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Biología Fundamental y de Sistemas

Análisis de la dinámica de los robledales (*Quercus pyrenaica* Willd.) frente al cambio global en el límite sur de su distribución (Sierra Nevada)

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*Hay un momento para todo y un tiempo para cada cosa
bajo el sol:*

*un tiempo para nacer y un tiempo para morir;
un tiempo para plantar y un tiempo para arrancar lo plantado;
un tiempo para matar y un tiempo para curar;
un tiempo para demoler y un tiempo para edificar;
un tiempo para llorar y un tiempo para reír;
un tiempo para lamentarse y un tiempo para bailar;
un tiempo para arrojar piedras y un tiempo para recogerlas,
un tiempo para abrazarse y un tiempo para separarse;
un tiempo para buscar y un tiempo para perder;
un tiempo para guardar y un tiempo para tirar;
un tiempo para rasgar y un tiempo para coser;
un tiempo para callar y un tiempo para hablar;
un tiempo para amar y un tiempo para odiar;
un tiempo de guerra y un tiempo de paz.*

Eclesiastés 3

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Resumen / Abstract

Resumen

El estudio de la dinámica ecológica de las poblaciones localizadas en los límites de su distribución se considera esencial para establecer unas directrices de gestión adecuadas bajo las incertidumbres climáticas actuales. Las poblaciones de los márgenes posteriores suelen estar adaptadas a las condiciones ambientales locales en el límite de la amplitud ecológica de la especie, y a menudo muestran una persistencia a largo plazo. Las respuestas locales a los cambios ambientales pueden diferir de la respuesta media de la especie y tales diferencias pueden promover o dificultar la supervivencia de las poblaciones del margen posterior de distribución en las condiciones actuales de cambio global. Los robledales de *Q. pyrenaica* en Sierra Nevada representan uno de los márgenes más meridionales del área de distribución de esta especie. Están localizados en una región de montaña que ha servido de refugio para la especie. Al igual que otras formaciones forestales Mediterráneas, han estado sometidos a intensas presiones antropogénicas a lo largo del tiempo, lo que ha provocado una reducción de su extensión y una modificación de su composición florística y de sus patrones estructurales. Históricamente, los robledales han sido explotados en monte bajo para la obtención de leña, carbón vegetal, taninos. También se aclararon para generar grandes zonas de pastoreo. Todas estas actuaciones condujeron a una sobreexplotación de los robledales, de tal forma que la configuración actual

de estas formaciones en Sierra Nevada parece depender en gran medida del uso del pasado. Sin embargo, a partir de la segunda mitad del siglo XX se produjo un abandono de las actividades tradicionales, resultando en una disminución de la presión antrópica sobre los ecosistemas forestales. Paradójicamente, muchos robledales presentan un estado de degradación avanzado (e.g. problemas de regeneración, altas densidades, estancamiento en el crecimiento, entre otros). Estos problemas pueden verse agravados en el contexto actual de cambio climático, sobre todo teniendo en cuenta la alta vulnerabilidad de esta especie al cambio climático, y especialmente para las zonas situadas en el borde posterior de su área de distribución como es Sierra Nevada. Por tanto, entender la ecología de las poblaciones situadas en el borde posterior de su distribución es clave para evaluar la respuesta de la especie a las condiciones ambientales cambiantes. El objetivo general de esta tesis doctoral es analizar la dinámica de funcionamiento frente al cambio global de los robledales de *Q. pyrenaica* situados en Sierra Nevada, una región montañosa que representa uno de los límites geográficos de su distribución, donde estas formaciones han sido objeto de intensas presiones antrópicas.

En el [capítulo 1](#) prestamos la introducción y los objetivos de la tesis doctoral. Posteriormente en el [capítulo 2](#) presentamos el área de estudio, realizamos algunos apuntes sobre *Quercus pyrenaica*, y esbozamos de forma genérica la metodología empleada en la realización de la tesis doctoral.

En el [capítulo 3](#), utilizando información ambiental de alta resolución e inventarios forestales, hemos determinado que la precipitación y la radiación son las variables más importantes que explican la distribución de las poblaciones de robledal dentro de su margen de distribución. Hemos identificado la existencia de tres grupos de poblaciones de robledal dentro de Sierra Nevada, debido principalmente a las condiciones microambientales. Encontramos una notable coincidencia entre la agrupación de las poblaciones derivada del análisis de las variables ambientales y la ordenación de las poblaciones según la composición de especies, lo que sugiere una relación entre la heterogeneidad de los factores ambientales y la variabilidad de la composición de especies para estos bosques. Esta diversidad de condiciones ecológicas para las poblaciones de *Q. pyrenaica* situadas en este borde

posterior, está en consonancia con los altos niveles de diversidad genética mostrados por las poblaciones de esta especie en Sierra Nevada.

En el [capítulo 4](#) hemos estudiado el patrón de colonización de los cultivos de montaña por parte de *Q. pyrenaica* en dos localidades de Sierra Nevada. Para ello analizamos la estructura de la fuente de semillas (bosques circundantes), la abundancia de arrendajo *Garrulus glandarius* (principal dispersor de bellotas de roble), y la abundancia de juveniles de *Q. pyrenaica* en los cultivos abandonados. Asimismo caracterizamos en la medida de lo posible la historia de gestión antes y después del abandono de cultivos. Los resultados indican que se está produciendo una recolonización natural de las tierras de cultivo abandonadas por parte de *Q. pyrenaica* en el borde posterior de su distribución. Encontramos diferencias en el patrón de colonización entre los sitios de estudio, que parecen estar relacionadas con las diferencias en la gestión anterior y posterior al abandono. Nuestros resultados demuestran que incluso en las actuales condiciones climáticas cada vez más secas, los bosques de *Q. pyrenaica* son capaces de recuperar los antiguos campos de cultivo abandonados en el mismo nivel altitudinal donde el robledal es la vegetación potencial. Este proceso natural puede aportar soluciones para la conservación de la biodiversidad, y mejora la mitigación del cambio climático y la adaptación al mismo.

En el [capítulo 5](#) realizamos una estimación de la capacidad de secuestro de carbono por parte de los robledales de *Q. pyrenaica* en Sierra Nevada. Asimismo, estudiamos las tendencias temporales de la provisión de este servicio ecosistémico. Los robledales de Sierra Nevada, al igual que los del resto de la Península Ibérica, han experimentado un aumento de la biomasa total en las últimas décadas, y por tanto de su capacidad como sumidero de carbono. Los datos estimados de secuestro de Carbono para los robledales de Sierra Nevada son superiores a los observados para otras zonas, indicando el alto potencial como sumidero de carbono de estos robledales, a pesar de estar situados en el límite sur de su distribución. Estos resultados parecen estar relacionados con el hecho de que los robledales de Sierra Nevada son relativamente más jóvenes en comparación con otros robledales (debido al intenso uso antrópico al que han estado sometidos), y las condiciones de refugio en las que se encuentran los robledales de Sierra Nevada. Por otro

lado, se encontraron diferencias respecto al potencial de secuestro de Carbono entre las poblaciones de robledal de Sierra Nevada. Aquellas poblaciones que han estado sometidas a menos perturbaciones antropogénicas presentan una mayor riqueza estructural, que se ve reflejado en valores más altos de biomasa, y por tanto, en un mayor potencial de secuestro de carbono.

En el [capítulo 6](#), combinando el estudio del verdor de la vegetación derivado de imágenes de satélite, con análisis dendrocronológicos de árboles adultos, hemos analizado la resiliencia a la sequía del crecimiento primario y secundario de los robledales de Sierra Nevada. Las tendencias de crecimiento reflejaron una fuerte influencia del uso del suelo en la estructura forestal actual. El crecimiento primario y secundario de esta especie, aún siendo muy sensible a la disponibilidad de agua, mostró una alta resiliencia a corto y largo plazo a los eventos de sequía. Los altos valores de resiliencia observados sugieren que las poblaciones de robledal de Sierra Nevada se encuentran en el borde posterior geográfico pero no climático ni ecológico. La resiliencia a la sequía que muestran los robledales de Sierra Nevada no es espacialmente homogénea, debido a las diferencias en las condiciones ecológicas y a los legados del uso del suelo. La gran variabilidad en las respuestas entre sitios muy cercanos geográficamente, parece indicar que las respuestas a la sequía son dependientes del sitio y pueden variar drásticamente en gradientes espaciales extremadamente estrechos, como los que ocurren en regiones de montaña. En los últimos años se ha observado una tendencia positiva en la productividad primaria y en el crecimiento secundario de los robledales de Sierra Nevada. Esta respuesta es diferente a la tendencia negativa de crecimiento que cabría esperar para las poblaciones situadas en el borde sur de su distribución, tal y como se ha observado para otras especies templadas y mediterráneas.

En el [capítulo 7](#) evaluamos cómo modificaciones en los patrones de disponibilidad de agua debido al cambio climático pueden afectar a la productividad de robledales de Sierra Nevada. Utilizando información derivada de imágenes de satélite junto con un sistema de ontologías, hemos observado la concurrencia de cambios en los patrones de innovación (disponibilidad de agua) y en la productividad primaria de los robledales de *Q. pyrenaica*. En las zonas donde se ha detectado un adelanto en la fecha

de fusión de la nieve, es decir, la nieve presenta una tendencia significativa a retirarse antes, también se ha observado un aumento significativo en la productividad primaria de verano para los robledales. Este acoplamiento entre las tendencias de producción primaria y las de duración de la nieve es más patente para las poblaciones de robledales occidentales de Sierra Nevada. Esta modificación en los patrones de disponibilidad de agua debido al cambio climático parece estar afectando a la productividad estacional de los robledales.

Finalmente, en el [capítulo 8](#) realizamos una revisión de los servicios ecosistémicos proporcionados por los robledales de *Q. pyrenaica*, combinando una revisión bibliográfica para todo el área de su distribución con un análisis espacio-temporal de la provisión de servicios ecosistémicos, usando los robledales de Sierra Nevada como caso de estudio. Los robledales proporcionan una gran cantidad de servicios ecosistémicos. Además del papel que presentan estos bosques como proveedores de servicios de regulación (*e.g.* sumidero de Carbono) o de provisión (*e.g.* uso de su madera para el envejecimiento del vino), se ha puesto de manifiesto la existencia de un gran número de servicios ecosistémicos culturales proporcionados por los bosques de *Q. pyrenaica*. El análisis espacio-temporal de la provisión de servicios ecosistémicos reveló diferencias en la oferta de servicios ecosistémicos entre las poblaciones de robledal de Sierra Nevada, siendo las poblaciones del sur las que presentan mayores valores de servicios de regulación y las del norte las que presentan mayores valores de servicios culturales. Observamos una variación temporal en el suministro de servicios ecosistémicos. Hasta mediados del siglo pasado, los servicios de provisión predominaban sobre los servicios de regulación y culturales. El abandono de las actividades tradicionales provocó una disminución de los servicios de provisión a favor de los servicios de regulación y, en las últimas décadas, de los servicios culturales. Nuestra recopilación de datos a escala local nos ha permitido cuantificar muchos de los servicios ecosistémicos prestados por los bosques de *Q. pyrenaica*, lo cual proporciona a los gestores del territorio una información

muy valiosa que puede ayudar en la planificación de actuaciones de gestión y conservación de esta formación forestal.

Abstract

The study of the ecological dynamics of populations located at the limits of their distribution is considered essential to establish appropriate management guidelines under current climatic uncertainties. Rear-edge populations are usually adapted to local environmental conditions at the limit of the ecological range of the species, and often show long-term persistence. Local responses to environmental changes may differ from the average response of the species, and such differences may promote or hinder the survival of the rear-edge populations under current conditions of global change. *Q. pyrenaica* populations of Sierra Nevada represent one of the southernmost margins of this species' range. They are located in a mountain region that has served as a refuge for the species. Like other Mediterranean forest formations, *Q. pyrenaica* woodlands have been subjected to intense anthropogenic pressures over time, which has led to a reduction in their extent and a modification of their floristic composition and structural patterns. Historically, *Q. pyrenaica* forests been exploited in coppices for firewood, charcoal and tannins. They were also cleared to generate large grazing areas. All these actions led to an overexploitation of the *Q. pyrenaica* woodlands, so that the current configuration of these formations in the Sierra Nevada seems to depend largely on past use. However, from the second half of the 20th century onwards, traditional activities were abandoned, resulting in a decrease in anthropic pressure on forest ecosystems. Paradoxically, many *Q. pyrenaica* forests present an advanced state of degradation (regeneration problems, high tree stand densities, growth stagnation, among others). These problems may be aggravated in the current context of climate change, especially considering the high vulnerability of *Q. pyrenaica* to climate change, and particularly for populations located at the rear edge of its distribution range

such as Sierra Nevada. Therefore, understanding the ecology of populations located at the rear edge of its distribution is key to evaluate the response of the species to changing environmental conditions. The general objective of this doctoral thesis is to analyze the functioning dynamics in the face of global change of *Q. pyrenaica* populations located in Sierra Nevada, a mountainous region that represents one of the geographical limits of its distribution, where these formations have been subject to intense anthropic pressures.

In the [chapter 1](#) we stated the introduction and the objectives of the doctoral thesis. Then, in the [chapter 2](#) we present the study area, we describe some of the features of *Q. pyrenaica*, and we outline in a generic way the methodology used to carried out the doctoral thesis.

In the [chapter 3](#), using high-resolution environmental information, and forest inventories, we have determined that precipitation and radiation are the most important environmental variables explaining the distribution of *Q. pyrenaica* populations within their range. We identified three clusters of *Q. pyrenaica* populations within the Sierra Nevada, mainly due to microenvironmental conditions. We also found a remarkable match between the populations clustering derived from analysis of environmental variables, and the ordination of the populations according to species composition, suggesting a relationship between the heterogeneity of environmental factors and the variability of species composition for these forests. The diversity of ecological conditions for *Q. pyrenaica* populations in this rear edge are consistent with the high genetic diversity shown by populations of this oak in the Sierra Nevada.

In the [chapter 4](#) we studied the colonization pattern of *Q. pyrenaica* into abandoned mountain croplands, in two localities of Sierra Nevada. For this purpose, we analyzed the structure of the seed source (surrounding forests), the abundance of *Garrulus glandarius* jays (main disperser of oak acorns), and the abundance of *Q. pyrenaica* juveniles in abandoned croplands. We also characterized as far as possible the management history prior- and after- crop abandonment. The results indicate that natural recolonization of abandoned croplands by *Q. pyrenaica* is occurring at the rear edge of their distribution. We found differences in the colonization pattern among

study sites, which seems to be related to differences in pre- and post-abandonment management. Our results demonstrate that even in the current increasingly dry climatic conditions, *Q. pyrenaica* woodlands are able to recover the abandoned former arable fields at the same altitudinal level where oak woodland is the potential vegetation. This natural process can provide solutions for biodiversity conservation, and enhances climate change mitigation and adaptation.

In the [chapter 5](#) we estimate the carbon sequestration capacity of *Q. pyrenaica* forests in Sierra Nevada. We also studied temporal trends in the provision of this ecosystem service. The *Q. pyrenaica* woodlands of Sierra Nevada, like those of the rest of the Iberian Peninsula, have experienced an increase in total biomass in recent decades, and therefore in their capacity as a carbon sink. The estimated carbon sequestration data for the *Q. pyrenaica* forests of Sierra Nevada are higher than those observed for other areas, indicating the high potential of these oak forests as carbon sinks, despite being located at the southern limit of their distribution. These results seem to be related to the fact that the Sierra Nevada *Q. pyrenaica* forests are relatively younger compared to other oak forests (due to the intense anthropic use to which they have been subjected), and the refuge conditions in which the Sierra Nevada oak forests are found. On the other hand, differences of carbon sequestration potential among Sierra Nevada *Q. pyrenaica* populations were found. Those populations that have been subjected to less anthropogenic disturbances have a greater structural richness, which is reflected in higher biomass values, and therefore, in a higher carbon sequestration potential.

In the [chapter 6](#), we analyzed the resilience to drought of relict Mediterranean *Q. pyrenaica* populations in Sierra Nevada in relation to historical records of land use, combining dendroecological growth of adult trees and greenness (EVI) as proxies for secondary and primary growth. The growth trends reflected a strong influence of old land-use legacies in the current forest structure. Trees were highly sensitive to moisture availability, but both primary growth and secondary growth expressed high resilience to drought events over the short and the long term. The high values of resilience observed suggest that the studied *Q. pyrenaica* populations are located in a geographical but not a climatic or ecological rear edge. Resilience of oak

stands to drought events was not spatially homogeneous across the mountain range, due to differences in ecological conditions and/or past management legacies. The large variability in the response to climate along the rear edge seems to indicate that responses to drought are site-dependent and can vary dramatically along extremely narrow spatial gradients, such as those occurring in mountain regions. In recent years, a positive trend in primary productivity and secondary growth of Sierra Nevada oak forests has been observed. This response is different from the negative growth trend that would be expected for populations located at the rear edge of their distribution, as has been observed for other temperate and Mediterranean species.

In the [chapter 7](#) we evaluate how modifications in water availability patterns due to climate change may affect the productivity of Sierra Nevada *Q. pyrenaica* woodlands. Using information derived from satellite imagery together with an ontology system, we observed the concurrence of changes in snowfall patterns (water availability) and primary productivity of oak woodlands in the Sierra Nevada. In areas where we have detected an earlier snowmelt date, *i.e.* snow cover present a significant trend to melt earlier, we have also observed a significant increase in summer primary productivity for *Q. pyrenaica* woodlands. This coupling between primary production and snow duration trends is most apparent for western oak woodland populations in the Sierra Nevada. This modification in water availability patterns due to climate change appears to be affecting the seasonal productivity of oak woodlands.

Finally, in the [chapter 8](#) we review the ecosystem services provided by *Q. pyrenaica* woodlands, combining a general literature review (*e.g.* for the entire area of their distribution), with a spatio-temporal analysis of ecosystem service supply, using the Sierra Nevada *Q. pyrenaica* woodlands as a case study. *Q. pyrenaica* forests provide a large number of ecosystem services. In addition to the role of these forests as providers of regulating services (*e.g* carbon sink) or provisioning services (*e.g* use of their wood for wine aging), the existence of a large number of cultural ecosystem services provided by oak forests has been revealed. Spatio-temporal analysis of ecosystem services revealed differences in the supply of ecosystem services among Sierra Nevada

oak woodland populations, with southern populations having higher values of regulating services and northern populations having higher values of cultural services. We observed temporal variation in the supply of ecosystem services. Until the middle of the last century, provisioning services predominated over regulating and cultural services. The abandonment of traditional activities led to a decline in provisioning services in favor of regulating services and, in recent decades, cultural services. Our compilation of data at the local scale has allowed us to quantify many of the ecosystem services provided by the *Q. pyrenaica* forests, which provides land managers with valuable information that can help in the planning of management and conservation actions for this forest formation.

Parte I

Introducción y Metodología

Introducción General

1.1. Vivir en los márgenes de distribución

La hipótesis Centro-Periferia (**CPH** de su siglas en inglés, *Centre-Periphery Hypothesis*) es un postulado biogeográfico que pretende explicar la variación de las características demográficas, genéticas y ecológicas de especies en sus áreas de distribución (Pironon *et al.*, 2015; Sexton *et al.*, 2009). Esta hipótesis asume que el rango de distribución de una especie es una representación geográfica de su rango ecológico, y por tanto las condiciones ambientales son óptimas en el centro de su área de distribución y más severas en las regiones periféricas (Pironon *et al.*, 2017) (Figura 1.1). Así, las poblaciones situadas en la periferia geográfica experimentan condiciones ecológicas (abióticas y/o bióticas) más desfavorables que conducen a menor densidad de población y eficacia ecológica (*fitness*, Brown, 1984). A medida que se alcanzan los límites de los recursos ecológicos de las especies, las poblaciones se vuelven más pequeñas y más aisladas espacialmente, y tienden a perder variación genética (García *et al.*, 2010a; Kark *et al.*, 2008). La hipótesis Centro-Periferia se ha utilizado ampliamente como base de diferentes hipótesis sobre procesos ecológicos y evolutivos, abordando desde el flujo genético entre poblaciones a otras cuestiones más aplicadas como la forma en la que las poblaciones responderán al cambio climático (Sagarin & Gaines, 2002).

Tradicionalmente se ha considerado que las poblaciones situadas en los márgenes de su rango de distribución presentan un peor rendimiento, son más vulnerables, y presentan una baja diversidad genética, en comparación con las situadas en el centro de su distribución. Sin embargo, en los últimos años se ha observado cómo algunos rasgos funcionales (e.g. supervivencia, fecundidad) no siempre siguen las predicciones de esta hipótesis (Pironon *et al.*, 2017). Varios trabajos de revisión que realizan una compilación de estudios de ecología y evolución basados en el supuesto de la hipótesis centro-periferia, encontraron evidencias empíricas a favor de esta hipótesis en un 40-50 % de los estudios analizados (Pironon *et al.*, 2017; Sagarin & Gaines, 2002). Eckert *et al.* (2008), en una revisión de estudios sobre la variación genética entre las poblaciones periféricas y centrales de 115 especies, encontraron que el 64 % de los estudios presentaban el esperado declive en diversidad genética en las poblaciones situadas en los márgenes. Sin embargo, constataron que las diferencias genéticas en la mayoría de los

estudios eran pequeñas, y sobre todo que los mecanismos que generan ese patrón no estaban claros. Éstas y otras revisiones (e.g. Abeli *et al.*, 2014), han puesto de manifiesto la existencia de numerosas excepciones a la hipótesis centro periferia, sobre todo en poblaciones de especies vegetales. Así por ejemplo, en especies forestales mediterráneas como *Pinus sylvestris*, se han observado tendencias de crecimiento mas positivas en poblaciones situadas en el límite inferior de su distribución que en las zonas centrales y en las zonas de latitudes mas al norte (Matías *et al.*, 2017). Asimismo, estudios en poblaciones periféricas de haya (*Fagus sylvatica*) han revelado una mayor resiliencia y estabilidad frente a eventos de sequía (Vilà-Cabrera *et al.*, 2019). Por otro lado, varios estudios genéticos sobre *Quercus pyrenaica*, han puesto de manifiesto una mayor diversidad genética en las poblaciones localizadas en Sierra Nevada, uno de sus límites de distribución meridional, que en otras áreas situadas en el centro de su distribución (Valbuena-Carabaña & Gil, 2013, 2017). Por tanto, ante las numerosas excepciones a la hipótesis CPH, algunos autores han apuntado la necesidad de llevar a cabo una nueva redefinición de la teoría para explicar los efectos de la marginalidad en plantas y para identificar patrones generales (Abeli *et al.*, 2014), y sobre todo, se ha señalado que se necesitan mas estudios que nos permitan una mejor comprensión de las dinámicas de las poblaciones situadas en los márgenes de su distribución (Fady *et al.*, 2016; Hampe & Jump, 2011; Jump *et al.*, 2010; Vilà-Cabrera *et al.*, 2019).

Las poblaciones localizadas en el frente de retroceso (*rear-edge, sensu* Hampe & Petit, 2005) son desproporcionadamente importantes para la conservación a largo plazo de la diversidad genética de la especie, así como para la historia filogeográfica y el potencial evolutivo de la especie (Hampe & Petit, 2005; Willis & Birks, 2006; Woolbright *et al.*, 2014). Comprender con detalle el funcionamiento de las poblaciones situadas en el frente de retroceso es esencial para su conservación, y para la compresión de las respuestas de las especies y poblaciones al cambio climático (Fady *et al.*, 2016; Hampe & Jump, 2011; Jump *et al.*, 2010).

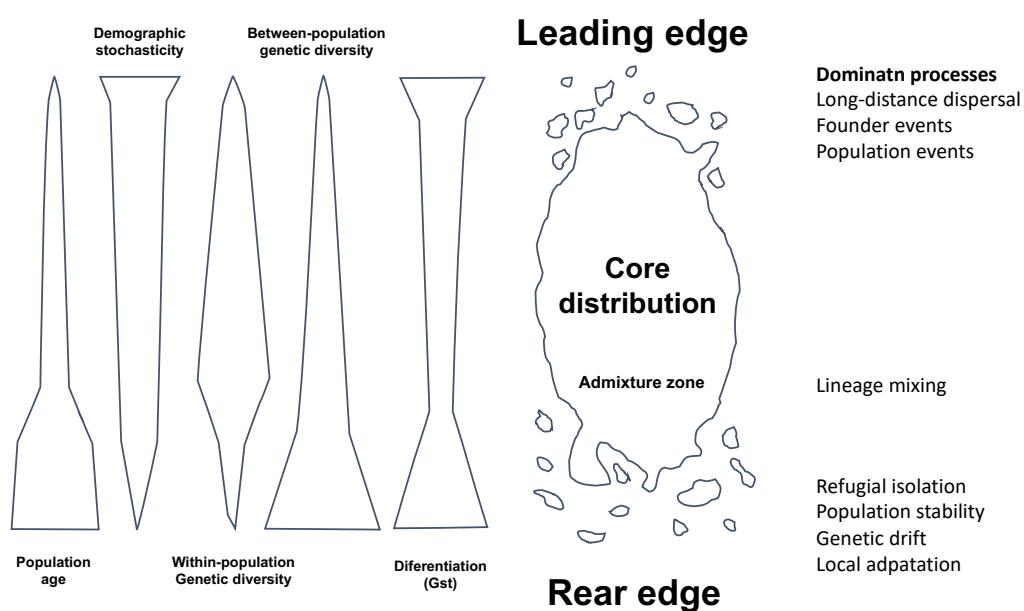


Figura 1.1. Representación esquemática de las poblaciones del frente de avance y de retroceso en respuesta al cambio climático. Varios autores sugieren que las poblaciones del borde posterior (*rear-edge*) pueden ser extremadamente importantes para la conservación a largo plazo de la diversidad genética, y por tanto es necesario prestarse especial atención a la modelización de los impactos del cambio climático sobre estas poblaciones. Dibujado a partir de (Hampe & Petit, 2005; Willis & Birks, 2006; Woolbright *et al.*, 2014)

1.2. ... y en zonas de montaña

Las áreas montañosas albergan aproximadamente la mitad de los *hotspots* de biodiversidad del planeta (Kohler *et al.*, 2014; Spehn & Körner, 2009). En ellas se observa una alta diversidad de condiciones ambientales, debido principalmente a que presentan amplios gradientes climáticos en pequeñas escalas espaciales (Kohler *et al.*, 2014; Zamora *et al.*, 2021). Esto, unido a la alta sensibilidad y vulnerabilidad que presentan sus ecosistemas aislados geográfica y ecológicamente, hace que las áreas de montaña actúen como sistemas de alerta temprana de los impactos del cambio global (Kohler & Maselli, 2009; Macchi & ICIMOD, 2010; Price *et al.*, 2011; Zamora *et al.*, 2017b; Zamora *et al.*, 2015) considerándose laboratorios naturales donde estudiar los impactos del cambio global (Doblas-Miranda *et al.*, 2015; Jump *et al.*, 2009; Zamora, 2010). Algunas especies, tienen localizadas las poblaciones que constituyen los bordes traseros de su distribución en zonas de montaña. Estas poblaciones se sitúan en zonas con una alta heterogeneidad de factores edáficos y topográficos, que parecen haber actuado como islas microclimáticas dentro de una región climática adversa, lo que ha sido de gran importancia para la persistencia de algunas especies (Abel Schaad *et al.*, 2014; Meineri & Hylander, 2017). Por ejemplo en Sierra Nevada, la heterogeneidad climática y topográfica existente, ofrece una gran diversidad de micro hábitats que ha permitido que esta región montañosa actúe como refugio de diferentes especies (Blanco-Pastor *et al.*, 2019; Gómez & Lunt, 2007; Médail & Diadema, 2009), incluso para especies de *Quercus* caducifolios durante el último periodo glacial (Brewer *et al.*, 2002; Olalde *et al.*, 2002; Rodríguez-Sánchez *et al.*, 2010).

En las regiones de montaña, además existen gradientes de escala más fina anidados dentro de cada montaña, que reproducen las condiciones de los bordes y del centro de distribución de las especies, haciendo muy complejas las interpretaciones de lo que ocurre con las especies que sitúan sus bordes de distribución en estas regiones, por lo que son zonas extremadamente importantes para su estudio (Jump *et al.*, 2009).

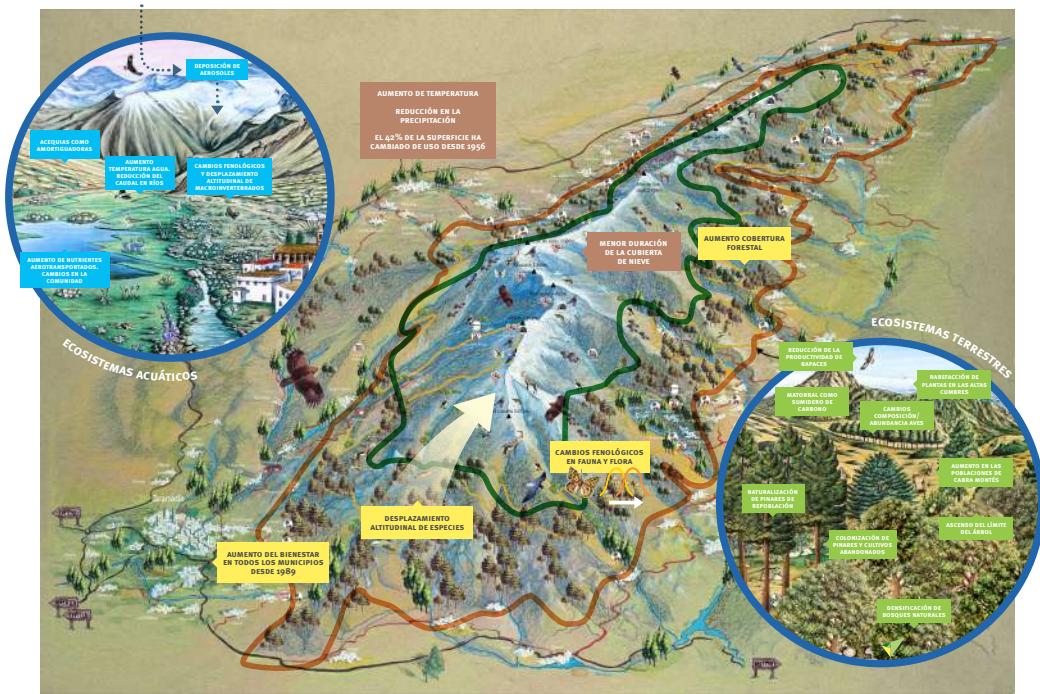


Figura 1.2. Principales impactos del cambio global en Sierra Nevada una región montañosa del sur de la Península Ibérica. Fuente: Zamora *et al.* (2015).

1.3. ... y con cambio climático

En la actualidad existen evidencias científicas de los efectos del cambio climático sobre los sistemas naturales (IPCC, 2013). Muchos procesos se están viendo alterados debido al cambio climático: cambios en el área de distribución de las especies (Thuiller *et al.*, 2005); alteraciones fenológicas (Estiarte & Peñuelas, 2015; Gordo & Sanz, 2005), invasiones de especies (González-Moreno *et al.*, 2014), aumento en la severidad e incidencia de plagas forestales (Hódar *et al.*, 2012; Hódar & Zamora, 2004), alteraciones en las interacciones ecológicas (Montoya & Raffaelli, 2010), por citar algunos. Estos y otros cambios están modificando la composición, estructura y el funcionamiento de los ecosistemas, así como los bienes y servicios que éstos proporcionan (Ding *et al.*, 2016). Para la región Mediterránea, los efectos del cambio climático se espera que sean más severos que en otras regiones de la Tierra (Giorgi, 2006; IPCC, 2013) y en los ecosistemas forestales mediterráneos estos cambios tendrán impactos significativos (Herrero &

Zavala, 2015; Peñuelas *et al.*, 2017; Regato, 2008; Resco de Dios *et al.*, 2006).

En la región Mediterránea se ha registrado en las últimas décadas un aumento generalizado de las temperaturas, así como un cambio en los patrones de precipitación (Cramer *et al.*, 2020; Giorgi & Lionello, 2008; Pérez & Boscolo, 2010). Para Sierra Nevada, usando datos de estaciones meteorológicas y mapas climáticos de alta resolución (Benito *et al.*, 2014), también se han encontrado tendencias positivas para la temperaturas mínimas y máximas anuales, así como un patrón generalizado de reducción de la precipitación anual desde la década de 1960 (Pérez-Luque *et al.*, 2021; Pérez-Luque *et al.*, 2016a).

Una de las característica del cambio climático, además del aumento en las temperaturas y el cambio en el régimen de precipitaciones, es el aumento de los eventos extremos, tales como sequías, tormentas, inundaciones, etc. (IPCC, 2013). A pesar de que la sequía es una característica del clima mediterráneo (Lionello, 2012), en las últimas décadas se ha registrado un incremento en la duración, frecuencia y severidad de los eventos de sequía (Coll *et al.*, 2017; Lloyd-Hughes & Saunders, 2002; Sousa *et al.*, 2011), particularmente en el sur de Europa (Páscoa *et al.*, 2017; Spinoni *et al.*, 2015; Stagge *et al.*, 2017; Vicente-Serrano *et al.*, 2014), donde además se ha observado una tendencia hacia veranos más secos (Spinoni *et al.*, 2017) (Figura 1.3). Este hecho cobra especial relevancia para el área Mediterránea, considerada una de las más vulnerables frente al cambio climático (Giorgi, 2006), ya que las proyecciones a futuro pronostican un aumento de la severidad de los eventos climáticos extremos (Hoerling *et al.*, 2012; IPCC, 2013; Spinoni *et al.*, 2018; Trenberth *et al.*, 2014).

El incremento en la frecuencia y severidad de las sequías está alterando el funcionamiento de los ecosistemas mediterráneos a diferentes escalas (Forner *et al.*, 2018; Liu *et al.*, 2020; Ogaya & Peñuelas, 2021; Peñuelas *et al.*, 2017), puesto que la sequía afecta a aspectos fisiológicos, funcionales, estructurales y demográficos de los ecosistemas forestales (Allen *et al.*, 2010; Assal *et al.*, 2016). No obstante, se están observando respuestas diferenciales de los ecosistemas forestales a la sequía (Anderegg *et al.*, 2020), poniendo de manifiesto la importancia de otros aspectos como el momento en el que

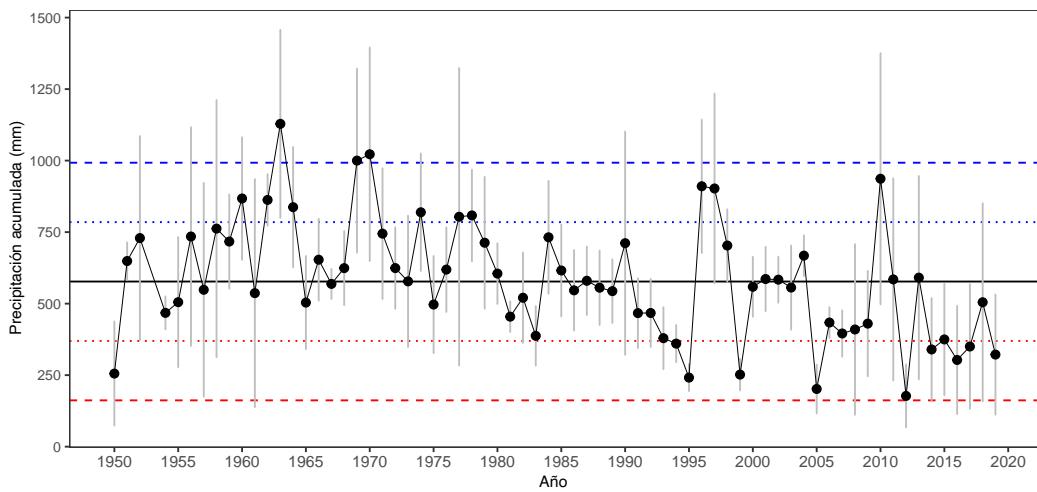


Figura 1.3. Evolución temporal de la precipitación acumulada (año hidrológico) durante el periodo 1950-2020 para Sierra Nevada (datos procedentes de 28 estaciones meteorológicas). Los puntos representan la media y las barras de error, el error estándar. La línea negra indica la precipitación acumulada media para todo el periodo (585 mm). Las líneas rojas representan -1 y -2 desviaciones estándar (líneas punteadas y discontinuas respectivamente). Las líneas azules representan +1 y +2 desviaciones estándar (líneas punteadas y discontinuas, respectivamente). Datos de (Pérez-Luque *et al.*, 2021)

ocurre la sequía (Huang *et al.*, 2018). Esto es de especial relevancia para especies de frondosas como el *Quercus pyrenaica* que presenta una fenología de crecimiento bien marcada (Pérez-de Lis *et al.*, 2016).

Q. pyrenaica presenta una alta vulnerabilidad al cambio climático en la Península Ibérica (Benito *et al.*, 2011; Benito-Garzón *et al.*, 2008; García-Valdés *et al.*, 2013), lo cual es particularmente importante en las zonas más cálidas de su distribución (Gea-Izquierdo & Cañellas, 2014). Las simulaciones basadas en modelos de distribución de especies pronostican un potencial desplazamiento del área de distribución, así como una disminución en la idoneidad del hábitat para esta especie (Benito *et al.*, 2011; Benito-Garzón *et al.*, 2008; Felicísimo, 2011; Felicísimo *et al.*, 2012; Mateo *et al.*, 2010; Ruiz-Labourdette *et al.*, 2011; Urbieta *et al.*, 2011), que potencialmente puede suponer una reducción en la superficie ocupada a consecuencia del aumento de temperatura pronosticado (Benito *et al.*, 2011; Benito-Garzón *et al.*, 2008). Esto es particularmente importante para Sierra Nevada, donde además de la disminución del área de ocupación se prevé una migración altitudinal (Benito *et al.*, 2011; Benito, 2009), así como un aumento de la

competencia con otras especies, ya que las zonas actualmente ocupadas por los robledales en Sierra Nevada serán óptimas para los encinares (Benito *et al.*, 2011).

1.4. ... y con cambios de uso

A menudo se pasa por alto que la actividad humana constituye un impulsor de cambio tan poderoso o incluso más que los impulsores naturales (*i.e.*, la variación natural del clima), en particular para las regiones con una larga historia de manejo, como la región Mediterránea (Doblas-Miranda *et al.*, 2017; Navarro-González *et al.*, 2013). En estas zonas, la susceptibilidad y la respuesta de los ecosistemas al cambio climático están condicionadas por los legados del uso del suelo (Mausolf *et al.*, 2018; Munteanu *et al.*, 2015). Los legados del uso pasado, interactúan con las perturbaciones climáticas recientes causadas por el hombre y pueden confundir su interpretación (Foster *et al.*, 2003). Esto es importante ya que en la Península Ibérica se ha constatado que una cuarta parte de los bosques actuales crecen en antiguos terrenos agrícolas y de pastoreo abandonados después de la década de 1950 (Vilà-Cabrera *et al.*, 2017). En consecuencia, la modificación antropogénica del hábitat y sus legados representan una dimensión crítica para las poblaciones situadas en su borde de distribución, ya que pueden intensificar, enmascarar o retrasar el declive poblacional impulsado por el clima en estas zonas (Sánchez de Dios *et al.*, 2020; Vilà-Cabrera & Jump, 2019).



Figura 1.4. Principales usos antrópicos del robledal. Pilas de leña para carboneo tradicional (1); quemas para la creación de áreas de pastoreo y cultivos (2); leñas para uso doméstico (3); pastoreo (4); y producción de bellotas (5). (Fuente: Pérez-Luque *et al.*, 2021a)

Los robledales de *Q. pyrenaica*, al igual que otras formaciones forestales, han sido objeto de intensas presiones de origen antrópico que han provocado la reducción de su área de distribución, así como la modificación en sus patrones florísticos y estructurales (Gavilán *et al.*, 2000; Gavilán *et al.*, 2007; Tárrega *et al.*, 2006). Históricamente se han explotado en monte bajo para la obtención de leñas, carbón, taninos y producción de casca (Ruiz de la Torre, 2006). También se han llevado a cabo clareos para crear pastos con bajas densidades de árboles maduros que proporcionan bellotas, leñas y amplias áreas para el pastoreo; e incluso a veces se quemaban para crear áreas de pastoreo (Valbuena-Carabaña & Gil, 2017). De hecho, el sobrepastoreo en estas formaciones provocaba unas importantes pérdidas de suelo, aspecto que se viene señalando por los gestores forestales desde final del siglo XIX (Laguna, 1872). Todos estos procesos antropogénicos han transformado tanto las estructuras de los robledales, que es difícil encontrar rodales que puedan considerarse como bosques naturales (Ruiz de la Torre, 2006). Esta presión antrópica también se ha observado en los robledales de Sierra Nevada (Jiménez Olivencia, 1991), donde el intenso aprovechamiento ganadero y forestal, la roturación de espacios para nuevos cultivos y pastos, la explotación de leña para uso doméstico o industrial, e incluso los incendios forestales, han ocasionado la reducción de la superficie que ocupaban estas formaciones (Camacho-Olmedo *et al.*, 2002b) (Figura 1.4). Así, por ejemplo,

el melojar de la Solana de la Dehesa de San Jerónimo, sufrió una tala masiva en la posguerra para utilizar la leña como gasógeno para los automóviles (Prieto, 1975). En algunas zonas de Sierra Nevada, la presión antrópica ha sido tan intensa, que se perdió por completo la cubierta forestal, ocasionando graves problemas de erosión (Mesa Garrido, 2019; Romero-Zurbano, 1909). Todas estas actuaciones condujeron a una sobreexplotación de los robledales cuya configuración actual en Sierra Nevada parece depender, al igual que otras formaciones vegetales, del uso del pasado (Navarro-González *et al.*, 2013). Sin embargo, a partir de la segunda mitad del siglo XX se produjo un abandono rural que produjo una disminución de la presión antrópica sobre los ecosistemas forestales. Es por ello que analizar la dinámica de los robledales frente a los cambios de uso del suelo resulta crucial dada la importancia que tiene el uso del pasado en la configuración actual de estos ecosistemas, más teniendo en cuenta que representan uno de los bordes más meridionales de su distribución.

1.5. Problemas de conservación del robledal en el borde de su distribución

Las principales amenazas que sufren los melojares parecen estar relacionadas con las transformaciones productivas y de usos del suelo generadas por los intensos cambios socioeconómicos ocurridos durante las últimas décadas (Piqué & Vericat, 2015; Vericat *et al.*, 2012). Este conjunto de efectos se ha convertido en el principal agente transformador de los melojares, que además pueden actuar de forma sinérgica con los impactos derivados del cambio climático. La sustitución de los robledales en el pasado por cultivos y pastos relegó al robledal a las laderas y pendientes más inclinadas (Allué, 1997; Blanco Castro *et al.*, 2005; García & Jiménez, 2009; Jiménez-Olivencia *et al.*, 2015). El abandono de los usos forestales tradicionales ha provocado posteriormente una acumulación de biomasa en el monte que incrementa la vulnerabilidad y la sensibilidad de estas formaciones ante los incendios forestales (Allué, 1997; Calvo *et al.*, 1999; García & Jiménez, 2009). Por otro

lado, debido a la gran capacidad de recuperación que presenta esta especie frente a perturbaciones puntuales (como un incendio) (Calvo *et al.*, 2003; Calvo *et al.*, 1999), el riesgo de sufrir incendios recurrentes aumenta debido a la acumulación de altas densidades de biomasa aérea (Cañellas *et al.*, 2008; Cañellas *et al.*, 2004).

Otras amenazas específicas sobre los melojares están relacionadas con los problemas de regeneración y baja supervivencia de las plántulas. Tradicionalmente se ha asumido que los robledales, debido a su debilitado estado de salud, producen pocas bellotas. De hecho, se han aclarado las masas con el objetivo de reducir la competencia por los recursos y mejorar el estado de la masa (Aldea *et al.*, 2017a; Cañellas *et al.*, 2004; Moreno-Fernández *et al.*, 2020), lo cual puede derivar en una mayor capacidad de reproducción y de producción de bellota (Bravo *et al.*, 2008). Sin embargo, se ha visto en algunas especies congénères que estos efectos se mantienen solo en el corto plazo (Sanchez-Humanes & Espelta, 2011), y que incluso pueden llegar a producir una disminución de la producción de bellota (Martiník *et al.*, 2017).

Los robledales, al igual que otras especies del género *Quercus*, también sufren la incidencia de plagas forestales, entre las que destaca el complejo de lepidópteros defoliadores. Este complejo que alberga a mas de 50 especies de diferentes familias de lepidópteros (Soria, 1988; Soria, 1987), debilita el estado de salud de las masas forestales, afectando también a la producción de bellota. En Sierra Nevada, se han detectado mas de 25 especies de este complejo defoliador (J.M. Muñoz *com. pers.*), comportándose algunas como plagas en determinados años (*e.g. Lymantria dispar, Tortrix viridiana*).

La dispersión de las bellotas se realiza principalmente por parte del arrendajo (*Garrulus glandarius*). En Sierra Nevada, se ha observado un descenso en la densidad de este córvido, pasando de 6.6 ind/10 ha en los años 80 a 1.25 ind/10 ha en la actualidad (Zamora & Barea-Azcón, 2015). Las bellotas de roble melojo son consumidas por varias especies de vertebrados como el ratón de campo (*Apodemus sylvaticus*), el jabalí (*Sus scrofa*) o el ganado doméstico (Gómez *et al.*, 2001; Perea *et al.*, 2014), que actúan en diferentes micro hábitats. Por ejemplo, los jabalís prefieren los espacios abiertos mientras que los ratones consumen selectivamente las bellotas situadas debajo de los

arbustos, por lo que disminuyen los lugares seguros para el reclutamiento (Gómez *et al.*, 2003).

La sequía estival junto con los daños causados por los ungulados provocan una considerable mortalidad de plántulas y juveniles de esta especie (Baraza *et al.*, 2004; Perea *et al.*, 2014). Las plántulas emergidas sufren unas altas tasas de mortalidad, debidas fundamentalmente al pisoteo y al consumo por parte de vertebrados como jabalíes, ratones y liebres (Gómez *et al.*, 2003; Perea *et al.*, 2014). Por otro lado, la herbivoría también se ve condicionada por las diferencias en las características químicas de las plántulas de especies arbóreas, propiciando un consumo diferencial por parte de los ungulados (Baraza, 2005; Baraza *et al.*, 2004; Baraza *et al.*, 2007). En Sierra Nevada, el roble y el arce (*Acer opalus* subsp. *granatensis*) presentan una alta calidad nutritiva en comparación con otras especies forestales con las que conviven (e.g pino albar, pino salgareño y encina), lo que supone una alta probabilidad de consumo, incluso cuando son juveniles. Además, el efecto de la herbivoría sobre la regeneración del roble, y de otras especies forestales, depende, también de la frecuencia y severidad con la que son ramoneados los individuos (juveniles), y de la capacidad de tolerancia que presentan. Así los juveniles de las especies con mayor probabilidad de consumo (menos resistentes), muestran una mayor recuperación tras la herbivoría (tolerancia) respecto a las especies menos palatables (Baraza *et al.*, 2007).

Otro factor a tener muy en cuenta respecto al reclutamiento del robledal es la intensidad y duración de la sequía estival. Se ha comprobado que el roble junto con la encina son las especies que presentan mayor probabilidad de reclutamiento en veranos secos (Mendoza *et al.*, 2009). Asimismo, cuando ocurren veranos más húmedos, aumenta drásticamente la supervivencia del banco de plántulas de roble (Mendoza *et al.*, 2009).

1.5.1. Conservación de los robledales

Q. pyrenaica está incluida con la categoría de "Preocupación menor" en la Lista Roja de Especies Amenazadas de la IUCN (Gorener *et al.*, 2017), así como en la Lista Roja Europea de Árboles (Rivers *et al.*, 2019). En algunos catálogos autonómicos aparece con diferentes grados de protección. En

Andalucía, se consideró como Vulnerable con riesgo menor pendiente de conservación (Vivero *et al.*, 2000). Asimismo se incluye en la Lista Roja de la Flora Vascular de Andalucía bajo la categoría "NT" (Casi Amenazada) (Cabezudo *et al.*, 2005). Finalmente, en Sierra Nevada siguiendo criterios UICN se ha catalogado como de menor riesgo, dependiente de la conservación (LRcd) (Blanca *et al.*, 1998; Blanca *et al.*, 2001; Lorite *et al.*, 2007; Lorite, 2016).

Los bosques de *Q. pyrenaica* están protegidos a nivel europeo por la Directiva Hábitats (92/43/CEE) (en el anexo I como "9230 Robledales galaico-portugueses con *Quercus robur* y *Quercus pyrenaica*") e incluidos en la Red Natura 2000. Aparecen en diferentes esquemas de clasificación de hábitats:

- EUNIS Hábitat Classification (Davies *et al.*, 2004): G1.7B4 Baetic [*Quercus pyrenaica*] forests
- Palearctic Habitat Classification 1996 (Devillers & Devillers-Terschuren, 1998): 41.6 *Quercus pyrenaica* forests

El 18.41 % de la distribución actual de los melojares en España aparece bajo algún nivel de protección ya que se encuentran en diversos espacios naturales protegidos. Asimismo aparece en la Lista Patrón de Hábitats Terrestres como 41.64 *Bosques béticos de Quercus pyrenaica*.

1.6. Conocimiento de la dinámica de los robledales en el borde de su distribución

Los robledales de Sierra Nevada han sido objeto de numerosos estudios, predominando los de índole ecológico y fitosociológico. Se han realizado trabajos de caracterización de los robledales desde un punto de vista fitosociológico, llevando a cabo clasificaciones basadas en la composición y abundancia de especies (*e.g.* Lorite *et al.*, 2008; Martínez-Parras & Molero-Mesa, 1982; Melendo & Valle, 2000). Asimismo, se ha abordado diferentes aspectos ecológicos, como por ejemplo (por citar algunos): efecto de la

herbivoría en el reclutamiento (e.g. Baraza *et al.*, 2004; Baraza *et al.*, 2007; Gómez *et al.*, 2003); el reclutamiento bajo diferentes escenarios de sequía (Mendoza *et al.*, 2009); la evaluación de las respuestas de los juveniles a diferentes escenarios lumínicos (Gómez-Aparicio *et al.*, 2008); la evaluación de la supervivencia de juveniles por encima del límite del árbol (Leverkus *et al.*, 2015). Por otro lado también se han abordado estudios genéticos de los diferentes tipos de robledales (e.g. Valbuena-Carabaña & Gil, 2013, 2017; Valbuena-Carabaña & Gil, 2011), así como estudios de la microbiota de estas formaciones (Cobo-Díaz *et al.*, 2017; Lasa *et al.*, 2019a; Lasa *et al.*, 2019b). Otros trabajos han evaluado el funcionamiento de estas formaciones usando índices derivados de teledetección (Alcaraz-Segura *et al.*, 2015; Dionisio *et al.*, 2012; Requena-Mullor *et al.*, 2018), así como las tendencias de crecimiento usando métodos dendrocronológicos (Gea-Izquierdo & Cañellas, 2014; Rubio-Cuadrado *et al.*, 2018). Destacan también los estudios de cambio de uso (Camacho-Olmedo *et al.*, 2002; Jiménez-Olivencia *et al.*, 2015), y aquellos donde se propone la utilización de plantas nodrizas para la restauración de robledales (Castro *et al.*, 2006; Gómez-Aparicio *et al.*, 2004). Éstos y otros estudios, han aportado una valiosa información sobre aspectos concretos de la ecología y el funcionamiento de los robledales. No obstante, en este memoria doctoral, pretendemos aumentar ese conocimiento centrandonos en varios aspectos relacionados con la dinámica de funcionamiento de esta formación frente al cambio global (cambios de uso y cambio climático) en el límite sur de su distribución.

1.7. Objetivos

Así pues el **objetivo** general de esta memoria doctoral es analizar la dinámica de funcionamiento frente al cambio global de los robledales de *Q. pyrenaica* situados en Sierra Nevada, una región montañosa que representa uno de los límites geográficos de su distribución, donde estas formaciones han sido objeto de intensas presiones antrópicas.

Los objetivos específicos son:

Caracterizar los robledales de Sierra Nevada desde un punto de vista ambiental

Bajo la hipótesis de que las poblaciones del límite sur de distribución geográfica de *Q. pyrenaica* localizadas en zonas de montaña son representativas de diferentes condiciones ambientales a escala local debido a los fuertes gradientes topográficos existentes, queremos analizar si las poblaciones de robledal de Sierra Nevada habitan en condiciones similares, y hasta qué punto la variabilidad ambiental se corresponde con diversidad florística. En este sentido, pretendemos: (i) determinar las variables ambientales que mejor explican la distribución de las poblaciones de melojo en Sierra Nevada; (ii) identificar grupos de poblaciones de robledal en función de la composición florística y las condiciones ambientales; y (iii) analizar si la agrupación de las poblaciones de melojo en función de las variables ambientales coincide con su agrupación en función de la composición florística.

Analizar el proceso de colonización de hábitats degradados próximos a las masas de robledal en Sierra Nevada

Tras el abandono de actividades tradicionales, queremos analizar el proceso de colonización de hábitats degradados (campos de cultivo abandonados) próximos a los robledales y explorar si existen diferencias entre las poblaciones en el límite sur de su distribución.

Cuantificar el papel de los robledales de Sierra Nevada como sumidero de carbono y analizar su tendencia temporal

El secuestro de carbono es uno de los servicios ecosistémicos más relevantes que proporcionan los bosques mediterráneos, siendo un indicador de la capacidad del ecosistema para contribuir a la regulación del clima. Los robledales, como ecosistemas mediterráneos representan un sumidero de carbono. El objetivo de este capítulo es cuantificar la capacidad de secuestro de carbono de los robledales de Sierra Nevada, situados en el borde de su distribución, explorando las posibles diferencias entre las poblaciones de robledal dentro de esta región montañosa. Asimismo estamos interesados en analizar la evolución temporal de este servicio ecosistémico

Analizar los efectos del cambio climático en la productividad de los robledales en Sierra Nevada

Pretendemos evaluar cómo las alteraciones en los patrones de disponibilidad hídrica debido al cambio climático pueden afectar a la productividad de esta formación forestal. Sabemos que los robledales presentan una estación de crecimiento bien definida y centrada en la estación estival. Por ello es de interés evaluar la productividad de los robledales (utilizando índices de vegetación obtenidos a partir de imágenes de satélite) frente a cambios en los patrones de disponibilidad hídrica. Nos centraremos en analizar modificaciones en la cantidad de agua (disminución de la disponibilidad de agua debido a eventos de sequía) así como alteraciones en la distribución temporal de la disponibilidad de agua (*p.ej.*: adelantos en la fusión de la cubierta de nieve).

Evaluar la resiliencia de los robledales en su borde de distribución frente a eventos de sequía

El cambio global supone un reto para los ecosistemas forestales localizados en el límite de su distribución debido a su vulnerabilidad a los eventos de sequía. Nuestro objetivo es analizar la resiliencia a varios eventos de sequía de las poblaciones relictas de *Q. pyrenaica* situadas en Sierra Nevada. Para ello, combinaremos información de teledetección y métodos dendroecológicos para evaluar el impacto de la sequía tanto en el verde de la vegetación (como indicador del crecimiento primario) como en el crecimiento radial de los árboles (como indicador del crecimiento secundario).

Identificar y cuantificar los servicios ecosistémicos proporcionados por los robledales en Sierra Nevada

Realizaremos una revisión de los principales servicios ecosistémicos proporcionados por los robledales combinando revisiones bibliográficas con conocimiento experto y datos de Sierra Nevada, con el objetivo de poner de relieve los diferentes servicios ecosistémicos que proporcionan estas formaciones para incorporarlas a las estrategias de gestión de estos ecosistemas.

Metodología general

2.1. El roble melojo

Quercus pyrenaica Willd. es un árbol caducifolio de hojas marcescentes que alcanza hasta 20-25 m, de copa amplia (Figura 2.1). La corteza es cenicienta o pardo-grisácea, gruesa y agrietada. El tronco aparece muchas veces tortuoso. Ramillas pardas cuando jóvenes, después grisáceas, tomentosas. Presenta un sistema radical muy potente con numerosas raíces horizontales, superficiales, copiosamente estoloníferas, que dan lugar a la formación de matas periféricas tapizantes. Hojas pinnatífidas o pinnatipartidas, de base truncada o cordada; las adultas de haz verde y glabrescente y envés densamente tomentoso, con los pelos estrellados, que a menudo se mantienen marchitas y sin caer durante gran parte del invierno. Flores unisexuales; las masculinas en amentos laxos, colgantes, con perianto de lóbulos hirsutos y estambres expertos; las femeninas con estilos en el interior de un involucro de numerosas escamas (cúpula), en grupos raciformes de 1 a 4, sentadas o cortamente pedunculadas. Fruto en aquenio (bellota), envuelto por la cúpula en su parte basal, solitario o en grupos de 2-3, de color pardo-amarillento. Florece en abril y mayo; las bellotas maduran en noviembre y diciembre del mismo año.



Figura 2.1. Características del roble melojo (*Quercus pyrenaica* Willd.). Fotos: M. Iglesias (raíces); A.J. Pérez-Luque.

Los robledales de roble melojo o melojares son formaciones dominadas por *Quercus pyrenaica* Willd. que se distribuyen desde el suroeste de Francia hasta el noreste de Marruecos, ocupando su mayor extensión en la Península Ibérica, donde abarcan una amplia variedad de sitios y nichos ecológicos (Figura 2.2) (de la Serna *et al.*, 2016; García & Jiménez, 2009; Nieto-Quintano *et al.*, 2016; Vilches de la Serna, 2014). Según el Inventario Forestal Nacional (Villanueva, 2005), estas formaciones ocupan 845 511 ha, lo que supone aproximadamente el 5 % de la superficie forestal de España.

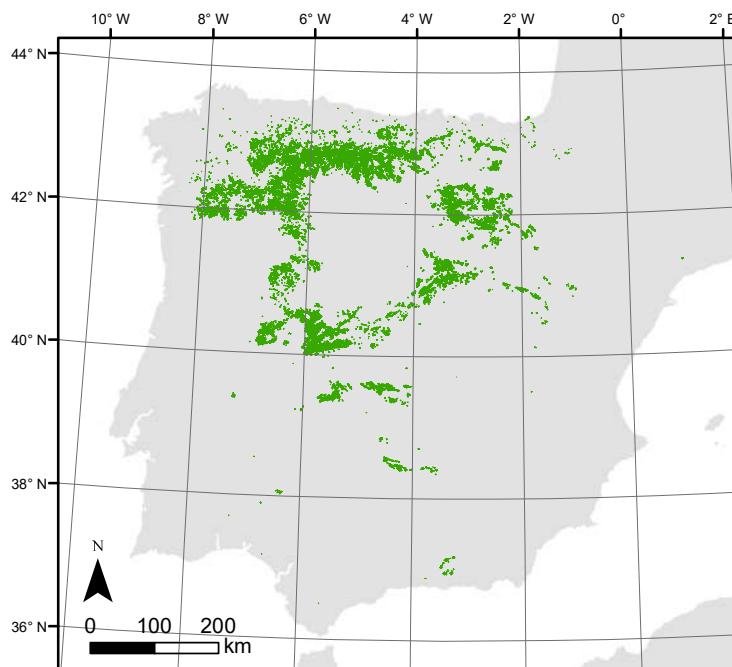


Figura 2.2. Distribución de los bosques de *Quercus pyrenaica* en la Península Ibérica.
Elaboración propia a partir del Mapa Forestal Español

Esta especie requiere de un mínimo de humedad estival para sobrevivir, que algunos autores han estimado en al menos 100 mm de precipitación entre mayo y agosto (Blanco Castro *et al.*, 2005; Prieto, 1975). En Sierra Nevada el aporte extra de humedad necesario proviene de dos vías: de los ríos y acequias de careo, o del aire húmedo proveniente del Mediterráneo (Martínez-Parras & Molero-Mesa, 1982; Prieto & Espinosa, 1977; Pérez-Raya *et al.*, 1990). En efecto, los melojares en Sierra Nevada aparecen en aquellos enclaves más húmedos y de menor índice de insolación, principalmente barrancos y fondos de valle donde se dan unas condiciones microclimáticas favorables, tal y

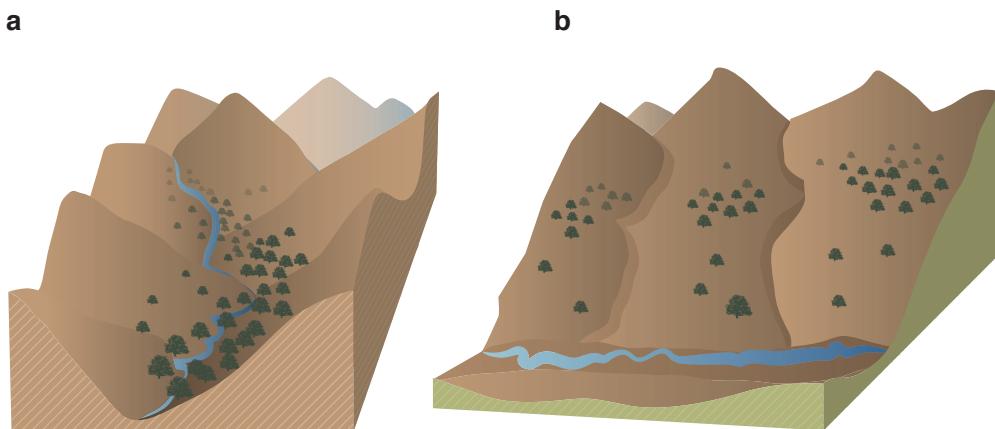


Figura 2.3. Disposición de las poblaciones de robledal en la cara norte (e.g. Robledal del valle del Río Genil)(a) y sur (e.g. Robledal de Cáñar)(b) de Sierra Nevada. Modificado a partir de Prieto y Espinosa (1977).

como ocurre en la zona occidental en orientaciones norte (ríos Alhama de Lugros, Maitena, Vadillo, Genil, Monachil, Dílar y Dúrcal) (Figura 2.3a); o situados ocupando una determinada altura en la vertiente sur (Alpujarras: loma de Cáñar, barranco del Poqueira, loma de Pitres-Busquístar) en donde actúan como una banda de vegetación que intercepta la humedad procedente del Mediterráneo (Lorite, 2001; Prieto & Espinosa, 1977) (Figura 2.3b). Estas diferencias también tienen reflejo en la composición florística de las poblaciones de ambas vertientes (Lorite *et al.*, 2008; Melendo & Valle, 2000).

2.2. Área de estudio

Sierra Nevada es una región montañosa situada en el sur de Europa, que ocupa más de 2 000 km² (Figura 2.4). Presenta un rango altitudinal que varía entre 860 y 3 482 m.s.n.m., incluyendo la cumbre más alta de la Península Ibérica (Mulhacén). El clima es mediterráneo, caracterizado por inviernos fríos y veranos calurosos, con una pronunciada sequía estival. La temperatura media anual desciende en altitud desde los 12-16°C por debajo de los 1 500 m.s.n.m. hasta los 0°C por encima de los 3 000 m.s.n.m. de altitud. La precipitación media anual es muy irregular, con valores que oscilan entre los 250 y los 700 mm anuales, dependiendo principalmente

de la altitud y de la compleja orografía (Peinó Calero, 2020; Pérez-Luque *et al.*, 2021). Las precipitaciones invernales son principalmente en forma de nieve por encima de los 2 000 *m.s.n.m.* de altitud (Pérez-Palazón *et al.*, 2015). Geológicamente, la zona central está compuesta por rocas silíceas, principalmente micaesquistos, rodeadas de calizas y dolomías (Rodríguez-Fernández, 2017). Esta región montañosa alberga un total de 2 353 taxones de plantas vasculares, representando el 33 % y el 20 % de la flora de España y de Europa respectivamente (Lorite, 2016). Además presenta una alta tasa de endemidad con 95 taxones vegetales endémicos (Lorite *et al.*, 2007; Lorite *et al.*, 2020). La cubierta forestal de Sierra Nevada está dominada por plantaciones de pino (*Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arnold subsp. *salzmannii* (Dunal) Franco, y *P. sylvestris* L.) que cubren aproximadamente 37 000 ha. Los bosques autóctonos están dominados principalmente por la encina (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) ocupando zonas de baja y media montaña (11 000 ha) y el roble melojo (*Quercus pyrenaica* Willd.) que va desde los 1 100 a los 2 000 *m.s.n.m.*, cubriendo unas 3 400 ha (Lorite, 2001; Pérez-Luque *et al.*, 2019).

Sierra Nevada contiene 27 hábitats tipo incluidos en la Directiva Hábitats, 28 especies de aves del Anexo I de la Directiva Aves y 15 especies de animales incluidas en el Anexo II de la Directiva Hábitats (1 reptil, 2 anfibios, 7 mamíferos y 5 invertebrados). Todo ello hace que esté considerada como uno de los hotspots de biodiversidad más importantes en la Región Mediterránea (Blanca, 1996; Blanca *et al.*, 1998; Cañadas *et al.*, 2014; Medail & Quezel, 1999). En Sierra Nevada hay 61 municipios con un total de mas de 90 000 habitantes, siendo sus principales actividades económicas la agricultura, el turismo, la ganadería, la apicultura, la minería, y el esquí (Fernández-Márquez & Salinas, 2009). El alto valor de biodiversidad y geodiversidad, así como su riqueza paisajística y cultural han hecho que Sierra Nevada presente varios reconocimientos y cuente con diversas figuras legales de protección. Además de contar con un Parque Nacional y un Parque Natural, Sierra Nevada es una Reserva de la Biosfera (MaB, Unesco). Está incluida en la red Natura 2000 como Zona de Especial Protección para las Aves y Lugar de Interés Comunitario (LIC).

