



Management of forest fire buffer zones: Implications for flowering plants and bees



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ABSTRACT

Pollination, especially by bees, has high importance for man and nature. Ongoing global declines in bee populations make their present and future conservation crucial. We investigated how management of natural areas affects plants and pollinators, in the context of fire prevention measures in Mediterranean forests. The standard forestry practice to reduce fire hazard includes construction of vegetation-thinned buffer zones near roads and human settlements. Such buffer zones are commonly maintained by livestock grazing or mechanical trimming to prevent forest regrowth. We conducted a controlled and replicated field experiment to assess the effects of these maintenance practices on flowering plants and bees. Vegetation was thinned in 32 experimental plots at the Mt. Carmel Nature Reserve, Israel, to simulate construction of fire buffer zones. Sixteen plots were either grazed by sheep or trimmed during the following year, while the remaining plots received no maintenance treatment. We surveyed the flowers (identified to species) and bees (identified to genus) in the plots over three years: before, during and after the maintenance interventions. Maintenance management (regardless whether by grazing or by trimming) affected the floral community composition, as did monitoring date and the plots' fire history (burnt either four or > 20 years earlier). However, the abundance and diversity of flowers and bees, and the bees' community composition, did not differ between plots that received maintenance treatments and their paired non-maintenance controls. We conclude that many aspects of flower and bee assemblages in the reserve are little affected, in the short term, by the maintenance practices of fire buffer zones. As our experiment was limited to a one-year grazing/trimming intervention, future studies should assess the longer-term effects of these management activities on pollination interactions.

1. Introduction

Biodiversity is essential for maintaining ecosystem functions in forests (Gamfeldt et al. 2013) and other managed landscapes (Bengtsson et al. 2003; Tschamtker et al. 2005). Pollination, a major natural ecosystem service, is needed for the existence of many plants and animals, as well as for providing food to human populations (Gallai et al. 2009). Insects, and especially bees, are considered key vectors for biotic pollination (Michener 2000). Bee communities worldwide are commonly comprised of many rare and threatened species and few dominant ones (Potts et al. 2003a, Kleijn et al. 2015; Winfree et al. 2015). Moreover, some pollinating insects are declining globally and their valuable services are at risk (Goulson et al. 2015; Potts et al. 2016). The domestic stock of honey bees is rising, yet at a much slower rate than the rate of increase in agricultural needs for honey bees as pollinators (Aizen & Harder 2009). To develop successful management

strategies that will conserve pollinator diversity and services, the factors affecting wild bee communities in natural and managed landscapes need to be elucidated (Rubene et al. 2015; Brown et al. 2017).

The Mediterranean Basin is a global biodiversity hotspot (Myers et al. 2000) and hosts highly diverse plant-pollinator interactions (Petanidou and Lamborn 2005). Long durations of high-intensity human disturbances in this area have led to species-rich plant communities (Cowling et al. 1996; Vulliamy et al. 2006), which deserve high conservation priority. Such conservation efforts must consider the substantial risk of forest fires, due to the long, hot and dry summers in the Mediterranean and its dense and flammable vegetation (Agee, 1996). The UNESCO-recognized Mount Carmel Biosphere Reserve in Israel is continually threatened by fire. It thus exemplifies the importance of a science-based land management program to protect its forests and human settlements. A large wildfire in 2010 took the lives of 44 people and burned about 25,000 km² of natural and planted forests.

