Universitat d'Alacant
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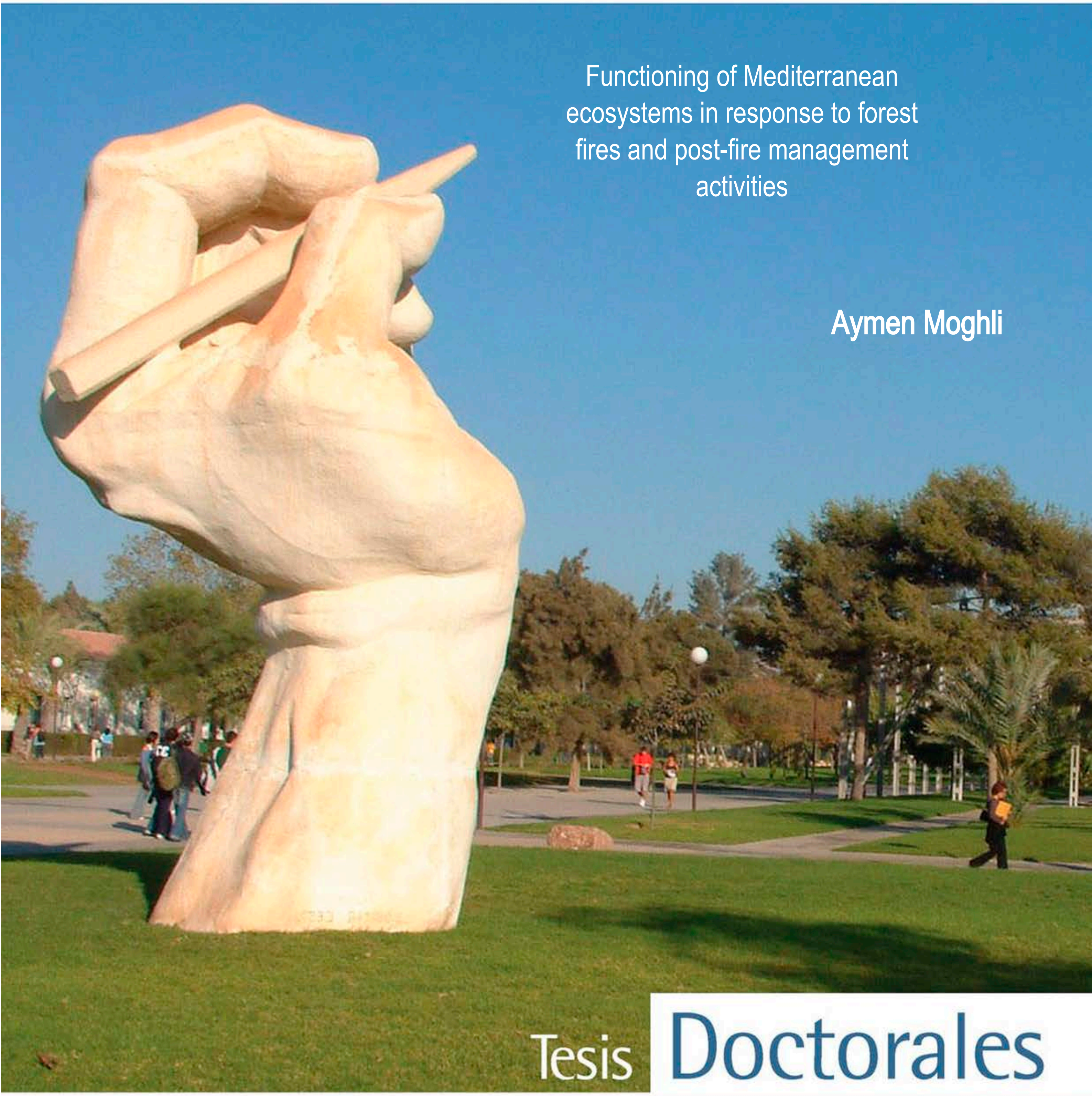
Functioning of Mediterranean ecosystems in response to forest fires and post-fire management activities

Aymen Moghli



Tesis Doctorales
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Functioning of Mediterranean ecosystems in response to forest fires and post-fire management activities

Aymen Moghli

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Departamento de Ecología

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El funcionamiento de los ecosistemas mediterráneos en respuesta a los incendios forestales y a las actividades de gestión post- incendio

Aymen Moghli

Tesis presentada para aspirar al grado de

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Fonctionnement des écosystèmes méditerranéens en réponse aux incendies de forêt et aux activités d'aménagement post-incendie

Aymen Moghli

Thèse présentée pour aspirer au degré de

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Hacen constar:

Que el trabajo descrito en la presente memoria "**Functioning of Mediterranean ecosystems in response to forest fires and post-fire management activities"** ha sido realizado bajo su dirección por **AYMEN MOGHLI** para optar al grado de Doctor por la Universidad de Alicante, y reúne todos los requisitos necesarios para su aprobación como Tesis Doctoral.

Alicante junio de 2022.

Dr. MANUEL JAIME BAEZA **Dr. VICTOR MANUEL SANTANA**

El doctorando

AYMEN MOGHLI

A mi Madre, mi Padre

A Aya, Chaima y Karima

قَالَ رَسُولُ اللهِ صَلَّى اللهُ عَلَيْهِ وَسَلَّمَ
(إِنْ قَامَتِ السَّاعَةُ وَفِي يَدِ أَحَدِكُمْ فَسِيلَةٌ، فَإِنِ اسْتَطَاعَ أَنْ لَا تَقُومَ حَتَّى يَغْرِسَهَا فَلْيَغْرِسْهَا)

“Si la Hora Final llega mientras tienes una plántula en tus manos y es posible plantarla antes de que llegue la Hora, debes plantarla".

El profeta del Islam

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……A todos y todas muchas gracias……

Contents

Abstract

In Valencia region (SE Spain), many post-fire communities are dominated by non-resprouting (seeder) species, because of the long history of land exploitation and subsequent abandonment during the last half of 20th century. These communities accumulate fine dry biomass and, therefore, can burn again easily. In fact, Mediterranean forests are suffering from an increase in wildfire frequency since the early 1970s. Wildfires shape the composition and functioning of Mediterranean ecosystems, but we do not know how these ecosystems respond to both the higher fire recurrence and shorter recovery times expected for future climatic scenarios. In this sense, Aleppo pine forest (*Pinus halepensis*) is one of the most fire affected vegetation of this type in the Mediterranean Basin and to know how it respond to fire is fundamental to design management plans. After fire, regeneration of this forest can be highly variable, and it can go from extremely dense tree stands (overstocked pine) to treeless shrublands dominated by seeder species. All these regenerated stands are fire prone with limited ability to deliver multiple ecosystem services. Although several management techniques are applied to redirect these post-fire ecosystems towards less vulnerable and more functional communities, we do not know yet which amongst them could serve to foster more diverse and multifunctional landscapes. Therefore, the general objective of this thesis is to investigate the functioning of these Mediterranean ecosystems as consequence of shifts in fire regime and forest management application, using different techniques, in different post-fire regenerated ecosystems (overstocked pine forests and dense shrublands). To do so, we calculate, within Mediterranean *Pinus halepensis* forests affected by wildfires, the supply of multiple ecosystem services (biodiversity conservation, carbon sequestration, disturbance regulation, food production, supporting services, and multifunctionality), through up to 25 aboveground and belowground attributes. Our main findings are (1) High fire recurrence and time since last fire interacted to determine ecosystem services but did not affect their synergies and trade-offs between them. Their combined effects reduced carbon sequestration and multifunctionality. Disturbance regulation diminished drastically with the first fire, with no effect of further fires. However, their effects dampened, and even became positive, for biodiversity conservation and food production services if provided enough time to recover. (2) Thinning in overstocked pine stands enhances ecosystem attributes associated with biodiversity conservation without compromising the provision of carbon sequestration. After 10 years, two levels of thinning, (600 and 1200 trees·ha-1), similarly affected ecosystem attributes, which suggest that 1200 trees·ha-1 suffice to enhance individual ecosystem attributes. (3)

Clearing within dense shrubland dominated by seeder species enhances ecosystem attributes associated with biodiversity conservation without compromising the capacity of ecosystem to sequester carbon. (4) Plantation of resprouting species combined with thinning and clearing, in overstocked pine forests and dense shrublands respectively, can enhance the provision of ecosystem services of disturbance regulation, food production and ecosystem multifunctionality. (5) Prescribed burning reduces the amount of dead fuel, increases biodiversity conservation, and improves food production. However, these effects become negative, in addition to the decline in disturbance regulation and multifunctionality, if prescribed burning is applied frequently. (6) Combining different management activities can enhance the supply of multiple ecosystem services simultaneously by reducing the trade-offs in between them and therefore, establish multifunctional Mediterranean landscapes.

Síntesis

En la Comunitat Valenciana (SE de España), muchas comunidades post-incendio están dominadas por especies no rebrotadoras (germinadoras), debido a la larga historia de explotación del suelo y posterior abandono durante la última mitad del siglo XX. Estas comunidades acumulan mucha biomasa fina y seca y, por tanto, se pueden volver a quemar fácilmente. De hecho, los bosques mediterráneos están sufriendo un aumento de la frecuencia de los incendios forestales desde principios de los años 70. Los incendios forestales determinan la composición y el funcionamiento de los ecosistemas mediterráneos, pero no sabemos cómo responden estos ecosistemas tanto a la mayor recurrencia de los incendios como a los menores tiempos de recuperación previstos para los futuros escenarios climáticos. En este sentido, el bosque de pino carrasco (*Pinus halepensis*) es uno de los tipos de vegetación más afectado por el fuego en la Cuenca Mediterránea y conocer cómo responde es fundamental para diseñar planes de gestión. Después del fuego regeneración de este tipo de bosque puede ser altamente variable y puede ir desde masas arbóreas extremadamente densas (pinares hiperdensos) hasta matorrales desarbolados dominados por especies germinadoras. Todos estos ecosistemas regenerados son propensos a los incendios y con una capacidad limitada para proveer servicios ecosistémicos de forma múltiple y simultánea. Aunque actualmente se aplican varias técnicas de gestión para reorientar estos ecosistemas post-incendio hacia comunidades menos vulnerables y más funcionales, aún no sabemos cuáles de ellas podrían servir para fomentar paisajes más diversos y multifuncionales. Por lo tanto, el objetivo general de esta tesis es investigar el funcionamiento de ecosistemas mediterráneos respecto a cambios en el régimen de incendios y a la aplicación de la gestión forestal, utilizando diferentes técnicas en diferentes ecosistemas regenerados tras el incendio (pinares hiperdensos y matorrales densos). Para ello, calculamos, dentro de bosques mediterráneos de *Pinus halepensis* afectados por incendios forestales, la provisión de múltiples servicios ecosistémicos (conservación de la biodiversidad, fijación de carbono, regulación de las perturbaciones, producción de alimentos, servicios de soporte y multifuncionalidad), a través de 25 atributos aéreos y del suelo. Nuestros principales resultados son: (1) La elevada recurrencia de los incendios y el tiempo transcurrido desde el último incendio interactuaron para determinar los servicios del ecosistema, pero no afectaron a las sinergias y compromisos entre ellos. Sus efectos combinados redujeron la fijación de carbono y la multifuncionalidad. La regulación de las perturbaciones disminuyó drásticamente con el primer incendio, sin que los incendios posteriores tuvieran ningún efecto. Sin embargo, este efecto se redujo, e incluso llegó a ser positivo, para los servicios de conservación de la biodiversidad y de producción de alimentos siempre que se dispusiera de tiempo suficiente (> 20 años) para su recuperación. (2) El aclareo en masas hiperdensas de pino mejora los atributos del ecosistema asociados a la conservación de la biodiversidad, sin comprometer la provisión de la fijación de carbono. Después de 10 años, los dos niveles de aclareo (600 y 1200 árboles·ha-1) afectaron de forma similar los atributos del ecosistema lo que sugiere que un aclareo de árboles·ha-1 es suficiente para mejorar los atributos individuales del ecosistema. (3) El desbroce en matorral denso dominado por especies germinadoras mejora los atributos del ecosistema asociados a la biodiversidad sin comprometer la capacidad del ecosistema de fijar el carbono. (4) La plantación de especies rebrotadoras combinada con el aclareo y el desbroce, en masas hiperdensas de pino y matorral denso respectivamente, puede mejorar la provisión de los servicios de la regulación de perturbación, producción de alimentos y la multifuncionalidad. (5) La quema prescrita reduce la cantidad de combustible muerto, aumenta la conservación de la biodiversidad y mejora la producción de alimentos. Sin embargo, estos efectos se vuelven negativos además de la disminución de la regulación de las perturbaciones y la multifuncionalidad si la quema prescrita se aplica con frecuencia. (6) La combinación de diferentes actividades de gestión puede mejorar el suministro de múltiples servicios ecosistémicos simultáneamente, reduciendo las compensaciones entre ellos y, por lo tanto, establecer paisajes mediterráneos multifuncionales.

CHAPTER I

General introduction

Forest fires in Mediterranean ecosystems

The Mediterranean Basin has suffered for millennia a high anthropization of its natural systems. Since the Neolithic Era, approximately 10,000 years ago, agriculture, livestock farming, and exploitation of other natural resources have been constant activities throughout its territory (Blondel, 2006; Blondel & Aronson, 1999). However, the intense industrialization of this region, in the European side , since the last century has led to an extensive abandonment of rural activity and, consequently, to a generalized abandonment of vast agricultural land (Le Houérou, 1993). This has led to the establishment of large extensions of landscapes in early stages of succession, and dominated by fast-growing species with high capacity to colonize open spaces (Sluiter & De Jong, 2007; Weissteiner et al., 2011).

In addition to the human factor, fire is considered one of the most important driving forces in the Mediterranean landscape. It has been considered that the Mediterranean ecosystem has a high regenerating capacity, that is, the capacity of recovering its composition and structure over time after disturbances (Trabaud et al., 1985). The recovery capacity is determined by the intrinsic survival strategies of the different species that allow their persistence after the fire. Resprouting species for example can survive after fire due to their belowground structure (e.g., tuber, rhizomes) that protects them from high temperatures and allow them to resprout after fire. Another group of species is unable to resprout after fire (i.e., obligate seeders), and their regeneration will depend on their seed bank (Pausas, Bradstock, et al., 2004). Also, there are species that present both strategies (facultative species; Pausas & Keeley, 2014), and other group of species enable to regenerate after fire, which their persistence would be conditioned by the colonization from adjacent unburned areas. In case of the obligate seeder species, to ensure their regeneration after disturbances they produce and store numerous seeds in soil or canopy seed banks. The recruitment of new individuals is determined by the conditions generated during and after the fire; for example, by breaking seed dormancy, in the case of the soil seed bank, or by opening the cones of species with serotinous fruits (mainly Pinus species) (Bond & Van Wilgen, 1996). These “seeders species”, are characterized by their high ability to colonize open spaces, their fast growth, and the high accumulation of large proportions of fine and dead fuel in their structure (Baeza and Santana 2015). Therefore, positive feedback loops could occur between fire and vegetation, placing the ecosystem in arrested stages of succession (Grigulis et al., 2005). This is of particular concern given that in recent decades there has been an increase in both the number of fires and the burned area, which will be further increased by future conditions of aridity and high temperatures predicted under climate change scenarios (Kovats et al., 2014). Indeed, recent studies reveal that the Mediterranean Basin is largely threatened by extreme wildfires events (EWE) and represents over 85% of the most vulnerable areas to fire in Europe (San-Miguel-Ayanz et al., 2017). These EWE overpass the suppression capacity of extinction means and they can burn high amounts of land in a short space of time (e.g., from hours to days) (Duane et al., 2021). Therefore, despite the number of fires can be stabilized in next decades, or even reduced in some areas, the more likely occurrence of EWE will still result in vast burned areas every year. All these facts make wildfires one of the priority targets in current and future forest research in the Mediterranean Basin.

Effect of fire regime shifts in Mediterranean ecosystems

Although wildfires are a natural disturbance in many forests worldwide, changes in the fire regime in terms of higher fire recurrence (the number of fires that occur in a specific site over a certain period of time) has occurred in the last decades (Kovats et al., 2014), and it is expected to increase further under future climatic scenarios (Enright et al., 2015; Lindner et al., 2010). Around the early 1970s, the burned area in the Mediterranean Basin has increased due to a higher fire frequency, which is twice as high as the historically observed (Pausas and Fernández-Muñoz 2012). Mediterranean ecosystems are considered resilient yet, fire regime shifts may alter this capacity by increasing regeneration failures. High fire recurrence with short fire intervals can reduce the regeneration capacity and may lead to local extinction either by eliminating the persistence structure or reducing species' ability to replenish their seed banks (Santana et al., 2014). In addition, shorter fire intervals may interact with lower post-fire regeneration capacity induced by climate change with drier conditions, leading to a syndrome termed "interval squeeze" (Enright et al., 2015). This can result in a simplification of the vegetation structure and changes from forest to shrublands (Karavani et al., 2018) .These changes may also affect ecosystem functions and services related to aboveground attributes and, thus, further effort in assess them should be put into it. For example, these structural changes can result in a reduction in habitat provision for birds and mammals. The absence of trees reduces seed dispersal by birds or mammals and therefore delays colonization of woody resprouting species (Pausas et al., 2006). These species are often related to ecosystem resilience as they reduce the response time after disturbance and decrease the probabilities of regeneration failure (Vallejo et al., 2006). Also, stand structural and compositional shifts from forest to shrublands observed within frequently burned ecosystems could reduce of carbon sequestration capability (Kashian et al., 2006; Pellegrini et al., 2020). Contrarily, the dominance of leguminous shrubs often seen after fires could enhance soil fertility, and more open canopies could favor forage production and understory diversity (Certini, 2005; Pausas & Keeley, 2019).

In addition to changes in vegetation attributes, fires also can affect soil nutrients which are crucial for the post-fire recovery of soil biota and vegetation (Duguy et al., 2007). Frequent fires may progressively produce a long-lasting impoverishment of soil fertility through erosion and repeated heating (Knicker, 2007; Mayor et al., 2016). Conversely, fire may enhance soil carbon and nutrients´ concentration by promoting the establishment of more productive plant species, as well as by ash inputs into soils (Boerner et al., 2009). Critically, however, studies that document changes in soils affected by more than one fire offer limited insight into long-term changes (Pereira et al., 2018). The latter hinders our ability to predict recovery time for these properties and to predict ecosystem service supply under different disturbance scenarios.

Post-fire forest management in Mediterranean ecosystems

Aleppo pine forests are among the main components of Mediterranean Basin vegetation affected by wildfires. *Pinus halepensis*, an autochthonous species from the Mediterranean Basin (Quézel, 2000), 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 & Cortina, 2004). After fire, regeneration may vary according to several factors related to the pre-fire site conditions (e.g., forest structure and composition, climatic conditions, soil depth, and bedrock type) and fire severity (Rodríguez-Garcia et al. 2022) . The regeneration could range from hyperdense pine stands (overstocked) to a low-density regeneration of pine individuals which gives place to a dense shrub layer (Figure 1) dominated by obligate seeders (e.g. *Ulex parviflorus*, *Cistus albidus,* and *Salvia officinalis*). These vegetation types, at the two extremes of the regeneration of burned Aleppo pine forests, present high levels of species competition for resources such as light, water and nutrients, shelter less biodiversity and accumulate high proportions of dead fuel. Thus, these dense and homogeneous ecosystems may present a high vulnerability to further disturbance (fires, pest outbreaks) and less functioning within which integrated management activities should be implemented (Agee & Skinner, 2005; Baeza et al., 2006; Santana et al., 2018).

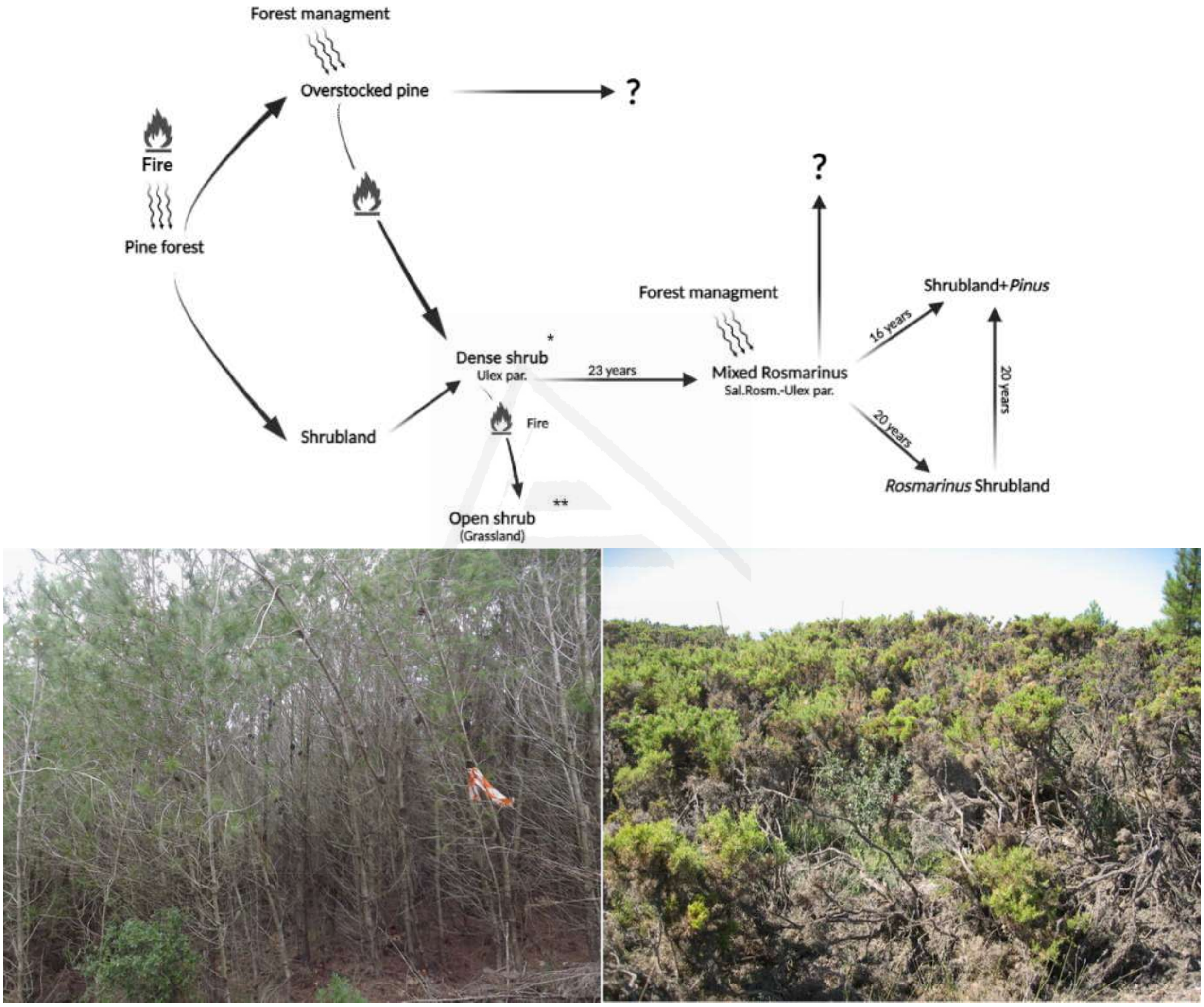

Figure 1: Conceptual model of vegetation dynamics after fire (based on Baeza et al., 2007) and treatment effects. Arrows are transition from one vegetation state to another. The arrows with a question mark indicate unknown transition. (*) means with pine regeneration and (**) means pine disappear. (Moghli et al., in preparation). The two photos represent the regenerated ecosystems after wildfire, overstocked pine forest (left, >75000 trees$\cdot$ha^{-1}) and dense shrubland dominated by seeder species (right).

