

Understory structure and function following release from cattle grazing and overstory thinning in Mediterranean conifer plantations

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Abstract

• **Key message** Cattle grazing and overstory cover restrict understory growth and interact in shaping the understory community structure in Mediterranean conifer plantations.
• **Context** Understanding how silvicultural manipulations drive understory structure and function in Mediterranean pine plantations is essential for their multifunctional management.
• **Aims** This paper aims to study the interactive effects of cattle grazing and overstory thinning on understory structure and function.
• **Methods** Ten plots (0.25 ha) were selected in East Mediterranean mature *Pinus brutia* plantation (rainfall = 600 mm year⁻¹) representing thinned (≈100 trees ha⁻¹, leaf area index (LAI) ≈ 1.6) and non-thinned

(≈230 trees ha⁻¹, LAI ≈ 3.5) areas. Two subplots (100 m²) within each plot were fenced in 2000 and 2006 while a third one remained grazed. Understory growth and species composition were measured in 2010.

• **Results** Thinning and grazing exclusion both positively influenced woody growth with their combined effect during 10 years leading to 20-fold increase in vegetation volume. An increase (15-fold) in herbaceous biomass was recorded 4 years after grazing exclusion but disappeared 10 years after exclusion due to increased woody cover. Species richness was not influenced by grazing but was positively affected by thinning. Understory composition was affected by grazing × thinning interaction with herbaceous ephemerals and short woody species being more frequent in grazed, thinned areas while larger woody species were more associated with ungrazed, non-thinned areas.

• **Conclusion** Grazing impacts on forest understories depend on overstory cover. We propose variable grazing-thinning combinations to meet multiple management objectives.

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1 Introduction

Conifer forest plantations are widely distributed throughout the Mediterranean (De Luis et al. 2013; Quezel 2000). In the East Mediterranean, these plantations are composed of drought-tolerant pine species of which the most common ones are *Pinus halepensis* Mill. and *Pinus brutia* Ten. Mediterranean pine forests are multifunctional (Osem et al. 2008; Perevolotsky and Sheffer 2009) and livestock grazing is an important form of land use in these forests (Evlagon et al. 2010; Mancilla-Leytón et al. 2012). While forest areas provide

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forage and husbandry for livestock, grazing is useful as a means for fuel load control and fire hazard reduction (Evlagon et al. 2012; Ne'eman et al. 1997).

Conifer-based afforestation in the Mediterranean was frequently associated with a degraded state of natural vegetation communities (Osem et al. 2008). However, during the last decades, the native vegetation slowly recovered and developed as an understory layer (Osem et al. 2009, 2012). The pace of this process varies among forest sites depending on habitat, disturbance, and silvicultural characteristics (Gómez-Aparicio et al. 2009; Hernandez-Tecles et al. 2015; Maestre and Cortina 2004).

The understory vegetation is increasingly recognized as an important component of forest ecosystem structure and function (Barbier et al. 2008; Vanderschaaf et al. 2000, 2004). The understory contains most of the plant diversity and provides critical food and habitat for wildlife and livestock (Bakker et al. 2010; Hegland et al. 2013; Kleintjes et al. 2004; Mosquera-Losada et al. 2009). Moreover, this vegetation layer, which developed in the conifer plantations, provides the basis for the transition of these simply structured systems toward a more diverse and complex state (Navarro-Cerrillo et al. 2013; Osem et al. 2008). However, the course of this process and the ways by which it is driven by environmental and silvicultural factors are still quite poorly understood (Gómez-Aparicio et al. 2009; Maestre and Cortina 2004). In particular, little is known about the impacts of livestock grazing on understory structure in Mediterranean pine forests.

The impacts of grazing in natural vegetation communities of the Mediterranean have been addressed quite extensively (Gutman et al. 2000; Hadar et al. 1999; Noy-Meir et al. 1989; Osem et al. 2004). Much less attention, however, has been directed toward forest plantations. It is well established that the survival and performance of plant species may be affected differentially by grazing through consumption and physical damage (Carmona et al. 2013; Kuiters and Slim 2002), competition release (Darabant et al. 2007; Khishigjargal et al. 2013), soil disturbance (Hamza and Anderson 2005; Trimble and Mendel 1995), nutrient redistribution (Bokdam and Gleichman 2000), and seed dispersal (Cosyns et al. 2005; Mancilla-Leytón et al. 2014). This and more, grazing effects, at the entire community level, may diverge across vegetation, habitat, and grazer characteristics (Ameztegui and Coll 2015; Randall and Walters 2011; Tyler et al. 2008). In forested sites, characteristics related to stand structure are particularly interesting since they are bound to silvicultural manipulation with major consequences on vegetation structure and function (Osem et al. 2013; Prevosto et al. 2011). For example, light penetration, determined through overstory cover, is a crucial factor determining vegetation performance in the forest understory (Jennings et al. 1999; Rodríguez-Calcerrada et al. 2008). Furthermore, soil resources'

availability and use efficiency in the understory also depend on competitive and microclimatic effects of the overstory (Devine and Harrington 2008; Rodríguez-Calcerrada et al. 2008). It was previously proposed that consequences of grazing on plant community structure are likely to vary and may even reverse in low vs. high productivity habitats (Cingolani et al. 2005; Proulx and Mazumder 1998). Thus, grazing may be expected to interact with overstory cover and related productivity variation, in shaping the understory structure. Studying this type of interaction may contribute largely to the understanding of plant diversity patterns in forests worldwide (Fortuny et al. 2014). Furthermore, it may assist foresters in managing the pine plantation to meet multiple management objectives.

