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Thinning and plantation of resprouting species redirect overstocked pine stands towards more functional communities in the Mediterranean basin

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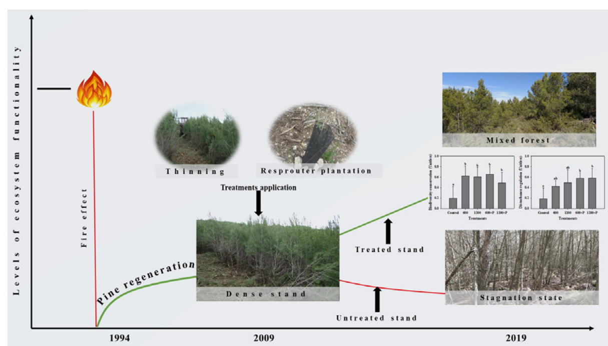
HIGHLIGHTS

- The combination of thinning and resprouter plantation improved ecosystem functions.
- Moderate thinning suffices to enhance individual aboveground attributes.
- Plantation of resprouter species helps to maximize ecosystem services.
- Ecosystem responses to management are driven by aboveground but not belowground attributes.

GRAPHICAL ABSTRACT



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ABSTRACT

Post-fire regeneration in *Pinus halepensis*' forests, one of the most abundant vegetation types in the Mediterranean basin, often generates overstocked and vulnerable stands. They accumulate a high fuel load, increasing the risk of further fires, and present high levels of vulnerability due to their reduced seed production. In addition, these dense stands substantially reduce the availability of light and nutrients, which may hinder the recruitment of other species, often generating mono-specific and homogeneous stands, which potentially supply fewer ecosystem services than mixed forests with more heterogeneous structures. In these dense pine stands, management is of high priority to reduce fire hazards and promote their functionality. In overstocked pine stands (>75,000 trees·ha^{-1}), we assessed the long-term effects (10 years) of two thinning levels (600 and 1200 trees·ha^{-1}), in combination with the plantation of *Quercus faginea* (a resprouter species typical of advanced successional stages in our study area) on 28 above and belowground ecosystem attributes, including fire hazard. After ten years, thinning and plantation interacted to enhance ecosystem attributes associated with disturbance regulation and biodiversity conservation (up to 200%) and food production (up to 90%), while no effects were observed on those attributes related to carbon sequestration and supporting services. These effects were mainly driven by aboveground attributes, as they responded more strongly to our treatments than those belowground. Our results are relevant for the restoration of Mediterranean degraded ecosystems, and show that tree thinning in overstocked pine stands, combined with the plantation of resprouter species, may not only reduce fire risks and accelerate post-fire succession but also enhance the supply of multiple ecosystem services in the long run.

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1. Introduction

Wildfires are one of the most important disturbances shaping ecosystem structure and functioning (Keeley et al., 2012; Whitman et al., 2019). In the Mediterranean basin, wildfires have occurred for millennia and are an inherent driver of ecological processes (Scott et al., 2014). In recent decades, however, land use (crop abandonment) and climatic changes (increasing aridity) have shifted fire regimes towards more frequent and larger fire events (Duane et al., 2021; Pausas and Fernández-Muñoz, 2012), which could compromise ecosystem resilience and functioning (Blondel and Aronson, 1995). In this context, it may be more pragmatic to shift management targets from fire suppression towards an integrated approach joining fire prevention and the promotion of more resilient landscapes (Moreira et al., 2020).

Pinus halepensis is an autochthonous species from the Mediterranean basin (Quézel, 2000). Presently, it is one of the most abundant species in this region favored, in part, by its ability to colonize abandoned crop fields and its past use in massive reforestation plans (Le Houerou, 2000; Maestre and Cortina, 2004). After a fire, *P.halepensis* may regenerate massively from seeds- protected and released from serotinous cones (Daskalakou and Thanos, 1996), often leading to extremely dense (overstocked) and even-aged pine stands that hinder individuals' development and increase fire risk (Le Houerou, 1974; Pausas et al., 2004a, 2004b). These dense, homogeneous, and monospecific stands are vulnerable to fire and other environmental disturbances (Bauhus et al., 2017). A second fire in this stagnant state is tied to high fire severities and local pine extinctions by immaturity risk (Baeza et al., 2007; Verkaik and Espelta, 2006). These stands, in addition, are probably less functional and host low species richness and, therefore, are a prior target in ecological management and restoration plans in the Mediterranean area.

Although these dense pine stands could eventually undergo self-thinning in the long run, their slow successional dynamics, together with their vulnerability to further fires and droughts, call for their active management to foster more desirable ecosystem stages. According to the ecosystem type and the goals intended to reach, different restoration activities (e.g. clearing, prescribed fires, thinning) are applied to manage these dense pine stands, among which tree thinning is the most usually recommended in order to reduce fuel load and enhance tree growth and stand heterogeneity (Agee and Skinner, 2005; Mitchell et al., 1983). Yet, our knowledge regarding the effectiveness of tree thinning is incomplete (Agee and Skinner, 2005; Moreira et al., 2011). Tree thinning may allow the establishment of less-flammable communities by reducing competition and allowing late-successional species to germinate and establish (Agee and Skinner, 2005; Baeza et al., 2003; Fernández and Vega, 2016). Besides, reduced competition may enhance pine trees' growth and seed production (González-Ochoa et al., 2004; Verkaik and Espelta, 2006). Furthermore, forests deliver multiple services to humans, ranging from the production of raw materials and regulation of water flow to soil protection and biodiversity conservation (Brockerhoff et al., 2017; Gamfeldt et al., 2013), and tree thinning may have contrasting effects on the supply of these multiple services. For example, tree thinning may increase tree size and understory diversity, enhancing the provision of habitat for fauna (Boch et al., 2013; Cruz-Alonso et al., 2019). However, thinning could also reduce the inputs of organic matter into the soil, due to reductions in litterfall and worsened microclimatic conditions (Wic Baena et al., 2013). The balance between the latter and enhanced tree growth may thus lead to either positive or negative effects on carbon sequestration (Grady and Hart, 2006; Jandl et al., 2007; Lopez-Serrano et al., 2006). Hence, to better understand the effectiveness of tree thinning in enhancing forest functioning, we need to address its effects on multiple ecosystem functions and services. Besides, we need to do so over long periods, as often recommended to properly evaluate the success of any ecological restoration or management practice (Dwyer et al., 2010; Gavinet et al., 2015; Jiménez and Navarro, 2016; Ruiz-Jaen and Aide, 2005; SER, 2004).

