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Distribución espacial, dinámica espacio-temporal, regeneración y diversidad en las comunidades de *Quercus faginea* del Pirineo Central Aragonés

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DISTRIBUCIÓN ESPACIAL, DINÁMICA ESPACIO-TEMPORAL, REGENERACIÓN Y DIVERSIDAD EN LAS COMUNIDADES DE *QUERCUS FAGINEA* DEL PIRINEO CENTRAL ARAGONÉS

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Spatial distribution, spatio-temporal dynamic, regeneration, and diversity in the *Quercus faginea* communities of the Aragón's Central Pyrenees

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Tesis doctoral

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TESIS DOCTORAL

Distribución espacial, dinámica espacio-temporal, regeneración y diversidad en las comunidades de *Quercus faginea* del Pirineo Central Aragonés

Memoria presentada por **Yacine Kouba** para optar al grado de Doctor
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A mes parents pour leur amour et surtout pour leur compréhension durant toutes ces années que j'ai passé loin d'eux

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“If you cannot do great things, do small things in a great way.”

Napoleon Hill (1883-1970)

American writer

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Esta tesis, de acuerdo con el informe correspondiente, autorizado por el director de la tesis y el Órgano Responsable del Programa de Doctorado, se presenta en formato de compendio de publicaciones científicas.

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Índice

Resumen/Summary

En muchos bosques Mediterráneos, *Quercus faginea* se considera como un componente estructural importante de las comunidades nativas porque ofrece hábitat para una amplia diversidad de comunidades de plantas y animales, y por lo tanto, es de gran interés para la conservación de los ecosistemas. A pesar de su importancia, esta especies es poco estudiada en comparación con otras especies tal como *Q. ilex* y *Fagus syvatica*. Esta tesis doctoral (i) analiza el efecto de los factores abióticos y el uso antrópico en la distribución de *Q. faginea* en el Pirineo Central, (ii) examina la dinámica espaciotemporal de los bosques de *Q. faginea* del Prepirineo Central durante el periodo entre 1957 y 2006, (iii) evalúa el papel del cambio del uso del suelo y el cambio climático en el establecimiento y la dinámica re-generacional de los bosques de *Q. faginea*, (iv) analiza la relación entre la expansión de *Q. faginea* observada en algunos campos abandonados y los cambios socioeconómicos en siete municipios del Prepirineo Central durante la segunda mitad del siglo XX, (v) estudia la organización de la diversidad florística a múltiples escalas espaciales e identifica los factores ambientales que han influenciado en la distribución espacial de la diversidad florística en los bosque de *Q. faginea*, e (vi) investiga el efecto del uso histórico del suelo en las comunidades vegetales (diversidad y composición florística) de los bosques de *Q. faginea* del Prepirineo Central.

En primer lugar hemos examinado el efecto de los factores abióticos y el uso antrópico en la distribución de *Q. faginea* en el Pirineo Central. Los mapas de presencia-ausencia de *Q. faginea*, de las variables abióticas y del uso antrópico se han derivado de los mapas disponibles, como por ejemplo el mapa del tercer Inventario Nacional Forestal; INF3, y fotografías aéreas, usando el sistema de información geográfica. El efecto de las variables abióticas y del uso del suelo en la distribución de *Q. faginea* se ha cuantificado usando el modelo bayesiano “Bayesian Model Averaging (BMA)”. A gran escala, las variables abióticas (clima y litología), fueron los factores que tuvieron el mayor efecto en la distribución espacial de *Q. faginea*, sin embargo, las plantaciones introducidas recientemente y la presión del ganado de las primeras décadas del siglo XX han afectado negativamente la distribución de *Q. faginea* en esta zona.

Para evaluar la dinámica espaciotemporal de los bosques de *Q. faginea* durante el periodo entre 1957 y 2006, hemos realizado los mapas de distribución de *Q. faginea* en el Prepirineo Central durante los años 2006 y 1957 usando el mapa del tercer Inventario Nacional Forestal (INF3) y las fotografías aéreas tomadas en 2006 y 1957. Las ganancias y pérdidas en los bosques de *Q. faginea* se cuantificaron usando la matriz de cambios. La fragmentación, el aislamiento, y la irregularidad de las manchas se evaluaron usando una seria de índices del paisaje. Los factores más probables que influyeron en estos cambios se identificaron por medio de modelos estadísticos. Los resultados mostraron cambios substanciales en los patrones espaciales de los bosques de *Q. faginea* en el Prepirineo Central durante los últimos 50 años. Estos cambios se han reflejado claramente en un incremento considerable de la fragmentación, del grado de aislamiento, y en la irregularidad de las manchas. Los cambios en los patrones espaciales de los bosques de *Q. faginea* se asocian particularmente al aumento en las plantaciones de pinos y la antigua deforestación asociada con el aumento de las tierras cultivadas y los pastos. Además las carreteras actuaron como "atractores" para los cambios de uso del suelo y la deforestación, lo que influyó fuertemente en la variabilidad espacial de los bosques de *Q. faginea*.

Para entender cómo los cambios del uso del suelo y el cambio climático han influenciado en la dinámica de las masas de *Q. faginea* y cómo han afectado al establecimiento de los individuos de esta especies durante el siglo XX, hemos seleccionado diez masas forestales dominadas por *Q. faginea* en el Prepirineo Central. En cada masa de Q*. faginea* se ha establecido un transecto de 500-m en un sitio elegido al azar. Cada transecto tiene 20 puntos de muestreo elegidos a un intervalo de 25-m. Usando el método "Point-quarter" en cada punto se ha identificado el árbol adulto de *Q. faginea* más cercano a este punto en los cuatro direcciones cardinales. Las siguientes variables se han recogido para cada uno de los cuatro árboles: diámetro a la altura del pecho (DBH) (cm), la altura del árbol (m), hábitat (monte bajo o terraza abandonada). Además se ha estimado la edad de 290 árboles en las diez masas muestreadas. Los datos de distribución de edad se analizaron usando la función "*Power function*" para estimar el reclutamiento de *Q. faginea* a lo largo del siglo XX. Para evaluar los efectos de las variables climáticas y del uso del suelo en el establecimiento de *Q. faginea*, hemos calculado los

coeficientes de correlación de Spearman (r_S) entre las variables climáticas y las que reflejan el uso de suelo, y el número de árboles establecidos observado y los residuales obtenidos de la función ajustada "*Power function*". Desde finales de 1930, el reclutamiento de los nuevos individuos en los bosques de *Q. faginea*, ha mostrado una alta variabilidad interanual y el reclutamiento más alto se produjo entre 1965 y 1975. El establecimiento de los árboles se correlacionó negativamente con la temperatura media de las máximas del verano, tamaño de la población de los pueblos cercanos, y la cantidad de ganado, y se correlacionó positivamente con las precipitaciones anuales, precipitaciones del invierno, y las precipitaciones del invierno-primavera.

Para estudiar la relación entre la expansión de *Q. faginea* y los cambios socioeconómicos en siete municipios del Prepirineo Central durante la segunda mitad del siglo XX, hemos cuantificado en primer lugar las ganancias (ha) en los bosques de *Q. faginea* por municipio entre 1957 y 2006, luego hemos correlacionado estas ganancias con los cambios -entre 1957 y 2006- en el tamaño de la población del municipio, y el número de agricultores y cabezas de ganado por cada municipio. La superficie de las nuevas áreas adquiridas por los bosques de *Q. faginea* ha aumentado significativamente con el decremento del tamaño de población, y el número de agricultores y cabezas de ganado. En general, la emigración rural que ha ocurrido en esta área desde los años sesenta ha generalizado un abandono masivo de las tierras agrícolas y una disminución en la presión ganadera, lo que ha permitido a *Q. faginea* colonizar algunas de las tierras abandonadas sobre todo en los municipios con una disminución notable del número de agricultores.

Para entender la organización de la diversidad florística a diferentes escalas espaciales (transecto, masa forestal, región) e identificar los factores ambientales que influyen en los patrones de la diversidad florística en los bosque de *Q. faginea*, se ha cuantificado la riqueza y la abundancia de las plantas vasculares en 30 transectos de 500-m establecidos en las 10 masas de *Q. faginea* muestreadas (3 transectos por masa) usando el método "Point-intercept". Además, se ha estimado la edad media por masa, el coeficiente de variación de edad de la masa forestal, la abundancia de *Q. faginea* (en cada uno de los 30 transectos), el tipo de bosque (monte bajo vs. bosque secundario), el área de la masa forestal, y la complejidad de la forma de la masa forestal (perímetro/área). Hemos usado la partición jerárquica-multiplicativa de la diversidad y el índice de Hill para evaluar los patrones de la diversidad florística a distintas escalas espaciales, y el análisis de redundancia (RDA) para examinar el efecto de las variables ambientales que describen las características de las masas de *Q. faginea* en la variación de la composición florística. Los resultados han revelado que la mayor parte de la diversidad florística (diversidad gama) en las masas de *Q. faginea* del Prepirineo Central es el resultado de la diferenciación florística entre las masas, dicho de otra manera, es resultado de la diversidad beta entre las masas de *Q. faginea*. Esta misma diversidad -diversidad beta- está estructurada en gran parte por unos factores que son muy influenciados por el uso histórico de la masa forestal como por ejemplo la edad media de la masa forestal, el coeficiente de variación de la edad, y la abundancia de *Q. faginea*.

Para investigar los efectos de la gestión histórica de los bosques y el uso histórico de las tierras agrícolas en las comunidades vegetales actuales de los bosques de *Q. faginea*, hemos comparado la diversidad y la composición de la comunidad vegetal entre masas de *Q. faginea* que han establecido en las terrazas abandonadas y las masas del monte bajo. Además las masas de *Q. faginea* se han evaluado basándose en su edad (jóvenes vs. viejas) y la intensidad de la gestión histórica. Los resultados han revelado diferencias significativas en cuanto a la composición florística entre las masas de *Q. faginea.* Esta variación florística es debida principalmente a diferencias en riqueza y equitabilidad “evenness” de especies que desarrollan en diferentes estadios sucesionales: especies de la fase inicial de la sucesión vegetal, especies de la fase intermedia de la sucesión vegetal, y especies de la fase final de la sucesión vegetal. Los resultados han revelado también que las masas viejas de *Q. faginea* albergan pocas especies que se consideran como especialistas de los bosques. Ello respalda la idea de que la recolonización de los bosques alterados por especies especialistas es muy difícil incluso cuando las masas forestales se dejan sin ningún tipo de gestión por mucho tiempo.

