Universidad de Granada

Departamento de Ecología

Tesis Doctoral

Ph.D. Thesis

Colonización de áreas incendiadas por quercíneas: análisis de la concordancia entre factores de dispersión y establecimiento y valoración económica de los servicios ecosistémicos

Post-fire oak colonisation: Analysis of the concordance among factors of dispersal and establishment and economic valuation of ecosystem services

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Dr. Jorge Castro Gutiérrez, Profesor Titular de Ecología de la Universidad de Granada, **Dr. José María Rey Benayas**, Catedrático de Ecología de la Universidad de Alcalá de Henares,

CERTIFICAN

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral “Colonización de áreas incendiadas por quercíneas: análisis de la concordancia entre factores de dispersión y establecimiento y valoración económica de los servicios ecosistémicos”, enmarcada en el programa de Biología Fundamental y de Sistemas, son aptos para ser presentados por el **Lic. Alexandro B. Leverkus** ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad de Granada.

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A Reme…

… y a Gabriel, Andrea y Paola

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alex

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- **Servicios de la avifauna (*highly mobile link species*) en mosaicos agroforestales: regeneración forestal y regulación de plagas** SERAVI (CGL2014-53308-P) MINECO, 2015-2019.
- **Desarrollo de configuraciones óptimas para un dispositivo protector de semillas ante depredadores (patente 201331441): puesta a punto para su lanzamiento al mercado** (PR/14/003). OTRI–UGR, 2015.
- **Testar en condiciones reales la eficacia de un nuevo dispositivo, protector de semillas ante depredadores, presentado en la oficina de patentes y marcas de España (solicitud patente 201331441)** (PR/14/D1). OTRI–UGR, 2014.
- **Efecto del fuego sobre la diversidad de insectos claves (Hormigas y Abejas) en el monte andaluz: aspectos funcionales e implicaciones para la conservación** (P12-RNM-2705). Jta. de Andalucía, 2014-2018.
- **Colonización post-incendio por encina de pinares de repoblación en función del manejo de la madera quemada: análisis de la concordancia entre los factores de dispersión y el establecimiento.** COILEX (CGL2008-01671/BOS). MICINN, 2009-2012.
- **Restauración y conservación de los ecosistemas madrileños: Respuesta frente al cambio global** REMEDINAL-2 (S2009/AMB-1783). Comunidad de Madrid, 2010-2013.
- **Efecto del manejo de la madera quemada sobre la regeneración forestal post-incendio: desarrollo de técnicas blandas de restauración ecológica** (10/2005). MAGRAMA, 2006-2009.

Contents

List of Publications

The following publications are reproduced as part of this Thesis with the permission of the journals:

Chapter 1

Leverkus, A.B., Castro, J., Puerta-Piñero, C., Rey Benayas, J.M., 2013. Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks. Ecological Engineering 53, 15–22.

Chapter 2

Leverkus, A.B., Rojo, M., Castro, J., 2015. Habitat complexity and individual acorn protectors enhance the post-fire restoration of oak forests via seed sowing. Ecological Engineering 83, 276–280.

Chapter 3

Leverkus, A.B., Puerta-Piñero, C., Guzmán-Álvarez, J.R., Navarro, J., Castro, J., 2012. Post-fire salvage logging increases restoration costs in a Mediterranean mountain ecosystem. New Forests 43, 601–613.

Chapter 4

Leverkus, A.B., Castro, J., Delgado-Capel, M.J., Molinas-González, C., Pulgar, M., Marañón-Jiménez, S., Delgado-Huertas, A., Querejeta, J.I., 2015. Restoring for the present or restoring for the future: enhanced performance of two sympatric oaks (*Quercus ilex* and *Quercus pyrenaica*) above the current forest limit. Restoration Ecology doi: 10.1111/rec.12259

Chapter 5

Castro, J., Puerta-Piñero, C., Leverkus, A.B., Moreno-Rueda, G., Sánchez-Miranda, A., 2012. Post-fire salvage logging alters a key plant-animal interaction for forest regeneration. Ecosphere 3, art90.

Appendix I

Castro J, Leverkus A.B. Dispositivo protector de semillas ante depredadores (Container for protecting seeds from predators). Patent Number: ES2428943-A1; Patent holder: Universidad de Granada; Spain.

The work carried out for this Thesis also contributed to the following publications (not reproduced):

Castro, J., Leverkus, A.B., 2012. La saca de la madera quemada perjudica la regeneración natural y asistida de especies forestales en el Parque Nacional de Sierra Nevada, in: Martínez Ruiz, C., Lario Leza, F.J., Fernández Santos, B. (Eds.), Avances en la Restauración de Sistemas Forestales. Técnicas de Implantación. SECF-AEET, Madrid, pp. 27–34.

Castro, J., Leverkus, A.B., Fuster, F., 2015. A new device to foster oak forest restoration via seed sowing. New Forests doi: 10.1007/s11056-015-9478-4

Castro, J., Leverkus, A.B., Marañón-Jiménez, S., Serrano-Ortiz, P., Sánchez-Cañete, E.P., Reverter, B.R., Guzmán-Álvarez, J.R., Kowalski, A.S., 2013. Efecto del manejo de la madera quemada sobre la restauración y regeneración post-incendio: implicaciones para la gestión y para el conjunto del ecosistema, in: Libro de Actas del 6^{o} Congreso Forestal Español. SECF, Vitoria-Gasteiz, pp. 1–19.

Leverkus, A.B., Castro, J., Puerta-Piñero, C., Rey Benayas, J.M., 2012. Efecto del manejo de la madera quemada y la profundidad de siembra de bellotas sobre el éxito de reforestación con encina de áreas incendiadas, in:

Martínez Ruiz, C., Lario Leza, F.J., Fernández Santos, B. (Eds.), Avances en la Restauración de Sistemas Forestales. Técnicas de Implantación. SECF-AEET, Madrid, pp. 35–40.

Leverkus, A.B., Castro, J., Rey Benayas, J.M., 2014. Regeneración post-incendio de la encina en pinares de repoblación mediterráneos. Ecosistemas 23, 48–54.

Leverkus, A.B., Gustafsson, L., Rey Benayas, J.M., Castro, J., 2015. Does post-disturbance salvage logging affect the provision of ecosystem services? A systematic review protocol. Environmental Evidence 4, art16.

Leverkus, A.B., Lorite, J., Navarro, F.B., Sánchez-Cañete, E.P., Castro, J., 2014. Post-fire salvage logging alters species composition and reduces cover, richness, and diversity in Mediterranean plant communities. Journal of Environmental Management 133, 323–331.

Summary

Recovering vegetation after forest disturbance may be achieved by active or passive restoration. Active methods involve sowing seeds or planting seedlings, whereas passive restoration relies on natural regeneration. The success of each strategy, and the trade-offs between their cost-effectiveness and outcomes, may depend on several factors such as interspecific interactions, climatic gradients, or post-disturbance management. For example, post-fire salvage logging –the felling and extraction of burnt trunks, often including the elimination of residuals– is widely applied after wildfires around the world and may alter habitat features that can affect seedling development and habitat selection by mutualistic and antagonistic species. As a result, post-fire wood management can have profound consequences for secondary succession and for the active and passive regeneration of the burnt area.

The objective of this Thesis is to analyse some of the factors that affect the success of the natural and assisted regeneration of the Holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) in relation to post-fire management in a pine afforestation that burned in 2005. For this, I study acorn dispersal and predation, seedling recruitment, and the success of a planting operation in the Natural and National Park of Sierra Nevada after the Lanjarón fire. Additionally, I provide an economic assessment of the cost of reforesting with different methods and an economic valuation of the ecosystem service supplied by a major acorn disperser, the European jay (*Garrulus glandarius* L.), and by the resprouting capacity of the Holm oak. For the study, three experimental plots of 18–30 ha were established along an altitudinal gradient. Each of the plots was divided in nine subplots, which constituted three replicates of each of three post-fire management treatments:

1. Salvage logging. The burnt pines were logged, separated from their branches, and piled, and the remaining biomass was masticated. This generated a homogeneous and open landscape.

2. Partial Cut plus Lopping. Some 90% of the burnt pines were cut down and separated from their main branches, producing a complex habitat difficult to transit.
3. Non-Intervention. No action was taken. This habitat was characterised by standing dead trees, which gradually collapsed throughout the five years after the fire.

The first four chapters of this Thesis focus on assisted regeneration, while the last two deal with natural regeneration.

Chapters 1 and 2 analyse the success of acorn sowing, with focus on acorn predation. Acorns were sown in two of the post-fire treatments, which differently affected foraging by wild boars and rodents. In **Chapter 1,** two different methods are tested to reduce acorn predation by rodents: deeper sowing and the application of a chemical repellent. As these methods were ineffective, in **Chapter 2** a physical protecting device, named seed shelter, was tested. The seed shelter eliminated acorn predation by small rodents. Its use in a structurally more complex treatment, which reduced acorn predation by wild boars, minimised overall acorn predation. The document that describes the patent of the seed shelter is included as **Appendix I**.

Chapters 3 and 4 analyse the success and implications of reforestation with nursery-grown seedlings. In **Chapter 3**, the survival of four species is tested in the three wood management treatments across two plots. The main objective of this chapter is to assess whether the cost of salvage logging may be compensated by the savings obtained by performing reforestation in a more accessible area devoid of dead boles and branches. The costs of all forestry activities were calculated and led to the conclusion that in burnt Mediterranean pine plantations salvage logging is not profitable. For **Chapter 4,** demographic and ecophysiological data are used to study the performance of two of the planted species (the evergreen *Q. ilex* and the deciduous *Q. pyrenaica* Willd.) at different elevation. While the lower plot was located within the known range of oak forests, the upper plot was above that range. Both species, particularly the deciduous oak, performed best at the upper plot, where survival still increased with elevation. The results are interpreted in the context of the implications of species range shifts for ecosystem restoration.

Chapters 5 and 6 analyse the natural regeneration of the Holm oak. Some large, mature Holm oaks were unaffected by the fire next to one of the study plots, and they acted as seed sources. **Chapter 5** investigates the preferences of European jays for the different post-fire treatments as habitat and as acorn caching locations. The burnt but standing pines still acted as habitat for jays, suggesting that leaving burnt trees standing may favour the natural colonisation by oaks of burnt pine forests if nearby seed sources exist. **Chapter 6** studies the spatial and temporal patterns of recruitment of young Holm oaks over seven years following the fire. The Non-Intervention areas favoured recruitment during the first years, but as the burnt pines collapsed, the main direction of seed dispersal changed towards patches of unburnt pines that remained within the plot. As these living pines reduced the growth of seedlings underneath them, there was a temporal shift in the demographic conflicts experienced by successive cohorts of oak recruitment.

In the **General Discussion**, besides expanding on the implications of the individual studies, I provide an economic assessment of the different options for assisted regeneration under several scenarios. The specific costs are calculated in **Appendix II**. Planting seedlings was the most costly method for assisted oak regeneration, and sowing with the seed shelter was the least expensive regardless of the expected range of potential costs of the device.

At the end of the Discussion I estimate the economic value of the ecosystem service of natural regeneration of oaks with the Replacement Cost method, considering the cost of reforestation on the one hand (Chapters 1 to 4) and the naturally regenerated seedling densities on the other hand (Chapters 5 and 6). Natural regeneration, including post-fire resprouting and seed dispersal, led to potential savings of hundreds of euros per hectare due to the reduced need for reforestation. The value of this service was particularly high near seed sources and in areas without post-fire human management, indicating that the common strategy of post-fire salvage logging may hamper the natural regeneration of oaks.

Resumen

Para recuperar la vegetación después de una perturbación forestal existen métodos de restauración activa y pasiva. La restauración activa implica la siembra de semillas o la plantación de plantones, mientras que la restauración pasiva se basa en la regeneración natural. El éxito de cada estrategia, así como el balance en cuanto al coste y resultados de estos métodos, dependen de varios factores, como las interacciones interespecíficas, los gradientes climáticos o el manejo post-perturbación. La saca de la madera tras un incendio, que implica la tala de los árboles quemados, la extracción de los troncos y el astillado o quema de los residuos, es común en amplias partes del mundo y puede alterar elementos del hábitat que afectan al desarrollo de las plantas y la selección de hábitat por parte de especies mutualistas y antagonistas. En consecuencia, el manejo post-incendio de la madera quemada puede tener profundas consecuencias sobre la sucesión secundaria y la regeneración, tanto activa como pasiva, del área incendiada.

El objetivo de esta Tesis es analizar algunos de los factores que afectan al éxito de la regeneración natural y asistida de la encina (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) en función del manejo post-incendio del hábitat en un pinar que ardió en el año 2005. Para ello se estudia la dispersión y depredación de bellotas, el reclutamiento de plántulas y el éxito de una plantación en el Parque Natural y Parque Nacional de Sierra Nevada tras el incendio de Lanjarón. Adicionalmente, se realiza una valoración económica de los costes de reforestación en función de los métodos empleados así como una valoración del servicio ecosistémico aportado por el principal dispersor de las bellotas, el arrendajo común (*Garrulus glandarius* L.), y por la capacidad de rebrote post-incendio de la encina. Para el estudio se establecieron tres parcelas experimentales de 18-30 ha que se distribuyeron a lo largo de un gradiente altitudinal. Cada parcela comprende nueve subparcelas, que constituyen tres réplicas de cada uno de tres tratamientos de la madera quemada:

1. Saca de la madera. Los pinos quemados fueron talados, separados de sus ramas y apilados, y la biomasa residual fue astillada. Ello generó un paisaje abierto y homogéneo.
2. Intervención Intermedia. Aproximadamente el 90% de los pinos quemados fueron talados, separados de sus ramas principales y troceados, lo cual produjo un hábitat complejo y difícil de transitar.
3. No Intervención. No se realizó ninguna acción. Este hábitat se caracterizó por la presencia de árboles quemados en pie, los cuales fueron cayendo gradualmente a lo largo de los cinco años posteriores al incendio.

Los primeros cuatro capítulos de esta Tesis analizan la regeneración asistida de la encina, mientras que los últimos dos tratan de la regeneración natural.

Los **Capítulos 1 y 2** analizan el éxito de la siembra de bellotas, con énfasis en la depredación de bellotas. Se realizaron siembras en dos de los tratamientos post-incendio, los cuales afectaron de diferente manera a la depredación por roedores o jabalíes. En el **Capítulo 1** se prueban dos métodos para reducir la depredación por roedores: la siembra a mayor profundidad y el uso de un repelente químico. Como estos métodos resultaron ineficaces, en el **Capítulo 2** se prueba un dispositivo protector llamado *seed shelter*. El *seed shelter* eliminó la depredación por pequeños roedores. Su uso en un tratamiento estructuralmente más complejo, que redujo la depredación por jabalí, minimizó las pérdidas por depredación. El documento que describe la patente del *seed shelter* se incluye como **Apéndice I**.

Los **Capítulos 3 y 4** analizan el éxito y las implicaciones de la reforestación con plantones de vivero. En el **Capítulo 3** se estudia la supervivencia de plantones de cuatro especies en los tres tratamientos post-incendio en dos de las parcelas. El principal objetivo de este capítulo es analizar si el coste de la saca de la madera se puede compensar mediante el ahorro obtenido al reforestar en una zona más accesible por la ausencia de ramas y troncos. Se calculó el coste de todas las actividades selvícolas y se concluyó que en pinares de reforestación mediterráneos que han ardido la saca de la madera no es rentable. Para el **Capítulo 4** se utilizan datos demográficos y ecofisiológicos para analizar el desarrollo de dos de las especies plantadas (la perennifolia *Q. ilex* y la caducifolia *Q. pyrenaica* Willd.) a diferente altitud. Mientras que una parcela se encontraba dentro del rango altitudinal de distribución de los bosques de *Quercus*, la otra se situaba por encima de dicho rango. Ambas especies, y en particular la caducifolia, mostraron mejor desarrollo en la parcela superior, donde la supervivencia aún aumentaba en altitud. Los resultados se interpretan en términos de las implicaciones de las migraciones altitudinales de las especies para la restauración de los ecosistemas.

Los **Capítulos 5 y 6** analizan la regeneración natural de la encina. Algunas encinas adultas cercanas a una de las parcelas no se vieron afectadas por el incendio y actuaron como fuente de bellotas. El **Capítulo 5** investiga las preferencias del arrendajo por los diferentes tratamientos post-incendio como hábitat y como sitios para esconder bellotas. Los árboles quemados que permanecían en pie actuaron como hábitat para el arrendajo, sugiriendo que no tumbar los árboles quemados puede favorecer la colonización natural por parte de la encina de bosques quemados si existe una fuente de bellotas. En el **Capítulo 6** se estudian los patrones espaciotemporales en el reclutamiento de encinas a lo largo de los siete años posteriores al incendio. Las zonas de No Intervención favorecieron el reclutamiento a lo largo de los primeros años, pero conforme caían los árboles quemados fue cambiando la dirección de la dispersión hacia unos rodales de pinos que no se quemaron y que se localizaban dentro de la parcela. Como estos pinos vivos redujeron el crecimiento de las plántulas emergidas debajo de su dosel, hubo un cambio direccional en los principales conflictos demográficos experimentados por cohortes sucesivas de reclutamiento de encinas.

En la **Discusión General**, además de discutir las implicaciones de los estudios individuales, presento un balance económico de los distintos métodos de regeneración asistida bajo diversos escenarios. Los detalles del cálculo se proveen en el **Apéndice II**. La plantación fue el método más caro para la regeneración asistida de la encina y la siembra mediante el *seed shelter* fue el más asequible sin importar el rango estipulado de costes del dispositivo.

Al final de la Discusión utilizo el método del Coste de Reposición para valorar en términos económicos el servicio ecosistémico de la regeneración natural de la encina, tomando en cuenta por una parte el coste de la reforestación (Capítulos 1 a 4) y por otra las densidades de encinas obtenidas mediante regeneración natural (Capítulos 5 y 6). La regeneración natural, incluyendo la capacidad de rebrote tras incendio y la dispersión de bellotas, produjo ahorros potenciales de cientos de euros por hectárea resultantes de la reducción en la necesidad de reforestar. El valor de este servicio fue particularmente elevado cerca de fuentes de bellotas y en zonas sin intervención humana post-incendio, lo cual indica que la estrategia habitual de sacar la madera después de un incendio puede obstaculizar la regeneración natural de la encina.

Introduction

1. Fire in the Mediterranean Region

Fire is a natural disturbance that has shaped the ecosystems of the Mediterranean Region since the onset of its characteristic climate. The hot, dry summers set the scene for high propagation of fires, which represent an important ecological and evolutionary factor (Moreno and Oechel, 1994; Pausas and Keeley, 2009). In fact, most of the plant species that currently occupy the Mediterranean Basin possess some strategy to regenerate after fire, such as the accumulation of a large seed bank in the soil with the ability to germinate after the stimulation of heat, or the capacity to resprout from roots or stems after the twigs and leaves have burned (Lloret, 2004; Pausas et al., 2004a). Thus, fire does not necessarily represent a catastrophe from the point of view of plants and ecosystems.

Fire allows early-successional species to establish and reproduce in otherwise highly competitive, mature stands in many ecosystems (Christensen Jr, 2014). Some plant species are even fire-dependent, for example due to the need of stimulation by heat for their seeds to germinate (Naveh, 1975; Lloret, 2004). As individual fire events are spatially limited and within one burn the intensity of fire usually varies, fires generate heterogeneity in space and time (Noss et al., 2006; Kulakowski and Veblen, 2007). This heterogeneity is essential for the persistence of species of different successional stages in the landscape and to enhance the resilience of the ecosystem to subsequent disturbances (Díaz-Delgado et al., 2003; Purdon et al., 2004; Thompson et al., 2007).

The Mediterranean Basin has suffered human impacts for longer than most other regions in the world, and this includes the use of fire (Pausas and Vallejo, 1999). Humans have altered the natural fire regime since the Palaeolithic by using fire to facilitate food gathering and hunting (Stewart, 1956). Since then, human presence in the region has become so intense that it is impossible to understand the current patterns of vegetation without taking into account the human use and management of it. In the last few decades, rural abandonment has reduced the intensity of management, grazing and wood gathering, and ultimately increased the amount of available fuel (Pausas and Vallejo, 1999; Pausas and Fernández-Muñoz, 2012). Climatic trends of aridification have favoured, and are predicted to keep favouring, the frequency and intensity of fires in the region (Pausas and Vallejo, 1999; Mouillot et al., 2002; Pausas and Fernández-Muñoz, 2012; IPCC, 2014). Besides, massive conifer plantations, mostly established in the mid-nineteenth century around the Mediterranean, and particularly in Spain, nowadays form dense, uniform stands with undesirable properties such as a lack of natural regeneration, high potential for fire propagation, and low resilience to fire (Maestre and Cortina, 2004; Pausas et al., 2004a, 2004b; Pausas et al., 2008; Gómez-Aparicio et al., 2009). As a consequence, there has been an increase in the amount, intensity and surface of fires in the region, and this trend is expected to continue (IPCC, 2014; Pausas and Fernández-Muñoz, 2012).

The observed and projected shifts in fire regimes may undermine ecosystem resilience by affecting the mechanisms underlying plant natural regeneration. For example, high fire frequencies may reduce the capacity of some species to resprout (Ferran et al., 1998). Also, the regeneration of seeder species –those whose post-fire regeneration relies on seeds– may fail when the fire interval is too short for the accumulation of a seed bank large enough to produce a new plant cohort (Pausas et al., 2008; Vallejo and Alloza, 2012). As a result, fire may represent an environmental challenge, as it may induce ecosystem shifts such as desertification in dry areas (Dury et al., 2011). Understanding the processes related to plant regeneration after fire is thus of paramount importance for the maintenance and enhancement of biodiversity and ecosystem services, as is taking effective post-fire management actions that favour the regeneration of the ecosystem.

2. Post-fire management: motivations and controversy

After a disturbance such as fire, biological legacies from the past ecosystem set the scene for plant regeneration (Franklin et al., 2000; Lindenmayer et al., 2008; Christensen Jr, 2014). Biological legacies left after a wildfire, such as remaining burnt trees, logs and branches, as well as surviving vegetation, may aid ecosystem recovery by retaining soil (Reeves et al., 2006), producing nutrient inputs (Brais et al., 2000; Marañón-Jiménez and Castro, 2013), acting as seed traps (Marzano et al., 2013), facilitating survival and population viability in disturbed areas (Franklin et al., 2000; Castro et al., 2011), and promoting plant and animal (re-) colonisation by providing habitat features, substrate, and food for many species (Noss and Lindenmayer, 2006; Lindenmayer et al., 2008). However, the ecological role of these biological legacies in post-fire ecosystems has long been neglected by managers and policymakers, associated with the lack of scientific evidence of their importance (McIver and Starr, 2000). In fact, the removal of large quantities of biological legacies (i.e. the burnt biomass), also called salvage logging, is one of the most common post-fire management strategies worldwide (McIver and Starr, 2000; Beschta et al., 2004; Noss and Lindenmayer, 2006; Lindenmayer et al., 2008).

Post-fire salvage logging consists in the felling and removal of the burnt trunks, often including the elimination of the remaining woody debris (Fig. 1). Major motivations for post-fire salvage logging differ, although the most important are economic (recovering part of the forest capital) and silvicultural (aiding the management and restoration of the burnt site by easing the access of forestry personnel) (Lindenmayer et al., 2004; Donato et al., 2006; Castro et al., 2010a; Lindenmayer et al., 2008). Advocates for salvage logging also argue that it reduces the risk of pest outbreaks and wildfire due to the elimination of substrate and fuels (D’Amato et al., 2011; Fraver et al., 2011). Finally, there is a social perception of ugliness and death that may be offset by removing the affected elements (Lindenmayer and Noss, 2006). However, these arguments are not always based on scientific evidence but rather on traditional practices, perceptions and deductions, and consequently this practice is surrounded by controversy. A report published in 2000 (McIver and Starr, 2000) reviewed the ecological effects of salvage logging and identified a lack of research on this topic. This review triggered a wide number of empirical studies around the world, and in the last 15 years all of the above-mentioned motivations for salvage logging have been questioned (e.g. fire risk; Donato et al., 2006; and forestry and economics; Bautista et al., 2004) and many other unaccounted effects have been described (McIver and Starr, 2000; Lindenmayer et al., 2008). There is increasing evidence that biological legacies are components of natural systems that promote ecosystem recovery and diversity, and that their extraction represents a further disturbance which acts synergistically with the original one and may lead to effects that would not be expected by one of the disturbances (i.e. fire or logging) alone (Beschta et al., 2004; Lindenmayer et al., 2004; DellaSala et al., 2006; Hutto, 2006; Lindenmayer et al., 2008).

Figure 1. Post-fire salvage logging A) with a tree harvester after a fire in 2014 near Uppsala, Sweden, and B) with chainsaws followed by extraction by mules after a fire in 2014 near Granada, Spain.

The impacts of post-disturbance salvage logging may strongly affect a whole set of ecosystem features and processes. The most obvious effect of this practice is that it alters the physical structure of ecosystems (D'Amato et al., 2011; Waldron et al., 2013). Further, several key ecosystem processes and services can be affected, and most studies point to negative effects. Salvage logging may impact the provision of ecosystem services through altering processes such as soil erosion and hydrological regimes (Reeves et al., 2006; Wagenbrenner et al., 2015), nutrient cycling (Marañón-Jiménez and Castro, 2013), carbon sequestration (Serrano-Ortiz et al., 2011), seed dispersal (Rost et al., 2009), tree regeneration (Fernández et al., 2008), resistance to invasive species (Holzmueller and Jose, 2012), and many others (Beschta et al., 2004; Karr et al., 2004; Lindenmayer and Noss, 2006; Lindenmayer et al., 2008; McIver and Starr, 2000).

Salvage logging can also affect particular elements of the biota and change species assemblages. Several studies have focused on how it may affect particular taxonomic groups such as birds (Hutto and Gallo, 2006; Nappi and Drapeau, 2009; Castro et al., 2010b), beetles (Koivula and Spence, 2006; Cobb et al., 2011), or mammals (Lindenmayer and Possingham, 1996; Hebblewhite et al., 2009). Most of them conclude that those species that depend either directly (e.g. for food or tree cavities), or indirectly (e.g. those that feed on the latter) on the wood tend to be among the most negatively affected (Thorn et al., 2015).

The response of plant communities has also been analysed in several studies, particularly in Europe (Marzano et al., 2013; Kramer et al., 2014; Leverkus et al., 2014) and North America (Purdon et al., 2004; Greene et al., 2006; Kurulok and Macdonald, 2007; Macdonald, 2007; D’Amato et al., 2011). Although the responses of plant community regeneration are greatly variable, several studies point out potential changes in community composition in burnt areas resulting from salvage logging (e.g. Purdon et al., 2004; Greene et al., 2006; D’Amato et al., 2011; Boucher et al., 2014; Leverkus et al., 2014), in particular due to reductions in forest species and increases in open-habitat species, and also a homogenisation of the plant community (Kurulok and Macdonald, 2007; D’Amato et al., 2011). Here arises one of the main questions surrounding this practice, which is: Does salvage logging affect forest regeneration? As mentioned before, the answer seems to be *yes*, but a wise response requires focusing on main tree species and the factors affecting their regeneration.

Several studies have, indeed, studied the effect of salvage logging on the natural regeneration of main forest-forming tree species (Spanos et al., 2005;

Donato et al., 2006; Goodman and Hungate, 2006; Fernández et al., 2007; Vega et al., 2009; Bottero et al., 2013; Marañón-Jiménez et al., 2013a; Marzano et al., 2013; Kramer et al., 2014). Salvage logging can affect tree regeneration either through direct effects of the activities of logging or through indirect effects due to habitat modifications resulting from the removal of biological legacies (Lindenmayer et al., 2008). Forestry work that involves dragging trunks (Fig. 1) represents a mechanical disturbance that can substantially damage both the soil and the naturally establishing vegetation (McIver and Starr, 2000; Van Nieuwstadt et al., 2001; Bautista et al., 2004). Besides, the removal of the tree boles implies changes in microclimatic conditions and in the habitat heterogeneity that provides the necessary conditions for many species (Lindenmayer and Noss, 2006; Castro et al., 2011; Leverkus et al., 2014). As a result, numerous mechanisms related to salvaging may operate to affect seedling recruitment. However, scant studies have been conducted to test the effects of post-fire salvage logging on different methods of regeneration, including natural and artificial techniques. Besides, oaks (*Quercus spp.*) have so far received little attention in these studies.

Many (if not most) studies on post-disturbance logging have some experimental flaw. Part of the scientific literature dealing with the ecological consequences of salvage harvesting consists in reviews which at least partially make forecasts about potential impacts suggested by comparing studies on the consequences of fire or logging alone (Lindenmayer and Ough, 2006; Reeves et al., 2006; González and Veblen, 2007). Other studies are based on empirical results of post-fire natural regeneration and/or the importance of the remaining biological legacies, and their predictions of negative impacts of logging lack empirical testing (van Nieuwstadt et al., 2001). Others have studied salvage-logged sites without the consideration of unsalvaged controls (Greenberg et al., 1992; Greenberg and McGrane, 1996). Among studies that do consider unsalvaged controls, many make use of areas that have been differently managed for reasons other than the experiment itself (e.g. Martínez-Sánchez et al., 1999; Purdon et al., 2004; Bradbury, 2006; Donato et al., 2006; Foster and Orwig, 2006; Kurulok and Macdonald, 2007; Macdonald, 2007; Fernández et al., 2008), for example due to the different economic potential of the remaining timber in different areas; thus, the interpretation of the effects of salvage logging could be confounded with effects of site characteristics such as soil productivity (Purdon et al., 2004). In fact, Macdonald (2007) found that unsalvaged, non-merchantable burnt forests might not serve as post-fire species and community reservoirs, which underlines the need of experimental approaches in which salvage logging and other treatments are randomly allocated to different areas. Some experiments have been carried out, but unfortunately with no replication (e.g. Martínez-Sánchez et al., 1999; Spanos et al., 2005; Beghin et al., 2010; Marzano et al., 2013), which makes it statistically impossible to make inferences to areas larger than the experiment itself. As a result, it would be more than desirable that more studies be conducted with proper replication and randomisation.

3. Forest restoration

Forest restoration is a major challenge worldwide, and it has enormous ecological and societal implications (Lamb and Gilmour, 2003; Egan et al., 2011). Besides compensating for the ongoing loss and degradation of ecosystems, including an ever-increasing amount and severity of forest disturbances worldwide (Schelhaas et al., 2003; Kurz et al., 2008; Pausas and Fernández-Muñoz, 2012), forest restoration can enhance biodiversity and recover the functioning of important ecosystem services such as water retention, atmospheric regulation, and the provision of forest goods and spiritual values (CBD, 2001; Lamb and Gilmour, 2003; MA, 2005; Rey Benayas et al., 2009; IUCN and WRI, 2014; Meli et al., 2015). Forest restoration also has substantial economic implications, arising both from the large investments in these activities (e.g. USDA Forest Service 2014) and the value of the restored ecosystem services (MA, 2005; Cunningham et al., 2015). The success of forest restoration is thus paramount to meet ecological and societal targets, and innovation can play an essential role in achieving this in an economically efficient manner.

The new challenges related to restoring forests are also bringing along new debates and controversies. The efforts to understand the processes of forest restoration have brought about scientific discussion on the question of whether human intervention is actually necessary. Ecosystems usually have mechanisms for regeneration after specific disturbances, such as the resprouting ability of many species after a fire, bird-mediated seed dispersal into degraded areas, and long-term successional dynamics that may ultimately lead to the regeneration of ecosystems with a more or less similar composition to the original one (Holling, 1973; Christensen Jr, 2014). However, ecosystem resilience may be compromised in many cases, for example due to the lack of seed sources or proper habitat for dispersers. In such cases, human intervention may be necessary to accelerate successional dynamics, with actions such as soil preparation, decontamination, or reforestation.

Active tree cover regeneration is usually addressed in one of two ways: planting nursery-grown seedlings (either with bare-rooted seedlings or enclosed in root containers) or seed sowing (Savill et al., 1997; Allen et al., 2001; Lamb and Gilmour, 2003; Dey et al., 2008). Seedling planting has several advantages over sowing, such as generally faster seedling growth (Allen et al., 2001; Löf et al., 2004; Fields-Johnson et al., 2010), higher survival rates (Dey et al., 2008; Valkonen, 2008; Fields-Johnson et al., 2010; but see Löf et al., 2004; González-Rodríguez et al., 2011), promotion of habitat heterogeneity and diversity (Twedt and Wilson, 2002), and the avoidance of seed predation (Stewart et al., 2000). However, seed sowing potentially generates a much lower impact on soil and vegetation during working operations, which in turn are easier to carry out, have more flexibility in terms of timing, and allow restoration in areas where seedling planting is too costly or difficult (Allen et al., 2001). Sowing also reduces the risk of transferring plant diseases from nurseries to the field (Sánchez et al., 2005). And, in particular, the economic cost of sowing is far lower than that of planting (Bullard et al., 1992; King and Keeland, 1999; Madsen and Löf, 2005; Farlee, 2013). The net balance between seedling planting and seed sowing, whenever the target species offers both possibilities, is thus context-dependent.

Despite much effort and great advances in the success of forest plantations (e.g. King and Keeland, 1999; Espelta et al., 2003a; Rey Benayas et al., 2005; Jiménez et al., 2007; Chirino et al., 2008; Löf and Birkedal, 2009), forest regeneration does not need to be constrained to purely active or passive approaches. Human intervention is usually present in some way or another, and a way to achieve successful regeneration of tree cover beyond planting trees may be to favour the presence of habitat elements that benefit natural regeneration. For example, seed dispersers may require certain habitat features, whose presence in a disturbed area may increase their abundance and consequently the entrance of seeds (Rost et al., 2009, 2010; Cavallero et al., 2013). On the contrary, the abundance and activity of granivorous animals may be favoured in certain post-disturbance habitats (Puerta-Piñero et al., 2010), and managing these habitats to reduce their activity could increase the success of natural recruitment. Thus, while passive restoration is based on letting nature take its own course, there are certain management decisions that may enhance this process without having to introduce seeds or plants from the nursery. Such an approach can potentially induce more natural dynamics, prevent the entrance of foreign genetic material, and produce benefits for society in terms of reducing management costs.

Besides ecological factors, managers must take into account other factors, including their usually limited restoration budgets, when defining courses of action. As several options usually exist for the restoration of an area, defining the actions to be taken to reach restoration objectives usually depends on trade-offs between the expected success of these possibilities and their economic cost. The cost of restoration actions will, in turn, rely on the direct cost of performing them, but also on their success (e.g. due to the need of replacing dead nursery seedlings). Further, other ecosystem processes that are affected by management actions may contribute to their economic balance, as ecosystem services that can be affected by management may have large economic value that is usually not considered (Costanza et al., 1997).

Ecosystems and organisms within them contribute to human wellbeing through ecosystem services, which are classified into provisioning, regulating, cultural, and supporting services (MA, 2005). While the demand for ecosystem services is globally increasing, the natural capacity to meet them is rapidly diminishing through human actions (CBD, 2001; MA, 2005; Kumar et al., 2010).

Land-use decisions are usually based on cost-benefit analyses, trade-offs between use and management options intended to maximise economic returns, although they seldom consider the value of ecosystem services, especially when they do not enter the market such as many regulating and supporting services (Heal, 2000; CBD, 2001; Kumar et al., 2010). Understanding and valuing ecosystem services has thus acquired paramount importance (Costanza et al., 1997; Bockstael et al., 2000; Turner et al., 2003; Wenny et al., 2011).

For example, birds can play a crucial role in natural regeneration (Rey and Alcántara, 2000; Purves et al., 2007; Rost et al., 2009; García et al., 2010). They act as mobile links within and between ecosystems, contributing to ecosystem function and resilience (Hutchins et al., 1996; Lundberg and Moberg, 2003), and to all four kinds of ecosystem services, one of the main ones being seed dispersal (Whelan et al., 2008). Through bird-mediated dispersal, plant species benefit from gene flow, escape from high-mortality areas, reach more favourable sites, and colonise new or degraded sites (Herrera, 1995; Rost et al., 2010; Cavallero et al., 2013). However, this ecosystem service is still poorly understood and greatly undervalued (Hutchins et al., 1996; Whelan et al., 2008; Wenny et al., 2011).

4. Oaks: relevance and regeneration

Oak forests are among the main vegetation types across the Northern Hemisphere. In the Mediterranean Basin, several oak species play crucial roles in maintaining biodiversity and ecosystem function (Thompson et al., 2009; Bugalho et al., 2011; Puerta-Piñero et al., 2011; Marañón et al., 2012). A major mechanism for colonisation by oaks is their mutualism with European jays (*Garrulus glandarius* L.). These corvids are the main long-distance dispersers of acorns across Europe (Bossema, 1979; Pons and Pausas, 2007), dispersing most acorns between 100 and 600 m and some up to 1 km from the parent tree (Gómez, 2003). Some of the cached acorns germinate and grow into adult oaks. Jays confer oaks the ability to colonise degraded lands such as abandoned cropland (Pons and Pausas, 2007; Rey Benayas et al., 2008). However, as jays prefer forests over open areas, acorn dispersal tends to be directional, with higher oak recruitment where trees already exist (Gómez, 2003). Trees could thus be considered supporting elements (*sensu* Liu et al., 2010), necessary for the provision of this ecosystem service (Hougner et al., 2006). However, there is still little quantitative information on how fire and subsequent management may affect the jay-oak interaction and subsequent acorn dispersal (Wenny et al., 2011).

Oaks are able to vigorously resprout after disturbances such as fire (Zavala et al., 2000; Rodrigo et al., 2004) (Fig. 2), which confers resilience to the forests they form. In Mediterranean Spain, much of the previous oak forest cover has been degraded or converted (WWF, 2011), and reforestation efforts in the last century have focused on rapid-growing species such as pines (Pausas et al., 2004b; Gómez-Aparicio et al., 2009; Ruiz-Benito et al., 2012; Vallejo et al., 2012). Although the use of pines usually guarantees the success of forestation due to their high survival and growth rates, pine plantations have low resistance and resilience to recurrent fires, as Mediterranean pine species are not able to resprout after a fire (Vallejo et al., 2012) and several species, such as *Pinus nigra* and *P. sylvestris*, lack any post-fire regeneration strategy. As a consequence, there is a current interest in regaining cover of resprouting hardwoods in the Mediterranean Region (Vallejo and Alloza, 2012), especially forests of *Quercus* (e.g. EEC Regulation No. 2080/92). Reforestations with oaks, including mixed pine/oak plantations, are nowadays common in Mediterranean Europe, and also in North America (King and Keeland, 1999; Allen et al., 2001; Rey Benayas et al., 2005; Jiménez et al., 2007; Dey et al., 2008). However, many reforestation programmes have failed as a consequence of high mortality rates, and great efforts have concentrated on all phases of the process, from the collection of seed, growth in the nursery, field conditioning, and subsequent management (King and Keeland, 1999; Espelta et al., 2003b; Rey Benayas et al., 2005; Jiménez et al., 2007; Chirino et al., 2008; Löf and Birkedal, 2009).

Figure 2. Burnt Holm oak vigorously resprouting five years after the Lanjarón fire (Granada).

The most common oak reforestation technique is the plantation of nursery-grown seedlings (King and Keeland, 1999; Navarro Cerrillo et al., 2005; Pemán et al., 2006). However, survival of planted seedlings may be low, particularly in the case of ecosystems with a dry summer such as those under Mediterranean climate. Mortality during the months of summer drought is, in fact, one of the main demographic filters for oak regeneration, whether natural or assisted (Rey Benayas et al., 2005; Castro et al., 2006; Valdecantos et al., 2006; Pérez-Ramos et al., 2012). In addition, oaks develop a tap root –a large, dominant root growing directly downward from which the rest of the root system sprouts laterally– whose morphology may be affected by the choice of reforestation method (Savill et al., 1997). In the case of nursery-grown oak seedlings, the tap root may be damaged or anomalously-shaped when grown in containers, or pruned in the case of bare-root transplanted seedlings (Allen et al., 2001; Tsakaldimi et al., 2009; Farlee, 2013). This may lead to a shallower root system with less access to soil moisture (Dey et al., 2008; McCreary, 2009; Tsakaldimi et al., 2009), and ultimately to an abnormal development and lower performance of the seedling under field conditions (Pemán et al., 2006; McCreary, 2009; Tsakaldimi et al., 2009; González-Rodríguez et al., 2011). As a result, proper access of seedlings to water and reductions in the physiological stress induced by summer drought are among the main factors that may aid oak forest restoration (Rey Benayas et al., 2005).

Several factors may enhance oak seedling survival during summer drought. One of them is the use of nurse plants, which can provide some shade, reduce soil temperatures, and boost seedling survival (Gómez-Aparicio et al., 2004; Castro et al., 2006). Alternatively, elements such as dead logs may also prove useful, with the additional advantages that they do not compete for underground resources but release nutrients (Castro et al., 2011). Seedling survival may thus be enhanced under circumstances of reduced drought stress due to improvements in the abiotic micro-environment (Zavala et al., 2000; Marañón-Jiménez et al., 2013a). Further, given the expected scenario of rising temperatures and increasing aridity in the Mediterranean Basin and other regions of the world (Easterling et al., 2000; IPCC, 2014), the potential distribution ranges of many tree species are shifting latitudinally towards the poles and altitudinally up the mountains (Jump et al., 2009; Kelly and Goulden, 2008; Matías and Jump, 2014), and this includes oaks (Benito et al., 2011; Rigling et al., 2013). Thus, the elevation at which plantations are carried out might affect seedling survival in ways beyond those expected from the past distribution of the target species.

The other method of active oak regeneration, acorn sowing, is largely discarded due to the high seed losses produced by vertebrate predators (Allen et al., 2001; Pulido and Díaz, 2005; Dey et al., 2008), including small rodents (Gómez, 2003; Tyler et al., 2006; Puerta-Piñero et al., 2010), wild ungulates (such as wild boars, *Sus scrofa* and red deer, *Cervus elaphus*), and livestock (Schmidt and Timm, 1991; Muñoz and Bonal, 2007; Gómez and Hódar, 2008; Puerta-Piñero, 2010). However, the surviving acorns are likely to yield high emergence (Fuchs et al., 2000; Allen et al., 2001; Pulido and Díaz, 2005) and seedling survival rates (Tietje et al., 1991; Pulido and Díaz, 2005; Mendoza et al., 2009; Matías et al., 2011). Seedlings emerged from acorns in the field tend to develop better root architectures for field conditions (Allen et al., 2001; Dey et al., 2008; Tsakaldimi et al., 2009; Zadworny et al., 2014). In particular, besides the potential benefits for seedling development, sowing can greatly reduce the cost of reforestation (Allen et al., 2001), potentially allowing the reforestation of larger areas with the same budget. Under these premises, the search for methods to reduce seed predation has long been recognised as a key issue to improve the effectiveness while reducing the cost of reforestation (Allen et al., 2001; Dey et al., 2008; Farlee, 2013).

Non-lethal methods to control acorn predation have been investigated for decades, such as creating habitat types that negatively affect seed predators (McCreary, 2009; Birkedal et al., 2010), adding perches to attract birds of prey (Farlee, 2013), increasing burial depth (Tietje et al., 1991; Fuchs et al., 2000), sowing at times of high food availability or providing alternative food sources to satiate predators (Sullivan, 1979; Dey et al., 2008), applying non-harmful chemical repellents (Williams and Funk, 1979; Nolte and Barnett, 2000; Willoughby et al., 2010), and employing physical protectors ranging from large-scale fencing to small wire mesh screens, perforated cans, or buried tubes (Schmidt and Timm, 1991; Crawley and Long, 1995; Löf et al., 2004; Madsen and Löf, 2005; Dey et al., 2008; McCreary, 2009; Farlee, 2013; Reque and Martin, 2015). None of them, however, have shown satisfactory results to date for large-scale restoration. Devices that offer physical protection, in particular, are generally ineffective, alter the normal development of roots, are difficult and expensive to produce, are large and uncomfortable to carry in the field, and/or require excessive post-sowing management. Consequently, sowing is still rarely used in reforestation largely because of the unresolved problem of seed predation.

5. Study area

This Thesis was conducted in the Lanjarón experimental plots on post-fire management (Fig. 3).

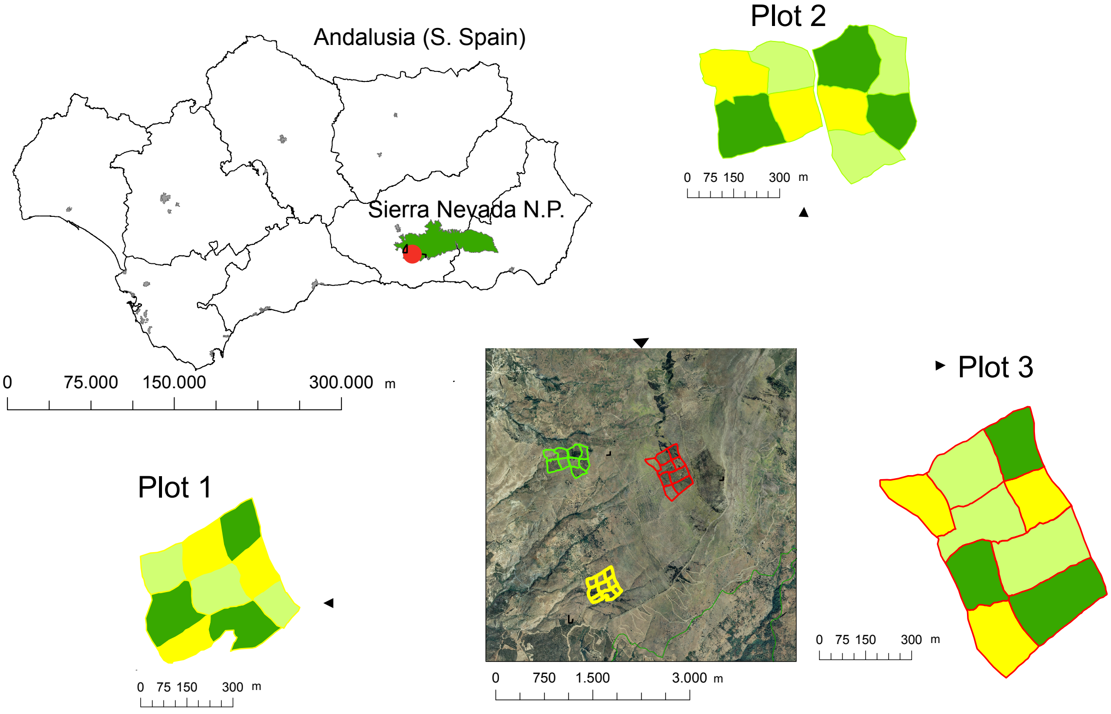

Figure 3. Experimental plots established after the 2005 Lanjarón fire. Dark green polygons correspond to replicates of the NI treatment, light green to PCL, and yellow to SL. The red point on the map indicates the approximate location of the fire. Orthorectified aerial photo (2007) courtesy of the Consejería de Medio Ambiente, Junta de Andalucía.

In September 2005, a fire affected 3417 ha of the Cáñar, Dúrcal, Lanjarón, Lecrín, and Nigüelas municipalities of the Granada province (Andalucía, Southern Spain). Of this area, some 1300 ha were pine plantations. The fire affected an elevation gradient across which pines had been planted in accordance with their climatic requirements (from lower to higher elevation: *Pinus pinaster* Ait., *P. nigra* Arn., and *P. sylvestris* L.). The fire was described as a high-intensity crown fire, as it killed most of the trees. However, heterogeneity in slope, wind, and other factors generated spatial heterogeneity, as some patches of pines within the affected area survived. The pine stand, 35-45 years old by the time of the fire, covered a large area and was surrounded by patches of natural vegetation, crops, and chestnut and almond tree orchards.

In spring 2006, three experimental plots were established in collaboration with the local Forest Service with the aim of testing the effects of post-fire management on several variables related to ecosystem regeneration (Fig. 3, Table 1). The plots were established on an elevation gradient on a SW-facing mountain slope, with micaschist as bedrock.

Each of the plots comprised nine subplots, which were randomly allocated to one of three replicates of one of three burnt-wood management treatments (Figs. 3 & 4). The treatments were as follows:

(1) Non-Intervention (NI), where no action was taken. The cumulative fall rate of burnt trees was 0.0% in 2006 and 2007, 11.3% in 2008, 79.8% in 2009, 97.4% in 2010 and 100% thereafter (estimated from 100 marked trees per plot; González-Molinas et al., in prep.). This led to yearly changes in the vertical structure of these habitats until 2010, when all the snags had collapsed.

(2) Partial Cut plus Lopping (PCL), where ca. 90% of the burnt trees were cut and felled, with the main branches lopped off but leaving all the biomass *in situ*.

(3) Salvage Logging (SL), where the trees were cut and their trunks cleared of branches with chainsaws. Trunks were manually piled in groups of 10–12, and the woody debris was chopped using a tractor with a mechanical masticator. The removal of trunks was planned, but this was eventually cancelled by the local Forest Service due to technical difficulties arising from the spatial arrangement of the plots.

The resulting experimental design corresponds to a generalized randomized block design (Quinn and Keough, 2002) with three blocks each containing three replicates of each of three treatments. The area of the replicates was similar across treatments according to Kruskall-Wallis tests, as were the parameters related to stand characteristics before the post-fire interventions (Leverkus et al., 2014).