Previous studies looking at the understory in East Mediterranean pine plantations have focused primarily on natural regeneration of tree species (Osem et al. 2009, 2013, 2015). In this study we pursued a more comprehensive understanding of the ways by which understory structure and function is driven by management factors. Specifically, we investigated the interactive effects of two major silvicultural and pasturing tools namely, overstory thinning and cattle grazing, on understory productivity and community structure. These characteristics were compared in grazed vs. ungrazed plots within thinned and non-thinned forest areas. We hypothesized that overstory thinning (i.e., overstory cover reduction) will increase understory productivity and, therefore, grazing impact on understory structure will depend on overstory cover. In our approach, we used woody vegetation volume and herb biomass for understory productivity while species richness and composition were used for community structure.

2 Materials and methods

2.1 Site

The study was performed in the Mount Horshan Forest area located in the Ramat Menashe region (34° 59' 58 E, 32° 35' 14 N) of Israel. The climate is typical east Mediterranean. Average annual rainfall amount is about 600 mm concentrated mainly between December and March. The drought season is long; typically 6 months with no rain. Daily average temperatures range between 11 °C in the winter and 26 °C in the summer. The elevation is 170 m a.s.l. Local soils are bright mountain rendzines which developed on soft chalk and marl. The typical native vegetation is sparse woodland dominated by *Quercus ithaburensis* Decne. accompanied by *Quercus calliprinos* Webb., *Pistacia palaestina* Boiss., *Pistacia lentiscus* L., and *Styrax officinalis* L. The experiment was carried out in a mature *P. brutia* (Calabrian pine) forest. Since the early 1970s, this

pine species, exotic to Israel, has gradually replaced the native *P. halepensis* (Aleppo pine) as the leading conifer used for afforestation in Israel. According to forest service documentation, the study area was subjected to controlled cattle grazing since 1990. Based on local foresters' knowledge, this area was under livestock grazing of varying intensity for decades prior to any documentation. Since 1990, cattle stocking rate has increased gradually from about 2.5 animal units month (AUM) ha⁻¹ to a level of 3 AUM ha⁻¹ within the last 7 years including the study period. The herd, a breed mixture of Charolais, Brahma, and Baladi, enters the forest in the beginning of November and forages freely until the end of April.

2.2 Experimental structure

A 50-year-old *P. brutia* plantation (approx. 10 ha) was selected for the study in 2000. Average tree stem diameter at breast height (DBH) and tree height were 32.5 ± 5.8 cm and 19.1 ± 0.8 m, respectively. The plantation has undergone two comprehensive thinning treatments, one at the age of ≈ 10 years and the other at the age of ≈ 20 years. Since then, a combination of natural mortality and limited silvicultural intervention (sanitation thinning, i.e., removal of dead trees) has resulted in the designated forest area exhibiting a patchy distribution of variable stand structure ranging in tree density: 4–30 trees ha⁻¹, stem basal area (BA) 4–23 m² ha⁻¹, overstory leaf area index (LAI) 1–3.6 m² m⁻², and overstory canopy cover 20–95%. Ten 50 × 50 m plots (0.25 ha) were randomly selected, five of them from thinned forest areas (i.e., thinned within the last 20 years, average tree density ≈ 100 trees ha⁻¹ and canopy cover $\approx 55\%$) while the other five from non-thinned areas (average tree density ≈ 230 trees ha⁻¹ and projected canopy cover $\approx 95\%$). In the center of each plot, two 10 × 10 m subplots were situated; one of them fenced to exclude grazing (ungrazed 10 years) while the other remained open (grazed subplot). In 2006, five additional 10 × 10 m subplots were fenced (ungrazed 4 years) three of which were located in thinned plots and two located in non-thinned plots. Thus, the experimental structure represented a split-plot design with thinned/non-thinned as the main plots and grazed, ungrazed 10 and 4 years as subplots. An area of 10 × 10 m was practically the largest subplot size that could be attained. This was due to the limited area of thinned/non-thinned plots (approx. 50 × 50 m) and the need to avoid marginal effects by keeping a 15-m buffer zone around the subplots' borders. For the same reason, the inclusion of a third subplot (ungrazed 4 years) was only possible in the larger five out of the ten research plots. Measurements of understory woody cover and height and herb biomass were implemented in all of the research plots during 2010. Understory species richness and composition were surveyed during 2010 only in the ungrazed 10 years and grazed subplots.