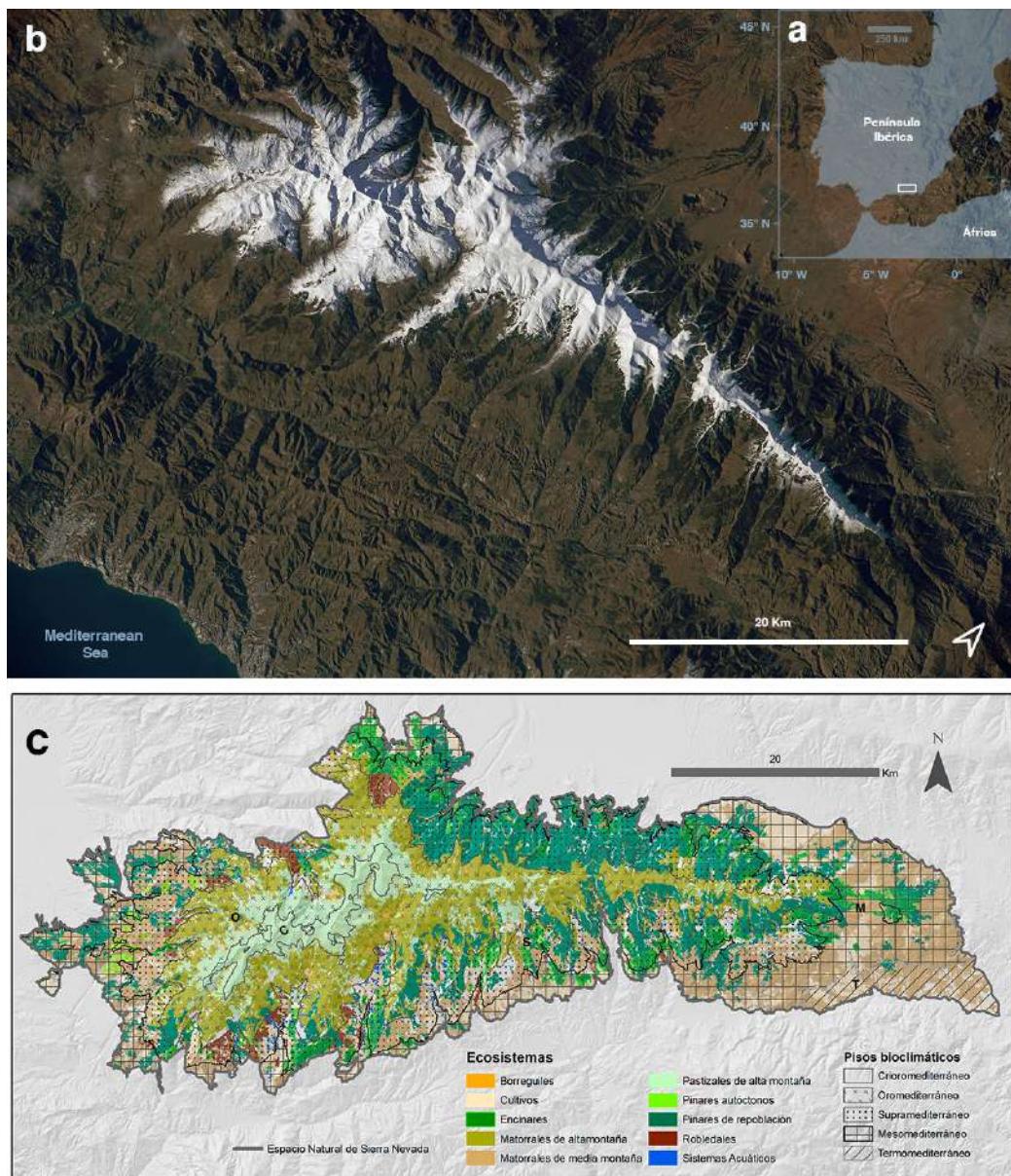


Figura 2.4. Localización (a) y vista de satélite de Sierra Nevada (b). Distribución espacial de los ecosistemas de Sierra Nevada (c). Se indican los pisos bioclimáticos. Imagen de la Estación Espacial Internacional tomada en diciembre de 2014; cortesía de *Earth Science and Remote Sensing Unit, NASA Johnson Space Center*.

Una de las características más importantes de Sierra Nevada es la existencia de marcados gradientes altitudinales, ecológicos y climáticos (Zamora *et al.*, 2021). Así por ejemplo, existe un fuerte contraste climático entre las laderas soleadas y secas orientadas al sur, y las laderas sombreadas y más húmedas orientadas al norte. La heterogeneidad climática y topográfica existente en Sierra Nevada ofrece una gran diversidad de micro hábitats, lo que ha permitido a esta región montañosa actuar como refugio de diferentes especies (Blanco-Pastor *et al.*, 2019; Gómez & Lunt, 2007; Médail & Diadema, 2009), incluyendo especies caducifolias de *Quercus* durante la última glaciación (Olalde *et al.*, 2002; Petit *et al.*, 2002; Rodríguez-Sánchez *et al.*, 2010).

La existencia de estos gradientes confiere a Sierra Nevada, y a las regiones montañosas en general, el carácter de un excepcional laboratorio natural de seguimiento del cambio global (Zamora, 2010; Zamora *et al.*, 2017b). De hecho, en 2008 se estableció el Observatorio de Cambio Global de Sierra Nevada (OBSNEV) (<https://obsnev.es>), un programa de seguimiento a largo plazo para evaluar el impacto del cambio global en los ecosistemas nevadenses (Aspizua *et al.*, 2010; Bonet-García *et al.*, 2011). Esta iniciativa está recopilando información útil y relevante sobre los efectos del cambio global en los sistemas sociecológicos de Sierra Nevada (Pérez-Luque *et al.*, 2016a; Ramos-Losada *et al.*, 2017; Zamora *et al.*, 2017a; Zamora *et al.*, 2015). Asimismo, y relacionado con la temática de la presente memoria doctoral, dentro de las metodologías de seguimiento de esta iniciativa, se vienen realizando diferentes análisis sobre los efectos del cambio global en las masas de robledal (ver por ejemplo Aspizua *et al.*, 2012; Bonet-García *et al.*, 2015a; Muñoz, 2012).

Melojares en Sierra Nevada

En Sierra Nevada, los melojares ocupan actualmente una extensión de 3 400 ha (Pérez-Luque *et al.*, 2019), distribuidas entre los 1 000 y 2 000 m.s.n.m., y situados exclusivamente sobre suelos silíceos. Aunque representan menos del 7 % de la superficie forestal existente en Sierra Nevada (Figura 2.4c), tienen una alta singularidad ecológica y presentan una alta diversidad de especies vegetales en comparación con las otras formaciones forestales (Gómez-Aparicio *et al.*, 2009; Pérez-Luque *et al.*, 2014). Además, albergan

diferentes especies vegetales consideradas relictas (Blanca *et al.*, 1998; Lorite *et al.*, 2008) (Ver apéndice A).

2.3. Análisis del patrón de colonización de cultivos abandonados

En el capítulo 4 se estudia el patrón de colonización de los cultivos de montaña abandonados. La aproximación que utilizamos consistió en el estudio de los diferentes módulos implicados en la dispersión (Lundberg & Moberg, 2003; Nathan *et al.*, 2012), a saber: fuente semillera (bosques de *Quercus pyrenaica*); vector de dispersión (animales dispersores de bellotas); y sumidero receptor de semillas (cultivos abandonados).

Se seleccionaron 5 cultivos abandonados situados en dos localidades de Sierra Nevada que representan las dos vertientes: robledal de San Juan (Robledal del río Genil; orientación NW); y robledal de Cáñar (orientación sur). Para cada uno de los cultivos abandonados, se llevó a cabo un análisis de la estructura forestal circundante y del patrón de regeneración. Para ello se distribuyeron al azar transectos lineales de vegetación (30x10 m) en el cultivo abandonado; en los bordes del bosque y dentro de los bosques circundantes (Figura 2.5). El número de transectos en cada uno de los cultivos abandonados fue proporcional al tamaño de los campos de cultivo abandonado (ver Tabla 4.1).

En cada transecto de vegetación se registraron todos los individuos y se midió la altura y el diámetro de los mismos (diametro base para individuos con altura <150 cm; y diámetro a la altura del pecho para individuos con altura >150 cm). Para cada transecto se calculó la abundancia de juveniles, sin diferenciar entre regeneración vegetativa y sexual debido a la dificultad que presenta la especie por su carácter rebrotador. Dentro de los juveniles se diferenciaron varias etapas de reclutamiento en función del tamaño de los individuos (*e.g.* Plieninger *et al.*, 2010). Consideramos cinco categorías de tamaño basadas en la altura (cada 30 cm).

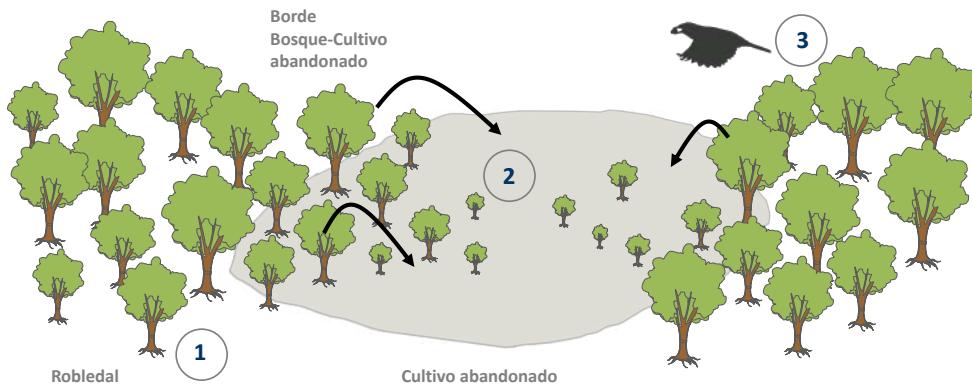


Figura 2.5. Esquema metodológico de análisis del patrón de colonización de cultivos. Se estudió la estructura de la fuente semillera (1), el estado de la comunidad de arrendajos (el principal dispersor de bellotas)(3), y la regeneración observada en los cultivos abandonados (2)

Para estudiar la comunidad de dispersantes se utilizó una serie temporal de datos de abundancia del arrendajo (*Garrulus glandarius*), el principal dispersor de las bellotas de *Quercus pyrenaica* en Sierra Nevada (Gómez *et al.*, 2003). Esta serie de datos procede del seguimiento de aves paseriformes realizado en el marco del Observatorio de Cambio Global de Sierra Nevada (Barea-Azcón *et al.*, 2012; Zamora *et al.*, 2017b). En concreto se utilizaron datos para los robledales de la zona de estudio (Robledal de Cáñar y Robledal de San Juan). Estos muestreos consistieron en censos realizados a lo largo de transectos lineales con un ancho de banda fijo de 50 m (25 a cada lado del observador), en donde se registraron todos los avistamientos (Barea-Azcón *et al.*, 2012; Zamora & Barea-Azcón, 2015).

Todos los datos fueron debidamente documentados y publicados en repositorios institucionales: véase Pérez-Luque *et al.* (2015b) para una descripción detallada del conjunto de datos de los transectos de vegetación; y Pérez-Luque *et al.* (2016b) para la descripción del conjunto de datos sobre aves paseriformes.

2.4. Estimación de biomasa a nivel de parcela

En el capítulo 5 se llevó a cabo una estimación de la biomasa utilizando ecuaciones alométricas (ver Montero *et al.*, 2005) a partir de datos de inventarios forestales. Los datos de campo se obtuvieron a partir de una recopilación de varios inventarios forestales y proyectos de investigación realizados en Sierra Nevada. En primer lugar, se seleccionaron las parcelas incluidas en la distribución actual de *Q. pyrenaica* en Sierra Nevada (Pérez-Luque *et al.*, 2019). A continuación se seleccionaron únicamente las parcelas con información completa (aquellas en las que se midieron todos los individuos arbóreos con DBH > 7,5 cm), y los rodales puros (composición > 70 %). De estas parcelas, se aplicó un filtro espacial para descartar las parcelas superpuestas, y un filtro temporal, descartando los inventarios de antiguos (es decir, de más de 10 años). Todas las parcelas seleccionadas se midieron entre 2012 y 2020.

Además de ello, y para tener una representación de todas las poblaciones de robledal, se muestrearon parcelas circulares adicionales (de 9 a 16 m de radio) entre octubre de 2019 y marzo de 2020. En cada parcela se marcaron y midieron todos los ejemplares arbóreos. Se anotó el diámetro a la altura del pecho (DBH) utilizando un calibre forestal graduado (precisión de 0.1 cm). La altura de cada árbol se midió utilizando un hipsómetro (Vertex 5, Haglöf Sweden) con una precisión de 0.1 metros. También se anotó para cada ejemplar el azimut y la distancia respecto al centro de la parcela, cuya posición fue registrada mediante la utilización de un GPS submétrico (Leica Zeno 20 GIS, Leica Geosystems, Suiza). Las parcelas se seleccionaron en proporción a la extensión de los diferentes estratos ecológicos, proporcionando rodales representativos con una variedad de estructura de rodal y condiciones de sitio en las diferentes poblaciones de robledal de Sierra Nevada.

2.5. Muestreos dendrocronológicos

En el capítulo 6, realizamos una estimación del crecimiento secundario de los robledales, para lo cual llevamos a cabo muestreos dendrocronológicos estándar para obtener series de crecimiento radial (Cook & Kairukstis, 1990; Fritts, 1976; Gutiérrez, 2008; Natalini *et al.*, 2017).

En cada sitio de muestreo (Robledal del Genil, GEN; y Robledal de Cáñar, CAN; ver capítulo 6), se seleccionaron entre 15 y 20 árboles de forma aleatoria. Para cada árbol focal (*target tree*), se tomaron entre 2-3 testigos (*cores*) de 5 mm de diámetro utilizando una barrena forestal o barrena de Pressler (Grissino-Mayer, 2003) (Figura 2.6). Los testigos se tomaron de forma perpendicular, y a una altura de 1.3 metros (Figura 2.7b). Cada testigo se etiquetó y se guardó en pajitas (preferiblemente de papel) para su transporte. Posteriormente en el laboratorio, los testigos se secaron al aire, y se montaron en soportes de madera para su posterior lijado y análisis (Figura 2.7b-c). Durante el montaje, los testigos se colocaron de tal forma que las fibras quedaran perpendiculares a la superficie de lectura, y dejando visible la sección transversal, facilitando así la observación de los anillos (Fritts, 1976; Natalini *et al.*, 2017). Para el lijado de las muestras se utilizó una lijadora eléctrica usando papeles de lija de granos sucesivamente más finos (desde 60 hasta 1200).

Posteriormente se procedió a la medición, desde la corteza hasta la médula, de la anchura de todos los anillos de crecimiento (*RW, ring width*) con una precisión de 0.01 mm, utilizando una mesa de medición LINTAB acoplada a un estereomicroscopio de alta resolución y a un ordenador con el software TSAP-Win (Rinntech, Heidelberg, Alemania). Una vez realizadas las mediciones, las series se sincronizaron visualmente y se dataron utilizando los estadísticos *Gleichläufigkeit* (GLK), *t*-valor e índice de datación cruzada (CDI, *crossdate index*) (Buras & Wilmking, 2015; Schweingruber, 1988). Se sincronizaron los testigos pertenecientes al mismo árbol entre sí, construyeron cronologías de individuo, para posteriormente generar cronologías de sitio. La datación cruzada visual se verificó utilizando el programa COFECHA, que calcula la intercorrelación entre series mediante segmentos solapados (Holmes, 1983). Este programa ayuda a evaluar la

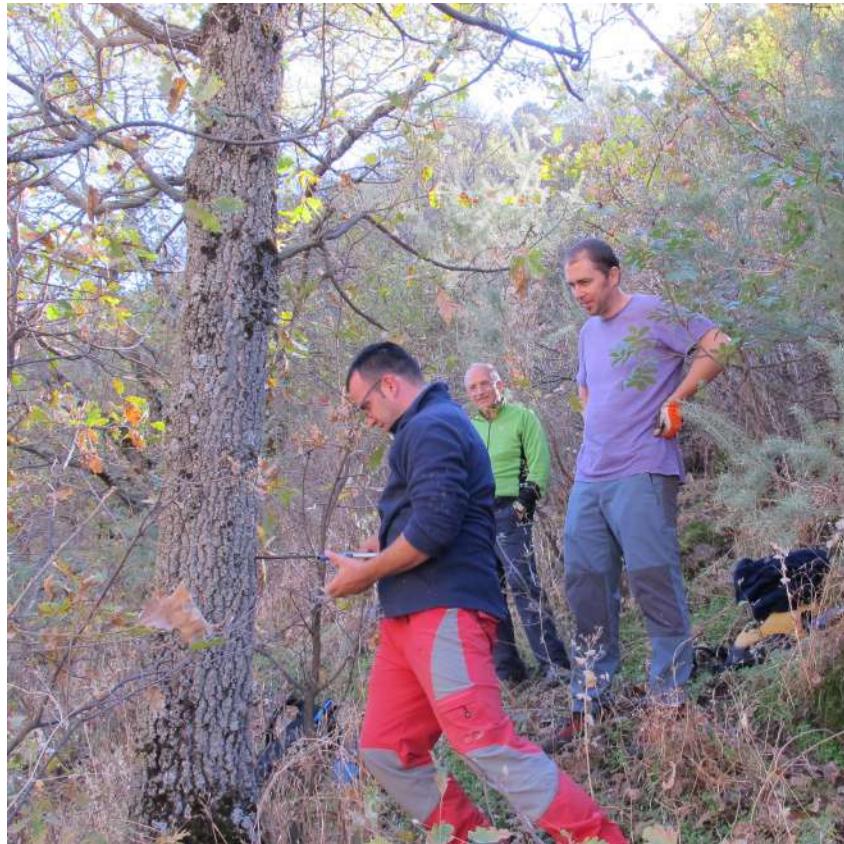


Figura 2.6. Obtención de testigos con Barrena de Pressler.



Figura 2.7. Barrena de Pressler (a) obteniendo testigos de un ejemplar de *Quercus pyrenaica*. Testigos montados sobre soporte de madera, antes (b) y después (c) de ser lijados.

calidad de la datación cruzada y a identificar posibles problemas dentro de una serie de anillos de crecimiento (Grissino-Mayer, 2001).

Estimación de la competencia

Para la estimación de la competencia de cada árbol focal (*target tree*) se emplearon diferentes **índices de competencia**. La mayoría de los índices de competencia descritos en la literatura forestal pueden dividirse en dos grandes clases: los *índices independientes de la distancia*, que utilizan únicamente información no espacial sobre el tamaño y el número de árboles agregados dentro de un área determinada (e.g. una parcela o un rodal); y los *índices dependientes de la distancia* que además incorporan las ubicaciones relativas de los árboles vecinos dentro del área (Burkhart & Tomé, 2012; Contreras *et al.*, 2011; Gea-Izquierdo & Cañellas, 2009). Los índices dependientes de la distancia, aunque son mas tediosos de obtener, presentan una mejor correlación con el crecimiento que los índices independientes de la distancia (Contreras *et al.*, 2011; Gea-Izquierdo & Cañellas, 2009; Maleki *et al.*, 2015). En nuestro caso empleamos los índices independientes de la distancia, *densidad* ($n \text{ árboles} \cdot ha^{-1}$) y *área basal* ($m^2 \cdot ha^{-1}$); así como el índice dependiente de la distancia *ratio de tamaños proporcional a la distancia* (*srd*, del inglés *size ratio proportional to distance*) calculado como

$$srd = \sum_{i=1}^n \left(\frac{dbh_j}{dbh_i} \right) \times \left[\frac{1}{(dist_{ij} + 1)} \right]$$

siendo dbh_i y dbh_j los diámetros a la altura del pecho del árbol i y el árbol focal (j) respectivamente; y $dist_{ij}$ la distancia entre ambos árboles.

Se muestrearon todos los árboles vivos con $DBH > 7.5$ cm dentro de una parcela circular de 10 m de radio, tomando como centro el árbol focal. Para cada árbol, se anotó la especie, se midió la altura y el DBH, así como la distancia y ángulo (*azimuth*) respecto al árbol focal (Figura 2.8).

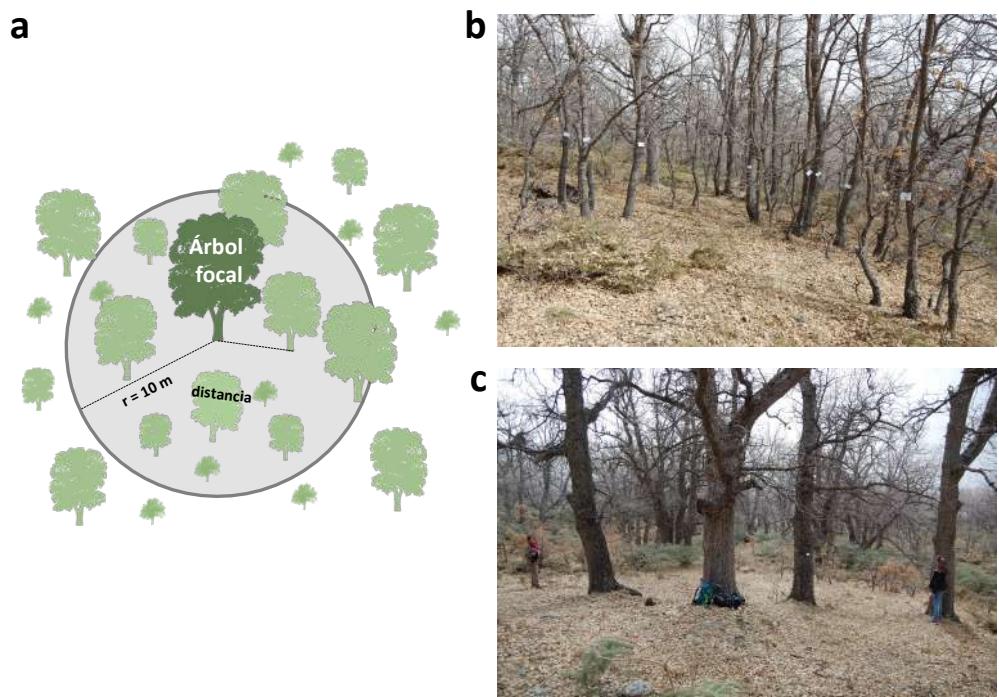


Figura 2.8. Esquema de los muestreos para estimación de la competencia (a). Se replantean parcelas de 10 m de radio en torno al árbol focal. Cada árbol vecino es identificado (b) y medido (c), anotando la distancia y azimuth respecto al centro, así como su altura y DBH.

2.6. Índices de Vegetación

La información derivada de las imágenes de satélite (teledetección) proporciona un medio relativamente barato y accesible para obtener series temporales de información, a distintas escalas espaciales, sobre diferentes atributos de los ecosistemas, lo que supone un gran potencial para el seguimiento de los cambios en el funcionamiento de los escosistemas (Alcaraz *et al.*, 2006; Alcaraz-Segura *et al.*, 2015; Cabello *et al.*, 2012; Pettorelli *et al.*, 2014; Pettorelli *et al.*, 2018).

Los índices de vegetación (IV) son los índices espectrales derivados de imágenes de satélite más utilizados. Estos índices se pueden utilizar para estimar la fracción de la radiación fotosintéticamente activa absorbida por la vegetación (fPAR), que representa el control principal de la producción primaria (Monteith, 1972), debido a la relación lineal existente entre ambas variables (Hatfield *et al.*, 1984). Gracias a la relación con la productividad primaria neta, los índices de vegetación se han empleado para derivar indicadores del funcionamiento ecosistémico, tales como el carbono total anual absorbido por la vegetación, o la estacionalidad y fenología de la dinámica de las ganancias de carbono (Alcaraz-Segura *et al.*, 2009a; Alcaraz-Segura *et al.*, 2009b; Cabello & Paruelo, 2009; Cazorla *et al.*, 2020; Dionisio *et al.*, 2012). En el marco de la presente memoria doctoral se utilizaron los índices **EVI**, Índice de Vegetación Mejorado (*Enhanced Vegetation Index*) (ver capítulo 6) y el **NDVI**, Índice de Vegetación de Diferencia Normalizada (*Normalized Difference Vegetation Index*) (capítulo 7). A partir de las series temporales construidas para cada índices, se obtuvieron diferentes indicadores sintéticos de la dinámica de la intercepción de radiación por parte de la vegetación, tales como el promedio anual y estacional, la estacionalidad o la fenología del ecosistema, con los que, posteriormente caracterizar y monitorear diferentes aspectos del funcionamiento de los ecosistemas (Cabello *et al.*, 2012).

El NDVI es un índice espectral que tiene en cuenta la diferente absorción de la radiación solar por parte de la vegetación en las bandas del rojo (*red*) e

infrarrojo (*NIR*) cercano dentro del espectro electromagnético. Su valor se computa como

$$NDVI = \frac{\rho_{NIR} - \rho_{red}}{\rho_{NIR} + \rho_{red}}$$

siendo ρ_{NIR} y ρ_{red} las reflectancias de las bandas infrarrojo cercano (*NIR*) y rojo respectivamente. Al tratarse de un índice normalizado, sus límites teóricos son -1 y 1, representando a la vegetación los valores superiores a cero (Huete *et al.*, 2002). El EVI, por su parte, es un índicepectral que tiene en cuenta la diferente absorción de la radiación solar por parte de la vegetación en las bandas del rojo e infrarrojo cercano (además de incluir la banda del azul como corrección) dentro del espectro electromagnético (Huete *et al.*, 2002). Su fórmula además incorpora una serie de constantes para corregir ciertos efectos de la atmósfera y el suelo:

$$EVI = G \times \frac{(\rho_{NIR} - \rho_{red})}{\rho_{NIR} + C_1 \times \rho_{red} - C_2 \times \rho_{blue} + L}$$

siendo ρ_{NIR} , ρ_{red} , y ρ_{blue} las reflectancias de las bandas infrarrojo cercano (*NIR*), rojo y azul respectivamente. L es el ajuste del fondo del dosel, C_1 y C_2 coeficientes de que corrigen la influencias de los aerosoles, y G el factor de ganancia. En el algoritmo de MODIS-EVI, los valores adoptados para esos coeficientes son: $L = 1$; $C_1 = 6$ y $C_2 = 7,5$ y $G = 2,5$ (Huete *et al.*, 2002).

Las imágenes de EVI y NDVI fueron derivadas del producto MOD13Q1 obtenido por el sensor MODIS (*Moderate Resolution Imaging Spectroradiometer*) (Didan, 2015). Estas imágenes tienen una resolución espacial de 231 m y temporal de 16 días (23 imágenes por año). Los datos de MODIS de la Colección 6 se obtuvieron utilizando la plataforma Google Earth Engine (Gorelick *et al.*, 2017). Seleccionamos los píxeles que cubren la distribución de los bosques de *Q. pyrenaica* en Sierra Nevada ($n = 928$ píxeles). Posteriormente se aplicó un filtrado de datos para seleccionar los valores válidos de los índices de vegetación. El filtrado se realizó utilizando los indicadores de calidad (banda *250m 16 days VI Quality*) que acompañan a cada imagen. A partir de esa información, filtramos aquellos valores afectados por alto contenido de aerosoles, nubes, nieve y sombras, siguiendo las recomendaciones de filtrado de datos de imágenes de satélite para regiones de montaña (Reyes-Díez *et al.*, 2015).

Para cada uno de los índices, generamos series temporales desde 2000 hasta 2014 (NDVI) (capítulo 7) y 2016 (EVI) (capítulo 6). De las series temporales generadas se derivaron los perfiles anuales (Figura 7.2) y se calcularon diferentes métricas (promedio anual, estacional, máximo, mínimo, etc) en función de las necesidades de estudio (ver capítulos 6 y 7).

2.7. Estimación de indicadores de la cubierta de nieve

La producción primaria de la vegetación depende de multitud de factores biofísicos. En regiones de montaña como Sierra Nevada, la nieve puede jugar un papel determinante en este sentido. La cantidad de agua suministrada por la nieve puede explicar, en parte, el funcionamiento de ecosistemas forestales cercanos al límite del árbol. En el capítulo 7 se evalúan las relaciones entre la duración de la cubierta de nieve y la productividad en los robledales de *Q. pyrenaica*. Para ello, además de los índices de vegetación antes mencionados, se ha generado una serie temporal sobre la dinámica de la cubierta de nieve en los robledales de Sierra Nevada (Bonet-García *et al.*, 2015b; Pérez-Luque *et al.*, 2016c). A partir del producto MOD10A2 de MODIS (Hall *et al.*, 2002), que presenta una periodicidad de 8 días y una resolución espacial de 500 m, se calculó el índice diferencial normalizado de nieve **NDSI** (*Normalized Difference Snow Index*). Se trata de un ratio de bandas espectrales que aprovecha la mayor reflectancia de la nieve en las longitudes de onda visible, y baja reflectancia en la región infrarroja de onda corta (Salomonson & Appel, 2006)

$$NDSI = \frac{\rho_{green} - \rho_{SWIR}}{\rho_{green} + \rho_{SWIR}}$$

siendo ρ_{green} y ρ_{SWIR} las reflectancias en las bandas visible e infrarrojo de onda corta respectivamente. Este índice ha demostrado ser un indicador robusto de la cobertura de nieve utilizando imágenes MODIS (Rittger *et al.*, 2013). Se derivaron diferentes indicadores que caracterizan la cubierta de nieve (Wang & Xie, 2009):

- *duración de la cubierta de nieve (scd, snow cover duration)*: se define como el número de días cubiertos de nieve por año hidrológico.
- *fecha de inicio de la cubierta de nieve (scod, snow cover onset date)*: primera fecha del año hidrológico en que el píxel tiene nieve. Este indicador es útil para identificar los cambios en el inicio de la temporada de nieve.
- *fecha de fusión de la capa de nieve (scmd, snow cover melting date)*: es la última fecha del año hidrológico en que el píxel tiene nieve. Este indicador proporciona información útil sobre el proceso de fusión de la nieve.

2.8. Conjuntos de datos y software utilizado

Todos los análisis estadísticos realizados a lo largo de esta memoria doctoral se han llevado a cabo con el software estadístico R (R Core Team, 2020), utilizando diferentes paquetes o librerías (Tabla 2.1). Se han utilizado diferentes sistemas de información geográfica. En el capítulo 3 utilizamos el software GRASS GIS (Neteler *et al.*, 2012) junto con los módulos r.sun, r.terraflow, r.param.scale, r.slope.aspect, r.terraflow, r.recode, v.extract, v.grow.distance y r.neighbors, para la generación de las diferentes variables ambientales usadas. Algunas de las visualizaciones espaciales se llevaron a cabo con ArcGIS (version 10.0; Redlands, CA: Environmental Systems Research Institute) y con QGIS (QGIS Geographic Information System. QGIS Association.). Otros software específicos utilizados vienen descritos en cada capítulo (*e.g.* software dendrocronológico en el capítulo 6).

Los datos constituyen uno de los productos valiosos de la ciencia (Costello *et al.*, 2013). Las series de datos son de gran importancia para comprender patrones ecológicos complejos y/o resolver problemas ambientales emergentes, por lo que su preservación, accesibilidad y reutilización en ecología resulta crucial (Pérez-Luque & Ros-Candeira, 2019). Muchos datos utilizados en esta memoria doctoral provienen de

diferentes fuentes de datos, que se han especificado y citado en cada capítulo. Además de ello, como parte del trabajo desarrollado, se han generado diferentes conjuntos de datos. Estos conjuntos de datos se han documentado convenientemente, utilizando estándares de metadatos como EML (*Ecological Metadata Language*), y Directiva INSPIRE (ISO-19139). Posteriormente los conjuntos de datos se han depositado e integrado en repositorios institucionales locales (Observatorio de Cambio Global de Sierra Nevada, www.obsnev.es) e internacionales (e.g. GBIF: Global Biodiversity Information Facility, <https://www.gbif.org/>; PANGAEA, <https://www.pangaea.de/>). Asimismo, para maximizar el valor de los datos generados y facilitar su acceso y su re-utilización, se escribieron diferentes artículos de datos (*Data Papers*) donde se documentaron de forma detallada, el contexto en el que fueron generados así como su contenido. De esta forma se apuesta por una mejor reutilización de los datos, cumpliendo los principios FAIR, es decir que los datos sean encontrables, accesibles, interoperables y reutilizables (Wilkinson *et al.*, 2016).

A continuación se muestran un listado de los conjuntos de datos documentados y el capítulo en el que se han utilizado:

- Dataset: Ecological diversity within Rear-Edge: A Case Study from Mediterranean *Quercus pyrenaica* Willd.. Depositado en: Figshare. doi: 10.6084/m9.figshare.13382969.v1 (capítulo 3)
- Dataset: Resilience to drought of relict Mediterranean *Quercus pyrenaica* populations in the southern Iberian (Sierra Nevada, Spain). Depositado en: PANGAEA. doi: 10.1594/PANGAEA.922054 (capítulo 6)
- Dataset: Enhanced Vegetation Index covering *Quercus pyrenaica* forests in Sierra Nevada (southern Spain). Depositado en: PANGAEA. doi: 10.1594/PANGAEA.922052 (capítulo 6)
- Dataset: Tree-ring measurements of *Quercus pyrenaica* (focal trees) from 1899 to 2016 (Sierra Nevada, Spain). Depositado en: PANGAEA. doi: 10.1594/PANGAEA.922053 (capítulo 6)
- Dataset: Species, total height, diameter at breast height of neighboring living trees and distance and azimuth with respect to *Quercus pyrenaica*

(focal trees) (Sierra Nevada, Spain). Depositado en: PANGAEA. doi: 10.1594/PANGAEA.922050 (capítulo 6)

- Dataset: Total height, diameter at breast height and tree ring code of *Q. pyrenaica* (focal trees) (Sierra Nevada, Spain). Depositado en: PANGAEA. doi: 10.1549/PANGAEA.922049 (capítulo 6)
- Dataset of Passerine bird communities in a Mediterranean high mountain (Sierra Nevada, Spain). Depositado en GBIF. doi: 10.15468/ow9noo (capítulo 4)
- Dataset of Global Change, altitudinal range shift and colonization of degraded habitats in mediterranean mountains (MIGRAME). Depositado en GBIF. doi: 10.15470/orboj4 (capítulo 4)
- Sinfonevada: Dataset of Floristic diversity in Sierra Nevada forests (SE Spain). Depositado en GBIF. doi: 10.15468/4gpr7e (capítulos 3, 5, y 8)

Y derivados de ellos se han generado diferentes artículos de datos (Data Papers) sometidos al proceso de revisión por pares y publicados en revistas indexadas:

- Pérez-Luque, A. J., F. J. Bonet, R. Pérez-Pérez, R. Aspizua, J. Lorite, and R. Zamora. 2014. Sinfonevada: Dataset of floristic diversity in Sierra Nevada forests (SE Spain). PhytoKeys 35:1-15.
- Pérez-Luque, A. J., R. Zamora, F. J. Bonet, and R. Pérez-Pérez. 2015. Dataset of MIGRAME project (global change, altitudinal range shift and colonization of degraded habitats in Mediterranean mountains). PhytoKeys 56:61-81.
- Pérez-Luque, A. J., J. M. Barea-Azcón, L. Álvarez-Ruiz, F. J. Bonet-García, and R. Zamora. 2016. Dataset of Passerine bird communities in a Mediterranean high mountain (Sierra Nevada, Spain). ZooKeys 552:137-154.

Tabla 2.1. Paquetes estadísticos utilizados en los análisis realizados en esta memoria doctoral.

Categoría	Paquetes de R utilizados
Análisis Estadísticos	ade4 (Dray & Dufour, 2007), bestglm (McLeod <i>et al.</i> , 2020), BIOMASS (Rejou-Mechain <i>et al.</i> , 2017), biostat (Gegzna, 2020), boot (Canty & Ripley, 2021), broom (Robinson <i>et al.</i> , 2020), car (Fox & Weisberg, 2019a), DHARMA (Hartig, 2020), DiscriMiner (Sanchez, 2013), dplR (Bunn <i>et al.</i> , 2021), easynls (Arnhold, 2017), effects (Fox & Weisberg, 2019b), factoextra (Kassambara & Mundt, 2020), ggsignif (Ahlmann-Eltze, 2019), glmulti (Calcagno, 2020), Hmisc (Harrell Jr <i>et al.</i> , 2020), klaR (Weihs <i>et al.</i> , 2005), lsmeans (Lenth, 2016), MASS (Venables & Ripley, 2002), multcomp (Hothorn <i>et al.</i> , 2008), multcompView (Graves <i>et al.</i> , 2019), MuMIn (Bartoñí, 2020), nFactors (Raiche & Magis, 2020), nlme (Pinheiro <i>et al.</i> , 2021), nlstools (Baty <i>et al.</i> , 2015), PMCMR (Pohlert, 2014), randomForest (Liaw & Wiener, 2002), rcompanion (Mangiafico, 2021), rrcov (Todorov & Filzmoser, 2009), rstatix (Kassambara, 2020b), scales (Wickham & Seidel, 2020), SPEI (Beguería & Vicente-Serrano, 2017), stats (R Core Team, 2020), TRADER (Jan <i>et al.</i> , 2014), treeclim (Zang & Biondi, 2015), trend (Pohlert, 2020), vegan (Oksanen <i>et al.</i> , 2019), VSURF (Genuer <i>et al.</i> , 2019), WRS2 (Mair & Wilcox, 2020), zoo (Zeileis & Grothendieck, 2005)
Análisis y Visualización espacial	dynamodel (Metcalfe <i>et al.</i> , 2018), exactextractr (Daniel Baston, 2020), ggmap (Kahle & Wickham, 2013), ggspatial (Dunnington, 2020), leaflet (Cheng <i>et al.</i> , 2021), mapdata (Brownrigg, 2018), maps (Brownrig <i>et al.</i> , 2018), mapview (Appelhans <i>et al.</i> , 2020), raster (Hijmans, 2020), rasterVis (Perpiñán & Hijmans, 2020), rgdal (Bivand <i>et al.</i> , 2020), rgeos (Bivand & Rundel, 2020), sf (Pebesma, 2018), sp (Pebesma & Bivand, 2005), stars (Pebesma, 2021)
Manipulación de Datos	anytime (Eddelbuettel, 2020), dplyr (Wickham <i>et al.</i> , 2020a), flextable (Gohel, 2020a), gtable (Wickham & Pedersen, 2019), gtsummary (Sjoberg <i>et al.</i> , 2020), lubridate (Golemund & Wickham, 2011), magrittr (Bache & Wickham, 2014), naniar (Tierney <i>et al.</i> , 2020), officer (Gohel, 2020b), pander (Darózzi & Tsegelskyi, 2018), plyr (Wickham, 2011), purrr (Henry & Wickham, 2020), reshape2 (Wickham, 2007), stringr (Wickham, 2019), tidylog (Elbers, 2020), tidyrr (Wickham, 2020b), tidyverse (Wickham <i>et al.</i> , 2019)
Obtención de datos y Documentación	finch (Chamberlain, 2019), pangaear (Chamberlain <i>et al.</i> , 2020b), RCurl (Temple Lang, 2020a), rdryad (Ram <i>et al.</i> , 2020), readODS (Schutten <i>et al.</i> , 2018), readr (Wickham & Hester, 2020), readxl (Wickham & Bryan, 2019), rfigshare (Boettiger <i>et al.</i> , 2015), rgifbif (Chamberlain <i>et al.</i> , 2020a), rvest (Wickham, 2020a), XML (Temple Lang, 2020b)
Otros	base (R Core Team, 2020), binaryLogic (Dörrhöfer, 2017), checkpoint (de Vries & Microsoft, 2020), devtools (Wickham <i>et al.</i> , 2020b), digest (Eddelbuettel <i>et al.</i> , 2020), grateful (Rodriguez-Sanchez, 2018), here (Müller, 2017), knitr (Xie, 2015), numform (Rinker, 2020), tab (Van Domelen, 2019), units (Pebesma <i>et al.</i> , 2016)
Visualización de datos	corrgram (Wright, 2018), cowplot (Wilke, 2019), DT (Xie <i>et al.</i> , 2021), egg (Auguie, 2019), ellipse (Murdoch & Chow, 2020), GGally (Schlöerke <i>et al.</i> , 2021), ggc当地 (Kassambara, 2019), ggExtra (Attali & Baker, 2019), ggord (Beck, 2020), ggplot2 (Wickham, 2016), ggpmisc (Aphalo, 2021), ggpubr (Kassambara, 2020a), ggrepel (Slowikowski, 2020), ggthemes (Arnold, 2021), grid (R Core Team, 2020), gridExtra (Auguie, 2017), gridSVG (Murrell & Potter, 2020), gt (Iannone <i>et al.</i> , 2020), jcolors (Huling, 2019), kableExtra (Zhu, 2019), lattice (Sarkar, 2008), latticeExtra (Sarkar & Andrews, 2019), lemon (Edwards, 2020), patchwork (Pedersen, 2020), plotly (Sievert, 2020), RColorBrewer (Neuwirth, 2014), scico (Pedersen & Crameri, 2020), sjPlot (Lüdecke, 2021), stargazer (Hlavac, 2018), viridis (Garnier, 2018a), viridisLite (Garnier, 2018b), visreg (Breheny & Burchett, 2017), xtable (Dahl <i>et al.</i> , 2019)

Parte II

Investigación

Ecological diversity within
rear-edge: a case study from
Mediterranean *Quercus pyrenaica*
Willd.

Antonio J. Pérez-Luque; Blas M. Benito; Francisco J. Bonet-García & Regino Zamora. 2021. *Forests*, 12(1): 10. doi:10.3390/f12010010

Abstract

Understanding the ecology of populations located in the rear-edge of their distribution is key to assess the response of the species to changing environmental conditions. Here we focus on rear-edge populations of *Quercus pyrenaica* in Sierra Nevada (southern Iberian Peninsula) to analyze their ecological and floristic diversity. We perform multivariate analyses using high-resolution environmental information and forest inventories to determine how environmental variables differ among oak populations, and to identify population groups based on environmental and floristic composition. We find that water availability is a key variable in explaining the distribution of *Q. pyrenaica* and the floristic diversity of their accompanying communities within its rear edge. Three cluster of oak populations were identified based on environmental variables. We found differences among these clusters regarding plant diversity, but no for forest attributes. A remarkable match between the populations clustering derived from analysis of environmental variables and the ordination of the populations according to species composition was found. The diversity of ecological behaviors for *Q. pyrenaica* populations in this rear edge are consistent with the high genetic diversity shown by populations of this oak in the Sierra Nevada. The identification of differences between oak populations within the rear-edge with respect to environmental variables can aid to plan the forest management and restoration actions, particularly considering the importance of some environmental factors in key ecological aspects.

3.1. Introduction

The study of ecological dynamics within the rear edge populations is considered essential to establish proper management guidelines under current climate uncertainties (Fady et al., 2016). Rear-edge populations are often adapted to local environmental conditions at the limit of the species' ecological amplitude, and often show a long-term persistence (Hampe & Petit, 2005). Local responses to environmental changes may differ from the species mean response (Benavides et al., 2013; Castro et al., 2004; Gea-Izquierdo & Cañellas, 2014; Matías et al., 2017), and such differences may either promote or hamper the survival of edge populations under global change (Benito-Garzón et al., 2011). Furthermore, the heterogeneity in the response to climate change observed across ecological and geographical gradients (Chen et al., 2015; Dorado-Liñán et al., 2019; Gea-Izquierdo et al., 2013; Pérez-Luque et al., 2020), justifies the need to incorporate fine-scale variation of environment variables throughout species ranges to better understand species responses to global change (De Frenne et al., 2013; Oldfather et al., 2020). This is particularly important for mountain landscapes, where the topographic complexity may cause a decoupling between the climate and the geographic spaces (Elsen & Tingley, 2015; Pironon et al., 2015).

The environmental heterogeneity (microclimate, geomorphology, topography, etc.) found in mountains allows the existence of a diverse plethora of ecological conditions at very fine spatial scales (Hannah et al., 2014; Körner & Spehn, 2019), offering an excellent opportunity to study ecological responses to future environmental changes (Kohler et al., 2014; Payne et al., 2017; Spehn & Korner, 2009; Zamora et al., 2017a). Some tree species, such as *Pinus sylvestris* and *Quercus pyrenaica*, have their rear-edge populations located in mountainous areas of southern Europe. The topographic heterogeneity of such habitats, which act as microclimatic islands within a region of unsuitable climate for the persistence of these species, is likely to have a significant impact on persistence of these populations (Meineri & Hylander, 2017). In these areas, the climate variation controlled by topography (Franklin et al., 2013; Potter et al., 2013) is hard to capture, and the fine scales non-climate factors (both biotic and abiotic) can be at least as much relevant for species distribution as climate (Lo et al.,

2010) by modulating the direct effect of regional climate on individuals. Additionally, there are finer scale gradients nested within each mountain range, which reproduce rear, optimum and leading edge conditions making the interpretation of what is currently occurring in the so-called rear edge extremely complex (Benavides et al., 2013; Oldfather et al., 2020). When environmental conditions are homogeneous, similar responses are expected which facilitate future forecast. Conversely, if the environmental conditions are heterogeneous, we expect a variety of responses, which forces us to consider different future scenarios at a very fine spatial scale, since climate change sensitivities could strongly vary at local scales (Gea-Izquierdo & Cañellas, 2014; Lindner et al., 2010; Tito et al., 2020).

Quercus pyrenaica Willd. (Pyrenean oak) is a deciduous Mediterranean tree species widely distributed throughout south-western France and the Iberian Peninsula reaching their southern limit in mountain areas of northern Morocco (Franco, 1990). The rear-edge populations of this species are restricted to high-mountain areas where these populations persists as isolated nuclei with ecological conditions very different from those of the main distribution area. *Q. pyrenaica* is considered one of the Mediterranean trees with a higher sensitivity to climate change (Benito-Garzón et al., 2008; García-Valdés et al., 2013). Several studies analyzed the potential effects of climate change on distribution of this species at different spatio-temporal scales (Benito et al., 2011; Benito-Garzón et al., 2008; Benito-Garzón et al., 2007; Felicísimo, 2011; Gea-Izquierdo et al., 2013; Ruiz-Benito et al., 2013; Ruiz-Labourdette et al., 2013; Urbieta et al., 2011) forecasting a decrease in the suitable area of this tree species, particularly in its southern range.

Considering that the conservation strategies for tree species need to take into account the peculiarities of the rear-edge populations (Fady et al., 2016; Hampe & Petit, 2005; Rehm et al., 2015), and the high vulnerability to climate change of *Q. pyrenaica* (García-Valdés et al., 2013), here we focus on the rear-edge populations of this species in the mountains of southern Iberian Peninsula to answer the question: Are the environmental conditions of the rear-edge populations of *Q. pyrenaica* in Sierra Nevada homogeneous?. The answer to this question may be useful to analyze how the predicted climate changes would impact the rear-edge population, providing

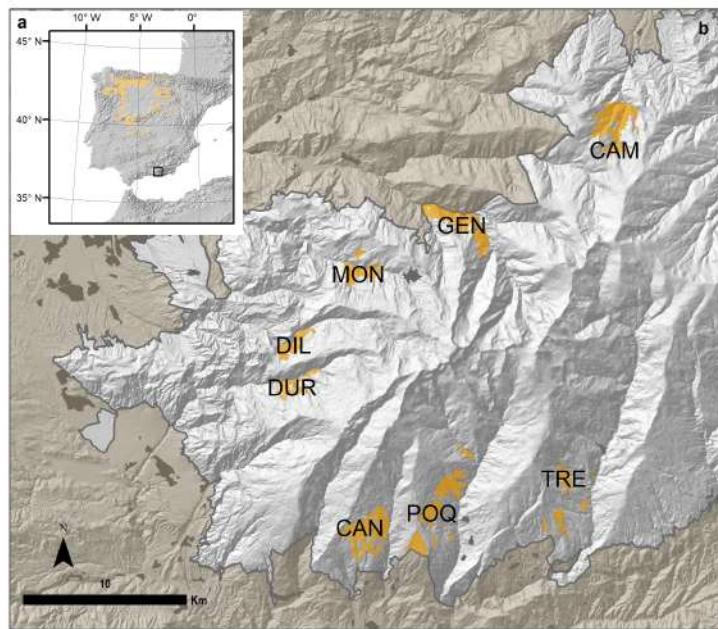


Fig. 3.1. Distribution of *Quercus pyrenaica* forests in the Iberian Peninsula (a) and location of the patches in Sierra Nevada mountain range (b). Name of each population as in Table 3.1.

valuable information for the development of efficient forest management and restoration plans. We selected rear-edge populations of *Q. pyrenaica* located in Sierra Nevada (Southern Iberian Peninsula), since peripheral forest tree populations located in mountain areas represent natural laboratories for resolving priority research questions (Fady et al., 2016). Particularly, we hypothesize that the rear-edge populations of *Q. pyrenaica* located in mountain areas are representative of different environmental conditions at local scale due to the strong topographic gradients available at the edge of its range. In this work we analyze whether these rear-edge populations inhabit similar environmental conditions. We also assess to what extent the environmental variability is matched by the floristic diversity of *Q. pyrenaica* forests. Specifically, the objectives of the work were: (i) to determine the most important environmental variables for the distribution of Pyrenean oak populations in Sierra Nevada; (ii) to identify groups of Pyrenean oak populations based on floristic composition and environmental conditions; and (iii) to unveil whether the rear-edge populations clustering according to environmental variables coincides with their grouping based on their floristic composition.

3.2. Material and Methods

3.2.1. Study area

The study was conducted at the Sierra Nevada (Andalusia, SE Spain; Figure 3.1), a mountainous region covering more than 2000 km² with an elevation range of between 860 and 3482 m.a.s.l. The climate is Mediterranean, characterized by cold winters and hot summers, with a pronounced summer drought. The annual average temperature decreases in altitude from 12-16 °C below 1500 m.a.s.l. to 0 °C above 3000 m.a.s.l.. Annual precipitation ranges from less than 250 mm in the lowest areas of the mountain range to more than 700 mm in the highest peaks. Winter precipitation is mainly in the form of snow above 2000 m.a.s.l.. Additionally, the complex orography causes strong climatic contrasts between south and north-facing slopes. This mountain range is considered one of the most important biodiversity hotspots in the Mediterranean region (Blanca et al., 1998), hosting 105 endemic plant species for a total of 2353 taxa of vascular plants (33% and 20% of Spanish and European flora, respectively) (Lorite, 2016). Forest cover in Sierra Nevada is dominated by pine plantations (*Pinus halepensis* Mill., *Pinus pinaster* Ait., *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco, and *Pinus sylvestris* L.) covering approximately 37000 ha. Native forests are mainly dominated by holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) occupying low and medium mountain areas (11000 ha.), and Pyrenean oak *Quercus pyrenaica* ranging from 1100 to 2000 m.a.s.l., covering about 3000 ha (Pérez-Luque et al., 2019).

Quercus pyrenaica is a deciduous species extending through southwestern France, the Iberian Peninsula and northern Morocco (Franco, 1990). The forests of this species reach their southernmost European limit in Andalusian mountains such as Sierra Nevada, where eight populations have been identified (Figure 3.1a; Table 3.1) on the basis of their isolated geographic locations in deep valleys separated by distances considerably longer than the average dispersal distances of the seeds by birds such as Eurasian jay (*Garrulus glandarius*) (Gómez, 2003; Valbuena-Carabaña et al., 2005). They are distributed on siliceous soils both in the northwestern and southern slopes of the mountain range and are often associated to major river valleys. These

Tab. 3.1. Description of the *Q. pyrenaica* populations in Sierra Nevada. For elevation, minimum and maximum values are in brackets. The latitude and longitude coordinates referred to polygon centroid.

Oak population	Code	River valley	Municipalities	Elevation (m)	Latitude	Longitude	Area (ha)
El Camarate	CAM	Alhama	Lugros	1740 (1441-2026)	37° 10' 29.49" N	3° 15' 24.33" W	457.15
Robledal de San Juan	GEN	Genil	Güejar-Sierra	1519 (1189-1899)	37° 7' 29.63" N	3° 21' 54.60" W	395
Loma de la Perdiz	MON	Monachil	Monachil	1780 (1564-1990)	37° 5' 54.87" N	3° 25' 46.65" W	204.55
Umbria de la Dehesa de Dílar	DIL	Dílar	Dílar	1764 (1478-1960)	37° 3' 33.61" N	3° 28' 29.07" W	154.07
Loma de Enmedio	DUR	Dúrcal	Dúrcal	1824 (1530-2035)	37° 1' 58.75" N	3° 28' 38.44" W	137.04
El Robledal de Cáñar	CAN	Chico	Cáñar	1687 (1366-1935)	36° 57' 28.04" N	3° 25' 57.10" W	436.2
Loma de la Matanza y Loma de Ramón	POQ	Poqueira	Soportújar, Pampaneira, Bubión, Capileira	1740 (1214-1981)	36° 57' 58.90" N	3° 22' 55.12" W	458.95
Loma de los Lotes	TRE	Treveléz	Pórtugos, Busquístar	1692 (1312-1963)	36° 58' 37.38" N	3° 17' 25.75" W	197.92

oak woodlands represent a rear edge of their distribution (Hampe & Petit, 2005), containing high levels of intraspecific genetic diversity (Valbuena-Carabaña & Gil, 2013). Their conservation status for southern Spain is “Vulnerable”, and it is expected to suffer from climate change, potentially reducing its suitable habitats in the near future (Gea-Izquierdo et al., 2013; Gea-Izquierdo et al., 2017).

The distribution of *Q. pyrenaica* forests in Sierra Nevada was delimited using the updated version of the forest map of Sierra Nevada at 1:10 000 scale (CMAOT, 2014; Pérez-Luque et al., 2019). Black and white orthophotographies from 2001 (0.5-m of spatial resolution) and false color aerial photographies (Color Infrared) from 2005 (1-m resolution) were used to correct errors by detailed photographic interpretation, resulting in a detailed map of oak forests (Figure 3.1b). Forest patches with at least 50 % tree cover of which 75 % cover being *Q. pyrenaica* were considered oak patches.

3.2.2. Environmental data

For each oak population we obtained the values of 30 environmental variables selected to represent different direct and indirect gradients important for plant distribution (Guisan & Zimmermann, 2000; Williams et al., 2012): temperature, water availability, topography, solar radiation and land-use (Table 3.2). Observed climate data (1960-2010) from 43 meteorological stations 50 km around Sierra Nevada, compiled by Sierra Nevada Global Change Observatory (Zamora et al., 2017a), were used as input to compute high resolution (100 x 100 m pixel-size) climate maps (Benito et al., 2014) based on the mapping method proposed by Ninyerola et al. (2000). Seasonal and annual maps with the averages of direct solar radiation and insolation time were computing using the GIS GRASS module r.sun (Neteler et al., 2012; Súri & Hofierka, 2004). From a high-resolution digital elevation model (10-m; Department of the Environment, Regional Government of Andalusia) several topographic variables were derived: elevation, slope, aspect, E-W and N-S gradients, topographic position (difference in elevation between a cell and surrounding cells within a 1000 meter radius) (Guisan et al., 1999). Also,

Tab. 3.2. Description of environmental variables and forest attributes used in our analysis

Category	Code	Description	Units
Climate	precYE	Annual precipitation	mm
	precSU	Summer precipitation	mm
	precAU	Autumn precipitation	mm
	precWI	Winter precipitation	mm
	precSP	Spring precipitation	mm
	tmaxSU	Summer mean maximum temperature	° C
	tmaxAU	Autumn mean maximum temperature	° C
	tmaxWI	Winter mean maximum temperature	° C
	tmaxSP	Spring mean maximum temperature	° C
	tminSU	Summer mean minimum temperature	° C
	tminAU	Autumn mean minimum temperature	° C
	tminWI	Winter mean minimum temperature	° C
	tminSP	Spring mean minimum temperature	° C
Topography	elev	Elevation	meter
	aspect	Aspect	°
	slope	Slope	°
	tpNS	North-South gradient	%
	tpEW	East-West gradient	%
	radSU	Summer direct radiation	$W \cdot h \cdot m^{-2}$
	radAU	Autumn direct radiation	$W \cdot h \cdot m^{-2}$
	radWI	Winter direct radiation	$W \cdot h \cdot m^{-2}$
	radSP	Spring direct radiation	$W \cdot h \cdot m^{-2}$
	radhSU	Mean duration of insolation in Summer	hour
	radhAU	Mean duration of insolation in Autumn	hour
	radhWI	Mean duration of insolation in Winter	hour
Landscape	radhSP	Mean duration of insolation in Spring	hour
	twi	Topographic wetness index	
	tpos	Topographic position	meter
	flow	Flow accumulation	
Forest structure	human	Anthropogenic influence	cells
	FCC	Forest canopy cover	%
	FCCTree	Forest canopy cover of Tree	%
	FCCShrub	Forest canopy cover of Shrub	%
	FCCHerb	Forest canopy cover of Herbaceous	%
	CCshann	Canopy Cover diversity	
	heiTree	Tree Height	m
	denTree	Density	trees ha^{-1}
	BA	Basal area	$m^2 \cdot h^{-1}$
	vol	Volume	$m^3 \cdot h^{-1}$
Forest biodiversity	diver	Plant diversity	
	rich	Richness	species number
Forest function	regTot	Total regeneration	total seedling number
	regQp	Pyrenean Oak regeneration	seedling number
	regQi	Holm Oak regeneration	seedling number

topographic wetness index and flow accumulation were computed using the r.terraflow module of GRASS GIS. As a surrogate of anthropogenic influence, we computed the frequency of human infrastructures in a 2000 meter radius buffer. Finally, for each environmental variable we extracted the values for all the 100 m size pixels contained within each oak population (Figure 3.2).

3.2.3. Forest attributes

To characterize oak patches, we selected several stand attributes relating to forest structure, function, and composition from Sierra Nevada Forest Inventory (SINFONEVADA, Pérez-Luque et al., 2014) (Table 3.2). By using this approach, we characterized the plant community both in terms of their species composition, and also regarding their ecological functioning (del Río et al., 2016; McElhinny et al., 2005). SINFONEVADA forest inventory was carried out during 2004-2005, and it includes an extensive network of plots distributed within the main forest units of Sierra Nevada mountain range. We selected 32 plots belonging to deciduous broadleaf forests category. All of them are located within the eight Pyrenean oak populations identified in Sierra Nevada. For each plot (20 x 20 m), all trees with diameter at breast height (dbh) > 7.5 cm were tallied by species and dbh. Regeneration, species composition and abundance were also recorded in two additional subplots (see Pérez-Luque et al., 2014, for a detailed description): a 5-m radius subplot where the seedling abundance of *Q. pyrenaica* was recorded; and a 10-m radius subplot where the species composition and abundance estimated by the Braun-Blanquet cover-abundance scale were measured (Braun-Blanquet, 1964) (See Table A.1).

Forest composition (richness) and plant diversity were used as indicator for overall forest biodiversity. Plant diversity was measured using the Shannon diversity index (Krebs, 1999). The total regeneration was used as proxy for forest functioning. Finally, as forest structure indicators we selected the following attributes: the total- and strata- (*i.e.* tree, shrub and herbaceous) canopy cover; canopy cover diversity; tree height, tree density, basal area and volume of adult tree. Canopy covers were computed as the proportion of plot area covered by the whole forest (total) and the different strata considered (tree, shrub and herbaceous respectively). Canopy cover diversity was quantified through the Shannon index for the proportion of plot area covered by different vegetation strata (tree, shrub and herbaceous) according with the following equation:

$$CCd' = \sum_{i=1}^n g_i \cdot \ln g_i$$

where g_i is the proportion of strata i of the total plot area and n is the number of strata (del Rio et al., 2003). Basal area was calculated as the sum of the basal areas of the adult trees assuming a circular cross-section of the trunk. Volume was calculated as sum of volume ($V = 0.55 \cdot \text{height} \cdot \text{diameter}^2$) of all *Q. pyrenaica* adult trees. Additionally, we also extracted the values of the environmental variables for the centroids of the plots and we added a species-composition matrix for each of the 32 selected plots.

3.2.4. Statistical analysis

To identify the main environmental gradients that characterize the oak forests at Sierra Nevada, we performed a principal component analysis (PCA) on the standardized variables (Figure 3.2). Over 75 % of the correlations (Sperman's r) among variables were significant ($p < 0.01$). We checked the adequacy of the environmental matrix by applying Kaiser-Meyer-Olkin test, a measure of sampling adequacy ($KMO=0.7138$, value greater than 0.5 is considered adequate (Dziuban & Shirkey, 1974). The Kaiser-Guttman rule [*i.e.* axes whose eigenvalues are larger than the average of all eigenvalues; Guttman (1954)], and the criterion that any principal component (PC) accounts for at least 10% of the total variance were used to determine the meaningful PCs to be retained for interpretation (Legendre & Legendre, 2012). The PCA variables with a correlation to the principal components that was higher than 0.7 were selected to describe the environmental gradients indicated by the principal factors. We applied Linear Discriminant analysis (LDA) to determine the environmental variables that best discriminated among Pyrenean oak patches and to identify different groups of populations (Legendre & Legendre, 2012; Williams, 1983).

Then, environmental variables and forest attributes were tested for differences among populations groups previously identified. Normality and homoscedasticity were checked using the Shapiro-Wilk test and Levene's test respectively. If normality and homoscedasticity assumptions were satisfied, we performed ANOVA analysis followed by the Tukey LSD for testing statistical significance. Otherwise, Kruskal-Wallis ANOVA for nonparametric

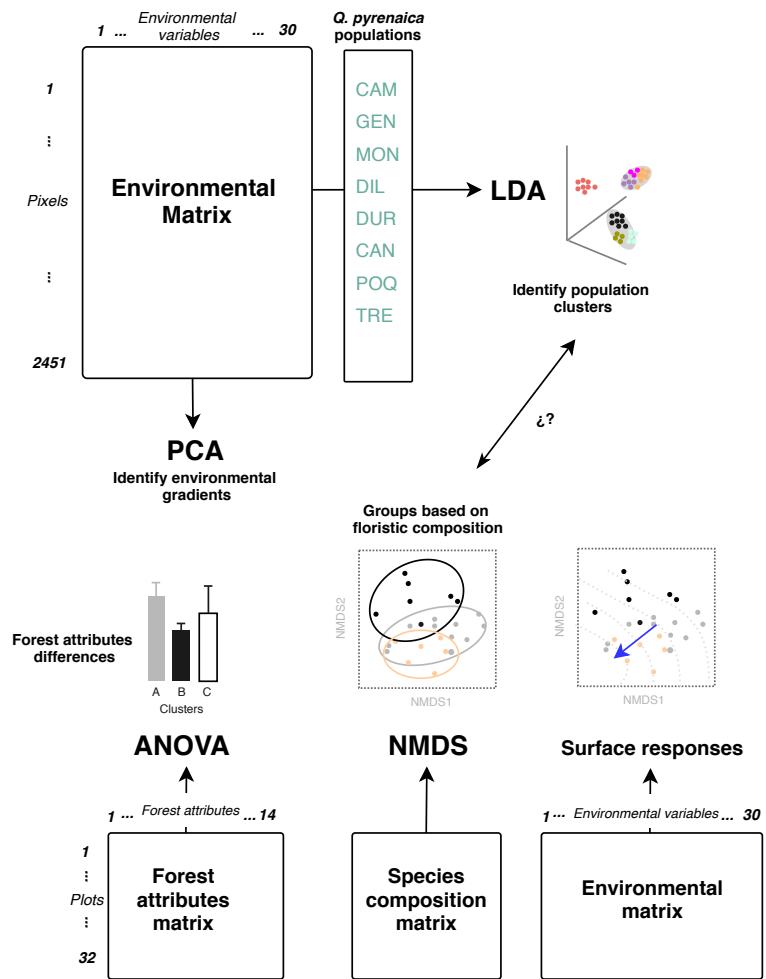


Fig. 3.2. Methodological scheme of the analyses. Using an environmental data matrix, the main environmental gradients that characterize the oak forests at Sierra Nevada were identified using a Principal Component Analysis (PCA). Linear Discriminant Analysis (LDA) was also applied to identify different groups of oak populations. With a matrix of floristic composition, a Non-metric Multidimensional Scaling (NMDS) ordination were applied to visualize patterns of species composition, interpret them according to the environmental factors, and identify groups of oak populations based on similarities between floristic composition. See material and methods for more details.

data were conducted followed by manual pairwise comparison using Mann-Whitney U-test.

Finally we used a Non-metric Multidimensional Scaling (NMDS) ordination analysis based on Bray–Curtis dissimilarity distance (Kruskal, 1964) to: (i) visualize patterns of species compositions, (ii) interpret them with respect to the environmental factors (*i.e.* relate the variability in species composition to environmental variables), and (iii) identify groups of Pyrenean oak populations based on similarities between floristic composition. NMDS involves the reduction of multidimensional similarity data to a low-dimensional ordination in which relative distance indicates relative similarity (*i.e.* plots with very similar species composition are close and *vice versa*) (Minchin, 1987). We compared two and three-dimensional solutions based on Kruskal's stress (as a measure of goodness of fit). We also studied the floristic-environment relationships by fitting linear trends on the ordination yielded by the NMDS. For these linear fittings, squared correlation coefficients and empirical p-values were calculated using random permutations ($n = 1000$) of the data (Oksanen, 2013). Finally we fitted non-parametrically smoothed surfaces of continuous environmental variables on the NMDS ordination. The smooth surfaces were fitted using generalized additive models (GAM) with thin plate splines, using the coefficient of determination (R^2) as goodness-of-fit statistic (*e.g.* Oksanen, 2013; Virtanen et al., 2006).

All analysis was conducted in R software (R Core Team, 2020) using the following packages: MASS (Venables & Ripley, 2002), nFactors (Raiche & Magis, 2020), and vegan (Oksanen et al., 2019). We also used the packages candisc (Friendly & Fox, 2020), ellipse (Murdoch & Chow, 2020), ggpibr (Kassambara, 2020a), ggord (Beck, 2020), factoextra (Kassambara & Mundt, 2020) and patchwork (Pedersen, 2020) for visualization.

3.3. Results

PCA of all measured environmental variables yielded three significant axes explained 62.11 % of the total variance (Table 3.3). The first PC axis was strong and negatively correlated with radiation and precipitation related

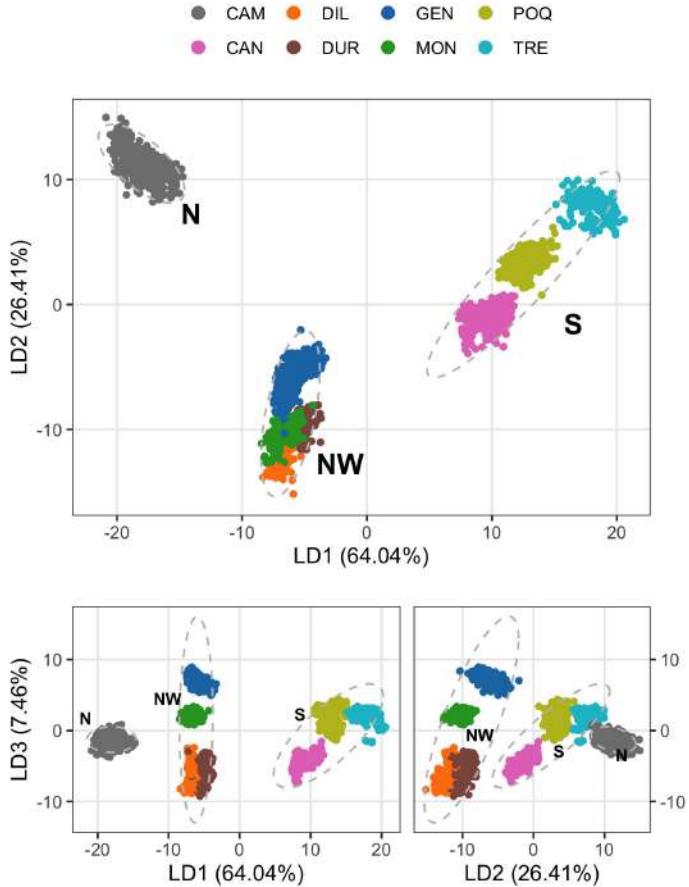


Fig. 3.3. Discriminant analysis ordination of *Quercus pyrenaica* populations. N: northern population group (CAM); NW: northwest population group (GEN, MON, DUR, DIL); and S: southern population group (CAN, POQ, TRE). Population's code as in Table 3.1. Numbers in brackets expressed explained variance (%) for each discriminant axis.

variables, and positively with northness gradient and slope (Table 3.3). Maximum average temperatures showed strongest negative correlations with the second PC axis. The third PC axis was negatively correlated with minimum average temperatures. The precipitation variables presented weak positive correlation with the third PC axis.