Table 1

	Plot		
	1	2	3
UTM coordinates (x; y)[a]	456070E-4089811N	455449E-4091728N	457244E-4091551N
Altitude (m a.s.l.)[a]	1477	1698	2053
Plot area (ha)	17.8	23.9	31.7
Subplot area (ha)[b]	2.0 ± 0.2	2.7 ± 0.2	3.5 ± 0.3
Slope (%)[c]	30.3	28.7	31.4
Mean daily min. temp. (ºC)[d]	6.8 ± 0.2	5.6 ± 0.2	3.4 ± 0.2
Mean daily max. temp. (ºC)[d]	17.1 ± 0.2	16.2 ± 0.2	13.4 ± 0.2
Mean ann. precip. (mm)[d]	536 ± 41	550 ± 40	630 ± 42
Dominant species	*Pinus pinaster/ P. nigra*	*Pinus nigra*	*Pinus sylvestris*
Tree density (trees/ha)[e]	1477 ± 46	1064 ± 67	1051 ± 42
Tree basal diameter (cm)[e]	17.7 ± 0.2	18.3 ± 0.1	15.7 ± 0.1
Tree diameter at 1.30 m (cm)[e]	13.3 ± 0.2	14.5 ± 0.2	10.7 ± 0.2
Tree height (m)[e]	6.3 ± 0.1	6.6 ± 0.1	6.2 ± 0.1

[a] Coordinates and altitude measured at the centroid of each plot (UTM zone 30N, Datum: ED-50)

[b] There was no significant difference in subplot area among treatments (Kruskal Wallis test; χ^2 = 2.6; df = 2; P >0.05); values in the table are mean ± 1SE

[c] Mean slope of the nine subplots

[d] Data obtained from interpolated maps of Sierra Nevada (1981 - 2010) generated at the Centro Andaluz de Medio Ambiente (CEAMA)

[e] Measured after the fire. Density sampled in each subplot by counting the trees in four randomly placed 25 x 25 m quadrats. Tree diameter and height were measured on 30 randomly chosen trees in these quadrats, thus 120 trees per subplot

Climate in the area is Mediterranean, with hot, dry summers and wet, mild winters. Mean precipitation recorded near Plot 1 averages 511.1 ± 48.8 mm (period 1989 - 2011; values for climatic variables are mean ± 1SE). Rainfall during the summer months (June - September) is 51.4 ± 7.0 mm (1989 - 2011). Mean minimum and maximum daily temperatures of the coldest month (January) recorded at a nearby meteorological station at 1652 m a.s.l. are 0.2 ± 0.5 and 7.8 ± 0.6^{o}C (1989 - 2014). Mean minimum and maximum daily temperatures of the hottest month (July) are 13.3 ± 0.6 and 22.3 ± 0.7^{o}C (1989-2014).

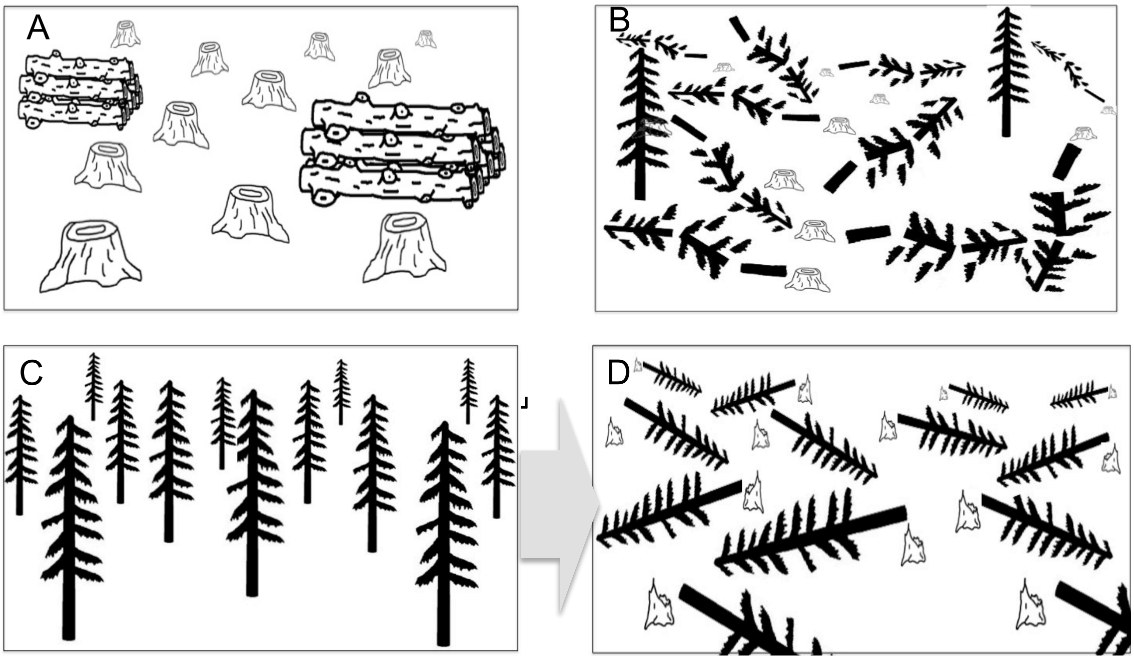

Figure 4. The post-fire treatments implemented in the study plots were A) Salvage Logging, B) Partial Cut plus Lopping, and C) Non-Intervention, where all the burnt trees collapsed within five years (D).

Further information, including details relevant to each chapter of this Thesis, are included in the Methods section of each chapter. Detailed soil properties of the plots may be found in Marañón-Jiménez and Castro (2013) and Marañón-Jiménez et al. (2013b), and an analysis of the vegetation two years after the fire in Leverkus et al. (2014).

6. Objectives and chapters of this Thesis

The main objective of this Thesis is to study how post-fire management and other factors such as elevation and interspecific ecological interactions affect the post-fire regeneration of *Quercus ilex* subsp. *ballota* (Desf.) Samp., the Holm oak. For this, I made use of the above-described plots to sample different aspects of post-fire Holm oak regeneration, ranging from natural recruitment to the human alternatives of sowing acorns and planting nursery-grown seedlings. I have divided this work into six chapters that investigate different aspects of each of three regeneration methods: acorn sowing, seedling planting, and natural regeneration. The main objectives of each chapter are described below.

Chapter 1 looks at assisted oak regeneration by searching ways to overcome acorn predation to enhance reforestation via seeding. Although seeding may be advantageous for regeneration due to economic and plant-morphological reasons, it is usually avoided due to seed predation. Two small-scale protective methods, namely deeper burial depth and a chemical repellent, were experimentally implemented in Plot 1 to try to reduce predation by rodents, and their single and combined effect was tested under areas with different habitat complexity due to different burnt-wood management. The hypotheses were that the protective methods and the habitat complexity would affect the behaviour of the main guilds of acorn predators (rodents and ungulates) and might provide a window of opportunity for acorn sowing.

Chapter 2 presents an alternative solution to the problem of the previous chapter. A new device was tested in another acorn predation experiment throughout the replicates of two of the burnt-wood treatments of Plot 1. The device, named seed shelter, was designed with the aim of protecting individual acorns from predation by small rodents. This chapter asks whether the use of this device in combination with large-scale habitat management could offer a dual solution to predation by rodents and large mammals to enhance reforestation success via sowing, building on the lack of success of the previously-tested methods. The seed shelter was patented, and its full description (in Spanish) is included in this Thesis as **Appendix I**.

Chapter 3 addresses the method of seedling planting for post-fire regeneration. It analyses the success of a large-scale reforestation project that used nursery-grown plants, and it tests the effect of post-fire management at Plots 2 and 3 on the performance of these transplanted seedlings. Beyond only focusing on seedling survival, this study also aims to evaluate the cost of the actions carried out during post-fire management and reforestation and to shed light on the controversy of whether salvage logging reduces the cost of post-fire management by easing reforestation.

Chapter 4 makes use of the transplanted oak seedlings of the previous chapter to study their survival and nutrient and water status as revealed by the analysis of leaf isotopic and nutrient composition. This chapter is placed in a global change scenario, leaving aside the wood management question and asking whether the increasing aridity in the region may be shifting the regeneration niche of two oak species up the mountain. The hypotheses were that seedlings at elevations greater than the current altitudinal limit of oak forests would show enhanced survival and water status due to the upward-shifting optimum climatic niche for plant establishment.

Chapter 5 addresses acorn dispersal by European jays into the burnt study area and the effects of post-fire management on this process. The hypothesis was that altering the vertical structure of the post-fire habitat would change the habitat preference of jays for caching acorns. Plot 1 was used for this study. Jays were monitored to discern the patterns of dispersal into the different treatments within the plot, and natural regeneration was thoroughly monitored across the plot surface.

Chapter 6 builds on the previous chapter by analysing how temporal changes in habitat features (i.e. the gradual collapse of burnt trees in the NI treatment) may have generated temporal shifts in the spatial recruitment patterns across different habitat types. I ask whether in highly dynamic landscapes, such as a forest that recently underwent strong disturbance, different cohorts of recruitment may experience different conflicts across ontogenetic stages due to the dynamic nature of ecosystem features. I based my analyses and conclusions on the yearly patterns of oak seedling emergence and their survival and growth until seven years after the fire, and related these to other ongoing processes.

The **General Discussion** makes use of the data gathered throughout Chapters 1 to 6 to calculate the cost of the different alternatives for active regeneration and to estimate the economic value of the ecosystem service of passive regeneration. Details for the cost estimations of the reforestation methods are presented in **Appendix II**. Altogether, this Thesis aims to shed light onto some of the processes that may aid or hamper the post-fire regeneration of native oak forests in Mediterranean mountain systems and to provide a balance of the cost-effectiveness of the different options.

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General Discussion

Throughout this Thesis I have analysed how several factors, including mutualistic and antagonistic interspecific interactions, as well as the effect of elevation under a changing climate, may affect the post-fire regeneration of *Quercus ilex* by natural or artificial regeneration in habitats differing in the management of the burnt wood and, consequently, in several habitat attributes. In this Discussion I will a) briefly discuss the conclusions and implications of the methods for post-fire oak regeneration tested throughout Chapters 1 - 6, b) provide an economic assessment of the different reforestation methods, and c) valuate the ecosystem service of natural regeneration in economic terms.

1. Implications

The artificial regeneration of most woody plant species in degraded or disturbed areas relies on either sowing seeds or planting nursery-grown seedlings (Savill et al., 1997; Allen et al., 2001; Twedt and Wilson, 2002; Lamb and Gilmour, 2003; Dey et al., 2008). In Chapters 1-4 of this Thesis, these two methods were tested for the Holm oak under several different environmental conditions, which in turn affected the performance of seedlings and the abundance and behaviour of antagonistic species.

The artificial regeneration of oaks via acorn sowing was generally not an effective method due to the great losses to wild boars and, particularly, small rodents. This result was not surprising, as the risk of losing large amounts of acorns to predators is very common and usually dissuades land managers from using this method (Dey et al., 2008; McCreary, 2009; Farlee, 2013). Still, some relevant advantages may be achieved through sowing, as it is generally the least costly method (Bullard et al., 1992; King & Keeland, 1999; Madsen & Löf, 2005; Farlee, 2013; Schmitt, 2013) and, besides, it allows the growth in the field of a deep tap root, which is usually abnormally-shaped or even pruned in the nurseries (Allen et al., 2001; Pemán García and Gil Pelegrín, 2008; Tsakaldimi et al., 2009; Farlee, 2013). Much effort has thus been placed in developing methods to protect acorns from predators (Schmidt and Timm, 1991; Tietje et al., 1991; Fuchs et al., 2000; Madsen and Löf, 2005; Dey et al., 2008; McCreary, 2009; Farlee, 2013; Reque and Martin, 2015), although the problem endures. In Chapter 1 of this Thesis, deeper burial and the application of capsaicin as a chemical repellent proved ineffective as methods to control acorn predation by mammals. Rodents were very quick in consuming most of the sown acorns, particularly in the more complex Non-Intervention post-fire habitat, which provided them with food and shelter (Haim and Izhaki, 1994; Herrera, 1995; Smit et al., 2008). Non-Intervention areas, however, had the advantage of reducing foraging by wild boars. This led to the hypothesis that large-scale management favouring a complex habitat structure –which would reduce acorn predation by large mammals– in combination with some yet-to-be-discovered protection for individual acorns –which should reduce predation by small mammals– may represent a solution to this long-lasting problem.

The seed shelter, which was conceived and designed as a physical acorn protector against small mammals (Appendix I), proved highly effective in this regard (Chapter 2). The device, consisting of two attached truncated cones, successfully allowed the exit of the root and stem through its narrow openings while virtually eliminating predation by mice and voles. Similar results were also found in a second field trial (Castro et al., 2015), although in this case some larger rodent, probably a rat or squirrel, was able to unbury two devices, leaving the open question of whether the seed shelter may be useful in situations where medium-sized acorn predators are abundant (e.g. rabbits; Crawley and Long, 1995). In any case, under the circumstances of the study, the combination of a complex post-fire habitat and the use of the seed shelter reduced acorn predation to a bare minimum of 5%, which confirmed the previously stated hypothesis. Besides, the device did not seem to affect seedling development (Castro et al., 2015), so it promises to represent a solution for reforestation with oaks. Currently, more research and talks to the private sector are under way to find an optimum final configuration and material for the seed shelter for its possible entry in the market.

As long as the outcomes of sowing remain unpredictable due to the problem of acorn predation, planting seedlings will likely continue to be the standard method for reforestation with oaks (García-Salmerón, 1995; Savill et al., 1997; King and Keeland, 1999; Espelta et al., 2003; Dey et al., 2008). Indeed, seedlings, including oaks, were planted by the local Forest Service around the Lanjarón study plots after the fire as a means to increase the cover of native vegetation. The plantation performed within the plots, which was an experimental extension of otherwise standard operations, revealed mortality rates of about half of the seedlings when pooling species, post-fire treatments, and plots/elevations (Chapters 3 & 4).

While high mortality rates of planted seedlings may compromise management objectives, replacing the seedlings is costly. The cost of planting seedlings with and without seedling replacement was evaluated in Chapter 3 for each of the burnt-wood treatments. While the Non-Intervention treatment slightly increased the direct cost of reforestation as compared to the Salvage Logging treatment, mostly due to the difficulty for the machinery and forestry staff to transit an area full of logs and branches spread over the ground, no treatment effect was obtained for the cost of seedling replacement. This was partially due to roughly similar mortality rates across treatments. However, whether with or without seedling replacement, the difference between treatments in the total cost of reforestation was about an order of magnitude smaller than the difference between treatments in the total cost of post-fire management (see Fig. 3 of Chapter 3). The sale of the wood provided a revenue roughly equal to the cost of transporting it to the mill, a common feature in these forests (Velasco and Hernández, 2012). The economic balance of salvage logging thus resulted to be very negative for this Mediterranean pine afforestation, which contrasts with other parts of the world where burnt trees are generally salvaged for economic purposes (hence the term *salvage*; Akay et al., 2006; Lindenmayer et al., 2008). This result adds to the growing body of evidence worldwide that in many cases the main motivations for post-fire salvage are, the least, controversial, and that applying this practice in a generalised way may have undesirable consequences (Saab and Dudley, 1998; McIver and Starr, 2000; Beschta et al., 2004; Karr et al., 2004; Lindenmayer et al., 2004; DellaSala et al., 2006; Donato et al., 2006; Lindenmayer and Noss, 2006; Stokstad, 2006; Smith et al., 2008; Castro et al., 2011; Serrano-Ortiz et al., 2011; Marañón-Jiménez et al., 2013; Marzano et al., 2013; Leverkus et al., 2014; Kishchuk et al., 2015).

The rather small effects of the burnt-wood treatments on the survival of planted seedlings contrasted with the comparatively large effects of elevation. The planted seedlings of the evergreen Holm oak and the deciduous Pyrenean oak performed best in a plot that is considered to be above the current distribution of oak forests than in a plot located within the forest range, and ecophysiological and demographic data revealed that this effect was related to drought stress (Chapter 4). The increasing aridification of large areas of the planet in the last decades has triggered species uphill range shifts in many parts of the world (Kelly and Goulden, 2008; Jump et al., 2009; Matías and Jump, 2014). However, realised species niches usually shift more slowly than their potential climatic niches due to constraints in seed dispersal, competition, and other factors (Jump et al., 2009; Benavides et al., 2013; Grassein et al., 2014). Assisted migration is a way to overcome these limitations. While academics debate on the pros and cons of assisted migrations (Hewitt et al., 2011), managers periodically face the challenge of deciding which species to select for the restoration of degraded areas. The results of Chapter 4 suggest that restoring degraded areas with consideration of the projected future climatic conditions should aid the persistence of target species by assisting their altitudinal migration while promoting ecosystem adaptation to climate change.

An option for ecological restoration that frequently escapes public knowledge and practical application is passive restoration, which is grounded on the concept of the resilience of ecological systems (Holling, 1973). Birds are highly effective and highly mobile seed dispersers, and they have the capacity to accelerate succession by introducing plants into degraded lands (Wenny, 2001; Lundberg and Moberg, 2003; Pejchar et al., 2008; Rey Benayas et al., 2008; Schupp et al., 2010; Zamora et al., 2010). However, the magnitude of seed dispersal may rely on the availability of suitable habitat for the dispersing birds, which may in turn be related to human management. In the Lanjarón area, European jays still found suitable habitat in places where post-fire management favoured the persistence of standing dead trees (Chapter 5). Further, jays dispersed acorns from adjacent, unburnt Holm oaks into the study area, and during the initial post-fire years new Holm oaks recruited, particularly in the Non-Intervention treatment. Other studies have similarly found that favouring the persistence of certain post-fire habitat features such as perches or piles of wood can aid natural regeneration by providing the necessary habitat for seed dispersers (Castro et al., 2010; Rost et al., 2010, 2012; Cavallero et al., 2013). The commonly applied regime of post-fire salvage logging could thus have negative consequences for forest regeneration (Donato et al., 2006; Greene et al., 2006; Macdonald, 2007; Beghin et al., 2010; Marañón-Jiménez et al., 2013; Marzano et al., 2013; Rodríguez Martínez et al., 2013; Brown et al., 2014; Leverkus et al., 2014).

The positive effect of post-fire Non-Intervention areas on oak seedling recruitment did not persist throughout the seven years of study (Chapter 6). As the burnt pines gradually collapsed, this treatment reduced its suitability as habitat for jays, and this translated into reduced oak seedling recruitment. The window of opportunity for natural oak colonisation after the fire was reduced to the first 4 to 5 years after the fire, and a new opportunity for natural recruitment will likely not open before either young, regenerating pines grow large enough to create suitable habitat for jays, or the recruited Holm oaks reach maturity and begin producing acorns. In any case, oak recruitment still occurred underneath some patches of unburnt pines, particularly after the collapse of the burnt trees. For the newly emerging oak seedlings, this implied growing in a different environment than the previous cohorts, in which their growth would be greatly constrained by the dense shade thrown by the pine canopy (Espelta et al., 1995; Zavala et al., 2000; Gómez, 2004; Pérez-Ramos et al., 2012; Galiano et al., 2013). While several studies have revealed that habitats may exert different pressure on different plant ontogenetic stages (Jordano and Herrera, 1995; Schupp, 1995; Gómez, 2004; Pulido and Díaz, 2005; Pérez-Ramos et al., 2012; van Ginkel et al., 2013), the results of this chapter also show that successive cohorts of recruitment may experience shifting ontogenetic conflicts at the landscape level resulting from habitat features that change directionally and modify the direction of seed dispersal.

The individual chapters of this Thesis provide assessments of some of the factors that may affect the post-fire regeneration of the Holm oak through various methods. In order to compare the effectiveness of these methods, in the following section I provide an economic balance of the different methods of artificial regeneration, based on the cost of obtaining the same number of surviving seedlings under the different strategies that were tested.

2. Which method to choose? Estimation of reforestation costs

With the reforestation methods that were tested in this Thesis, the question naturally arises: Which method is best for reforestation with Holm oaks? Ultimately, the best method will be the one that achieves management targets at the lowest cost, so that deciding among the different reforestation methods requires knowledge of the potential trade-offs between their cost and their success. To answer the above question in a hopefully meaningful way, here I provide an economic assessment of the different methods of oak reforestation that were tested throughout this Thesis. For this I make use of empirical data, standard costs, and several assumptions and scenarios related to the parameters that affect the final costs. The aim is to allow comparing the different methods under the same metric by showing the amount of money necessary to obtain a specific final result (i.e. a specific number of living oaks) under the different methods of reforestation.

Table 1 summarises the estimated cost of reforestation with the different methods and under a set of different scenarios. These include a) three scenarios on the time required to sow one unprotected acorn (0.5 min, 1 min, or 2 min, always assuming that it takes twice this time to sow an acorn with a seed shelter), and b) three scenarios on the cost of one assembled seed shelter (€ 0.05, € 0.10, or € 0.20). Due to the effects of the post-fire treatments on mortality rates (e.g. acorn predation; Chapters 1 & 2) and on the difficulty for reforestation works (Chapter 3), the costs are provided independently for each of the treatments. The metric used is the amount of euros necessary to obtain 400 seedlings that survive to the next year in one hectare. This allows assessing the overall efficacy of each method (i.e. it explicitly contemplates mortality) and it provides a common metric to allow comparing the analysed methods. The rankings in Table 1 are a sequence from the least (1) to the most (13) expensive reforestation scenario, as derived from the costs shown in the table. For more detailed methods and results, see Appendix II.

The least costly method for reforestation in all post-fire treatments was acorn sowing with the seed shelter under the assumption that it takes maximum 2 minutes for the forestry staff to sow each acorn with seed shelter, and under any of the specified cost scenarios (Table 1; rankings 1 to 6). On the contrary, the most expensive methods in all treatments were standard sowing under the scenarios of ≥ 1 min per sown acorn, and seedling planting (Rankings 11 to 13).

To better visualise the trade-offs between the cost of the different methods and scenarios, see Figure 1. The figure shows that planting was generally the most expensive option for reforestation, except if compared to standard sowing when the time to sow one acorn surpassed 2 min. Panel A shows that the proposed range of the timely requirement for sowing might not limit the economic competitiveness of sowing with the seed shelter as compared to either standard sowing or planting (i.e. the coloured seed shelter lines always lie below the planting and standard-sowing lines). Panel B suggests that under the scenario of 0.5 min per sown acorn (which assumes 1 min per sown acorn with a seed shelter; red lines) the use of the device would be economically competitive compared to standard sowing up to a price of around € 1.00 per assembled unit (which is where the solid seed shelter line and the dashed standard-sowing line intersect), while under the scenario of 1 minute per sown acorn (purple lines) the maximum cost of the device for remaining competitive compared to standard sowing would rise to around € 2.00. Both of these prices are much greater than the expected price, so under the tested parameters it seems likely that the seed shelter may provide a cost-effective alternative. The difference between panels A and B in the distance between the coloured solid lines suggests that the total cost of the seed shelter method is more sensitive to the time required for sowing than it is to the cost of an assembled unit within the proposed price and time ranges. Thus, future development of the product should address the optimisation of field operations.

Table 1

	Reforestation cost for 400 surviving seedlings in 1 ha (€)												
	Sowing												
	Time to sow 1 standard acorn*												
	0.5 min				1 min				2 min				
		Sowing with seed shelter				Sowing with seed shelter				Sowing with seed shelter			
		Unitary cost of seed shelter (€)				Unitary cost of seed shelter (€)				Unitary cost of seed shelter (€)			
Post-fire treatment	Standard sowing	0.05	0.10	0.20	Standard sowing	0.05	0.10	0.20	Standard sowing	0.05	0.10	0.20	Planting
SL	570.57	258.55	292.79	361.27	1020.61	454.02	488.26	556.74	1909.99	846.13	880.37	948.85	3265.02
NI	784.21	301.94	335.32	402.09	1432.28	542.07	575.45	642.22	2712.98	1023.78	1057.16	1123.93	4644.93
PCL	1577.57	249.77	281.87	346.07	2832.55	440.35	472.45	536.65	5312.64	822.66	854.76	918.96	3850.87
Ranking** SL & NI	7	1	2	3	11	4	5	6	12	8	9	10	13
Ranking** PCL	10	1	2	3	11	4	5	6	13	7	8	9	12

*Assumes that the time required to sow with a seed shelter is twice the indicated amount

** The Rankings position the options/scenarios from least to most expensive

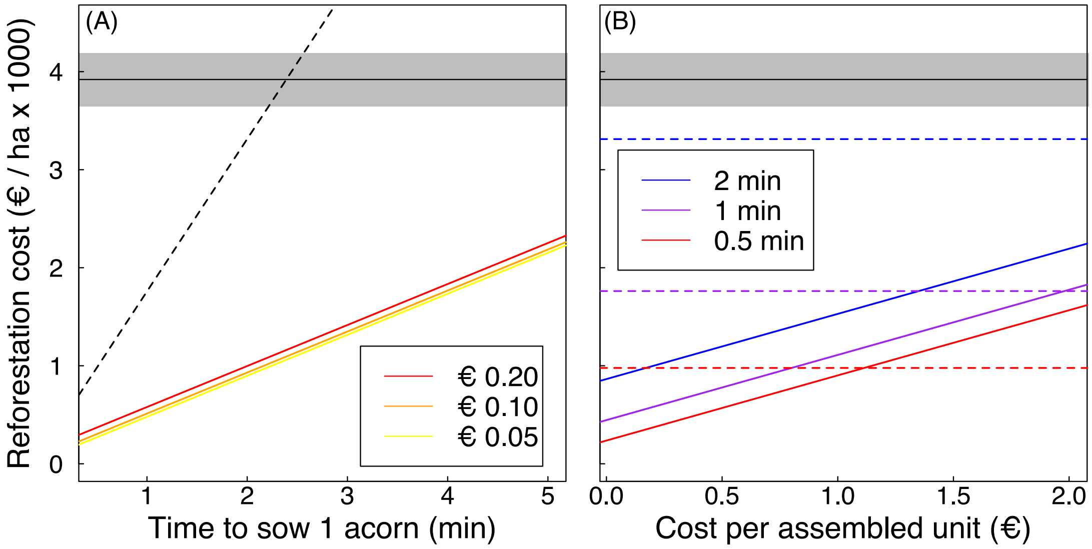

Figure 1. Cost of different reforestation methods. The black horizontal line indicates the average cost of planting across all the management replicates, and the grey shaded area delimits its 95% confidence interval. The dashed lines are for standard sowing and coloured solid lines for sowing with the seed shelter. The colours of the lines indicate the effects on the estimated total cost of sowing to obtain 400 living seedlings of changing (A) the cost of an assembled seed shelter unit, and (B) the per unit timely requirement for sowing in the field. Note that the time required to sow an acorn with a seed shelter is assumed to be twice the indicated amounts.

As outlined in Chapters 1 and 2, acorn sowing has a high potential as an alternative reforestation method due to its lower cost, and it may even show advantages for seedling development over planting, if the problem of acorn predation was solved. Although the results here presented suggest that standard sowing could under some circumstances be less expensive than planting even despite the high losses to acorn predators, the unpredictability of sowing outcomes due to fluctuating predator abundances is a serious risk that managers tend to avoid. From the results of this Thesis it appears that the seed shelter might represent a solution for acorn sowing. Although the calculations here presented rest on several static assumptions (see Appendix II) that require testing under many different conditions, it seems plausible that this device could be economically competitive with respect to other methods of artificial regeneration and reduce the unpredictability of sowing. All of this, of course, in case it reaches the market.

3. Economic valuation of the ecosystem service

As outlined in the Introduction, ecosystems and organisms within them contribute to human wellbeing through so-called ecosystem services. Although ecosystem services represent an enormous value for human society globally (Costanza et al., 1997), their value often escapes our knowledge and consequently the cost-benefit analyses that underlie land-use and management decisions (MA, 2003). In particular, supporting and regulating ecosystem services are essential in maintaining all other services (Kumar et al., 2010), but they are often undervalued by land owners and policy makers. Being public goods and usually not traded in markets, they are easily susceptible to negative externalities (CBD, 2001; Kumar et al., 2010; Wenny et al., 2011). Valuing ecosystem services in economic terms has thus acquired paramount importance in recent decades (Costanza et al., 1997; Chichilnisky and Heal, 1998; Liu et al., 2010), and various methods have been developed for this purpose (Farber et al., 2002).

Without a market for most supporting and regulating services, and lacking public awareness and sufficient information on their economic importance, cost-based approaches like the replacement cost method are most useful for their valuation (Heal, 2000). This method consists of measuring the economic value of an ecosystem service by the cost of replacing it by a human activity (Farber et al., 2002). Examples include valuing the cost of replacing natural water regulation by the construction of a treatment plant (Chichilnisky and Heal, 1998), coral reef shore protection by the creation of artificial protection (Howorth, 1982), or natural crop pollination by performing manual pollination (Allsopp et al., 2008). Using the replacement cost method, Hougner et al. (2006) studied the economic value of jay-mediated acorn dispersal in the Stockholm National Park as the value of planting or seeding instead. Similarly, Puerta-Piñero et al. (2011) used forest inventory data to analyse the savings to the Spanish Forest Service obtained by the avoided need for reforestation due to the natural post-fire regeneration of oaks.

The data presented throughout this Thesis allow applying the replacement cost method to calculate the economic value of natural regeneration resulting from seed dispersal and post-fire resprouting, and also to analyse differences in this value arising from the different post-fire habitats. I used the data on seedling recruitment of Chapters 5 and 6 and the estimated costs of reforestation of Chapters 1 to 4, put together in Appendix II, to calculate the economic value of oak natural regeneration in the experimental plot. This represents an improvement over other valuation studies based on theoretical estimates, where data are often missing or incomplete (Hougner et al., 2006; Puerta-Piñero et al., 2011).

Human alternatives to seed dispersal

To valuate an ecosystem service with the replacement cost method, it is essential to identify the least-cost human alternative that would obtain an identical outcome (Bockstael et al., 2000; Heal, 2000; Pagiola et al., 2004; Söderqvist and Soutukorva, 2009). In Appendix II, I analysed the cost of two alternative methods for oak reforestation: seeding and planting. I also estimated the cost of sowing with the use of an acorn protector, the seed shelter, which resulted to be the most inexpensive altermative under several scenarios. However, for the purpose of this valuation I do not consider the cost of using the seed shelter, as 1) the device is still not in the market (beyond prototypes for research purposes), and 2) this is not a standard technique for reforestation and it is consequently not expected that managers would incur the cost (and the risk) of using it. Further, standard sowing is most often avoided by managers due to the unpredictability and frequent poor results resulting from acorn predation (Dey et al. 2008; McCreary 2009; Farlee 2013), and thus here I use the cost of planting to calculate the replacement value of natural regeneration.

Ecosystem service valuation: Methods

I based the estimation of the economic value of natural regeneration on the assumed management target of obtaining a density of 400 oaks per hectare. This would normally be achieved by planting sufficient seedlings that 400 survive. However, if some of these seedlings were obtained through natural regeneration, then fewer plants would need to be planted to achieve the target. I thus took the densities of oak seedlings encountered throughout the post-fire habitats of Plot 1 (as defined in Chapter 6), substracted them from 400, and calculated the cost of planting the remaining number of seedlings (assuming that the changes in seedling density resulting from planting fewer seedlings would not change the per unit cost of planting, and that planting in the PIN habitat would cost as much as in the treatment that was least expensive to reforest). I then value the ecosystem service as the potential savings that arise from the difference between the cost of planting to obtain the deafault of 400 surviving seedlings and planting the amount necessary to reach 400 seedlings when taking into account those already present due to natural regeneration. I calculated this for a) the pre-management saplings, b) the post-management seedlings, and c) all plants combined (for definitions, see Chapter 6).

Ecosystem service valuation: Results

Planting across the whole plot at a density of 400 seedlings per hectare would cost € 68726, from which about 10% would be saved if oak natural regeneration were taken into account to meet the management objective (Table 2). If the total savings due to natural regeneration are divided by the surface of the plot (17.67 ha), the average value of post-fire oak regeneration is 359 €/ ha.

Table 2

Post-fire habitat	Savings (€ / ha) Pre-mgt saplings	 Post-mgt seedlings	 All plants	Total savings (€)*	Full cost planting (€)**
NI	112.58	92.11	204.69	1161.25	26351.55
SL	410.53	21.26	431.79	2154.90	16294.31
PCL	199.77	35.05	234.82	1290.09	21157.39
PIN	92.04	1061.12	1153.16	1738.61	4922.64
Total				6344.85	68725.89

* Savings across the whole surface of the post-fire habitat due to natural regeneration

** Cost of planting to obtain 400 live seedlings per hectare across the whole surface of the post-fire habitat

The value of oak natural regeneration varied among post-fire habitats. Although here I do not present statistical tests for these differences, three main patterns arise from Table 2. First, the savings per hectare in the SL and PCL habitats were fairly large for pre-management (mostly resprouting) seedlings, and comparatively very small for post-management seedlings. Second, the savings in NI due to pre-management and post-management seedlings were quite similar. And third, the savings in PIN due to post-management seedlings were more than ten-fold those of pre-management seedlings.

Ecosystem service valuation: Discussion

The results of this Thesis indicate that the ecosystem service of natural regeneration of oaks in the Lanjarón study area may provide a value of € 205 to € 1150 per hectare, resulting from acorn dispersal by jays and from young resprouting oaks. Although this value came free of cost, it was highly dependent on the management strategy employed after the fire, particularly in cases where not all the trees were killed, and it relied on the existence of either resprouting individuals or a nearby seed source. The obtained economic values are roughly in line with another estimate for Spain (Puerta-Piñero et al., 2011) yet below long-term estimations for the Stockholm National Urban Park (Hougner et al., 2006). As discussed below, the replacement cost method proved appropriate to calculate the value of natural post-fire regeneration.

Being a non-market approach, thus not based on people’s preferences, makes the replacement cost method controversial for economists (Farber et al., 2002). However, it is considered adequate if three conditions are met (Bockstael et al., 2000; Heal, 2000; Pagiola et al., 2004; Söderqvist and Soutukorva, 2009):

1. The human activity should generate quantitatively and qualitatively identical outcomes than the ecosystem service being replaced. As I calculated the cost of replacing the exact amount of seedlings that recruited naturally, the human alternative is quantitatively identical. However, I did not account for the spatial variability in seed dispersal, which represents a disadvantage for managers by making the outcomes

less predictable. Nevertheless, I also based the costs of planting on average values although they, too, varied. In fact, natural regeneration through seed dispersal may show advantageous over planting for several reasons: a) it is a continuous process that reduces vulnerability to the allocation of management resources (Lundberg et al., 2008), b) it reduces the risks related to fluctuating environmental conditions (Hougner et al., 2006; Wenny et al., 2011), c) it allows the normal development of tap roots (Pemán García and Gil Pelegrín, 2008; Tsakaldimi et al., 2009), d) it enhances gene flow and genetic diversity (Lundberg et al., 2008), and e) it avoids damage to the soil and vegetation by machinery. Thus, human alternatives may have disadvantages compared to dispersal, their cost resulting in a conservative estimate for the natural service.

2. The human activity must be the least-cost alternative available. Seed sowing was generally the least-cost alternative available in the market. However, planting was used as a reference due to condition 3 below (also see *Methods* above). If new, less expensive, and reliable methods for reforestation became available in the market and common, as could happen with the seed shelter (Castro et al., 2015; Leverkus et al., 2015a), the savings in reforestation (i.e. the economic value of natural regeneration) would become smaller.
3. Society should be ready to incur the costs. Willingness to pay for the human alternative of planting exists, as reforestations were carried out around the study plots. Besides, as planting is generally more widespread than sowing, the replacement cost was calculated under a realistic alternative scenario to natural regeneration.

I did not use discount rates to calculate the value of the ecosystem service. Discount rates indicate how much less present money is worth in the future (Hein, 2006), and it could be argued that seed dispersal is worth less than what was calculated because a part of it occurs later than a one-time reforestation. However, neither natural nor artificial regeneration have immediate results– both may have the consequence of producing a forest in the long term (particularly in the case of slow-growing species such as *Q.ilex*). The objective of reinforcing ecosystem resilience through enhancing resprouting species (Thompson et al., 2009) is yet another future-oriented objective. This contrasts with the short-term economic view imposed by discount rate application, which may easily encourage unsustainable management practices (CBD, 2001; Hein, 2006).

For the provision of the ecosystem service of seed dispersal, the service providers, namely jays (Luck et al., 2009), required the standing living or dead pines as supporting elements to perform their function (Hougner et al., 2006). However, the presence of these supporting elements also enhanced the activity of the main ecosystem service *antagonisers* –species acting against ecosystem services (Luck et al., 2009)–, in this case rodents (Puerta-Piñero et al., 2010). Still, the overall effect of the trees and snags on seedling recruitment remained positive as long as they remained standing, and the economic value of dispersal was particularly high in the patches of surviving pines, which endured throughout the study period.

In the SL and PCL post-fire habitats, which were mostly –or totally– devoid of standing trees, the ecosystem service of natural regeneration relied mainly on the resprouting capacity of the Holm oak. Resprouting is, in fact, one of the main post-fire regeneration strategies of plants in the Mediterranean Basin (Lloret, 2004; Pausas et al., 2004). In the large, dense plantations of pines that abound in the region –several of which, such as *Pinus nigra* or *P. sylvestris*, lack post-fire regeneration strategies–, the presence of resprouting, late-successional species such as the Holm oak may thus confer resilience to stand-replacing disturbances and provide direct value to society by reducing, or even eliminating, the need to perform reforestation.

Besides seed dispersal, post-fire management can affect other ecosystem services, such as nutrient cycling, water retention, carbon absorption, and habitat provision (McIver and Starr, 2000; Lindenmayer et al., 2008; Leverkus et al., 2015b). These, in turn, must be balanced with other factors, such as local post-fire plague risks and social acceptance, to make decisions on post-fire management. With this Thesis I hope to provide a small part of the cost-benefit equation of burnt wood management.

As a final remark, economic valuations alone do not lead to sustainable practices (Kumar et al., 2010). Still, it is important to investigate how ecosystem services change under different environmental scenarios to aid land managers in making informed decisions (Luck et al., 2009). While it is impossible to calculate the full value of the services provided by an ecosystem (Heal, 2000), and any full attempt may risk to be regarded as a *serious underestimate of infinity* (Toman, 1998), providing managers with alternative economic assessments may aid decision-making towards sustainability and towards *enhancing the infinite value of nature*.

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Conclusions

1. Both active and passive regeneration allow enhancing the cover of desired species in degraded areas. The trade-offs between these two approaches in terms of outcomes and economic balance are the result of several interacting factors related to land management, interspecific interactions, and other external factors such as climate.

2. The success of active regeneration of holm oaks through seeding acorns is often hampered by mammals that depredate the acorns. Large-scale management leading to a more complex habitat structure may impede foraging by large ungulates such as wild boars. This may, however, increase the abundance and activity of small mammals such as mice, which find protection in such areas. Thus, finding effective protection from rodents for individual acorns is necessary to enhance the success of acorn sowing.

3. Deeper burial of acorns and the application of capsaicin seem ineffective to deter rodents from predating acorns. However, a new device named seed shelter, designed to prevent predation by small mammals, may greatly increase the success of acorn sowing and provide a cheap and reliable alternative to seedling planting. This device is not yet in the market.

4. Planting nursery-grown seedlings, a more widespread method of active regeneration with species of *Quercus*, is often used to justify post-fire salvage logging, as this practice eases reforestation works and reduces their cost. However, the savings obtained by planting in salvaged burnt forests as compared to unsalvaged areas are an order of magnitude lower than the cost of salvaging. Thus, in burnt Mediterranean pine afforestations, where the profit of transporting and selling the timber is small or inexistent, planting does not justify the cost of salvage actions.

5. The aridification of Mediterranean mountains may yield enhanced performance of reforestation in areas previously considered to be above the altitudinal distribution of target species. Restoring with consideration of uphill range shifts may aid the persistence of target species while enhancing ecosystem adaptation to climate change.

6. Obtaining an established holm oak seedling generally costs less through standard acorn sowing than through planting, but the outcomes of sowing are unpredictable. Sowing with the seed shelter may be more cost-efficient and reliable than either of these standard techniques.

7. Passive regeneration of holm oaks involves resprouting and the mutualistic interaction with European jays, a major long-distance disperser. After a fire, burnt and partially damaged pine trees that remain standing still act as suitable habitat for jays to cache acorns. Post-fire management favouring these structures in the presence of nearby seed sources may yield enhanced natural colonisation of the burnt area by oak seedlings.

8. Dynamic, heterogeneous landscapes where seed dispersal changes directionally following gradual alterations in habitat attributes may yield shifting demographic conflicts across successive cohorts of plant recruitment.

9. Natural regeneration of oaks represents an ecosystem service that may reduce the need for post-fire reforestation. As such, it may also reduce the cost of these actions, and produce savings of hundreds of euros per hectare.

Conclusiones

1. La restauración activa y pasiva permiten repoblar zonas degradadas con las especies deseadas. El balance en cuanto al éxito y el coste de estas alternativas es el resultado de factores relacionados con el manejo del ecosistema, las interacciones interespecíficas y otros factores extrínsecos como el clima.

2. El éxito de la siembra de bellotas de encina a menudo se ve diezmado por mamíferos depredadores de bellotas. El manejo de hábitats que favorezca una elevada complejidad estructural de los mismos puede reducir el forrajeo de grandes mamíferos como el jabalí. Sin embargo, ello puede incrementar la abundancia y actividad de mamíferos más pequeños, como los ratones, que encuentran protección en estas zonas. Para incrementar el éxito de las repoblaciones con bellota es esencial desarrollar métodos eficaces para proteger a las bellotas de los roedores.

3. Una mayor profundidad de siembra y el uso de capsaicina parecen ineficaces para prevenir la depredación de bellotas por roedores. Sin embargo, un nuevo dispositivo, llamado *seed shelter* y diseñado para prevenir la depredación por pequeños mamíferos, podría aumentar sustancialmente el éxito y la fiabilidad de las siembras de bellota como alternativa a la plantación. Este dispositivo aún no está en el mercado.

4. La plantación, un método más extendido para la regeneración activa de especies de *Quercus*, es a veces utilizada para justificar la saca de la madera después de un incendio, al facilitar ésta las labores y reducir los costes de repoblación. Sin embargo, el ahorro obtenido por reforestar en zonas incendiadas donde se ha extraído la madera en comparación con zonas sin saca es un orden de magnitud menor que el coste mismo de la saca. En pinares de repoblación mediterráneos, donde el beneficio del transporte y la venta de la madera es reducido o nulo, la plantación no justifica el coste de sacar la madera quemada.

5. La aridificación de las montañas mediterráneas puede generar un mayor éxito de las repoblaciones forestales en zonas anteriormente consideradas por encima de la distribución altitudinal de las especies de interés. La restauración con consideración de los ascensos altitudinales en el rango de distribución potencial de las especies favorecerá tanto la permanencia de las especies de interés como la adaptación de los ecosistemas al cambio climático.

6. Obtener una encina establecida es generalmente más barato mediante siembra que mediante plantación, pero los resultados de la siembra son impredecibles. Sembrar con el *seed shelter* puede resultar más rentable y fiable que cualquiera de los dos métodos tradicionales.

7. La regeneración pasiva de la encina involucra la capacidad de rebrote y la relación mutualista con el arrendajo, un importante dispersor de bellotas a larga distancia. Después de un incendio, los pinos quemados o parcialmente afectados que se mantienen en pie aún actúan como hábitat apropiado para la dispersión de bellotas. Las estrategias de manejo post-incendio que favorezcan la presencia de estas estructuras en la cercanía de fuentes de bellotas pueden favorecer la colonización natural por encinas de la zona quemada.

8. Los paisajes heterogéneos y dinámicos en los que la dirección de la dispersión de semillas cambia direccionalmente como resultado de transformaciones graduales en las propiedades del hábitat pueden generar cambios en los conflictos demográficos sufridos por cohortes sucesivas de reclutamiento.

9. La regeneración natural de la encina supone un servicio ecosistémico que puede reducir la necesidad de reforestación post-incendio. De este modo, puede reducir el coste de estas acciones y producir ahorros de cientos de euros por hectárea.

Chapter 1

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Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks

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Abstract

Acorn sowing is a reforestation technique that can potentially render high-quality oak seedlings and high seedling survival, although it is often discarded due to high rates of seed predation. Predator activity can be modified by habitat complexity due to its effect on accessibility and protection for different predators. In this study we analysed how habitat complexity generated by different post-fire management treatments, sowing depth, and capsaicin (a chemical repellent) affect acorn predation by two guilds of post-dispersal predators that differ in size and foraging behaviour. We carried out two acorn predation experiments. In Experiment #1 we buried acorns at two depths (2 and 8 cm) in two post-fire burnt-wood management treatments of different habitat complexity, namely: 1) Salvage Logging (SL), where the burnt trunks were cut and piled and the branches were masticated (lower habitat complexity), and 2) Non-Intervention (NI), with no action after the fire and 100% of the trees naturally fallen by 2009, thus leaving a habitat with lying burnt logs and branches (higher habitat complexity). In Experiment #2 we repeated Experiment #1, with the addition of capsaicin as a mammal repellent treatment. Most acorns were consumed in both years (ca. 90%), mainly by rodents. In Experiment #1 predation by boars accounted for 4.1% of overall predation, and it was about twice as high in SL than in NI, likely due to the physical difficulty for large mammals to forage in an area with a complex structure created by lying logs and branches. In contrast, rodents consumed ca. 1.4 times more acorns in NI than in SL, which led to overall greater predation in NI in both experiments. This was likely due to the protection provided by the branches for the rodent community. Deeper burial reduced predation by small percentages, although in Experiment #1 it had a negligible effect in NI. Capsaicin did not reduce predation, and it reduced seedling emergence to half. This study suggests that habitat complexity created by trunks and branches reduced predation by wild boars, but favoured rodent acorn predation. We conclude that other methods for the protection of individual acorns need to be identified to increase the success of oak reforestation via seeding.

Keywords: acorn removal, capsaicin, post-fire management, rodents, seed predation, seed sowing

Abbreviations: BWM= Burnt-wood management treatment(s); SL= Salvage Logging treatment; NI= Non-Intervention treatment

1. Introduction

Seed sowing and seedling planting are universal methods for the restoration of woody plant species in disturbed areas (Twedt and Wilson, 2002; Pausas et al., 2004; Dey et al., 2008; Cortina et al., 2009). Planting has the advantage of using already emerged seedlings. It avoids mortality from seed predation, which otherwise acts as a filter that can destroy a great proportion of available seeds (Crawley and Long, 1995; Herrera, 1995; Gómez, 2004; Pulido and Díaz, 2005), and consequently hinder regeneration via seeding. However, planting has the major inconvenience of being far more costly and time-consuming than seeding (Bullard et al., 1992; Stanturf et al., 2000; Espelta et al., 2003; Allen et al., 2004). Through seeding, many seeds can be sown in little time and at a relatively low cost, and in case they escape seed predation, high germination rates and adequate seedling performance can be obtained (Fuchs et al., 2000; Pulido and Díaz, 2005; Cortina et al., 2009; Puerta-Piñero, 2010). Even if part of the sown seeds are lost before reaching the seedling stage (e.g. by predation or fungal attack), the higher number of seeds that can be sown, compared to the seedlings that can be planted at a similar cost, might compensate (Bullard et al., 1992; Pausas et al., 2004).

Oak woodlands are one of the main vegetation types in the Northern Hemisphere. These forests have suffered disturbances during millennia, and currently they are one of the main targets in restoration policy (e.g. EEC Regulation No. 2080/92; US Wildlife Habitat Incentives Programs). The most common oak reforestation technique is via plantations of nursery-grown seedlings (King and Keeland, 1999; Espelta et al., 2003; Cortina et al., 2009; Del Campo et al., 2010). However, survival of planted seedlings may be low, particularly in the case of ecosystems with a dry summer such as those under Mediterranean climate conditions (Rey Benayas et al., 2005; Castro et al., 2006; Valdecantos et al., 2006; Del Campo et al., 2010). Besides, nursery-grown oak seedlings often suffer suboptimal root architectures which are not appropriate for Mediterranean drought conditions (Peman et al., 2006; Dey et al., 2008; Tsakaldimi et al., 2009). Furthermore, planting, associated with machinery removing naturally established vegetation and digging holes on mountain slopes, usually causes important damage to the soil (Pulido, 2002; Espelta et al., 2003). In some cases, machines are not even capable of entering certain areas due to the steep slopes, while a person would not have difficulties in passing and sowing acorns. These arguments question whether the investment in oak planting and subsequent management is actually worthwile compared to seeding.

Acorn sowing is largely discarded for oak reforestation due to the high seed loss produced by vertebrate predators (Allen et al., 2004; Pulido and Díaz, 2005; Dey et al., 2008; Cortina et al., 2009), including small rodents (Gómez, 2003; Tyler et al., 2006; Puerta-Piñero et al., 2010a), wild ungulates (such as wild boars, *Sus scrofa* and red deer, *Cervus elaphus*), and livestock (Schmidt and Timm, 2000; Muñoz and Bonal, 2007; Gómez and Hódar, 2008; Puerta-Piñero, 2010). However, the emergence rate of surviving acorns after sowing tends to be high (Fuchs et al., 2000; Allen et al., 2004; Pulido and Díaz, 2005). In addition, the survival rates of emerged oak seedlings can be similarly high, with values that can surpass 50% and even approach 100% several years after sowing (Tietje et al., 1991; Pulido and Díaz, 2005; Mendoza et al., 2009; Matías et al., 2011). Seedlings emerged from acorns in the field tend to develop better root architectures for field conditions (Allen et al., 2004; Dey et al., 2008; Tsakaldimi et al., 2009). Another advantage of sowing is that it provides flexibility, as the temporal span when acorns can effectively be sown is wider than that of planting (Allen et al., 2004). Seeding may also result in less vegetation uniformity of the reforested area, potentially resulting in better wildlife habitat (Twedt and Wilson, 2002). Thus, seed sowing has the potential to be an effective and cost-efficient method for oak woodland restoration if seed predation was reduced. Consequently, finding a way for acorns to overcome post-dispersal seed predation is a key issue that could promote oak woodland reforestation (Schmidt and Timm, 2000; Gómez, 2004; Smit et al., 2008).

