

ARTICLE

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Long-term proliferation of large annual thistles in dry Mediterranean rangelands

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Abstract

Spiny plants comprise a large, ecologically and economically important functional group in Mediterranean rangelands. The increasing abundance of large annual thistles in grazed grasslands entails major consequences for ecosystem services. This study aims to quantify the contribution of large annual spiny plants to rangeland vegetation cover and productivity and to identify management- and climate-related drivers of spiny plant distribution and performance. Using a 15-year dataset from an extensive herbaceous pasture experiment in northeastern Galilee, Israel, we examined the effects of livestock management and climate on the cover and biomass of two dominant annual thistle species, *Scolymus maculatus* and *Carthamus glaucus*. These thistles constitute a significant proportion of pasture productivity, contributing more than 50% and 25% under high and moderate stocking density, respectively. Despite the similarity in life-form and life-history characteristics, each demonstrates a distinct response to both management intensity and annual climatic parameters. High stocking density had a positive effect on both cover and biomass of *S. maculatus*. Conversely, *C. glaucus* biomass estimates were higher under moderate stocking density. Distance from feeding site had significant contrasting effects on each of the focal thistles. Relative humidity and temperature were the most sensitive climatic parameters in explaining the variation in cover and biomass of the two thistles. The directionality of the two species' responses suggests that *S. maculatus* attains higher biomass than *C. glaucus* under dry and warm conditions. The proliferation of both large thistles under variable stocking densities and climatic conditions increases productivity but reduces the palatable vegetation of Mediterranean rangelands by 27%–50%.

KEYWORDS

climate change, productivity, spiny plants, stocking density, supplemental feeding, thistles

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INTRODUCTION

Annual herbaceous rangeland species' stature is subject to a trade-off between resources and herbivory. Tall growth forms and fast growth rates allow better competition for light but increased susceptibility to grazing (Milchunas et al., 1988). Spininess releases (at least partially) annual spiny plants from these constraints by deterring herbivores and reducing palatability. Thus, large herbaceous spiny plant species increase in abundance in grazed vegetation due to their relatively low palatability and increase in size due to the partial release from resource-herbivory trade-off (Adler, 2008; Chollet et al., 2014). In Mediterranean regions, increased abundance of spiny plants under grazing may decrease rangeland carrying capacity and paradoxically increase rangeland productivity, through altered plant size, density, and resource allocation (Dovrat et al., 2019, 2020).

Spiny plants are a well-known component of Mediterranean herbaceous plant communities (Sternberg et al., 2000). Spines or thorns are found on the leaves, stems, and/or flowers of 10% (268 of 2657) of all vascular plant species in Israel (Danin & Fragman-Sapir, 2016). The Asteraceae family stands out, as 42% of its species (90 of 224) bear spines on at least one of their above-ground parts and it contributes 38% of Israel's spiny annuals (Appendix S1: Figure S1).

Studies on the distribution of spiny plants along ecological and geographical gradients are scarce, and emerging patterns, for example, regarding the effect of elevation and aridity, are inconclusive (Moreno et al., 2010; Song et al., 2020). This may be related to the effects of sampling across different spiny plant life forms, and in the case of grazing, to the effects of different types of herbivores.

Ungulates have been abundant in the Eastern Mediterranean for thousands of years, particularly in the last 10,000 years (Perevolotsky & Seligman, 1998) when domestication of animals led to a significant increase in their prevalence (Ronel & Lev-Yadun, 2012). Spininess is a plastic inducible trait that provides defense against vertebrate herbivory and is favored under grazing (Armani et al., 2020; Rebollo et al., 2002). Several studies in Mediterranean rangelands have demonstrated that the abundance and productivity of spiny plants increase under grazing (Golodets et al., 2010; Sternberg et al., 2015). However, few have attempted to quantify the contribution of spiny plants to total vegetation productivity, and little is known about the effect of stocking density and spatially explicit variation in the response of spiny plants to supplemental cattle feeding. Moreover, the effects of climate and seasonality on this group have not been examined to date.

In semiarid Mediterranean ecosystems, cattle are provided with water troughs, and since the available annual vegetation begins to lose its nutritional value after flowering, the cattle are provided with nitrogen-rich supplemental feed (poultry litter), ad-lib, at designated feeding sites (Becchetti et al., 2016). The soil surrounding these sites is enriched with nitrogen, phosphorus, and potassium (Mathews et al., 1994; Vinograd et al., 2019; West et al., 1989) via cows' feces and urine, as well as from scattering of the supplemental feed. The nitrogen concentration of the soil decreases linearly with distance from the water troughs and feeding sites (Dubeux et al., 2009, 2014; Sigua & Coleman, 2006). Large thistle abundance may increase near the water troughs and feeding sites, due to their relatively low palatability and their ability to capture high inputs of soil nitrogen (Leghari et al., 2016).