The discriminant analysis yielded three significant functions explaining 97.9 % of variance (Table 3.3). The ordination plot (Figure 3.3) showed a clear separation of oak populations into three clusters: a single-oak-population (CAM) cluster, namely N in the Figure 3.3; the second cluster (NW) formed by the GEN, MON, DIL and DUR oak populations; and the southern cluster

Tab. 3.3. Results of the principal component and discriminant analysis. The three first axis for PCA and LDA are shown. Loadings and correlations of the environmental variables on principal component axis are reported. For LDA, canonical correlations of environmental variables with each discriminant function are shown.

Variable	PC1 load	PC1 cor.	PC2 load	PC2 cor.	PC3 load	PC3 cor.	LDA 1	LDA 2	LDA 3
Topography									
twi	-0.022	-0.069	-0.010	-0.024	0.023	0.046	-0.009	0.005	0.018
flow	0.024	0.073	0.011	0.026	-0.008	-0.015	0.004	-0.003	0.005
elev	-0.158	-0.489	-0.016	-0.035	0.142	0.280	0.000	-0.014	0.105
slope	0.222	0.690	-0.068	-0.155	0.157	0.309	0.032	0.034	-0.073
tpos	-0.163	-0.507	-0.019	-0.042	-0.043	-0.085	-0.021	-0.013	0.006
aspect	-0.210	-0.650	-0.012	-0.026	-0.087	-0.172	-0.044	-0.043	0.075
tpEW	0.082	0.255	0.092	0.209	-0.017	-0.033	0.029	0.065	0.044
tpNS	0.238	0.737	0.031	0.070	0.092	0.182	0.076	0.070	-0.070
radWI	-0.270	-0.836	-0.030	-0.067	-0.101	-0.198	-0.071	-0.076	0.081
radSU	-0.276	-0.857	-0.023	-0.051	-0.119	-0.235	-0.067	-0.077	0.084
radSP	-0.287	-0.889	0.031	0.071	-0.152	-0.299	-0.045	-0.059	0.090
radAU	-0.292	-0.906	0.005	0.011	-0.141	-0.279	-0.056	-0.069	0.090
radhWI	-0.286	-0.888	-0.014	-0.032	-0.127	-0.251	-0.073	-0.083	0.098
radhSP	-0.283	-0.878	0.024	0.054	-0.150	-0.295	-0.051	-0.054	0.101
radhSU	-0.138	-0.428	0.111	0.252	-0.105	-0.207	-0.003	0.003	0.061
radhAU	-0.190	-0.590	0.096	0.218	-0.112	-0.220	-0.018	-0.003	0.074
Landscape									
human	-0.143	-0.443	-0.069	-0.156	0.165	0.326	-0.067	0.013	0.107
Climate									
precWI	-0.191	-0.593	-0.178	-0.404	0.301	0.594	-0.081	0.024	-0.076
precSP	-0.178	-0.551	-0.068	-0.153	0.264	0.520	-0.044	0.087	0.074
precSU	-0.226	-0.702	-0.084	-0.190	0.243	0.479	-0.073	0.069	0.092
precAU	-0.223	-0.692	-0.173	-0.391	0.225	0.444	-0.157	-0.043	-0.074
precYE	-0.223	-0.692	-0.145	-0.329	0.274	0.539	-0.092	0.032	-0.001
tminWI	0.042	0.131	-0.342	-0.775	-0.267	-0.525	0.003	-0.001	-0.024
tminSP	0.036	0.110	-0.293	-0.664	-0.311	-0.613	0.007	-0.008	0.001
tminSU	0.022	0.068	-0.189	-0.429	-0.357	-0.705	0.014	-0.011	0.045
tminAU	0.035	0.109	-0.276	-0.625	-0.321	-0.633	0.009	-0.009	0.008
tmaxWI	0.051	0.159	-0.353	-0.800	0.133	0.262	-0.021	0.014	-0.176
tmaxSP	0.063	0.196	-0.355	-0.804	0.091	0.180	-0.009	-0.014	-0.155
tmaxSU	0.056	0.175	-0.396	-0.897	0.015	0.030	-0.010	0.004	-0.120
tmaxAU	0.054	0.166	-0.372	-0.843	0.100	0.196	-0.018	0.011	-0.160
Eigenvalue	9.618		5.130		3.886		150.351	67.162	19.108
Variance	32.061		17.100		12.953		61.780	27.597	7.851
Cumulated variance	32.061		49.161		62.114		61.780	89.378	97.229
Canonical correlation							0.997	0.993	0.975

(S) composed by the southern oak populations CAN, POQ and TRE. Southern oak populations were separated out from northern populations along the first LDA axis (Figure 3.3), which showed slight negatively correlation with autumn rainfall. The second and third LDA axes showed weak correlations with all variables (Table 3.3).

The three oak clusters showed significantly differences for most of the environmental variables analyzed (Table 3.4). Only winter minimum temperatures ($\chi^2 = 5.35$; p-value = 0.069) and insolation time during summer ($\chi^2 = 0.306$; p-value = 0.306) was similar among the three oak clusters (Table 3.4). Post-hoc analysis showed that for most of the environmental variables we found pairwise significant differences between all the three oak clusters (Table 3.4).

Forest attributes did not significantly differ among the above described oak clusters except for plant diversity and herbaceous canopy cover (Table 3.4). The N cluster showed higher value of Shannon diversity index (2.27 ± 0.17) than NW cluster (*Mann-Whitney U* = 22.0; p-value < 0.01). For stand attributes relating to forest structure only the herbaceous canopy cover showed significantly differences ($\chi^2 = 11.18$; p-value = 0.004; Table 3.4) between N and NW clusters (*Mann-Whitney U* = 15.0; p-value < 0.01). For all other forest structure attributes, despite there are no significant differences, the N cluster showed the lowest values (Table 3.4). No significant differences were recorded for regeneration variables.

A three-dimensional solution of the NMDS was chosen because its correlation with the original data was higher than for a two-dimensional solution (Linear fit $R^2=0.793$ vs. 0.713). Additionally, lower Kruskal's stress value was observed for the three-dimensional solution (Stress=0.159 vs. 0.226). The NMDS ordination of the forest stands according to their floristic composition was significantly correlated with precipitation variables, elevation and marginally with winter maximum temperatures (Figure 3.4; Table 3.5). The precipitation variables showed highly and negative correlations with NMDS axis 2 (Table 3.5). The NMDS axis 1 were negatively correlated with elevation ($R^2 = 0.464$) and minimum temperatures, and positively correlated with slope and winter maximum temperatures (Table 3.5). The NMDS ordinations with fitted vectors and surfaces for significant variables

Tab. 3.4. Mean values of environmental variables and forest attributes for the three identified clusters of *Q. pyrenaica* forests derived from the discriminant analysis. The Chi-squared statistics of the nonparametric Kruskal-Wallis test is shown except for those variables analyzed using ANOVA test (*fccShru*, *fccTree* and *rich*). Values within brackets correspond to standard errors. Standard errors are shown in parentheses. Different letters indicate statistically significant differences between clusters oak populations.

variable	statistic	p.value	d.f.	groupA (N)	groupB (NW)	groupC (S)
Forest attributes						
BA	4.43	0.109	2	0.71 (0.47) a	7.11 (2.00) ab	7.71 (2.78) b
denTree	3.17	0.204	2	61.57 (31.95) a	226.97 (65.10) a	282.47 (86.03) a
fccHerb	11.18	0.004	2	6.50 (0.60) a	2.83 (0.51) b	4.33 (1.12) ab
fcc	4.45	0.108	2	7.50 (0.57) a	8.50 (0.54) a	8.67 (0.99) a
heiTree	1.15	0.563	2	4.19 (1.67) a	6.96 (1.83) a	7.45 (1.76) a
CCShann	2.09	0.352	2	0.85 (0.06) a	0.92 (0.04) a	0.93 (0.04) a
vol	3.63	0.163	2	7.50 (4.92) a	90.05 (29.24) a	76.66 (34.22) a
fccShru	1.96	0.159	2,29	2.75 (0.86) a	4.50 (0.51) a	5.33 (1.54) a
fccTree	1.41	0.261	2,29	1.75 (0.62) a	3.33 (0.58) a	2.67 (0.80) a
regTot	0.18	0.913	2	19.38 (6.25) a	47.56 (16.16) a	32.67 (15.82) a
regQi	3.89	0.143	2	5.75 (3.40) a	0.17 (0.09) a	3.50 (2.08) a
regQp	0.39	0.823	2	7.62 (3.21) a	46.39 (16.16) a	29.17 (16.30) a
diver	8.67	0.013	2	2.27 (0.17) a	1.57 (0.13) b	1.83 (0.09) ab
rich	2.95	0.068	2,29	16.62 (1.95) a	11.72 (1.21) a	14.17 (0.70) a
Environmental						
flow	66.22	0.000	2	345.35 (97.91) a	175.73 (32.95) b	169.57 (21.93) c
twi	60.74	0.000	2	4.90 (0.08) a	5.08 (0.05) b	5.40 (0.05) c
elev	32.38	0.000	2	1740.05 (6.52) a	1669.84 (6.22) b	1710.33 (4.20) c
tpEW	442.28	0.000	2	40.37 (1.47) a	54.36 (0.84) b	28.34 (0.58) c
tpos	201.90	0.000	2	-22.52 (1.73) a	-22.46 (1.64) a	-1.25 (0.75) b
aspect	656.80	0.000	2	160.25 (5.50) a	113.33 (2.33) b	262.06 (3.14) c
slope	568.14	0.000	2	26.10 (0.33) a	29.93 (0.28) b	20.32 (0.25) c
radWI	1301.22	0.000	2	1489.98 (50.78) a	770.18 (31.99) b	3013.85 (25.28) c
radAU	1238.90	0.000	2	5854.49 (40.75) a	5205.08 (30.85) b	6808.90 (17.59) c
radSU	1242.79	0.000	2	3056.60 (59.95) a	2140.28 (41.68) b	4619.39 (26.39) c
radSP	1064.83	0.000	2	6835.85 (29.69) a	6352.91 (25.49) b	7419.43 (14.46) c
radhWI	1565.28	0.000	2	4.77 (0.10) a	2.98 (0.08) b	8.10 (0.05) c
radhAU	125.57	0.000	2	10.44 (0.05) a	10.37 (0.04) a	11.01 (0.03) b
radhSP	1117.91	0.000	2	7.42 (0.06) a	6.47 (0.06) b	9.13 (0.04) c
radhSU	2.36	0.307	2	11.49 (0.05) a	11.37 (0.04) a	11.58 (0.03) a
tpNS	1363.86	0.000	2	62.33 (0.93) a	73.73 (0.66) b	27.76 (0.54) c
dist	2094.16	0.000	2	47.10 (0.04) a	39.52 (0.11) b	25.26 (0.04) c
human	983.67	0.000	2	0.00 (0.00) a	6.95 (0.38) b	19.53 (0.45) c
precYE	1143.00	0.000	2	690.32 (1.66) a	741.43 (1.10) b	778.13 (0.95) c
precWI	926.56	0.000	2	233.38 (0.43) a	246.53 (0.27) b	253.85 (0.28) c
precAU	1703.96	0.000	2	253.82 (0.45) a	267.02 (0.29) b	290.49 (0.35) c
precSP	576.54	0.000	2	135.36 (0.39) a	148.30 (0.32) b	148.28 (0.21) c
precSU	847.35	0.000	2	67.76 (0.39) a	79.57 (0.32) b	85.51 (0.20) c
tmaxWI	184.76	0.000	2	8.22 (0.05) a	9.40 (0.05) b	9.16 (0.04) c
tmaxAU	170.76	0.000	2	16.22 (0.05) a	17.19 (0.05) b	16.97 (0.04) c
tmaxSP	46.60	0.000	2	13.95 (0.04) a	14.35 (0.04) b	14.21 (0.03) c
tmaxSU	87.50	0.000	2	24.93 (0.04) a	25.46 (0.04) b	25.29 (0.03) c
tminWI	5.35	0.069	2	0.45 (0.04) a	0.42 (0.02) a	0.37 (0.02) a
tminAU	28.56	0.000	2	7.15 (0.04) a	6.93 (0.02) b	6.89 (0.02) b
tminSP	18.45	0.000	2	4.55 (0.04) a	4.37 (0.02) b	4.35 (0.02) b
tminSU	80.11	0.000	2	13.13 (0.04) a	12.68 (0.03) b	12.68 (0.03) b

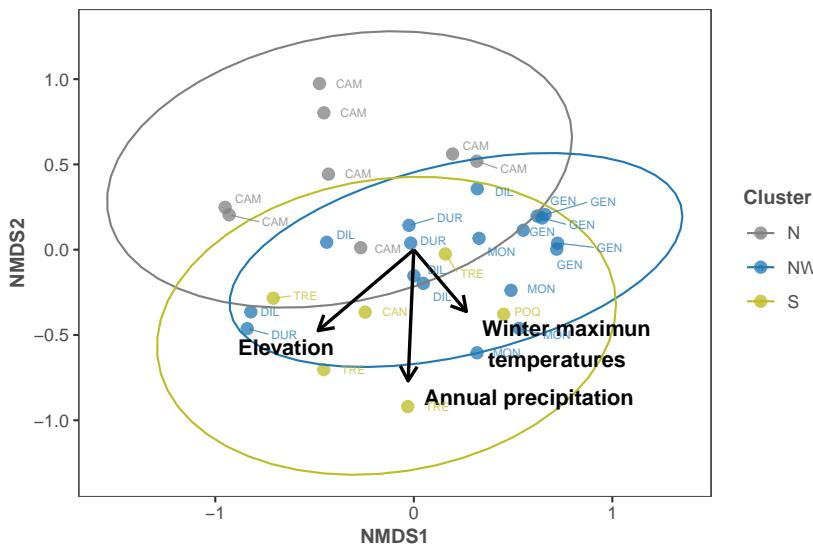


Fig. 3.4. NMDS ordination of the plots. Points represent plot sites displayed according to their similarity in species composition. Proximity in the statistical space indicates plot sites with a similar species composition. Arrows represent vectors of significantly environmental variables explaining the ordination (see Table 3.5). Each plot coloured according to the three oak-populations clusters derived from discriminant analysis. Only two dimensions of the NMDS is illustrated for ease of representation.

are shown in Figure 3.5. All these variables showed a non-linear significant relationship with the ordination pattern (R^2 values for surfaces were slightly higher than linear R^2 values; Table 3.5).

3.4. Discussion

3.4.1. Ecological diversity within the rear-edge

The rear-edge populations of *Quercus pyrenaica* located in mountain areas are not ecologically homogeneous, neither for their environmental conditions nor for their plant species composition. In this study, we find separate groups of *Q. pyrenaica* populations within Sierra Nevada (rear-edge) driven by radiation and rainfall as main discriminant variables (Figure 3.3). The differences among populations based on environmental variables, are in line with differential ecological dynamics reported for *Q. pyrenaica* forests in the Sierra Nevada by other studies. For instance, primary productivity

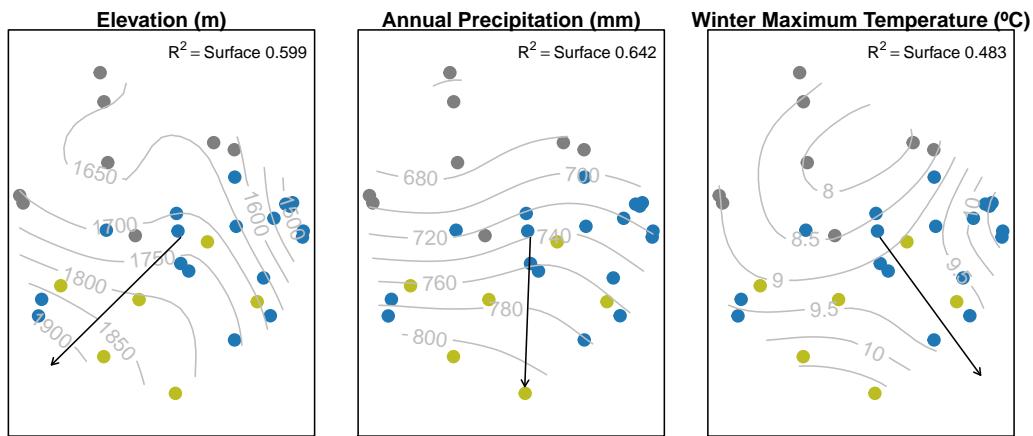


Fig. 3.5. NMDS ordination with fitted environmental vectors and regression surfaces. Length and direction of the arrows indicate the strength and sign of the linear correlation of environmental variable with ordination scores. The surfaces show smooth trends of the relationship between environmental variables and plot scores.

of these forest measured using remote sensing showed a heterogeneous spatial behavior, with oak woodlands of the southern slopes displaying a greater annual vegetation greenness than those from the northern slopes (Dionisio et al., 2012; Pérez-Luque et al., 2015a; Pérez-Luque et al., 2020). Also, differences have been found in both seasonal dynamics of greenness (Dionisio et al., 2012), and in temporal trends for primary productivity in the last years related with differential snow-cover trends in contrasting slopes (Alcaraz-Segura et al., 2016; Pérez-Luque et al., 2015a).

Interestingly, our results also showed differences in species diversity among population groups derived from clustering based on environmental variables. These results are consistent with those provided by Lorite et al. (2008), who pointed out that differences observed for the floristic component in the *Q. pyrenaica* populations of Sierra Nevada are related to the microclimatic conditions. Thus, the oak woodlands located in the northern of Sierra Nevada showed greater floristic similarity with those located at the center of the *Q. pyrenaica* distribution than those located at southern slopes of Sierra Nevada (geographically closer) (Lorite et al., 2008). The floristic differences between Sierra Nevada oak populations could also be related to the anthropogenic impact suffered by those populations, since the anthropic disturbances can affect the floristic patterns of the woodlands of this species, as it has been documented for oak woodlands in central Spain (Gavilán et al., 2000). Thus,

Tab. 3.5. Results of the NMDS. Maximum linear correlations (R^2) of the environmental variables (vector) with the NMDS ordination patterns are shown. Significance of the correlations was calculated using 1000 permutations. Non-linear surface responses using GAM are also shown

Variable	Vector			Response Surface	
	Vector R^2	Vector p-value	F	Response Surface R^2	p-value
Climate					
precWI	0.583	0.001	4.89	0.587	0.000
precSP	0.509	0.001	6.23	0.644	0.000
precSU	0.584	0.001	7.76	0.693	0.000
precAU	0.526	0.001	2.93	0.460	0.000
precYE	0.613	0.001	6.14	0.640	0.000
tminWI	0.071	0.547	0.73	0.175	0.106
tminSP	0.091	0.436	0.63	0.155	0.121
tminSU	0.138	0.223	0.51	0.130	0.140
tminAU	0.101	0.384	0.54	0.137	0.144
tmaxWI	0.234	0.047	3.21	0.483	0.001
tmaxSP	0.112	0.363	0.87	0.202	0.069
tmaxSU	0.206	0.081	1.78	0.341	0.014
tmaxAU	0.225	0.057	2.97	0.463	0.002
Landscape					
human	0.127	0.277	0.14	0.040	0.319
Topography					
twi	0.057	0.649	0.52	0.131	0.133
flow	0.032	0.830	0.00	0.000	0.604
elev	0.464	0.002	5.12	0.598	0.000
slope	0.053	0.631	0.14	0.040	0.293
tpos	0.131	0.261	0.27	0.072	0.232
aspect	0.050	0.696	0.00	0.000	0.646
tpEW	0.050	0.698	0.34	0.090	0.217
tpNS	0.008	0.970	0.31	0.081	0.211
radWI	0.021	0.899	0.12	0.034	0.326
radSU	0.017	0.918	0.00	0.000	0.841
radSP	0.024	0.864	0.00	0.000	0.580
radAU	0.014	0.937	0.00	0.000	0.660
radhWI	0.028	0.837	0.05	0.014	0.384
radhSP	0.038	0.782	0.00	0.000	0.613
radhSU	0.139	0.190	0.01	0.004	0.421
radhAU	0.115	0.280	0.19	0.052	0.274

the CAM oak population (N-cluster) showed both the highest plant species diversity and richness (Table 3.4 and Supplementary), which may be related to a better conservation status, as this populations has been less exposed to intense anthropogenic activity (Jiménez Olivencia, 1991). Conversely, the southern oak populations (CAN, POQ and TRE) showed a poorer floristic composition conditioned by both climate and intense land use (Al Aallali et al., 1998; Camacho-Olmedo et al., 2002).

We found a remarkable match between the population's clustering derived from analysis of environmental variables (Figure 3.3) and the ordination of the populations according to species composition (Figure 3.4 and Figure 3.5). These findings suggest a linkage between the heterogeneity of environmental factors and the variability of species composition for these woodlands. The diversity of ecological conditions for *Q. pyrenaica* populations in this rear edge are in line with the high levels of genetic diversity shown by populations of this oak in the Sierra Nevada (Valbuena-Carabaña & Gil, 2013, 2017). The climatic and topographical heterogeneity that exists in the Sierra Nevada offers a great diversity of microhabitats, which has allowed this mountain range to act as a refuge for different species (Blanco-Pastor et al., 2019; Gómez & Lunt, 2007; Médail & Diadema, 2009), including for deciduous *Quercus* species during the last glacial period (Brewer et al., 2002; Olalde et al., 2002; Rodríguez-Sánchez et al., 2010). In fact, there are fossil and genetic evidences for different *Quercus* species that strongly suggest they survived only in southerly refugia during the last glacial maximum (Bhagwat & Willis, 2008; Birks & Willis, 2008; Brewer et al., 2002; Petit et al., 2002). The persistence in a refugium suggests a combination of a moderately suitable local environment buffering against the regional climate, and a relative tolerance to climate change, by either pronounced phenotypic plasticity, and/or adaptive capacity (Gavin et al., 2014). This could be very well the case of *Q. pyrenaica*, a species harboring a high genetic diversity (Valbuena-Carabaña & Gil, 2013), located in a mountain region with a complex topography that could protect local populations against rapid climate shifts and allow species to persist despite regionally unfavorable environments.

3.4.2. The importance of summer rainfall at the micro-habitat level.

The distribution of *Q. pyrenaica* is known to be conditioned by summer drought period with a minimum of 100-150 mm of summer rainfall (Blanco Castro et al., 2005; García & Jiménez, 2009). Bioclimatic analysis for this species revealed the importance of rainfall and ombrothermic indexes in the separation of temperate and Mediterranean forests (del Río et al., 2007). At more detailed scale, the distribution for this oak is driven by a complex gradient related with temperature, rainfall and radiation (Gavilán et al., 2007; Urbieta et al., 2011). Our study unveils a separation in the environmental space between oak populations at the rear-edge related with the spatial pattern of precipitation for this mountain region (Pereira et al., 2016). Thus, summer and annual rainfall are among the most important factors in explaining the distribution of *Q. pyrenaica* forests in Sierra Nevada (Table 3.3). The northern and northwestern populations of *Q. pyrenaica* at Sierra Nevada are located in valley bottoms with and northern orientation, where the relative humidity is greater as result of a lower solar radiation. On the other hand, the populations of the southern slopes of Sierra Nevada get an extra supply of water from moist air from the neighboring Alborán sea (Martínez-Parras & Molero-Mesa, 1982). The differences in water availability among oak populations could affect several ecological processes such as tree-growth (Gea-Izquierdo & Cañellas, 2014; Pérez-Luque et al., 2020), seedling germination and survival (Gómez et al., 2003; Gómez-Aparicio et al., 2008; Mendoza et al., 2009), and the regeneration of the species (Gómez et al., 2001), mainly due to the key role of water availability in the microsites facilitating the germination and establishment of seedlings.

3.4.3. Implications for forecasting and modelling.

The factors controlling species distributions may vary depending on the scale of observation. At large scale areas, the distribution of a species is likely to be controlled by climatic regulators (Guisan & Thuiller, 2005), whereas at local scales factors related to biological interactions play a relevant role in shaping species distributions (Sánchez de Dios et al.,

2009; Urbíeta et al., 2008). At the site level, we found that moisture availability is the environmental factor that better separates the studied oak populations into clearly differentiated clusters. The identification of different population groups based on environmental variables at fine-scale is important when modelling the distribution and forecasting the impact of global change on the species. Our results suggest that incorporating the local adaptations of individual populations into predictive models might help avoid misrepresenting the potential range shift of species under changing climate conditions (Benito-Garzón et al., 2011). This is particularly important for species with rear-edges located in mountain ranges, since these areas provide a broad diversity of microhabitats due to climatic and topographical heterogeneity (Médail & Diadema, 2009). For instance, some recent works have performed out high-resolution models of the distribution of relict trees in Mediterranean southern mountains (e.g. *Abies pinsapo*, *Pinus sylvestris* and *P. nigra*) providing useful information for forest management actions (López-Tirado & Hidalgo, 2014).

3.5. Concluding remarks: biodiversity from the genetics to the landscape.

We identified several groups of oak populations within the rear-edge of the *Q. pyrenaica* forest mainly due to microhabitats conditions. The different clusters of oak populations are supported both by discriminant analysis of environmental variables and by ordination analysis based on the floristic composition on the target populations. The diversity in the ecological conditions within these populations results from both to the environmental heterogeneity created by the slopes and the contrasting exposures of the valleys they inhabit, and the anthropic use of these ecosystems (e.g. Navarro-González et al., 2013; Pérez-Luque et al., 2020). The confluence of these factors generates a multitude of environmental conditions on a fine scale, which are reflected in the distribution, composition and functioning of the *Quercus pyrenaica* forests. *Quercus pyrenaica* woodlands are highly diverse at all organization levels, from a genetic perspective, i.e. high levels

of genetic differentiation within species (Valbuena-Carabaña & Gil, 2013) and differences between populations (Valbuena-Carabaña & Gil, 2011); to ecosystem-functioning level, *i.e.* diversity in terms of primary production and growth (Alcaraz-Segura et al., 2016; Pérez-Luque et al., 2015a), and diversity of resilience to disturbances (*e.g.* Pérez-Luque et al., 2020). Such ecological heterogeneity is also made evident by the accompanying plant communities, which are very different depending on the oak population considered, being such differences correlated with the differences in environmental conditions among populations.

Mountains such as Sierra Nevada, not only act as elevation gradients along which plant communities are distributed and replaced, in fact, they constitute an ecological mosaics in which other factors besides elevation, *e.g.* the exposure and the history of human management, create a broad range of responses from the oak woodlands and its very diverse associated vegetation, from genetics to landscape. Understanding the differences that exist between oak populations within the rear-edge with respect to environmental variables help us to plan both the forest management and restoration actions, especially taking into account the importance of some environmental factors in key ecological aspects (*e.g.* regeneration and growth, Gómez-Aparicio et al., 2008; Pérez-Luque et al., 2020). Our results also show the importance of the rear-edge mountain areas as refuges for within-species diversity, and the role of species' southern ranges as hotspots of within-species diversity (Hampe & Jump, 2011; Jump et al., 2010). All this knowledge will be important to prioritize the conservation measures, and to design adaptive management actions targeting these populations, in order to maintain their ecological processes and biodiversity.

Colonization pattern of abandoned croplands by *Q. pyrenaica* in a Mediterranean mountain region

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Abstract

Land abandonment is a major global change driver in the Mediterranean region where anthropic activity has played an important role shaping landscape configuration. Understanding the woodland expansion towards abandoned croplands is critical to develop effective management strategies. In this study we analyze the colonization pattern of abandoned croplands by *Quercus pyrenaica* in Sierra Nevada mountain range (southern Spain). We aimed to assess differences among populations within the rear-edge of the *Q. pyrenaica* distribution. For this purpose we characterized (i) the colonization pattern of *Q. pyrenaica*, (ii) the structure of the seed source (surrounding forests), and (iii) the abundance of the main seed disperser (Eurasian jay, *Garrulus glandarius*). The study was conducted in five abandoned croplands located in two representative populations of *Q. pyrenaica* located in contrasting slopes. Vegetation plots within three habitat-types (mature forest, edge-forest and abandoned cropland) were established to compute the abundance of oak juveniles. Abundance of European jay was determined using data of bird censuses (7-year). Our results indicate that a natural recolonization of abandoned croplands by *Q. pyrenaica* is occurring in the rear edge of the distribution of this oak species. Oak juvenile abundance varied between study sites. Neither surrounding-forest structure nor the abundance of jays varied significantly between study sites. The differences in the recolonization patterns seem to be related to differences in the previous-and post abandonment management.

4.1. Introduction

Land-use change is considered the main global change driver worldwide (Butchart et al., 2010; Winkler et al., 2021) affecting biodiversity (Sala, 2000), modifying ecological processes (Lindenmayer et al., 2012), and altering the provision of ecosystem services (Hasan et al., 2020). Croplands abandonment and afforestation are the main processes of land-use change in the Northern hemisphere (Rey Benayas, 2007; Winkler et al., 2021). In Mediterranean region, where anthropic activity has played an important role shaping landscape configuration, cropland abandonment has been widespread during the second half of the last century (Martínez-Fernández et al., 2015; Pías et al., 2014; Valbuena-Carabaña et al., 2010). Land-use change models predict an increase in this trend in the future (Perpiña Castillo et al., 2021; Rounsevell et al., 2006). The abandonment of traditional activities has left many Mediterranean landscapes in an almost barren state, with poor vegetation cover (Rey Benayas, 2007; Sheffer, 2012). Consequently, a natural vegetation regeneration process started with a spontaneously recovery of abandoned croplands (Alvarez-Martínez et al., 2014; de Natale et al., 2007; Debussche et al., 1999; Peñuelas & Boada, 2003; Piussi, 2000).

Thus, the abandonment of traditional uses since the middle of the last century (MacDonald et al., 2000), has caused a decrease in anthropogenic pressure on Mediterranean forest ecosystems (Valbuena-Carabaña et al., 2010), being particularly important for mountain areas (Alvarez-Martínez et al., 2014; de Natale et al., 2007; Jiménez-Olivencia et al., 2015; Pías et al., 2014). The dramatic rural exodus occurred in mountain areas due to changes in socio-economic conditions (European Environment Agency, 2010), resulting an abandonment of traditional activities and significant environmental changes (Alvarez-Martínez et al., 2014; de Natale et al., 2007; MacDonald et al., 2000; Piussi, 2000; Rutherford et al., 2008; Zimmermann et al., 2010). Moreover the abandonment of mountain agricultural areas is causing an increase in forest expansion via the spontaneous recovery of vegetation (Alvarez-Martínez et al., 2014; Piussi, 2000), that can causes a homogenization of the landscape (Mietkiewicz et al., 2017) with several ecological consequences (Zimmermann et al., 2010).

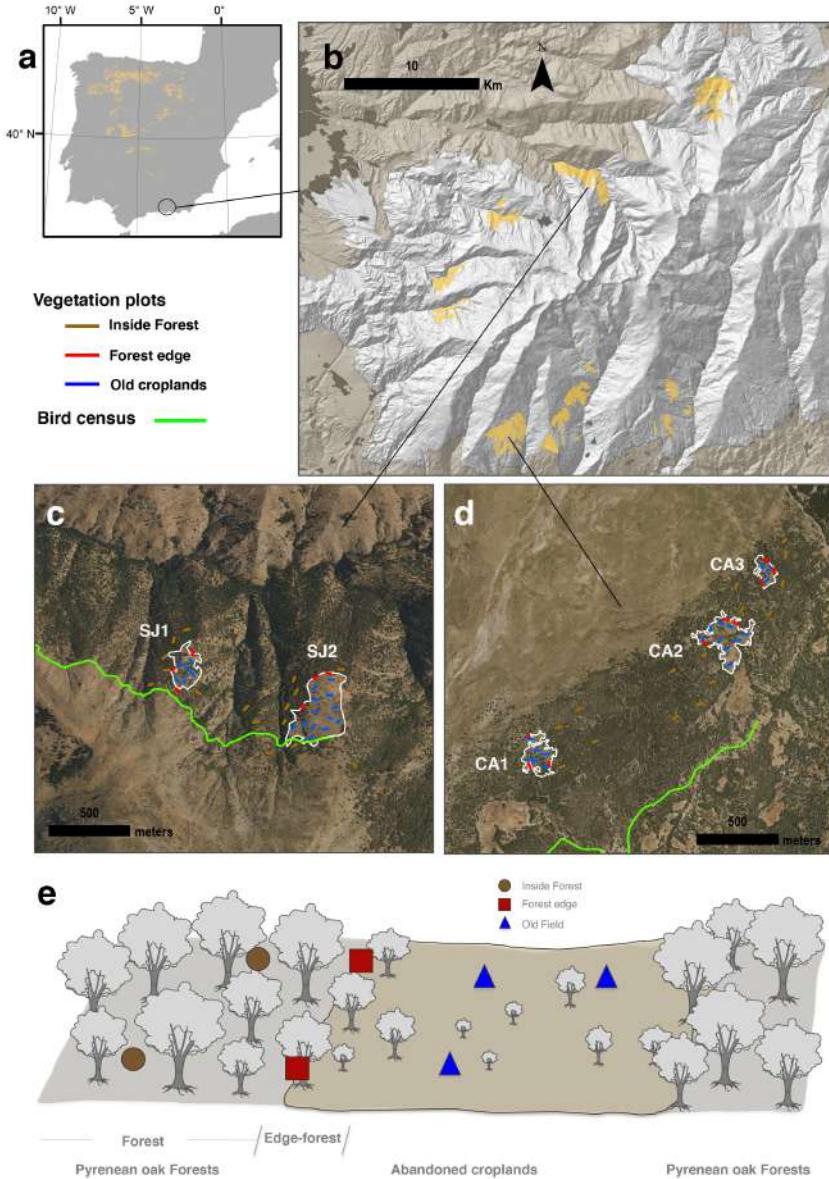


Fig. 4.1. Distribution of *Q. pyrenaica* forests in the Iberian Peninsula (a), and in Sierra Nevada mountain range (b). Location of the old croplands (white lines) in the study sites: Robledal de San Juan (SJ) (c), and Robledal de Cáñar (CA) (d). Names of the old croplands as in Table 4.1. Sampling design (e). Vegetation plots were randomly placed in the abandoned croplands (triangles), and inside the forest (circles) surrounding the old field. Several plots were also located at forest-old field edge (squares).

Quercus pyrenaica Willd. woodlands, like other forest formations in the Mediterranean region, have been subjected to intense anthropogenic pressures over time (Alba-Sánchez et al., 2021; García & Jiménez, 2009), which have led to the reduction of their distribution area, as well as to the modification of their floristic and structural patterns (Calvo et al., 1999; Gavilán et al., 2000; Tárrega et al., 2006). Historically, the woodlands of *Q. pyrenaica* have been exploited mainly for firewood, charcoal, and tannins (Ruiz de la Torre, 2006; Sánchez Palomares et al., 2008). Some areas were also burned and thinned to create pastures with low densities of mature trees that provide acorns, firewood, and large areas for grazing (Alvarez et al., 2009; Herrera Calvo, 2016; Valbuena-Carabaña & Gil, 2017). All these anthropogenic processes have transformed the oak woodlands in a deep way that it is difficult to find stands that can be considered natural forests (Ruiz de la Torre, 2006). Nonetheless, the decrease in anthropogenic pressure has paradoxically caused that many of the *Q. pyrenaica* oak stands present a state of advanced degradation, showing growth stagnation, lack of fruiting, and also symptoms of branch dieback (Bravo et al., 2008; Cañellas et al., 2004; Piqué et al., 2018; Piqué & Vericat, 2015; Valbuena-Carabaña & Gil, 2014).

Therefore, understanding the woodland expansion towards abandoned croplands would become critical to develop effective management strategies, particularly for populations representing the rear-edge of their distribution (Hampe & Petit, 2005) which need a particular attention due to their high conservation value (Fady et al., 2016). The study of ecological dynamics within the rear-edge populations is considered essential to establish proper management guidelines under current climate uncertainties (Fady et al., 2016; Jump et al., 2010). Rear-edge populations are often adapted to local environmental conditions at the limit of the species ecological amplitude, and often show a long-term persistence (Hampe & Petit, 2005). Local responses to environmental changes may differ from the species mean response (Benavides et al., 2013; Castro et al., 2004; Matías et al., 2017), and such differences may either promote or hamper the survival of edge populations under global change (Fady et al., 2016; Jump et al., 2010). In this work we analyze the colonization pattern of abandoned croplands by *Quercus pyrenaica* in Sierra Nevada mountain region. This mountain has undergone significant land use changes in the last 50 years (Jiménez-Olivencia et al., 2015) with increases

Tab. 4.1. Main characteristics of the abandoned croplands studied.

Site	Cropland				Number of plots		
	Code	Abandonment Age (years)	Elevation (m)	Area (ha)	Cropland	Edge	Forest
Robledal de Cáñar	CA1	> 60	1796-1866	3.29	6	3	4
	CA2	< 30	1789-1858	5.80	9	3	7
	CA3	40 - 60	1851-1892	1.56	3	3	4
Robledal de San Juan	SJ1	40 - 60	1507-1674	3.47	6	3	6
	SJ2	30 - 40	1575-1746	10.36	13	3	10

of forest densities (see chapter 5; also Jiménez-Olivencia et al., 2015), and tree growth (see chapter 6; Pérez-Luque et al., 2020). We are interested in exploring the colonization pattern of abandoned croplands by *Q. pyrenaica* on both slopes of the Sierra Nevada. We aimed to assess differences among populations in the rear edge of its distribution. Our specific goals are (*i*) to analyze the colonization pattern of abandoned cropland by *Q. pyrenaica* and its relationship with time after abandonment; (*ii*) to explore differences on the structure of the seed source (mature woodlands); and (*iii*) to compare the abundance of the main seed disperser (Eurasian jay, *Garrulus glandarius*).

4.2. Material and methods

4.2.1. Sampling Description

We sampled 5 abandonment croplands located at two Pyrenean oak forests in contrasting slopes of Sierra Nevada (southern Spain): Robledal de San Juan (SJ), located at the northern aspect (37°7'29.63"N, 3°21'54.60"W; Güejar-Sierra, Granada, Spain); and Robledal de Cáñar (CA), located at the southern aspect (37°57'28.04"N, 3°25'57.1"W; Cáñar, Granada). We selected oak populations located at contrasting slopes since differences in environmental variables have been reported for those oak woodlands (Pérez-Luque et al., 2021b). Each cropland was delimited using land-use and land-cover map of Andalusia for 1956 (CMA, 2007) combined with a detailed photographic interpretation of the black and white 1956 orthophotos (1-m spatial resolution) (see Navarro-González et al., 2012, for more details). The estimation of the age abandonment for each cropland were performed

combining interpretation of orthophotographies with information from local neighbors. We compiled all available aerial ortophotographies of the study areas from Fototeca Digital of the Spanish National Geographic Institute (<http://fototeca.cnig.es/>). These dates were verified using information about past land-use, compiled from local neighbours (by local workshops and interviews with retired elder: farmers, shepherds and loggers; see details in Moreno-Llorca et al., 2014; Moreno-Llorca et al., 2016). The estimated rank of ages could be considered accurate (see Table 4.1).

For each abandonment cropland, vegetation plots (30 m x 10 m) were randomly distributed in the old field; at the forest edges; and inside the surrounding forests (Figure 4.1). The number of plots within the old fields and surrounding forests were proportional to the size of the abandonment cropland (Table 4.1). A total of 83 vegetation plots were sampled in autumn 2012. In each vegetation plot all tree species were recorded, and tree height and diameter were measured. For each transect we computed the juvenile abundance as the number of individuals smaller than 150 cm on height. We did not distinguish the reproductive and vegetative origins of young oaks, since it is difficult due to the resprouting trait of this species. In addition to the juvenile abundance, we explored differences between several recruitment stages based on individual size (e.g Plieninger et al., 2010). We considered five size categories based in height (every 30 cm). All data were properly documented and published in an international repository (see Pérez-Luque et al., 2015b, for a detailed description of the dataset). To explore the main bird disperser in our study sites, we used bird censuses carried out by the Sierra Nevada Global Change Observatory (<https://obsnev.es/>). This dataset contains bird censuses at different ecosystems types of Sierra Nevada since 2008 (for more details see Barea-Azcón et al., 2012; Pérez-Luque et al., 2016b). We only used data for the Eurasian jay (*Garrulus glandarius*), since it is the main disperser of *Quercus pyrenaica* (Gómez, 2003). We assumed that jays can move acorns into abandoned croplands based on the habitat-preferences to cache acorns reported by Pons and Pausas (2007), and also considering preliminary data on jays flights carried out in our study sites by Zamora et al. (2013), who found a high proportion of flights of this bird at the same elevation, and around 40% of open areas as arrival habitat. Since we were interested in the comparison of the Eurasian jay populations

between the two study sites, we computed the annual bird abundances (in terms of birds/10 ha) for each site during a 7-year period (2008-2013). The sampling procedures was the line-transect method with a bandwidth of 50 m (25 m on each side). Transects length were 2.80 km for Cáñar site (CA), and 3.22 km for San Juan site (SJ). Sight and sound records within the sample area were accepted as contacts. All transects were sampled in the early morning. Eurasian jay abundance was calculated in terms of birds/10 ha. All counts in one month were averaged, and the yearly result was obtained from the average of all the months studied. For more details about bird censuses see Barea-Azcón et al. (2012) and Zamora and Barea-Azcón (2015).

4.2.2. Data analysis

We used the vegetation plots carried out inside the forest (habitat type = forest) to analyze the structure of the seed source (surrounding forest). Several parameters related to forest structure and functioning were computed: tree density, juvenile abundance, tree species composition, tree size related statistics (*i.e.* mean, median, maximum, 75 and 90 percentiles of tree-height), and basal area (BA). Differences between sites were assessed using the non-parametric Mann–Whitney U-test, since data did not meet normality nor/either homocedasticity assumptions. We also compared whether there was variation within plots belonging to the same sites. ANOVA analyses were performed to explore differences of bird disperser abundance (*G. glandarius*) between sites and across years.

The variation of the juvenile abundance between study sites, habitat type, and their interaction (site-habitat type), was analyzed using Generalized Linear Models with a Tweedie distribution with a log link (Dunn & Smyth, 2018). Study sites and habitat type were the explanatory variables. Prior to the analysis, data exploration was applied following protocols described by Zuur et al. (2010) and Ieno and Zuur (2015). As the dataset comprised count data, we initially used the Poisson and the Negative Binomial distribution. However, these models were overdispersed. A variance power parameter of 1.28 (1.20-1.40, 95% confidence interval) were used in the Tweedie GLM model. This parameter was estimated using the `tweedie.profile`

Tab. 4.2. Forest attributes of northern (SJ) and southern (CA) sites. U Mann-Withney statistics with significance at 0.05 level. Mean and SE are shown

Variable	Southern site (CA)	Northern site (SJ)	U statistic	p value
% of Q. pyrenaica	96.11 ± 1.28	100 ± 0	3.688	0.0001
Tree density (ind/ha)	1671.11 ± 229.21	1587.5 ± 161.67	4.808	0.9369
Juvenile abundance (ind/ha)	1004.44 ± 195.72	883.33 ± 127.18	4.852	0.7667
Adult abundance (ind/ha)	584.44 ± 80.47	704.17 ± 63.31	4.448	0.1780
Maximum tree height (m)	13.93 ± 0.65	13.75 ± 0.71	4.824	0.8736
Tree height mean (m)	4.32 ± 0.6	5.09 ± 0.37	4.330	0.0855
Tree height median (m)	3.19 ± 0.83	3.57 ± 0.66	4.564	0.3527
Tree height 75 percentile (m)	5.73 ± 1.02	8.29 ± 0.6	4.343	0.0922
Tree height 90 percentile (m)	10.07 ± 0.95	11.22 ± 0.54	4.605	0.4399
Basal Area (m ² /ha)	37.56 ± 4.23	33.58 ± 3.6	4.912	0.5400

Tab. 4.3. Model selection for the oak juvenile abundance, sorted by minimum AICc value.

model.name	df	logLik	AICc	ΔAICc	Nagelkerke R ²
Habitat type + Site + Habitat type × Site	6	-221.89	457.78	0	0.970
Habitat type + Site	4	-231.83	473.65	15.87	0.955
Habitat type	3	-236.21	480.42	22.64	0.946
Site	2	-291.06	588.12	130.34	0.116
null model	1	-293.09	590.19	132.41	0

function of the tweedie R package (Dunn, 2017; Dunn & Smyth, 2005). Model comparison (univariate models) was carried out using the Akaike's information criterion (AIC) (Burnham & Anderson, 2010). The model accuracy was tested by Nagelkerke's pseudo- R^2 , used as a measure of goodness of fit. The significance of the explanatory variables in the selected model was tested using the likelihood ratio tests (LRT). Wald z-tests and Tukey's HSD-corrected *post hoc* comparisons were used to test for differences in juvenile abundance among sites and habitat-type.

4.3. Results

The forest structure of *Quercus pyrenaica* woodlands did not show significant differences for the forest attributes between study sites (Table 4.2). *Quercus pyrenaica* woodlands of southern site (CA) showed higher tree density but smaller tree heights (mean, median and percentiles) than those on the northern site (SJ) (Table 4.2). In addition, higher abundance of juveniles

was found for CA site, which also showed greater basal area than SJ site (Table 4.2).

Regarding the abundance of *Garrulus glandarius*, no differences between study sites were found ($F_{1,82} = 2.387$; $p = 0.126$; CA = 1.69 ± 0.21 and SJ = 1.33 ± 0.22 birds/10ha), neither across years in the studied period (2008-2014) ($F_{6,82} = 1.234$; $p = 0.297$). The interaction term was also not significant ($F_{6,82} = 1.26$; $p = 0.284$).

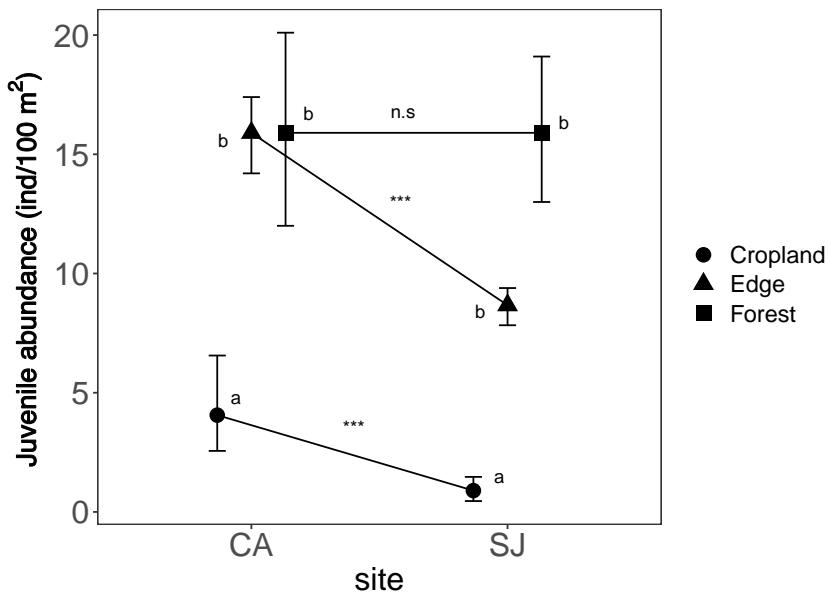


Fig. 4.2. Interaction plot for the oak juvenile abundance. Habitat-type differences within each site were indicated with different letters. Differences between sites for each habitat-type were indicated with asterisk. CA: Robledal de Cáñar site (southern slopes); SJ: Robledal de San Juan site (northern slopes).

The juvenile oak abundance model including all terms (*i.e.* full model) showed higher strength of empirical support than did models for each of the independent variables (*i.e.* univariate models) (Table 4.3). Oak juvenile abundance differed among habitat types ($F_{2,77} = 72.95$; $p < 0.0001$), and between study sites ($F_{1,77} = 8.16$; $p = 0.0054$; Table 4.4).

A decreasing gradient of oak-juvenile abundance was found across habitat-type, from higher values in forest type (15.90 ± 1.30 juvenile/100m²) to lower values inside the old croplands (2.43 ± 0.55 juvenile/100m²; Figure 4.2). The abundance of oak juveniles in the old croplands of the

Tab. 4.4. ANOVA table of the selected GLM model for the abundance of *Quercus pyrenaica* juvenile across study sites and habitat types. F-value and p-values are displayed.

Variable	SS	df	F	p-value
Habitat type	233.89	2	72.95	0.0001
Site	13.09	1	8.16	0.0054
Habitat type × Site	27.19	2	8.48	0.0004
Residuals	123.43	77		

southern site (CA) was significantly higher (4.06 ± 0.98 juvenile/100m²) than in those of the northern site (SJ; 0.90 ± 0.26 juvenile/100m²).

The size distribution of juveniles was also different among the study sites (Figure 4.3). An even size-distribution of the oak juveniles was observed in the old croplands of northern site. Conversely, higher contribution of small oak juveniles (< 30 cm) were found at old croplands of southern site (Figure 4.3).

A positive relation was found between the oak juvenile abundance and the estimate age of crop abandonment (Figure 4.4) with higher oak juvenile abundances in the earlier abandoned croplands

4.4. Discussion

We observed a colonization process of *Quercus pyrenaica* into abandoned croplands in this mountain region despite the strong recruitment constraints described for this species (Bravo et al., 2008; Gómez et al., 2003; Perea et al., 2014). Forest expansion towards abandoned croplands has been recorded in several marginal habitats in other European mountainous regions (Alvarez-Martínez et al., 2014; Améztegui et al., 2010; Ameztegui et al., 2016; de Natale et al., 2007; Kozak, 2003; Lasanta-Martínez et al., 2005; Piussi, 2000; Vicente-Serrano et al., 2004), as consequence mainly of rural depopulation and decrease on herbivores pressure (European Environment Agency, 2016; MacDonald et al., 2000). Our results show a relationship between juvenile-oak abundance and the estimated age of crop abandonment (Figure 4.4). As the time after crop abandonment increases, species heterogeneity and functional diversity of the ecosystem increases (Hermy & Verheyen, 2007;

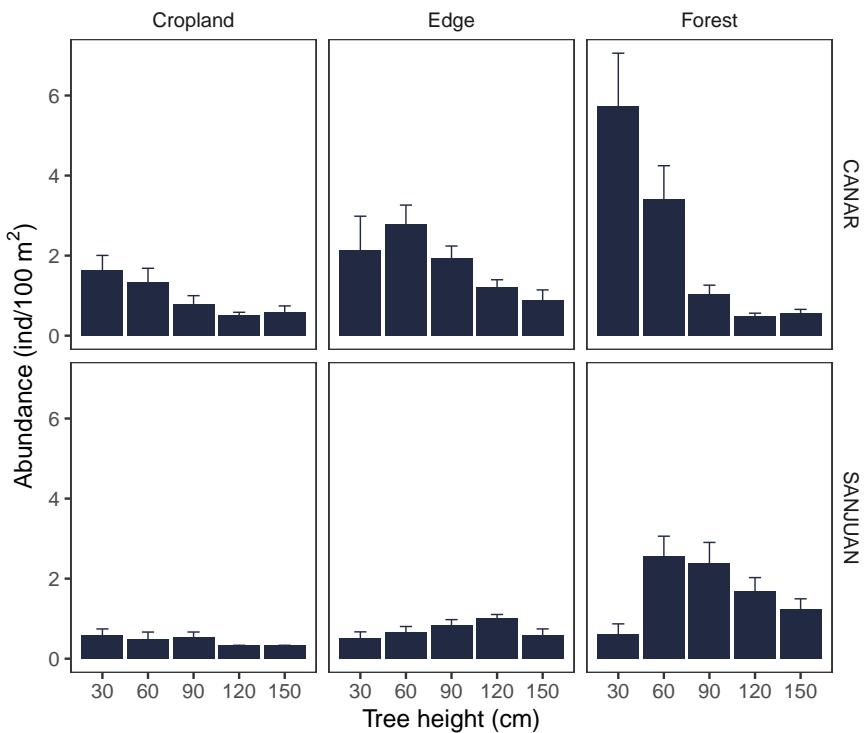


Fig. 4.3. Juvenile abundance classified by tree-size (see material and methods) by habitat-type in the two study sites. Mean and standard error are shown.

Puerta-Piñero et al., 2012), boosting the multifunctionality of the ecosystems (Cruz-Alonso et al., 2019).

It has been also reported that both age of the surrounding forests and previous land use could influence the colonization pattern (Minotta & Degioanni, 2011). In this sense, it is expected that the colonization process will continue, since the forests surrounding our study areas are relatively young. Dendrochronological estimates of the forest age for our study woodlands, ranged approximately 90-100 and 200 years for northern and southern oak populations respectively (Gea-Izquierdo & Cañellas, 2014; Pérez-Luque et al., 2020), which is younger than the estimated ages for these forests along their distribution range (Gea-Izquierdo & Cañellas, 2014). Cruz-Alonso et al. (2019), in a study of the recovery of multifunctionality in Mediterranean forests, reported for this oak species, a minimum of 80 years after the abandonment for the recovery of the reference multifunctionality.

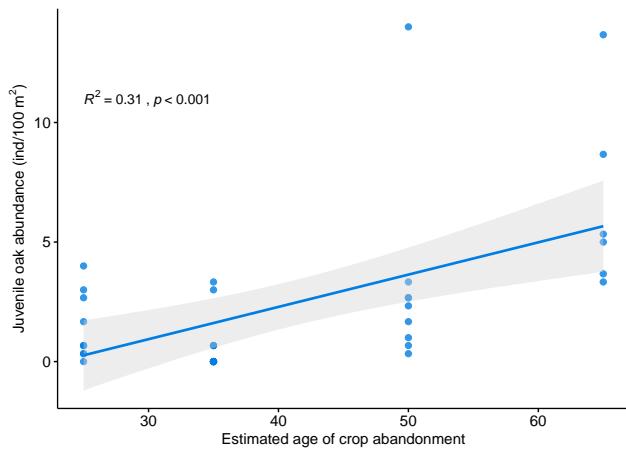


Fig. 4.4. Relation of the juvenile oak abundance with the estimated age of crop abandonment.

The colonization pattern of abandoned croplands varies within the rear-edge of the *Q. pyrenaica*. Our results showed different abundances of oak juveniles between sites, with higher abundances at the southern sites (CA) (Table 4.4; Figure 4.2). It is known that the distance to the source and the structure of the seed source influenced the propagule input into new habitats (Hewitt & Kellman, 2002; Kurek et al., 2019; Nathan, 2006). In our study sites, all the abandoned croplands are surrounded by native forests. Thus, the observed differences in oak juvenile abundance would not seem explained by the distance to the seed source (Table 4.1). Regarding to the structure of the seed source, we found no differences between the study sites (Table 4.2). Forest attributes potentially related to the acorn production (e.g. tree density, basal area, Gea-Izquierdo et al., 2006) are not different for surrounding forests between study sites (Table 4.2). Although in our work we have not carried out an estimation of acorn production that would allow us to compare between study sites, previous studies analyzing the variation in reproductive parameters and comparing the acorn production across oak woodlands of Sierra Nevada, found slight differences among oak populations, with higher acorn yield for southern oak woodlands than northern one (Leal, 2013). However, the data series used by Leal (2013) was very short (only two years) and *Quercus pyrenaica* have a marked mast-seeding behaviour (Bravo et al., 2008; Gómez et al., 2001). Besides that, there not seem to be marked differences in the current seed source that could explain our observed differences in the abundance of juveniles in the abandoned crops.

Another key aspect for the tree colonization of abandoned croplands is the dispersion vectors. *Q. pyrenaica* acorn are mainly dispersed by woodmouse (*Apodemus sylvaticus*) and Eurasian jay (*Garrulus glandarius*) (Gómez et al., 2003; Perea et al., 2014). We used a time series (a 7-year period) to analyze the abundance of jays at each study site. The aim of using this time series was to explore whether there were differences between study sites with respect to the abundance of this bird acorn-disperser. We are aware of the limitation of using these data, *i.e.* we do not know if the abundance of jays at both sites has followed the same temporal trajectory, but we have used the longest time series we have for both sites, to at least find out if there are differences between the sites in recent years. Our results showed similar abundances of this acorn disperser between the two study sites. Therefore, the observed differences in oak juvenile abundance do not appear to be explained by differences in abundance of this acorn disperser. Having observed no differences in the seed source neither in the main dispersal vector, a logical next step would be to explore differences on the seed arrival site.

For the recolonization of abandoned croplands, besides the importance of factors related to dispersal in time (seed bank related) and space (distance related), the previous use to which the crop field has been subjected is a key factor determining the abundance of native tree species (Hermy & Verheyen, 2007; Navarro-González et al., 2013). The colonization pattern of woody species is affected by fine-scale variations in abiotic factors (Leverkus et al., 2016; Milder et al., 2013), but it has been observed that land-use history mainly controlled the forest expansion rates (Alvarez-Martínez et al., 2014; Perring et al., 2016). The forest history of our study sites, inferred from several compiling studies (Jiménez-Olivencia et al., 2015; Mesa-Torres, 2009; Moreno-Llorca et al., 2014; Moreno-Llorca et al., 2016; Pérez-Luque et al., 2020; Titos, 1990), indicated that both sites were subjected to intense anthropic uses in the past. At the northern site (SJ), uplands areas were dedicated to grazing, and in the forest areas there were also some croplands with grazing. In addition, timber extraction for mining were recording at this site. Southern site (CA) has been exploited for firewood, charcoal and acorns, with less presence of livestock use. Although we could not estimate the intensity of use to which both zones have been subjected before the

abandonment of crops, the northern zone seems to have had a management history with higher grazing intensity than the southern site (Moreno-Llorca & Zamora, 2012; Moreno-Llorca et al., 2014; Moreno-Llorca et al., 2016).

In addition to the land-use legacies previous to the cropland abandonment, another relevant question would be the management history after the crop cessation, focusing on the livestock pressure, since herbivory impose severe constraints to the establishment and regeneration of this oak species (Gómez et al., 2003; Perea et al., 2014). There is no data available on the temporal evolution of grazing pressure at detailed scale in our study sites. Only Robles-Cruz (2008) showed an general quantification for several ecosystems of Sierra Nevada. Notwithstanding, several studies and reports, combining interviews with shepherds and reviewing of historical documents, have determined the recent livestock history in several oak woodlands of the Sierra Nevada (Moreno-Llorca & Zamora, 2012; Moreno-Llorca et al., 2014; Moreno-Llorca et al., 2016). For our study sites it has been observed both higher numbers of herds and sheperds, and more livestock density in the northern site (SJ) than in the southern one (CA), which could be translated into a greater herbivore pressure that would explain our observed differences in juvenile oak abundance within the abandoned croplands. This distinct herbivory pressure in the two study sites could explain the differences observed in the juvenile oak abundance not only at cropland habitat type either both at edge and forest habitat type. The exploration of abundance juveniles by size categories between habitats type for each study site showed lower abundance values for northern site (Figure 4.3). The size-age structure is also more homogeneous at the northern site, reinforcing the hypothesis of higher herbivore pressure. Gómez et al. (2003) found that herbivory rather than abiotic factors is the main cause of seedling mortality of *Q. pyrenaica* in Sierra Nevada. Thus, herbivores killed most of the seedlings, although the way in which they severed the seedlings was very diverse Gómez et al., 2003. They found that trampling by livestock and acorn predation by wild boards and hares were the main causes of the mortality observed, but the browsing by livestock is marginal (only 1% of the mortality) (Gómez et al., 2003). Another factor to consider is the presence of shrubs which can act as nurse plants. Facilitation by nurse plants has been reported as an essential process for the regeneration of some tree species (Castro et al., 2006; Gómez-Aparicio

et al., 2004). The survival of *Q. pyrenaica* substantially increases when it is under individual pioneer shrubs (Castro et al., 2006; Costa et al., 2017). Shrubs may protect *Q. pyrenaica* seedlings from browsing and trampling of vertebrate herbivores. They also offer safe sites that reduce the high mortality rates during the summer in the early stages of recruitment (Baraza et al., 2004; Castro et al., 2006). Although we did not estimate the cover and diversity of shrub species in our studied abandoned crops, previous studies in the surrounding forests of the same localities did not find differences in the diversity and richness of shrubs within oak forests (Muñoz, 2012).

4.5. Concluding remarks

The results of our study show that, even in the current increasingly dry climatic conditions, *Q. pyrenaica* woodlands are able to recover the abandoned former arable fields at the same altitudinal level where oak woodland is the potential vegetation. Thus, the Pyrenean oak woodland is clearly expanding in Sierra Nevada mountain range, a rear edge of the distribution of this oak species. This natural process can provide solutions for conservation of biodiversity, and enhances the mitigation of, and the adaptation to climate change (Chazdon et al., 2020, and references therein). Besides this, active restoration could aid to recovery the oak forest multifunctionality (Cruz-Alonso et al., 2019) in the abandoned croplands that are being colonized by tree species.

The differences in the recolonization patterns within the rear-edge seems be related to differences in the management prior to and after abandonment of mountain croplands. A higher herbivory pressure after cropland abandonment seems to limit the forest expansion towards marginal habitats. Related to this, and in order to improve the forest expansion, it would be recommended to take advantage of the presence of native shrubs that offer safe sites. Those safe sites could aid to reduce the mortality of *Q. pyrenaica* seedlings, and therefore increase the establishment probabilities of this oak species. This also would aid to increase heterogeneity within the ongoing secondary forest, which also increase the resilience to perturbations y the recovery of the ecosystem multifunctionality (Cruz-Alonso et al., 2019; Stritih

et al., 2021). On the other hand, attention also is needed to maintain healthy seed sources (surroundings forests), and a stable seed disperser community, particularly the Eurasian jay, since acorn dispersion by this bird species is considered a key process in the regeneration of *Quercus* forests after land abandonment (Pausas et al., 2006).

Carbon sequestration of coppiced forests of *Q. pyrenaica*. An study case from the rear-edge of its distribution

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(In prep.)

5.1. Introduction

Forest ecosystems are suppliers of several ecosystems services to humans (Iverson et al., 2018; Martínez Pastur et al., 2018; Noce & Santini, 2018). Forest ecosystem services include provisioning services (e.g. wood and non-wood forest products), regulating services (e.g. climate regulation), habitat or support services, and cultural services. In Mediterranean region, humans have been exploiting forest resources for centuries (Valbuena-Carabaña et al., 2010), however in the last decades a strong abandonment of traditional activities in mountains regions have been observed, mainly due to the rural exodus and the low economic value of forest products activities (Chauchard et al., 2007; Debussche et al., 1999; MacDonald et al., 2000). As a result, many forests currently have high tree-density stands, with an increased competition for resources, which can lead to widespread weakening of stand, increasing the vulnerability of forests to abiotic and biotic disturbances (Tardieu et al., 2018). This may be especially relevant for forests stands located at the rear-edge of the species distribution (Hampe & Petit, 2005), which are usually considered more vulnerable to climate change compared with populations at the centre of a species' range (Fady et al., 2016; Pironon et al., 2017; Rehm et al., 2015).

Q. pyrenaica (Pyrenean oak) is a marcescent Mediterranean tree species widely distributed throughout southwestern France and the Iberian Peninsula, reaching their southern limit in mountain areas of northern Morocco (Franco, 1990). The rear-edge populations of this species are restricted to high-mountain areas where these populations persists as isolated nuclei with ecological conditions very different from those of the main distribution area (Pérez-Luque et al., 2021b). Due to its ability to resprout from stumps and the entire root system, most stands of this species have been coppiced for centuries mainly for firewood, charcoal, tannins and woody pasture production (Sánchez Palomares et al., 2008; Ximénez de Embún, 1961). All these anthropogenic processes have transformed native woodland structures (Tárrega et al., 2006), and nowadays it is difficult to find stands of this oak that can be qualified as natural or pristine forests (Ruiz de la Torre, 2006). Paradoxically, after the diminution of human pressure on woodlands over the last decades, the abandoned coppices of *Q. pyrenaica* present an advanced

state of degradation with important ecological, economic and social problems (Bravo et al., 2008; Montoya & Mesón, 1979; Piqué et al., 2018; Piqué & Vericat, 2015; Vericat et al., 2012). Due to the importance of this species, several management practices (e.g. conversion to high forest) have been proposed to improve the state of abandoned coppices (Bravo et al., 2008; Montoya, 1982, 1983; Serrada et al., 1992; Vericat et al., 2012), although they have not been very successful, partly due to the lack of a comprehensive understanding of the physiological mechanisms underpinning tree stagnation (Salomón et al., 2017; Valbuena-Carabaña & Gil, 2017). In view of this situation, it is essential to seek for alternative management practices to the traditional uses of the abandoned coppices (Mesón & Montoya, 1985; San Miguel et al., 2012). Some management alternatives based on pastoral use have been proposed (Herrera Calvo, 2016), but to our knowledge few proposals have focused on the provision of the ecosystem services provided by this oak forests (but see Piqué et al., 2018; Piqué & Vericat, 2015).

The carbon sequestration is one of the most relevant ecosystems services provided by Mediterranean forests (Gauquelin et al., 2018; Noce & Santini, 2018). Carbon stock can be assumed as an indicator of the capacity of ecosystems to contribute to climate regulation because their potential to influence atmospheric CO₂ concentration (Lauterbach, 2007; Luyssaert et al., 2008). Mediterranean forests represent a carbon sink expected to increase over coming decades (Cañellas et al., 2017; Pasalodos-Tato et al., 2017). Improving carbon estimation and our understanding of the effects of forest management could be useful for forest managers, which could include carbon sequestration among the different objectives pursued in the forests management (Ruiz-Peinado et al., 2017). Several studies have been conducted to determine carbon sequestration by forest ecosystems in the Mediterranean region based on data from forest carbon inventories, field measurements, remote sensing, laser scanning and growth simulation (e.g. Cañellas et al., 2008; Chiesi et al., 2005; García et al., 2010b; Guerra-Hernández et al., 2016; Simonson et al., 2016; Vayreda et al., 2012). LIDAR (Light Detection And Ranging) has emerged as an effective technique for quantifying aboveground biomass in forests (Beland et al., 2019; Lefsky et al., 2002; Xiao et al., 2019) and has been also used for quantifying carbon stocks (Simonson et al., 2016; Zhao et al., 2018). In this study

we combined Airborne Laser Scanning LIDAR data and field inventories to estimate the biomass of Pyrenean oak woodlands (*Q. pyrenaica*) of Sierra Nevada (southern Spain), and then to assess the carbon sequestration capacity of those forests and their role as carbon sink. The specific objectives are: (i) to estimate the potential capacity of these ecosystems to sequester carbon dioxide and to evaluate the temporal trends for this ecosystem service; (ii) to explore the factors that explain the C stock for *Q. pyrenaica* woodland in Sierra Nevada; and (ii) to analyse the differences in biomass and carbon sequestration among oak populations within this mountain region.