In the Mediterranean Basin, one of the targets in post-fire management focuses on restoring the mature communities dominated by resprouting species to the detriment of highly flammable overstocked stands or denseshrubland (Moreira et al., 2011; Vallejo et al., 2006). For this purpose, the integrated implementation of several restoration activities such as thinning, clearing, and the introduction of resprouting species is suggested (Figure 2). These management activities are applied in order to reduce fuel loads and enhance tree growth. At the same time they look for enhancing habitat heterogeneity and establish mixed-forests which are often reported as more functional ecosystems (Pretzsch & Forrester, 2017). Indeed, the establishment of forest containing a higher degree of species-mixing promises the delivery of a wide range of ecosystem goods and services at higher level in comparison to monospecific forests (Gamfeldt et al., 2013). Prescribed fire is also another management activity commonly applied, as a more economical alternative to the mechanical clearing, in order to reduce fuel load and establish open spaces that enhances forage production (Fernandes et al., 2013; Santín et al., 2008). Several studies have assessed the effectiveness of post-fire restoration activities, yet they do so by focusing on single attributes instead of the overall functions or by assessing their effectiveness in the short term (Baeza et al., 2003; Carra et al., 2021; Lucas-Borja et al., 2021; Santana et al., 2018; Wic Baena et al., 2013). This may underestimate the effectiveness of restoration activities as they may affect ecosystem functioning in different ways. Thinning and clearing for example may reduce fuel load and fire hazards, but it may also decrease organic carbon by limiting the amount of litterfall and shifting the microclimatic conditions (Grady & Hart, 2006). Similarly, prescribed fires (Figure 4) may reduce fire risk and severity, but it may reduce soil fertility and increase runoff and erosion risk due to vegetation removal (Carra et al., 2021). Thus, addressing the effects of management strategies in the long term by integrating different ecosystem functions in standardized indices may permit a less biased perception of restoration success, and lead to a better forest management (Cruz-Alonso et al., 2019; Manning et al., 2018). This management is of high importance to maintain a vegetation mosaic that maximizes the supply of multiple ecosystem services simultaneously at the landscape level.

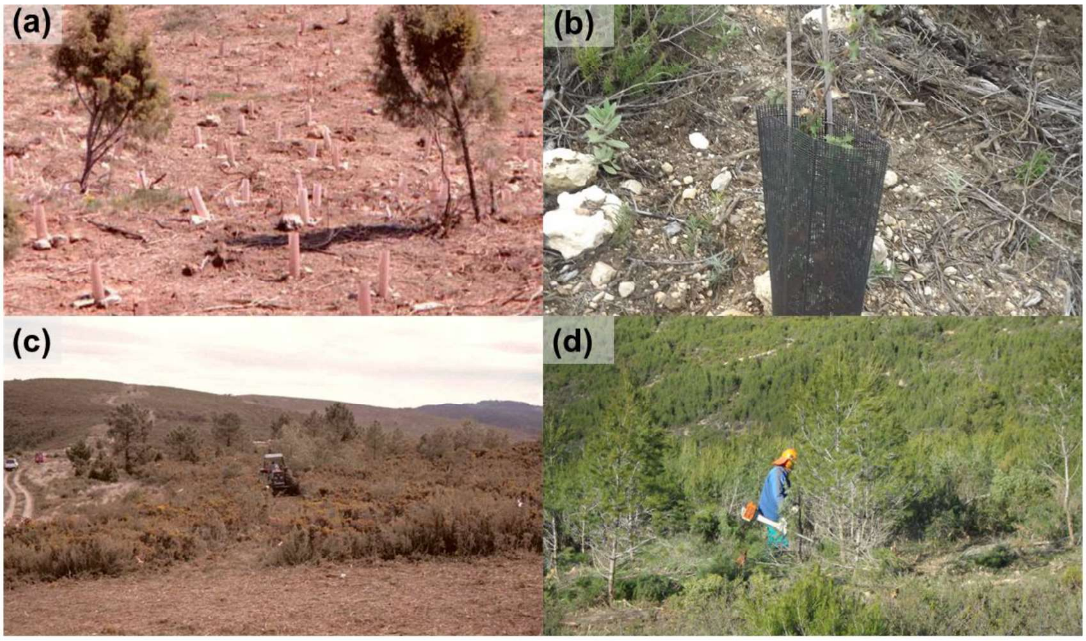

Figure 2. Mechanical treatments **a** and **c** plantation of resprouting species (*Q. ilex*, *Rhamnus alaternus* and *Pistacia lentiscus*) and clearing within dense shrublands **b** and **d** plantation of resprouting species (*Quercus faginea*) and thinning within overstocked pine stand.

The scaling aspect has been and still is one of the most important knowledge gaps about the sustainable management of Mediterranean forest (Scarascia-Mugnozza et al., 2000). Most of the studies that assess management activities are carried out at stand/management scale, contrarily to disturbances impacts which are considered at landscape scale (Nocentini et al., 2022). Managing ecosystem services across landscapes is a key challenge in forest management due to the multiple response of ecosystem functions and services (Raudsepp-Hearne et al., 2010). Thus, recent studies suggest that combining different management techniques at larger spatial scales could maximize multifunctionality at landscape level in which management and policy-makers often focus (Hölting, Jacobs, et al., 2019). This maximization of landscape-level multifunctionality could occur if different restoration techniques establish communities that supply a different set of ecosystem services (Felipe-Lucia et al., 2014; Raudsepp-Hearne et al., 2010). In this context, the 2010-2020 Mediterranean Forest Research Agenda highlighted the importance of predicting the effect of forest management on the provision of multiple goods and services, and the design of management models that take into a count the ecosystem functioning from stand to landscape level (Palahí et al., 2009).

Figure 4. Application of prescribed fires within dense shrubland.

Ecosystem services and multifunctionality

Ecosystem functioning studies have often focused on how individual functions are affected by their drivers. However, this approach has shown many limitations due to the contrasting and multiple effects of these drivers (e.g., forest fire). In recent years, there have been an upsurge of interest in 'ecosystem multifunctionality', a concept that has developed and increasingly studied in the largely separate fields of biodiversity and– ecosystem science. This ecosystem multifunctionality has become a common target in land management research and landscape-scale policy (Garland et al., 2021; Manning et al., 2018; Soliveres et al., 2016). To date, there has been no single common accepted definition of multifunctionality, nor any agreed ways of measuring it but it potentially refers to 'the capacity of an area to supply multiple ecosystem functions or services simultaneously at high levels' (Garland et al., 2021; Hölting, Beckmann, et al., 2019; Manning et al., 2018; Van Der Plas et al., 2016).

Multifunctionality can be estimated with indicators, functions and/or ecosystem services that an ecosystem may supply (Figure 5). In most biodiversity– ecosystem functioning studies the main methods for quantifying ecosystem multifunctionality are the 'averaging' (or sum) approach or the 'threshold' approach. The averaging approach consists in taking the average, or sum, of the standardized values of each function. However, the threshold approach consists in counting the number of functions that pass a given threshold, or a range of thresholds (Figure 6), usually expressed as a percentage of the highest observed level of functioning (Byrnes et al., 2014). Thus, quantifying and integrating different community-level functions in standardized indices is recommended to avoid a biased perception of management effectiveness (Cruz-Alonso et al., 2019; Manning et al., 2018). This information could lead to better forest management practices that effectively increase ecosystem health and functions.

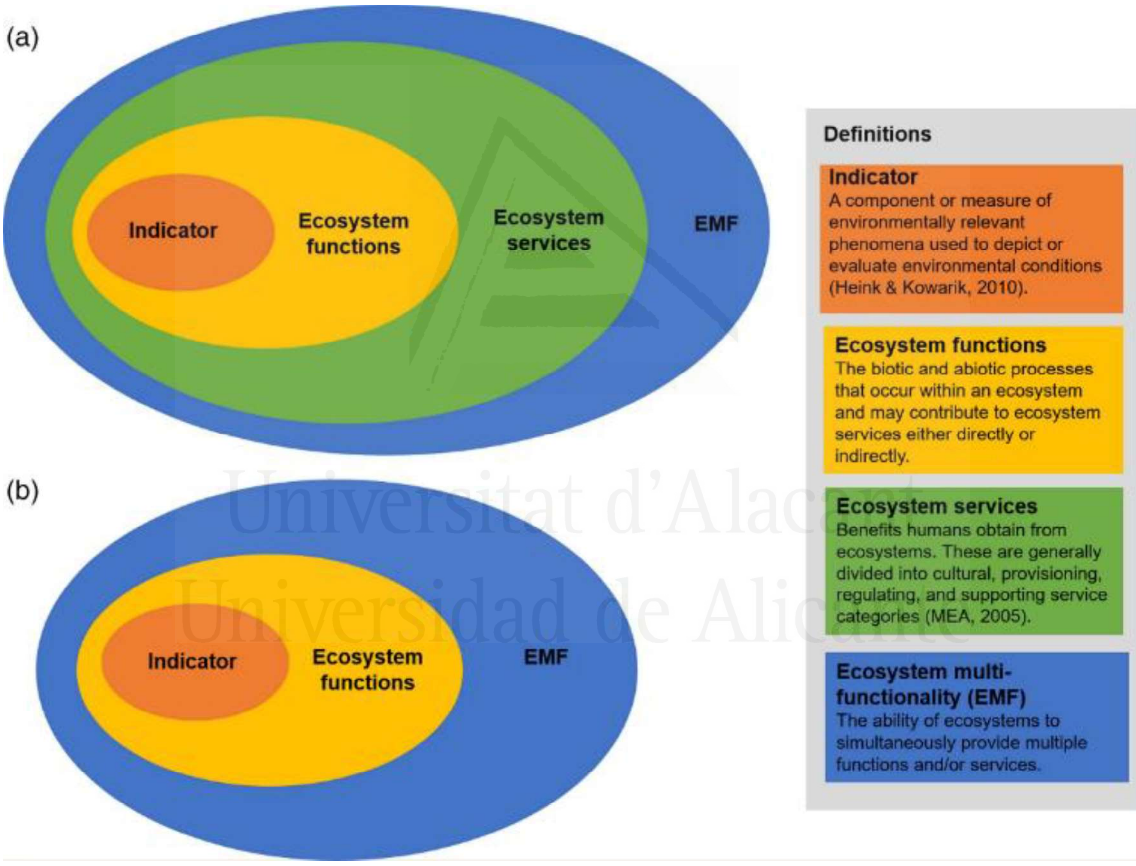

Figure 5: Conceptual diagram explaining that ecosystem multifunctionality (EMF) can be comprised of (a) ecosystem functions and services or (b) solely ecosystem functions, and that these functions can be measured either directly, or with the use of indicators (Garland et al., 2021).

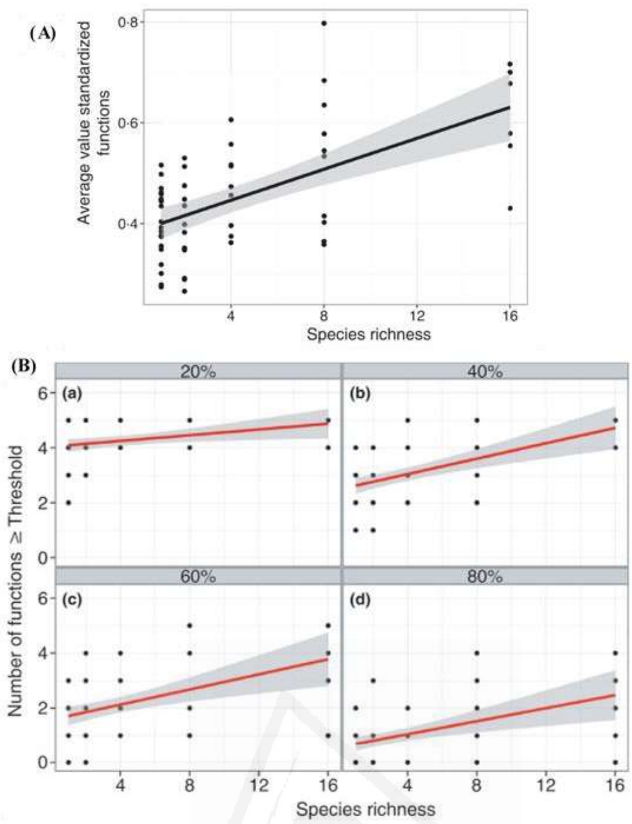

Figure 6: The relationship between planted species richness and multifunctionality, defined as (A) the average of the standardized value of functions (Slope estimate = 0,0133 ± 0,0028 SE, Diversity F1,22 = 22,554, P < 0,001, R2 = 0,36) and (B) number of functions reaching a threshold of some percentage of the maximum observed function. Panels show the relationship for four different thresholds (20%, 40%, 60%, and 80% of maximum) in plots in the German portion of the BIODEPTH experiment (Byrnes et al., 2014).

Studies about ecosystem services and post-fire management in Mediterranean Ecosystems

Studies considering the provision of multiple ecosystem services in response to wildfire and post-fire management activities in Mediterranean forests are still scarce. To identify research progress and knowledge gaps, we searched Scopus database for published documents as scientific articles that were explicitly related to fire or post-fire forest management with ecosystem services in Mediterranean ecosystems worldwide for the period 2010–2022. The literature survey was carried out in May 2022 using the following terms in the combined field of title, abstract, and key words: ("fire" AND "Mediterranean" AND "ecosystem service") OR ("forest management" AND "Mediterranean" AND "ecosystem service"). A total of 4675 publications on fire and forest management in Mediterranean ecosystem were published between 1943-2022. Of all these documents, 3178 (ca. 68%) were published between 2010- May 2022, 86.7% of which are scientific articles. Only ca. 4% (119 scientific articles) included the supply of at least one ecosystem service when studying fire and forest management in Mediterranean ecosystems. In addition, Spain is a pioneer region for fire and forest management studies, since 24% of all articles were released in Spanish Mediterranean ecosystems. These results suggest that, although there is an increasing interest in considering the supply of ecosystem services when assessing the effect of fire and forest management in Mediterranean ecosystems (Figure 7), more studies in this sense are still needed to fulfill the knowledge gaps.

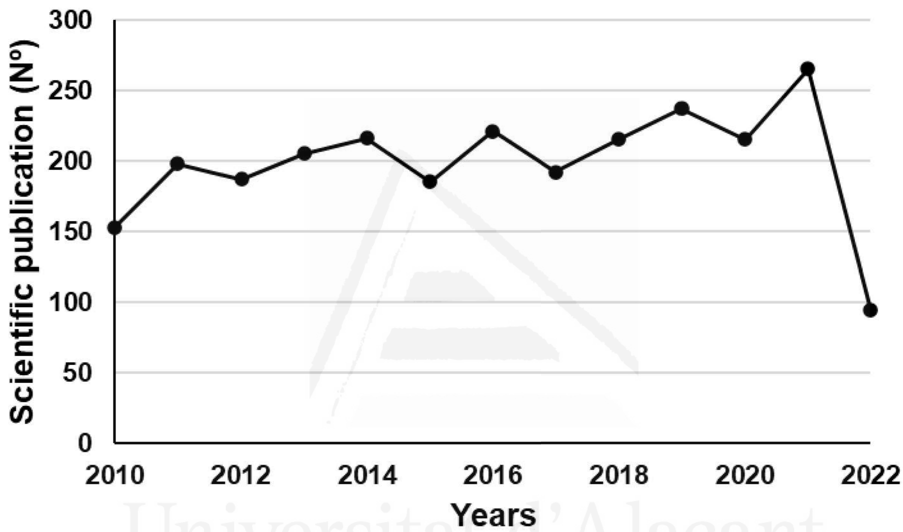

Figure 7. The evolution of the scientific published documents (2010-May 2022) about fire and forest management effects in Mediterranean ecosystems.

Main objectives and hypotheses of the doctoral thesis

This study was focused on Mediterranean *Pinus halepensis* forests affected by wildfires located in Valencian Community (SE Spain). The general objectives of this thesis is to investigate the functioning of this typical Mediterranean ecosystem depending on both (i) different regimes of fire recurrence, and (ii) different forest management activities over the most problematic post-fire regenerated ecosystems (i.e., overstocked pine forests and dense shrublands). Particularly, we calculate the supply of multiple ecosystem services (biodiversity conservation, carbon sequestration, disturbance regulation, food production, supporting services, and multifunctionality), through up to 25 aboveground and belowground attributes. In addition, these ecosystem services were integrated within a standardized index "Multifunctionality", that is, the capacity of the ecosystem to supply multiple ecosystem services at high level simultaneously. We hypothesized that (i) the supply of different ecosystem functions and services will vary according to the resulting vegetation, which in turn is determined by shifts in the fire regime, (ii) shifts in the fire regime will impinge in the synergies and trade-offs related to the provision of ecosystem services in these burned Mediterranean forests, (iii) management activities aiming to reduce vegetation density such as thinning and clearing, combined with the plantation of resprouting species will redirect the regenerated ecosystems towards less vulnerable and more functional communities, (iv) combining different forest management at landscapes scale can maximize the supply of multiple ecosystem services. Specifically, we tried to answer these hypotheses in the following chapters, where the specific questions and objectives are described below:

Chapter 2: ***Fire Recurrence and Time Since Last Fire Interact to Determine the Supply of Multiple Ecosystem Services by Mediterranean Forests.*** Concretely, we examine how interactions between fire recurrence (up to 4 fires) and time since last fire (TSLF; up to 35 years) influence ecosystem services. Here we provide a valuable contribution to the literature since studies about the interactions between aspects of the fire regime are still relatively rare. Furthermore, the ecosystem services are not independent from each other, as there may be synergies and trade-offs in their provision (Raudsepp-Hearne et al., 2010). Changes in these synergies and trade-offs in response to forest management are starting to be known (Felipe-Lucia et al., 2018), but we know little about how they respond to natural disturbances such as wildfires. In this sense, we tried to assess how fire recurrence, time since last fire, and their interactions affect synergies and trades-off in Mediterranean ecosystem services. Specifically, we asked the following questions: (i) how does fire recurrence affect the supply of ecosystem services and the overall ecosystem multi- functionality? (ii) does TSLF interact with fire recurrence to determine these ecosystem services? and (iii) do fire recurrence and TSLF affect synergies and trade-offs between ecosystem services?

Chapter 3: ***Thinning and plantation of resprouting species redirect overstocked pine stands towards more functional communities in the Mediterranean Basin.*** Through a field study, the long-term effects in main ecosystem services and functions (10 years) of two thinning levels (600 and 1200 tree·ha^{-1}), in combination with the plantation of *Quercus faginea* in overstocked regenerated pine forests were assessed. In such stands, thinning is implemented to reduce fuel load and increase tree growth (Manrique-Alba et al., 2020). In addition, planting of resprouting species is another restoration activity that aim to increase the diversity and resilience of ecosystems (Gavinet et al., 2016). However, our knowledge regarding their effectiveness is still incomplete since they are often implemented separately. Besides, most studies focus on individual ecosystem function and/or at short term, while several studies showed the importance of addressing multiple function that one ecosystem can simultaneously provide (Lefcheck et al., 2015). We hypothesized that the combination of thinning and plantation of resprouting species will (i) have positive effects on both above- and below-ground forests attributes, (ii) reduce fire risk and (iii) increase the supply of ecosystem services.

Chapter 4: ***Combining post-fire management strategies can maximize landscape multifunctionality in Mediterranean ecosystems.*** Through a field study, the long-term effect in main ecosystem services and functions of main management actions were assessed. These actions included plantation of resprouting species combined with thinning and clearing, as well as punctual and repeated prescribed burns. Management was applied in the most problematic post-fire vegetation types after a *Pinus halepensis* forest is burned (i.e., stands with high regeneration of pine and dense shrublands). *Pinus halepensis* forest is one of the main components of Mediterranean Basin ecosystems and high extension of this vegetation type is burned every year. After fire, the regeneration can be extremely dense pine forests or dense shrublands dominated by seeders (gorse). These vegetation types have low functionality, have a high fire risk because the accumulation of large proportions of fine dead biomass, as well as can remain stagnant for long periods of time. Therefore, it is fundamental to ascertain which management actions can be more effective in driving these systems to more desired states not only at stand scale but also at landscape scale. The main questions of this chapter were which management strategies, applied within overstocked pine forests and dense shrubland, allow the best recovery of ecosystem functions regarding the unburned (reference) ecosystem levels, (iii) how species compositional shifts regulate the provision of ecosystem services and multifunctionality and (iii) how can we manage these different ecosystems to obtain functional landscapes?

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CHAPTER II

“Fire recurrence and time since last fire interact to determine the supply of multiple ecosystem services by Mediterranean forests”

Ecosystems
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ECOSYSTEMS

Fire Recurrence and Time Since Last Fire Interact to Determine the Supply of Multiple Ecosystem Services by Mediterranean Forests

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Abstract

Wildfires shape the composition and functioning of Mediterranean ecosystems, but we do not know how these ecosystems respond to both the higher fire recurrence and shorter recovery times expected for future climatic scenarios. We sampled 29 plots with different fire recurrences (from 0 to 4 fires over the past decades) and time since the last fire (up to 35 years; hereafter TSLF) in Southeast Spain, to assess the effect of fire recurrence and TSLF on 25 ecosystem attributes, five related ecosystem services (biodiversity conservation, carbon sequestration, disturbance regulation, food production, and supporting services), plus the synergies and trade-offs between them. High fire recurrence (number of fires) and TSLF interacted to determine ecosystem services but did not affect the synergies and trade-offs between them. Fire recurrence reduced many ecosystem functions and ecosystem multifunctionality. However, this effect dampened, and even became positive, for biodiversity conservation and food production services provided enough (> 20 years) time to recover. The combined effects of fire recurrence and TSLF, however, reduced carbon sequestration and had no overall effects on supporting services. Disturbance regulation, in turn, diminished drastically with the first fire, with no effect of further fires or their interaction with TSLF. Our results show which ecosystem services will suffer more from an increase in fire recurrence, and where restoration and management efforts should focus to maximize the provision of those services more demanded by stakeholders.

Key words: Biodiversity; Carbon sequestration; Ecosystem services; Ecosystem multifunctionality; Disturbance regulation; Synergies; Trade-offs.

Highlights

- Fire recurrence reduced many ecosystem services and ecosystem multifunctionality
- Long times since fire (TSLF) may buffer ecosystem services from fire recurrence
- Ecosystem services' synergies and trade-offs are consistent to different fire regimes

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Resumen

Los incendios forestales determinan la composición y el funcionamiento de los ecosistemas mediterráneos, pero no se conoce cómo estos ecosistemas responden tanto a una mayor recurrencia de incendios como a menores tiempos de recuperación que se espera escenarios climáticos futuros. Se han muestreado 29 parcelas con diferente recurrencia de incendios (de 0 a 4 incendios en la última década) y tiempo desde el último incendio (hasta 35 años; en adelante TSLF) en el sureste de España Se intenta evaluar el efecto de la recurrencia de incendios y el TSLF en 25 atributos de los ecosistemas, cinco servicios ecosistémicos relacionados (conservación de la biodiversidad, fijación de carbono, regulación de perturbación, producción de alimentos, servicios de mantenimiento), además de las sinergias y compromisos entre ellos. La recurrencia de incendios redujo muchas funciones del ecosistema y la multifuncionalidad. Sin embargo, este efecto se atenuó e incluso llegó a ser positivo para los servicios de conservación de la biodiversidad y de producción de alimentos siempre que se dispusiera de tiempo suficiente (>20años) de recuperación. No obstante, los efectos combinados de la recurrencia y del TSLF redujeron la fijación de carbono y no tuvieron efectos globales sobre los servicios de soporte. El servicio de regulación de las perturbaciones, por su parte, disminuyó drásticamente con el primer incendio sin que incendios posteriores o su interacción con el TSLF tuvieran efecto. Nuestros resultados muestran qué servicios ecosistémicos se verán perjudicados por un aumento de la recurrencia de incendios, y donde deberían centrarse los esfuerzos de restauración y gestión para maximizar la provisión de aquellos servicios más demandados.

