

Regeneration dynamics of woody vegetation in a Mediterranean landscape under different disturbancebased management treatments

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Keywords

Disturbance treatments; Grazing; Mediterranean; Regeneration; Woody vegetation

Nomenclature Feinbrun-Dothan et al. (1998)

Received 29 June 2016 Accepted 30 August 2016 Co-ordinating Editor: Martin Hermy

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Abstract

Question: Mediterranean landscapes have been affected for millennia by agropastoral disturbances such as grazing and vegetation clearing. Increased levels of fine-scale habitat heterogeneity that resulted from these disturbances contribute to reduced wildfire risk and increased species diversity. Disturbance-based management tools utilize disturbances in order to promote biodiversity and reduce fire risk, but are complicated to apply effectively due to the natural regeneration ability of many woody species following disturbances. Therefore, their successful application requires a better understanding of woody regeneration dynamics. Here, we asked how disturbance-based management treatments affected the spatiotemporal dynamics of woody vegetation across 11 yrs in a Mediterranean landscape.

Location: Ramat HaNadiv LTER, northern Israel.

Methods: We analysed vegetation dynamics in a field experiment comprising five treatments: cattle grazing, goat grazing, shrub clearing, shrub clearing followed by goat grazing and undisturbed control. We used image analysis of high-resolution aerial photographs to map woody patches in our study plots. We then quantified the spatial pattern of woody vegetation using multiple landscape indices, and conducted a comparative analysis of woody regeneration rates under different management treatments.

Results: Cattle grazing did not inhibit woody regeneration, as regeneration rates were similar to those found in undisturbed control plots. Shrub clearing led to rapid woody regeneration (7% yr⁻¹), while a combination of shrub clearing and intense goat grazing halted woody regeneration completely. Finally, intense goat grazing not only prevented woody regeneration but led to significant decline in woody cover (1% yr⁻¹).

Conclusions: Our results highlight the rapid regenerative response of woody vegetation to severe disturbances, and the growth rates we found can serve as guidelines for long-term management regimes aimed at maintaining low woody cover and biomass in fuel breaks and buffer zones.

Introduction

Mediterranean vegetation has been affected by thousands of years of human activities, which included grazing, shrub clearing and fire (Geri et al. 2010). These disturbances have created complex landscapes that are characterized by spatial heterogeneity of habitats at different spatial scales (Pickett & Cadenasso 1995). This spatial heterogeneity, which is manifested by structural fragmentation of woody vegetation patches (Bar Massada et al. 2008), contributes to high species diversity (Gabay et al. 2011), reduced wildfire risk (Dufour-Dror 2011) and high scenic diversity (de La Fuente de Val et al. 2006). The positive effects of agropastoral disturbances on various aspects of Mediterranean landscapes facilitated their application as disturbancebased management tools, which aim to preserve biodiversity of various taxa and reduce wildfire risk (Scarascia-Mugnozza et al. 2000).

Two main forms of disturbance-based management are grazing, by goats or cattle, and mechanical shrub clearing. The relationships between herbivores and the plants they consume have strong effects on different organization levels: grazing can lower the biomass of plants, change the species composition and alter the abiotic substrate (via soil compacting and nutrient enrichment; Gabay et al. 2011). Plant species that are less desirable can establish more easily when preferable species are consumed by herbivores (Pignatti 1983). Livestock species affect the vegetation in different ways. Cows are grazers, and mostly consume herbaceous vegetation, but may also consume the leaves of woody species in the dry season when there is no green herbaceous vegetation (Brosh et al. 2006). Therefore, their effect on the structure of woody vegetation is mostly indirect, via physical processes such as trampling (Perevolotsky et al. 2002). In contrast, goats are mostly browsers, preferring to consume the leaves of woody species, and therefore have a direct effect on the structure and dynamics of woody vegetation (Bartolomé et al. 1998).