5.2. Material and Methods

5.2.1. Study site and oak woodlands

The study area is located in Sierra Nevada (37°N, 3°W), a high-mountain range of southern of Andalusia with elevations of up to 3 482 *m.a.s.l.*. The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought and increasing aridity with decreasing altitude, and marked variability according to elevation and aspect. In Sierra Nevada there are eight Pyrenean oak populations (2 400 ha), distributed from 1 100 to 2 000 *m.a.s.l.* and often associated with major river valleys. Those eight oak populations could be grouped in three clusters, based on their structure and floristic composition: the northern (N), the northwestern (NW), and the southern (S) clusters (see chapter 3; also Pérez-Luque et al., 2021b). *Q. pyrenaica* woodlands in this mountain region represent a rear edge of their habitat distribution (Hampe & Petit, 2005). They are the richest forest formation in vascular plant species of Sierra Nevada, containing several endemic and endangered plant species (Lorite et al., 2008), and they also harbor high levels of intraspecific genetic diversity (Valbuena-Carabaña & Gil, 2013). However, these relict forests have undergone intensive human use throughout history (Camacho-Olmedo et al., 2002). Furthermore, the conservation status of this species for southern Spain is considered "Vulnerable" and it is expected to suffer from climate change, reducing its

Tab. 5.1. Allometric equations to compute biomass fraction of *Q. pyrenaica* (Ruiz-Peinado et al., 2012). DBH: Diameter at breast height; h: Tree height.

Tree fraction	Equation
Stem and thick branches	$W_{stem} = 0.0261 \text{ DBH}^2$
Medium branches	$W_{b2-7} = -0.0260 \text{ DBH}^2 + 0.536 \text{ h} + 0.00538 \text{ DBH}^2 \text{ h}$
Thin branches and leaves	$W_{b2} = 0.898 \text{ DBH} - 0.445 \text{ h}$
Roots	$W_{root} = 0.143 \text{ DBH}^2$

suitable habitats in the near future (Benito et al., 2011; Gea-Izquierdo et al., 2013; Gea-Izquierdo et al., 2017).

5.2.2. Biomass data

We used two types of field data, inventories (previous collected, 90 plots), and field data (20 plots) collected for this study.

Field data were obtained from a compilation of several forest inventories carried out in the Sierra Nevada mountain range (Table 5.2). In a first step, we selected plots included in the current distribution of Pyrenean oak in Sierra Nevada (Pérez-Luque et al., 2019). Then, only plots with complete information (*i.e.* those where all tree individual with dbh > 7.5 cm were measured), and pure stands (*i.e.* *Q. pyrenaica* composition > 70%) were selected. A spatial filter was also applied to discard overlapping plots. We also discarded old forests inventories (*i.e.* more than 10 years). All selected plots were measured between 2012 and 2020. In order to have a representation of all the oak populations, additional circular plots (radius 9 to 16 m) were sampled between October 2019 and March 2020. The plots were selected in proportion to the extension of the different ecological strata, providing representative stands with a variety of stand structure and site conditions. A sub-meter global satellite receiver (Leica Zeno 20 GIS, Leica Geosystems, Switzerland) was used to survey plot centers. We tagged and measured all tree individuals within the circular plot. Diameter at breast height (DBH) was measured to the nearest 0.1 cm with a graduated caliper, and tree height was measured to the nearest 0.1 m with a hypsometer. Azimuth and distance of each measured tree from the plot center were also recorded. A total of 113

Tab. 5.2. Field data used to compute the biomass of *Q. pyrenaica*. For DBH (Diameter at breast height) and Tree height, the average values and range (in brackets) are shown.

Source	n plots	area (m ²)	year	# trees	DBH (cm)	Tree height (m)
Dataset of Global Change, altitudinal range shift and colonization of degraded habitats in Mediterranean mountains (MIGRAME) (Pérez-Luque et al., 2015b)	30	300	2012	1422	10.77 (7.5–105)	4.27 (1.1–18)
Sierra Nevada Global Change Observatory (Aspízua et al., 2012; Zamora et al., 2017a)	3	400	2011,2012	122	19.03 (8–36)	9.57 (4.7–16.4)
Protection of key ecosystem services by adaptive management of climate change endangered mediterranean socioecosystems (Barea-Azcón et al., 2017). Forest inventories from Action C6 of the project	16	706.85	2015, 2017	650	13.26 (7.6–50)	6.96 (3.6–14)
Protection of key ecosystem services by adaptive management of climate change endangered mediterranean socioecosystems (Barea-Azcón et al., 2017). Forest inventories associated with dendrochronological plots	2	254.47–530.93	2018	191	7.73 (2.1–42.2)	4.48 (1.1–13.6)
Forest inventories from dendroecological research (see chapter 6; Pérez-Luque et al., 2020)	39	314.16	2018	457	26.3 (2.86–122.55)	10.31 (3–20.4)
This study field data	23	254.47–706.85	2019,2020	382	24.32 (2.91–67)	11.42 (1.7–20.6)

plots (254 to 400 m²) were finally selected with a total of 3 224 measured trees (Table 5.2).

5.2.3. Biomass and Carbon estimation

The biomass of individual trees was estimated according to published species-specific allometric equations (Ruiz-Peinado et al., 2012). For each tree, dry biomass was estimated as a sum of the different fractions (Carvalho & Parresol, 2003): stem plus branches with a diameter > 7 cm (W_{stem}); branches with a diameter between 2 and 7 cm (W_{b2-7}), branches with a diameter of less than 2 cm with leaves (W_{b2}), and the belowground fraction (W_{root}) the roots. Biomass of each fraction were computed using the equations developed for *Q. pyrenaica* (Ruiz-Peinado et al., 2012) (Table 5.1).

The carbon content in each biomass fraction was calculated by multiplying each value by 0.475, i.e. the species-specific carbon content of the biomass for this species (Ibáñez et al., 2002; Montero et al., 2005). The equivalent tree CO₂ sequestration was estimated by multiplying the tree carbon content by 3.67, i.e. the ratio between CO₂ molecular weight and C atomic weight. Biomass and carbon storage of individual trees were aggregated at plot level and scaled-up to hectarea to obtain the values of biomass for each fraction (Mg ha⁻¹), and the total carbon storage (Mg ha⁻¹) at the plot level.

5.2.4. Airborne Laser Scanning (ALS) Data and processing

Airborne Laser Scanning (ALS) data were acquired in 2014, with up to four returns measured per pulse, within the Spanish National Plan for Aerial Orthophotography (PNOA, by its Spanish language acronym) were used to generate the biomass map. The nominal point density was 0.5 points m⁻² with a vertical accuracy better than 0.20 m. The data were examined for extent, point density and consistency with overlapping points from adjacent scanning lines being removed. Gap filling was carried out when data from additional flight lines were available. The point clouds were classified into

ground and non-ground using the Multiscale Curvature Classification (MCC) algorithm (Evans & Hudak, 2007). Non-ground returns were labelled as vegetation as no infrastructure is present in the study area. The classified point cloud (ground class) was used to derive a digital elevation model (DEM). The DEM was subsequently used to compute the height above ground (*i.e.* normalized height) for the points classified as vegetation. Based on the height above ground, four generic groups of lidar metrics were generated at 20-m spatial resolution: canopy metrics, strata metrics, first returns metrics and all returns metrics. For example, canopy metrics included canopy closure at different heights (*i.e.*, 1-, 2-, 4-, 6-, 8-, 10-, and 12-m) while strata metrics included canopy closure and forest density for specific strata (*i.e.*, 0-0.5 m, 1-6 m, 1-8 m, 1-10 m, 1-12 m, 1-16 m, 1-24 m, 2-4 m, 2-6 m,..., 8-16 m, 8-24 m). Percentiles were computed using first returns as well as all returns metrics. Canopy closure metrics were defined as the proportion of first returns over a specific height threshold. Strata-specific canopy closure and forest density metrics were defined as the proportion of first returns and, respectively, all returns falling within specific height thresholds. Such metrics, representing proxies of forest structural characteristics, were aggregated at plot level and correlated with field-based plot biomass estimates to select optimum predictor variables for forest biomass. A two-step variable selection approach was used to identify the best lidar predictors for each biomass fraction. First, correlation among all 250 lidar variables was assessed and highly correlated ($|r| > 0.7$) variables were excluded from the dataset after retaining those with the highest correlation with biomass response variables (W_{stem} , W_{b2} , $W_{\text{b2-7}}$, W_{root} , and W_{total}). Second, the VSURF variable selection algorithm was implemented in R (Genuer et al., 2019) to identify the best predictors for each response variable. Briefly, this algorithm computes random forest models and variables are selected based on their importance value and on their capacity to decrease the OOB (out-of-bag) error of these models (more details can be found in VSURF package description, see Genuer et al., 2019).

Biomass maps were generated based on the selected predictor lidar variables using a Support Vector Machines (SVM) classification. The SVM model's stability and error were computed by randomly splitting the dataset ($n=113$ plots) into calibration and validation metrics (using a 60:40 rule). 100 random iterations were carried out to compute average error metrics

including the average root mean squared error (RMSE), the relative RMSE (RMSE%) and the correlation (r) between predicted and observed biomass. SVM biomass models were applied over the extents of the eight oak populations. For each biomass fraction, we compared the performance of the plot-scale biomass measurements (field data) with the predicted values derived from the ALS modelling. We used graphical methods and computed a Pearson correlation coefficient.

5.2.5. Cartography of biomass and C Stocks

For each of the estimated biomass fractions obtained from the modelling, we generated a map of biomass and sequestered C for each of the oak populations studied. The distribution of *Q. pyrenaica* forests in Sierra Nevada were obtained from vegetation and ecosystem maps of Sierra Nevada at 1:10 000 scale (CMAOT, 2014; Pérez-Luque et al., 2019). The pixel size selected to compute the ALS-derived metrics and to map the biomass and C stock was 20 m × 20 m, representing an area of 400 m², similar to the field plot dimensions (mean = 439 m², range 254 - 706.85) (Table 5.2).

5.3. Temporal evolution of tree biomass in *Q. pyrenaica* stands

We explored the temporal variation of biomass for this species at national level, and then only for plots located in our study area. To analyze the temporal evolution of the tree biomass of *Q. pyrenaica* forests, we used data from Spanish National Forest Inventory (SNFI), an extensive national database of forest surveys distributed systematically across the forested area of Spain. We used data from the second (SNFI2, Villaescusa & Díaz, 1998) and the third Spanish Forest Inventory (SNFI3, Villanueva, 2005), carried out during 1986-1996 and during 1997-2007, respectively. The SNFI is based on a network of circular plots which allows forest characterization and includes exhaustive information on the structure and composition of canopy and understory woody species. Each plot consisted of four concentric circles

of *radii* 5-, 10-, 15- and 25-m, in which DBH and total height were measured in all trees of DBH > 7.5-, 12.5-, 22.5- and 42.5-cm, respectively (Alberdi et al., 2016). Of the SNFI3 plots where *Q. pyrenaica* was present ($n = 6382$ plots), we selected only plots measured previously in the SNFI2, and with *Q. pyrenaica* as the main dominant species ($n = 2269$). For each plot, we computed aboveground and belowground biomass of each *Q. pyrenaica* adult tree using allometric equations (Table 5.1) (Ruiz-Peinado et al., 2012). We scaled-up to hectarea and aggregated at plot level. The temporal variation of biomass was estimated as the difference between biomass value of the same plot at the SNF3 and at the SNF2:

$$\Delta \text{Biomass} = B_{i,\text{SNFI3}} - B_{i,\text{SNFI2}}$$

5.4. Statistical analysis

We analyzed differences of the ALS-derived biomass and carbon dioxide sequestration for each fraction among the different oak populations and oak-population clusters. Non parametric Kruskal-Wallis test were used because data do not fit normality, homocedasticity or independence. Multiple pairwise comparisons after this test were made using Dunn's test with Bonferroni's correction. We also explored differences in the forest structure among oak-populations clusters. For this purpose, we computed several forest attributes for each field plot: mean tree height (m), average DBH (cm), basal area ($\text{m}^2 \text{ ha}^{-1}$) and tree density (trees ha^{-1}). Differences for stand attributes among oak-population clusters were also analyzed with the non-parametric Kruskal-Wallis test, followed by multiple pairwise comparisons using Dunn's test with Bonferroni's correction.

We used generalized linear models (GLM) to analyze the effect of the different explanatory variables and their interactions on the forest C stock (*i.e.*: W_{total} , W_{stem} , W_{root}). As explanatory variables we selected: topographic variables (elevation, slope and aspect); competition related-variables (tree density); stand-structural variables (Shannon structural diversity index and vertical strata richness); and microclimatic variables (topographic wetness index, a surrogate of the moisture content). Topographic variables were derived

from a digital elevation model at 5 x 5 meters resolution (Spanish National Geographic Institute). For each plot we compute the tree density (trees ha⁻¹), and the strata richness (number of different diametric classes) using the DBH. We considered the following diametric classes: <2.5 cm; each 5 cm-intervals; and >52.5 cm. We also characterized the structural diversity by computing a Shannon-Weber structural diversity index following (del Rio et al., 2003). This index is considered a surrogate of structural heterogeneity (McElhinny et al., 2005; v. Gadow et al., 2012). The topographic wetness index is an estimate of the predicted water accumulation and is considered a surrogate of soil-moisture (e.g. Petroselli et al., 2013; Zinko et al., 2005). It was derived from the high-resolution digital elevation model using the dynatopmodel R package (Metcalfe et al., 2018). Stepwise model selection was applied starting from the saturated model and removing the least significant term until there was no further decrease in the Bayesian Information Criterion (BIC). We considered all models within 2 BIC units as equivalent in terms of fit.

All analyses were conducted using the R software (R Core Team, 2020), and the vegan (Oksanen et al., 2019), randomForest (Liaw & Wiener, 2002), nlstools (Baty et al., 2015), nlme (Pinheiro et al., 2021), biostat (Gegzna, 2020), glmulti (Calcagno, 2020), MuMIn (Bartoń, 2020) and VSURF packages (Genuer et al., 2019).

5.5. Results

5.5.1. Biomass modelling

The LIDAR-metrics that best predicted the each-fraction biomass values are presented in Table B.1. The rumple index, elevation, canopy height maximum and 99th percentile of canopy height were the LIDAR-metrics better explained the biomass model for the W_{stem}, W_{b2-7} and W_{total} fractions (Table B.1), and they also were selected in biomass model for the W_{root} and W_{b2} fractions. The better models provided R² values ranged from 0.17 (W_{b2}) to 0.45 (W_{stem}) (Table B.1).

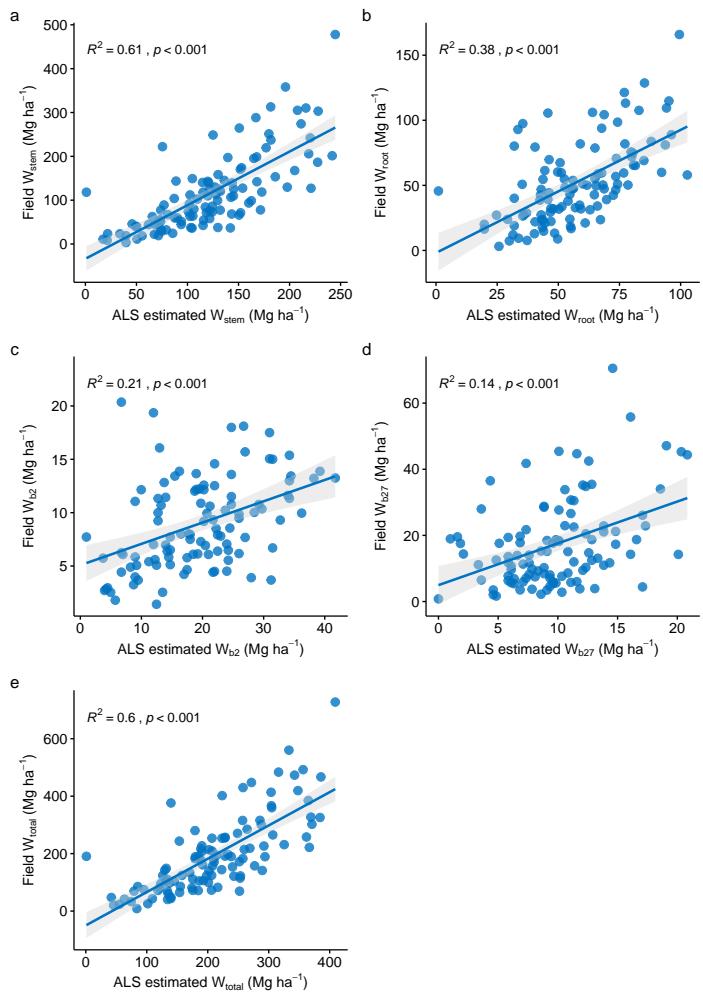


Fig. 5.1. Scatterplots of the field-measured biomass fractions and the most accurate model-estimated values of the biomass fractions in the same plot. R^2 and significance values of the correlation are included

The evaluation of the observed (field-measured) *versus* the ALS-estimated values for all biomass fractions are presented in Figure 5.1. The higher correlations were obtained for W_{stem} and W_{total} fractions which showed 0.61 and 0.60 R^2 values respectively. The other biomass components showed significant but weaker correlations, particularly the W_{b2-7} fraction with a R^2 value of 0.14 (Figure 5.1).

Tab. 5.3. Stand characteristics, field-measured and ALS-derived biomass (Mg ha^{-1}) and potential carbon dioxide sequestration ($\text{Mg CO}_2 \text{ ha}^{-1}$) values for Pyrenean oak-population clusters in Sierra Nevada. Statistics and significance value for Kruskal-Wallis tests were shown. Different letters indicate statistically significant differences between oak-population clusters (Dunn's test, $p < 0.05$). Total values of ALS-derived Biomass (Mg) and Potential CO_2 sequestration (Mg CO_2) for all *Q. pyrenaica* forests in Sierra Nevada are shown. Values in bracket show total values for each oak-population cluster.

Stand features	N	NW	S	Statistic	p-value
Tree height (avg.)	14.69 ± 0.81 a	9.10 ± 0.55 b	7.81 ± 0.36 b	15.23	<0.001
Tree height (min)	10.32 ± 1.49 a	4.02 ± 0.52 b	3.71 ± 0.31 b	11.20	0.004
Tree height (max)	18.54 ± 0.68 a	14.76 ± 0.40 b	13.89 ± 0.33 b	12.67	0.002
DBH	39.36 ± 6.00 a	20.18 ± 1.24 b	20.88 ± 1.54 b	8.43	0.015
Basal Area	35.99 ± 6.61 a	28.08 ± 2.34 a	28.81 ± 2.26 a	1.31	0.518
Tree density	405.51 ± 165.87 a	898.86 ± 104.02 a	838.35 ± 106.01 a	3.69	0.159
<i>Field-measured biomass</i>					
W _{stem}	182.89 ± 33.18	113.21 ± 11.41	117.18 ± 11.72	4.30	0.116
W _{b2-7}	28.82 ± 5.37	17.49 ± 1.85	17.31 ± 1.69	5.25	0.072
W _{b2}	8.75 ± 2.06	9.73 ± 0.74	8.63 ± 0.48	1.06	0.587
W _{root}	65.52 ± 12.04	51.12 ± 4.26	52.46 ± 4.11	1.31	0.518
<i>ALS-derived measured</i>					
W _{stem}	84.29 ± 0.50 a (1.03 10^6)	83.35 ± 0.37 a (1.98 10^6)	89.16 ± 0.33 b (2.62 10^6)	2296.42	<0.001
W _{b2-7}	8.71 ± 0.04 a (0.10 10^6)	8.24 ± 0.03 b (0.18 10^6)	8.37 ± 0.02 c (0.24 10^6)	1446.20	<0.001
W _{b2}	13.16 ± 0.08 a (0.16 10^6)	13.10 ± 0.06 a (0.31 10^6)	14.18 ± 0.05 b (0.42 10^6)	2138.11	<0.001
W _{root}	49.32 ± 0.21 a (0.59 10^6)	46.56 ± 0.16 b (1.08 10^6)	47.74 ± 0.13 c (1.4 10^6)	2978.22	<0.001
W _{total}	152.06 ± 0.81 a (1.85 10^6)	147.27 ± 0.60 b (3.48 10^6)	157.13 ± 0.53 c (4.61 10^6)	2369.70	<0.001
CO ₂ stock stem	146.93 ± 0.86 a (1.03 10^6)	145.30 ± 0.64 a (1.89 10^6)	155.44 ± 0.57 b (2.44 10^6)	2296.42	<0.001
CO ₂ stock b27	15.19 ± 0.06 a (1.79 10^6)	14.37 ± 0.05 b (3.44 10^6)	14.59 ± 0.04 c (4.57 10^6)	1446.20	<0.001
CO ₂ stock b2	22.95 ± 0.15 a (0.28 10^6)	22.85 ± 0.11 a (0.54 10^6)	24.73 ± 0.10 b (0.73 10^6)	2138.11	<0.001
CO ₂ stock root	85.98 ± 0.37 a (0.17 10^6)	81.17 ± 0.27 b (0.31 10^6)	83.23 ± 0.22 c (0.42 10^6)	2978.22	<0.001
CO ₂ stock total	265.07 ± 1.41 a (3.22 10^6)	256.72 ± 1.05 b (6.07 10^6)	273.91 ± 0.93 c (8.04 10^6)	2369.70	<0.001
<i>Total</i>					

5.5.2. Differences on biomass and C stock among Pyrenean oak populations

The cartography for total biomass (W_{total}) and the potential dioxide carbon sequestration of are shown in Figure 5.2. The total estimated biomass (aboveground and belowground) existing in the *Q. pyrenaica* woodlands of Sierra Nevada amounted to 9.94 Tg (1 Tg = 10^{12} g), which represents a potential sequestration of 17.33 Tg of CO₂ (Table 5.5).

The spatial distribution of the estimated biomass in the *Q. pyrenaica* forests of Sierra Nevada showed a general pattern with higher values mostly concentrated at southernmost oak woodlands. We observed that the MON population, belonging to NW cluster, showed the higher values for the estimated biomass and for the dioxide carbon sequestration potential (Figure 5.2; Table B.2).

The comparison of field-derived measures between oak-cluster populations revealed differences for tree height and DBH, but no for Basal Area and Tree density (Table 5.3). The oak woodlands of N-cluster showed significantly taller trees with larger DBH than those of the NW and S (Table 5.3, Figure 5.3). Lower tree density and higher basal area were observed for N oak-woodlands, but the differences were not significant with the other oak-populations. No differences were found for field-biomass estimation between oak-populations (Table 5.3).

Significant differences for ALS-estimated biomass were found among oak-clusters (Table 5.3). The values for the stem fraction (W_{stem}) and small branches (W_{b2}) biomass fractions were significantly higher for S oak-populations than for those in the N and NW, the latter showing no differences (Table 5.3). The total biomass (W_{total}) was significantly different between oak-population clusters with higher values for southern oak populations (Figure 5.3). Root biomass (W_{root}) and medium branches biomass (W_{b2-7}) were significantly higher for northern oak-populations (N) (Table 5.3; Figure 5.3).

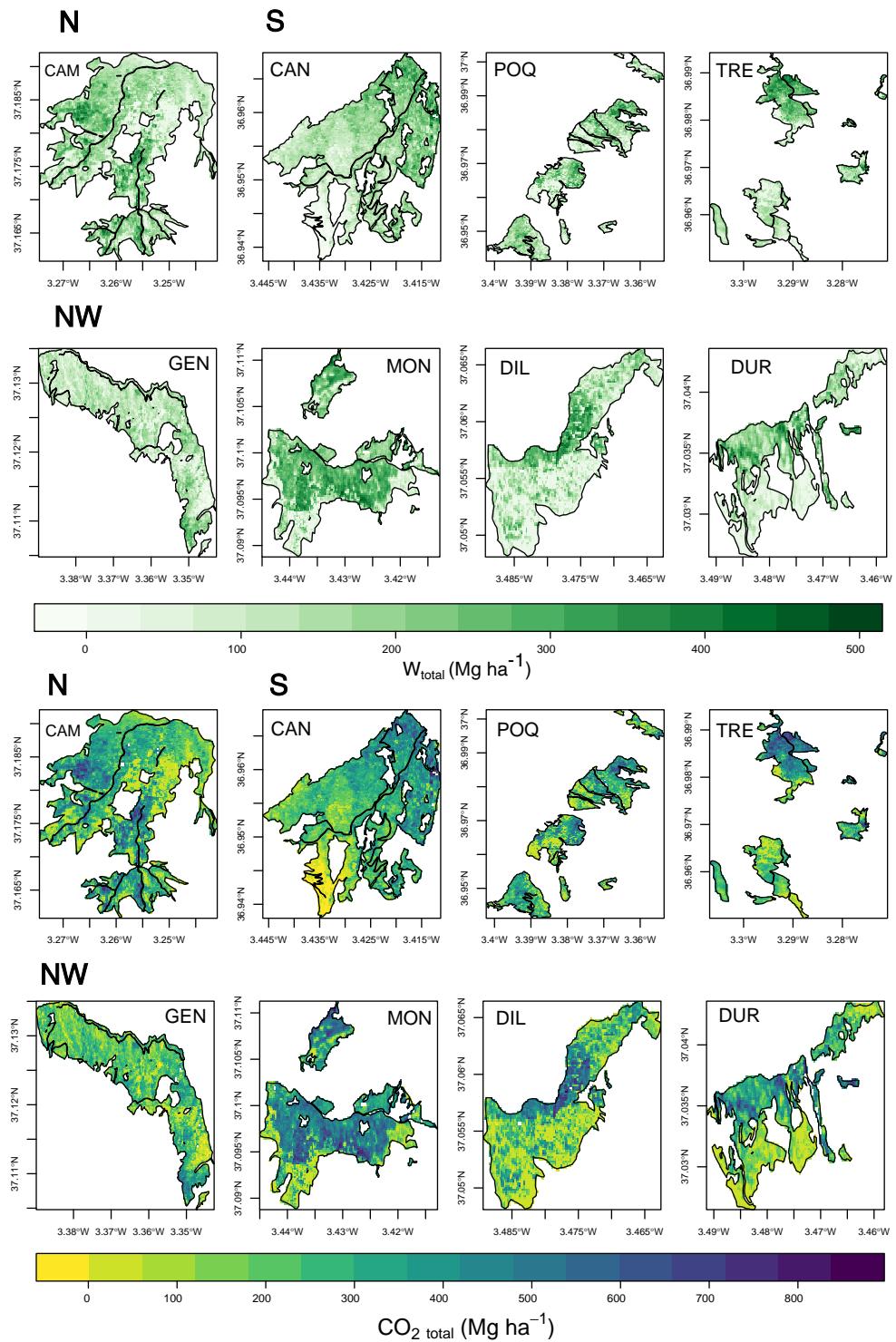


Fig. 5.2. Total biomass (W_{total}) (a) and Potential Carbon sequestration (b) for each of the eight Pyrenean oak populations of Sierra Nevada. Different spatial scales were used for ease of visualization.

Tab. 5.4. Summary of the best model (in terms of Bayesian Information Criterion) of total (W_{total}), stem (W_{stem}), and root (W_{root}) biomass (Mg ha $^{-1}$) as a function of field-plot variables.

Effects	W_{total}			W_{stem}			W_{root}		
	Estimate	Z-value	p-value	Estimate	Z-value	p-value	Estimate	Z-value	p-value
Intercept	-1094.19 ± 292.09	-3.75	<0.001	-721.44 ± 188.25	-3.83	<0.001	-224.74 ± 68.09	-3.3	0.001
L_{\ln} Tree density (trees ha $^{-1}$)	102.04 ± 44.97	2.27	0.03	73.14 ± 28.98	2.52	0.01	22.08 ± 10.48	2.11	0.04
Elevation (m)	0.31 ± 0.05	6.77	<0.001	0.17 ± 0.03	5.83	<0.001	0.07 ± 0.01	6.83	<0.001
Structural diversity index	2617.14 ± 828.65	3.16	0.002	1809.87 ± 534.06	3.39	0.001	542.41 ± 193.18	2.81	0.006
L_{\ln} Tree density × Structural diversity index	-349.22 ± 122.01	-2.86	0.005	-242.94 ± 78.63	-3.09	0.003	-76.26 ± 28.44	-2.68	0.009
Degree of freedom	101	101		101	101		101	101	
AIC	1196	1103		887	887		903	903	
BIC	1212	1119		903	903		931	931	
Deviance Explained	0.413	0.373		0.381	0.381		0.381	0.381	

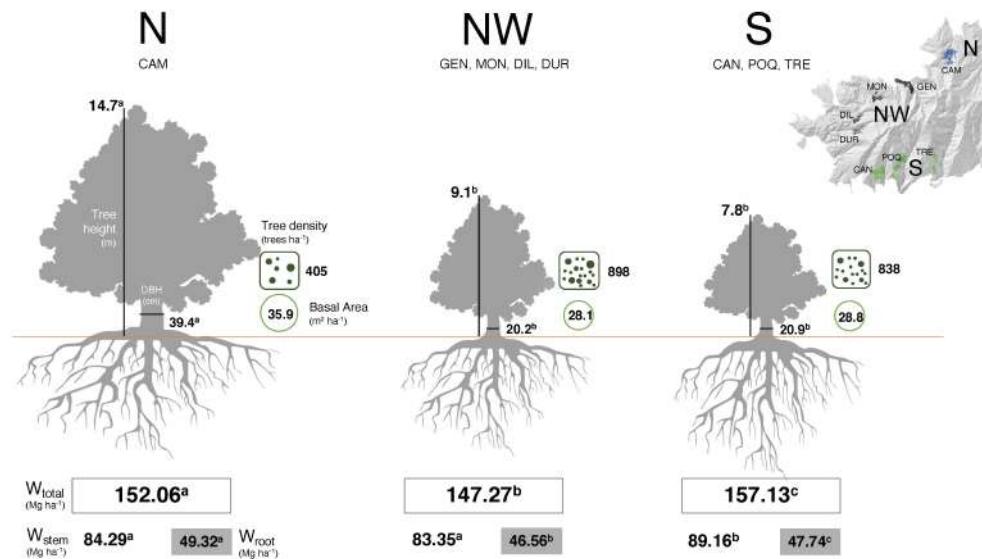


Fig. 5.3. Comparison of stand features and ALS-estimated biomass fractions between oak-population clusters of *Quercus pyrenaica* woodlands in Sierra Nevada. The distribution of oak-cluster are shown upper-right. Different letters indicate statistically significant differences between oak-population clusters (Dunn's test, $p < 0.05$) after Kruskal-Wallis test.

5.5.3. Predictions of Stand Biomass

The best GLM models selected for total (W_{total}), stem (W_{stem}) and root (W_{root}) biomass explained 70.3%, 67.3% and 63.1% of variance respectively (Table 5.4 and Table B.3). The elevation and the shannon structural diversity index showed positive effects on estimated biomass (Table 5.4; Figure 5.4). Tree density negatively affected the estimated total biomass. The interaction between tree density and the shannon structural diversity index was significantly (Table 5.4), indicating that the total biomass increased with the increase structural diversity at lowest and medium tree densities, but decreased at high values of tree density (Figure 5.4).

5.5.4. Temporal evolution of Biomass in *Q. pyrenaica* stands

A general pattern of increase in aboveground tree biomass was observed for most analyzed plots (Table 5.5), with a total increase of 19 172 Mg ha⁻¹

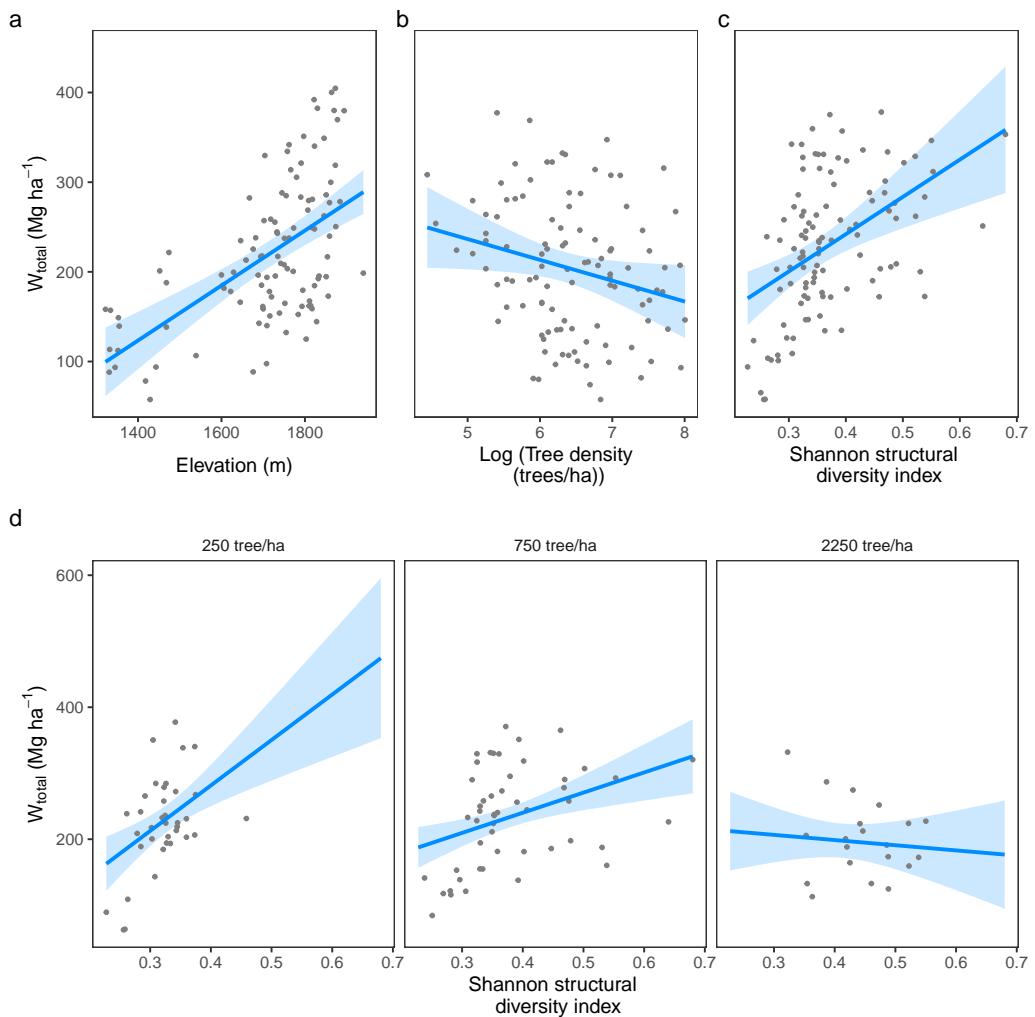


Fig. 5.4. Predicted effects of the (a) elevation (meters), (a) tree density (trees ha^{-1}), (c) shanon structural diversity index, and (d) tree density \times shanon structural diversity index, on the total biomass (W_{total} ; Mg ha^{-1}).

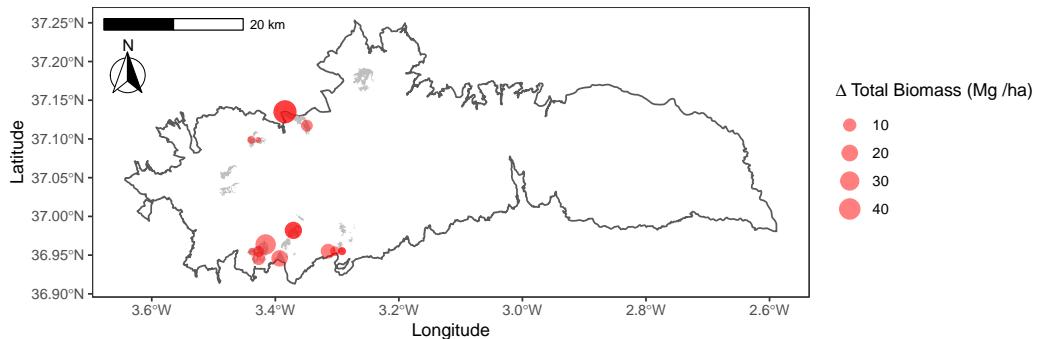


Fig. 5.5. Variation of tree biomass between the second and third Spanish National Forest Inventories, for plots (points) located on Sierra Nevada which have *Q. pyrenaica* as the main species. Size point indicates the variation in total biomass ($\Delta \text{Mg ha}^{-1}$).

between the two national forest inventories. About 89 % of the plots showed an increase in aboveground tree biomass, with an average of 11.46 Mg ha^{-1} (Table 5.5). This general pattern was also observed for plots located in Sierra Nevada (Figure 5.5).

5.6. Discussion

5.6.1. Carbon sequestration by Sierra Nevada oak woodlands.

Total estimated biomass values in Sierra Nevada oak woodlands ranged from $147.27 - 157.13 \text{ Mg ha}^{-1}$ (Table 5.3), with aboveground biomass (sum of W_{stem} , W_{b2} and $W_{\text{b2.7}}$ fractions) ranging from $104.69 - 111.71 \text{ Mg ha}^{-1}$. Our results are consistent with the mean aboveground biomass density cited by the IPCC guidelines as the default value for temperate mountain systems ($130 (20 - 600) \text{ Mg ha}^{-1}$) in Europe (IPCC, 2006). Using data from the Spanish Third National Forest Inventory, Vayreda et al. (2012) reported an average value for stand C stock of 45 Mg ha^{-1} along the distribution

Tab. 5.5. Temporal evolution of the total biomass (Mg ha^{-1}) of *Q. pyrenaica* and the total carbon (Mg ha^{-1}) between the second (SNFI2) and third (SNFI3) Spanish National Forest Inventories. Plots were aggregated by loss/gains of the tree numbers (Δ trees), and also by increase/decrease of biomass during the period analyzed. The total variation in biomass (i.e. sum for all plots), and the average variation per plot are shown for each category.

Δ trees	Biomass	# plots	Δ total biomass (Mg ha^{-1})	Average variation per plot (Mg ha^{-1})	Total Carbon
<0	Decrease	159	-1060.39	-6.67 (0.86)	-1846.85
	Increase	123	921.40	7.49 (0.86)	1604.77
>0	Decrease	33	-287.19	-8.7 (2.82)	-500.19
	Increase	1586	18183.25	11.46 (0.41)	31669.16
0	Decrease	56	-141.40	-2.53 (0.59)	-246.28
	Increase	312	1556.16	4.99 (0.48)	2710.32

of *Q. pyrenaica* in the Iberian Peninsula. Those values were lower than the estimated carbon stock (above- and below-ground) in our study which ranged from $69.95 - 74.63 \text{ Mg ha}^{-1}$ (Table 5.3). At a more regional scale, our results showed higher values than those found in the central range of the species distribution, where aboveground biomass varied between $63.8 - 98 \text{ Mg ha}^{-1}$ (Gallardo Lancho & González Hernández, 2004). Estimates of dioxide carbon sequestration for *Q. pyrenaica* pure stands ($122.19 - 152.82 \text{ Mg ha}^{-1}$) located in the Central Mountain Range (Spain) (Cañellas et al., 2008; Cañellas et al., 2017) were also lower than our results ($256.72 - 273.91$) (Table 5.3). Despite the potential differences derived from the carbon estimation method (i.e. LIDAR estimation versus field-ground based estimation; biomass expansion factors), several factors could explain the differences found in our results with respect to the values reported for other studies. First, it is generally accepted that there is an age-related decline in stand biomass accumulation (Xu et al., 2012, and references therein) with the productivity of old-growth forests being usually lower than younger forests (Kutsch et al., 2009). Oak woodlands of Sierra Nevada are composed of relatively young trees (Gea-Izquierdo & Cañellas, 2014; Pérez-Luque et al., 2020; Rubio-Cuadrado et al., 2018) in comparison with other woodlands of the species along their distribution area (Gea-Izquierdo & Cañellas, 2014). The strong anthropic perturbations in these oak has conditioned their structure. For instance, some of the oak woodlands were massively cut down during Spanish Civil

post-war period for use as wood gas for vehicles (e.g. MON population; Prieto, 1975), or for use in intense mining activities (e.g. GEN population; Pérez-Luque et al., 2020). Therefore, we can consider that many of the oak woodlands of Sierra Nevada oaks are relatively young, which might explain the high potential for C accumulation obtained in our study, since it has been shown that forest created as a result of drastic land-use changes exhibited faster growing rates, and therefore higher potential C accumulation, than pre-existing forests (Vilà-Cabrera et al., 2017). Differences in carbon stock between young oak coppices and mature forests were reported for other *Quercus* species (Bruckman et al., 2011; Cotillas et al., 2016). Therefore, it is likely that the high total ecosystem C values obtained in our area of study could be partly explained by the stands age-development stage (Makineci et al., 2015). Secondly, the water availability is generally the most limiting factor driving radial growth of *Q. pyrenaica* along its distribution range in the Iberian Peninsula (Gea-Izquierdo & Cañellas, 2014). In Sierra Nevada, northern and northwestern oak populations are located in valley bottoms with high values of relative humidity; and southern ones get the extra supply of water from moist air from the Mediterranean sea. Therefore water availability does not seem to be strongly limiting the oak-growth in this mountain region. In fact, in the last decades positive trends have been observed for greenness and secondary growth of oak woodlands in Sierra Nevada (Gea-Izquierdo & Cañellas, 2014; Pérez-Luque et al., 2020; Rubio-Cuadrado et al., 2018) suggesting that this mountain range could act as an ecological refugee for this species. Thus those positive growth trends could explain the high values of carbon sequestration obtained in our study.

5.6.2. Factors explaining biomass in the oak woodlands

Regarding the factors explaining biomass, we found a positive effect of the structural richness on total biomass, and therefore on C stock (Figure 5.4). Our results are consistent with general patterns obtained for tree species in Iberian Peninsula (Vayreda et al., 2012). In structural-heterogeneous stands, trees occupy different horizontal and vertical layers, thus they can maximize

the resources (e.g. light Forrester, 2014), whereas homogeneous stand structure may reduce complementary effects (Gonçalves, 2018; Vayreda et al., 2012). Being surrounded by size-diverse neighbours allow trees to fill the available canopy space around them and hence capture more light (Forrester, 2014; Vanhellemont et al., 2018). Our results show that the higher the tree density, the lower the total biomass (Figure 5.4). Previous studies on forests located on NW of Spain, reported tree stand density as one of the main factors affecting potential biomass production and carbon sequestration (Castaño Santamaría et al., 2013). Tree growth of *Q. pyrenaica* is inversely influenced by competition (Cañellas et al., 2004; Fernández-de Uña et al., 2015; Fernández-de Uña et al., 2016). Thus, trees respond to reduced competition through the structural shifts such as increased radial growth (Cañellas et al., 2004; Fernández-de Uña et al., 2016), and therefore a potential increase in biomass. We also found an interaction effect between the tree-density and stand structure diversity (Figure 5.4) which suggests that at high tree-densities resources are not maximized, even if structural diversity exists. Despite the importance of the water availability in the growth of *Q. pyrenaica* (Gea-Izquierdo & Cañellas, 2014; Moreno-Fernández et al., 2020), none of the best models selected for W_{total} , W_{stem} or W_{root} , included the topographic wetness index (Table B.3). This would seem suggest that the water requirement of this species in this mountain is met by the location of the oak populations within Sierra Nevada, and therefore would reinforce the role of this mountain region as an ecological refugee for this species.

5.6.3. Biomass differences within oak woodlands

We found that oak woodlands of the Northern cluster showed stands with taller and greater trees (Table 5.3), and also high values of biomass (Figures 5.2 and 5.3). It could be related with lower intensity of anthropogenic disturbances in comparison with the other oak woodlands, mainly because the northern oak woodlands had greater protection during the second half of the last century (Jiménez Olivencia, 1991), and currently also have the highest level of legal protection within the protected area (Anónimo, 2011). The less anthropogenic disturbances have resulted in well-conserved forests with a greater species diversity (Pérez-Luque et al., 2021b), and also a stable

stand structure with high values of biomass (Figures 5.2 and 5.3). For other species of *Quercus* it has been observed that forests with less disturbance have a higher potential for carbon storage (Balboa-Murias et al., 2006; Cotillas et al., 2016; Stojanović et al., 2017).

Our results also highlighted how differences in stand structure conditioned stand tree biomass (Table 5.4, Figure 5.4). High dense stands, *i.e.* northwestern oak populations, showed lower total biomass than less dense stands (northern or southern oak populations) (Figure 5.3). High stand density increase tree competition, limiting stand growth which provokes loss of vitality and reduction in acorn production (Bravo et al., 2008; Piqué et al., 2018), and according to our results, the higher the tree density the lower the capacity of these forests to act as carbon sinks (Figures 5.3, 5.4). In addition, an accumulation of biomass, coupled with a loss of structural diversity (Figure 5.4), would increase the risk of forest fires due to the large amount of biomass (Cañellas et al., 2004; Piqué & Vericat, 2015; Serrada et al., 1992)

5.6.4. Trends of carbon sequestration by oak woodlands

We observed an increase in aboveground tree biomass between the two inventories for plots located in oak woodlands (Table 5.5, Figure 5.5). Recent studies have reported a positive trend for primary production and for secondary growth in oak woodlands in Sierra Nevada (Alcaraz-Segura et al., 2016; Dionisio et al., 2012; Pérez-Luque et al., 2015a; Pérez-Luque et al., 2020). In addition, an increase in the area occupied by oak forests (Camacho-Olmedo et al., 2002a) as well as the densification of existing forest have been found (Jiménez-Olivencia et al., 2015). All these results indicated that this ecosystem service, *i.e.* carbon sequestration, have suffered an increase in the last decades in our study area. Land-use changes have extensively affected C storage of terrestrial ecosystems for several areas of south Europe (Muñoz Rojas et al., 2011; Muñoz Rojas et al., 2015). Abandonment of traditional activities and rural exodus are the main drivers explaining the densification and expansion of forests particularly in mountainous regions

such as Sierra Nevada (Jiménez-Olivencia et al., 2015; MacDonald et al., 2000). Considering the positive trend observed for the increase in biomass, and the lack of direct human-drive disturbances as these forests are in a protected area, it would expect a positive trend in forest carbon stock, such as has been recorded in many forests in the Mediterranean region in the last decades (FAO & Plan Bleu, 2018). It also agrees with the predictions under different scenarios forecasting a forest growth in the next decades (Aparicio et al., 2015). However, it should be taken with caution, since some early signs of saturation of forests as a carbon sink are being documented in Europe (Nabuurs et al., 2013).

5.7. Management implications

Several studies indicated that reductions of tree-density on oak coppices forests, by moderate thinning, causes an increase in the tree growth and biomass for *Q. pyrenaica* woodlands (Aldea et al., 2017a; Aldea et al., 2017b; Cañellas et al., 2004; Moreno-Fernández et al., 2020), and also for other *Quercus* species (e.g. Cotillas et al., 2009; Fernández-de Uña et al., 2015). This reduction in the stand density could increase the carbon sequestration of the woodland by a higher structural diversity which maximized the use of resources (Castaño Santamaría et al., 2013). Esta reducción de la densidad, además implica una menor cantidad de biomasa de pequeño tamaño, mejorando las condiciones para los incendios.

Land-use legacies and climate
change as a double challenge to
oak forest resilience: mismatches
of geographical and ecological
rear edges

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Ecosystems 10.1007/s10021-020-00547-y

Abstract

Global change challenges ecosystems in xeric locations transformed by intensive human use. Resilience to drought of relict Mediterranean *Quercus pyrenaica* populations in the southern Iberian Peninsula was analyzed in relation to historical records of land use, combining dendroecological growth of adult trees and greenness (EVI) as proxies for secondary and primary growth. The growth trends reflected a strong influence of old land-use legacies (e.g. firewood removal) in the current forest structure. Trees were highly sensitive to moisture availability, but both primary growth and secondary growth expressed high resilience to drought events over the short and the long term. Resilience and the tree growth response to climate followed a water-stress gradient. A positive growth trend since the late 1970s was particularly evident in mesic (colder and wetter) high-elevation stands, but absent in the most xeric (warmer and drier) stands. The high values of resilience observed suggest that the studied *Q. pyrenaica* populations are located in a geographical but not a climatic or ecological rear edge. Resilience of oak stands to drought events was not spatially homogeneous across the mountain range, due to differences in ecological conditions and/or past management legacies. This is particularly relevant for rear-edge populations where topographic and biophysical variability can facilitate the existence of refugia.

6.1. Introduction

The response of species to changing environments (*e.g.* distributional shifts) can be determined largely by population responses at range margins (Hampe & Petit, 2005). Peripheral populations are usually considered more vulnerable compared with populations at the center of a species' range [*i.e.* center-periphery hypothesis; Sagarin and Gaines (2002); Pironon et al. (2017)]. Geographically marginal populations have often been assumed to represent ecologically marginal populations. This means lower performance, higher vulnerability, and thus higher risk of extinction than for populations at the core of the species' range (Pironon et al., 2017; Rehm et al., 2015; Vilà-Cabrera et al., 2019). Nonetheless, recent reviews report that species- and population-specific responses do not always support this hypothesis (Abeli et al., 2014; Oldfather et al., 2020; Sexton et al., 2009). This is partly because a rear-edge is a multidimensional concept including an ecological (*i.e.* climatic and edaphic), a geographical, and a genetic component (Vilà-Cabrera et al., 2019), but also an anthropogenic dimension (*i.e.* land-use). In this respect, to fully understand changes in distribution and abundance of species as a consequence of global change, it is crucial to identify and understand mismatches between the geographical and the ecological rear edges (Vilà-Cabrera & Jump, 2019).

Limits of species distribution are strongly determined by climatic factors and biotic interactions (Gaston, 2009; Sexton et al., 2009). Climate change is expected to cause major shifts in the distribution and abundance of plant communities, and signs already indicate that more intense and longer droughts are altering forest dynamics (Allen et al., 2010). Drought frequency and severity have increased in recent decades, with a trend towards drier summers, particularly for Southern Europe (Stagge et al., 2017; Vicente-Serrano et al., 2014). In this climatic-change context, population loss and range retractions are expected in boreal, temperate, and Mediterranean species at the lowest latitudes and elevations, as well as in drought-prone areas of a species' distribution, *i.e.* the rear edge. The rear-edge populations are likely to be more sensitive to minor climatic and microtopographic variations and therefore the effects of droughts are expected to be particularly noteworthy (Hampe & Petit, 2005; Vilà-Cabrera et al., 2019).

It is often overlooked that human activity constitutes a driver of change as powerful or even more powerful than natural drivers, *i.e.* natural variation in climate, particularly for regions with long land-use history such as the Mediterranean Region (*e.g.* Doblas-Miranda et al., 2017; Navarro-González et al., 2013). In these areas, the susceptibility and response of ecosystems to climate change are conditioned by legacies of historical land-use activity (*e.g.* Mausolf et al., 2018; Munteanu et al., 2015). The past land-use legacies interact with recent human-caused climate disturbances and may confound their interpretation (Foster et al., 2003). For example, recent works showed that a quarter of current forests in the Iberian Peninsula, are growing on former agricultural and grazing land abandoned after the 1950s (Vilà-Cabrera et al., 2017). Consequently, anthropogenic habitat modification and its legacies represent a critical dimension of marginality as they may intensify, confound or delay climate-driven population decline at rear edges (Sánchez de Dios et al., 2020; Vilà-Cabrera & Jump, 2019). In this context, our work seeks to identify the impacts and responses to natural (*e.g.* severe drought) and human disturbances (*e.g.* logging) on oak forests at their southern geographical range. A historical perspective should help us to interpret the responses of ecosystems to disturbances (Foster et al., 2003), particularly regarding marginal rear-edge populations (Vilà-Cabrera et al., 2019).

The assessment of resilience to climate and human disturbances provides critical information concerning the capacity of forests to maintain their structure and render valuable ecosystem services. Resilience is the capacity of an ecosystem to persist and maintain its state and functions in the face of disturbance (Hodgson et al., 2015; Holling, 1973). Lloret et al. (2011) proposed an approach, which decomposes resilience into three components: resistance to drought, recovery after drought and resilience. This resilience is determined by the forest's ability to mitigate the disturbance (resistance) and the capacity to recover from the impact (recovery) (Ingrisch & Bahn, 2018). This conceptual approach has recently become widely used to assess forest resilience, because it allows a simple, yet highly efficient assessment of short-term responses of trees to drought. Nevertheless, not exempt from criticism, this approach needs to be applied carefully to avoid potential bias at different levels (Schwarz et al., 2020). In this sense we assessed forest resilience both over the short-term to several recent extreme drought

episodes, as well as over the long-term to climate change (*i.e.* warming on the last few decades), using two different proxies to characterize resilience. Dendroecological estimates of growth (*i.e.* tree-ring width) are commonly used proxies to characterize tree vitality and have commonly been used to study growth changes in response to drought at the individual tree level (Dobbertin, 2005; Fritts, 1976). Remote sensing can be used to analyze the impact of drought on ecosystems at the stand level (*e.g.* Zhang et al., 2013). Tree-ring records complement remote-sensing data with a longer time scale. Tree rings can reflect tree-growth anomalies induced by climate or other disturbance over decades to centuries (Babst et al., 2017) and provide an accurate measure of growth responses to droughts (Bhuyan et al., 2017). The combination of remote sensing and dendroecology has been used to assess the effects of droughts on vegetation along ecological gradients (*e.g.* Coulthard et al., 2017; Vicente-Serrano et al., 2013), and also to evaluate growth resilience to drought in several tree species (*e.g.* Gazol et al., 2018; Peña-Gallardo et al., 2018).

In the present study, we assess resilience of *Quercus pyrenaica* (Pyrenean oak) from southern relict forests at the rear edge of the species distribution, where species performance is considered to be threatened by climate change (Gea-Izquierdo et al., 2013; Gea-Izquierdo et al., 2017). For this, we combined remote-sensing information and dendroecological methods to evaluate the impact of drought both on canopy greenness (as a proxy for primary growth) and radial tree growth (as a proxy for secondary growth). For the analysis of forest resilience to climate, we took into account the land-use history of these transformed forests, thoroughly reviewing historical documents to reconstruct forest history at the study sites, and analyzing how anthropogenic drivers have shaped the current forest structure. Based on this analysis, we developed a rationale that integrates the ecological and anthropogenic components of marginality to determine the regional and local scale mechanisms shaping the probability of persistence (or extinction) of rear-edge oak populations. Our main hypothesis is that range edge stands will show low resilience to extreme droughts, but that the vulnerability to drought will be reduced quickly across a fine-scale topographic gradient of decreasing aridity. To test this hypothesis, we: (*i*) quantified how recent extreme drought events influenced primary and secondary growth of *Q. pyrenaica* forests at

their present geographical rear edge; (ii) analyzed the long-term resilience of these forests to extreme drought events, using time-series of radial growth; (iii) reviewed historical documents to reconstruct forest-management history and to infer how it impacted tree growth and stand dynamics over time; (iv) and examined differences in the resilience metrics between populations under contrasting ecological conditions (*i.e.* xeric vs. mesic) along environmental gradients within the rear edge in order to detect vulnerability to climate change at the small spatial scale.

6.2. Material and Methods

6.2.1. Tree species and study site

Quercus pyrenaica forests extend throughout south-western France and the Iberian Peninsula, reaching their southern limit in mountain areas of northern Morocco (Franco, 1990). In the Iberian Peninsula, these forests occupy siliceous soils under meso-supramediterranean and mesotemperate areas and subhumid, humid, and hyperhumid ombroclimate. Pyrenean oak is a deciduous species that requires over 650 mm of annual precipitation and some summer precipitation. As a submediterranean species, it has lower drought tolerance than evergreen Mediterranean taxa (del Río et al., 2007).

The forests of this species reach their southernmost European limit in Andalusian mountains such as Sierra Nevada (37°N, 3°W), a high-mountain range with elevations of up to 3482 m *a.s.l.*. The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought and increasing aridity with decreasing altitude, and marked variability in annual rainfall according to elevation and aspect. Sierra Nevada is considered a glacial refuge for deciduous *Quercus* species (Olalde et al., 2002). Eight Pyrenean oak patches (2400 ha) have been identified in this mountain range (Figure 6.1), from 1100 to 2000 m *a.s.l.* and often associated with major river valleys. Today, *Quercus pyrenaica* woodlands in this mountain region represent a rear edge of their habitat distribution (Hampe & Petit, 2005). They are the richest forest formation in vascular plant species of Sierra Nevada, containing several endemic and endangered plant

Tab. 6.1. Characteristics of sampled plot. Lat = latitude; Long = longitude. Dbh and height of all trees, Basal Area (BA), Density and SDR (size ratio proportional to distance) are computed for all trees within a 10-m radius of focal trees (see Materials and methods). Temp.: annual average of mean monthly minimum and maximum temperatures. Values shown here correspond to site averages. Standard deviations are shown in parentheses. Different letters indicate statistically significant differences between sites (Kruskal-Wallis test followed by Dunn's test, $p < 0.05$). Stands were monospecific, hence all results correspond to oak data.

Site	Lat (°)	Long (°)	Elevation (m)	Slope (°)	Prec. (mm)	Temp. (°C)	Cored trees			Stand competition			SDR		
							#trees	(#cores)	Dbh (cm)	Height (m)	Age (years)	Dbh (cm)	all Height all (m)	BA (m ² ha ⁻¹)	Density (trees ha ⁻¹)
CA-High	36.97	-3.42	1846 - 1884	12.11	731	3.4- (3.28)	15 (30)	69.8 (20.5)	15.4 (1.8) a	161.0 (24.3) a	34.1 a	10.8 (4.4) (24.31) a	39.13 (147.1) a	348.0 (0.63) a	0.91
CA-Low	36.96	-3.42	1691 - 1751	12.86	658	4.7- (2.98)	15 (30)	45.9 (8.6) a	12.6 (1.6) b	148.5 (16.5) a	21.7 b	9.0 (2.8) (14.4) b	18.02 (7.11) ab	409.6 (226.0) a	0.89 (0.44) a
SJ	37.13	-3.37	1322 - 1474	27.33	555	4.9- (5.59)	20 (48)	31.9 (3.7) b	11.8 (2.3) b	72.6 (11.1) b	20.6 (8.1) b	9.7 (3.6) ab	11.64 (5.47) b	339.0 (130.3) a	1.11 (0.52) a

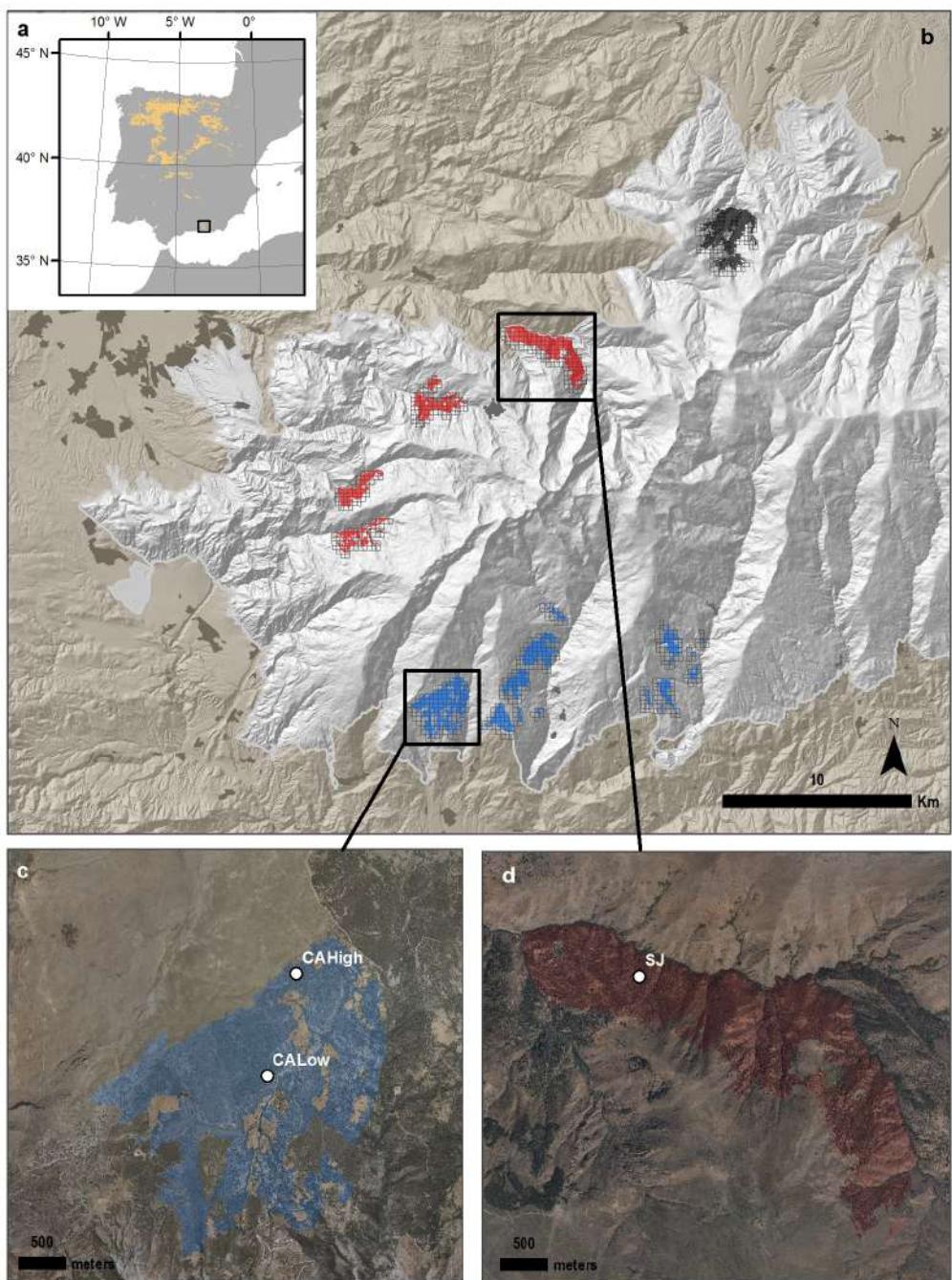


Fig. 6.1. Distribution of *Quercus pyrenaica* forests in the Iberian Peninsula **a** and in Sierra Nevada mountain range **b**. Different colors indicate oak-population clusters identified in Sierra Nevada (Pérez-Luque et al., 2015b). For each population, a grid with the MODIS pixels is shown (see Material and methods). Detailed location of the dendroecological sampling sites: northern (San Juan, SJ) **c**, and southern ones (Cáñar: CA-Low and CA-High) **d**. Color orthophotography of 2009 from Regional Ministry of the Environment.

species (Lorite et al., 2008). They also harbor high levels of intraspecific genetic diversity (Valbuena-Carabaña & Gil, 2013). These relict forests have undergone intensive human use throughout history (Camacho-Olmedo et al., 2002). Furthermore, the conservation status of this species for southern Spain is considered “Vulnerable” and it is expected to suffer from climate change, potentially reducing its suitable habitats in the near future (Gea-Izquierdo et al., 2013; Gea-Izquierdo et al., 2017).

6.2.2. Climatic data and drought episodes

The Iberian Peninsula underwent several extreme drought episodes in the last three decades (e.g. 1995, 1999, 2005, 2012 Vicente-Serrano et al., 2014). The 2005 and 2012 drought events have been documented as being among the worst in recent decades for the southern Iberian Peninsula (Páscoa et al., 2017), appearing as extreme drought in our climatic data (Figure C.1; Table C.2). We focused on these two drought events because they were included in the period having remote-sensing information of high spatial resolution (MODIS started on 2000; see below). Nevertheless, for radial growth-time series, a greater number of older drought events were also analyzed to contextualize the results for 2005 and 2012 and to evaluate forest resilience to drought over a longer term (see Table C.2). A drought event was identified using the SPEI (Standardized Precipitation-Evapotranspiration Index) (Vicente-Serrano et al., 2010) (SPEI 12-months scale), following a procedure similar to the one proposed by Spinoni et al. (2015). We used 0.5° grid cells covering Sierra Nevada taken from the Global SPEI Database (<http://spei.csic.es/database.html>). A severe drought event starts when SPEI falls below the threshold of -1.28 (Páscoa et al., 2017; Spinoni et al., 2018). A drought event is considered only when SPEI values fall below that threshold for at least two consecutive months. For each drought event, we computed: the *duration* as the number of consecutive months with the SPEI lower than a certain threshold; the *severity* as the sum of the absolute SPEI values during the drought event; the *intensity* and the *Lowest SPEI* refer to the mean and lowest value of SPEI respectively during the drought event.

To explore the relationships between climatic variables and tree-growth variables we used climate data obtained from the European Daily High-Resolution Observational Gridded Dataset (E-OBS v16) (Haylock et al., 2008). Monthly precipitation and minimum and maximum temperatures had a 0.25 x 0.25 ° resolution for the 1950-2016 period. Grid cells were selected to cover each sampled site. The SPEI 6-months scale index was used to characterize the drought conditions for the period 1961-2014.

6.2.3. Greenness data to assess ecosystem resilience

Vegetation greenness of *Quercus pyrenaica* was characterized by means of the Enhanced Vegetation Index (EVI), derived from MOD13Q1 product of the MODIS sensor. EVI data consists of 16-day maximum value composite images (23 per year) of the EVI value with a spatial resolution of 250 m x 250 m. MODIS EVI data were compiled for the period 2000 - 2016. We selected the pixels covering the distribution of *Quercus pyrenaica* forests in Sierra Nevada ($n = 928$ pixels). Any values affected by clouds, snow, shadows or high content aerosols, were filtered out following recommendations for mountain regions (Reyes-Díez et al., 2015).

The mean Annual EVI (EVI_{mean}) as a surrogate of mean annual primary production was computed for each pixel for the period 2000 - 2016. The EVI standardized anomaly (EVI_{sa}) was computed pixel-by-pixel, in order to minimize bias in the evaluation of anomalies and to provide more information concerning their magnitude (Samanta et al., 2012). For each pixel, an annual EVI value was calculated by averaging EVI valid values. Then, the standardized anomaly was computed as:

$$EVI_{sa,i} = (EVI_{mean,i} - EVI_{mean,ref}) / \sigma_{ref}$$

where $EVI_{sa,i}$ is the EVI standardized anomaly for year i ; $EVI_{mean,i}$ the annual mean value of EVI for year i ; $EVI_{mean,ref}$ the average of the annual EVI values for the period of reference 2000-2016 (all except year i); and σ_{ref} the standard deviation for the reference period. Each pixel was categorized according

the EVI standardized anomalies as “greening” ($EVI_{sa} > 1$), “browning” ($EVI_{sa} < -1$) or “no-changes” ($-1 > EVI_{sa} > 1$) (Samanta et al., 2012).

Rather than other vegetation indices such as the NDVI, EVI_{mean} was chosen because it is highly stable under the use of any filter (Reyes-Díez et al., 2015) and because it showed highly significant correlations with annual ($r = 0.81$) and seasonal EVI values ($r_{spring} = 0.76$ and $r_{summer} = 0.88$).