Annual plant species are typical of water-limited environments in which rainfall is highly unpredictable and confined to a relatively short winter period (Hahm et al., 2019; Lozano-Parra et al., 2018). The herbaceous vegetation in the rangelands of northern Israel reaches its peak vegetative growth during spring (March–April), flowering and setting seed, and then wilting and drying up after seed dispersal, in early summer (May) (Golodets et al., 2013). The phenology of annual thistles of the Asteraceae family may be asynchronized with the phenology of most herbaceous species in the community. Seedlings develop initially as rosettes, establishing a deep root system, then sending up a flowering stalk later in the season, reaching peak growth and flowering in May–June, when most of the other annual plants have already wilted and died (Ronel et al., 2010). The rosettes' low stature provides a size refuge from grazing and occupies a relatively large area to prevent nearby competitors' germination. The two dominant, large annual thistle species in the system—*Carthamus glaucus* M. Bieb. and *Scolymus maculatus* L.—usually complete their life cycle by July, and at the latest, August. The aboveground parts of both species carry spines on their cauline leaves, rosettes, and inflorescence heads, with the stems of *S. maculatus* bearing spiny wings that are absent in *C. glaucus*.

Global climate change can lead to changes in community composition in grazed Mediterranean grasslands via a gradual long-term increase in the relative proportion of large thistles. The combined effect of high grazing pressure and a decline in rainfall amounts, predicted for Mediterranean areas (Golodets et al., 2013), can reduce the resilience of the ecosystem by causing a dramatic shift in community composition and productivity (Dovrat et al., 2020; Siero et al., 2019).

In addition to their potential contribution to biomass production, large annual thistles also utilize a large proportion of the available soil nutrients. This means that a community with a higher proportion of spiny species relative to palatable grasses should demonstrate a higher mineral content. However, since these species are mostly not eaten, these extra nutrients and proteins are essentially “locked away” in the spiny plants and are unavailable for cattle consumption. Similarly, spiny plants may make a significant contribution to rangeland productivity; however, this does not necessarily translate to a higher amount of available herbage for the cattle.

Increased abundance of large annual thistles in grazed grasslands may carry major consequences for ecosystem services, manifested in reduced rangeland carrying capacity, which is becoming increasingly problematic over time rather than being a localized problem. We therefore maintain that it is imperative to obtain a clearer understanding of the dynamics of large annual thistles under cattle grazing. The specific objectives of this study were to: (1) determine the long-term contribution of large annual thistles to rangeland biomass production; (2) analyze the variation in large annual thistle cover and biomass with respect to stocking density and the heterogeneous soil nutrient enrichment resulting from supplemental summer feeding; and (3) identify plant species-specific responses of spiny plants to variation in annual climatic indices under a changing climatic regime.

MATERIALS AND METHODS

Site description

Vegetation and climate data were obtained from a long-term ecological research (LTER) study at the Karei Deshe Experimental Range Station (32°55' N, 35°35' E, 150 m above sea level) in northeastern Galilee, Israel. The climate is Mediterranean with mean annual precipitation of 567 mm, mean annual maximum and minimum temperatures of 25.9 and 16.1°C, respectively. The vegetation at this site is classified as Mediterranean Batha (Zohary, 1973), dominated by grasses and forbs. Annuals comprise 74% of the species pool ($n = 166$) and constitute more than 50% of the plant cover (Sternberg et al., 2000). The dominant perennial species are the hemicryptophytes, *Hordeum bulbosum*, *Bituminaria bituminosa*, *Echinops gaillardotii*, *Echinops adenocaulos*, and *Ferula communis* (Noy-Meir et al., 1989). Most other species are annuals, including grasses (*Avena sterilis* and *Hordeum spontaneum*), legumes (*Medicago polymorpha* and *Trifolium pilulare*), composites, crucifers, and umbellifers.

The two dominant large annual thistles in the system are *S. maculatus* and *C. glaucus*. Sampled in July 2019, the mean height of uneaten *S. maculatus* and *C. glaucus* was 98.5 ± 6.4 cm and 78.7 ± 5.3 cm, respectively.

Experimental treatments

The experimental treatments included two stocking densities: heavy stocking density (1.1 cows ha⁻¹) and moderate stocking density (0.55 cows ha⁻¹), this experimental setup has been in operation since 1994 (Henkin et al., 2015). The total experimental area covered 58.7 ha and was divided into two large fenced paddocks: 27.6 ha for the heavy grazing treatment and 31.1 ha for the moderate grazing treatment. The cattle graze in the experimental paddocks for approximately seven months per year, from mid-January to late August. Deferment of grazing after the onset of the rainy season in late autumn allows for vegetation establishment and early growth of the pasture. In the years of the study, grazing commenced in early February. Each experimental paddock contained a feeding site for supplemental summer feed, positioned near the entrance. The experimental treatments were sampled annually for 14 years (2005–2018) in three distances from the cattle feed points (300, 400, and 500 m from feed points).