The management of habitat complexity is a way to influence plant-animal interactions, including the potential reduction of post-dispersal seed predation on sown seeds. Movement decisions and foraging behaviour of animal species are affected by habitat complexity (Fuchs et al., 2000; Gómez, 2004; Puerta-Piñero, 2010; Puerta-Piñero et al., 2010a). Indeed, the same habitat characteristics may affect different guilds of predators in different ways (Matías et al., 2009; Smit et al., 2008; Puerta-Piñero, 2010). For instance, small seed predators such as rodents tend to concentrate their activity in areas with a rather complex habitat structure, as this reduces the risk of predation they perceive (Schupp, 1988; Torre and Díaz, 2004) and provides more suitable conditions for them (Haim and Izhaki, 1994). By contrast, seed predation by large mammals such as ungulates could be lower where a higher habitat complexity impedes their movements and partially avoids their penetration (Forget et al., 2005; Gómez and Hódar, 2008; Smit et al., 2008; Puerta-Piñero, 2010).

Besides managing habitat complexity at larger landscape scales, acorn-scale solutions such as deep sowing or the use of chemical repellents could also improve seed survival. Burial can increase the likelihood of surviving to acorn predation (Crawley and Long, 1995; Herrera, 1995; Fuchs et al., 2000; Gómez, 2004; Pulido and Díaz, 2005). Buried acorns can also find more favourable temperatures and moisture levels than on the ground surface (Li and Ma, 2003; Tietje et al., 1991; Dey et al., 2008), and this positive effect is likely to increase up to a certain depth (Tietje et al., 1991; Fuchs et al., 2000). The use of chemical substances that act as predator repellents is another technique to reduce predation that has been little explored (Nolte and Barnett, 2000; Willoughby et al., 2011). Capsaicin is a natural repellent obtained from chilli peppers (genus *Capsicum*; EPA, 1996) that produces a burning sensation in mammals by irritating mucose tissues, and it has successfully been used as a mammal repellent under controlled conditions (e.g. Nolte and Barnett, 2000; Willoughby et al., 2011). However, the capacity of this substance to reduce seed predation has scarcely been tested under field conditions (but see Barnett, 1998).

In this study we investigate whether the effectiveness of seed sowing could be enhanced in landscapes managed to reduce predation by large mammals while individual acorns are protected to minimise their predation by rodents. For this, a post-fire landscape was managed to create two treatments differing in habitat complexity: one where all the burnt trees were removed (the usual post-fire treatment, called salvage logging, with low habitat complexity), and one where burnt wood was left *in situ* creating a complex mesh of fallen logs and branches (high habitat complexity). We hypothesised that i) acorn predation would vary among burnt-wood management treatments, ii) deeper-buried acorns would suffer lower predation rates, and iii) capsaicin would deter predation on acorns. As a result, we aimed to explore whether appropriate management of burnt wood, sowing depth, and the use of chemical repellents could create a suitable scenario for the restoration of oak forests through seed sowing.

2. Materials and methods

2.1. Study site and species

The study site is located in the Sierra Nevada National Park, SE Spain, where a fire burned 1300 ha of pine forest (3420 ha in total) in September 2005. The site was located in an affected *Pinus pinaster* and *P. nigra* reforestation stand at 1477 m a.s.l. (36º 57’ 9.8949 N, 3º 29’ 36.2381’’ W) located in the Lanjarón municipality. Pine tree density in the study area was 1477 ± 46 individuals ha^{-1}, with a basal trunk diameter of 17.7 ± 0.2 cm (mean ± SE; Castro et al., 2011). It is situated on a SW-oriented hillside (slope: 30.3 ± 5.7%) with micaschist as bedrock. Climate in the area is Mediterranean, with warm, dry summers and mild, rainy winters. Mean annual precipitation recorded at the site was 501 ± 49 mm (1988-2011) and mean annual temperature was 12.3 ± 0.4 °C (1988-2008). The study years (2010 and 2012) greatly differed in terms of precipitation. Precipitation from January through June 2010 (time period of the experiments) was 555.7 mm, while in 2012 it was only 145.1 mm during the same months.

Holm oaks (*Quercus ilex* subsp. *ballota* L.) naturally coexisted with the pines in the study area, and are considered the potential climax vegetation of the area according to climatic, edaphic and historical data (Valle, 2003). The holm oak is a sclerophyllous evergreen tree, abundant in the Mediterranean area of the Iberian Peninsula. Acorns ripen in autumn and are dispersed primarily by the European jay *Garrulus glandarius* (Castro et al., 2012). The main post-dispersal acorn predators in the area are wild boars and rodents such as *Apodemus sylvaticus* and *Mus spretus* (Gómez and Hódar, 2008; Puerta-Piñero et al., 2010a; Unpublished data).

2.2. Experimental design

Seven months after the fire (April 2006), the local Forest Service established a plot with three randomly distributed replicates of two treatments that differed in their degree of post-fire burnt-wood management (BWM hereafter) and thus in the resulting post-fire habitat complexity (Fig. 1):

1) Salvage logging (SL). In this treatment, all the burnt trees were cut and their trunks cleared of their main branches using chainsaws. Trunks were piled in groups of 10-15 and left *in situ*, and the woody remains were treated with a mechanical masticator. This created an open landscape where ungulates could move and forage easily (Puerta-Piñero et al., 2010a).

2) Non-Intervention (NI). Here the burnt trees were left standing and no further action was taken. Trees fell naturally, with a cumulative fall rate (measured with 100 marked pines per replicate in February of each year) of 0.0% in 2006, 12.33 ± 3.38% in 2007, 92.88 ± 1.18% in 2008, and 100% in 2009 (Castro et al., 2012). Thus, during the study period (2010 and 2012), this treatment was characterised by a complex structure of trunks and branches spread all over the ground.

The six replicates had an average size of 2.0 ± 0.2 hectares, with no significant differences in size between treatments (Kruskal-Wallis test).

2.3. Habitat complexity

In 2012, we sampled habitat complexity in the experimental BWM treatments. For this we established eight linear transects of 25 m in each of the thee replicates of both treatments. The transects were defined by randomly selecting eight starting points within each replicate, and drawing a straight line in the direction of the maximum slope. We noted the nature of the highest contact (soil, live plants, or woody debris) and its height every 0.5 m along each transect as well as at 1 m to both sides of the transect (thus 150 points per transect). Height was categorised in six different classes (0= 0 cm; 1= 1-10 cm; 2=11-25 cm; 3= 26-50 cm; 4= 51-100 cm; 5= >100 cm).

2.4. Acorn Predation Experiments

We studied acorn predation in two complementary experiments performed in 2010 (Experiment #1) and 2012 (Experiment #2).

Experiment #1 was carried out to investigate the combined effects of post-fire BWM and depth of burial on acorn predation. It was set up in January 2010. We sowed 150 viable acorns per replicate of each treatment (900 acorns monitored in total). Half of the acorns in each replicate were sown at 2 cm depth (shallow, hereafter), mimicking biotic dispersal (Gómez, 2003; Muñoz and Bonal, 2007), and the other half at 8 cm (deep, hereafter), which simulates potential human sowing for reforestation purposes (Allen et al., 2004; Dey et al., 2008). Acorns were individually placed within the replicates, at least 10 m apart from each other, and at alternated sowing depths. Burial holes were made with a pick, removing the ground as little as possible. A numbered wooden stick was set into the ground to mark the buried acorn. Viability of the acorns was checked before sowing through the flotation method (Gómez, 2004). We monitored acorn removal after 10, 40, and 90 (± 3) days of sowing. In each revision, the fate of the acorns was visually recorded (predated vs. non-predated), as well as predator identity (rodent vs. wild boar). The latter is easily identifiable, as rodents dig a narrow hole to unbury the acorns, while wild boars leave plants uprooted and the soil turned over (Puerta-Piñero, 2010). In the last revision, performed at the time of germination, we confirmed the removal of acorns by digging 40 randomly selected sowing points per BWM replicate with a pick. In 100% of the cases we confirmed that the results of the visual revision had been correct. Removed acorns were considered predated because previous studies found that > 98% of acorns found by rodents are finally predated and that there is no secondary caching by the main acorn dispersers in the area (Muñoz and

Bonal, 2007; Gómez et al., 2008). Out of the 900 experimental acorns, 14 were lost during the study, so the statistical analyses were made on the remaining (N = 886).

Experiment #2 was carried out to test the effects of burial depth in both BWM treatments (as in Experiment #1), combined with the use or not of capsaicin as a rodent repellent. It was performed in January 2012. We used the same post-fire BWM replicates and burial depths as in Experiment #1. Natural capsaicin (65% capsaicin, 35% dihydrocapsaicin) was obtained from Sigma-Aldrich. We diluted it in an emulsion of diethyl ether and sorbitan trioleate at 24 g l^{-1} (Willoughby et al., 2011). We applied a total of 0.325 g of capsaicin per kg of acorns, a proportion that has been shown to be effective in controlled multiple-choice experiments with mice and squirrels on wheat (Willoughby et al., 2011). For each experimental combination (BWM x burial depth x capsaicin) we sowed 35 acorns, totalling 840. Acorns within each BWM replicate were placed at systematically alternated depth x capsaicin combinations. Methods were as described above. One visual revision was made 7 +/- 2 days after sowing. A second visual revision was made by the time of germination in May, 100 +/- 7 days after sowing. After this last revision we again confirmed acorn removal by digging up 40 randomly selected sowing points per BWM replicate with a pick, and again we confirmed 100% of accuracy of the visual revision. Five acorns were lost during the study, so our effective sample size was N = 835.

2.5. Effect of capsaicin on seedling emergence

At the time of sowing in the field in Predation Experiment #2, we performed an experiment to test the effect of capsaicin on seedling emergence. A total of 80 acorns (40 treated with capsaicin as described above and 40 control with no capsaicin added) were sown in plastic containers using a substrate prepared by mixing 67% natural soil from the experimental plot in Lanjarón and 33% sand. Acorns were planted at 6 cm depth, using an alternating distribution. The experiment was conducted in a nursery at outdoor conditions near the University of Granada (735 m a.s.l.). The containers (300 cm^3) were covered with wire mesh to prevent predation by domestic rodents, and were periodically irrigated during the trial. We monitored their emergence after 60, 80, 86, 94, 103, 114, and 154 days.

2.6. Data analyses

Habitat structure was analysed with hierarchical ANOVAs that used percentage cover of each cover type (soil, live plants, wood) as dependent variables, with all height classes pooled. BWM was the only explanatory factor, and we specified the sampling error structure [sides of a transect (left, centre, right) within transects within BWM replicates]. The percent cover data were arcsine-transformed prior to analysis.

Acorn predation at the end of Experiment #1 was analysed using a generalized linear model (GLM) with binomial response and logit as link function, considering the effects of BWM, Depth, the BWM by Depth interaction, and Replicate nested in BWM. The effect of predator identity was later tested with contingency analysis. For Experiment #2 a similar model was built, using BWM, Depth, Capsaicin, all the possible interactions among these factors, and Replicate nested in BWM as explanatory factors. These models were simplified following Crawley (2007).

We performed a survival analysis to test the effect of capsaicin on seedling emergence with time after sowing. For this we used a GLM with gamma errors. We used Capsaicin as the only explanatory factor. For the final values of acorn emergence, we fitted a GLM with quasi-binomial errors and Capsaicin as explanatory factor.

Statistical analyses were performed using R version 2.15.0 (R Development Core Team, 2012).

3. Results

3.1. Habitat complexity

Open soil covered 39.2 ± 6.0% in SL (mean ± SE of the mean, calculated using the means of the three replicates) and 25.6 ± 4.8% in NI (Table 1), although this difference was not significant ($P > 0.05$). Cover of live plants did not significantly vary with BWM either ($P > 0.05$), and had values of 46.8 ± 7.2% in NI and 49.7 ± 7.2% in SL (Table 1). In contrast, cover of woody debris was significantly greater in NI (27.6 ± 2.8%) than in SL (11.1 ± 2.4%; $F = 18.55$; df = 1; $P = 0.02$).

3.2. Acorn predation experiments

Acorn predation for Experiment #1 reached an overall value of 41.3 ± 1.7% after 10 days, 78.8 ± 1.4% after 40 days, and 87.6 ± 1.1% after 90 days (mean ± SE of the mean). Predation by the end of the experiment was significantly affected by all factors (Table 2). Predation was higher in NI (99.1 ± 0.4%) than in SL (76.1 ± 2.0%), and was slightly greater at 2 cm (89.7 ± 1.4%) than at 8 cm (85.5 ± 1.7%) depth. There was a significant BWM x Depth interaction, as depth had a stronger effect in SL than in NI (Table 2; Fig. 2). Predation was greater in some replicates of the BWM treatments than others, this effect being highly significant (Table 2; Fig. 3). Rodents accounted for 95.9% of the predated acorns, while wild boars consumed the remaining 4.1% (differences among predator agents: $\chi^2 = 652.28$, d.f. = 1, $P < 0.0001$). Predation by rodents was similarly affected by all factors (Table 2), with higher values in NI than in SL (96.8 ± 0.8% vs 70.9 ± 2.2%, respectively). In contrast, predation by wild boars in

NI was about half what it was in SL (2.3 ± 0.7% and 5.0 ± 1.0%, respectively; χ^2 = 4.78, d.f. = 1; P = 0.03).

In Experiment #2, 80.1 ± 1.4% of the acorns had been consumed after 7 days, and 90.0 ± 1.0% at the end of the experiment. Only BWM, Depth and Replicate had a significant effect on predation (Table 3). Predation was greater in NI (99.8 ± 0.2%) than in SL (80.2 ± 2.0%), and slightly greater for shallow (91.6 ± 1.4%) than for deep acorns (88.5 ± 1.6%). Capsaicin did not have a significant effect (Table 3), not even in the first revision (χ^2 = 1.7, P = 0.19; rest of the model not shown). Overall, only 3 acorns were consumed by wild boars (all in SL), and the remaining by rodents.

3.3. Effect of capsaicin on seedling emergence

Capsaicin significantly delayed average emergence time by 9 days (df = 1, χ^2 = 0.52, P = 0.001; Fig. 4). Besides, capsaicin application reduced the final values of seedling emergence from 63% to 33% (df = 1; F = 7.1; P = 0.009).

4. Discussion

We analysed the effect of the habitat complexity generated by different burnt-wood management treatments on mammal acorn consumption in a burnt Mediterranean forest, as well as the potential of sowing depth and the use of capsaicin for reducing acorn predation. We had initially hypothesised that an appropriate habitat management, combined with deeper sowing and/ or the use of a chemical repellent could provide a window of opportunity for oak reforestation via sowing. However, contrary to our expectation, predation rates were very high in all experimental combinations, reaching an overall value of ca. 90% in both years. Nevertheless, our results still provide useful insights to be considered for oak reforestation via acorn sowing.

4.1. Effect of burnt-wood management and sowing depth

Our results show that acorn predation was greater in the treatment with higher habitat complexity generated by logs and branches spread on the ground (NI). On the other hand, predation was reduced with deeper burial, although this difference was generally low and in Experiment #1 it was more apparent in the treatment with lower structural complexity (SL) and negligible in NI. All this may be explained by the foraging behaviour of the main predator guild. On one hand, rodents accounted for most of the predation (nearly 100% in Experiment #2) and they predated very fast, with values that could surpass 70% after just one week. This reduced the opportunities for predation by larger and less abundant mammals such as ungulates. Greater predation rates in NI could be related to potential benefits obtained by the rodent community, as the woody debris on the ground created a habitat where rodent populations could profit from more abundant food, shelter, and nest sites, as well as better thermoregulatory conditions (Herrera, 1995; Loeb, 1999; Smit et al., 2008). Furthermore, the logs and branches could have led to a lower perceived predation risk (Torre and Díaz, 2004; Muñoz and Bonal, 2007). Non-intervention areas could consequently both sustain greater rodent abundances, as well as change rodent foraging behaviour by allowing them to spend more time foraging and digging than in salvage logged areas (Haim and Izhaki, 1994; Torre et al., 2002; Muñoz and Bonal, 2007). A more careful search for food would consequently explain the lower effectiveness of deeper burial obtained in NI in Experiment #1.

Predation by wild boars was low in this study. However, the results support that the management of burnt wood could help reduce acorn losses to this predator, as in Experiment #1 the NI treatment reduced predation by wild boars to half. This was likely due to the physical difficulty for a large mammal to forage in an area with a complex structure created by logs and branches (Relva et al., 2009; Puerta-Piñero, 2010; Puerta-Piñero et al., 2010a). As wild boars can represent a major threat for oak reforestation via seed sowing (Gómez, 2004; Pulido and Díaz, 2005; Smit et al., 2008), the higher post-fire habitat complexity could represent a relevant benefit for reforestation under circumstances of greater predation pressure by these ungulates.

In short, both experimentally tested burnt-wood management practices generated trade-offs between acorn predation by the two different predator guilds. A high habitat complexity created by elements that hamper ungulate foraging may greatly reduce the potential impact of this guild. In contrast, rodents can benefit from the protection of logs and branches, causing high predation even on deeper-sown acorns. The actual effect of burnt-wood management on seeding outcomes will thus depend on the spatial and temporal context of predator abundances.

4.2. Effects of capsaicin on acorn predation and seedling emergence

The application of capsaicin did not reduce acorn predation. This contrasts with previous studies that have shown its effectiveness as a mammal repellent in other situations (Nolte and Barnett, 2000; Jensen et al., 2003; Willoughby et al., 2011). The absence of an effect of capsaicin was evident even one week aftert sowing, so we may discard a potential loss of effectiveness with time due to field conditions. The lack of an effect of capsaicin despite using the same application methods as Willoughby et al. (2011) in multiple-choice feeding trials could be explained by two main hypotheses. First, under field conditions rodents might not have a sufficient natural food supply as to reject the repellent-treated alternative. In the cited cafeteria experiment rodents had a plentiful supply of untreated food, and this could have led them to be more selective than in our study. Second, this effect could have been exacerbated by a potential food shortage in 2012, the year in which capsaicin was applied. Precipitation from January through June 2012 measured at the experimental site was about one-fourth of the precipitation in those months in 2010. The drought during the 2012 rainy season could have led to an even lower food supply for the rodent community, which in turn would have become less selective and searched more carefully for any available food (Puerta-Piñero et al., 2010b). This idea is supported by the results of the first revision of our experiments, as predation by rodents occurred much faster in 2012 than in 2010. Besides not reducing acorn predation, capsaicin reduced seedling emergence by half. This result is in accordance with some studies which have found that the application of capsaicin reduced seed germination of other species (Barnett, 1998; Siddiqui and Uz-Zaman, 2005) but disagrees with others (Gosling and Baker, 2004). However, we are not aware of previous studies addressing the effects of capsaicin on the germination or emergence rates of *Quercus* seeds. According to our results, capsaicin does not seem to be an effective way for promoting oak reforestation.

4.3. Conclusions and insights for future research

Our results show that burnt-wood management and burial depth interact in complex ways and that their potential benefits for oak reforestation via seed sowing depend on the abundance of the different predator guilds. Although the impact of wild boars on sown acorns was low in our site, the opposite could be the case in other situations. Alternatives to control the activity of wild boars (and potentially of other ungulates) such as fencing (Dey et al., 2008) are expensive and in many cases logistically very difficult if possible to carry out. In contrast, burnt logs and branches are common elements after a fire. They come at no additional economic cost, and their use as physical structures to protect acorns against ungulate predation could be useful for oak reforestation. On the other hand, the presence of the burnt wood in our study favoured predation by rodents, and even eliminated the potential benefit of deeper burial. As rodents were by far the most important predator guild, burnt-wood management can be a way to increase seeding success only if effective methods to protect individual acorns from rodents are implemented. Capsaicin was not an appropriate method, as it did not protect against acorn predation and it even reduced seedling emergence.

We suggest that more research should be conducted in two lines. First, other methods to protect individual acorns should continue to be explored for both their ecological and their economic efficacy. These methods could include small fences (Crawley and Long, 1995; Tietje et al., 1991), wire mesh screens (Schmidt and Timm, 2000; Dey et al., 2008), or other repellents (Nolte and Barnett, 2000; Willoughby et al., 2011). Second, we need to better understand the population trends of predators with post-fire succession. For example, the rodent community may disappear after a fire (Fons et al., 1993; Haim and Izhaki, 1994), and the succession of recolonisers may differ under distinct burnt-wood management (Haim and Izhaki, 1994). This temporal gap could be regarded as a window of opportunity for acorn sowing coupled with the greater habitat complexity achieved by burnt-wood management to deter ungulate predation.

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Figure legends

Figure 1. Photographs of the burnt-wood management treatments: a) Salvage Logging, and b) Non-Intervention. The fire occurred in September 2005, treatments were implemented in spring 2006, and the photos are from 2012. Photo a) courtesy of R. Marzano, photo b) by JC.

Figure 2. Percent acorn predation in the Non-Intervention (NI) and the Salvage Logging (SL) post-fire management treatments in 2010. Graphs show differences between deep (8 cm) and shallow (2 cm) buried acorns for both treatments. The dark grey areas on the upper part of the bars indicate predation by boars, and the lower part by rodents. Note that mean differences between deep and shallow acorns were larger in the SL than in the NI treatment.

Figure 3. Spatial distribution of predated (grey points) and non-predated (black points) acorns sown at (a) 2 cm and (b) 8 cm depth in 2010. Post-fire treatments are Salvage Logging (SL) and Non-Intervention (NI).

Figure 4. Percent seedling emergence with and without the application of capsaicin. These acorns were sown in plastic containers and isolated from predators, and emergence was monitored.

Table 1. Indicators of habitat complexity in the Salvage Logging and Non-Intervention burnt-wood management treatments. Numbers in the table indicate the percentage of sampling points that had their highest contact at the specified combination of height and structural element. Note that only the highest contact at each sampling point was recorded. An increase in woody cover at greater height classes in NI relative to SL can be observed.

Non-Intervention					Salvage logging				
	Structural element					Structural element			
Height (cm)	Open soil	Live plants	Wood	Total	Height (cm)	Open soil	Live plants	Wood	Total
0	25.6	0.0	0.0	25.6	0	39.2	0.0	0.0	39.2
1-10	0.0	3.6	2.1	5.8	1-10	0.0	6.4	5.2	11.6
11-25	0.0	5.2	6.2	11.4	11-25	0.0	6.2	2.8	9.0
26-50	0.0	11.2	9.9	21.1	26-50	0.0	11.3	1.9	13.2
51-100	0.0	20.0	7.1	27.1	51-100	0.0	22.3	1.1	23.4
>100	0.0	6.8	2.2	9.0	>100	0.0	3.5	0.0	3.5
Total	25.6	46.8	27.6	100.0	Total	39.2	49.7	11.1	100.0

Table 2. Generalized Linear Model with the effects of burnt-wood management treatment (BWM: Non-Intervention and Salvage Logging), acorn sowing depth (shallow: 2 cm vs. deep: 8 cm), and replicate nested in BWM on overall acorn predation (all predators) and predation by rodents alone in Experiment #1 (2010).

		Overall predation		Predation by rodents	
	d.f.	χ^2	P	χ^2	P
Treatment (T)	1	131.57	**<0.0001**	124.46	**<0.0001**
Depth (D)	1	4.00	**0.05**	5.23	**0.02**
T x D	1	4.20	**0.04**	5.00	**0.03**
Replicate [T]	4	82.40	**<0.0001**	72.56	**<0.0001**

Table 3. Generalized Linear Model with the effects of burnt-wood management treatment (BWM: Non-Intervention and Salvage Logging), acorn sowing depth (shallow: 2 cm vs. deep: 8 cm), application of capsaicin, and BWM replicate nested in treatment on overall acorn predation in Experiment #2 (2012).

Term	df	χ^2	P
Treatment (T)	1	114.1	**<0.0001**
Depth (D)	1	4.7	**0.03**
Capsaicin (C)	1	1.8	0.18
D x C	1	0.1	0.82
D x T	1	0.8	0.36
C x T	1	1.0	0.31
T x D x C	1	0.0	1
Replicate [T]	4	182.7	**<0.0001**

Figure 1

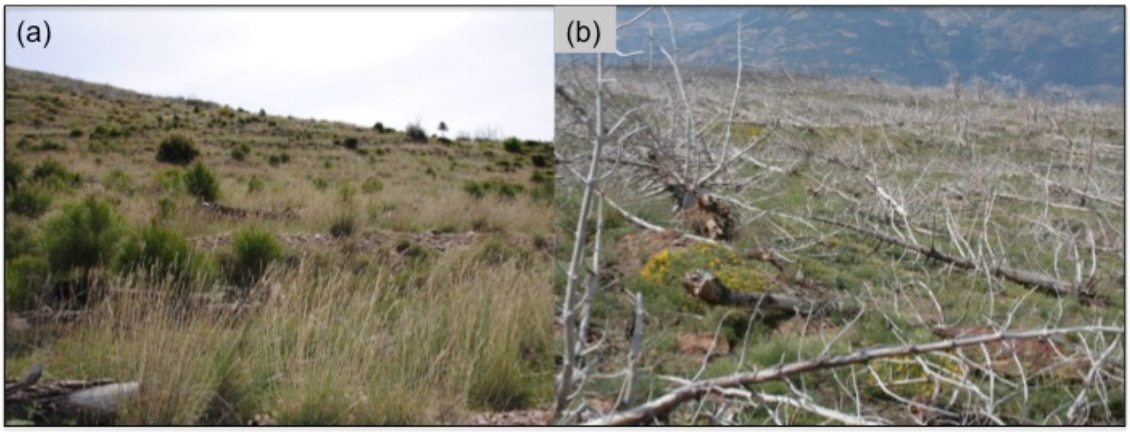


Figure 2

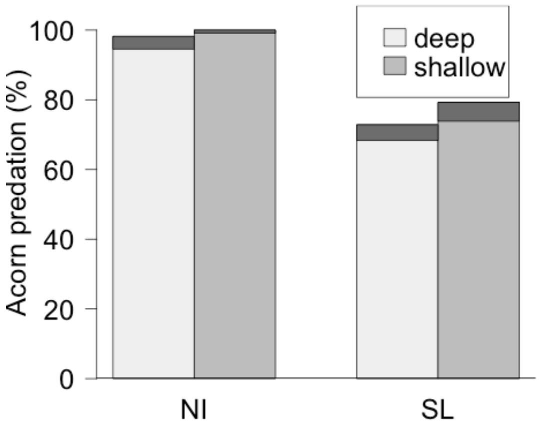


Figure 3

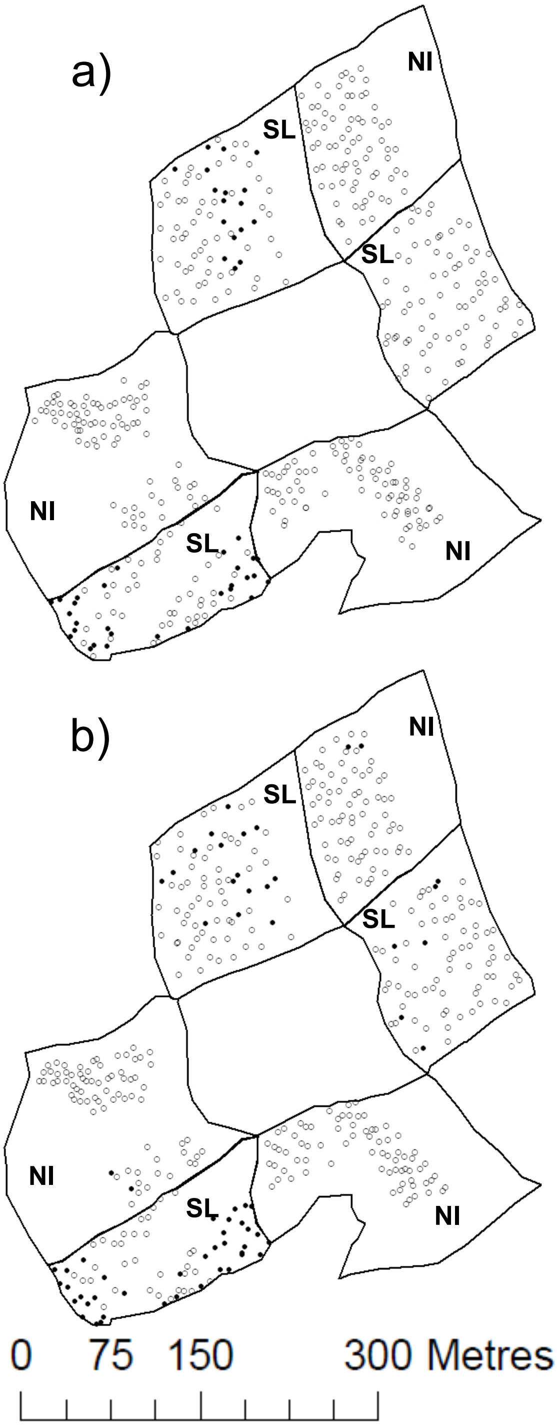
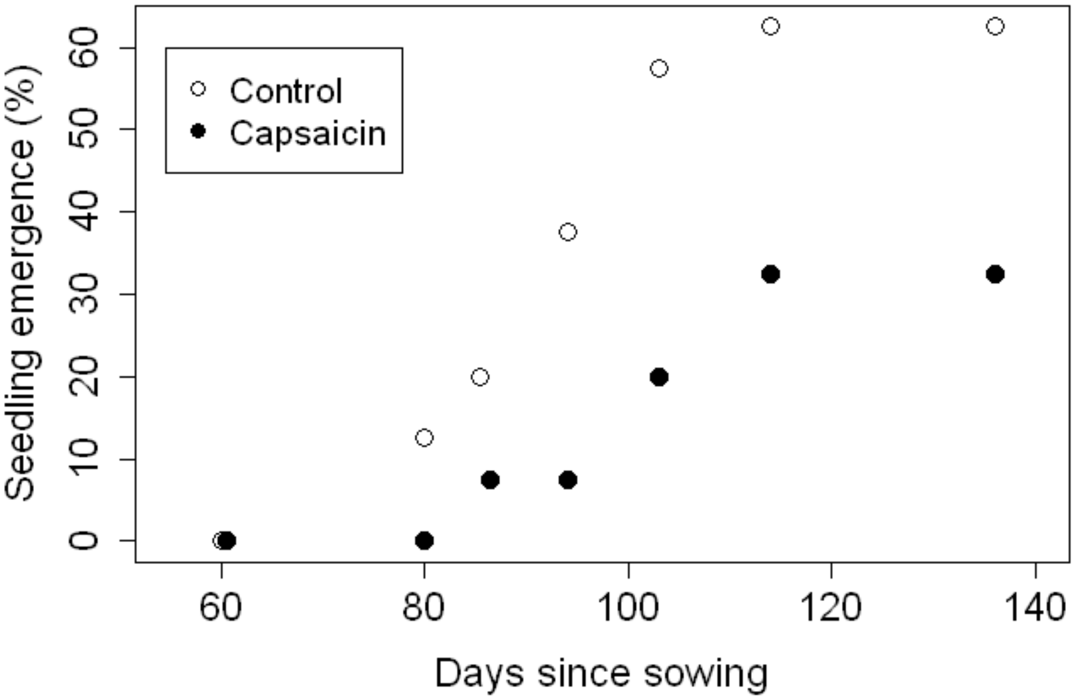


Figure 4


Control
Capsaicin
Seedling emergence (%)
0
10
20
30
40
50
60
60
80
100
120
140
Days since sowing

Chapter 2

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Habitat complexity and individual acorn protectors enhance the post-fire restoration of oak forests via seed sowing

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Abstract

Oak reforestation via direct sowing has advantages over planting for economic and plant-morphological reasons, but the risk of high acorn predation usually dissuades land managers from using this method. In a previous study we hypothesised that overcoming acorn predation would require both large-scale solutions to reduce predation by large mammals –which we had effectively obtained through ecosystem management leading to greater habitat complexity– and small-scale protection to tackle predation by small mammals –which we had been unsuccessful to encounter. In this study we aimed to test this hypothesis under the same management areas but with a new acorn-scale protective device named seed shelter. We carried out an acorn predation experiment in Sierra Nevada (S Spain), in a burnt area with three replicates of each of two post-fire management treatments: Non-Intervention (NI), with high habitat complexity due to the abundance of lying burnt trees, and Salvage Logging (SL), with low habitat complexity due to the previous felling and piling of the tree trunks and chopping of the branches. In each replicate we sowed 50 acorns with seed shelter and 50 acorns without (N= 600 acorns). After 129 days, predation by rodents averaged 17% for control acorns, while the seed shelter reduced this to nil. Predation by boars (17.5% overall) was not affected by the seed shelter but it was reduced to one-sixth in the NI treatment (5% vs 30% in SL), so we obtained the lowest overall predation rates in the combined NI + seed shelter treatment (5%). We thus corroborated our hypothesis that combining large-scale management with an acorn-scale protection can greatly increase the success of sowing. We expect these outcomes to increase the effectiveness of direct sowing and to raise the share of this practice in reforestation, especially for species that develop best with direct sowing such as oaks.

Keywords: *Quercus*, ecosystem restoration, seed removal, seed sowing, seeding, innovation, seed protector

Abbreviations: BWM= Burnt-wood management treatment(s); SL= Salvage Logging treatment; NI= Non-Intervention treatment

1. Introduction

Millions of hectares of land are reforested every year to counteract deforestation and the degradation of natural ecosystems. Oaks (*Quercus spp.*) are a frequently-used species for reforestation (e.g. EEC regulation no. 2080/92), as they are widely distributed across the Holarctic. Oaks provide numerous ecosystem services (Marañón et al., 2012), but they are encountering population decline and difficulties in their regeneration in many parts of their distribution range (Dey et al., 2008; Pulido and Díaz, 2005; Thomas et al., 2002). Much hope, effort, and money are thus placed into reforestation with oaks, yet stories of low success are very common (Dey et al., 2008; Navarro Cerrillo et al., 2005; Rey Benayas et al., 2005).

Seedling planting and seed sowing are the two possibilities for reforestation with oaks. While planting oaks has the advantage of using already-established seedlings, it often renders high seedling mortality and/or low-quality plants (Rey Benayas et al., 2005; Zadworny et al., 2014), as nursery-grown seedlings often present root architectures that are suboptimal for field conditions (Tsakaldimi et al., 2009). In contrast, sowing has the advantage of producing seedlings that are better acclimated to local conditions, besides having about one-half to one-third of the economic cost of planting (Bullard et al., 1992; King and Keeland, 1999; Madsen and Löf, 2005). However, sowing is usually opted out because of the frequent high levels of acorn predation and the uncertainty that results from oscillations in predator populations (Dey et al., 2008; Madsen and Löf, 2005). Finding a way to reduce acorn predation could thus increase the success and reliability of acorn sowing and of forestation practice in general.

Reducing seed predation can be achieved by taking advantage of habitat features that affect the activity of seed predators. For example, areas covered by shrubs or coarse woody debris can represent a physical obstacle for foraging by ungulates (Ripple and Larsen, 2001), although they can also provide food and shelter for rodents (Gómez, 2004). Due to such contrasting effects of habitat on different predator guilds there is hardly any optimal solution to increase acorn survival to predation. In a previous study in an area where the management of wood after a forest fire in Sierra Nevada (S Spain) generated areas with low or high habitat complexity (Leverkus et al., 2013) we concluded that combining high habitat complexity at a large scale (which reduced foraging by wild boars; Leverkus et al., 2013; Puerta-Piñero et al., 2010) with some small-scale protection from rodents might effectively increase acorn survival. However, such small-scale protection was yet to be discovered– we tested deeper burial and a chemical repellent but without much success (Leverkus et al., 2013).

Devices designed to represent a barrier for seed predators are usually ineffective, large, expensive, difficult to handle, or a combination of those (Dey et al., 2008; Madsen and Löf, 2005; Pemán et al., 2010; Reque and Martin, 2015). In this short communication we test the effectiveness of a new, simple device –named seed shelter (Castro et al. 2015)– designed to protect individual acorns from small predators in areas where different management schemes have led to greater or lower habitat complexity due to the presence or absence of deadwood. For this we performed an acorn predation experiment in the above-mentioned post-fire habitats. Our working hypotheses were that: i) the seed shelter device would represent a physical barrier that would reduce acorn predation by rodents, and ii) the use of the seed shelter in areas with greater habitat complexity would yield the greatest acorn survival due to the cumulative effect of the seed shelter reducing predation by rodents and of habitat complexity on reducing foraging by ungulates (wild boars). Overall, we expect to find a way to turn acorn sowing into an effective and reliable method to produce high-quality oak seedlings.

2. Materials and Methods

2.1 Study site

This study was carried out in the Sierra Nevada National Park (S Spain), in an area of the Lanjarón municipality where a fire burned about 1300 ha of pine afforestations in September 2005. The area has Mediterranean climate, with hot, dry summers and mild, wet winters. Holm oak forests (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) are the main climax vegetation in the area (Valle, 2003). The main acorn predators are wild boars (*Sus scrofa*) and rodents like *Apodemus sylvaticus* and *Mus spretus* (Gómez and Hódar, 2008; Puerta-Piñero et al., 2010).

In spring 2006, an experimental site was established in a burnt *Pinus pinaster* and *P. nigra* afforestation at 1477 m a.s.l. to test the effects of burnt-wood management on different processes related to ecosystem restoration (37º57’ N, 3º29’ W; see supplementary kml file). This site included three replicates of each of two burnt-wood management (BWM) treatments, which had an area of 2.0 ± 0.2 ha (Leverkus et al., 2012). The treatments were: a) Salvage Logging (SL), where the burnt tree trunks were felled, separated from their main branches and piled, and the remaining woody debris was mechanically masticated; b) Non-Intervention (NI), where no action was taken and all the trees had fallen by 2009. The physical structure of the SL treatment was an open area easily accessible by humans, while the NI treatment was covered in branches and trunks that complicated movement (Leverkus et al., 2013; Puerta-Piñero et al., 2010). For further details on the study area and the experimental site, see Castro et al. (2012) and Leverkus et al. (2012, 2013).

2.2 Acorn predation experiment

In January 2014 we began an experiment to test the effects of habitat complexity and individual acorn protection on seed predation. For this, we established 50 sowing points per BWM replicate (6 replicates), and in each point we sowed two *Q. ilex* acorns 30 cm away from each other: one with and one without seed shelter (600 acorns in total). The seed shelter (patent #201331441, University of Granada; Castro et al., 2015) consists of two identical truncated cones or pyramids joined at their larger opening and filled with substrate. The rationale is that a large seed could be held in the wide middle of the seed shelter and that the small upper and lower openings would be large enough to allow the stem and the roots to grow out, yet small enough to prevent the entrance of a rodent. For the present study we used prototypes made of polypropylene (Fig. 1).

We visually inspected each sowing point after 8, 25, 81, and 129 days to identify whether acorns were predated or not and, if predated, to establish the guild of the predator (as described in Leverkus et al., 2013). Acorns with seed shelters that were extracted by wild boars but not opened (i.e. where the acorns were not consumed) were marked as predated because they would likely not produce viable seedlings. During the last revision we dug up all the points to be certain of the fate of all acorns, to record the germination of non-predated acorns, and to remove the devices from the field. We assumed that removed acorns were depredated because studies in the area found that

>98% of the acorns handled by the main acorn dispersers are consumed (Gómez et al., 2008).

2.3 Habitat complexity

We sampled the complexity of the habitat in both BWM treatments with linear transects. In each BWM replicate we randomly placed four transects of 25 m and established sampling points one meter to each side at every meter of the transect. At each point we defined five height classes (1-10, 11-25, 26-50, 51-100, 101-200 cm) and estimated the percentage of these ranges contacted by live vegetation or woody debris.

2.4 Statistical analyses

For all analyses we used R version 2.15.0 (R Development Core Team 2012).

To analyse habitat structure relative to BWM treatment, we fitted hierarchical ANOVA models for each cover type (plant or wood) and height class separately. We specified transects within the replicates as the random effects. To reduce the percentage of zeros in the data, we averaged the values of the left and right side of each point of the transects. For each transect we also calculated the percentage of points with cover of bare soil, and we used ANOVA to assess the possible effect of BWM treatment. Cover data were arcsine, square root transformed previous to analysis (Crawley, 2013).

To test the effects of *BWM* and *Seed shelter* on final acorn predation, we fitted a generalized linear mixed model (glmm) with binomial errors, using the lmer function from the lme4 package (Bates et al. 2012). In these models we specified the spatial structure of the experiment (sowing points located within BWM replicates) as random effects, and *BWM*, *Seed shelter*, and the *BWM* x *Seed shelter* interaction as fixed effects. To analyse predation by the individual predator guilds (boars or rodents) we considered the acorns predated by the other guild as “non-predated” and repeated the analysis. For computational reasons we had to simplify the specification of the experiment’s spatial structure with only BWM replicate as a random effect in the predator-specific models. Finally, to test the effect of *BWM* and *Seed shelter* on the germination of non-predated acorns, we fitted a glmm with binomial errors, considering the replicate of BWM as a random effect.

We tested for the significance of the terms in the mixed models through likelihood ratio tests, with model simplification (Crawley, 2013).

3. Results and discussion

3.1 Habitat structure

The cover of live plants did not significantly differ among treatments, although there was a trend of greater cover in NI for all height classes (Table 1). The cover of woody debris was significantly greater in NI than in SL in all height classes above 10 cm (Table 1). In contrast, the cover of bare soil was greater in SL (34.3%) than in NI (21.2%) but not significantly so ($F_{1,22}$= 1.84, P= 0.19). The lying logs and branches thus created a more complex habitat structure in the NI treatment than in SL, as found in previous sampling (Leverkus et al., 2013), and this may influence the foraging behaviour of acorn predators (Leverkus et al., 2013; Puerta-Piñero et al., 2010).

3.2 Acorn predation

Acorn predation averaged 26% across all the sown acorns, an extremely low value compared to other studies in the same area in previous years, in which overall predation reached up to 90% (Leverkus et al., 2013; Puerta-Piñero et al., 2010). In particular, predation by rodents was surprisingly low (17% for acorns without seed shelters) compared to those previous studies, when rodents generally consumed >80% of the acorns. Wild boars, on the other hand, consumed 17.5% of the acorns, thus more than in previous years when this value ranged from negligible to about 10% (Leverkus et al., 2013; Puerta-Piñero et al., 2010). These results highlight the strong fluctuations that can occur in the populations of acorn predators, especially rodents (Ostfeld and Keesing, 2000). Although it could be tempting to overemphasize this case and others as general successes of sowing due to high acorn survival, such events usually come at times of low rodent population densities (Dey et al., 2008), and the unpredictability that surrounds them turns sowing into a high-risk activity usually avoided by land managers.

Rodents consumed more acorns in the NI treatment (22.0%) than in SL (12.0%; χ^2=5.06, P>0.01; values and analysis for acorns without seed shelters) and, contrarily, boars consumed more acorns in the SL treatment (30%) than in NI (5%; χ^2= 4.97, P>0.05; Fig. 2). As previously found (Leverkus et al., 2013; Puerta-Piñero et al., 2010), the greater habitat complexity generated by the lying logs and branches in the Non-Intervention treatment had opposing effects on the two main predator guilds. Large mammals, in this case wild boars, likely found the areas without post-fire intervention difficult to transit, as the fallen trees acted as physical barriers to their movement (Puerta-Piñero et al., 2010). And, on the other hand, smaller animals like rodents may have found more resources and protection below the branches, resulting in greater rodent populations and/or activity (Herrera, 1995; Muñoz and Bonal, 2007). What arises from the present study is that the net effect of the management of habitat complexity on acorn consumption greatly depends on the relative abundance and activity of these predator guilds. In the present study, with low rodent activity, overall predation was much lower in the high-complexity NI treatment (16%) than in SL (36%; Fig. 2) due to the positive effect of SL on predation by boars, while in previous years, with much greater rodent activity (Leverkus et al., 2013), predation was always greater in NI (up to 99%) than in SL, this being due to the positive effect of NI on predation by rodents. Thus, habitat complexity alone cannot be used to predict whether greater or smaller overall levels of acorn consumption will occur because this will also depend on the relative abundance of the different predator guilds.

Not a single acorn within a seed shelter was consumed by a rodent, suggesting that we might have come across an effective solution to the long-lasting problem of predation of sown seeds by small mammal predators (Bullard et al., 1992; Dey et al., 2008; Herrera, 1995; Leverkus et al., 2013; Puerta-Piñero et al., 2010; Pulido and Díaz, 2005). On the other hand, wild boars consumed acorns irrespectively of the seed shelters (χ^2=0.01, P=0.90; Fig. 2), as they were able to dig up the devices easily and even break them and consume the acorns within them in many cases. The use of the seed shelters consequently does not entirely solve the problem of acorn predation, as wild boars and other wild and domestic ungulates can cause great acorn losses too (Gómez and Hódar, 2008; McCreary, 2009; Muñoz and Bonal, 2007). A potential solution arises from the significant interaction effect of burnt-wood management and the use of the seed shelter on overall predation (χ^2=7.90, P<0.01): the device had a greater proportional effect in NI (where the relative effect of rodents was also greatest and the seed shelter reduced predation by 77%) than in SL (where boars had the greatest relative effect and the seed shelter reduced predation by only 30%). As a result, only 5% of acorns in NI with a seed shelter were consumed (Fig. 2). The efficacy of the seed shelters may thus be greatest in situations where low predation is expected by large animals. In post-fire restoration, a way to achieve this, as shown by our results, is by favouring ecosystem management that leads to greater habitat complexity –i.e. with little or no intervention after the fire–, with the additional advantage that the deadwood remaining after such management may improve microclimatic conditions and provide nutrients that altogether enhance seedling establishment, survival and growth (Leverkus et al., 2012; Marañón-Jiménez et al., 2013; Marzano et al., 2013).

3.3 Germination

Significantly more of the non-predated acorns with seed shelters germinated (82%) than without seed shelters (51%; χ^2= 34.42, P>0.001), while BWM had no significant effect on germination. We believe that the positive effect of the device on germination could be related to the quality of the substrate included inside the device, or to potentially higher moisture retention or enhanced microclimatic conditions inside the device (Castro et al., 2015). Thus, the seed shelter seems to provide an additional advantage for reforestation although further research on the underlying mechanisms is necessary.

4. Conclusions

In this study the seed shelter, a physical device, proved effective to prevent seed predation by rodents, while it did not reduce predation by wild boars. Although predation by rodents was low during the study compared to other years, our results confirm that the use of a device such as the one tested here –which may eliminate predation by small rodents– in combination with a complex habitat structure –which can greatly reduce predation by larger mammals– could lead to an effective use of direct sowing for reforestation. The seed shelter has high potential for reforestation with many large-seeded species, for which post-sowing seed predation rates are usually high and whose production under nursery conditions may impose limitations for seedling development. These include many late-successional species in forests of different parts of the world, such as the Fagaceae in the Holarctic. Although more research into the use of biodegradable materials and the cost-effectiveness of this method as compared to planting are needed, our results strongly support the usefulness of individual seed protectors for oak forest restoration via direct acorn sowing provided that features of the landscape reduce the access of larger animals.

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Table 1

Effects of burnt-wood management on habitat complexity at the different height classes.

Height (cm)	Live Plants				Wood			
	$F_{1,22}$	P	Mean NI	Mean SL	$F_{1,22}$	P	Mean NI	Mean SL
1-10	1.03	0.32	28.2 ± 1.9	20.4 ± 1.6	1.94	0.18	9.7 ± 1.1	12.4 ± 1.4
11-25	2.11	0.16	19.3 ± 1.6	12.3 ± 1.3	9.43	<0.01	5.5 ± 0.7	3.6 ± 0.7
26-50	1.43	0.24	15.4 ± 1.5	9.6 ± 1.2	86.57	<0.001	2.9 ± 0.3	0.3 ± 0.1
51-100	2.71	0.11	8.9 ± 1.0	4.7 ± 0.7	26.31	<0.001	1.3 ± 0.2	0.0 ± 0.0
101-200	0.51	0.48	1.8 ± 0.4	1.3 ± 0.3			0.4 ± 0.1	0.0 ± 0.0

Habitat complexity was measured as the percentage of the height range covered by either live plants or wood averaged across transects. Values indicate the mean ± 1 SE of the mean for all transects. Due to the lack of points contacting wood at the highest class in the SL treatment, no statistical test was performed for this treatment comparison. Treatments were SL= Salvage Logging; NI= Non-Intervention.

Figure 1

Photos of the seed shelter prototype used for this study. Two identical flat shapes, punched out of 0.8-mm polypropylene sheets (a), were folded together to create truncated pyramids, which were then assembled with simple folds and slots to create the complete seed shelter (b). Before joining the two parts, they were filled with substrate [1/3 sand and 2/3 peat (Kekkilä Garden Brown 025W)] and an acorn was placed in the middle. The entire device was then placed belowground in the field with its upper opening at ground level (c), which left the acorn within at 5-6 cm depth. The acorns without seed shelter were placed at the same depth.

