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Original Article

Persistent increase in understory vegetation following thinning and grazing exclusion in a semiarid pine forest

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Abstract

Forests function as hotspots for plant functional diversity, hosting numerous nontree plant species in the understory. In tropical, temperate, and Mediterranean forests, density reduction (thinning) treatments have been shown to enhance the abundance of understory plants, including shrubs and herbs. These plant functional types are also known to dominate semiarid steppes and savannas. Yet, it is unknown if thinning in a semiarid forest could have such effects on understory vegetation. Here, we tested the effects of thinning and grazing exclusion on shrub cover and herbaceous biomass in a field manipulation experiment in a semiarid pine forest. Understory development was measured in 21 experimental plots (0.5 ha each) in the dry seasons of the years 2009–22. Fifteen plots were thinned to 300, 200, or 100 trees ha^{-1} (0%, 33%, and 67% thinning, respectively) and grazing was excluded from half of each plot. Six additional plots were left unthinned at 400–200 trees ha^{-1}, and served as controls. Herbaceous biomass increased significantly with thinning, from ~5 to ~10 kg ha^{-1} in most years. Shrub cover tended to increase with 67% thinning from ~2% to ~4%, and both shrubs and herbs increased with time. While annual precipitation amount did not directly affect the understory, herbs responded positively to last year precipitation. Ungrazed plots showed higher shrub and herb development than grazed plots, but overall, grazing effect was not significant. Our results show a persistent increase in understory vegetation following thinning in a semiarid pine forest. The gaps formed by thinning created conditions for regrowth of the native nontree vegetation, diversifying the forest structural diversity and its ecosystem services. Yet this change might not sustain under drying conditions.

Keywords: shrubs; herbs; forest understory; forest density; grazing exclusion; pine forest

Introduction

Although typically dominated by trees, forests host a wide variety of other plant life forms, including ferns, vines, herbs, and shrubs (Trentini et al. 2017). This diversity of plant functional types forms the basis for the high biodiversity in global forests (Guo et al. 2022). A diverse forest understory can provide ecosystem services and benefits, e.g. mitigation of soil erosion (Liu et al. 2020) and an increase in carbon storage (Zhang et al. 2023). Conversely, understory vegetation might compete with trees, tree seedlings, or increase fire hazard (Behm et al. 2004). Despite these potential impacts, when new forests are planned and planted, little attention is given to nontree plant forms.

One management tool that can enhance understory development is forest density reduction, i.e. thinning, often involving micrometeorological changes. Responses of understory herbs and shrubs to forest thinning were studied primarily in wet conifer forests (Supplementary Table S1). For example, thinning in pine plantations in wet parts of Northeastern Argentina was shown to increase biodiversity and related ecosystem functions. Specifically, ferns and vines increased more steadily than grasses, and in turn more than shrubs (Trentini et al. 2017). In that study, canopy openness, solar radiation, air temperature, and soil bulk density were higher in thinning treatments than in control plots, while soil water content was lower Additionally, thinning may be a useful management tool to encourage understory herbs growth on expense of low shrubs and weedy species (Lindh and Muir 2004). Shrubs and herbs also differ in their responses to micrometeorological variation. For example, in a mixed-conifer forest in the Sierra Nevada (USA), herbs associated positively with greater soil moisture, while shrubs associated positively with greater diffuse light and lower soil moisture (North et al. 2005). In a plantation forest in France, soil water content in the forest area was higher under low pine cover without shrubs than it was in the medium and high pine cover (Prévosto et al. 2020). In a Mediterranean forest, intense thinning (67%) increased herb species richness from 16 to 37 at the stand scale compared to 48 species in clearcut areas (Zangy et al. 2021). Carbon (C) storage is another benefit: in a northeastern forest in China, tree C pools increased by 75% within 10 years following 30% thinning, while shrub C pools increased >5-fold and herb C was unchanged (Zhang et al. 2023). Overall, thinning mostly facilitated herbs and shrubs cover, abundance, and richness (Supplementary Table S1). Yet, it is unknown if thinning in a semiarid forest could have similar effects on understory vegetation.

In many terrestrial ecosystems, shrubs, and herbs (including grasses) are major plant growth forms, that compete for limited resources like light, water, and nutrients. For example, two-thirds of the aboveground net primary production (ANPP) in a

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Patagonian steppe were accounted for by perennial grasses and one-third by shrubs (Fernandez et al. 1991). In another study, competition between grasses and shrub seedlings had no effect on either germination or survival of these functional types (Weber–Grullon et al. 2022). Shrub encroachment into semiarid grasslands (aridity index between 0.2 and 0.5) is facilitated by precipitation, but an increase in herbivore activity due to the increased available biomass, can also counterbalance this effect (Weber-Grullon et al. 2022). In forests, shrubs and herbs can have convergent or divergent responses to thinning, depending on the context. In a subtropical plantation of *Cryptomeria japonica* in Taiwan measured 9 years after 25% or 50% thinning, grass cover increased but not shrub cover (Tsai et al. 2018). Whereas in a northeastern forest in China, thinning facilitated shrubs more than herbs (Zhang et al. 2023). After thinning in Douglas-fir plantations in the US Northwest, grasses increased their cover more than shrubs (Thomas et al. 1999). Shrub-herb competition was also documented in a study from a Mediterranean forest: An increase (15-fold) in herbaceous biomass was recorded 4 years after grazing exclusion but disappeared 10 years after exclusion due to increased woody cover (Osem et al. 2017).

Herbivory adds another level of complexity to the aforementioned interactions among forest density, understory composition, and micro-environment (Weber-Grullon et al. 2022). In a Patagonian shrub–grass steppe, sheep grazing did not affect shrub and grass cover, but decreased the abundance of non-grass herbs due to grazers' nutritional preferences (Golluscio et al. 2009). In a Mediterranean pine forest, cattle grazing and overstory cover restricted understory growth and interacted in shaping the understory community structure, whereby grazing and thinning decreased understory height (Osem et al. 2017). In another study, grasses showed an immediate response to grazing, with 8% higher cover in ungulate exclosures than in adjacent grazed areas (Kramer et al. 2015). That study concluded that conifer thinning and ungulate exclusion may increase grass cover, however, during drought periods, these positive effects are only short-term. In one of the earlier studies on the topic, shrub and herb production was quantified in relation to precipitation amount, in a Patagonian steppe (Fernandez et al. 1991). ANPP was 79 ± 19 g m^{-2} $year^{-1}$ in a 191 mm rainfall year, ranging between 21 and 75 g m^{-2} $year^{-1}$ in drier years. Interestingly, while there was a large reduction in ANPP during a year of extreme drought, there were no increases in ANPP during years with above-average precipitation.