Vegetation sampling

The vegetation was monitored annually in spring (late March to mid-April), at peak primary production of the herbaceous vegetation. Transects were sampled along three perpendicular distances: 300, 400, and 500 m from the cattle feed points. The transects (100–500 m long) traverse the paddocks from fence to fence. Plant cover and species composition were estimated using the step-point method (Mueller-Dombois & Ellenberg, 1974). Every 2 m, a thin rod was placed vertically in the vegetation (74–250 points per transect). Living plant species (i.e., green tissues) in contact with two certain heights (3–10 and 30–50 cm) on the rod were recorded. In cases where no vegetation was encountered, bare ground and rock cover were recorded. Relative cover was calculated by dividing the sum of encounters of each species with the sum of all encounters along the transect. Biomass sampling took place during the same period. Quadrats of 25 × 25 cm were randomly placed along the transects in the paddocks. All aboveground palatable standing biomass was harvested. Twenty samples were harvested in each paddock during each year of the study. The harvested samples were oven-dried at 65°C for three days and then weighed.

Climate parameters

Climatic parameters were recorded for 14 years (2005–2018) by a meteorological station located at the experimental site. We analyzed three groups of climatic parameters: temperature, humidity, and rainfall. For each climatic parameter group, we calculated indicators of spread (distribution) and amount, in the form of annual mean and seasonal monthly mean. Seasonal indices were calculated for the annual growth period, that is, winter and spring (October–May). To analyze extreme winter values of temperature and relative humidity, we calculated the mean daily maximum and minimum values and then pooled them for a winter monthly mean. To analyze precipitation, we constructed measures of seasonal temporal spread and accumulated annual amount. We used “rain until sampling” to test the effect of mean accumulated rain amount from the first rain event until April, for spring sampling, and December rain percentage, and amount, for early winter precipitation, which is critical for germination of annual plants.

Data analysis

Large annual thistle cover and biomass

The historical long-term (2004–2018) dataset that we used included yearly samples of nonspiny plant biomass and cover samples of both spiny and nonspiny plants, but did not include the relative fraction of the spiny plant biomass out of total aboveground plant biomass. To determine the association between cover and biomass for the spiny species, we used two datasets from studies conducted at Karei Deshe during 2003 and 2019. These datasets included direct measurements of the biomass and cover of spiny and nonspiny plants in the experimental plots, as well as in control plots that were excluded from grazing (10 exclosures ranging in size from 16 to 36 m²). We used nonlinear extrapolation to estimate the relative fraction of the spiny plant biomass from total aboveground biomass given the annual relative cover of spiny plants and the annual biomass of nonspiny plants. The calibration equation is presented in Appendix S1.

Statistical analysis

Preliminary analysis of the data showed that the shared response of the two focal annual thistles to different environmental parameters can mask species-specific responses; we therefore analyzed each species independently. For each of the two focal species' cover or biomass

(dependent variable), we constructed a model with two fixed categorical factors: stocking density (two levels) and distance from feeding site (three distances). We tested each of these factors and their interaction on each of the focal species' cover and biomass. We then expanded the model using the best continuous explanatory factor, screened from a range of 16 climatic parameters. To find the climatic parameters that best predict cover and biomass for each of the two thistle species, we used multifactorial ANOVAs. To compare and rank multiple competing models to select the best approximation model, we used forward selection and the corrected Akaike information criterion (AIC_c) for small sample size. We used a post hoc Bonferroni test for multiple comparisons between stocking densities and distances from feeding sites. We conducted Shapiro–Wilk tests for normality of errors and Levene's test for homogeneity of variances. In cases where ANOVA assumptions were not met, we used mathematical transformations (arcsine square root). Statistical analyses were performed using IBM SPSS Statistics for Windows, version 25.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Total productivity and thistle biomass

Productivity surveys in spring 2019 showed that total aboveground biomass was significantly affected by stocking density ($F_{1,29} = 7.317$, $p \leq 0.05$) and was lower under no grazing compared with moderate and heavy stocking densities ($p \leq 0.05$; Figure 1). Thistle biomass in spring 2019 was significantly higher under heavy stocking density relative to moderate stocking density ($F_{1,10} = 10.112$, $p \leq 0.05$; Figure 1). The long-term mean annual biomass estimate (extrapolated from the relative cover of thistles) for *C. glaucus* and *S. maculatus* throughout the 15 years of the experiment (2004–2018) was 630 and 240 kg ha⁻¹, respectively, under heavy stocking density, and 250 and 340 kg ha⁻¹, respectively, under moderate stocking density. Thistles were absent from the no-grazing exclosures.

Biomass and cover are two measures of abundance that differ for the two dominant thistles. Examining the long-term changes in biomass–cover ratio can be proven insightful for each of the two species performance under distinct management. For *C. glaucus* we found no difference in the biomass–cover slope under moderate or heavy stocking densities (Appendix S1: Figure S2a). However, for *S. maculatus*, the slope was significantly higher under moderate stocking with high biomass indices against low relative cover (Appendix S1: Figure S2b).