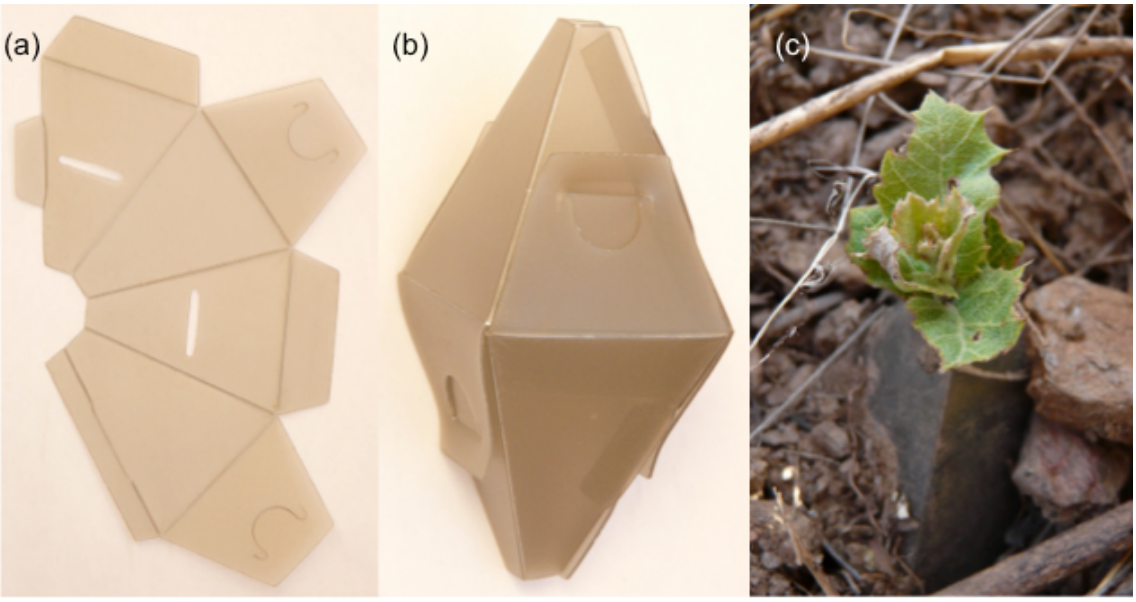
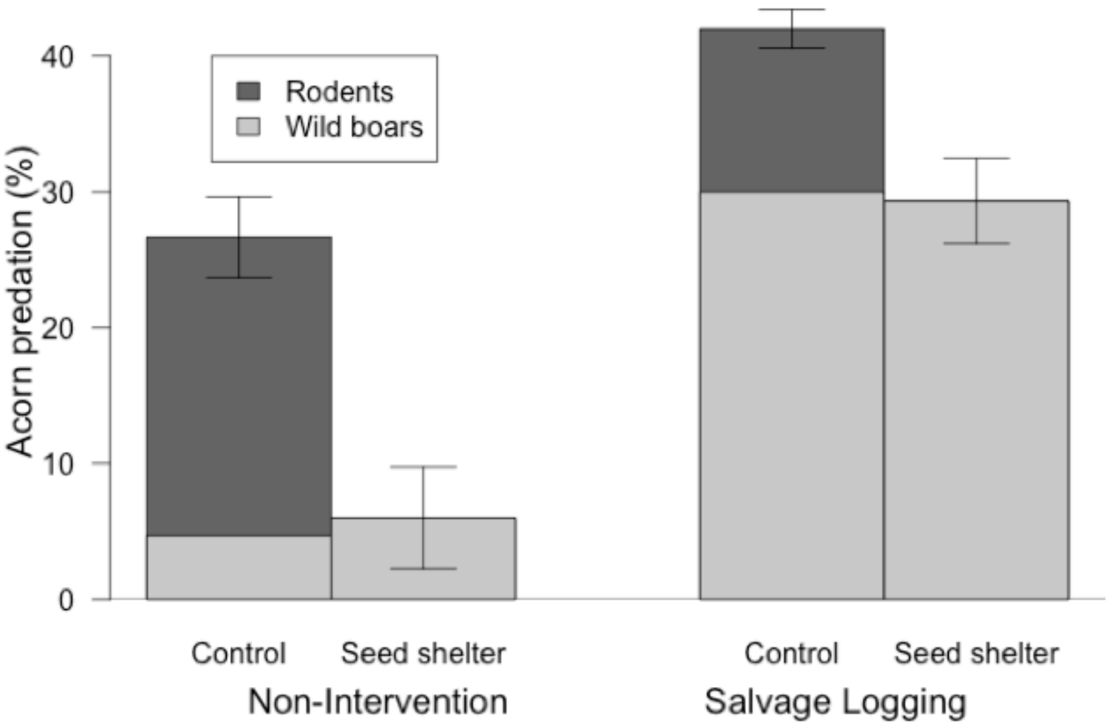


Figure 2

Acorn predation by the main predator guilds in the experiment as affected by burnt-wood management and the use of the seed shelter. Error bars indicate ± 1 SE of the mean of total acorn predation between the three replicates.



Chapter 3

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Post-fire salvage logging increases restoration costs in a Mediterranean mountain ecosystem

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Abstract

Post-fire salvage logging (i.e. felling and removing burnt trees, often eliminating the remaining woody debris) is a practice routinely performed by forest managers worldwide. In Mediterranean-type ecosystems, salvage logging is considered a measure to reduce future reforestation costs, but this assumption remains largely untested. We made a cost analysis of different management schemes, addressing the immediate post-fire burnt-wood management as well as the costs and success of subsequent reforestation efforts. Two experimental 25-ha plots were established in a burnt pine reforestation of SE Spain, in which three replicates of three post-fire treatments were applied: non-intervention (NI), partial cut plus lopping (PCL; felling and lopping off the branches from most of the trees, leaving all biomass *in situ*), and salvage logging (SL). After four years, a mechanised reforestation was undertaken, and seedling mortality was monitored for two years. The cost of all management operations was recorded *in situ*, and the cost of re-planting the dead seedlings was estimated according to the expenses of previous reforestation. Initial cost of wood management was greatest in SL and zero in NI. Reforestation cost was highest in NI and lowest in SL, and seedling-mortality rates proved lowest in PCL (43%, vs. 51% and 52% in SL and NI, respectively). Considering all the post-fire management operations, salvage logging did not provide particular economic advantages for forest restoration, and had an overall cost of 3436±340 €/ha. By contrast, NI and PCL reduced total restoration costs by 50 and 35%, respectively, and PCL indeed promoted restoration success. We suggest that the full cost of management operations needs to be considered when evaluating the economic implications of post-fire salvage logging.

Keywords: Forest economics, nurse objects, post-fire restoration, salvage logging.

Introduction

Fire is a common disturbance in many forests, deeply affecting ecosystems and human societies around the world (FAO 2007; Bowman et al. 2009; Thompson et al. 2009). After fire, human intervention is common in order to restore the forest, as natural regeneration of tree species may be slow or even hampered for different reasons [e.g. seedbed limitations (Mallik et al. 2010), post-fire environmental conditions (Tercero-Bucardo et al. 2007), or seed and seedling predation (Ordóñez and Retana 2004; Denham 2008; Puerta-Piñero et al. 2010)]. In many cases, the final action to restore the forest is the direct planting of tree seedlings (Savill et al. 1997, Zhang et al. 2008, Ahtikoski et al. 2009, Moreira et al. 2012). Before reforestation is undertaken, other management measures are typically implemented, with post-fire manipulation of the burnt wood particularly common (McIver and Starr 2000; Lindenmayer et al. 2008; Castro et al. 2011). Very often, the logs are cut and removed, and the remaining coarse woody debris (e.g. branches and log remnants) is eliminated by chopping, mastication, or fire (Bautista et al. 2004; Castro et al. 2011). Such operations are called post-fire salvage logging (McIver and Starr 2000; Lindenmayer et al. 2008).

Salvage logging is extensively implemented worldwide (McIver and Starr 2000; Lindenmayer et al. 2008; Castro et al. 2011), with several reasons commonly presented to support such actions. In certain regions the main motivation is economic, as timber may still provide commercial benefits after the fire, hence the term “salvage logging” (salvaging part of the capital in the burnt area; McIver and Starr 2000; Lindenmayer et al. 2008). However, in many cases burnt wood is not a profitable resource, e.g. due to small size of the affected timber stand, low quality of the wood, high costs of wood extraction due to landscape features, or regional lack of a timber-production industry.

The unprofitable nature of SL is a common situation in mountain forests of the Mediterranean basin (Bautista et al. 2004; Castro et al. 2011). In such cases, the purposes of salvage logging are mainly silvicultural (McIver and Starr 2000; Castro et al. 2010a, 2011), the preparation of the ground for subsequent reforestation being one of the main reasons (Castro et al. 2009). It is assumed that reforesting the area through direct planting will be less costly and more efficient if the reforestation is conducted in an open (salvaged) area than in a place covered by burnt logs and branches (Bautista et al. 2004). The underlying logic assumes that the economic balance of conducting salvage logging is positive when considering reduced reforestation efforts and costs.

The economic balance of conducting salvage logging for reforestation purposes will depend, however, on trade-offs among various factors related to the difficulty of working and operating machinery. For example, the time needed for natural treefall and wood decomposition, or structural characteristics of the stand such as tree size or density, should determine the difficulty of reforestation in unsalvaged areas (Catry et al. 2012), and consequently its cost. Post-fire non-intervention measures may increase the costs of reforestation according to the above-mentioned factors, yet the costs of burnt-wood management would be nil. Moreover, in areas with low accessibility (e.g. remote or roadless areas, or rugged terrain with steep slopes) the removal of burnt logs might not be possible, and hence any reforestation would need to be conducted in the presence of the burnt wood. In summary, less intense post-fire management strategies than salvage logging might raise the costs of future reforestation, but the full economic balance is not clear when considering the lower initial wood-management costs of these alternatives. In this line, economical motivations for any kind of post-fire management should be based on its economic efficiency considering all the steps of management

(Mavsar et al. 2012). However, the economics of post-fire management are still one of the unresolved questions regarding fires (Barbati et al. 2009).

In addition to economic issues, post-fire salvage logging may have ecological implications relative to the naturally or artificially established vegetation. For example, the remaining coarse woody debris may act as a nurse structure that provides improved microclimatic conditions (Castro et al. 2011), protection against herbivores or seed predators (Ripple and Larsen 2001; Puerta-Piñero et al. 2010), and enhanced nutrient availability (Brown et al. 2003; Lindenmayer et al. 2008; Marañón-Jiménez 2011). These improved conditions could lead to higher plant survival and growth rates in places where salvage logging is not practised (e.g. Donato et al. 2006; Castro et al. 2011), and thus boost the success of restoration efforts, with economic returns. Contrarily, if salvage logging leads to a greater proportion of reforested trees to die, this could reduce the economic benefits of a less costly initial reforestation under this treatment.

In this study, we analyse the costs of first conducting three different post-fire wood management treatments and then of reforestation. These treatments included Non-Intervention (NI, no action taken), Partial Cut plus Lopping (PCL, an intermediate level of intervention), and Salvage Logging (SL, removal of burnt logs). Reforestation was performed in all the treatments, and mortality of the planted trees was monitored for two years. The costs of all the actions (Fig. 1) were monitored, and the cost of subsequent re-planting efforts depending on the mortality rates of the planted seedlings was also calculated. We hypothesise that costs and success of reforestation will depend on previous burnt-wood management, and that the overall cost of restoration will derive from the trade-offs among the differential difficulty of management operations under the three treatments. No analogous studies are available explicitly addressing the full cost analysis of different management schemes for post-fire forest restoration. Few studies are available tackling the economics of stand establishment (Ahtikoski et al. 2009), let alone in combination with post-fire wood management.

Methods

Study site and experimental design

The study site is located in the Sierra Nevada Natural and National Park (SE Spain), where in September 2005 a fire burned 1300 ha of pine reforestations. Two plots of ca. 25 ha were established after the fire at different altitudes. The first plot was located at 1698 m a.s.l. (Low Plot, hereafter), and the second plot at 2053 m a.s.l. (High Plot). They were similar in terms of orientation (SW), slope (30.1±1.2%; throughout the paper, values are mean ± 1 SE of the mean), bedrock type (micaschists) and parameters related to tree characteristics (Table 1). Before the fire, the pine species present in each plot differed according to their ecological requirements along this elevational/moisture gradient. Black pine (*Pinus nigra*) dominated in the Low Plot, and Scots pine (*P. sylvestris*) in the High Plot. Both species are native in the region, although they were extensively planted in the area some 40 years earlier for forestry purposes. The plantations were carried out using terraces established with bulldozers, previously a common reforestation practice on hillsides in Spain. Each terrace stairstep is composed of a steep backslope, approx. 1 m high, and bed ca. 3 m wide.

Within each plot, three replicates of three burnt-wood management treatments were implemented in a random spatial distribution: 1) Non-Intervention (NI), where no action was taken. 2) Partial Cut plus Lopping (PCL), where ca. 90% of burnt trees were cut and felled, with the main branches lopped off but leaving all the biomass *in situ*. 3) Salvage Logging (SL), where trees were cut and the trunks cleared of branches with chainsaws. Trunks were manually piled in groups of 10-12, and the woody debris was chopped using a tractor with a mechanical masticator. The removal of trunks was planned, but this was eventually cancelled by the Forestry Service due to technical difficulties arising from the spatial arrangement of the plots. However, in the rest of the affected area this step was undertaken. The burnt trees fell naturally, so that 0.0% had fallen by February 2006 and 2007, 13.3±0.3% by 2008, 83.5±4.0% by 2009, and 98.3±1.0 by 2010 (Castro et al. 2010a). Thus, by the time of reforestation (2010; see below), there were nearly no standing trees in any treatment.

The size of the resulting 18 experimental replicates averaged 3.09±0.20 ha, with no significant differences among treatments (Kruskal-Wallis test; $p = 0.24$). There were no differences among treatments (within each plot) in terms of slope, tree density, basal trunk diameter, or tree height (Kruskal-Wallis tests; $p > 0.05$). All post-fire management treatments were implemented between March and May 2006 (about seven months after the fire). The fire was moderate to high in severity, consuming or totally scorching most of the tree crown. Grasses and forbs dominated the understory during the years of study. Kruskal-Wallis tests showed no differences in plant cover between plots (Table 1; sampled two years after the fire), but cover slightly differed among treatments, being 73.9±1.8% in NI, 71.5±2.0 in PCL, and 67.6±2.2% in SL (both plots pooled; $F = 2.55$, d.f. = 2, $p = 0.052$; see Table 1 for methodology).

Climate in the area is Mediterranean, with hot, dry summers and wet, mild winters. Mean annual rainfall recorded by a nearby meteorological station placed at 1465 m a.s.l. is 470±50 mm (1988-2008 period). Mean temperature according to another meteorological station placed at 1652 m a.s.l. is 12.3±0.4 ºC, ranging from a minimum yearly average of 7.6±0.5 ºC to a maximum of 16.2±0.6 ºC (1994-2008 period).

Site reforestation

Reforestation was carried out by the local forestry service (Andalusian Regional Environment Ministry) between March and April 2010 (4 years after burnt-wood management) in all replicates of both plots. A surface of ca. 1.5 hectares was used in each replicate. Around 600 holes of 60 x 60 x 60 cm were made with a mini-tracked excavator 51/ 70 HP, resulting in an average planting density of 400 seedlings per hectare. Holes were made in terrace beds. The excavator dug the soil, broke it up, and returned it to the hole, leaving a worked soil bulk that could easily be dug by hand. Forestry employees manually planted seedlings from trays after digging the machine-worked soil with a pick. The seedlings, 1-2 years old by the time of planting, were potted in a volume of ca. 300 cm^3. The species used were *Crataegus monogyna*, *Berberis hispanica*, *Quercus pyrenaica*, and *Quercus ilex*, all naturally present in the area. 150 seedlings per species were planted in each experimental replicate, totalling 10,800 planted seedlings. The species were planted in a mixed order, thus distributed all across the reforested area. Afterwards, a random subsample of 75 plants per species were tagged and monitored for mortality after two growing seasons (in September 2011). A few seedlings were lost, and therefore eliminated from subsequent analysis. In the end, a total of 4950 seedlings were monitored for mortality.

Economic assessment of management operations

Management operation costs were calculated for all the steps described in Fig. 1. The forestry staff registered the resources (man and machine hours, materials) spent for each replicate in every management step in order to calculate these costs. The cost of Burnt-Wood Management operations was calculated considering the hours of machine, workers, and foremen needed. Reforestation costs were similarly calculated, considering the different steps involved and the time employed by employees and machinery, as well as the price of tree seedlings. All costs were later transformed to a one-hectare basis for each treatment. See Appendix 1 for cost calculation details.

The total sum of all the steps is here termed “Restoration”. For this, we considered two scenarios (Fig. 1). For Restoration Scenario I, we assumed that there was no replacement of dead seedlings. This is a realistic scenario for the local forestry service, as very often, due to logistic and economic reasons, the seedlings that do not survive are not replaced (Mavsar et al. 2012). For Restoration Scenario II, we assumed that there was Seedling Replacement. In this case, the number of seedlings being re-planted would be the same as the number of seedlings that died in each replicate. This is also a realistic scenario, as seedling replacement is usually done taking advantage of the holes made in the original Reforestation. As Seedling Replacement was not performed under field conditions, we estimated the Planting costs per seedling as being the same as during Reforestation, multiplying this by the number of dead seedlings per hectare in each experimental replicate (thus excluding the costs of Hole Digging). The costs were estimated at the time when each management step was completed using real costs at that time. All costs are presented in Euros (€).

The Forest Service sold the wood to a sawmill located 177 Km from the burnt site, with a sell price of 30 € per tonne. Costs of wood extraction to the log-loading area with the log-fowarder were 2.5 € per tonne, and the cost of wood transport by truck to the sawmill was 26 € per tonne (a value similar to the cost estimated for wood transport in Spain calculated by Velasco and Hernández, 2012). As a result, the benefit of wood selling roughly covered the cost of wood extraction plus transport (Direction of the National and Natural Park of Sierra Nevada, personal comm.). We did not consider these variables in our analyses because they added no relevant modification in the global economic balance and, as the potential benefits of salvage logging depend on timber quality, distance from roads, market conditions, and forest ownership (Vallejo et al. 2012), analyzing the cost of extraction and the benefit from the sale would have reduced the portability of our results to other burnt areas.

Data analyses

The mortality of seedlings was analysed using a generalized linear model (glm) with binomial errors (corrected for overdispersion by using quasibinomial errors) and logit as link function. A full model with plot, treatment, and species was created and simplified, beginning with the highest-order interactions present in the model and hierarchically moving on to the single factors. Significance of the effect of factors and interactions on seedling mortality was checked by performing likelihood ratio tests on the models with and without that specific factor or interaction (Crawley 2007). Significant increases in deviance with model simplification indicated a significant effect of the interaction or factor being removed. The minimal adequate model (MAM) was the one where all non-significant factors or interactions had been removed. To check for *ad hoc* differences among factor levels, the levels were pairwise merged into a single level of the same factor. Significant changes in deviance among the MAM and the model with the new factor, given by likelihood ratio tests, indicated that the merged factor levels significantly differed from one another (Crawley 2007).

Differences in management costs among treatments were analysed for each management operation independently (Burnt-Wood Management, Hole Digging, Planting, and Seedling Replacement), as well as for Reforestation (Hole Digging +

Planting), Restoration Scenario I (Burnt-Wood Management + Reforestation), and Restoration Scenario II (all steps added; Fig. 1), using non-parametric Kruskal-Wallis tests. Given that both plots are similar in terms of tree density, tree size, slope, etc. (see Table 1), we assumed that plot is not a factor that determined the costs of the different management steps. We thus pooled plot for these analyses, resulting in a sample size of 6 replicates per treatment. Where treatment had a significant effect, differences among treatment levels were evaluated by a non-parametric multiple comparison test for balanced data (Nemenyi test; Zar 1996).

For analyses, we used R, version 2.12.0 (R Development Core Team 2010).

Results

Seedling mortality differed among treatments, the lowest value being recorded in PCL (43%), followed by SL (51%), and NI (52%, all replicates of each treatment pooled; Fig. 2, Table 2). Mortality was lower in the High Plot, and also differed among species, although the pattern was consistent across treatments and plots, as reflected by the lack of interactions among factors (Table 2; overall mortality: *Q. ilex*, 40%; *C. monogyna*, 41%; *Q. pyrenaica*, 51%; *B. hispanica*, 60%).

The cost of Burnt-Wood Management significantly differed among treatments ($\chi^2 = 15.30$, df = 2, p = 0.0005), being zero in NI and highest in SL (Fig. 3A). The cost of Hole Digging differed slightly among treatments ($\chi^2 = 5.77$, df = 2, p = 0.06), being lowest in SL (407±23 €/ ha), followed by PCL (545±57 €/ ha), and NI (559±32 €/ ha; all costs of reforestation actions correspond to 1 ha planted with 400 plants). The cost of Planting did not differ among treatments (p = 0.45), averaging 504±48 €/ ha. The Reforestation cost (adding Hole Digging and Planting) significantly varied with treatment ($\chi^2 = 7.05$, df = 2, p = 0.03; Fig. 3B), with the highest value in NI and the lowest in SL. Seedling Replacement costs did not differ among treatments (Kruskal-Wallis test, $p = 0.58$; Fig. 3C). Restoration Scenario I costs significantly varied with treatment ($\chi^2 = 14.36$, df = 2, $p < 0.001$; Fig. 3D). Finally, Restoration Scenario II costs significantly varied with treatment ($\chi^2 = 12.12$, df = 2, $p < 0.005$), being greatest in SL (3436±340 €/ ha), followed by PCL (2258±187 €/ ha), and NI (1707±160 €/ ha; Fig. 3E).

Discussion

Our results show that the overall cost of post-fire restoration, including the cutting and extraction of the burnt wood as well as the posterior reforestation and seedling replacement actions, was clearly greater (as much as 100%) for salvage logging than for the intermediate or non-intervention treatments. As expected, the experimental reforestation costs were lowest in SL due to the greater difficulty for hole-digging machinery, as well as for forestry staff, to work in unsalvaged areas (Catry et al. 2012). The felled logs and collapsed branches represented obstacles for post-fire forestry work that were greatly avoided when the burnt biomass was removed. In fact, this is one of the reasons for performing salvage logging in areas where it is unprofitable (Castro et al. 2009). However, while the differences in reforestation costs among treatments in our study were counted in hundreds of Euros per hectare, the differences in burnt-wood management costs were an order of magnitude greater, and thus offset the higher cost of reforestation in the non-SL treatments. In addition, seedling mortality was similar (NI treatment) or lower (PCL treatment) than in salvaged areas, with the potential to affect costs of seedling replacement whenever this step is conducted. Lower seedling mortality in PCL is consistent with results found for natural regeneration of a pine species in this burnt area (Castro et al. 2011), and it is likely promoted by the improvement of microclimatic conditions by logs and branches (acting as nurse structures; Castro et al. 2011) and by the increase in soil nutrients through decomposition in relation to both SL and NI (Marañón-Jiménez 2011). In summary, less intense post-fire management than salvage logging provided an overall reduction of restoration costs and even increased reforestation success.

Despite the greater restoration cost of salvage logging in this study, it is important to bear in mind that costs are context-dependent, and that a large set of management needs and decisions are based on site characteristics. For example, in many areas of the planet, the burnt wood still provides economic benefits (Van Nieuwstadt et al. 2001; Brown et al. 2003; Lindenmayer et al. 2008). Salvage logging is also performed for reasons other than to facilitate future reforestation, such as for pest and fire control, and aesthetic reasons (McIver and Starr 2000; Bautista et al. 2004; Noss and Lindenmayer 2006; Lindenmayer et al. 2008; Castro et al. 2010a). Although these reasons are controversial and recent studies are showing that the presence of burnt wood is not necessarily related to greater fire or pest risk (Ross 1997; Donato et al. 2006; Thompson et al. 2007; Jenkins et al. 2008; Toivanen et al. 2009), the overall fact is that the consequences of different post-fire burnt-wood management largely depend on the particular circumstances of the affected area. For example, in our study case the trees were relatively small (dbh ca. 13 cm), and the area is windy and snowy in the winter. All this implies that i) trees did not provide commercial benefits (in addition to the lack of a local wood industry), ii) trees fell in a relatively short time span (4 years), and iii) the branches collapsed rapidly due to the snow load, eliminating structural elements that would have hampered reforestation. In fact, it was a surprise that the reforestation could be carried out mechanically even in the non-intervention treatment. All this added up to the higher costs of salvage logging operations with respect to the other treatments, showing that the final outcome will depend on structural particularities of the burned stand as well as on local market conditions.

In addition to the evaluation of the direct costs of management operations, the results of this study could be magnified in economic terms if other ecosystems services were considered. There is an increasing call to implement less intense post-fire management operations based on the contention that burnt wood is an essential ecosystem component that may affect a large set of ecosystem functions and processes (McIver and Starr 2000; DellaSala et al. 2006; Lindenmayer and Noss 2006; Lindenmayer et al. 2008). In fact, salvage logging has been shown to increase the levels of erosion in relation to non-salvaged areas (Inbar et al. 1997; Karr et al. 2004), degrade watersheds (Karr et al. 2004), and reduce animal diversity and species richness (Haim and Izhaki 1994; Hebblewhite et al. 2009; Castro et al. 2010b; Bros et al. 2011) as well as seed dispersal by birds (Rost et al. 2009, 2010), nutrient availability for plants (Marañón-Jiménez 2011), and carbon sequestration (Serrano-Ortiz et al. 2011). These are essential supporting and regulating ecosystem services (Millennium Ecosystem Assessment 2003; United Nations Environment Programme 2010) that may be evaluated in economic terms (Costanza et al. 1997; Heal 2000; Farber et al. 2002; Hougner et al. 2006), and if accounted for they would likely increase the economic benefit of management regimes less intense than salvage logging.

In summary, our study provides an evaluation of the costs of different management schemes addressing the immediate post-fire management of the burnt wood as well as the costs and success of subsequent reforestation efforts. The results show that, from an economic point of view, post-fire salvage logging was not the best option, and that less intensive post-fire management may lead to cost reductions and increased reforestation success. The cost-benefit output of salvage logging will depend on the socio-economic and the ecological contexts of the affected area, and it might even be economically positive in other circumstances. However, our results clearly support the contention that these kinds of trade-offs should be carefully evaluated before post-fire management actions are taken with economic aims.

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	Low Plot	High Plot
UTM Coordinates (x,y)[a]	455449; 4091728	457244; 4091551
Area (hectares)	23.9	31.7
Altitude (m a.s.l.)[a]	1698	2053
Slope (%)[b]	28.7	31.4
Tree density (units/ ha)[c]	1064±67	1051±42
Basal trunk diameter (cm)[d]	18.3±0.1	15.7±0.1
Dominant species	*Pinus nigra*	*Pinus sylvestris*
Plant cover (%)[e]	69.1±1.7	72.9±1.6

Table 1. Summary of the main characteristics of the study plots. [a]Measured at the centroid of the plot. [b]Average of the nine replicates for each plot. [c]Sampled after the fire by counting the trees in four randomly placed 25 × 25 m quadrats per replicate; values are Mean ±1 SE. [d]Measured after the fire for 30 random trees per quadrat (120 trees per replicate). [e]Sampled two years after the fire (July 2007) in 8 randomly established 25 m-long linear transects per replicate. The nature of the contact (soil or vegetation) was noted every 50 cm along the transect in the central position and at 1 m to both sides of the transect (150 points per transect, 1200 per replicate). See Castro et al. 2010a for further details.

Factor/ interaction	df	Δ deviance	p-value (F test)
Species	3	140.87	**<0.0001**
Plot	1	257.13	**<0.0001**
Treatment	2	37.00	**0.02**
Species x Treatment	6	6.08	0.97
Species x Plot	3	3.00	0.90
Treatment x Plot	2	4.67	0.63
Species x Treatment x Plot	6	15.42	0.82

Table 2. Generalized linear model for seedling mortality. Results shown for each term are those of the likelihood ratio tests among models with and without that term. For each term removed, the degrees of freedom of the interaction or factor of interest, the increase in deviance that is produced by removing it from the model, and the p- values associated with that increase, are shown. Significant results are highlighted. *Ad hoc* analyses show that, among species, only *Q. ilex* and *C. monogyna* did not significantly differ from one another in terms of mortality (p = 0.72), and among treatments only NI and SL did not show significantly different mortality rates (p = 0.96).

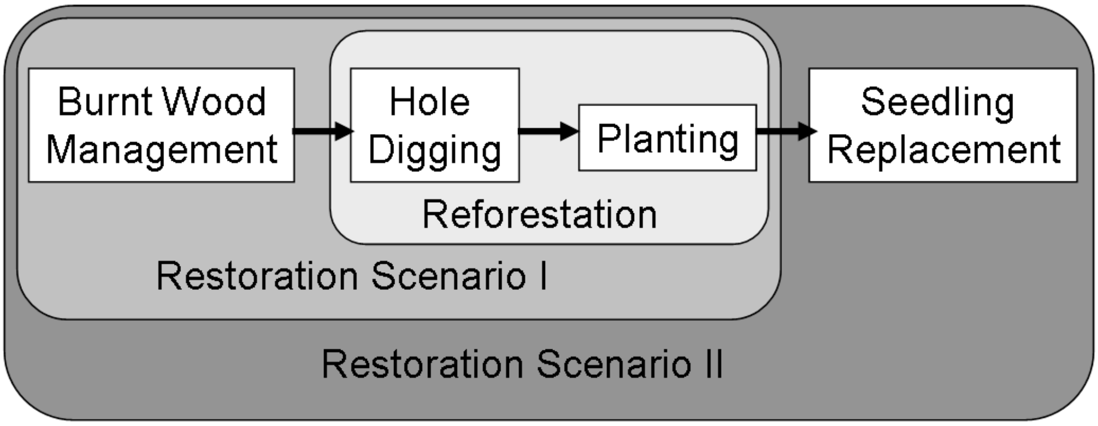

Fig. 1 Conceptual diagram of the steps involved in the post-fire restoration works, with the nomenclature employed throughout the manuscript. “Burnt-Wood Management” was the first step taken after the fire; it involved cutting the burnt trees (in the SL and PCL treatments) as well as the mastication of the remaining coarse woody debris (in SL only); by definition, none of these actions were taken in NI. “Hole Digging” and “Planting” were performed in all replicates of all treatments, and both these steps are what we call “Reforestation”. “Burnt-Wood Management” and “Reforestation” are experimental actions, which we called “Restoration Scenario I”. “Seedling Replacement” consists of the reposition of dead seedlings, in our case counted after two growing seasons (this step was not carried out in the field, but the cost was still calculated). The sum of the four steps is “Restoration Scenario II”. Treatments are Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

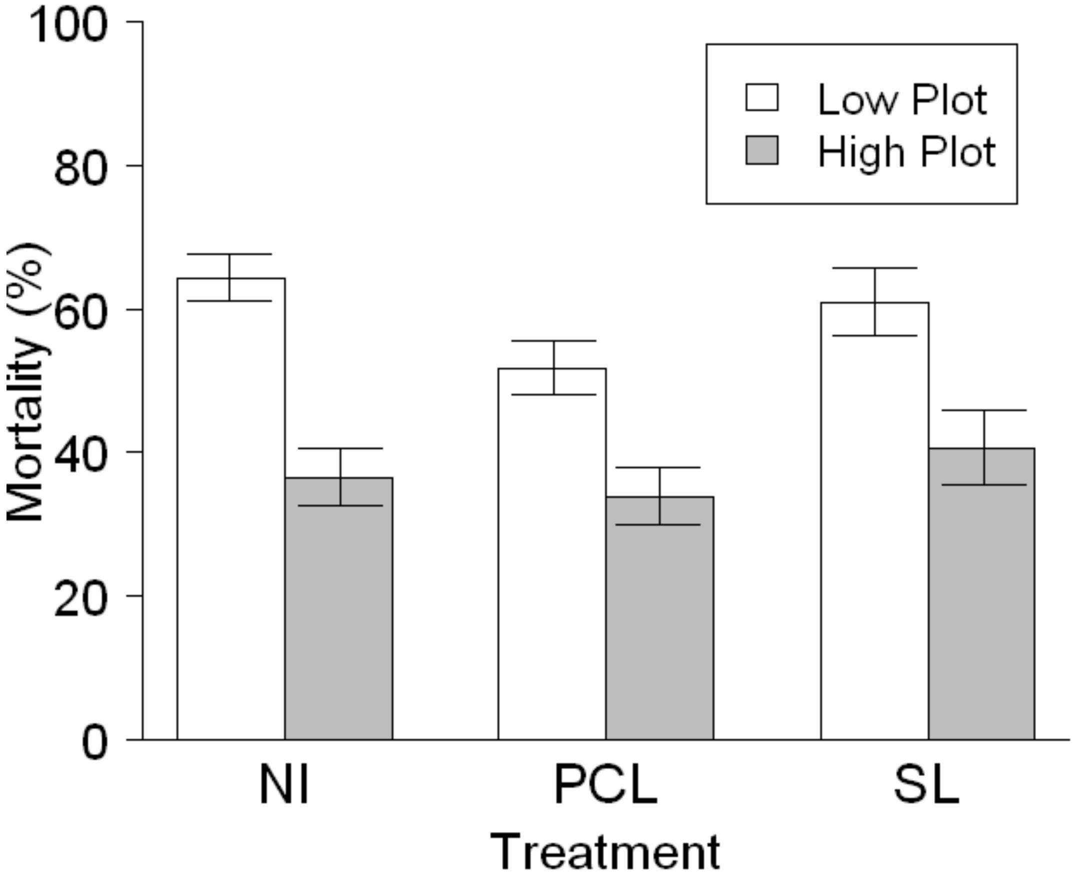

Fig. 2 Seedling mortality after 2 years according to the burnt-wood management treatment in both plots. Treatments are Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL). Among treatments, only NI and SL did not have significantly different mortality rates ($p = 0.96$). Error bars indicate ±1 SE of the mean.

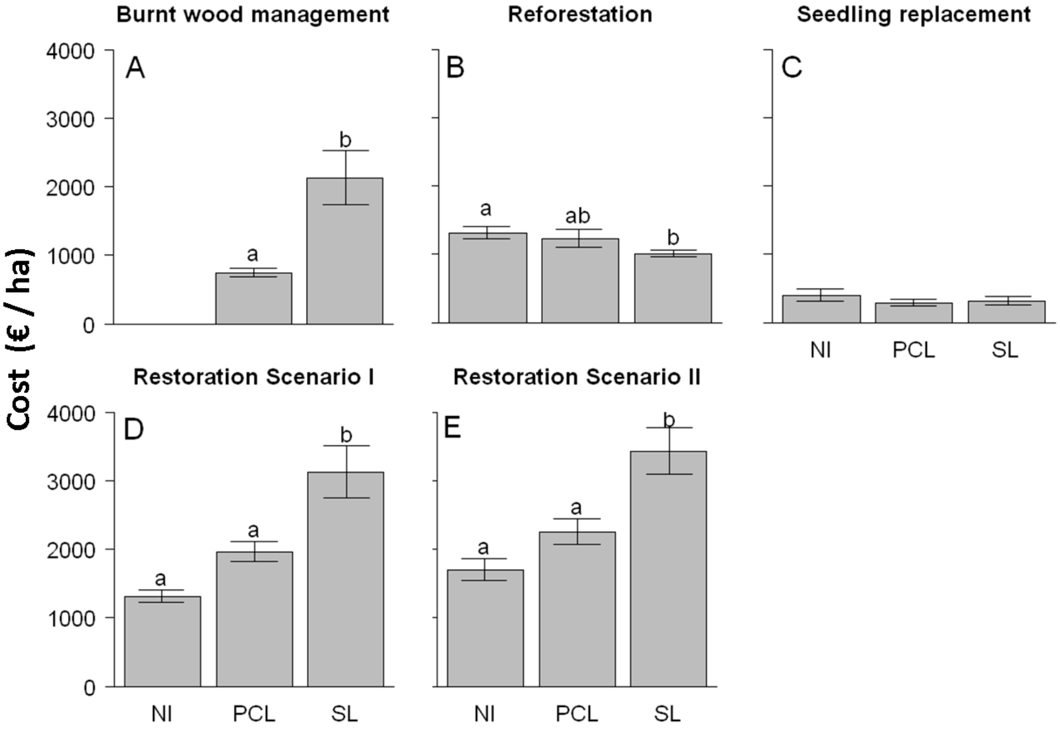

Fig. 3 Costs of the steps involved in post-fire restoration relative to the burnt-wood management treatment. Burnt-Wood Management (A) involves the cutting of trees (carried out in PCL and SL) and the elimination of remaining coarse woody debris (only performed in SL); by definition, the cost of this in NI is nil. Reforestation (B) includes Hole Digging and seedling Planting at a density of 400 seedlings/ ha. Seedling Replacement (C) takes into account the cost of re-planting the dead seedlings in each replicate, using the existing holes. Restoration Scenario I (D) includes Burnt-Wood Management and Reforestation (A + B). Restoration Scenario II (E) is the sum of these and Seedling Replacement (A + B + C). Values shown in the plots are means ±1 SE (of the mean) for one hectare. Different letters show significant differences among treatments at $p = 0.1$ from *ad hoc* Nemenyi tests. For Burnt-Wood Management, as costs of NI were nil by definition, differences among PCL and SL were given by a Mann-Whitney U test. Treatments were: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

Appendix I

Costs per hectare of the different management operations in the experimental replicates. The prices employed are standard TRAGSA (Empresa de Transformación Agraria, S.A.) prices, which at the time of the experiment were the guideline for reforestations by the local forestry service. For every cost column, the hours spent by the machinery and staff in each action were multiplied by the corresponding TRAGSA costs. The costs used were as follows: 14.55 €/ h for workers, 15.87 €/ h for foremen, 51.91 €/ h for the machine used for Hole Digging, and 62.87 €/ h for the machine used for woody debris mastication during Burnt-Wood Management (machines include driver). One foreman is needed for every 6 workers. The cost of one seedling was put at 0.34 €. An additional 7% of indirect costs was added for each management step (office work, transportation, etc.). The costs of Seedling Replacement covered the replanting of seedlings that died after 2 years of plantation, using the holes initially dug by the machinery. Scenario I of Restoration includes Burnt-Wood Management, Hole Digging, and Planting, and Scenario II covers all these as well as Seedling Replacement. Data on timings were provided by EGMASA (Empresa de Gestión Medio Ambiental S.A.), who was responsible for the management operations. Costs are given as €/ ha. Treatments are Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

Plot	Treat	Repl	Monitored plants	Mortality (%)	Cost Burnt Wood Mgt	Cost Hole Digging	Cost Planting	Cost Seedling Replacement	Cost Restoration Scenario I	Cost Restoration Scenario II
Low	NI	1	287	74.6	0.0	489.0	1045.0	779.2	2313.2	1534.0
Low	NI	2	291	61.5	0.0	444.5	572.2	351.9	1368.6	1016.7
Low	NI	3	290	56.9	0.0	555.7	721.1	410.3	1687.0	1276.8
Low	SL	1	295	73.9	902.7	466.7	751.1	555.1	2675.7	2120.6
Low	SL	2	256	48.4	2056.6	333.4	630.0	305.2	3325.1	3020.0
Low	SL	3	300	60.7	2530.1	355.6	653.1	396.2	3934.9	3538.8
Low	PCL	1	275	57.1	708.3	644.6	591.6	337.8	2282.3	1944.5
Low	PCL	2	300	58.7	626.6	377.8	652.2	382.6	2039.3	1656.7
Low	PCL	3	272	39.0	906.7	355.6	529.0	206.2	1997.5	1791.3
High	NI	1	298	37.2	0.0	644.6	741.0	276.0	1661.6	1385.6
High	NI	2	194	29.4	0.0	600.1	498.8	146.5	1245.4	1098.9

High	NI	3	292	42.8	0.0	622.3	940.3	402.5	1965.2	1562.7
High	SL	1	300	38.7	2155.3	422.3	539.8	208.7	3326.1	3117.4
High	SL	2	312	36.4	1403.7	400.1	482.0	271.9	2557.6	2285.7
High	SL	3	297	26.6	3699.7	466.7	498.8	132.7	4797.9	4665.2
High	PCL	1	183	38.8	848.6	622.3	1212.7	470.5	3154.1	2683.6
High	PCL	2	284	27.5	500.2	666.8	587.1	161.2	1915.4	1754.1
High	PCL	3	224	33.0	883.0	600.1	508.5	168.0	2159.5	1991.6

Chapter 4

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Restoring for the present or restoring for the future: Enhanced performance of two sympatric oaks (*Quercus ilex* and *Quercus pyrenaica*) above the current forest limit

Running head: Enhanced oak performance above altitude limits

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Abstract

Reforestation is common to restore degraded ecosystems, but tree-species choice often neglects ongoing environmental changes. We evaluated the performance of planted seedlings of two oak species at two sites in a Mediterranean mountain (Sierra Nevada, SE Spain): one located within the current altitudinal forest range and one above the upper forest limit. The forest service planted 1350 seedlings of the deciduous Pyrenean oak and the evergreen Holm oak in a post-fire successional shrubland. After two years seedlings were monitored for survival, and a subset of 110 Pyrenean oaks and 185 Holm oaks were harvested for analyses of biomass and foliar nutrient status, $\delta^{13}C$, and $\delta^{18}O$. Both species showed the highest survival and leaf N status above the upper forest limit, and survival increased with altitude within each plot. The deciduous oak benefited most from planting at higher altitude, and it also had greater biomass at the higher site. Correlations between foliar N, $\delta^{18}O$, and $\delta^{13}C$ across elevations indicate tighter stomatal control of water loss and greater water-use efficiency with increasing plant N status at higher altitude, which may represent a so-far overlooked positive feedback mechanism that could foster uphill range shifts in water-limited mountain regions. Given ongoing trends and future projections of increasing temperature and aridity throughout the Mediterranean region, tree-species selection for forest restoration should target forecasted climatic conditions rather than those prevailing in the past. This study highlights that ecosystem restoration provides an opportunity to assist species range shifts under rapidly changing climate.

Keywords: isotopic analysis, stable isotopes, uphill shifts, climate change, reforestation, assisted colonization

Implications for practice

- Due to ongoing climate warming and aridification in large areas of the planet, optimum conditions for reforestation may now include sites that were previously beyond species distribution ranges, especially for more drought-sensitive tree species.
- In mountain areas with increasing aridification due to climate change, proper conditions for forest restoration may now be found at higher elevation than in the past, as species climatic niches are shifting uphill.
- Restoring with consideration of future climatic conditions will assist species uphill range shifts under rapidly changing climate, as natural shifts are often limited by biotic and abiotic constraints.
- Assisted colonization of degraded ecosystems may aid the persistence of target species while enhancing ecosystem adaptation to climate change.

Word count: 6507

Introduction

Restoration activities are widespread to recover the integrity and sustainability of ecosystems, enhance biodiversity, and recover ecosystem services (SER 2004; MA 2005). Given the importance of past vegetation as an indicator of the current potential vegetation in degraded areas, a traditional paradigm is to take the ecosystems of the past as reference models to be re-established (Hobbs & Harris 2001; Harris et al. 2006; Choi et al. 2008). Consequently, reforestation –among the most frequent restoration activities in terrestrial ecosystems– often aims at regaining the cover of native plant species whose presence in the area was recorded in the past. However, these efforts are doomed to fail in cases in which the environmental conditions required by the planted species are no longer present or are predicted to change in the near future, for example due to climate change (Hobbs & Harris 2001; Harris et al. 2006; Choi et al. 2008; Woodworth 2013). In fact, the potential distribution ranges of many tree species are shifting latitudinally towards the poles and altitudinally up the mountains as a consequence of increasing temperatures and drought frequency and intensity (Kelly & Goulden 2008; Jump et al. 2009; Matías & Jump 2014). These range shifts are particularly evident in mountains due to the much smaller distances over which the changes occur as compared to latitudinal shifts (Jump et al. 2009). Mountains thus provide ideal study systems to evaluate the success of forest restoration under rapidly changing climatic conditions.

Oak forests are among the most widespread vegetation types in the Northern Hemisphere and they provide numerous ecological, societal, and economic services. In many places these ecosystems have been degraded or encounter difficulties in their regeneration (Dey et al. 2008; MacDougall et al. 2010), so reforestation with species of *Quercus* is frequently considered in restoration policy (e.g. EEC regulation no. 2080/92). Deciduous and evergreen oak species coexist in large areas of their distribution ranges. When they coexist, evergreen oaks typically dominate drier positions of the landscape, whereas deciduous oaks are often restricted to higher elevations and/or wetter areas (Blanca et al. 2001; Blondel et al. 2010). Evergreen trees exhibit a more conservative water-use behavior than deciduous ones due to a tighter control of stomatal conductance and a greater sensitivity to leaf-to-air water vapor pressure differences (Mediavilla & Escudero 2003; López-Iglesias et al. 2014). Under the expected scenario of rising temperatures and increasing aridity in the Mediterranean Basin (Easterling et al. 2000; IPCC 2012), environmental conditions should become less favorable for oak forest regeneration within their current range, especially for deciduous oak species with lower drought tolerance (Gea-Izquierdo et al. 2013).

In this study we seek to investigate the success of reforestation with two sympatric oak species in a Mediterranean mountain area (Sierra Nevada, SE Spain). We planted seedlings of an evergreen (*Quercus ilex*) and a deciduous (*Q. pyrenaica*) oak species, both of which form native forests and woodlands in the Mediterranean region. The study considered two altitudes within distinct vegetation belts: i) ~1700 m a.s.l. (above sea level), where both oak species currently form mature forests, and ii) ~2050 m a.s.l., an area above the current distribution range of forests in Sierra Nevada. Seedlings were monitored during two years for demographic parameters (survival and growth), and leaf nutrient concentrations (N, P) and isotopic composition ($\delta^{13}C$ and $\delta^{18}O$) were measured at the end of the second growing season. This allows evaluating the ecophysiological response of the oak seedlings to the environmental conditions prevailing at these sites of contrasting elevation.

Stable isotope ratios provide time-integrated information on plant physiological response to changing abiotic conditions (Dawson et al. 2002). In C3 plants, leaf carbon isotopic ratios– $\delta^{13}C$, the ratio of ^{13}C to ^{12}C– are related to the ratio of intercellular to atmospheric CO_2 concentrations (Farquhar et al. 1989), and can provide a time-integrated measure of intrinsic water-use efficiency (WUE_i). WUE_i is defined as the ratio between net photosynthetic rate (A) and stomatal conductance to water vapour (g_s) (Dawson et al. 2002). Water shortage and drought stress induce the progressive closure of stomata, which reduces both A and g_s, although A is reduced to a lesser extent than g_s, which thus increases WUE_i. At the same time, the lower diffusion of CO_2 into the leaf due to stomatal closure increases the intercellular concentration of ^{13}C, leading to more of the heavy isotope being assimilated and the photosynthate becoming more enriched in ^{13}C (Farquhar et al., 1989). Leaf oxygen isotopic composition ($\delta^{18}O$) is affected by the isotopic signature of the source water used by the plant, but also by changes in stomatal conductance and transpiration. Since foliar $\delta^{18}O$ is affected by g_s (so that higher values of g_s lead to lower leaf $\delta^{18}O$ values) but not by A, leaf $\delta^{18}O$ data can greatly aid the interpretation of leaf $\delta^{13}C$ data (Barbour 2007). This is so because stomatal limitations to photosynthesis affect both $\delta^{13}C$ and $\delta^{18}O$, whereas biochemical limitations influence $\delta^{13}C$ but not $\delta^{18}O$ (Scheidegger et al. 2000). Measuring foliar nutrient concentrations and plant growth parameters can further aid in the interpretation of leaf $\delta^{13}C$ and $\delta^{18}O$ data (e.g. Querejeta et al., 2008).

Given the current trend of increasing aridification in the Mediterranean Basin (IPCC 2012) and in the study area in particular (Ruiz Sinoga et al. 2011), we hypothesize that the establishment and performance of the two oak species will be favored at higher elevation as a response of species range shifts. On the other hand, given the greater drought sensitivity of Mediterranean deciduous species compared to evergreen species (Mediavilla & Escudero 2003, Gea-Izquierdo et al. 2013; López-Iglesias et al. 2014), we hypothesize that the deciduous *Q.pyrenaica* will show a greater response to changes in elevation and climate between sites than the evergreen *Q.ilex*.

The results of this study should help to elucidate whether the potential altitudinal distribution/ regeneration niche of the target oak species might have expanded upslope in response to the prevailing warmer and drier conditions, and also reveal whether the success of ecosystem restoration in mountain areas may be enhanced by considering changes in climatic conditions.

Methods

Study species

Quercus ilex L., the Holm oak, is a sclerophyllous evergreen tree widely distributed across the Western Mediterranean Basin. *Quercus pyrenaica* Willd., the Pyrenean oak, is a deciduous tree distributed from SW France through N Morocco. In the southern Iberian Peninsula, both species grow up to 1800 m a.s.l., as part of the Supramediterranean vegetation belt (Costa-Tenorio et al. 1998; Valle 2003), whereas the vegetation above this altitude is dominated by stunted and cushion shrubs characteristics of the Oromeditarranean belt (Valle 2003; Appendix S1; Table S1). In S Spain, *Q. pyrenaica* forests are frequently mixed with *Q. ilex*, although the deciduous *Q. pyrenaica* often substitutes its evergreen counterpart at higher elevations and at more mesic sites (Costa-Tenorio et al. 1998). Despite the key importance of the conservation of both types of oak forests (Lorite et al. 2008; WWF, 2011), they have been extensively degraded, and they currently occupy small, fragmented patches within their potential range (Costa-Tenorio et al. 1998; García & Jiménez Mejías, 2009; WWF, 2011). In particular, the Sierra Nevada populations of *Q. pyrenaica* are relict in Andalusia due to intensive human exploitation and land-use changes (Pérez Luque 2011).

Study site and experimental design

The study was conducted between 2010 and 2011 in the Sierra Nevada National and Natural Park (SE Spain), in an area that was affected by a wildfire that burned 3400 ha of shrublands and 40 to 60 year-old pine plantations in September 2005 (Leverkus et al. 2012). Pine species had been planted at different elevation according to their climatic requirements, and the fire was of high severity across the burnt area (Marañón-Jiménez et al. 2013). Two plots of >20 ha in surface and ~1.5 km apart were established in collaboration with the local Forest Service to test the success of native-forest restoration: one at 1,700 m a.s.l. (Low Plot, hereafter; altitude of the centroid of the plot), and the other one at 2,050 m a.s.l., with higher rainfall and lower temperatures in the latter (High Plot; Table 1; Fig. 1). These altitudinal (and, consequently, climatic) differences led both plots to be categorized onto different bioclimatic belts or life zones (Blanca et al. 2001; Valle 2003). The Low Plot was in the Supramediterranean belt, where forests of both oak species are part of the historical vegetation. The High Plot was located in the Oromediterranean belt, thus above the current altitudinal limit of native forests (Valle 2003). Both plots were dominated by early-successional shrubs and perennial grasses that regenerated abundantly after the fire (Table 1). Plant species composition differed among plots, with typical species from the Supramediterranean and lower elevation vegetation belts at the Low Plot and species from the Oromediterranean belt at the High Plot (Appendix S1; Table S1). The plots had similar bedrock (micaschist) and soil type (Haplic phaeozems; Marañón-Jiménez *et al.*, 2013). Soil texture, nutrient content, mineral composition, and other properties were similar between plots. Only soil pH, bulk density, and N differed slightly among plots (Table 1), in a way that could be expected due to the differences in elevation (Reich & Oleksyn 2004). The plots also had similar slope (ca. 30%), although they were both terraced 40-60 years prior to the study to ease the plantation of pines, thus minimizing potential effects of slope on seedling development. Both plots had a dominant W/ SW aspect (Table 1, Fig. S1).