2.3 Measurements

2.3.1 Overstory characteristics

Stand density, tree height, and DBH were measured separately in each of the ten study plots. Density was determined based on total plot tree count while height and DBH were measured in a sample of 20% or ten trees at least. Average tree density was 233.3 ± 8.9 trees ha⁻¹ in the non-thinned plots and 100.4 ± 13.0 trees ha⁻¹ in the thinned plots. Average tree height and stem diameter were similar among the thinned (18.6 ± 1.18 and 33 ± 10.1 cm, respectively) and non-thinned plots (19.6 ± 0.43 m and 32 ± 1.5 cm, respectively). To account for possible within-plot variation, leaf area index (LAI) and canopy cover were measured at the subplot level over three evenly distributed 10-m transects. Leaf area index was determined using the optical tracing radiation and architecture of canopies device (TRAC, Chen et al. 1997) while for overstory canopy cover (projected canopy cover, %), a sighting tube was used (Jennings et al. 1999). Average canopy cover and LAI for the six different thinning-grazing combinations are presented in Table 1. Canopy cover and LAI were approximately twofold larger in the non-thinned than in the thinned plots ($P < 0.0001$) but did not differ among the grazing treatments.

2.3.2 Understory woody vegetation

Understory woody vegetation comprising dwarf shrubs (e.g., *Cistus creticus* L., *Sarcopoterium spinosum* L.); shrubs (e.g., *Rhamnus lycioides* L., *P. lentiscus* L.); vines (e.g., *Ephedra foeminea* Forssk., *Smilax aspera* L.); and regenerating trees (e.g., *Q. calliprinos* Webb., *Q. ithaburensis* Decne.), was measured during summer (July) 2010. The line intercept method (Osem et al. 2012) was used in each subplot along five evenly distributed transects of 10-m length (altogether, 125 transects). Woody growth was quantified by the following three parameters: (1) surface cover—the proportion of surface covered by vegetation; (2) average height (weighted by cover); and (3) specific vegetation volume—the product of surface cover [proportion] × area [m²] × average height. A woody vegetation patch was defined as a unit of continuous cover by a single woody species, and by measuring all such patches separately, we could calculate surface cover for any single species or species group, as well as for the total woody understory. For further details, see Osem et al. (2012).

2.3.3 Understory herbaceous vegetation

Understory herb biomass which comprised a variety of ephemeral species (mostly annuals) was measured during spring (April) 2010. Four representative herbaceous samples were taken in each subplot during peak standing crop (April)

Table 1 Average projected canopy cover (PCC, %) and leaf area index (LAI) for six combinations of overstory thinning and cattle grazing treatments. Mount Horshan

Thinning treatment	Grazing treatment	PCC [%]	LAI
Non-thinned	Ungrazed 10 years	95.56 ± 2.22	3.57 ± 0.17
	Ungrazed 4 years	96.34 ± 3.21	3.63 ± 0.21
	Grazed	94.45 ± 2.68	3.41 ± 0.38
Thinned	Ungrazed 10 years	51 ± 6.7	1.61 ± 0.47
	Ungrazed 4 years	44.15 ± 9.43	1.33 ± 0.33
	Grazed	58.33 ± 4.20	1.78 ± 0.14

Non-thinned plots that were not thinned within the last 20 years, *Thinned* plots that were thinned within the last 20 years, *Ungrazed 10 years* subplots that were protected from grazing within the last 10 years, *Ungrazed 4 years* subplots that were protected from grazing within the last 4 years, *Grazed* subplots unprotected from grazing

by clipping aboveground biomass within 400 cm² quadrats. Samples were oven dried (65 °C, 48 h) and weighed.

2.3.4 Understory community structure

Plant species richness and composition were measured during spring (April) 2010. In each subplot, four samples of 10 m² were laid and all plant species occurring in each sample (10 m²) and within the entire subplot area (100 m²) were listed. Species richness for each treatment was determined via the average number of species per subplot (100 m²). Species abundance was determined via species incidence—the number of samples in which a species occurred out of the total number of samples (four) within a subplot.

2.4 Data analyses

Analyses of variance (ANOVA) were used to examine variation in vegetation parameters with respect to overstory thinning (thinned, non-thinned) and grazing (grazed and ungrazed 10 and 4 years). In order to address the experimental design (split-plot), a nested statistical model was used (grazing nested within thinning). Assumptions for ANOVA were tested through both the Levene and Bartlett tests for homogeneity of variances and the Shapiro-Wilk test for normal distribution of error. Mathematical transformations of data were used when necessary to correct deviations from normality and/or homogeneity of variances. If assumptions for ANOVA were still not met, analyses of variance were conducted using rank-transformed data, as outlined by Conover and Iman (1981). The Tukey-Kramer HSD test was used for post hoc comparisons. Figures throughout the text indicate the average and standard error ($A \pm SE$).

Ordination analyses were applied to examine the variation in the species composition as affected by grazing (grazed, ungrazed 10 years) and overstory canopy cover (measured

for each subplot). Linear models were chosen according to the protocol described by Braak ter and Smilauer (2012). Redundancy analysis (RDA) was applied to investigate the relationship between grazing treatment and overstory canopy cover on the one hand, and species composition on the other. The significance of these effects was determined by means of the Monte Carlo permutation tests. The statistical packages used were JMP 9 (SAS Institute, Cary, NC, US) and Canoco v5 (Braak ter and Smilauer 2012).