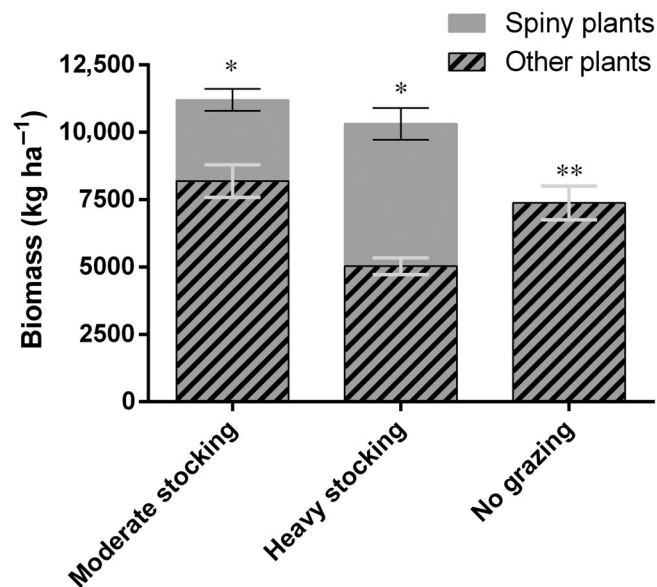


FIGURE 1 Aboveground biomass of spiny plants and nonspiny plants under moderate and heavy stocking densities, and no grazing (control). Mean biomass ($\pm$ SE) was measured directly from harvested plants sampled in control and grazed plots in 2019 at flowering time (peak standing herbaceous biomass). Statistically significant differences between spiny and nonspiny plants within treatments are designated by asterisks (** $p \leq 0.005$; * $p \leq 0.05$).

Effect of distance from feeding site and stocking density on large thistle cover and biomass

Relative cover of *C. glaucus* and *S. maculatus* changed significantly with distance from the feeding site (Table 1). The relative cover of *C. glaucus* increased with distance from the feeding site and was significantly higher at a distance of 500 m than at a distance of 300 m (Figure 2a). The relative cover of *S. maculatus* decreased with distance from the feeding site and was significantly higher at a distance of 300 m than at distances of 400 and 500 m (Figure 2b). Relative cover of *S. maculatus* was significantly higher under heavy stocking density than under moderate stocking density (Figure 2b, Table 1). In contrast, the relative cover of *C. glaucus* did not differ significantly between moderate and heavy stocking densities (Figure 2a, Table 1). The interaction term between distance from the feeding site and stocking density was not significant for the relative cover of either thistle species (Table 1).

The biomass estimates of *C. glaucus* and *S. maculatus* varied significantly with distance from the feeding site (Table 1). The biomass of *C. glaucus* increased with distance from the feeding site and was significantly higher at a distance of 500 m than at a distance of 300 m

TABLE 1 Relative cover and biomass of two large annual thistles.

Source	df	F	p	Partial η^2
Cover				
<i>Carthamus glaucus</i>				
Distance	2	8.07	***	0.173
Stocking	1	2.38	ns	0.03
RH max	1	5.52	*	0.067
Distance $\times$ stocking	2	0.639	ns	0.016
<i>Scolymus maculatus</i>				
Distance	2	9.30	***	0.195
Stocking	1	28.6	***	0.271
T max Oct–May	1	9.29	**	0.108
Distance $\times$ stocking	2	1.23	ns	0.031
Biomass				
<i>C. glaucus</i>				
Distance	2	8.13	***	0.174
Stocking	1	15.6	***	0.168
RH max	1	2.71	ns	0.034
Distance $\times$ stocking	2	0.126	ns	0.003
<i>S. maculatus</i>				
Distance	2	9.03	***	0.19
Stocking	1	27.8	***	0.265
RH max	1	6.72	ns	0.08
Distance $\times$ stocking	2	1.19	ns	0.03

Note: Results of multifactorial ANOVAs of the effects of distance from feeding site (“distance”), stocking density (“stocking”), and a single most relevant climatic parameter (as a continuous factor) on relative cover and biomass of *C. glaucus* and *S. maculatus*.

Abbreviations: ns, not significant; RH max, maximum relative humidity; T max, maximum temperature.

* $p \leq 0.05$; ** $p \leq 0.005$; *** $p \leq 0.001$.

(Figure 3a). Conversely, the biomass of *S. maculatus* decreased with distance from the feeding site and was significantly higher at a distance of 300 m than at distances of 400 and 500 m (Figure 3b). Similarly, the biomass estimates of both thistles varied significantly with stocking density. The biomass of *C. glaucus* was significantly higher under moderate stocking density, while the biomass of *S. maculatus* was significantly higher under heavy stocking density (Figure 3, Table 1). The interaction term between distance from feeding site and stocking density was not significant for biomass of either species (Table 1). Alongside with the effects of the distance from the feeding site on thistles distribution, we found no effect of distance from the feeding site on either total biomass or nonspiny biomass (Appendix S1: Table S1).