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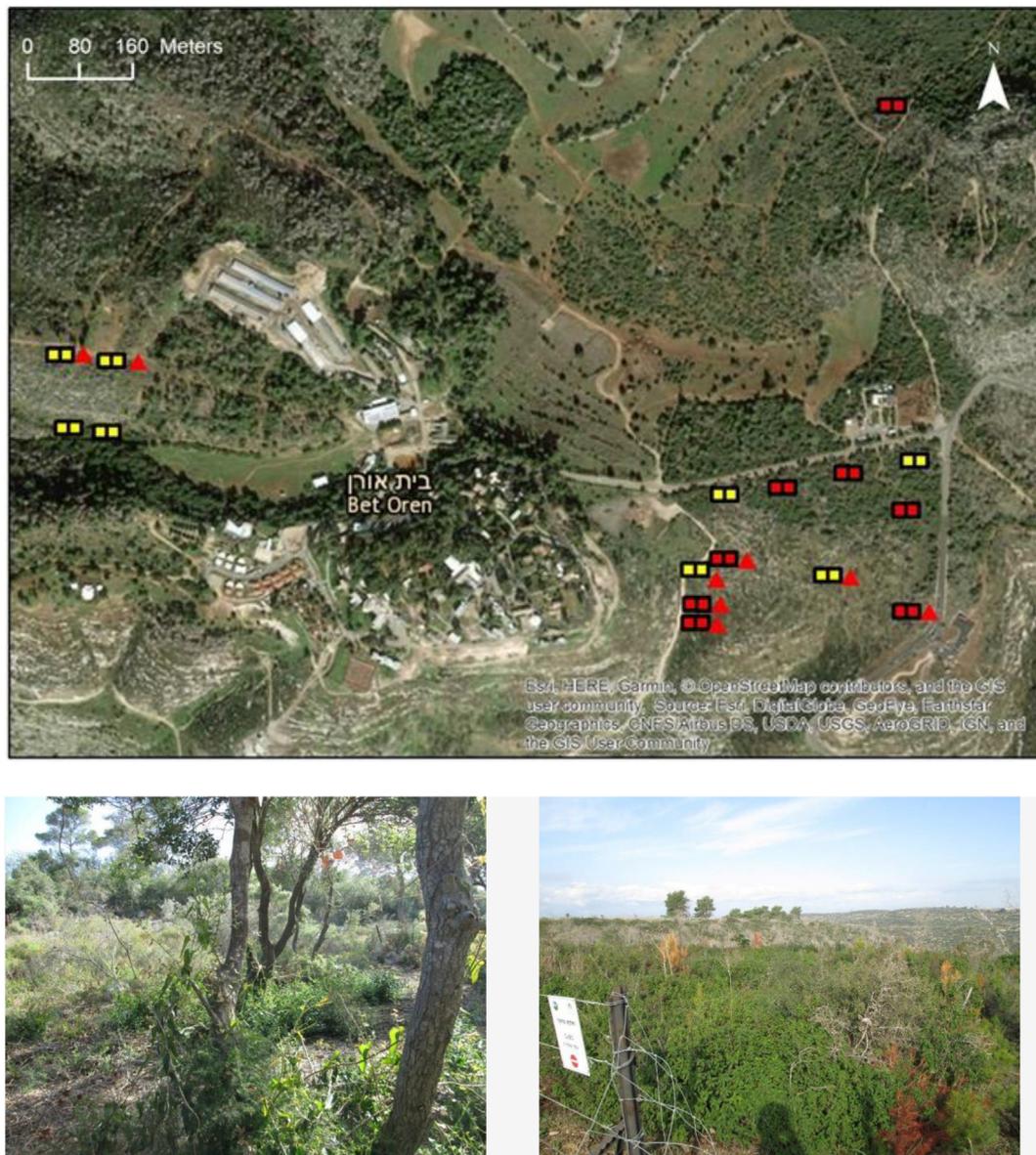


Fig. 1. Top: Satellite map of the research area near Kibbutz Beit Oren. Red rectangles represent mechanical cutting and their control plots, and yellow rectangles represent sheep grazing and their control plots. Rectangle sizes are drawn to scale. Plots marked with red triangles were burnt in 2010 and the remaining plots had not experienced forest fires for at least 20 years. Bottom: Illustration images of a maintenance (left) and a no-maintenance control (right) plot. Photos by Na'ama Tessler. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

To decrease the risks of such devastating fires in the future, various management strategies are implemented, mainly to establish 'fire buffer-zones' (also termed 'fuel breaks') around populated areas and along roadsides, in which woody biomass is drastically reduced. The natural fast regrowth of the Mediterranean shrubs and trees following clear-cutting causes rapid closure of the vegetation and accumulation of new woody biomass (Ne'eman and Perevolotsky, 2000). Therefore, the buffer zones need to be repeatedly maintained, using mechanical cutting or grazing as key management tools. Such actions may affect the community composition and abundance of flowering plants and bees. Here, we ask how standard protocols for grazing and cutting, used for maintenance of fire buffer zones, affect pollination interactions in the Mt. Carmel reserve.

Studies that focused on management of Mediterranean ecosystems found that livestock grazing often (Bashan and Bar-Massada 2017; Henkin 2011) but not always (Riedel et al., 2013) effectively clears forested areas and prevents regrowth. The effects of grazing on plant community composition are highly diverse (Hadar et al. 1999; Henkin

2011). They are influenced by (among other things) the type of grazer, the grazing intensity and the interaction of the grazing animal with its pasture environment. For example, moderate cattle grazing increased plant species richness relatively to un-grazed areas in Mediterranean grasslands (Noy-Meir 1995). Grazing by goats, on the other hand, reduced the number of plant species in herbaceous habitats and increased them in woody patches (Gabay et al. 2011). Previous research from Mt. Carmel provides initial evidence for beneficial local effects of grazing on flowering plants and pollinators. Honey bee (*Apis mellifera* L.) abundance in the reserve tended to increase with grazing intensity (Potts et al. 2003a). Cattle grazing had a positive influence on floral diversity, and indirectly also increased the species richness of native bees, as they sustain themselves on flowers (Vulliamy et al. 2006).

An additional set of experiments tested the effects of tree cutting and thinning on herbaceous plants in Mediterranean forests. Clear-cutting of all trees in Spanish pine-dominated stands significantly affected the composition of the understory plant community, while thinning (removal of 25% or 50% of the trees) produced milder effects

(Alday et al. 2010). In a second study from Spain, thinning of a pine forest (removal of 1/3 of the trees) did not affect overall species richness and diversity in the herbaceous plant community, but did increase the proportion of annual and nitrogen-fixing species (Nunes et al. 2014).