3 Results

3.1 Woody understory growth

Woody understory cover was significantly affected by grazing with higher cover found in the ungrazed subplots (non-thinned ungrazed 10 years = 70.0 ± 10.4%; non-thinned ungrazed 4 years = 40.5 ± 16.2%; thinned ungrazed 10 years = 103.4 ± 13.3%; thinned ungrazed 4 years = 70.9 ± 4.7%) than in the grazed ones (non-thinned grazed = 15.1 ± 3.3%, thinned grazed = 13.6 ± 5.3%) but no significant difference was detected between the two ungrazed treatments (Table 2). No significant effect of overstory thinning was found on woody understory cover. When looking at woody vegetation volume, a positive effect of both thinning and grazing exclusion was found with a significant positive effect of time since grazing exclusion (i.e., ungrazed 10 vs. 4 years, Table 2, Fig. 1).

3.2 Herbaceous understory biomass

Herb biomass during peak standing crop (early spring) was significantly affected by grazing treatment while no significant effect of overstory thinning was detected (Table 3, Fig. 2). Average herb biomass was approx. 15-fold larger in subplots ungrazed since 2006 (ungrazed 4 years) than those under continuous grazing (grazed). However, in the subplots ungrazed since 2000 (ungrazed 10 years) herbaceous biomass was low and did not differ significantly from the grazed plots.

3.3 Understory community structure

Altogether, 95 plant species were found in the forest understory within the research area. Of these, ten species were trees, nine shrubs and dwarf shrubs, five vines, 19 geophytes and hemicryptophytes, and 52 therophytes. Species richness was significantly influenced by thinning. It was found higher (by more than 30%) in thinned than in non-thinned areas (Table 4, Fig. 3). No significant effect of grazing exclusion on species richness was found. When looking at species composition through ordination analysis (RDA) significant changes in species composition were found across grazing and thinning

Table 2 ANOVA ($N = 25$) of the effect of grazing (grazed and ungrazed 4 and 10 years) and overstory thinning (thinned, non-thinned) on understory woody vegetation cover and volume. Mount Horshan Forest, July 2010

	Factor	DF	<i>F</i>	<i>P</i> value	Post hoc	
Woody cover $R^2 = 0.80$ $P = 0.0001$	Grazing	2	31.23	0.0001	Ungrazed 10 years	A
					Ungrazed 4 years	A
	Grazed	B				
Woody volume $R^2 = 0.73$ $P = 0.0001$	Thinning	1	1.359	0.0834		
	Graz. × Thin.	2	1.248	0.31		
	Grazing	2	17.97	0.0001	Ungrazed 10 years	A
Ungrazed 4 years					A	
Grazed	B					
Thinning	1	10.18	0.0051	Thinned	A	
				Non-thinned	B	
Graz. × Thin.	2	04.3	055.0			

treatments. This and more, a separate analysis revealed a significant thinning × grazing interaction (Table 5). While some species responded mainly to grazing and not to thinning, other species were sensitive to thinning and hardly responded to grazing. In addition, some species responded to both thinning and grazing in various ways. Thus, species responses were variables occurring in all directions of the ordination matrix, reflecting shifts in species composition in response to different combinations of thinning and grazing (Fig. 4, Tables 5 and 6). Most (90%) of the species showing the strongest association with grazed areas were ephemeral herbaceous species (eight therophytes and one hemicryptophyte) in addition to one (10%) aromatic dwarf shrub. Of the species most associated with ungrazed areas, only 50% were ephemerals (four therophytes and one hemicryptophyte) in addition to two broadleaved trees (20%), two dwarf shrubs (20%), and one vine species (10%). Across thinning treatments, mostly associated with thinned areas were seven ephemerals (70%, six therophytes and one hemicryptophyte) and three dwarf shrubs (30%) while non-thinned areas attracted four ephemeral

species (40%, three geophytes and one hemicryptophyte) in addition to three broadleaved tree species (30%), one vine (10%), one dwarf shrub, and one shrub (10%) species. When looking at treatment combinations, species clearly associated with grazed thinned areas were all therophytes while those associated with grazed non-thinned areas were tree, dwarf shrub, and hemicryptophyte species. Two therophytes and two dwarf shrub species were associated with ungrazed-thinned areas while tree, shrub, geophyte, and vine species were associated with ungrazed non-thinned areas.

4 Discussion

4.1 Understory productivity

The effect of overstory thinning on understory woody growth was substantial with a reduction of overstory light interception (indexed through LAI) by ~50% leading to the total understory woody volume of ungrazed plots being more than 2.5-fold larger in the thinned as in the non-thinned areas. This supported our basic assumption regarding overstory cover as a determinant of understory productivity. In addition, grazing exclusion for 10 years resulted in the woody vegetation volume increasing by nearly tenfold in both thinned and non-thinned areas. According to our observation, this effect was mostly through the continuous consumption of developing young shoots and leaves by the cattle (Gutman et al. 2000). Altogether, the combined effect of increased growing space (through thinning) and disturbance cease (grazing exclusion) for 10 years resulted in the understory woody volume being as much as 20-fold greater.

