND proportion of woody vegetation in landscape, *AREA* mean size of woody patches, *PD* patch density, *ED* edge density

The significance of the differences according to Wilcoxon Rank Sum test

There was a clear and consistent contrast between treatments in terms of the correlation between vegetation structure and species richness (Table 5). In control plots, richness consistently decreased with vegetation cover and patch size, and increased with fragmentation (patch- and edge density). In browsed plots, an opposite trend occurred, as richness increased with vegetation cover and decreased with fragmentation. These findings were consistent for open patches as well as for closed patches (with a single exception). In control plots, correlation values were significant in 9 of 12 cases, while only 4 of 12 correlation values were significant in browsed plots.

Discussion

Impacts of goats on patch characteristics

The opening of woody patches by goats and the increased number of broken branches accumulated on the ground underneath woody plants changed environmental conditions under woody patches (Fig. 1). Although browsing occurred mostly on woody patches, it also affected conditions in the adjacent open patches (Fig. 1b, d, e). Increased soil temperatures in herbaceous patches with goats might be the result of the reduction in woody patch size, which

Table 5 Spearman correlation values (r_{sp}) and significance (P) between each of the four landscape metrics and three richness measures

Landscape metric	Richness	Control		Browsed	
		r_{sp}	P	r_{sp}	P
% Woody vegetation	Richness in plot	−0.9	0.004	0.41	NS
	Richness in open patches only	−0.87	0.004	0.6	NS
	Richness in woody patches only	−0.8	NS	−0.6	NS
Patch area	Richness in plot	−0.8	0.02	0.82	NS
	Richness in open patches only	−0.87	0.004	0.7	NS
	Richness in woody patches only	−0.9	0.048	0.7	0.016
Patch density	Richness in plot	0.8	0.044	−0.82	0.044
	Richness in open patches only	0.87	0.008	−0.7	NS
	Richness in woody patches only	0.9	NS	−0.7	0.004
Edge density	Richness in plot	0.8	0.012	−0.82	NS
	Richness in open patches only	0.87	0.008	−0.7	NS
	Richness in woody patches only	0.9	NS	−0.8	0.012

reduced shading on adjacent open patches. The higher soil moisture in patches subjected to browsing compared to unaffected patches might be the outcome of soil trampling by goats, which increased soil micro-relief and improved surface detention of water (Archer and Smeins 1991).

Water permeability was higher in browsed plots in open patches, but not in woody patches. The lack of change in soil moisture in woody patches might have stemmed from the habit of goats to browse mostly on the edge of woody plants, so that there was only a slight change in the way browsed woody plants blocked raindrops and affected soil moisture in the patch. In woody patches, the rate of soil drying up was lower in the presence of goats (Fig. 1d, e), possibly because of the broken branches that covered the ground due to goats' activity and impeded soil water evaporation.

As environmental conditions affect plants germination and growth, changing environmental conditions by introduction of goats may indirectly affect the plant community, regardless of their direct effect by consumption. Therefore, although herbaceous vegetation in woody patches is relatively protected from direct consumption by goats, browsing still may affect it by modifying environmental conditions.

Impacts of goats on landscape structure

In Mediterranean woodlands, goats function mainly as browsers rather than grazers (Dumont et al. 1995; Papachristou et al. 2005). Therefore, goats may affect landscapes predominantly by modifying woody plant architecture through canopy browsing. Depending on plant size, browsing may concentrate on the edge of tall shrubs or on the entire canopy of low shrubs. We observed that during browsing, goats broke branches and reduced the size of woody patches (Table 4). In addition, browsing reduced leaf cover and canopy density. At a larger scale, the reduction in woody patch size that followed browsing resulted in reduction in woody vegetation cover at the landscape scale (Table 4). In addition, patch density increased because of structural fragmentation of large woody patches and their division into multiple small patches.

In a mosaic of woody- and herbaceous vegetation, browsing on woody vegetation can affect landscapes by suppressing woody patches and transforming a patchy landscape dominated by woody vegetation into a landscape dominated by herbaceous vegetation (Cingolani et al. 2008; Fabricius et al. 2002). In regions with a long history of browsing, its exclusion may result in a landscape dominated by woody vegetation (Bartolome et al. 2000; Verdu et al. 2000). Intensive browsing that significantly reduces woody biomass may decrease the differences in abiotic conditions between herbaceous and woody patch types and thereby increase landscape homogeneity. Our results indicate that 2 years of heavy browsing pressure reduced woody patch size and cover of woody vegetation, but retained the two-phase structure of the landscape. Since similar grazing pressure has been in effect for thousands of years, the resilience of the system is high (Focardi and Tinelli 2005), and the woody vegetation could recover from goat browsing once it is reduced or excluded.

Impacts of goats on the plant community

Significant interactions between the effects of patch type and goats on species richness and density (Table 2) support the hypothesis that the responses of plant species to herbivory are affected by the structure and properties of patch types (Osem et al. 2007). Whereas goats prefer foliage of woody plants, they may also consume herbaceous vegetation. Since herbaceous vegetation in open patches is accessible, it may be exposed to more consumption. Consequently, in open patches the direct impact of herbivores on herbaceous vegetation is stronger than the indirect impact. For that reason, species richness in open patches did not increase following the introduction of goats despite the improved soil water conditions. In our study, goats did not consume herbaceous vegetation during Dec.–Apr. since they were excluded from the plots between the germination and sampling periods. However, they may directly affect the herbaceous community by consuming seeds.