Evidence for the effects of tree thinning on pollination interactions is mainly based on studies from temperate-climate and boreal forests. Clear-cutting of trees below power lines increased the species and functional diversity of insect-pollinated plants (Steinert et al. 2018). Thinning of trees at forest edges that bordered farmland increased the total insect species richness and the abundance of butterflies, but did not affect the abundance of bumblebees (Korpela et al. 2015). Harvesting of pine trees in biofuel production plantations increased the abundance and diversity of bees (Miljanic et al., 2019). Clear-cutting of conifers for timber harvesting generally benefited pollinator abundance and diversity (reviewed by Rivers et al. 2018), as did post-fire salvage logging (Heil & Burkle 2018). Nevertheless, an earlier meta-analysis found that the effect size of logging on bees is generally small (Winfree et al. 2009).

It is still unknown whether mechanical cutting also benefits flowers and bees in Mediterranean ecosystems (Rivers et al. 2018). Moreover, a comparison of the effects of livestock grazing vs. mechanical cutting on the diversity of flowering plants and their visitors is still lacking. The present work aims to address this knowledge gap and describe the effects of fire buffer-zone maintenance practices on pollination systems in a managed Mediterranean forest. Because fire buffer-zones are repeatedly managed, the short-term effects of such maintenance activities are important and our study focuses on them.

2. Material and methods

2.1. Study site

The research plots were in the Mount Carmel Biosphere Reserve, Israel (Fig. 1) and were monitored during the spring seasons of 2014–2016. The area has a typical Mediterranean climate with six months of long, hot and dry summers (average \pm SD daily summer temperatures during the 2014–2016 study period were 24.3 ± 0.4 °C). There are about three months (December–February) of short, cool and rainy winters (average \pm SD daily winter temperatures were 13.6 ± 0.2 °C). The mean annual precipitation during 2014–2016 was 494.3 ± 178.2 mm, Israel Meteorological Service, <https://ims.gov.il/>). The reserve comprises 150 km² of Aleppo pine (*Pinus halepensis* Mill.) woodland in a mosaic of areas that differ in the age of their post-fire regenerating phrygana vegetation. *Pinus halepensis* and *Quercus calliprinos* Webb. are the dominant trees, accompanied by multi-stemmed trees, shrubs and dwarf-shrubs (e.g., *Pistacia lentiscus* L., *Cistus salviifolius* L., *Salvia fruticosa* Mill.). Several major fires (1974, 1983, 1989, 1998 [two fires], 1999 and 2010) have resulted in large stands of phrygana dominated by *Cistus* spp., *Satureja thymbra* L. and *S. fruticosa*, with species-rich annual herbaceous vegetation (Potts et al., 2003a). A full floristic description of this habitat is provided by Zohary (1982).

2.2. Experimental design

Thirty-two quadratic plots of 20 × 20 m were established in the spring and summer of 2014. The 20-meter edge length was selected to match the recommended design of fire buffer zones in Israel (strips of 10–70 m, depending on vegetation and topography; Dufour-Dror, 2011). The woody vegetation in the plots was mechanically thinned and pruned to simulate the creation of fire buffer zones, according to the standard protocol of the local forestry department. The main action was thinning of the shrubs and the number of stems of the trees, including their low lateral branches. These activities aim to reduce fuel load, restrict the spread of fire at ground level and prevent its vertical spread from ground to canopy (Ne'eman and Perevolotsky, 2000). Two

maintenance treatments were applied to inhibit natural regeneration of the woody biomass: (1) Cutting of the herbaceous and the regenerating woody vegetation in the fall of 2014, using a mechanical line trimmer and leaving behind fine slash (n = 8 plots). (2) Ten hours of monthly grazing by 100 sheep per plot during January–August 2015 (n = 8 plots). No maintenance treatments were applied in 2016. A no-maintenance control plot was set up next to each management plot as a reference with similar local conditions (totaling 16 plots, Fig. 1). The trees in the control plots were thinned in the spring-summer of 2014 to mimic the initial management of fire buffer zones. However, they received no further treatment afterwards, thus the control plots simulated fire buffer zones with no maintenance management. Cutting plots and their adjacent control plots were fenced to prevent unintended grazing by domestic or wild mammalian herbivores. In the sheep grazing treatment, the control plots were set up as enclosures within two large grazed areas of 58,700 and 7,100 m².

One half of the research plots of each treatment were established in an area that had been burnt by the large canopy forest fire of 2010, while the remaining plots were established in an area that has not been burnt for at least 20 years (Fig. 1). This was done to reduce the effects of fire history on flower and visiting insect composition (Ponisio et al. 2016).