Here, we tested the effects of thinning and grazing exclusion on shrub cover and herbaceous biomass in a field manipulation experiment in a semiarid Aleppo pine forest. Aleppo pine (*Pinus halepensis*) is the most common tree species in natural and planted forests of the Mediterranean basin (Patsiou et al. 2020). In thinned Aleppo pine stands, shrubs were studied as facilitators of oak seedling establishment (Gavinet et al. 2016). Soil water content in the forest area was higher under low pine cover without shrubs than it was in the medium and high cover (Prévosto et al. 2020). In Israel, both thinning and grazing exclusion positively influenced understory woody plant growth with their combined effect over 10 years leading to a 20-fold increase in shrub volume (Osem et al. 2017). In a follow-up study at that site, resource availability, rather than spatial resource heterogeneity, was the main factor shaping understory diversity (Zangy et al. 2021). Herbaceous ephemerals and short woody species were more frequent in grazed, thinned areas while larger woody species were more associated with ungrazed, non-thinned areas of the Aleppo pine forest. Due to its drought resistance properties (Wagner et al. 2022, 2023), Aleppo pine populates forests beyond the Mediterranean zone, up until the "dry timberline," at annual rainfall <300 mm (Klein 2020). Despite the advanced knowledge of shrub and herb dynamics in semiarid grasslands (Fernandez et al. 1991, Golluscio et al. 2009, Weber-Grullon et al. 2022), less is known about this aspect in semiarid forests.

In 2000, a research station was established at Yatir forest, Israel, a planted Aleppo pine forest on the edge of the Negev desert (Grünzweig et al. 2003). Trees were planted in the late 1960s over a low shrubland that suffered millennia of livestock grazing and centuries of over-grazing (Waisel 1984). Still, the shrubland surrounding the forest is highly diverse, with >400 native plant species, 98% of which are herbaceous or shrubs (Gil-Klein et al. 2021). The most common annual herb species are the grasses *Hordeum spontaneum* and *Bromus fasciculatus*, and the most common low shrub species are *Sarcopoterium spinosum*, *Ratema ratem*, and *Artemisia siberi*. Together, these species growing outside the forest create patches of herbaceous annuals and perennials with a maximum height of 30–50 cm (Grünzweig et al. 2007). While the herbs dominate in the wet season and until the end of the spring, the shrubs cover 19% of the surface, with the rest being rock (20%) and bare soil (61%). Contrastingly, the pine forest, with a density of 300 trees ha^{-1} and a semi-closed canopy, has very little understory, and hence a low plant functional diversity. The aboveground carbon (C) content of the adjacent shrubland was measured at 60 ± 20 g C m^{-2}, expectedly lower than the C content of the forest 35 years after planting, 1553 ± 178 g C m^{-2} (Grünzweig et al. 2007).

In late 2009, a thinning and grazing experiment was established at Yatir forest. In the years that passed, there was an increased tree growth following thinning, due to higher light availability (Tsamir et al. 2019). In addition, stand density and grazing exclusion positively affected pine seed germination (Pozner et al. 2022). Seedling survivorship was higher in wetter years, but multiyear seedling growth was stunted by grazing. Considering the site history, and the earlier observations of tree and seedling growth responses to thinning and grazing, we predicted that: (Ares et al. 2009) thinning-induced increase in light availability should increase the understory vegetation in the forest, by allowing regrowth of the native herbs and shrubs. (Bartoń 2022) Grazing exclusion should further promote shrub regrowth, and, to a larger extent, herbaceous vegetation growth, assuming that the latter is the preferred food for the animals. (Bates and Sarkar 2007) Overall, the understory vegetation should increase in wet vs. dry years.

Materials and methods

Yatir forest, site, and climate

Yatir forest is a semiarid forest of *P. halepensis* Mill., located at the southern edge of the Judean hills in Israel (31°20′49″ N; 35°03′07″ E, mean elevation of 650 m a.s.l.). The forest covers 3000 ha which have been planted mostly between 1965 and 1969. It extended southward the distribution range of Aleppo pine, whose limit is ∼10 km north of Yatir. Although it can be regarded as a plantation, its non-commercial character and low management led to a structure that resembles those of many natural Aleppo pine forests. The surrounding native vegetation consisted of sparse desert fringe shrubland with seasonal herbaceous vegetation between February and April, now creating the understory of the planted forest. The semiarid climate is defined by hot-dry summers and cool-rainy winters (Pozner et al. 2022). The mean annual precipitation is 280 mm, and the mean diurnal air temperature and relative humidity are 10°C and 65% in January and 26°C and 50%

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in July, respectively. During 2009–22, 8 out of the 14 years had precipitation below 280 mm, and were defined as drought years. Precipitation was measured continuously at the standard rain station of KKL (31°20°18.1″N 35°02′03.0″E, elevation 650 m a.s.l, situated ∼1.5 km from the Yatir research station). The forest bedrock consists of chalk and limestone, and the soil is shallow loess down to 20–40 cm depth. Soil texture is clay-loam (42% sand, 17% silt and 41% clay; Klein et al. 2014). Rock erosion created round hills with moderate slopes that have a high fraction of stoniness and surface rock cover (48% and 37%, respectively; Preisler et al. 2019). The water-table is 300 m below the surface. Due to the depth of the water-table, and lack of runoff, precipitation during the wet season (November–April) fundamentally supports the existence of vegetation at the site (Schiller and Atzmon 2009).