Palabras claves: biodiversidad; fijación de carbono; servicios ecosistémicos; multifuncionalidad ecosistémica; regulación de las perturbaciones; sinergias; compromisos.

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CHAPTER III

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

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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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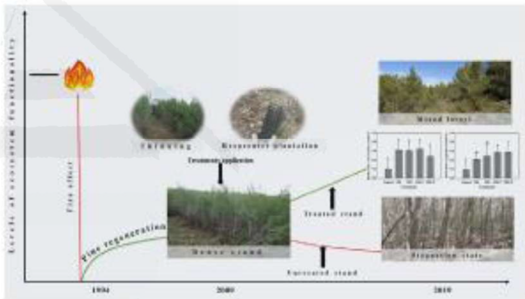
HIGHLIGHTS

- 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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Resumen

La regeneración post-incendio en los bosques de Pinus halepensis, uno de los tipos de vegetación más abundantes en la cuenca mediterránea, suele generar rodales hiperdensos y vulnerables. Acumulan una alta carga de combustible, aumentando el riesgo de nuevos incendios, y presentan altos niveles de vulnerabilidad debido a su reducida producción de semillas. Además, estas masas densas reducen sustancialmente la disponibilidad de luz y nutrientes, lo que puede dificultar el reclutamiento de otras especies, generando a menudo masas monoespecíficas y homogéneas, que potencialmente proporcionan menos servicios ecosistémicos que los bosques mixtos con estructuras más heterogéneas. En estas masas densas de pinos, la gestión es prioritaria para reducir el riesgo de incendios y promover su funcionalidad. En las masas hiperdensas de pino (>75.000 árboles ha-1), evaluamos los efectos a largo plazo (10 años) de dos niveles de aclareo (600 y 1200 árboles ha-1), en combinación con la plantación de Quercus faginea (una especie rebrotadora típica de las etapas sucesionales avanzadas en nuestra área de estudio) sobre 28 atributos del ecosistema aéreos y del suelo, incluyendo el riesgo de incendio. Después de diez años, el aclareo y la plantación interactuaron para mejorar los atributos del ecosistema asociados con la regulación de las perturbaciones y la conservación de la biodiversidad (hasta un 200%) y la producción de alimentos (hasta un 90%), mientras que no se obtuvieron efectos sobre los atributos relacionados con la fijacion de carbono y los servicios de mantenimiento. Estos efectos se debieron principalmente a los atributos sobre aéreos, ya que respondieron más fuertemente a nuestros tratamientos que los del suelo. Nuestros resultados son relevantes para la restauración de ecosistemas degradados mediterráneos, y muestran que el aclareo de árboles en masas de pino hiperdensas, combinado con la plantación de especies rebrotadoras, puede no sólo reducir el riesgo de incendio y acelerar la sucesión post-incendio, sino también mejorar el suministro de múltiples servicios ecosistémicos a largo plazo.

Palabras claves: Masas densas de pino, funcionamiento ecosistémico, servicios ecosistémicos, control de combustible, bosque mixto de pino; actividades de restauración.

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Chapter IV

Combining post-fire management strategies can maximize landscape multifunctionality in Mediterranean ecosystems.

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Combining post-fire management strategies can maximize landscape multifunctionality in Mediterranean ecosystems. *(in preparation)*

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Resumen

1. Los bosques mediterráneos están sufriendo un aumento en la frecuencia y severidad de los incendios forestales, lo que a menudo genera masas arbóreas extremadamente densas o matorrales sin árboles dominados por especies germinadoras, ambos con una capacidad limitada para promover la biodiversidad y los servicios ecosistémicos. Aunque varias técnicas de gestión pueden orientar los ecosistemas post-incendio hacia comunidades menos vulnerables y más funcionales, aún no sabemos cuáles de ellas podrían servir para fomentar paisajes más diversos y multifuncionales.
2. Evaluamos, a escala de rodal y de paisaje, cómo diferentes combinaciones de gestión regulan las respuestas de múltiples propiedades de los ecosistemas (vinculadas a la conservación de la biodiversidad, la fijación de carbono, la producción de alimentos, la regulación de las perturbaciones y los servicios de soporte) en dos ecosistemas dominantes después de incendios en bosques de *Pinus halepensis* (bosques de pinos hiperdensos y matorrales densos). Consideramos la

plantación de especies rebrotadoras en combinación con el aclareo de árboles (pinares hiperdensos), el desbroce (matorral denso), y las quemas prescritas (matorrales densos), comparando las consecuencias de estas combinaciones de gestión con los ecosistemas no gestionados (control) y no quemados (referencia). Esta evaluación se realizó a medio-largo plazo hasta 30 años desde la aplicación de los tratamientos. También creamos y analizamos paisajes artificiales para encontrar qué combinaciones de ecosistemas y tipos de gestión producen los niveles más altos de multifuncionalidad del paisaje (altos niveles de múltiples funciones simultáneamente).

3. La reducción de la densidad de la vegetación a escala de rodal mediante el aclareo y el desbroce, combinada con la plantación de especies rebrotadoras, mejora los atributos del ecosistema asociados a la conservación de la biodiversidad, la captura de carbono, la regulación de las perturbaciones y la multifuncionalidad. Así, en combinación con la quema prescrita, se establecerían paisajes más funcionales que maximizarían la provisión de servicios ecosistémicos.
4. **Síntesis**: Nuestros resultados revelan el potencial de los aclareos y desbroces, combinados con la plantación de especies rebrotadoras, para mejorar el suministro de múltiples servicios ecosistémicos a largo plazo y reducir el riesgo de incendios. Nuestro estudio proporciona una nueva visión a los gestores que ayuda a restaurar los ecosistemas mediterráneos degradados hacia paisajes menos vulnerables y más funcionales.

Palabras claves: desbroce, matorral denso, servicios ecosistémicos, multifuncionalidad, pino hiperdenso, quemas prescritas, especies rebrotadoras, aclareo.

Abstract

1. Mediterranean forests are suffering an increase in wildfire frequency and severity, which often generates either extremely dense tree stands or treeless shrublands dominated by seeder species, both with a limited ability to promote biodiversity and ecosystem services. While several management techniques can redirect post-fire ecosystems toward less vulnerable and more functional communities, we do not know yet which amongst them could serve to foster more diverse and multifunctional landscapes.
2. We assess at stand and landscape scales, how different management combinations regulate multiple ecosystem properties (linked to biodiversity conservation, carbon sequestration, food production, disturbance regulation and supporting services) in two dominant post-fire ecosystems after *Pinus halepensis* forests are burned (overstocked pine forests and dense shrublands). We considered plantation of resprouting species in combination with tree thinning (overstocked pine forests), clearing (dense shrublands) and prescribed burns (dense shrublands), comparing the consequences of these management combinations to unmanaged (control) and unburned (reference) ecosystems. This assessment was performed in the medium-long term, up to 30 years since treatments´ application. We also created and analyzed artificial landscapes to find which combinations of ecosystem and management types produce the highest levels of landscape multifunctionality (high levels of multiple functions simultaneously).
3. Reducing vegetation density at stand scale by thinning and clearing combined with plantation of resprouting species enhance ecosystem attributes associated with biodiversity conservation, carbon sequestration, disturbance regulation and multifunctionality. Thus, combined with prescribed burning would establish more functional landscapes that maximize the provision of ecosystem services.
4. ***Synthesis:*** Our results unfold the potential of tree thinning and clearing both combined with the plantation of resprouting species in enhancing the supply of multiple ecosystem services in the long run while reducing fire risks. Our study provides new insight to land-managers that help restoring degraded Mediterranean ecosystem towards less vulnerable and more functional landscapes.

Keywords: clearing, dense shrubland, ecosystem services, multifunctionality, overstocked pine, prescribed burns, resprouting species, thinning.

1. Introduction

In the Mediterranean region the extensive abandonment of agricultural lands in the 20th century has created large landscapes dominated by early-successional species characterized by their high colonization ability and fast growth (Baeza & Santana, 2015; Weissteiner et al., 2011). Presently, *Pinus halepensis* is one of the most abundant tree species due to its ability to colonize abandoned crop fields and its past use in massive reforestation plans (Le Houerou, 2000; Maestre & Cortina, 2004). When pine forest is affected by fire, the regenerated ecosystem varies greatly, from a massive regeneration represented by overstocked pine forests (>75,000 trees·ha^{-1}) to a low pine regeneration accompanied by a dense shrub layer dominated by seeders (Baeza et al., 2007; Moghli et al., 2022). These post-fire ecosystems are characterized by the accumulation of large proportions of dead fine biomass, which make them stands of high fire risk (Baeza et al., 2002; Marino et al., 2010). Thus, integrated restoration actions in these ecosystems are of high priority to establish functional landscapes are of high necessity.

According to the regenerated ecosystem and the objectives, a wide range of post-fire restoration activities may be carried out by managers to redirect these burned *P. halepensis* forests towards more functional ecosystems. These activities include thinning, clearing, plantation of resprouting species, and prescribed burns, and collectively focus on reducing fuel load and favoring mature communities dominated by resprouting species to the detriment of highly flammable seeding communities (Agee & Skinner, 2005; Moghli et al., 2022; Santana et al., 2018). Also, these restoration activities are applied in order to enhance tree growth and habitat heterogeneity, and establish mixed-forests often reported as more functional ecosystems (Pretzsch & Forrester, 2017). However, studies addressing the effectiveness of post-fire restoration activities have commonly focused on single attributes (Alday et al., 2015; Baeza & Roy, 2008; Juan-Ovejero et al., 2021) and/ or at short term (Lucas-Borja et al., 2021), rather than on the provision of multiple ecosystem services in the long run, which is the main aim to these restoration activities (but see Moghli et al., 2022). Different post-fire restoration activities may have contrasting effects depending on the ecosystem function of interest, which could lead to trade-offs in the supply of ecosystem services. For example, thinning and clearing may reduce fuel load and fire hazards, but it may also decrease organic carbon by limiting the amount of litterfall and shifting the microclimatic conditions (Grady & Hart, 2006). Similarly, prescribed burning may reduce fire risk and severity, but it may reduce soil fertility and increase runoff and erosion risk due to vegetation removal (Carra et al., 2021). Thus, addressing the effects of management strategies by integrating different ecosystem functions in standardized indices may permit a less biased perception of restoration success, and could lead to better forest management (Cruz-Alonso et al., 2019; Manning et al., 2018). This management is fundamental to maintain a vegetation mosaic that maximizes the supply of multiple ecosystem services simultaneously at the landscape level.

Precisely these potential trade-offs derived from the contrasting effects of different post-fire restoration techniques on different ecosystem services, suggests that the combination of different management techniques at larger spatial scales could maximize landscape multifunctionality where management and policy making often focus (Hölting et al., 2019). This maximization of landscape-level multifunctionality could occur if different restoration techniques render communities that supply a different set of ecosystem services (i.e., ecosystem service bundles; Felipe-Lucia et al., 2014; Felipe-Lucia & Comín, 2015; Raudsepp-Hearne et al., 2010)), or if each of those communities is dominated by different species "specialized" in the supply of a particular service (Van Der Plas, Manning, Allan, et al., 2016). Yet, the vast majority of empirical evidence regarding the effect of post-fire restoration practices often focus on individual functions at the stand scale, while those considered at the landscape level are very scarce (Nocentini et al., 2022). Indeed, the latter has been highlighted as a major research gap by the 2010-2020 Mediterranean Forest Research Agenda (Palahí et al., 2009). Developing tools and methods to assess the effects of forest management on multiple forest goods and services, and related resources in an integrated stand-to-landscape scale are still key challenges.

Here, we assess the long-term effects (up to 30 years) of different post-fire management activities within the most problematic ecosystems resulting from burned *P. halepensis* forests: tree thinning (600 trees· ha^{-1}) ± plantation of resprouting species within overstocked pine forests, and clearing ± plantation of resprouting species, single prescribed burn, and repeated prescribed burn (three times) within dense shrublands. We evaluate their effects on five ecosystem services (biodiversity conservation, carbon sequestration, disturbance regulation, food production and supporting services) summarizing 22 above and belowground attributes. We asked the following questions: (i) which management strategies allow the recovery of ecosystem attributes and functioning in overstocked pine forests and dense shrublands, (ii) how species compositional shifts regulate the provision of the ecosystem services and multifunctionality and (iii) which are the combinations of treatments that maximize landscape-level multifunctionality?

2. Material and methods

2.1. Study area

The study area is in the Valencian region, South-eastern Spain. It is a mountainous area with a mosaic dominated by *Pinus halepensis* forests accompanied by agricultural lands, abandoned croplands and shrublands (Baeza et al., 2007). This landscape is the result of centuries of human exploitation and wildfire incidence. Agricultural activity has led to the extirpation of mature vegetation dominated by broad-leaved resprouting species (e.g., Quercus ilex, *Q. coccifera,;* Sheffer, 2012) . The posterior abandonment of agricultural lands, exacerbated since the last half of the 20th century, has promoted the dominance of pine forests because its high natural colonization capacity (Sheffer, 2012; Weissteiner et al., 2011) . When pine forests are burned, frequently regenerate in a dense vegetation dominated by obligate seeders. Depending on the pine regeneration success, vegetation varies from a dense *Ulex parviflorus* gorse accompanied by some pine individuals to overstocked pine stands with densities ranging between 75,000 to 220,000 trees·ha^{-1} (Fig 1). Some other obligate seeders such as *Salvia rosmarinus* and *Cistus albidus* are also present along with isolated resprouting shrub individuals (e.g., *Quercus coccifera, Rhamnus alaternus, and Pistacia lentiscus*). Soils present similarities and mostly develop on dolomitic limestones and marls. Because active and abandoned agricultural lands are mainly developed in marls, soils in our study are mainly regosols developed from marls. Climate is Mediterranean with a mean annual temperature and rainfall of 13~17 ºC and 450~700 mm respectively. The three experimental designs we covered in this work aimed to evaluate the performance of contrasting post-fire restoration techniques in these two major post-fire communities: overstocked pine stands and pine shrublands. In the study region, dense pine stands regenerated from previous fires represent the third part of the burnt area and seeder-dominated shrublands represent more than the 11% of the total affected vegetation between 1991-2019 (Alloza et al., 2021).

2.2.Experimental design

2.2.1. *Clearing and plantation of resprouting species in dense shrub ecosystems*

Within the study area, we selected three sites affected by a wildfire in 1979 (Table S1). These sites regenerated in dense gorselands with sparse *P. halepensis* individuals. In 2003, twenty-four years after fire, three neighboring plots of ca.1000 m^2 were selected within each site, to experimentally set up three combinations of two post-fire restoration techniques (selective clearing ± plantation of resprouting species); such as: (i) Clearing, (ii) Clearing + Plantation of resprouting species and (iii) control (untreated hereafter "dense shrub") ($N = 9$; 3 treatment combinations × 3 sites). Clearing consisted in removing *U. parviflorus* individuals mechanically. Whenever possible, pine trees and resprouting shrubs were preserved. The plantation consisted in opening holes mechanically and planting 1-year-old seedlings of three native woody resprouting species typical of mature stages: Holm oak (*Q. ilex*), Italian buckthorn (*Rhamnus alaternus*) and Mastic tree (*Pistacia lentiscus*) following a 1:1:1 ratio and an interspersed distribution with a density of ca.4000 individuals·ha^{-1}. Two years after plantation, the seedling survival of *Q. ilex* and *R. alaternus* was above 83% and between 52-68% for *P. lentiscus* (Valdecantos et al., 2009). For further details about the experiment see (Santana et al., 2018).

2.2.2. Prescribed burns in dense shrub ecosystems

In addition to shrub clearing and plantation of resprouting species, prescribed burns are commonly applied as a more economical alternative to mechanical techniques to remove flammable shrubs. Also, prescribed burns may direct the ecosystem towards more open communities that promote forage production (Fernandes et al., 2013; Santín & Doerr, 2016). Within the study area we selected three sites affected by three different wildfires in 1984. In 1994, they regenerated in dense shrubs dominated by *Ulex parviflorus* and other obligate seeders such as *Salvia Rosmarinus, Cistus albidus* and *Thymus piperella* with an herbaceous stratum composed mainly by the grass *Brachypodium retusum*. There were a few small, isolated individuals of woody resprouting species like *Quercus coccifera* and *Juniperus oxycedrus.* From 1994 to 2016, subsequent controlled burns have been applied each ca. 10 years within the dense shrub. Therefore, we had two neighboring plots of 30×30m on each site with similar characteristics but different burning recurrences: (i) dense shrub (unburned), (ii) burned once in 1994 and (iii) burned three times in 1994, 2006 and 2016 (*N*=9; 3 fire treatments × 3 sites). These prescribed fires were experimental fires, applied in spring under moderate weather conditions (air temperature < 25ºC, air humidity>42%, wind speed <5km·h^{-1}), therefore they are may be considered as a good proxy for prescribed burning (for further information see Baeza et al., 2002; Santana et al., 2011).

2.2.3. *Thinning and plantation of Quercus faginea in overstocked pine ecosystems*

Within the study area, we selected three sites affected by a wildfire in 1994 which regenerated in overstocked pine stands. In 2009, we experimentally reduced tree density by thinning (600 trees·ha^{-1} vs unthinned control) and planted a resprouting species (*Quercus faginea*; 300 seedlings · ha^{-1} vs no plantation) with three 0.5 ha per treatment (*N* = 9; 2 treatment combinations + unmanaged plot × 3 sites). Firstly, we reduced pine density using a tractor furnished with a vertical-axle chain drive that chopped vegetation and left it on the soil as mulch. Due to their keystone role in these ecosystems, the few individuals of resprouting species present were left standing when possible. The survival of planted *Quercus faginea* was 37% after 10 years. See Moghli et al., (2022) for more details. Prescribed burns technique can be applied within pine stands but, at the best of our knowledge, is not applied in overstocked forests because the high density of trees makes difficult to control fire.

2.2.2. Unburned "reference" sites.

To compare the effect of our treatments within each ecosystem type with the unburned ecosystems (hereafter reference ecosystem), we selected, within our study area, three sites dominated by *Pinus halepensis* forests (Table S2) located near to our study plots that had not been burned at least for the past 70 years.

2.3. Field sampling and laboratory analysis

In Spring 2019, we measured in each plot 22 vegetation and soil attributes (hereafter above- and belowground attributes). These attributes are linked to biodiversity conservation, capacity to capture carbon (either on woody biomass or into the soil), disturbance regulation (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 (Table S3).

2.3.1. Aboveground attributes

In each plot, we assessed plant cover using the point intersect method (Greig-Smith, 1983) across parallel transects (five transects of 10m within clearing and prescribed burns plots and three transects of 30 m long within the thinned plots). We recorded each species' contact every 20 cm using a graduated metal rod of 3mm diameter. This was also used to calculate i) species richness, ii) estimation of the beekeeping potential using available literature about the honey production capacity of each species (Mateu, 2016; Sanchís et al., 1992), and iii) calculate habitat complexity as an index related to the provision of habitat for animals (e.g. birds, reptiles and mammals) using the cover of the different vegetation strata and litter (Val et al., 2018). We assessed the natural colonization of resprouting species by measuring their density and richness within 10·10m subplot. Within the same 10·10 m subplot, we measured tree biomass (mainly *P. halepensis* and *P. pinaster*) estimated from allometric equations using the basal stem diameter (Baeza & Santana, 2015). We measured the understory biomass in six 1·1m quadrats per treatment selected randomly, where all vegetation and litter were harvested. Then in the laboratory, we separated the clipped material into dead and living biomass, and woody and herbaceous biomass. The separated samples were later oven-dried at 80ºC for 48h and weighed.

2.3.2. Belowground attributes

At each plot, we collected five soil samples at two depths (0-5cm and 5-15cm) after removing the herbs, litter, and woody debris. Before the analyses, we air-dried and sieved (< 2 mm) the soil samples. We measured the soil organic C using the loss-on-ignition method (Davies, 1974) and the available phosphorus following Olsen et al (1954) procedure. We also measured the enzymatic activities β-glucosidase and acid phosphatase related to the cycling of C and P following the Tabatabai (1994) method. Also, we measured the total oxidized nitrogen (TON; nitrates + nitrites) and total ammonium following (ISO, 1998), and Potential nitrogen mineralization (PNM) following the methodology of Stanford and Smith (1972). We measured all soil attributes at the topsoil (0-5cm). In addition, we assessed the functional status of each study plot using the landscape functional analysis (LFA; Tongway and Hindley, 2004). This method allows the calculation of the stability, infiltration, and nutrient cycling indices.

2.3.3. Ecosystem services and multifunctionality

We organized the different vegetation and soil variables, after removing those highly correlated with others (r ≥0.7) and standardizing them to a common range (between 0 and 1), into five categories of ecosystem services (Table S3, Fig S1): i) biodiversity conservation, ii) carbon sequestration, iii) disturbance regulation, iv) food production and v) supporting. Then we calculated the overall multifunctionality, as the average of the five ecosystem services (see Maestre et al (2012) for a related approach).

2.3.4. Artificial landscapes simulation

To analyze the effect of treatments at different scales, ranging from plots to landscape scale, we created artificial landscapes from the observed plots (see Van Der Plas et al., 2016 for related approach). We created all the possible combination, without repetition, using 8 plots (one plot as the minimal sample size for a given treatment × 8 treatments). We had a total of 4686825 possible combinations. We also created two landscapes scenarios of untreated plots (mean of each treatment × 8) to compare them with the managed landscapes. Reference plots were not considered in the creation of the artificial landscapes, because we compare landscapes that already burned where different treatments are applied. Since different landscape configurations could render relatively similar multifunctionality levels, from all possible landscapes, we selected the best 100. The selection was performed according to the highest values of either ecosystem service or overall multifunctionality. We quantified the contribution of each treatment in the 100 landscapes configuration by calculating the number of times a treatment participates in the construction of a landscape scenario. To assess the landscapes configuration, we selected the 10 best landscapes (to provide better representation) providing the highest values.

2.4. Statistical Analysis

We performed a one-way analysis of variance (ANOVA) with treatments (4 levels for overstocked pine, and 8 levels for dense shrub) for each of the measured variables individually, and for those ecosystem services to which they were related. We applied a Kruskal-Wallis one-way analysis of variance on ranks when ANOVA assumptions were not reached. We performed Tukey and Dunn's post-hoc tests in case of significant differences ($P < 0.05$) to compare between the different treatments. We performed

PERMANOVA analysis to assess the effect of treatments on species composition (using data from the point-intercept transects) within each type of post-fire ecosystem. 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; common species) and using 4th-root transformed-data (i.e., almost presence/absence data; rare species). We visualized the overall dissimilarity in species composition, the provision of ecosystem services and multifunctionality among treatments by using a non-metric multidimensional scaling (NMDS) from '*vegan*' package using a Bray-Curtis dissimilarity distance. Vectors of plant species and ecosystem services was fitted in the NMDS ordination analysis using the *envfit* function implemented with 1000 random permutations. The latter provides the directions of vectors, their amount of variance explained (R^2), and their significance (*P*-value). It is noteworthy that although the ages of the post-treatment vegetation are not equal, they are comparable as they are all sampled in the medium-long term after their application >10 years, therefore we assume that the dynamics are comparable. We also performed Kruskal-Wallis one-way analysis of variance on ranks followed by Tukey post-hoc between the best 10 landscape scenarios and untreated landscapes (overstocked pine and dense shrub) and between the best scenario that provide the highest values of multifunctionality vs landscapes established only with one treatment. All analyses were done using R software version 3.5.2 (R Core Team, 2017).