2.3. Monitoring protocol

Each plot was monitored for (1) the species-level composition and abundance of flowers and the dominant flowering plant species and (2), and the genus-level composition and abundance of flower-visiting bees. Flower-visiting bees were observed by patrolling along the two diagonals of each plot for 15 min in total, and recording bees in a 1-m strip on both sides of each diagonal. Flowers were recorded in 1 × 1 m sampling quadrats, placed at 1-m intervals along the diagonals. Only quadrants with > 50% exposed soil area, which were suitable for plant growth and were later analyzed for flower abundance and composition, were used for observations. The number of observation quadrants therefore varied among plots and ranged from 8 to 17 (mean \pm SE: 12.94 ± 1.66). To reduce disturbance to the natural bee community within the national park, bees were visually identified to genus in the field with no capturing when possible. About 10% of the individuals could not be reliably identified in the field. They were collected and their identification was confirmed in the lab. 94% of these individuals were correctly identified in the field, providing us with an estimate of our identification accuracy. For bee identification we used a reference collection established by Dr. Simon Potts that is housed at the Institute of Evolution, University of Haifa, Israel. The specimens in this collection were identified by researchers of the Bee Systematics and Biology Unit, Oxford University Museum of Natural History, UK (Potts et al. 2003a). Plots within each pair (comprising a maintenance plot and its neighboring control plot) were observed successively on the same day in each monitoring session. To reduce the probability of observing the same visiting bees in unpaired plots, proximate plot pairs were not sampled on the same day, and the plot pairs that were sampled on the same day were as far as possible from each other. The minimal time interval between visits to neighboring pairs of plots was one week.

Flower-visiting bees were classified to genera, their visits to flowers were counted, and the visited flower species were recorded. Marking and fencing of 24 plots (assigned to cutting, grazing and control treatments) out of the 32 was completed before May 2014. A pre-maintenance monitoring session was conducted in these plots during February–April 2014. This monitoring session allowed us to test whether the maintenance and control plots differed *a-priori*, before any maintenance management was applied. We monitored all 32 plots in 2015, once in February–March and once again in April–May, to capture changes along the season during the year on which the maintenance treatments were applied. In 2016, the plots were monitored once, during February–April, to detect any potential post-maintenance effects.