Yatir thinning and grazing experiment

During fall 2009, the plots were thinned from various stand densities (200–400 trees ha^{-1}) to three stand density levels: 300, 200, and 100 trees ha^{-1} (five plots per density; Tsamir et al. 2019; Fig. 1; Supplementary Fig. S1). In addition, six control plots were unthinned and remained in their original densities: two plots at 200 trees ha^{-1}, three plots at 300 trees ha^{-1}, and a single plot at 400 trees ha^{-1}. These forest densities remained stable throughout the years 2010–2022. The harvest was non-commercial and did not affect the size distribution of trees (see below). In 2010–11, fenced grazing exclosures (0.25 ha each) were created in each of the 15 thinned plots (Fig. 1; Supplementary Fig. S1). Grazing in Yatir forest is managed by the Israel Forest Service (KKL) and is limited to up to 2500–3000 animals per day throughout the forest (i.e. 0.83–1 grazer ha^{-1} day^{-1}). The typical flock consists of 150–500 sheep (*Ovis aries*) and up to 10 goats (*Capra hircus*), grazing daily during the grazing season. The grazing season starts in February, when the herbaceous vegetation develops, and a heavy grazing regime continues until the end of the wet season (April). Over the following period of April to May, the herbaceous vegetation dries and this results in a low grazing rate. In the dry period of June to August, the flocks modify their grazing pattern and graze the herbaceous ripened seeds and woody vegetation until the end of the grazing season in July–August. The Yatir thinning and grazing experiment is part of the long-term ecological monitoring (Dor-Haim and Assaraf 2022) network in Israel (https://lter-israel.org.il/), belonging to the European Long-Term Ecological Research (LTER) (https://elter-ri.eu/).

Herbaceous biomass, shrub cover, and tree stem increment

To avoid a potential edge effect, sampling within the plots was conducted excluding a 15 m buffer zone from all sides, i.e. at an area of 40 × 40 m or 30 × 80 m. Herbaceous biomass was measured at the end of the wet season (April) in each of the following 6 years: 2015 through 2018 and in 2021 and 2022. In each plot, 10 points were randomly picked, and a 20 × 20 cm wood frame was laid in each point, yielding a total sampling area of 0.4 m^2 per plot. At each point, all aboveground herbaceous material was collected into paper bags, which were dried in a drying oven (3 days at 60°C). Herbaceous dry weight (g) was considered as biomass and was upscaled to kg ha^{-1}. Shrub cover was measured at the end of the dry season (typically in September or October) in 2009–22, except for the years 2011, 2012, and 2017, i.e. in 11 years. Shrub cover was measured within two permanent belt transects of 30 × 4 m (sampling area of 240 m^2 per plot). Within this area, we measured the width and length of each shrub, and assuming an oval shape, calculated the shrub cover area. Dividing the total

Figure 1. Areal views of Yatir forest and the thinning and grazing field experiment. Drone images taken in April 2019, showing the forest canopy (top) and one of the field experiment plots (bottom). The bottom picture shows a thinned plot at 200 trees ha^{-1}, with gaps in between trees, where herbaceous vegetation can be seen growing at the end of the wet season, mostly in the grazing exclusion area (white lines indicate the grazing exclusion fence). Photo credit: Peleg Bar-On, The Weizmann Tree Lab.

area of all measured shrubs by the measurement area yielded the shrub cover (%). Herbaceous biomass and shrub cover data are reported in Supplementary Tables S2 and S3, respectively. Tree stem increment was measured using manual dendrometers monitored for extension or shrinkage six times a year (tree girth band D1, UMS, Munich, Germany). Dendrometers were installed on 7 trees of each plot. Trees were selected to represent the size distribution (DBH categories) of all trees in each plot, as measured at the start of the experiment (DBH = 12–32 cm). For each plot, a mean annual increment was calculated every year. To allow for direct comparison among the three plant functional types (herbs, shrubs, and trees), tree and shrub data were transformed into biomass data, using allometric equations which were developed for the respective plant species *in situ*. For the trees, we used the allometric equation for *P. halepensis* at this site (Grünzweig et al. 2007). For the shrubs, we used the allometric equation developed for the most common species, *Sarcopoterium spinosum*, at Lehavim (15 km west of our site; Sternberg and Shoshany 2001). This was the only allometric equation existing for shrubs growing in Yatir. Considering the growth form of *Sarcopoterium spinosum*, the equation should be valid for *Artemisia siberi* and other shrubs

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Table 1. Anova-like results of the selected generalized linear mixed models for shrub cover and herbaceous biomass in Yatir forest.

Source	F-value	DF	P-value
Effects on herbaceous biomass	(split-plot design)		
Forest density	3.82	2,12	**.052**
Precipitation (previous year)	7.78	1,101	**.006**
Year	21.07	1,101	**<.001**
Effects on shrub cover			
Year	50.16	1,175	**<.001**

Effects with p-values < 0.05 are shown in bold to indicate statistical significance.

species, although not for *Ratema ratem*, of which a few individuals exist in some of the plots.

Statistical analysis

Statistical analyses of shrub cover and herbaceous biomass followed a split-plot experimental design, using hierarchical linear modeling to account for nested data, interaction effects, and temporal autocorrelation. Tree density was the between-plot factor, and grazing treatment was the within-plot factor, allowing for the assessment of their interactive effects on vegetation responses under varying environmental conditions (see model equations below). To meet normality and homoscedasticity assumptions, shrub cover data were square root transformed, and herbaceous biomass data were log-transformed. Precipitation from the current and two preceding years was included to assess potential lag effects, given delayed biological responses in arid ecosystems (Klein et al. 2019). Continuous predictors (e.g. precipitation metrics) were standardized for interpretability. Statistical modeling was performed in R using "lme4" and "lmerTest" (Bates et al. 2015, Kuznetsova et al. 2017), incorporating random effects. The initial model for both response variables included interactions between tree density, grazing treatment, and the precipitation metrics, while accounting for subplot-level variability. To account for temporal autocorrelation, an ARMA (1,0) correlation structure was used in the mixed-effects model, as implemented in the nlme package (Pinheiro and Bates 2000). Variance inflation factors were computed using "car" (Fox and Weisberg 2018) to assess multicollinearity. Model selection followed an exhaustive approach via MuMIn's (Bartoń 2022) "dredge" function, ranking models by Akaike Information Criterion corrected for small sample sizes. The best model for herbaceous biomass retained Year, Previous Year Precipitation, and Density as fixed effects, while for shrub cover, Year was the sole fixed effect (see model equations below and Supplementary Tables S4 and S5 for selected models). Fixed effect significance was evaluated using marginal F-tests as implemented in the "anova" function for "lme". Model summaries, including F-values statistics and P-values, were reported in an ANOVA-style table (Table 1). Model diagnostics included residual and random effect plots to check for heteroscedasticity or non-normality (Supplementary Figs S2 and S3). Effect sizes were reported for the significant predictors of the selected models (Fig. S4). Coefficient plots visualized significant predictors (Supplementary Figs S5 and S6).