3. Results

3.1. Effect of treatments on the provision of ecosystem services and multifunctionality

Our treatments within both overstocked pine and dense shrub ecosystem (Fig.1) affected the ecosystem attributes and the provision of ecosystem services in different ways (Fig. 2, S3 and S4, Tables S4 to S13). Overall, reducing plant density (either by tree thinning, or shrub clearing by mechanical removal or prescribed burning) increased biodiversity conservation compared to the reference ecosystem and the untreated ecosystems (overstocked pine forest or dense shrub ecosystems; Fig. 2). In dense shrublands, biodiversity conservation within clearing ± plantation treatments were higher than repeated prescribed burns. These effects were the result of the positive effects of reducing vegetation density on species richness and habitat heterogeneity ($P<0.05$).

Overstocked pine forest and thinning ± plantation treatments showed the highest values of carbon sequestration, with no significant differences in between them, compared with the reference ecosystem ($F_{3,8}=10.64$, $P>0.05$, Table S10). Clearing in shrubland increased the carbon sequestration compared with the reference ecosystem, and prescribed burn and repeated prescribed burns ($\chi^2=14.71$, $P<0.05$, Table S12). From all the treatments applied, only the untreated dense shrublands, shrub clearing (with no plantation) and repeated prescribed burns reduced disturbance regulation, with the rest of post-fire restoration techniques showing high values, similar to those found in the reference ecosystem. Although prescribed burn increased the herbaceous biomass (Fig. S3), our treatments did not significantly affect food production. Similarly, our treatment did not affect disturbance regulation except clearing + plantation which increased it compared with all treatments except prescribed burn (Fig 2).

Post-fire restoration techniques did not affect multifunctionality within overstocked pine forest but clearing + plantation increased it in shrublands compared with the untreated dense shrublands and repeated prescribed burns. The later, showed the lowest values of multifunctionality, compared with all treatments (Fig.2).

3.2. Effect of plant species compositional shifts on the provision of ecosystem services and multifunctionality

Our treatments induced compositional shifts, both in abundant (overstocked pine $F_{3,8}=1.86$, dense shrub: $F_{5,15}=2.61$, $P<0.05$) and rare species ($F_{5,15}=2.30$, $P<0.05$; Fig. 3 and S5, Table S14 and S16). Overstocked pine plots were dominated mainly by *P. halepensis*, however, the thinned plots showed more mixed species composition (e.g., *Pistacia lentiscus*, *Thymus piperella*, *Polygala rupestris*). Within the dense shrubland, reference ecosystem, clearing, clearing +plantation and prescribed burn treatments showed more mixed species composition than the untreated ecosystems (Fig 3; Table S16). The abundance of common species was the main cause of the observed compositional shifts within both overstocked pine and dense shrubland ecosystems (Table S14). Plant compositional changes also influenced ecosystem functioning, with different species promoting different services (Fig 3, Tables S16). Carbon sequestration both above- and belowground (and supporting services in shrublands) was related to the abundance of the dominant woody species (*P.halepensis* in forests *and Salvia rosmarinus* in shrublands; R^2 =0.42, P.value <0.05). The provision of food production in both ecosystems was related to the herbaceous species and species of beekeeping interest (i.e. *Stipa offneri* R^2=0.38, P.value<0.05*, Lavandula latifolia* R^2=0.30, P.value<0.05), (R^2 =0.45, P.value <0.05; R^2 =0.36, P.value <0.05 in overstocked pine and dense shrub respectively). herbaceous species was also the main determinant of supporting services in the overstocked pine forests (Fig. 3). The treatments of prescribed burn and repeated prescribed burns were the main driver of the abundance of herbaceous species. The provision of high levels of disturbance regulation was related to the abundance of resprouting species (i.e., *Rhamnus alaternus* R^2 =0.28, P.value<0.05*, Pistacia lentiscus;* R^2 =0.64, P.value<0.05), mainly present in unburned reference plots.

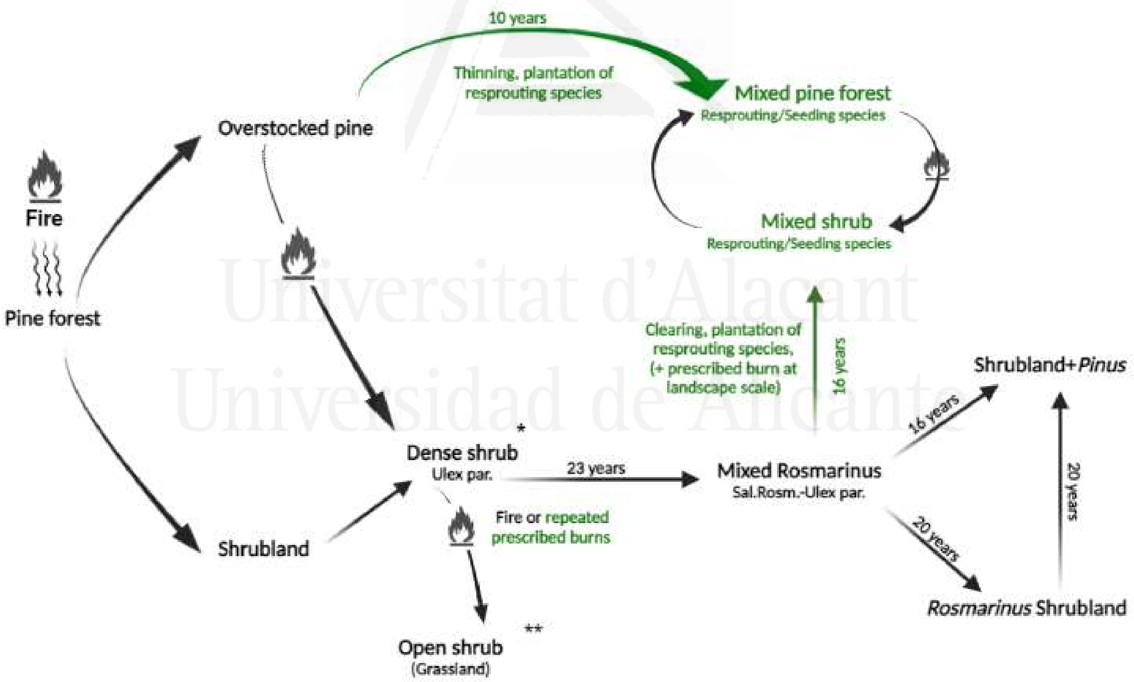

Figure 1. Conceptual model of vegetation dynamics after fire (based on Baeza et al., 2007) and treatment effects. Arrows show transition from one vegetation state to another. Arrows in green color indicate the expected effect of management activities The arrows with a question mark indicate unknown transition. (*) means with pine regeneration and (**) means pine disappearance.

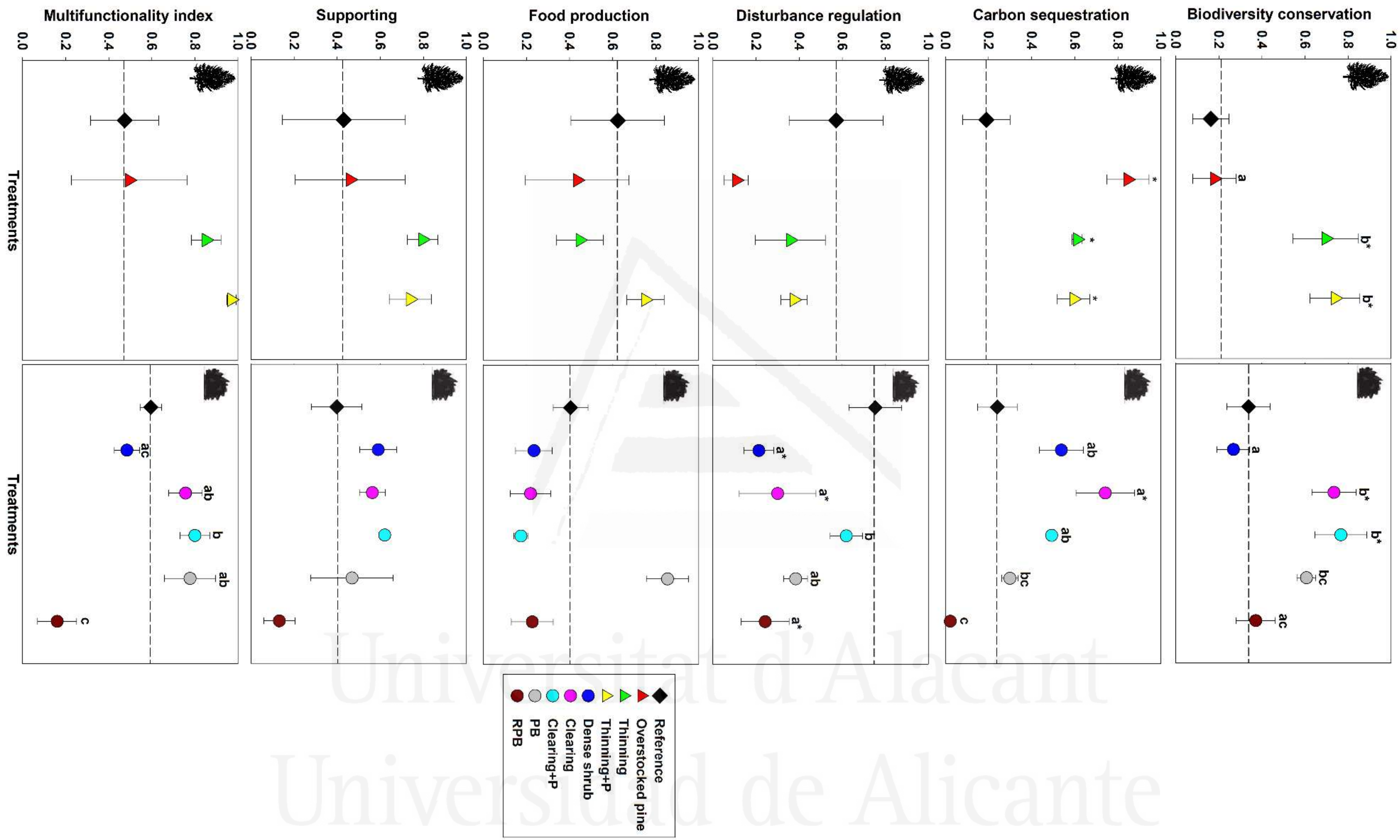

Fig. 2. Mean (±SE) of five ecosystem services and multifunctionality index within overstocked pine forest (left) and dense shrubland (right). Different letters mean significant differences between the different treatments. Asterisk means significant difference with the reference (unburned) ecosystem. Dashed lines are used to better visualize the reference ecosystem level.

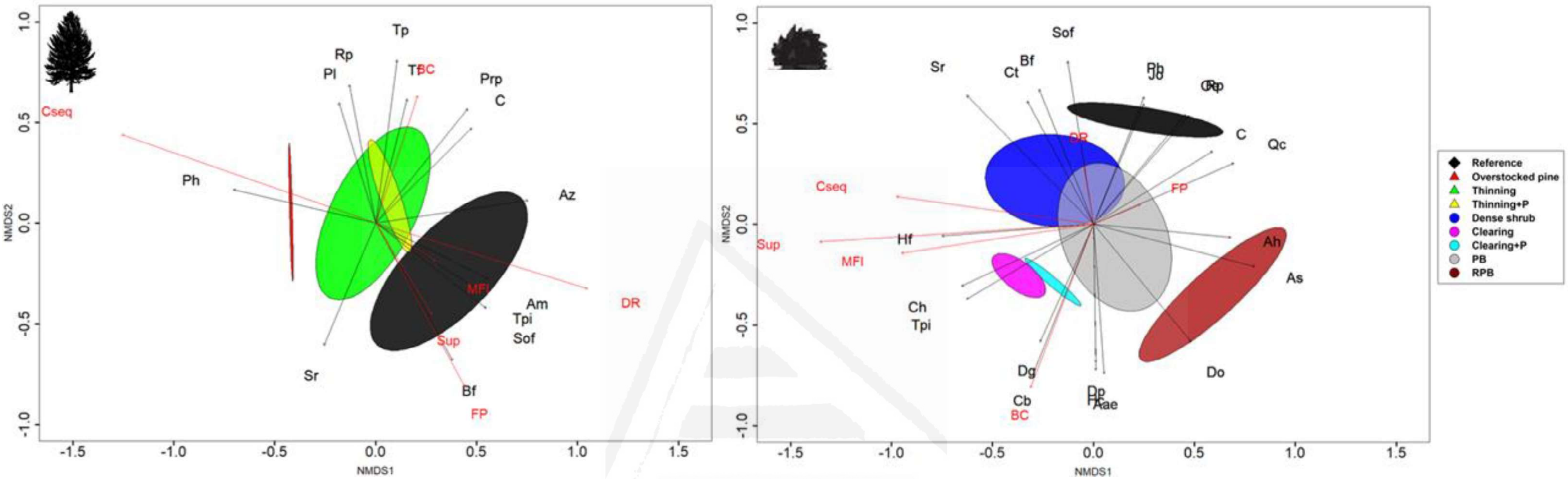

Fig. 3. The non-metric multidimensional scaling (NMDS; panels in the top) NMDS was performed using 75 plant species (abundant species using raw data) found in all study plots. Left and right panels show the treatments applied within overstocked pine forest and dense shrub respectively. The ellipses show 95% standard error for different treatments. Species shown are those significantly related to the compositional changes. Species legend: Am: *Aphyllantes monspeliensis*, Az: *Argyrolobium zanonii*, Aa: *Asparagus acutifolius*, Ah: *Atractylis humilis*, Bp: *Brachypodium phoenicoides*, Br: *Brachypodium retusum*, Bf: *Bupleurum fruticescens*,Ct: *Carduus tenuiflorus*, Cb: *Centaurea boissieri*, C: *Centaurea sp*, Ca: *Cistus albidus*, Cc: *Cistus clusii*, Cmo: *Cistus monspelliensi*, Cs: *Cistus salviflorus*, Cp: *Compuesta sp*, Cm: *Coronilla minima*, Csc: *Coronilla scorpioides*, Dc: *Dacus caota*, Dgn: *Daphne gnidium*, Dp: *Dorycnium pentaphyllum*, Ev: *Echium vulgare*, Em: *Erica multiflora*, Ei: *Euphorbia isatidifolia*, E: *Euphorbia sp*, Fe: *Fumana ericoides*, Fl: *Fumana laevis*, Ft: *Fumana thymifolia*, Gs: *Genista scorpius*, Hc: *Helianthemum cinereum*, Hs: *Helianthemum syriacum*, Jo: *Juniperus oxycedrus*, Ls: *Linum suffruticosum*, Li: *Lonicera implexa*, Oe: *Olea europaea*, Of: *Ononis fruticosa*, Om: *Ononis minutissima*, Ps: *Paronychia suffruticosa(polygonifolia)*, Pr: *Phagnalon rupestre*, Pl: *Phlomis lychnitis*, Pc: *Phlomis crinita*, Ph: *Pinus halepensis*,Pp: *Pinus pinaster*, Ple: *Pistacia lentiscus*,Prp: *Polygala rupestris*,Qc: *Quercus coccifera*,Qi: *Quercus ilex*, Ru: *Reseda undata*, R: *Rosa sp*, Ro: *Rosmarinus officinalis*, Rpe: *Rubia peregrina*, Ss: *Sedum sediforme*, Sm: *Senecio malacitanus*, Sd: *Staehelina dubia*, Sof: *Stipa offneri*, Tf: *Teucrium flavum*, Tp: *Teucrium pseudochamaepitys*, Tvi: *Thapsia villosa*, Tpi: *Thymus piperella*, Tv: *Thymus vulgaris*, Up: *Ulex parviflorus*. Black and red vectors represent the effect of plant species and ecosystem services, are fitted using the *envfit* function implemented with 1000 random permutations. PB: prescribed burn, RPB: Reapeated prescribed burn. BC: Biodiversity conservation, Cseq: carbon sequestration, DR: disturbance regulation, FP: Food Production, Sup: supporting, MFI multifunctionality.

3.3. Effect of treatments on the provision of ecosystem services and multifunctionality at the landscape level.

Our results show that combining thinning +plantation (24% included within the most multifunctional landscapes), clearing (18%) and clearing + plantation (24%) provide the highest levels of landscape-level multifunctionality (Fig. 4). The latter is related to the large benefits of thinning and thinning + plantation for biodiversity conservation, together with the positive effects of combining clearing and clearing + plantation to enhance disturbance regulation. These treatments (reducing density + introducing resprouting species) also had positive effects for food production and supporting services if combined at least with 13% of prescribed burns and 13% of the burned area should remain unmanaged (Fig. S6). To maximize carbon sequestration, the most effective alternative is to leave part of the post-fire communities untreated, as >25% of the landscapes maximizing this service were covered by overstocked pine forest and/or dense shrublands. Nonetheless, clearing and thinning are also suitable techniques to enhance carbon sequestration at the same that other services are promoted (Fig 4). The landscapes that combined different treatment had more capacity to provide ecosystem services than untreated landscapes. The combination of the best landscape scenario that maximize multifunctionality showed similar capacity of provision compared with the best treatment for each ecosystem services (Fig S7).

4. Discussion

The high incidence of wildfires in Mediterranean forests has generated a substantial amount of research regarding post-fire restoration techniques to diminish vulnerability and enhance ecosystem services. However, there have been few attempts to collectively evaluate the success of these restoration techniques across the main different types of post-fire communities (overstocked pine forests and dense shrublands dominated by seeder species). Furthermore, different post-fire restoration techniques have contrasting functional consequences, yet we know very little about how to combine these techniques in order to generate landscape configurations that maximize the supply of the multiple ecosystem services we rely upon. We found that, at the stand scale, reducing vegetation density by thinning and clearing combined with plantation of resprouting species are suitable techniques to restore degraded ecosystems. These techniques together with prescribed fire can establish multifunctional Mediterranean landscapes, however repeated prescribed burns were less effective at both scales (Fig 4, S6 and S7). This is due to the positive effect of prescribed burn in promoting the abundance of herbaceous species which in turn enhance food production (Fig. 2 and S3). Overall, these results are mainly driven by the response of biodiversity conservation, carbon sequestration and disturbance regulation. Food production and supporting services, however, were not affected by our treatments. Our findings point out the importance of considering multiple ecosystem functions at contrasting spatial scales when assessing the success of post-fire management, and the importance of combining different techniques to accelerate the successional process and establish mixed landscapes that supply multiple ecosystem services simultaneously.

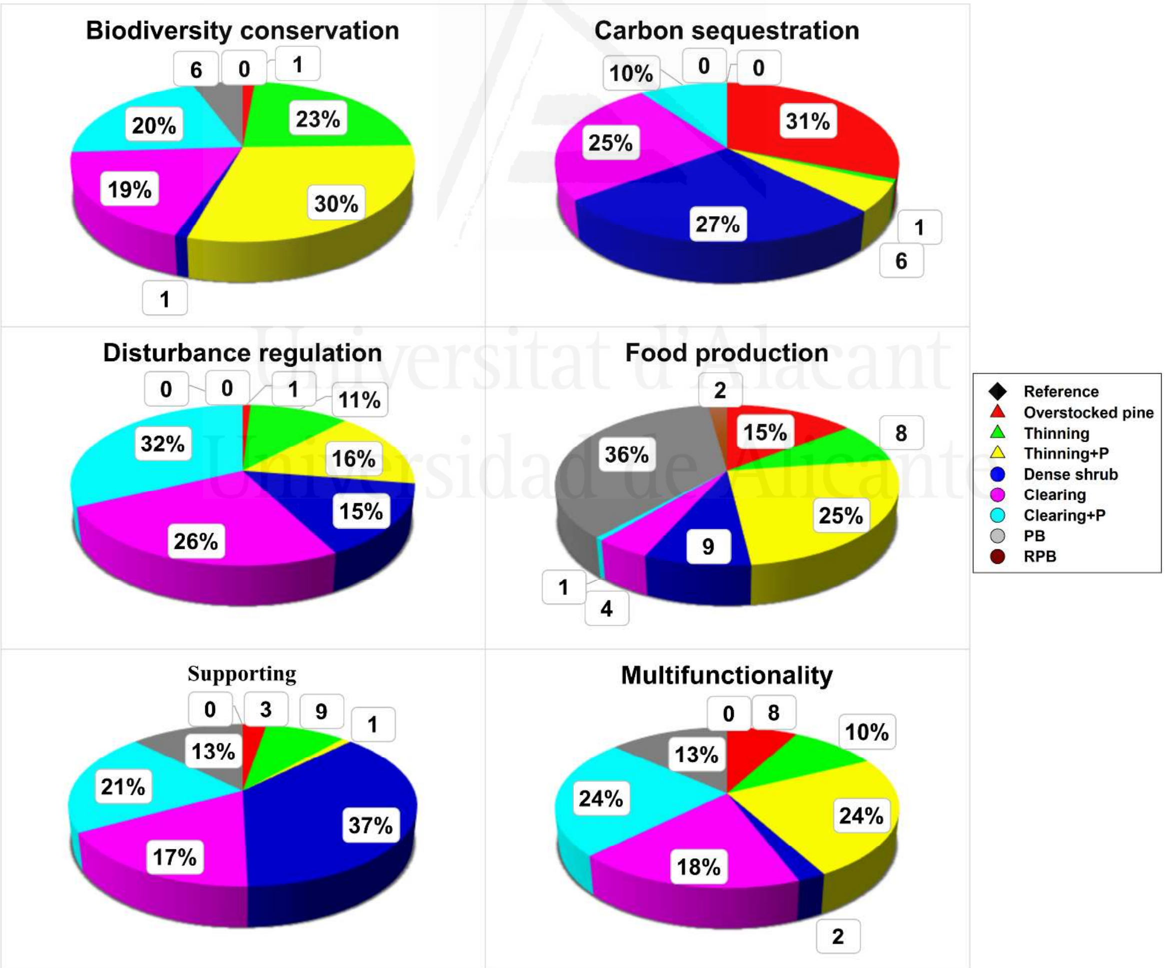

Fig. 4. The impact of treatments (calculated as the number of times a given treatment participates in the landscape creation) in establishing 100 landscapes (out of 4600000 possible combinations created from 8 plots) that provide the highest levels of ecosystem services and multifunctionality.

Thinning and clearing treatments, both combined with plantation of resprouting species, were the most effective techniques to accelerate the successional process and redirect degraded and vulnerable communities dominated by seeders species towards mixed forests with more abundance of resprouting species (Fig 1 and 2). The later are often reported as more resistant and functional ecosystems (Pretzsch & Forrester, 2017). Reducing vegetation density generally enhances the availability of light, soil moisture and nutrients, which in turn induce several structural and compositional shifts (Agee & Skinner, 2005; Wic Baena et al., 2013). The compositional changes in the plant community induced by the treatments also determine ecosystems functions and the supply of ecosystem services (Fig 3). The application of thinning and clearing, in combination with the plantation of resprouter species, have positive effects in increasing native species richness and habitat complexity, and reducing dead fuel load (Fig 2, S3; see also (González-Ochoa et al., 2004; Jiménez & Navarro, 2016; Manrique-Alba et al., 2020; Santana et al., 2018; Verkaik & Espelta, 2006). In addition, it enhanced soil properties in dense shrub ecosystem, such as organic carbon, available phosphorus, and infiltration rates (Fig. S4). Reducing vegetation increased biodiversity conservation which was even higher than reference ecosystem in plots where treatments of thinning, clearing and their combination with plantation of resprouting species are applied (Fig 2; Fig S4). Open and heterogeneous habitats provide more colonization opportunities for new plant species and provide a greater range of habitat for animals (Val et al., 2018). The effect of increasing species richness and habitat heterogeneity may also enhance ecosystem functioning due to the positive relationship between biodiversity and multifunctionality (Pretzsch & Forrester, 2017). Also, reducing vegetation density by clearing with plantation of resprouting species enhanced disturbance regulation within dense shrublands. This result is due to the presence of woody resprouting species, both by plantation and natural colonization (i.e *P. lentiscus*, *R. alaternus*), and the low dead fuel load (Fig 4). In the other hand, reducing vegetation density may potentially reduce the capacity of ecosystem to sequester carbon (de las Heras et al., 2013), yet this was not our case. Carbon sequestration was not decreased by reducing the density of *P. halepensis* and *S. rosmarinus*, its main determinant species in overstocked pine and dense shrubland respectively. In addition, carbon sequestration was even higher than the reference ecosystem in dense shrublands (Fig 2). This is probably due to the compensatory woody plant growth as consequence of the reduced competition compared to the untreated plots

(Dwyer et al., 2010; Manrique-Alba et al., 2020), as well as to the chopped vegetation left on the soil as mulch which may supply organic matter (Prosdocimi et al., 2016). This may also suggest that these types of regenerated ecosystems could be an opportunity, if they are properly managed, to increase the capacity of Mediterranean forest to sequester carbon.