Another common form of disturbance treatment is tree or shrub clearing. In Mediterranean landscapes, clearing has two main effects: (1) selective clearing and pruning can lead to change in woody species composition with time; and (2) woody vegetation dominated by large trees (Maquis) may convert to a low shrubland (Batha; Pignatti 1983). Plant species that are useful for construction or heating will no longer dominate the landscape, thus paving the way for opportunistic species with rapid regeneration capability that may overtake their vacated niche (Young & Evans 1978). Furthermore, repeated clearings may transform species composition (Agra & Ne'eman 2011) and can transform single-stemmed trees and shrubs to a multiple-stem structure (Hallé et al. 1978), which alters the spatial structure of the habitat.

The application of disturbance-based management in Mediterranean ecosystems is complicated not only due to differences in the effects of grazing and clearing on the structure and composition of the vegetation, but also because many woody species have different evolutionary adaptations to the main forms of disturbance (i.e. grazing, clearing and fire). These adaptations are manifested by three separate mechanisms for coping with disturbances: (1) high capability of regrowth and re-sprouting after all severe disturbances; (2) mechanical or chemical defence mechanisms against browsing; and (3) rapid establishment of large canopy or soil seed banks (Geeson et al. 2003; Ne'eman et al. 2004).

The ability of woody species to recover quickly from disturbances by regrowth of new shoots requires continuous or periodic application of pruning or cutting in order to delay woody regeneration or to prevent it altogether (Seligman & Perevolotsky 1994). For example,

Perevolotsky et al. (2002) found that mechanically cleared shrublands can recover back to their initial structure already after 6 yrs. Cattle grazing, on the other hand, did not inhibit the recovery process significantly. Other studies (Carmel & Kadmon 1999: Nader et al. 2007) have revealed that a combination of disturbance management treatments (i.e. mechanical clearing and grazing) provides a much more effective prevention scheme than any single treatment if the management objective is to prevent vegetation regeneration in order to maintain habitat patchiness. Nevertheless, establishing the most effective composition of management treatments is not straightforward, as grazingbased treatments need to account for the differences in dietary preferences between goats and cattle, as well as for seasonal changes in diet. Furthermore, the intensity of grazing has a strong influence on vegetation composition, structure and its regenerative response (Celaya et al. 2010; Glasser et al. 2012), so management activities aimed at biodiversity conservation (which benefits from a heterogeneous vegetation structure) might not align with those aimed at fire prevention (which requires the removal of most of the woody cover).

The main objective of this research was to examine the regeneration dynamics of woody vegetation across space and time following different management treatments that are commonly applied in Mediterranean landscapes. We specifically focused on four types of treatment: periodic goat grazing, periodic cattle grazing, shrub clearing and shrub-clearing followed by periodic goat grazing. We expected that shrub clearing alone would lead to very high regeneration rates, and a combination of goat grazing and shrub clearing would be effective enough for maintaining open habitat that can serve as a fuel break. We also expected that intensive goat grazing would inhibit woody vegetation regeneration, while cattle grazing would have only minor impacts on the dynamics of woody vegetation compared to an undisturbed control.

Methods

Study area

The study was conducted at Ramat HaNadiv Nature Park (Fig. 1), located at the southern tip of Mt. Carmel, northern Israel (34°56′ E, 32°32′ N). The park, encompassing 500 ha, has an eastern Mediterranean climate, with an average annual temperature of 19 °C and an annual rainfall between 500 and 600 mm (Hadar et al. 1999). Vegetation formations include Mediterranean Batha (dwarf shrubs and herbaceous vegetation) and Garrigue (medium height shrublands), dominated by *Phillyrea latifolia, Pistacia lentiscus* and *Calicotome villosa* (Geffen et al. 1999). The landscape is characterized by a fine-grained mosaic of woody patches of different heights and sizes, herbaceous clearings,