Herbaceous biomass initial model

$$\begin{aligned} &Ln\,[HerbaceousBiomass]\,ij \\ &= \beta_0 + \beta_1 \cdot Density_{ij} + \beta_2 \cdot Grazing_{ij} + \beta_3 \cdot Precipitation_{ij} \\ &\quad + \beta_4 \cdot Precipitation_{LastYear\,ij} + \beta_5 \cdot Precipitation_{TwoYearsAgo_{ij}} \\ &\quad + \beta_6 \cdot Density_{ij} \cdot Grazing_{ij} + + \beta_7 \cdot Year_{ij} + u_j + \upsilon_{ij} + \varepsilon_{ij} \end{aligned}$$

where

$Ln\,[HerbaceousBiomass]\,ij$ is the natural logarithm of the herbaceous biomass for subplot i in plot j.
β_0 is the intercept.
$\beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7$ are the fixed effects coefficients for Density, Grazing, Precipitation, Precipitation Last Year, Precipitation Two Years Ago, Year, and the interaction between Density and Grazing, respectively.
u_j is the random effect associated with plot j, assuming $u_j \sim N\left(0, \sigma_u^2\right)$.
υ_{ij} is the random effect associated with subplot i nested within plot j, assuming $\upsilon_{ij} \sim N\left(0, \sigma_\upsilon^2\right)$.
ϵ_{ij} is the residual error for subplot i in plot j, assuming $\varepsilon_{ij} \sim N\left(0, \sigma_\varepsilon^2\right)$.

Additionally, temporal autocorrelation in the data was modeled using an **ARMA (1,0)** correlation structure to account for potential lagged effects over time, with **Year** as the time variable nested within the hierarchical structure of **Plot/subplot.**

Herbaceous biomass selected model

$$\begin{aligned} &Ln\,[HerbaceousBiomass]\,ij \\ &= \beta_0 + \beta_1 \cdot Density_{ij} + \beta_2 \cdot Precipitation_{LastYear\,ij} \\ &\quad + \beta_3 \cdot Year_{ij} + u_j + \upsilon_{ij} + \varepsilon_{ij} \end{aligned}$$

where

$Ln\,[HerbaceousBiomass]\,ij$ is the natural logarithm of the herbaceous biomass for subplot i in plot j.
β_0 is the intercept.
$\beta_1, \beta_2, \beta_3$ are the fixed effects coefficients for Density, Precipitation Last Year, and Year, respectively.
u_j is the random effect associated with plot j, assuming $u_j \sim N\left(0, \sigma_u^2\right)$
υ_{ij} is the random effect associated with subplot i nested within plot j, assuming $\upsilon_{ij} \sim N\left(0, \sigma_\upsilon^2\right)$.
ϵ_{ij} is the residual error for subplot i in plot j, assuming $\varepsilon_{ij} \sim N\left(0, \sigma_\varepsilon^2\right)$.

Additionally, temporal autocorrelation in the data was modeled using an **ARMA (1,0)** correlation structure to account for potential lagged effects over time, with **Year** as the time variable nested within the hierarchical structure of **Plot/subplot.**

Shrub Cover initial model

$$\begin{aligned} &Sqrt\,[ShrubCover]\,ij \\ &= \beta_0 + \beta_1 \cdot Density_{ij} + \beta_2 \cdot Grazing_{ij} + \beta_3 \cdot Precipitation_{ij} \\ &\quad + \beta_4 \cdot Precipitation_{LastYear\,ij} + \beta_5 \cdot Precipitation_{TwoYearsAgo_{ij}} \\ &\quad + \beta_6 \cdot Density_{ij} \cdot Grazing_{ij} + \beta_7 \cdot Year_{ij} + u_j + \upsilon_{ij} + \varepsilon_{ij} \end{aligned}$$

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where

$Sqrt\,[ShrubCover]\,ij$ is the square root of the shrub cover for subplot i in plot j.
β_0 is the intercept.
$\beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7$ are the fixed effects coefficients for Density, Grazing, Precipitation, Precipitation Last Year, Precipitation Two Years Ago, Year and the interaction between Density and Grazing, respectively.
$u_j$is the random effect associated with plot j, assuming $u_j \sim N\left(0, \sigma_u^2\right)$
v_{ij} is the random effect associated with subplot i nested within plot j, assuming $v_{ij} \sim N\left(0, \sigma_v^2\right)$.
ϵ_{ij} is the residual error for subplot i in plot j, assuming $\varepsilon_{ij} \sim N\left(0, \sigma_\varepsilon^2\right)$.

Additionally, temporal autocorrelation in the data was modeled using an **ARMA (1,0)** correlation structure to account for potential lagged effects over time, with **Year** as the time variable nested within the hierarchical structure of **Plot/subplot.**

Results

The effect of thinning and grazing on forest shrubs and herbs

Forest thinning was performed at the end of the drought year of 2009, which was followed by additional droughts in the years 2011 and 2013 (Fig. 2a), as well as several wet years (2012, 2014–16), and then mostly drought years (except for the very wet 2020). Despite this variation in precipitation, shrub cover and herbaceous biomass mostly increased (Fig. 2). Evidently, the effect of "Year" was positive and significant in the statistical models for both shrubs and herbs (Table 1; Supplementary Fig. S4). Still, there was an immediate drop in shrub cover in 2010 with respect to pre-thinning values (Fig. 2b). Considering that shrubs are perennial, this drop probably relates to the disturbance caused by the thinning activities on the ground (e.g. through the use of heavy machinery), rather than reflecting a thinning stress. Shrub cover recovered to pre-thinning values by 2015, with consistent increases at the 100 trees ha^{-1} plots (Fig. 2b), yet the density effect was not significant. The herbaceous biomass measurement missed the peak precipitation year of 2020, yet an increase could still be seen in 2021 (Fig. 2d). Overall, forest density significantly affected herbaceous biomass, but not shrub cover (Table 1; Supplementary Fig. S4). In ungrazed plots, shrub cover showed an increase trend as stand density decreased, reaching up to 5% at 100 trees ha^{-1} in the wet year of 2020, and only 2% at 300 trees ha^{-1} (Fig. 2b). Although overall the shrub cover tended to increase as stand density decreased, grazed plots showed a weaker trend (Fig. 2b and c). Herbaceous biomass was also significantly higher at 100 trees ha^{-1} compared to 200 or 300 trees ha^{-1}, which were otherwise similar in most years (Fig. 2d; Supplementary Fig. S4). Looking at the changes in shrub cover across forest densities (Fig. 3a), a thinning-induced increase is observed in ungrazed plots in most years, and values increase along the years. The major increase is at the lowest density of 100 trees ha^{-1} (Fig. 3a). In grazed plots, this trend was true in some years (e.g. 2018 and 2016; Fig. 3b), but reversed in other years (e.g. 2013 and 2014). Herbaceous biomass increased with thinning, but in 2 out of 6 measurement years, the highest values were at 200 trees ha^{-1} (Fig. 3c). The overall effect of grazing on both shrubs and herbs was not significant (Table 1).