Contrarily to mechanical clearing, prescribed burn and repeated prescribed burns showed less diversity with dominance of herbaceous species (Fig. 2 and 3,S3,S4), yet enhance food production services and reduce flammability (Agee & Skinner, 2005). In fact, fire has been traditionally used (by early hunter-gatherer for example) to increase forage production (Pausas & Keeley, 2019) , yet at the cost (i.e. trade-offs) of other services of interest (e.g., biodiversity conservation, disturbance regulation, carbon sequestration and multifunctionality; Fig. 2). Repeated heating derived from prescribed burns can reduce the availability of nutrients and infiltration, litter and seeds into the soil, and also replace woody late-successional species with opportunistic herbaceous species (Santana et al., 2014). This is also in line with many studies showing that prescribed burns, although having low intensity may increase the risk of erosion, runoff and shifts on soil properties (Carra et al., 2021; Wright et al., 2021). These changes substantially dampen the carbon sequestration potential and reduce the capacity of ecosystems to recover after additional wildfires (Figs 2, S3 and S4; Wright et al., 2021). This result suggests that although prescribed burn reduce vegetation density and dead fuel load, it may negatively affect the functioning of ecosystems if applied frequently. Therefore, these findings support the concept of considering the multiple ecosystem functions, and the potential trade-offs that treatments may produce when managing at landscape scale. (Cruz-Alonso et al., 2019; Felipe-Lucia et al., 2018; Manning et al., 2018).

Mixed landscapes can maximize the supply of multiple ecosystem services (Pretzsch & Forrester, 2017). Our results show that landscapes configurations combining thinning and clearing both with plantation of resprouting species (enhancing biodiversity conservation, disturbance regulation and with high levels of carbon sequestration), together with some minor prescribed burn (mainly enhancing forage production) may enhance simultaneously the provision of multiple ecosystem services of interest in the Mediterranean Basin (Fig 4 and S6 and S7). While the importance of heterogeneity to establish landscapes that maximize the supply of ecosystem services have been repeatedly highlighted (Liang et al., 2016; Pretzsch & Forrester, 2017), we lacked quantitative and empirical evidence regarding the most beneficial configurations to maximize landscape multifunctionality. Our study shows that maintaining <25% of untreated ecosystems combined with thinning and thinning +P (13-25%) clearing (<25%) and clearing +P (25%), and prescribed fire (13%) may establish multifunctional landscapes (Fig S6). Importantly, applying a potential treatment for a given ecosystem services, for example, thinning +plantation of resprouter species to promote the supply of biodiversity conservation at high levels, can not maximize all the other ecosystem services simultaneously at landscape scale (Fig S7). This is a key challenge in ecosystem management to determine how to manage multiple ecosystem services across landscapes as they may exist trade-offs between ecosystem services (e.g., biodiversity conservation vs carbon sequestration) induced by restoration activities (Raudsepp-Hearne et al., 2010) However, combining different management activities can enhance the supply of multiple ecosystem services simultaneously and establish multifunctional Mediterranean landscapes.

5. Conclusion

Our study shows the effectiveness of thinning and clearing, both combined with plantation of resprouter species, within two post-fire regenerated ecosystems (overstocked pine and dense shrub) to redirect them towards more functional and less vulnerable communities. Together, combined with some, but minor, prescribed burn can establish landscapes that maximize the provision of the main ecosystem services supplied by Mediterranean ecosystems. We also highlight the importance of considering the diversity of functions and services that an ecosystem may supply, as they respond in different ways to the forest management. Our study provides insights for land managers and policymakers as how to manage multiple ecosystem services across different scales to establish multifunctional Mediterranean landscapes.

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Supplementary information

Table S1. Topographic and environmental features of the managed study sites.

Site	Ecosystem type	Treatments	Unburned reference site	Latitude–longitude	Elevation (m)	Aspect
Albaida	Overstocked pine	Thinning± plantation	Alcoy	38º50'N- 0º30'W	500	N
Bocairente	Overstocked pine	Thinning± plantation	Alcoy	38º46'N- 0º36'W	641	N
Mariola	Overstocked pine	Thinning± plantation	Alcoy	38º43'N- 0º39'W	816	N
Roñoso	Dense shrubland	Clearing± plantation	Ayora	39º07´N,0º57´W	1032	NE
Morera	Dense shrubland	Clearing± plantation	Ayora	39º07´N, 0º57´W	978	NE
Gachas	Dense shrubland	Clearing± plantation	Ayora	39º01´N, 0º53´W	978	NE
Teresa	Dense shrubland	Prescribed burns	Ayora	39º07'N, 0º57'W	1040	NE
Penyesrojes	Dense shrubland	Prescribed burns	Onil	38º39'N, 0º39'W	941	NE
Pardines	Dense shrubland	Prescribed burns	Alcoy	38º40'N, 0º34'W	900	NE

Table S2. Topographic and environmental features of the unburned sites.

Site	Ecosystem type	Latitude–longitude	Elevation(m)	Aspect
Alcoy	Mature pine forest	38º40'N-0º34'W	900	NE
Ayora	Mature pine forest	39º08'N- 0º55'W	774	NE
Onil	Mature pine forest	38º39'N-0º39'W	940	NE

Table 3. 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
	Total biomass		No, highly correlated with live aroboreal biomass already included in carbon sequestration
	Woody biomass		No, highly correlated with live aroboreal biomass already included in carbon sequestration
	Organic carbon	Belowground	Yes
Disturbance regulation	Richness of resprouting shrubs	Aboveground	Yes
	Abundance of resprouting shrubs		Yes
	Arboreal dead biomass		Yes
	Dead shrub biomass		Yes
	Stability index		Yes
	Infiltration		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
	Nutrients		Yes
Other	pH	Belowground	No
	Electrical Conductivity		No

Table S4. Results of Kruskal-Wallis test applied to evaluate the effect of treatments within overstocked pine forests on ecosystem attributes when the assumptions of the one-way ANOVA test are not met.

Variable	**Chi-squared**	**p-value**
Resprouter richness	6.89	0.08
Resprouter abundance	6.26	0.10
Shrub live biomass	2.49	0.48
Shrub dead biomass	7.09	0.07
Herbaceous	7.51	0.06
Litter	9.51	**0.02**
Tree live biomass	9.97	**0.02**
Tree dead biomass	9.97	**0.02**
woody biomass	9.97	**0.02**
Organic carbon	6.69	0.08
Infiltration	7.17	0.07
Total Oxidized Nitrogen	1.19	0.75

Table S5. Dunn's test results of multiple comparisons between treatments that had significant effects on ecosystem attributes in Table S4

	Comparison	Z	P.value
Litter	600 - 600+P	0.91	0.37
	600 - Overstocked pine	-0.91	0.37
	600+P - Overstocked pine	-1.81	0.07
	600 - Reference	**-2.04**	**0.04**
	600+P - Reference	**-2.94**	**0.00**
	Overstocked pine - Reference	-1.13	0.26
Tree live biomass	600 - 600+P	0.79	0.43
	600 - Overstocked pine	-2.15	**0.03**
	600+P - Overstocked pine	-2.94	**0.00**
	600 - Reference	-1.13	0.26
	600+P - Reference	-1.92	**0.05**
	Overstocked pine - Reference	1.02	0.31
Tree dead biomass	600 - 600+P	0.79	0.43
	600 - Overstocked pine	-2.15	0.03
	600+P - Overstocked pine	-2.94	0.00
	600 - Reference	-1.13	0.26
	600+P - Reference	-1.92	0.05
	Overstocked pine - Reference	1.02	0.31
woody biomass	601 - 600+P	-0.69	0.15
	601 - Overstocked pine	-0.59	0.14
	600+P - Overstocked pine	-0.49	0.14
	601 - Reference	-0.38	0.13
	600+P - Reference	-0.28	0.12
	Overstocked pine - Reference	-0.18	0.11

Table S6. Results of one-way ANOVA applied to evaluate the effect of treatments within overstocked pine forests on ecosystem attributes.

Variable		Df	SS	Mean Sq	F.value	Pr(>F)
Species richness	Treatment	3	49.46	16.49	3.01	0.09
	Residuals	8	43.78	5.47		
Beekeeping potential	Treatment	3	2881.00	960.40	1.21	0.37
	Residuals	8	6354.00	794.30		
Habitat complexity	Treatment	3	0.20	0.07	7.24	**0.01**
	Residuals	8	0.07	0.01		
Phosphorus	Treatment	3	35.78	11.93	4.79	**0.03**
	Residuals	8	19.91	2.49		
Beta glucosidase	Treatment	3	3.59	1.20	1.11	0.40
	Residuals	8	8.63	1.08		
Acid phosphatase	Treatment	3	3.31	1.10	0.65	0.61
	Residuals	7	11.88	1.69		
Potential mineralized N	Treatment	3	755.20	251.70	1.58	0.27
	Residuals	8	1272.40	159.10		
Total ammonium	Treatment	3	73.07	24.36	1.89	0.21
	Residuals	8	103.02	12.88		
Nutrients cycling index	Treatment	3	229.50	76.51	1.74	0.25
	Residuals	7	308.10	44.02		
Stability index	Treatment	3	55.37	18.46	1.72	0.25
	Residuals	7	75.15	10.74		

Table S7. Results of Tukey-post hoc tests comparison between treatments that had significant effects on ecosystem attributes in Tables S6. diff = mean difference, lwr and upr = the lower and upper confidence interval respectively, p adj is the adjusted p value.

	Comparison	diff	lwr	upr	p adj
Habitat complexity.	600+P-600	0.01	-0.24	0.26	1.00
	Overstocked pine-600	-0.21	-0.46	0.04	0.11
	Reference-600	-0.29	-0.54	-0.04	**0.03**
	Overstocked pine-600+P	-0.21	-0.47	0.04	0.10
	Reference-600+P	-0.30	-0.55	-0.05	**0.02**
	Reference-Overstocked pine	-0.08	-0.33	0.17	0.73
Phosphorus	600+P-600	-2.66	-6.79	1.46	0.24
	Overstocked pine-600	-2.31	-6.44	1.81	0.34
	Reference-600	-4.87	-9.00	-0.75	**0.02**
	Overstocked pine-600+P	0.35	-3.77	4.48	0.99
	Reference-600+P	-2.21	-6.33	1.92	0.38
	Reference-Overstocked pine	-2.56	-6.68	1.57	0.27

Table S8. Results of Kruskal-Wallis test applied to evaluate the effect of treatments within dense shrubland on ecosystem attributes.

Variable	Chi-squared	p-value
Specie richness	16.18	**0.01**
Resprouters richness	15.82	**0.01**
Resprouters abundance	14.37	**0.01**
Habitat complexity	5.99	0.31
Beekeeping potential	8.90	0.11
Shrub live biomass	13.43	**0.02**
Shrub dead biomass	10.87	0.05
Tree live biomass	13.53	**0.02**
Tree dead biomass	13.94	**0.02**
woody biomass	10.04	0.07
Herbaceous biomass	7.55	0.18
Litter	15.15	**0.01**
Total biomass	9.08	0.08
Organic carbon	16.00	**0.01**
Phosphorus	11.46	**0.04**
Acid phosphatase	12.51	**0.03**
Beta glucosidase	4.92	0.43
Total ammonium	4.22	0.52
Total oxidized nitrogen (TON)	1.379	0.93
PMN	7.49	0.19
Stability index	8.62	0.13
Infiltration index	11.18	**0.05**
Nutrients cycling index	11.15	**0.05**

Table S9. Dunn's test results of multiple comparisons between treatments that had significant effects on ecosystem attributes in Table S8

	Comparison	Z	P.value
Specie richness	Clearing - Clearing + Plantation	0.07	0.95
	Clearing - Dense shrub	**2.76**	**0.01**
	Clearing+ Plantation – Dense shrub	**2.68**	**0.01**
	Clearing - PF	1.09	0.28
	Clearing + Plantation - PF	1.02	0.31
	Dense shrub - PF	-1.50	0.13
	Clearing - Reference	1.78	0.08
	Clearing + Plantation - Reference	1.71	0.09
	Dense shrub - Reference	-0.70	0.48
	PF - Reference	0.69	0.49
	Clearing - RPF	**2.90**	**0.00**
	Clearing + Plantation - RPF	**2.83**	**0.00**
	Dense shrub - RPF	0.59	0.56
	PF - RPF	1.81	0.07
	Reference - RPF	1.12	0.26
Resprouters richness	Clearing - Clearing + Plantation	0.00	1.00
	Clearing - Dense shrub	1.66	0.10

	Comparison	Z	P.value
	Clearing + Plantation - Dense shrub	1.66	0.10
	Clearing - PF	**2.58**	**0.01**
	Clearing + Plantation - PF	**2.58**	**0.01**
	Dense shrub - PF	1.32	0.19
	Clearing - Reference	0.69	0.49
	Clearing + Plantation - Reference	0.69	0.49
	Dense shrub - Reference	-0.86	0.39
	PF - Reference	-1.88	0.06
	Clearing - RPF	**2.88**	**0.00**
	Clearing + Plantation - RPF	**2.88**	**0.00**
	Dense shrub - RPF	1.66	0.10
	PF - RPF	0.30	0.77
	Reference - RPF	**2.18**	**0.03**
Resprouter abundance	Clearing - Clearing + Plantation	-1.61	0.11
	Clearing - Dense shrub	-0.08	0.94
	Clearing + Plantation - Dense shrub	1.79	0.07
	Clearing - PF	1.38	0.17
	Clearing + Plantation - PF	**3.00**	**0.00**
	Dense shrub - PF	1.67	0.09
	Clearing - Reference	-1.09	0.28
	Clearing + Plantation - Reference	0.53	0.60
	Dense shrub - Reference	-1.18	0.24
	PF - Reference	**-2.47**	**0.01**
	Clearing - RPF	1.22	0.22
	Clearing + Plantation - RPF	**2.83**	**0.00**
	Dense shrub - RPF	1.48	0.14
	PF - RPF	-0.16	0.87
	Reference - RPF	**2.31**	**0.02**
Shrub live biomass	Clearing - Clearing+Plantation	-0.72	0.47
	Clearing - Dense shrub	**-2.17**	**0.03**
	Clearing + Plantation - Dense shrub	-1.33	0.18
	Clearing - PF	**-2.37**	**0.02**
	Clearing + Plantation - PF	-1.64	0.10
	Dense shrub - PF	-0.57	0.57
	Clearing - Reference	-1.45	0.15
	Clearing + Plantation - Reference	-0.72	0.47
	Dense shrub - Reference	0.49	0.62
	PF - Reference	0.92	0.36
	Clearing - RPF	0.46	0.65
	Clearing + Plantation - RPF	1.18	0.24
	Dense shrub - RPF	**2.70**	**0.01**
	PF - RPF	**2.83**	**0.00**
	Reference - RPF	1.91	0.06
	Clearing - Clearing Plantation	0.73	0.46

	Comparison	Z	P.value
Tree live biomass	Clearing - Dense shrub	0.27	0.79
	Clearing + Plantation - Dense shrub	-0.58	0.56
	Clearing - PF	**2.30**	**0.02**
	Clearing + Plantation - PF	1.56	0.12
	Dense shrub - PF	**2.38**	**0.02**
	Clearing - Reference	-0.20	0.84
	Clearing + Plantation - Reference	-0.93	0.35
	Dense shrub - Reference	-0.50	0.62
	PF - Reference	**-2.50**	**0.01**
	Clearing - RPF	**2.30**	**0.02**
	Clearing + Plantation - RPF	1.56	0.12
	Dense shrub - RPF	**2.38**	**0.02**
	PF - RPF	0.00	1.00
	Reference - RPF	**2.50**	**0.01**
Tree dead biomass	Clearing - Clearing + Plantation	0.93	0.35
	Clearing - Dense shrub	-0.04	0.97
	Clearing + Plantation - Dense shrub	-1.11	0.27
	Clearing - PF	**2.30**	**0.02**
	Clearing + Plantation - PF	1.36	0.17
	Dense shrub - PF	**2.69**	**0.01**
	Clearing - Reference	0.13	0.89
	Clearing + Plantation - Reference	-0.80	0.42
	Dense shrub - Reference	0.19	0.85
	PF - Reference	**-2.16**	**0.03**
	Clearing - RPF	**2.30**	**0.02**
	Clearing + Plantation - RPF	1.36	0.17
	Dense shrub - RPF	**2.69**	**0.01**
	PF - RPF	0.00	1.00
	Reference - RPF	**2.16**	**0.03**
Litter	Clearing - Clearing + Plantation	0.53	0.60
	Clearing - Dense shrub	-1.33	0.18
	Clearing + Plantation - Dense shrub	-1.94	0.05
	Clearing - PF	-1.45	0.15
	Clearing + Plantation - PF	**-1.97**	**0.05**
	Dense shrub - PF	-0.34	0.73
	Clearing - Reference	-1.71	0.09
	Clearing + Plantation - Reference	**-2.24**	**0.03**
	Dense shrub - Reference	-0.65	0.52
	PF - Reference	-0.26	0.79
	Clearing - RPF	1.25	0.21
	Clearing + Plantation - RPF	0.72	0.47
	Dense shrub - RPF	**2.77**	**0.01**
	PF - RPF	**2.70**	**0.01**
	Reference - RPF	**2.96**	**0.00**

	Comparison	Z	P.value
Organic carbon	Clearing - Clearing + Plantation	0.59	0.55
	Clearing - Dense shrub	1.75	0.08
	Clearing + Plantation - Dense shrub	1.06	0.29
	Clearing - PF	**2.37**	**0.02**
	Clearing + Plantation - PF	1.78	0.08
	Dense shrub - PF	0.99	0.32
	Clearing - Reference	**2.89**	**0.00**
	Clearing + Plantation - Reference	**2.30**	**0.02**
	Dense shrub - Reference	1.60	0.11
	PF - Reference	0.53	0.60
	Clearing - RPF	**3.09**	**0.00**
	Clearing + Plantation - RPF	**2.50**	**0.01**
	Dense shrub - RPF	1.82	0.07
	PF - RPF	0.72	0.47
	Reference - RPF	0.20	0.84
Available phosphorus	Clearing – Clearing + Plantation	0.46	0.65
	Clearing - Dense shrub	0.11	0.91
	Clearing + Plantation - Dense shrub	-0.42	0.68
	Clearing - PF	**2.04**	**0.04**
	Clearing + Plantation - PF	1.58	0.11
	Dense shrub - PF	**2.24**	**0.03**
	Clearing - Reference	**2.37**	**0.02**
	Clearing + Plantation - Reference	1.91	0.06
	Dense shrub - Reference	**2.62**	**0.01**
	PF - Reference	0.33	0.74
	Clearing - RPF	0.92	0.36
	Clearing + Plantation - RPF	0.46	0.65
	Dense shrub - RPF	0.95	0.34
	PF - RPF	-1.12	0.26
	Reference - RPF	-1.45	0.15
A. Phosphatase	Clearing - Clearing + Plantation	-0.65	0.51
	Clearing - Dense shrub	1.80	0.07
	Clearing + Plantation - Dense shrub	2.56	**0.01**
	Clearing - PF	1.96	0.05
	Clearing + Plantation - PF	2.61	**0.01**
	Dense shrub - PF	0.46	0.64
	Clearing - Reference	1.46	0.14
	Clearing + Plantation - Reference	2.04	**0.04**
	Dense shrub - Reference	0.07	0.94
	PF - Reference	-0.29	0.77
	Clearing - RPF	1.85	0.06
	Clearing + Plantation - RPF	2.43	**0.01**
	Dense shrub - RPF	0.51	0.61
	PF - RPF	0.10	0.92

	Comparison	Z	P.value
	Reference - RPF	0.36	0.72
Infiltration index	Clearing - Clearing + Plantation	-0.33	0.74
	Clearing - Dense shrub	0.08	0.94
	Clearing + Plantation - Dense shrub	0.46	0.65
	Clearing - PF	1.28	0.20
	Clearing + Plantation - PF	1.61	0.11
	Dense shrub - PF	1.41	0.16
	Clearing - Reference	0.89	0.37
	Clearing + Plantation - Reference	1.22	0.22
	Dense shrub - Reference	0.95	0.34
	PF - Reference	-0.39	0.69
	Clearing - RPF	2.40	**0.02**
	Clearing + Plantation - RPF	2.73	**0.01**
	Dense shrub - RPF	2.70	**0.01**
	PF - RPF	1.12	0.26
	Reference - RPF	1.51	0.13
Nutrients index	Clearing - Clearing + Plantation	-0.33	0.74
	Clearing - Dense shrub	0.30	0.76
	Clearing + Plantation - Dense shrub	0.68	0.49
	Clearing - PF	1.45	0.15
	Clearing + Plantation - PF	1.78	0.08
	Dense shrub - PF	1.37	0.17
	Clearing - Reference	0.99	0.32
	Clearing + Plantation - Reference	1.32	0.19
	Dense shrub - Reference	0.84	0.40
	PF - Reference	-0.46	0.65
	Clearing - RPF	**2.43**	**0.01**
	Clearing + Plantation - RPF	**2.76**	**0.01**
	Dense shrub - RPF	**2.51**	**0.01**
	PF - RPF	0.99	0.32
	Reference - RPF	1.45	0.15

Table S10. Results of one-way ANOVA applied to evaluate the effect of treatments within overstocked pine forests on ecosystem services

		Df	SS	Mean Sq	F value	Pr (>F)
Biodiversity conservation	Treatment	3	0.90	0.30	7.46	0.01
	Residuals	8	0.32	0.04		
Carbon sequestration	Treatment	3	0.67	0.22	10.64	0.00
	Residuals	8	0.17	0.02		
Disturbance regulation	Treatment	3	0.32	0.11	1.78	0.23
	Residuals	8	0.49	0.06		
	Treatment	3	0.21	0.07	0.73	0.56

Food production	Residuals	8	0.75	0.09		
Supporting	Treatment	3	0.32	0.11	0.88	0.49
	Residuals	8	0.97	0.12		

Table S11. Results of Tukey-post hoc tests comparison between treatments that had significant effects on ecosystem attributes in Tables S13. diff = mean difference, lwr and upr = the lower and upper confidence interval respectively, p adj is the adjusted p value.

	Comparison	diff	lwr	upr	p adj
Biodiversity conservation	600+P-600	0.04	-0.48	0.57	0.99
	Overstocked pine-600	**-0.52**	**-1.04**	**0.01**	**0.05**
	Reference-600	**-0.53**	**-1.06**	**-0.01**	**0.05**
	Overstocked pine-600+P	**-0.56**	**-1.08**	**-0.04**	**0.04**
	Reference-600+P	**-0.58**	**-1.10**	**-0.05**	**0.03**
	Reference-Overstocked pine	-0.02	-0.54	0.51	1.00
Carbon sequestration	600+P-600	-0.02	-0.39	0.36	1.00
	Overstocked pine-600	0.24	-0.14	0.61	0.27
	Reference-600	**-0.42**	**-0.80**	**-0.04**	**0.03**
	Overstocked pine-600+P	0.25	-0.13	0.63	0.22
	Reference-600+P	**-0.41**	**-0.78**	**-0.03**	**0.04**
	Reference-Overstocked pine	**-0.66**	**-1.04**	**-0.28**	**0.00**

Table S12. Results of Kruskal-Wallis test applied to evaluate the effect of treatments within dense shrubland on ecosystem services and multifunctionality (MFI).