Climate in the area is typical Mediterranean, with mild, wet winters and hot, dry summers. Mean precipitation recorded at a nearby meteorological station at 1652 m a.s.l. averages 511.1 ± 239.1 mm (period 1989-2011; values for climatic variables are mean ± SD). Rainfall during the summer months (June- September) was 60.9 mm in 2010, 12.9 mm in 2011, and 52.8 ± 35.0 in the period 1989-2009. Mean minimum and maximum daily temperatures of the coldest month (January) were -1.1 and 6.8ºC in 2010, -0.7 and 5.5 in 2011, and 0.5 ± 2.6 and 8.6 ± 2.7ºC in 1989-2009. Mean minimum and maximum daily temperatures of the hottest month (July) were 18.1 and 27.3ºC in 2010, 16.6 and 25.5ºC in 2011, and 17.9 ± 2.1 and 27.5 ± 2.2ºC in 1989-2009. The differences in climatic conditions between the two plots were estimated from interpolated maps obtained from the Sierra Nevada Global Change Observatory for 1981-2010 (http://linaria.obsnev.es/). These rendered a mean rainfall of 550 ± 215 mm at the Low Plot and 630 ± 227 mm at the High Plot, a mean minimum daily temperature of 5.6 ± 1.2ºC at the Low Plot and 3.4 ± 1.2ºC at the High Plot, and a mean maximum daily temperature of 16.2 ± 1.1 at the Low Plot and 13.4 ± 1.1ºC at the High Plot.

In March-April 2010 the local Forest Service conducted an experimental oak plantation in the study plots. An excavator dug holes of approx. 60 x 60 x 60 cm in the terrace beds, in which forestry workers planted the seedlings at approx. 400 seedlings ha^{-1} (Leverkus et al. 2012). The seedlings of the two species were intermingled across each experimental plot (Fig. 1; Appendix S2; Fig. S2).

Seedling survival

A subsample of 642 and 540 *Q. ilex* (Low and High Plot, respectively) and 549 and 501 *Q. pyrenaica* seedlings (Low and High Plot) were tagged to monitor seedling survival, and their position was recorded with a Leica GPS SR20 with external antenna. These seedling numbers were obtained after a resampling procedure to eliminate small differences in sample size among different post-fire management areas (Appendix S3;

Table S2). Survival was monitored in June 2010 to discard seedlings that died due to transplanting shock, and thereafter at the end of the first summer (September 2010), first winter (June 2011), and second summer (September 2011). We also intended to monitor damage due to ungulate herbivores, but it was negligible and not further considered. We acknowledge that there is no spatial replication of each elevation (greatly due to the complex logistics of collaborating with different stakeholders). However, given that the seedlings were planted in a large area (>20 ha) at each altitude, that the plots had similar topographic and soil characteristics, and that seedlings of the two species were completely intermingled, we consider that the design allows to compare the performance of these two oak species at different elevation. In addition, it was possible to evaluate the effects of altitude gradients within each plot (150-170 m) on seedling performance, given the existence of precise data on seedling position.

Seedling biomass, nutrient content, and isotopic composition

In September 2011 (two years after planting), a total of 87 and 90 *Q. ilex* (Low and High Plot, respectively) and 45 and 42 *Q. pyrenaica* seedlings (Low and High Plot) were harvested for biomass, leaf nutrient (N and P), and leaf isotopic (δ^{13} C, δ^{13} O) measurements. As for seedling survival, these numbers were obtained after a resampling procedure (Appendix S3; Table S2). Harvested seedlings differed from those tagged for survival monitoring, but they were within the same area and randomly selected among live individuals at the time of sampling. The exact position of these seedlings was not recorded. After harvesting, seedlings were oven-dried at 40ºC for 48 hours, and leaves and stems were separately weighed. Leaves from the 2011 growing-season cohort (i.e. all *Q. pyrenaica* leaves, but only current-year *Q. ilex* leaves) were finely ground prior to analyses. Nitrogen concentration was measured with the combustion furnace technique at 850ºC (Leco TruSpec autoanalyser, St. Joseph, MI, USA), and phosphorus with the molybdovanadate method (AOAC 1975) with a Perkin Elmer 2400 spectrophotometer (Waltham, MA, USA). The samples were dried at 105ºC by a thermogravimetric analyzer (Leco TGA 701), and nutrient concentrations referred to dry weight.

For the analysis of foliar $\delta^{13}C$, we used two replicate samples of 0.5-0.6 mg weighed in tin capsules. Samples were then placed in the autosampler of a Carlo Elba 1500 NC elemental analyzer connected to an Isotope Ratio Mass Spectrometer (Thermo Finnigan Delta plus XL). For foliar $\delta^{18}O$ analysis, three replicate subsamples of 0.3 mg were weighed in silver capsules and mixed with 0.6 mg of graphite. The samples were then placed in the autosampler of a High Temperature Conversion elemental analyzer connected to an Isotope Ratio Mass Spectrometer. The ISODAT NT software provided the $\delta^{18}O$ and $\delta^{13}C$ (‰) values, and the average value of the subsamples was calculated for each seedling. We expressed the isotopic composition of the samples in delta notation as:

$$\delta^{xx}E\ (‰) = 1000*(R_{samp}/R_{stand}-1)$$

where ^{xx}E is the heavy isotope which is compared to the lighter one; R refers to the molar ratio of the heavy to the light isotope (i.e. ^{13}C:^{12}C or ^{18}O:^{16}O); samp refers to the sample; and stand refers to an international standard (V-PDB for C and V-SMOW for O). We used international and internal standards for analyses. Isotopic composition was measured at the Stable Isotope Laboratory of the Instituto Andaluz de Ciencias de la Tierra (Granada, Spain).

Statistical analyses

We analyzed the effect of elevation on two-year seedling survival at two spatial scales. First, across plots we used a two-way factorial analysis of deviance with quasibinomial errors, with *Elevation* (a categorical factor defined by Plot), *Species*, and the interaction between them as explanatory factors. Second, within each plot we used logistic regression models to test the effect of *Elevation* (a continuous variable with measurements for each individual seedling) on seedling survival, also including *Species* and the *Species* x *Elevation* interaction in the model. The models were simplified to test for the significance of these terms (Crawley 2013).

Plant biomass, foliar nutrient concentrations, and isotopic ratios were analyzed with two-way ANOVA, considering *Elevation*, *Species*, and the interaction between them as explanatory variables. Previous to analysis, data were transformed to improve homogeneity of variance. To test for correlations between foliar isotopic ratios, nutrient concentrations, and seedling aerial biomass, we calculated Pearson´s product-moment correlation coefficients for the seedlings of each *Species* x *Elevation* combination separately. For correlations with $\delta^{18}O$ we first removed outliers (as defined in Crawley 2013). For analyses we used R version 2.15.0 (R Development Core Team 2012).

All analyses were carried out after resampling procedures with 10,000 permutations to homogenize the number of seedlings from each post-fire management area in each plot (Appendix S3). In each permutation we ran the models and extracted the appropriate test statistics (F-values in all cases). The reported P-values were later calculated from the average F-values and degrees of freedom from the permutations. All the means and correlation coefficients presented here are averages of the values obtained in the permutations.

Results

Of all the planted oak seedlings, 61% were recorded alive after the first summer, 63% after the first winter (because some seedlings resprouted), and 54% after the second summer. Two-year survival was significantly greater at the High Plot (67%) than at the Low Plot (43%), and greater for *Q. ilex* (59%) than for *Q. pyrenaica* (48%; Table 2; Fig. 2). Seedling survival significantly increased with seedling elevation within each of the plots (Low Plot: $F=13.08$, $P<0.001$; High Plot: $F=18.96$, $P<0.01$), and this effect was consistent among species (i.e. no *Species* x *Elevation* interactions). The model coefficients for the slope of the *Elevation* effect were consistently positive within each plot (Low Plot: 0.0079; High Plot: 0.0044).

Seedling aerial biomass (stems, leaves, or total) was greater for *Q. ilex* than for *Q. pyrenaica* at both elevations, and greater at the High Plot than at the Low Plot for both species. Differences in biomass between elevations were largest for *Q. pyrenaica*, leading to significant *Species* x *Elevation* interactions (Table 2; Fig. 3).

There were no significant differences in foliar $\delta^{13}C$ between species, but *Q. ilex* showed significantly higher foliar $\delta^{18}O$ than *Q. pyrenaica* at both elevations. Seedlings showed higher foliar $\delta^{13}C$ values at the High Plot than at the Low Plot, although this effect was only significant for *Q. ilex* when analyzing the two species separately (Table 2; Fig. 4). Both species showed higher foliar $\delta^{18}O$ values at the High Plot than at the Low Plot (Table 2; Fig. 4).

Quercus pyrenaica had higher foliar N and P concentrations than *Q. ilex* at both elevations, and foliar N concentrations were higher in the High Plot than in the Low Plot in both species (Table 2; Fig. 4). However, this difference was greater in *Q. pyrenaica* (15% higher in the High Plot) than in *Q. ilex* (10%), as indicated by a significant *Species* x *Elevation* interaction (Table 2, Fig. 4). Foliar P concentrations also tended to be higher at the High than at the Low Plot in *Q. ilex*, (Fig. 4), although not significantly.

Seedling aerial biomass was positively correlated with foliar N in both oak species at the High Plot, negatively correlated with foliar $\delta^{13}C$ in *Q. ilex* at the Low Plot, and also negatively correlated with $\delta^{18}O$ in *Q. pyrenaica* at the High Plot (Table 3). Foliar $\delta^{13}C$ and $\delta^{18}O$ values were positively correlated with each other in *Q. pyrenaica* at both elevations, and in *Q. ilex* at the higher elevation (Table 3). Foliar $\delta^{13}C$ was positively correlated with foliar nutrient status (N and/or P concentrations) in both oak species, except for N in *Q. ilex* and P in *Q. pyrenaica* at the lower elevation. Foliar $\delta^{18}O$ was also positively associated with foliar N concentration in *Q. pyrenaica* at both elevations. When pooling data across elevations, both foliar $\delta^{13}C$ and $\delta^{18}O$ were positively correlated with foliar N concentrations in each oak species separately (Fig. 5).

Discussion

The seedlings of both oak species showed higher 2-year survival when planted above the upper forest limit than at a lower elevation where native oak forests are currently present. In addition, biomass growth and leaf nutrient status and isotopic composition further support that seedlings performed better at the higher-elevation site, primarily due to an improved leaf N status and a reduction in drought stress, especially for the deciduous *Q. pyrenaica*. Interestingly, seedling survival followed a clear positive trend with increasing elevation across and within plots (even within the plot located above the current forest range), further supporting an uphill shift in the climatic niche for regeneration of these oak species. These results suggest that the historical or present distribution range of tree species may no longer necessarily be a good predictor of seedling performance and establishment potential in this Mediterranean mountain ecosystem, which has been undergoing climate warming and aridification in recent decades.

Strong effects of drought stress on seedlings of both species were evidenced by demographic and physiological data. We observed high mortality rates, especially during the first but also during the second summer, while virtually no winter mortality occurred. We also found positive correlations between foliar $\delta^{13}C$ and $\delta^{18}O$ in surviving seedlings of both species (except for *Q. ilex* at the lower site), indicating that seedling growth was limited by water stress and stomatal constraints on photosynthesis (Scheidegger et al. 2000). Summer drought is indeed one of the main demographic filters acting on seedlings in Mediterranean-type mountain ecosystems and a major cause of failure in ecosystem restoration activities (Castro et al. 2002; Gómez-Aparicio et al. 2004; Castro et al. 2006). The facts that mortality decreased with increasing altitude and that biomass growth was greater at the higher-elevation site, most likely due to the cooler and wetter summer conditions associated with higher altitude, further support that drought was a critically important stress factor for both oak species during the study period.

Biomass, leaf isotopic composition, and nutrient concentration data indicate that *Q. pyrenaica* seedlings derived a greater benefit from planting at the higher elevation than *Q. ilex* seedlings. *Quercus pyrenaica* seedlings showed massive mortality (over 60%), negligible biomass growth, and much lower N concentrations at the drier, lower-elevation site, which highlights the low drought tolerance of this species. Furthermore, *Q. pyrenaica* seedling biomass was positively correlated with leaf N concentration and negatively correlated with foliar δ^{18}O values across individuals at the higher-elevation area, indicating enhanced seedling growth with increasing foliar nutrient status and decreasing water stress (as suggested by lower δ^{18}O values; Barbour et al. 2000; Scheidegger et al. 2000; Barbour 2007).

Quercus ilex also showed 50% higher survival as well as 10% higher foliar N and P concentrations at the higher-elevation plot despite its greater drought tolerance. Plant nutrition might have been improved at higher elevation due to the slightly greater soil N content and lower soil pH and bulk density (Table 1). The negative association between seedling aerial biomass and foliar δ^{13}C across *Q. ilex* individuals at the lower elevation area also suggests decreasing seedling growth with increasing water stress (Farquhar *et al.*, 1989; Dawson *et al.*, 2002). Still, the enhanced biomass growth at higher altitude was not statistically significant for *Q. ilex* seedlings, and was small if compared to that shown by *Q. pyrenaica* seedlings. This result is in good agreement with previous knowledge on the contrasting water requirements of these sympatric oak species: whereas the evergreen *Q. ilex* can successfully cope with severe summer drought, *Q. pyrenaica* requires wetter conditions during the summer (Blanca et al. 2001;

Gea-Izquierdo et al. 2013). More broadly, deciduous oak species show greater reductions in stomatal conductance in response to water stress than evergreen species (Acherar & Rambal 1992). The sclerophyllous leaves of *Q. ilex* confer it a greater ability to control transpiration by closing stomata during drought (Schiller et al. 2007). A tighter stomatal control of transpiration water losses in *Q. ilex* than in *Q. pyrenaica* (supported by higher leaf δ^{18}O values in *Q. ilex*; Barbour 2007) may thus explain the better performance of *Q. ilex* seedlings at the drier, lower-elevation area.

Quercus ilex (but not *Q. pyrenaica*) leaves were more enriched in ^{13}C at the higher-elevation site, which is in agreement with the well-known trend of increasing plant δ^{13}C values with increasing altitude due to decreased carbon isotope discrimination (Körner et al. 1988, 1991). However, contrary to expectation, foliar δ^{18}O values in both oak species were also greater at the high-elevation site. This result is striking, given that plants would be expected to become more depleted (rather than more enriched) in ^{18}O with increasing altitude due to the lower temperatures and vapor pressure deficits, more depleted meteoric water δ^{18}O values, and higher precipitation and water availability found at higher elevations in Mediterranean mountain areas (Dawson et al. 2002; Barbour 2007). This result may be explained by several non-mutually exclusive mechanisms. First, lower temperatures with increasing altitude also cause the viscosity of water to increase, which can slow the transport of water from the soil to the leaves (Roderick & Berry 2001), thereby decreasing stomatal conductance (Cernusak et al. 2013) and increasing leaf δ^{18}O values. Second, a delayed leaf phenology at the colder, higher-elevation site (with greater physiological activity during the dry summer) may also have contributed to more enriched leaf δ^{18}O at higher elevation. And third, it is well established that photosynthetic capacity and water-use efficiency increase with increasing foliar N concentration (Field & Mooney 1986;

Körner 1989; Sparks & Ehleringer 1997), which may allow improved stomatal control of water loss (thus leading to higher leaf $\delta^{18}O$ and $\delta^{13}C$ values). Given the global trends of increasing leaf nutrient status (N and P) with increasing altitude and colder temperatures (Körner 1989; Reich & Oleksyn 2004), we propose that improved stomatal control of water loss due to enhanced nutrient status could be a so-far overlooked but important positive feedback mechanism that could foster upward range shifts in water-limited mountain regions. Further studies in different geographical locations are warranted to test this intriguing hypothesis.

Implications for management

The current distribution of native oak forests and woodlands in Sierra Nevada reaches 1800 m a.s.l. (eventually 1900 on South-facing slopes). The fact that seedlings of both oak species performed better above this upper limit as compared to a lower altitude considered more appropriate for oak forest establishment, and with seedling survival still increasing with altitude at the higher plot, may indicate an uphill shift of the climatic optimum for oak forest regeneration in Sierra Nevada. In fact, many studies show that upward shifts of species ranges are already happening under ongoing climate change and will be widespread in the near future (Kelly & Goulden 2008; Jump et al. 2009; Matías & Jump 2014). In Sierra Nevada, mean annual rainfall has shown decreasing trends during the last decades, including crucially important autumn rainfall after the long summer-drought period (Ruiz Sinoga et al. 2011). Further, climate models predict an average temperature increase of 4.8ºC by the end of the XXI century in these mountains (Benito et al. 2011), which would induce a yearly uphill shift of 14.8 and 13.4 m in the climatic niche of *Q. ilex* and *Q. pyrenaica,* respectively (Benito et al. 2011). Recent changes and future projections imply that areas currently occupied by subalpine shrublands are becoming suitable for the Pyrenean oak, and that areas currently occupied by the Pyrenean oak are becoming suitable for the Holm oak (Benito et al. 2011), so the results reported here fall within the expected trend (cf. Gea-Izquierdo et al. 2013). Follow-up monitoring of the planted oaks in the coming decades are required to investigate whether the seedlings growing at high altitudes reach maturity and are able to reproduce naturally, and further experimental studies replicated under a wide range of environmental conditions –such as precipitation, land use, and temperature (Barbero et al. 1992, Pérez Luque 2011)– would provide invaluable insights into the extent of oak range shifts in water-limited Mediterranean mountain ecosystems.

Despite widespread uphill shifts in the climatic niches of plant species in Mediterranean mountain regions under climate change (e.g. Kelly & Goulden 2008), natural events of species upward migration may be constrained by the potential for seedling establishment, which may in turn rely on species interactions involving seed dispersal, competition, facilitation, parasitism, or herbivory (Jump et al. 2009; Benavides et al. 2013; Grassein et al. 2014). In our study area, successional vegetation of the Oromediterranean life zone (e.g. cushion shrubs) is abundantly regenerating at the higher-elevation site despite evidence indicating that the area may already be suitable for the growth of oak forests. Numerous processes may be slowing oak colonization at higher elevation, the first being acorn dispersal. European jays (*Garrulus glandarius* L.), the main long-distance acorn dispersers in the area, preferentially cache acorns in forest areas (Pons & Pausas 2008; Castro et al. 2012), which they do not encounter above the forest limit. Further, seed predation by rodents and wild boars in the area has been shown to decimate the acorns available for germination and growth (Gómez et al. 2003; Leverkus et al. 2013). Current post-fire vegetation regeneration patterns at the higher-elevation area are thus likely the result of the competitive dominance of resprouting shrubs and the presence of a well-established seed bank (Leverkus et al. 2014), and also of the time lag required for the migration of competing tree species from lower elevations.

The slow natural colonization rates of species with shifting potential ranges may partially be overcome through ecosystem restoration activities. As our results suggest, assisted colonization –taking species beyond their past or present distribution limits to sites projected to become more favorable in the future (Hoegh-Guldberg et al. 2008)– may improve transplant survival and performance in water-limited mountain areas and might also assist tree-species uphill range shifts under ongoing climate change. Although assisted colonization remains controversial (Hewitt et al. 2011), the debate overlooks the need of managers to define target ecosystems to be restored in degraded areas and the fact that species that were previously present in a place may often no longer thrive there. By ignoring climate change projections, reforestation efforts would be increasingly likely to fail or produce maladapted forests (Millar et al. 2007), including a wasteful use of limited resources for ecosystem restoration. Assisted colonization in degraded ecosystems could thus provide an effective means for aiding the persistence of target species while favoring forest adaptation to climate change (Millar et al. 2007; Seddon 2010; Lunt et al. 2013). Under "the premise of an uncertain but certainly variable future" (Millar et al. 2007), ecosystem restoration should be adaptive and have dynamic references and targets to enhance plant performance and ecosystem resilience under the environmental challenges expected during this century.

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Tables

Table 1. Key properties of the study plots.

[a] Above sea level; values are the range of elevation

[b] 10th and 90th percentile of pixel values calculated in ArcGIS from Digital Elevation Models

[c] Values indicate mean ± 1 SE of the mean hereafter

[d] Properties measured a few weeks after the fire. Pine density within each plot was sampled in 36 quadrats of 25 x 25 m, and tree height on 30 randomly-chosen trees within each quadrat.

[e] See Appendix S1 for indicator species and percent cover of most abundant species.

[f] Sampled in 2008. Soil texture data are based on 3 samples per plot and were analyzed with Mann-Whittney U-tests. The rest of the soil properties are based on 20 samples per plot and were analyzed with Student's t-tests. Significance levels are: ns (not significant), * (P<0.05), ** (P<0.01), *** (P<0.001)

Variable	Low Plot		High Plot
Elevation (m a.s.l.) [a]	1600-1760		1970-2120
Area (ha)	21		32
Aspect (Degrees) [b]	222-283		225-264
Direct solar radiation at summer solstice (W h m^{-2}) [b]	6406-6893		6722-7060
Bioclimatic belt	Supramediterranean		Oromediterranean
Dominant pre-fire afforested species	*Pinus nigra*		*Pinus sylvestris*
Pine density (individuals ha^{-1}) [c,d]	1064 ± 67		1051 ± 42
Pine height (m) [d]	6.6 ± 0.1		6.2 ± 0.1
Average plant cover in 2007 [e] *			
Perennials (%)	42.9		61.8
Annuals (%)	26.3		11.1
Bare soil (%)	30.9		27.1
Soil properties [f] †			
Texture	Sandy loam		Sandy loam
Clay (%)	12.5 ± 1.5	ns	8.8 ± 0.3
Fine loam (%)	16.7 ± 1.3	ns	12.5 ± 0.4
Coarse loam (%)	11.9 ± 0.7	ns	9.7 ± 0.4
Sand (%)	58.9 ± 3.2	ns	69.0 ± 0.1
Stoniness (% vol.)	41.8 ± 1.3	ns	45.2 ± 1.7
Bulk density (g cm^{-3})	1.3 ± 0.1	*	1.2 ± 0.1
Cation Exchange Capacity (cmol^{+} kg^{-}	5.3 ± 0.3	ns	4.6 ± 0.3

^{1} soil)			
pH	7.3 ± 0.1	***	6.7 ± 0.1
Nutrient content			
Soil Organic Matter (%)	3.32 ± 0.18	ns	3.57 ± 0.18
C_{tot} (%)	1.17 ± 0.10	ns	1.30 ± 0.13
N_{tot} (%)	0.07 ± 0.01	**	0.09 ± 0.01
NH_4^+ (ppm)	3.10 ± 0.82	ns	3.66 ± 0.85
NO_3^- (ppm)	1.17 ± 0.35	ns	1.47 ± 0.28
P_{inorg} (ppm)	1.87 ± 0.15	ns	2.64 ± 0.38

* For detailed species composition and abundance see Leverkus et al. (2014).

[†] Data extracted from Marañón-Jiménez et al. (2013).

Table 2. Results of ANOVA for plant biomass and leaf nutrient and isotopic composition.

[a] Weight and nitrogen data were square root-transformed prior to analysis.

[b] Phosphorus data were log-transformed prior to analysis.

[c] Average residual degrees of freedom of the simulations (fewer than the rest because some of the harvested seedlings had no P measurement)

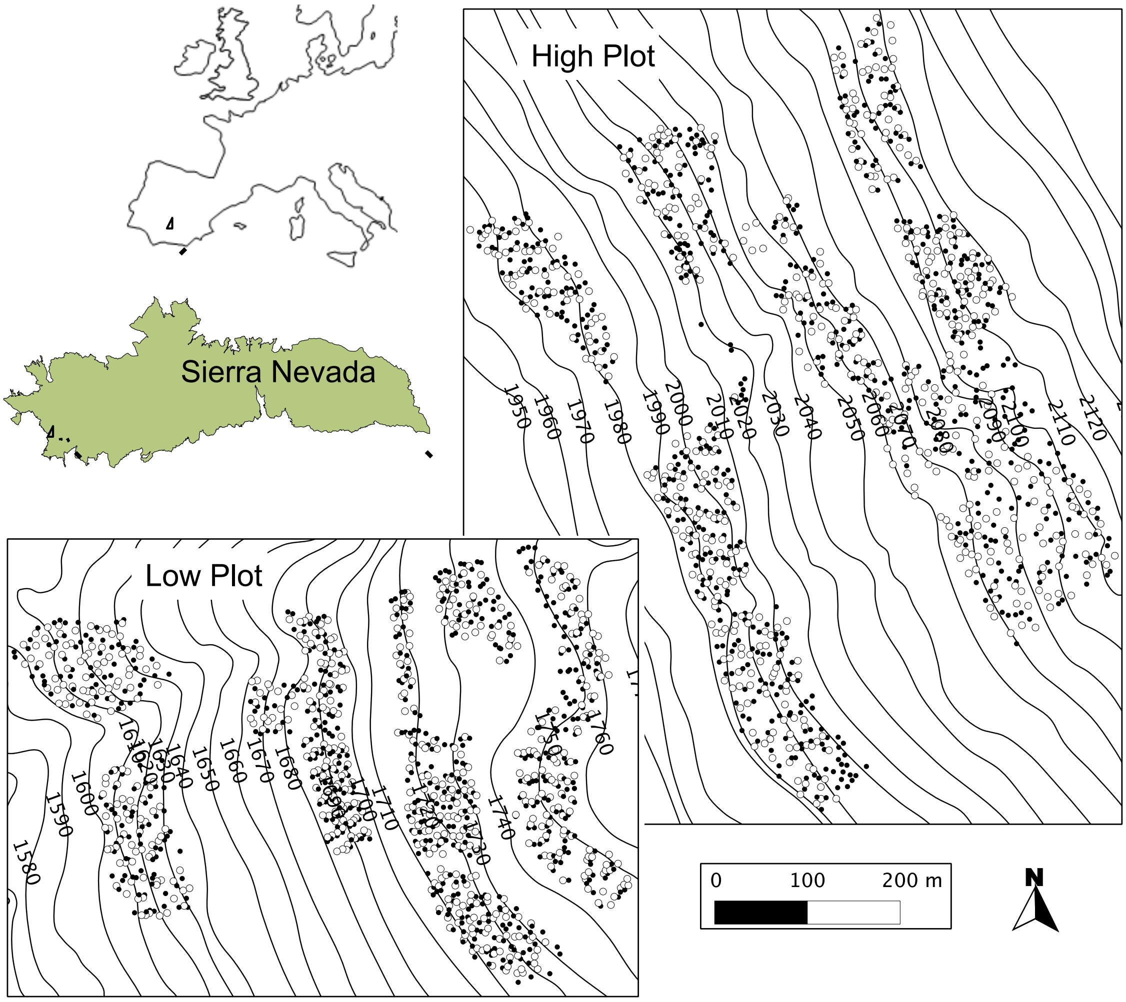
		Elevation		*Species*		*Elevation* x *Species*	
Response	Df	F	P	F	P	F	P
2-yr survival	1,2229	132.4	<0.001	30.8	<0.001	0.8	0.38
W_{leaf} [a]	1,260	11.9	<0.001	190.7	<0.001	7.0	<0.01
W_{stem} [a]	1,260	14.8	<0.001	113.4	<0.001	3.5	0.06
W_{tot} [a]	1,260	14.2	<0.001	177.3	<0.001	6.3	<0.05
$\delta^{13}C$	1,260	35.3	<0.001	1.9	0.17	17.1	<0.001
$\delta^{18}O$	1,260	38.5	<0.001	44.7	<0.001	0.5	0.48
N (%) [a]	1,260	61.2	<0.001	226.3	<0.001	4.3	<0.05
P (mg/g) [b]	1,252.9 [c]	1.9	0.17	189.2	<0.001	1.5	0.22

Table 3. Pearson correlation coefficients between plant biomass and leaf nutrient and isotopic composition. W_{tot}= total weight of aerial biomass; N= nitrogen concentration; P= phosphorus concentration.

	Q. ilex				*Q. pyrenaica*			
	Low Plot		High Plot		Low Plot		High Plot	
Variables	r	P	r	P	r	P	r	P
W_{tot}-N	0.07	0.50	0.22	<0.05	-0.06	0.70	0.28	0.07
W_{tot}-$\delta^{13}C$	-0.21	0.05	-0.05	0.61	-0.13	0.39	-0.22	0.16
W_{tot}-$\delta^{18}O$	0.11	0.31	-0.13	0.23	-0.13	0.39	-0.26	0.10
$\delta^{13}C$-$\delta^{18}O$	0.17	0.11	0.28	<0.01	0.31	<0.05	0.32	<0.05
$\delta^{13}C$-N	0.17	0.12	0.33	<0.01	0.49	<0.001	0.39	<0.05
$\delta^{13}C$-P	0.41	<0.001	0.27	<0.05	-0.10	0.52	0.38	<0.05
$\delta^{18}O$-N	0.15	0.17	0.07	0.51	0.29	0.06	0.29	0.07

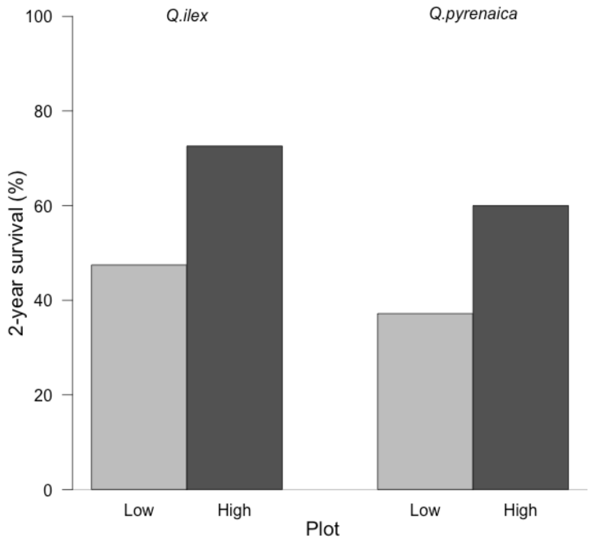
Figures

Figure 1



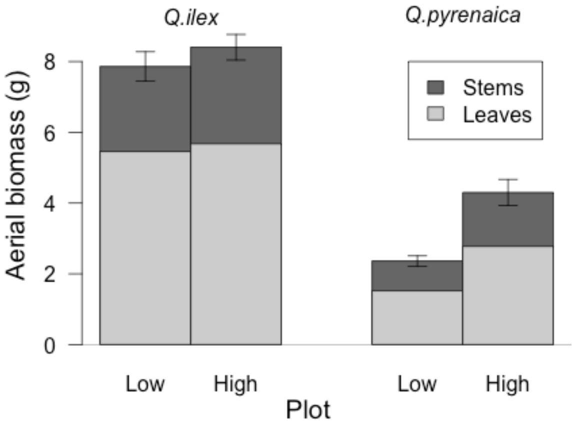
Map of the study plots showing the position of the monitored seedlings of *Quercus ilex* (black points) and *Quercus pyrenaica* (white points). Lines are 10-m topographic contour lines and values are in meters above sea level. Note that the seedlings of both species were intermingled within each plot; for spatial analysis, see Appendix S2.

Figure 2



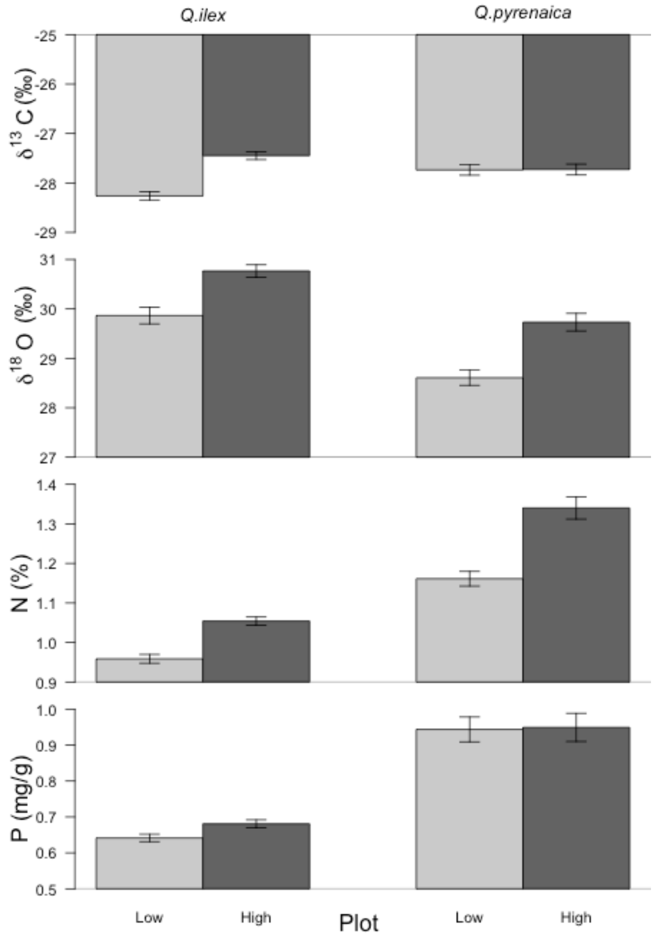
Seedling survival for *Quercus ilex* and *Q. pyrenaica* after the second growing season (in September 2011).

Figure 3



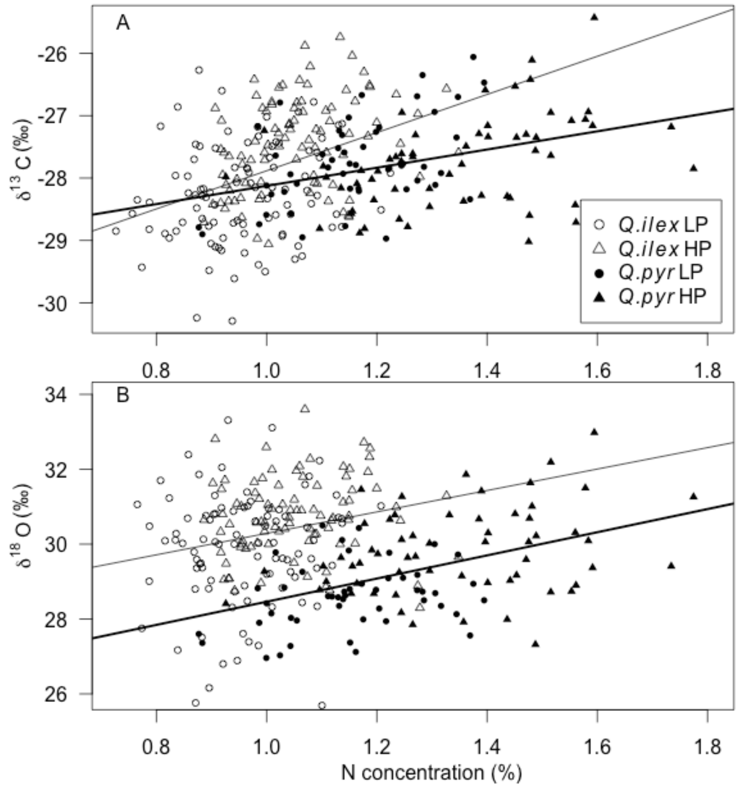
Mean biomass of aerial tissues for each species and plot/elevation. Error bars indicate ± 1 SE of average total aerial biomass (stems + leaves).

Figure 4



Average leaf isotope ratios and nutrient concentrations. Error bars indicate ± 1 SE of the mean.

Figure 5



Correlations between leaf N concentration and isotopic composition across plots/elevations. Thin lines are lines of best fit for *Q. ilex*, and thick lines for *Q. pyrenaica*. Correlation coefficients are: A) for δ^{13}C: *Q. ilex* (r= 0.40, P< 0.001), *Q. pyrenaica* (r= 0.37, P< 0.001); B) for δ^{18}O: *Q. ilex* (r= 0.23, P< 0.01), *Q. pyrenaica* (r= 0.47, P< 0.001). LP= Low Plot; HP= High Plot. For correlation coefficients separated by plot/elevation, see Table 3. The figure shows the data for all seedlings, while analyses were made after a resampling procedure (Appendix S3).

Appendix S1: Indicator Species Analysis

In order to characterize the differences in vegetation between the plots and to locate them onto the corresponding vegetation belts of Sierra Nevada, we carried out an Indicator Species Analysis and revised on which belt the resulting species are usually located.

Methods

We used data from Leverkus et al. (2014) to determine which species were indicators of the Low and High Plots two years after the fire (the Low and High Plots correspond to Plots 2 and 3 from the cited study; Plot 1 was not considered in this study). To obtain the data, in each plot we sampled 72 linear transects, and for each transect we estimated the percent cover of each species by using 150 contact points. With these data we carried out Indicator Species Analysis (Dufrêne & Legendre 1997) with the “labdsv” package in R (Roberts 2012), which indicates the species that are usually present at a site (fidelity) and not present at the other site (specificity). In our case, the sites are the two plots. We report only significant indicator species ($P < 0.05$) with an indicator value greater than 25 (Dufrêne & Legendre 1997). The natural occurrence of the resulting species in the Supra- and Oromediterranean vegetation belts was established according to Blanca et al. (2009) and to expert knowledge when necessary. For more detailed sampling and statistical methods, see Leverkus et al. (2014).

Results

We found 15 species that were significant indicators of the Low Plot and 12 species of the High Plot (Table S1). All the species indicative of the Low Plot are typical of the

Supramediterranean belt and lower elevations, while several of the species found to be indicators of the High Plot are typical of greater elevations. These results indicate that the Low and the High Plot are located on the Supra- and Oromediterranean belt, respectively. This result is in accordance with what would be expected from the elevation of the plots.

Table S1 also shows the percent cover of all the abundant species in each plot, i.e. those with values greater than 3%. All of these species except one (*Euphorbia flavicoma*) were also indicators of the plot where they were found to be abundant, reflecting that the composition of the plant communities of the two plots differed in terms of their most abundant species. For a more detailed description of plant composition of the plots, see Leverkus et al. (2014).

References for Appendix S1

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Table S1. Cover of the most abundant plant species and results of Indicator Species Analysis. [*] Species characteristic of the Supramediterranean and lower vegetation belts. [†] Species characteristic of the Oromediterranean vegetation belt. [‡]Species generally present in the Supra- and Oromediterranean belts, with greater abundance in the latter. [††] Indicator and P-values only shown for significant indicator species.

Plot	Species	Cover (%)[**]	Ind. value[††]	P
Low	*Eryngium campestre*[*]		91.67	0.0001
Low	*Andryala integrifolia*[*]		83.60	0.0001
Low	*Carlina corymbosa*[*]		77.22	0.0001
Low	*Koeleria vallesiana*[*]	5.4	76.00	0.0001
Low	*Dactylis glomerata*[*]	3.1	73.61	0.0001
Low	*Adenocarpus decorticans*[*]	4.6	68.34	0.0001
Low	*Reseda alba*[*]		64.53	0.0001
Low	*Festuca scariosa*[*]	3.0	54.64	0.0001
Low	*Vaccaria hispanica*[*]		53.04	0.0001
Low	*Picnomon acarna*[*]		38.76	0.0001
Low	*Ulex parviflorus*[*]		34.72	0.0001
Low	*Chondrilla juncea*[*]		30.76	0.0001
Low	*Ononis spinosa*[*]		27.78	0.0001
Low	*Thapsia villosa*[*]		27.60	0.0001
Low	*Erysimum mediohispanicum*[*]		27.25	0.0001
Low	*Euphorbia flavicoma*	3.1		
Low	Annuals	26.3		
High	*Senecio nebrodensis*[‡]	15.1	98.49	0.0001
High	*Sesamoides purpurascens* subsp. *prostrata*[†]	10.7	97.14	0.0001
High	*Genista versicolor*[†]	3.8	93.06	0.0001
High	*Verbascum nevadense*[‡]	3.5	73.61	0.0001
High	*Plantago holosteum*[‡]		62.50	0.0001
High	*Onopordum acaulon*		62.11	0.0001
High	*Reseda phyteuma*	3.0	58.59	0.0001
High	*Corynephorus canescens*		56.70	0.0001
High	*Linaria aeruginea*		54.17	0.0001
High	*Acinos alpinus* subsp. *meridionalis*		51.39	0.0001
High	*Festuca indigesta*[†]		44.78	0.0001
High	*Arrhenatherum elatius* subsp. *bulbosum*		44.35	0.0094
High	*Euphorbia flavicoma*	4.6		
High	Annuals	11.1		

[**] Plant cover for species with >3%; see Leverkus et al. (2014) for details.

Appendix S2: Spatial analysis of seedling distribution

To confirm that the seedlings of both species were randomly distributed respect to each other (thus allowing the use of individual seedlings as replication units in statistical analyses) we carried out a spatial analysis.

Methods

We analyzed the spatial distribution of the planted seedlings with $K_{ij}(r)$, an analogous function to Ripley's K that is used for multitype point patterns (Diggle 1983; Dixon 2002). This function counts, for each point of type *i*, the number of points of type *j* that are closer than r units away from it. If the points of both types are randomly distributed, then $K(r) = \pi r^2$. To stabilize the variance and linearize the graphical output of K(r), a variation of it, the *L* function, is frequently used (Dixon 2002; Fortin et al. 2002):

$$L(r) = \sqrt{K(r)/\pi}$$

Values of L(r) greater than r indicate clustering between point types, while lower values indicate a spatial segregation.

We used the "spatstat" package in R (Baddeley & Turner 2005) to analyze the spatial distribution of all planted oak seedlings in each plot separately. The "point types" were the two species that were used. We calculated the empirical "L" line (as described above) with border correction (Ripley 1988) and then built 99% confidence intervals through simulation. We randomly allocated one of both species to each planted seedling 1000 times and calculated the L function with each of these simulated data sets. Then, for each distance (r) we used the 5th and the 996th highest values of the simulated L(t) lines as lower and upper limits of the confidence intervals. Values above this envelope indicate that plants of both species are more attracted to each other than expected by a random Poisson process, while values below indicate repulsion between plants of both species (Fortin et al. 2002).

Results

The oak seedlings showed a significant attraction among species at both plots for all distances above ~13 m and a random distribution at lower distance (Fig. S2). This means that the plants of both species were randomly located across the area at small distances, and at medium to large distances they were closer to plants of the other species than expected by random.

This result falls within expectation. Although the seedlings of both species were not systematically alternated during plantation, the general trend was to plant the seedlings one species after the other. The result was that seedlings of both species were mixed across the reforested area, contrary to having clumps of each species in different places.

References for Appendix S2

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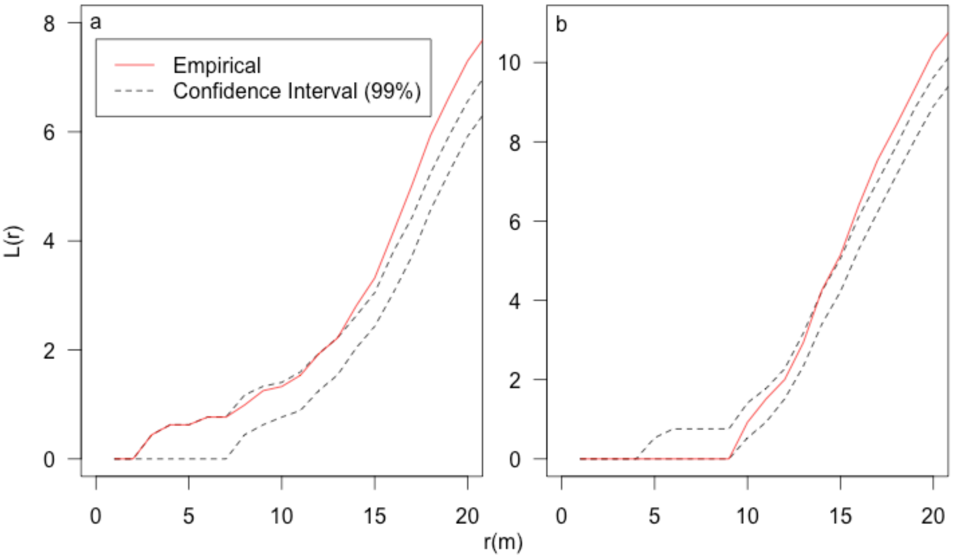
Figure S2



Results of the L(r) function. The solid red line, marking the empirical L(r) function, is greater than the 99% confidence envelopes in both (a) the High Plot and (b) the Low Plot for all distances above ca. 13 m, indicating attraction between species. Below 13 m, the empirical lines lie within the envelopes, indicating a random distribution between species.

Appendix S3: Experimental area and resampling procedure

Description of the experimental area

Pre-fire vegetation at both plots consisted of dense, ~40 year-old pine plantations, mainly with black pine (*Pinus nigra*) at the Low Plot and Scots pine (*P. sylvestris*) at the High Plot. Both pine species were commonly used in past decades to establish a tree cover in long-deforested areas in Sierra Nevada. They are native in Southern Spain but would not naturally occur at the study site; in fact, pine regeneration after the fire was negligible (Leverkus et al. 2014).

The two plots were located on the same hill and had a dominant W/ SW aspect (Fig. S1). As a consequence, the incident solar radiation was roughly similar between plots (calculated in ArcGIS from a Digital Elevation Model for the day of summer solstice), although it was somewhat greater in the High Plot due to a slight W/NW aspect at the Low Plot (Table 1, Fig. S1).

Between April and May 2006 (some eight months after the fire), the Forest Service implemented three treatments that differed in the management of the burnt wood: (1) Non-Intervention (NI), where no action was taken; (2) Partial Cut plus Lopping (PCL), where ca. 90% of burnt trees were cut and felled, with the main branches lopped off but leaving all the biomass in situ; (3) Salvage Logging (SL), where trees were cut and the trunks cleared of branches with chainsaws and piled, leaving a landscape devoid of branches and with a low habitat complexity (Leverkus et al. 2012, 2013). Each of the study plots contained nine subplots, which constituted three randomly-located replicates of each of the above-mentioned treatments. These subplots had similar size (3.1 ± 0.2 ha), which did not significantly differ between treatments (Kruskal-Wallis test; $P > 0.05$). Where trees remained standing, they fell throughout the second (13.3%), third (83.5%), and fourth (98.3%; cumulative values) year after the fire, and thus there were virtually no standing trees by 2010 (the year of planting) in any of these treatments (Marañón-Jiménez 2012). The present study was conducted in the context of these treatments. During planting operations, the excavator moved the fallen logs (where present) to create open 2-m bands where it could pass through, and the seedlings were introduced in 80 x 80 x 80 cm holes dug by the machine. As a result, the surface immediately surrounding the seedlings was similar across burnt-wood management treatments, consisting basically in an open area with little competing vegetation or coarse woody debris.

Although the original design also considered the management of the burnt wood, our statistical analyses were conducted considering only *Species* and *Elevation* (i.e. Plot) as independent variables because this study focuses on the response of two oak species to different elevation. We consider this to be correct because seedlings were intentionally planted in a wide area at each elevation (ca. 25 ha) in order to encompass the environmental variability affecting seedlings at the plot scale. Besides, the seedlings of both species were intermingled across each plot (see Fig. 1 of the manuscript and Appendix S2 for spatial analysis), and thus we were able to use individual seedlings as replicate units. Because seedlings were not harvested in identical numbers across treatments for each species and plot, we carried out a resampling procedure to eliminate potential confounding effects.

Resampling procedure: Methods

We harvested a different number of seedlings in each burnt-wood management treatment from each species x plot combination (Table S2). Consequently, in case this management variable had any influence on the parameters we measured, data analysis could potentially suffer from confounding effects. In this study we aimed to study the effect of planting at different elevation on two oak species. As we did not aim to contrast the effect of the management variable for the present work, this means that an equal amount of samples from each treatment for each species x elevation combination needed to be used in analysis. To achieve this we carried out a resampling procedure. In each of 10,000 permutations we randomly chose a number of individuals per treatment equal to the minimum number available for that species and plot. The GLM and ANOVA described in the *Statistical analyses* section of the main text were carried out in each of these permutations, and the F-values were extracted and averaged across all the permutations. We then calculated the corresponding P-values based on the average F-values and the appropriate degrees of freedom (Table 2 of the text). Similarly, we calculated Pearson´s product-moment correlation coefficients in each permutation, and with the average of these values and the appropriate degrees of freedom we calculated the P-values shown in Table 3 of the text. The means and standard errors presented in the paper are also the means of the values obtained in the permutations. The number of seedlings used in the statistical analyses after resampling can be found in Table S2.

References for Appendix S3

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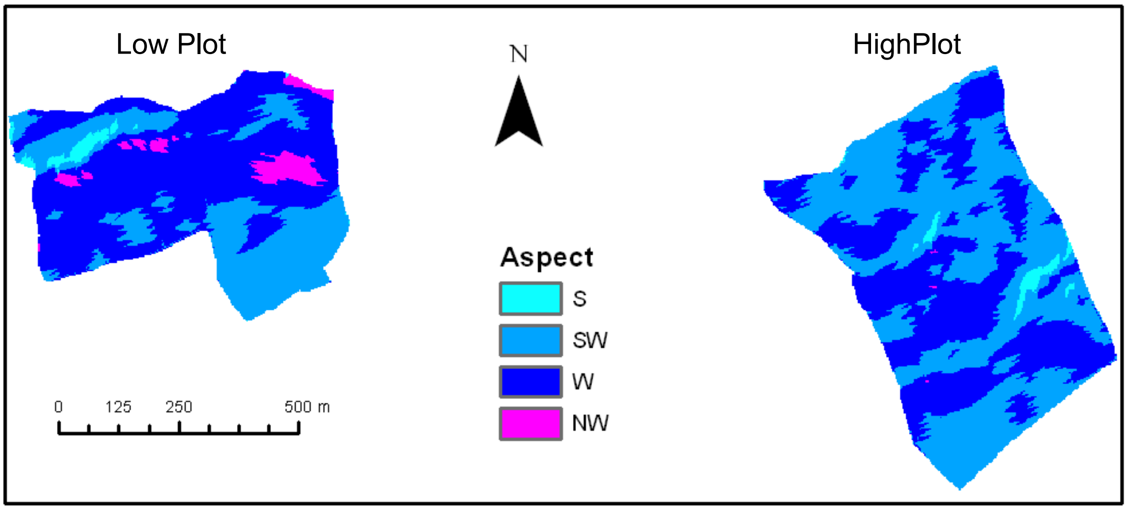
Figure S1



Within-plot variations in aspect. The map was created on the basis of a digital elevation model, which was in turn interpolated from 10 m topographic contour lines. The distance between the plots in the figure is at the same scale as the plots.