Unlike the woody understory, we found no significant effect of thinning on herb biomass in both grazed and ungrazed areas. This was in opposition to what may have been expected considering known effects of overstory cover on light and water availability as demonstrated in numerous previous

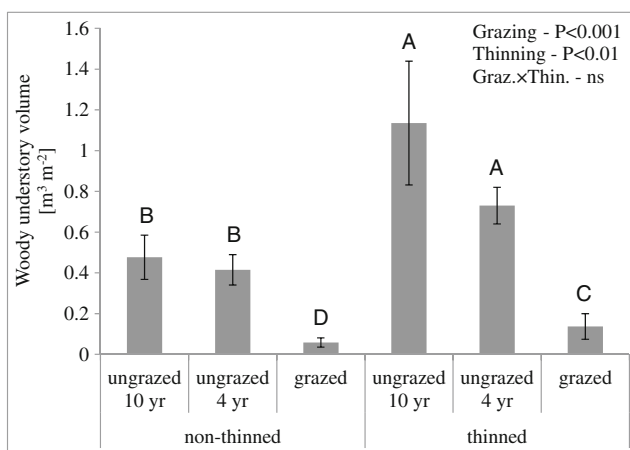


Fig. 1 Understory woody vegetation volume in Mount Horshan Forest, July 2010, as affected by cattle grazing and overstory thinning. Bars indicate SE, $N = 25$

Table 3 ANOVA ($N = 25$) of the effect of grazing (grazed and ungrazed 4 and 10 years) and overstory thinning (thinned, non-thinned) on understory herbaceous vegetation biomass. Mount Horshan Forest, April 2010

	Factor	DF	F	P value	Post hoc
$R^2 = 0.54$ $P = 0.0101$	Grazing	2	9.5355	0.0015	Ungrazed 4 years
					Ungrazed 10 years
					Grazed
	Thinning	1	0.2941	0.5941	
Graz. \times Thin.	2	0.0675	0.9349		

studies in (Bakker and Moore 2016; Harrington et al. 2003; Hernandez-Teclas et al. 2015; Kleintjes et al. 2004; Krzic et al. 2003; Sabo et al. 2009). However, when looking at the effect of grazing, a dynamic pattern was revealed where a substantial increase (15-fold) in herb biomass occurred in areas ungrazed for 4 years while no significant difference was found between areas ungrazed for 10 years vs. those under grazing. It should be noted that the two grazing exclusion treatments were measured at the same time (spring 2010). We propose the following explanation: Shortly after grazing exclusion, opportunistic herb species enjoyed the combination of grazing cease with available growing space due to undeveloped woody understory. This has led to a rapid increase in herb biomass. However, at longer time span, as the woody understory developed, the herbaceous vegetation was gradually forced back toward its biomass levels prior to grazing exclusion.

In a study of a water-limited (precipitation ≈ 600 mm year⁻¹) Ponderosa pine (*P. ponderosa*) ecosystem in southwestern USA, no effect was found following 90 years of livestock (sheep and cattle) grazing exclusion on understory herb cover (Bakker and Moore 2016). Looking at a more humid system (1500 mm year⁻¹), Brockway and Lewis (2003) reported no effect on herb biomass following 4 years of cattle grazing exclusion in a longleaf pine (*Pinus palustris*) ecosystem in south-central Alabama, USA. In both cases, the minor grazing effect

was explained by low grazing pressure. In young lodgepole pine (*Pinus contorta*) stands in south-central British-Columbia (380–900 mm year⁻¹), Sullivan et al. (2012) found that cattle grazing exclusion, for 10 years, had no effect on herb biomass in low productivity plots but increased it significantly in fertilized plots. This variation was attributed to differences in grazing intensity, i.e., grazing was more intense in the fertilized plots where herb production was greater. In another study of Himalayan conifer forest stands in western Bhutan (620 mm year⁻¹), Wangchuk et al. (2014) reported significant increase in herb species abundance following 5 years of cattle grazing exclusion.

With regard to the lack of overstory cover influence on herb biomass in our system, we propose that grazing was responsible for compensating overstory thinning effect on herbaceous understory through increased consumption rate in thinned patches with higher herb productivity (Sullivan et al. 2012; Bakker and Moore 2016). In the ungrazed areas, however, it was the accelerated woody understory growth which occurred in thinned areas that compensated for the lower overstory cover, keeping the herbaceous vegetation under strong competitive pressure (Harrington 2011). This was in addition to the fact that an important portion of the herb biomass, following grazing exclusion, was contributed by two perennial grasses namely *Piptatherum blanchetianum* and *Piptatherum miliaceum* which appeared to be unaffected by the range of overstory cover levels presented in our system.