6.2.4. Field sampling and dendroecological methods to assess individual tree resilience

Trees were sampled during the autumn of 2016 at two locations in contrasting N-S slopes of Sierra Nevada: San Juan (SJ), a xeric site located at the northern aspect (around 1400 m); and Cáñar (CA), a wetter site located at the southern aspect (Figure 6.1; Table 6.1). For the southern site, two elevations were sampled: CA-Low (around 1700 m) and CA-High (around 1860 m), constituting the current low-elevational limit for the species (CA-Low) and the maximum altitude currently reached by trees (CA-High), respectively, in the site sampled. Despite the proximity of these two elevations (less than a 200-m difference) the stands differ markedly in their structure and characteristics (Table 6.1). The three sampling sites followed a moisture gradient: SJ < CA-Low < CA-High (Table 6.1). All the sites were oak monospecific and representative of the population clusters identified for the species in this mountain range (Pérez-Luque et al., 2015b). At each site, between 15 and 20 trees from either the single dominant-codominant layer in CA or the open canopy in SJ were randomly sampled. Two cores of 5 mm in diameter were taken from each tree at breast height (1.3 m) using an increment borer. Diameter at breast height (DBH) and total height were measured for each tree. In addition, stand competition affecting target trees was assessed by recording distance, azimuth, DBH, species, and total height of all neighboring living trees with $DBH > 7.5$ cm within a circular plot with a 10-m radius. Several competition indices were calculated: the distance independent indices *density* ($\text{trees} \cdot \text{ha}^{-1}$), and *basal area* ($\text{BA}, \text{m}^2 \cdot \text{ha}^{-1}$);

and the distance dependent index size ratio proportional to distance (see Gea-Izquierdo & Cañellas, 2009, for more details) as:

$$\text{srd} = \sum_{i=1}^n (dbh_j/dbh_i) \cdot [1/(dist_{ij} + 1)]$$

Tree cores were air dried, glued onto wooden mounts, and sanded. Annual radial growth (ring width, RW) was determined with a measuring device coupled to a stereomicroscope, for an accuracy of 0.001 mm. Individual ring series were first visually and statistically cross-dated with TSAP software (Rinntech, Heidelberg, Germany), using the statistics Gleichläufigkeit (GLK), t-value and the crossdating index (CDI). Cross-dating validation was finally verified using COFECHA (Holmes, 1983).

The growth trends were analyzed at different time scales. To study the growth response to the inter-annual variability of climate (short-term response), pre-whitened residual chronologies (RWI) were used. These were calculated from ratios between raw growth measurements and individual cubic splines with a 50% frequency cutoff at 30 years (Fritts, 1976). Tree-ring width series were standardized and detrended using dplR (Bunn, 2010). Mean residual site chronologies were established by computing the biweight robust mean of all prewhitened growth indices for the trees of the same site (Fritts, 1976). The statistical quality of each chronology was checked via the expressed population signal (EPS). A threshold value of EPS > 0.85 was used to determine the cutoff year of the time span that could be considered reliable.

The long-term growth response was analyzed using basal area increment (hereafter BAI, $\text{cm}^2 \cdot \text{year}^{-1}$). In theory, BAI represents a more accurate indicator of growth than ring width, because it removes variation in growth attributable to increasing stem circumference after 30-40 years of juvenile growth (Biondi & Qeadan, 2008). Raw ring widths and measured DBH were used to compute BAI (Piovesan et al., 2008) with the following equation:

$$\text{BAI} = \pi(r_t^2 - r_{t-1}^2)$$

where r is the radius of the tree and t is the year of tree-ring formation. For each individual tree, a mean BAI series was calculated. Then, mean site BAI chronologies were determined by averaging individual tree BAI time series.

6.2.5. Disturbance analyses and land-use history review

Disturbance chronologies were built using tree-ring width to identify abrupt and sustained increases (release events from competition) or decreases (suppressions) in radial growth (Nowacki & Abrams, 1997) as indirect estimates of possible disturbance events (*e.g.* logging, drought-induced neighbor mortality) in the past. Growth changes (GC) were calculated for the individual tree-ring series using a 10-year running window as either positive (PGC) or negative (NGC) growth changes:

$$\%GC = \left[(M1 - M2) / M2 \right] \times 100$$

where $M1$ is the preceding 10-year median and $M2$ is the subsequent 10-year median (Rubino & McCarthy, 2004).

Site-disturbance chronologies were constructed by annually averaging the individual disturbance series. To separate growth peaks caused by disturbance events and expressing stand-wise disturbances from those caused by climate, we considered a threshold of 50% of GC and more than 50% of the individual trees displaying the same growth changes (*e.g.* Gea-Izquierdo & Cañellas, 2014). In addition, the history of the forest and management of our sampling sites was inferred from a detailed analysis of historical land-use changes. For this, existing historical documents were exhaustively reviewed to compile information on socio-economical activities affecting the forests being studied (Table C.4). We exhaustively reviewed existing documentary sources: historical documents and maps; detailed mining reports; official information on recent wildfires events and forest-management practices; livestock farming; traditional irrigation channels; and studies concerning the socioeconomic dynamics of forests on Sierra Nevada at different spatio-temporal scales (see Table C.4 for references).

Tab. 6.2. Characteristics of the mean tree-ring chronologies. Length values in parentheses indicate the number of years replicated with more than five series. *RW* = mean annual ring width (standard deviation in parenthesis). *MS* = mean sensitivity. *AR(1)* = mean autocorrelation of raw series. *Rbt* = mean correlation between series. *EPS* = mean expressed population signal. *EPS* and *Rbt* were calculated for the mean residual chronologies of growth indices.

Site	First year	Last year	Length (years)	# trees	# cores	RW (mm)	MS	AR(1)	Rbt	EPS
CA-Low	1836	2016	181 (164)	15	30	1.253 (0.781)	0.208	0.799	0.520	0.897
CA-High	1819	2016	198 (188)	15	30	1.500 (0.879)	0.203	0.827	0.522	0.907
SJ	1921	2016	96 (90)	20	48	1.725 (1.207)	0.319	0.692	0.637	0.959

6.2.6. Assessing resilience to drought at the forest stand and individual-tree levels

To evaluate the effects of drought events on ecosystem resilience (using greenness data) and individual tree resilience (using BAI data), we used resilience indices proposed by Lloret et al. (2011). The Resistance index estimated as the ratio between performance during and before the disturbance ($\text{Resistance} = \text{Drought}/\text{PreDrought}$) quantifies the severity of the impact of the disturbance in the year it occurred. The Recovery index, computed as the ratio between performance after and during disturbance ($\text{Recovery} = \text{PostDrought}/\text{Drought}$), represents the ability to recover from disturbance relative to its severity. Finally, the Resilience index ($\text{Resilience} = \text{PostDrought}/\text{PreDrought}$) is the capacity to reach pre-disturbance performance levels. The values of these indices were computed for tree growth (BAI) and greenness (EVI mean) during each drought event. The predrought and postdrought values of each target variable (*i.e.* BAI or EVI) were computed as the mean value over a period of three years before and after the drought event, respectively. A period of three years was chosen because we found similar results on comparing periods of two, three, and four years (Figure C.3b), and this time period has been used in other studies (*e.g.* Gazol et al., 2018). Resilience metrics for BAI data were additionally computed for the most severe drought events since 1940 ($n = 8$; Table C.2) and compared with drought severity.

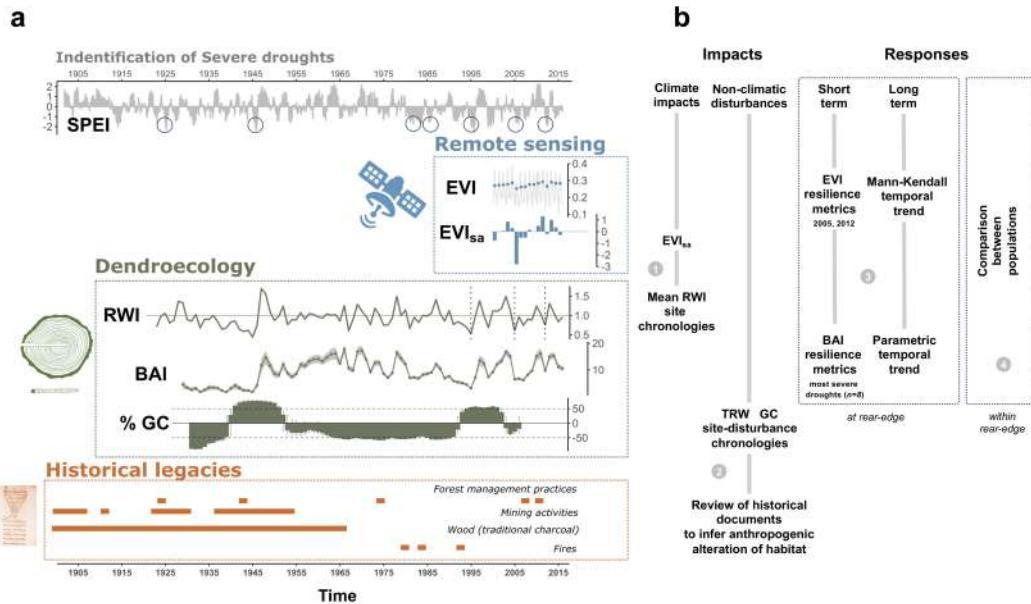


Fig. 6.2. Schema of the different metrics **a** and analyses **b** used in the manuscript (see Material and methods for details). The severe drought events since 1901 were identified using SPEI-12 and characterized in terms of duration, severity and intensity. Climate impacts on vegetation were assessed for greenness and tree-growth. Non climatic disturbances on vegetation were quantified using growth changes on tree growth (%GC) and were also related with anthropogenic alterations inferred from review of historical documents. Responses of vegetation to disturbances were explored in the short- and the long-term using resilience metrics and temporal trends respectively for both EVI and BAI. Resilience metrics of BAI were computed for the eight most severe drought events since 1950, and their relationship with drought severity were explored. For the 2005 and 2012 drought events we also compared EVI and BAI resilience metrics among the three *Q. pyrenaica* populations. Numbers (grey circles) indicate the study aims to which the analyses are related.

6.2.7. Statistical analysis

Differences between sites for height, DBH, and competition indices were analyzed using non-parametric Kruskal-Wallis rank sum tests. When significant differences were detected, multiple comparisons were run using the Dunn test with Bonferroni adjustment to correct for significance.

The severe drought events since 1901 were identified using SPEI-12. They were characterized in terms of duration, severity and intensity (see Spinoni et al., 2015). In a first step, the impact of drought in greenness and growth was explored using the *EVI_{sa}* and the mean RWI site chronologies (Figure 6.2). Additionally the relationships between climatic variables and tree-growth variables (RWI and BAI site chronologies) were assessed using bootstrapped Pearson's correlations estimated using treeclim (Zang & Biondi, 2015). The non-climatic disturbance impacts on tree-growth were evaluated using site disturbance chronologies (built using growth changes on tree growth).

Responses of vegetation to disturbances were explored in the short- and the long-term using resilience metrics (resilience, resistance and recovery) and temporal trends respectively for both EVI and BAI (Figure 6.2). Resilience metrics of BAI were computed for the eight most severe drought events since 1950 (including 2005 and 2012), and their relationship with drought severity were explored. Resilience metrics of EVI were computed only for 2005 and 2012 drought events. Temporal trends of *EVI_{mean}* (pixel scale) and BAI (mean BAI site chronologies) were examined using non-parametric (Mann-Kendall) and parametric test (Pearson) respectively.

For each of the three resilience indices studied, we used robust two-way ANOVAs to test for differences between drought events (2005 and 2012) and the oak populations studied (northern and southern exposures). These tests were used because original and log-transformed data did not follow the assumptions of normality or homogeneity of variance (Wilcox, 2012). Robust measures of central tendency (M-estimator based on Huber's Psi) were used because they were close to the mean value in all cases (Wilcox, 2012). When the robust ANOVA test was run, data were bootstrapped 3000 times and trimmed automatically to control the potential influence of outliers. Post-hoc differences were assessed pairwise using a similar bootstrap test. All the

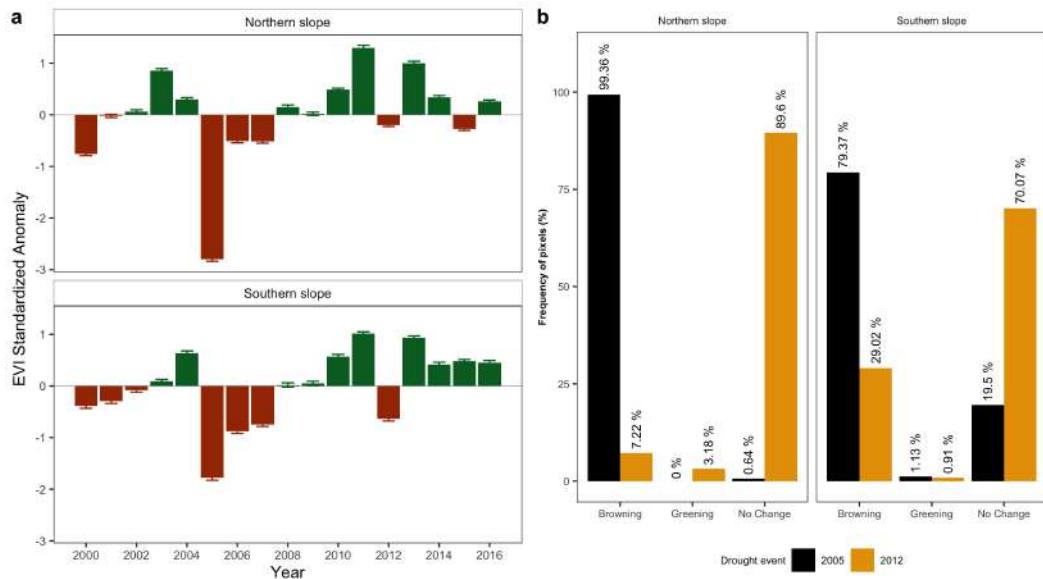


Fig. 6.3. EVI standardized anomaly during the period 2000-2016 for northern and southern populations **a**. Error bars show standard error. See main text for details on EVI calculation. Percentage of pixels showing browning, greening or no changes during the 2005 and 2012 drought events according to EVI standardized anomalies **b**. See main text for an explanation of greening and browning.

robust ANOVA and *post-hoc* tests were carried out using the WRS2 R package (Mair et al., 2017). The level of significance was set to 0.05 and adjusted for multiple comparisons.

6.3. Results

6.3.1. Temporal trends in vegetation greenness

The analysis of temporal trends in greenness showed that 78.9% of the EVI pixels followed a positive trend for the 2000-2016 period. The lowest values of EVI standardized anomalies for the study period were recorded during the 2005 drought, and the minimum EVI values were expressed in the northern (dry) population (Figure 6.3a). A “browning” episode ($\text{EVI}_{\text{sa}} < -1$) was found during this drought event, whereas no changes in greenness in response to the 2012 drought were detected (Figure 6.3b).

6.3.2. Analysis of radial-growth trends and disturbances

The trees of the southern population were older than those from the northern one (Table 6.2). In addition, trees from the southern population at high elevation were taller and their growth was significantly greater than that of trees from the other two sites. Stand competition measured as plot basal area was greatest in CA-High (Table 6.1, Figure 6.4a). The growth and height of trees from the northern and the low-elevation southern population were similar (Figure 6.4a and Figure C.3a). Only trees from the southern sites (*i.e.* the wetter exposure) showed significant positive growth trends since the late 1970s (Figure 6.4a), this trend being far more pronounced for the wetter and colder high elevation site (CA-High).

Drought events reduced radial growth for all sites (Figure C.2a). The strongest reduction in radial growth occurred in response to the 1995 drought (the worst drought spell in our climatic record, Table C.2) for all sites. Tree-growth reductions in response to drought followed a moisture gradient. Tree-growth reductions in response to the studied drought events were lower in the southern sites (CA-High and CA-Low) than in the northern site (SJ), especially for 2005 and 2012 (Figure C.2a). The weakest growth reductions were found in trees from the wettest site (CA-High).

The response of tree growth to water availability was greater than to temperatures. Cumulative precipitation of the hydrological year and seasonal SPEI values (*i.e.* for the Hydrological year, Spring and Summer) were the climatic variables exhibiting the highest (positive) relationship with growth for all populations (Figure C.6a). Nevertheless, there were differences between populations: the positive relationship with SPEI was highest in the more xeric northern population ($r > 0.6$ vs. $r < 0.5$; Figure C.6a).

The northern site (SJ) showed two major release events ($GC > 50\%$ occurring in more than 50% of trees sampled): the first during the 1940s (the most evident) and the second in 1995-2000 (Figure 6.4b). These periods alternated with periods of suppression. By contrast, the two southern sites showed no release events except for CA-High at the beginning of the 1830s and no suppression events in the last 50 years.

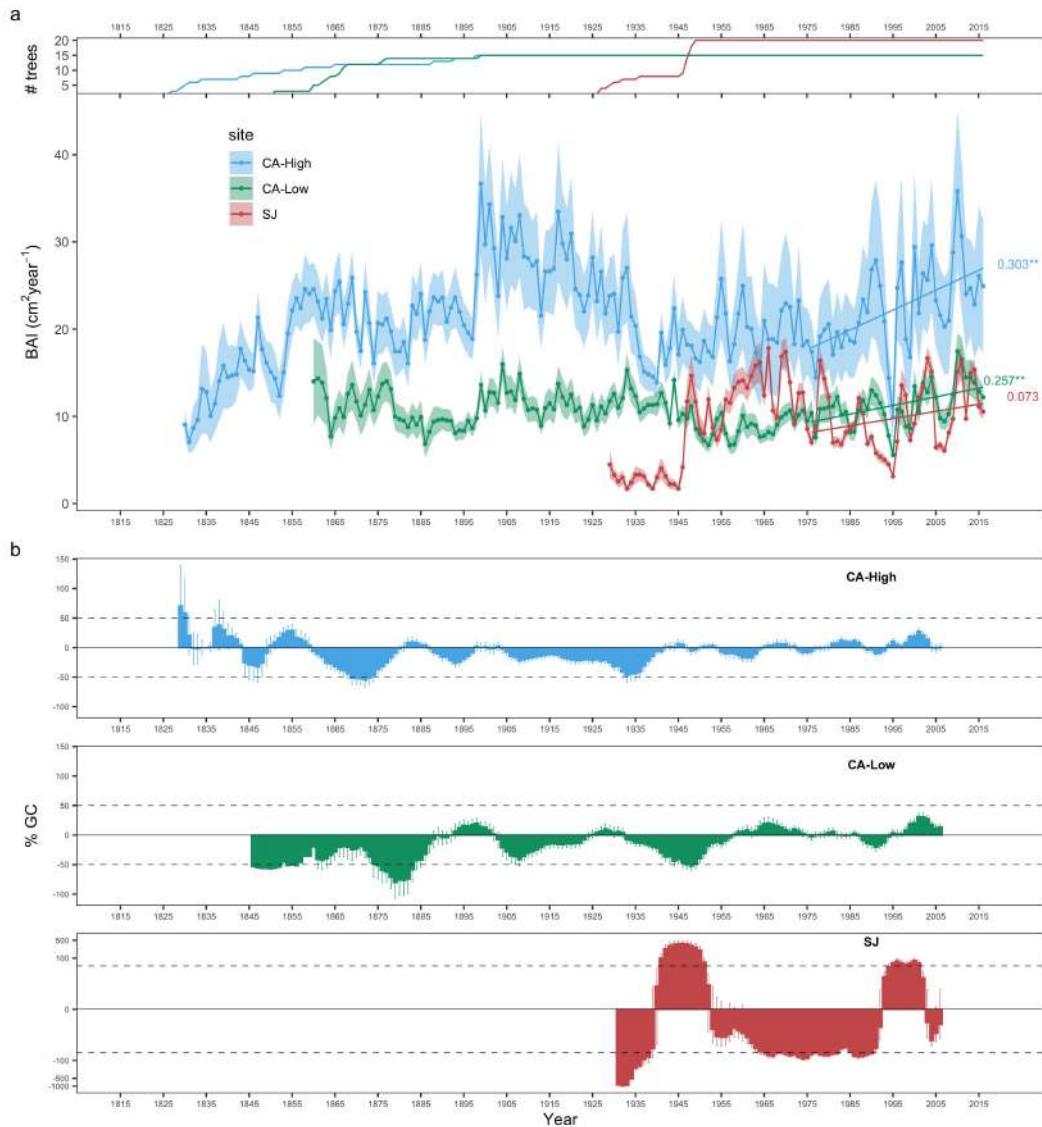


Fig. 6.4. Basal Area Increment (BAI) chronologies of *Q. pyrenaica* for northern population (SJ; red) and southern ones: low-elevation (CA-Low; green) and high-elevation (CA-High, blue) sites **a**. Shading areas correspond to standard error of the mean. Number of series is displayed in the upper plot. Only years replicated with $\# \text{ series} > 5$ are shown. Linear trends since 1975 are indicated for all sites (numbers indicate r^2 values; asterisks indicate significant linear trend, $p < 0.001$). Comparison of median growth change (GC) following Nowacki and Abrams (1997) for *Q. pyrenaica* sites **b**. Dashed black lines indicate a threshold of 50% of GC (see Material and methods). Note that y-axes do not correspond in all of the three panels for the sake of clarity. Error bars indicate standard error.

6.3.3. Resilience, resistance and recovery to drought events at the stand and individual-tree levels

Resilience and resistance varied in the same direction whereas recovery varied inversely to resilience and resistance. During the last two drought events, resilience metrics for greenness and tree growth significantly differed between drought events (Table C.1). The 2005 drought event reduced greenness and growth more than that of 2012 (Table C.3) but the metrics of resilience generally covaried in the same direction during those two drought events. For EVI, resilience and resistance values were significantly higher for 2012, the most severe event, than for 2005 (Table C.3; Figure 6.5b); whereas recovery values were higher for 2005 than for the 2012 drought event. For BAI, the resilience, resistance and recovery values were higher for 2012 than for 2005 (Table C.3, Figure 6.5c).

The recovery and resistance for greenness and growth varied significantly between sites. Resilience calculated for greenness also differed between sites but not for tree growth ($p = 0.534$; Table C.1). The two southern populations showed lower recovery values than did the northern site both for greenness and tree growth, but resistance and resilience values were significantly higher for the southern site (Table C.3).

Resilience metrics of tree-growth for drought events since 1950 (*i.e.* shared period among the three chronologies excluding the juvenile years, Table C.2) revealed a positive relationship between drought severity and recovery, significant for all oak populations (Figure 6.5a). A similar pattern was found for resilience but proved significant only for SJ. Importantly, non-significant patterns resulted when we excluded 1995, except for recovery in SJ (Figure C.5). The trees showed the highest value of tree-growth resilience for 1995, the worst drought event in our study area, particularly SJ where our results suggest a major release event also after 1995 (Figure 6.4b).

6.4. Discussion

By using a combined approach of remote-sensing information and dendroecology, we quantified the growth of adult trees and greenness (EVI) as proxies for secondary and primary growth of relict Mediterranean *Quercus pyrenaica* populations in the southern Iberian Peninsula. These relict oak populations, driven by historical land-use, have been resilient to climate change at their present rear edge. However, resistance, resilience, and forest recovery after extreme drought events were strongly influenced by mountain exposure, local environmental conditions, and management legacies. This means that the geographical and the ecological rear edges do not necessarily match and, at a small spatial scale, tree performance can vary markedly along the rear edge under climate change.

6.4.1. High sensitivity and variability in the oak sensitivity to climate at the rear edge

Severe drought negatively affects both primary and secondary growth of *Q. pyrenaica* forests. This was expressed by the observed reduction in greenness and tree growth in response to the 2005 and 2012 drought events as well as by radial-growth suppression during extreme drought events (Corcuera et al., 2006; Gea-Izquierdo & Cañellas, 2014). Furthermore, the greatest reduction of tree growth was detected during the 1995 drought, a characteristic negative precipitation anomaly that caused severe and extensive damage in the Mediterranean Iberian Peninsula (Gazol et al., 2018; Peñuelas et al., 2001).

The tree responses to drought are site-dependent (Babst et al., 2013), particularly for rear-edge populations (Cavin & Jump, 2017; Dorado-Liñán et al., 2017c). Greenness and tree growth were more affected by drought events in drier northern populations than in wetter southern oak populations of Sierra Nevada. The northern site showed higher browning intensity than did the southern sites during the 2005 drought event, and stronger correlations of tree-growth with SPEI (hydrological year and summer) at the northern site can be interpreted as higher sensitivity to drought at drier sites (Gea-

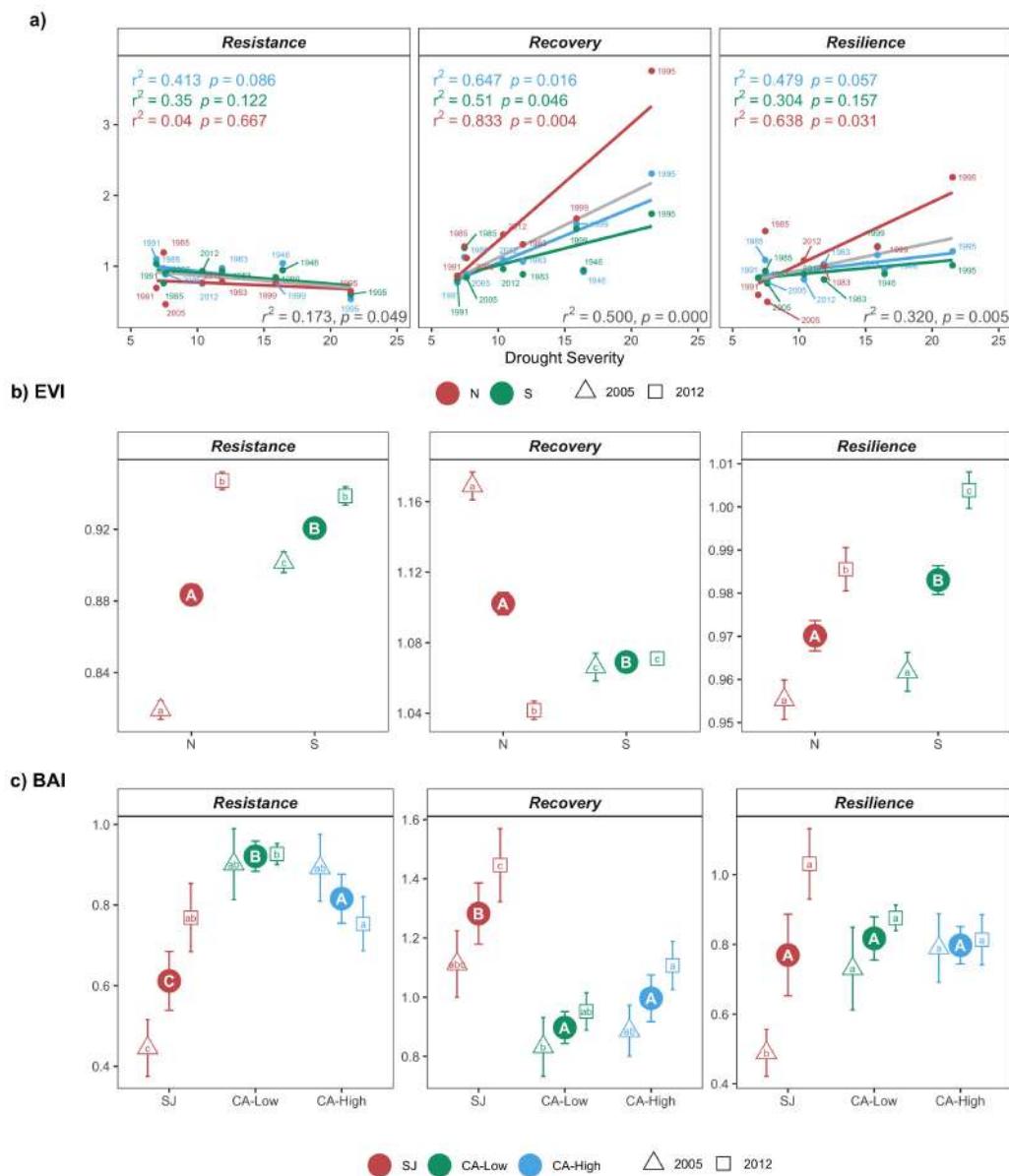


Fig. 6.5. Resilience metrics of tree-growth for eight severe drought events since 1950 (see main text for details) as a function of drought severity a. Points indicate resilience metrics for oak populations: SJ (red), CA-High (blue) and CA-Low (green). Resilience metrics were computed for each population (sample depth > 10) and drought event. Gray lines represent overall relationships for each Resilience metrics. Comparison of the response of **Q. pyrenaica** forests to drought in terms of resistance, recovery, and resilience of greenness (a) and tree growth (c). For EVI, northern populations (red circle) were compared with southern ones (green circle). For BAI, the more xeric northern population (San Juan, SJ; red circle) was compared with the two southern populations, Cáñar-High (CA-High; blue circle) and Cáñar-Low (CA-Low; green circle). Different letters indicate significant post hoc differences between groups (see Material and methods for details).

Izquierdo & Cañellas, 2014). Greenness was less sensitive to drought than tree growth, particularly for drier sites. These findings agree with previous works showing tree growth to be a more sensitive metric of forest resilience than is net primary productivity (e.g. Babst et al., 2013; Coulthard et al., 2017; Gazol et al., 2018; Peña-Gallardo et al., 2018), suggesting that the growth reduction could be mediated by sink more than by source limitations (Fatichi et al., 2014; Körner, 2013). On the other hand, trees at CA-High registered higher BAI than did those located at lower elevations (CA-Low and SJ; Figure 6.4). This shows the high variability in the response to climate exhibited along a narrow gradient, which was especially noteworthy for southern sites, as these lie close to each other and both are considered to constitute the rear edge for the species.

As with many other forest species under Mediterranean climates, moisture availability is generally the most limiting factor driving radial growth of *Q. pyrenaica* along its distribution range in the Iberian Peninsula (Gea-Izquierdo & Cañellas, 2014). Thus, our results are consistent with those of previous studies highlighting the influence of precipitation on tree-ring growth in different oak species (e.g. Di Filippo et al., 2010; García-González & Souto-Herrero, 2017; Gea-Izquierdo et al., 2011; Tessier et al., 1994). A positive effect of moisture availability and negative impact of temperature expressing a limiting effect of high vapor-pressure deficit and potential evapotranspiration can be expected at drought-limited rear-edges. Yet, at the rear edge, the growth of some tree species (e.g. *Abies alba*) has been shown to be more sensitive to moisture-related variables (Martínez-Sancho & Gutiérrez Merino, 2019), while others species were more sensitive to temperatures (e.g. *Pinus sylvestris*, Herrero et al., 2013), and still other species responded simultaneously to both temperature and moisture-related variables (e.g. *Fagus sylvatica*, Dorado-Liñán et al., 2017a; Dorado-Liñán et al., 2017b; *Pinus nigra* subsp. *salzmanii*, Sánchez-Salguero et al., 2012). This diversity in the response of tree species to precipitation and temperature suggests that vulnerability to climate change is not consistently expressed within the rear edge, therefore evidencing that geographically marginal forests are not necessarily climatically or ecologically marginal (see Dorado-Liñán et al., 2019, and references therein).

6.4.2. Relict oaks show high resilience to drought at different spatio-temporal scales: do the geographical and ecological rear-edges match?

Despite the severe drought events in recent decades (Table C.2), we found a positive trend for vegetation greenness of *Q. pyrenaica* for the last 16 years. This is consistent with previous findings stressing a recent short-term increase in primary productivity for these forests coinciding with a rather wet decade in the 2000s after a dry decade in the 1990s (Pérez-Luque et al., 2015a). For tree growth, positive trends also appeared in the last decade, particularly for the southern high-elevation site (CA-High, Figure 6.4a). Similar long-term trends have been described for this species along its distribution range only at high-elevation wet and cold sites (Gea-Izquierdo & Cañellas, 2014). This could be related to a non-linear positive effect of warming for species at cold-limited high-elevation sites (Gea-Izquierdo & Cañellas, 2014; Salzer et al., 2009). Importantly, for rear edges threatened by climate change, negative growth trends were expected, as shown for some temperate and Mediterranean species (Camarero et al., 2015b; Dorado-Liñán et al., 2017b; Sánchez-Salguero et al., 2012).

Although the 2012 drought event was more severe and intense than that of 2005 (Table C.2), resilience values for greenness and tree growth were greater for 2012. This could be due to the different timing of the two droughts. The 2012 event was a winter drought (Trigo et al., 2013) occurring earlier than the shorter 2005 drought. The latter matched the period of maximum growth for oak forests in late spring (Figure C.4). This would highlight the importance of the timing of the drought as a key factor determining tree recovery after drought (Camarero et al., 2015a; Huang et al., 2018). For tree growth, the highest values of resilience were found for the two most severe events (1995 and 1999; Table C.2) and tree-growth resilience was positively related to drought severity (Figure 6.5a).

The high drought-resilience values reported here, in addition to the potential role of local adaptation [*i.e.* high values of genetic resilience for oak forests

on Sierra Nevada; Valbuena-Carabaña and Gil (2013); Valbuena-Carabaña and Gil (2017)], suggest that land-use also has a key role to determine tree resilience to drought and the range edge of species. Our findings agree with those of studies showing that the assumed higher vulnerability of current geographical dry edges does not necessarily hold (e.g. Cavin & Jump, 2017). In our case, this can be explained by the fact that the current geographical rear-edge does not match with the potential ecological rear edge for the species because this has been modified and determined mostly by human use. Martínez-Vilalta (2018) pointed out the importance of local adaptation and plasticity, and also of local environmental factors on the vulnerability shown by rear-edge populations. Our results highlight the ample small-scale variability at the ecological boundary and thus the rear edges need to be more clearly defined and delineated. All the above points, together with the characteristic high resprouting ability of the species, show the long-term persistence of these populations (Bellingham & Sparrow, 2000). It should be mentioned that we studied only adult individuals established decades or centuries ago, meaning that it needs to be assessed whether the high resilience found is expressed at the species level (*i.e.* also including regeneration) or only in adult trees. The rear-edge might differ for different ontogenetic stages. It is important to assess whether seedling regeneration and recruitment are vulnerable, as in other Mediterranean species at some locations including their xeric limit (Castro et al., 2004; Gea-Izquierdo et al., 2015; Vilà-Cabrera et al., 2011).

6.4.3. Land-use legacies in relation to forest response under climate change and to the present rear edge

The review of historical documents revealed that forest clearings, firewood removal, charcoal production, and mining have strongly affected the forests on Sierra Nevada (Table C.4), where an estimated historical loss of broadleaf *Quercus* species has approached 90% in tree cover at medium and low elevations (Jiménez-Olivencia et al., 2015). Together with the analysis of the disturbance chronologies, the observed notable differences in stand

structure, tree size, and age suggest different forest histories and a different management origin (*i.e.* land-use legacy) between northern (coppice) and southern populations (high forest, open woodland). On the northern slopes of Sierra Nevada (*e.g.* the SJ site), land uses have been historically distributed along an elevational gradient: grasslands and shrublands for cattle farming at the highest elevations; next forest stands with some croplands; and, finally, irrigated terraces with tree crops at the lowest elevations (Jiménez-Olivencia et al., 2015). In addition, other activities such as mining must have altered the forest structure, *e.g.* the SJ site has many small mines and quarries that were exploited intermittently throughout history. The release growth event expressed in the 1940s concurs with a period of maximum mining activity in this area (1925 to 1957), during which timber use increased for mine tunnels and furnaces, these also requiring large amounts of firewood to melt the mineral (Table C.4). This heavy exploitation of the neighboring forest resources must have affected a significant part of this oak woodland, as shown by growth of the remnant trees at the northern site (Figure C.2b).

On the other hand, woodlands on the southern slopes (*e.g.* CA site) were mixed with a greater percentage of croplands along the elevational gradient where oaks grow (Jiménez-Olivencia et al., 2015). Firewood, charcoal, and acorns were intensively exploited at the southern sites, until at least the mid-20th century, when these activities sharply declined due mainly to rural abandonment and the use of gas and fossil fuels (Valbuena-Carabaña & Gil, 2013). At the CA-High site, the only positive release event found for the earliest years could be related to the conversion from closed forest to an open silvopastoral system, a common management practice often applied in the past in many Iberian oak woodlands (Cañellas et al., 2004; Gea-Izquierdo et al., 2011) and which has been documented for this site (Valbuena-Carabaña & Gil, 2013).

The other release event observed for the SJ site during the period 1995-2000 was lower than during 1940, but also affected most trees (Figures Figure 6.4 and Figure C.2b). No records of forest practices in this area over the last 30 years have been found (Bonet et al., 2016), and no logging was recorded during the period 1995 - 2000 (F.J. Cano-Manuel *personal communication*). Therefore this release might be related to natural drought-induced mortality

after 1995, as has been reported for other Mediterranean tree species after severe drought (e.g. Lloret et al., 2004; Peñuelas et al., 2001).

6.5. Conclusions

Two main results could be highlighted from our research. First, the high values of resilience in our study suggest that *Quercus pyrenaica* populations in Sierra Nevada are located in a geographical, but not a climatic, ecological rear edge (*sensu* Martínez-Vilalta, 2018; Vilà-Cabrera et al., 2019). Contrary to our expectations, the trees exhibited high resilience in the response to drought, particularly over the long-term. The high resilience values observed could also be related to stabilizing mechanisms promoting community resilience or enhancing resilience of already established adult individuals [e.g. stress tolerance capacity linked to local adaptation; Lloret et al. (2012)], that can buffer the impact of extreme events, as has been described for other species (e.g. *Pinus sylvestris*, Herrero & Zamora, 2014). Second, these resilience responses of oak forest to drought events are not spatially homogeneous throughout the mountain range, due to differences in ecological conditions and/or past management legacies. In fact, there was much small-scale variability in the response to climate along the rear edge that we had not *a priori* considered in our study. The differences found in tree growth, climatic sensitivity and tree resilience between close neighboring sites showed that responses to drought were site dependent and could drastically vary in extremely narrow spatial gradients. In other words: in mountains, heterogeneity of ecological conditions at fine scales is the rule, enabling the existence of microrefugia and lengthening species persistence (Olalde et al., 2002; Serra-Díaz et al., 2015). This is particularly relevant to define the real extent and nature (*i.e.* geographical and/or ecological) of rear-edge populations where topographic and biophysical variability facilitates the existence of microrefugia.

The analysis of tree-growth dynamics revealed suppression and release events that were consistent with legacies left by land use in local forest dynamics, as inferred from an exhaustive review of historical documents. This suggest that the rear edge therefore needs to be redefined in space but also in

time (Vilà-Cabrera et al., 2019), partly because of land-use legacies and their effect on the possible mismatch between the current distribution of species (*i.e.* determining the “available” geographical rear edge) and the potential ecological (limiting) rear edge of species. The rear-edge concept should also consider historical aspects in addition to the geographic, climatic, and genetic ones (Vilà-Cabrera et al., 2019), particularly in areas with a long history of human management, such as Mediterranean mountains. Therefore, anthropogenic habitat modification and its legacies represent a critical dimension of marginality as they may intensify, confound or delay climate-driven population decline at the rear edges (Vilà-Cabrera et al., 2019). This is relevant for tree species that are highly sensitive to climate change, such as *Quercus pyrenaica*, not only for conservation *per se* of the species, but for all ecosystem services that these forests offer. In this sense, it needs to be analyzed the resilience of all demographic stages of species, to assure that the observed resilience in adult trees it is also manifested in its demographic recruitment dynamic expressed by the natural regeneration. The rear-edge could also differ for different age cohorts or in seedlings compared to resprouts.

An ontological system based on
MODIS images to assess
ecosystem functioning of Natura
2000 habitats: A case study for *Q.*
pyrenaica forests

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Abstract

The implementation of the Natura 2000 network requires methods to assess the conservation status of habitats. This paper shows a methodological approach that combines the use of (satellite) Earth observation with ontologies to monitor Natura 2000 habitats and assess their functioning. We have created an ontological system called Savia that can describe both the ecosystem functioning and the behaviour of abiotic factors in a Natura 2000 habitat. This system is able to automatically download images from MODIS products, create indicators and compute temporal trends for them. We have developed an ontology that takes into account the different concepts and relations about indicators and temporal trends, and the spatio-temporal components of the datasets. All the information generated from datasets and MODIS images, is stored into a knowledge base according to the ontology. Users can formulate complex questions using a SPARQL end-point. This system has been tested and validated in a case study that uses *Quercus pyrenaica* Willd.. forests as a target habitat in Sierra Nevada (Spain), a Natura 2000 site. We assess ecosystem functioning using NDVI. The selected abiotic factor is snow cover. Savia provides useful data regarding these two variables and reflects relationships between them.

7.1. Introduction

European Union has developed a set of environmental directives focused on nature conservancy (Evans, 2012). Their main aims are: 1) to halt the biodiversity loss according to the Convention on Biological Diversity (CBD (Secretariat de la Convention on Biological Diversity), 2003), 2) to promote the implementation of policies for achieving sustainable development in a context of global change.

The Birds (79/409/EEC; 2009/147/EU) as well as the Habitats Directives (92/43/EEC) seek a favorable conservation status for all listed habitats and species all throughout the European territory (Louette et al., 2011). For these objectives, it is mandatory to implement methods to assess the conservation status of habitats and species. This is a challenging task that requires taking into consideration the concept of monitoring (Lindenmayer & Likens, 2010; Pereira & Cooper, 2006). According to Lindenmayer and Likens (2010), the protocols used to satisfy legislation requirements must be focused on identifying trends in structural and functional features of habitats. These authors assert that “mandated monitoring” (required by legislation) can help in assessing the changes in the conservation status of habitats (Lindenmayer & Likens, 2010).

Satellites gather huge amounts of information that could be useful to monitor and to assess the conservation status of habitats (Vanden Borre et al., 2011). Such information would be adequate to assess both structural (distribution) and functional changes (productivity, phenology, etc.) in the Natura 2000 habitats. For example, a wide set of products derived from MODIS (Moderate Resolution Imaging Spectroradiometer) sensor are useful for monitoring ecosystem function at a landscape scale (250-1000 m resolution)(Hall et al., 2002; Huete et al., 2002; Justice et al., 2002). Other satellites such as Quickbird or IKONOS provide information at a finely detailed spatial resolution (0.5-4 m resolution), which is useful to monitor habitat distribution and structure [Forster et al. 2008 Approaches Utilising; Hyde et al. (2006); Wang et al. (2004)]. The most important advantage of satellite Earth observation in relation to habitat monitoring could be its capacity to allow comparisons among different locations (Vanden Borre et al., 2011). The

temporal homogeneity (the same information is gathered with a predefined periodicity) is also a key feature to implement monitoring protocols using (satellite) Earth observation. However, the information collected from satellites cannot be processed and interpreted straightforwardly by most scientists and decision makers (Kalluri et al., 2003). Both the overwhelming amount of data to process/analyse as well as the inherent complexity of the variables measured makes it difficult to create an operational system for assessing habitat functioning (Xue et al., 2011).

Ontologies are knowledge-representation techniques defined as a specification of a conceptualization (Gruber, 1993) within a domain of interest (habitat functioning in our case). A conceptualization is “an abstract, simplified view of the world that we wish to represent for some purpose” (Gruber, 1993). A computer can “understand” an ontology, because ontologies are structured according to concepts and relationships on which a computer can “reason”, as opposed to unstructured files like documents (Antoniou & Van Harmelen, 2004). The use of ontologies can foster comprehensive data discovery and integration (Gruber, 1993; Jones et al., 2006), adding semantic meaning to data. Thus, these techniques can promote the use of remote sensing by environmental managers and ecologists (Silva et al., 2005).

While ontologies help to represent the domain, knowledge bases are used to store facts and complex information defined according to ontologies. Consequently, an inference engine, a software tool that applied logical rules to the knowledge base, can reason about those facts, deduce implicit facts, or resolve semantic queries (Hayes-Roth et al., 1983). Although ontologies are commonly used in different disciplines (Bard & Rhee, 2004; Renear & Palmer, 2009), they are not common in Ecology (Madin et al., 2007; Madin et al., 2008; Williams et al., 2006), or Earth observation (Arvor et al., 2013; Fallahi et al., 2008; Fonseca & Llano, 2011; Hashimoto et al., 2011; Oliva-Santos et al., 2014; Wiegand & García, 2007).

In this work, we describe the design and implementation of an ontological system (called Savia, <http://obsnev.es/ontologia/index>) that combines the advantages of (satellite) Earth observation with the knowledge-representation capabilities of ontologies to create a tool that displays

indicators and trends regarding habitat functioning. This work had two objectives: *a*) to assess the functioning of a Natura 2000 habitat and its relationships with abiotic factors (thematic objective), and *b*) to use ontologies to create a operational system that satisfies the first objective (methodological objective). Our work provides a novel case study to the body of knowledge regarding the use of ontologies in Earth observation. It is also of value because we compute temporal indicators and trends to assess the conservation status of habitats. Finally, we show how ontologies can help to bridge the gap between ecologists and remote-sensing experts.

7.2. Study area and data

7.2.1. Study area

Sierra Nevada (SE Spain) is a mountainous area (ranging from 860 m to 3482 m *a.s.l.*) covering more than 2000 km² (Figure 7.1a). The climate is Mediterranean, characterized by cold winters and hot summers, with a pronounced summer drought.

Sierra Nevada is considered one of the most important biodiversity hotspots in the Mediterranean region (Blanca et al., 1998) and has several types of legal protection: Biosphere Reserve, National and Natural Park, and Nature 2000 site. Sierra Nevada is also a LTER (Long-Term Ecological Research) site. We have focused this work on one habitat of Sierra Nevada: forests dominated by *Quercus pyrenaica* Willd.. This habitat (EU habitat code 9230) is included in the Annex I of the Habitats Directive and its conservation status is not well known (EIONET, 2013), partly due to lack of detailed ecological studies (García & Jiménez, 2009). The Pyrenean oak forests extend from southwestern France to the Iberian Peninsula (Franco, 1990) (Figure 7.1a), reaching their southernmost European limit in Sierra Nevada, where nine oak patches (2400 ha) have been identified (Figure 7.1b), ranging between 1100-2000 m *a.s.l.*.

Quercus pyrenaica is considered as vulnerable in southern Spain (Vivero et al., 2000) and the populations inhabiting Sierra Nevada are considered

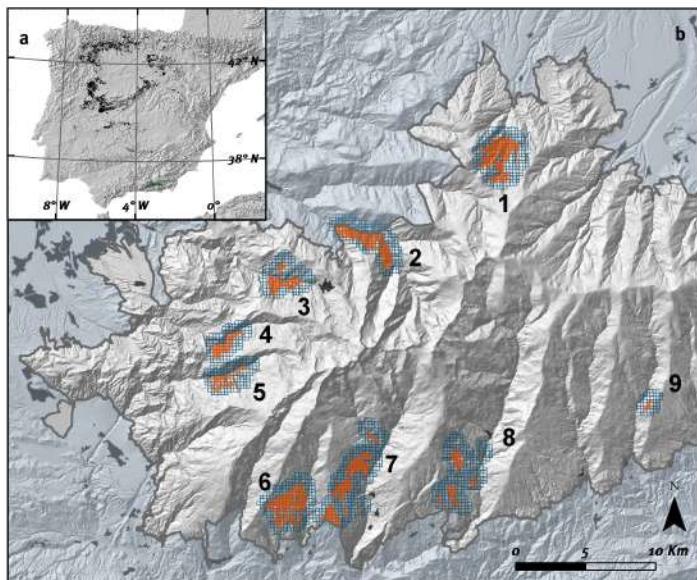


Fig. 7.1. Location of Sierra Nevada mountains. The distribution of *Quercus pyrenaica* in the Iberian Peninsula is shown in black (a). The patches of *Quercus pyrenaica* in Sierra Nevada are shown in orange (b). The grey line shows the boundary of the natural protected area of Sierra Nevada. The pixels used to compute the vegetation and snow indicators are included (blue grid).

relict forests (Melendo & Valle, 2000). They have undergone intensive anthropic use in recent decades (Camacho-Olmedo et al., 2002b). They are also expected to suffer the impact of climate change, due to their climate requirements (wet summers): *Quercus pyrenaica* requires between 650 and 1200 mm of annual precipitation and minimal summer precipitation between 100 and 200 mm. Thus, simulations of the climate-change effects on this habitat point to a reduction in suitable habitat for Sierra Nevada (Benito et al., 2011; Benito, 2009).

7.2.2. Data sets and derived information

We have selected two MODIS products: MOD13Q1 to assess the habitat functioning and MOD10A2 to study the behaviour of an abiotic factor (snow cover). MOD13Q1 provides information on vegetation index NDVI (Normalized Difference Vegetation Index). The spatial resolution of this product is 250 m and the temporal resolution is 16 days. MOD10A2 provides information about snow cover extent (Hall et al., 2002). It has a periodicity

of 8 days and a spatial resolution of 500 m. Each MOD10A2 pixel is labelled as snow if it has had snow on one of the previous 8 days. We selected MODIS products because both their spatial resolution and temporal resolutions are appropriate for the scope of this study. We homogenized the different spatial and temporal resolutions in these two products to produce the final data at 500 m of spatial resolution and 16 days of temporal resolution. For the spatial resolution, we intersected the two grids to assign the identifier of any MOD10A2 pixel to its overlapping one in MOD13Q1. For temporal homogenization, we aggregated the data from MOD10A2 (8 days) to gain information regarding at least MOD13Q1 scale (*i.e.* more than 16 days). We used the MODIS time series from 2000 to 2012.

NDVI seasonal measurements (aggregation of NDVI values by season) are suitable tools to quantify productivity and biomass (Running et al., 2004; Turner et al., 2006), seasonality (Piñeiro et al., 2006; Potter & Brooks, 1998) and other phenological measurements (Cleland et al., 2007). These measurements have been used to characterize ecosystem functioning (Cabello et al., 2012). We have calculated indicators regarding these ecological functions using the mean NDVI profiles provided by MODIS (Figure 7.2) *sensu* Alcaraz-Segura et al. (2009b):

- *annual and seasonal mean* (NDVI-I) which can be used to estimate fAPAR (Fraction of Absorbed Photosynthetically Active Radiation) (Sellers et al., 1996) and thus net primary production (Paruelo et al., 1997; Sellers et al., 1992; Tucker et al., 1985).
- *annual relative range* (RREL); difference between maximum and minimum NDVI divided by annual mean. This variable provides an indicator of the seasonality of the photosynthetic activity (Paruelo & Lauenroth, 1995).
- *maximum and minimum NDVI values* (MAX and MIN) and *months* (MMAX and MMIN) in which they occur. They provide an additional description of phenology, indicating the intra-annual distribution of the periods with maximum and minimum photosynthetic activity (Hoare & Frost, 2004; Lloyd, 1990).

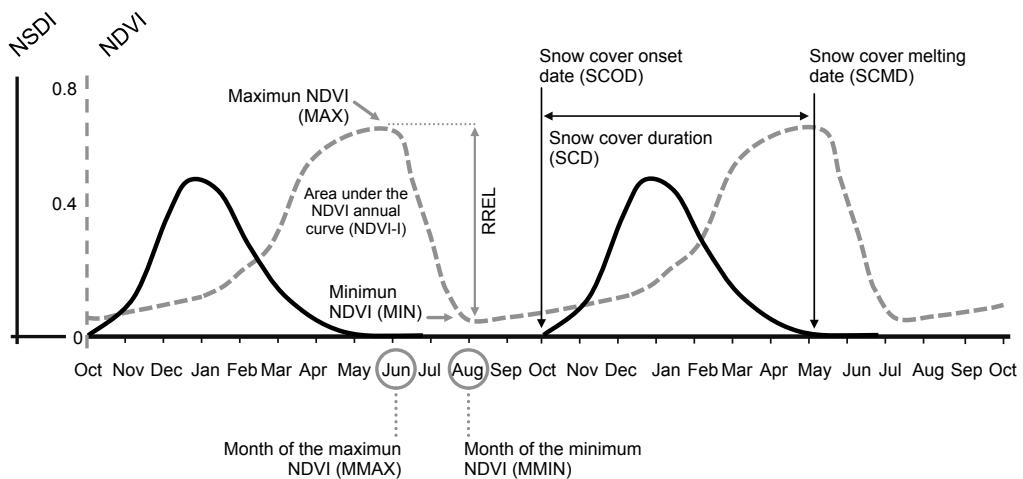


Fig. 7.2. Attributes derived of Normalized Difference Vegetation Index (NDVI) and snow-cover profiles. Modified from (Alcaraz-Segura et al., 2009b; Wang & Xie, 2009).

NDSI (Normalized Difference Snow Index) is a spectral band ratio that takes advantage of the fact that snow reflectance is high in the visible wavelengths and low in the shortwave infrared region (Salomonson & Appel, 2006). This index has proven to be a robust indicator of snow cover using MODIS images(Rittger et al., 2013). We have calculated several indicators from MOD10A2 images (Wang & Xie, 2009) (Figure 7.2):

- *snow-cover duration (SCD)*: is defined as the number of days covered by snow per hydrological year (describe a time period of 12 months for which precipitation totals are measured).
- *snow-cover onset dates (SCOD)*: is defined as the first date in the hydrological year that the pixel has snow. This indicator is useful to identify shifts in the starting of snow season.
- *snow-cover melting dates (SCMD)*: is the last date in the hydrological year that the pixel has snow. This indicator provides useful information about the melting process.
- *snow-cover melting cycles (SCMC)*: number of melting cycles in each pixel per hydrological year.

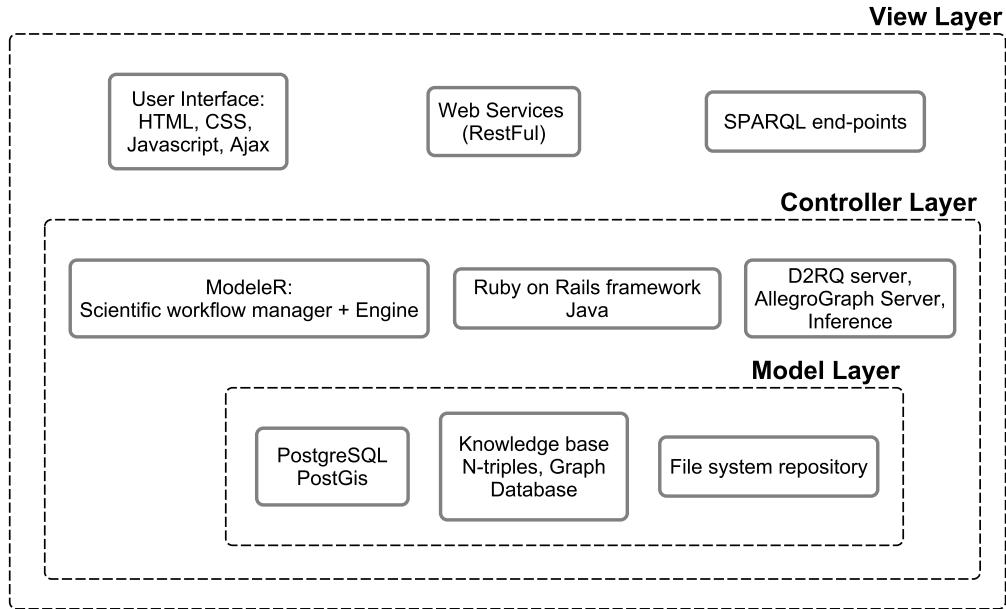


Fig. 7.3. System architecture.

7.3. Knowledge retrieval: ontologies and semantic processing

Savia was designed taking into account a client-server architecture (Figure 7.3). The system contains different modules that extract relevant knowledge from the raw data. These modules act in a user-transparent way and are detailed in the following subsections, highlighting image processing, the development of the ontology, how instances are generated, and the final query system.

Embedding MODIS images in a database and calculating thematic indicators

HDF (Hierarchical Data Format) files are downloaded from NASA servers and processed using a workflow that makes the process automatic and reproducible. This workflow is stored and documented in a model repository called ModeleR (Bonet et al., 2014a; Pérez-Pérez et al., 2012). The workflow extracts information contained in any HDF files and stored it in a relational database (see structure in Figure 7.4). NDVI and NDSI values are stored in a

table that is linked to a vector layer containing the centroids of MODIS pixels. These raw data are used to aggregate and calculate the different indicators in Savia. The results are integrated again into the relational database, that is part of the Sierra Nevada LTER site information system (Bonet-García et al., 2011).

The indicators described in Section 2.2 were calculated for each pixel and temporal stage (by hydrological year, *i.e.* the period between October 1st of one year and September 30th of the next; and by season) using SQL queries. The temporal trend for each pixel was calculated using the nonparametric Mann-Kendall trend test (Kendall, 1970; Mann, 1945). The analyses were computed in R (R Core Team, 2020) with Kendall package (McLeod, 2011). We set 0.05 the alpha level for the test, and slopes with p-values > 0.05 were considered significant.

7.3.1. Creating the ontology

The ontology must represent both the information (MODIS products, indicators, and temporal trends) and the concepts used to add ecological meaning to the data (Figure 7.5). To build the ontology, we used Time Ontology in OWL (Web Ontology Language) (Hobbs & Pan, 2004) and Basic Geo (WGS84 lat/long) Vocabulary (Brickley, 2003) external ontologies. The OWL-Time ontology promoted by W3C (World Wide Web Consortium) (W3C, 2013), provides a vocabulary for expressing instants and intervals, together with information concerning durations and date/time information (Hobbs & Pan, 2004). The Basic Geo is an RDF (Resource Description Framework) vocabulary for representing latitude, longitude, altitude information as well as other information related to spatial-located items.

Thus, the ontology takes into account three different parts (Figure 7.5):

1. Representing spatial information. The main concept is the Pixel, which represents a pixel from a MODIS image. Some pixels that share similar functions (*i.e.* be covered by the same habitat) may belong to a Patch. Finally, some patches sharing the same dynamics may belong to a Group. The properties called *PixelBelongsToPatch* and *PatchBelongsToGroup* help to define the relationships between the previously defined concepts.

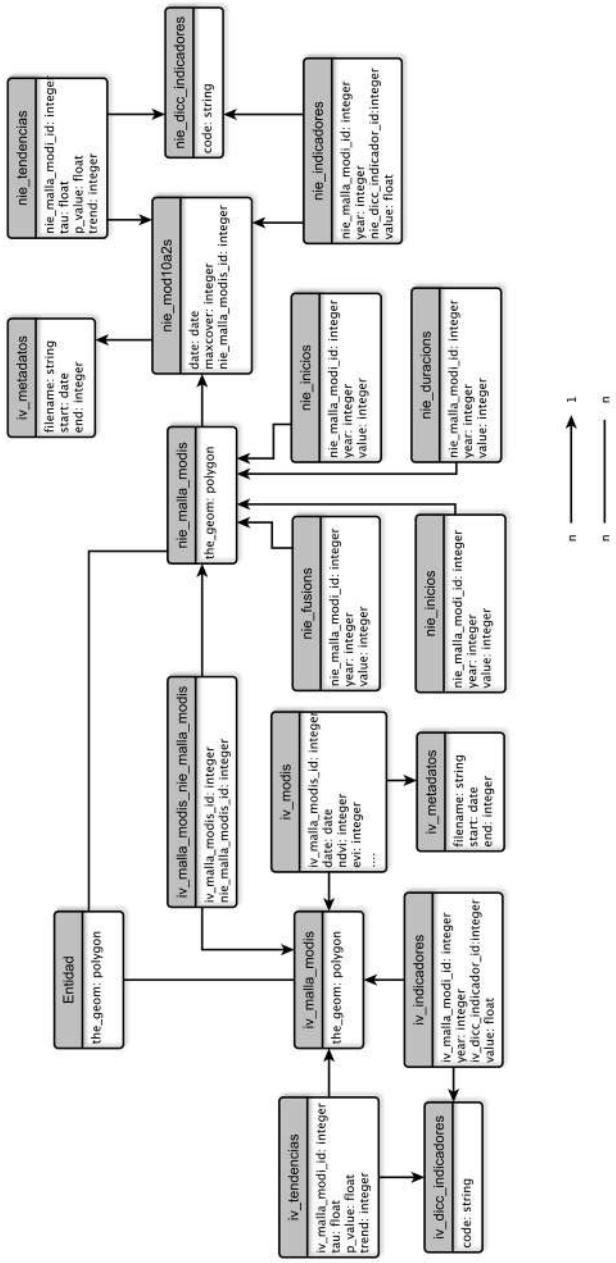


Fig. 7.4. Database schema. For each MODIS product the relational model stores three types of information: (i) spatial distribution of the pixels (**nie_malla_modis** and **iv_malla_modis** tables); (ii) values of NDVI and NDSI from original HDF files (**nie_mod10a2s** and **iv_modis** tables); and (iii) the metadata associated with each original image (**nie_metadata_modis** and **iv_metadata_modis** tables). The database also contains an auxiliary table to manage spatial entities (i.e. *Quercus pyrenaica* patches). Finally, there was a set of tables containing the aggregated information and indicators obtained after processing the raw data (see Section 2.2) (tables **iv_tendencias**, **iv_nie_inicios**, **nie_nie_fusions**, **nie_nie_tendencias**)

PixelIsNearTo is another useful property that adds the functionality of proximity to any pixel. The distance threshold used was 500 m between pixels (500 m is the spatial resolution of MODIS snow products). This property is symmetric because when a pixel A is near B, B is also near A.

2. Indicators. This part contains a concept (*IndicatorValues*) that represents the different values that take an indicator (see Section 2.2) at a given time point (through the concept called time: Year and the property *HasYear*) and in a given place (through the concept Pixel and the property *IndicatorValuesLocateInPixel*). We have also included a concept to describe all the indicators (Snow-cover duration, Snow-cover onset date, NDVI_i annual, Maximum NDVI, etc.). These concepts are grouped according to their thematic area (Snow and Vegetation). Each indicator has a property called value that is measured using a given specific unit.
3. The temporal trends are described in a concept called *IndicatorTrend*. This concept shows the temporal trend of a single point for the whole time series (it is linked to *Pixel* via *PixelHasIndicatorTrends*). We have also created a concept for each temporal trend calculated for the previously described indicators (Trend of Snow cover duration, Trend NDVI_i annual, etc.). These concepts are also grouped according to their thematic area (Snow Trend, Vegetation Trend). All these concepts have the following properties:
 - a) *value_tau* and *p_value*: These properties contain the statistic (*value_tau*) and the significance (*p_value*) reached by the Mann-Kendall trend analysis.
 - b) *value_trend*: Categorical property ranges from -1 (significant negative trend) to 1 (significant positive trend). It is calculated according to the values of *value_tau* and *p_value*.

This schema was implemented using OWL DL (Description logic) that allows an enhanced expression level and does not limit the values for cardinality (Smith et al., 2004). The structure of the ontology created can be downloaded following this link: <http://iecolab.es/indicators.rdf>

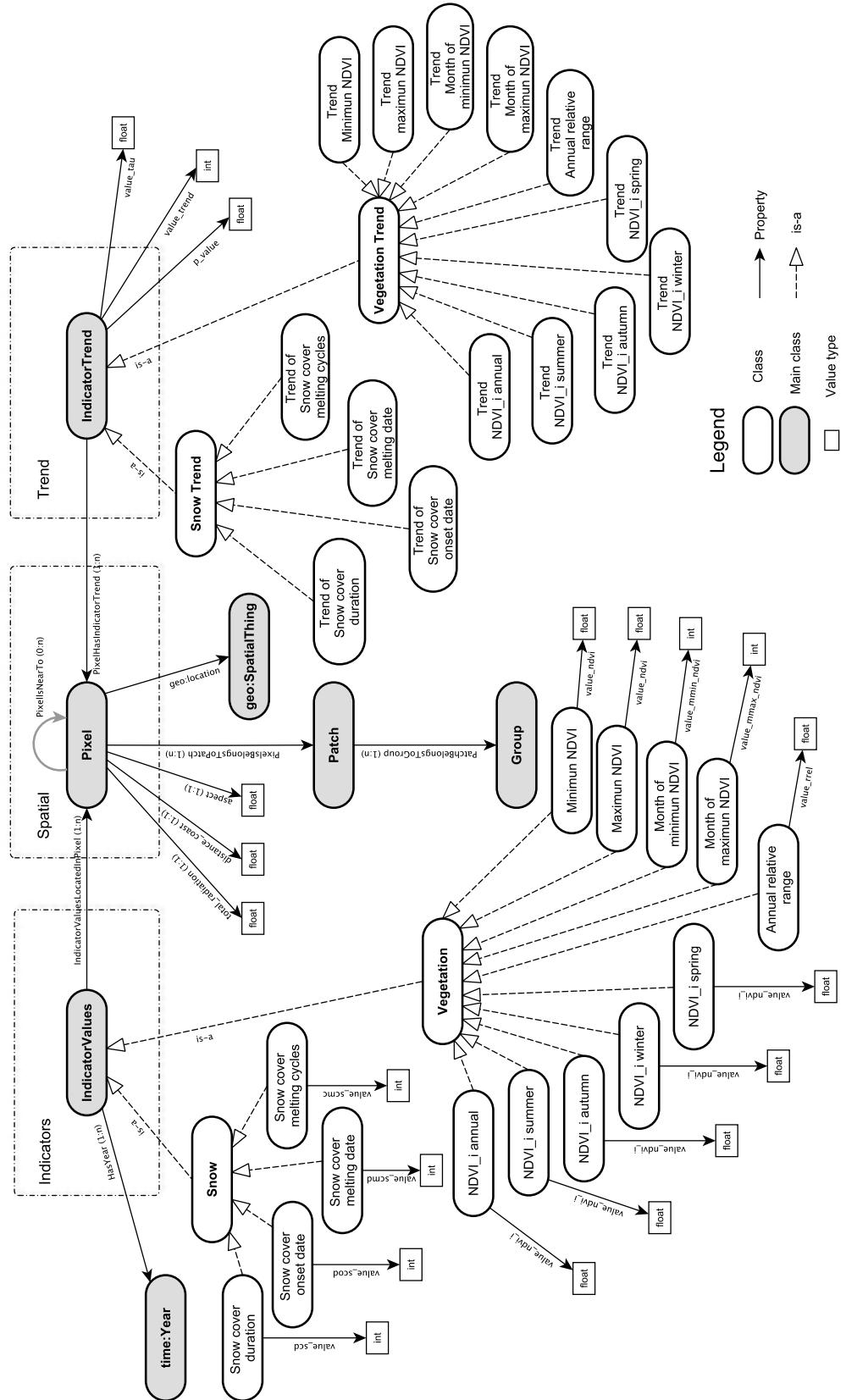


Fig. 7.5. Detailed representation of the ontology created. Three main parts are considered: spatial information, indicators, and temporal trends of the indicators

7.3.2. Knowledge base, SPARQL endpoint and inference

The next step after creating the ontology is to map the records in the database that contain the data to the ontology. Firstly, we used D2RQ (Bizer et al., 2004) to map the relational database to OWL ontology. This software allows instance data to be retrieved from relational databases on-the-fly during the execution of SPARQL queries. Nevertheless, this procedure is time consuming and demands powerful computational capabilities. Thus, we dumped the mapping created with D2RQ into an intermediate N-triples file to avoid this drawback (Sarkar et al., 2011). This file was created with the data existing in the database and has all the triplets contained in the knowledge base.