In addition to tree thinning, the introduction of resprouter species is often implemented as a post-fire restoration technique to enhance ecosystem resilience due to their ability to survive and regenerate after the fire (Vallejo and Alloza, 1998; Gavinet et al., 2016; Santana et al., 2018). Resprouter species are typical of late-successional stages and thus their reintroduction increases diversity in monospecific stands and accelerates secondary succession. The introduction of resprouter species can also enhance the supply of additional ecosystems services in forests, as they provide food and shelter to animals and may help to generate multi-species and heterogeneous stands (Cavard et al., 2011; Curt et al., 2013; Jactel and Brockerhoff, 2007). Resprouter species also have positive impacts on carbon storage, soil fertility, and nutrient cycling (e.g., López-Poma and Bautista, 2014; Maestre et al., 2009) and could thus balance out the potentially negative effects of tree thinning in these ecosystem attributes. Despite their complementarities and potential synergistic effects, fire prevention management (via tree thinning) and post-fire restoration (via the introduction of resprouter shrubs and trees) have typically been studied in isolation and with a different focus (short-term fuel reduction for the former, long term improvement of productivity, increase ecosystem resilience and diversity for the latter). In addition, the success of the introduction of these resprouter species can be enhanced if competition diminishes with tree thinning. Therefore, studying the combined effect of these two complementary strategies as integrated fire management may help to foster multifunctional landscapes at the same time that fire risk is minimized (Gavinet et al., 2016; Santana et al., 2018; Valdecantos et al., 2009).

Here, we assessed the long-term effects (10 years) of two thinning levels (600 trees$\cdot$ha^{-1} and 1200 trees$\cdot$ha^{-1}) and plantation of a resprouter species (with and without plantation), within overstocked pine stands (>75,000 trees$\cdot$ha^{-1}), on ecosystem services (biodiversity conservation, carbon sequestration, ecosystem resilience, food production, and supporting services) summarizing 28 above and belowground ecosystem attributes. These treatments aimed to i) reduce fire hazards and the vulnerability of the stands, and ii) increase the provision of ecosystem services and ecosystem functioning. We hypothesized that the combination of thinning and plantation of resprouter species will have positive effects on both above- and below-ground forests attributes, reduce fire risk and increase the supply of ecosystem services.

2. Material and methods

2.1. Study area

The study area is located in South-eastern Spain. Within this area, we selected three wildfires that had occurred during the summer of 1994 in areas of similar soil, climatic and pre-fire vegetation characteristics. We selected three sites (Table S1) with a burned surface of more than five hectares distributed in the Mariola (38°43′N, 0°24′W) and Benicadell (38° 49′N, 0°24′W) mountain ranges. Site altitudes range from 500 to 800 m above sea level, and the climate is dry sub-humid Mediterranean. Mean annual temperatures range from 13.1–16.5 °C and mean annual rainfall from 450 to 700 mm (Table S1). Bedrock is limestone and soils are Calcaric Cambisol. Before the fire, the vegetation consisted of a mature Aleppo pine (*P. halepensis*) forest, which is commonly characterized by tree densities of 1672 ± 1333individuals$\cdot$ha^{-1}, (Moghli et al., unpublished data). Currently, the vegetation is a homogeneous and dense young pine forest (26 years) with a high-density regeneration of pine (75,000–220,000 trees$\cdot$ha^{-1}). Beneath the tree layer, there is a senescent shrubland layer dominated by obligate seeder species such as *Ulex parviflorus*, *Rosmarinus officinalis,* and *Cistus albidus*. There are also a few small isolated individuals of woody resprouting species such as *Quercus coccifera*, *Juniperus oxycedrus, Pistacia lentiscus,* and *Quercus ilex.*

2.2. Experimental design

In autumn/winter 2009, we experimentally reduced tree density by thinning (two levels: 600 and 1200 trees·ha^{-1}) and planted a resprouter species (*Quercus faginea*; 300 seedlings·ha^{-1} vs no plantation) following a full-factorial design with four 0.5 ha plots ($N = 12$; 4 treatment combinations × 3 sites). In addition to these treatments, we left three 0.5 ha plots unmanaged as a control, with the original pine density (75,000–220,000 trees·ha^{-1}, Table S1) and without plantation. Pine density was reduced first with a tractor equipped with a vertical-axle chain drive that chopped vegetation and left it on the soil as mulch. The tractor created corridors that facilitated a posterior manual clearing until the desired density was achieved. In addition to pines, other seeder shrubs species like *Ulex parviflorus*, *Cistus albidus,* and *Rosmarinus officinalis* were also removed. When possible, the few individuals of resprouting species present were left standing due to their keystone role in these ecosystems (e.g., Cortina et al., 2011). The plantation was performed immediately after thinning. The planting holes (30·30·30 cm) for introducing *Q. faginea* were dug mechanically by a tractor supplemented with a backhoe. Seedlings introduced were two years old and produced in a nearby forest nursery (Basal diameter: mean = 3.53 cm; SD = 0.82). Plantation of additional resprouter species was not considered in this study, as individuals of other resprouter species of interest (*Q. ilex*, *Q. coccifera*, *P. lentiscus,* and *J. oxycedrus*) were already present in the area.