In young lodgepole pine stands, Sullivan et al. (2012) reported no effect of thinning treatments on herb biomass attributed to relatively open canopy conditions in all stands. In a study of Ponderosa pine ecosystem, Bakker and Moore (2016) reported limited effect of thinning on understory herb biomass attributed to increased woody understory growth following thinning. Similarity, Harrington (2011) reported in longleaf pine (*P. palustris*) plantations in South Carolina, USA (1200 mm year⁻¹) short-term positive effects of thinning on herbaceous vegetation cover which gradually diminished over 14 years following thinning due to developing woody understory. The importance of woody-herbaceous vegetation interaction determining consequences of grazing in the forest understory was also demonstrated by Randall and Walters (2011) who reported in aspen (*Populus grandidentata*) forests in

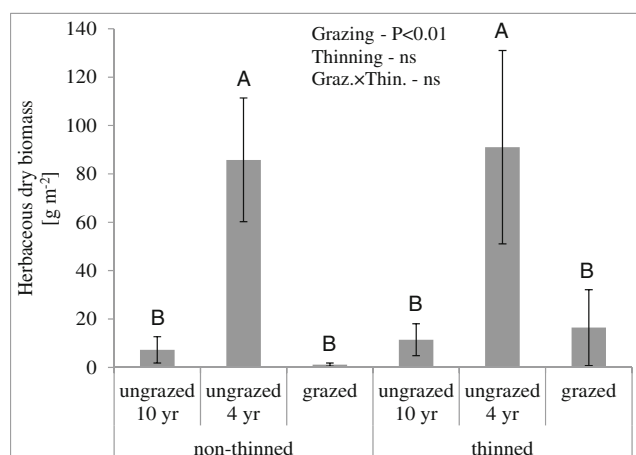


Fig. 2 Understory herbaceous vegetation biomass in Mount Horshan Forest, April 2010, as affected by cattle grazing and overstory thinning. Bars indicate SE, $N = 25$

Table 4 ANOVA ($N = 20$) of the effect of grazing (grazed and ungrazed 10 years) and overstory thinning (thinned, non-thinned) on understory plant species richness. Mount Horshan Forest, April 2010

	Factor	DF	F	P value	Post hoc
Number of species in 100 m ² $R^2 = 0.41$ $P = 0.0308$	Grazing	1	0.19	0.663	
	Thinning	1	9.76	0.0065	Thinned A 33.66 Non-thinned B 25.28
	Graz. \times Thin.	1	1.68	0.213	

Michigan (1000 mm year⁻¹) positive effects of deer browsing on herb biomass attributed to reduction of competing woody vegetation. The dynamic interaction of herbaceous vs. woody understory following grazing exclusion and overstory thinning as found in our system as well as in a variety of other silvopastoral systems, highlights time as an important axes along which consequences of overstory thinning and grazing cessation on understory structure and function may diverge considerably (Mosquera-Losada et al. 2009).

4.2 Understory community structure

We found no effect on understory species richness following 10 years of grazing exclusion in both thinned and non-thinned areas. However, while the total number of species was unaffected, significant variations in species frequencies were found across grazing treatments indicating that grazing was important in controlling understory community structure. Our analyses revealed a list of species, mostly ephemeral herbs (90%), that were associated with grazed areas while a different set of species comprising larger portion of woody species (50%) was more associated with ungrazed areas. Interestingly, plant traits that were associated with grazing were mostly related to plant size (small) and life cycle

(annual) rather than to physical or chemical defense mechanisms.

Differently than grazing exclusion, overstory thinning resulted in a significant positive influence on species richness. Increased species richness by thinning may indicate positive resource availability-diversity relationship as previously shown in various ecosystems (Liang et al. 2016; McClain et al. 2015). When examining the variation in species frequencies across thinning treatments, it became apparent that the species associated with non-thinned plots were mostly woody species (trees, shrubs, and vines, 60%) in addition to relatively large hemicryptophytes and geophytes (40%). In contrast, species associated with thinned areas were mostly therophytes (60%) in addition to relatively short woody species (dwarf shrubs, 30%). This may be partly explained by the fact that thinned areas were more heavily grazed than non-thinned ones. Indeed, when considering the combined effect of grazing and thinning on species composition, it was evident that the combination of grazing and thinning clearly favored small-sized herbaceous ephemerals while larger-sized woody species were more associated with the ungrazed non-thinned areas.

The finding of woody species being more associated with ungrazed vs. grazed areas is in agreement with our previously discussed finding regarding understory woody volume. However, the positive effect of thinning on woody volume as found in our system seems to contradict the fact of woody species being more associated with non-thinned areas as revealed by our RDA analysis. In a previous study within the same system, we found the effect of overstory thinning and grazing on tree recruitment in the forest understory to depend on sapling size. While smaller saplings (<20 cm in height) were generally more abundant in grazed non-thinned areas, larger saplings were more abundant in the ungrazed-thinned areas (Osem et al. 2015). Higher frequency of tree and shrub species in the understory of non-thinned plots may be related to better seedling establishment of large seeded woody species such as *Q. calliprinos*, *S. officinalis*, and *Phillyrea latifolia* resulting from facilitative effects of the overstory (Alon and Kadmon 1996) and related ground litter layer (Sayer 2006). It should be noted, however, that while these woodland species exhibit better regeneration in the understory of the pine forests, their growth at later phases was shown to be restricted by