Fig. 1. An aerial photo of the experimental setting. The original LTER treatment blocks appear on the left, while the five cattle grazing blocks we added *a posteriori* appear on the right. Treatment abbreviations are: C = control, CG = cattle grazing, G = goat grazing, P = shrub clearing, P+G = shrub clearing followed by goat grazing.

exposed rocks and bare ground (Perevolotsky et al. 2002). Vegetation formations, including the dominant plant species, are dictated by the soil water accumulation potential and the rock-soil formation (Bar & Kaplan 2005). On top of these drivers, vegetation structure and composition reflect a long history of disturbances. In 1980, a fire burned large areas of the park. In areas affected by the fire, woody vegetation has been regenerating, and consequently there is a decrease in the number and size of open herbaceous patches, and an increase in areas dominated by dense woody vegetation (Perevolotsky & Seligman 1998).

Experimental design

In 2004, a Long-Term Ecological Research (LTER) site was formed in the northwestern part of the park (Fig. 1). The site hosts a long-term field experiment focusing on the effects of disturbances on various ecological phenomena. The experiment comprises four groups of five blocks (each ca. 1200 m²), with each block allocated at random within the boundaries of the experimental site. Each block is subjected to one of four treatments: (1) intensive goat grazing (G), applied during several periods throughout the year, mostly in the spring and summer (ca 1156 goat days 1000 m⁻²·yr⁻¹); (2) shrub clearing (P), conducted once in 2004 and again in 2010 where shrubs were removed mechanically down to ground level; (3) shrub clearing followed by goat grazing (P+G) where shrubs were cleared in 2004 and goat grazing was re-applied every year (ca. 971 goat days 1000 m^{-2} ·yr⁻¹); and (4) control (C) with no disturbance. Blocks with non-control treatments were

surrounded by electric fences to prevent grazing by cattle and native ungulates. Since the original field experiment did not include a cattle grazing treatment (while cattle grazing is a common tool for fuel-break maintenance in Israel), we added five randomly located blocks of the same size (ca. 1200 m²) in an adjacent area grazed by cattle just to the east of the experimental blocks. This area has the same edaphic and topographic characteristics as the original experimental blocks. Thus the fifth (5) treatment is moderate cattle grazing (CG), which is applied from 3 to 5 months per year, mainly in the spring and summer (ca. 16.8 cattle days 1000 m⁻²·yr⁻¹). While cattle grazing intensity is much lower than grazing intensity by goats, these intensities are not directly comparable because goats are browsers while cattle are grazers.

Vegetation mapping

We obtained orthorectified aerial photographs of the study site from 2003 (the year prior to the establishment of the field experiment) to 2015, excluding 2005 and 2012 (11 images overall). All images were taken in the summer months, when there is no herbaceous cover. The spatial resolution of the images varied among years, and ranged from 7.5 cm to 25.0 cm. All images except two were in true colour (the images of 2003 and 2006 were panchromatic).

We classified each image into three thematic classes (woody vegetation, bare ground and rocks) using a maximum likelihood supervised classification approach (Otukei δ Blaschke 2010). Following the classification, we assessed classification accuracy using two measures, total accuracy (Congalton 1991) and Cohen's kappa (Foody 2002). To facilitate the computation of classification accuracy, we generated 100 reference points on each image, which we allocated in a stratified random scheme across pixels of the three classes, and then classified manually as belonging to each one of the three classes. In all images, both classification accuracy and Cohen's kappa were >0.9, implying high classification accuracy. We conducted the mapping process as well as its accuracy assessment in ArcMap v 10.2.2.

Landscape and patchiness indices

Based on the classified images, we created binary images of 'woody vegetation' and 'non-vegetation' to serve as the basis for calculating vegetation structure. We then quantified three landscape and patchiness indices for each experimental block in each image: (1) woody cover: the proportion of woody vegetation in the block; (2) mean patch density: the total number of contiguous patches of woody vegetation in each block, divided by block area (1200 m²); and (3) mean patch area: the mean area of contiguous woody patches in the block. We calculated all patchiness indices in the Patch Analyst 5.1 extension of Arc Map (Rempel et al. 2012).