2.3. Field sampling and laboratory analysis

In Spring 2019, twenty-five years after the fire and ten years after management, we measured 28 vegetation and soil attributes (hereafter above- and belowground attributes) at each plot. These attributes are linked to biodiversity conservation, capacity to capture carbon (either on woody biomass or into the soil), resistance and resilience to further fires, food production (forage for livestock or wild animals, potential production of honey), or the capacity to capture, store and recycle nutrients (see Table 1 and text below for details).

2.3.1. Aboveground attributes

We assessed plant cover across three 30 m-long transects, parallel to each other and separated by 5 m, within each plot. Using the point-intersect method (Greig-Smith, 1983), we recorded each species contact every 20 cm with a graduated metal rod (3 mm diameter) (150 points per transects with a total of 750 points per plot). These measurements were also used to i) calculate species richness, ii) estimate the potential of beekeeping from literature about the honey production value of each species (Mateu, 2016; Sanchís et al., 1992), and iii) calculate habitat complexity (an index related to habitat provision for birds, lizards, and mammals, using the cover of different vegetation strata and litter (Val et al., 2017). The effect of treatments on the natural colonization of resprouting species was assessed by measuring their density and richness within one 10·10 m subplot in each plot. In the same 10·10 m subplots, we measured the arboreal biomass (*P. halepensis*) estimated from allometric equations using the basal stem diameter (Baeza and Santana, 2015). Understory biomass was measured in six 1·1 m quadrats per treatment (two quadrats per transect) selected randomly, where all vegetation and litter were harvested. In the control plot, *P. halepensis* biomass was also assessed in these six quadrats because of the high individuals' density. In the laboratory, the clipped material was separated into dead and living biomass, and into woody and herbaceous biomass. Samples were then oven-dried at 80 °C for 48 h and weighed. Dead biomass and the vertical cover were used to calculate (i) the vertical fuel discontinuity as the gap (cm) between the understory and canopy layers, which is linked to the vulnerability of the ecosystem to further fires (Sánchez-Pinillos et al., 2019), and (ii) the dead fuel bulk density (DFBD) as a flammability indicator (i.e. the height of shrub (m)/dead biomass (g.·m^{-2}) (Fernandes and Cruz, 2012; Santana et al., 2011). In addition, we calculated the percentage of dead biomass (pDB) within each plot regarding the total biomass.

2.3.2. Belowground attributes

Five soil samples (top 5 cm) were collected within each study plot. Herbs, litter, and woody debris were removed before collecting soil samples. Soil samples were air-dried and sieved (<2 mm) before the

Table 1
Summary of the variables measured and included in the calculation of the related ecosystem services.

Ecosystem service	Variable measured	Above/belowground	Included in the calculation?
Biodiversity conservation	Plant species richness	Aboveground	Yes
	Habitat complexity		Yes
Carbon sequestration	Arboreal live biomass	Aboveground	Yes
	Shrub live biomass		Yes
	Organic carbon	Belowground	Yes
Disturbance regulation	Richness of resprouter shrubs	Aboveground	Yes
	Abundance of resprouter shrubs		Yes
	Arboreal dead biomass		No, highly correlated to total dead biomass already included in disturbance regulation service
	Dead shrub biomass		No, highly correlated to total dead biomass already included in disturbance regulation service
	Dead fuel bulk density		No, highly correlated to total dead biomass already included in disturbance regulation service
	Percentage of dead biomass		No, highly correlated to total dead biomass already included in disturbance regulation service
	Vertical continuity		Yes
Food production	Beekeeping potential	Aboveground	Yes
	Herbaceous biomass		Yes
Supporting	Litter	Aboveground	Yes
	Available phosphorus	Belowground	Yes
	Total oxidized nitrogen		Yes
	Total ammonium		Yes
	Potential nitrogen mineralization		Yes
	Acid phosphatase		Yes
	Beta glucosidase		Yes
Other	pH	Belowground	No
	Electrical Conductivity		No

analyses. In a mixture of soil: deionized water (1:5), the soil pH and electrical conductivity (EC) were measured. Soil organic C was analyzed using the loss-on-ignition method (Davies, 1974). The enzymatic activities β-glucosidase and acid phosphatase related to the cycling of C and P were analyzed following the procedure described by Tabatabai (1994). The total oxidized nitrogen (TON; nitrates + nitrites) and total ammonium were analyzed following (ISO, 1998). Potential nitrogen mineralization (PNM) was assessed following Stanford and Smith (1972).

2.3.3. Ecosystem services

After removing those highly correlated to others ($r > 0.7$; Fig. S1, Table 1), we re-organized the 28 above- and belowground ecosystem attributes measured into five categories of ecosystem services: i) carbon sequestration: woody biomass and soil organic carbon, as the main carbon pools in terrestrial ecosystems (Heimann and Reichstein, 2008), ii) biodiversity conservation: plant species richness and habitat complexity (linked to the diversity of vertebrate animals, insects and belowground biota; Scherber et al., 2010; Val et al., 2017), iii) food production: beekeeping potential and herbaceous biomass (as an indicator of forage available for both livestock and wild herbivores), iv) disturbance regulation: resprouter abundance and dead fuel biomass, related to the vulnerability of ecosystems to further fires and their capacity to regenerate after fire (the inverse of dead fuel biomass was used, so higher values mean less vulnerability and therefore higher disturbance regulation services), and v) supporting services: litter biomass, available phosphorus, β-glucosidase, acid phosphatase, TON, and total ammonium. All variables were standardized between 0 and 1 to equally weigh the influence of each variable on the supply of each related service, and also to obtain comparable coefficients in the statistical analyses described below. Then, we obtained an overall measurement of ecosystem functioning using a multifunctionality index summarizing these five services into a single metric. The multifunctionality index was calculated as the Gini-Simpson diversity index (Simpson, 1949; Eq. (1)) using the function 'diversity' of the vegan package in R (Oksanen et al., 2019). This metric considers the number of ecosystem services, their supplies, as well as the balance between them, and avoid the overestimation if a plot supplies only few, but very high levels of ecosystem services (Hölting et al., 2019).

$$Geni\ Simpson\ Diversity\ Index = 1 - \sum_{i=1}^{N} Pi^2 \quad (1)$$

(N = total number of ecosystem services (5); pi = the supply of each ecosystem service (i) proportionally to the supply of all ecosystem services in the plots).