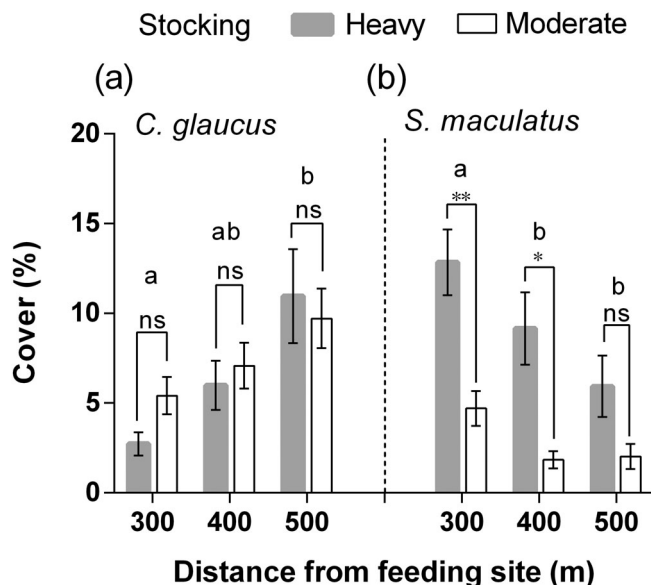


FIGURE 2 Relative cover of two large annual thistles as a function of distance from feeding site. Bars represent the mean relative cover ($\pm$ SE) of *Carthamus glaucus* (a) and *Scolymus maculatus* (b), under heavy and moderate stocking densities. Statistically significant differences are designated by different letters (between distances, post hoc Bonferroni $p \leq 0.05$) and asterisks (between stocking densities, $**p \leq 0.005$; $*p \leq 0.05$). ns, not significant.

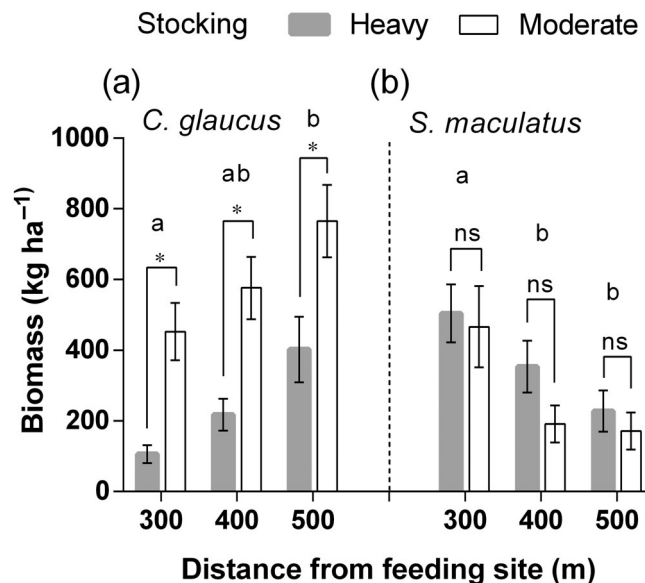


FIGURE 3 Mean biomass (extrapolated from the relative cover of thistles) of two large annual thistles as a function of distance from feeding site. Bars represent the mean biomass ($\pm$ SE) of *Carthamus glaucus* (a) and *Scolymus maculatus* (b), under heavy and moderate stocking densities. Statistically significant differences are designated by different letters (between distances, post hoc Bonferroni $p \leq 0.05$) and asterisks (between stocking densities, $*p \leq 0.05$). ns, not significant.

Effect of climatic variables on large thistle cover and biomass

Climatic variables demonstrated significant contrasting effects on the cover and biomass of both species. Warm, drier years were associated with higher cover of *S. maculatus*. The model that included winter and spring daily maximum temperature, combined with stocking density and distance from feeding site, provided the best prediction for *S. maculatus* cover ($R^2 = 0.416$) throughout the 14 years of climate parameter sampling (2005–2018), according to AIC_c (Appendix S1: Table S2). In contrast, *C. glaucus* cover increased in cooler, humid years. The models that included daily maximum relative humidity, along with stocking density and distance from feeding site, gave the best prediction according to AIC_c ($R^2 = 0.235$; Appendix S1: Table S3).

For most of the climatic parameters tested, we found contrasting behavior for the two large dominant thistle species: a positive linear association of *S. maculatus* with mean maximum temperature ($R^2 = 0.249$, $p \leq 0.001$; Figure 4a), and total annual rainfall ($R^2 = 0.11$, $p \leq 0.05$; Figure 4b), under heavy and moderate stocking densities, respectively, while in contrast a significant negative linear association of *C. glaucus* with mean maximum

temperature under heavy stocking density ($R^2 = 0.10$, $p \leq 0.05$; Figure 4a).

The biomass of *S. maculatus* declined in cooler, humid years. A model comprising daily maximum relative humidity, combined with stocking densities and distance from feeding site, provided the best prediction for *S. maculatus* biomass according to AIC_c ($R^2 = 0.33$; Appendix S1: Table S4). In contrast, *C. glaucus* biomass increased in cooler, humid years. A model comprising daily maximum relative humidity with stocking density and distance from feeding site provided the best prediction for the biomass production of this species according to AIC_c ($R^2 = 0.31$; Appendix S1: Table S5).

We found a significant negative linear association between the biomass estimate for *C. glaucus* and mean maximum temperature from October to May under heavy stocking density ($R^2 = 0.16$, $p \leq 0.001$; Figure 5a) and a significant positive linear association between *C. glaucus* and mean maximum relative humidity from October to May ($R^2 = 0.17$, $p \leq 0.001$; Figure 5b). For the *S. maculatus* biomass estimate, we found no linear association with mean maximum temperature from October to May under heavy stocking density or with mean maximum relative humidity from October to May under moderate stocking density (Figure 5a,b).