Data analysis

Our analysis aimed at quantifying how different disturbance treatments affected the temporal dynamics of woody vegetation structure, as represented by the different patchiness indices. We first evaluated whether our patchiness indices were correlated, to omit indices that are redundant, a typical problem in the analysis of landscape metrics (Riitters et al. 1995; Li & Wu 2004). We then used a linear mixed effects model to determine the effect of different disturbance management treatments on the patterns of woody vegetation dynamics across time (woody vegetation patterns were woody cover, mean patch area and mean patch density, as described in the previous section). The model included two fixed effects, year and treatment, and one random intercept effect, block number, to account for the nested structure of the data and the multiple measures per block (five replicates of each treatment across multiple years). On top of the full model (which included all disturbance types), we generated sub-models for each treatment separately to quantify the temporal dynamics of vegetation pattern (i.e. the average rate of vegetation change across years) in any given treatment. The shrub clearing treatment (P) was divided into two separate periods (2004-2009 and 2010-2015) due to the re-application of mechanical clearing in 2010. We evaluated the significance of model terms using Wald's χ^2 tests. Beyond the above models that quantified the full temporal dynamics

of vegetation patterns, we also used one-sided paired *t*-tests to compare woody vegetation cover in 2003 (prior to the initiation of the disturbance regime) to its value in 2014 (a decade into the disturbance regime) to test if vegetation cover was still lower than its pre-disturbance level (as our assumption was that disturbances reduce woody cover, but woody species can regenerate). We conducted all statistical analyses in R (R Foundation for Statistical Computing, Vienna, AT) using the Lme4 and car packages.

Results

Spatial and temporal dynamics of woody vegetation across treatments

We retained all three patchiness indices as the correlations among them were always <0.5. Woody cover exhibited marked differences in dynamics among most treatments (Fig. 2). Woody cover levels differed significantly among treatments (Type II Wald's test, $\chi^2(5) = 63.13$, P < 0.001),

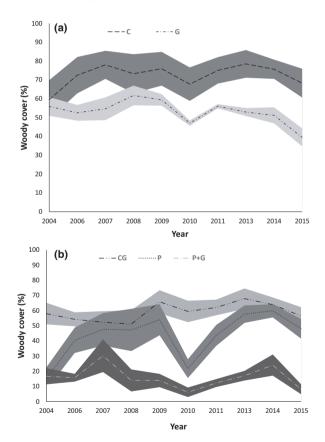


Fig. 2. Temporal dynamics of woody vegetation cover under different disturbance treatments. Line types represent means of different treatments, and ribbons represent SE around the means. Panel (a) depicts the control treatment (C) and the goat grazing treatment (G). Panel (b) depicts the cattle grazing treatment (CG), the shrub clearing treatment (P; the drop in 2010 reflects the outcome of an additional clearing treatment in that year) and the shrub clearing plus goat grazing treatment (P+G).

with all treatments except cattle grazing exhibiting significantly lower levels of woody cover compared to the undisturbed control (Table 1). In all treatments except control, woody cover in 2014 (a decade since the initial application of disturbances), was significantly lower than its values in 2003, 1 yr before establishment of the field experiment (paired *t*-test, df = 4 in all cases; shrub clearing: t = 11.09, P < 0.001; shrub clearing plus grazing: t = 6.81, P = 0.001; goat grazing: t = 7.65, P < 0.001; cattle grazing: t = 4.65, P = 0.004). Similarly to woody cover, patch density and mean patch area differed significantly across treatments, except for cattle grazing, when compared to the undisturbed control (Table 1; Type II Wald's test, $\chi^2(5) = 74.92$, P < 0.001; Type II Wald's test, $\gamma^2(5) = 13.98$, P = 0.015 for patch density and mean patch area, respectively).