In our experimental design, there were 6 control plots that were unthinned and remained in their original densities: 2 plots at 200 trees ha^{-1}, 3 plots at 300 trees ha^{-1}, and a single plot at 400 trees ha^{-1}. In terms of herbaceous biomass, these plots showed the same trend of negative relationship with forest density (Supplementary Table S2; Supplementary Fig. S7). Specifically, the unthinned 400 trees ha^{-1} plot had on average only 1.1 ± 0.5 kg ha^{-1} herbaceous biomass. The unthinned 300 and 200 trees ha^{-1} plots had on average 4.7 ± 0.7 and 13.3 ± 4.6 kg ha^{-1} herbaceous biomass; values that were even higher than those of the thinned plots. The situation for shrubs was very different: all unthinned plots had negligible shrub cover, rarely above 2% (Supplementary Table S3; Supplementary Fig. S7).

The effect of annual precipitation on forest shrubs and herbs

The effect of the current year annual precipitation (representing the wet season just preceding the measurement) was not significant on both shrubs and herbs. However, in two plots, there was a significant positive relation between precipitation and shrub cover (Supplementary Fig. S5). Shrub cover increased with annual rainfall amount, from negligible cover (0 or <0.5%) in drought years (200 mm or less), to 2%–4% in wet years (>300 mm; Supplementary Fig. S5). While the increase is seemingly small by number, it is considerable for such perennial plants. For herbs, there was a single plot showing a significant negative effect of the current year's precipitation, and a similar trend was observed in most other plots, although not significant (Supplementary Fig. S6). Next, we examined the relation between the shrub and herb indices and rainfall of the previous year; and of two years before (see Methods for model equations). For herbs, a significant positive effect was achieved with rainfall of the previous year (Table 1; Supplementary Fig. S4).

Biomass partitioning among plant functional groups in a semiarid pine forest

In the years 2015, 2016, 2018, and 2022, we were able to measure both shrub cover and herbaceous biomass. Therefore, data from these years was used to test for relationships between these two functional groups. There was no consistent relationship between shrub cover and herbaceous biomass across years and study plots. Still, in one case we observed a significant negative relationship between the groups, indicating a tradeoff, at 100 trees ha^{-1} in 2016 (Supplementary Fig. S8). Conversely, in another case there was a significant positive relationship between the groups, at 100 trees ha^{-1} in 2022 (Supplementary Fig. S8). Next, we added the tree biomass component to complete the three plant functional types in the semiarid pine forest. Overall, shrub biomass, reflecting perennial growth, was ~20-fold higher than herbaceous biomass, reflecting annual growth. Tree biomass in the study plots ranged between ~19 069 and 76 402 kg ha^{-1}, i.e. several orders of magnitude higher than shrub or herbaceous biomass. This meant that visualization of the three groups together required a logarithmic scale (Fig. 4). The stacked columns showed the increase in total plant biomass from 2015 to 2022, yet this increase was more evident at 100 trees ha^{-1} than in the other, less thinned plots (Fig. 4). Also, at 100 trees ha^{-1}, shrubs and herbs had a larger, and more stable, share of the total plant biomass partitioning, 8‰–11‰ (permill) compared to 1‰–4‰ in the higher densities. In the unthinned plots, shrubs, and herbs also had a small share of the total plant biomass partitioning, 0‰–4‰ (data not shown).