In many mesic forests in Mediterranean environments, Q. faginea is an important structural component of native plant communities because it provides habitat for a wide diversity of plant and animal communities and, therefore, is of great interest for ecosystem conservation. In spite of the importance of this species, exist few studies compared to other species such as Q. ilex and Fagus syvaltica. This PhD thesis (i) analyzes the effects of abiotic and anthropogenic factors on the distribution of Q. faginea forests in the Central Pyrenees, (ii) examine the spatiotemporal dynamics of Q. faginea forests over period from 1957 to 2006, (iii) assess the roles of land-use and climate change on the establishment and regeneration dynamics of Q. faginea forests in the Central Pre-Pyrenees, (iv) analyzes the relationship between the observed expansion of Q. faginea in some abandoned lands and socioeconomic changes (i.e. population number, number of farmers and livestock) in seven municipalities of the Central Pre-Pyrenees during the second half of the 20th century, (v) study the organization of plant diversity at multiple spatial scales and identify the environmental factors that might have patterned plant species diversity in human-altered oak forests, and (vi) investigate the effects of the previous land management on contemporary plant communities (plant diversity and composition) in the oak forests of the Central Pre-Pyrenees.

Firstly we examined the effects of abiotic and anthropic factors on the distribution of Q. faginea in the Central Pyrenees. Information on the presence-absence of Q. faginea, and abiotic and anthropic variables, were derived using GIS based on the available maps (e.g. the third Spanish National Forest Inventory map; IFN3) and aerial photographs. The effect of abiotic and land use variables on Q. faginea distribution was quantified using Bayesian Model Averaging (BMA). On a broad scale, abiotic variables; i.e. climate and lithology, were the factors that had the greatest effect on the spatial distribution of Q. faginea; although, recently introduced pine plantations and previous livestock pressure have had a negative effect on the distribution of Q. faginea in the region.

To assess the spatiotemporal dynamics of Q. faginea forests over period from 1957 to 2006 we created maps of Q. faginea distribution over the Central Pre-Pyrenees in 2006 and 1957 using the third Spanish National Forest Inventory map (IFN3) and aerial photographs from 2006 and 1957. Gains and losses in Q. faginea forests were *quantified by means of construction of matrix of changes. Patch fragmentation, isolation, and irregularity were assessed using a set of standard landscape metrics. We also identified, the probable factors influencing these changes using statistical models (e.g. Bayesian Model Averaging; BMA). The results revealed substantial changes in the spatial patterns of Q. faginea forests over the last 50 years. These changes have been clearly reflected in noteworthy increase of fragmentation, isolation degrees, and patch irregularity. Changes in the spatial patterns of Q. faginea forests were particularly driven by the vast introduction of pine plantations and the former deforestation, associated with increasing the amount of croplands and pastures. In addition, roads acted as attractors for changes in land use and deforestation, which influenced strongly the spatial variability of Q. faginea forests.*

To understand how changes in land use and climate influence the dynamics of Q. faginea forest stands and how they affected tree establishment in the 20th century we selected ten stands that were dominated by Q. faginea in the Central Pre-Pyrenees. Within each stand, a 500-m linear transect was established at a randomly chosen location. Each transect had sampling points (n=20) at 25-m intervals. Using the "Point-quarter" method at each point, we identified the closest adult Q. faginea tree in each of the four cardinal directions. The following variables were recorded for each of the four trees: diameter at breast height (DBH) (cm), tree height (m), habitat (coppice stand or abandoned terrace). The age of 290 trees were also estimated in the teen sampled stands. The age distribution data was analyzed by using "Power function" to estimate the establishment of Q. faginea trees along the 20th century. To assess the effects of climate and land use variables on Q. faginea establishment, we calculated Spearman correlation coefficients (rs) between the climate and land use variables and both the observed number of trees established and the residuals obtained from the fitted "Power function". Since the late 1930s, Q. faginea became established episodically, and the highest peak occurred between 1965 and 1975. Tree establishment was negatively correlated with mean summer maximum temperature, population size of nearby villages, and the amount of livestock, but was positively correlated with annual, winter, and winter-spring precipitation.

To study the relation between the expansion of Q. faginea and socioeconomic changes in seven municipalities of the Central Pre-Pyrenees over the second half of the 20th *century, we first quantified the gains (ha) in Q. faginea forests per municipality between 1957 and 2006, then we correlated these gains with changes -between 1957 and 2006- in population size and the number of farmers, and livestock in each municipality. The amount of gains in Q. faginea increased significantly with a decrease in population size and the number of farmers and livestock. Overall, the rural emigration that occurred in this area since 1960s has generated a massive abandonment of agricultural lands and a decrease in livestock pressure, which allowed Q. faginea to colonize some of the abandoned lands, essentially in the municipalities that known a high reduction in the number of farmers.*

To understand how plant species diversity changes across different spatial scales (i.e. transect, stand, and entire region) and to identify the environmental factors that might have patterned plant species diversity in Q. faginea forests, the richness and abundance of all vascular plant species were quantified for 30 500-m transects established in the ten sampled oak stands (3 transects per stand) by using "Point-intercept" method. Furthermore, for each stand we estimated the mean age, coefficient of variation of tree age, Q. faginea abundance (in each of the 30 transects), stand size, and stand-form complexity (Perimeter/area of stand). We used multiplicative diversity partitioning and Hill Index to assess plant diversity patterns at the three spatial scales, and redundancy analysis (RDA) to test the effects of environmental variables that describe Q. faginea stands' characteristics on the compositional variation of plant species. The results revealed that a great part of plant diversity (gama diversity) in the Q. faginea stands of the Central Pre-Pyrenees is a result of floristic differentiation among stands (i.e. among-stands beta diversity). This beta diversity is mainly structured by the factors that are strongly influenced by the historical use of oak stands, such as mean stand age, the coefficient of variation of tree age, and Q. faginea abundance.

To investigate the effects of previous forest management and agricultural land use on contemporary plant communities in oak forests, we compared the plant diversity and composition of abandoned coppices and secondary growth stands. In addition, the stands were assessed based on their ages (young vs. old stands), and historical management intensity. The finding revealed a significant compositional differentiation between stands. This compositional variation is due to differences in *the richness and evenness of plant species of different habitat preferences (i.e. early-, mid-, late-successional species). The results showed also that the old oak stands harbored a considerably small share of forest specialists, which support the suggestion that the re-colonization by forest specialists can be difficult, even if the stand is left unmanaged for a long time.*

Introducción general

La problemática de los bosques

La gestión de los bosques, no para la explotación sino para asegurar la diversidad biológica y obtener de ellos servicios ambientales, es uno de los temas que desarrolla la gestión forestal. La gestión de los bosques para asegurar la diversidad biológica tiene como objetivo usar los procesos naturales que suceden dentro del bosque para optimizar los servicios ambientales y disminuir el impacto de las perturbaciones en los bosques (Rdemacher et al., 2004). Varias investigaciones han demostrado que los cambios en el uso del suelo son las causas principales de la degradación de los bosques naturales (Ewers et al., 2006; Freitas et al., 2010; Kobayashi and Koike, 2010). El tipo y la intensidad de los cambios del uso de suelo influyen en la perdida de hábitat y la fragmentación de los bosques. La fragmentación de los bosques implica la reducción del tamaño de las manchas del bosque y el incremento del grado de aislamiento entre ellas. Como consecuencia, las poblaciones locales se restringen a pequeñas manchas aisladas y vulnerables a la extinción (Sawchik et al., 2002). Por otra parte los cambios en el uso de suelo junto con el cambio climático pueden afectar significativamente al establecimiento de los árboles así como a la estructura y dinámica de los bosques, sobre todo en las zonas que han sido sometidas a una fuerte explotación humana (Barbero et al., 1990; Améztegui et al., 2010; Chauchard et al., 2010).

Por otro lado muchos estudios han mostrado que la disponibilidad del agua en el suelo es el factor principal que afecta el crecimiento y la regeneración de los bosques (Ogaya et al., 2003; Linares et al., 2010; Pulido and Díaz, 2005). La variabilidad inter-anual en las precipitaciones afecta significativamente al reclutamiento de los nuevos individuos (Urbieta et al., 2008). Sin embargo, las diferencias anuales en las precipitaciones no es el único factor que afecta la regeneración del bosque. En las zonas áridas con clima continental las precipitaciones junto a las temperaturas juegan un papel muy importante en la determinación de la disponibilidad del agua en el suelo (Larcher, 2000; Vicente-Serrano et al., 2010). Además, la frecuencia y la intensidad de los fenómenos meteorológicos extremos como por ejemplo las sequias severas, las cuales se espera que van a aumentar en las zonas áridas como consecuencia del cambio climático (IPCC, 2007), tienen importantes repercusiones en la conservación de los bosques. En las zonas donde predominan las sequias severas, los bosques van a verse afectados a causa del aumento de las condiciones de sequía.

Esta reconocido que los bosques proporcionan hábitat a un rango muy amplio de plantas (Battles et al., 2001). El reconocimiento de la importancia ecología de la biodiversidad ha motivado a los forestales a trabajar para mantener la diversidad biológica en los bosques. Muchos estudios han destacado la importancia de la estructura del dosel arbóreo y la estructura espacial de las manchas de los bosques en la diversidad y la composición de las especies del sotobosque. En los bosques, el dosel arbóreo (los arboles dominantes en un bosque) puede influenciar la disponibilidad de los recursos para las especies de los estratos arbustivo y herbáceo. El dosel arbóreo influye en la cantidad de luz que llega a estos estratos, el sustrato, el pH y los nutrientes del suelo (Augusto et al., 2002; Härdtle et al., 2003; Aubert et al., 2004; Hart & Chen, 2006). Por otra parte las propiedades estructurales del bosque (edad de los árboles, la distribución del diámetro a la altura del pecho y la densidad del bosque) pueden afectar fuertemente la diversidad y la composición de los estratos arbustivo y herbáceo (Augusto et al., 2002; Estevan et al., 2007). Además el tamaño y la complejidad de las manchas de bosque, que pueden considerarse como reflejo de las perturbaciones y la gestión histórica de un bosque, pueden afectar también la diversidad y la composición de las especies a nivel de las masas forestales (Estevan et al., 2007; Lomba et al., 2011).