Variable	Chi-squared	p-value
Biodiversity conservation	14.98	**0.01**
Carbon sequestration	14.71	**0.01**
Disturbance regulation	12.67	**0.03**
Food production	9.84	0.08
Supporting	9.42	0.09
MFI	14.58	**0.01**

Table 13. Dunn's test results of multiple comparisons between treatments that had significant effects on ecosystem attributes in Table S15**.**

Variable	Comparison	Z	P.unadj
Biodiversity conservation	Clearing – Clearing + Plantation	-0.07	0.95
	Clearing - Dense shrub	**2.74**	**0.01**
	Clearing + Plantation- Dense shrub	**2.81**	**0.00**
	Clearing - PB	0.53	0.60
	Clearing + Plantation- PB	0.59	0.55
	Dense shrub - PB	**-2.13**	**0.03**
	Clearing - Reference	**2.17**	**0.03**

Variable	Comparison	Z	P.unadj
	Clearing + Plantation- Reference	**2.24**	**0.03**
	Dense shrub - Reference	-0.23	0.82
	PB - Reference	1.64	0.10
	Clearing - RPB	1.84	0.07
	Clearing + Plantation- RPB	1.91	0.06
	Dense shrub - RPB	-0.61	0.54
	PB - RPB	1.32	0.19
	Reference - RPB	-0.33	0.74
Carbon sequestration	Clearing – Clearing + Plantation	1.12	0.26
	Clearing - Dense shrub	1.03	0.31
	Clearing + Plantation- Dense shrub	-0.27	0.79
	Clearing - PB	**2.11**	**0.04**
	Clearing + Plantation- PB	0.99	0.32
	Dense shrub - PB	1.41	0.16
	Clearing - Reference	**2.30**	**0.02**
	Clearing + Plantation- Reference	1.18	0.24
	Dense shrub - Reference	1.63	0.10
	PB - Reference	0.20	0.84
	Clearing - RPB	**3.29**	**0.00**
	Clearing + Plantation- RPB	**2.17**	**0.03**
	Dense shrub - RPB	**2.77**	**0.01**
	PB - RPB	1.18	0.24
	Reference - RPB	0.99	0.32
Disturbance regulation	**Clearing – Clearing + Plantation**	**-1.97**	**0.05**
	Clearing - Dense shrub	0.27	0.79
	Clearing + Plantation- Dense shrub	**2.55**	**0.01**
	Clearing - PB	-0.59	0.55
	Clearing + Plantation - PB	1.38	0.17
	Dense shrub - PB	-0.95	0.34
	Clearing - Reference	**-2.11**	**0.04**
	Clearing + Plantation - Reference	-0.13	0.90
	Dense shrub - Reference	**-2.70**	**0.01**
	PB - Reference	-1.51	0.13
	Clearing - RPB	0.07	0.95
	Clearing +Plantation - RPB	**2.04**	**0.04**
	Dense shrub - RPB	-0.19	0.85
	PB - RPB	0.66	0.51
	Reference - RPB	**2.17**	**0.03**
MFI	Clearing – Clearing + Plantation	-0.13	0.90
	Clearing – Dense shrub	1.86	0.06
	Clearing + Plantation – Dense shrub	**2.01**	**0.04**
	Clearing - PB	-0.07	0.95
	Clearing + Plantation - PB	0.07	0.95
	Dense shrub - PB	-1.94	0.05
	Clearing - Reference	1.12	0.26
	Clearing +Plantation - Reference	1.25	0.21

Variable	Comparison	Z	P.unadj
	Dense shrub - Reference	-0.57	0.57
	PB - Reference	1.18	0.24
	Clearing - RPB	**2.76**	**0.01**
	Clearing + Plantation - RPB	**2.89**	**0.00**
	Dense shrub - RPB	1.33	0.18
	PB - RPB	**2.83**	**0.00**
	Reference - RPB	1.64	0.10

Table S14. Results of the Permutational Multivariate Analysis of Variance (PERMANOVA), showing the effects of treatments within overstocked pine forests and dense shrubland on species composition (abundant, and abundant + rare species using raw data and nearly presence/absence data, respectively). Df = degrees of freedom, SS = sum of squares (type III), R2 = variance explained by the model, F = pseudo-F, Pr(>F) = P value.

			Df	SS	R2	F	Pr(>F)
Overstocked pine	Abundant species	Treatment	3.00	0.69	0.41	1.86	0.03
		Residual	8.00	0.98	0.59		
		Total	11.00	1.67	1.00		
	Rare species	Treatment	3.00	0.34	0.31	1.20	0.23
		Residual	8.00	0.76	0.69		
		Total	11.00	1.11	1.00		
Dense shrub	Abundant species	Treatment	5.00	1.80	0.46	2.61	0.00
		Residual	15.00	2.18	0.54		
		Total	20.00	4.08	1.00		
	Rare species	Treatment	5.00	1.36	0.43	2.30	0.00
		Residual	15.00	1.77	0.57		
		Total	20.00	3.13	1.00		

Table 15. Determination coefficients (R^2) and their significance (*P*) determined by NMDS ordination (Ecosystem services supplied within overstocked pine and dense shrub ecosystems). R and P were obtained using 1000 random permutations

		NMDS1	NMDS2	r2	Pr(>r)
Overstocked pine	Biodiversity conservation	0.31	0.95	0.14	0.50
	Carbon sequestration	-0.94	0.33	0.56	0.02
	Disturbance regulation	0.96	-0.30	0.38	0.11
	Food production	0.48	-0.88	0.27	0.26
	Supporting	0.53	-0.85	0.09	0.65
	MFI	0.84	-0.54	0.04	0.82
Dense shrub	Biodiversity conservation	-0.36	-0.93	0.17	0.18
	Carbon sequestration	-0.99	0.14	0.22	0.13
	Disturbance regulation	-0.16	0.99	0.02	0.83
	Food production	0.92	0.39	0.01	0.89
	Supporting	-1.00	-0.06	0.42	0.01
	MFI	-0.99	-0.15	0.21	0.12

Table S16. Determination coefficients (R^2) and their significance (*P*) determined by NMDS ordination (abundant species within overstocked pine and dense shrub ecosystems). R and P were obtained using 1000 random permutations

Species	**Overstocked pine**		**Dense shrub**	
	R2	**Pr(>r)**	**R2**	**P**
Aphyllantes monspeliensis	0.58	**0.01**	0.34	**0.032**
Argyrolobium zanonii	0.66	**0.01**	0.04	0.695
Asparagus acutifolius L.	0.35	0.15	0.00	1.000
Asphodelus aestivus	0.00	1.00	0.34	**0.020**
Atractylis humilis	0.03	0.91	0.31	**0.026**
Biscutella sp.	0.00	1.00	0.00	1.000
Brachypodium phoenicoides	0.12	0.57	0.33	**0.029**
Brachypodium retusum	0.02	0.92	0.07	0.535
Bupleurum fruticescens	0.71	**0.00**	0.43	**0.007**
Carduus tenuiflorus	0.38	0.08	0.39	**0.006**
Carex humilis	0.00	1.00	0.43	**0.012**
Centaurea boissieri	0.38	0.08	0.38	**0.026**
Cistus albidus	0.06	0.75	0.12	0.310
Cistus clusii	0.01	0.95	0.31	**0.044**
Cistus salviflorus	0.37	0.12	0.00	1.000
Compuesta sp	0.51	**0.03**	0.34	**0.021**
Coronilla minima	0.04	0.84	0.17	0.272
Dacus caota	0.28	0.32	0.00	1.000
Dactylis glomerata	0.00	1.00	0.39	**0.011**
Daphne gnidium	0.29	0.23	0.11	0.382
Digitalis obscura	0.00	1.00	0.37	**0.011**
Dorycnium hirsutum	0.00	1.00	0.35	**0.023**
Dorycnium pentaphyllum	0.10	0.58	0.24	0.103
Echinops ritro	0.00	1.00	0.08	0.475
Erica multiflora	0.27	0.31	0.39	**0.009**
Erica terminalis	0.00	1.00	0.12	0.401

Euphorbia isatidifolia	0.06	0.72	0.00	1.000
Euphorbia characias	0.00	1.00	0.11	0.351
Euphorbia serrata	0.00	1.00	0.20	0.101
Euphorbia sp	0.00	1.00	0.20	0.116
Fumana ericoides	0.05	0.91	0.35	**0.026**
Fumana laevis	0.38	0.08	0.13	0.350
Fumana thymifolia	0.00	1.00	0.10	0.392
Galactites tomentosa	0.00	1.00	0.20	0.101
Galium aparine	0.00	1.00	0.10	0.414
Galium valentinum	0.00	1.00	0.02	0.859
Genista scorpius	0.45	0.08	0.45	**0.008**
Helianthemum cinereum	0.14	0.53	0.48	**0.005**
Helianthemum syriacum	0.04	1.00	0.10	0.414
Helictotrichon filifolium	0.00	1.00	0.49	**0.005**
Herbacea1	0.00	1.00	0.44	**0.007**
Juniperus oxycedrus	0.22	0.35	0.31	**0.037**
Lavandula latifolia	0.00	1.00	0.30	**0.040**
Lonicera implexa	0.01	0.96	0.17	0.272
Olea europaea	0.16	0.46	0.34	**0.011**
Phagnalon rupestre	0.28	0.26	0.18	0.177
Phlomis crinita	0.38	0.08	0.07	0.568
Pinus halepensis	0.56	**0.01**	0.29	**0.049**
Pinus pinaster	0.27	0.41	0.00	0.980
Pistacia lentiscus	0.64	**0.00**	0.00	0.966
Plantago lanceolata	0.00	1.00	0.05	0.772
Polygala rupestris	0.73	**0.01**	0.19	0.154
Quercus coccifera	0.24	0.28	0.27	0.058
Quercus ilex	0.08	0.67	0.21	0.115
Reseda undata	0.28	0.32	0.00	1.000
Rhamnus alaternus	0.00	1.00	0.28	**0.046**
Salvia rosmarinus	0.57	**0.02**	0.62	**0.001**
Rubia peregrina	0.58	**0.02**	0.35	**0.019**
Sangisorba minor	0.00	1.00	0.08	0.475
Satureja montana	0.00	1.00	0.20	0.136
Satureja obovata	0.00	1.00	0.08	0.451
Senecio malacitanus	0.28	0.32	0.00	1.000
Sideritis leucanta	0.00	1.00	0.10	0.414
Staehelina dubia	0.07	0.83	0.00	1.000
Stipa offneri	0.39	0.10	0.38	**0.015**
Stipa sp.	0.00	1.00	0.34	**0.019**
Teucrium chamaedrys	0.00	1.00	0.08	0.475
Teucrium flavum	0.68	**0.01**	0.20	0.101
Teucrium homotrichum	0.00	1.00	0.12	0.360
Teucrium libanitis	0.00	1.00	0.20	0.135
Teucrium pseudochamaepitys	0.86	**0.00**	0.17	0.236
Thapsia villosa	0.13	0.57	0.00	1.000
Thymus piperella	0.42	0.08	0.55	**0.002**
Thymus vulgaris	0.28	0.26	0.21	0.143
Ulex parviflorus	0.25	0.27	0.08	0.499

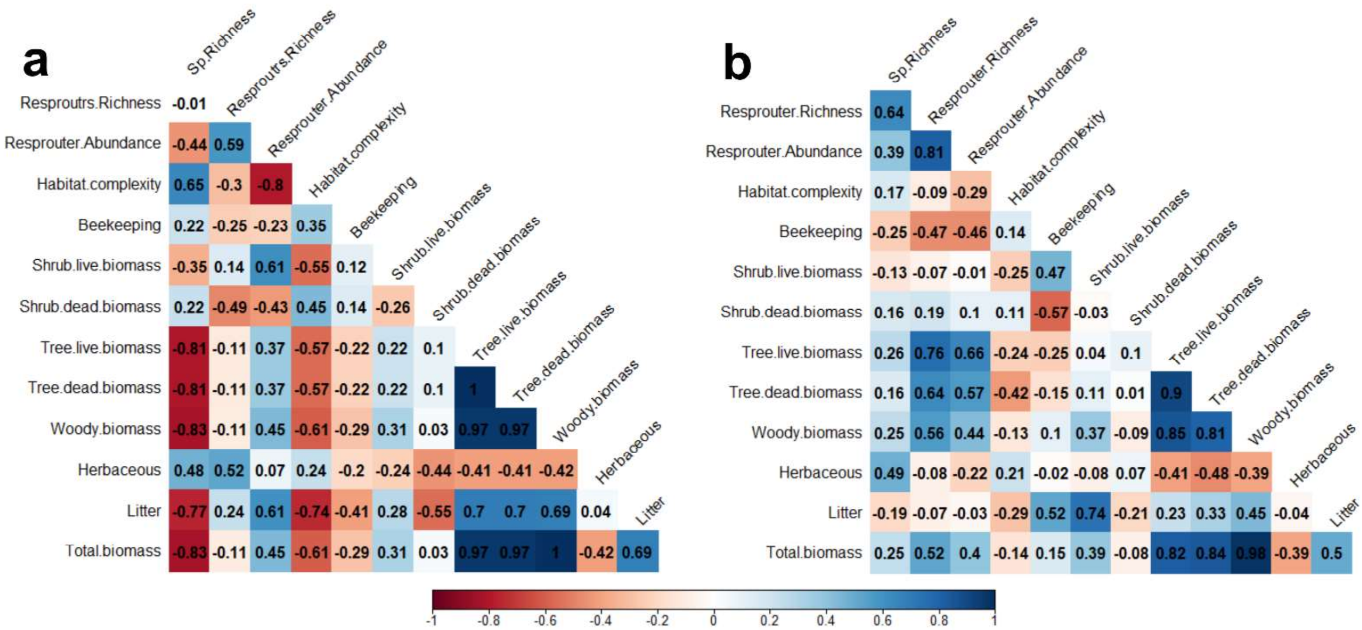

Fig S1. Spearman´s correlation matrix between aboveground attributes (N=12). Correlation analyses were performed to assess the relationship between variables, and only those providing non-redundant information (r < 0.7) were retained to calculate the related ecosystem services.

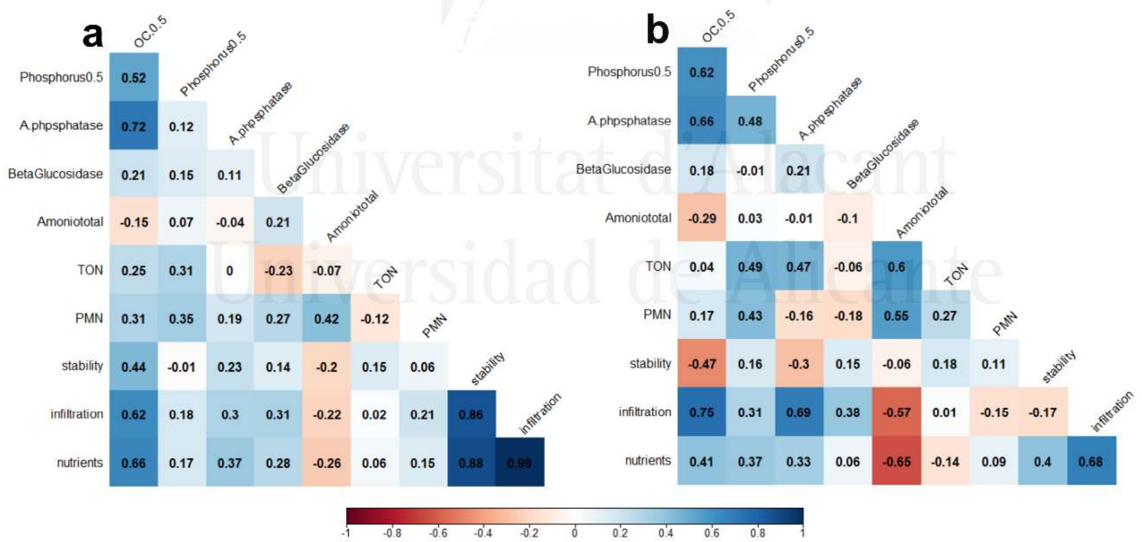

Fig S2. Spearman´s correlation matrix between belowground attributes (N=10). Correlation analyses were performed to assess the relationship between variables, and only those providing non-redundant information (r < 0.7) were retained to calculate the related ecosystem services. OC is the organic carbon, A. phosphatase: acid phosphatase. TON: the total oxidized nitrogen, PMN: potential nitrogen mineralization. All soil samples were taken at the first top 5 cm.

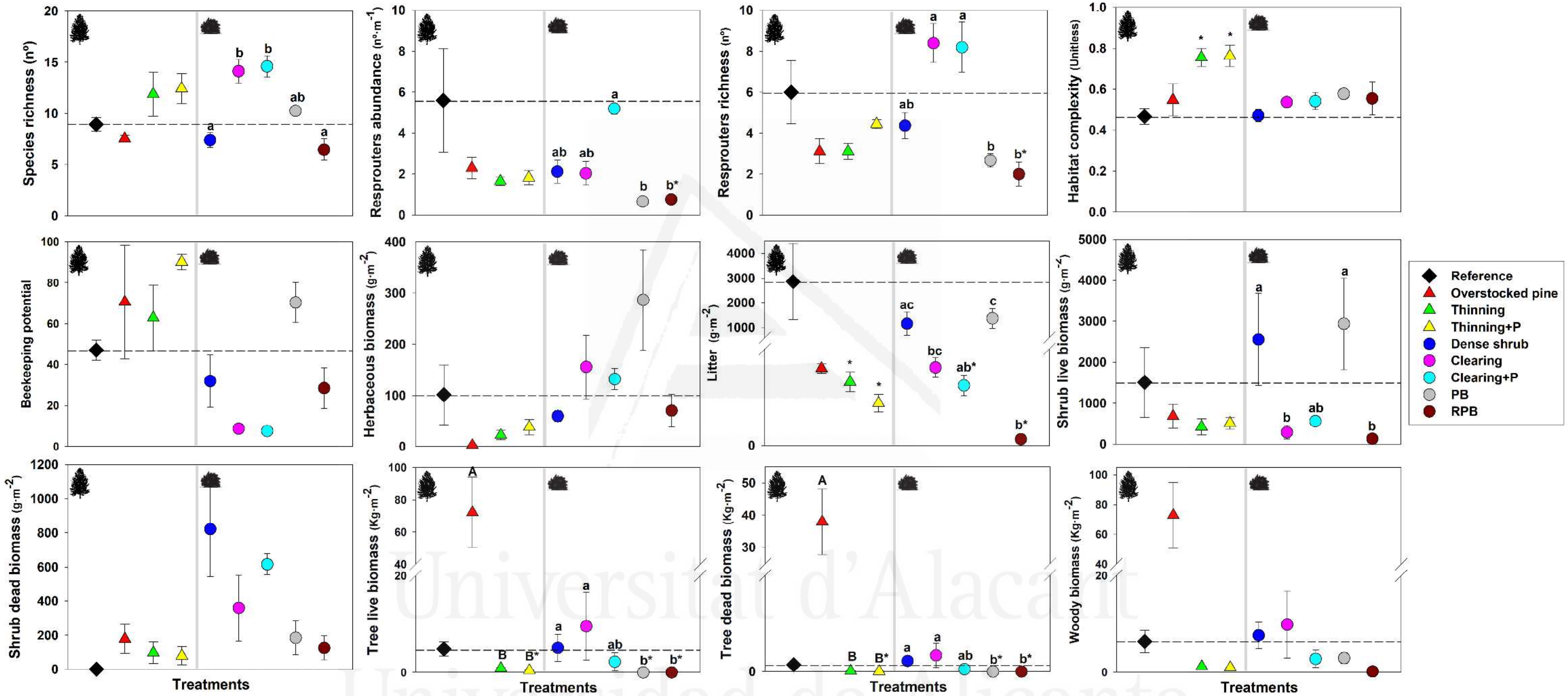

Fig S3. Mean (±SE) of aboveground attributes within overstocked pine forest (right) and dense shrubland (left). Different letters mean significant differences and no letters means no significant differences were found in between the different treatments. Asterisk means significant difference with reference (unburned) ecosystem. Dashed line is used to better visualize the reference ecosystem level.

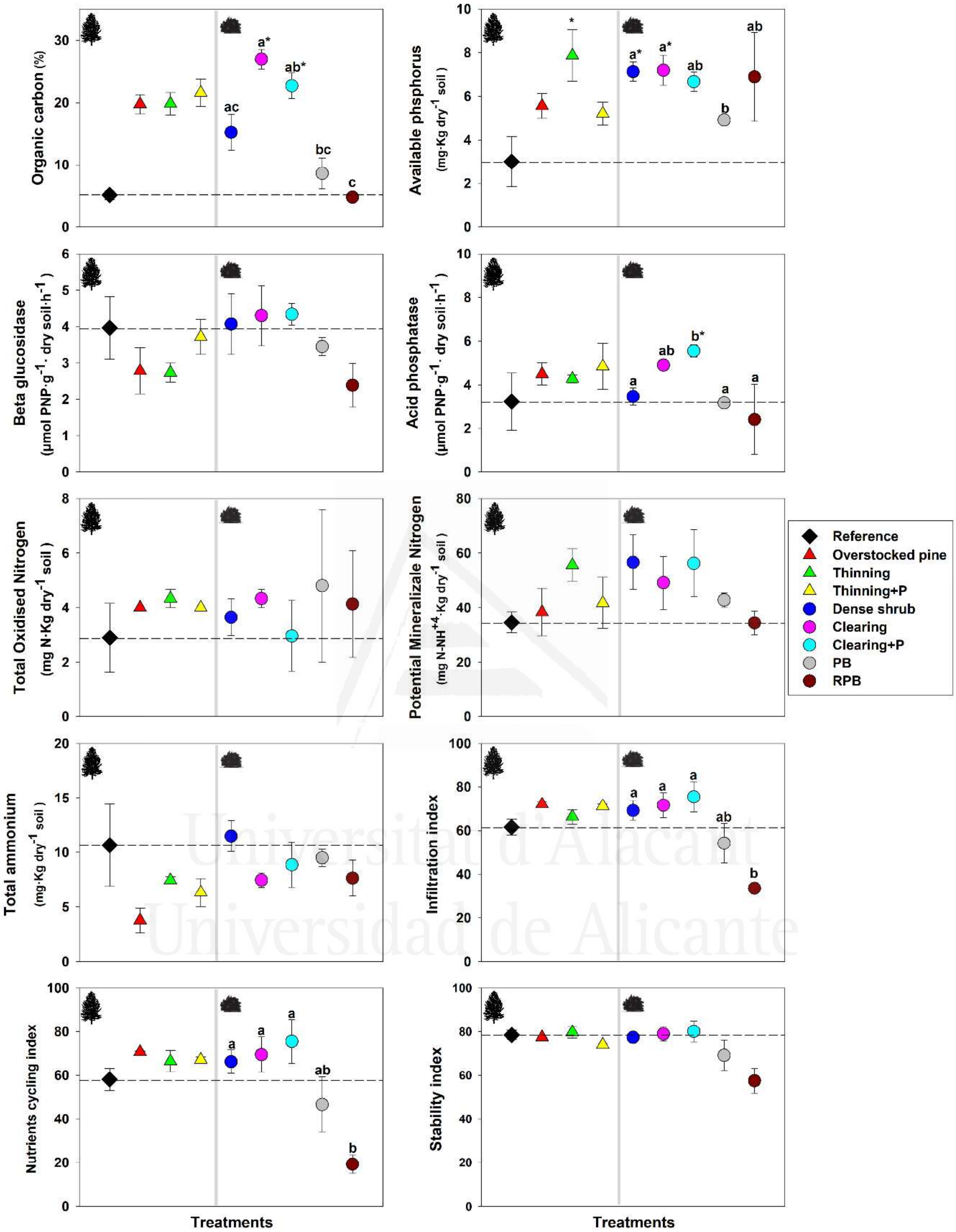

Fig S4. Mean (±SE) of belowground attributes within overstocked pine forest (right) and dense shrubland (left). Different letters mean significant differences and no letters means no significant differences were found in between the different treatments. Asterisk means significant difference with reference (unburned) ecosystem. Dashed line is used to better visualize the reference ecosystem level.