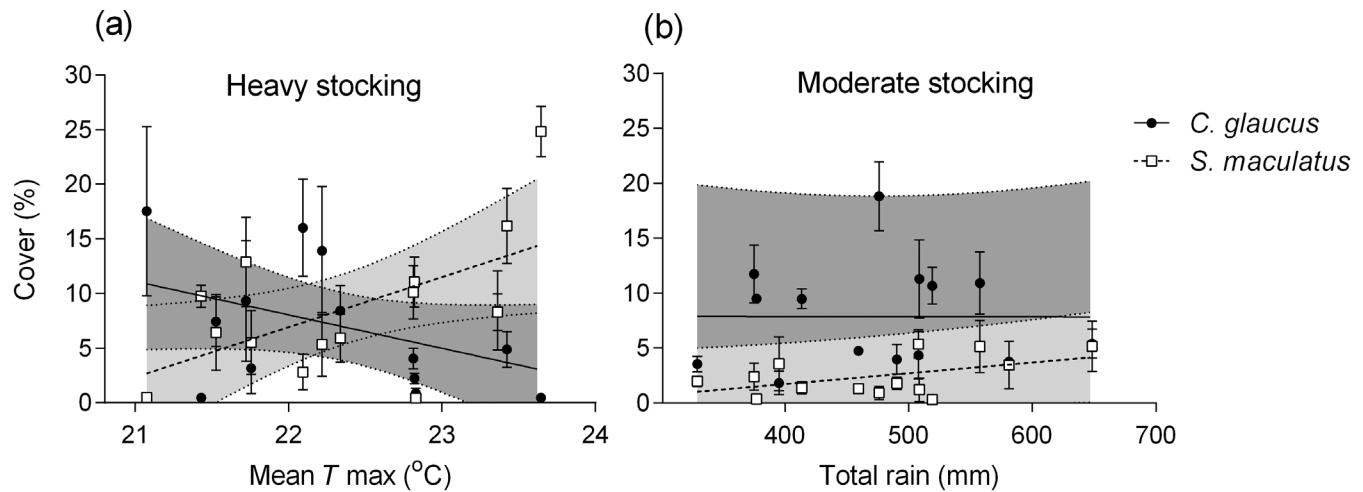


FIGURE 4 Relative cover of *Carthamus glaucus* and *Scolymus maculatus* against: (a) mean maximum temperature (T_{max}) under heavy stocking density and (b) mean total amount of rain under moderate stocking density.

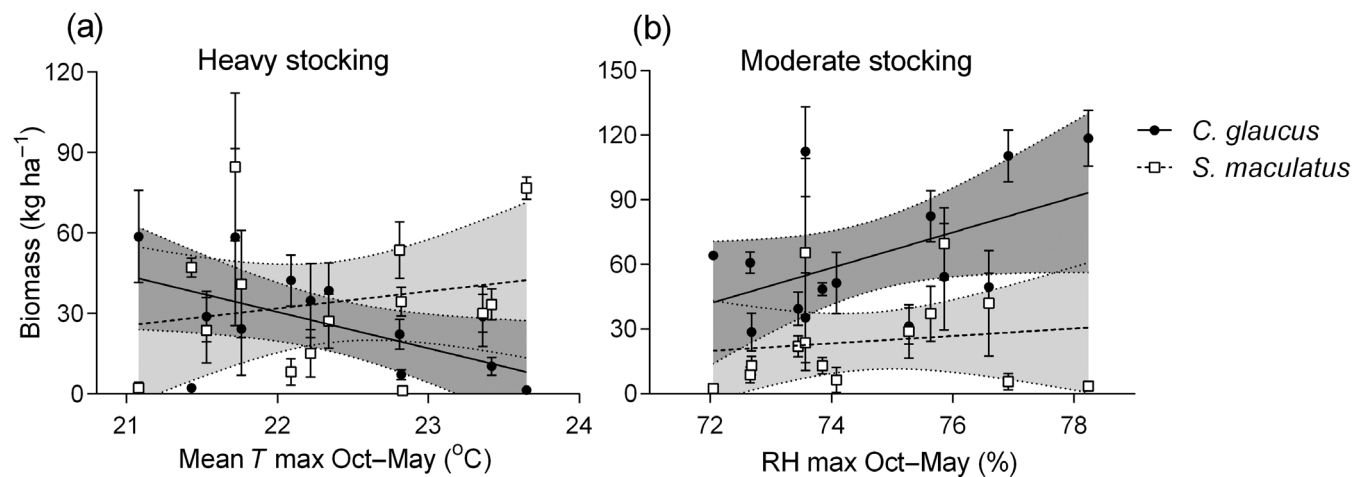


FIGURE 5 Biomass estimate of *Carthamus glaucus* and *Scolymus maculatus* against: (a) mean maximum temperature (T_{max}) from October to May under moderate stocking density and (b) mean maximum relative humidity (RH max) from October to May under heavy stocking density.