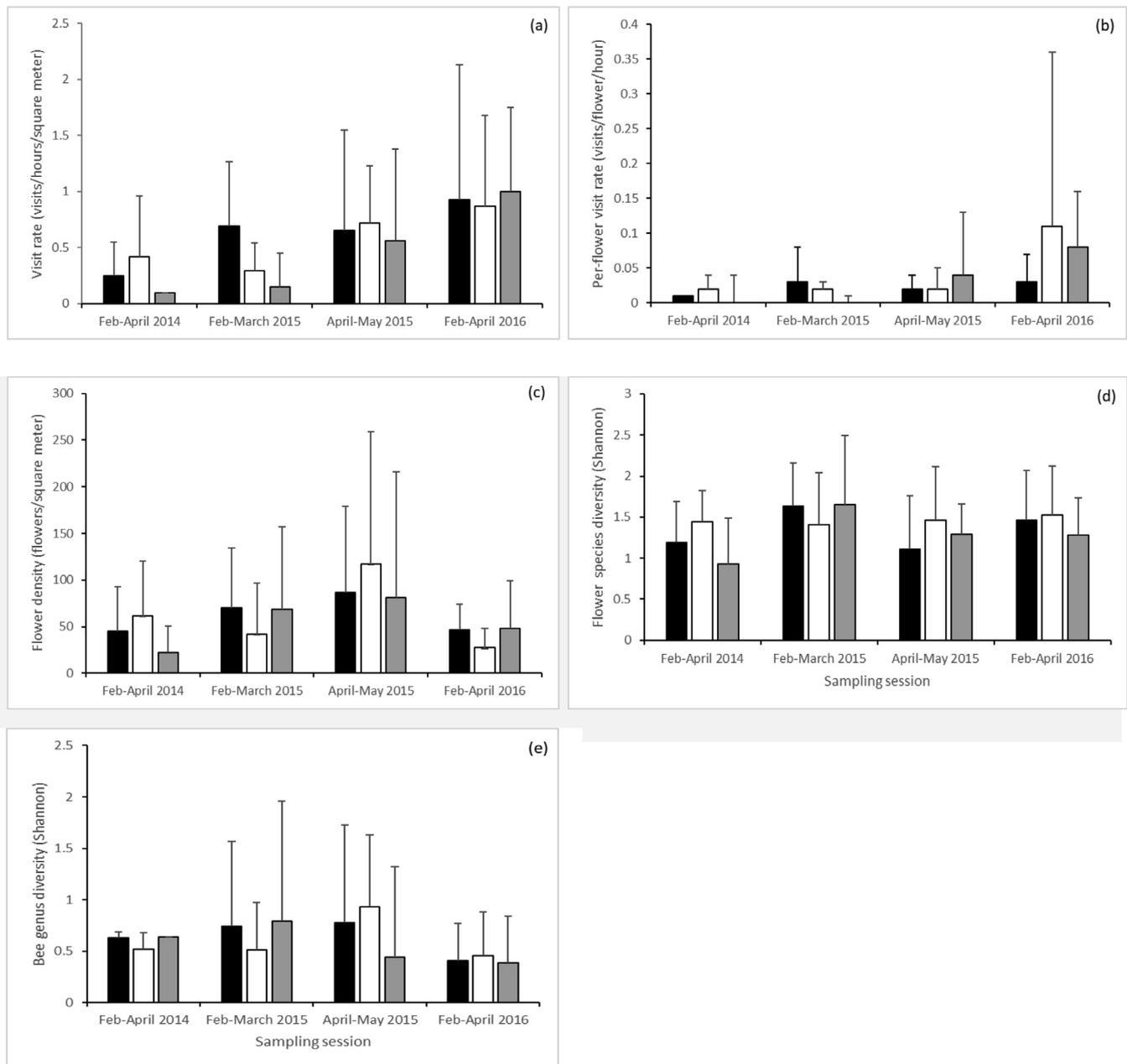


Fig. 2. Mean \pm SD values of the pollination-related variables in the experimental plots, grouped by monitoring session and maintenance treatment. (a) per-area visit rates, (b) per flower visit rates, (c) flower density, (d) flower species diversity, (e) bee genus diversity.

This design resulted in four monitoring sessions over three years. Each plot comprised a sampling unit within a session.

2.4. Data analysis

2.4.1. Flower density, visit rates and diversity indices

The density of flowers, per-area and per-flower rates of bee visits, and diversity indices for flower species and bee genera were computed for each of the plots within each of the four sampling sessions. We calculated the mean number of flowers per 1 m² sampling square as a measure of floral density. Bee visits were observed during 15-minute walks along the two diagonal transects, excluding the time needed to move from one transect to the other. We therefore multiplied the recorded numbers of visits by 4 to obtain hourly rates. Dividing these values by the area observed during the transect walk (113.14 m²) yielded the per-area visit rates (number of bee visits/hour/m²). Hourly

per-flower visit rates were calculated by dividing the number of visits/hour/m² by the mean floral density (no. flowers/m²) in each plot. Floral species-level diversity and bee genus-level diversity were estimated using the Shannon index.

We used generalized linear mixed models (lme4; Bates et al. 2015) to test whether the plots allocated to different treatments differed in pollination-related parameters in 2014, before the maintenance treatments were applied. We defined the allocated treatment (control, cut, or grazed) and fire history (burnt or unburnt in the 2010 fire) as fixed factors in each model. Plot ID ($n = 16$ pairs of plots) was included as a random factor to account for the pairing of maintenance and control plots. The dependent variables in the models were the bees' per-area visit rate, floral density, per-flower visit rate, flower diversity and bee diversity.

We analyzed the data from 2015 to 2016 (three monitoring sessions conducted during and after the maintenance operations) in a second set

Table 1

Composition of bees observed while visiting flowers during the transect walks. Data from the three monitoring sessions of 2015–2016 were pooled.

Bee genus	No. individuals observed	Percentage of all individuals
<i>Apis</i>	1215	66.94
<i>Halictus</i>	214	11.79
<i>Andrena</i>	189	10.41
<i>Anthophora</i>	79	4.35
<i>Chelostoma</i>	47	2.59
<i>Lasioglossum</i>	21	1.16
<i>Hylaeus</i>	16	0.88
<i>Xylocopa</i>	15	0.83
<i>Eucera</i>	12	0.66
<i>Hoplitis</i>	5	0.28
<i>Bombus</i>	2	0.11
Total	1815	

of generalized linear mixed models. Treatment, sampling session, their interaction and fire history were defined as fixed factors. Plot ID ($n = 16$) was defined as a random factor because of the spatial (paired maintenance and control plots) and temporal (repeated sampling) dependence between samples. We considered the same dependent variables as for the 2014 data.

We first defined a full model, and then created reduced models by sequentially removing fixed factors and interactions, for each of the GLMMs. We used likelihood tests to compare between models and to calculate P -values for each of the explanatory variables.

2.4.2. Flower species and bee genus community composition

We tested the effects of monitoring session, fire history and management on the composition of flower and bee communities in 2015–2016 using Permutational Multivariate ANOVA (PERMANOVA) tests. In this multivariate analysis, the numbers of individuals per bee genus/flower species were used as dependent variables. Thus, the dataset included 96 observations (32 plots \times 3 monitoring sessions). The tests were implemented using the ‘adonis’ function in the R package ‘vegan’ (Oksanen et al. 2013). We first considered maintenance (yes or no), monitoring session (February–March 2015, April–May 2015 or February–April 2016), burning history (burnt or unburnt in 2010) and their interactions as explanatory variables. After detecting a significant effect of maintenance on floral community composition (see results section), we conducted a second PERMANOVA analysis to test whether the type of maintenance (cutting vs. grazing) affected the floral community. We included monitoring session and fire history in this model as well and excluded the non-maintenance control plots from the dataset. We used Mantel tests to calculate correlations between bee/flower community dissimilarity and distances between plots.