Particularmente en los países desarrollados muchos bosques natural que no están bajo ningún tipo de gestión han sido explotados intensivamente en el pasado (Barbero *et al.* 1990). Muchos autores han argumentado que, en los bosques que han sido modificados por el hombre, las actuales características estructurales, espaciales, y topográficas de las masas forestales vienen determinadas en gran medida por el tipo y la intensidad del uso histórico de estos bosques (Flinn & Vellend 2005; Hermy & Verheyen 2007). Además, la antigua intensa gestión forestal y las actividades agrícolas podrían haber afectado fuertemente a la composición florística en estos bosques (Flinn & Vellend 2005). Por lo tanto, un profundo conocimiento de las consecuencias de las decisiones históricas, en cuanto a la gestión forestal, a largo plazo es crucial para predecir la respuesta de las comunidades vegetales a posibles perturbaciones futuras incluso el cambio climático. Por último, los problemas que enfrentan los bosques imponen la necesidad de tenerlos en cuenta a la hora de realizar los planes de gestión forestal, lo que puede permitir un desarrollo sostenible de los bosques y una mejor conservación de la biodiversidad.

Los bosques de *Quercus faginea*

Descripción de la especies

El nombre *Quercus faginea* se impone en la literatura botánica tras la publicación y difusión del género en *Flora Europea* (Schwarz, 1964). Anteriormente hubo una profunda discusión sobre cuál debería ser el nombre admitido (Vicioso, 1950). Según Arroyo (2002) El vocablo "*Quercus*", que nomina este género de las *Fagáceas*, proviene de la unión de dos étimos celtas. Por un lado "*Quer*" (=bello) y por otro *"cuez"* (=árbol): "árbol hermoso", y así pasó a los romanos, que de forma indistinta llamaban a robles y encinas "*quercus"*. Precisamente de la lengua latina proviene "*faginea*"; de "*fagus*" (=haya) por su parecido a la hoja de la haya. Así lo describe Lamarck en 1785, en su *Encyclopédie méthodique: botanique* "*chêne à feuilles de Hêtre"* como las hojas de Haya. El nombre vulgar "quejigo" proviene del latín "*cecidium"* (agalla), ya que es muy frecuente la aparición de estos engrosamientos en sus hojas (Arroyo, 2002). Numerosos mitos griegos y romanos hacen referencia a las quercíneas, siendo común a todos ellos la creencia popular de que en el interior de estos árboles habitaban las *Dríades* o *Hamadríades*, ninfas que nacían con el árbol y lo protegían (Arroyo, 2002).

El quejigo es un árbol de tamaño medio que no suele sobrepasar los 20 metros, aunque a veces se ve reducido al porte arbustivo por motivos naturales o antrópicos (Sancho et al., 1998). La copa es redondeada o aovada, con el follaje no muy denso. El tronco es por lo general tortuoso, y en su corteza destacan líquenes, que lo hacen característico (Arroyo, 2002). Las hojas son de color verde lustroso por el haz y pálido por el envés, con el borde recorrido por dientes poco profundas, a veces punzantes; semicaducas. Las flores son muy sencillas y van reunidas en grupitos sobre amentos colgantes. El fruto es una bellota cuya cúpula está recubierta de escamas aovadas, algo prominentes en el dorso y de aspecto aterciopelado; las bellotas se disponen en grupos y nacen sobre cortos pedúnculos.

Los quejigos aparecen tanto sobre sustratos calizos como silíceos, aunque parecen preferir los ricos en bases, sobre los que forma extensas masas donde es dominante (Sancho et al., 1998; Villar et al., 1997). El quejigo abunda en calizas, arcillas y margas; también ocupa margas yesosas, areniscas o conglomerados. Vive también sobre gran variedad de sustratos ácidos, aunque sobre éstos no son abundantes las masas puras (Sancho et al., 1998; Arroyo, 2002).

Esta gran amplitud en sustratos litológicos que ocupan los quejigares ocasiona que sean también muy variados los tipos de suelos (Sancho et al., 1998). Predomina los cambisoles cálcicos, pero también eúticos, dístricos, gléycos y húmecos; en las áreas de mayor pluviometría, luvisoles cálcicos o crómicos; y en valles vaguadas sobre fluvisoles eúticos; en llanuras sedimentarias a veces se encuentran sobre planosoles (Sancho et al., 1998).

El quejigo vive en zonas con temperatura media anual entre 9 y 12º C, siendo el límite máximo tolerable los 39º C (Arroyo, 2002). Prefiere que las precipitaciones ronden los 800 mm anuales, pero progresa con 400 mm, y es capaz, por lo tanto, de habitar estaciones que van desde el "seco" al "sub húmedo" (Arroyo, 2002; Sancho et al., 1998). Es de media luz, por lo cual las nuevas plantas soportan algo de sombra los primeros años. Tiene un crecimiento lento que después de mantener su vestimenta seca durante el invierno reverdece a partir de mayo. La reproducción puede realizarse por semilla (en casi todos los casos), cepa (con mayor vitalidad y longevidad) o raíz (muy rara vez) (Arroyo, 2002). Es además muy importante señalar que el quejigo contrariamente a otras especies de frondosas es capaz de producir semilla fértil durante su etapa arbustiva (Arroyo, 2002). Es una especies que se asocia con frecuencia o se pone en contacto con encinas, melojos y alcornoques; puede formar híbridos fácilmente con otros quejigos (*Quercus canariensis*) y robles (*Quercus pubescens*), que dificultan su identificación.

Quercus faginea Lam comprende un conjunto variable de estirpes (Ruíz de la Torre, 1988, Sancho et al., 1998, Arroyo, 2002):

- *Quercus faginea ssp. alpestris*. Tiene las hojas muy coriáceas, frecuentemente abarquilladas con nervación y dientes muy irregulares. Habita en las montañas del Sur de España y Norte de Marruecos, donde alcanza importantes altitudes.
- *Quercus faginea ssp*. *faginea.* El borde de la hoja es ondulado, y menos coriáceo. Crece en toda España y casi a cualquier altitud, siendo la variedad más frecuente de las tres.
- *Quercus faginea ssp*. *broteroi*. Hoja más grande que los anteriores, casi plana. Requiere climas suaves y húmedos. Es más frecuente en el cuadrante sur-occidental de la Península Ibérica

Distribution de la especies

El quejigo es una especie exclusiva del Mediterráneo occidental (España, Portugal y el Norte de África). Fuera de la península su representación es bastante escasa, muy puntual en Europa (lo podemos encontrar en Francia e Italia) y algo mejor representada en el norte de África (lo podemos encontrar en Marruecos y Túnez) (Figura 1), aunque con masas fragmentadas y circunscritas a territorios muy concretos (Sancho et al., 1998).

Figura 1: Distribución mundial del *Quercus faginea*

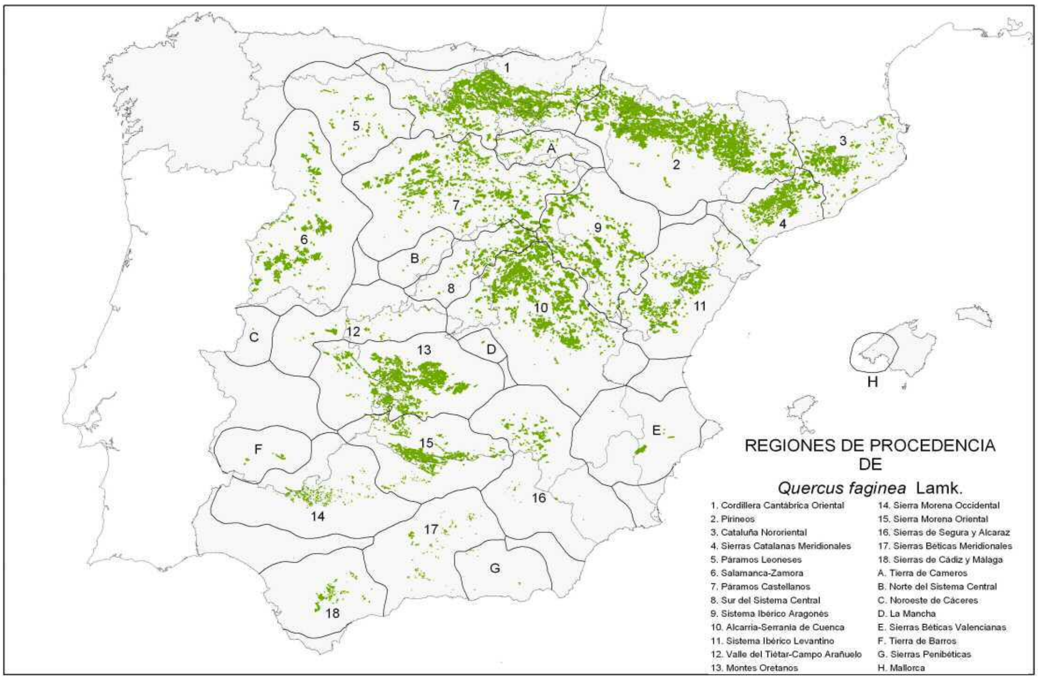

Figura 2: Distribución de *Q. faginea* en España (Sancho et al., 1998)

En España el quejigo presenta una distribución muy dispersa; se encuentra prácticamente en todas las provincias (Figura 2), salvo Pontevedra, La Coruña, Lugo y Guipúzcoa. Sus masas más importantes se sitúan en el cuadrante nororiental de la Península (Sancho et al., 1998). En gran parte de España aparece como especies subordinada en formaciones de otras frondosas (encina, alcornoque) o coníferas (pinos, sabinas) (Sancho et al., 1998).