Temporal dynamics of woody vegetation within treatments

Different disturbances exhibited varying trends of woody cover dynamics across time (Fig. 2). Woody vegetation in the control treatment (Fig. 2a) exhibited a small yet significant increase over the years ($\beta = 0.58 \pm 0.28$ (\pm SE), $\chi^2 = 4.31$, P = 0.037). A similar trend occurred in the cattle grazing treatment (Fig. 2b; $\beta = 0.78 \pm 0.27$, $\chi^2 = 8.16$, P = 0.004). The two separate periods of the shrub clearing treatment (Fig. 2b) exhibited the most rapid increase in woody vegetation cover over the years (Fig. 3; $\beta = 7.43 \pm 1.43$, $\chi^2 = 28.40$, P < 0.001; and $\beta 2 = 5.57 \pm$ 1.16, $\chi^2 = 24.27$, P < 0.001, for the first and second period, respectively). Therefore, without further intervention, woody cover might regain its former state (prior treatment) in ca. 10 yrs. In contrast, goat grazing (Fig. 2a) led to an opposite trend, in which woody cover decreased significantly throughout the years ($\beta = -1.00 \pm 0.39$, $\chi^2 = 6.48$, P = 0.01). The combination of shrub clearing and goat grazing (Fig. 2b) resulted in the long-term stabilization of woody cover, as it remained unchanged across time $(\beta = -0.41 \pm 0.44, \chi^2 = 0.87, P = 0.34).$

Mean patch area increased significantly over the years following both shrub-clearing events ($\beta 1 = 1.65 \pm 0.66$, $\chi^2 = 6.20$, P = 0.012; $\beta 2 = 0.80 \pm 0.31$, $\chi^2 = 6.698$, P = 0.009, for the first and second post-clearing periods, respectively). Patch density increased significantly over the years under goat grazing ($\beta = 0.007 \pm 0.003$, $\chi^2 = 4.66$, P = 0.03) and decreased significantly in the years following the first shrub-clearing event ($\beta = -0.03 \pm 0.008$, $\chi^2 = 11.90$, P < 0.001). Both patch density and mean patch area did not change significantly over the years in any other treatment, thus under cattle grazing or undisturbed control, woody vegetation changes only in overall amount, but not in spatial configuration.

Discussion

Treatment effects on woody vegetation

In this study, we found that long-term application of different disturbance-based management treatments leads to diverging trajectories of woody vegetation dynamics in a Mediterranean habitat. Moderate cattle grazing did not inhibit woody growth, and mechanical clearing led to rapid regrowth after treatment application. A combination of mechanical clearing and intense goat grazing inhibited regrowth, and intensive goat grazing led to a decrease in woody vegetation cover. While the differential impacts of disturbances on woody vegetation at any single point in time are well known from previous studies (e.g. Sal et al. 1999; Bar Massada et al. 2008; Agra & Ne'eman 2011; Dias et al. 2016), our findings highlight the differences in annual rates of natural regeneration and in the long-term dynamics of vegetative response. As such, they have clear implications for planning disturbance-based management regimes in Mediterranean landscapes.

Growth and regeneration of woody vegetation

The continuation of vegetation growth under control conditions (0.5% cover yr^{-1}) probably reflects the on-going regeneration of the study area from the 1980 wildfire, and

Table 1. Coefficients of LMM of the effects of different disturbance treatments on woody cover, patch density and mean patch area. Treatment effects are contrasted against the undisturbed control (e.g. treatments with negative effects have lower values of woody cover, patch density or mean patch area compared to the control). The 'Year' covariate is the mean slope of woody cover, patch density or mean patch area across all treatments.