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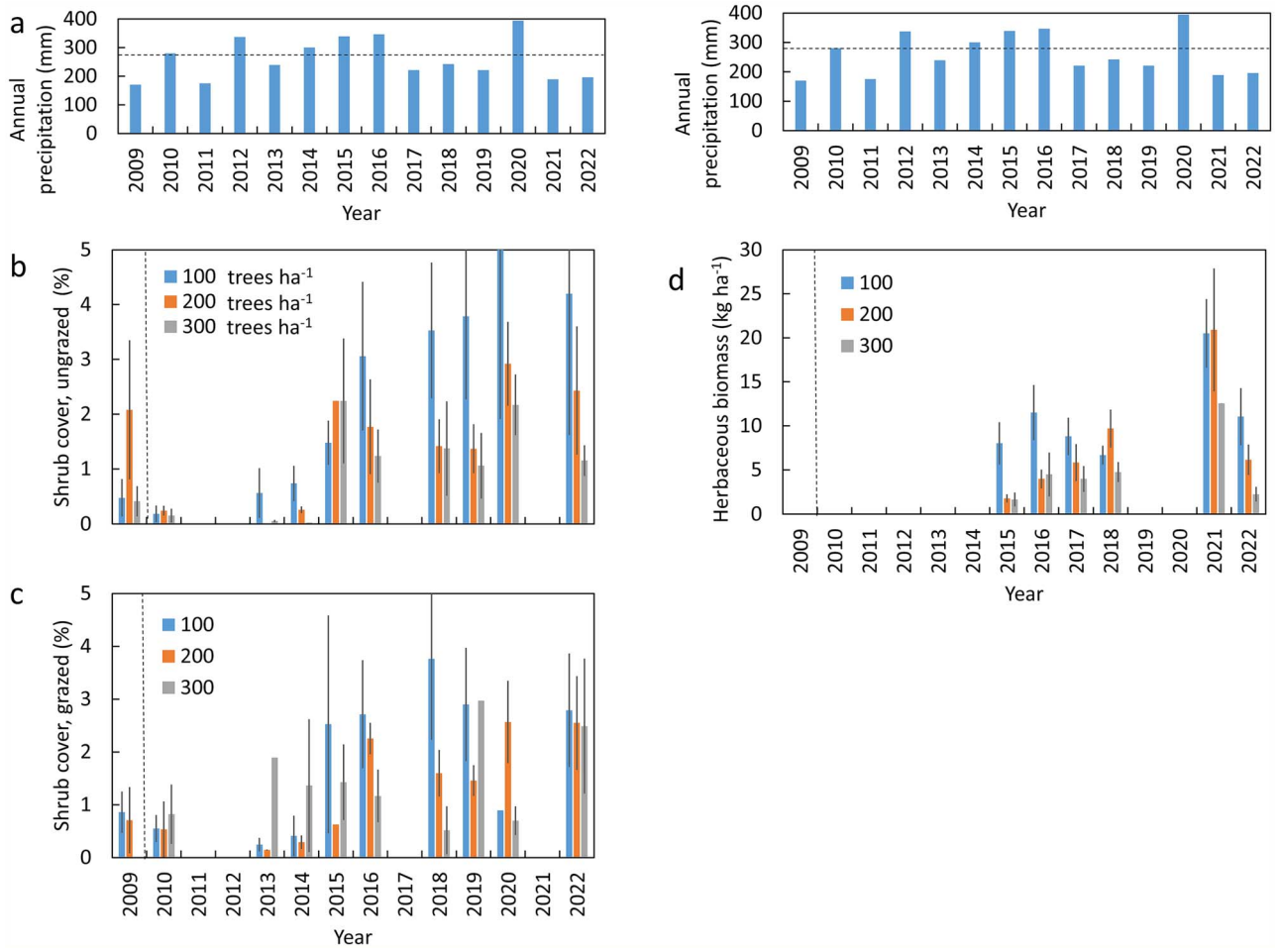

Figure 2. Annual precipitation and nontree plant growth in Yatir forest in 2009–22. (a) Annual rainfall (mm); the horizontal dash line indicates the 30-year mean of 280 mm. Note that panel (a) is replicated for convenience. (b) Shrub cover (%) in ungrazed plots; (c) shrub cover (%) in grazed plots; and (d) herbaceous biomass (kg ha^{-1}) in Yatir thinning and grazing plots (means ± SE). The vertical dash line indicates the beginning of the experiment. Shrub cover is in ungrazed plots; herbaceous biomass in grazed plots. Years with missing columns are due to insufficient data.

Discussion

In this long-term forest manipulation study, we bring evidence of a persistent increase in understory vegetation following thinning in a semiarid pine forest. Afforestation in this area fulfilled its landscaping role (creating a green canopy landscape; Fig. 1) and enhanced the carbon storage by replacing low vegetation with trees (Fig. 4). Later on, thinning was tested as means to minimize drought-induced tree mortality (Klein et al. 2019, Preisler et al. 2019) and ensure the sustainability of the forest under warming and drying conditions (Tsamir et al. 2019). Here, we show that thinning carried an additional benefit by creating the conditions required for the partial regrowth of native herbs, which were partly inhibited under the forest canopy in the semiarid conditions. Therefore, our first prediction, regarding thinning-induced understory regrowth, was confirmed for herbs (Table 1). Interestingly, this happened in spite of the drier and hotter soil in the newly created forest gaps in summer (Pozner et al. 2022, Wang et al. 2022). In addition, both shrubs and herbs increased with time, as shown by the significant positive effect of "Year" (Table 1; Supplementary Fig. S4). Our second prediction was that grazing exclusion should further promote shrub regrowth, and, to a larger extent, herbaceous vegetation growth, assuming that it is the preferred food for the animals. Contrary to our prediction, the grazing effect was not part of the selected statistical model for both functional groups (Supplementary Tables S4 and S5). This non-significant effect of grazing might reflect a counterbalancing act of plant compensatory growth following grazing, also known as grazing-induced growth stimulation, which is known across ecosystems (Georgiadis et al. 1989, Noy-Meir 1993, Li et al. 2020, Penner and Frank 2021). The third prediction was that overall, the understory vegetation should increase in wet vs. dry years; however, precipitation had a delayed significant effect on herbs, but not on shrubs.

Facilitation of understory carbon storage

Our observations match earlier reports from more mesic sites about regrowth of low vegetation following forest thinning and the resulted increase in resource availability (Lindh and Muir 2004, Trentini et al. 2017, Zangy et al. 2021; Supplementary Table S1). For example, in a northeastern China forest with 30% thinning, tree biomass increased from 80 000 to 140 000 kg ha^{-1} after 10 years, while shrub biomass increased >5-fold, from 800 to 4400 kg ha^{-1}, and herb biomass was unchanged, at 500 kg ha^{-1} (Zhang et al. 2023). The higher numbers in the Chinese study compared to ours probably relate to the higher precipitation, 660 vs. 280 mm year^{-1}. Therefore, to study the understory facilitation permitted by the thinning, we need to compare our data with those measured locally outside Yatir forest. Here we showed that shrub cover

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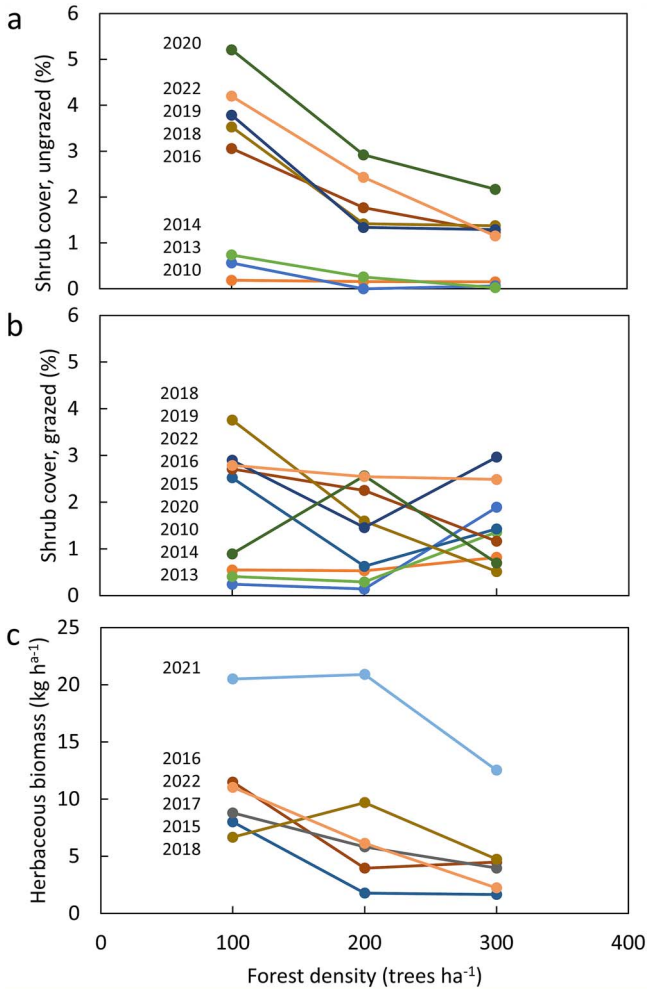