Table S2

Number of seedlings available (within parentheses) and used for analyses after resampling (outside parentheses)

	Low Plot		High Plot	
	Q. ilex	*Q. pyrenaica*	*Q. ilex*	*Q. pyrenaica*
Seedling survival				
NI	214 (218)	183 (210)	180 (198)	167 (197)
SL	214 (214)	183 (210)	180 (229)	167 (222)
PCL	214 (217)	183 (183)	180 (180)	167 (167)
Total	642 (649)	549 (603)	540 (607)	501 (586)
Harvested seedlings				
NI	29 (30)	15 (19)	30 (30)	14 (25)
SL	29 (29)	15 (15)	30 (31)	14 (14)
PCL	29 (35)	15 (17)	30 (30)	14 (20)
Total	87 (94)	45 (51)	90 (91)	42 (59)

Chapter 5

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Post-fire salvage logging alters a key plant-animal interaction for forest regeneration

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Running head: Salvage logging hampers oak colonization

Abstract

Post-fire salvage logging is widely implemented worldwide, but there is an increasing concern about its potential impact on the ecosystem. Moreover, there is scant information about the effect of salvage logging on ecosystem processes mediated by species interactions. We manipulated a burnt pine forest to experimentally analyze the effect of burnt-wood management on the colonization of Holm oak (*Quercus ilex*) mediated by acorn dispersal by Eurasian jays (*Garrulus glandarius*). Three replicates of three treatments were established in an 18-ha plot: salvage logging (SL), non-intervention (NI), and partial cut plus lopping (PCL; felling and lopping most of the trees but leaving all the biomass *in situ*). We hypothesized that different burnt-wood management could alter jays' landscape perception and thus the pattern of seed dispersal and seedling recruitment. We monitored jay abundance in each treatment for three winters and three breeding periods, and jay flights of potential acorn dispersal between nearby oak trees and the treatments. We also searched for oak seedlings recruited in the experimental plot for five years following the fire. Jays were recorded significantly more times (87%) in NI, and movements to this treatment during the acorn dispersal period were also more frequent (81% of the flights). Oak seedlings were also more abundant in NI (ca 55%) than in SL or PCL (ca. 25% each), despite a strong effect of small remnants of live pines. The results show that the burnt forest, if unsalvaged, still provides a suitable habitat for jays, while salvage logging reduces the strength of this key plant-animal interaction for oak natural regeneration. Non-intervention policies after a forest fire therefore provide the opportunity for adaptive management that helps reduce restoration costs and increase the resilience of the system.

Keywords: *Garrulus glandarius*; jay-oak interaction; oak colonization; *Quercus ilex*; resilience; salvage harvesting; seed dispersal; Sierra Nevada National Park; succession.

Introduction

After a forest fire it is customary that the local forest service (whether directly or through private counterparts) removes the burnt logs from the site, a process that is referred to as salvage logging and that often involves the elimination of the remaining woody debris such as branches and snags by chopping, mastication, etc. (McIver & Starr 2000; Lindenmayer et al. 2008). Post-fire salvage logging is widely implemented worldwide (McIver & Starr 2000; Van Nieuwstadt et al. 2001; Lindenmayer & Noss 2006; Mavsar et al. 2011), and renders a landscape devoid of most of the forest biomass and a simplification of the post-fire habitat (Lindenmayer et al. 2008; Bros et al. 2011). Several reasons are invoked to support this practice, coming from economics (return of economic capital of wood), silvicultural (*e.g.* greater ease of future reforestation, reduction of fire and pest risk), visitor safety, or even aesthetics (McIver & Starr 2000; Lindenmayer et al. 2008; Mavsar et al. 2011). Many of these reasons are, however, controversial (e.g. Castro et al. 2011), and an increasing number of studies are showing that salvage logging may have strong negative impacts on ecosystem processes, such as a reduction of the natural capacity for the regeneration of tree species (Donato et al. 2006; Castro et al. 2011), lesser diversity of plant and animal communities (McIver & Starr 2000; Castro et al. 2010a), or increases in soil erosion and watershed runoff (Beschta et al. 2004; Karr et al. 2004; Lindenmayer et al. 2008). Consequently, there is a growing appeal for the implementation of post-fire policies of non-intervention or less aggressive intervention, on the basis of the evidence that snags and decaying burnt wood are components of natural systems that promote ecosystem recovery and diversity (Beschta et al. 2004; Lindenmayer et al. 2004; DellaSala et al. 2006; Castro et al. 2010a).

The analysis of the effect of salvage logging on organisms has largely focused on its impact on diversity or on specific groups of species, whereas its effect on ecosystem processes has been focused on abiotic factors such as microclimate, hydrology, erosion, or nutrient cycling (Lindenmayer et al. 2008; Marañón-Jiménez & Castro 2012). However, very little is known about the effect of salvage logging on ecosystem processes mediated by species interactions. It is well known that animal species are affected by intermediate to severe disturbances that modify habitat structure and complexity (e.g. Cody 1985), including the removal of dead trees (e.g. Hutto 2006; Relva et al. 2009; Castro et al. 2010a; Puerta-Piñero et al. 2010). The degree to which post-fire salvage logging changes the habitat could then be of great importance for key plant-animal interactions, as is the case with seed dispersal (Rost et al. 2009; Castro et al. 2010a; Rost et al. 2010). This can affect the resilience of the ecosystem in terms of the time needed for natural regeneration after fire. The way in which post-fire management affects these interactions will determine the success or failure of other important ecosystem services such as ground cover, carbon fixation, or the scenic view of the landscape, among others (Millennium Ecosystem Assessment 2005; Lindenmayer et al. 2008; Serrano-Ortiz et al. 2011).

In this study, we experimentally analyze the effect of burnt-wood management on the interaction between a tree (the Holm oak, *Quercus ilex* L.) and its main seed disperser (the Eurasian jay, *Garrulus glandarius* L.). Oaks are major components of forests in the Holarctic (Archibold 1995; Breckle 2002). Jays are the main disperser of the oaks as well as other *Fagaceae* species (Bossema 1979). Jays move and cache an enormous amount of acorns during the fall for later consumption, with dispersal distances that average several hundred meters and can reach up to a few kilometers (Kollmann & Schill 1996; Gómez 2003; Pons & Pausas 2007). Part of the cached acorns are not consumed for several reasons (e.g. cached in excess, forgotten, or the death of the jay that cached them), and can therefore emerge as seedlings (Kollmann & Schill 1996; Pulido & Díaz 2005). Furthermore, jays move and cache a large fraction of acorns into conifer forests, either natural or planted (Mosandl & Kleinert 1998; Gómez 2003). As a result, it is common to find an oak seedling and sapling bank in the understory of coniferous forests due to jay dispersal, provided that both jays and mature oaks are present in the area (Mosandl & Kleinert 1998; Lookingbill & Zavala 2000; Puerta-Piñero et al. 2012a).

In September 2005, the "Lanjarón" fire (Sierra Nevada, SE Spain) burned a pine stand located mostly in the potential domain of the Holm oak. The landscape surrounding the burnt pine forest has small clusters of Holm oak as well as isolated individual trees that survived the fire (Fig. 1). Working in cooperation with the local Forest Service, we established three experimental treatments that differed in the post-fire management of burnt trees, ranging from the common salvage logging to non-intervention. We hypothesize that the burnt forest, if not salvaged, might still be a suitable habitat for jays to move and hide acorns, as the basic habitat structure of the forest still persists (high density of standing logs and a relatively high habitat complexity in the overstory), while in the salvaged areas the activity of jays will be reduced given that it is devoid of tree remains. This might translate as an impact of the conventional salvage logging on the natural colonization capacity of the oaks, with potential implications for post-fire colonization of oaks and forest regeneration in large areas of the planet. Our specific objectives are to determine whether: 1) post-fire burnt-wood management alters habitat selection by jays; 2) acorn dispersal by jays is affected by salvage logging; and 3) this behavior translates in differences in the pattern of seedling recruitment among management treatments.

Methods

Study system and experimental design

The study site was located in Sierra Nevada Natural and National Park (SE Spain), where in September 2005 the Lanjarón fire burned *ca.* 1,300 ha of pine reforestations planted 35 to 45 years ago for forestry purposes (mainly soil protection). A plot of 17.8 ha (UTM x,y position at the centroid: 456070, 4089811) was established at 1477 m a.s.l. in the burnt pine stand. At this elevation, oak forests are considered the climax vegetation according to edaphic and climatic properties as well as historical records (Valle 2003). Pine species present in this plot were *Pinus pinaster* and *P. nigra* (Castro et al. 2010b). The area surrounding the experimental plot is dominated by shrublands and patches of almond and chestnut orchards, with scattered individuals and small clusters of mature Holm oak trees that did not burn (Fig. 1).

From 21 April 2006 to 10 May 2006 (*ca.* seven months after the fire), the Forest Service implemented three replicates of three treatments in the plot, following a random spatial distribution: 1) "Non-Intervention" (NI), leaving all of the burnt trees standing. The trees fell in the course of consecutive years (mostly during the winter). Cumulative tree fall rate (measured in February of each year) was 0.0% by 2006 and 2007, 13.3±0.3% by 2008, 83.5±4.0 by 2009, and 98.3±1.0 by 2010 (measured from 100 marked trees per replicate, mean±SE in all cases; Castro et al. 2010b). Thus, the NI treatment kept a vertical structure of standing trees until autumn 2009. 2) "Partial Cut plus Lopping" (PCL), a treatment where *ca*. 90% of the burnt trees were cut and felled, with the main branches also lopped off, but leaving all the cut biomass *in situ* on the ground. 3) "Salvage Logging" (SL), trees were cut and the trunks cleaned of branches with the use of chainsaws. Trunks were manually piled (groups of 10-15) and the woody debris was masticated using a tractor with a mechanical masticator. The three treatments therefore differed in the degree of intervention (maximum in SL, minimum in NI) and in the habitat structure generated (low vertical structure in SL, intermediate in PCL, and highest in NI), parameters that may affect habitat selection by jays. Replicate size (2.0 ha in average) was similar among treatments (Kruskal-Wallis test, $P>0.05$). Pine density before treatment implementation was 1477±46 individuals per hectare (mean±SE; estimated by counting the number of trees in four 25x25 m quadrats per experimental replicate two months after the fire) and did not differ among treatments. Tree size (basal trunk diameter) was 17.7±0.2 cm (estimated for 30 random trees per quadrat, thus 120 trees per replicate) and did not differ among treatments either (Castro et al. 2010b).

Salvage logging is the usual post-fire action taken by the local Forest Service, and it was fully implemented throughout the rest of the surrounding burnt area where the experimental plot was located, including the removal of trunks with a log forwarder. The plan was also to remove the trunks with a log forwarder from the experimental SL treatment. However, the Forest Service eventually cancelled this last step due to difficulties in operating machinery within the spatial arrangement of the experimental replicates. Thus, the logging operation performed in the experimental SL treatment was less intense than the usual salvage logging. On the other hand, small patches of partially burnt but live pines remained after the fire and survived through the rest of the study period (Fig. 1). In particular, there were patches of live pines totaling 0.95 ha in replicate 1 of treatment NI, 0.30 ha in replicate 2 of treatment NI, and 0.26 ha in replicate 1 of treatment SL (Fig. 1). This was expected to affect habitat selection by jays given their preference for conifer forest to hide acorns (Bossema 1979; Pons and Pausas 2007).

Holm oak acorns are dispersed in the area from October to December, mainly by the Eurasian jay (Gómez 2003), and acorns emerge as seedlings through the following spring. Small rodents such as *Apodemus sylvaticus* and *Mus spretus* are acorn dispersers to a lesser extent (Muñoz & Bonal 2007; Gómez et al. 2008), although with a low average distance (below 5 m; Gómez et al. 2008). In addition, rodents finally depredate most (up to 98%) of the acorns they handle (Gómez et al. 2008; Puerta-Piñero 2010). Acorn dispersal by rodents to distances of more than several dozen meters is therefore negligible at the landscape level compared to jay dispersal (Muñoz & Bonal 2007; Pons & Pausas 2007; Gómez et al. 2008; Puerta-Piñero 2010). In our experimental plot, the mean distance between replicates and the nearest oak patches was 452.4 m, and the minimum distance was 41.0 m, which is further than what would be expected from dispersal by rodents (Fig. 1); thus, we may consider that the seedlings found in the experimental plot originated from acorns dispersed by jays.

Habitat selection by jays

We monitored habitat selection by jays by point censuses during breeding and winter periods. We located one sampling point at the center of each replicate of each treatment, and used it permanently as the sampling point. A total of 252 censuses (84 per treatment; 6 min per census) were made during six sampling periods: three autumn-winters (2006, 2007, and 2008; “winters”, hereafter) and three breeding seasons (2007, 2008, and 2009), distributed as follows: 4 censuses for the first winter, 6 censuses for the first breeding season, 5 censuses for the second and third winter and second breeding season, and 3 censuses for the third breeding season. We conducted the winter censuses from November to February, and breeding season censuses during May and June. We assessed jay abundance by either visual location or hearing, recording all the individuals detected within the limit of the experimental replicate during the time of census. We considered only jays that were stopped within the limits of the corresponding replicate at the moment of census (thus ignoring those that flew across). Counts started three minutes after the arrival of the observer to each of the sampling points. We only performed censuses under good weather conditions, without rainfall and with low or no wind (Bibby et al. 1992).

Acorn dispersal by jays

We sampled the spatial pattern of acorn dispersal by jays across treatments in 2008 by observing jay flights during the natural dispersal period (mid-October to mid-November). Two observers (communicating by radio) were simultaneously placed in two strategic positions at a distance that allowed the visual covering of the entire plot and surrounding Holm oak patches, as well as the tracking of flights (Fig. 1). Any jay flight to the plot, from the plot, or between surrounding vegetation was followed with binoculars and noted. Sampling was done during six days, from October 25 to November 13, coinciding with the period of maximum acorn dispersal. They started at 8:00 am (solar time) and lasted for 3-4 hours, depending on jay activity, and only under good weather conditions (without rainfall and with low or no wind). For the observations of jays in the present study, we stayed at sufficient distances to monitor a large area and to track flights to experimental treatments. This precluded the observation of acorn transport in the beak or the gut in some cases. Nonetheless, jay flights from oak patches to other sites in this period imply acorn dispersal in most of the cases (Gómez 2003; Puerta-Piñero et al. 2012a), so we considered such flights as putative acorn dispersal. Some of the flights occurred between the experimental plot and oak patches located close to the plot (Fig. 1; Appendix 1). For those cases, we later calculated flight distances with GIS (as the distance between the centroid of the oak patch and the centroid of the replicate). Mean distance from Holm oak patches to experimental replicates was 373.2±24.2 m, and did not differ among treatments (Kruskal-Wallis test; $\chi^2 = 0.20$, df = 2, p = 0.90).

Holm oak seedling recruitment

We monitored Holm oak seedling recruitment throughout the plot from spring to early summer 2006 to 2010. To accomplish this, we thoroughly searched the surface of each treatment replicate every year, and we marked and noted UTM coordinates of any new seedling (sensu lato, see below) with a GPS system. Holm oak seedlings have the ability to resprout after a fire (Rodrigo et al. 2004). Thus, the 2006 seedlings corresponded either to dispersal in 2005 (thus after the fire but before treatment implementation) or to resprouts of seedlings that were present in the understory before the fire. Because it was difficult to unequivocally differentiate these two categories, we marked them as a single category (2006 cohort). In any case, it is clear that all of them originated from acorns dispersed before treatment implementation, so they were not used for analysis. Seedlings found in spring 2007-10 correspond to acorns dispersed the previous autumn, all after treatment implementation. For seedlings from 2007 onwards, the soil around the root was excavated when necessary to confirm the presence of attached acorn or cotyledon marks as a test of its recent emergence.

Data analysis

We analyzed habitat selection by jays with a chi-square goodness of fit test using the sum of all censuses per replicate. Potential acorn dispersal by jays was analyzed with two complementary approaches. First, the total number of flights to the experimental plot or from the experimental plot was analyzed with a chi-square test. Second, for those dispersal movements from oak patches to the plot (and thus with known starting and ending point), we used a generalized linear mixed model (glmm) with poisson errors. We constructed and step-wise simplified a full model with treatment, the distance between each oak patch and the experimental replicates, and their interaction as fixed factors. We considered oak patch (three patches were present) as a random factor. Likelihood ratio tests allowed testing for the significance of the change in log-likelihood obtained by the deletion of a term, which would justify the retention of this term in the model. In the minimum adequate model only significant terms were retained. An observation-level random term was included in the model to test for overdispersion. The total number of seedlings in each experimental replicate (seedling recruitment) was also analyzed with a glmm with poisson errors, using burnt-wood management treatment and proportion of replicate area covered by live pines as fixed factors. To account for temporal pseudoreplication, we allowed for a random effect of year on each replicate (with replicates nested within treatments). We further ran the model excluding from the experimental replicates the area of live pine patches and the seedlings they contained in order to explore the results reducing the potential interference of live pines. For this purpose, we similarly used a glmm with the same random effects structure, but with only the factor treatment. Model simplification and overdispersion testing was carried out as described above. Statistical analyses were carried out in R (R Development Core Team 2011), with the use of the package lme4 (Bates et al. 2011).

Results

Habitat selection by jays

A total of 23 jay records were made through the three sampled years, 20 of them in the NI treatment (0.25 records per 6 min census), 3 in PCL (0.04 per census), and zero in SL ($P<0.001$). For the NI treatment, no significant differences were found between periods (winter versus breeding season) in the number of records, nor were there differences among replicates (9, 5 and 6 records for replicates 1, 2 and 3, respectively; $P>0.05$).

Acorn dispersal by jays

We registered a total of 167 jay flights (Appendix 1), of which 63 were arrivals to the experimental plot and 51 were departures. Among movements into the plot, jays entered the NI treatment in 81.0%, PCL in 15.9%, and SL only in 3.1% of the cases ($P<0.001$). Jays similarly departed NI in most of the cases when leaving the experimental plot (92.2% of the cases; Appendix 1). A total of 28 flights were registered from nearby oak patches to the experimental plot (Appendix 1) with a known departure and arrival point. Distance from the oak patches to the experimental replicates did not significantly influence the number of jay flights in a specific route, nor did the treatment by distance interaction. Only the factor treatment affected the number of flights (Table 1), supporting that jays positively selected the NI treatment.

Holm oak seedling recruitment

A total of 244 seedlings emerged after treatment implementation during the four years of study (28, 38, 140 and 38 in the years 2007-2010, respectively; Fig. 2, Appendix 2). Seedlings were more abundant in NI (66.0% of the seedlings) than in PCL (11.5%) or SL (22.5%), although treatment was not a significant factor in the model (Table 2; Fig. 2). The presence of live pines affected post-treatment seedling distribution, as the proportion of replicate area covered by live pines significantly determined the number of recruited seedlings (Table 2; Fig. 2). When seedlings under live pines were excluded from the analysis, the model still did not show a significant effect of treatment on number of recruited seedlings, although significance improved considerably (Table 2). The lack of significance for seedling recruitment could be related to the large variability in number of seedlings among replicates and years. In fact, if data from the replicates were pooled, the number of seedlings greatly differed among treatments, with the highest proportion of seedlings encountered in NI (52.0%), followed by SL (26.0%) and PCL (22.0%; Chi-squared test, d.f.=2, $P<0.01$).

Discussion

The analysis of the different phases involved in Holm oak colonization of burnt areas supports a strong concordance between habitat selection by jays for foraging across seasons, potential acorn dispersal, and new seedling establishment in the treatment with no post-fire intervention. Jays preferentially used the non-intervention treatment during both the winter and the breeding seasons, still showed a clear preference for movements into this treatment during the acorn dispersal period, and their caching behavior led to the emergence of more seedlings (52% of the total, excluding those below live pines) in non-intervention than in the other treatments. By contrast, salvage logging reduced the natural recruitment of new oaks, as it created a habitat not used by the main seed disperser (Castro et al. 2010a). Furthermore, it is likely that the conditions of our experimental salvage logging even produced an over-estimation of the role of jays in the salvage logging treatment, as the permanence of trunk piles could have increased the use of this habitat for caching (see Rost et al. 2009, 2010 for a similar pattern for frugivorous, bird-dependent seed dispersal). In addition, seedling recruitment in the salvaged areas is largely dependent on the presence of live trees that survived the fire (either isolated or in small clusters), as those trees were highly attractive to jays. Patches of live pines might have similarly increased recruitment in replicates of non-intervention, but the results show that when seedlings below these patches were excluded from analysis the significance of the treatment improved considerably. In addition, the replicate of non-intervention that had no live pines registered more records for both jay habitat selection and jay flights during the dispersal period than all the replicates of the other treatments together (Table S1). Similarly, this particular non-intervention replicate contained more recruited seedlings than any replicate of the other two treatments when live pine patches were excluded (Table S2). Overall, the non-intervention treatment clearly had a positive effect on jay activity and oak recruitment.

It is well known that the Eurasian jay disperses acorns and other nuts to conifer forests (Gómez 2003), and that this interaction results in an effective oak recruitment in the understory of these forests (Mosandl & Kleinert 1998; Lookingbill & Zavala 2000). In fact, our results show a strong effect of small patches of live pines. However, the potential use of burnt forests by jays as a suitable habitat for foraging and acorn caching remained untested. Jay selection of live unburnt conifer forest for caching acorns seems to be related to the lower predation risk posed by their own predators, to the suitability of this forest type for breeding (when cached food is more crucial), or to the avoidance of competitors (intra or interspecific) for cached acorns (Andrén 1990; Rolando 1998). Furthermore, jays use visual cues (such as trunks or rocks) to select caching sites that can be memorized for future food recovery (Bennett 1993; Clayton & Krebs 1994; Lanner 1996). All of these characteristics may still be found in a burnt, unsalvaged forest: vertical habitat complexity and tree overstory which may reduce jay predation risk (as opposed to a salvaged area), enough distance to acorn sources to reduce competition, and a large number of visual cues (tree trunks) to hide acorns (see Castro et al. 2010a for similar results of jay habitat selection in the same burnt site across an altitudinal gradient). Our results therefore corroborate our working hypothesis as the burnt forest, if not salvaged, was a suitable habitat for jay activity, likely because of the habitat complexity still provided by the standing, burnt trees. By contrast, in the salvaged areas the activity of jays was reduced given that it was devoid of trees. The low selection by jays of a treatment where most trees were cut and lopped (PCL treatment) supports the relevance of keeping a vertical structure of trees (even burnt) for jay habitat selection.

The maintenance of the jay-oak interaction after a fire provides the opportunity for adaptive management that helps reduce restoration costs. The ecological and economic role of jays has been demonstrated for oak forest expansion and maintenance at a landscape level (Mosandl & Kleinert 1998; Gómez 2004, Hougner et al. 2006; Purves et al. 2007; Puerta-Piñero et al. 2012b). In our study, the result of the post-treatment activity of jays, spanning only five years after the fire, resulted in the recruitment of 23 oaks per hectare in the NI treatment (sum of oak seedlings divided by the surface of the three replicates). Although low, we should consider that this is the net result after different post-dispersal processes occur, such as seed predation by other predators (that was in fact high in the area during the study years; Puerta-Piñero et al. 2010), germination, or emergence (Gómez 2004; Puerta-Piñero 2010). In addition, the maintenance of the burnt, standing trees after the fire helps to increase the resilience of the system, as it provides a mechanism to accelerate succession and the long-distance colonization and regeneration of the burnt area. Many *Pinaceae* members from the Palaearctic cannot resprout and do not form serotinous cones that resist fire (*e.g.* most *Pinus* species, *Picea abies*, *Larix decidua* or *Abies* spp.; see Richardson 1998 for *Pinus*), therefore relying on seed dispersal (usually of dozens of meters; *e.g.* Debain et al. 2007) for regeneration. Jays disperse nuts to larger distances, and thus might accelerate the recovery of a tree cover in burnt coniferous forests.

The effect of post-fire burnt-wood management on the jay-oak interaction reported here might also be common to millions of hectares in the world where oak and conifer forests coexist. First of all, the Eurasian jay is the main disperser of *Quercus* species as well as other *Fagaceae* (e.g. *Fagus* spp.) throughout the Palaearctic Region (Bossema 1979). Second, *Pinaceae* and *Fagaceae* species (either oaks or beech) are also species that comprise main forests in the Palaearctic, very often with large ecotone areas between them (Archibold 1995; Breckle 2002). Finally, the positive selection by jays of non-intervened burnt forest is probably a consequence of their niche requirements, as suggested above. Thus, it is likely that an outcome similar to that reported in this study will also apply to large areas of Eurasia wherever mature oak (or other *Fagaceae*) trees (whether forests or scattered individuals) are in contact with a burnt conifer forest.

In conclusion, our results demonstrate that post-fire salvage logging negatively affects a key, positive plant-animal interaction for forest regeneration. Different post-fire treatments altered jay behavior in terms of seed dispersal, which subsequently altered the spatial pattern of seedling recruitment. Recent studies are showing that salvage logging alters other interactions as well, such as herbivory (increasing its impact after log removal; Relva et al. 2009), ungulate-wolf interaction (Hebblewhite et al. 2009), or seed dispersal by frugivorous birds (Rost et al. 2009, 2010). All this supports that salvage logging may interfere with a wide array of species interactions, adding to the growing body of evidence that shows its potential impact at the ecosystem level.

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Table 1. Results for number of acorn-dispersal flights, i.e. flights from nearby oak patches to the experimental replicates during autumn 2008.

	Number of flights		
Explanatory variable	F	df	P
Distance[a] [†] * Treatment[‡]	0.22	2	0.81
Distance	0.43	1	0.52
Treatment	10.76	2	**<0.0005**

Note: Reported values refer to the changes in log-likelihood obtained by the elimination of the explanatory variable from the model. The minimal adequate model contained only treatment as a fixed factor. Ad hoc analyses showed that among treatments only NI significantly differed from the other two treatments. In the model, 95% confidence intervals showed no significant oak patch-related random effect on jay flights, so the results shown are for a glm with quasipoisson errors. Among the 28 analyzed flights, 24 were to NI, 3 to PCL, and only 1 to SL.

[†] Distance from the oak patch (flight starting point) to the experimental burnt-wood management replicates (arrival point).

[‡] Burnt-wood management treatments are: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

Table 2. Results for number of seedlings recruited in the experimental treatments, for the total amount of seedlings (Total) and for those excluding the seedlings found under live pines (see Fig. 1).

		Number of seedlings		
	Explanatory variable	Chisq	df	P
Total	Treatment[†]	0.26	2	0.88
	Proportion live pines[‡]	5.54	1	**<0.02**
Excluding seedlings under live pines	Treatment	3.80	2	0.15

Note: Reported values refer to the changes in log-likelihood obtained by the elimination of the explanatory variable from the model. The minimal adequate model contained only the proportion of replicate area covered by live pines as a fixed factor, as well as the random term (a random intercept and slope of sampling year for each experimental replicate).

[†] Experimental burnt-wood management treatments: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

[‡] Percentage of area covered by patches of live pines in a particular experimental replicate, calculated using GIS.

Figure legends

Figure 1. Orthorectified aerial photograph of the study plot two years after the fire. The polygons indicate the boundaries of the experimental treatment replicates: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL). One of the clusters of unburnt oaks that did not burn and that are acting as seed source into the study plot is indicated by the red circle. Some trees within the plot partially burned during the fire but survived. As a result, clusters of live pines finally remained in replicates 1 and 2 of NI, and replicate 1 of SL, indicated in the figure by the dashed lines. Green trees in the top left corner mainly correspond to chestnut *Castanea sativa* trees. Photo courtesy of the National Park of Sierra Nevada.

Figure 2. Percentage of seedlings recruited in the different treatments. Note that jays and other predators consume a huge proportion of the cached acorns, so the reported seedlings are the net result of the mutualistic interaction between jays and the Holm oak. Numbers above columns indicate the total percentage of seedlings per treatment. Treatments are: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL). Under live pines refers to seedlings located in patches of pines that survived the fire within the replicates of the experimental treatments; these patches were located in 2 replicates of NI and 1 replicate of SL (see Fig. 1 and Appendix 2).

Figure 1

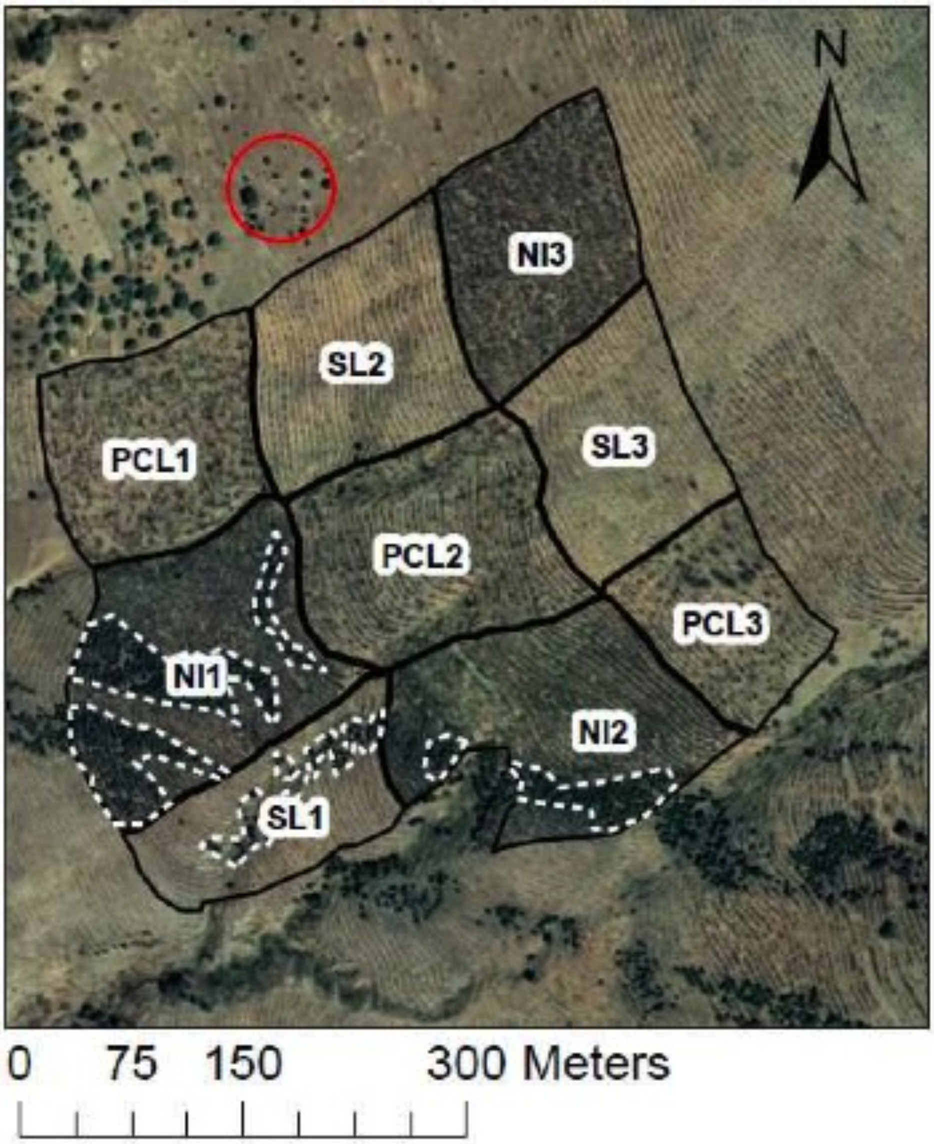
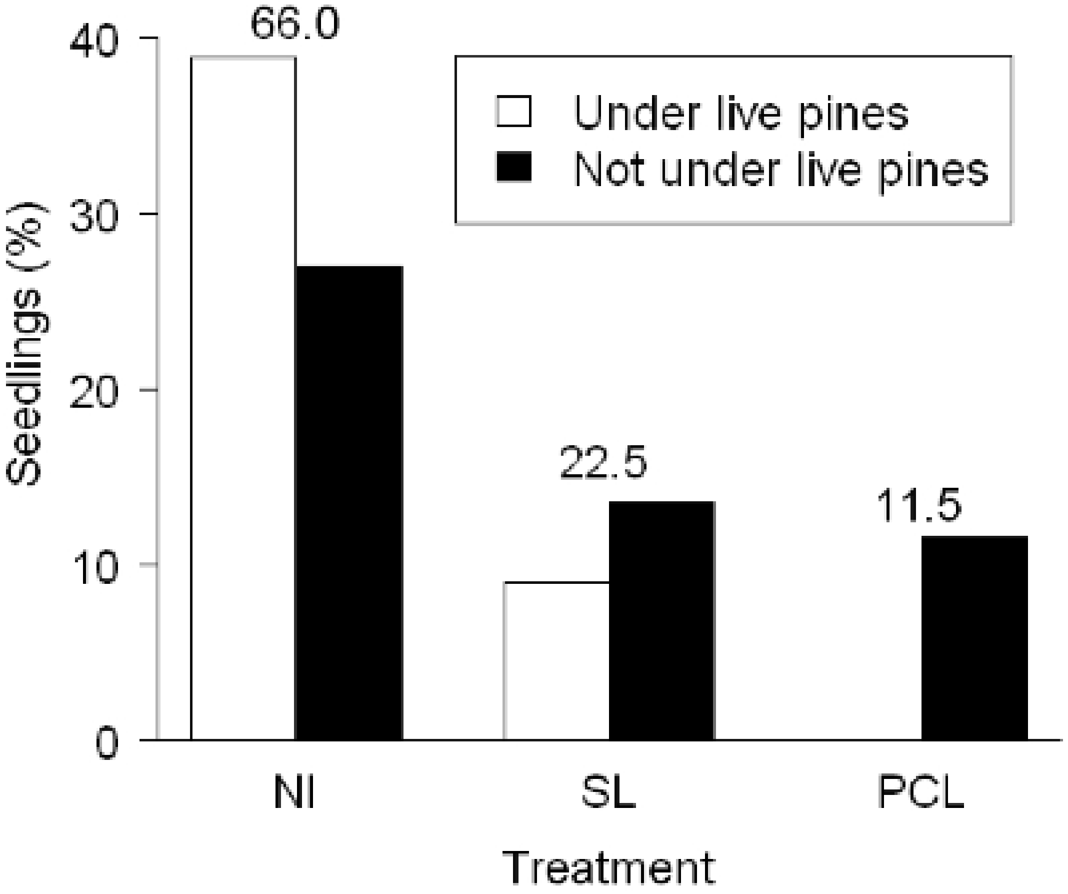


Figure 2


66.0
Under live pines
Not under live pines
Seedlings (%)
40
30
20
10
0
22.5
11.5
NI
SL
PCL
Treatment

Appendix 1. Summary of the flights of jays during the acorn-dispersal period in autumn 2008.

Site	Arrivals	Departures	Arrivals from oak patches[#]
Treatment NI[†]	**51**	**47**	**24**
NI-1	27	26	12
NI-2	13	9	6
NI-3	11	12	6
Treatment PCL[†]	**10**	**4**	**3**
PCL-1	1	0	0
PCL-2	7	4	2
PCL-3	2	0	1
Treatment SL[†]	**2**	**0**	**1**
SL-1	2	0	1
SL-2	0	0	0
SL-3	0	0	0
Subtotal experimental plot[‡]	63	51	28[††]
Subtotal Oak patches	51	60	5
Subtotal other vegetation patches[§]	44	19	22
Total[¶]	158	130	55

Note: We recorded a total of 167 flights, which we divided into arrivals and departures from/ to the experimental plot, oak patches, and other vegetation patches.

[†] Sums of the three replicates of each treatment (underneath). Treatments are: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

[‡] Sum of NI, PCL, and SL.

[§] Flights among patches outside the experimental plot or the oak patches. These movements were mostly to live pine patches not affected by the fire, and to almond tree and chestnut orchards.

[¶] Arrival or departure was unknown in some of the flights, so the totals are below 167 (the total number of flight registered).

[#] These arrivals are a subset of the total arrivals.

[††] These were acorn-dispersal flights from oak patches to the experimental plot with known departure and arrival points (thus with known flight distances). These are the data used for analysis shown in Table 1.

Appendix 2. Total numbers of seedlings from acorns dispersed by jays after the fire in each experimental replicate during the sampling period, lasting four years (acorns dispersed from autumn 2007 to autumn 2010).

Treatment[†]	Replicate	Altitude (m a.s.l.)	Replicate area (ha)	Area covered by live pines (ha) [‡]	Total seedlings	Seedlings under live pines[§]
NI	1	1432	2.62	0.95	122	85
NI	2	1486	2.42	0.30	14	10
NI	3	1533	1.89	0.00	25	0
PCL	1	1430	1.88	0.00	11	0
PCL	2	1474	2.32	0.00	16	0
PCL	3	1516	1.29	0.00	1	0
SL	1	1432	1.46	0.26	42	22
SL	2	1474	2.06	0.00	6	0
SL	3	1522	1.73	0.00	7	0

[†] Burnt-wood management treatments are: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

[‡] Three of the nine replicates had patches of live pines: NI-1, NI-2, and SL-1 (see Fig. 1).

[§] Subset of the total seedlings in each replicate that were found under live pines. These were zero in the replicates that did not have patches of live pines.

Chapter 6

Shifting demographic conflicts across recruitment cohorts in a dynamic post-fire Mediterranean landscape

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Summary

1. Demographic conflicts in plant ontogeny arise when habitats favour certain stages of recruitment but disfavour others, and spatial heterogeneity may induce different demographic conflicts across the landscape.
2. We asked whether a dynamic, heterogeneous landscape might produce temporal shifts in the demographic conflicts experienced by successive cohorts of naturally recruited plants due to ongoing changes in habitat features. As early successional habitats are characterised by rapid change, we used a burnt pine afforestation in southern Spain to study the recruitment and performance of a late-successional tree species (*Quercus ilex*) across seven years in four replicated post-fire habitats. These differed in structure and included patches of unburnt forest and three management alternatives of burnt trees: salvage logging, partial cutting, and non-intervention.
3. Some oaks resprouted after the fire and were mainly located near major acorn sources; in contrast, post-fire oak seedling emergence was greatest in habitats with standing live or dead trees, likely due to habitat selection by European jays, *Garrulus glandarius,* for dispersal. The dead pines gradually collapsed and reduced their suitability for dispersal, so subsequent seedling cohorts mainly recruited within patches of live pines.

4. The live pines generally enhanced the survival of oak seedlings and resprouts located underneath their canopy but greatly reduced their growth as compared to the other post-fire habitats, thus representing a demographic conflict that was absent elsewhere.
5. As a consequence of the shift in the preferred habitat for dispersal, oak seedlings from successive cohorts experienced a gradual improvement in their likelihood of survival but a reduction in growth. The progressive increase in this demographic conflict hinged on the reduction in the presence of vertical structures in the habitat with dead pines.
6. *Synthesis* Oak seedling recruitment success was the result of a complex scenario that involved temporal variation in the direction of seed dispersal and spatial variation in habitat suitability for seedling establishment and growth. Temporal changes in habitat structure in dynamic, heterogeneous landscapes can change the direction of seed dispersal and lead to shifts in the demographic conflicts affecting plant recruitment across seed/seedling cohorts.

Keywords

Plant ontogeny, life-stage conflicts, plant demography, seed dispersal, succession, pine plantation, directional change

Introduction

Plant recruitment is a complex process mediated by interacting biotic and abiotic factors that act across different ontogenetic stages (Fenner and Thompson, 2005; Gómez-Aparicio, 2008). The physical structure of habitats may affect processes such as seed dispersal, seedling establishment and sapling growth in different ways. For example, habitats with a low plant cover may yield high survival to post-dispersal seed predators yet low seedling survival due to high solar irradiance, leading to the uncoupling of demographic stages of recruitment (Gómez, 2004; Pérez-Ramos et al., 2012; van Ginkel et al., 2013). Spatial heterogeneity may cause habitats within the same landscape to show different suitability for different recruitment stages, and potentially different trade-offs between the performance of plant ontogenetic stages across the landscape (Jordano and Herrera, 1995; Schupp, 1995; Gómez, 2004; Pulido and Díaz, 2005; Pérez-Ramos et al., 2012).

From the perspective of a recruitment cohort, the microhabitats that favour the transition from one phase of the cycle to the next will define the probabilities of occurrence of the next transition. As a consequence, the habitat features that actually affect demographic processes may constitute only a subset of those existing in the landscape. For example, directional acorn dispersal by European jays (*Garrulus glandarius* L.) into forests, a common process across Eurasia (Bossema, 1979; Mosandl and Kleinert, 1998; Gómez, 2003), may ultimately result in the reduction of the amount of solar irradiance under which oak seedlings emerge as compared to the available light conditions in the landscape (Gómez et al., 2004), and this can strongly affect seedling emergence, survival and growth (Zavala et al., 2000; Gómez et al., 2004; Espelta et al., 2005). Although much has been learnt about how different habitats affect different stages of plant recruitment and how demographic filters acting heterogeneously across the landscape may define the conditions for the next demographic stage (Louda, 1983; Schupp, 1995; Wenny, 2000; Pulido and Díaz, 2005), most studies on this topic do not consider the effects of ongoing habitat modifications, as they are usually conducted in scenarios where a range of habitats are tested simultaneously (e.g. Herrera et al., 1994; Pulido and Díaz, 2005) or are constrained to short-term changes such as those of fluctuating weather conditions (e.g. Wenny, 2000; Quero et al., 2011). As a consequence, we still know little about how temporal changes in dynamic habitats may translate into different habitat suitability for recruitment and potentially into different conflicts across plant ontogeny for successive recruitment cohorts. Increasing our understanding of such processes may help predict patterns of plant recruitment in rapidly-shifting habitats.

The initial years after large disturbances are considered among the most dynamic for ecosystem processes. Rapidly-changing conditions affect both abiotic components involved in seedling establishment, such as light or nutrient availability (DeLuca et al., 2002; Ward et al., 2014), and biotic components such as competition or habitat selection by seed dispersers and predators (Keith and Bradstock, 1994; Dafni et al., 2012). In addition, disturbances create spatial heterogeneity (Noss et al., 2006), which may contribute to defining the timing and trajectory of succession in plant communities (Frelich and Reich, 1995; Franklin et al., 2000; Christensen Jr, 2014). Further, post-disturbance management has the potential to affect biological legacies and their associated spatial and temporal patterns (Lindenmayer et al., 2008; Peterson et al., 2009), which may produce additional variation and ultimately trigger new successional pathways (Purdon et al., 2004; Macdonald, 2007; Leverkus et al., 2014). Post-disturbance ecosystems are thus characterised by spatially and timely variable features that may affect plant recruitment, and subsequent management can induce further changes.

In this study we aimed to investigate the effects of dynamic, early-successional habitats in a heterogeneous landscape on different stages of the recruitment of the Holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.), which forms forests around much of the western Mediterranean Basin. We monitored oak recruitment across seven years in an experimental landscape consisting of a burnt, even-aged pine afforestation adjacent to patches of unburnt, acorn-producing Holm oaks. Four distinct habitats were created within this landscape, consisting of unburnt patches of pines plus three post-fire management treatments that modified habitat structure. Given that European jays are the main dispersers of acorns, and that their selection of habitat for dispersal is largely determined by habitat characteristics (Bossema, 1979; Mosandl and Kleinert, 1998; Gómez, 2004), we hypothesised that (1) the emergence of oak seedlings would differ across post-disturbance habitats. As these habitats generated different abiotic conditions and oak seedlings show enhanced survival under moderate shade due to the alleviation of hot and dry summer conditions in Mediterranean-type ecosystems (Zavala et al., 2000; Gómez, 2004; Puerta-Piñero et al., 2007), we also hypothesised that (2) seedling survival would be higher in habitats with a surviving canopy cover. Shade, if excessive, may limit the growth and development of Holm oak seedlings (Espelta et al., 1995), so we hypothesised that (3) post-disturbance habitats would affect the growth of the surviving seedlings. Further, we expected that (4) the effect of habitat upon recruitment would change across time due to ongoing changes in habitat characteristics. Overall, we expect the resulting patterns in the emergence, survival and growth of the different cohorts of post-fire Holm oak seedlings to be a function of the temporally variable suitability of the existing habitats for different stages of recruitment. In brief, this study aims to investigate how the patterns of plant recruitment are modulated by the transient dynamics of habitat features.

Methods

Study site

The study was carried out in the Sierra Nevada Natural Park (SE Spain), where in September 2005 the Lanjarón fire burned ca. 1,300 ha of 35 to 45 year-old pine afforestations. An experimental plot of 17.8 ha was established at 1477 m a.s.l. in the burnt pine stand (37º 57' N, 3º 29' W). At this elevation, Holm oak forests are considered the climax vegetation according to edaphic and climatic conditions as well as historical records (Valle 2003). The pine species present in this plot were *Pinus pinaster* and *P. nigra*, two native species that, however, do not grow naturally in the area and lack resprouting capacity. Shrublands and patches of almond and chestnut orchards dominated the area surrounding the experimental plot, including scattered individuals and small clusters of mature Holm oak trees that did not burn (Fig. 1). The plot was SW-oriented and had an average slope of 30.3% and micaschist as bedrock. Climate is typical Mediterranean, with warm, dry summers and mild, rainy winters. Mean annual rainfall is 501.1 ± 48.8 mm (values are mean ± 1 SE throughout the text; 1988-2011), of which only 4.7 +/- 1.3 mm correspond to July-August. Mean yearly minimum and maximum temperatures are 6.8 ± 0.2ºC and 17.1 ± 0.2ºC, respectively (1981-2010).

Experimental design

In April 2006, nine adjacent subplots of 2.0 ± 0.2 ha were established in collaboration with the local Forest Service (Fig. 1). Each subplot constituted one in three replicates of one of three post-fire management treatments differing in habitat structure. Some patches of surviving pines covered ca. 1.5 ha across three of these subplots and were left standing (Fig. 1). These patches of surviving pines generated distinctive elements within the landscape, so we considered them as a fourth habitat type. As a result, there were three replicates of each of the following four post-fire habitats:

1) Non-Intervention (NI): no action was taken, thus leaving a dense stand of standing bunrt trees.

2) Partial Cut plus Lopping (PCL): ca. 90% of the burnt trees were felled, with their main branches lopped off but leaving all the cut biomass *in situ*, spread over the ground. The logs and branches initially covered some 45% of the ground surface (Castro et al., 2011).

3) Salvage logging (SL): all the burnt trees were cut and cleared of their branches with chainsaws. The trunks were piled in groups of 10-15, and the woody debris was mechanically masticated. This produced an open landscape devoid of coarse woody debris except for the trunk piles.

4) Surviving Pines (PIN): Patches of unlogged, surviving pines.

Pine density (1477 ± 46 individuals ha^{-1}; counted in 36 quadrats of 25 x 25 m) and basal trunk diameter (17.7 ± 0.2 cm; estimated from 30 random trees per quadrat, thus 120 trees per subplot) were homogeneous across the whole plot before treatment implementation. The treatments created four habitats that differed in vertical structure, a parameter that exerts a strong effect on the foraging behaviour of the main acorn disperser in the area, the European jay (Gómez, 2003; Castro et al., 2012). Moreover, the burnt trees in the NI and PCL habitats collapsed in the course of our study period (mostly during the winters). The cumulative fall rate of burnt trees was 0.0% in 2006 and 2007, 13.3 ± 0.3% in 2008, 83.5 ± 4.0% in 2009, 98.3 ± 1.0% in 2010 and 100% thereafter (always estimated in February from 100 marked trees per subplot in treatments NI and PCL). This induced yearly changes in the vertical structure of these habitats until 2010, when the last snags collapsed. Previous research, conducted when most of the burnt trees in NI remained standing, showed that jays dispersed acorns from the unburnt Holm oaks into the subplots after the fire, preferentially into the NI habitat (Castro et al., 2012). Flights to the patches of unburnt pines were not monitored in this study, but the positive selection of pine forest by European jays for acorn dispersal is well established (Mosandl and Kleinert, 1998; Gómez, 2003).

Figure 1. Aerial view in 2006 of the study plot, delimited by the white line. Triangles are located on the replicates of the Non-Intervention habitats, squares on Partial Cut plus Lopping, and circles on Salvage Logging. The polygons delimited in black are the patches of surviving pines (the PIN habitat), and the dashed black polygon at the upper left side indicates the location of unburnt holm oaks acting as seed sources for the plot. The parallel lines on the ground are terraces perpendicular to the slope, made to ease reforestation some 45 years previous to the study. All the terraced area was covered by a homogeneously-aged pine stand before the fire, and the burnt pines beyond the plot boundaries were salvage/ sanitation logged. Each side of the plot measured approx. 450 m. Photo courtesy of the Sierra Nevada National Park.

The nearest group of holm oaks acting as seed sources was located between 40 and 450 m from the edge of the plot, which constitutes adequate distance for dispersal by jays (Gómez, 2003; Pons and Pausas, 2007) but is too far for dispersal by rodents (Gómez et al., 2008). Besides, rodents appear to act primarily as acorn consumers, rather than dispersers, in the area (Gómez et al., 2008), so here we assume that all the post-management seedlings (see definition below) resulted from dispersal by jays.

Seedling recruitment

We monitored the recruitment of *Q. ilex* seedlings between spring and early summer of 2006 through 2012, for which we exhaustively searched the ground surface of the entire study plot, tagging each individual seedling and taking their GPS coordinates. We monitored seedling survival and measured stem height, base diameter and crown diameter in April 2012.