Alternatively, we also calculated the multifunctionality index using the averaging approach, as the mean of the five ecosystem services (see Maestre et al., 2012 for a related approach). Since the results from the latter were very similar to those presented here ($r = 0.82$; $P < 0.0001$), we do not discuss them further.

2.4. Statistical analysis

Due to the nature of our experimental design, we assigned each treatment combination as a different level in a single factor (5 levels or treatment-types in total): i) control-unthinned (untreated), ii) thinned to 1200 trees·ha^{-1} without plantation (1200), iii) 1200 trees·ha^{-1} + plantation of resprouter species (1200 + P), iv) 600 trees·ha^{-1} without plantation (600), and v) 600 trees·ha^{-1} with plantation of resprouter species (600 + P). One-way analysis of variance (ANOVA) with treatment (5 levels, with transects as pseudo-replicate for the variables, assessed using three transects per plot) as the sole predictor were performed for each of the measured variables individually, and for those ecosystem services to which they were related. Kruskal-Wallis one-way analyses of variance on ranks were performed when the ANOVA assumptions were not reached. Tukey and Dunn's post-hoc tests were respectively performed in case of significant differences ($P < 0.05$) in parametric and non-parametric analysis to compare between the different treatments.

In addition, to identify the collective effect of treatments on all belowground (all soil properties) and aboveground attributes (all vegetation variables), a Permutational Multivariate Analysis of Variance (PERMANOVA) was carried out using the *adonis* function from *vegan* package implemented with 1000 permutations (Oksanen et al., 2019). The same analysis was also carried out to assess the effect of treatments on species composition (using data from the point-intercept transects). To compare the influence of abundant or rare species in the compositional responses, we compared PERMANOVA results using raw cover data (and therefore accounting mainly for changes in the most abundant species) and using 4th-root transformed-data (i.e., almost presence/absence data, and therefore giving equal weight to changes in rare or abundant species). In both cases (common species only, or common + rare), we visualized the overall dissimilarity in species composition among treatments by using a non-metric multidimensional scaling (NMDS) using a Bray-Curtis dissimilarity distance. Vectors of plant species were fitted in the NMDS ordination using the *envifit* function implemented with 1000 random permutation. The later provides the directions of vectors, their amount of variance explained (R^2), and their significance (P). All analyses were done using R software version 3.5.2 (R Core Team, 2017).

3. Results

3.1. Tree thinning, more than plantation of resprouter species, enhances individual aboveground ecosystem attributes

Thinning and plantation of *Quercus faginea* affected aboveground attributes in different ways (Fig. 1, Table 2, Fig. S2, Tables S2–S5). Compared with untreated plots, all treatments increased herbaceous biomass (ANOVA: $F_{4,44} = 3.03, P < 0.05$) while reduced arboreal living biomass (Kruskal-Wallis: $\chi^2 = 9.12, P < 0.05$), arboreal dead biomass ($\chi^2 = 9.05, P < 0.05$), dead fuel bulk density ($\chi^2 = 9.11, P < 0.05$), and the percentage of dead biomass ($\chi^2 = 9.72, P < 0.05$). In addition, excepting the 1200 + P treatment, all treatments increased species richness up to 65% ($F_{4,44} = 5.40, P < 0.05$) and habitat heterogeneity ($F_{4,44} = 5.45, P < 0.05$). Our treatments also changed significantly species composition with respect to the control, unthinned plots (Fig. S3, Tables S6–S8), but showed no differences between them. Whereas control plots were strongly dominated by *P. halepensis*, all thinned plots showed a more balanced species composition, with species typical of the Mediterranean basin. These compositional changes were caused both by changes in the abundance of common and rare species in response to our treatments (Figs. S3 and S8). The 1200 + P treatment increased resprouters' richness up to 54% ($F_{4,44} = 4.42, P < 0.05$) and 600 + P increased vertical fuel discontinuity ($F_{4,44} = 3.53, P < 0.05$).

Contrarily to aboveground attributes, thinning and plantation of *Quercus faginea* had no effects on belowground attributes compared with untreated plots (Fig. 2, Tables 2 and S9). The PERMANOVA analysis confirmed these results and showed that our treatments induced significant changes on aboveground attributes overall ($P < 0.01$) while did not show significant effects on belowground attributes (Table 2). In general, we did not observe significant differences between our different thinning and plantation treatments, but only between those and the untreated plots. Therefore, looking at each ecosystem attribute individually, our results suggest that thinning to 1200 trees · ha^{-1} would be the most efficient restoration technique to enhance forest functioning.