Los bosques de *Quercus faginea* del Pirineo Central Aragonés

Características de los bosques de Quercus faginea

En el Pirineo Aragonés, los bosques de *Q. faginea* son unos de los más extendidos en el piso montano (Figura 3), donde soportan un clima muy continental y seco. Forman en este caso la transición entre las comunidades esclerófilas de encina y pino carrasco y los bosques de alta montaña mediterránea de *Pinus sylvestris* y *P. nigra* (Sancho et al., 1998). *Q. faginea* no puede subir a los picos en el Pirineo porque las bajas temperaturas del invierno provocan heladas, lo que inhibe el establecimiento y el crecimiento de las plántulas de esta especies. Forman bosques más bien bajos (5-10 m), con el estrato arbóreo poco sombrío, muchas veces aclarado por perturbaciones (Figura 3). Los estratos arbustivo y herbáceo tienen una densidad variable dependiendo del grado de apertura del dosel arbóreo. Desde un punto de vista fitosociológico, se encuentra mezclado con pinares (*Pinus* ssp) naturales o repoblados o encinares (*Quercus ilex*). Hay además, algunas masas de *Q. faginea* puro con presencia de algunas especie arbustivas como *Buxus sepervirens*, *Quercus coccifera* y *Juniperus communis*. En esta comunidad también podemos encontrar *Genista scorpius*, *Arctostaphylos uva-ursi*. Protegidos por el *Buxus sepervirens* aparecen a finales de invierno narcisos (*Narcissus* ssp) y *Viola alba.* En sus claros hallaremos plantas mediterráneas como *Thymus vulgares*, *Lavandula latifolia*, *Linum suffruticosum*, *Linum narbonense*. De un punto de vista de la ecología del paisaje, los bosques de *Q. faginea* forman en algunos sitios masas grandes continuas y en otros sitios forma teselas pequeñas fragmentadas y aisladas. En su límite altitudinal superior, *Q. faginea* contacta en función de la humedad con formaciones de pino silvestre (*Pinus sylvestris*) o con hayedos (*Fagus sylvatica*).

Figura 3: Una foto de un bosque de quejigo en el Prepirineo (elaboración propia)

Es importante señalar también que en Pirineo Central hay dos tipos de bosques de quejigo:

1. Los quejigares que se consideran como montes bajos: desde la antigüedad se han explotado bastante para leñas, carbón y pastos, por lo que forman masas fragmentadas y muy aclaradas (Sancho et al., 1998). En los alrededores de los pueblos se han conservado algunos árboles centenarios por su producción de bellota.

2. Los quejigares recientemente formados en las terrazas abandonadas: Estos bosques se han establecido en las tierras abandonadas, antiguamente usadas como tierras agrícolas. Se han instalado especialmente durante la segunda parte del siglo

veinte como resultado de la sucesión vegetal natural (invasión del quejigo en las terrazas abandonadas).

La gestión histórica de Quercus faginea en el Pirineo Central Aragonés

Los usos de esta especie han variado poco a lo largo de la historia, pero sí ha existido variación en su intensidad de acuerdo a los niveles de desarrollo demográfico y tecnológico de las sociedades humanas (Sancho et al., 1998). Los principales productos obtenidos tradicionalmente de esta especie han sido las leñas, seguidos con menor importancia por la madera y la bellota.

La utilización de los quejigares como fuente de combustible, ya sea en forma de leña o de carbono se debe a la buena calidad de este producto. Desde la antigüedad existen testimonios de esta dedicación, así Teofrasto en su “Historia de las Plantas” y Plinio el Viejo en su “Historia Natural” hacen referencias frecuentes al uso generalizado y buena calidad de la leña y el carbón de los quejigos en particular y los robles en general (Anbré, 1962; Díaz-Regaños, 1988; Sancho et al., 1998). La leña y el carbón del quejigo se han empleado como fuentes de energía en las actividades domésticas de las sociedades rurales pero también en actividades industriales (Sancho et al., 1998). Este aprovechamiento ha sido la principal causa de la deforestación y alteración de los quejigares.

A partir de la edad moderna la presión sobre los bosques en general se acelera debido al aumento demográfico con el consiguiente aumento de la demanda de combustible, madera y terreno para el cultivo (Sancho et al., 1998; Barbero et al., 1990). También se ha constatado el uso de madera de esta especie para la obtención de vigas y pilares en la construcción, pero se trata de un uso puntual debido a la dificultad de encontrar ejemplares con porte adecuado.

A parir de la primera mitad del siglo veinte, el descuaje de masas de quejigo para el cultivo agrícola y la extensión de los pastos han causado fuerte impacto en los bosques del quejigo del Pirineo Aragonés, determinando la configuración actual de la estructura de estos bosques. En el caso más extremo ha conducido a la disminución del área ocupada por los bosques de quejigo y la sustitución de la especie. La introducción de las plantaciones de pinos (especialmente *Pinus niga* y *Pinus syvestris*) a partir de segunda mitad del siglo veinte ha reducido el área total ocupada por los bosques de quejigo. Estas especies, que se caracterizan por un crecimiento rápido, están ocupando áreas que estaban ocupadas anteriormente por el quejigo. El abandono de las tierras no fértiles, que ha sucedido en el Pirineo Aragonés, particularmente desde la segunda mitad del siglo veinte, ha permitido al quejigo recolonizar algunas zonas de estas tierras abandonadas como consecuencia de un proceso de sucesión vegetal natural.

Zonas de estudio

Situación geográfica y descripción de la zona de estudio

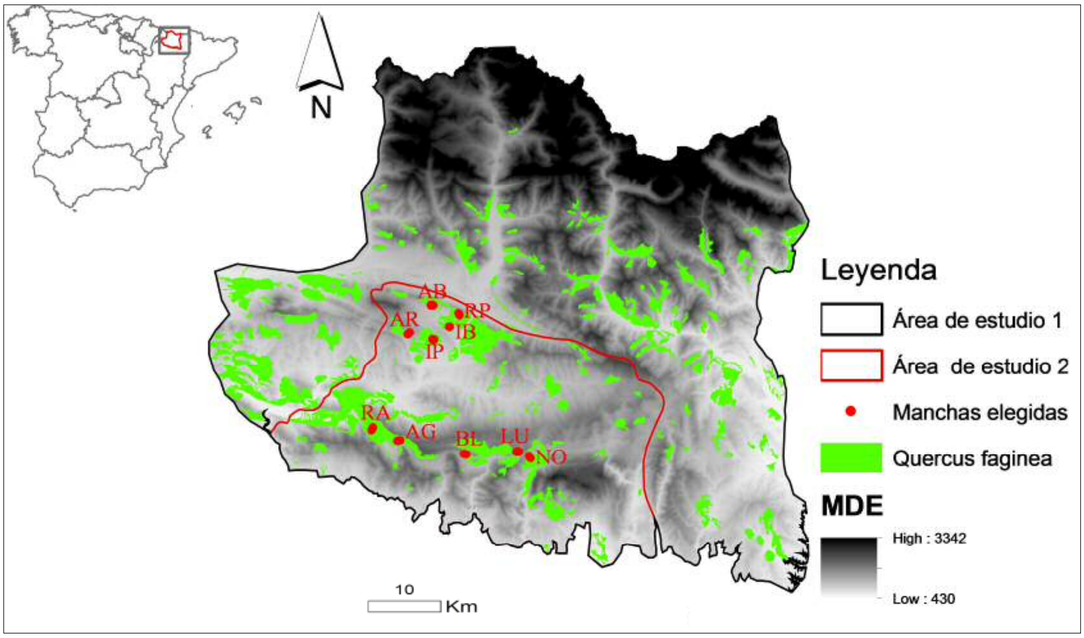

Figura 4: Modelo Degital de Elevaciones (MDE; CINTA, 2013) y delimitación de las áreas de estudio

En primer lugar se ha seleccionado una zona muy amplia del Pirineo Central Aragonés con un área de 4394 Km^2 (Figura 4). Esta zona abarca la mayor parte de los bosques del quejigo en el Pirineo Central Aragonés. Geográficamente el área de estudio está situada en la provincia de Huesca y está delimitada por el río Cinca en el este, el río Aragón en el oeste, la cuidad de Huesca en el sur y por las fronteras con Francia en el norte. La zona tiene un carácter rural, incluye 324 núcleos de población, ninguno de ellos, a excepción de los municipios de Jaca, Fraga y Sabiñánigo con población mayor de 4000 habitantes. Esta zona se ha elegido para estudiar a gran escala el efecto de los factores abióticos y el uso de suelo sobre la distribución espacial de *Q. faginea*. En segundo lugar se ha elegido una zona reducida en el Prepirineo Aragonés con un área de 1363 Km^2 (Figura 4). La zona incluye una gran parte de la sierra de Guara, la sierra de Javierre, sierra de Bonés, sierra de Belarre, sierra Alta, sierra Caballera, sierra de la Gabardiella, sierra de Aineto, sierra de San Pedro, sierra de Portiello, sierra de Bescos, sierra de Villacampa, y sierra de Picardiello. Esta zona se ha seleccionado para estudiar a escala media la evolución espaciotemporal de los bosques de quejigo, así como identificar los factores del uso antrópico que han conducido la dinámica espaciotemporal de esta especies. Por último se han seleccionado diez masas forestales dominadas por el quejigo (elegidas según el tipo de hábitat, es decir si es un monte bajo o una terraza abandonada) en el Prepirineo. Las diez masas están situadas cerca de los siguientes pueblos: Abena (AB), Ara (AR), Arguís (AG), Belsúe (BL), Ipies (IP), Ibort (IB), Lucera (LU), Nocito (NO), Rapun (RP), y Rasal (RA) (Figura 4). En estas masas se ha estudiado la dinámica de las masas de quejigo durante el siglo XX, así como se ha estudiado el efecto del uso histórico de estas masas forestales en la diversidad y composición florística.

Litología, geomorfología y relieve

Tradicionalmente se han distinguido dos unidades geológicas y geomorfológicas en el Pirineo: El *Pirineo Axial* formada por materiales del ciclo hercínico (principalmente sedimentos paleozoicos y plutones graníticos) y el *Prepirineo* constituido por sedimentos deformados durante el ciclo alpino con predominio de materiales calcáreos (Soler & Puigdefábregas, 1970, 1972). Este último consta a su vez de cuatro partes (Figura 5): las Sierras Interiores (dominadas por calizas “Cretáceo-Paleoceno” y areniscas del “flysch luteciense”), la Depresión Prepirenaica (dominada por margas, areniscas, y los conglomerados del Oligoceno), las Sierras Exteriores (dominadas por areniscas ludiense, margas, calizas, y conglomerados), y la Depresión del Ebro (viene dominada por relieves planos con cerros tabulares o sasos entre vales u hondonadas y materiales sedimentarios miocénicos) (Villar et al., 1997). Hay que señalar que la Depresión del Ebro no forma parte de nuestra zona de estudio.