On the other hand, herbaceous vegetation within woody patches is less accessible, although it may be eaten during browsing of woody plant foliage. Therefore, in woody patches, the main impact is indirect, by canopy modulation that alters abiotic conditions and landscape structure. As woody plants have an important impact on herbaceous plant species in Mediterranean woodland (Agra and Ne'eman 2009), changing their structure by browsing affects the herbaceous community.

Opening the canopy of woody plants creates new sites for species that could not arrive or persist before the experimental browsing. The majority of species found in foraged woody patches characterize disturbed habitats; they have wind-dispersed seeds that facilitate quick colonization of new sites. The modification of shrub structure facilitated the establishment of species that inhabited only open patches prior to the introduction of goats. Following the experimental browsing, these species populated both open and woody patch types, and their frequency in the plots increased. In open patches, the frequency of species that are vulnerable to foraging decreased following the introduction of goats; in fact, some species virtually disappeared from the foraged plots (for example, *Scabiosa prolifera* and *Picris galilae*). These changes indicate that goat activity can redistribute herbaceous species in the landscape and thus modify plant community structure. Analysis of changes in plant composition in each patch type separately is necessary, to gain a better understanding of the impact of herbivores in heterogeneous systems. Analysis of herbivory impacts in the whole plot without reference to different patch types may overlook significant alterations in plant communities.

Grazing pressure

In our experiment, goats did not forage throughout the whole year round, but only in rotation for 9 months (April–December). In total, each 1000 m^2 plot was exposed to about 1,518 goat foraging hours in a year, which are equivalent to 41.6 foraging hours ha^{-1} day^{-1}. Observations showed that in traditional systems goats spent 5–8 h a day foraging (Negi et al. 1993; Penning et al. 1997). Therefore, 41.6 foraging hours ha^{-1} day^{-1} are equivalent to a single foraging day with a foraging pressure of 5.2–8.3 goats ha^{-1}. Such foraging pressure is high and can be found in commercial herds in Mediterranean woodlands (Alados et al. 2004; Gangoso et al. 2006). The foraging regime in our experiment differed from traditional foraging activity, mainly because we controlled foraging by fencing and avoided foraging during the growing season of the herbaceous plants. Nevertheless, our experimental conditions created a similar foraging pressure on the vegetation, in terms of exposure hours, as traditional systems. Therefore, our experiment simulated heavy goat pressure in natural Mediterranean woodland foraging systems.

Linking impacts at landscape scale and community level

Our results show that woody cover largely affects herbaceous species composition. Without browsing, development of dense woody patches was correlated with lower species richness (Table 5). The dominance of woody patches reduced the size and number of open patches and thus decreased habitat diversity. Since open patches form a species-rich niche, it was predicted that the reduction in size and numbers of open patches, together with reduction in habitat diversity, would result in reduction in species richness over the whole plot (Wright et al. 2004).

We therefore predicted that opening the woodland through goat browsing would increase species richness at the plot. However, the reduction in woody cover and woody patch size in the browsed plots did not significantly increase species richness in the plot (Table 5). This could be a result of damage to species in open patches (Table 1). Even though in our study goats did not consume herbaceous plants directly, they may have had a negative effect on plant species richness through seed consumption (Chaideftou et al. 2009) and soil compaction (Alados et al. 2004). These effects on herbaceous vegetation change the relationship between species richness and landscape structure, as shown in Table 5.

This study presents the results of 2 years of heavy grazing. The experiment is a part of a long-term research in Ramat Hanadiv Park, which studies short- and long-term impacts of grazing. In the future, we intend to assess the same parameters of environmental conditions, landscape structure, and herbaceous plant community after 10 years of grazing, to study the differences between short- and long-term effects.

Conclusions

Our study highlights the importance of considering the various impacts of browsing and grazing on different patch types in a landscape mosaic. We show that in a landscape composed of woody and open patches, the impact of herbivory depends on patch type. In open patches, herbivores affect herbaceous vegetation mainly by consumption of plants and seeds, whereas in woody patches the effect on herbaceous vegetation is mainly indirect, through modification of patch properties. The dual function of browsers as consumers and as ecosystem engineers initiated two opposing trends of change in species richness, depending on patch type: in open patches, direct consumption of herbaceous vegetation reduced species richness, whereas in woody patches modification of abiotic conditions increased species richness. We argue that at the short-term, the main effect of ecosystem engineering by browsing is redistribution of species between patch types.

Animal behavior and patch traits determine whether foraging animals affect the vegetation mainly as consumers or as engineers; therefore consideration of the effects of browsing and grazing on ecological systems should take into account landscape structure and patch type properties. The number, size, and distribution of the various patch types determine the relative effects of foraging animals as consumers or engineers, and thus determine their overall effect on plant communities. Landscape structure should be taken into account when considering the employment of livestock as a management tool for reducing woody vegetation cover and promoting high plant species richness (Verdu et al. 2000).

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