To store the knowledge base, our tests with the open-source Apache Fuseki and Jena (<http://jena.apache.org/>) frameworks yielded unsuccessful results as soon as the data volume started to grow. Because we need an efficient implementation that can be scaled to large, enterprise-class data (Wilkinson et al., 2004), we also conducted some tests with AllegroGraph (<http://www.franz.com/agraph/allegrograph/>) and Virtuoso (<http://virtuoso.openlinksw.com/>), choosing the former option because of its capabilities and user-friendly management environment. This software is a triplestore that uses a graph database and it has the ability to encode values directly into its triples. To enhance the results of the queries, a reasoning task can be also triggered within the generation of the system output process. AllegroGraph provides a built-in inference engine that derives implicit information from the knowledge base. Thus, users can easily turn it on by toggling that option in the query builder interface to enrich their queries. The inference engine is useful to find relations on different types of indicators and other implicit properties such as *PixelIsNearTo*. For example, Savia can answer questions concerning implicit knowledge of pixels with a positive trend on seasonal mean of NDVI near others with a negative trend in snow-cover melting dates.

7.4. Study Case

For the improvement of the conservation status of habitats, it is necessary to implement management plans according to the Annex 6 of the Habitats Directive. Our system provides knowledge useful to design those management plans. We have used *Q. pyrenaica* forests in Sierra Nevada (Spain) to explore the importance of snow duration in the functioning of *Q. pyrenaica* forests. We have chosen this habitat as a case study for two reasons: *a*) its interesting ecological dynamics (deciduous forest in a Mediterranean mountain), and *b*) the need to manage these forests in a global-change context.

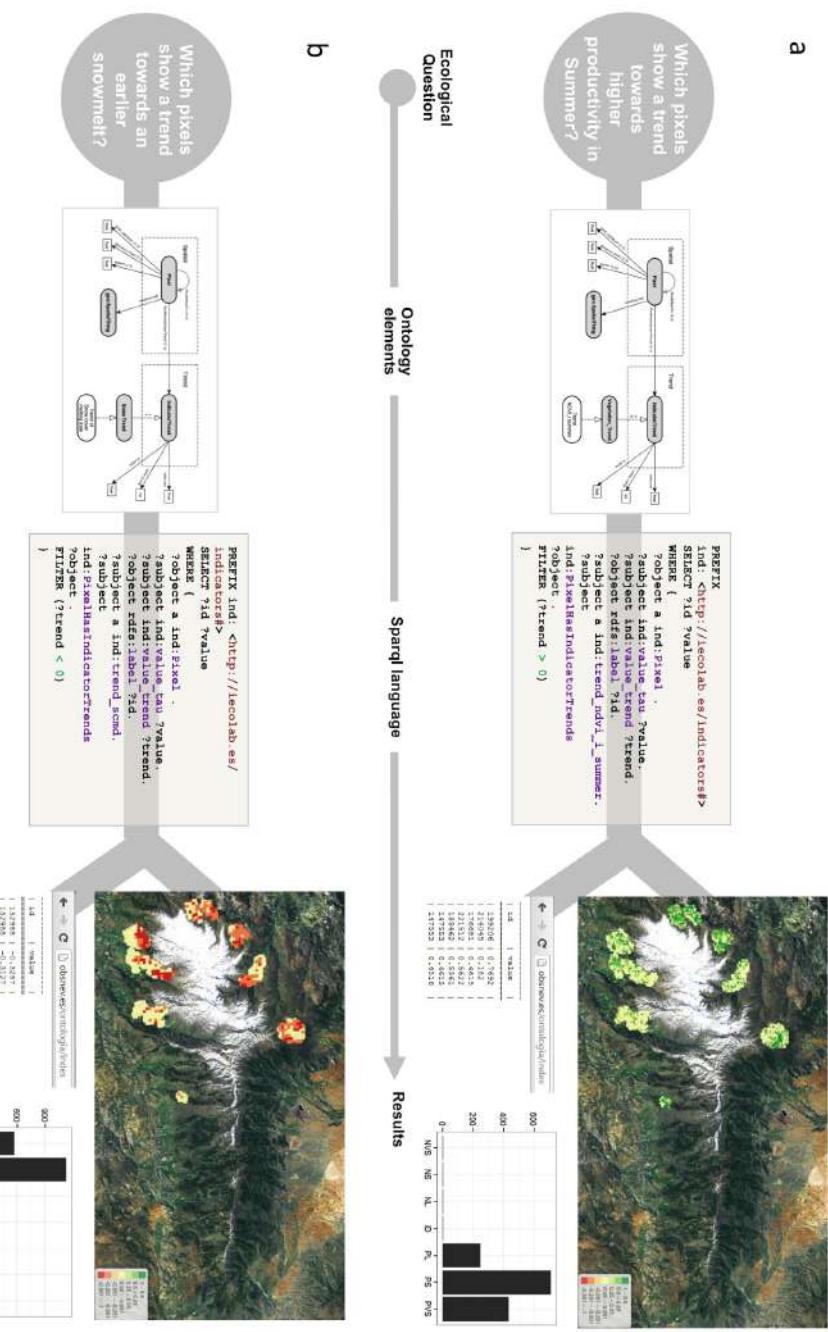
We have structured the case study according to three questions that will provide two types of results. Some of them will help in the understanding of the ecological functioning of the target habitat. And others will demonstrate how ontologies are useful tools to make remote sensing information more accessible for non-expert users.

7.4.1. Which pixels show a trend towards higher productivity in summer?

Q. pyrenaica forests show a well-defined growth season centred in summer (Alcaraz et al., 2006; Dionisio et al., 2012). Some works have pointed out changes in habitat functioning: increase in annual vegetation greenness in Sierra Nevada (Alcaraz-Segura et al., 2010; Alcaraz-Segura et al., 2008) and seasonal functional changes in *Q. pyrenaica* woodlands (Marty, 2008), during the last decade.

This question aims to explore whether our target habitat is undergoing changes in summer productivity, specifically which *Q. pyrenaica* forests of Sierra Nevada have shown a positive trend of the value of summer productivity (summer NDVI).

Fig. 7.6. Scheme showing how the ontology solves questions regarding habitat functioning (a) and the behaviour of an abiotic factor (b). For each ecological question, different ontology elements are used to answer it. Then SPARQL language is used to query the knowledge base. Finally, results can be shown in different formats: map, csv or histogram. See first and second question of the study case. All pixels are displayed on the resulting map, but for those that have a significant positive trend the tau value is retrieved. In the map, we show seven different colours corresponding to this classification of tau values: [1, 0.5], [0.5, 0.25], [0.25, 0.05], [0.05, -0.051], [-0.051, -0.251], [-0.251, -0.501], [-0.501, -1].



7.4.2. Which pixels show a trend towards an earlier snowmelt?

Several studies have pointed out a trend towards higher temperatures and lower precipitation for the Mediterranean area (García-Ruiz et al., 2011; Giorgi & Lionello, 2008). Significant declines in snow-cover extent and duration has been reported in some European mountains (Marty, 2008; Moreno Rodríguez et al., 2005; Nikolova et al., 2013; Scherrer et al., 2004). Climate projections forecast an increase of +4.8°C at the end of the 21st century (Benito et al., 2011) for Sierra Nevada and it is expected that snowmelt will occur earlier in the year and will be more rapid (García-Ruiz et al., 2011).

The second question that we raised concerns the observed changes in snowpack in Sierra Nevada. We are interested specifically in which pixels show a trend towards earlier snowmelt during spring-summer. This question is crucial, given that *Q. pyrenaica* forests need water in summer for growth.

7.4.3. Which *Q. pyrenaica* patches show a trend towards a more productive summer and earlier snowmelt?

This question explores the relationships and co-occurrence between biological production and snow-cover features.

Snow-related variables can explain the distribution of plant communities in the landscape (Jones et al., 2001). This causal relationship is more important at high elevation (Bonet García & Cayuela, 2009) in Sierra Nevada. But snow cover also explains part of the ecosystem functioning. Trujillo et al. (2012) found that vegetation greenness increases with snow accumulation. This relationship varies with elevation, reaching a maximum between 2000-2600 m.

Some works have pointed out the influence of snow on greenness in Pyrenean oak forests (Alcaraz-Segura et al., 2009b; Dionisio et al., 2012), but to date

we have found no studies that analyse the coupling between snow cover and forest greening. Water availability is a key issue on the distribution of *Q. pyrenaica* (del Río et al., 2007; Gavilán et al., 2007). This combination of plant growth and water scarcity makes summer a critical season for the functioning of this habitat.

The third question assesses the capacity of our ontology to show relationships similar to those described above. We have explored the co-occurrence of significant trends in biological production and snow-cover melting date in *Q. pyrenaica* forests. In other words, we have analysed which *Q. pyrenaica* forests show a trend towards higher productivity and earlier melting date in summer.

7.5. Results

We translated the above questions from natural language into ontology. For the first and second questions (Sections 4.1 and 4.2) we used two concepts (*Pixel*, *IndicatorTrend*) and some properties describing these concepts (*value_trend*, *value_tau*, *PixelHasIndicatorTrends*, *Trend NDVI_i summer*, *Trend of Snow cover melting date*) included in the ontology. Specifically:

- “select all *Pixel* where *IndicatorTrend* is positive for summer NDVI-*I* indicator” for question 4.1 (Figure 7.6a)
- “select all *Pixel* where *IndicatorTrend* is negative for snow-cover melting date” for question 4.2 (Figure 7.6b)

We used SPARQL language to query the knowledge base.

Regarding the first question, we found that 75% of pixels had a positive significant trend for summer NDVI (Figure 7.6a). For these, more than 80% showed a strong or very strong positive trend. In general, *Q. pyrenaica* patches located on the north face of Sierra Nevada showed a higher amount of significant pixels than the southern ones did (see map in Figure 7.6a).

The second question showed that almost 70% of the pixels covered by *Q. pyrenaica* forests had a strong or very strong negative and significant trend

towards an earlier melting date (Figure 7.6b). Similar to NDVI, the northern patches showed a higher amount of significant pixels than the southern ones.

The third question is more difficult to translate to the ontology because it takes into account two datasets and more concepts than the previous questions. We have included a concept called Patch, being a subset of pixels that share some ecological features (they belong to the same *Q. pyrenaica* population). This question also includes other concepts already mentioned (*Pixel*, *IndicatorTrend*) and properties describing those concepts (*value_trend*, *value_tau*, *PixelHasIndicatorTrends*). We also calculated the percentage of pixels per Patch that showed trends towards more productive summers and earlier snowmelt. These elements were used to translate the original question to another one that was more suitable for the ontology: select all Pixels where the *IndicatorTrend* is positive for the summer NDVI-I indicator (*Trend NDVI_i summer*) and negative for snow-cover melting date (*Trend of Snow-cover melting date*). We used SPARQL language to query the knowledge base. The results can be displayed both in a map and table format (Figure 7.7).

Savia provides two types of answers for this question: *a)* A table (Figure 7.7) shows the different *Q. pyrenaica* patches ranked according to the percentage of pixels having the described trends in summer productivity and snow-cover melting date. *b)* A binary map showing the pixels (grouped by *Patch*) that satisfy both conditions (Figure 7.7). All the patches that share the same behaviour are considered as Groups.

7.6. Discussion and Conclusions

The system that we have created adds a semantic component to remote-sensing images using ontologies to describe this information. Savia is an operational system that is available for any user via the web (<http://obsnev.es/ontologia/index>). Our system implements a query builder user interface that allows users to build questions using SPARQL. It also includes a set of predefined questions to show its capabilities. Furthermore, users can select different output file formats to display results (csv, text or map). All the analytical procedures needed to run this system have been documented

using a model repository called ModeleR (Bonet et al., 2014a; Pérez-Pérez et al., 2012). The ontology created reuses and extends public ontologies like OWL-Time and Basic Geo (WGS84 lat/long) Vocabulary. The database containing MODIS images was translated into facts within a knowledge base. This requires a mapping between the database and the concepts contained in the ontology. The dynamical queries to knowledge base, using the mapping tool, were one of the most relevant bottlenecks that we have found during the implementation of the system, and we finally used enterprise-ready software to optimise queries to the knowledge base. We also used an inference engine to solve complex queries that require using advanced properties in the ontology (transitivity and symmetry, mainly).

We tested the ontological system in a case study focusing on *Q. pyrenaica* habitat in Sierra Nevada. We identified significant trends in summer NDVI for 75% of pixels covered by the target habitat. These pixels were located mainly in northern-faced patches (aspect was calculated using DEM). These results could be explained by a different pattern of summer productivity among the *Q. pyrenaica* patches. We have also described similar trends in snow patterns: 70% of pixels show a significant and negative trend towards an earlier melting date. Most of those pixels are also located in northerly facing patches. This result could have several hydrological and ecological implications: a) water from the melted snow is available for vegetation earlier each year, which could help deciduous trees to overcome the summer drought, b) the ground is free of snow during a longer period each year, which could provide extra area to treeline communities for altitudinal shifts.

The ontology has also helped to unveil the co-occurrence of significant trends both in snow cover (abiotic factor) and ecosystem functioning (NDVI). Thus, western patches display a high percentage of pixels showing this co-occurrence. The ecological implications of this co-occurrence can be explained by arguing that the earlier snowmelt provides water to *Q. pyrenaica* trees when they are in the middle of their growing season. This earlier amount of water supply encourages trees to be more productive in summer. On the other hand, the southern patches also show this co-occurrence in the opposite way: The lack of significant trends in summer productivity for southern patches could be explained by the lack of pixels with trends towards

earlier snowmelt in these areas. Although these results are still preliminary, we have established a link between the status of an abiotic factor and the functioning of ecosystems. Some forest activities can be scheduled according to the trends observed. It could be useful, for example, to reinforce the western patches by planting *Q. pyrenaica* trees. These new trees could take advantage of the productive summers in order to create denser forests. These ecological results are similar to others found in different habitats Trujillo et al. (2012).

The results (both ecological and methodological) demonstrate that the information in the MODIS time series is useful to assess the functioning of a terrestrial Natura 2000 habitat. We have described the temporal behaviour of *Q. pyrenaica* forests in Sierra Nevada, distinguishing among patches located in areas with different environmental conditions. We have also showed temporal trends in several functioning indicators. The trends discovered would help managers to assess the conservation status of this habitat. They can also build management plans using the knowledge provided by our ontology (*i.e.* to decide where to locate plantations taking into account the productivity trends). We have also described the behaviour of a key abiotic factor: snow cover; and we calculated trends for several snow-cover related indicators (snow duration, snow-cover melting date, etc.). Those could help managers to identify places where snow-cover trends could change in the coming years. Finally, we have detected relationships between trends in habitat productivity and snow-cover melting date for the target habitat. All this knowledge is offered to users (mainly managers and scientists) through a web portal, the use of which does not require expertise in remote sensing. Thus, we believe that this work is a worthwhile example of a web-based expert system created using an interdisciplinary approach.

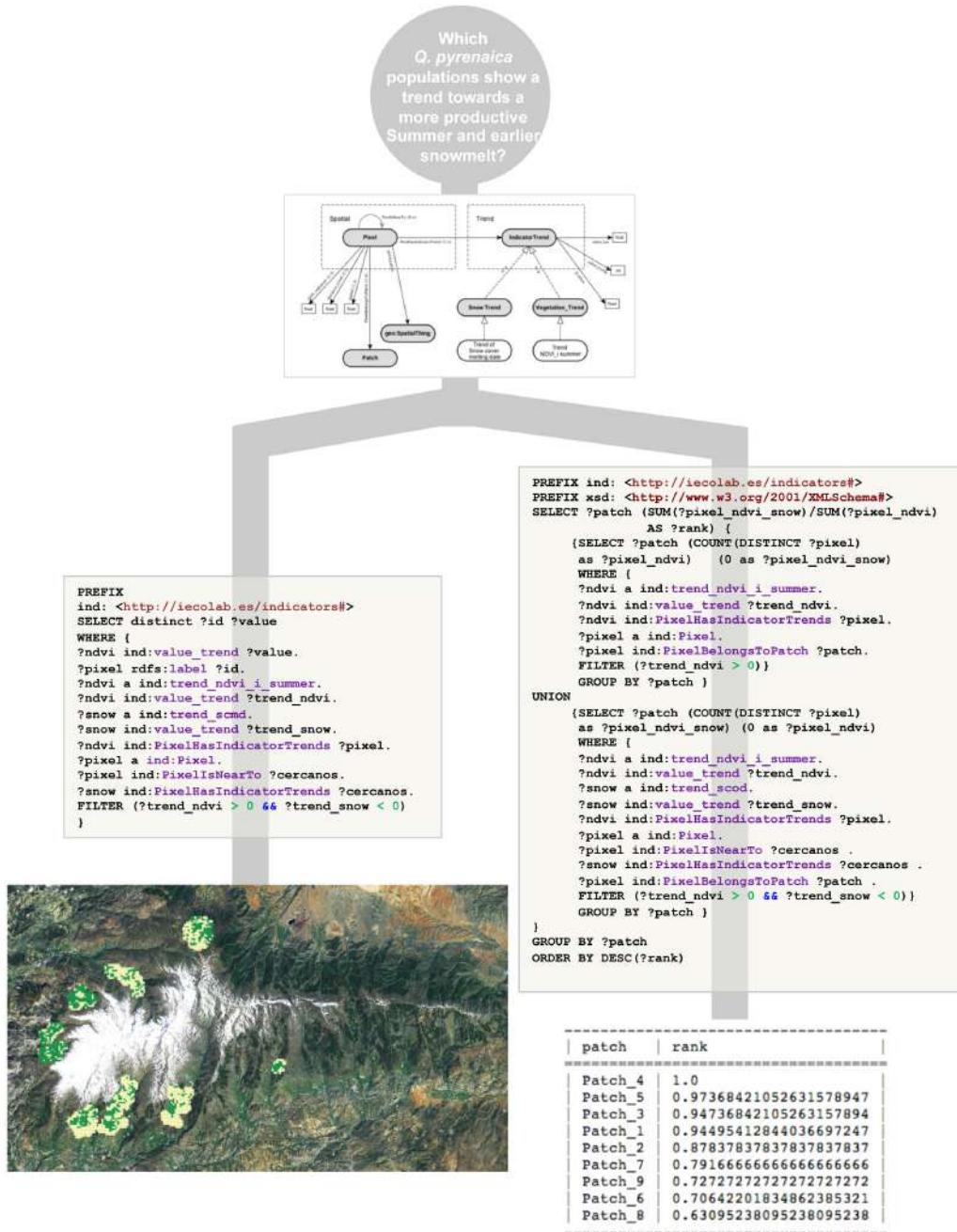


Fig. 7.7. Scheme showing the process of answering a complex query by the ontology. The question takes into account trends in habitat functioning as well as trends in snow-cover melting date. We first show the concepts used by the ontology to answer the query, then the SPARQL code and finally the results found. The left branch provides a map showing those pixels with trends towards more productive summers and earlier snowmelt date. The right branch offers a table ranking the Pyrenean oak patches according to the percentage of pixels that satisfies both conditions.

Ecosystem services provided by
Quercus pyrenaica Willd. oak
forests. A study case from Sierra
Nevada mountain range (southern
Spain)

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(Submitted to *Forest Systems*)

Abstract

Quercus pyrenaica (melojo) forests are relevant part of the Iberian landscape and have suffered intense anthropic pressures causing modifications in their structure and composition. Historically they were exploited in coppice for charcoal, firewood, or they were thinned and even burned to create grazing areas. Abandonment of traditional exploitation since the middle of the last century has led to a decrease in anthropic pressure on these ecosystems. Paradoxically, some of these oak woodlands present a state of advanced degradation (stagnation of growth; scarce regeneration; etc), with stands with high densities and high biomass accumulation, increasing the fire risk. Taking into account this situation, and considering the vulnerability of this species to global change, it is necessary to find alternatives to the traditional uses of coppice management, particularly for those stands located in their rear edge, such us the oak woodlands of Sierra Nevada (southern Spain), due to their relevance for the species conservation. In this work we present a comprehensive review of the main ecosystem services (ES) provided by melojo oak forests. Then, using the Sierra Nevada (SN) melojo oak populations as study-case, we explore more in depth the ES provided by these woodlands. We combined expert knowledge and datasets from different sources (e.g. grey literature, monitoring programs) to quantify the ES provided by these forests. We also explored the spatio-temporal pattern of some ES among the melojo oak populations within SN mountain range. Provisioning (e.g. use of melojo oak wood in the wine production) and regulating services (e.g. carbon sequestration and soil fertility) were widely reported in the literature review meanwhile no studies assessing cultural ES were found in our literature review. However, this pattern changes when the ES were analyzed in more detail as in our study case, highlighting the existence of diverse cultural services provided these forests in SN. We found differences among the supply of ES within the melojo oak populations, with southern populations have higher values of regulating services and northern ones exhibited higher values for cultural services. A temporal variation in the supply of ES of melojo forests was observed. Until the middle of the last century, provisioning services predominated over regulating and cultural services (poor valued). The abandonment of traditional activities led to a decrease of provisioning services in favor of regulating services, and in

the last decades, cultural services. Our compilation of local scale data has allowed us to quantify many of ES supplied by the *Q. pyrenaica* forests, which could aid to natural resource managers with more information and tools to help them in the decision-making process.

8.1. Introduction

Mediterranean forests are subjected to significant and simultaneous climatic and anthropogenic pressures (Doblas-Miranda et al., 2017; FAO & Plan Bleu, 2018), and climate change is expected to strongly affect the Mediterranean Region (Cramer et al., 2020; Cramer et al., 2018; Giorgi & Lionello, 2008). Besides, the impacts of global change on Mediterranean forest ecosystems are altering the provision of ecosystem services (Lindner et al., 2014; Lindner et al., 2010; Noce & Santini, 2018; Peñuelas et al., 2017; Serrada Hierro et al., 2011) particularly in mountainous regions, which have shown a high vulnerability to climate change (Schröter et al., 2005). Notwithstanding, Mediterranean forests provide a wide range of ecosystem services (ES), and represent a great asset and opportunities for the future of the Mediterranean basin (Gauquelin et al., 2018; Noce & Santini, 2018). Hence, the importance of Mediterranean forests derives both from their current value in terms of area and goods and services, and from the potential role they are likely to play in the future as providers of ES (FAO & Plan Bleu, 2018).

Among the Mediterranean type forests, the oak woodlands, *i.e.*, those dominated by oak tree species (*e.g.* *Quercus ilex*, *Q. suber*, *Q. robur*, *Q. faginea*, *Q. petraea*, *Q. pubescens*, *Q. pyrenaica*, *Q. canariensis*) are key ecosystems providing variety of ES (Marañón et al., 2020). For example, their capacity to sequester carbon and therefore to regulate the climate and to mitigate the effects of climatic change is a remarkable regulating service. Oak forests contribute to soil fertility and to the regulation of air, soil and water quality (Marañón et al., 2012). These woodlands also provide several raw materials: cork, firewood, acorns (Bugalho et al., 2011). In addition, their role as providers of a wide variety of cultural services, such as recreational, aesthetic and spiritual has been also highlighted (Löf et al., 2016). To conserve these forests and their biodiversity, and to manage them in a sustainable way, it is important to be aware of their real and potential supply of ES.

The case of melojo woodlands (*Quercus pyrenaica*) in the Western Mediterranean Region

Quercus pyrenaica Willd. (Pyrenean oak, *melojo*) is a marcescent tree species widely distributed throughout southwestern France and the Iberian Peninsula with some populations at the mountain areas of northern Morocco (Franco, 1990) (Figure 8.1). In the Iberian Peninsula, these forests (in this chapter we will refer to *Quercus pyrenaica* forests as *melojo* oaklands or *melojo* woodlands) occupy siliceous soils under meso-supramediterranean and mesotemperate areas and subhumid, humid, and hyperhumid ombroclimate (de la Serna et al., 2016; Gavilán et al., 2018). The rear-edge populations of this species are restricted to high-mountain areas where they persist as isolated nuclei with ecological conditions very different from those of the main distribution area (Pérez-Luque et al., 2021b). Sierra Nevada mountains (37°N, 3°W, Spain) represent one of the southernmost European limits for this species (Figure 8.1b). In this mountain area, considered a glacial refuge for deciduous *Quercus* species (Olalde et al., 2002), there are eight *melojo* oak patches, occupying a total of 2400 ha, and ranging from 1100 to 2000 m.a.s.l.. Among the forest ecosystems in Sierra Nevada, *melojo* woodlands are the richest regarding vascular plant species, containing a large number of endemic and endangered plant species (Lorite et al., 2008). They also harbor high levels of intraspecific genetic diversity (Valbuena-Carabaña & Gil, 2013, 2017).

Q. pyrenaica woodlands, like other forests in Mediterranean area, have been subjected to intense anthropogenic pressures over time (García & Jiménez, 2009), resulting in a reduction of their extension and a modification of their floristic composition (Gavilán et al., 2000; Pérez-Luque et al., 2021b; Serrada et al., 1992) and of their structural patterns (Calvo et al., 1999; Tárrega et al., 2006). Historically, these woodlands have been exploited in coppices for obtaining several products such as firewood, charcoal, tannins, casca (*i.e.* parts of the bark used to extract tannins), and many other traditional uses (Ruiz de la Torre, 2006; Sánchez Palomares et al., 2008). For instance, after the Spanish Civil war (since 1940's), some oak woodlands were massively cut down to use the firewood as fuel for automobiles (*e.g.* Dehesa de San Jerónimo, Sierra Nevada) (Prieto, 1975). Forest management

for coppices consisted of clear-cutting in rotation periods of 12-20 years, causing the profusion of shoots from the stool highly appreciated by livestock (Bravo et al., 2008). Thinning and sometimes even burned have also been carried out to create pastures with low densities of mature trees that provide acorns, firewood and large areas for grazing (Alvarez et al., 2009; Herrera Calvo, 2016; Valbuena-Carabaña & Gil, 2017). In fact, overgrazing in these formations have caused strong soil erosion loss, which was noticed by forest managers since the end of the 19th century (Laguna, 1872). In some areas, the strong anthropic pressure provoked the loss of the forest cover. For instance, in southern slopes of Sierra Nevada mountains, oak woodlands were almost completely removed at the beginning of the 20th century, which led to some of its watershed being considered among the most torrential in Spain (Romero-Zurbano, 1909). All these anthropogenic processes have transformed the melojo woodlands in a deep way that it is difficult to find stands that can be considered natural forests (Ruiz de la Torre, 2006).

The abandonment of livestock and forestry traditional uses since the middle of the last century due to rural abandonment (MacDonald et al., 2000), has caused a decrease in anthropogenic pressure on Mediterranean forests, being particularly important for mountain areas (Jiménez-Olivencia et al., 2015; Jiménez-Olivencia et al., 2015; Pías et al., 2014; Valbuena-Carabaña et al., 2010). Paradoxically, and considering this decrease in anthropogenic pressure, many of the oak stands present a state of advanced degradation, showing growth stagnation, lack of fruiting, and also signs of branch dieback (Bravo et al., 2008; Cañellas et al., 2004; Piqué et al., 2018; Piqué & Vericat, 2015; Valbuena-Carabaña & Gil, 2014). Many stands, derived from the high resprout capacity of *Q. pyrenaica*, also have high tree density that would increase their vulnerability to drought, as has been reported in other forests across the world (McDowell et al., 2020). The high tree density together with the accumulation of biomass and high horizontal continuity, would increase the risk of fire (Bravo et al., 2008; García & Jiménez, 2009). In addition, these problems may be aggravated in the current context of climate change (increase in temperatures and higher incidence of extreme events such as droughts) (IPCC, 2013; Spinoni et al., 2018), particularly considering the high vulnerability of this species to climate change (Benito et al., 2011; García-Valdés et al., 2013; Gea-Izquierdo et al., 2013; Sánchez de Dios et al.,

2009), and especially for areas located in the rear edge of their distribution range such as Sierra Nevada mountain range.

In view of this current situation of vulnerable (to global change drivers) forest stands, affected by the progressive abandonment of traditional land uses during the last decades, the need of defining alternative uses for melojo oak woodlands has been pointed out (Mesón & Montoya, 1985; San Miguel et al., 2012), and some management alternatives have been proposed (e.g. sylvopastoral uses, see Herrera Calvo, 2016). Melojo woodlands are human-shaped ecosystems with high conservation value, and consequently, management is required to guide their development (Hobbs et al., 2006). In this sense, the identification and characterization of the main ES and their spatio-temporal pattern, becomes a crucial to develop landscape planning and forest management strategies in a global change context (Piqué et al., 2018).

Ecosystem services provided by melojo woodlands depend on the intensity of human use. Both overuse and abandonment of melojo woodlands provided very different scenarios for the provision of ES and for the socioeconomic demand for them. Despite the wide variety of ES provided by oaks is worldwide acknowledged, very little has been written specifically about the provision of ES by oak-dominated forests (Marañón et al., 2012; Marañón et al., 2012; Moreno-Llorca et al., 2012). Some works have carried out a general valuation of the ES provided by the different *Quercus* woodlands at regional and national scales (Marañón et al., 2012; San Miguel et al., 2012; Sousa et al., 2020), and some studies provided temporal trend analysis of ES from an economic perspective (see Caparrós et al., 2013, for an example for woodland pastures of California and Spain). However, to our knowledge, there is no comprehensive review of the ES provided by *Q. pyrenaica* woodlands.

The aim of this work is to carry out a review of the main ES provided by *Q. pyrenaica* woodlands. Firstly, we conducted a literature review to know the general state of the art and to summarize some of the most relevant ES provided by these formations. Secondly, using the Sierra Nevada oak populations as study-case we explore more in depth the ES provided by these woodlands. For this purpose, we combined expert knowledge and a wide variety of data coming from ecological monitoring programs and

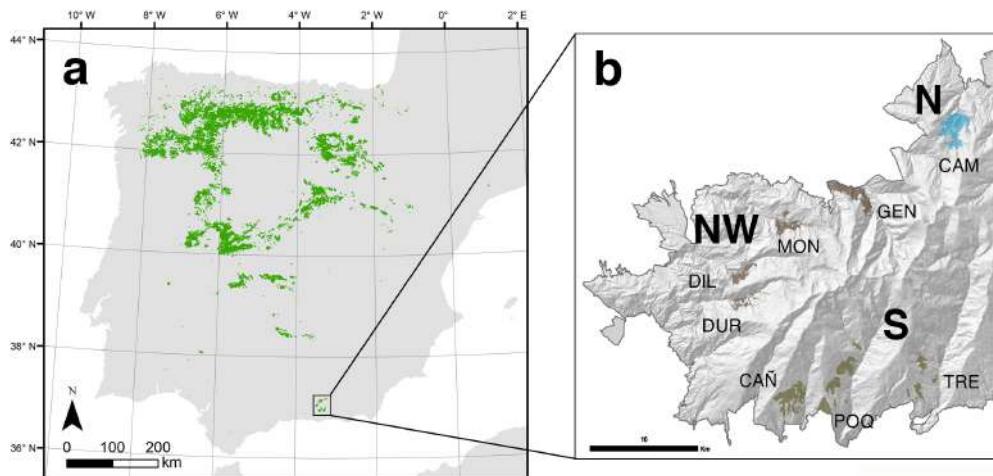


Fig. 8.1. (a) Distribution of *Quercus pyrenaica* forests in the Iberian Peninsula, and location of the oak populations in Sierra Nevada mountain range (b). In Sierra Nevada three oak populations clusters have been identified (Pérez-Luque et al., 2021b): N=Northern (CAM: Camarate); NW = Northwestern (GEN: Genil, MON: Monachil, DIL: Dílar, DUR: Dúrcal); S=Southern (CAÑ: Cáñar, POQ: Poqueira; TRE: Trevélez). Source: Spanish National Forest Map (1:50.000).

several research projects to quantify as far as possible the ES provided by these forests. We are also interested in exploring how the ES are spatially distributed in this mountain region. For this, we searched for differences on the supply of ES between the melojo oak populations within Sierra Nevada mountain range. Finally, using time series of several indicators, we have assessed the temporal changes of ES supply by *Q. pyrenaica* in our study area.

8.2. Material and methods

Study area

Sierra Nevada is a mountainous region located in the south-eastern Iberian Peninsula ($37^{\circ}14'$ - $36^{\circ}54'$ N; $2^{\circ}37'$ - $3^{\circ}39'$ W) covering more than 2000 km^2 with an elevation range of between 860 and 3482 m.a.s.l.. The climate is Mediterranean, characterized by cold winters and hot summers, with a pronounced summer drought. The annual average temperature decreases in altitude from 12-16 °C below 1500 m.a.s.l. to 0 °C above 3000 m.a.s.l.. Annual precipitation ranges from less than 250 mm in the lowest

Tab. 8.1. Indicators used to evaluate the temporal evolution of the ES supply by *Q. pyrenaica* woodlands in Sierra Nevada. All data referred to Robledal de Cáñar oak woodland (southern slope of Sierra Nevada), except visitors numbers corresponding to all Sierra Nevada Protected Area. For each indicator the ES category are indicated: (R) regulation; (S) provisioning and supporting; (C) cultural.

Indicator	Units	Data Source - References	Temporal range
Population	Inhabitants	Institute of Statistics and Cartography of Andalusia	1940 - 2016
Apiarian uses (S)	Number of hives	Public Forest use plans. Moreno-Llorca et al. (2014), Moreno-Llorca et al. (2016)	1978 - 2011
Acorn harvesting (S)	Hectoliters	Public Forest use plans. Moreno-Llorca et al. (2014), Moreno-Llorca et al. (2016); Mesa-Torres (2009)	1950 - 1966
Sheep farming (S)	Number of animals	Moreno-Llorca et al. (2014), Moreno-Llorca et al. (2016); Mesa-Torres (2009)	1950 - 2011
Visitors numbers (C)	Visitor numbers	Sierra Nevada Natural and National Protected Area	1999 - 2019
EVI vegetation Index (R)	dimensionless	MODIS; Pérez-Luque et al. (2015a) and Pérez-Luque et al. (2020)	2000 - 2016
Biomass increment(S)	Mg ha ⁻¹ year ⁻¹	Spanish NFI. Pérez-Luque et al. (2021a)	1995 - 2007
Forest Area (S, R)	ha	Navarro-González et al. (2012)	1956 - 2007
Oak tree density (S)	n trees ha ⁻¹	Zamora et al. (2017b)	1956 – 2005

areas of the mountain range to more than 700 mm in the highest peaks. Winter precipitation is mainly in the form of snow above 2000 m.a.s.l.. Topographically, the area is heterogeneous, with strong climatic contrasts between the sunny, dry south-facing slopes and the shaded, wetter north-facing slopes. This mountain range is considered one of the most important biodiversity hotspots in the Mediterranean region (Blanca et al., 1998), hosting 105 endemic plant species for a total of 2353 taxa of vascular plants (33% and 20% of Spanish and European flora, respectively) (Lorite, 2016). Forest cover in Sierra Nevada is dominated by pine plantations (*Pinus halepensis* Mill., *Pinus pinaster* Ait., *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco, and *Pinus sylvestris* L.) covering approximately 37000 ha. Native forests are mainly dominated by holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) occupying low and medium mountain areas, and melojo oak ranging from 1100 to 2000 m.a.s.l. (Pérez-Luque et al., 2019).

Selection of ecosystem services and their assessment

To analyze the ES provided by melojo forests, we have carried out two different phases. Firstly, we performed a general literature review to explore the state of the art on the ES provided by these forests regardless of their specific location. Secondly, considering the results of the general literature review, we have carried out a more comprehensive analysis of the ES provided by the melojo forests in Sierra Nevada. We have characterized their supply for Sierra Nevada mountain region, and where data were available, we have quantified them, and compared between melojo populations identified in Sierra Nevada. Finally, we explored temporal evolution of indicators for several ES when data were available. For the classification and definition of ecosystem services, we used the CICES V5.1 (Common International Classification of Ecosystem Services) approach (Haines-Young & Potschin, 2018). We have considered three categories of ecosystem services: provisioning, regulating and cultural, and for each of them, we have identified different ES indicators. Due to the large number of ES studied, we have considered it more practical to explain for each of the ES, the indicator(s) used to quantify it (see details in the following section).

To characterize the scientific literature that evaluate the ES of the melojo oak woodlands, we performed initially a systematic search in the ISI Web of Knowledge (search date: October 2020). We compiled references published in indexed journals included in the Journal of Citation Reports (JCR), in English language, since 1970 to 2020, that evaluated a wide variety of ES indicators in these woodlands. First, we conducted a search for papers on the study species with the term "*Quercus pyrenaica*" in the title, keywords or abstract, which produced 393 results. We applied a second criterion, to extract papers that analyzed possible services, including a broad list of terms (also in the title, keywords or abstract) related to ES (Table D.1). The combination of both produced 188 results. After reviewing their abstracts, we selected 60 papers that met the premise of evaluating ES in melojo oak woodlands (Table D.2). We omitted papers focused exclusively on descriptive aspects of these ecosystems (e.g. floristic composition or ecosystem structure), their biodiversity (e.g. species richness) which were not directly related to ecosystem service indicators.

For each of the ES reviewed, we initially described the general status of the services in these woodlands using the compiled references. Then, we performed a quantification for the Sierra Nevada oak woodland populations, when data were available. The values for the quantification were obtained both from the literature review and from several research datasets in combination with the expert criterion (Table 8.2). For those ES with data availability, we performed a quantification using a spatiotemporal approach: *i*) we assessed how ES provision varies across the space in each of the oak population clusters identified in Sierra Nevada (*i.e.* Northern (N), Northwestern (NW), and Southern (S)) (see Pérez-Luque et al., 2021b); and *ii*) we explored the temporal variation in the provision of ES using available time series of several indicators of ES (Table 8.1).

8.3. Ecosystem Services provided by *Q. pyrenaica* woodlands

The compilation of literature carried out has shown us those services that have been most frequently evaluated in works focused on *Q. pyrenaica* woodlands (see Table D.1). Provisioning services were the most frequently ES evaluated within the 60 papers selected in the literature review. Among them, the studies focused on investigating the effect of melojo wood in the wine production process stand out ($n = 26/60$) (*e.g.* Castro-Vázquez et al., 2013; Fernández de Simón et al., 2010), since barrels are frequently built with the wood of this species. In addition, we found different studies evaluating mushroom production (*e.g.* Oria-de Rueda et al., 2010), the effect of this species on livestock production (*e.g.* Núñez et al., 2012), or the production of wood or biomass for energy ($n = 6/60$) (*e.g.* Miranda et al., 2009). Regarding regulation services, several studies assessed the role of forests in soil quality and fertility ($n = 12/60$), or their capacity for carbon sequestration and storage ($n = 12/60$; *e.g.* Alvarez et al., 2014). There also a high proportion of studies on soil carbon ($n = 8/60$; *e.g.* Fonseca et al., 2019). Finally, it should be noted that, applying the above-mentioned search criteria,

Tab. 8.2. Ecosystem Services (ES) indicators used in this study. For each indicator the ES category, references, units, and data source are indicated. (R): regulation; (S): provisioning and supporting; (C): cultural. (*) extracted from the literature; (**) own calculations. (+) indicators with data for oak populations of Sierra Nevada.

Ecosystem Service	ES indicator used	Bibliographic References	Units	Data Source	Data for Sierra Nevada	
Experiential	Number of use of photographs (*)	(Moreno-Llorente et al., 2020)	Number of photographs	(Ros-Candela et al., 2020)	Yes (-)	
Landscape (C)	Physical use of Landscape (C)	Wikiloc tracks (**)	Routes density;	Wikiloc	Yes (-)	
Recreational	Visitors numbers (C)	Visitors numbers (**)	Total routes	Sierra Nevada National Protected Area	Yes (+)	
Scientific (C)	Research requests	(Zamora et al., 2016)	Visitor numbers	National Protected Area	Yes (+)	
Scientific (C)	Density of socio-ecological monitoring methodologies (**)	(Zamora et al., 2016)	Number of Research requests	Sierra Nevada Natural and National Protected Area	Yes (+)	
Symbolic (C)	Singular trees (*)	(Irurita-Fernández et al., 2003; Sánchez-García et al., 2003)	Density of monitoring methodologies	Sierra Nevada Natural and National Protected Area	Yes (+)	
Biodiversity (S)	Bird richness (**)	(Barea-Azcón et al., 2012; Pérez-Luque et al., 2021a; Pérez-Luque et al., 2016b; Zamora & Barea-Azcón, 2015)	Species number	Andalusia Government Observatory	Regional Yes	
Biodiversity (S)	Fungal diversity (*)	(Moreno-Arroyo, 2004; Ortega et al., 2010)	Species number	Sierra Nevada Global Change Observatory	Yes (+)	
Biodiversity (S)	Microbial diversity (*)	(Valbuena-Carabaña & Gil, 2013; Valbuena-Carabaña & Gil, 2013, 2017; Cobo-Díaz et al., 2017; Lasa et al., 2019a; Lasa et al., 2019b)	Species number	Basic Mycological Inventory of Andalucía	Yes (+)	
Biodiversity (S)	Woody richness (*)	(Lorite et al., 2008; Pérez-Luque et al., 2014)	Species number	Andalusia Government Observatory	Yes	
Food provision (S)	Wild mushrooms production (*)	Raya-López et al. (2017)	kg Fungi ha ⁻¹ year ⁻¹	CUSTIA Plan for the Sustainable Use and Conservation of Mushrooms and Truffles in Andalucía	Yes (+)	
Tanning (S)	Percentage of tannins (*)	(Doce et al., 2007; Fernández de Simón et al., 2006; Torner-Ochoa, 1952)	% of tannins present at bark	Plan for the Sustainable Use and Conservation of Mushrooms and Truffles in Andalucía	Yes	
Timber (S)	Biomass increment	(Pérez-Luque et al., 2021c)	Mg ha ⁻¹ year ⁻¹	Spanish National Forest Inventory	Yes	
Wine Ageing (S)	Phenological compounds (*)	(Cadahía & Fernández de Simón, 2004; Fernández de Simón et al., 2008; Fernández de Simón et al., 2009; Gallego et al., 2012; Gallego, 2013; Martínez-Gil et al., 2020; Ramilo et al., 2017)	Inventory	Inventory	Yes	
Climate Regulation (R)	Carbon sink (**)	Pérez-Luque et al. (2021c)	Mg CO ₂ ha ⁻¹	LIDAR and Forest Inventories MODIS	Yes (+)	
Climate Regulation (R)	Climate Vegetation Index (NDVI, EVI) (*)	(Alcaraz-Segura et al., 2016; Cazorla et al., 2020; Dionisio et al., 2012; Pérez-Luque et al., 2015a)		ClimaNevada	Yes (+)	
Climate Regulation (R)	Regulation of temperature (**)	(Zamora et al., 2021)			Yes	
Regulation (R)	Control of erosion (R)	Soil erosion Control (*)	(Mesón & Montoya, 1985; Salomón et al., 2017)	Mg SOC ha ⁻¹	SoilGrid database	Yes (+)
Regulation (R)	Soil Fertility	Soil Organic Carbon (**)	Batjes et al. (2020) and Batjes et al. (2017), Hengl et al. (2017)			

no studies on the evaluation of cultural services in the melojo woodlands have been found.

8.3.1. Regulating services

Soil climate regulation

Tree canopy cover is key to regulate soil temperature (Ellison et al., 2017), which is one of the main factors affecting ecological functions such as seed germination or plant growth and development, and being as important as air temperature, since it can limit root formation (Alvarez-Uria & Körner, 2007). The marcescent feature of *Q. pyrenaica* allows the accumulation of leaf litter layer on the ground during a part of the year. This accumulation can have positive effects on seedling establishment because it acts as a thermal insulator (Loydi et al., 2014), helping to alleviate the damage effects of freezing on seeds (Cavender-Bares et al., 2005; Esteso-Martínez & Gil-Pelegrín, 2004; Löf et al., 2019; Loydi et al., 2014). This buffer effect can also be important once germination starts, since negative temperatures can suspend the process and damage the radicle and epicotyl (Aizen & Woodcock, 1996). However, negative effects on seed germination and establishment could prevail (e.g. pathogen proliferation; allelopathic effects) when litter accumulation exceeds a certain threshold (Loydi et al., 2014; Xiong & Nilsson, 1999).

It has also been noticed the importance of the forest cover on the regulation of extremes temperatures registered during the summer period (De Frenne et al., 2021). This cover provides a cooler environment, reducing potential evapotranspiration and alleviating the water stress to which these formations are subjected in summer (Zamora et al., 2021). This can be particularly important for populations located at the warm rear-edge of the species distribution, such as the studied here. For instance, using microclimatic data from a sensor network deployed in a melojo oak stand located at southern slopes of Sierra Nevada, Zamora et al. (2021) found strong variations of the air and soil temperatures registered inside the forest compared with those registered on forest's open areas. The soil temperatures varied up to

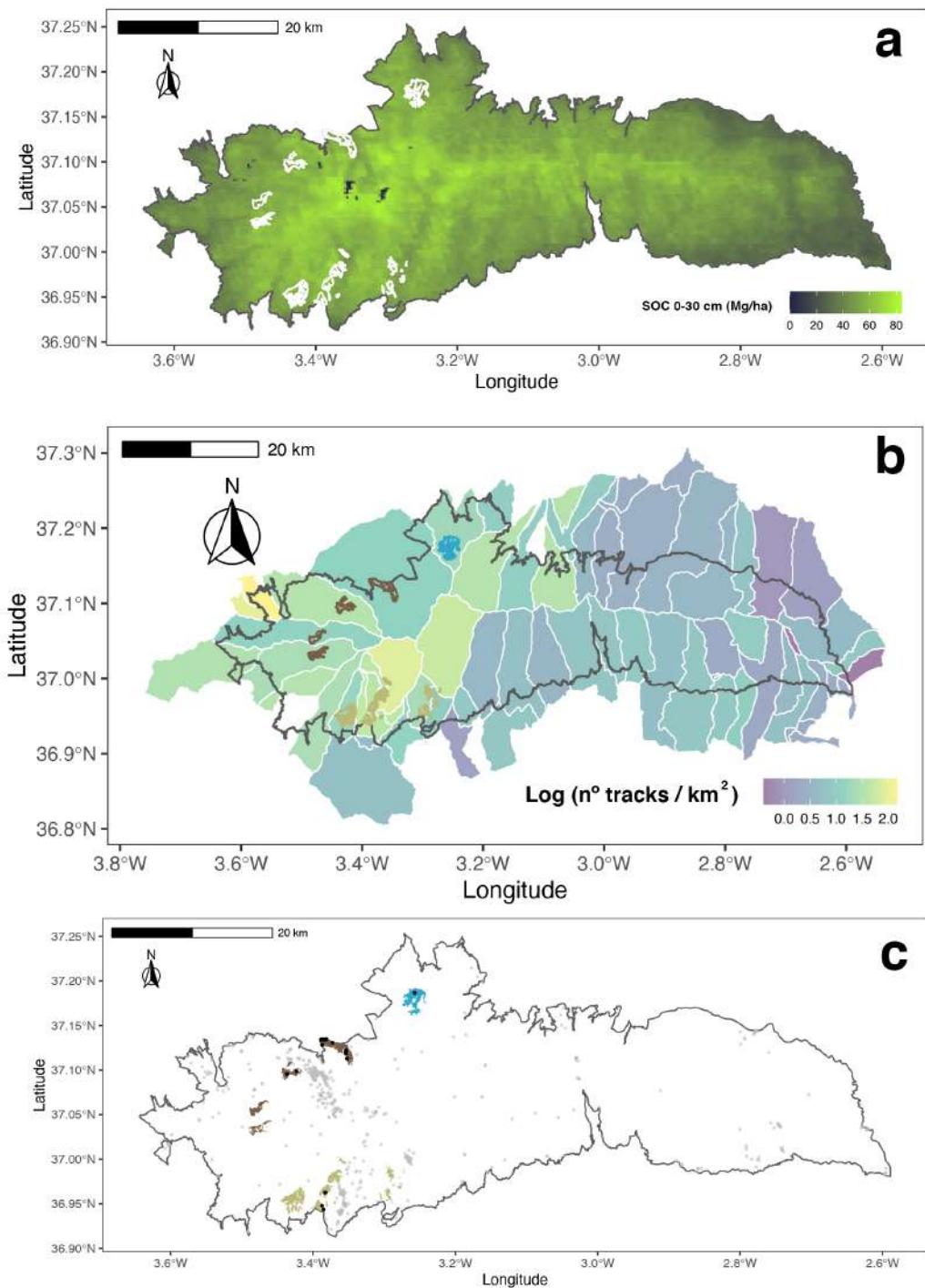


Fig. 8.2. (a) Distribution of the Soil organic carbon in Sierra Nevada. Oak populations in white. Drawn with data from SoilGrid database (see Hengl et al., 2017). (b) Density of Wikiloc routes for the municipalities of Sierra Nevada (Data from January 2020). Data are shown in Logarithmic scale. (c) Location of photos taken in Sierra Nevada uploaded to the Flickr platform ($n = 778$). Black dots indicate photos located in oak woodland. Drawn with data from Ros-Candeira et al. (2020). Oak woodland populations are shown. Colors correspond to northern (blue), northwestern (brown) and southern (green) cluster's of oak woodlands identified for Sierra Nevada (Pérez-Luque et al., 2021b)

15°C between microhabitats on a day of maximum temperatures during the summer period.

Climatic regulation: carbon sequestration and storage

The role of forest ecosystems on climate regulation by storing and sequestering large amounts of carbon is widely acknowledged (Gauquelin et al., 2018; Noce & Santini, 2018). In the Mediterranean region, forests' carbon stocks have increased for decades and this process is expected to continue in the future (Cañellas et al., 2017), although recent studies have shown a potential slowing down related to the increases in forest stand development levels in Mediterranean forests (Roces-Díaz et al., 2021).

Recently, a thematic mapping of the biomass and carbon sequestration potential of woodlands of Sierra Nevada has been generated (Pérez-Luque et al., 2021c) (see also chapter 5). These authors, combining remotely obtained information from aerial LIDAR (*Light Detection And Ranging*) with information from field work, estimated a total biomass (aboveground- and belowground-biomass) of 9.94 Tg (1 Tg = 10^{12} g) in the forests of the Sierra Nevada, which represents a sequestration of 17.33 Tg of CO₂.

In addition to their relevance on carbon storage, the soil organic carbon (SOC) is particularly relevant for different soil processes, and it is involved in different ES, among which regulating and provisioning services stand out (Francaviglia et al., 2018). For example, SOC content correlates positively with soil fertility, playing a key role determining the physical, chemical and biological qualities of a soil (Victoria et al., 2012). There are no studies quantifying SOC in Sierra Nevada oak melojo populations (but see Cobo-Díaz et al., 2017, for punctual estimation). We used the SoilGrid database (<https://soilgrids.org/>) which provided map of estimated SOC at a 250-m spatial resolution (Batjes et al., 2020; Batjes et al., 2017; Hengl et al., 2017). For Sierra Nevada, this dataset reported an average SOC content (mean SOC at 0-30 cm depth) of 51.8 Mg ha⁻¹ (20-80 Mg ha⁻¹) (Figure 8.2a), while the oak forests have an average SOC value of 53.5 Mg ha⁻¹ (45-67 Mg ha⁻¹), with southern oaks populations showing significantly higher values than northern ones.

Erosion control

Forests play a key role in the reduction of the erosive rainfall impact on soil, that is a very important regulating service. The root system of *Q. pyrenaica* consists of two well-differentiated types (Allué, 1995): (i) the main root, characteristic of the genus, which allows for powerful anchoring to the soil; and (ii) a layer of roots close to the soil surface and parallel to it, which could emit large number of shoots that form a dense network. These root systems help to maintain soil integrity by preserving landslides (Mesón & Montoya, 1985; Salomón et al., 2017) (Figure 8.3a). In addition, the extraordinary regrowth capacity of *Q. pyrenaica*, both of stump and roots, gives it functional advantages over other species, such as its response to disturbances (e.g., fires), particularly on sloping areas (Ruiz de la Torre, 2006; Valbuena-Carabaña & Gil, 2017). This resprouts profusion is key on soil protection, reducing the impact of erosive processes and the soil loss (Mesón-García, 1984).

8.3.2. Supporting and provisioning services

Biodiversity

Q. pyrenaica forests in Sierra Nevada have high values of phytosociological uniqueness (Lorite et al., 2008), which could be explained because they act as habitat providers for other relict species (Blanca et al., 1998; Lorite, 2016; Losa et al., 1986). In fact, the role of refugee of Sierra Nevada for this oak ecosystem (Brewer et al., 2002; Olalde et al., 2002; Rodríguez-Sánchez et al., 2010), translates into a great diversity of plant species, being the forest formation with the greatest richness in Sierra Nevada, although it only represents 7% of the forest areas (Pérez-Luque et al., 2014). *Q. pyrenaica* woodlands in Sierra Nevada provide optimal conditions for the presence of several plant species, some of which are cataloged under different threatened categories at regional level (Lorite, 2016; Losa et al., 1986; Melendo & Valle, 2000), such as the hybrid mustard (*Sorbus hybrida* L.) considered critically endangered (CR), the endangered (EN) goat willow (*Salix caprea* L.), the holly (*Ilex aquifolium* L.) and the yew (*Taxus baccata* L.) considered vulnerable (VU), and others with a lower level of threat (e.g. near threat, NT) (e.g. the rowan, *Sorbus aria* (L.) Crantz; or the maple *Acer opalus* subsp.

granatense (Boiss.) Font Quer & Rothm.). Many of these species are also considered relict species that find favorable microclimatic conditions in the melojo oak woodlands of Sierra Nevada, which make them a refuge for those species.

Birds populations of *Q. pyrenaica* forests of Sierra Nevada have been studied since 1980's (Barea-Azcón et al., 2012; Zamora & Barea-Azcón, 2015; Zamora & Camacho, 1984). A total of 73 species of passerine bird species has been recorded within these oak forests (Pérez-Luque et al., 2016b). Recent analysis shown differences in their diversity between Sierra Nevada oak populations, with lower values for southern oak populations than for northern-ones (Pérez-Luque et al., 2021a). No differences was found for bird abundance, but a general decrease of several key species (*Garrulus glandarius*) were recorded since 1980 (Zamora & Barea-Azcón, 2015).

Although there are no studies analyzing specifically the fungal composition of oak forests in Sierra Nevada, several works have shown the richness associated to the fungal communities of this type of forests at regional and national scales. Thus, an exhaustive review of the diversity of mycorrhizae-forming macromycetes in the *Quercus* forests of the Iberian Peninsula recorded 174 fungi species in *Q. pyrenaica* formations (Ortega et al., 2010), of which five are included in the Red List of Fungi to be Protected in the Iberian Peninsula. At regional level, the Basic Mycological Inventory of Andalusia (IMBA, *Inventario Micológico Básico de Andalucía*), reported 214 records belonging to 149 fungi taxa, inhabit in *Q. pyrenaica* forests (Moreno-Arroyo, 2004).

Trees provide a diversity of habitats in which other species can live. For instance, *Quercus* species are key in the development of the biological cycle of some insects, such us the oak gall wasp (Hymenoptera: Cynipidae). The galls support species-rich, closed communities of inquilines and parasitoids that have become a model system in community ecology (Stone et al., 2002). For instance, in melojo forests of Sierra Nevada have been recorded 30 species of cynipids (representing 21% of the Iberian species of this family) (Nieves-Aldrey, 2013). There are not many studies on the diversity that can be found in *Q. pyrenaica* forest soils. In Sierra Nevada, some studies have reported that microbial community of melojo oak forests is dominated by

a few very abundant taxa (Cobo-Díaz et al., 2017; Lasa et al., 2019a; Lasa et al., 2019b).

Finally, in relation to the genetic diversity within species, it has been traditionally assumed that continued coppicing of over centuries has led to a decline in the genetic diversity of the *Q. pyrenaica*, as a result of the strong inter-stem competition and the propagation of a limited number of genotypes (Bravo et al., 2008; Sánchez Palomares et al., 2008). However, several studies have pointed out the high diversity that Sierra Nevada *Q. pyrenaica* populations harbor (Valbuena-Carabaña & Gil, 2013; Valbuena-Carabaña & Gil, 2013, 2017; Valbuena-Carabaña & Gil, 2014), highlighting the importance of conserving the populations of this species at the rear-edge of their distribution, since they act as a reservoir of genetic diversity.

Wine aging and tanning

A relevant characteristic of oak trees is their ability to emit volatile organic compounds (VOCs), which in addition to giving the wines their characteristic flavor, act as an attractant for different insects. More than 50 volatile organic compounds belonging to 12 different chemical classes have been characterized in melojo oak (Ramilo et al., 2017). The phenolic compounds produced by *Q. pyrenaica* have similar chemical composition to those produced by the main oaks used in wine aging, such as American oak (*Q. alba*) or French oak (*Q. petraea*) (Gallego et al., 2012). In fact, the results of comparative analysis between wines aged in barrels from these three oak species, have indicated that the wine aged in melojo oak presents oenological features similar to those of the other oaks, being also very positively valued by the wine tasters (Cadahia & Fernández de Simón, 2004; Fernández de Simón et al., 2008; Fernández de Simón et al., 2009). All these results highlight the current use of *Q. pyrenaica* wood and its derivatives from for wine aging, which had not been previously used in cooperage (Gallego, 2013; Martínez-Gil et al., 2020) (Figure 8.3b).

The bark and leaves of *Q. pyrenaica* contain a great diversity and a high percentage of tannins (8% of bark and 2-10% of the wood corresponds to tannins) (Doce et al., 2007; Fernández de Simón et al., 2006; Torner-Ochoa,

1952)). For this reason, it has been used as a tanning agent for leather, particularly the bark, since it contains higher percentage of tannins than other *Quercus* species (8% versus 2-3%) (Torner-Ochoa, 1952).

Food provision: Edible fungi

Mycological resources have high ecological, social, recreational and economic importance contributing to increasing the environmental asset value of the forests (Martínez-Peña et al., 2015). Data on mushroom production and picking are scarce, scattered, and heterogeneous. However, several regional initiatives have carried out preliminary assessment of mycological resources of forests, such as the RECAMAN initiative in Andalusia ("Inncome and Capital of the Andalusian Mountains"; *REnta and the CApital of the Montes de ANdalucía*) (Martínez-Peña et al., 2015). Likewise, the "Plan CUSSTA" (*Plan for the Sustainable Use and Conservation of Mushrooms and Truffles in Andalusia*) is carrying out periodic field sampling to determine the production of mushrooms in different forest formations in Andalusia (Raya-López et al., 2017). Preliminary results for three years showed that in *Q. pyrenaica* forests, the main marketable species are: *Amanita caesarea* ($3.63 \text{ kg ha}^{-1} \text{ year}^{-1}$), *Boletus aereus* ($4.73 \text{ kg ha}^{-1} \text{ year}^{-1}$), *Cantharellus subpruinosus* ($7.8 \text{ kg ha}^{-1} \text{ year}^{-1}$), *Hydnnum rufescens* ($0.23 \text{ kg ha}^{-1} \text{ year}^{-1}$), *Lepista nuda* ($0.1 \text{ kg ha}^{-1} \text{ year}^{-1}$), *Macrolepiota procera* ($0.41 \text{ kg ha}^{-1} \text{ year}^{-1}$) and *Russula cyanoxantha* ($0.03 \text{ kg ha}^{-1} \text{ year}^{-1}$).

Timber and firewood

The wood of *Q. pyrenaica* has not been appreciated as much as that of other oaks for built, although it has been used to obtain firewood directly or for charcoal production (Montoya & Mesón, 1979). For instance, some of the oak populations of Sierra Nevada have been intensely historically exploited to obtain firewood (e.g. Robledal de Cáñar, Moreno-Llorca et al., 2016; Valbuena-Carabaña & Gil, 2013). In addition, other uses of timber have been documented in this mountain range, such as its use in mining in the northernwestern oak woodlands of Sierra Nevada ("Robledal de San Juan", Güejar-Sierra, Granada) where it was used for mine tunnels and furnaces,



Fig. 8.3. (a) Structure of the complex root system of several specimens of *Q. pyrenaica*. (b) Melojo oak barrels for wine aging. (c) Collection of wild fungi in the surroundings of Robledal de Cánar. Pictures from R. Salomón (a), A.J. Pérez-Luque (b) and B. Fernández de Simón (c)

and also as firewood to melt the mineral (Titos, 1990). All these intense exploitation of timber have altered structure of these forests (Pérez-Luque et al., 2020). Notwithstanding, since the 1970s, anthropogenic pressure has been reduced, which lead an increase of tree density, and also in the basal area and average tree size (González-Díaz et al., 2020). This general pattern, observed for most of the forests of the Iberian Peninsula (Astigarraga et al., 2020; González-Díaz et al., 2020), has been also confirmed for melojo oak forests. Thus, using data from second and third Spanish NFI, Pérez-Luque et al. (2021a) (see also chapter 5) assessed the temporal variation on tree biomass of the forests. This analysis showed a total increase of 19172 Mg ha⁻¹ between the two campaigns, with most of the field plots showing an increase pattern on biomass (89% of the plots). This increase could be considered an asset for local populations around the oak woodlands, who could use the forest for firewood extraction

8.3.3. Cultural services

Recreational values

Nature recreation represents a valuable ecosystem service that has a substantial economic value and contributes considerably to income and employment of local communities (Schägner et al., 2017). Monitoring visitors to natural areas have been used often to estimate their recreational values in many areas (Schägner et al., 2017). We used this type of data obtained directly from pyroelectric sensors located in places within Sierra Nevada Protected Area to monitor visitors to this mountain range. We selected two singular oak woodlands of Sierra Nevada for which data are available: Dehesa del Camarate, popularly known as "Bosque Encantado" (Enchanted Forests), and Vereda de la Estrella. We compared the visits in the two oak woodlands with total visitors registered for all sensors installed in this mountain range during a year ($n = 14$; October 2018 to October 2019). Preliminary results showed that those two oak woodlands have a high number of visits (41145 visitors representing 37.36% of total of annual visitors registered), particularly during autumn season, when they represent almost the total number of visits (Figure 8.4).

Recreational sports activities

One way to analyze the physical use of the landscape, and therefore its value as a provider of this cultural service, consists of quantifying the recreational activities performed in nature (e.g. Roces-Díaz et al., 2018). We used the density of routes (hiking, biking, running and other types of outdoor activities) existing in the Wikiloc portal (www.wikiloc.com) (data query in January 2020) for all the municipalities belonging to the Sierra Nevada Natural Protected Area. For each municipality, the total number of routes, and their density (number of routes / surface area of the municipality in ha) were calculated. Each of the oak populations of Sierra Nevada were assigned to the municipalities in which they are present. Of the 47998 routes obtained for the Sierra Nevada mountain range, 49.94% were in the 14 municipalities where oak woodland are present (Figure 8.2b). The density of routes in these municipalities ranged from $5.24 - 41.8$ routes km^{-2} (Table D.3) being for most of them much higher than the average density of routes of the Sierra Nevada municipalities (17.88 routes km^{-2}).

Scientific knowledge

We used two indicators describing research activities to show the relevance of melojo woodlands regarding this ES. Firstly, we explored the spatial pattern of these activities in Sierra Nevada during the period 2009-2013 (Zamora et al., 2017b). For this, we used a database compiling the research authorization documents for the Sierra Nevada Protected Area to generate a density map with the hotspots areas of research activities for this area. Then we extracted the information for the oak populations. Most of the research authorizations are concentrated in the western side of the Sierra Nevada (Figure 8.5b) particularly in the high summits area. The mean values of research permissions for *Q. pyrenaica* oak woodlands in the period studied was 3.03 ± 0.06 , with Genil and Cáñar oak populations (northwestern and southern oak populations respectively, contains the high concentration of research requests (Figure 8.5b). Secondly, we created a density map of sampling protocols deployed in the Sierra Nevada (Zamora et al., 2017b) using data from Sierra Nevada Global Change Observatory (Zamora et al., 2016). All the social-ecological monitoring protocols within this initiative

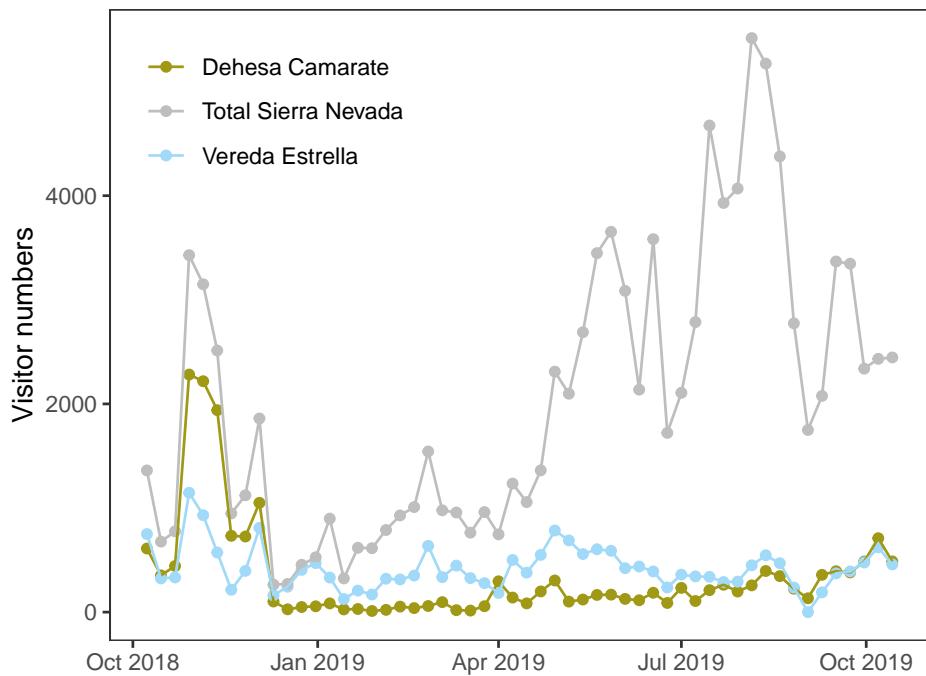


Fig. 8.4. Evolution of the visitors numbers in two oak woodlands, *Dehesa del Camarate* (green), and *Vereda de la Estrella* (blue), comparing with the total of Sierra Nevada (gray). Data come from automatic counters (pyroelectric sensors) located at different points in the Sierra Nevada.

were geolocated to generate a concentration map of sampling protocols by applying geostatistical hotspot detection techniques (Kernel density estimation) (Zamora et al., 2016) (Figure 8.5a). The results showed that the melojo oak woodlands are located in areas of high density of scientific activity (both sampling protocol density and research requested areas) in comparison with the other forest ecosystems of the Sierra Nevada.

Aesthetic values

To explore the aesthetical values of these forests, we used data from Moreno-Llorca et al. (2020) who assessed a series of cultural services in Sierra Nevada by using data from the Flickr platform (www.flickr.com). These authors analysed a total number of 778 photographs and 18 they geolocated in *Q. pyrenaica* woodlands (Figure 8.2c). Although this value is low with respect to the total number, it may be due to the fact that the highest density of photos in the analyzed dataset is located around the ski resort, at high altitude areas, and at village areas (mainly the Alpujarras) (Ros-Candeira et al., 2020). If we analyse forest separately (*i.e.* native pine, holm oak, melojo oak forests, and pine plantations), the photos taken in melojo oak woodlands represent 32% of the total.