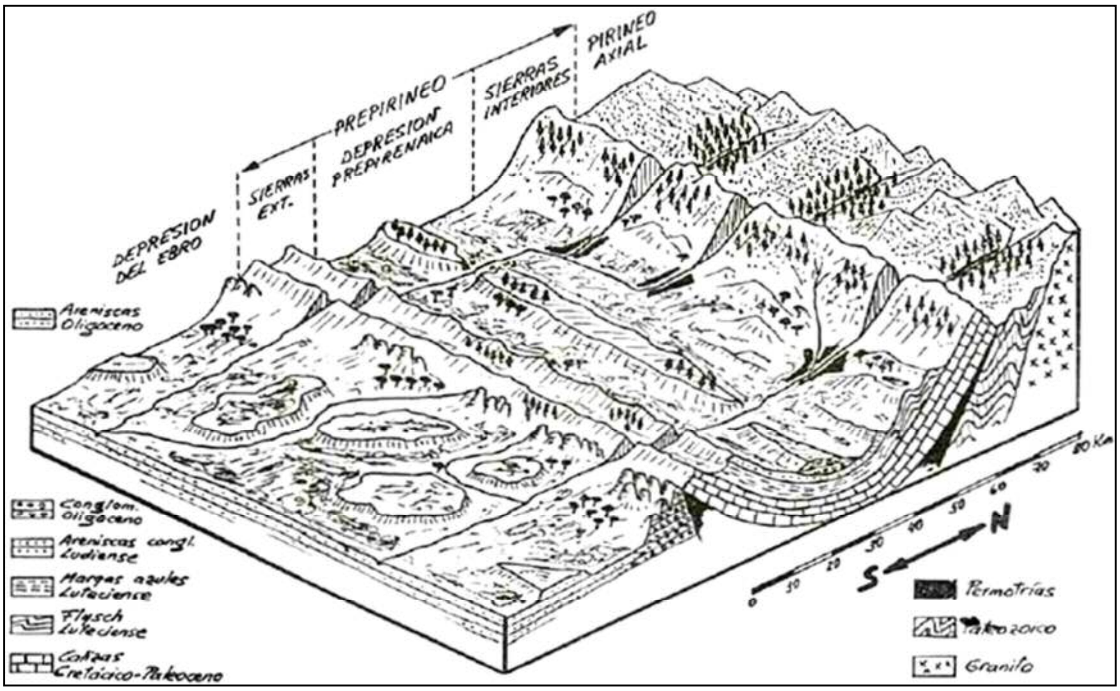

Figura 5: Bloque-diagrama geológico y estructural del Pirineo Aragonés (Villar et al., 1997)

Clima

De oeste a este se establece una transición climática, de forma que la parte más occidental tiene características oceánicas mientras que en la parte más oriental se percibe mejor la influencia mediterránea (Lasanta et al., 2002).

Las principales características climatológicas del área de estudio son las siguientes:

<u>Las precipitaciones</u>: Las precipitaciones anuales superan los 500 mm en toda el área de estudio, aproximándose a los 2000 mm en las crestas de los picos más altos (Lasanta et al., 2002). La cantidad de lluvia desciende rápidamente hacia el sur. Así, Sabiñánigo recibe entre 800 y 900 mm anuales de promedio, y Aínsa unos 1000 mm (Del Valle, 2000). La precipitación vuelve a aumentar algo en el Prepirineo, sobre todo en el Occidental (Loarre) y en el central (Guara), donde se superan los 1000 mm (Del Valle, 2000). Las estaciones más lluviosas son la primavera y el otoño (Del Valle, 2000). El verano es la estación más seca, pero en ocasiones pueden caer precipitaciones intensas de tipo tormentoso (Del Valle, 2000).

<u>La temperatura</u>: La temperatura media anual oscila entre 9º C y 11º C para las localidades más bajas, con importantes contrastes estacionales y diarios (Lasanta

et al., 2002). Por encima de 1600 m la temperatura media anual no supera 6º C (Creus, 1987). La isoterma de 0º C se sitúa a 1600 m para el periodo de diciembre a marzo (Lasanta et al., 2002). La temperatura media desciende rápidamente con la altura, a razón de 0,6º C por cada 100 m de ascenso aproximadamente. Por ello, la temperatura depende mucho del factor topográfico. La temperatura media anual en Candanchú es de 5,2º C y los meses con este valor por debajo de 0º C son diciembre, enero y febrero. En Jaca la temperatura anual asciende hasta 11º C y ningún mes tiene valores medios por debajo de 0º C (Del Valle, 2000). El mes más frío suele ser enero, y el más cálido julio. En ocasiones se registran valores mínimos muy bajos, próximos a -20º C, pero muy esporádicamente, sólo cuando se producen invasiones de aire ártico o siberiano en invierno (Del Valle, 2000).

Diferencias espaciales en precipitación y temperatura: Las características medias descritas hasta ahora varían mucho entre unas zonas y otras. Estas variaciones espaciales principalmente son:

-A medida que avanzamos hacia el sur, la temperatura tiende a aumentar y la precipitación a disminuir.

-A medida que nos desplazamos desde el oeste hacia el este la precipitación también tiende a disminuir y la temperatura a aumentar (suponiendo que nos mantenemos a la misma altura), aunque estas tendencias son compensadas en parte por la mayor elevación de la Cordillera.

Paisaje y pisos bioclimáticos

En el Pirineo Aragonés los paisajes se ordenan en función de la altitud, pues ésta determina las condiciones climáticas, que es un factor decisivo en la instalación de la vegetación y las actividades humanas (Benlloch, 2002). Por otro lado las variaciones ambientales y orográficas de esta zona condicionan la existencia de los diferentes pisos bioclimáticos (Figura 6). Las cumbres de las montañas, por encima de los 2800 m de altitud, constituyen el piso nival, dónde sólo unas pocas plantas localizadas en ambientes favorables consiguen sobrevivir. Por debajo del nival se extiende el piso alpino que se encuentra por encima de 2200-2300 m de altitud y se caracteriza por unas condiciones climáticas extremadamente duras. En este piso únicamente pueden desarrollarse plantas herbáceas y subarbustivas que en gran

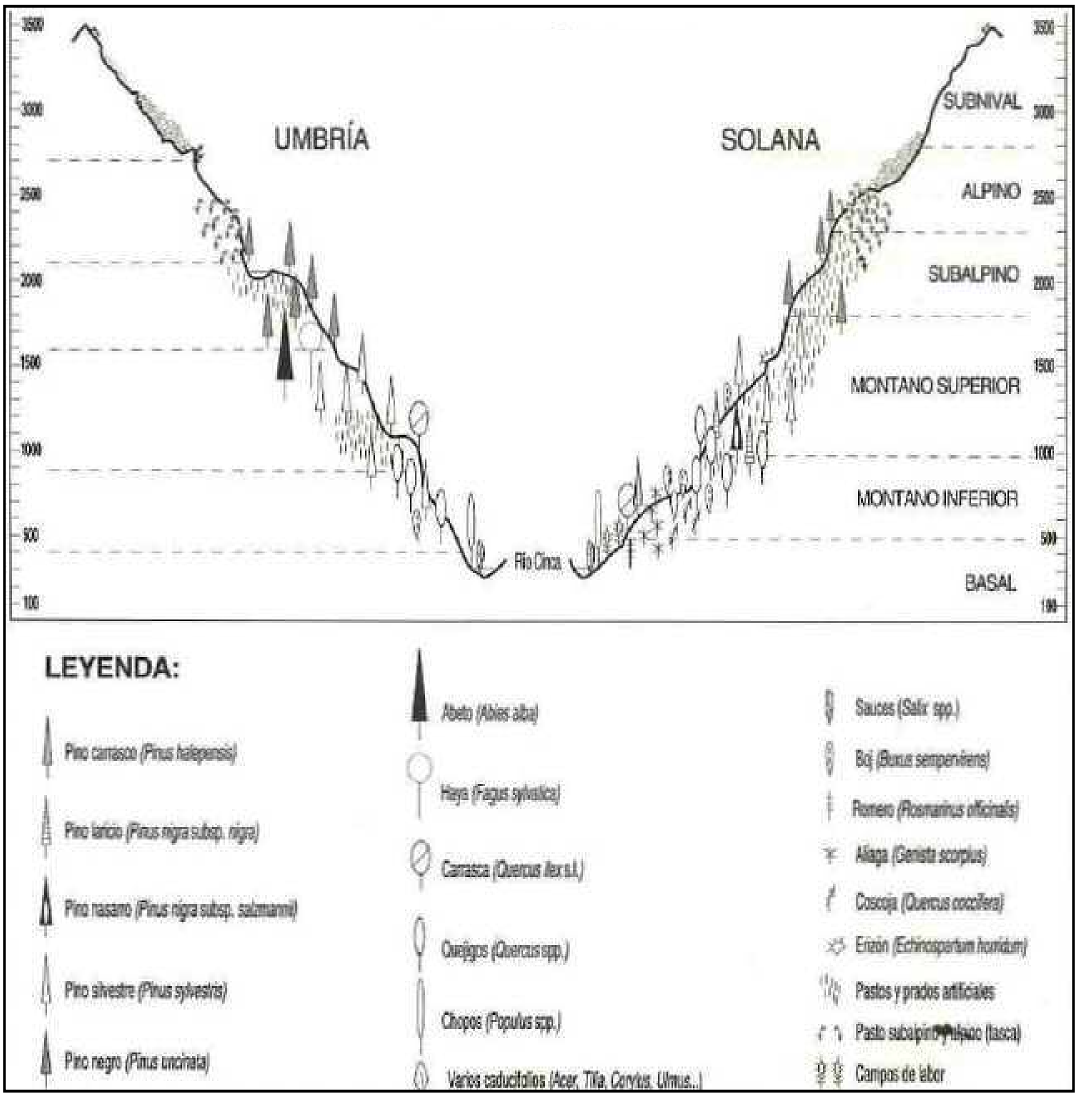

Figura 6: Pisos bioclimáticos y sus comunidades vegetales en el Pirineo Aragonés (Villar et al., 1997)

parte permanecen muchos meses (más de seis) bajo la nieve, lo que les protege (Benlloch, 2002). En las zonas donde se ha llegado a formar algo de suelo, la vegetación natural correspondiente a pastizales alpinos densos con dominio de especies vivaces caméfitas hemicriptófitas (Benlloch, 2002; Bueno, 2011) entre las que se encuentran muchos endemismos (Villar et al., 1997). El piso subalpino (entre 1800 y 2200 m aproximadamente) está ocupado principalmente por pinares de pino negro (*Pinus uncinata*) y en enclaves más húmedos aparecen abetales (*Abies alba*) (Benlloch, 2002). Hay que señalar que la potencialidad de los pastos de alta montaña llevó a los pirenaicos a ampliar el área de pastoreo a costa de estos pinares de pino negro. Así, muchas de las zonas más accesibles y de mejores suelos han sido deforestadas para su aprovechamiento como pastos

(García-Ruíz, 1976; Monserrat, 1968; Benlloch 2002). El piso montano húmedo (superior) está ocupado por hayedos (*Fagus silvatica*) y abetales (*Abies alba*), que se sitúan entre los 1000 y 1700 metros. El pino silvestre (*Pinus silvestris*) es el árbol típico del piso montano seco (inferior), donde convive con el abetal (*Abies alba*), llegando en ocasiones a subir hasta los dominios del pino negro (*Pinus uncinata*) (Benlloch, 2002). La explotación generalizada de todos los bosques del piso montano ha favorecido la dispersión del pino silvestre (*Pinus silvestris*), que espontáneamente ocupa los claros del quejigo (*Q. faginea*), los del hayedo (*Fagus silvatica*) y los del abetal (*Abies alba*). En los claros de los pinares de zonas secas aparece el erizón (*Echinospartum horridum*). En las zonas húmedas de los valles se asientan los bosques mixtos de frondosas, con gran variedad de especies (Benlloch, 2002). El piso basal del pirineo, fue destruido en gran parte para destinarlo al aprovechamiento agrícola. El quejigo ocupa una banda que se extiende por todo el Prepirineo, preferentemente en alturas comprendidas entre los 500 y 1000 metros. A menor altura que el quejigo crece la carrasca (*Quercus ilex*) que ocupa las solanas calizas del Prepirineo, con ella conviven *Buxus sepervirens*, *Juniperus communis*, *Juniperus sabina* y *Arctostaphylos uva-ursi*.