3.2. The combined effect of tree thinning and plantation of resprouter species enhance ecosystem services

When looking at the five ecosystem services instead of the individual attributes, our results regarding the different restoration treatments changed substantially. Two out of five ecosystem services were affected

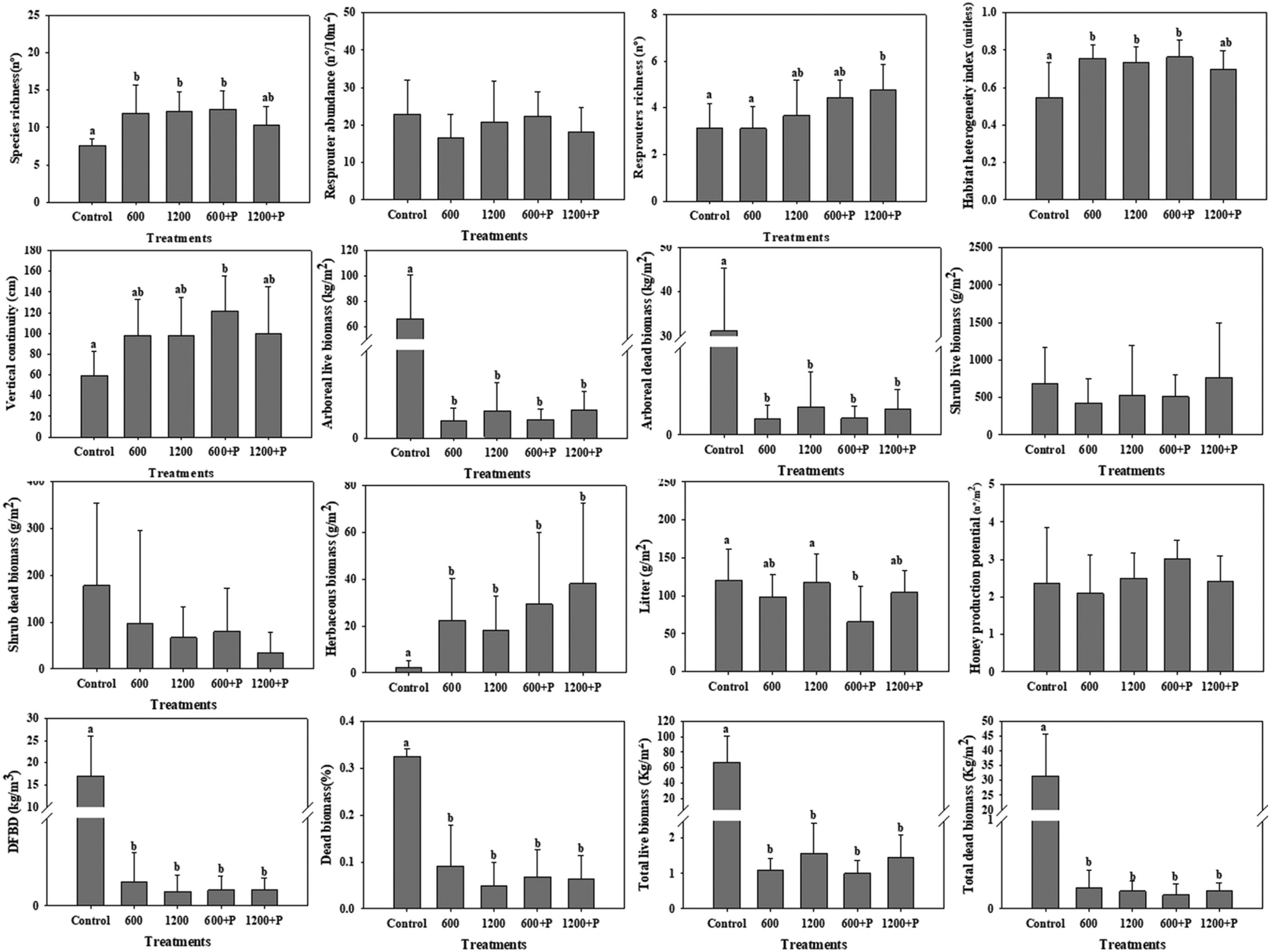

Fig. 1. Mean (±SE, N = 15) of aboveground attributes. Different letters mean significant differences according to our one-way ANOVA and no letters means that no significant differences were found in between the different treatments.

Table 2
Results of the Permutational Multivariate Analysis of Variance, showing the effects of treatments on overall above and belowground attributes. Df = degrees of freedom, SS = sum of squares (type III), R2 = variance explained by the model, F = pseudo-F.

	Aboveground attributes					Belowground attributes				
	Df	SS	R^2	F	*P*-value	Df	SS	R^2	F	*P*-value
Treatments	4	0.821	0.261	3.540	0.001	4	0.260	0.362	1.420	0.108
Residual	40	2.320	0.739			10	0.457	0.638		
Total	44	3.141	1			14	0.717	1		

by the combination of both tree thinning and plantation of a resprouting species (Fig. 3, Tables S10 and S11). This suggests that the non-significant changes observed for individual attributes summed up to significant differences when pooling these functions. Specifically, this is the case of functions related to food production and disturbance regulation services (compare 1200 and 600 vs 1200 + P and 600 + P in Fig. 3). Plots with plantation of *Quercus faginea* showed the highest values of disturbance regulation (up to 2 times higher) compared with untreated plots ($F = 3.68, P < 0.05$), and only those plots with the lowest tree density and plantation of resprouter species (600 + P) significantly enhanced food production (up to 90%) regarding untreated plots ($F = 2.62, P < 0.05$). It is worth noting that after 10 years, the survival of planted *Quercus faginea* was 37% and 42%, and the growth of basal diameter was 0.57 ± 0.07 mm·year^{-1} and 0.44 ± 0.05 mm·year^{-1} within 600 and 1200 trees · ha^{-1}, respectively, with no significant difference between these two levels of thinning (Fig. S4). Compared to untreated plots, all treatments increased up to 2 times biodiversity conservation ($F = 8.58, P < 0.05$); they also increased ecosystem multifunctionality, although this increase was only marginally significant ($\chi^2 = 8.23, P < 0.08$). However. no effects were observed on carbon sequestration and supporting services.