Statistical analyses were conducted in R version 3.5.1 (R Development Core Team, 2017).

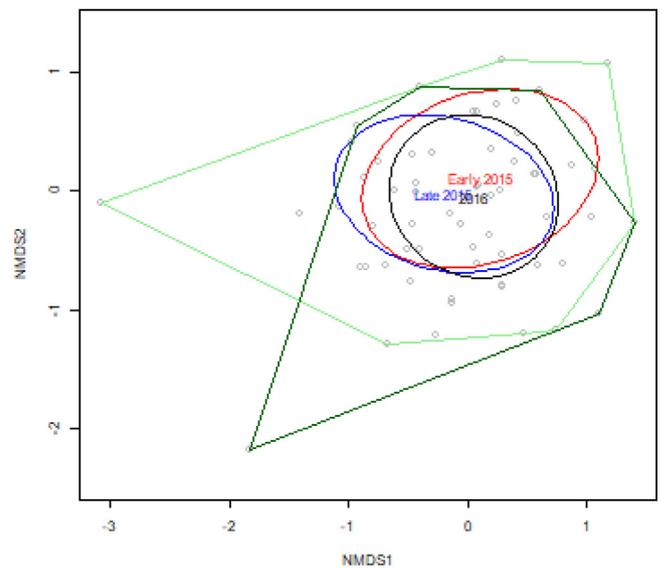
3. Results

3.1. The pre-maintenance monitoring session

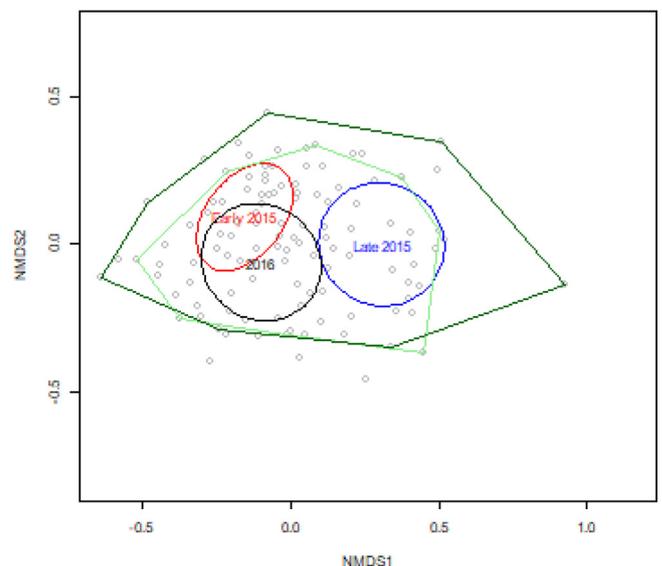
The plots were monitored for a pre-maintenance sample in the spring of 2014, after the initial thinning and trimming of the above-ground woody vegetation. Fig. 2 summarizes the mean per-area and per-flower visit rates, floral density and species diversity, and bee genus diversity for the plots assigned for future non-maintenance (control), cutting or grazing. The treatment allocated to the plots, their fire history and the interaction between these factors did not affect any of these dependent variables (Table S1).

3.2. Flower density, bee visit rates, and diversity measures in 2015–2016

The bees’ per-area and per-flower visit rates increased along the



(a) Bee communities



(b) Flower communities

Fig. 3. NMDS plots visualizing the effects of monitoring session (red, blue and black ellipses) and burning history (light green – recently burnt, dark green – unburnt) on the composition of bee (a) and flower (b) communities. Each plot-monitoring session combination is represented by a grey circle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

three monitoring sessions of 2015–2016 (Fig. 2a–b, GLMMs with likelihood tests for the effects of monitoring session: $\chi^2_1 = 6.25$, $P = 0.012$ for per-area visit rate, $\chi^2_1 = 4.45$, $P = 0.035$ for per-flower visit rate). Maintenance treatment, its interaction with monitoring session, and burning history did not significantly affect the rates of bee visits per area and per flower. None of the explanatory variables influenced flower density, flower diversity and bee diversity (Fig. 2c–e, Table S2).

Table 2

The abundant species of flowering plants (> 5% of all flowers) in the three monitoring sessions of 2015–2016, combined over all plots. The relative frequency (% of all flowers) of flowers from each species is reported.