Uso de suelo

En función de las características climáticas y del relieve se escalonan los usos del suelo en la zona de estudio. El nivel superior del Pirineo Aragonés corresponde a los pastos supraforestales, que aparecen frecuentemente por encima de los 1600 m. Inmediatamente por debajo de los pastos supraforetales se sitúa el nivel forestal, mejor conservado en las umbrías (Lasanta, 2002). Como consecuencia de la deforestación

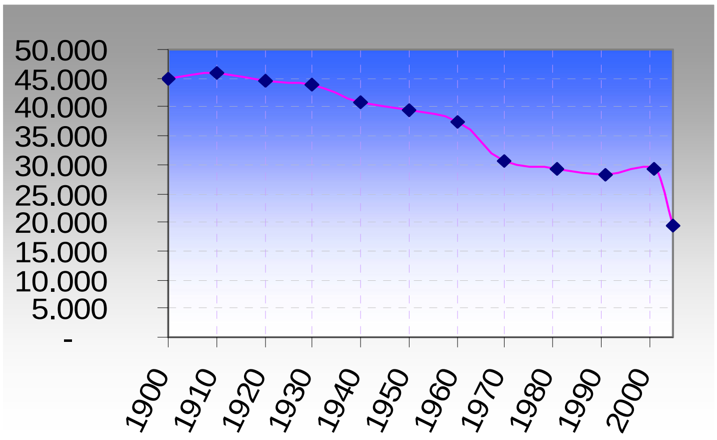

Figura 7: Evolución de la población en la zona de estudio entre 1900 y 2000 (elaboración propia a partir de los datos del Instituto Aragonés de estadística).

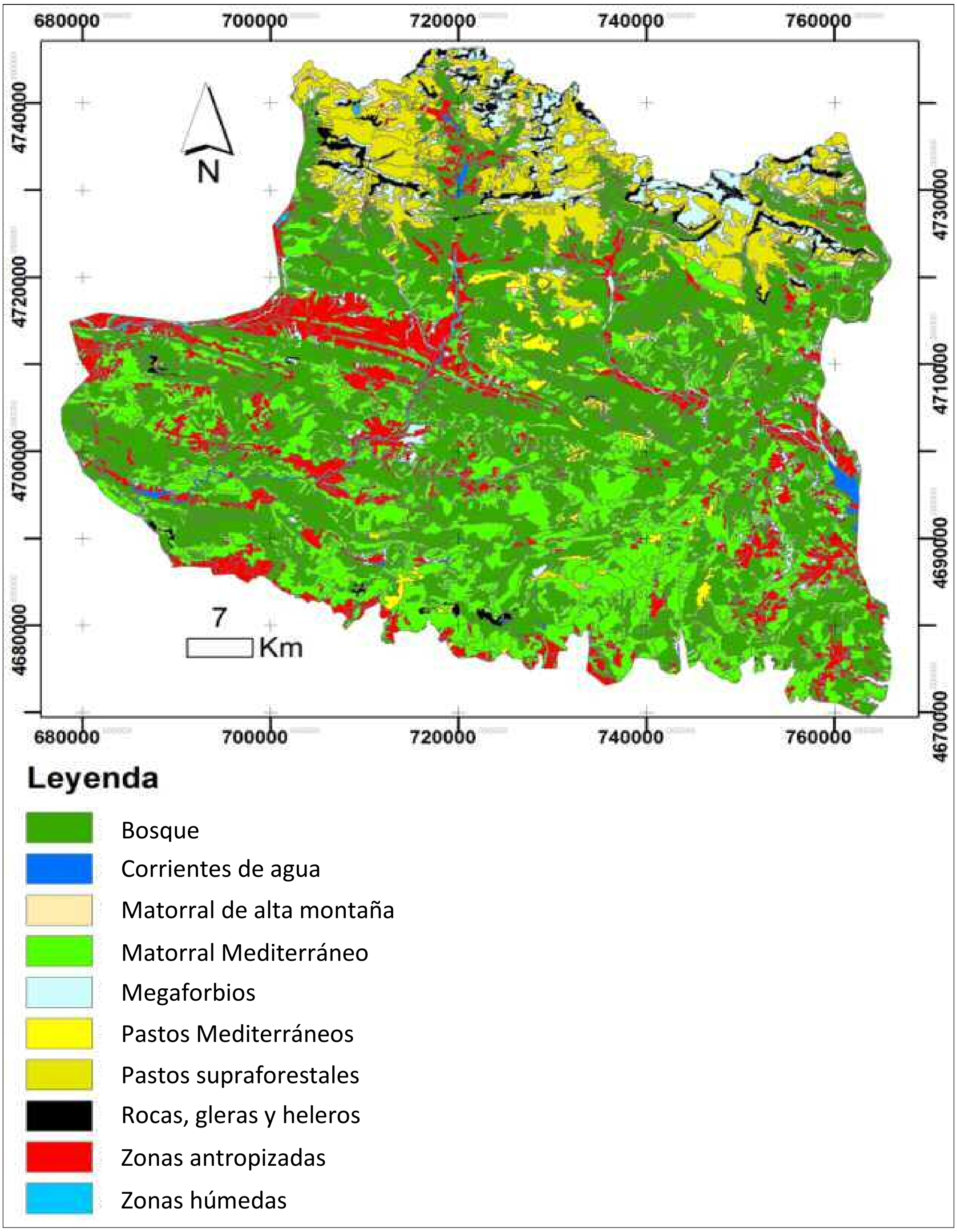

Figura 8: Mapa de usos de suelo en la zona de estudio (elaboración propia a partir del mapa de CORINE Land Cover 2000)

tradicional para el cultivo, el espacio agrícola se sitúa en el nivel inferior del Pirineo ocupando los fondos de valle y la parte baja de las laderas, si bien durante la segunda mitad del siglo XIX y las primeras décadas del siglo XX, la extensión del espacio cultivado fue muy superior, ocupando las actividades agrícolas sectores de los niveles superiores del Pirineo Aragonés (Lasanta, 2002). A partir de los años sesenta se produjo una emigración masiva de la población local (Figura 7) hacia las ciudades en búsqueda de mejores condiciones de vida, lo que ha generalizado una despoblación y envejecimiento de los pueblos y un abandono masivo de las tierras y campos agrícolas. Como consecuencia de este abandono la superficie labrada se reduce a un tercio (Garcia Ruiz & Lasanta, 1990). Una parte de las áreas abandonadas las repuebla el Patrimonio Forestal de Estado, mientras el resto se recupera de forma natural. La Figura 8 demuestra los diferentes usos del suelo en la zona de estudio.

Justificación de la tesis

Pocos trabajos han tratado de estudiar los bosques de quejigo del Pirineo Aragonés aunque es una especie que juega un papel muy importante en la conservación de la diversidad biológica en esta zona. En el Pirineo Aragonés además de la antigua deforestación severa de los bosques de quejigo para el incremento de las tierras agrícolas y los pastos, esta especie está condicionada por los factores abióticos como el clima y la litología, por lo tanto definir los factores abióticos y los relacionados con el cambio del uso de suelo que afectan a la distribución y la evolución espaciotemporal de esta especie tiene una gran importancia a la hora de realizar los planes de gestión de estos bosques. Por otra parte se desconoce el efecto del cambio climático y el cambio del uso de suelo en la dinámica re-generacional de las masas del quejigo. Estudios realizados en otros ecosistemas han mostrado que estos factores pueden afectar negativamente al establecimiento de los árboles y el reclutamiento de nuevos individuos (Améztegui et al., 2010; Chauchard et al., 2010; Gimmi et al., 2010). Se desconoce también el efecto del uso histórico de los bosques de quejigo en la riqueza, diversidad, y composición de las especies que en ellos habitan, aunque muchos estudios han destacado la importancia del uso histórico en la diversidad y la composición de las especies vegetales que albergan (Estevan et al., 2007; Fahey & Puettmann, 2008; Lomba et al., 2011). En esta tesis se realiza un estudio multidisciplinario sobre los bosques del quejigo que aborda distintos enfoques: la distribución espacial, la evolución espaciotemporal, la dinámica de las masas forestales, y la diversidad florística.

Objetivos y organización de la tesis

Esta tesis doctoral está estructurada en seis grandes capítulos que cubren las diferentes etapas y aspectos de esta investigación (Tabla 1).

Como punto de partida estudiamos los factores abióticos y el uso antrópico que afectan a la distribución espacial del quejigo a gran escala (capítulo 1). El propósito fue determinar qué variables abióticas y las relacionadas con el uso del suelo definen mejor la distribución espacial del quejigo en el Pirineo Aragonés. Como forma complementaria hemos clasificado estas variables según la importancia que tiene cada variable en la distribución espacial de esta especie.