The seedlings that established each spring corresponded to acorns dispersed during the previous autumn. However, holm oaks have a strong resprouting capacity (Zavala et al., 2000), so the seedlings found in 2006 corresponded either to dispersal in autumn 2005 (i.e. after the fire but before treatment establishment) or to resprouting seedlings that were present in the understory before the fire. As we could not unequivocally distinguish these two origins, we labeled them all as *pre-management* seedlings. Some resprouting stems were fairly tall and clearly produced by an adult individual. As for this study we were interested in the recruitment dynamics at the seedling/sapling stage, we did not consider large resprouts and restricted the tagging to those individuals <35 cm tall at the time of first sampling. All the seedlings encountered from 2007 onwards were labelled as *post-management* seedlings.

Solar irradiance

To characterise solar irradiance in the post-fire habitats we took hemispheric photographs at 0.4 m above the ground. We used a horizontally levelled Canon Digital SLR camera with a Sigma 4.5 mm f/2.8 EX DC HSM circular fisheye lens. Photos were taken at dawn on the 20th and 27 th of May 2014, by when all the snags had fallen. We took 30 photographs at random locations beneath and another 30 outside the canopy of live pines; for the ones outside the canopy we considered 10 locations in SL, 10 in PCL and 10 in NI. From the images we obtained values of Global Site Factor (GSF) –which combines year-round direct and indirect solar radiation– with HemiView version 2.1.1 (Delta-T Devices Ltd., Cambridge, UK).

Statistical analyses

The following analyses were performed in R, vers. 3.1.1 (R Core Team, 2014).

We analysed the effect of post-fire habitats on GSF with one-way ANOVA and compared between-habitat differences with Tukey HSD tests.

To analyse the effect of post-fire habitats on the distribution of oak seedling recruitment we fitted point process models with the spatstat package

(Baddeley and Turner, 2005). This model considered a non-homogeneous Poisson process, with seedling density depending on post-fire habitat. The latter was included as a spatial covariate, with a raster image of the plot of 1 x 1 m pixels containing different values for each of the four post-fire habitats. This model was performed for all the seedlings together, the pre-management seedlings only, all post-management seedlings together, and each cohort of post-management seedlings independently (2007-12).

To study the effect of post-fire habitat on seedling survival we fitted generalised linear models (glm) with a binomial error structure (quasi-binomial to account for over-dispersion) for each cohort separately. The significance of the treatment factor was studied with analysis of deviance. The significance of individual contrasts between habitats was analysed by merging levels of the habitat factor, rerunning the model and comparing the two models (Crawley, 2013). The cohorts of 2006 to 2009 were analysed at this stage.

We tested the effect of post-fire habitat on seedling growth with one-way ANOVA. Response variables were the size values obtained in 2012 for stem height, base diameter and mean crown diameter. We report the data of seedlings of the cohorts recruited from 2006 to 2009.

Results

Solar irradiance

Post-fire habitat significantly affected solar irradiance ($F_{3,56}$= 96.9; $P < 0.001$). The GSF values under the canopy of surviving pines (0.42 ± 0.03%) were less than half than in any other habitat (0.94 ± 0.01% on average). However, there were no differences in GSF among the NI, SL and PCL habitats.

Spatio-temporal pattern of seedling recruitment

We found a total of 1217 Holm oak seedlings across the 7 years of study, which resulted in an average of 71.9 seedlings ha^{-1}. Of these, 64% were pre-management seedlings (including post-fire resprouts, which likely constituted the largest fraction). Seedling recruitment in subsequent years oscillated between 8 and 149 seedlings per year across the 18-ha study site (Fig. 2).

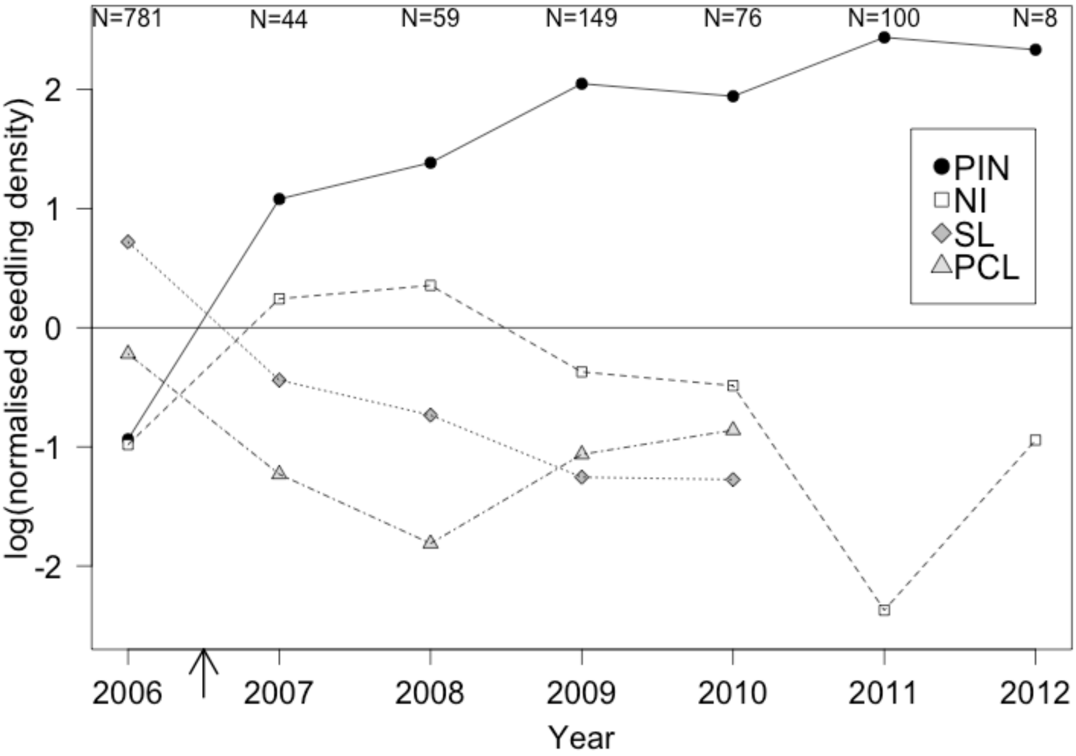

Figure 2. Normalised seedling density in the post-fire treatments for the recruitment cohorts of 2006 to 2012 (the fire occurred in 2005). Data points show the logarithm of the seedling density found in a given habitat and year divided by the average seedling density across habitats in that year (the latter is indicated by the horizontal line at y = 0). There was no recruitment in the SL and PCL habitats in 2011 and 2012. Values at the top are the number of seedlings recruited each year across the study area. The arrow under the X axis shows the timing of post-fire management. Note the change in the distribution of seedling recruitment among habitats from 2006 (pre-management seedlings) to 2007 (post-management seedlings). Post-fire habitats were: PIN = Pines (patches of pines that survived the fire and were left standing); NI = Non-Intervention; SL = Salvage Logging; PCL = Partial Cut plus Lopping.

The spatial pattern of all oak seedlings (including pre- as well as post-management seedlings) was not homogeneous, as the model considering a non-homogeneous Poisson distribution with post-fire habitat as covariate performed significantly better than a model with a homogeneous distribution (Chisq = 520.46, P<0.001). The non-homogeneous model also performed best when analysing the seedlings found in each year separately. However, the direction and magnitude of the spatial pattern of recruitment changed over time. The 2006 pre-management seedlings were mainly encountered near the main acorn sources, as 61% of them were located in the three plots that were closest to the unburnt patches of mature oaks (Fig. 3a). The NI and PIN habitats were associated with significantly lower pre-management seedling densities than SL or PCL (Table 1; note though that this result is a statistical artefact, as the treatments were applied *after* the emergence of these seedlings and had no effect on their densities; it is reported only for comparison between the spatial pattern of pre-management and post-management seedlings).

Table 1. Effect of post-fire habitats on the density of Holm oak seedlings encountered each year

		Post-fire habitat †		Contrasts with NI					
				PIN		SL		PCL	
Seedling cohort	N	X^2	P	Zval	P	Zval	P	Zval	P
2006	781	415.98	***	1.04		16.10	***	5.82	***
07-12	442	748.67	***	18.93	***	-3.06	**	-5.17	***
2007	41	17.52	***	1.62		-1.09		-2.74	**
2008	58	51.88	***	3.46	***	-2.20	*	-3.51	***
2009	159	240.37	***	10.50	***	-1.99	*	-2.65	**
2010	76	106.93	***	7.45	***	-1.14		-1.07	
2011	100	386.62	***	7.77	***	0.29		-0.01	
2012	8	28.62	***	2.93	**	0.00		0.00	

† Habitats were: NI = Non-Intervention; PIN = Surviving Pines; SL = Salvage Logging; PCL = Partial Cut plus Lopping

Once the post-fire habitats were established, the spatial distribution of newly recruited oak seedlings changed dramatically. The density of all post-management seedlings, recruited between 2007 and 2012, was lowest in the SL and PCL plots and greatest in the PIN plots (Table 1; Figs. 2, 3b) despite the latter being the furthest away from the seed sources (Fig. 1). Moreover, the effect of post-fire habitat on seedling recruitment also changed over time for post-management seedlings. The NI habitat exerted a positive effect on oak seedling recruitment compared to the PCL and/or SL habitats in the first years after post-fire management (2007-09; Table 1), but there was no significant difference among these three habitats after 2009. From 2008 onward, the density of newly recruited seedlings was significantly greater in the PIN than in the NI, PCL or SL habitats (Table 1; Fig. 2). The magnitude of this effect consistently increased until in 2011-12 the density of newly recruited oak seedlings under live pines was one order of magnitude greater than in the rest of the area (Fig. 2). As a result, the study site ended up having different clusters of recruited oaks, some due to the presence of young oaks previous to the fire and others due to post-fire seed dispersal (Fig. 3c).

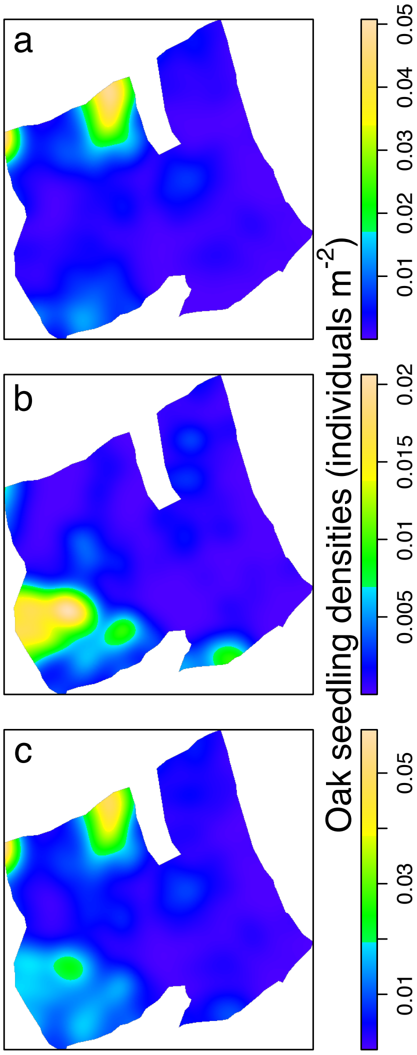

Figure 3. Kernel-smoothed seedling densities encountered in the study area for a) pre-management seedlings, b) post-management seedlings, and c) all seedlings combined. The maps show the intensities of the point pattern generated by seedlings within the plot. The change in the overall spatial pattern of recruitment between pre- and post-management seedlings is evidenced by comparing maps a) and b). A portion of Replicate 2 of SL, which was next to the mature oaks that acted as seed sources, was removed from monitoring and analysis due to very high densities of pre-management seedlings, likely resprouts.

Effect of post-fire habitats on seedling survival and growth

Post-fire habitats significantly affected the survival of recruited seedlings encountered in 2006 and 2008 but not in 2007 or 2009 (Table 2). In 2006 and 2008, the highest survival was underneath the canopy of the surviving pines (Fig. 4). In 2008 the PCL treatment led to high survival too, although this was based on only three individuals (Table S1).

Table 2. Effect of post-fire habitat on Holm oak seedling survival and size in 2012

	Year of seedling encounter											
	2006			2007			2008			2009		
Response var.	df	F	P	df	F	P	Df	F	P	df	F	P
Seedling surv.	777	6.0	<0.001	40	2.7	0.06	55	5.4	<0.01	145	0.5	0.65
Stem diam.	439	15.2	<0.001	20	6.6	<0.01	23	6.4	<0.01	73	21.7	<0.001
Stem height	439	10.8	<0.001	20	9.9	<0.001	23	2.7	0.09	73	14.6	<0.001
Crown diam.*	439	18.4	<0.001	20	6.9	<0.01	23	1.7	0.21	73	16.4	<0.001

* Average of two perpendicular crown measurements

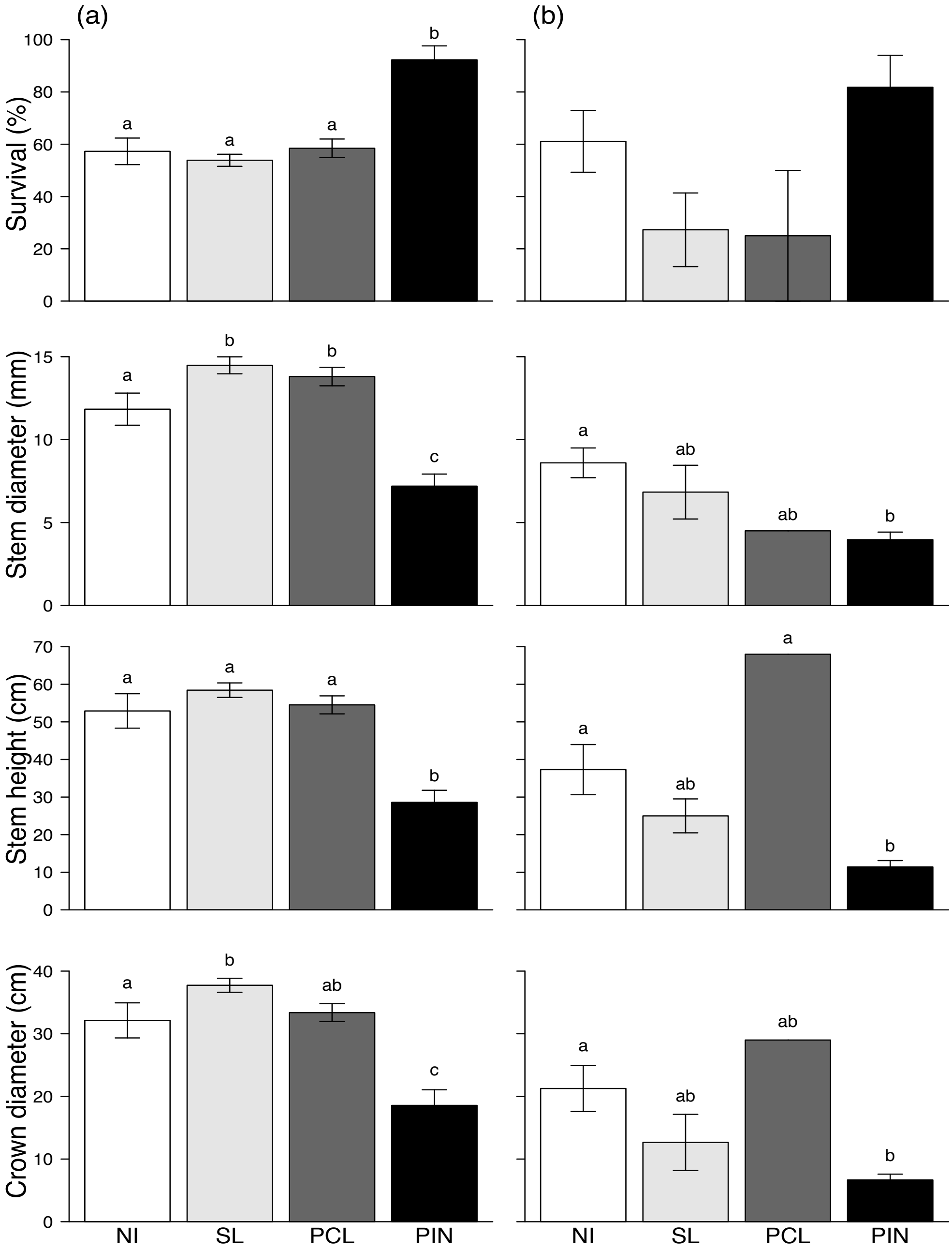

Figure 4. Average survival and size (measured in 2012) of the Holm oak seedlings/ saplings encountered in (a) 2006 and (b) 2007 across post-fire habitats. While most of the 2006 oaks were likely to be resprouting individuals that were present before the fire, the 2007 seedlings emerged from acorns dispersed in 2006 and were 5-year-old saplings at the time of measurement. Post-fire habitats are: NI= Non-Intervention; SL= Salvage Logging; PCL= Partial Cut plus Lopping; PIN= Surviving Pines. Error bars indicate ± 1 SE. Letters above the bars indicate significant between-habitat differences after post-hoc tests. The values for these and the 2008 and 2009 seedling cohorts, as well as the number of individuals across habitats, can be found in Table S1.

The PIN habitat had a negative effect on final stem diameter for the seedlings of each of the analysed cohorts (2006-09; Table 2; Fig. 4; Fig. 5). The PIN habitat also negatively affected stem height and crown diameter for seedlings of all cohorts except for the 2008 cohort. Mean values for seedling survival and size for each treatment for the first two cohorts (the pre-management plants of 2006 and the 2007 cohort) are shown in Figure 4, and for all the analysed cohorts (2006-09), including the significance of the contrasts between treatments, are shown in Table S1.

Figure 5. Specimens of Holm oaks recruited in 2007, thus after the fire, a) in an open area and b) under the canopy of pines that survived the 2005 fire. The photos were taken in 2013.

Discussion

We found heterogeneous Holm oak recruitment across the studied post-fire landscape as a result of spatiotemporal disparities in habitat features. Two kinds of biological legacies affected the densities of juvenile oaks seven years after the fire: first, resprouting individual oaks; and second, the habitat structure generated by standing live and dead trees, which generated new spatial and also temporal demographic patterns. The presence of live trees yielded high oak seedling recruitment throughout the study period, while the standing dead trees had a similar positive, but timely limited effect on recruitment due to their gradual collapse. Most of the resprouts and seedlings recruited in early years were located out of the post-fire canopy of live pines, where they showed moderate survival yet adequate growth. In contrast, the seedlings under live pines, which gradually increased in proportion throughout the study period, showed enhanced survival yet lesser growth. Our study thus shows a shift in the demographic filters encountered by different recruitment cohorts. It also highlights the importance of studying plant recruitment not only across different ontogenetic stages but also with explicit consideration of timely habitat shifts in order to understand the mechanisms underlying plant recruitment, especially in rapidly-changing environments such as forests shortly after disturbance.

Spatial patterns of seedling recruitment

After a stand-replacing disturbance, biological legacies from the past ecosystem set the scene for plant regeneration (Franklin et al., 2000; Lindenmayer et al., 2008; Christensen Jr, 2014). In our study, two main kinds of post-fire legacies affected the densities of juvenile oaks. First, oak individuals that survived the fire and resprouted accounted for about two thirds of the juvenile oaks that we found. Inherent to this legacy was the spatial distribution of the resprouts, which was strongly skewed towards the subplots located near the main acorn sources. This distribution was likely due to the important yet limited dispersal distances covered by European jays, the main acorn dispersers in the area (Gómez, 2003; Castro et al., 2012) and, in general, in the Palaearctic (Bossema, 1979; Mosandl and Kleinert, 1998; Pulido and Díaz, 2005). As a consequence, oak seedling densities within pine plantations tend to decline nonlinearly with distance to mature oaks (Gómez-Aparicio et al., 2009), and this was likely the baseline condition in our study area before the fire.

A second kind of biological legacy, namely standing live and dead pines, affected oak demographic processes. Seed dispersal by European jays was likely still the main mechanism for colonisation after the fire (Castro et al. 2012). As jays are forest dwellers (Bossema, 1979; Pons and Pausas, 2008), they tend to direct their dispersal towards areas with high tree cover, especially coniferous forest (Gómez, 2003; Pons and Pausas, 2007). Our results show that, once heterogeneous habitats were created after post-fire management within the burnt plantation, oak seedling recruitment was positively associated to the habitats with standing live or dead trees. The standing trees attracted seed dispersal by jays (Castro et al. 2012), leading to patches of high oak densities far away from the mature Holm oaks. This contrasts with the resprouts, which emerged from acorns dispersed mainly near acorn sources when all the area was covered by a homogeneous pine afforestation. As a consequence, there was a strong shift between the spatial distribution of resprouts and that of seedlings dispersed after spatially heterogeneous post-fire habitat structures were created by the fire and subsequent management.

Temporal patterns of recruitment

We observed a shift between the distribution of different cohorts of post-management seedlings, which derived from the different persistence in time of standing dead and live trees. The standing dead trees in the NI habitat had a similar positive effect on oak seedling recruitment as the live trees in PIN during the first years, but their gradual collapse led the positive effect of the NI habitat to decrease over time and ultimately vanish, likely because the vertical habitat structure preferred by jays disappeared (Castro et al., 2012). Another factor that may have gradually reduced oak recruitment in NI is that the trees that collapsed generated a complex habitat structure that induced high levels of acorn predation by rodents (Leverkus et al., 2013, 2015), a major demographic filter for oak recruitment (Herrera, 1995; Pulido and Díaz, 2005; Gómez et al., 2008; Pérez-Ramos et al., 2012; Rey Benayas et al., 2015). The abundance and activity of rodents may have increased as a consequence of the protection provided by the lying logs (Puerta-Piñero et al., 2010; Leverkus et al., 2013, 2015). As a result, the collapse of the standing snags gradually reduced habitat suitability for acorn dispersers and enhanced the suitability for acorn consumers, thus triggering a directional reduction in the recruitment of oaks in the NI plots. In contrast, the reduction of dispersal in NI may have had an indirect positive effect on dispersal to areas of live pines, where an increasingly greater proportion of seedlings emerged during and after the collapse of the dead trees.

Ontogenetic conflicts

Another fundamental difference between the effects of standing live and dead trees on oak demography was that the patches of live pines generally enhanced oak seedling survival but reduced their growth as compared to the rest of post-fire habitats. Greater survival was likely a result of alleviated summer temperatures in the shade, as summer drought strongly limits oak seedling establishment and survival in Mediterranean landscapes (Rey Benayas et al., 2005; Castro et al., 2006; Gómez-Aparicio et al., 2008; Mendoza et al., 2009a; Pérez-Ramos et al., 2012; Rey Benayas et al., 2015). The amelioration of these conditions may lead to greater probabilities of survival through reductions in evaporation, photo-inhibition and carbon starvation in young Holm oak seedlings (Zavala et al., 2000; Rey Benayas et al., 2005). On the contrary, competition from adult pines had a strong negative influence on the growth of oak seedlings recruited beneath their canopy, as these seedlings were much smaller than those recruited elsewhere. Besides providing shade, dense pine stands are highly water demanding (Maestre and Cortina, 2004). Pines have a shallow but extensive root system, and water deficit beneath them can even be greater than outside their canopy under dry conditions (Valladares and Pearcy, 2002). Another common feature of dense pine stands is a reduction in light availability –in this study the pines reduced global solar irradiance to half. Thus, although the Holm oak is shade tolerant and indeed benefits from moderate shade in its early life stages (Espelta et al., 1995; Zavala et al., 2000; Gómez, 2004; Espelta et al., 2005), the shade of dense canopies limits growth (Espelta et al., 2005; Mendoza et al., 2009b), and this trade-off has also been found in other studies (Zavala et al., 2000; Pérez-Ramos et al., 2012; Galiano et al., 2013).

As the emergence of seedlings showed temporal variability across post-fire habitats and habitats affected the physical environment, the different oak seedling cohorts were subject to different conditions that could affect their performance. The seedlings recruited during the early years after the fire were mostly located outside the canopy of live pines and, as a consequence, they showed moderate survival rates and strong growth. In contrast, in later years the seedlings emerged mainly under the canopy of live pines (a trend that is likely to continue for some years/decades), and they showed enhanced survival but little growth. As a consequence, there was a shift in the ontogenetic conflict experienced by seedlings: from a greater likelihood of dispersal to areas less favourable for survival but more favourable for growth to a greater likelihood of dispersal to areas more favourable for survival but less favourable for growth. In summary, our results show that seed dispersal effectiveness (*sensu* Schupp et al., 2010) may change through time in heterogeneous environments, and its explicit consideration may provide finer resolution to understand the mechanisms underlying the successional patterns.

Disturbance, succession and windows of opportunity for oak forest regeneration

Tree plantations are globally recognised as habitats where natural succession is often arrested (Cannell, 1999; Maestre and Cortina, 2004; Brockerhoff et al., 2008; Gómez-Aparicio et al., 2009; Ruiz-Benito et al., 2012). In particular, pine plantations like the one studied here occupy thousands of hectares in the Mediterranean Basin, have a high risk of fire propagation and hence present strong management challenges (Maestre and Cortina, 2004; Pausas et al., 2004a, 2004b; Gómez-Aparicio et al., 2009). In such ecosystems, which are usually dominated by a dense, mono-specific and even-aged stand, plants remaining as legacies of past ecosystems and processes mediated by seed dispersers offer an opportunity for succession (Gómez-Aparicio et al., 2009; Zamora et al., 2010; Navarro-González et al., 2013), provided that canopy gaps are opened at some stage to allow the competitive release of the understory. Our study shows that oaks remaining as legacies and dispersal from nearby oaks may yield a high potential for the naturalisation of the stand, provided that disturbance such as fire or other kinds of gap openings create a window of opportunity for the regeneration of oaks.

Beyond its consideration as a disturbance with large negative connotations, fire could act as the necessary mechanism for the colonisation and persistence of oaks in such landscapes. Active policies of fire management (such as prescribed fires) in landscapes where both seed sources (mature oaks) and mutualistic organisms (jays) are present may provide the basis for oak forest restoration. Habitat heterogeneity, obtained by variable fire intensities and post-fire management techniques, and in other cases variable pre-fire conditions, may prove valuable to enhance different stages of tree recruitment in Mediterranean landscapes.

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Supporting Information

Table S1. Average survival and size (measured in 2012) of seedlings

Seedling cohort	Habitat*	N †	Surv (%)	N ‡	Stem diam. (mm) ¶	Stem height (cm)¶	Crown diam. (cm) ¶
2006	NI	96	57.3 a	55	11.8 ± 1.0 a	52.9 ± 4.6 a	32.1 ± 2.8 a
	SL	464	53.9 a	250	14.5 ± 0.5 b	58.9 ± 1.9 a	37.7 ± 1.1 b
	PCL	195	58.5 a	114	13.8 ± 0.6 b	54.5 ± 2.4 a	33.4 ± 1.4 ab
	PIN	26	92.3 b	24	7.2 ± 0.7 c	28.6 ± 3.2 b	18.6 ± 2.5 c
2007	NI	18	61.1	11	8.6 ± 0.9 a	37.3 ± 6.7 a	21.3 ± 3.7 a
	SL	11	27.3	3	6.8 ± 1.6 ab	25.0 ± 4.5 ab	12.7 ± 4.5 ab
	PCL	4	25.0	1	4.5 ab	68 a	29 ab
	PIN	11	81.8	9	4.0 ± 0.5 b	11.4 ± 1.7 b	6.7 ± 0.9 b
2008	NI	27	40.7 a	11	7.1 ± 0.9 a	30.3 ± 5.5	14.1 ± 1.9
	SL	9	0.0 b	0	-	-	-
	PCL	3	66.7 a	2	10.0 ± 1.0 a	17.0 ± 2.0	16.3 ± 2.3
	PIN	20	65.0 a	13	4.8 ± 0.4 b	18.9 ± 2.6	10.4 ± 1.4
2009	NI	31	45.2	14	5.3 ± 0.6 a	22.0 ± 2.5 a	13.7 ± 2.5 a
	SL	11	63.6	7	5.7 ± 0.8 a	23.3 ± 4.0 a	11.8 ± 2.0 ab
	PCL	13	61.5	8	9.6 ± 1.0 b	37.4 ± 5.7 a	23.4 ± 4.5 b
	PIN	94	51.1	48	3.5 ± 0.2 c	13.1 ± 1.2 b	6.7 ± 0.6 c

* Post-fire habitats are: NI = Non-Intervention; SL = Salvage Logging; PCL = Partial Cut plus Lopping; PIN = Surviving Pines

† Total number of plants monitored

‡ Number of plants surviving until 2012

¶ Values are mean ± 1SE; letters indicate significant differences according to post-hoc Tukey's Honest Significant Difference tests

Appendix I

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(54) Título: **Dispositivo protector de semillas ante depredadores**

(57) Resumen:

Dispositivo protector de semillas ante depredadores.

La presente invención consiste en un dispositivo o contenedor para proteger semillas alojadas en su interior ante depredadores como roedores u otros vertebrados de mayor tamaño, que comprende una pieza contenedora, en cuyo interior se coloca la semilla, caracterizado porque dicha pieza contenedora tiene forma sensiblemente piramidal o troncocónica, seccionada por un plano paralelo o no a su base.

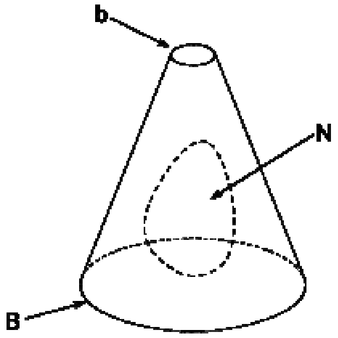


Figura 1

ES 2 428 943 B2

Aviso: Se puede realizar consulta prevista por el art. 40.2.8 LP.

DESCRIPCIÓN

DISPOSITIVO PROTECTOR DE SEMILLAS ANTE DEPREDADORES

SECTOR DE APLICACIÓN DE LA INVENCIÓN

La presente invención puede encuadrarse dentro de las prácticas y dispositivos que contribuyen a hacer más efectivas y rentables económicamente las operaciones de forestación o siembra de cualquier especie vegetal de interés cuyas semillas tengan una alta tasa de depredación. En particular, se refiere a un dispositivo que protege a las semillas colocadas en su interior ante depredadores de semillas como roedores o ungulados.

ESTADO DE LA TÉCNICA

Trabajos de forestación

La forestación o reforestación para la regeneración de la cubierta vegetal, o el cultivo de especies leñosas con fines agrícolas o agroforestales, es una actividad que afecta a una ingente superficie de terreno cada año a nivel mundial, y que involucra grandes sumas de dinero. Cuando la especie presenta un peso de semilla por encima de cierto límite (generalmente mayor de 1 g, ya sea la semilla propiamente dicha desde el punto de vista botánico o ésta acompañada de parte o conjunto del fruto) la siembra de semilla suele descartarse, especialmente en el sector forestal, en beneficio de la plantación de plantones previamente crecidos en vivero, debido fundamentalmente a que las semillas sembradas en campo sufren altas tasas de depredación por roedores u otros animales de mayor tamaño como jabalíes o cabras.

Sin embargo, la plantación de plantones de muchas especies arbóreas y arbustivas ha mostrado muchos problemas. Con frecuencia las tasas de supervivencia son bajas, y las plantas tienen tasas de crecimiento igualmente bajo y un desarrollo anómalo debido a problemas en el desarrollo de las raíces al pasar del contenedor en el que se transportan al suelo. Por el contrario, la siembra de semillas en campo da lugar, generalmente, a plantas vigorosas y con un buen desarrollo aéreo y radicular, por lo que resulta más ventajosa siempre que consiga evitar el impacto de los depredadores de semillas. A modo de ejemplo, las plantaciones que se realizan en España con especies del género *Quercus* muestran con frecuencia altas tasas de mortalidad y un escaso crecimiento de las plantas, mientras que la siembra de bellotas, si se logra impedir el ataque de los depredadores de semillas, rinde porcentajes de supervivencia muy altos (alcanzando generalmente valores entre el 50 y el 100%) y un desarrollo adecuado del juvenil. Nos encontramos así con la situación de que la siembra de semillas es un método muy apropiado para asegurar un adecuado crecimiento y desarrollo de las plantas (en particular árboles y arbustos) en relación a la plantación, pero presenta el problema de la alta depredación.

Dispositivos protectores de plantas y semillas ante depredadores

Para intentar solucionar el problema de depredación de semillas y plantas jóvenes se han desarrollado numerosos dispositivos.

Los inventores conocen diversos dispositivos para proteger a las plantas ante los depredadores o agentes meteorológicos, tales como los descritos en el modelo de utilidad ES1035385U o en la patente ES2137474T3, junto con otros tubos protectores, mallas protectoras, etc. cuya protección se limita a la parte aérea de la planta y están diseñados básicamente para proteger a los plantones. Otros dispositivos, como el descrito en la patente ES2015647, incorporan en su fabricación agentes activos de acción repulsiva contra los depredadores, pero se refieren igualmente a una estructura protectora para la parte aérea de la planta. También se conocen otros dispositivos destinados a la protección, en semillero, del tallo o parte aérea, como el descrito en el modelo de utilidad ES1054588U.

Sin embargo, apenas se ha prestado atención a la protección de las semillas (o frutos, en sentido amplio). Algunos dispositivos permiten encerrar semillas en su interior, como el descrito en la patente ES1048430, pero está completamente abierto por su parte superior y su base, de modo que no impide el acceso de los depredadores, y está concebido fundamentalmente para la protección de las raíces de las plantas ante la competencia de otras especies.

El único dispositivo, conocido por el solicitante, que tiene un objetivo claramente dirigido a las semillas es el descrito en la patente ES2383420. El dispositivo consiste en esencia en un cilindro que tiene una parte aérea mucho mayor que la parte subterránea, de modo que pretende solucionar tanto la depredación de semillas como, aparentemente, la herbivoría sobre la planta. Por otro lado, su uso en campo puede resultar engorroso, pues hay que colocar las semillas entre unos alambres y bloquear el acceso de los depredadores por la parte superior del cilindro con alguna estructura globosa que queda suspendida sobre la semilla. Además, la estructura descrita no parece fácil de transportar montada y, en caso de estar desmontada para su elaboración *in situ*, se requeriría mucho tiempo.

No obstante, el principal inconveniente que presentan este y otros dispositivos similares es que poseen una parte que sobresale del suelo para proteger la planta una vez la semilla germine. Con esta configuración, que produce un impacto visual considerable, el paso de los animales o cualquier otro factor que provoque la caída o inclinación del cilindro puede afectar negativamente al desarrollo del plantón y a su supervivencia.

OBJETO DE LA INVENCIÓN

La invención que aquí se describe permite proteger las semillas ante los depredadores una vez sembradas en campo, de modo que la semilla pueda germinar sin que sea depredada por roedores u otros vertebrados de mayor tamaño. Mediante el uso de la presente invención se podrá incrementar el éxito de establecimiento y reclutamiento de muchas especies forestales o de interés agronómico que sufren altísimas tasas de depredación post-siembra, pero para las que los métodos alternativos de regeneración (plantación de un plantón) no resultan exitosos por problemas de mortalidad de las plantas o de mal desarrollo de su sistema radicular. La invención ofrece una alternativa que será más exitosa para la forestación o el cultivo de árboles y arbustos y a menor costo, y potencialmente sería útil para millones de hectáreas en las que se desarrollan programas de forestación o reforestación, o de cultivos forestales a escala mundial.

La ventaja que aporta esta invención es enorme en el campo de la selvicultura, pues permite forestar usando semillas en lugar de plantones previamente cultivados en vivero. Esto es esencial para muchas especies arbóreas que se usan en forestaciones y reforestaciones, tanto en España como en el mundo, dado que suelen presentar semillas de gran tamaño, muy apetecibles por los depredadores (roedores o ungulados), que consumen prácticamente todas y por tanto anulan los esfuerzos de siembra. Sin embargo se conoce bien que muchas de estas especies tendrían mayor éxito de regeneración si se utilizasen semillas en lugar de plantones cultivados en vivero siempre y cuando se evite el problema de la depredación de semillas. El uso de esta invención permitirá por tanto tener más éxito en las forestaciones al tiempo que reducirá los costos.

La presente invención puede utilizarse también para la protección de semillas en el campo de la agricultura y en cualquier ámbito de las ciencias agroforestales en el que la siembra de semillas sea el mejor método para el desarrollo de la planta pero esté limitada por la actividad de los depredadores de semillas.

Por su configuración, la ubicación del dispositivo descrito en el terreno es totalmente subterránea (lo que elimina el impacto visual y reduce daños de los animales), es fácilmente transportable y manejable, e incluso puede comercializarse conteniendo ya la semilla de interés de modo que sólo haya que enterrarlo.

DESCRIPCIÓN DE LOS DIBUJOS

Las figuras presentadas en esta memoria tienen mero carácter ilustrativo y no limitativo.

Figura 1.- Representación esquemática de la pieza contenedora de un dispositivo protector de semillas de forma troncocónica. (B) representa la base mayor del tronocono y (b) la base menor. (N) representa la semilla situada en el interior del dispositivo.

Figura 2.- Representación esquemática de la pieza contenedora de un dispositivo protector de semillas ante depredadores con forma de tronco piramidal. (B) representa la base mayor del tronco piramidal y (b) la base menor. (N) representa la semilla situada en el interior del dispositivo.

Figura 3.- Representación esquemática del dispositivo protector de semillas enterrado. (N) representa la semilla situada en su interior antes de germinar, (X) representa la planta una vez que ha brotado y (R) representa las raíces de la planta.

Figura 4.- Representación esquemática de la pieza contenedora del dispositivo protector de semillas ante depredadores consistente en un elemento con forma de troncocono (C) que presenta una línea de apertura (L) que une la base mayor (B) con la base menor (b).

Figura 5.- Representación esquemática de la apertura del dispositivo protector tras el crecimiento de la planta. (C) representa la pieza contenedora del dispositivo y (X) representa la planta.

Figura 6.- Representación esquemática de la pieza contenedora de un dispositivo protector de semillas ante depredadores consistente en un troncocono (C) que presenta una línea de apertura (L) que une la base mayor (B) con la base menor (b). (T) representa una tapa que comprende una malla y se sitúa en la base mayor.

Figura 7.- Representación de una realización particular del dispositivo protector de semillas ante depredadores en la que (O) representa perforaciones en la pared de la pieza contenedora.

Figura 8.- Representación de una realización particular del dispositivo protector de semillas ante depredadores en la que (P) representa púas que se proyectan desde la pared de la pieza contenedora hacia fuera.

Figura 9. Representación de una realización particular del dispositivo protector de semillas ante depredadores en la que (O) representa perforaciones en la pared del troncocono y (P) representa púas que se proyectan desde la pared de la pieza contenedora hacia fuera.

Figura 10.- Representación esquemática de un dispositivo protector de semillas formado por dos elementos trococónicos, (C1) y (C2), unidos por su base mayor y su disposición en el terreno. (X) representa la planta una vez que ha brotado y (R) representa las raíces de la planta, que alcanzan mayor profundidad.

Figura 11.- Representación esquemática de un dispositivo protector de semillas formado por dos elementos trococónicos unidos por su base mayor y su disposición alterada en el terreno. (X) representa la planta una vez que ha brotado, (R) representa las raíces de la planta y (M) representa el túnel que escavaría un roedor.

Figura 12.- Representación esquemática de un dispositivo protector de semillas formado por una pieza contenedora (C1) a la que se le añade un elemento cilíndrico (C3) unido a su base mayor

Figura 13.- Representación esquemática de un kit que comprende el dispositivo contenedor de semillas (D), semillas (N) y un sustrato (S). (W) representa una bandeja.

DESCRIPCIÓN DE LA INVENCIÓN

A lo largo de la presente invención, se entenderá por "*semilla*" a la semilla propiamente dicha desde el punto de vista botánico (esto es, embrión, tejidos de reserva y cubiertas seminales) o a ésta junto a las partes del fruto con las que se disperse, maneje y/o comercialice, que es el caso de la mayor parte de las angiospermas.

Se entenderá por "*<u>parte superior del dispositivo</u>*" a la zona del mismo que, una vez enterrado, queda más cerca de la superficie.

Se entenderá por "*<u>pieza contenedora</u>*" un elemento cuya forma y dimensiones permiten colocar al menos una semilla en su interior.

Así, la presente invención consiste en un dispositivo o contenedor para proteger semillas alojadas en su interior ante depredadores como roedores u otros vertebrados de mayor tamaño, que comprende una pieza contenedora, en cuyo interior se coloca la semilla y en el que dicha pieza contenedora tiene forma sensiblemente piramidal o troncocónica (Fig. 1 y 2), seccionada por un plano paralelo o no a su base. De forma preferente, la forma geométrica de la pieza contenedora será un tronco cónico o piramidal con bases paralelas.

El dispositivo se coloca enterrado de forma que la base menor de dicha pieza contenedora queda ubicada más cerca de la superficie (Fig. 3).

El dispositivo y, particularmente la pieza mencionada, se confeccionarán preferentemente en un material biodegradable capaz de desintegrarse al cabo de unos meses, una vez que la planta haya crecido lo suficiente y no sea necesario proteger la semilla.

Además, la parte más ancha de su parte superior, correspondiente a la base menor, debe permitir la salida del tallo (Figura 3, **X**) en los primeros meses de crecimiento de la planta, y al mismo tiempo impedir la entrada de roedores u otros depredadores de pequeño tamaño que cavan alrededor de la semilla, **N**.

De forma particular, para permitir la salida del tallo e impedir la entrada de roedores u otros depredadores de pequeño tamaño que cavan alrededor de la semilla, el dispositivo se configura de forma que la mayor distancia entre dos puntos cualesquiera de la base menor, **b**, de la pieza contenedora, **C**, está comprendida entre 3 y 20 mm, preferentemente entre 5 y 12 mm. A modo de ejemplo, si la pieza contenedora tiene forma troncocónica, esa distancia se corresponderá con el diámetro de su base menor. Asimismo, se entiende que esta medida corresponde a la parte interior de la base menor de la pieza contenedora por lo que el grosor de esta pieza no influirá sobre esta característica.

En otra realización particular (Fig. 4), en la superficie de la pieza contenedora mencionada, **C**, se practica al menos un corte, rebaje o hilera de perforaciones o microperforaciones, en adelante "*línea de apertura*", **L**, desde la base mayor, **B**, a la base menor, **b**, para facilitar la rotura o apertura del contenedor (Fig. 5) cuando el tallo de la planta, **X**, que nace de la semilla, que brotará a través de la base menor, ejerza presión sobre dicha pieza contenedora. De esta forma, la planta quedará liberada del contenedor una vez que alcance el tamaño suficiente, y se evitará su estrangulamiento.

De forma alternativa, aunque conceptualmente equivalente, la pieza contenedora puede estar confeccionada a su vez por varias piezas unidas o que se pueden unir entre sí por medios que permitan una fácil separación, como hilos biodegradables, pequeños elementos plásticos que se puedan romper con la presión del tallo; o medios no permanentes de unión como puede ser un sistema de machihembrado a presión.

En una realización particular (Fig. 6), el dispositivo comprende además una tapadera perforada, rejilla o red de malla, **T**, situada en su parte inferior, correspondiente a su base mayor, **B**. Este elemento permite la salida de la raíz de la planta pero impide la entrada de depredadores que puedan cavar bajo el dispositivo para acceder a su interior.

En otra realización particular (Fig. 7), la pieza contenedora comprende una pluralidad de perforaciones, **O**, que faciliten el intercambio de humedad entre su interior, donde se aloja la semilla, y el medio exterior

En otra realización particular (Fig. 8), la pieza contenedora comprende una pluralidad de púas o elementos puntiagudos, **P**, dispuestos sobre su cara exterior, que impiden su destrucción y el consumo de las semillas contenidas en su interior por depredadores de mayor tamaño como jabalíes, ciervos, cabras, etc.

En otra realización particular (Fig. 9), la pieza contenedora combina las dos características anteriores y comprende una pluralidad de perforaciones, **O**, y una pluralidad de púas o elementos puntiagudos, **P**, dispuestos sobre su cara exterior.

Para simplificar el diseño y el proceso de fabricación, en una realización aún más particular, estas púas se pueden confeccionar al realizar las perforaciones en la superficie de la pieza contenedora, de forma que el material retirado da lugar a la púa.

En otra realización particular (Fig. 10), el dispositivo comprende además un segundo elemento, **C2**, que se une a la pieza contenedora, **C1**, por su base mayor, quedando situada en posición opuesta a la primera. Para facilitar su uso, es preferible que ambos elementos estén separados y puedan unirse tras la colocación de la semilla y el sustrato en su interior.

Esta realización presenta, principalmente, las siguientes ventajas: Protege la raíz durante más tiempo; dirige la raíz pivotante de la planta de forma perpendicular al suelo, permitiendo que alcance una mayor profundidad; y facilita la inserción del dispositivo en el terreno. Adicionalmente, el dispositivo seguiría siendo útil sin necesidad de mantener una posición concreta e incluso si se removiese la tierra y cambiase su posición (Fig. 11).

En otra realización alternativa (Fig. 12), a la pieza contenedora **C1**, se le añade, unido a su base mayor, un elemento cilíndrico o prismático, **C3**, preferentemente con la misma sección que la base mayor de la pieza contenedora, dando lugar a una prolongación de la base de la pieza contenedora.

De forma particular, en su superficie también se practica al menos una línea de apertura, desde la base mayor a la base menor.

En particular, la segunda pieza contenedora podrá ser de distinta altura que la primera pieza contenedora. Podrá igualmente contener perforaciones para facilitar el intercambio de humedad con el suelo circundante y púas para proteger al conjunto de la cápsula ante depredadores de mayor tamaño, como se ha descrito anteriormente.

Otra forma de realización que simplificaría el proceso de forestación, y que también es objeto de la presente invención, consiste (Fig. 13) en la elaboración industrial de kits o conjuntos que comprenden el dispositivo protector, **D**, cuyo interior está relleno con sustrato, **S**, y al menos una semilla, **N**, y que pueden ser distribuidos en bandejas forestales, **W**.

Opcionalmente se pueden incorporar otros elementos que se consideren necesarios como fertilizantes, geles de retención de humedad, etc.

De esta forma, el conjunto que comprende el dispositivo, la semilla y el sustrato está preparado para ser insertado en el hoyo de plantación reduciendo el tiempo de manejo en campo y permitirá equipar la semilla de cada especie con el tipo de sustrato más adecuado, e incrementará el valor añadido de la producción de la invención. Además permite emplear tratamientos promotores de la germinación de las semillas y el crecimiento de las plantas de forma segura y ajena al proceso de plantación.

En resumen, se presenta un dispositivo protector de semillas frente a depredadores que comprende una pieza contenedora, **C**, en cuyo interior se puede colocar al menos una semilla, consistente en un elemento hueco, con forma sensiblemente piramidal o troncocónica seccionada por un plano paralelo o no a su base. De forma preferente, el dispositivo está caracterizado porque la mayor distancia entre dos puntos cualesquiera de la base menor, **b**, de la pieza contenedora, **C**, está comprendida entre 3 y 20 mm, preferentemente entre 5 y 12 mm.

En otra realización particular, la pieza contenedora se practica al menos un corte, rebaje o hilera de microperforaciones, **L**, desde su base mayor a su base menor.

En otra realización particular, el dispositivo se caracteriza porque la pieza contenedora posee una pluralidad de orificios, **O**, practicados en su superficie que facilitan el intercambio de humedad y nutrientes con el terreno. De forma adicional o alternativa, otra realización del dispositivo comprende una pluralidad de púas o pinchos, **P**, colocados en la parte exterior de la pieza contenedora.

En otra realización particular, el dispositivo comprende adicionalmente, una tapadera perforada, rejilla o red de malla, **T**, que se une a la base mayor de la pieza contenedora, impidiendo el acceso de animales por su parte inferior al mismo tiempo que permite el crecimiento de las raíces.

En otros modos de realización particulares, en lugar de emplear una tapa, el dispositivo descrito comprende un segundo elemento hueco, con forma sensiblemente piramidal o troncocónica, **C2,** seccionado por un plano paralelo o no a su base, que se une a la pieza contenedora por su base mayor, quedando situado en posición opuesta a la primera, o bien comprende un segundo elemento hueco, con forma sensiblemente cilíndrica o prismática, **C3**, unido a la base mayor de la pieza contenedora. En distintas realizaciones aún más particulares, este segundo elemento puede disponer de al menos un corte, rebaje o hilera de microperforaciones que facilite su desgarro y posterior degradación una vez que la planta alcance un tamaño suficiente. Este segundo elemento también puede poseer, de forma alternativa o adicional, una pluralidad de orificios practicados en su superficie y/o una pluralidad de púas o pinchos colocados en su parte exterior.

Finalmente, también se presenta un kit para la plantación de semillas que comprende el dispositivo objeto de la invención, cuyo interior se rellena con al menos una semilla y sustrato.

MODOS DE REALIZACIÓN DE LA INVENCIÓN

Modo de realización 1

Un modo de realización sencillo es un dispositivo protector de semillas ante depredadores que consiste únicamente en una pieza contenedora fabricada con material biodegradable que se degrade, aproximadamente, en el plazo de un año.

La pieza contenedora tiene forma troncocónica. Su base menor tiene un diámetro de 10 mm y su base mayor un radio de 40 mm. La altura de dicha pieza contenedora es de 100 mm.

Las dimensiones de la base menor impiden que los roedores accedan a la semilla por la parte superior del dispositivo y la altura de la pieza contenedora es suficiente para impedir que excaven hasta acceder a la semilla por la parte inferior del dispositivo.

Modo de realización 2

Otro modo de realización, que permitiría utilizar otro tipo de materiales biodegradables, es un dispositivo que consiste únicamente en una pieza contenedora de forma troncocónica. Su base menor tiene un diámetro de 10 mm y su base mayor un diámetro de 40 mm. La altura de dicha pieza contenedora es de 100 mm.