Variable	Woody Cover		Patch Density		Mean Patch Area	
	Estimate (\pm SE)	P-Value	Estimate (\pm SE)	P-Value	Estimate (\pm SE)	P-Value
Cattle Grazing	-13.3 (7.7)	0.099	0.028 (0.023)	0.254	-15.68 (7.73)	0.055
Goat Grazing	-19.36 (7.7)	0.02	0.06 (0.023)	0.012	-21.09 (7.73)	0.012
Shrub Clearing + Goat Grazing	-56.62 (7.7)	< 0.001	0.15 (0.023)	< 0.001	-25.55 (7.73)	0.003
Shrub Clearing (First Period)	-30.37 (7.89)	< 0.001	0.093 (0.029)	< 0.001	-22.45 (8.12)	0.006
Shrub Clearing (Second Period)	-27.44 (7.89)	< 0.001	0.19 (0.029)	< 0.001	-21.54 (8.12)	0.008
Year	0.4 (0.22)	0.069	0.002 (0.002)	0.25	-0.45 (0.32)	0.16

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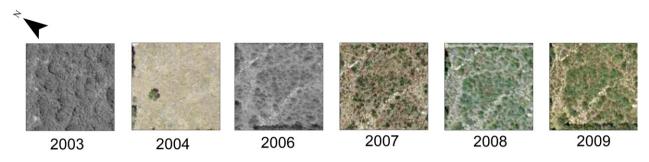


Fig. 3. Spatiotemporal dynamics of woody vegetation in a single shrub clearing treatment plot from 2004 to 2009. The 2003 panel depicts the area before the first application of the clearing treatment.

the growth rates we found are similar to those reported before in the same study area (Perevolotsky et al. 2002). Woody cover increased slightly faster under moderate cattle grazing, which is the most common land-use type in the study area (Glasser et al. 2013), and the most widespread livestock type in the Mediterranean zone of Israel. At the peak of the green season (early winter to late spring), cattle do not browse woody vegetation but rather feed on the herbaceous species (Grant et al. 1985; Hadar et al. 1999; Fraser et al. 2009; Papachristou & Platis 2011; Rosa García et al. 2013), as they prefer herbaceous plants over shrubs when they are readily available. Only after all other plant resources have been depleted will cattle switch to moderate consumption of woody species, depending on grazing intensity (Brosh et al. 2006; Henkin et al. 2011). Consequently, the effects of cattle on woody vegetation cover and structure are mostly indirect, via trampling (Seligman & Perevolotsky 1994).

Our finding on the continuous growth of woody vegetation under cattle grazing contrasts with those of some previous studies (Carmel & Kadmon 1999; Casasús et al. 2007). Carmel & Kadmon (1999) analysed 28 yrs of woody regeneration rates in northern Israel and reported a net decline in woody cover due to grazing. Another study in the Spanish Pyrenees (Casasús et al. 2007), which followed the dynamics of vegetation for 6 yrs, found that even medium-intensity grazing can prevent the regeneration of woody vegetation. These contrasting results might be explained by differences in the dominant woody species (Phillyrea latifolia, the dominant shrub in our study site, vs Quercus calliprinos, a tree/shrub in the study area of Carmel & Kadmon 1999; and Pinus nigra trees in the study area of Casasús et al. 2007) or differences in stocking rates and grazing season among studies.

Woody vegetation exhibited the fastest regeneration rates following shrub-clearing treatments (twice in 11 yrs), with 5–7% increase in cover per year. Therefore, without further treatment, full regeneration to predisturbance cover (ca. 70% on average) will occur in

about 10 yrs. While being highly effective in creating open habitats that can reduce wildfire spread, mechanical shrub clearing is expensive (Nader et al. 2007). Moreover, to be effective in preventing wildfire, fuel breaks require annual maintenance to prevent resprouting and rapid regeneration of woody plants. Towards that end of the experiment, we found that the combination of goat grazing and shrub clearing was the most effective treatment in maintaining open patches. These plots were characterized by an almost static vegetation structure that had on average 62.5% less woody cover compared to undisturbed plots. These results are similar to those found in a field experiment in Greece (Papachristou & Platis 2011), in which oak regeneration following shrub clearing was compared among control plots, cattle-grazed plots and goat-grazed plots. They found that goat grazing led to significantly lower shoot volume than cattle grazing and control conditions, and this effect was still evident 5 yrs after the application of clearing.