Monitoring session		Monitoring session		Monitoring session	
February-March 2015		April-May 2015		February-April 2016	
Species	%	Species	%	Species	%
<i>Scandix iberica</i>	32.1	<i>Lotus collinus</i>	42.7	<i>Calicotome villosa</i>	21.6
<i>Valerianella vesicaria</i>	9.8	<i>Chaetosciadium trichospermum</i>	25.3	<i>Scandix iberica</i>	11.8
<i>Rubia tenuifolia</i>	7.4	<i>Teucrium divaricatum</i>	21.0	<i>Cistus salvifolius</i>	11.6
<i>Sinapis alba</i>	7.1	<i>Synelcosciadium carmeli</i>	13.9	<i>Trifolium resupinatum</i>	9.1
				<i>Euphorbia hierosolymitana</i>	7.8

3.3. Community composition of visiting bees and flowers in 2015–2016

Honey bees (*Apis mellifera*) dominated the bee community in 2015–2016. *Halictus* and *Andrena*, medium-sized ground nesters, were the most abundant genera of wild bees (Table 1). None of the explanatory variables (presence/absence of maintenance management, monitoring session and burning history) significantly affected the genus-level composition of bee visitors in the PerMANOVA analysis (Fig. 3a, Table S3).

We recorded 147 species of flowering plants in 2015–2016. Abundant species, defined as those that comprised > 5% of the total number of flowers in all monitoring sessions combined, are listed in Table 2. The composition of flowering species was most strongly influenced by monitoring session, and to a lesser extent by fire history and maintenance (Fig. 3b, Table 3). As the presence of maintenance significantly affected flower composition, we ran an additional PerMANOVA test to determine whether the flower community differed between cutting and grazing plots. The input dataset for this analysis included only the maintenance plots in all three monitoring sessions. The results indicate no effect of the type of management (cutting or grazing) on the flower communities, while the effects of fire history and monitoring session remained significant (Table 4).

Mantel tests were performed to evaluate the effect of the distances among plots on the differences in their flower and bee communities. We did not find significant correlations between dissimilarity in flower species or bee genera community compositions and the distances between the plots they occupied, in any monitoring session (*P*-values for the Mantel tests: 0.462, 0.184, and 0.216 for flowers during February-March 2015, April-May 2015 and February-April 2016, respectively. *P* = 0.259, 0.453 and 0.795 for bees during these three monitoring sessions, respectively).

4. Discussion

Our experiment simulated the creation and maintenance of fire

Table 3

PERMANOVA results for the effects of maintenance management, fire history, monitoring session and their interactions on the composition of the flowering species community.

Factor	DF	SS	Mean Square	F	R ²	P
Treatment (Maintenance/Control)	1	0.683	0.683	1.687	0.014	0.006
Fire history (Burnt/Unburnt)	2	1.879	0.939	2.319	0.038	0.001
Monitoring session (Feb-Mar 2015/April-May 2015 /February-April 2016)	2	3.222	1.611	3.977	0.065	0.001
Treatment × History	2	1.175	0.588	1.451	0.023	0.011
Treatment × Session	2	1.299	0.649	1.603	0.026	0.002
History × Session	2	1.067	0.534	1.318	0.021	0.030
Treatment × History × Session	2	1.057	0.528	1.304	0.021	0.035
Residuals	97	39.291	0.405		0.791	
Total	110	49.673			1	

buffer zones in experimental plots within a Mediterranean forest. The pre-maintenance monitoring session in 2014 confirmed that all plots were initially similar in the abundance of flowers and bees and in floral diversity. These pollination-related variables did not differ between plots that received a maintenance treatment (either cutting or grazing) and their paired no-maintenance control plots in 2015–2016 as well. Maintenance, alone and in interaction with other variables, significantly affected the composition of flowers, and explained 12.8% of the variance in flower assemblages among plots. These findings differ from a previous study in the Mt. Carmel reserve, in which the intensity of cattle grazing correlated positively with the diversity of both flowers and native bees (Vulliamy et al. 2006). The dissimilarity between our findings and those of Vulliamy et al. (2006) may reflect differences in herbivore species and in their grazing pressure. Different grazing species were shown to affect plant biomass and to reduce regeneration to varying degrees, both in Mt. Carmel (Bashan and Bar-Massada, 2017) and in temperate forests (Öllerer et al. 2019). In addition, the rather low grazing intensity, as used by the local shepherds, which was applied in our experiment, may have been insufficient to affect flower and bee populations.

The composition of bees did not respond to the maintenance treatments, despite the effect of maintenance on the floral communities. This could be partly due to the small size of our research plots and their proximity to each other, which could have allowed some bees to forage in more than one plot type. These features of our experimental setup are ecologically realistic because they reflect actual “real-life” conditions; fire buffer zones in the Mt. Carmel reserve are constructed as narrow strips along roads and around villages, next to patches of dense forest, maquis, or phrygana. Thus, pollinators can probably easily fly in and out of the fire buffer zones.