4. Discussion

Overstocked pine stands are fire-prone and low functioning ecosystems, and therefore managing them to reduce fire risk and enhance multifunctionality is of high priority (Agee and Skinner, 2005). Herein, we show which attributes, and their related ecosystem services are enhanced by tree thinning and resprouter plantation 10 years after their application. We found that tree thinning to 1200 trees · ha^{-1} may suffice to enhance many ecosystem attributes of interest, but that only the combination of thinning and plantation of resprouter species (*Quercus faginea)* may be able to maximize disturbance regulation (including fire risk control) and food production services in the long run. Therefore, combining these two restoration techniques, often applied individually, might be a suitable integrated management to redirect dense pine forests towards mixed forests, often reported as more functional and less vulnerable (Pretzsch and Forrester, 2017). Multifunctionality as a whole did not change significantly in response to our treatments, perhaps due to the contrasting responses of the different functions to such treatments. However, the ecosystem services of biodiversity conservation, food production, and disturbance regulation were enhanced by, at least, one of the treatments, with their highest values observed within the combination of thinning (600 trees·ha^{-1}) + plantation of *Quercus faginea* seedlings (Fig. 3). In general, the observed effects were caused by changes in aboveground attributes, as they responded more strongly to the treatments than those belowground.

Thinning to 1200 trees·ha^{-1} suffice to enhance individual (aboveground) ecosystem attributes…

Our results show that reducing pine density may allow, as expected, the establishment of new species due to lower competition levels, or because of the higher availability of light and nutrients (Agee and Skinner, 2005; Fernández and Vega, 2016). All treatments increased the number of species, excepting the 1200 + Plantation, and induced significant changes in species composition compared to untreated plots after 10 years, while no difference was observed between them (Fig. S3, Tables S6 and S7). These results suggests that our treatments may redirect overstocked pines towards more diverse and even communities (Fig. S3). It is noteworthy that the observed increase of species richness was the result of the establishment of native species typical of Mediterranean ecosystems, and not caused by the invasion of exotic species, as also observed in previous studies focused on the effects of pine tree thinning in Mediterranean environments (González-Ochoa et al., 2004; Jiménez and Navarro, 2016; Manrique-Alba et al., 2020; Ruano et al., 2013; Verkaik and Espelta, 2006). In addition to the effects on plant composition, canopy opening and breaking the homogeneity of vegetation via tree thinning enhanced habitat heterogeneity (Fig. 1, Tables S2 and S4), which may provide a greater range of habitat for animals (Val et al., 2017). Increasing species richness and habitat heterogeneity is of special importance for ecosystems in terms of biodiversity preservation (both the number of species and the diversity of functional traits) and may have large consequences on ecosystem multifunctionality due to the oft-reported positive biodiversity-functioning relationships in woodlands (Jucker et al., 2014; Liang et al., 2016; but see van der Plas, 2019), and the positive effects of heterogenous forest structure on ecosystem multifunctionality (Felipe-Lucia et al., 2018; Pretzsch and Forrester, 2017).

The differences between the two levels of thinning were undetectable 10 years after their application for many of the multiple ecosystem attributes measured. The same was found for the survival and growth of the introduced *Quercus faginea* seedlings (Fig. S4) which are similar to those found for the same species elsewhere (Gavinet et al., 2015). This result suggests very similar effects of thinning to 1200 vs 600 trees·ha^{-1}. The difference between these two thinning treatments, however, could be accentuated over the following years, when remnant trees develop further and begin to compete for resources. For example, Manrique-Alba et al. (2020) found that the effects of moderate thinning on tree growth and drought response started to fade after 20 years. Furthermore, we should mention that heavy thinning could increase the possibility of herbivorous pest outbreaks (e.g. *Pachyrhinus spp.*) (González-Ochoa and De Las Heras, 2002), although we did not observe particularly high herbivory damage in the present study, neither it has been reported in other studies (e.g. Ruano et al., 2013).

…but combining thinning with plantation of resprouter species is best to maximize disturbance regulation and food production services

Dense pine stands may not facilitate the establishment of shrubs, including resprouter species (Gómez-Aparicio et al., 2009; Maestre et al., 2003). However, we found that combining tree thinning with the plantation of resprouter species effectively increased resprouters species richness, both by their direct introduction (in the case of *Q. faginea*) and by enhancing natural colonization (Fig. 1, Table S2). It is worth noting that a selective shrub clearing, in addition to tree thinning, may be an essential step to halt the arrested succession states, by opening a window of opportunity for new bird-dispersed seedlings of resprouter species to establish. Although we did not experimentally evaluate the interaction between tree and shrub clearing, the latter is in concordance with previous studies (Gómez, 2004; Pons and Pausas, 2007; Santana et al., 2018). In this sense, the selective clearing (elimination of seeders) that foster resprouter species' presence would enhance ecosystem resilience by both reducing the response time after disturbance (resprouter species take less time to regrow after a fire) and reducing the probabilities of regeneration failures (Pausas et al., 2004a, 2004b; Quintana et al., 2004; Riva et al., 2016).