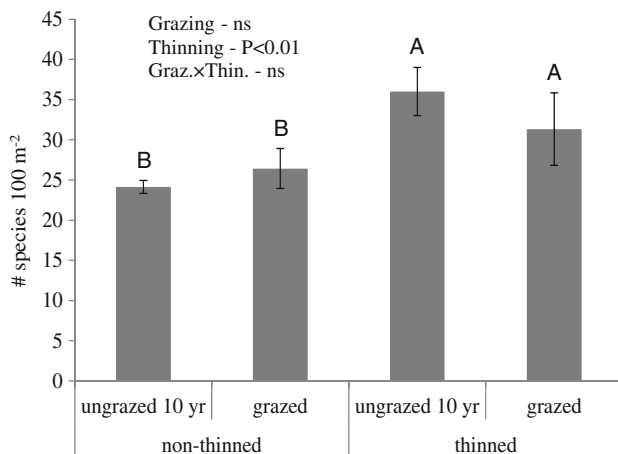


Fig. 3 Understory plant species richness in Mount Horshan Forest, April 2010, as affected by cattle grazing and overstory thinning. Bars indicate SE, $N = 20$

Table 5 Redundancy analysis (RDA, $N = 20$) of the effect of grazing (grazed, ungrazed 10 years) and overstory canopy cover on understory vegetation composition within 100 m² subplots. Mount Horshan Forest, April 2010

	Sum of all canonical eigenvalues	F ratio	P value	Number of permutations
Grazing	8.2	1.599	0.022	499
Canopy cover	9.00	1.771	0.008	499
Graz. × Cover	17.4	1.784	0.004	499

overstory shading (Cooper et al. 2014). This is supported by the fact that woody vegetation volume as measured in our study was much higher in thinned than in non-thinned plots. Thus, while the frequencies of the larger woody species were higher in non-thinned plots due to higher density of small-sized individuals, the volume of these species was much greater in the thinned plots as a result of more developed individuals.

Variable outcomes of grazing effects on understory richness and composition were reported from diverse forest ecosystems. For example, positive effects of livestock grazing on understory richness were reported in a long-term study of Ponderosa pine ecosystem in southwestern USA (Bakker et al. 2010) as well as in boreal Aspen (*Populus tremuloides*)

stands in BC Canada (Krzic et al. 2003), Savana woodlands in south India (Mandle and Ticktin 2013), and in Himalayan mix conifer forest (Wangchuk et al. 2014). While in one case increased species richness under grazing was attributed to higher prevalence of exotic species (Bakker et al. 2010), in another system, it was explained by enhanced colonization of endemic species (Krzic et al. 2003). On the other hand, no effect of cattle grazing on understory diversity was reported in a longleaf pine ecosystem (Brockway and Lewis 2003) while negative effects of deer browsing on understory richness were found in Aspen forests associated with the reduction of understory woody cover (Randall and Walters 2011).

Similarly to our findings, several studies have found no or minor effects of grazing on understory richness while highlighting variations in species composition. For example, cattle grazing increased the abundance and richness of annual grasses but reduced those of perennial forbs in Eucalyptus savanna in southwestern Australia (Fensham and Skull 2016). Deer browsing in old growth pine forest system in Norway increased the richness of low-growing functional groups as forbs, graminoids and mosses whereas the richness of taller growing woody species of the forest understory decreased (Hegland et al. 2013). In a Mediterranean stone pine (*Pinus pinea*) forest in southwestern Spain Mancilla-Leytón and Martín Vicente (2012) reported significant effects of goats browsing on the relative abundance of woody species.

Reported effects of overstory cover and thinning treatments on understory species richness are also somewhat variable. For example, positive effects of overstory openness on understory richness were reported in ponderosa pine ecosystem (Bakker et al. 2010), savanna woodlands (Mandle and Ticktin 2013), as well as in Mediterranean *P. halepensis* forest (Navarro et al. 2010). In contrast, Sanchez-Jardn et al. (2014) reported in lenga beech (*N. pumilio*) forests in Chilean Patagonia reduced understory species richness with increased canopy openness.

Several studies have highlighted the importance of spatial and temporal scales regarding the effects of overstory thinning and grazing on understory community structure. In a ponderosa pine ecosystem, for example, negative effects of overstory cover on understory richness were only apparent at small spatial scales while positive effects of livestock grazing were more substantial with increasing spatial scale

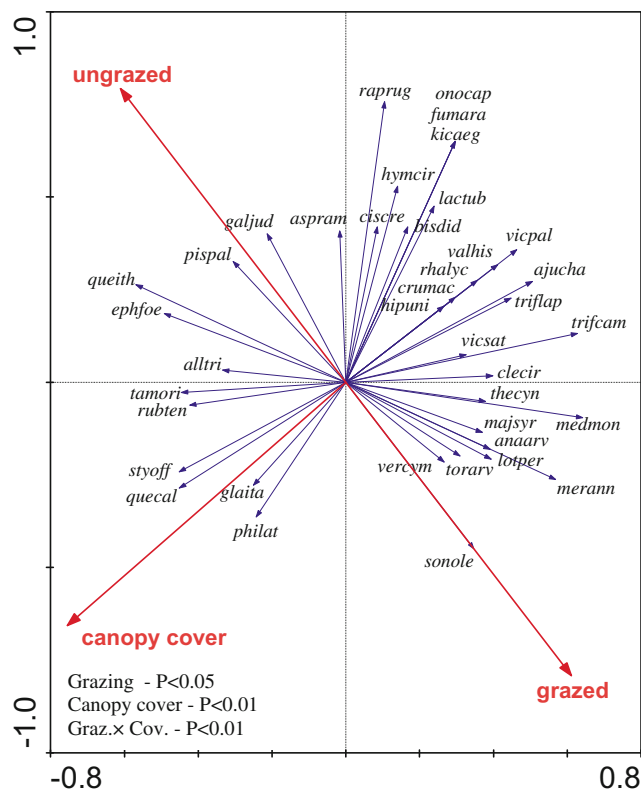


Fig. 4 Redundancy analysis (RDA, $N = 20$) of the effect of cattle grazing and overstory canopy cover (%) on understory vegetation composition within 100 m² subplots. Mount Horshan Forest, April 2010. Species full names are listed in Table 6