DISCUSSION

Processes that are mostly considered at global and long-term scales can often be overlooked at local and regional scales despite their capacity to drive significant changes in ecosystem function. To understand the proliferation of large annual thistles in semiarid rangelands, we selected two environmental factors, distance from feeding site (resource) and stocking density (disturbance), and monitored thistle cover and ecosystem function in the form of annual productivity of thistles. The significant findings of this study include the following: (1) the spatiotemporal scale at which thistles dominate the rangeland ecosystem; (2) the strong impact of supplemental feeding on large annual thistle abundance and

distribution; and (3) contrasting species-specific trends in response to climatic parameters and their interaction with distance from feeding site and stocking density.

According to the “biomass ratio hypothesis,” the effect of species traits on ecosystem properties and functioning depends on the dominant species in the community (Grime, 1998). The “snapshot” taken in 2019 of directly measured biomass of spiny and nonspiny plants provides evidence for the proportion of large annual spiny plant species under both heavy and moderate stocking densities and for their absence in the ungrazed plots. Large annual thistles comprised over 50% of the aboveground biomass under heavy stocking density, and 27% under moderate stocking density in 2019. This proportion translates to a

massive amount of herbage resources that are mostly unavailable for livestock.

Supplemental feeding of livestock with poultry litter during the dry season to meet their nutritional demands is a common practice in water-limited rangelands. Our findings suggest that distance from the supplemental feeding sites can have a significant effect on spiny plant distribution (cover) and performance (biomass). The two focal thistle species in our system display contrasting distribution and performance trends with respect to distance from the feeding site.

In Mediterranean rangelands, the accumulation and persistence of soluble nitrogen, phosphorus, and potassium in the upper soil layer varies with nutrient and with local biogeochemical conditions (Vinograd et al., 2019). This variation in soil nutrient accumulation can favor certain species over others (Braden et al., 2019). Thus, specific traits related to the ability to exploit soil resources (e.g., size of zone explored by roots, root impact density, specific root length, root diameter—see Tardy et al., 2017) may explain the discrepancies between the two species.

The effect of stocking density on productivity, diversity, and ecosystem resilience has been studied extensively in Mediterranean semiarid rangelands (e.g., Henkin et al., 2011; Osem et al., 2002; Perevolotsky & Seligman, 1998). Our results confirm findings on the effect of grazing on the large annual thistle functional group in Mediterranean herbaceous communities. Sternberg et al. (2000, 2015) report an increase in annual thistle cover under early and heavy stocking densities. Our examination of species-specific responses of annual thistles suggests that moderate stocking density leads to higher biomass of *C. glaucus*, while heavy stocking density leads to higher cover and biomass of *S. maculatus* and a decrease in the amount of palatable biomass.

Disturbance intensity and frequency can shape the composition of the soil seed bank (Eriksson & Eriksson, 1997), thus determining annual thistle abundance and distribution. Seed banks are traditionally defined as transient or persistent. Transient seeds are viable for less than one year, while persistent seeds can remain viable for one or more years (Walck et al., 2005). Previous studies suggest that the *C. glaucus* seed bank is transient (Sternberg et al., 2003) but may be persistent (Sofer-Arad, 2006). As for *S. maculatus*, seeds mostly germinate after 2–3 years (Sofer-Arad, 2006). Furthermore, soil disturbance can shift seed bank composition, for example, from persistent to transient (Bueno et al., 2011). Nevertheless, our findings show that high grazing density and proximity to the feeding site give an advantage to *S. maculatus*, which maintains a persistent seed bank. In general, species with persistent seed banks, such as

S. maculatus, are considered better gap colonizers and may be less affected by the climatic conditions prevailing in the previous year (Aboling et al., 2008); thus, they are less affected by the soil disturbance caused by cattle trampling than species with transient seed banks, such as *C. glaucus* (Kohler et al., 2006).

A long history of grazing at the community level favors species with low stature and delayed onset of flowering (Fernández Alés et al., 1993; Peco et al., 2012). Large annual thistles are not entirely released from the effect of grazing despite their structural defense in the form of spines, thorns, and prickles (Thomsen et al., 1993), and their asynchronized delayed phenology. Palatability declines with thistle development, but *C. glaucus* and *S. maculatus* are still eaten as seedlings (pre-spiny stage) and rosettes (low-stature growth form). Preliminary direct estimates of the susceptibility of *C. glaucus* and *S. maculatus* to grazing suggest that *C. glaucus* is eaten more than *S. maculatus*. This may provide a further explanation for increasing species cover with distance from the supplemental feeding site, although additional quantitative estimates of cattle diet selection throughout the year combined with species-specific measures of regeneration rates following defoliation at different phenological stages are needed to confirm this.

Semiarid rangelands are at high risk of degradation due to overexploitation and the interaction of livestock grazing with climate change (Eldridge et al., 2016). Climate change models for the Eastern Mediterranean Basin predict a reduction in mean annual rainfall coupled with an increase in seasonal and interannual rainfall variation (Ozturk et al., 2015; Tabari & Willems, 2018). Interannual fluctuations in climatic factors can influence plant community structure (Manning & Baer, 2018) and have a carryover effect on the annual plant seed bank (Smith et al., 2008). In grassland ecosystems, increased climate variability is expected to interact with disturbances, such as fire and grazing (Koerner et al., 2014). Climatic conditions and grazing density can thus act as filters on the regional species pool by removing species that lack traits for persisting under a particular set of conditions (De Bello et al., 2005). While rainfall determines the beginning and end of the growing season, temperature and relative humidity heavily influence the rate of herbage production during the growing season (Roche et al., 2009). Our analysis suggests that relative humidity and temperature were the most sensitive climatic parameters in explaining the variation in cover and biomass of the two thistles (Appendix S1: Tables S2–S5). The directionality of the effects of these climatic parameters differs between the two species. Maximum relative humidity had a negative effect on *S. maculatus* relative cover and biomass but a positive effect on the cover and biomass of *C. glaucus*.