Singular trees

Singular, large and/or monumental trees, in addition to perform key ecological functions (*e.g.* nutrient cycling; support complex assemblages of species, Lindenmayer & Laurance, 2017), are creditors of natural value *per se* (Asciuto et al., 2016). They are considered part of a social realm, providing numerous socio-cultural benefits to society (Blicharska & Mikusiński, 2014; Moya & Moya, 2013). Singular trees provide humans with aesthetic, symbolic, religious and historical values (Blicharska & Mikusiński, 2014). They can be considered as singular trees by their age, dasometric (height, diameter at breast height), and socio-cultural (*e.g.* surrounding landscape, local myths, legends and traditions, witnessing historical events) characteristics, so their conservation could contribute to the protection of both ecological and also social values (Blicharska & Mikusiński, 2014). There are several individuals

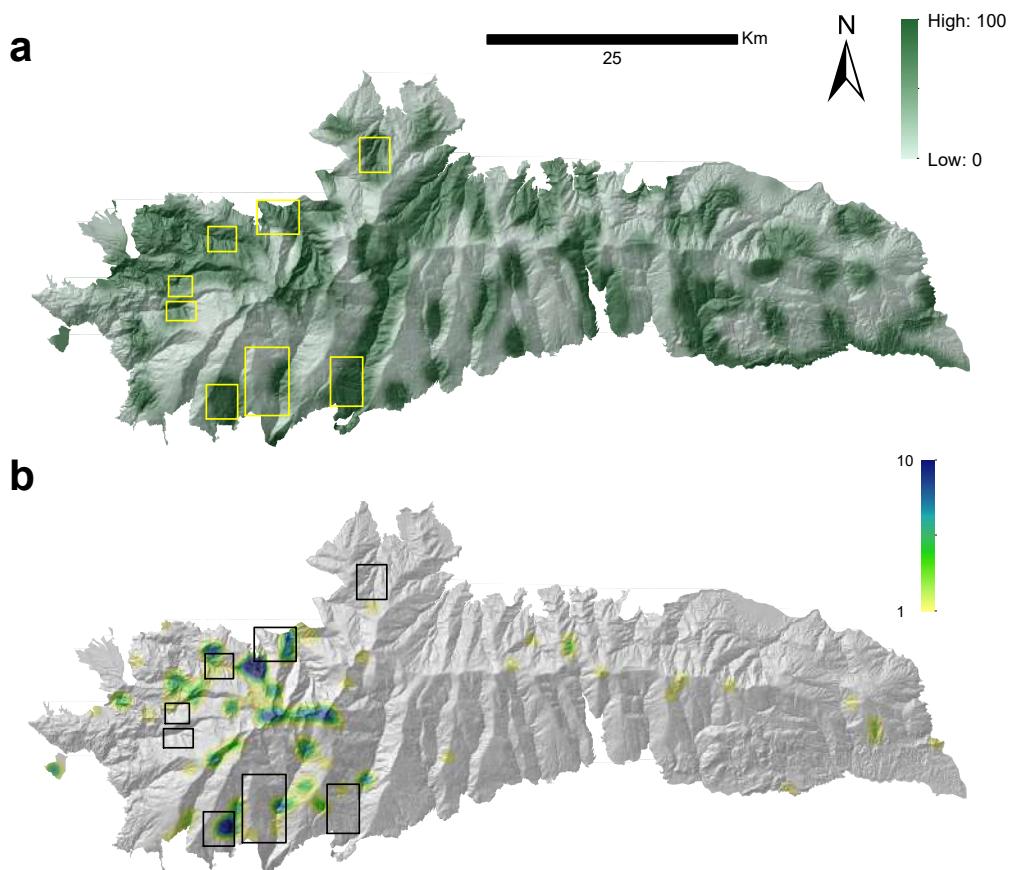


Fig. 8.5. Spatial localization of the research authorizations (Number of research authorizations) performed in Sierra Nevada in the period 2009-2015 (a); and map of density (scaled density) of socioecological monitoring protocols carried out in Sierra Nevada since 2008 (b). For both maps the spatial bounding boxes of each oak population are shown. Drawn from (Zamora et al., 2016; Zamora et al., 2017b)

of *Q. pyrenaica* in the study area, located in Busquístar (Alpujarras, southern slopes of Sierra Nevada), considered singular and/or monumental because of their extraordinary dimensions (Irurita-Fernández et al., 2003), reaching tree heights of up to 19.5 meters and base perimeter of 6.7 meters. Likewise, there are some oak woodlands in Sierra Nevada that shelter specimens and/or singular populations of other species. For instance, the "Abedular del Barranco de los Alisos", located in the Dúrcal oak woodland (Martínez-Labarga et al., 1990). It is a small grove of about 300 individuals of birch (*Betula pendula* subsp. *fontqueri*) with an average height of 12 m. Other examples are the grove of birch trees located at the "Barranco de los Alisos", in the Dúrcal melojo population; or the Aliseda de la Cueva del Santo, where there are more than 100 alders (*Alnus glutinosa*) accompanied by melojo oak and chestnut trees. In Andalusia region, there are also other melojo stands catalogued as singular, such as those located in the Sierra del Aljibe (Alcalá de los Gazules, southern Iberian Peninsula), whose specimens do not stand out for their dimensions but their location is unique and of great interest, representing a southern limit of distribution of the species (Sánchez-García et al., 2003).

8.3.4. Spatial pattern for Ecosystem Services and ecosystem functioning of melojo forest of Sierra Nevada

Q. pyrenaica populations in Sierra Nevada represent a rear-edge of the distribution of this oak species. Peripheral populations are usually considered more vulnerable compared with populations at the center of a species' range (i.e. center-periphery hypothesis Pironon et al., 2017). However, the expected lower performance and higher vulnerability for the peripheral populations do not always meet (e.g. Abeli et al., 2014; Oldfather et al., 2020; Pérez-Luque et al., 2020). For instance, several studies analyzed the evolution of productivity of melojo oak forests using vegetation indices derived from remote sensing (e.g. Enhanced Vegetation Index, EVI), and found that Sierra Nevada melojo forests, despite their high seasonality, are the most productive ecosystems in Sierra Nevada (Alcaraz-Segura et al., 2016; Cazorla

et al., 2020; Dionisio et al., 2012; Pérez-Luque et al., 2015a). These forests also showed a positive trend in productivity since 2000, highlighting their importance in carbon gain and therefore as carbon sinks (Pérez-Luque et al., 2015a) despite their expected low performance.

The quantification of some ES provided by melojo oak populations in Sierra Nevada, allows us to compare the supply of ES among those populations, and to describe what ES category predominate for each of the oak population cluster's in this mountain range (Table 8.3). This also allows us to explore the spatial pattern of ES supply by the melojo oak forest. Regarding the regulating services evaluated, we observed that the southern populations have higher values for carbon sequestration potential, mean EVI and soil organic carbon than for the other clusters (Figure 8.6), despite the theoretically greater vulnerability due to their location in the southernmost areas of Sierra Nevada. For cultural services, the NW populations present high values for sports activities, number of visitors, and density of sampling protocols (scientific value). Finally, for provisioning and support services we observed a variable pattern depending on the service evaluated.

8.3.5. Temporal evolution of Ecosystem Services provision within *Q. pyrenaica* forests in Sierra Nevada

Analyzing the temporal change of ES is key to understand how human societies have been using natural resources in different time periods. Besides, this approach helps us to understand the temporal trade-offs among ES. We compiled datasets of several ES indicators for which long temporal series were available (Table 8.1). Those data were available mainly for one of the oak woodlands (Robledal de Cáñar) located on the southern slope of Sierra Nevada (CAN, Figure 8.1b).

Both overuse and abandonment of melojo woodlands provide very different scenarios for the provision of ES and for the socioeconomic demand for them. From ancient (not determined) times until the period 1960-1970 there was an intense use of the resources provided by the oak forests. Local

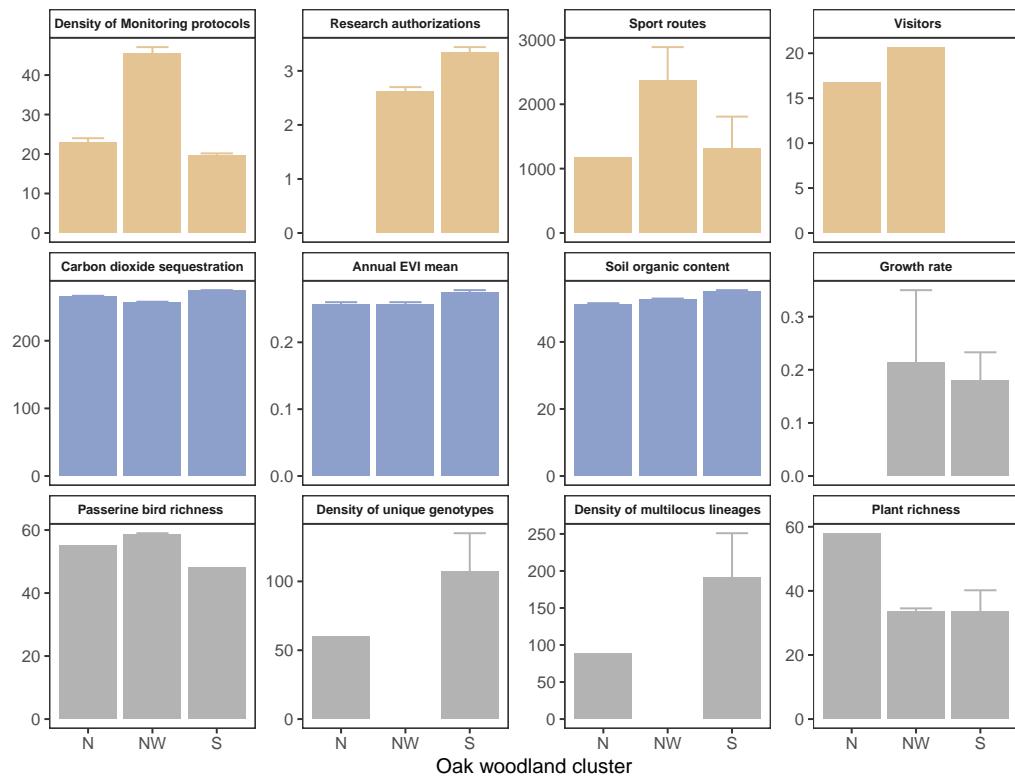


Fig. 8.6. Comparison of ecosystem services (cultural: yellow; regulation: blue; supporting: gray) for oak populations cluster identified in Sierra Nevada. See Table 8.3 for a detailed description

inhabitants used firewood from the forests for charcoal and fuel, reflected by the lower oak-tree density of the forests. Oak acorns were harvested for livestock feed (mainly pigs), as reflected in the auction records of the public forests. Therefore, many forest patches were cleared to create pastures for livestock and mountain crops, which explains the lower amount of forest area. In this period, provisioning ES prevailed over the regulating (poorly considered) or the cultural (not considered). Afterwards, due to changes in socio-economic conditions, a process of depopulation of rural areas (rural exodus) began, resulting in the abandonment of traditional activities as were reflected by several indicators (Figure 8.7). For instance, a decrease in the number of sheep (at least since 1956) and beekeeping (at least since 1980). This pattern also shows that provision ES of *Q. pyrenaica* forests tend to be less important in Sierra Nevada. It is consistent with other land uses not shown in the graph due to the lack of quantitative data (e.g., wood extraction, extent of agriculture within the forest, etc.). This behavior means, in terms of ES, that there is a trend towards less intense use of some provisioning services in melojo forests in Sierra Nevada. This decrease in the indicators related to provisioning ES coincides with an increase of the area occupied by melojo forests, and a gradual increase in their tree density (both at least since the end of 1950s). This pattern is also reflected in the forest's primary production (at least since 2000) as EVI temporal series shown (Figure 8.7). Consequently, increased forest productivity is also reflected in a raise in aboveground forest biomass. The consequences in terms of ES, is a reduction of the provisioning services as opposed to an increase in regulating services, mainly due to a recovery of the forest following the almost complete abandonment of traditional activities. On the other hand, after the declaration of Sierra Nevada as natural protected area (1989), there was an increase in the supply of cultural ES, as reflected for example in the increase in the number of visitors (Figure 8.7). The underlying pattern that seems to explain the above-describe trends is also shown in Figure 8.7: the steady and consistent decrease in human population since at least 1960. Our study area has suffered a strong drainage in human population mainly due to the migration to big cities. This demographical pattern could explain the observed decrease in the use of provisioning services, as well as the increase in their production (due to the land abandonment). Besides, the

increase in the interest of melojo forests by visitors is also compatible with this demographic situation: the currently more urban people enjoy visiting natural areas during their spare time.

Using the sequence of trends described above, we can infer a temporal evolution of the ES provided by melojo forests in Sierra Nevada (Figure 8.8). During the first half of XXth century, human activity was intense in our study area. This means that the most relevant ES were those related with the provision of goods (e.g., timber, grassland, crops, etc.). This situation implied an intense use of land that sometimes could threatened some regulating ES (e.g., soil protection, habitat for endangered species, etc.). During the 1950-60s, the situation changed: due to changes in the macroeconomical situation, an intense migration process began to shift population from rural areas to big cities. This involved the abandonment of previous land use and therefore the underutilization of provisioning ES. The creation of two overlapping protected areas (Natural Park in 1989 and National Park in 1999) reinforced this trend by discouraging intense human activities in the area. The reduction in the intensity of use and therefore the decline of provisioning ES could have fostered a process of secondary succession in the melojo forests. This implied the recovery of many regulating ES such as soil or habitat protection. In the transition from overexploitation to abandonment of the oak forest, many ecosystem services linked to the functioning of an increasingly biodiverse and complex forest ecosystem are being favored. However, in some cases a tradeoff is attained in relation to ecosystem services such as carbon storage. For example, increased forest encroachment implies higher aboveground carbon storage but also higher risk of severe wildfires and therefore carbon losses. Finally, once Spain became a world class tourism attraction (from 2000 onwards), the most relevant ES in our zone are those cultural related to leisure activities.

8.4. Concluding remarks

In this work we combined a literature review with expert criterion to identify and to characterize the main ecosystem services provide by *Q. pyrenaica* woodlands. The literature review revealed the existence of many works

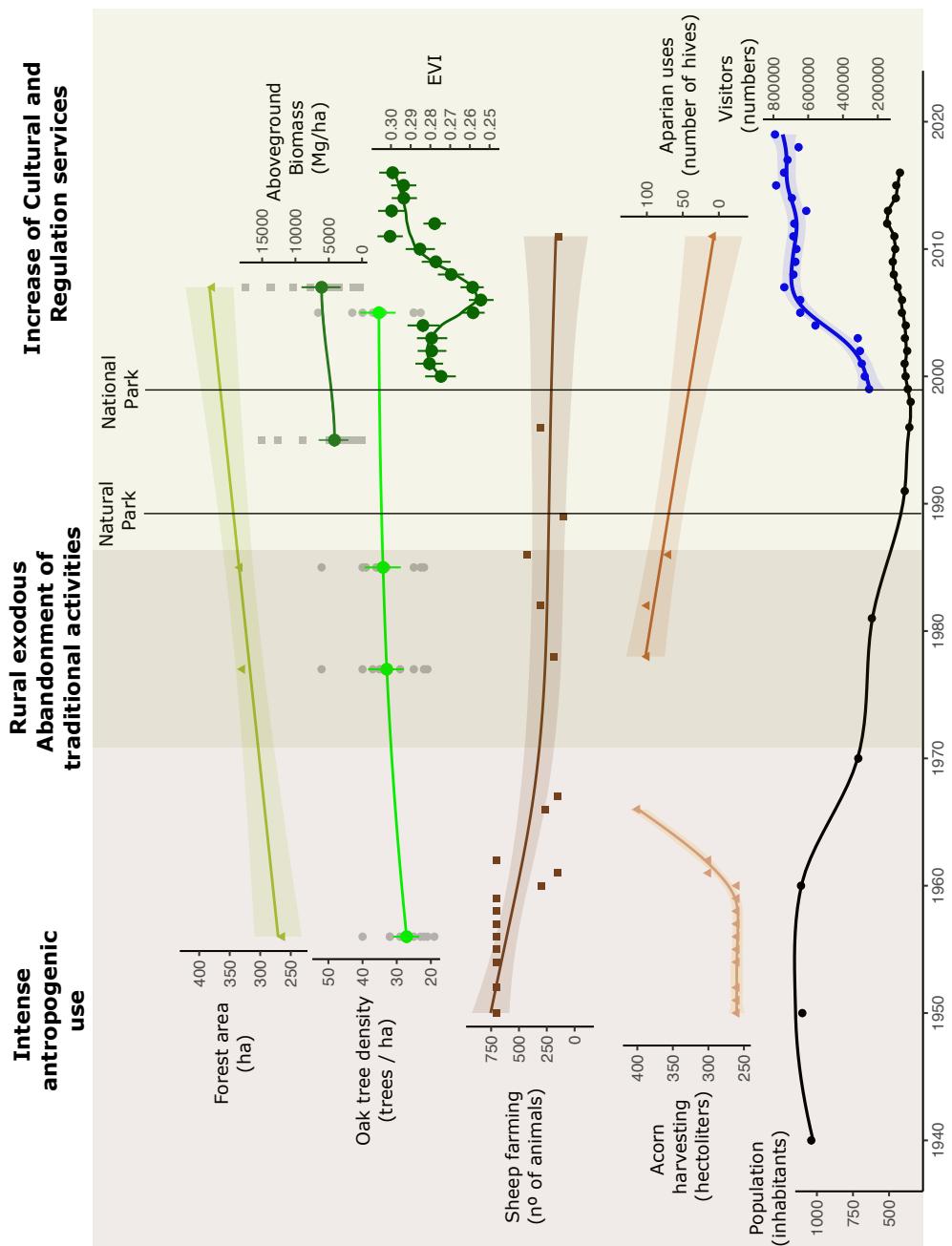


Fig. 8.7. Temporal evolution of indicators of ES supply by *Q. pyrenaica* woodlands in Sierra Nevada. See Table 8.1 for description of the sources. All data referred to Robledal de Cáñar oak woodland (southern slope of Sierra Nevada), except visitors numbers corresponding to all Sierra Nevada Protected Area.

related to wine ageing, highlighting the potential of this species for wine production (Table D.2). Interestingly, this ES has not been identified in our local scale search. It is also remarkable that no work has been found in our literature review that evaluates cultural services in these forests. However, this pattern changes when the ecosystem services are analyzed in more detail as in our case study. Thus, the combination of expert criteria with data at a more local scale allowed us to highlight the existence of diverse cultural ecosystem services provided by these forests.

Our compilation of local scale data has allowed us to quantify many of these ES, which on the one hand highlights the relevance of these forest formations, and on the other hand, provides to natural resource managers with more information and tools to help them in the decision-making process. Because melojo forest is a human-shaped ecosystem, management is required to guide their development (Hobbs et al., 2006). How we manage this new ecosystem effectively is a point for debate. In this sense, incorporating information on ecosystem services can significantly help managers to make decisions due to its integrative and interdisciplinary nature. Our study also adds some interesting insights for the study of ES provided by forests. For instance, we observed a highly variable temporal pattern of some ES, such as the recreational values. Some melojo woodlands of Sierra Nevada concentrate a large part of the visitors recorded in the Sierra Nevada Natural Area (Figure 8.4) during a specific time period. This highlights the need to consider the temporal dimension of the ES evaluated, and to pay attention to the pressure that these ecosystems may be suffering temporarily due to the high number of visitors. Therefore, from a natural resource management point of view, it is necessary not only to analyze the ES provided by an ecosystem, but also we would consider the spatio-temporal pattern of the ES supply. In this sense, it would be interesting to carry out detailed studies to provide managers with a comprehensive assessment of the possible impacts of visitors.

Another relevant outcome is the differences identified within melojo forests regarding their capacity to provide ES. We observed that southern populations seem to be able to sequester more carbon than northern ones. Besides, northwestern populations are specifically valuable for the cultural services

that they provide. The main conclusion regarding these facts is that we need to specifically assess the capacity of ES provision at a local scale. Only by doing so, we would be able to quantify the provision of ES considering the specific biophysical features of each target area.

Finally, we have assessed the change in ES provision patterns across time of this forest system with high conservation values. Both ancient overuse and current abandonment of melojo woodlands provided contrasting scenarios for the provision of ES and for the socioeconomic demand for them in Sierra Nevada. Although the history of land use patterns in our target area is well known, we have described that history using the framework of ES. We observed how the land use could modified the temporal provision of the ES in the melojo forests.

All these results provide enough evidence for us to advocate for the promotion of local scale studies like this one. The combination of literature research with analysis of local long term series and with detailed understanding of the target populations, has allowed us to unveil ES patterns that otherwise would have been kept hidden. Besides, thanks to the existence of the ES conceptual framework, our results can be easily compared with other studies done in other areas. Thus, we conclude that local scale studies can be a good way to gather information on ES supply both at a local and at larger scales.

Tab. 8.3. Quantification of several Ecosystem Services (ES) for Sierra Nevada oak population clusters (see Pérez-Luque et al., 2021b). N: Northern populations, NW: Northwestern populations; S: Southern populations.

ES Indicator	Definition	Units	N	NW	S
Plant richness	Mean richness of plant species recorded in forest inventories	Species number	58	33.5 ± 1.04	33.5 ± 6.69
Passerine bird richness	Mean richness of passerine birds recorded at bird censuses on oak woodlands	Species number	55	58.5 ± 0.5	48
Genetic diversity	Density of genotypes represented by one stem (unique genotypes, GU) per hectare	Genotypes Uniques ha ⁻¹	60	107.5 ± 27.5	
Genetic diversity	Density of multilocus lineages (MLL) per hectare	Multilocius Lineages ha ⁻¹	89	191 ± 60	
Biomass increment	Increment of Biomass amount (Growth rate) between two National Forest Inventories (SNFI2 and SNFI3)	Mg Biomass ha ⁻¹ year ⁻¹	0.214 ± 0.136	0.18 ± 0.053	
Recreational values	Percentage of visits (visits registered in the oak woodland / total visits registered in Sierra Nevada)	%	16.69	20.68	
Sport activities (total routes)	Mean of total routes registered at Wikilock in the Municipalities where oak woodlands are located	Sport activities	1170	2367.5 ± 520.36	1318 ± 489.95
Scientific authorizations	Average values of the Kernel Density Estimate of the research permissions	Number of autorization research		2.61 ± 0.09	3.34 ± 0.1
Scientific sampling density	Average of Normalized Kernel Density Estimation of the Density of scaled value (0-100) Monitoring methodologies		22.94 ± 1.07	45.56 ± 1.52	19.57 ± 0.59
EVI mean	Average of annual EVI mean for all pixels covering oak woodlands populations (period 2000-2018)		0.257 ± 0.003	0.256 ± 0.004	0.275 ± 0.003
Potential sequestration	Average values of the CO ₂ potential sequestration	Mg CO ₂ ha ⁻¹	265.07 ± 1.41	256.72 ± 1.05	273.91 ± 0.93
SOC	Average values of the mean Soil organic content at a 0-30 cm depth	Mg SOC ha ⁻¹	51.27 ± 0.29	52.59 ± 0.34	55.11 ± 0.33

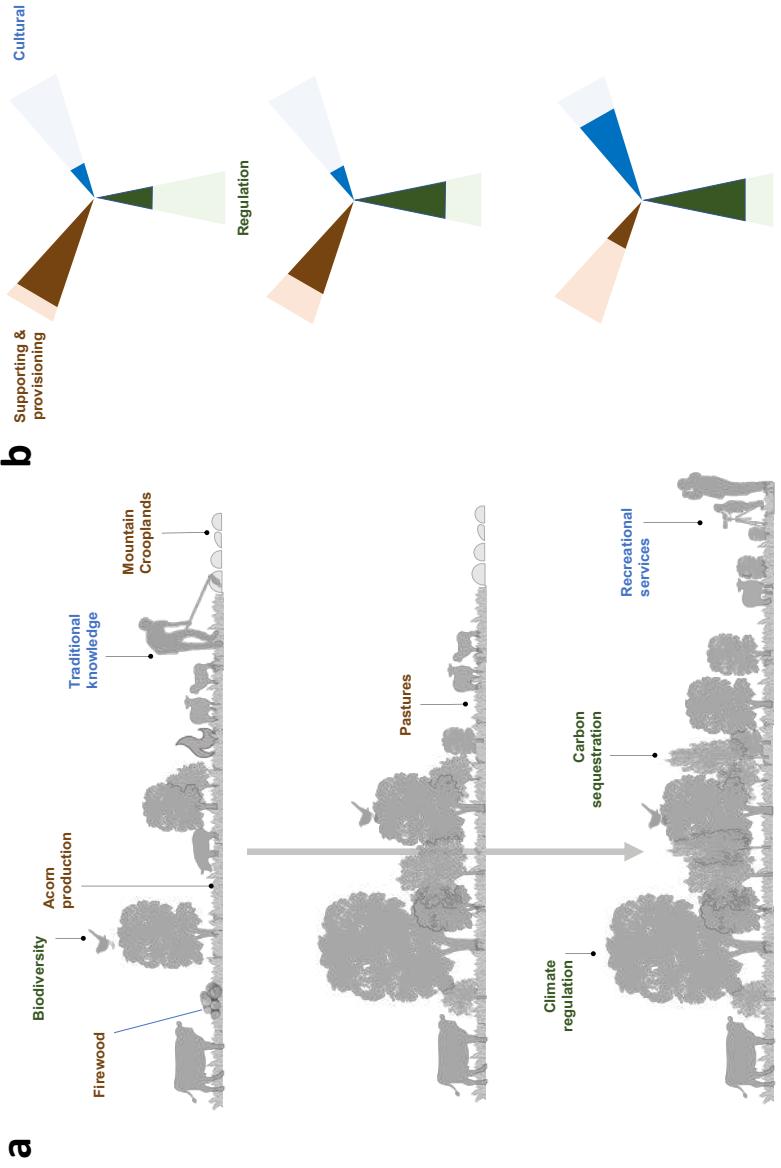


Fig. 8.8. (a) Temporal evolution of anthropic uses associated with Sierra Nevada oak forests, and their effect on the provision of ecosystem services (b). For each category of ecosystem services, an estimate of the supply at each time point is shown.

Parte III

Discusión General

Discusión General

Diversidad ecológica dentro del borde posterior de distribución de *Q. pyrenaica*.

La distribución de *Q. pyrenaica* está condicionada por el periodo de sequía estival, necesitando un mínimo de 100-150 mm de precipitación estival para su supervivencia (Blanco Castro et al., 2005; García & Jiménez, 2009). Varios autores han señalado la importancia de los índices pluviométricos y ombrotérmicos en la separación entre bosques templados y mediterráneos para esta especie a lo largo de su área de distribución (del Río et al., 2007). A escalas más detalladas, la distribución de esta especie se rige por un complejo gradiente relacionado con la temperatura, la precipitación y la radiación (Gavilán et al., 2007; Urbíeta et al., 2011). En el capítulo 3, hemos encontrado que la precipitación estival y anual son factores muy importantes para explicar la distribución de los bosques de *Q. pyrenaica* en Sierra Nevada. De hecho, hemos observado diferentes grupos de poblaciones de *Q. pyrenaica* en esta región montañosa discriminados principalmente por la precipitación y la radiación. Los robledales situados al norte y al noroeste, se localizan en fondos de valle con orientaciones norte, donde la humedad relativa es mayor como consecuencia de una menor radiación solar. Por otro lado, las poblaciones de la vertiente sur de Sierra Nevada reciben un aporte extra de agua procedente del aire húmedo del mar (Martínez-Parras & Molero-Mesa, 1982). Las diferencias en la disponibilidad de agua entre las poblaciones de robles podrían afectar a varios procesos ecológicos como la germinación y supervivencia de las plántulas (Gómez et al., 2003; Gómez-Aparicio et al., 2008; Mendoza et al., 2009), así como a la regeneración de la especie (Gómez et al., 2001), debido principalmente al papel clave de la disponibilidad de agua a escala de micrositio, que facilitan la germinación y el establecimiento de las plántulas. Asimismo, como se ha observado para otras especies de *Quercus* (e.g. Di Filippo et al., 2010; García-González & Souto-Herrero, 2017; Gea-Izquierdo et al., 2011; Tessier et al., 1994), la disponibilidad de agua es uno de los principales factores limitantes que afectan al crecimiento secundario de *Q. pyrenaica* (ver resultados obtenidos en el capítulo 6).

Las poblaciones de *Q. pyrenaica* situadas en Sierra Nevada, que representan un borde posterior (*rear-edge*), no son ecológicamente homogéneas, ni en sus condiciones ambientales ni en su composición de especies. Al explorar las

características de las poblaciones de roble melojo en Sierra Nevada, hemos observado la existencia de grupos separados de poblaciones basándose en sus características ambientales, siendo la radiación y la precipitación las principales variables discriminantes (ver capítulo 3). Esta heterogeneidad va en la línea de otros estudios que señalan una dinámica ecológica diferencial para estos bosques en Sierra Nevada. Así por ejemplo, la productividad primaria de estos ecosistemas (medida mediante el uso de teledetección) difiere entre las poblaciones de *Q. pyrenaica* de Sierra Nevada, con los robledales de la vertiente sur mostrando un mayor veredor anual de la vegetación que los de la vertiente norte (ver capítulo 7 Dionisio et al., 2012; Pérez-Luque et al., 2015a; Pérez-Luque et al., 2020). Asimismo, otros estudios encontraron diferencias en la dinámica estacional del veredor (Dionisio et al., 2012), y en la tendencia temporal de la productividad primaria (Alcaraz-Segura et al., 2016; Pérez-Luque et al., 2015a), esto último parece estar relacionado con la diferente tendencia observada para la cubierta de nieve en las vertientes norte y sur de Sierra Nevada (ver capítulo 7).

Curiosamente, también hemos encontrado diferencias en la diversidad de especies entre los grupos de poblaciones derivadas de la agrupación basada en variables ambientales (ver capítulo 3). Estos resultados son consistentes con los aportados por Lorite et al. (2008), que señalaron que las diferencias observadas para el componente florístico en las poblaciones de *Q. pyrenaica* de Sierra Nevada están relacionadas con las condiciones microclimáticas. En este sentido, los robledales situados en el norte de Sierra Nevada presentan mayor similitud florística con los situados en el centro de la distribución de *Q. pyrenaica* que con los que se localizan en la vertiente sur de Sierra Nevada (geográficamente más cercanos) (Lorite et al., 2008). Además de los factores climáticos, las diferencias florísticas entre las poblaciones de *Q. pyrenaica* en Sierra Nevada también podrían estar relacionadas con el impacto antropogénico sufrido, ya que las perturbaciones antrópicas pueden afectar a los patrones florísticos, como se ha documentado para los robledales del centro de la Península Ibérica (Gavilán et al., 2000). Por ejemplo, el robledal del Camarate (que representa el grupo de población Norte en Sierra Nevada, ver capítulo 3) mostró una mayor diversidad y riqueza de especies vegetales, lo que puede estar relacionado con un mejor estado de conservación, ya que esta población ha estado menos expuesta a la intensa actividad antropogénica.

(Jiménez Olivencia, 1991). Por el contrario, las poblaciones de robledal situadas en la vertiente sur, mostraron una composición florística más pobre condicionada tanto por el clima como por el intenso uso del suelo (Al Aallali et al., 1998; Camacho-Olmedo et al., 2002). Por tanto, podemos atrevernos a afirmar la importancia del uso del suelo para entender el estado actual de los robledales de *Q. pyrenaica* dentro del borde posterior de su distribución.

La notable coincidencia entre la agrupación de las poblaciones derivada del análisis de las variables ambientales y la ordenación de las poblaciones según la composición de especies, sugieren una relación entre la heterogeneidad de los factores ambientales y la variabilidad de la composición de especies para estos bosques. Esta diversidad de condiciones ecológicas para las poblaciones de *Q. pyrenaica* situadas en este borde posterior, está en consonancia con los altos niveles de diversidad genética mostrados por las poblaciones de esta especie en Sierra Nevada (Valbuena-Carabaña & Gil, 2013, 2017). La heterogeneidad climática y topográfica que existe en Sierra Nevada ofrece una gran diversidad de micro hábitats, lo que ha permitido que esta región montañosa actúe como refugio de diferentes especies (Blanco-Pastor et al., 2019; Gómez & Lunt, 2007; Médail & Diadema, 2009), incluso para las especies de *Quercus* caducifolios durante el último periodo glacial (Brewer et al., 2002; Olalde et al., 2002; Rodríguez-Sánchez et al., 2010). De hecho, existen evidencias fósiles y genéticas que sugieren que diferentes especies de *Quercus* sólo sobrevivieron en refugios del sur durante el último máximo glacial (Bhagwat & Willis, 2008; Birks & Willis, 2008; Brewer et al., 2002; Petit et al., 2002). La persistencia en un refugio sugiere una combinación de un entorno local moderadamente adecuado que amortigua el clima regional, y una relativa tolerancia al cambio climático, ya sea por una pronunciada plasticidad fenotípica, y/o por la capacidad de adaptación (Gavin et al., 2014). Este podría ser muy bien el caso de *Q. pyrenaica*, una especie que alberga una alta diversidad genética (Valbuena-Carabaña & Gil, 2013), situada en una región montañosa con una topografía compleja que podría proteger a las poblaciones locales contra los rápidos cambios climáticos y permitir que las especies persistan a pesar de los entornos regionales desfavorables.

La identificación de diferentes grupos de poblaciones en función de las variables ambientales a escala de detalle (ver capítulo 3), es importante a la hora de modelizar la distribución de una especie y prever los impactos del cambio global sobre ella, ya que los factores que controlan la distribución de las especies pueden variar en función de la escala de observación (Guisan & Thuiller, 2005; Sánchez de Dios et al., 2009; Urbieta et al., 2008). Los resultados que hemos obtenido en el capítulo 3, que indican una separación de poblaciones de *Q. pyrenaica* en función de la disponibilidad de agua, sugieren la necesidad de incorporar estos resultados en los modelos de predicción del impacto de cambio climático sobre esta especie. Incorporar las adaptaciones locales de las poblaciones en los modelos predictivos, puede ayudar a evitar representaciones erróneas del desplazamiento del área de distribución de las especies bajo condiciones climáticas cambiantes (Benito-Garzón et al., 2011). Esto es especialmente importante en el caso de las especies con bordes posteriores situados en regiones de montaña, ya que estas zonas ofrecen una amplia diversidad de micro hábitats debido a la heterogeneidad climática y topográfica (Médail & Diadema, 2009). Por ejemplo, algunos trabajos recientes han realizado modelos de alta resolución de la distribución de especies arbóreas relictas en montañas Mediterráneas del sur (e.g. *Abies pinsapo*, *Pinus sylvestris* y *P. nigra*) proporcionando información útil para las acciones de gestión forestal (López-Tirado & Hidalgo, 2014).

Los robledales de *Q. pyrenaica* en Sierra Nevada frente al cambio climático

Varios son los trabajos que han documentando un aumento generalizado de las temperaturas, así como un cambio en los patrones de precipitación para la región Mediterránea (e.g. Cramer et al., 2020; García-Ruiz et al., 2011; Giorgi & Lionello, 2008; Pérez & Boscolo, 2010). Estos patrones generales también han sido observados para Sierra Nevada, donde varios estudios, a partir de datos de estaciones meteorológicas y usando mapas climáticos de alta resolución, han encontrado tendencias positivas para las temperaturas mínimas y máximas anuales, así como un descenso generalizado en la

precipitación desde 1960 (Benito et al., 2014; Pérez-Luque et al., 2021; Pérez-Palazón et al., 2015; Pérez-Luque et al., 2016a). Esos cambios observados en las variables climáticas parecen afectar a varios procesos ecológicos, como por ejemplo la dinámica de la cubierta de nieve en ambientes de montaña (Trujillo et al., 2012). Así, en algunas montañas europeas se han registrado descensos significativos en la extensión y duración de la cubierta de nieve (Marty, 2008; Moreno Rodríguez et al., 2005; Nikolova et al., 2013; Scherrer et al., 2004). En Sierra Nevada, además de estos cambios, se han observado modificaciones en la fecha de inicio y de fusión de la cubierta de nieve (Pérez-Luque et al., 2016a). Específicamente se han documentado para los últimos 20 años un retraso en la fecha de inicio de la presencia de nieve, y un adelanto en la fecha de fusión de la nieve (Pérez-Luque et al., 2016a). Por ejemplo, para el 70% de los píxeles que coinciden con la distribución de los robledales en Sierra Nevada, hemos encontrado tendencias hacia una fecha de deshielo más temprana (ver capítulo 7).

Las alteraciones en los patrones de disponibilidad hídrica, tal y como apuntábamos en los objetivos de esta memoria doctoral, pueden afectar al funcionamiento ecosistémico de los robledales en Sierra Nevada. Mediante el uso del sistema de ontologías (ver capítulo 7), hemos observado tendencias temporales significativas para el NDVI de verano en los robledales. En concreto, el 75% de los píxeles que cubren los robledales han mostrado tendencias positivas significativas. El sistema de ontologías desarrollado, nos ha ayudado a desvelar la co-ocurrencia de tendencias significativas tanto en la cobertura de nieve (factor abiótico) como en el funcionamiento del ecosistema (NDVI). Por ejemplo, en las poblaciones de robledal situadas en la parte más occidental de Sierra Nevada, la mayor parte de sus píxeles muestran esta co-ocurrencia. Las implicaciones ecológicas de esta co-ocurrencia pueden explicarse argumentando que el deshielo más temprano proporciona agua a los árboles de *Q. pyrenaica* cuando están en la mitad de su temporada de crecimiento. Este suministro de agua más temprano puede favorecer que los árboles sean más productivos en verano. Por otro lado, las poblaciones de robledal situadas en el sur de Sierra Nevada, también muestran esta co-ocurrencia en sentido contrario: la falta de tendencias significativas en la productividad de verano para ésta poblaciones, podría explicarse por la falta de píxeles con tendencias hacia un deshielo más

temprano en estas zonas. Aunque estos resultados hay que considerarlos con cautela, parecen indicar la existencia de un vínculo entre el estado de un factor abiótico (duración de la cubierta de nieve) y el funcionamiento de los ecosistemas (productividad), tal y como ha sido documentado en otras regiones montañosas (Dye & Tucker, 2003; Wan et al., 2014). Estos resultados pueden utilizarse en la programación de algunas actuaciones forestales de mejora de los robledales. Por ejemplo, si entre las actuaciones forestales se contemplara la realización de refuerzos poblacionales mediante plantación, éstas se pueden realizar en aquellas poblaciones donde se haya observado un patrón de mayor disponibilidad de agua, lo cual aumentaría la posibilidad de éxito de la actuación, teniendo en cuenta la importancia de la disponibilidad de agua para esta especie (ver capítulo 3).

En Sierra Nevada, al igual que en otras zonas del sur de Europa, se ha observado en los últimos años un aumento en la duración, frecuencia y severidad de los eventos de sequía (ver capítulo 6 y apéndice C; Páscoa et al., 2017; Spinoni et al., 2015; Stagge et al., 2017; Vicente-Serrano et al., 2014), con una tendencia hacia veranos más secos (Spinoni et al., 2017). Esta situación está alterando el funcionamiento de los ecosistemas mediterráneos a diferentes escalas (Forner et al., 2018; Liu et al., 2020; Ogaya & Peñuelas, 2021; Peñuelas et al., 2017), puesto que la sequía afecta a aspectos fisiológicos, funcionales, estructurales y demográficos de los ecosistemas forestales (Allen et al., 2010; Assal et al., 2016). No obstante, se están observando respuestas divergentes de los ecosistemas forestales a la sequía (Anderegg et al., 2020), poniendo de manifiesto la importancia de otros aspectos, como por ejemplo, el momento en el que ocurre la sequía (Huang et al., 2018). Esto es de especial relevancia para especies como *Q. pyrenaica* que presenta una fenología de crecimiento bien marcada con su máximo de crecimiento en final de primavera y verano (Pérez-de Lis et al., 2016).

Los eventos de sequía severa afectan a la dinámica de crecimiento de *Q. pyrenaica*. Los resultados del capítulo 6 muestran claramente una reducción en el crecimiento primario (verdor medido usando EVI) y en el crecimiento secundario (BAI) para los eventos de sequía de 2005 y 2012. Asimismo, observamos que durante los eventos de sequía extrema, como la registrada

en 1995, se produjo la mayor reducción del crecimiento radial. Ese evento de sequía causó graves y extensos daños en los ecosistemas Mediterráneos de la Península Ibérica (Gazol et al., 2018; Peñuelas et al., 2001).

Las respuestas de los árboles a la sequía son dependientes del sitio (Babst et al., 2013), particularmente para las poblaciones situadas en su borde posterior de distribución (Cavin & Jump, 2017; Dorado-Liñán et al., 2017c). Tal y como hemos observado en el capítulo 6, tanto el verdor de la vegetación (EVI), como el crecimiento secundario de los árboles (BAI), se vieron más afectados por los eventos de sequía en las poblaciones de robledal situadas en la cara norte de Sierra Nevada que las situadas en la cara sur. Específicamente, encontramos que las poblaciones situadas en la cara norte mostraron anomalías de EVI más negativas para la sequía de 2005 que las situadas en la cara sur. Asimismo, las correlaciones entre el crecimiento secundario de los árboles y el índice SPEI (tanto del año hidrológico como de verano) fueron más intensas para las poblaciones de la cara norte, lo cual se puede interpretar como una mayor sensibilidad a la sequía en los sitios más secos (Gea-Izquierdo & Cañellas, 2014). Por otro lado, es interesante destacar la gran variabilidad en respuesta al clima mostrada por las poblaciones de roble a lo largo de un estrecho gradiente. Por ejemplo, los árboles situados en las zonas altas del robledal de Cáñar mostraron un BAI superior a los situados en elevaciones más bajas, aunque ambos sitios de muestreo se encuentren muy cerca el uno del otro.

No obstante, a pesar de los severos eventos de sequía de las últimas décadas, llama poderosamente la atención la tendencia positiva para el verdor de la vegetación mostrada por los bosques de *Q. pyrenaica* durante los últimos 20 años (ver resultados de los capítulos 6 y 7). De igual modo, para el crecimiento de los árboles también observamos tendencias positivas en la última década para los robledales de Sierra Nevada. Estos resultados concuerdan con las tendencias a largo plazo exhibidas por esta especie en lugares húmedos y fríos a lo largo de su área de distribución (Gea-Izquierdo & Cañellas, 2014). Esto podría estar relacionado con un efecto positivo no lineal del aumento de temperaturas, para las especies situadas en sitios a mayor altitud con crecimiento limitado por el frío (Gea-Izquierdo & Cañellas, 2014; Salzer et al., 2009).

Un aspecto importante a destacar es que, para las poblaciones situadas en los bordes posteriores de distribución que se encuentran amenazadas por el cambio climático, se esperaban tendencias de crecimiento negativas, tal y como se ha mostrado para algunas especies templadas y mediterráneas (Camarero et al., 2015b; Dorado-Liñán et al., 2017b; Sánchez-Salguero et al., 2012). Sin embargo, nuestros resultados (ver capítulos 6 y 7), indican que las poblaciones de robledal en Sierra Nevada, situadas en uno de los bordes posteriores de distribución, mostraron tendencias positivas para el EVI (crecimiento primario) y en el BAI de los árboles (crecimiento secundario).

Los robledales de *Q. pyrenaica* en Sierra Nevada frente a los cambios de uso

Los cambios de uso del suelo se consideran los principales impulsores del cambio global (Butchart et al., 2010; Winkler et al., 2021), afectando a la biodiversidad (Sala, 2000), modificando diferentes procesos ecológicos (Lindenmayer et al., 2012) y alterando la provisión de servicios ecosistémicos (Hasan et al., 2020). Los bosques de *Q. pyrenaica*, al igual que otras formaciones forestales de la región Mediterránea, se han visto sometidos a intensas presiones antropogénicas a lo largo del tiempo (Alba-Sánchez et al., 2021; García & Jiménez, 2009), que han llevado a la reducción de su área de distribución, así como a la modificación de sus patrones florísticos y estructurales (Calvo et al., 1999; Gavilán et al., 2000; Tárrega et al., 2006). Históricamente, los bosques de *Q. pyrenaica* han sido explotados principalmente para la obtención de leña, carbón vegetal y taninos (Ruiz de la Torre, 2006; Sánchez Palomares et al., 2008). Algunas zonas se quemaron y aclararon para crear pastos con bajas densidades de árboles maduros que proporcionaban bellotas, leña y grandes áreas para el pastoreo (Alvarez et al., 2009; Herrera Calvo, 2016; Valbuena-Carabaña & Gil, 2017). Todos estos procesos antropogénicos han transformado los robledales de una manera tan profunda que es difícil encontrar rodales que puedan considerarse bosques naturales (Ruiz de la Torre, 2006).

La revisión de diversos documentos históricos (ver capítulos 4 y 6) ha revelado que las cortas, la extracción de leña, la producción de carbón

vegetal y la minería, entre otras actividades antropogénicas, han afectado intensamente a los bosques de Sierra Nevada. De hecho, estudios previos han estimado una pérdida histórica de en torno al 90% de la cobertura arbórea para especies caducifolias de *Quercus* en elevaciones medias y bajas de Sierra Nevada (Jiménez-Olivencia et al., 2015). Las diversas estructuras forestales que encontramos en la actualidad en las poblaciones de *Q. pyrenaica* de Sierra Nevada (ver resultados en capítulos 3, 4, 5 y 6) parecen ser fruto de intensas y diferentes historias de uso y manejo que han sufrido estas formaciones forestales (Figura 5.3). En la vertiente norte de Sierra Nevada (por ejemplo el robledal de San Juan, GEN) los usos del suelo se han distribuido históricamente a lo largo de un gradiente de elevación: pastizales y matorrales para la ganadería en las cotas más altas; a continuación, masas forestales con algunos cultivos; y, por último, terrazas de regadío con cultivos arbóreos en las cotas más bajas (Jiménez-Olivencia et al., 2015). Además, otras actividades como la minería debieron alterar la estructura del bosque. Así por ejemplo, el entorno del robledal de San Juan (GEN) tiene muchas minas y canteras pequeñas que fueron explotadas intermitentemente a lo largo de la historia. De hecho, estos usos históricos se ven reflejados en los resultados de los análisis dendrocronológicos indicados en el capítulo 6. Así por ejemplo, un evento de liberación del crecimiento arbóreo en la década de 1940 expresado en el registro dendrocronológico del robledal de San Juan, coincide con un periodo de máxima actividad minera en esta zona (1925 a 1957). Durante ese periodo se incrementó el uso de la madera para los túneles y hornos de las minas, que además requerían grandes cantidades de leña para fundir el mineral (Tabla C.4) (Titos, 1990). Esta fuerte explotación de los recursos forestales en el entorno de estas minas, debió afectar a una parte importante de este robledal, como demuestra el crecimiento de los árboles remanentes en este robledal. Por otro lado, los bosques situados en la vertiente sur de Sierra Nevada (por ejemplo el robledal de Cáñar, CAN), se mezclaron con un mayor porcentaje de tierras de cultivo a lo largo del gradiente de elevación (Jiménez-Olivencia et al., 2015). La leña, el carbón vegetal y las bellotas se explotaron intensamente en estos robledales, hasta al menos mediados del siglo XX, cuando estas actividades disminuyeron bruscamente debido principalmente al abandono rural y al uso de gas y combustibles fósiles (Bonet et al., 2014b; Mesa-Torres,

2009; Moreno-Llorca et al., 2016; Valbuena-Carabaña & Gil, 2013). En las zonas altas de estos robledales, los registros dendrocronológicos indican una liberación de crecimiento en los primeros años registrados (en torno a 1830-1840) que podría estar relacionado con la conversión del bosque cerrado a un sistema silvopastoral abierto, una práctica de gestión común aplicada en el pasado en muchos robledales ibéricos (Cañellas et al., 2004; Gea-Izquierdo et al., 2011) y que ha sido documentada para este sitio (Valbuena-Carabaña & Gil, 2013).

Sin embargo, a partir de la segunda mitad del siglo XX, se produjo un abandono de las actividades tradicionales (MacDonald et al., 2000; Martínez-Fernández et al., 2015; Pías et al., 2014; Valbuena-Carabaña et al., 2010), que ha provocado una disminución de la presión antrópica sobre los ecosistemas forestales mediterráneos (Peñuelas & Sardans, 2021; Valbuena-Carabaña et al., 2010), siendo especialmente importante para las zonas de montaña (Alvarez-Martínez et al., 2014; de Natale et al., 2007; Jiménez-Olivencia et al., 2015; Pías et al., 2014). El dramático éxodo rural en las zonas de montaña se produjo debido a los cambios en las condiciones socioeconómicas (European Environment Agency, 2010), dando lugar, además de al abandono de las actividades tradicionales, a importantes cambios ambientales (Alvarez-Martínez et al., 2014; de Natale et al., 2007; MacDonald et al., 2000; Piussi, 2000; Rutherford et al., 2008; Zimmermann et al., 2010). Así por ejemplo, varios estudios han demostrado que los cambios de usos están afectando ampliamente al almacenamiento de carbono de los ecosistemas terrestres en varias zonas del sur de Europa (Muñoz Rojas et al., 2011; Muñoz Rojas et al., 2015). En este sentido, tras el abandono de las actividades tradicionales se ha observado una densificación de las masas forestales en áreas de montaña (Jiménez-Olivencia et al., 2015). Los resultados del análisis de la evolución temporal de la biomasa arbórea en las parcelas del Segundo y Tercer Inventario Nacional Forestal (ver capítulo 5), indican un aumento de la biomasa en el 89% de las parcelas de *Q. pyrenaica* en la Península Ibérica. Este resultado, junto con el incremento del área ocupada por esta formación en Sierra Nevada en las últimas décadas (Camacho-Olmedo et al., 2002a) y la constatación de la existencia de un proceso de densificación forestal (Jiménez-Olivencia et al., 2015), ponen de manifiesto un incremento en la capacidad potencial de secuestro de carbono de estos bosques. Por tanto,

considerando esta tendencia, y la casi ausencia de perturbaciones directas de origen humano, al estar estos bosques en una zona protegida, cabría esperar un aumento potencial de las existencias de carbono forestal, como la que se ha registrado en muchos bosques de la región Mediterránea en las últimas décadas (FAO & Plan Bleu, 2018). Esto además coincide con las predicciones bajo diferentes escenarios que prevén un crecimiento forestal en las próximas décadas (Aparicio et al., 2015). Sin embargo, debe tomarse con cautela, ya que se están documentando algunos signos de saturación de los bosques como sumideros de carbono (Nabuurs et al., 2013).

Al igual que hemos apuntado para otras variables a lo largo de esta memoria doctoral, existe heterogeneidad en la biomasa aérea entre las poblaciones de roble en Sierra Nevada (ver capítulo 5), condicionado fundamentalmente por las diferentes intensidades de uso a las cuales han estado sometidas dichas poblaciones en los últimos años. Así por ejemplo, la estructura forestal del robledal del Camarate (grupo N), con árboles más altos y más grandes, y por tanto mayores valores de biomasa, podría relacionarse con una menor intensidad de las perturbaciones antropogénicas en comparación con los otros robledales. Los robledales del Camarate tuvieron una mayor protección durante la segunda mitad del siglo pasado (Jiménez Olivencia, 1991), y actualmente también tienen el mayor nivel de protección legal dentro del espacio protegido (Anónimo, 2011). Las menores perturbaciones antropogénicas han dado lugar a bosques mejor conservados con una mayor diversidad de especies (Pérez-Luque et al., 2021b), y también a una estructura de rodales estable con altos valores de biomasa (Figura 5.3). Para otras especies de *Quercus*, también se ha observado que los bosques con menos perturbaciones tienen un mayor potencial de almacenamiento de carbono (Balboa-Murias et al., 2006; Cotillas et al., 2016; Stojanović et al., 2017). Nuestros resultados ponen de manifiesto cómo las diferencias en la estructura del rodal condicionaron la biomasa arbórea del mismo. Los rodales muy densos (e.g. poblaciones del NW) mostraron una biomasa total inferior a la de los rodales menos densos (poblaciones de roble del N o del S) (Figura 5.3). Una mayor densidad arbórea aumenta la competencia de los árboles, limitando el crecimiento de la misma, lo que provoca la pérdida de vitalidad y la reducción de la producción de bellota (Bravo et al., 2008; Piqué et al., 2018) y según nuestros resultados, cuanto mayor es la densidad

de los árboles, menor es la capacidad de estos bosques para actuar como sumideros de carbono (Figura 5.4). Además, esta mayor acumulación de biomasa, unida a una pérdida de diversidad estructural, aumenta el riesgo de incendios forestales debido a la gran cantidad de biomasa acumulada (Cañellas et al., 2004; Piqué & Vericat, 2015; Serrada et al., 1992).

El abandono de las actividades tradicionales en montaña, como por ejemplo los cultivos de montaña, también está provocando un aumento de la expansión forestal hacia las tierras de cultivo abandonadas (Alvarez-Martínez et al., 2014; Piussi, 2000), que puede provocar una homogeneización del paisaje (Mietkiewicz et al., 2017) con diversas consecuencias ecológicas (Zimmermann et al., 2010). Así, a pesar de las fuertes limitaciones de reclutamiento descritas para esta especie (Bravo et al., 2008; Gómez et al., 2003; Perea et al., 2014), hemos constatado la existencia de un proceso de colonización de *Quercus pyrenaica* hacia tierras de cultivo abandonadas en Sierra Nevada (ver capítulo 4). Este fenómeno de expansión forestal hacia las tierras de cultivo abandonadas también se ha registrado en otras regiones montañosas europeas (Alvarez-Martínez et al., 2014; Améztegui et al., 2010; Ameztegui et al., 2016; de Natale et al., 2007; Kozak, 2003; Lasanta-Martínez et al., 2005; Piussi, 2000; Vicente-Serrano et al., 2004) como consecuencia principalmente de la despoblación rural y de la disminución de la presión de los herbívoros (European Environment Agency, 2016; MacDonald et al., 2000). En Sierra Nevada, hemos observado que el proceso de colonización de cultivos por parte del robledal es diferente entre las poblaciones estudiadas. Encontramos que en las poblaciones del sur (Robledal de Cáñar), la cantidad de juveniles de *Q. pyrenaica* en el interior de los cultivos abandonados era mayor que en las poblaciones de la vertiente norte. De los diferentes aspectos analizados que puedan explicar esas diferencias, encontramos que la distancia a la fuente semillera, la estructura del bosque circundante a los cultivos abandonados, y la población de arrendajo (*Garrulus glandarius*, el principal dispersante de bellotas del roble) no presentan diferencias significativas para las poblaciones estudiadas (ver capítulo 4).

Además de la importancia de los factores relacionados con la dispersión y con la variación a escala fina de los factores abióticos (Leverkus et al., 2016; Milder et al., 2013), la historia de uso a la que han sido sometidos los

cultivos de montaña abandonados (antes y después de su abandono) es un factor clave que determina la abundancia de las especies arbóreas nativas (Alvarez-Martínez et al., 2014; Hermy & Verheyen, 2007; Navarro-González et al., 2013; Perring et al., 2016). La historia de uso y gestión de nuestros sitios de estudio, inferida a partir de varios trabajos de recopilación histórica (Jiménez-Olivencia et al., 2015; Mesa-Torres, 2009; Moreno-Llorca et al., 2014; Moreno-Llorca et al., 2016; Pérez-Luque et al., 2020; Titos, 1990), señala que ambos sitios estuvieron sometidos a intensos usos antrópicos en el pasado. En las poblaciones de la vertiente norte (por ejemplo, robledal de San Juan), las zonas altas estaban dedicadas al pastoreo, y en las áreas de bosque también había algunas tierras de cultivo con pastoreo, mientras que el robledal de Cáñar (vertiente sur) ha sido explotado para leña, carbón vegetal y bellotas, con menor presencia de uso ganadero. Aunque no hemos podido estimar la intensidad de uso a la que han estado sometidas ambas zonas antes del abandono de los cultivos, la zona norte parece haber tenido una historia de manejo con mayor intensidad de pastoreo que el sitio sur (Moreno-Llorca & Zamora, 2012; Moreno-Llorca et al., 2014; Moreno-Llorca et al., 2016). Por otro lado, es importante conocer la historia de uso tras el abandono del cultivo de montaña, centrándonos en la presión ganadera, ya que la herbivoría impone severas limitaciones al establecimiento y regeneración de esta especie (Gómez et al., 2003; Perea et al., 2014). Aunque no se dispone de datos sobre la evolución temporal de la presión de pastoreo a escala de detalle en nuestros lugares de estudio, varios estudios e informes, combinando entrevistas con pastores y revisión de documentos históricos, han inferido la historia ganadera reciente en varios robledales de Sierra Nevada (Moreno-Llorca & Zamora, 2012; Moreno-Llorca et al., 2014; Moreno-Llorca et al., 2016). Así, se ha observado tanto un mayor número de rebaños y pastores, como una mayor densidad ganadera en el robledal de San Juan (vertiente norte) que en el de Cáñar (vertiente sur), lo que podría traducirse en una mayor presión herbívora. Esta distinta presión herbívora podría explicar las diferencias observadas en la abundancia de robles juveniles tanto en el interior de los cultivos abandonados como en el borde y en el interior del bosque circundante (ver Figura 4.3). La herbivoría, más que los factores abióticos, es la principal causa de mortalidad de plántulas de *Q. pyrenaica* en Sierra Nevada (Gómez et al., 2003), pero las plántulas mueren en su mayoría

por el efecto del pisoteo por parte del ganado silvestre y doméstico, más que por el ramoneo (que es una causa de muerte marginal para las plántulas de roble) (Gómez et al., 2003).

Las diferencias en los patrones de recolonización dentro del borde posterior parecen estar relacionadas con las diferencias en la gestión antes y después del abandono de las tierras de cultivo de montaña. Una mayor presión de herbivoría tras el abandono de las tierras de cultivo parece limitar la expansión del bosque hacia los hábitats marginales. En este sentido, y con el fin de mejorar la expansión del bosque, sería recomendable aprovechar la presencia de arbustos nativos que ofrecen lugares seguros ayudando a reducir la mortalidad de las plántulas de *Q. pyrenaica*, y por lo tanto aumentar las probabilidades de establecimiento de esta especie. Esto también ayudaría a aumentar la heterogeneidad en el desarrollo del bosque secundario que se está estableciendo, lo que aumentaría la resiliencia a las perturbaciones y la recuperación de la multifuncionalidad del ecosistema (Cruz-Alonso et al., 2019; Stritih et al., 2021). Por otro lado, también es necesario prestar atención al mantenimiento de las fuentes semilleras en buen estado de salud (bosques de alrededor), y de una comunidad estable de dispersores de semillas, particularmente del arrendajo, ya que la dispersión de bellotas por parte de esta especie de ave se considera un proceso clave en la regeneración de los bosques de *Quercus* tras el abandono del terreno (Pausas et al., 2006).

Vulnerabilidad de las poblaciones que viven en los márgenes de distribución: el caso de los robledales de Sierra Nevada

Las poblaciones de *Q. pyrenaica* situadas en su borde posterior de distribución presentan una alta sensibilidad a la disponibilidad de agua, siendo generalmente el factor que más limita el crecimiento secundario de esta especie (e.g. capítulo 6, Gea-Izquierdo & Cañellas, 2014). Esta sensibilidad a las variables relacionadas con la humedad se ha observado también en otras especies arbóreas cuyas poblaciones se sitúan en su margen posterior de distribución (e.g. *Abies alba* Martínez-Sancho & Gutiérrez Merino, 2019).

Sin embargo, otras especies son más sensibles a las temperaturas (e.g. *Pinus sylvestris*, Herrero et al., 2013) o responden simultáneamente a las variables relacionadas con la temperatura y la humedad (e.g. *Fagus sylvatica*, Dorado-Liñán et al., 2017a; Dorado-Liñán et al., 2017b; *Pinus nigra* subsp. *salzmanii*, Sánchez-Salguero et al., 2012). Esta diversidad en la respuesta de las especies arbóreas a la precipitación y a la temperatura, sugiere que la vulnerabilidad al cambio climático no se expresa de forma consistente dentro del borde posterior, evidenciando por tanto que los bosques geográficamente marginales no son necesariamente climática o ecológicamente marginales (ver Dorado-Liñán et al., 2019, y las referencias en dicho trabajo).

En el capítulo 6, combinado el uso de la teledetección, la dendrocronología, y la revisión de documentos históricos, hemos constatado que las poblaciones de roble en Sierra Nevada presentan unos altos valores de resiliencia a la sequía (crecimiento primario y secundario). Estos valores junto con el papel potencial de la adaptación local (e.g. altos valores de resiliencia genética para los robledales de Sierra Nevada, Valbuena-Carabaña & Gil, 2013), sugieren que la historia de gestión (usos del suelo) también tiene un papel clave para determinar la resiliencia de los árboles a la sequía en el borde posterior de distribución. Nuestros resultados coinciden con otros estudios que muestran que la supuesta mayor vulnerabilidad a la sequía en las poblaciones situadas en los márgenes geográficos de distribución actual no necesariamente se mantienen (e.g. Cavin & Jump, 2017). En nuestro caso, esto puede explicarse por el hecho de que el actual borde posterior de distribución geográfica no coincide con el potencial borde posterior ecológico de la especie, ya que éste ha sido modificado y determinado en su mayor parte por la intervención del hombre (*i.e.* historia de uso).

Los valores de resiliencia, resistencia y recuperación de los robledales de Sierra Nevada tras los eventos de sequía están fuertemente influenciados por la orientación y las condiciones ambientales locales, así como por la historia de manejo de los mismos. La adaptación y plasticidad local de algunas especies, así como la variación de los factores ambientales a escala local, se consideran factores importantes que determinan la vulnerabilidad de algunas especies en los bordes posteriores de distribución (Martínez-Vilalta, 2018). Asimismo, hemos encontrado una amplia variabilidad de los valores

de resiliencia a pequeña escala en los robledales en Sierra Nevada. Estos resultados sugieren que los márgenes posteriores de distribución geográficos y ecológicos no necesariamente coinciden, y que a escalas espaciales más pequeñas, la vulnerabilidad frente al cambio climático puede variar dentro del propio margen posterior de distribución de la especie.

Las poblaciones de *Q. pyrenaica* en Sierra Nevada están localizadas en un borde marginal geográfico, pero no en un borde marginal ecológico (*sensu* Martínez-Vilalta, 2018; Vilà-Cabrera et al., 2019). Contrariamente a lo esperado, los robles mostraron una alta resiliencia en respuesta a la sequía, especialmente a largo plazo. Estos altos valores pueden estar relacionados con mecanismos estabilizadores que promueven la resiliencia de los individuos adultos ya establecidos (e.g. capacidad de tolerancia al estrés vinculada a la adaptación local Lloret et al., 2012), y que pueden estar amortiguando el impacto de los eventos climáticos extremos, como se ha descrito para otras especies (e.g. *Pinus sylvestris*, Herrero & Zamora, 2014).

Las respuestas de resiliencia del robledal a los eventos de sequía no son espacialmente homogéneas en Sierra Nevada, debido a las diferencias en las condiciones ecológicas y/o a los legados de gestión del pasado. De hecho, existe mucha variabilidad a pequeña escala en la respuesta al clima a lo largo del borde posterior de distribución que no habíamos considerado *a priori*. Las diferencias encontradas en el crecimiento de los árboles, la sensibilidad climática y la resiliencia de los árboles entre sitios muy cercanos mostraron que las respuestas a la sequía dependen del sitio, y pueden variar drásticamente en gradientes espaciales extremadamente estrechos. En las regiones montañosas, la heterogeneidad de las condiciones ecológicas a escalas finas es la regla, lo que permite la existencia de microrrefugios y la prolongación de la persistencia de las especies (Olalde et al., 2002; Serra-Díaz et al., 2015). Esto es especialmente relevante para definir la extensión real y la naturaleza (geográfica y/o ecológica) de las poblaciones del borde posterior, donde la variabilidad topográfica y biofísica facilita la existencia de microrrefugios.

Por otro lado, el análisis de la dinámica de crecimiento arbóreo reveló eventos de supresión y liberación que eran consistentes con los legados de uso inferidos de la revisión exhaustiva de documentos históricos. Esto sugiere

que el concepto de borde posterior necesita ser redefinido en el espacio, pero también en el tiempo (Vilà-Cabrera et al., 2019), en parte debido a la importancia de los legados de uso y su efecto en el posible desajuste entre la distribución actual de las especies (*i.e.* determinando el borde posterior “geográfico disponible”) y el borde posterior ecológico potencial (limitante) de las especies. El concepto de retaguardia o de borde posterior de distribución (*i.e. rear edge*) también debería considerar aspectos históricos además de los geográficos, climáticos y genéticos (Vilà-Cabrera et al., 2019), especialmente en áreas con una larga historia de gestión humana, como las montañas Mediterráneas. Por lo tanto, la modificación antropogénica del hábitat y sus legados representan una dimensión crítica de la marginalidad, ya que pueden intensificar, confundir o retrasar el declive poblacional impulsado por el clima en los bordes posteriores de distribución (Vilà-Cabrera et al., 2019). Esto es relevante para las especies arbóreas muy sensibles al cambio climático, como *Quercus pyrenaica*, no sólo para la conservación *per se* de la especie, sino para todos los servicios ecosistémicos que ofrecen estos bosques. En este sentido, sería necesario analizar la resiliencia de todos los estadios demográficos de las especies, para asegurar que la resiliencia observada en los árboles adultos se manifiesta también en su dinámica de reclutamiento demográfico expresada por la regeneración natural. La resiliencia también podría ser diferente para las distintas cohortes de edad o en las plántulas en comparación con los rebrotes.

Provisión de servicios ecosistémicos de los robledales de Sierra Nevada

Como se ha apuntado a lo largo de esta memoria doctoral, el conocimiento de la dinámica de funcionamiento de los robledales de Sierra Nevada, es fundamental para desarrollar estrategias de gestión adecuadas bajo las incertidumbres climáticas actuales (Fady et al., 2016; Jump et al., 2010). Las poblaciones situadas en los bordes posteriores de su distribución, merecen *per se* una atención especial debido a su alto valor de conservación (Fady et al., 2016). Son poblaciones que suelen estar adaptadas a las condiciones ambientales locales en el límite de la amplitud ecológica de la especie, y

a menudo muestran una persistencia a largo plazo (Hampe & Petit, 2005). Además, las respuestas locales a los cambios ambientales pueden diferir de la respuesta media de la especie (Benavides et al., 2013; Castro et al., 2004; Matías et al., 2017), y estas diferencias pueden favorecer o dificultar la supervivencia de las poblaciones situadas en los límites de distribución en los escenarios de cambio global (Fady et al., 2016; Jump et al., 2010).

Un aspecto importante en el estudio de las poblaciones situadas en los límites de distribución, además de su dinámica de funcionamiento, es la provisión de servicios ecosistémicos considerando tanto los usos del suelo como los escenarios de cambio climático. Como hemos visto en los capítulos 5 y 8, además es importante tener en cuenta cómo ha variado a lo largo de las últimas décadas esta provisión de servicios ecosistémicos; y de cara a la gestión actual, la variabilidad existente de provisión de servicios ecosistémicos entre las diferentes poblaciones de robledal, que pueden ayudar a dirigir las actuaciones de gestión de estas formaciones forestales.