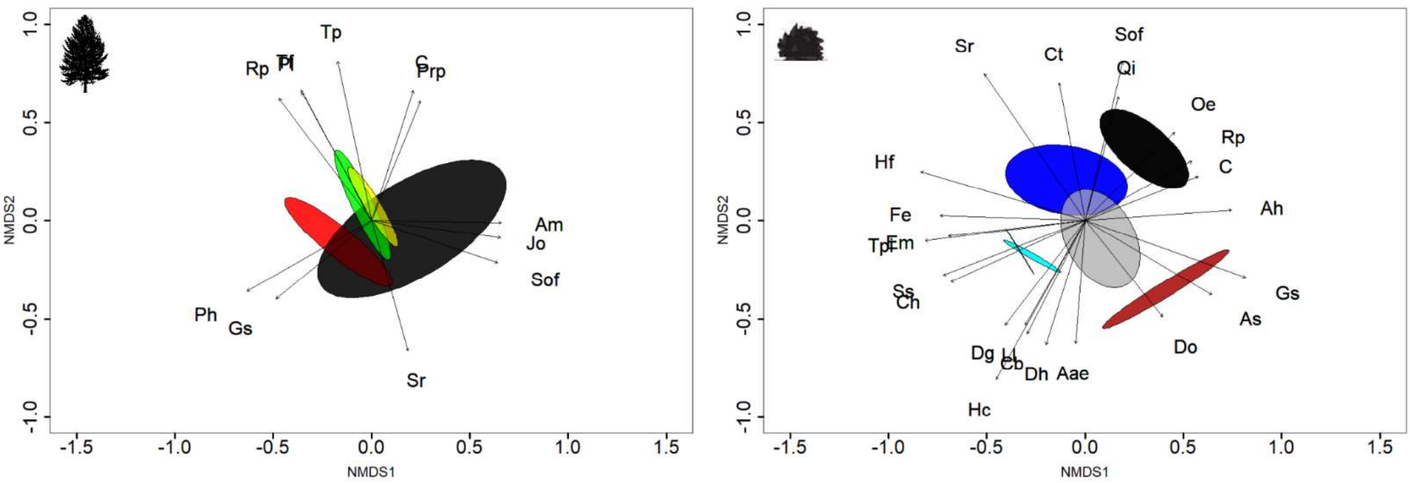

Fig S5. The non-metric multidimensional scaling (NMDS) of treatments to assess their effects on rare species using double square-root transformation (nearly presence/absence data). NMDS was performed using 75 plant species found in all study plots.Left and right panels show the treatments applied within overstocked pine forest and dense shrub respectively. The ellipses show 95% standard error for different treatments. Species shown are those significantly related to the compositional changes. Species legend: Am: *Aphyllantes monspeliensis*, Az: *Argyrolobium zanonii*, Aa: *Asparagus acutifolius*, Ah: *Atractylis humilis*, Bp: *Brachypodium phoenicoides*, Br: *Brachypodium retusum*, Bf: *Bupleurum fruticescens*,Ct: *Carduus tenuiflorus*, Cb: *Centaurea boissieri*, C: *Centaurea sp*, Ca: *Cistus albidus*, Cc: *Cistus clusii*, Cmo: *Cistus monspelliensi*, Cs: *Cistus salviflorus*, Cp: *Compuesta sp*, Cm: *Coronilla minima*, Csc: *Coronilla scorpioides*, Dc: *Dacus caota*, Dgn: *Daphne gnidium*, Dp: *Dorycnium pentaphyllum*, Ev: *Echium vulgare*, Em: *Erica multiflora*, Ei: *Euphorbia isatidifolia*, E: *Euphorbia sp*, Fe: *Fumana ericoides*, Fl: *Fumana laevis*, Ft: *Fumana thymifolia*, Gs: *Genista scorpius*, Hc: *Helianthemum cinereum*, Hs: *Helianthemum syriacum*, Jo: *Juniperus oxycedrus*, Ls: *Linum suffruticosum*, Li: *Lonicera implexa*, Oe: *Olea europaea*, Of: *Ononis fruticosa*, Om: *Ononis minutissima*, Ps: *Paronychia suffruticosa(polygonifolia*), Pr: *Phagnalon rupestre*, Pl: *Phlomis lychnitis*, Pc: *Phlomis crinita*, Ph: *Pinus halepensis*,Pp: *Pinus pinaster*, Ple: *Pistacia lentiscus*,Prp: *Polygala rupestris*,Qc: *Quercus coccifera*,Qi: *Quercus ilex*, Ru: *Reseda undata*, R: *Rosa sp*, Ro: *Rosmarinus officinalis*, Rpe: *Rubia peregrina*, Ss: *Sedum sediforme*, Sm: *Senecio malacitanus*, Sd: *Staehelina dubia*, Sof: *Stipa offneri*, Tf: *Teucrium flavum*, Tp: *Teucrium pseudochamaepitys*, Tvi: *Thapsia villosa*, Tpi: *Thymus piperella*, Tv: *Thymus vulgaris*, Up: *Ulex parviflorus*

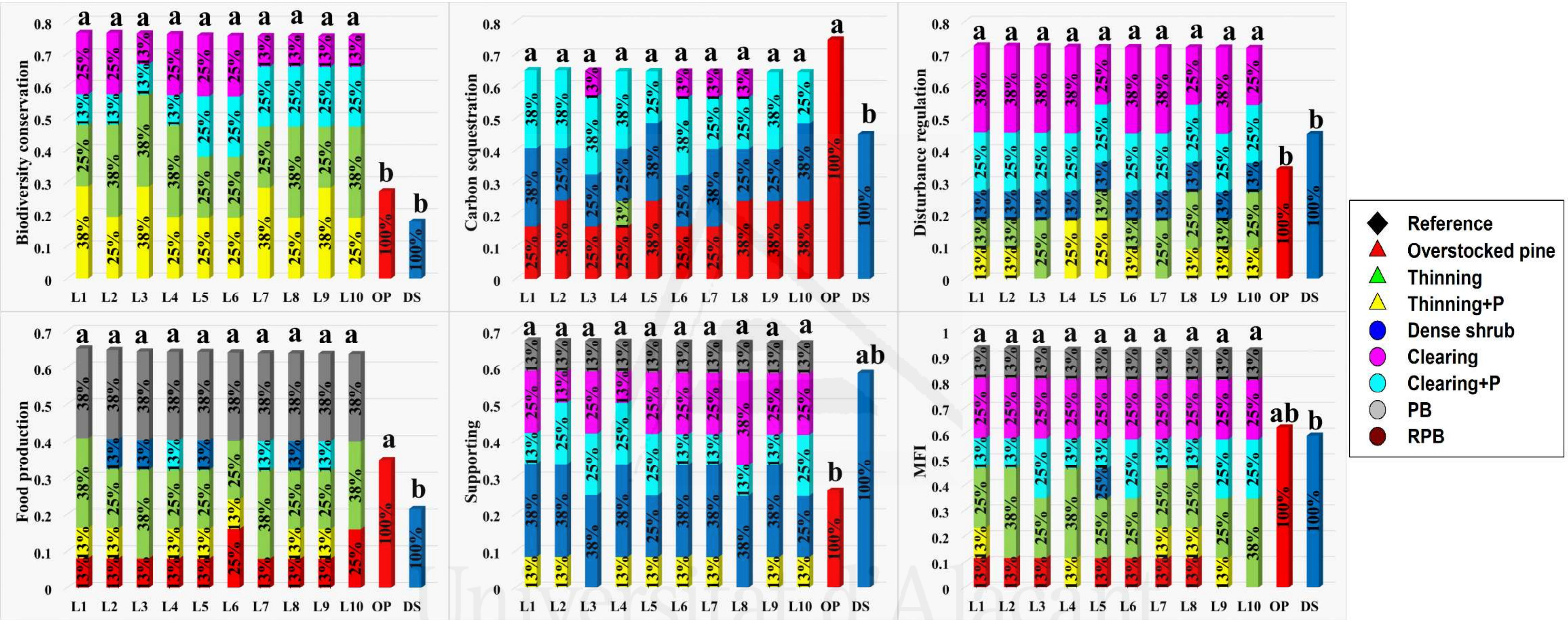

Fig S6. Configuration of 10 (+2 untreated) artificial landscapes (out of 4686825 landscapes created from the combination of 8 plots) that provide the highest levels in function of each ecosystem service and multifunctionality. Landscapes are created by combining three study plots. Bars show the means of ecosystem services and multifunctionality (MFI). Different letters mean significant differences. PB and RPB are prescribed burn and repeated prescribed burns respectively.

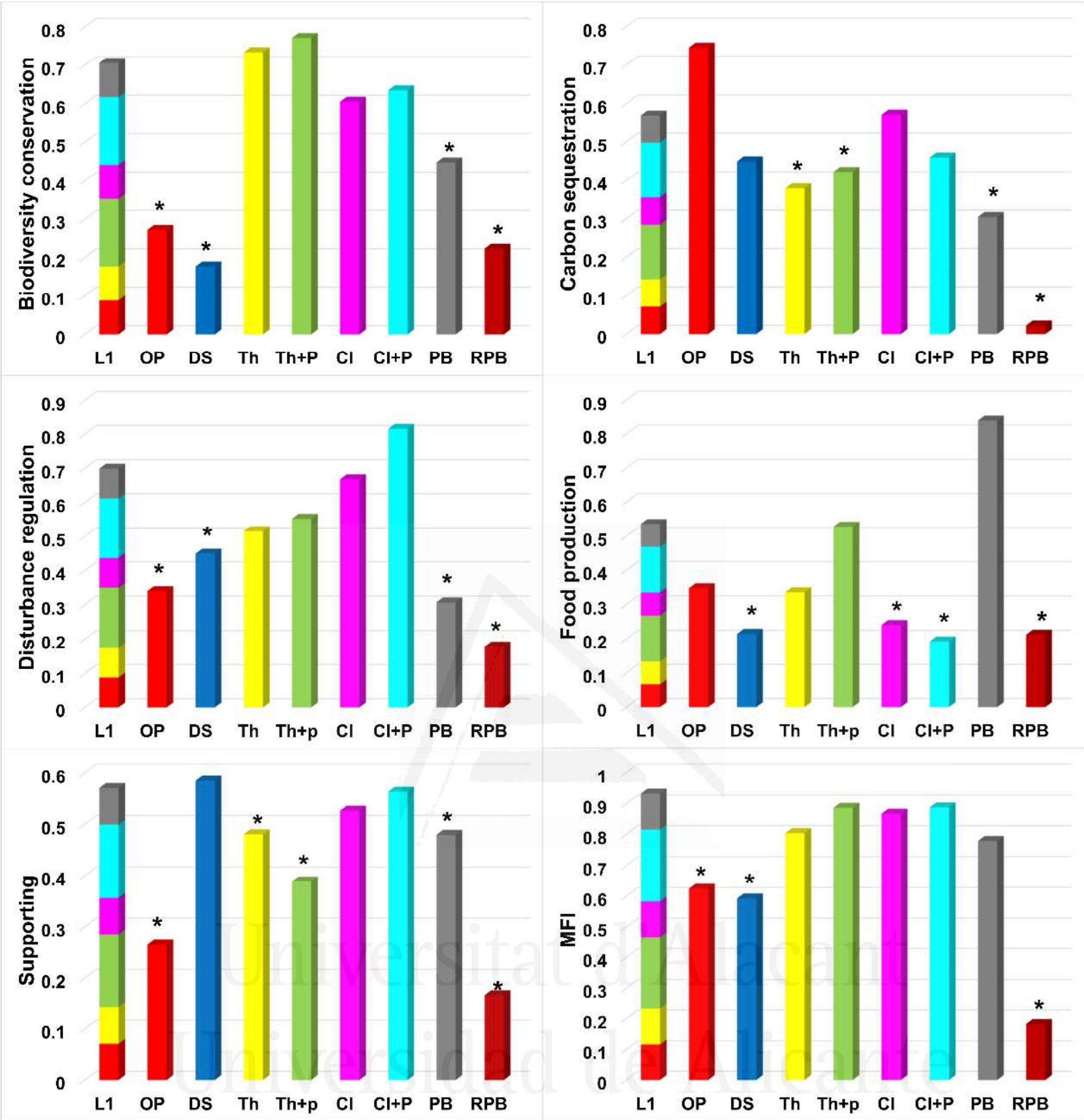

Fig S7. Mean of ecosystem functions and multifunctionality within nine landscapes scenarios; 8 homogenous landscapes established by one treatment (OP: overstocked pine, DS: dense shrub, Th: Thinning, Th+P: thinning + plantation, Cl: clearing, Cl+P: clearing + plantation, PB: prescribed burn, RPB: repeated prescribed burns) compared to the best scenario (L1, that provide the highest values of multifunctionality) of each ecosystem services. Asterisk means significant difference with the best scenario (L1)

Chapter V

Conclusions

(1) High fire recurrence and time since last fire interacted to determine ecosystem services but did not affect the synergies and trade-offs between them. Their combined effects reduced carbon sequestration and multifunctionality. Disturbance regulation diminished drastically with the first fire, with no effect of further fires. However, their effects dampened, and even became positive, for biodiversity conservation and food production services if provided enough time to recover.

(2) Thinning in overstocked pine stands enhances ecosystem attributes associated with biodiversity conservation without compromising the provision of carbon sequestration. After 10 years, the two levels of thinning, (600 and 1200 trees·ha^{-1}), similarly affected ecosystem attributes, which suggest that 1200 trees·ha-^{1} suffice to enhance individual ecosystem attributes.

(3) Clearing within dense shrubland dominated by seeder species enhances ecosystem attributes associated with biodiversity conservation without compromising the capacity of ecosystem to sequester carbon.

(4) Plantation of resprouting species combined with thinning and clearing, in overstocked pine forests and dense shrublands respectively, can enhance the provision of ecosystem services of disturbance regulation, food production as well as ecosystem multifunctionality.

(5) Prescribed burning reduces the amount of dead fuel, increases biodiversity conservation, and improves food production. However, these effects become negative, in addition to the decline in disturbance regulation and multifunctionality, if prescribed burning is frequently applied.

(6) Combining different management activities at landscape scale enhances the supply of multiple ecosystem services simultaneously by reducing the trade-offs in between them and therefore, establishes multifunctional Mediterranean landscapes.

Chapter VI

Resumen ampliado

En esta sección se presenta el resumen de la investigación, la metodología general y los principales resultados obtenidos en el marco de esta tesis doctoral. Estos resultados se organizan principalmente en tres puntos diferentes que se refieren a los capítulos 2, 3 y 4 de la tesis.

Los incendios forestales son una de las perturbaciones más importantes que configuran la estructura y el funcionamiento de muchos ecosistemas propensos al fuego (por ejemplo, los ecosistemas mediterráneos) y está afectando cada vez más a ecosistemas poco expuestos al fuego (por ejemplo, los bosques tropicales y los bosques caducifolios templados) (Mayor et al., 2016; Pellegrini et al., 2018). En la Cuenca Mediterránea, los incendios forestales se han producido durante milenios y son un motor inherente de los procesos ecológicos (Scott et al., 2014). Sin embargo, en las últimas décadas, cambios del uso del suelo (abandono de los cultivos) y el cambio climático (aumento de la aridez) han cambiado los regímenes de incendios hacia eventos de fuego más frecuentes y de mayor amplitud (Duane et al., 2021; Pausas & Fernández-Muñoz, 2012) lo que podría comprometer la resiliencia y el funcionamiento de los ecosistemas (Blondel & Aronson, 1995). Los ecosistemas mediterráneos se consideran resilientes al fuego, sin embargo, los cambios en el régimen de incendios pueden alterar esta capacidad de respuesta aumentando los posibles fallos de regeneración de la vegetación. Alta recurrencia de incendios con intervalos cortos de tiempos puede reducir la capacidad de regeneración y puede llevar a la extinción local de especies, ya sea eliminando las estructuras de persistencia o reduciendo la capacidad de las especies para reponer sus bancos de semillas (Santana et al., 2014). Esto se refleja en una simplificación de la estructura de la vegetación (Enright et al., 2015), con cambios de bosque a matorral (Karavani et al., 2018). Estos cambios pueden afectar, en diferentes maneras, a funciones y servicios del ecosistema como la diversidad vegetal y animal, la producción de forraje, el secuestro de carbono y la disponibilidad de nutrientes. Ante los efectos que se esperan debido a la alta recurrencia de incendios y el corto tiempo transcurrido después del último incendio sobre los atributos del ecosistema, necesitamos conocer no sólo las respuestas en la estructura y la composición de vegetación, sino también en las múltiples funciones y servicios que proporcionan. Además, estos servicios ecosistémicos no son independientes entre sí, por lo que pueden existir sinergias (por ejemplo, entre la producción de forraje y el secuestro de carbono) o compromisos (por ejemplo, los servicios culturales y la producción de madera son difíciles de maximizar simultáneamente, Felipe-Lucia et al., 2018). El efecto de la gestión y restauración en estas sinergias y compromisos han recibido cierta atención recientemente (Felipe-Lucia et al., 2018; Raudsepp-Hearne et al., 2010) pero el efecto de las perturbaciones naturales todavía no han sido estudiadas en profundidad (Turner et al., 2013). De hecho, los pocos estudios que evalúan la relación entre los incendios forestales y los múltiples servicios ecosistémicos se centran en pocas mediciones empíricas (Pausas & Keeley, 2019) y muy pocos de ellos se centran en los bosques mediterráneos, que se encuentran entre los ecosistemas más afectados por los incendios forestales.

Los bosques de pino carrasco (*Pinus halepensis*) se encuentran entre los principales componentes de la vegetación de la Cuenca Mediterránea que se ve afectada por incendios forestales. *P. halepensis*, una especie autóctona de la Cuenca Mediterránea (Quézel, 2000), es una de las especies más abundantes en esta región favorecida, en parte, por su capacidad para colonizar campos de cultivo abandonados y su uso en el pasado en planes de reforestación masiva (Le Houerou, 2000; Maestre & Cortina, 2004). Tras el incendio, la regeneración puede variar en función de varios factores, como por ejemplo la estructura y composición del bosque, las condiciones climáticas, la profundidad y tipo de suelo y la severidad del incendio (Rodríguez-García et al. 2022). Esta regeneración puede oscilar entre un pinar hiperdenso (>75.000 individuso ha^{-1}) o una baja densidad de pino que da lugar a un denso estrato arbustivo dominado por germinadoras obligadas (por ejemplo, *Ulex parviflorus, Cistus albidus y Salvia rosmarinus*). Estos ecosistemas presentan altos niveles de competencia entre especies por recursos como la luz, el agua y los nutrientes, albergan menos biodiversidad y acumulan altas proporciones de combustible muerto. Por lo tanto, estos ecosistemas densos y homogéneos pueden presentar una alta vulnerabilidad a nuevas perturbaciones (incendios, brotes de plagas), así como un menor funcionamiento. En este contexto, puede ser más pragmático cambiar los objetivos de gestión de la supresión de incendios hacia un enfoque integrado que combine la prevención de incendios y la promoción de paisajes más resilientes (Moreira et al., 2020). Sin embargo, el desarrollo de estrategias de gestión y restauración adecuadas para mitigar los cambios en el régimen de incendios mediante la mejora de las funciones de los ecosistemas y la provisión de servicios ecosistémicos a diferentes escalas siguen siendo un reto de investigación por explorar (Nocentini et al., 2022; Palahí et al., 2009).

El objetivo general de esta tesis es investigar los principales efectos en el funcionamiento de los bosques Mediterráneos como consecuencia de los cambios en el régimen de incendios y los efectos de diferentes tipos de manejo y gestión en las comunidades vegetales. En concreto, investigamos estos efectos evaluando la capacidad de los ecosistemas (afectados/tratados) en proporcionar múltiples servicios ecosistémicos (conservación de biodiversidad, fijación de carbono, regulación de perturbación, producción de alimentos y servicios de apoyo). Estos servicios han sido calculados a través de más de 25 atributos relacionados con la estructura y la composición de la vegetación y las propiedades del suelo. Además, estos servicios ecosistémicos se integraron en un índice estandarizado de "multifuncionalidad del ecosistema", es decir la capacidad del ecosistema de proporcionar múltiples servicios ecosistémicos en altos niveles y de manera simultánea. Planteamos las hipótesis de que (i) el suministro de las diferentes funciones de los ecosistemas habría variado según la vegetación resultante, lo que a su vez estaría determinado por los cambios en el régimen de incendios. (ii) los cambios en el régimen de incendios afectarían a las sinergias y compromisos de los bosques mediterráneos (iii) la reducción de la densidad de la vegetación mediante actividades de gestión, combinada con las plantaciones de especies rebrotadoras, reorientaría los ecosistemas regenerados hacia paisajes mediterráneos menos vulnerables y más funcionales.

En los siguientes puntos se describen los capítulos correspondientes a la investigación de la tesis doctoral.

1. La recurrencia de los incendios y el tiempo transcurrido desde el último incendio interactúan para determinar el suministro de múltiples servicios ecosistémicos por parte de los bosques mediterráneos.

Para este capítulo se seleccionaron 29 parcelas de 30 × 20 m ubicadas en siete zonas en la Comunidad Valenciana, Sureste de España (Capitulo II Tabla S1). Estas parcelas eran antiguos campos de cultivo abandonados en la última mitad del siglo XX. Estos campos han sido colonizados principalmente por *Pinus halepensis*. Estos pinares y sus respectivas etapas afectadas por el fuego son representativos de los sistemas naturales y seminaturales que dominan extensas áreas de la Cuenca Mediterránea (Sheffer, 2012).

Se analizaron los efectos de la recurrencia de incendios (5 niveles: 0, 1, 2, 3 y 4 incendios), tiempo transcurrido tras el último incendio (TSLF, desde 1 hasta 35 años después del último incendio), así como su efecto combinado en la multifuncionalidad de los ecosistemas (i.e., la capacidad de los ecosistemas de proporcionar múltiples funciones y servicios ecosistémicos a altos niveles simultáneamente). Para ello, evaluamos los efectos de la recurrencia de los incendios y del TSLF en cinco servicios ecosistémicos (conservación de la biodiversidad, secuestro de carbono, regulación de las perturbaciones, producción de alimentos y servicios de apoyo), basados en 25 atributos de los ecosistemas aéreos y del suelo (ver la parte metodología general para más información sobre cómo se calcularon los diferentes atributos). Nos planteamos las siguientes preguntas: (i) ¿cómo afecta la recurrencia de incendios a la provisión de servicios ecosistémicos y a la multifuncionalidad general del ecosistema? (ii) ¿Interactúa el TSLF con la recurrencia de incendios para determinar los servicios del ecosistema? y (iii) ¿afecta la recurrencia de los incendios y el TSLF a las sinergias y compromisos entre los servicios de los ecosistemas?