Correspondingly, maximum temperature had a positive effect on the cover of *S. maculatus* and a negative effect on the cover of *C. glaucus*. *S. maculatus* may be more adapted to warmer, dry conditions than *C. glaucus* and consequently proliferate during a sequence of warmer, dry years. The persistent seed bank of *S. maculatus* can enable it to maintain a viable seed bank between recruitment episodes during years that are less favorable climatically. This can partly explain this species' advantage over *C. glaucus*, which has a transient seed bank. The spatial distribution pattern of *C. glaucus* and *S. maculatus* in Israel mostly overlaps, though *S. maculatus* shows a wider distribution range into the central mountain ridge and southern coastal plains, beyond the rift valley region where *C. glaucus* mostly occurs (Danin & Fragman-Sapir, 2016). This indirectly indicates wider temperature, humidity, and drought resistance of *S. maculatus*, encompassing all four vegetation zones (Mediterranean, Irano-Turanian, Saharan, and Sudanian), which is expected to expand its distribution in the long term following regional warming (Harrison, 2020).

Shifts in the availability of resources such as soil nutrients and light can determine the intensity of interspecific competition among annual plants in both resource-rich and resource-poor ecosystems (Aschehoug et al., 2016). Removal of palatable species due to grazing may result in stronger competition for light between the remaining large and less palatable thistle species. Moreover, the intensity of the competitive interaction is expected to be stronger between species sharing the same life-history traits and adaptations. The negative correlation in relative abundance between the two dominant thistles suggests interspecific competition.

Shifts in rangeland plant community composition and dominance of spiny species are not inherently limited to Eastern Mediterranean grasslands, but occur in other rangeland ecosystems, for example, in Australia (Sindel, 1991) and North America (Enloe et al., 2007; Li et al., 2020). Given the decline in rangeland quality due to large annual thistle dominance, we suggest several direct and indirect management tools. Since the two dominant species display contrasting responses to the fertilization effect of supplemental feeding and grazing density, we suggest the use of species-specific management procedures. Reducing the stocking density below 0.55 cows ha⁻¹ year⁻¹ and adjusting the timing of grazing to early spring when defoliation of the leaf rosette occurs will allow optimal suppression of thistle growth, survival, and reproductive output. Both species possess the capacity to regrow following herbivory and canopy damage during most stages of their life cycle. This ability allows them to outcompete other annuals in the community that are more susceptible to herbivory. Thus, repeated exposure to grazing during the more vulnerable life stages may be

necessary for their control. Sternberg et al. (2003) found that the proportion of annual thistles in the seed bank was lowest following heavy stocking density late in the season (May–October), and highest following continuous (January–October) heavy stocking density.

Measures related to the impacts of supplemental feeding to improve thistle control include reduction of poultry litter spillover and construction of feedlots disconnected from the ground. Additional options for direct eradication and control of annual thistles include limited use of mechanical removal or use of selective herbicides. These options may not be feasible for many managers due to limited access, terrain complexity, and the sheer size of the areas requiring effective treatment.

This study has shown that despite their similarity in life-form and life-history characteristics, each of the two dominant thistle species in this grazing system demonstrates a distinct response to management intensity (stocking density and distance from feeding site) and climatic factors (humidity, temperature, and rainfall). *S. maculatus* was found to be competitive under the strong disturbance scenario in the form of high stocking density and high concentrations of soil nutrients. In contrast, *C. glaucus* was positively affected by distance from the feeding site, while stocking density had little effect on its relative cover. The pattern of interspecific relative cover association suggests that *C. glaucus* may be competitively excluded by *S. maculatus* to areas with lower soil nitrogen content. Both thistles display a stronger demographic response to the redistribution of soil resources than to stocking density. This is not surprising given that the pattern of animal distribution, that is, realized cattle densities in the vicinity of the feeding sites, may be an order of magnitude higher than the planned stocking densities and given the legacy effect of soil nutrients at sites of high livestock density.

We found no interaction between the effect of distance from the feeding site and the effect of stocking density for either species; these two factors drive the system in the same direction and apparently operate in an additive manner. Further investigation of soil nutrients, specifically soil nitrogen content and the nitrogen content of plant tissues (aboveground and belowground), may provide a better understanding of the mechanisms driving these species' performance.

AUTHOR CONTRIBUTIONS

Guy Dovrat conceived the research idea. Carly Golodets, Guy Dovrat, and Haim Gorelik collected data. Ori Segev performed statistical analyses and wrote the paper with contributions from Carly Golodets, Guy Dovrat, and Zalmen Henkin. All authors discussed the results and commented on the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Segev & Dovrat, 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.7047588>.

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