Figure 3. Nontree plant growth in Yatir forest across three forest densities. (a) Shrub cover (%) in ungrazed plots; (b) shrub cover (%) in grazed plots and (c) herbaceous biomass (kg ha^{-1}) in grazed plots. Year of observation is indicated for specific curves, differentiated by colors. Data points are means of 4–5 plots per density. Error bars were removed for visualization purposes.

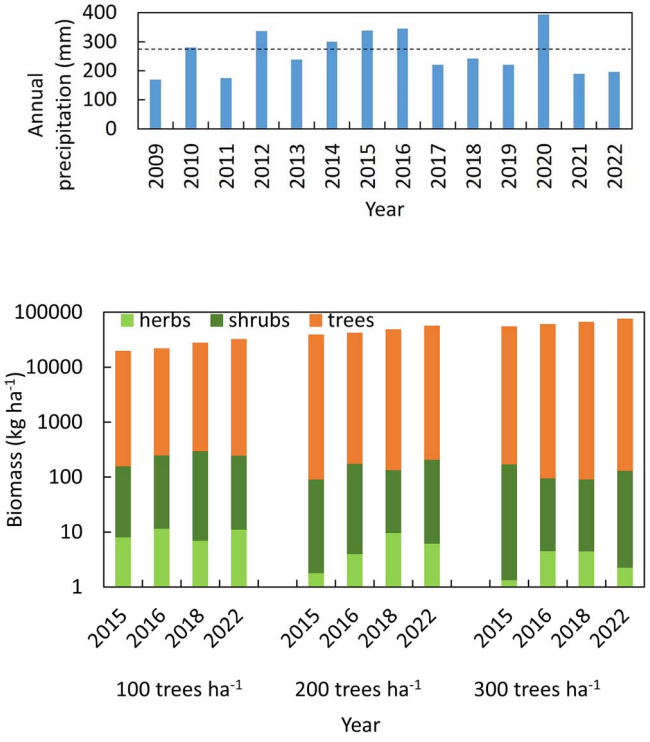

Figure 4. Plant biomass partitioning (herbs, shrubs, and trees) in Yatir forest in four different years and across three forest densities. Note the logarithmic scale in the y-axis due to scale differences among the groups (~10, ~150, and ~50 000 kg ha^{-1} for herbs, shrubs, and trees, respectively).

inside the forest increased from 1–2% to 4% (Fig. 2b), but that is still low compared with the shrub cover outside the forest, reported at 19% (Grünzweig et al. 2007). Based on C content calculations made in that earlier study, shrub biomass outside the forest was 1200 kg ha^{-1}, while tree biomass (35 years after planting) was 31 060 kg ha^{-1}. Here, we observe shrub biomass in the range of 86–290 kg ha^{-1}, and tree biomass (55 years after planting, but following thinning) between 19 069 and 76 402 kg ha^{-1} (Fig. 4). These numbers indicate that while shrub recovery was noticeable 12 years after the thinning, it was still a quarter of the native value, at most. It is possible that the shrub cover will continue to increase in the coming years, as it has been happening so far. On the other hand, considering the limited resources (water, nutrients, light), our numbers might represent the ecosystem capacity, as shown in dry years (Supplementary Fig. S7). Finally, all these numbers refer to aboveground biomass, and exclude the belowground fraction, which is considerable for Aleppo pine in Yatir (Grünzweig et al. 2007), and is probably lower, shallower, and shorter-lived in the herb and shrub species. Specifically for the shrubs, persistence of the root system could explain the multiannual dynamics (Figs 2 and 3), supporting aboveground growth in wet years vs. self-pruning in dry years.

Thinning effect vs. density effect

An additional question related to our study is whether the observed responses relate to the thinning itself (i.e. the fast change in plot conditions, sometimes causing a "thinning stress"), or rather reflect a value which could be expected from the stand density *per se*. Using our unthinned control plots, we showed that while shrubs benefited from the thinning itself, herbs did not, irrespective of thinning history (thinned or planted; Supplementary Table S3; Supplementary Fig. S7). How can this difference be explained? Our site is unique in having mostly perennial shrubs and annual herbs, lacking perennial herbs, which are important in other ecosystems (Fernandez et al. 1991). It is hence possible that the annual herbs grew as function of resources (light, water, nutrients), which are governed by forest density, regardless of plot history. However, the perennial shrubs, which grow over decades, needed a dramatic change in plot conditions in order to be released from competition with trees and to establish.

The nonsignificant effect of grazing

Another question regards the grazing treatment: Why was the grazing effect not significant?