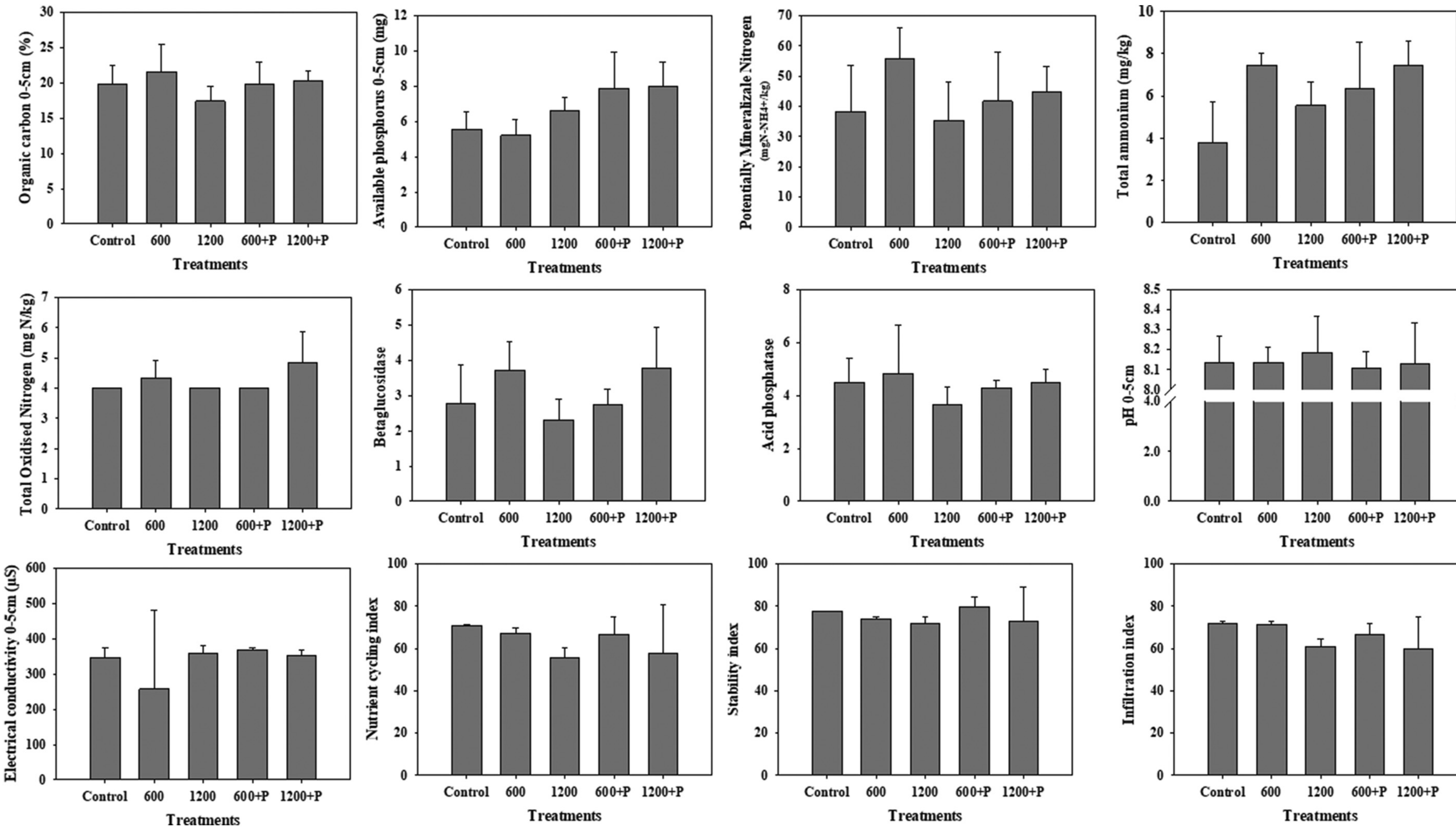

Fig. 2. Mean (±SE, N = 15) of belowground attributes. Different letters mean significant differences and no letters means no significant differences were found in between the different treatments.