Most of the bees in our study were identified without capturing in the field because of conservation concerns. This procedure limited our ability to detect management effects on community composition in two ways. First, we identified bees to genus level only, thus were unable to document potential species-specific effects of the grazing and cutting treatments. Further investigations, focused on specific bee species, are needed to address this limitation. Second, some bee genera (e.g., *Lasioglossum*, *Andrena* and *Halictus*) are very difficult to distinguish in the field. Potential errors in identification may have introduced additional noise into our analyses of bee community composition. We partially addressed this problem by capturing a subset (~10%) of the bees, confirming the identifications that were done on the wing, and assessing the identification error rate (~6%). Furthermore, pollen-deposition observations, which were conducted in our study plots in 2014–2015 by a different team of researchers, yielded a similar composition of bee genera as our observations (Ballantyne et al. 2017). This indirectly supports the accuracy of our genus-level identifications.

The rate of bee visits to flowers, per-area and per-flower, increased along the 2015–2016 monitoring sessions. Monitoring session was also the main variable that affected the composition of the flower community. Similarly, plant species composition in post-fire Australian forests

Table 4

PERMANOVA results for the effects of maintenance type (cutting vs. grazing), fire history, monitoring session and their interactions on the composition of the flower species community. Only cut and grazed plots were included in this analysis.

Factor	DF	SS	Mean Square	F	R ²	P
Type of maintenance (Cutting/Grazing)	1	0.449	0.449	1.070	0.021	0.348
Fire history(Burnt/Unburnt)	1	0.700	0.697	1.663	0.033	0.007
Monitoring session (Feb-Mar 2015/April-May 2015 /February-April 2016)	2	1.830	0.915	2.182	0.086	0.001
Maintenance × History	1	0.426	0.426	1.016	0.020	0.440
Maintenance × Session	2	0.984	0.492	1.174	0.047	0.131
History × Session	2	0.834	0.417	0.994	0.039	0.501
Maintenance × History × Session	2	0.853	0.426	1.016	0.040	0.454
Residuals	36	15.098	0.419		0.713	
Total	47	21.17			1.000	

was highly influenced by the timing of the vegetation surveys, but unaffected by grazing and fire history (Hill & French 2004). The community of flowering species in our study is a mix of perennial and annual plants and its composition changed from year to year, as expected in a mosaic of patches during the first years of post-fire regeneration (Dafni et al. 2012). Post-fire succession and the seasonal progression of flowering thus likely explain the effects of monitoring session. For example, annual herbs were the main dominant flowering species in early 2015. By 2016 shrubs increased their abundance in the flowering community, as predicted during secondary succession. These processes were unaffected by the presence or absence of maintenance treatments, since this variable did not interact with monitoring session. Unlike the flower community, the bees' genus-level composition was not affected by monitoring session in our study.

Beyond the main research question, our experimental design also allowed us to compare plots that experienced the 2010 wildfire with plots that did not. Similar to previous studies from Mt. Carmel, fire history influenced the composition of flowers in our plots, but not the genus-level composition of bees (Potts et al. 2003b; Dafni et al. 2012). Interestingly, fire history did affect the composition of bee assemblages at the species level, both in the Mt. Carmel reserve and elsewhere (Potts et al. 2003b; Rubene et al. 2015). However, Potts et al. (2003b) also report a peak in flower and bee abundance two years after a fire, which declined as the post-fire regeneration proceeded. In our experiment, on the other hand, variables related to flower density and bee activity were unaffected by the plots' fire history. Studies from other ecosystems also report diverse effects of post-fire conditions on bee density and species richness, ranging from positive (e.g., Van Nuland et al. 2013) to neutral (e.g., Rubene et al. 2015). This range of responses was suggested to reflect differences among pollinators in generation length and flight ranges, which determine their vulnerability to fires (Brown et al. 2017).

Overall, we recorded mild changes in the plant and pollinator communities in response to low-intensity grazing and cutting, as currently applied to maintain the fire buffer zones in the Mt. Carmel reserve. Earlier studies that evaluated the effects of livestock grazing (Sternberg et al. 2000; Gabay et al. 2011) and precipitation (Tielbörger et al. 2014) on Mediterranean plant communities report similar robustness. Species that are resistant to environmental fluctuations may have been selected under the highly variable abiotic conditions and long-term human disturbances that characterize Mediterranean ecosystems. Our study suggests that bee communities are similarly resistant to some habitat manipulations, at least over a time span of 1–2 years. However, long-term monitoring of Mediterranean plant-pollinator communities in Greece (over four years) and in Spain (over two decades) revealed high between-year variability in the composition of species and their interactions (Petanidou et al. 2008; Herrera 2019). Moreover, the bee composition in our study differed remarkably from that recorded in 1999–2000 in nearby sites on Mt. Carmel (Potts et al. 2003a). For example, the relative abundance of the family Andrenidae more than doubled between 1999 and 2000 and 2015–2016, while the frequency of the family Halictidae declined by ~50%. These indications

for high inter-annual variability and slow change rates in flower and bee communities call for longer-term investigations of their response to forestry management interventions.

CRediT authorship contribution statement

Alon Ornai: Investigation, Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Gidi Ne'eman:** Conceptualization, Funding acquisition, Supervision, Writing - original draft, Writing - review & editing. **Tamar Keasar:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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