Potential reasons include both biotic and abiotic factors. We mentioned the possible balance by plant compensatory growth (Noy-Meir 1993), yet additional factors are likely at play. It is important to note that the current grazing regime is regulated and is lower than the historical over-grazing. In a study in New Mexico (USA), grass cover exhibited an immediate response, with ungulate exclosures containing 8% higher cover than areas without exclosures (Kramer et al. 2015). The results suggest that conifer thinning and ungulate exclusion may elicit a positive

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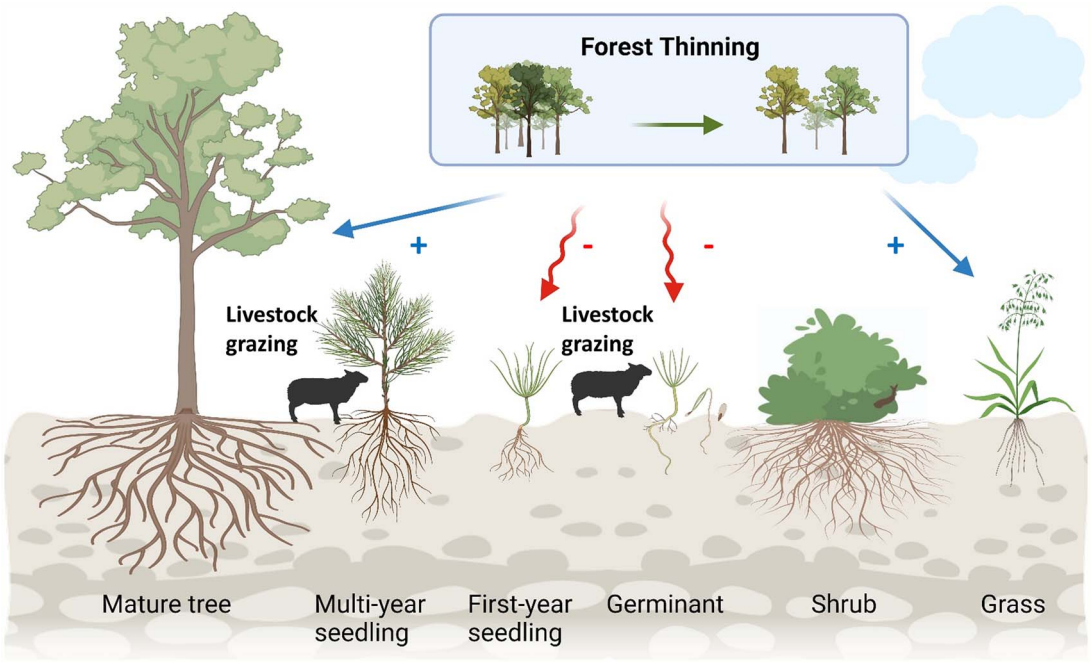

Figure 5. A summary of thinning and grazing effects on the different plant functional groups in Yatir forest. Forest thinning has a positive effect on mature trees, shrubs, and grasses (straight arrows) and a negative effect on germinants and first-year seedlings (wavy arrows). Grazing has a negative effect on multiyear seedlings (seedlings older than 1 year) and germinants (sheep icon; not to scale). Based on Tsamir et al. (2019); Pozner et al. (2022); and this study. Created with BioRender and Vecteezy.

response; however, in the presence of drought, the positive effects are only short-term. In addition, different grazing dynamics, such as rotation times, can produce different vegetation responses (Li et al. 2020), and one must consider that grazing in our site was managed on a seasonal basis and not exerting continuous pressure. Abiotic factors are also at play. Interestingly, this earlier study was performed in a site with mean annual precipitation of 474 mm (Li et al. 2020), where drought years have similar precipitation as the mean at our site. Thus, it is possible that potential grazing effects at our site are overridden by the low water availability. In that regards, herbs were less sensitive than shrubs to inter-annual differences (Table 1), i.e. annual precipitation (Figs 4 and 5), probably because they grow in the wet season only. In a yet drier ecosystem, without trees (Patagonian steppe), biomass growth of perennial grasses and shrubs was 790 kg ha^{-1} $year^{-1}$ in a 191 mm rainfall year, ranging between 210 and 750 kg ha^{-1} $year^{-1}$ in drier years, but not increasing in years with above-average precipitation (Fernandez et al. 1991). These numbers compare with our numbers for (long-term) shrub biomass (Supplementary Fig. S5).

Relationships between shrubs and herbs

Last, we investigated the relationships between the plant functional groups; both herbs and shrubs populate the forest understory, mainly in the newly formed gaps. In a Mediterranean forest site 50 km north of Yatir, a 15-fold increase in herbaceous biomass was recorded 4 years after grazing exclusion but disappeared 10 years after exclusion due to increased woody cover (Osem et al. 2017). The tradeoff between shrub and herb biomass which was observed in 2016 (Supplementary Fig. S8) might suggest such competition. However, a positive relationship was observed at the same plot 6 years later (Supplementary Fig. S8). It is possible that after 3 wet years in a row (2014–16), increased growth might have led to shrub-herb competition, whereas a dry year (2022) might offer more room for expansion of both functional groups.

Forest understory responses to thinning and grazing

In addition to the interactions discussed above, other interactions are also at play. In this long-term forest manipulation study and its preceding studies within the same experiment (Tsamir et al. 2019, Pozner et al. 2022), we showed that while mature pine trees and herbs benefited from the thinning, shrub response was context-dependent, and pine seed germination and seedling survival were lower (Fig. 5). However, since forest regeneration in Yatir is almost zero, seedling survival would anyhow require additional intervention. Grazing effects were either negative (specifically, on pine germination and seedlings older than 1 year; Fig. 5), or not significant. Whether there was competition between pine seedling and the understory components studied here remains to be tested. Additionally, the coming years will show if the increase in understory vegetation continues, or rather stabilizes. To test if increased understory vegetation is accompanied by increased species diversity, we are now planning botanical surveys of the plots.

Conclusion

(1) Twelve years following thinning and grazing exclusion in a semiarid pine forest, native shrubs and herbs have moderately expanded.
(2) The effect of thinning on herb growth was positive and significant and was mostly related to last year's precipitation. The effect of thinning on shrub growth was not significant.
(3) The effect of grazing on shrubs and herbs was not significant.

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Author contributions

Stav Livne-Luzon (Formal analysis, Methodology, Writing—review & editing), Yael Grunwald (Formal analysis, Methodology, Validation, Writing—review & editing), Ella Pozner (Data curation, Methodology), Eyal Rotenberg (Conceptualization, Methodology, Validation), Dan Yakir (Conceptualization), and Tamir Klein (Conceptualization, Formal analysis, Funding acquisition, Supervision, Validation, Writing—original draft)

Supplementary data

Supplementary data are available at *Forestry* online.

Conflict of interest

None declared.

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Data availability

All data related with this paper are included in the figures and supplementary materials. Data will be uploaded to Figshare.com upon manuscript acceptance.

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