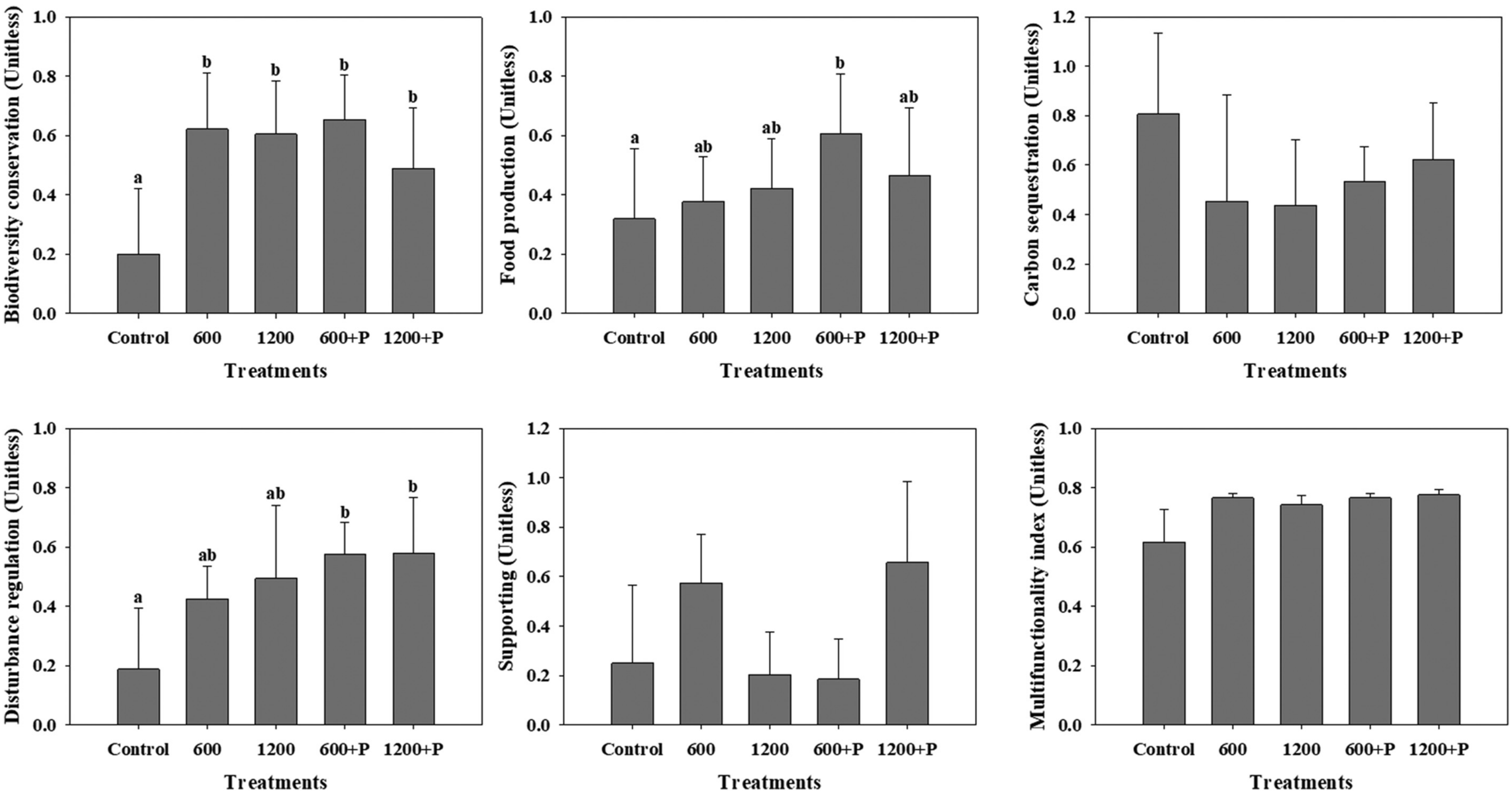

Fig. 3. Mean (±SE, N = 15) of five ecosystem services and multifunctionality index. Different letters mean significant differences and no letters means no significant differences were found in between the different treatments.

Regarding the effect of the treatments on fuel structure, a lower density of pines and plantation of *Quercus faginea* (600 + Plantation) increased the gaps between the understory and canopy layers (Fig. 1, Table S2), and therefore reduced the risk of vertical fire propagation (Reinhardt et al., 2006; Sánchez-Pinillos et al., 2019). Furthermore, by removing trees, all treatments reduced dead biomass (up to 30%) and dead fuel bulk density, a surrogate of flammability, decreasing, therefore, the ecosystem's fire risk (Fig. 1, Tables S3 and S5). Together with the lower flammability, the lower probability of ignition due to the increased presence of resprouters (with a lower accumulation of dead fuel and high moisture content) promoted by our treatments (Fig. 1, Table S2) could further reduce fire risk (Baeza and Santana, 2015; Santana and Marrs, 2014).

Tree removing and plantation of resprouter species did not only reduce fire risk and increased biodiversity conservation, but also enhanced the production of food, especially in the 600 + plantation treatment (Fig. 3). Although reducing shrub biomass by clearing, honey production did not decline, probably due to, besides the plantation of *Quercus faginea*, the establishment of new species with potential for honey production, such as *Rosmarinus officinalis, Cistus albidus, Ulex parviflorus, and Erica multiflora*. In addition, a lower density of pines allowed the establishment of herbaceous vegetation increasing forage availability. Collectively, our results show that a combination of tree thinning and plantation of resprouter species is a useful and integrated restoration and fuel management approach that facilitates successional trajectories towards less fire-prone and more resilient and functional communities.

Importantly, reductions in tree biomass due to thinning management may potentially dampen the ability of ecosystems to sequester carbon (De Las Heras et al., 2013). However, our treatments did not affect carbon sequestration (Fig. 3, Tables S10 and S11). This result can be explained by compensatory growth (and therefore enhanced organic matter input into the soil) of the remaining trees and shrubs, due to reduced competition and higher resources availability compared with untreated plots (Dwyer et al., 2010; Manrique-Alba et al., 2020). Considering the young age (25 years) of the forests in our study sites, and the die-off processes characterizing dense pine stands in the longer term, the negligible effects of our treatments on carbon sequestration could shift to positive if dense pine stands stagnate their growth rates and thinned forests continue to grow (Ruiz-Peinado et al., 2017). Regardless of the future response of trees' growth rate to our treatments, the amount of litter, which is the main source of nutrient inputs and organic carbon of forest soils (Meentemeyer et al., 1982), decreased by our 600 + plantation treatment, similarly to previously reported negative effects of thinning on the amount of litter (Jiménez and Navarro, 2016). There is, therefore, a research need for more long-term assessments on the net carbon balance of tree thinning in dense forest stands to evaluate if increased growth of the remaining woody species compensates for the lost tree biomass and the reduced litter production (see modeling example in Dwyer et al., 2010 as a potential way forward).

5. Conclusions

In this work, we observed that the combination of thinning and plantation of resprouting species within overstocked pine stands may facilitate the establishment of more functional and fire-resistant forests in the long term (10 years). Our study shows that our treatments may enhance the supply of ecosystem services, such as biodiversity conservation, food production, and disturbance regulation without compromising carbon sequestration. Our study also highlights the necessity of considering the different functions that ecosystems may provide as they respond differently to treatments. This simultaneous consideration may highlight treatment effects less noticeable when studying functions individually (as we observed with the plantation of resprouter species). We conclude that establishing mixed forests with heterogeneous structures via tree thinning and plantation of resprouter species enhances forest functionality while reducing fire risk. These findings are fundamental to manage post-fire dense pine regeneration in Mediterranean areas.

CRediT authorship contribution statement

Aymen Moghli: Conceptualization, Investigation, Methodology, Formal analysis, Data curation, Writing – original draft, Visualization. **Victor M. Santana:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision, Funding acquisition, Resources. **Santiago Soliveres:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Validation. **M. Jaime Baeza:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition, Resources, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150715.

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