Este estudio muestra que los cambios en los regímenes de incendios pueden alterar sustancialmente el suministro de importantes servicios y funciones ecosistémicas de los bosques mediterráneos. Nuestros resultados mostraron que el incremento de la recurrencia de incendios redujo la multifuncionalidad del ecosistema. La multifuncionalidad fue un 20% menor en bosques quemados de uno a tres veces respecto a los bosques no quemados, y 70% menos en bosques quemados cuatro veces. La recurrencia de incendios y TSLF interactuaron para determinar tres de los cinco servicios medidos: conservación de biodiversidad, producción de alimentos y fijación de carbono. Si los incendios forestales se vuelven más frecuentes, como se espera (Turco et al., 2014), esto disminuiría de forma crítica la capacidad de los bosques mediterráneos para almacenar carbono, detener la pérdida de biodiversidad o producir alimentos. La proporción de los servicios de conservación de biodiversidad y producción de alimentos se redujo bajo el efecto de la recurrencia, aunque este efecto negativo se atenuó, e incluso pasó a ser positivo si el TSLF es lo suficientemente largo (20 años o más). Por lo tanto, para mejorar la provisión de estos servicios, la gestión y la vigilancia deberían tener como objetivo minimizar los riesgos de incendio en aquellos ecosistemas que ya se han quemado alguna vez, para darles el tiempo suficiente para recuperarse. Esto último podría conseguirse bien reduciendo la carga de combustible o reintroduciendo especies con baja inflamabilidad (por ejemplo, especies rebrotadoras) en las zonas quemadas con mayor frecuencia (Santana et al., 2018).

La fijación de carbono mostró una respuesta positiva al TSLF (pero disminuyó con la recurrencia de incendios, y sobre todo después del segundo incendio coincidiendo con la pérdida del estrato arbóreo en la mayoría de los casos. De hecho, esta respuesta fue impulsada principalmente por los cambios en la biomasa leñosa. Estos resultados están en relación con estudios que reportan que si los incendios recurrentes afectan antes de que los árboles hayan tenido la oportunidad de alcanzar la madurez reproductiva pueden producir disminuciones en la biomasa arbórea, la productividad y la resiliencia (Mayor et al., 2016; Pellegrini et al., 2018; Tapias et al., 2001; Turner et al., 2019). Esto conlleva una importante reducción de la capacidad de secuestrar carbono. Por otro lado, los servicios de regulación de las perturbaciones y de soporte no se vieron afectados por los cambios en el régimen de incendios. Sin embargo, en comparación con las parcelas no quemadas, estos dos servicios ecosistémicos disminuyeron aproximadamente un 40% y un 30% respectivamente después del primer incendio. Además, el efecto de la recurrencia sobre la densidad del combustible muerto, un atributo importante relacionado con el riesgo de incendio (y por tanto asociado a los servicios de regulación de las perturbaciones), fue negativo. En general, la mayoría de los efectos observados fueron modulados por los atributos relacionados con la estructura y la composición de la vegetación más que los que están relacionados con las propiedades de suelo. Además, la sinergias y compromisos entre los diferentes servicios ecosistémicos no fueron afectados por la recurrencia del fuego, el TSLF, ni su interacción. Esto sugiere que las relaciones entre los servicios ecosistémicos proporcionados por los ecosistemas mediterráneos son consistentes y no están impulsadas por los cambios estructurales y composicionales de la vegetación. Esto está parcialmente en desacuerdo con los resultados encontrados en los bosques templados, ya que las sinergias y compensaciones de los servicios que proporcionan se vieron fuertemente afectadas por los cambios estructurales relacionados con la gestión (Felipe-Lucia et al., 2018). La falta de respuesta podría estar relacionada con otros factores no considerados en este estudio como la influencia de las características del paisaje. Sin embargo, nuestros resultados coinciden en parte con estos hallazgos anteriores, dado que la conservación de la biodiversidad (relacionada con la heterogeneidad del hábitat) se correlacionó positivamente con la producción de alimentos y los servicios de regulación de las perturbaciones en todos nuestros sitios de estudio. Nuestros resultados sugieren, además, que la recurrencia de incendios puede reducir las sinergias entre los servicios de los ecosistemas o incluso cambiarlas por compromisos. Este resultado hace necesario realizar futuras investigaciones para evaluar si el TSLF y los cambios estructurales y de composición de la vegetación asociados son un factor importante que mejora las sinergias de los ecosistemas, como sugieren tanto Felipe-Lucía et al. (2018) en bosques templados como Lucas-Borja & Delgado-Baquerizo (2019) en ecosistemas Mediterráneos.

2. El aclareo y la plantación de especies rebrotadoras redirigen las masas de pino hiperdensas hacia comunidades más funcionales en la Cuenca Mediterránea

En este capítulo analizamos los efectos a largo plazo (10 años) de dos niveles de aclareo (600 árboles·ha^{-1} y 1200 árboles·ha^{-1}) con y sin la plantación de una especie rebrotadora (*Quercus faginea*) en rodales con una regeneración hiperdensa de pino sobre varios servicios ecosistémicos. En concreto, estos servicios ecosistémicos fueron los deconservación de la biodiversidad, captura de carbono, resiliencia del ecosistema, producción de alimentos y de soporte, y se determinaron a partir de 28 atributos del ecosistema aéreos y del suelo. Los objetivos de estos tratamientos fueron (i) reducir los riesgos de incendio y la vulnerabilidad de los rodales, y (ii) aumentar la provisión de servicios ecosistémicos y el funcionamiento del ecosistema. Nuestra hipótesis fue: la combinación de aclareo y plantación de especies rebrotadoras tendrá efectos positivos en los atributos relacionados con la estructura y la composición de la vegetación y las propiedades del suelo, reducirá el riesgo de incendios y aumentará la provisión de servicios ecosistémicos. Para ello, seleccionamos tres incendios forestales ocurridos durante el verano de 1994 en zonas con características similares edáficas, climáticas y de composición de la vegetación anteriores al incendio. En concreto, seleccionamos tres zonas (Capitulo III. Tabla S1) localizadas en las sierras de Mariola (38°43′N, 0°24′W) y Benicadell (38° 49′N, 0°24′W). La vegetación se regeneró en masas homogéneas y densas de *P. halepensis* mezclado con un matorral dominado por especies germinadoras como *Ulex parviflorus, Salvia rosmarinus, y Cistus albidus.* En otoño/invierno de 2009, se redujo experimentalmente la densidad de árboles mediante aclareos (dos niveles: 600 y 1200 árboles-ha^{-1}) y plantamos una especie rebrotadora (*Quercus faginea*; 300 plántulas-ha^{-1} y sin plantación) siguiendo un diseño factorial completo con cuatro parcelas de 0,5 ha (N=12; 4 combinaciones de tratamiento × 3 sitios). Además de estos tratamientos, dejamos tres parcelas de 0,5 ha sin gestionar como control con la densidad de pinos original (75.000-220.000 árboles-ha^{-1}, Capitulo II-Tabla S1) y sin plantación (ver Capitulo III para más información sobre el experimento).

En este estudio, encontramos que el aclareo de árboles hasta 1200 árboles·ha^{-1} puede ser suficiente para mejorar muchos atributos del ecosistema de interés, pero que solo la combinación de aclareo y plantación de especies rebrotadoras (*Q. faginea*) puede ser capaz de maximizar la regulación de las perturbaciones (incluyendo el control del riesgo de incendios) y los servicios de producción de alimentos a largo plazo. Por lo tanto, la combinación de estas dos técnicas de restauración, a menudo aplicadas individualmente, podría ser una gestión integrada adecuada para redirigir los bosques densos de pinos hacia bosques mixtos, a menudo reportados como bosques más funcionales y menos vulnerables (Pretzsch & Forrester, 2017). La multifuncionalidad en su conjunto no cambió significativamente en respuesta a nuestros tratamientos, quizás debido a las respuestas contrastadas de las diferentes funciones a dichos tratamientos. Sin embargo, los servicios ecosistémicos de conservación de la biodiversidad, la producción de alimentos y la regulación de las perturbaciones fueron mejorados por, al menos, uno de los tratamientos, con sus valores más altos observados en la combinación de aclareo (600 árboles·ha^{-1}) + plantación de *Q. faginea*. De hecho, las parcelas con plantación de *Q. faginea* mostraron los valores más altos de regulación de la perturbación (hasta 2 veces más altos) en comparación con las parcelas no tratadas, y sólo aquellas parcelas con la menor densidad de árboles y plantación (600 + P) mejoraron significativamente la producción de alimento (hasta un 90% más) respecto a las parcelas no tratadas. Además, en comparación con las parcelas no tratadas, todos los tratamientos aumentaron hasta 2 veces la conservación de la biodiversidad. También aumentó la multifuncionalidad del ecosistema, aunque este aumento fue sólo marginalmente significativo. Estos resultados son la consecuencia de que los efectos que el aclareo suele proporcionar como reducir la competencia entre especies incrementa la disponibilidad de los recursos (por ejemplo, luz, agua y nutrientes) (Agee & Skinner, 2005). Esto, además, permite reducir la carga del combustible muerto y disminuye la vulnerabilidad de estos ecosistemas frente a nuevos incendios. Asimismo, la plantación de especies rebrotadoras a menudo se reportan como especies clave en la restauración de ecosistemas degradados y vulnerables debido a su efecto positivo en la resistencia y la resiliencia a las perturbaciones (Gavinet et al., 2015; Santana et al., 2018; Vallejo & Alloza, 1998). No se observaron, sin embargo, efectos en la fijación de carbono ni en los servicios de soporte. Esto es probablemente debido, en el caso de fijación de carbono, al crecimiento compensatorio de los pinos (Dwyer et al., 2010; Manrique-Alba et al., 2020) y a las respuestas contrastadas y débiles de los atributos relacionados con las propiedades del suelo en el caso de los servicios de soporte.

3. **La combinación de estrategias de gestión post-incendio puede maximizar la multifuncionalidad del paisaje en los ecosistemas mediterráneos.**

En este estudio, evaluamos los efectos a largo plazo (hasta 40 años) de diferentes estrategias de gestión post-incendio dentro de los ecosistemas resultantes de bosques quemados de *P. halepensis*: aclareo de árboles (600 árboles·ha^{-1}) ± plantación de especies rebrotadoras dentro de rodales hiperdensas de pino, y desbroce ± plantación de especies rebrotadoras, quema prescrita única y quema prescrita repetida (cada 10 años) en matorrales densos. Evaluamos sus efectos en cinco servicios ecosistémicos (conservación de la biodiversidad, fijación de carbono, regulación de las perturbaciones, producción de alimentos y servicios de soporte) utilizando 22 atributos de la parte aérea y subterránea del ecosistema. Todos los tratamientos tenían como objetivo aumentar la provisión de servicios ecosistémicos, mejorar el funcionamiento del ecosistema, a la vez que se reduce el riesgo de incendios y la vulnerabilidad del ecosistema. Nos planteamos las siguientes preguntas: (i) ¿qué estrategias de gestión, aplicadas dentro de los pinares hiperdensos y los matorrales densos, permiten la recuperación de los atributos y el funcionamiento de los pinares con respecto a los niveles de los pinares maduros no quemados (en adelante, de referencia), (ii) ¿cómo los cambios en la composición de las especies regulan la provisión de los servicios del ecosistema y la multifuncionalidad? y (iii) ¿cómo podemos gestionar estos diferentes ecosistemas para obtener paisajes funcionales? Para ello, se seleccionaron diferentes zonas quemadas en la Comunidad Valenciana, Sureste de España. En primer lugar, se seleccionaron tres zonas afectadas por un incendio en 1979, que dio lugar a un matorral denso con pinos dispersos. En 2003 se aplicaron tratamientos de desbroce con y sin plantación de especies rebrotadoras (*Quercus ilex, Rhamnus alaternus y Pistacia lentiscus*). En segundo lugar, se seleccionó otra zona afectada por un incendio en 1984, que también dio lugar a una regeneración de matorral denso con pinos dispersos. En estas últimas zonas se aplicaron quemas prescritas a partir de 1994 hasta el 2016 con una frecuencia de aproximadamente cada 10 años, por lo tanto, se obtuvo parcelas tratadas 3 veces. Finalmente, en este estudio también se incluye las parcelas con alta regeneración de pino tratadas con un aclareo (600 árboles·ha^{-1}) ± plantación de especies rebrotadoras explicadas en el capítulo anterior. En este diseño de parcelas, se añadieron otras parcelas no quemadas consideradas como ecosistemas de referencia lo más cercanas posibles a los tratamientos de gestión realizados.

Los resultados de este estudio mostraron que, a escala de parcela, la reducción de la densidad de la vegetación mediante aclareos y desbroces, combinada con la plantación de especies rebrotadoras, son técnicas adecuadas para restaurar los ecosistemas degradados y, junto con la aplicación puntual del fuego prescrito, pueden establecer paisajes mediterráneos multifuncionales. Los tratamientos de aclareo y desbroce, ambos combinados con la plantación de especies rebrotadoras, demostraron su eficacia para acelerar el proceso de sucesión y reorientar las comunidades degradadas y vulnerables dominadas por especies germinadoras hacia bosques mixtos dominados por especies rebrotadoras. Estos bosques mixtos suelen ser reportados como ecosistemas más resistentes, resilientes y funcionales (Gavinet et al., 2015; Pretzsch & Forrester, 2017; Santana et al., 2018). Estos tratamientos impulsaron cambios en la composición de especies que se tradujo en un incremento de la riqueza de especies debido a la alta disponibilidad de recursos y la baja competencia entre especies generada al reducir la densidad de vegetación (Agee & Skinner, 2005; Santana et al., 2018). Al contrario de lo que ocurre con una quema prescrita, los incendios prescritos repetidos mostraron una menor diversidad con predominio de especies herbáceas (por ejemplo, *Brachypodium retusum*). Esto se debe probablemente al fuego repetido que cambia las propiedades del suelo, limitando la disponibilidad de recursos (por ejemplo, nutrientes) y a que afecta negativamente a la capacidad de rellenado del banco de semillas del suelo. Este tipo de gestión desplazaría el matorral denso con mayor presencia de especies leñosas hacia sistemas con mayor presencia de especies herbáceas y oportunistas (Santana et al., 2014). Además, estos cambios en la composición de especies determinaron la provisión de servicios ecosistémicos.

Los bosques mixtos pueden establecer paisajes funcionales que proporcionan múltiples servicios ecosistémicos a altos niveles (Pretzsch & Forrester, 2017). Los resultados del capítulo II (Moghli et al., 2021) sugieren que existen sinergias entre la conservación de la biodiversidad, la regulación de las perturbaciones y la producción de alimentos en los ecosistemas mediterráneos. En efecto, los resultados de este estudio muestran que la combinación de aclareos y desbroces con la plantación de especies rebrotadoras y la quema prescrita puede mejorar simultáneamente la provisión de estos servicios ecosistémicos y establecer paisajes multifuncionales en la Cuenca Mediterránea. La reducción de la densidad de la vegetación en todos los tratamientos aplicados, excepto las quemas prescritas repetidas, aumentó la conservación de la biodiversidad, que fue incluso superior a la del ecosistema de referencia en las parcelas en las que se aplicaron tratamientos de aclareo, desbroce y su combinación con la plantación de especies rebrotadoras. Por otro lado, la reducción de la densidad de la vegetación puede reducir potencialmente la capacidad del ecosistema para secuestrar carbono (De las Heras et al., 2013), sin embargo, no se vio afectada por el aclareo en el pinar hiperdenso e incluso fue superior al ecosistema de referencia por desbroce del matorral denso. Las quemas prescritas repetidas afectaron negativamente al secuestro de carbono, que es el resultado de la eliminación de la biomasa leñosa y de la reducción del carbono orgánico del suelo, así como de la cantidad de hojarasca, el principal aporte de nutrientes y carbono orgánico de los suelos forestales. El desbroce con la plantación de especies rebrotadoras mejoró la regulación de las perturbaciones en los matorrales densos; sin embargo, el resto de los tratamientos, excepto la quema prescrita, mostraron bajos niveles de resistencia a nuevas perturbaciones. Nuestros resultados señalan la importancia de considerar múltiples funciones de los ecosistemas, a largo plazo, cuando se evalúa el éxito de la gestión post incendio, y la importancia de combinar diferentes técnicas para acelerar el proceso de sucesión y establecer paisajes mixtos que suministren simultáneamente múltiples servicios ecosistémicos.

4. Metodología general:

En este apartado se explica la metodología del muestreo de campo y los análisis de laboratorio realizados para estudiar los efectos de la recurrencia de incendios, el tiempo transcurrido después el ultimo incendio, y los diferentes tratamientos (aclareo, desbroce, plantación de especies rebrotadoras y quemas prescritas) sobre la provisión de servicios ecosistémicos de los bosques mediterráneos.

En cada parcela se midieron 25 atributos (relacionados con la estructura y composición de la vegetación y propiedades del suelo, relacionados con el potencial de conservación de la biodiversidad, la capacidad para la fijación de carbono en la biomasa leñosa y en el suelo, la resistencia potencial a perturbaciones adicionales (ya sean más incendios o procesos erosivos del suelo), su potencial para producir alimentos (forraje para el ganado o para animales silvestres, producción potencial de miel), o su capacidad para capturar, almacenar y reciclar nutrientes. En cada parcela se establecieron varios transectos permanentes (tres de 30 m) en las zonas de pinar denso y cinco transectos de 10 m de longitud en las otras parcelas para evaluar la cobertura de especies vegetales. La diversidad (riqueza de especies, índice de diversidad de Shannon) se calculó mediante el método del punto-intersección (Greig-Smith, 1983). Las medidas se tomaron cada 20 cm y en cinco alturas (0-5 cm, 5-15 cm, 15-25 cm, 25-50 cm, 50-150 cm) (250 puntos/parcela). El potencial apícola se estimó como la abundancia de plantas de interés para la producción de miel, según la literatura publicada (Mateu, 2016; Sanchís et al., 1992). La cantidad de especies leñosas rebrotadoras que se reclutaron en cada parcela se evaluó en una subparcela de 10 ×10 m que se ubicó al azar dentro de cada parcela.

La biomasa arbustiva y herbácea se midió en cinco cuadrículas de 1×1 m por parcela (una cuadrícula/transecto), y se recogió toda la vegetación y la hojarasca. En el laboratorio, el material recolectado se separó en biomasa viva y muerta. Las muestras se secaron en el horno hasta peso seco y se pesaron. La biomasa de las grandes especies leñosas se estimó mediante ecuaciones alométricas utilizando el diámetro basal del tallo (Baeza & Santana, 2015) de todos los individuos arbóreos encontrados en un cuadrado de 10 ×10 m (la misma subparcela utilizada para medir la densidad de las especies rebrotadoras). La biomasa leñosa total se calculó sumando la biomasa arbustiva y arbórea. La biomasa arbustiva muerta y la cobertura arbustiva vertical se utilizaron para calcular la densidad aparente del combustible muerto (peso/volumen del combustible) como una medida de la inflamabilidad (es decir, biomasa arbustiva muerta (g/m^2) / altura del arbusto (m), (Santana et al., 2011).

Para analizar los potenciales efectos de los tratamientos en los atributos del suelo, se recogieron cinco muestras de suelo (en los mismos cinco cuadrados de 1 ×1 m que las muestras de biomasa) dentro de cada parcela de estudio. Todos los suelos se muestrearon a principios de verano, para evitar la variación estacional de las variables medidas. Las muestras de suelo se secaron en laboratorio y se tamizaron (< 2 mm) antes de los análisis. El pH del suelo y la conductividad eléctrica se determinaron en una mezcla de suelo: agua desionizada (1:5). El carbono orgánico del suelo se obtuvo mediante la oxidación con dicromato de Walkley-Black (Nelson & Sommers, 1996). El fósforo disponible se obtuvo siguiendo el método de Olsen et al (1954). Las actividades enzimáticas β- glucosidasa y fosfatasas relacionadas con el ciclo del carbono y el fósforo se analizaron siguiendo el procedimiento descrito por Tabatabai (1994). Cada atributo del suelo, excepto las actividades enzimáticas, se midieron en dos submuestras de suelo a dos profundidades (0-5 y 5-15 cm). Como evaluación adicional del estado funcional de cada parcela de estudio, se utilizó el análisis funcional del paisaje (Landscape Functional Analysis-LFA; Tongway & Hindley, 2004) para medir índices que reflejan la estabilidad, la infiltración y el reciclaje de nutrientes.

Después de eliminar los atributos altamente correlacionados entre sí, y por lo tanto proporcionan información redundante, las diferentes variables de vegetación y suelo se organizaron, mediante el cálculo de sus promedios después de ser estandarizados entre 0-1, en cinco categorías de servicios de los ecosistemas: (i) conservación de la biodiversidad: riqueza de especies vegetales (relacionada también con la diversidad de insectos y biota subterránea; Scherber et al., 2010), y complejidad del hábitat (un índice compuesto relacionado con la provisión de hábitat para aves, reptiles y mamíferos, utilizando la cobertura de diferentes estratos de vegetación y hojarasca, según Val y otros (2017), (ii) fijación de carbono: biomasa leñosa viva y carbono orgánico del suelo, como principales fuentes de almacenamiento de carbono en los ecosistemas terrestres (Heimann & Reichstein, 2008), (iii) producción de alimentos: potencial apícola y biomasa herbácea (como indicador de la disponibilidad de forraje tanto para el ganado como para la fauna silvestre), ambos con una gran importancia económica en la zona de estudio, (iv) regulación de las perturbaciones: relacionada con la capacidad del ecosistema para resistir la erosión del suelo (índice de estabilidad), la probabilidad de volver a quemarse (la densidad aparente del combustible muerto, multiplicado por - 1 para reflejar la resistencia a nuevos incendios), y la capacidad de volver a regenerar tras un incendio adicional (abundancia de especies rebrotadoras), y (v) servicio de apoyo: índice de ciclo de nutrientes, β-glucosidasa y fosfatasa. Calculamos un índice de multifuncionalidad como la media de los cinco servicios ecosistémicos (ver Allan et al., 2015 para un enfoque relacionado). Como alternativas, en lugar del enfoque del promedio, también calculamos la multifuncionalidad utilizando la función de umbral múltiple, definida como el número de funciones que alcanzan algún porcentaje (40, 60 y 80% en nuestro caso) del máximo observado (Byrnes et al., 2014) en el Capítulo II y la multifuncionalidad como el índice de Gini Simpson (ver Hölting et al (2019) para un enfoque relacionado).

5. Conclusiones

1. La elevada recurrencia de los incendios y el tiempo transcurrido desde el último incendio interactuaron para determinar los servicios del ecosistema, pero no afectaron a las sinergias y compromisos entre ellos. Sus efectos combinados redujeron la fijación de carbono y la multifuncionalidad. La regulación de las perturbaciones disminuyó drásticamente con el primer incendio, sin que los incendios posteriores tuvieran ningún efecto. Sin embargo, este efecto se redujo, e incluso llegó a ser positivo, para los servicios de conservación de la biodiversidad y de producción de alimentos siempre que se dispusiera de tiempo suficiente (> 20 años) para su recuperación.
2. El aclareo en masas hiperdensas de pino mejora los atributos del ecosistema asociados a la conservación de la biodiversidad, sin comprometer la provisión de la fijación de carbono. Después de 10 años, los dos niveles de aclareo (600 y 1200 árboles·ha^{-1}) afectaron de forma similar los atributos del ecosistema lo que sugiere que un aclareo de 1200 árboles·ha^{-1} es suficiente para mejorar los atributos individuales del ecosistema.
3. El desbroce en matorral denso dominado por especies germinadoras mejora los atributos del ecosistema asociados a la biodiversidad sin comprometer la capacidad del ecosistema de fijar el carbono.
4. La plantación de especies rebrotadoras combinada con el aclareo y el desbroce, en masas hiperdensas de pino y matorral denso respectivamente, puede mejorar la provisión de los servicios de la regulación de perturbación, producción de alimentos, así como la multifuncionalidad.
5. La quema prescrita reduce la cantidad de combustible muerto, aumenta los servicios de conservación de la biodiversidad y la producción de alimentos. Sin embargo, estos efectos se vuelven negativos en estos servicios como la regulación de perturbaciones y la multifuncionalidad si la quema prescrita se aplica con frecuencia.
6. La combinación de diferentes actividades de gestión a escala de paisaje puede mejorar el suministro de múltiples servicios ecosistémicos simultáneamente, reduciendo las compensaciones entre ellos y, por lo tanto, establecer paisajes mediterráneos multifuncionales.

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