En un siguiente paso, a una escala espacial más reducida hemos estudiado la dinámica espaciotemporal de los bosques de quejigo durante el periodo entre 1957 y 2006 (capítulo 2). En este capítulo hemos comparado la configuración espacial de las manchas del quejigo entre 1957 y 2006, lo que nos ha permitido identificar los cambios ocurridos en los bosques de quejigo durante los últimos 50 años. Hemos identificado los factores que han provocado dichos cambios en la estructura espacial de los bosques de quejigo durante este periodo.

Una vez estudiadas la distribución espacial y la dinámica espaciotemporal del quejigo, tratamos de definir el papel del cambio climático y el cambio del uso de suelo en el establecimiento de los árboles del quejigo y en la dinámica regeneracional de los bosques del quejigo (capítulo 3). Para dar este paso, estudiamos la relación entre el establecimiento de los árboles, con las variables climáticas (precipitaciones y temperaturas) y las variables relacionadas con el cambio del uso de suelo (densidad de población de los núcleos urbanos y la cantidad del ganado en la zona estudiada). Como forma complementaria hemos comparado el crecimiento anual medio secundario, el crecimiento apical y el diámetro a la altura del pecho de los individuos de quejigo entre las terrazas abandonadas y los montes bajos.

Los trabajos anteriores (capítulo 2 y 3) han revelado la instalación de nuevas masas de quejigo en el Prepirineo Aragonés, especialmente en las terrazas abandonadas, durante la segunda parte del siglo XX. Así que, el propósito del cuarto artículo fue estudiar la relación entre los cambios socioeconómicos que han ocurrido en el Prepirineo Aragonés durante la segunda mitad del siglo veinte y la expansión del quejigo. Particularmente, se ha examinado la hipótesis de que la colonización del quejigo de algunas zonas del Prepirineo Aragonés es el resultado de la reducción de la presión antrópica en el territorio como consecuencia del abandono de las tierras agrícolas y la disminución de la presión pastoral.

Tabla 1: Resumen de los objetivos de cada uno de los capítulos de la tesis

Capítulo 1	¿Qué variables abióticas afectan la distribución del quejigo? ¿Qué variables antrópicas afectan la distribución del quejigo? ¿Cuál es la importancia de cada variable?
Capítulo 2	¿Cómo han evolucionado las manchas de quejigo entre 1957 y 2006? ¿Cuáles son los factores que han favorecido la extensión del quejigo? ¿Cuáles son los factores que han conducido a la reducción de la superficie de quejigo?
Capítulo 3	¿Cómo ha evolucionado la dinámica re-generacional de los bosques de quejigo durante el siglo veinte? ¿Qué factores climáticos han afectado al establecimiento de los árboles de quejigo durante el siglo veinte? ¿Qué factores antrópicos han afectado al establecimiento de los árboles de quejigo durante el siglo veinte?
Capítulo 4	¿Cuál es la relación entre los cambios socioeconómicos que han ocurrido en el Prepirineo Aragonés durante la segunda mitad del siglo veinte y la expansión del quejigo?
Capítulo 5	¿Cómo está organizada la diversidad florística a distintas escalas espaciales en los bosques de quejigo? ¿Cuáles son los factores que controlan la composición florística a nivel de masas forestales?
Capítulo 6	¿La gestión histórica de los bosques de quejigo ha conducido a una homogenización florística o al contrario a una heterogeneidad florística a escala regional?

En el capítulo 5 se han estudiado los patrones de la diversidad florística en los bosques de quejigo a distintas escalas espaciales (partición jerárquica de la diversidad). Hemos tratado de definir el papel de las características estructurales, espaciales, y topográficas de las masas de quejigo en gobernar y generar esos patrones.

Por último (capítulo 6) hemos estudiado el efecto del uso histórico de los bosques de quejigo en la composición florística actual a nivel de masas forestales. Con este fin hemos comparado la composición florística entre masas forestales en distintos estados de sucesión y con diferentes usos históricos.

Cada capítulo de esta tesis está constituido por un artículo enviado, aceptado, o publicado en una revista científica, por lo que la mayoría de los capitulos están redactados en inglés.

Métodos

Cartografía

#1. <u>El mapa de distribución de *Q. faginea* en la zona de estudio en 2006:</u> el primer paso fue la elaboración del mapa de distribución de *Q. faginea* en la zona de estudio. Este mapa fue elaborado a partir del tercer Inventario Nacional Forestal (IFN3; MMA, 2007). Para ello se seleccionaron las manchas de bosque en las que el quejigo era una de las tres especies arbóreas más abundantes. Las manchas de distribución de la vegetación fueron corregidas con la ayuda de las fotos aéreas orto-rectificadas a escala 1:30000 del Plan Nacional de Ortofotografía Aérea (PNOA, 2006). Debido a que *Q. faginea* se hibrida con *Q. pubescens*, haciendo difícil la identificación de individuos (Himrane *et al.,* 2004; Loidi & Herrera, 1990), hemos incluido los híbridos (principalmente *Q. subpyrenaica*) con *Q. faginea*. Para la elaboración de dicho mapa se ha usado una unidad mínima cartografiable (UMC) de 0,1 ha por mancha.

#2. <u>El mapa de distribución de *Q. faginea* en 1957:</u> se ha elaborado mediante la interpretación visual de las fotos aéreas del año 1957 a escala 1:32000 proporcionados por el Centro Cartográfico y Fotográfico del Ejército del Aire, usando los polígonos del mapa de 2006 como guía. Basándonos en los trabajos publicados (Molinillo *et al.*, 1997; Monserrat, 1990) y en nuestra propia inspección de las fotos aéreas, hemos asumido que sólo las zonas que eran ocupadas por matorral en 1957 podrían haberse transformado en manchas de *Q. faginea* en 2006, por lo que las manchas de matorral se han incluido en el mapa de 1957. De la misma manera que el mapa de 2006, se ha usado una unidad mínima cartografiable (UMC) de 0,1 ha por mancha.

#3. Los mapas topográficos: incluyen la elevación (m, sobre el nivel del mar), pendientes (%), curvatura (zonas cóncavas/zonas convexas), y el mapa de la insolación (Wh/m^2). Estos mapas se han derivado del Modelo Digital del Terreno de Aragón con una resolución de 20-m (CINTA, 2007).

#4. Los mapas climáticos: incluyen el mapa del balance hídrico, el mapa del número de días con heladas por año, los mapas de medias de las temperaturas máximas y mínimas mensuales. Dichos mapas se han obtenido del Atlas Climático de Aragón (DAM, 2007).

#5. Mapas que reflejan las actividades antrópicas: en esta tesis se han usado distintos mapas que reflejan las actividades antrópicas: la distancia al pueblo más próximo, la distancia a la carretera más próxima, la distancia a la repoblación de pinar más próxima, la distancia a la mina más próxima, y las distancias de coste a pastizales, vías pecuarias, y campos agrícolas. Los mapas de distancias se realizaron usando la opción 'Euclidian distance' de ArcGIS que calcula la distancia euclidiana entre cada pixel y el pueblo, la carretera, la plantación, o la mina más próxima. La distancia de coste es una combinación de la distancia entre dos puntos y la pendiente que los separa, se ha calculado usando la opción 'Cost distance' de ArcGIS. Otros detalles sobre el proceso de elaboración de los mapas que reflejan el uso antrópico así como las fuentes de los mapas usados como base están incluidos en los capítulos 1, 2, y 4.

Trabajo de campo

Se han seleccionado diez masas forestales dominadas por *Q. faginea* en el Prepirineo Aragonés (Más detalles sobre los criterios de selección de las masas forestales están proporcionados en los capítulos 3 y 5). Se han usado dos tipos de muestreo en las masas seleccionadas:

#1. <u>Muestreo de las propiedades estructurales del bosque:</u> En cada masa forestal se ha realizado un transecto de 500-m, con 20 puntos de muestreo (un intervalo de 25-m). Usando el método Point-Quarter (Cottam & Curtis, 1956), en cada punto se ha identificado el arbol adulto de *Q. faginea* más cercano en las cuatro direcciones cardinales (Figura 9). Se ha considerado como árbol adulto los individuos con altura superior a 2-m o aquellos individuos con un DBH ≥ 4cm. Para estimar la densidad del bosque, se ha calculado la distancia entre el punto de muestreo (el punto central) y los cuatro árboles.

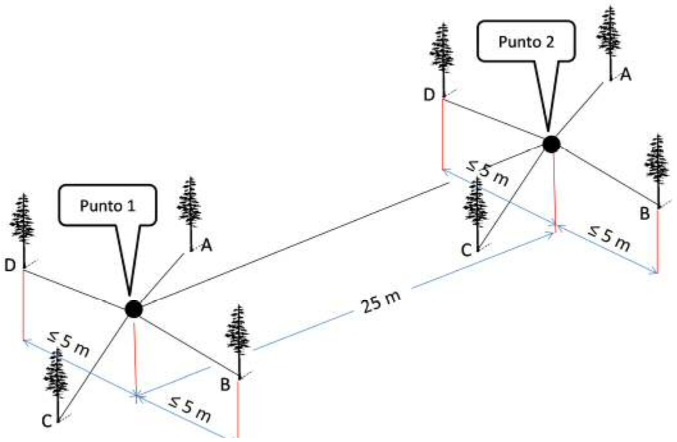

Figura 9: Esquema representativo del diseño de muestreo de las propiedades estructurales del bosque

En cada cuadricula (delimitada por los arboles A, B, C, y D) se han realizado las siguientes mediciones por cada uno de los cuatro arboles: DBH (cm), la altura del arbol (m), como se ha registrado el tipo de hábitat (monte bajo o terraza abandonada). Así como, se han sacado cores o rodajas de 2 árboles en cada cuadricula para estimar la edad de los árboles (ver más detalles en el capítulo 3).

#2. <u>Muestreo de la diversidad florística:</u> En 2009 y 2010, durante el periodo del pico de crecimiento (mayo y junio), se han muestreado las plantas vasculares en las diez masas forestales seleccionadas. En cada masa forestal se ha establecido tres transectos de 500-m (30 transectos en total) (Figura 10). Hemos usado el método de Point-Intercept (Goodall, 1952) para estimar la abundancia y la riqueza de las plantas en cada transecto. Ello implica registrar

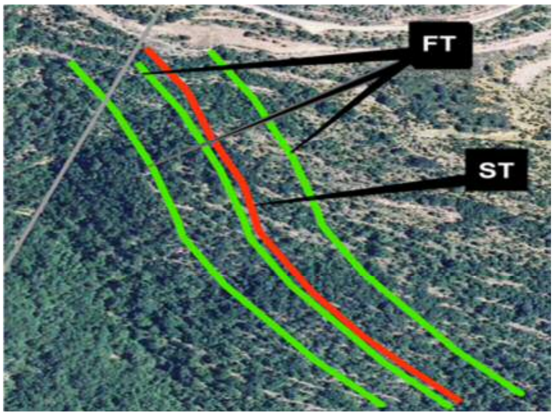

Figura 10: Localización de los 3 transectos de diversidad floristica (FT) y el transecto de propiedades estructurales del bosque (ST) en una masa forestal.

a un intervalo de 40-cm la identidad de los individuos que estan en contacto con el puntero. Los individuos que no eran fáciles de identificar en el campo se han traído al laboratorio para identificarlos posteriormente por un experto en botánica.