Perhaps the least expected result in terms of vegetative response to disturbance was our finding that high-intensity goat grazing led to a consistent decline in woody cover over the years. As the vegetation was expected to regrow rapidly between grazing periods (i.e. months when grazing was excluded), we expected that grazing would inhibit growth. A similar result was found in the Judean mountains, where goat grazing decreased woody cover from 58.4% to 37.1% during a 9-yr period (Perevolotsky & Haimov 1992). In contrast, a previous analysis in our study area found that in goat-grazed plots, woody cover increased by 8.26% between 2004 and 2010 (Glasser et al. 2013). The difference between our results and those of Glasser et al. (2013) might be attributed to the fact that they measured woody cover only in 2004 and 2010, and thus their results are sensitive to annual fluctuations in woody cover; our results, in contrast, reflect a long-term trend in measurements that is less sensitive to annual fluctuations. While the average rate of decline was rather slow in our study system (1% cover yr^{-1}), its consistency raises a question about long-term effects of grazing on vegetative response (Eldridge et al. 2015). We suggest that it is likely that with cessation of grazing, the vegetation will regenerate back to its previous form (Hartley 2015), as shown in many other areas around the Mediterranean Basin (Perevolotsky & Haimov 1992; Perevolotsky & Seligman 1998; Carmel & Kadmon 1999; Fernández-Lugo et al. 2013).

Ecological outcomes and economic benefits

While our study did not focus on the effects of vegetation patterns on ecological processes, we can infer from past studies in the same study area and similar landscapes. For wildfire prevention, the optimal spatial structure of vegetation would be one that minimizes the cover of woody vegetation and reduces woody patch sizes to a minimum (Graham et al. 2004; Bohlman et al. 2016). Our results show that one-time mechanical clearing, followed by periodic application of intensive goat grazing, can successfully maintain an open landscape. The repeated application of goat grazing prevents the need for another session of mechanical clearing, which reduces long-term costs and prevents damage to the habitat (Nader et al. 2007). Yet beyond wildfire prevention, disturbance-based management is often used to promote biodiversity of various taxonomic groups. A previous study in the same study site (Gabay et al. 2011) showed that herbaceous species richness was highest at intermediate levels of woody cover, which are obtained when grazing effects are weak and habitat heterogeneity is high. Therefore, the vegetation structure that promotes biodiversity might be different than the one that prevents wildfire spread, and hence management activities for biodiversity conservation and wildfire prevention need to be carefully interweaved at the landscape scale.

Conclusion

Disturbance-based management activities, which build upon millennia of human activities that shaped Mediterranean landscapes, are effective tools for managing the spatial structure of woody vegetation as well as its temporal dynamics. Our results highlight the complex regeneration dynamics of woody vegetation under different disturbance-based management activities, and provide insight into the potential efficiency of different disturbance treatments. As such, they can be used by land managers in Mediterranean landscapes in planning how to best apply disturbance regimes to maintain a desired state of vegetation structure, which in turn can reduce wildfire risk (if low woody cover is maintained) or promote biodiversity (by maintaining intermediate levels of woody cover and high levels of habitat heterogeneity).

Acknowledgements

We thank Liat Hadar, Tzach Glasser and the staff of Ramat HaNadiv Nature Park for their assistance and suggestions. Gidi Ne'eman, David Eldridge and two anonymous reviewers provided comments and suggestions that greatly improved this manuscript. This study was funded by a research grant from Ramat HaNadiv Nature Park. DB and AB designed the research, DB collected the data, DB and AB analysed the data and wrote the manuscript.

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