Con respecto al papel de estos bosques como potencial sumidero de carbono, en el capítulo 5 hemos estimado que los robledales de Sierra Nevada presentan unos altos valores de biomasa forestal aérea ($104.69 - 111.71 \text{ Mg ha}^{-1}$, ver Tabla 5.3). Estos resultados son coherentes con los estimados para los ecosistemas forestales montañosos por el IPCC para Europa ($130 (20 - 600) \text{ Mg ha}^{-1}$; IPCC, 2006). Sin embargo, nuestros resultados discrepan con las estimaciones realizadas por diferentes autores para robledales a lo largo de su rango de distribución. Por ejemplo, Vayreda et al. (2012), usando datos del Tercer Inventory Forestal Nacional de España, encontró para los robledales de *Q. pyrenaica*, un valor medio para el stock de carbono de 45 Mg ha^{-1} . Estos valores eran inferiores al stock de carbono estimado en nuestro estudio, que oscilaba entre 69.95 y 74.63 Mg ha^{-1} . A una escala más regional, nuestros resultados mostraron valores más altos que los encontrados por otros trabajos realizados en el rango central de la distribución de la especie, donde la biomasa aérea varió entre $63,8 - 98 \text{ Mg ha}^{-1}$ (Gallardo Lancho & González Hernández, 2004). Asimismo, otras estimaciones del secuestro de dióxido de carbono en rodales puros de *Q. pyrenaica* situados en el Sistema Central (Península Ibérica), arrojaron valores inferiores a los nuestros. A pesar de las posibles diferencias derivadas del método de estimación del carbono (e.g.

estimación utilizando LIDAR vs. estimación usando medidas en campo), otros factores podrían explicar las diferencias encontradas en nuestros resultados con respecto a los valores reportados para otros estudios. En primer lugar, está generalmente aceptado que existe un declive relacionado con la edad en la acumulación de biomasa de los rodales (Xu et al., 2012, y referencias incluidas en ese trabajo), siendo la productividad de los bosques viejos generalmente menor que la de los bosques más jóvenes (Kutsch et al., 2009). Los robledales de Sierra Nevada están compuestos por árboles relativamente jóvenes (Gea-Izquierdo & Cañellas, 2014; Pérez-Luque et al., 2020; Rubio-Cuadrado et al., 2018) en comparación con otros bosques de la especie a lo largo de su área de distribución (Gea-Izquierdo & Cañellas, 2014). Como hemos visto en esta memoria doctoral, las fuertes perturbaciones antrópicas en estos robledales han condicionado su estructura. Por ejemplo, algunos de los robledales fueron masivamente talados durante la época de la posguerra para su uso como gasógeno para los vehículos (e.g. robledal San Jerónimo, MON; Prieto, 1975), o para su uso en intensas actividades mineras (e.g. fundición de mineral en el entorno del robledal de San Juan, GEN Pérez-Luque et al., 2020). Por lo tanto, podemos considerar que muchos de los robledales de Sierra Nevada son relativamente jóvenes, lo que podría explicar el alto potencial de acumulación de C obtenido en nuestro estudio, ya que se ha demostrado que los bosques creados como resultado de cambios drásticos en el uso del suelo exhiben tasas de crecimiento más rápidas, y por lo tanto una mayor acumulación potencial de C, que los bosques preexistentes (Vilà-Cabrera et al., 2017). Asimismo, otros estudios han mostrado diferencias en el stock de carbono entre formaciones jóvenes y bosques maduros para diferentes especies de *Quercus* (Bruckman et al., 2011; Cotillas et al., 2016). Por tanto, es probable que los altos valores de C estimados para los robledales de Sierra Nevada pueda explicarse en parte por el estado de desarrollo de estas masas forestales (Makineci et al., 2015). En segundo lugar, la disponibilidad de agua es generalmente el factor más limitante que impulsa el crecimiento radial del *Q. pyrenaica* a lo largo de su rango de distribución en la Península Ibérica (Gea-Izquierdo & Cañellas, 2014). En Sierra Nevada, los robledales de la vertiente N y NW se localizan en fondos de valle con altos valores de humedad relativa, mientras que las de la vertiente S reciben el aporte extra de agua del aire húmedo

procedente del mar Mediterráneo. Por lo tanto, la disponibilidad de agua no parece estar limitando el crecimiento del roble en esta región montañosa. De hecho, como se comentó previamente, se han observado tendencias positivas para el verdor (EVI) y el crecimiento secundario de los robledales de Sierra Nevada, sugiriendo que Sierra Nevada podría actuar como un refugio ecológico para esta especie. Estas tendencias positivas de crecimiento podrían explicar los altos valores de secuestro de carbono obtenidos en las poblaciones de robledal de Sierra Nevada en comparación con las aportadas por otros estudios, aunque sería necesario realizar un estudio más detallado de las tendencias de crecimiento y la biomasa comparando entre poblaciones situadas en el centro de su distribución y aquellas localizadas en los bordes de distribución.

En el capítulo 8 hemos llevado a cabo una revisión exhaustiva de los principales servicios ecosistémicos que proporcionan los bosques de roble melojo a nivel general. La recopilación bibliográfica realizada ha mostrado que los servicios ecosistémicos que han sido evaluados con mayor frecuencia corresponden con los servicios de aprovisionamiento. Destacan los estudios centrados en investigar el efecto de la madera de melojo en el proceso de elaboración del vino (e.g. Castro-Vázquez et al., 2013; Fernández de Simón et al., 2010), ya que las barricas se construyen frecuentemente con la madera de esta especie. Además, encontramos diferentes estudios en los que se evalúa la provisión de setas (e.g. Oria-de Rueda et al., 2010), o la producción de madera o biomasa para energía (e.g. Miranda et al., 2009). En cuanto a los servicios de regulación, varios estudios evalúan el papel de los robledales en la calidad y fertilidad del suelo, o su capacidad de secuestro y almacenamiento de carbono (e.g. Alvarez et al., 2014). También hay una alta proporción de estudios sobre el carbono del suelo (e.g. Fonseca et al., 2019). Por último, cabe destacar que con los criterios de búsqueda utilizados (ver capítulo 8), no se ha encontrado ningún estudio sobre la evaluación de los servicios culturales en los bosques de *Quercus pyrenaica*.

Posteriormente, utilizando las poblaciones de roble melojo de Sierra Nevada como caso de estudio, hemos explorado la variación espacio-temporal de la provisión de servicios ecosistémicos por parte de esta formación forestal. Combinamos conocimiento experto y diferentes fuentes de datos (literatura

gris, datos de proyectos de investigación, programas de seguimiento, etc) para cuantificar en la medida de lo posible los servicios ecosistémicos proporcionados por estos bosques. Respecto al patrón espacial, hemos podido observar cómo existen diferencias de provisión de servicios ecosistémicos entre las poblaciones de robledal en Sierra Nevada. Los robledales de la vertiente sur de Sierra Nevada presentan mayores valores de servicios de regulación, mientras que los robledales situados en la vertiente norte exhiben mayores valores para los servicios culturales. Nuestra recopilación de datos a nivel local nos ha permitido cuantificar muchos de los servicios ecosistémicos suministrados por los bosques de *Q. pyrenaica* en Sierra Nevada, lo que podría ayudar a los gestores de recursos naturales con más información y herramientas para ayudarles en el proceso de toma de decisiones.

En cuanto a los servicios de regulación evaluados, observamos que los robledales situados en la vertiente sur de Sierra Nevada presentan valores más altos para el potencial de secuestro de carbono, el EVI medio y el carbono orgánico del suelo que el resto de poblaciones de robledal, a pesar de la esperada mayor vulnerabilidad debido a su localización en las zonas más meridionales de Sierra Nevada. Estos resultados están en consonancia con los resultados encontrados en otros trabajos (ver capítulo 6), que destacaban mayores valores de resiliencia a las perturbaciones de los robledales de la vertiente sur. Para los servicios culturales, los robledales situados en el noroeste de Sierra Nevada presentan valores elevados para las actividades deportivas, el número de visitantes y la densidad de los protocolos de muestreo (valor científico). Finalmente, para los servicios de provisión, observamos un patrón variable en función del servicio evaluado. Esta cuantificación de algunos de los servicios ecosistémicos proporcionados por las poblaciones de roble melojo en Sierra Nevada, nos ha permitido comparar el suministro de servicios ecosistémicos entre dichas poblaciones, y describir qué categoría de servicios ecosistémicos predomina en cada uno de los grupos de poblaciones de roble en Sierra Nevada. Por otro lado, hemos observado un patrón temporal de suministro de servicios ecosistémicos condicionado principalmente por los usos antrópicos a los que ha estado sometido esta formación forestal. Hasta la década de 1970 el suministro de servicios ecosistémicos que predominaba en esta formación era el de abastecimiento y provisión. Aunque los servicios de

regulación podían estar presentes (*e.g.* control de la erosión en algunas zonas escarpadas, por el característico sistema radicular de esta especie), los robledales eran usados como proveedores de leñas, carboneo, pastos para el ganado, bellotas, entre otros (*i.e.* servicios de provisión y abastecimiento). Poco a poco se fueron abandonando algunas actividades tradicionales, lo que provocaba la disminución del suministro de algunos servicios de abastecimiento frente a un ligero incremento de los servicios de regulación por parte del bosque. Posteriormente tras el abandono generalizado de las actividades tradicionales, se produjo una reducción drástica en la provisión de servicios de abastecimiento. Asimismo, debido en parte a la expansión del bosque hacia cultivos abandonados, y a la densificación de las masas de robledal existente, se aumentó la provisión de servicios de regulación (*e.g.* regulación climática, secuestro de carbono). Por otro lado, fruto de las políticas de protección de los recursos naturales (*e.g.* declaración de espacio natural protegido) y de un aumento de la concienciación sobre los valores ambientales que proporciona la naturaleza (Mace, 2014), entre otras razones, se produjo un aumento de la provisión de servicios culturales por parte de estas formaciones forestales.

Además de la evolución temporal de la provisión de servicios ecosistémicos, nuestro trabajo también añade algunas ideas interesantes para el estudio de los servicios ecosistémicos proporcionados por los robledales. Por ejemplo, observamos un patrón temporal muy variable de algunos servicios ecosistémicos, como el valor recreativo. Algunos bosques de melojo de Sierra Nevada concentran gran parte de los visitantes registrados en el Espacio Natural de Sierra Nevada durante un periodo de tiempo concreto. Esto pone de manifiesto la necesidad de considerar la dimensión temporal de los servicios ecosistémicos evaluados, y de prestar atención a la presión que estos ecosistemas pueden estar sufriendo temporalmente debido al elevado número de visitantes. Por lo tanto, desde el punto de vista de la gestión de los recursos naturales, no sólo es necesario analizar los servicios ecosistémicos que proporciona un ecosistema, sino que también habría que considerar el patrón espacio-temporal de la oferta de dichos servicios. En este sentido, sería interesante realizar estudios detallados para proporcionar a los gestores una evaluación completa de los posibles impactos de los visitantes. Consideramos por tanto, que nuestra recopilación de datos a nivel local nos

ha permitido cuantificar muchos de los servicios ecosistémicos suministrados por los bosques de *Q. pyrenaica*, lo que proporciona a los gestores información y herramientas clave para ayudarles en el proceso de toma de decisiones.

Parte IV

Conclusiones

Conclusiones

1. Las poblaciones de *Quercus pyrenaica* situadas en límite meridional de su distribución y que se localizan en zonas de montaña, no son ecológicamente homogéneas, ni por sus condiciones ambientales ni por su composición de especies vegetales. En Sierra Nevada, la diversidad de "comportamientos" ecológicos que muestran las poblaciones de *Q. pyrenaica*, es consistente con la alta diversidad genética de dichas poblaciones.
2. La disponibilidad de agua es una variable clave que explica la distribución del roble melojo en Sierra Nevada, así como la diversidad florística de las comunidades vegetales que le acompañan.
3. Para Sierra Nevada, se han identificado tres grupos de poblaciones de *Q. pyrenaica*. Estos grupos de poblaciones presentan diferencias respecto a la diversidad vegetal que albergan. Se ha encontrado una notable coincidencia entre la agrupación de poblaciones derivada del análisis de las variables ambientales y la ordenación de las poblaciones según la composición de especies.
4. La identificación de diferencias, tanto en condiciones ambientales como en composición florística, entre los grupos de poblaciones de robledal dentro del límite sur de su distribución, puede servir de ayuda en la planificación de la gestión forestal y las actuaciones de restauración de estas poblaciones, particularmente considerando la importancia de algunos factores ambientales (e.g. disponibilidad de agua) en aspectos ecológicos clave.
5. A pesar de las fuertes limitaciones de reclutamiento descritas para *Q. pyrenaica*, se ha observado la existencia de un proceso de recolonización natural de los cultivos de montaña abandonados por parte de *Q. pyrenaica*. El robledal está siendo capaz de colonizar zonas abandonadas dentro de la misma banda altitudinal donde habita. Teniendo en cuenta las previsiones de cambio climático, sería interesante estudiar la capacidad de colonización por encima de su límite altitudinal.

6. El proceso de recolonización de cultivos abandonados por parte de *Q. pyrenaica* está condicionado por el uso previo y posterior al abandono del cultivo. En Sierra Nevada, se han observado diferencias en la recolonización de los cultivos por parte del *Q. pyrenaica*. Diferentes historias de manejo condicionan la abundancia de regeneración dentro de los cultivos abandonados. Así, una mayor presión herbívora tras el abandono de las tierras de cultivo parece limitar la expansión del bosque hacia éstas tierras.
7. Los robledales de Sierra Nevada, al igual que los del resto de la Península Ibérica, han experimentado un aumento de la biomasa total en las últimas décadas. La biomasa total estimada para los robledales de *Q. pyrenaica* en Sierra Nevada asciende a 9.94 Tg (1 Tg = 10^{12} g), lo que representa un secuestro potencial de CO₂ de 17.33 Tg.
8. Los robledales de Sierra Nevada, a pesar de estar situados en el límite sur de su distribución, presentan un alto potencial de secuestro de Carbono. Los datos estimados de stock de Carbono para los robledales de Sierra Nevada son superiores a los observados para otras zonas. Estas diferencias parecen estar relacionadas con el hecho de que los robledales de Sierra Nevada son relativamente más jóvenes en comparación con otros robledales (debido al intenso uso antrópico al que han estado sometidos). No obstante sería necesario realizar estudios que analicen en profundidad las diferencias en la capacidad de secuestro de carbono de esta formación a lo largo de su rango de distribución, y los factores que las explican.
9. Existen diferencias respecto al potencial de secuestro de Carbono entre las poblaciones de robledal de Sierra Nevada. Aquellas poblaciones que han estado sometidas a menos perturbaciones antropogénicas presentan una mayor riqueza estructural, que se ve reflejado en valores mas altos de biomasa, y por tanto, en un mayor potencial de secuestro de carbono.
10. El aumento de temperatura registrado en las últimas decadas está ocasionando cambios en la dinámica de los ecosistemas de montaña. Mediante el uso de un sistema de ontologías se ha observado

la concurrencia de cambios en el patrón de innovación y en la productividad de los robledales de Sierra Nevada. En las zonas donde se ha detectado un adelanto en la fecha de fusión de la nieve, también se ha observado un aumento significativo en la productividad primaria de verano para los robledales. Esta modificación en los patrones de disponibilidad de agua debido al cambio climático parece estar afectando a la productividad estacional de los robledales. Este acoplamiento entre las tendencias de producción primaria y las de duración de la nieve es más patente para las poblaciones de robledales occidentales de Sierra Nevada, donde el 60% de los pixeles muestran un adelanto en la fecha de retirada de la nieve y un aumento de la productividad en verano.

11. Los robledales proporcionan una gran cantidad de servicios ecosistémicos. Además del papel que presentan estos bosques como proveedores de servicios de regulación (*e.g* sumidero de Carbono) o de provisión (*e.g.* uso de su madera para el envejecimiento del vino), se ha puesto de manifiesto la existencia de un gran número de servicios ecosistémicos culturales proporcionados por los bosques de *Q. pyrenaica*. La revisión de servicios ecosistémicos realizada para los robledales de Sierra Nevada, combinando criterio experto junto con datos locales, proporciona a los gestores del territorio una información muy valiosa que puede ayudar en la planificación de actuaciones de gestión y conservación de esta formación forestal.
12. Los robledales localizados en el límite sur de su área de distribución muestran una gran resiliencia a la sequía. El crecimiento primario y secundario de esta especie, aún siendo muy sensible a la disponibilidad de agua, mostró una alta resiliencia a corto y largo plazo a los eventos de sequía. Los altos valores de resiliencia observados sugieren que las poblaciones de robledal de Sierra Nevada se encuentran en el borde posterior geográfico pero no climático ni ecológico.
13. En los últimos años se ha observado una tendencia positiva en la productividad primaria y en el crecimiento secundario de los robledales de Sierra Nevada. Esto podría estar relacionado con un efecto positivo del calentamiento para las especies que se encuentran en lugares de

alta elevación limitados por el frío. Asimismo, es importante destacar que esta respuesta es diferente a la tendencia negativa de crecimiento que cabría esperar para las poblaciones situadas en el borde sur de su distribución, tal y como se ha observado para otras especies templadas y mediterráneas.

14. La resiliencia a la sequía que muestran los robledales de Sierra Nevada no es espacialmente homogénea, debido a las diferencias en las condiciones ecológicas y a los legados del uso del suelo. La gran variabilidad en las respuestas entre sitios muy cercanos geográficamente, y que se manifiesta a través de diferencias en el crecimiento, distinta sensibilidad climática y diferente resiliencia a la sequía, parece indicar que las respuestas a la sequía son dependientes del sitio y pueden variar drásticamente en gradientes espaciales extremadamente estrechos, como los que ocurren en regiones de montaña.
15. El concepto de borde posterior de distribución de una especie, necesita considerar los usos del pasado como un aspecto más, además de los aspectos geográficos, climáticos y genéticos, sobre todo en regiones con una larga tradición de modificaciones antropogénicas del territorio.

Conclusions

1. The rear-edge populations of *Quercus pyrenaica* located in mountain areas are not ecologically homogeneous, neither for their environmental conditions nor for their plant species composition. The diversity of ecological behaviors for *Q. pyrenaica* populations in Sierra Nevada are consistent with the high genetic diversity shown by populations of this oak in this rear edge.
2. Water availability is a key variable explaining the distribution of melojo oak and the floristic diversity of their accompanying communities in Sierra Nevada.

3. For Sierra Nevada, three clusters of *Q. pyrenaica* populations were identified based on environmental variables. These population groups also differ in terms of the plant diversity they harbor. A remarkable match between the populations clustering derived from analysis of environmental variables and the ordination of the populations according to species composition was found.
4. The identification of differences, both in environmental conditions and floristic composition, between groups of oak woodland populations within the southern limit of their distribution, can help in the planning of forest management and restoration actions for these populations, particularly considering the importance of some environmental factors (e.g. water availability) in key ecological aspects.
5. A colonization process of *Q. pyrenaica* into abandoned croplands in the Sierra Nevada mountain region has been observed despite the strong recruitment constraints described for this species. The melojo oak is being able to colonize abandoned areas within the same altitudinal level where it lives. Considering the climate change forecasts, it would be interesting to study the colonization capacity above its altitudinal limit.
6. The recolonization of abandoned mountain croplands by *Q. pyrenaica* is conditioned by the previous- and post-abandonment use of the croplands. In Sierra Nevada, differences have been observed in the recolonization of crops by the *Q. pyrenaica*. Different management histories condition the abundance of regeneration of *Q. pyrenaica* within abandoned crops. Thus, increased herbivory pressure after the abandonment of croplands seems to limit the expansion of the forest into mountain croplands.
7. The *Q. pyrenaica* forests of Sierra Nevada, like those of the rest of the Iberian Peninsula, have experienced an increase in total biomass in recent decades. The total biomass estimated for oak woodlands in the Sierra Nevada amounts to 9.94 Tg (1 Tg = 10^{12} g), which represents a potential CO₂ sequestration of 17.33 Tg.

8. The oak forests of Sierra Nevada, despite being located at the rear-edge of their distribution, have a high potential for carbon sequestration. The estimated values of carbon stock for the Sierra Nevada *Q. pyrenaica* forests are higher than those observed for other areas. These differences seem to be related to the relatively younger age of the *Q. pyrenaica* trees of Sierra Nevada compared to other oak forests (due to the intense anthropic use to which they have been subjected). However, it would be necessary to carry out studies that analyze in depth the differences in the carbon sequestration capacity of this formation throughout its distribution range, and the factors that explain them.
9. There are differences in carbon sequestration potential among *Q. pyrenaica* populations in the Sierra Nevada. Those populations that have been subjected to less anthropogenic disturbances have a greater structural richness, which is reflected in higher biomass values, and therefore, in a greater potential for carbon sequestration.
10. The increase in temperature recorded in recent decades is causing changes in the dynamics of mountain ecosystems. Using an ontology system, the concurrence of changes in the snowfall pattern and productivity of Sierra Nevada oak forests has been observed. In areas where an earlier snowmelt date has been detected, a significant increase in summer primary productivity has also been observed for *Q. pyrenaica* woodlands. This modification in water availability patterns due to climate change appears to be affecting the seasonal productivity of oak woodlands. This coupling between primary production and snow duration trends is most apparent for the western oak woodland populations of the Sierra Nevada, where 60% of the pixels show an earlier snow melting date and an increase in summer productivity.
11. Melojo woodlands provide a large number of ecosystem services. In addition to the role of these forests as providers of regulating services (carbon sink) or provisioning services (use of their wood for wine aging), a large number of cultural ecosystem services provided by oak forests have been highlighted. The review of ecosystem services supplied by Sierra Nevada *Q. pyrenaica* forests, combining expert criteria with local data, provides to natural resource managers with

more information and tools to help them in the decision-making process (e.g. conservation actions for the *Q. pyrenaica* woodlands).

12. *Q. pyrenaica* forests located in the southern limit of its distribution area shown a great resilience to drought. Trees were highly sensitive to moisture availability, but both primary growth and secondary growth expressed high resilience to drought events over the short and the long term. The high values of resilience observed suggest that the Sierra Nevada *Q. pyrenaica* populations are located in a geographical but not a climatic or ecological rear edge.
13. A positive trend in primary productivity and secondary growth of Sierra Nevada *Q. pyrenaica* woodlands has been observed in recent years. This could be related to a positive effect of warming for species found in cold-limited high elevation sites. It is also important to note that this response is different from the negative growth trend that would be expected for populations at the southern edge of their distribution, as has been observed for other temperate and Mediterranean species.
14. Resilience of Sierra Nevada *Q. pyrenaica* woodlands to drought events was not spatially homogeneous across the mountain range, due to differences in ecological conditions and/or past management legacies. The large variability in responses among close neighboring sites, manifested by differences in tree growth, climatic sensitivity, and tree resilience, suggests that responses to drought are site-dependent and could drastically vary in extremely narrow spatial gradients, such as those occurring in mountainous regions.
15. The rear-edge concept should also consider historical aspects in addition to the geographic, climatic, and genetic ones, particularly in areas with a long history of human management, such as Mediterranean mountains.

Parte V

Bibliografía y Apéndices

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Material Suplementario del Capítulo 3

Tab. A.1. Species present in each population.

Scientific name	CAM	GEN	MON	DIL	DUR	CAN	POQ	TRE
<i>Acer opalus</i> subsp. <i>granatense</i>	1		1	1				
<i>Adenocarpus decorticans</i>	1	1	1	1	1		1	1
<i>Agrostis canina</i>	1							
<i>Andryala integrifolia</i>								1
<i>Arenaria armerina</i> subsp. <i>armerina</i>	1							
<i>Armeria villosa</i> subsp. <i>bernisii</i>	1		1		1			
<i>Arrhenatherum elatius</i> subsp. <i>bulbosum</i>				1		1		
<i>Artemisia absinthium</i>					1			
<i>Artemisia barrelieri</i>					1			
<i>Artemisia campestris</i> subsp. <i>glutinosa</i>	1	1	1	1	1	1		1
<i>Avenula bromoides</i> subsp. <i>pauneroi</i>		1	1	1	1			
<i>Berberis hispanica</i>	1		1	1				1
<i>Brachypodium retusum</i>				1				1
<i>Carlina corymbosa</i>	1				1		1	1
<i>Carthamus lanatus</i>		1			1	1		1
<i>Celtis australis</i>				1				
<i>Centaurea monticola</i>							1	
<i>Centaurea ornata</i>		1						
<i>Centaurea pulvinata</i>				1				
<i>Cerastium gibraltaricum</i>	1		1		1			1
<i>Chondrilla juncea</i>	1							
<i>Cirsium odontolepis</i>					1			
<i>Cirsium pyrenaicum</i>							1	
<i>Clematis vitalba</i>					1			
<i>Clinopodium vulgare</i> subsp. <i>arundanum</i>	1		1					

<i>Corynephorus canescens</i>		1	1			
<i>Cotoneaster granatensis</i>	1		1	1		
<i>Crataegus granatensis</i>	1					
<i>Crataegus monogyna</i> subsp. <i>brevispina</i>	1	1	1	1	1	1
<i>Crocus nevadensis</i>	1					
<i>Cytisus galianoi</i>	1					
<i>Cytisus scoparius</i> subsp. <i>reverchonii</i>	1		1	1	1	
<i>Dactylis glomerata</i>	1	1				
<i>Dactylis glomerata</i> subsp. <i>hispanica</i>			1	1	1	1
<i>Daphne gnidium</i>						1
<i>Dianthus pungens</i> subsp. <i>brachyanthus</i>			1	1	1	
<i>Digitalis purpurea</i>		1				
<i>Echinospartum boissieri</i>			1			
<i>Elymus hispanicus</i>	1					
<i>Erinacea anthyllis</i>						1
<i>Eryngium campestre</i>	1	1	1		1	1
<i>Euphorbia characias</i>				1	1	1
<i>Euphorbia nevadensis</i>				1		
<i>Festuca elegans</i>	1		1			1
<i>Festuca hystrix</i>			1	1		
<i>Festuca indigesta</i>	1			1	1	1
<i>Festuca scariosa</i>	1	1				
<i>Fraxinus angustifolia</i>		1				
<i>Genista cinerea</i> subsp. <i>speciosa</i>			1			
<i>Genista versicolor</i>	1			1	1	1
<i>Halimium atriplicifolium</i>				1		1
<i>Helianthemum hirtum</i>	1		1		1	
<i>Helichrysum italicum</i> subsp. <i>serotinum</i>					1	1
<i>Helleborus foetidus</i>	1	1	1	1		1
<i>Hieracium pilosella</i> subsp. <i>tricholepium</i>	1				1	
<i>Hormatophylla spinosa</i>	1				1	
<i>Hypericum perforatum</i>			1		1	1
<i>Juncus effusus</i>						1
<i>Juniperus communis</i>	1					
<i>Juniperus sabina</i>	1					
<i>Koeleria vallesiana</i>	1			1	1	1
<i>Lathyrus pratensis</i>					1	
<i>Lonicera arborea</i>	1	1			1	
<i>Marrubium supinum</i>	1				1	1
<i>Ononis aragonensis</i>			1	1		
<i>Ononis spinosa</i>		1		1		1
<i>Phlomis crinita</i>						1
<i>Pistacia terebinthus</i>		1				
<i>Plantago lanceolata</i>						1
<i>Plantago radicata</i> subsp. <i>granatensis</i>	1					
<i>Populus nigra</i>					1	
<i>Potentilla reuteri</i>	1				1	
<i>Prunus avium</i>	1	1				
<i>Prunus dulcis</i>			1			
<i>Prunus mahaleb</i>		1				
<i>Prunus ramburii</i>	1					1
<i>Ptilostemon hispanicus</i>					1	1
<i>Quercus coccifera</i>		1				

<i>Quercus faginea</i>		1					
<i>Quercus ilex</i> subsp. <i>ballota</i>	1		1		1	1	1
<i>Quercus pyrenaica</i>	1	1	1	1	1	1	1
<i>Retama sphaerocarpa</i>			1				
<i>Ridolfia segetum</i>			1				1
<i>Rosa canina</i>	1	1	1	1	1	1	1
<i>Rosa corymbifera</i>		1					
<i>Rosa micrantha</i>							1
<i>Rosa pouzinnii</i>		1					
<i>Rosa sicula</i>		1					
<i>Rubus ulmifolius</i>	1	1		1	1		1
<i>Rumex induratus</i>				1			
<i>Salix caprea</i>				1			
<i>Sanguisorba minor</i>		1			1		1
<i>Santolina rosmarinifolia</i> subsp. <i>canescens</i>					1		
<i>Santolina rosmarinifolia</i> subsp. <i>rosmarinifolia</i>	1		1				
<i>Scabiosa turolensis</i>		1					
<i>Sedum forsterianum</i>		1					
<i>Sedum sediforme</i>		1					1
<i>Silene mellifera</i>			1	1			1
<i>Smilax aspera</i>		1					
<i>Solidago virgaurea</i>			1				
<i>Sorbus aria</i>	1		1				
<i>Teucrium capitatum</i>			1				
<i>Teucrium similatum</i>		1					
<i>Thymus mastichina</i>	1			1		1	1
<i>Thymus serpyloides</i> subsp. <i>serpyloides</i>					1		1
<i>Thymus zygis</i>						1	1
<i>Vicia sp.</i>		1	1		1		
<i>Vinca difformis</i>				1			
Total	54	25	34	31	32	14	17
							36

B

Material Suplementario del Capítulo 5

Tab. B.1. Predictor variables selected for each model obtained to estimate each biomass fraction from LIDAR data.

Biomass fraction	Predictors	RMSE	RMSF (%)	R ²
W_{stem}	Rumple index Elevation (m) 99th percentile of canopy height (m) Maximum canopy height (m)	64.1	54.5	0.4489
W_{root}	Rumple index Cover estimate (%) (All_cover_above_mean) Elevation (m) 99th percentile of canopy height (m) Proportion of returns with height between 2-5m compared to all returns (%) Maximum canopy height (m)	25	49.4	0.3364
W_{b2}	Rumple index Elevation (m) Canopy cover (%) (FIRST RETURNS_1st_cover_above_mean) Canopy cover (%) (FIRST RETURNS_all_1st_cover_above_mean) CV canopy height (m) (FIRST RETURNS_elev_CV_0p5plus) 99th percentile of canopy height (m) Proportion of returns with height between 2-5m compared to all returns (%)	3.9	44.2	0.1681
$W_{\text{b2-7}}$	Rumple index Elevation (m) 99th percentile of canopy height (m) Maximum canopy height (m)	9.2	52	0.4761
W_{total}	Rumple index Elevation (m) 99th percentile of canopy height (m) Maximum canopy height (m)	94	48	0.4761

Tab. B.2. Biomass (Mg ha^{-1}) and Potential carbon sequestration (Mg ha^{-1}) values for Pyrenean oak populations in Sierra Nevada. Different letters indicate statistically significant differences between sites (Kruskal-Wallis test followed by Dunn's test, $p < 0.05$).

Pyrenean oak population									
	CAM	GEN	MON	DIL	DUR	CAN	POQ	TRE	
W _{stem}	84.29 ± 0.50 a	82.50 ± 0.46 a	109.32 ± 0.83 d	68.61 ± 0.97 c	63.71 ± 0.88 c	93.51 ± 0.51 b	86.85 ± 0.51 e	85.06 ± 0.75 ae	
W _{b2-7}	8.71 ± 0.04 a	8.15 ± 0.03 e	9.90 ± 0.06 f	7.41 ± 0.07 c	7.11 ± 0.07 d	8.36 ± 0.03 b	8.44 ± 0.04 g	8.25 ± 0.05 b	
W _{b2}	13.16 ± 0.08 a	13.01 ± 0.08 a	17.17 ± 0.14 d	10.88 ± 0.16 c	9.85 ± 0.14 c	14.91 ± 0.09 b	13.81 ± 0.09 e	13.47 ± 0.13 ae	
W _{root}	49.32 ± 0.21 a	43.80 ± 0.18 e	60.33 ± 0.35 f	41.70 ± 0.44 c	39.30 ± 0.38 d	48.47 ± 0.19 ab	47.79 ± 0.21 b	46.07 ± 0.29 g	
W _{total}	152.06 ± 0.81 a	142.12 ± 0.74 d	193.77 ± 1.37 e	124.91 ± 1.59 c	117.67 ± 1.45 c	162.95 ± 0.83 b	154.21 ± 0.84 f	151.19 ± 1.22 a	
C _{root}	85.98 ± 0.37 a	76.36 ± 0.32 e	105.17 ± 0.61 f	72.69 ± 0.76 c	68.51 ± 0.66 d	84.50 ± 0.33 ab	83.32 ± 0.37 b	80.31 ± 0.51 g	
C _{stem}	146.93 ± 0.86 a	143.82 ± 0.80 a	190.57 ± 1.45 d	119.61 ± 1.69 c	111.06 ± 1.53 c	163.01 ± 0.89 b	151.40 ± 0.89 e	148.28 ± 1.31 ae	
C _{b2}	22.95 ± 0.15 a	22.68 ± 0.13 a	29.93 ± 0.24 d	18.97 ± 0.28 c	17.17 ± 0.25 c	25.99 ± 0.15 b	24.08 ± 0.15 e	23.48 ± 0.22 ae	
C _{b2-7}	15.19 ± 0.06 a	14.22 ± 0.05 e	17.26 ± 0.11 f	12.92 ± 0.13 c	12.40 ± 0.12 d	14.57 ± 0.06 b	14.71 ± 0.06 g	14.38 ± 0.09 b	
C _{total}	265.07 ± 1.41 a	247.74 ± 1.29 a	337.79 ± 2.38 d	217.76 ± 2.78 e	205.12 ± 2.53 c	284.07 ± 1.44 b	268.83 ± 1.46 f	263.56 ± 2.13 a	

Tab. B.3. Model selection for total (W_{total}), stem (W_{stem}), and root (W_{root}) biomass (Mg ha^{-1}). Models selected in terms of BIC ($\Delta \text{BIC} < 2$ units) are indicated in bold.

Response	covariates	df	logLik	BIC	ΔBIC	weight
W_{total}	Ln Tree density + elevation + Structural diversity index + Structural diversity index:ln Tree density	6	-592.02	1212.0	0.00	0.595
	Ln Tree density + elevation + Structural diversity index	3	-600.47	1214.9	2.91	0.139
	Ln Tree density + elevation + Structural diversity index + Structural diversity index:ln Tree density + Structural diversity index:elevation	5	-596.15	1215.6	3.60	0.098
	Ln Tree density + elevation + Structural diversity index + Structural diversity index:elevation + Structural diversity index	7	-591.57	1215.8	3.76	0.091
W_{stem}	Ln Tree density + elevation + Structural diversity index + Structural diversity index:ln Tree density	6	-545.46	1118.9	0.00	0.672
	Ln Tree density + elevation + Structural diversity index + Structural diversity index:ln Tree density + Structural diversity index:elevation	7	-544.96	1122.6	3.67	0.107
	Ln Tree density + elevation + twi + Structural diversity index + Structural diversity index:ln Tree density	7	-545.12	1122.9	3.99	0.091
	Ln Tree density + elevation + Structural diversity index + elevation:ln Tree density + Structural diversity index:ln Tree density	7	-545.46	1123.6	4.66	0.065
W_{root}	elevation	4	-552.47	1123.6	4.70	0.064
	Ln Tree density + elevation	3	-443.77	901.5	0.00	0.431
	Ln Tree density + elevation + Structural diversity index + Structural diversity index:ln Tree density	6	-437.67	903.3	1.78	0.177
	Ln Tree density + elevation + twi + twi:elevation	5	-440.48	904.3	2.75	0.109
	elevation + twi	4	-443.23	905.1	3.58	0.072

Material Suplementario del Capítulo 6

Tab. C.1. Robust two-way ANOVAs of the resilience metrics of greenness (EVI) and tree growth (BAI) for the two drought events (in 2005 and 2012) and site.

		Resistance		Recovery		Resilience	
Factor		F	p	F	p	F	p
EVI	Drought event	799.9	<0.001	312.0	<0.001	207.2	<0.001
	Site	153.2	<0.001	105.4	<0.001	29.8	<0.001
	Drought event × Site	234.7	<0.001	364.3	<0.001	6.1	0.014
BAI	Drought event	6.0	0.019	29.5	<0.001	44.3	<0.001
	Site	59.3	<0.001	53.1	<0.001	1.3	0.534
	Drought event × Site	32.2	<0.001	4.4	0.134	30.0	<0.001

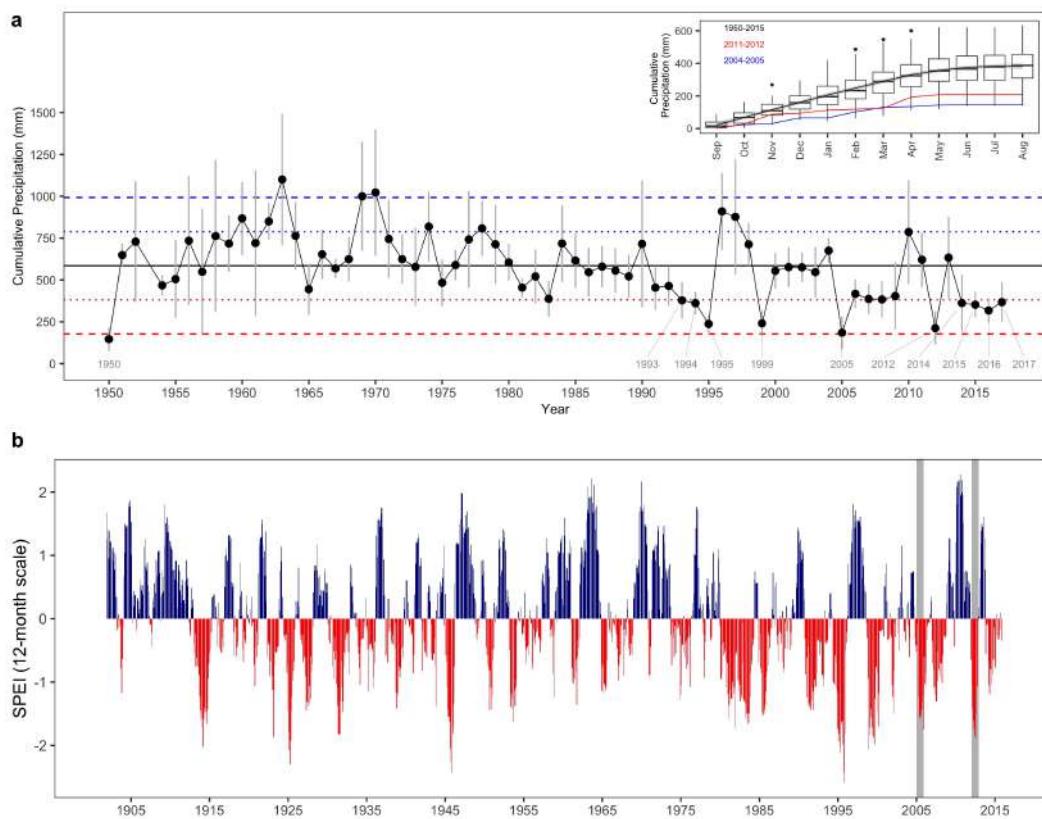


Fig. C.1. a) Temporal evolution of cumulative precipitation (hydrological year) during the period 1950-2017. Points represent the mean, and error bars the standard error. The black line indicates mean for the entire period (585 mm). The red lines represent -1 and -2 standard deviation (dotted and dashed lines, respectively). The blue lines represent +1 and +2 standard deviation (dotted and dashed lines, respectively). Years with average values below -1SD are labeled. Data from 28 meteorological stations distributed around the Sierra Nevada area (from the National Spanish Meteorological Services, AEMET). Inset plot: cumulative precipitation during the hydrological years 2004-2005 (blue line) and 2011-2012 (red line). The boxplot representing the average from 1950-2015 period. Data from meteorological station Granada, Base Aérea. b) Drought severity in Sierra Nevada for the 1901-2016 period based on the Standardized Precipitation-Evapotranspiration Index (SPEI). Data from Global SPEI database (<http://spei.csic.es/database.html>). We took the SPEI data for a 12-month scale and for all 0.5°grid cells covering Sierra Nevada. Horizontal gray bars indicate the years 2005 and 2012.

Tab. C.2. Drought events for the 1901-2016 period for Sierra Nevada ranked according to drought severity calculated from the SPEI index (12 months scale).

Duration (months)	Intensity	Severity	Lowest SPEI	Months	Year
11	-1.957	21.524	-2.585	Jan - Nov	1995
11	-1.581	17.391	-2.024	Nov - Sep	1913-1914
9	-1.823	16.409	-2.42	May - Jan	1945-1946
9	-1.764	15.88	-2.056	Dec - Aug	1998-1999
8	-1.482	11.859	-1.654	Feb - Sep	1983
6	-1.728	10.367	-1.906	Mar - Aug	2012
5	-1.905	9.527	-2.3	Jan - May	1925
5	-1.522	7.611	-1.571	May - Sep	2005
5	-1.493	7.463	-1.537	May - Sep	1985
5	-1.385	6.926	-1.444	Apr - Aug	1991
4	-1.714	6.855	-1.833	May - Aug	1931
4	-1.363	5.453	-1.441	May - Aug	1927

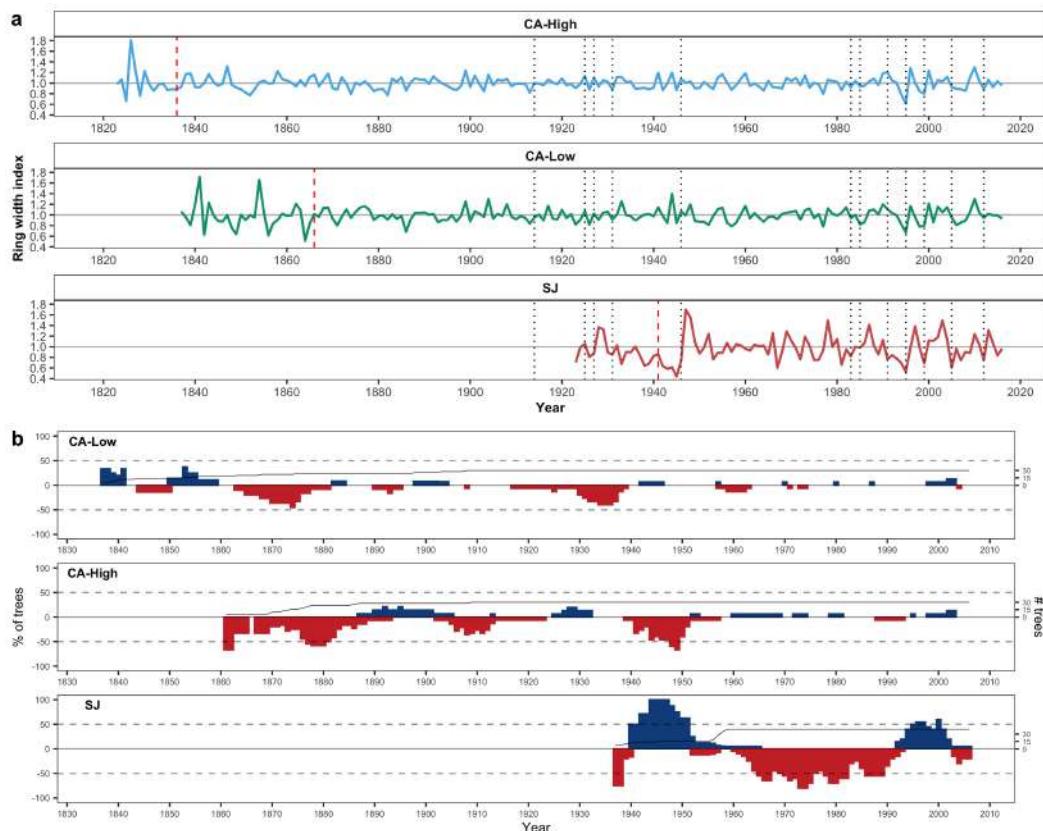


Fig. C.2. a) Residual tree-ring chronologies determined for the *Q. pyrenaica* sites. Dashed red lines indicate the start of the reliable period ($\text{EPS} > 0.85$). Dotted black lines show the severe drought years identified in our climatic data (Table S3 and Figure S1). b) Percentage of *Q. pyrenaica* trees affected by GC > 50 % by site. Black line shows number of trees (right-axis). Data for number of trees > 2 is shown.

Tab. C.3. Robust measures of central tendency of resilience indices for greenness (EVI) and tree growth (BAI), grouped by drought events, site, and interaction. Measures of central tendency are M-estimators based on Huber's Psi. In parentheses are the 95% confidence intervals using 3000 bootstraps. Total corresponds to the average of 2005 and 2012

Variable	Sites	2005			2012			Total		
		Resistance	Recovery	Resilience	Resistance	Recovery	Resilience	Resistance	Recovery	Resilience
EVI	Northern slope	0.819 (0.814 - 0.824)	1.169 (1.161 - 1.177)	0.955 (0.951 - 0.960)	0.947 (0.942 - 0.952)	1.042 (1.036 - 1.047)	0.986 (0.980 - 0.990)	0.884 (0.878 - 0.889)	1.102 (1.096 - 1.108)	0.97 (0.967 - 0.974)
	Southern slope	0.902 (0.896 - 0.907)	1.066 (1.058 - 1.074)	0.962 (0.957 - 0.966)	0.939 (0.934 - 0.944)	1.071 (1.067 - 1.075)	1.004 (1.000 - 1.008)	0.921 (0.917 - 0.925)	1.069 (1.065 - 1.073)	0.983 (0.980 - 0.986)
All	All	0.858 (0.854 - 0.863)	1.12 (1.113 - 1.126)	0.958 (0.955 - 0.962)	0.943 (0.940 - 0.947)	1.057 (1.054 - 1.060)	0.995 (0.991 - 0.998)			
	CA:High	0.892 (0.809 - 0.975)	0.887 (0.800 - 0.973)	0.79 (0.691 - 0.888)	0.753 (0.686 - 0.820)	1.107 (1.026 - 1.188)	0.813 (0.741 - 0.885)	0.816 (0.755 - 0.876)	0.996 (0.917 - 1.075)	0.798 (0.744 - 0.851)
CA:Low	All	0.901 (0.813 - 0.989)	0.832 (0.733 - 0.932)	0.73 (0.612 - 0.849)	0.926 (0.900 - 0.953)	0.952 (0.889 - 1.015)	0.876 (0.839 - 0.913)	0.921 (0.883 - 0.958)	0.897 (0.843 - 0.951)	0.817 (0.755 - 0.879)
	SJ	0.445 (0.375 - 0.516)	1.112 (1.000 - 1.224)	0.489 (0.421 - 0.556)	0.769 (0.684 - 0.853)	1.446 (1.322 - 1.569)	1.031 (0.930 - 1.132)	0.612 (0.539 - 0.685)	1.282 (1.179 - 1.386)	0.769 (0.652 - 0.886)
All	All	0.721 (0.644 - 0.798)	0.946 (0.879 - 1.013)	0.653 (0.585 - 0.721)	0.819 (0.776 - 0.863)	1.161 (1.081 - 1.240)	0.911 (0.865 - 0.957)			

Tab. C.4. Review of the forest and management history of the sampling sites. Historical documents were exhaustively reviewed to compile information on socio-economical activities affecting forests: historical documents and maps (e.g. Titos, 1990); detailed mining reports (e.g. Maestre, 1858); official information on recent wildfire events and forest-management practices (e.g. Bonet et al., 2016); livestock farming (e.g. Moreno-Llorca et al., 2016); traditional irrigation ditches (e.g. Ruiz-Ruiz, 2017) and other studies reviewing the socioeconomic dynamics of forest of Sierra Nevada at different scales (e.g. Jiménez-Olivencia et al., 2015).

Use	Cáñar (CA sites)	Güejar-Sierra (SJ site)	References
Land uses	Oak woodlands mixed with a high percentage of croplands even reached high elevation (mainly barley, rye and potatoes). Irrigated crops near the village (<i>regadío de vega</i>)	Grasslands and shrublands for cattle farming located at high elevations. Then forests formations (oak woodlands) with some croplands (herbaceous mainly and potatoes). Irrigated terraces with tree crops (chestnut trees, cherry trees)	Calatrava and Sayadi (2019); Jiménez-Olivencia et al. (2015); Moreno-Llorca et al. (2016); Zoido and Jiménez Olivencia (2015)
Forest Management Practices	Nearby areas were afforested (pine plantations) to avoid soil erosion in 1925, 1928, 1950 and 1970.	Afforestation of the upper areas of the Genil River basin (1942) Puntual afforestation (creation of small <i>dispersal islands</i>) (2008)	Bonet et al. (2016); Moreno-Llorca et al. (2016); J. Navarro and F.J. Cano-Manuel <i>personal communications</i>
	Selective thinning during 2007 in small area near <i>Casa Forestal</i> Tree cleaning near trails-path (2009-2010)	Tree cleaning (2006 - 2007) near our study site (<i>La Hortichuela</i>) Puntual afforestation (creation of small <i>dispersal islands</i>) (2008)	
Forest structure	Inventories of trees made by the Spanish Navy during the second half of 18th century. For Cáñar site more than two millions of trees were reported, most of them <i>new trees</i> (<i>new trees</i> = 2010200; <i>growing trees</i> : 10791), and no <i>old trees</i> were counted, suggesting recent wood fellings	Inventories of trees made by the Spanish Navy during the second half of 18th century. For San Juan location circa 700000 trees were reported: <i>new trees</i> = 639550; <i>growing trees</i> = 56700; and <i>old trees</i> = 220)	Cruz (1991); Wing (2015)
Fires	Several small fires. 1979: 44 ha of Pyrenean oak forests (near <i>Casa Forestal</i>). 1984: 189 ha of Pine plantation and Holm oak forests (<i>El Jaral</i>). 1994: 65 ha of Pine plantation (<i>Puente Palo</i>)	Not recorded in the area since 1975	Bonet et al. (2014b), CMA (2018), and Moreno-Llorca et al. (2016)
Fruit production (acorns)	Old references have indicated traditional acorn gathering. Auctions of public forests to collect acorns (1927; 1954)		Bonet et al. (2014b); Catastro (1752); Mesa-Torres (2009)
Wood	Traditional charcoal (<i>carboneo</i>) and firewood extraction activities through history. Several references indicated the firewood activity of this site since 1572. At the beginning of the last century (1900s), 3 - 4 woodcutters collected firewood from Pyrenean forests daily.	Some references of wood removal for subsistence (1826; 1847). Massive logging during the first decades of 20th century. As a result, several old photos show areas without trees where oak forests stand today (1925; 1932)	Bonet et al. (2014b); Catastro (1752); Ferrer (1999); López (1776); Mesa-Torres (2009); Madoz (1846); Titos (1997)
Mining activities	No mining in the area, only scattered private excavations	Intermittent exploitation throughout history. Historical documents indicated two periods of intense mining: the second half of the 19th century after the publication of detailed mineralogical reports and during the first decades of the 20th century until 1960, which is the last year with evidence of mining. Evidence of several furnaces to melt minerals (Cooper)	Maestre (1852) ; Maestre (1858); Mesa-Torres (2009); Titos (1990)
Quarries		Exploitation of serpentinites quarries from 16th to 19th century (<i>Jaspe Verde</i>)	Navarro et al. (2014)
Traditional irrigation channels	An irrigation channel (<i>Acequia de la Era Alta</i>) is located uphill of the CA-High site (i.e. >2000 m), which functioned from March to June	Several historical irrigation channels, known as <i>acequias de careo</i> , were used since the Middle Ages to cultivate these valleys. Most are abandoned and deteriorated, probably at least since the 1960s.	Martín-Civantos (2014); Martín-Montañés et al. (2015); Ruiz-Ruiz (2017)

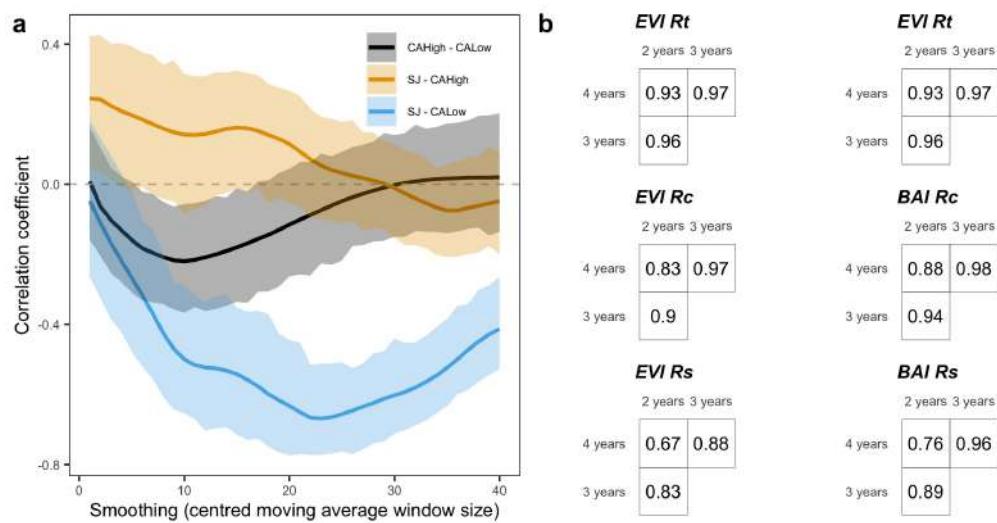


Fig. C.3. a) Correlation among site chronologies (CA-High, CA-Low and SJ) in different time domains after pre-filtering the time series with increasing size of the moving-average window (1 to 40 years). Each site chronology was smoothed using centered moving averages with different window sizes (1 to 40 years), and then Pearson's correlation coefficient between the each pair of chronologies was calculated. Significance was tested using 1000 bootstrap replicates and with 95% confidence intervals built using the R package boot. b) Correlation between indices of resilience (*Rt*, resistance; *Rc*, recovery; *Rs*, Resilience) using periods of several lengths (2, 3 and 4 years after a drought).

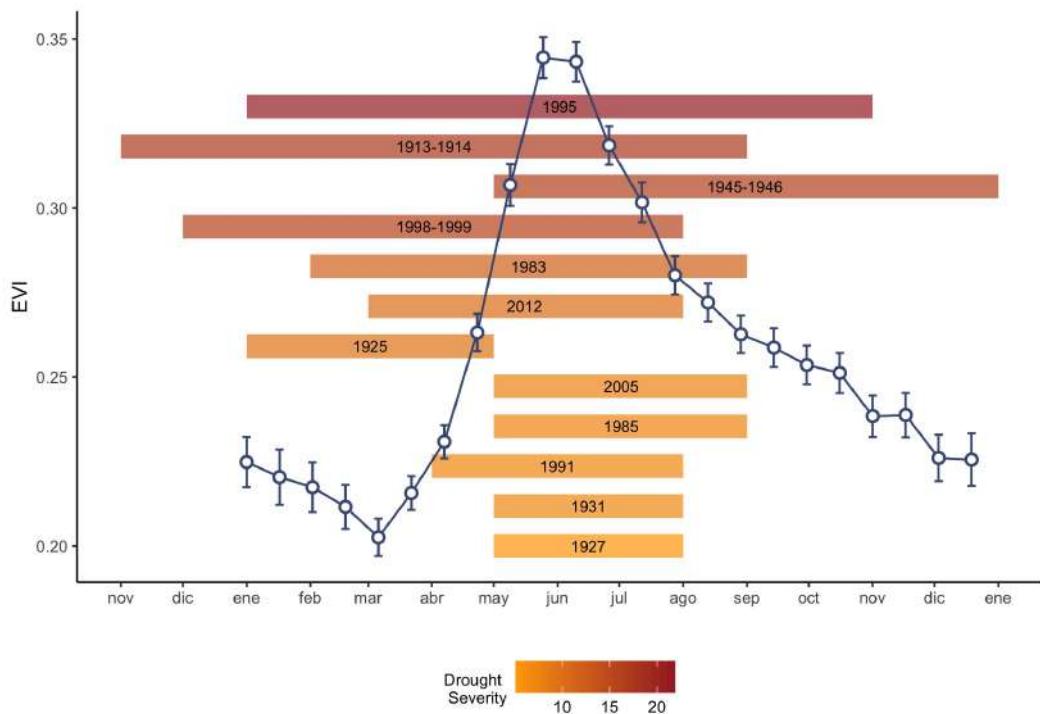


Fig. C.4. EVI annual profile (average of the period 2000-2016) for *Q. pyrenaica* forests in Sierra Nevada and drought events. Horizontal bars correspond to the most severe droughts for Sierra Nevada since 1900 (computed as in Table S3). Their position indicates the start and end months of each drought event. Bars lengths show the duration of the drought event (number of consecutive months with SPEI lower than -1.28, see Páscoa et al., 2017).

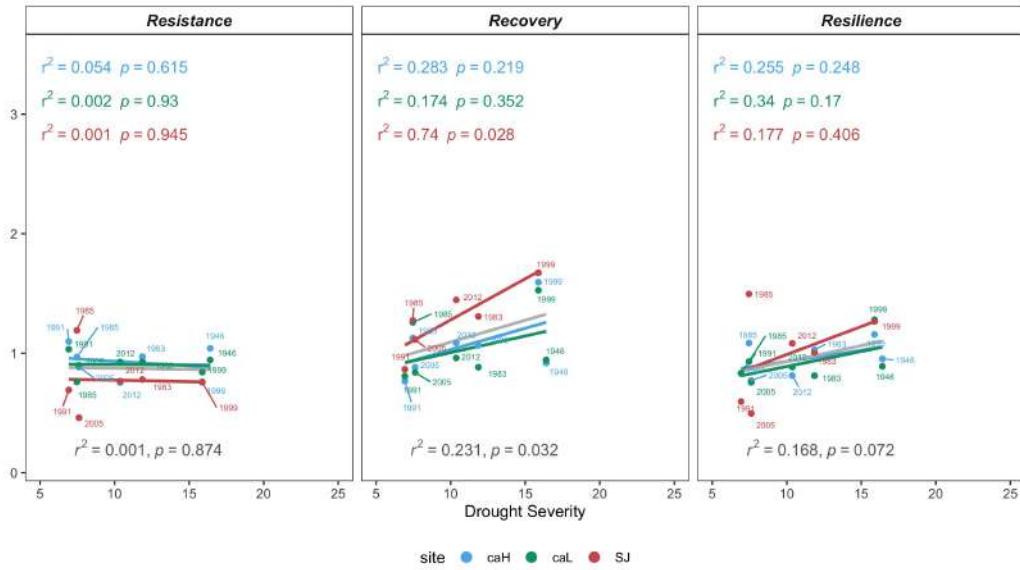


Fig. C.5. Resilience metrics of the tree growth for severe drought events since 1950 (excluding 1995 drought event). Left: Resistance; Center: Recovery; Right: Resilience. Points indicate resilience metrics for oak populations: SJ (blue), CA-High (red) and CA-Low (green). Resilience metrics were computed for each population (sample depth > 10) and drought event. The gray line represents overall relationship for each Resilience metrics.

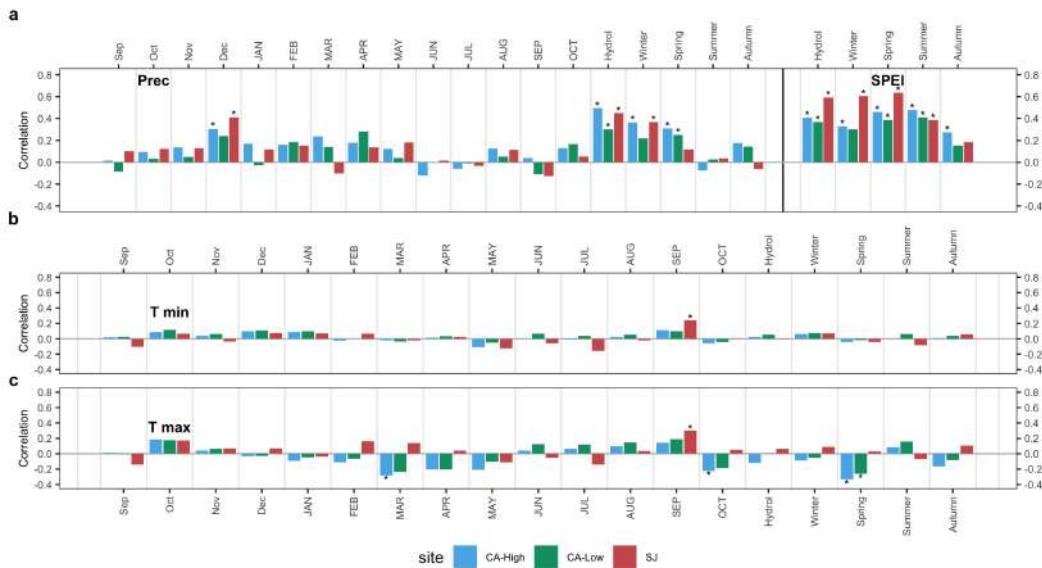


Fig. C.6. Correlation coefficients found by relating tree-ring residual chronologies (RWI) of *Q. pyrenaica* and monthly climatic data: precipitation and 6-month SPEI (a), minimum (b) and maximum (c) temperatures. green bars: northern site (SJ); light blue bars: low-elevation southern site (CA-Low); and dark blue bars: high-elevation southern site (CA-High). Asterisks indicate significant ($p < 0.05$) correlation coefficients.

D

Material Suplementario del Capítulo 8

Tab. D.1. Search terms used in the literature review.

TOPIC (i.e. Title OR Keywords OR Abstract)	Results
"Quercus pyrenaica"	393
"ecosystem service*" OR "ecologic* process*" OR "ecologic* function*" OR "provision*" OR "regulat*" OR "cultural" OR "support*" OR "food" OR "mushroom*" OR "fruit*" OR "berry" OR "berries" OR "cattle" OR "stock" OR "livestock" OR "sheep*" OR "goat*" OR "game" OR "hunt*" OR "wine" OR "fresh water" OR "water supply" OR "drink* water" OR "water yield*" OR "firewood" OR "wood" OR "timber" OR "coal" OR "climat* regulat*" OR "carbon sequest*" OR "carbon stock*" OR "carbon stor*" OR "soil fertilit*" OR "soil nutri*" OR "nutri* cycle*" OR "soil carbon*" OR "organic carbon" OR "water regulat*" OR "soil water" OR "water cycle" OR "water stor*" OR "water qualit*" OR "water depurat*" OR "water filtrat*" OR "water clean*" OR "snow regulat*" OR "snow storage" OR "soil erosion" OR "soil protection" OR "erosion protection" OR "erosion control" OR "soil loss" OR "water erosion" OR "landscape qualit*" OR "aesthetic*" OR "landscape value*" OR "recreation*" OR "social percept*" OR "spiritual value" OR "scientific knowledge"	188

Tab. D.2. Main descriptors of references compiled describing ecosystem services providing by *Q. pyrenaica*.

Main Ecosystem Services	Study area	References
Biomass	Castilla y León	Cañellas et al. (2004)
	Castilla y León	Laina et al. (2013)
	Castilla y León	Río and Sterba (2009)
	Portugal	Nunes et al. (2013)
Biomass, Soil quality	Castilla y León	Rapp et al. (1999)
Carbon sequestration	Guadarrama	Alvarez et al. (2014)
Energy	Extremadura	Miranda et al. (2009)
Food	Spain	Akcan et al. (2017)
	Portugal	Ferreira-Dias et al. (2003)
Food (mushrooms)	Palencia	Oria-de Rueda et al. (2010)
Livestock	Ávila	Núñez et al. (2012)
	Castilla y León	Doce et al. (2009)
	Castilla y León	Ammar et al. (2009)
	Castilla y León	Ammar et al. (2008)
		Doce et al. (2007)
Productivity	Portugal	Nunes et al. (2015)
Soil carbon	Palencia	Herrero et al. (2016)
	Sistema Central	Díaz-Pinés et al. (2011)
	Salamanca	Turrión et al. (2009)
Soil carbon; Carbon storage	Braganza (Portugal)	Fonseca et al. (2019)
Soil fertility	Spain	Campo and Gallardo (2012)

Tab. D.2. Main descriptors of references compiled describing ecosystem services providing by *Q. pyrenaica*.

Main Ecosystem Services	Study area	References
Soil quality	Castilla y León	Tárraga et al. (2009)
	Castilla y León	Turrión et al. (2008)
	Castilla y León	Menéndez et al. (2007)
	Castilla y León	Tárraga et al. (2006)
	Castilla y León	Schneider et al. (2001)
	Castilla y León	Gallardo et al. (1999)
	Castilla y León	Martin et al. (1997)
Soil quality; Soil carbon	Leza Valley (La Rioja)	Lasanta et al. (2020)
	Guadarrama	Fernández-Getino et al. (2020)
	Portugal	Fernández-Alonso et al. (2018a)
Soil respiration	Guadarrama	Fernández-Alonso et al. (2018b)
Wine	Salamanca	Martínez-Gil et al. (2020)
	Portugal	Jordão et al. (2019)
	Portugal	McCallum et al. (2019)
	Portugal	Del Galdo et al. (2019)
	Galicia	Díaz-Maroto and Sylvain (2016)
	Europe	Ghadiriasli et al. (2018)
	Portugal	Delia et al. (2017)
	Portugal	Tavares et al. (2017)
	Portugal	Castro-Vázquez et al. (2013)
	Portugal	Castro-Vázquez et al. (2013)
	Portugal	Jordão et al. (2012)
	Spain	Gallego et al. (2012)
	Iberian peninsula	Alañón et al. (2011)
	France	Fernández de Simón et al. (2010)
Wine	Castilla y León	Rodríguez-Bencomo et al. (2008)
	Spain	Fernández de Simón et al. (2009)
	Spain	Fernández de Simón et al. (2008)
	Spain	Fernández de Simón et al. (2006)
	La Rioja	Jordão et al. (2006)
	Álava	De Coninck et al. (2006)
	Álava	Fernández de Simón et al. (2003)
		Cadahía et al. (2003)
		Fernández de Simón et al. (1999)
		Cadahía et al. (2001)
		Fernández de Simón et al. (1996)

Tab. D.3. Wikilock routes density (routes km⁻²), and routes total numbers, for the municipalities of Sierra Nevada where Pyrenean oak woodland are located

Oak population	CAM	GEN	MON	DIL	DUR	CAN	POQ	TRE
Tracks density	18.51	13.79	35.63	14.22	24.36	32.48	52.77	29.89
Total tracks	1170	3290	3170	1140	1870	555	1491	1908

Entréme donde no supe,
y quedéme no sabiendo,
toda ciencia trascendiendo

Yo no supe dónde entraba,
pero, cuando allí me vi,
sin saber dónde me estaba,
grandes cosas entendí;
no diré lo que sentí,
que me quedé no sabiendo,
toda ciencia trascendiendo

Coplas hechas sobre un éxtasis de harta contemplación
San Juan de la Cruz, 1572-1577

Colophon

Esta tesis doctoral se ha escrito con L^AT_EX. Se ha utilizado una modificación de la plantilla *Clean Thesis* (<http://cleanthesis.der-ric.de/>), desarrollada por Ricardo Langer.

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