Table 6 Abbreviations for species in Fig. 4

Species code	Species name	Life form
Ajucha	<i>Ajuga chamaepitys</i> L.	Hemicytopyte
Alltri	<i>Allium trifoliatum</i> Kollmann	Geophyte
Anaarv	<i>Anagallis arvensis</i> L.	Theropyte
Aspram	<i>Asphodelus ramosus</i> L.	Hemicytopyte
Bisdid	<i>Biscutella didyma</i> L.	Theropyte
Ciscre	<i>Cistus creticus</i> L.	Dwarf shrub
Clecir	<i>Clematis cirrhosa</i> L.	Vine
Crumac	<i>Crucianella macrostachya</i> Boiss.	Theropyte
Ephfoe	<i>Ephedra foeminea</i> Forssk.	Vine
Fumara	<i>Fumana arabica</i> (L.) Spach	Dwarf shrub
Galjud	<i>Galium judaicum</i> Boiss.	Theropyte
Glaita	<i>Gladiolus italicus</i> Mill.	Geophyte
Hipuni	<i>Hippocrepis unisiliquosa</i> L.	Theropyte
Hymcir	<i>Hymenocarpus circinnatus</i> (L.) Savi	Theropyte
Kicaeg	<i>Kickxia aegyptiaca</i> (L.) Nabelek	Dwarf shrub
Lactub	<i>Lactuca tuberosa</i> Jacq.	Hemicytopyte
Lotper	<i>Lotus peregrinus</i> L.	Theropyte
Majsyv	<i>Majorana syriaca</i> (L.) Kostel.	Dwarf shrub
Medmon	<i>Medicago monspeliaca</i> (L.) Trautv.	Theropyte
Merann	<i>Mercurialis annua</i> L.	Theropyte
Onocap	<i>Onobrychis caput-galli</i> (L.) Lam.	Theropyte
Philat	<i>Phillyrea latifolia</i> L.	Tree
Pispal	<i>Pistacia palaestina</i> Boiss.	Tree
Quecal	<i>Quercus calliprinos</i> Webb.	Tree
Queith	<i>Quercus ithaburensis</i> Decne.	Tree
Raprug	<i>Rapistrum rugosum</i> (L.) All.	Theropyte
Rhalyc	<i>Rhamnus lycioides</i> L.	Shrub
Rubten	<i>Rubia tenuifolia</i> D'Urv.	Vine
Sonole	<i>Sonchus oleraceus</i> L.	Theropyte
Styoff	<i>Styrax officinalis</i> L.	Tree
Tamori	<i>Tamus orientalis</i> Thiebaut L.	Vine
Thecyn	<i>Theligonum cynocrambe</i> L.	Theropyte
Torarv	<i>Torilis arvensis</i> (Huds.) Link	Theropyte
Trifcam	<i>Trifolium campestre</i> Schreb.	Theropyte
Triflap	<i>Trifolium lappaceum</i> L.	Theropyte
Valhis	<i>Valantia hispida</i> L.	Theropyte
Vercym	<i>Veronica cymbalaria</i> Bodard	Theropyte
Vicpal	<i>Vicia palaestina</i> Boiss.	Theropyte

(Bakker et al. 2010). In longleaf pine plantations in South Carolina, USA, positive effects of thinning on herbaceous species richness were only apparent at the short-term and gradually diminished over 14 years in association with increasing understory woody cover (Harrington 2011). In Himalayan mix conifer forest, Wangchuk et al. (2014) demonstrated how effects of grazing on understory richness may depend on the spatial scale of overstory logging.

5 Conclusions and management implications

Our findings supported the basic research hypothesis according to which overstory cover and grazing interact in shaping understory community structure. Our results highlight the importance of woody vs. herbaceous vegetation dynamics following release from grazing and overstory thinning for understanding understory community structure. We propose that variation in understory community structure was mainly determined through differences in the combination of grazing resistance and shade tolerance levels exhibited by different species and/or functional groups within the plant community. Integrating previous findings with those of our study, we come up with the following management implications: Overstory thinning and grazing should be regarded as complementary management tools. Considering the multifunctionality of Mediterranean forests, no single optimum of thinning-grazing regime exists. Instead, grazing-thinning combinations should be implemented according to well defined management goals as may be illustrated through the following examples: Heavy thinning and continuous grazing to maintain fire fuel breaks; grazing exclusion under high overstory cover to encourage native broadleaved tree recruitment; grazing exclusion and overstory thinning to encourage conifer recruitment and tree growth; a dynamic mosaic of variable grazing and thinning levels to enhance forest species diversity and structural complexity.

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