En la superficie de esta pieza contenedora se realiza un corte, **L**, (línea de apertura) desde su base mayor, **B**, a su base menor, **b**. El corte se realiza a lo largo de una generatriz, de forma que la pieza contenedora no pierde su consistencia y mantiene su forma.

Con este corte se evita que la planta quede estrangulada al crecer si el material no se ha degradado adecuadamente (Fig. 5).

Modo de realización 3

Dispositivo protector de semillas ante depredadores con forma troncocónica (Fig. 6), consistente en una pieza contenedora, de forma troncocónica, de 4 cm de altura, cuya base menor, **b**, tiene un diámetro de 10 mm y su base mayor, **B**, un diámetro de 40 mm; y una tapadera perforada, **T**, con un diámetro de 40 mm y perforaciones de 9 mm de diámetro.

Además, la pieza contenedora presenta una línea de apertura, **L**, que une su base mayor con su base menor.

A la hora de realizar la siembra, la semilla y el sustrato deseados se insertan en el troncocono, tras lo que se coloca la tapadera mediante presión o cualquier otro medio que permita su anclaje.

El dipositivo, con la semilla y el sustrato en su interior, se inserta en el suelo con la base mayor hacia abajo.

El tallo de la planta, una vez germine la semilla, saldrá por la parte superior del troncocono, mientras que la raíz de la planta saldrá a través de las perforaciones de la tapadera. El troncocono se abrirá a través de la línea de apertura, **L**, una vez crezca la planta.

El conjunto del dispositivo permitirá proteger la semilla ante depredadores vertebrados como roedores, que no podrán acceder a su interior. También dificultará el consumo de semillas por vertebrados de mayor tamaño como jabalíes o cabras.

Modo de realización 4

Dispositivo protector de semillas ante depredadores con forma troncocónica (Fig. 9), consistente en una pieza hueca, con forma troncocónica, de 4 cm de altura, cuya base menor, **b**, tiene un diámetro de 10 mm y su base mayor, **B**, un diámetro de 40 mm.

El troncocono presenta en su pared perforaciones, **O**, de 3 mm de diámetro que incrementan el intercambio de humedad con el suelo una vez que la estructura se haya enterrado. Presenta igualmente púas, **P**, que se proyectan desde la pared del troncocono hacia afuera. El objetivo de estas púas es ahuyentar tanto a roedores como, especialmente, a depredadores de mayor tamaño como jabalíes o cabras.

El dispositivo se puede complementar con una tapa, tal y como se indica en el modo de realización anterior.

Modo de realización 5

Dispositivo protector de semillas ante depredadores (Fig. 10) consistente en una pieza contenedora, **C1**, a la que se añade un segundo elemento, **C2**, de forma que queden unidos por su base mayor.

La pieza contenedora, **C1**, consiste en una pieza hueca, con forma troncocónica, de 40 mm de altura, cuya base menor tiene un diámetro de 10 mm y su base mayor un diámetro de 40 mm,

El segundo elemento, **C2**, consiste en una pieza hueca con forma troncocónica, de 100 mm de altura, cuya base menor tiene un diámetro de 10 mm y su base mayor un diámetro de 40 mm.

La primera pieza contenedora presenta, a lo largo de una de sus generatrices, un corte, a modo de línea de apertura, **L**, que continúa a lo largo de la segunda pieza contenedora, uniendo también sus bases mayor y menor.

El dispositivo se entierra en el suelo manteniendo la pieza contenedora, **C1**, en la parte más cercana a su superficie.

Este modo de realización impide el acceso de roedores a la parte interior del dispositivo al mismo tiempo que dirige las raíces hacia zonas más profundas. Adicionalmente, el dispositivo sigue siendo útil sin necesidad de mantener una posición concreta e incluso si se removiese la tierra y cambiase su posición (Fig. 11).

Modo de realización preferido

En un modo de realización preferido, el dispositivo consta de dos troncoconos de tamaño idéntico que se encajan uno sobre el otro por presión. La base mayor de cada troncocono tendrá un diámetro de 30 mm y la base menor un diámetro de 10 mm. La altura de cada troncocono es de 30 mm. Estas dimensiones son suficientes para albergar una bellota en su interior y al mismo tiempo impedir la entrada de roedores por la única abertura que quedará libre (la de menor diámetro de cada troncocono) una vez que las dos mitades (troncoconos) de la estructura se ensamblen, y permitirá la salida del tallo (por la parte superior) y de la raíz (por la parte inferior) a través del orificio de menor diámetro.

Ambos troncoconos presentarán un corte a modo de línea de apertura que permitirá la apertura de cada troncocono una vez el tallo o la raíz de la planta en crecimiento ejerza presión. El protector será de un material suficientemente resistente como para evitar la rotura por roedores, pero será igualmente de un material biodegradable que permita su degradación una vez que la planta ya está creciendo. Los dos troncoconos presentarán perforaciones que permitirán el intercambio de humedad con el suelo. El troncocono superior del dispositivo presentará púas para reducir el riesgo de consumo por vertebrados de gran tamaño (como jabalíes o cabras) que puedan localizar la bellota una vez sembrada.

El troncocono superior irá acompañado de una funda o carcasa cilíndrica, encajada por presión, que encerrará las púas, lo que facilitará su embalaje y manejo durante el transporte.

Para su utilización, una vez en campo, se eliminará la carcasa, se separarán los dos troncoconos, y se rellenará el inferior con tierra, colocando la semilla encima de la misma. Posteriormente se puede añadir más tierra o colocar directamente el troncocono superior mediante presión, para terminar de rellenar con sustrato a través del orificio de menor diámetro del troncocono superior.

Se puede añadir cualquier sustrato o compuesto deseado, como fertilizante, geles para retener humedad, etc. Posteriormente la estructura resultante se insertará en el suelo tras hacer el agujero deseado con el uso de una herramienta apropiada (pico, azada, etc.).

REIVINDICACIONES

1. Dispositivo protector de semillas frente a depredadores que comprende una pieza contenedora, en cuyo interior se puede colocar al menos una semilla, caracterizado porque dicha pieza contenedora consiste en un elemento hueco, con forma sensiblemente piramidal o troncocónica seccionada por un plano paralelo o no a su base y la mayor distancia entre dos puntos cualesquiera de la base menor de dicha pieza contenedora está comprendida entre 3 y 20 mm.
2. Dispositivo según reivindicación 1 caracterizado porque la mayor distancia entre dos puntos cualesquiera de la base menor de la pieza contenedora está comprendida entre 5 y 12 mm.
3. Dispositivo según cualquiera de las reivindicaciones anteriores en el que a la pieza contenedora se practica al menos un corte, rebaje o hilera de perforaciones desde su base mayor a su base menor.
4. Dispositivo según cualquiera de las reivindicaciones anteriores, caracterizado porque la pieza contenedora posee una pluralidad de orificios practicados en su superficie.
5. Dispositivo según cualquiera de las reivindicaciones anteriores, que además comprende una pluralidad de púas o pinchos colocados en la parte exterior de la pieza contenedora.
6. Contenedor para proteger semillas según cualquiera de las reivindicaciones anteriores que además comprende una tapadera perforada, rejilla o red de malla que se une a la base mayor de la pieza contenedora.
7. Dispositivo según cualquiera de las reivindicaciones 1 a 5, que además comprende un segundo elemento hueco, con forma sensiblemente piramidal o troncocónica seccionado por un plano paralelo o no a su base, que se une a la pieza contenedora por su base mayor, quedando situado en posición opuesta a la primera.
8. Dispositivo según cualquiera de las reivindicaciones 1 a 5, que además comprende un segundo elemento hueco, con forma sensiblemente cilíndrica o prismática, unido a la base mayor de la pieza contenedora.
9. Dispositivo según cualquiera de las reivindicaciones 7 u 8, caracterizado porque se practica al menos un corte, rebaje o hilera de perforaciones al segundo elemento.
10. Dispositivo según cualquiera de las reivindicaciones 7 a 10, caracterizado porque el segundo elemento posee una pluralidad de orificios practicados en su superficie.

11. Dispositivo según cualquiera de las reivindicaciones 7 a 10, que comprende una pluralidad de púas o pinchos colocados en la parte exterior del segundo elemento.
12. Kit para la plantación de semillas que comprende un dispositivo según cualquiera de las reivindicaciones anteriores cuyo interior se rellena con al menos una semilla y sustrato.

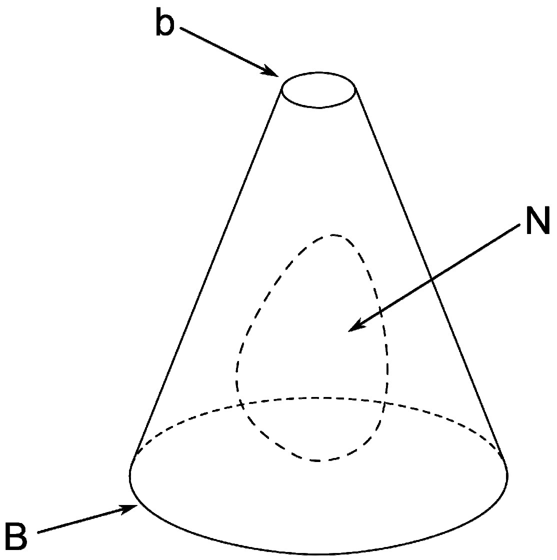


Figura 1

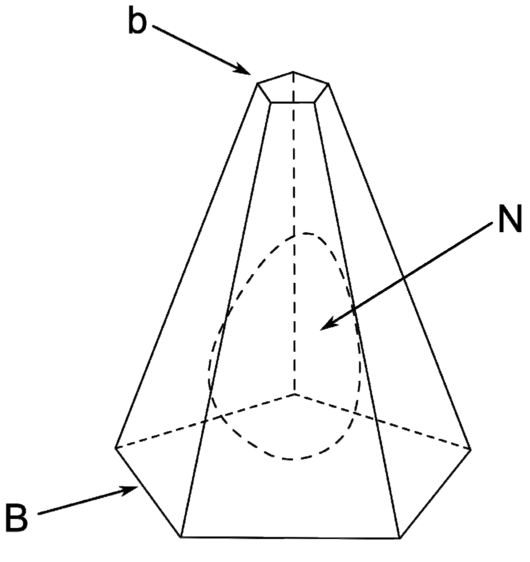
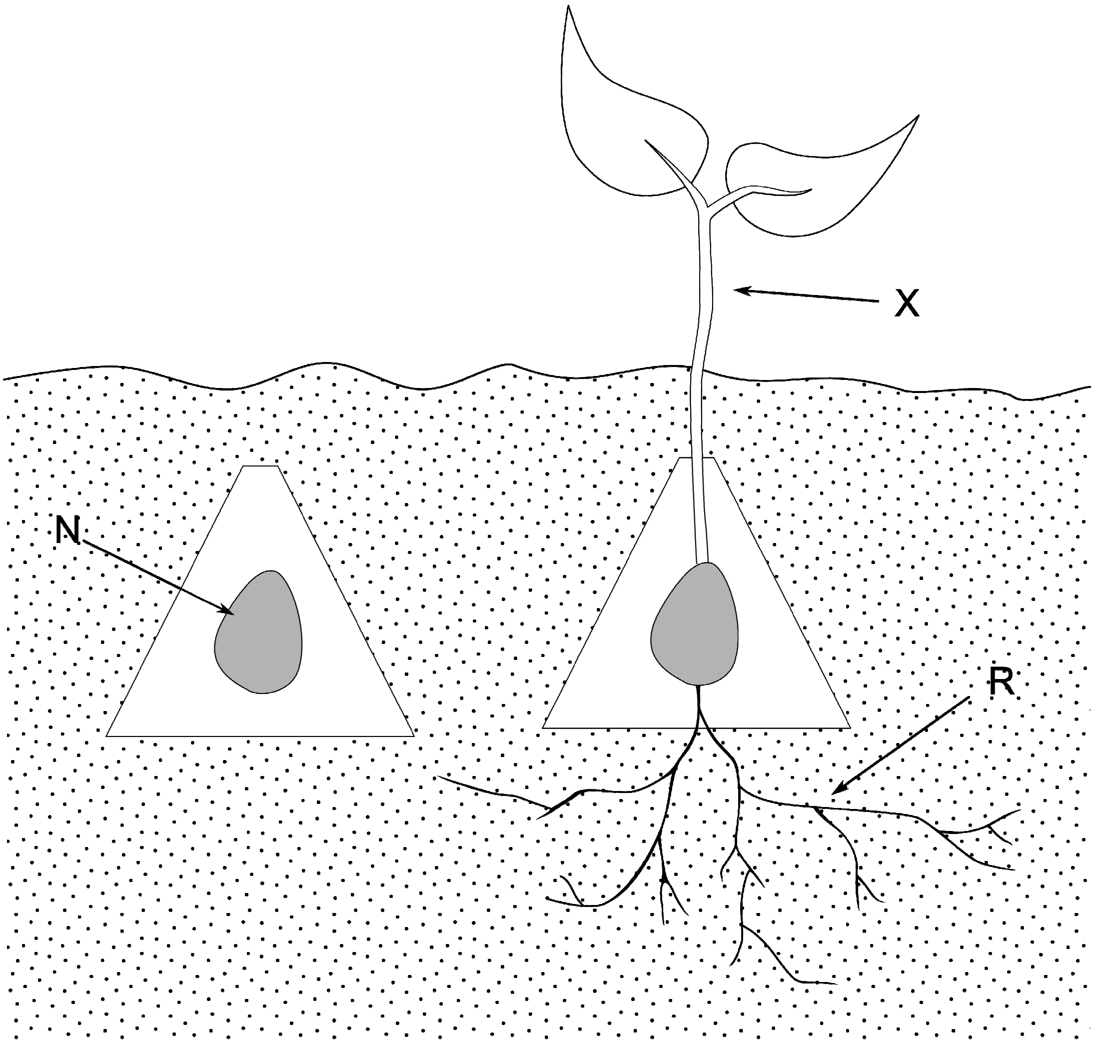


Figura 2



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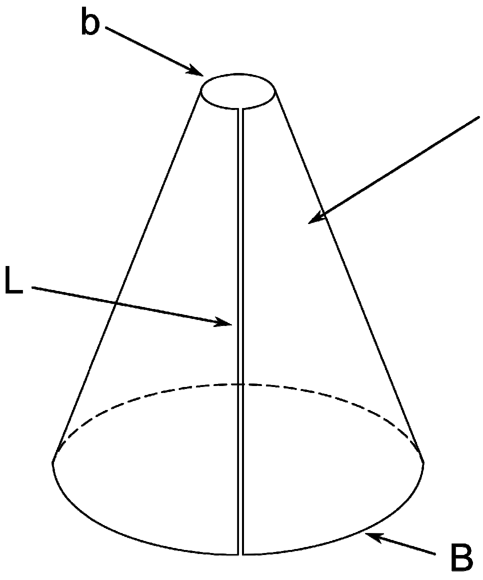
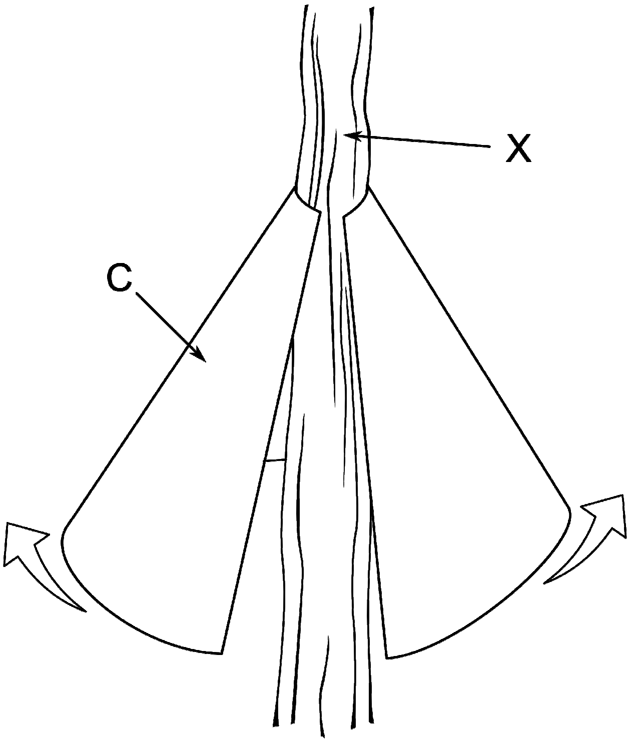


Figura 4



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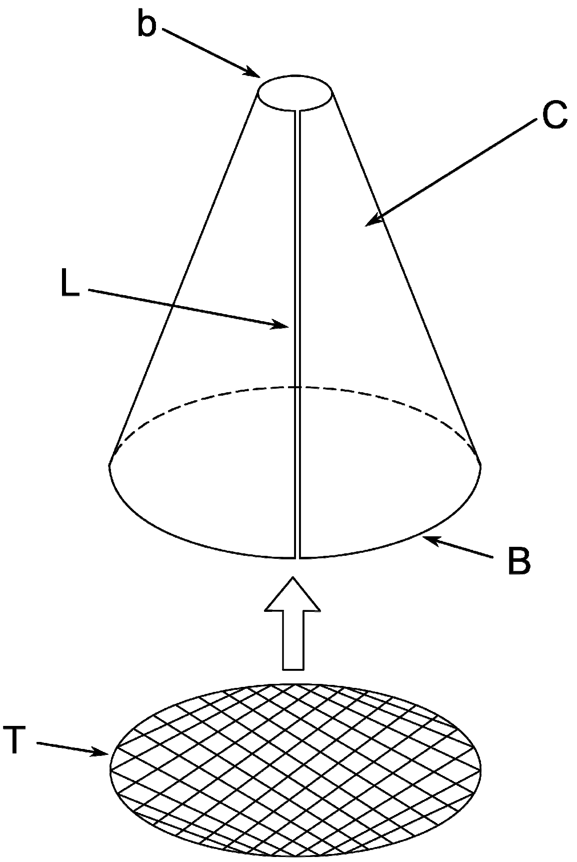

Figura 6

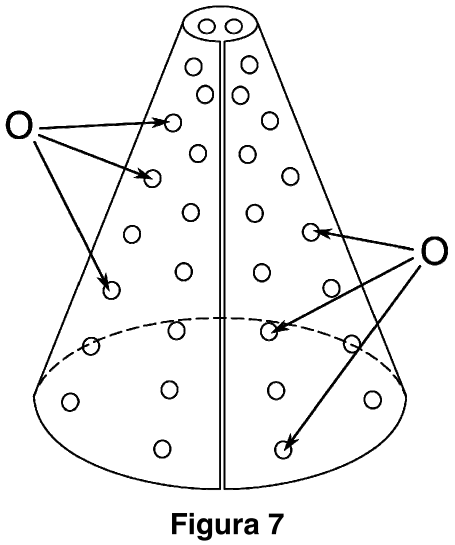

Figura 7

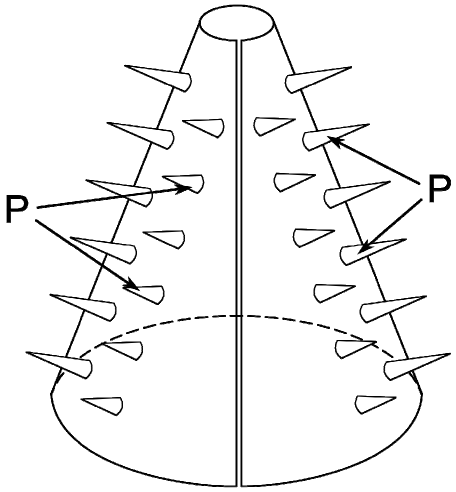

Figura 8

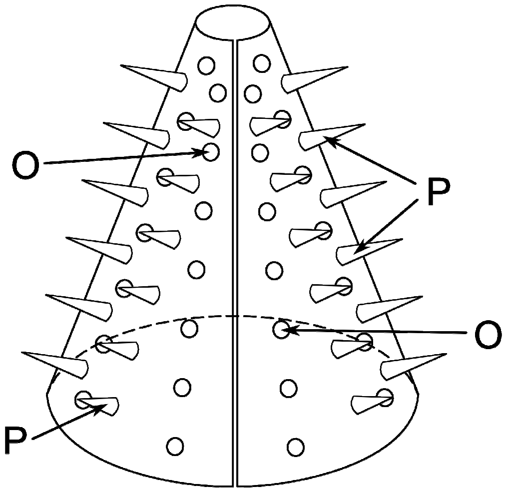

Figura 9

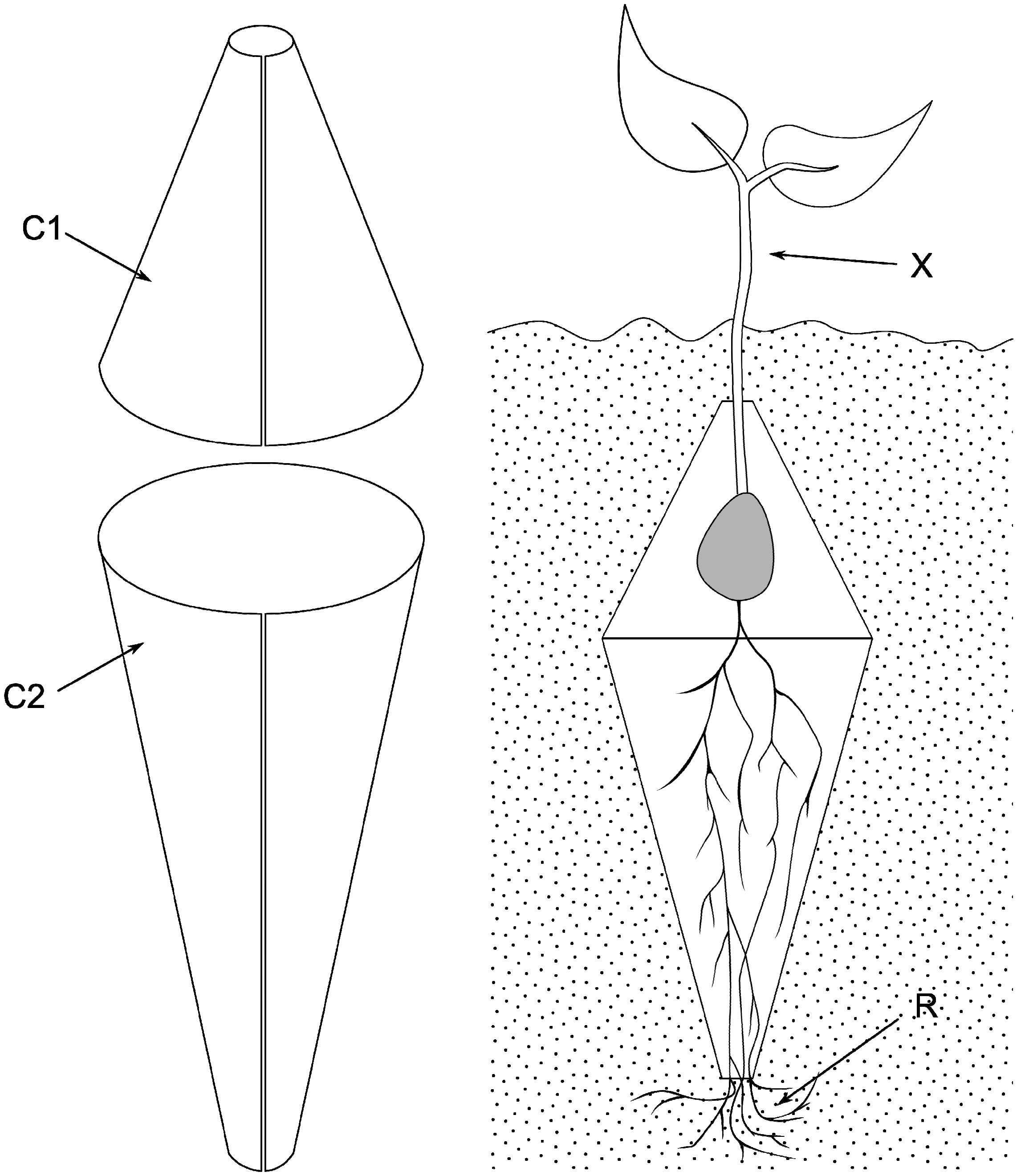

Figura 10

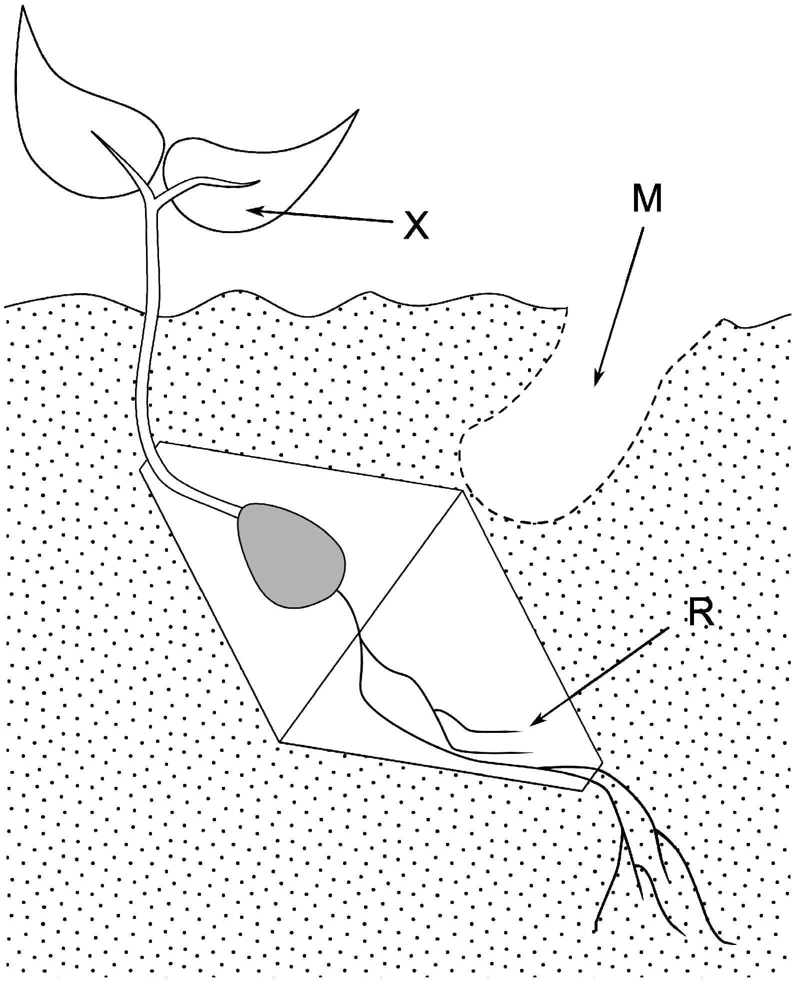

Figura 11

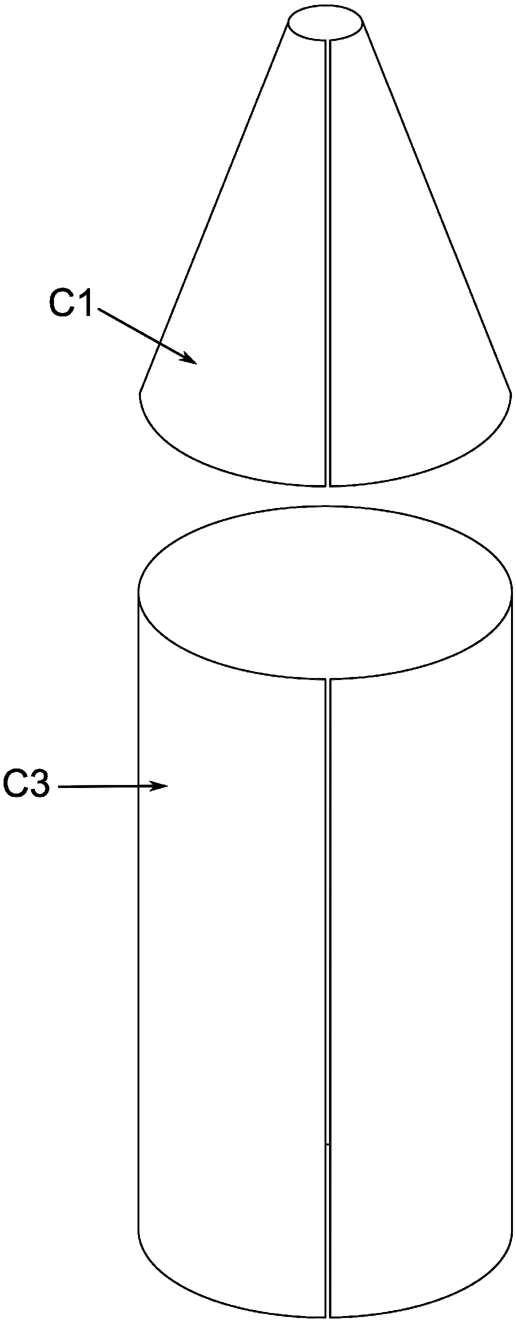

Figura 12

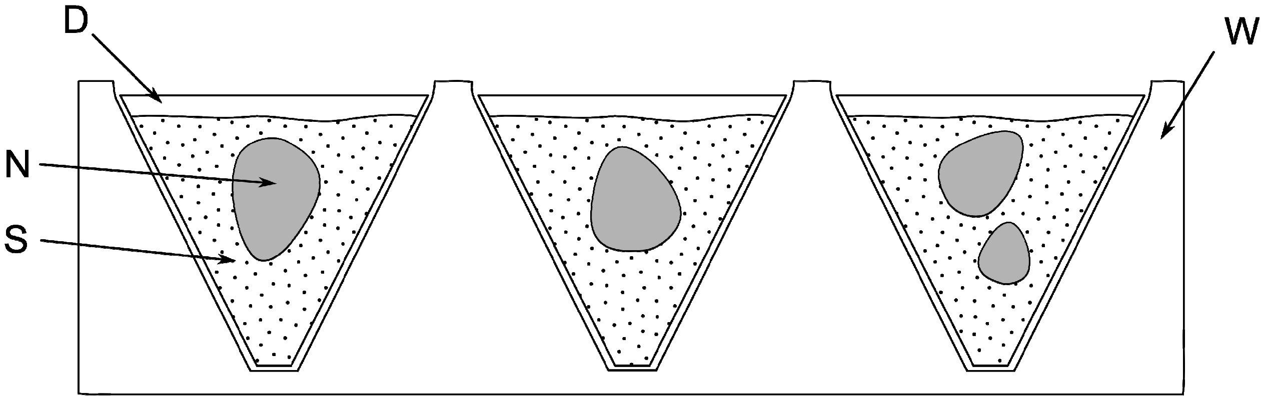

Figura 13

OFICINA ESPAÑOLA
DE PATENTES Y MARCAS

ESPAÑA

㉑ N.º solicitud: 201331441

㉒ Fecha de presentación de la solicitud: 02.10.2013

㉜ Fecha de prioridad:

INFORME SOBRE EL ESTADO DE LA TECNICA

(51) **Int. Cl. :** ***A01C1/06*** (2006.01)

DOCUMENTOS RELEVANTES

Categoría	(56) **Documentos citados**	**Reivindicaciones afectadas**
X Y	ES 2192932 A1 (UNIV CATALUNYA POLITECNICA) 16.10.2003, resumen; reivindicaciones.	1,13 5
Y	KR 20080089147 A (SO CHANG HO et al.) 06.10.2008, figuras.	5
A	ES 2383420 A1 (UNIV VALLADOLID) 21.06.2012, figuras.	1-13
A	US 2010263274 A1 (CORAK STEVEN J et al.) 21.10.2010, figuras.	1-13

Categoría de los documentos citados

X: de particular relevancia	O: referido a divulgación no escrita
Y: de particular relevancia combinado con otro/s de la misma categoría	P: publicado entre la fecha de prioridad y la de presentación de la solicitud
A: refleja el estado de la técnica	E: documento anterior, pero publicado después de la fecha de presentación de la solicitud

El presente informe ha sido realizado

☒ para todas las reivindicaciones ☐ para las reivindicaciones nº:

Fecha de realización del informe	**Examinador**	**Página**
28.10.2013	I. Rueda Molíns	1/4

Documentación mínima buscada (sistema de clasificación seguido de los símbolos de clasificación)

A01C

Bases de datos electrónicas consultadas durante la búsqueda (nombre de la base de datos y, si es posible, términos de búsqueda utilizados)

INVENES, EPODOC

Fecha de Realización de la Opinión Escrita: 28.10.2013

Declaración

Novedad (Art. 6.1 LP 11/1986)	Reivindicaciones	1-13	**SI**
	Reivindicaciones		**NO**
Actividad inventiva (Art. 8.1 LP11/1986)	Reivindicaciones	2-4, 6-12	**SI**
	Reivindicaciones	1, 5, 13	**NO**

Se considera que la solicitud cumple con el requisito de aplicación industrial. Este requisito fue evaluado durante la fase de examen formal y técnico de la solicitud (Artículo 31.2 Ley 11/1986).

Base de la Opinión.-

La presente opinión se ha realizado sobre la base de la solicitud de patente tal y como se publica.

1. Documentos considerados.-

A continuación se relacionan los documentos pertenecientes al estado de la técnica tomados en consideración para la realización de esta opinión.

Documento	Número Publicación o Identificación	Fecha Publicación
D01	ES 2192932 A1 (UNIV CATALUNYA POLITECNICA)	16.10.2003
D03	KR 20080089147 A (SO CHANG HO et al.)	06.10.2008
D04	ES 2383420 A1 (UNIV VALLADOLID)	21.06.2012
D05	US 2010263274 A1 (CORAK STEVEN J et al.)	21.10.2010

2. Declaración motivada según los artículos 29.6 y 29.7 del Reglamento de ejecución de la Ley 11/1986, de 20 de marzo, de Patentes sobre la novedad y la actividad inventiva; citas y explicaciones en apoyo de esta declaración

NOVEDAD Y ACTIVIDAD INVENTIVA (artículos 6 y 8 de la Ley 11/1986)

En la solicitud de patente se reivindica un dispositivo protector de semillas ante depredadores.

En los documentos D01, D02, D03 y D04 se divulgan diferentes dispositivos para proteger a las semillas.

En las reivindicaciones 1 y 5 de la solicitud de patente se reivindica un dispositivo protector de semillas frente a depredadores que comprende una pieza contenedora, en cuyo interior se puede colocar al menos una semilla, caracterizado porque dicha pieza contenedora consiste en un elemento hueco, con forma sensiblemente piramidal o troncocónica seccionada por un plano paralelo o no a su base y que posee una pluralidad de orificios practicados en su superficie. En la reivindicación 13 se reivindica un kit para la plantación de semillas que comprende el citado dispositivo, una semilla y sustrato.

El documento D01 divulga un método de preparación de semillas, para cultivos agrícolas y reforestación capaz de proteger la semilla de depredadores (tal y como se indica en el resumen del documento D01) caracterizado porque la semilla es introducida en una cápsula cerrada de cualquier geometría y tamaño junto a uno o varios productos, materiales o útiles tales como: abonos orgánicos, nutrientes Dicha cápsula puede ser cerrada o presentar un agujero dejado por un precinto previamente eliminado (tal y como se indica en la página 2 del documento D01).

En el documento D02 se muestra una cápsula que contiene una semilla con el fin de proteger posibles daños que se pudieran producir tras la siembra. Dicha cápsula presenta unos cortes para ventilación de la semilla.

Por tanto, teniendo en cuenta el documento D01, las reivindicaciones 1 y 13 de la solicitud de patente, presentan novedad pero no actividad inventiva. Si además se toma en consideración el documento D02, la reivindicación 5, tampoco presenta actividad inventiva, según lo establecido en los artículos 6 y 8 de la Ley 11/1986.

Appendix II

Appendix II. Estimation of reforestation costs

In this Appendix, I provide details on the methods employed to calculate the cost of reforestation. The costs of obtaining 400 living oaks through the methods of reforestation tested in Chapters 1 to 4 of this Thesis –standard sowing, sowing with the seed shelter, and seedling planting– are provided.

1. Standard sowing

Methods

To estimate the cost of acorn sowing in the burnt-wood replicates of Plot 1, I used 1) standard data on the wages of forestry employees and on the price of acorns, 2) three assumptions on the time needed for sowing, and 3) empirical data on acorn and seedling survival. The aim is to calculate the money necessary to obtain 400 living holm oak seedlings via sowing.

First, the standard cost of hiring a forestry employee is 14.55 €/ h (including the employee's salary, insurance, and taxes). Six employees are always accompanied by one foreman, whose cost is 15.87 €/ h. The cost of 1 kg of acorns, assumed to contain 100 units, is € 4.04. A further 7% is added to the final amount as indirect costs resulting from transport to the area, office work, etc. These are standard, tabulated costs used by the local Forest Service (Leverkus et al., 2012).

Second, I used empirical data from this Thesis and from the literature to estimate the number of acorns that need to be sown to obtain 400 seedlings. Several demographic filters act on acorns before they can become established oaks, the main ones involving acorn predation, seedling emergence, and one-year seedling survival in the case of Mediterranean ecosystems (Gómez, 2004; Pulido and Díaz, 2005; Pérez-Ramos et al., 2012). As acorns are usually pre-germinated before sowing (Pemán García et al., 2013), here I only contemplate mortality due to acorn predation and one-year seedling survival. For the purpose of this broad calculation, I averaged the acorn predation values obtained in the post-fire treatments across seven trials, where acorns were placed at 2-5 cm belowground (Puerta-Piñero et al., 2010; Leverkus et al., 2013, 2015a), thus avoiding the use of the values obtained under the experimental treatments of deeper burial, capsaicin, or seed shelters. I then took one-year *Q.*

ilex seedling survival data from three studies performed in Sierra Nevada (Table 1). I averaged these values, weighting over sample size. The number of acorns needed to obtain 400 seedlings is calculated as 400 divided by the product of the survival of acorns and seedlings.

Table 1

Reference	N	One-year seedling survival (%)
(Gómez, 2004)	500	67.2
(Mendoza et al., 2009)*	450	64.5
(Mendoza et al., 2009)*	225	78.1
Weighted mean		68.3

* Two trials of one study. Values are averaged across habitats and exclude the watering treatment. One-year survival was obtained with the DigitizeIt software (I. Bormann; www.digitizeIt.de).

Third, to estimate the time required by employees for sowing in the different post-fire treatments I used the following line of thought. The acorn sowing experiments of this Thesis (Leverkus et al., 2015b, 2013) were not performed by the Forest Service but rather by myself with the aid of several colleagues, and they included activities such as taking GPS coordinates and marking the location of each acorn with wooden sticks. This made the whole process unrealistically time consuming, so that the time employed would not be useful to calculate sowing costs under a realistic scenario (in contrast with the planting experiment, which was performed by forestry staff; Leverkus et al., 2012, 2015b). Due to the lack of realistic, empirical data, I calculated the potential cost of sowing operations on the basis of different assumptions on the time required for it. I assumed that to sow one acorn in the Salvage Logging treatment (mostly devoid of obstacles for forestry employees) it would take a) 0.5 min, b) 1 min, or c) 2 min. The time requirement in the other treatments would be larger due to their greater structural complexity arising from the lying burnt boles and branches, as was obtained in the economic assessment of planting (Leverkus et al., 2012). Here I assume that the difference in the time needed for sowing in the different treatments is independent of sowing density (although, in reality, a greater density would yield smaller between-treatment differences due to the smaller proportion of time required for walking between sowing points). In the plantation experiment, workers planted an average of 17.45 seedlings/ hour in the SL treatment, 16.83 seedlings/ hour in PCL, and 13.89 seedlings/ hour in NI (data provided by forestry personnel). As the above scenarios on the timely requirement to sow one acorn are for the SL treatment, this time was multiplied by a work efficiency factor of 17.45/ 16.83 = 1.04 for sowing in the PCL treatment and by 17.45/ 13.89 = 1.26 for the NI treatment.

The final cost of sowing was then calculated as the sum of the cost of the required worker and foreman hours (multiplied by the work efficiency factor) and the price of acorns, all multiplied by 1.07 to add the indirect costs and by the mortality factor (see Table 2).

Results

Survival to acorn predation across the seven trials averaged 17.6% in the NI treatment, 20.1% in SL, and 7.5% in PCL. Average 1-year seedling survival was 68.3% (Table 1). The number of acorns necessary to obtain one surviving seedling was thus N= 1/ (0.176 x 0.683) = 8.32 acorns in NI, 7.28 acorns in SL, and 19.52 acorns in PCL. These values, which are the inverse of the transition probabilities from sown acorns to 1-year-old seedlings (Gómez-Aparicio, 2008), are here regarded as *mortality factors* by which the cost of sowing 400 acorns needs to be multiplied in order to obtain 400 surviving seedlings (Table 2).

The cost of sowing was lowest in SL, followed by NI, and highest in PCL. The lowest cost was obtained in SL under the scenario that workers require 0.5 min to sow one acorn, and the highest cost was in PCL under the scenario of requiring 2 min (Table 2).

2. Sowing with seed shelters

Methods

I calculated the hypothetical cost of sowing acorns with the seed shelter (Leverkus et al. 2015a). As the device is not yet commercially available and thus lacks a market price, I put its price, including the substrate and its assembly, at a) € 0.05, b) € 0.10, or c) € 0.20. I assume that the device a) eliminates predation by rodents, and b) does not affect seedling survival. I re-calculated the mortality factor of seeding by using the mean values of acorn predation but excluding predation by rodents from the same trials considered above (Puerta-Piñero et al., 2010; Leverkus et al., 2013, 2015a). I also assumed that, due to the need to carry the seed shelters in the field and to bury them, the fieldwork would take twice as long as for standard sowing. Thus, the scenario of 0.5 min to sow one acorn assumes 1 min to sow one acorn with seed shelter. All other assumptions, scenarios, and methods are as for standard sowing.

Table 2

Scenario: Time to sow 1 acorn in SL (min)	Ttmt (a)	Work efficiency (b)	Worker hours (c)	Foreman hours (d)	Cost 4 kg acorns (€) (e)	Worker cost (€) (f)	Foreman cost (€) (g)	Subtotal (€) (h)	Indirect costs (€) (i)	Mortality factor (j)	Total cost (€) (k)
0.5	SL	1.00	3.32	0.55	16.16	48.31	8.78	73.25	5.13	7.28	570.57
	NI	1.26	4.18	0.70	16.16	60.87	11.06	88.09	6.17	8.32	784.21
	PCL	1.04	3.45	0.58	16.16	50.24	9.13	75.53	5.29	19.52	1577.57
1	SL	1.00	6.68	1.11	16.16	97.19	17.67	131.02	9.17	7.28	1020.61
	NI	1.26	8.42	1.40	16.16	122.46	22.26	160.89	11.26	8.32	1432.28
	PCL	1.04	6.95	1.16	16.16	101.08	18.38	135.62	9.49	19.52	2832.55
2	SL	1.00	13.32	2.22	16.16	193.81	35.23	245.20	17.16	7.28	1909.99
	NI	1.26	16.78	2.80	16.16	244.20	44.39	304.75	21.33	8.32	2712.98
	PCL	1.04	13.85	2.31	16.16	201.56	36.64	254.36	17.81	19.52	5312.64

(a) Post-fire management treatments were: Salvage Logging (SL), Non-Intervention (NI), and Partial Cut plus Lopping (PCL)

(b) Considers differences in the accessibility of post-fire treatments; see Methods of this Appendix

(c) 400 acorns x the timely requirement for 1 acorn x (b)

(d) One foreman for every 6 workers; (c) / 6

(e) Standard cost; 1 kg = 100 acorns

(f) = 14.55 € / h x (c)

(g) = 15.87 € / h x (d)

(h) = (e) + (f) + (g)

(i) = 0.07 * (h)

(j) Considers mortality due to seed predation and 1-year seedling survival

(k) = ((h) + (i)) * j

Results

The estimated survival to predation was 93.8% in NI, 97.7% in PCL, and 91.5% in SL. To obtain one surviving seedling with the seed shelter, one would thus require N = 1/ (0.938 x 0.683) = 1.56 acorns in the NI treatment, 1.60 in SL, and 1.50 in PCL. Replacing the mortality factors of Table 2 by the new factors, and including the different scenarios of the cost of the seed shelter, we obtain the hypothetical costs of sowing with the seed shelter (Table 3).

The lowest cost was always obtained in the PCL treatment, followed by SL, and highest in NI (Table 3). However, the difference in cost between treatments was much less pronounced than under standard sowing. The effect of the time needed for sowing was much greater than that of the price of the seed shelter. For example, in the SL treatment, multiplying the time required for sowing by four increased the total cost of sowing by a factor of 3.27 (under the scenario of € 0.05 per seed shelter), while multiplying the cost of the seed shelter by four increased the total cost of sowing by a factor of only 1.40 (under the scenario of 1 min per seed shelter) (Table 3).

3. Planting

Methods

The cost of the planting operation of the Lanjarón plots was calculated in Leverkus et al. (2012). These costs were calculated under the realistic management scenario that the seedlings that died after the first year would be replaced. However, mortality is also likely to occur among replacement seedlings, so that the desired number of surviving seedlings would still not be reached after replacement. This is why, in order to compare the different reforestation techniques in terms of the cost of achieving 400 live seedlings in one hectare, I recalculated the cost of planting as the quotient of the cost of planting 400 plants in each of the post-fire treatments divided by the obtained probability of seedling survival. I used the values of Table 3 of Leverkus et al. (2012) for this calculation and averaged them over the replicates of each burnt-wood treatment.

Table 3

Scenario: seed shelter cost (€/ unit)	Scenario: Time to sow 1 seed shelter (min)	Ttmt (a)	Work efficiency (b)	Worker hours (c)	Foremen hours (d)	Cost 4 kg acorns (€) (e)	Cost 400 s. sh. (€) (f)	Worker cost (€) (g)	Foremen cost (€) (h)	Subtota l (€) (i)	Indirect costs (€) (j)	Mortality factor (k)	Total (€) (l)
0.05	1	SL	1.00	6.68	1.11	16.16	20.00	97.19	17.67	151.02	10.57	1.60	258.55
		NI	1.26	8.42	1.40	16.16	20.00	122.46	22.26	180.89	12.66	1.56	301.94
		PCL	1.04	6.95	1.16	16.16	20.00	101.08	18.38	155.62	10.89	1.50	249.77
	2	SL	1.00	13.32	2.22	16.16	20.00	193.81	35.23	265.20	18.56	1.60	454.02
		NI	1.26	16.78	2.80	16.16	20.00	244.20	44.39	324.75	22.73	1.56	542.07
		PCL	1.04	13.85	2.31	16.16	20.00	201.56	36.64	274.36	19.21	1.50	440.35
	4	SL	1.00	26.64	4.44	16.16	20.00	387.61	70.46	494.23	34.60	1.60	846.13
		NI	1.26	33.57	5.59	16.16	20.00	488.39	88.78	613.33	42.93	1.56	1023.78
		PCL	1.04	27.71	4.62	16.16	20.00	403.12	73.28	512.56	35.88	1.50	822.66
0.1	1	SL	1.00	6.68	1.11	16.16	40.00	97.19	17.67	171.02	11.97	1.60	292.79
		NI	1.26	8.42	1.40	16.16	40.00	122.46	22.26	200.89	14.06	1.56	335.32
		PCL	1.04	6.95	1.16	16.16	40.00	101.08	18.38	175.62	12.29	1.50	281.87
	2	SL	1.00	13.32	2.22	16.16	40.00	193.81	35.23	285.20	19.96	1.60	488.26
		NI	1.26	16.78	2.80	16.16	40.00	244.20	44.39	344.75	24.13	1.56	575.45
		PCL	1.04	13.85	2.31	16.16	40.00	201.56	36.64	294.36	20.61	1.50	472.45
	4	SL	1.00	26.64	4.44	16.16	40.00	387.61	70.46	514.23	36.00	1.60	880.37
		NI	1.26	33.57	5.59	16.16	40.00	488.39	88.78	633.33	44.33	1.56	1057.16
		PCL	1.04	27.71	4.62	16.16	40.00	403.12	73.28	532.56	37.28	1.50	854.76
0.2	1	SL	1.00	6.68	1.11	16.16	80.00	97.19	17.67	211.02	14.77	1.60	361.27
		NI	1.26	8.42	1.40	16.16	80.00	122.46	22.26	240.89	16.86	1.56	402.09
		PCL	1.04	6.95	1.16	16.16	80.00	101.08	18.38	215.62	15.09	1.50	346.07
	2	SL	1.00	13.32	2.22	16.16	80.00	193.81	35.23	325.20	22.76	1.60	556.74
		NI	1.26	16.78	2.80	16.16	80.00	244.20	44.39	384.75	26.93	1.56	642.22
		PCL	1.04	13.85	2.31	16.16	80.00	201.56	36.64	334.36	23.41	1.50	536.65
	4	SL	1.00	26.64	4.44	16.16	80.00	387.61	70.46	554.23	38.80	1.60	948.85
		NI	1.26	33.57	5.59	16.16	80.00	488.39	88.78	673.33	47.13	1.56	1123.93
		PCL	1.04	27.71	4.62	16.16	80.00	403.12	73.28	572.56	40.08	1.50	918.96

(a) Post-fire management treatments were: Salvage Logging (SL), Non-Intervention (NI), and Partial Cut plus Lopping (PCL)

(b) Considers differences in the accessibility of post-fire treatments; see Methods of this Appendix

(c) 400 acorns x the timely requirement for 1 acorn x (b)

(d) One foreman for every 6 workers; (c)/ 6

(e) Standard cost; 1 kg = 100 acorns

(f) Cost scenario x 400 units

(g) = 14.55 € / h x (c)

(h) = 15.87 € / h x (d)

(i) = (e) + (f) + (g) + (h)

(j) = 0.07 * (i)

(k) Considers mortality due to seed predation and 1-year seedling survival

(l) = ((i) + (j)) * k

Appendix II

Results

The new calculation resulted in an average planting cost of € 4645 ± 337 in NI, € 3265 ± 729 in SL, and € 3851 ± 877 in PCL (mean ± SD). As already mentioned, these values are higher than those provided in Leverkus et al. (2012) because they include planting enough seedlings to compensate mortality and obtain 400 live seedlings.

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