Análisis de los datos

Dado el gran número de métodos usados para el análisis de datos, en este apartado solo nos concentramos en los métodos más relevantes.

#1. Análisis Bayesiano del Modelo Lineal Generalizado: La estadística bayesiana es una alternativa a la estadística clásica en los problemas típicos estadísticos como son estimación, prueba de hipótesis y predicción. La estadística bayesiana proporciona un completo paradigma de inferencia estadística y teoría de la decisión con incertidumbre. En esta tesis se ha usado la función "bic.glm" que realiza el Modelo Bayesiano Promediado (BMA) para el Modelo Lineal Generalizado (GLM). Esta función utiliza "Bayesian Information Criterion (BIC)" para comparar los modelos y el algoritmo ''leaps and bounds'' para identificar los modelos más probables (Raftery et al., 1997; Thomson et al. 2007). En el BMA, la probabilidad posterior de que el coeficiente de una variable tiene un valor diferente de cero, se usa como medida de influencia de esta variable en la variable respuesta (Hoeting et al., 1998). BMA se ha usado en este trabajo de tesis para identificar los factores que afectan a la distribución espacial de *Q. faginea* (capítulo 1), así como para saber cuáles son los factores que han afectado a la dinámica de *Q. faginea* entre 1957 y 2006 (capítulo 2).

#2. Partición Jerárquica de la varianza (HP): Este método se usa para calcular el porcentaje de la varianza total explicado "independientemente" por cada variable explicativa (Chevan & Sutherland, 1991). HP se ha usado en el capítulo 1 para clasificar los factores que afectan a la distribución espacial de *Q. faginea* basando en la varianza explicada independientemente por cada variable.

#3. Índice de Moran (Moran's *I*): Uno de los indicadores más viejos para estimar autocorrelación espacial (Moran, 1950). Se aplica a zonas con puntos donde se miden variables y compara el valor de la variable en una localidad con el valor en las localidades vecinas. Dado pares de localidades separadas por ciertas distancias, es la propiedad de variables aleatorias de tomar valores que son más similares (autocorrelación positiva) o menos similares (autocorrelación negativa) que lo esperado por pares de localidades aleatoreamente asociados (Legendre, 1993). El Índice de Moran se ha usado en los capítulos 1 y2 para definir la distancia mínima (entre las observaciones) a partir de la cual desaparece la autocorrelación espacial (Índice de Moran igual a cero) en las variables respuesta.

#4. Análisis de la Varianza Multivalente semi-paramétrico (PERMANOVA): Técnica de análisis multivariante que permite cubrir los casos dónde hay más de una variable dependiente que no pueden ser combinadas de manera simple (por ejemplo, usando ANOVA) (Anderson, 2001). PERMANOVA utiliza las distancias entre cada par de observaciones para obtener una matriz de distancia (como el análisis de componentes principales normalmente conocido por sus siglas en inglés, PCA) sobre la que luego se calcula la significación de las variables explicativas con simulaciones de Monte Carlo. Aplica análisis de permutaciones sobre las matrices de distancia. Este análisis nos permite saber si las variables explicativas tienen un efecto sobre el conjunto de las variables respuesta (ejemplo: la matriz de sitios × especies). Calcula también la variabilidad explicada por cada una de las variables explicativas. Este método se ha usado en el capítulo 6 para identificar los factores ambientales que controlan la variación de la composición florística en los bosques de *Q. faginea*.

#5. Escalamiento multidimensional no métrico (NMDS): El NMDS es una técnica multivariante de interdependencia que trata de representar en un espacio geométrico de pocas dimensiones las proximidades existentes entre un conjunto de objetos. El NMDS es un método de ordenación adecuado para datos que no son normales o que están en una escala discontinua o arbitraria (Minchin, 1987). NMDS es una técnica ampliamente utilizada en ecología para detectar gradientes en comunidades biológicas, tiene la ventaja de permite reducir la dimensionalidad de los datos originales y visualizar los resultados en un gráfico de ordenación. Los ejes resultantes de la ordenación NMDS se pueden también relacionar con distintas variables ambientales para determinar de manera indirecta el efecto de éstas sobre la matriz de sitios × especies. Hemos usado este método (capítulo 6) para examinar las diferencias en la composición florística entre masas forestales con distintas características (estructurales, espaciales, y topográficas).

#6. Análisis de Redundancia (RDA): Es una técnica multivariante que permite representar en un espacio geométrico de pocas dimensiones las proximidades existentes entre un conjunto de objetos condicionado por una serie de variables predictoras. El RDA es una técnica de ordenación restringida (constrained ordination; Legendre & Legendre, 2012), lo que significa que la ordenación de los objetos representa solamente la estructura de los datos que maximiza la relación con una segunda matriz de variables predictoras. RDA relaciona dos matrices: la matriz de variables dependientes (por ejemplo una matriz de sitios × especies) y la matriz de variables independientes (por ejemplo una matriz de variables ambientales). La relación entre ambas matrices se hace por medio de una combinación de técnicas de regresión multivariante y análisis de componentes principales (Bocard et al., 2011). En esta tesis (capítulo 5), RDA se ha usado para estudiar la relación entre las características estructurales, espaciales, y topográficas de las masas forestales y la composición florística.

#7. Partición Multiplicativa de la diversidad (MP): Este método está basado en la idea de Wittaker (1972): diversidad gama (γ) es igual a la diversidad alfa (α) multiplicada por la diversidad beta (β). Jost (2006) ha recomendado el uso de los números equivalentes (Hill numbers) en lugar de los índices de diversidad conocidos (p.e. riqueza, Shannon), y ha demostrado que el uso de los números equivalentes permite satisfacer los requisitos de la MP. La MP se ha usado en esta tesis (capítulo 5) para evaluar los patrones de biodiversidad a múltiples escalas espaciales (transecto, masa forestal, y área de estudio).

#8. Métricas de paisaje: Una métrica describe la estructura espacial de un paisaje en un tiempo determinado. Se utilizan como herramientas para caracterizar la geometría y las propiedades espaciales de un parche (una entidad espacialmente homogénea) o un mosaico de parches (Leitao & Ahern, 2002). En esta tesis (capítulo 2) se han usado las siguientes métricas para cuantificar y comparar la configuración espacial de las manchas de *Q. faginea* entre 1957 y 2006: (1) el número total de manchas de *Q. faginea*, (2) el tamaño medio de mancha (ha), (3) la distancia media entre las manchas (m), (4) el area total ocupada por *Q. faginea* (ha), (5) la longitud total de los bordes de las manchas (km), (6) la media de la ratio perímetro-área de mancha.

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CAPITULO 1

Effects of abiotic and anthropogenic factors on the spatial distribution of *Quercus faginea* in the Spanish Central Pyrenees

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Abstract

Abiotic factors often are the most important factors influencing a species' distribution. Nevertheless, when investigating the underlying causes of a species' distribution, it is important to assess both the abiotic and the anthropogenic factors (land-use variables) that might have influenced the species' distribution. That is especially true in the Mediterranean Basin, where natural ecosystems have undergone significant changes in response to anthropogenic pressures in the region. In this study, we examined the effects of abiotic and anthropogenic factors on the distribution of *Quercus faginea* in the Spanish Central Pyrenees. Information on the presence-absence of *Q. faginea*, and abiotic and anthropogenic variables, were derived using GIS based on digital maps and aerial photographs. To identify and quantify the factors that have affected significantly the spatial distribution of *Q. faginea*, we used Bayesian Model Averaging and hierarchical partitioning. In the Spanish Central Pyrenees, on a broad scale, abiotic variables; i.e. climate and lithology, were the factors that had the greatest effect on the spatial distribution of *Q. faginea*; however, recently introduced pine plantations and previous livestock pressure has had a negative effect on the distribution of *Q. faginea* in the region.

Keywords: Species distribution models (SDM), explanatory models, Bayesian Model Averaging, hierarchical partitioning, land-use variables.

Introduction

An understanding of the factors that influence the distribution of a species is important because it enables us to estimate the drivers of a species' distribution within a region. To model the relationship between a species and its environment, ecologists often use empirically based statistical models (e.g., Coudun et al. 2006; Segurado and Araújo 2004; Thuiller et al. 2004). Statistical models of species distributions (i.e., presence-absence of species) quantify the relationships between the dependent variable and a set of explanatory variables such as temperature, slope, and elevation. These models can be used as (1) explanatory: To make inferences about which variables are important in controlling the distribution of the focal species , i.e., examine the underlying causes of a species' distribution by examining the statistical significance of an explanatory variable influence on dependent variable or (2) predictive models: To estimate the spatial distribution of environments that are suitable for species distribution by creating a predictive map using the relationship between dependent variable and the predictors. But, in many cases, these models are used only to predict the potential distribution area of a species (i.e. as predictive models), while the underlying causes tend to be a secondary consideration. Consequently, few modeling studies have addressed those causes (e.g., Graham et al. 2004; Nally 2000).

Usually, the spatial distributions of terrestrial species are studied in the context of abiotic variables only, i.e., climate (e.g. Araújo et al. 2005), climate and topography (e.g. Raxworthy et al. 2007), climate and soil conditions (e.g. Coudun et al. 2006), and climate and lithology (e.g. Gastón et al. 2009). These abiotic variables are postulated to be the most important factors influencing the distribution of a species. However, human land use (e.g., agricultural and livestock activities and reforestations) may affect the distribution of plant species (Randin et al. 2009; Dirböck et al. 2003) or communities (Fischer 1990). In the Mediterranean Basin, one of the world's biodiversity hotspots (Myers et al. 2000), human activities have contributed significantly to the fragmentation of natural communities and the loss of species (Maltez-Mouro et al. 2009). For instance, plantations recently introduced in mountainous areas of Spain have replaced the native forests with faster growing species (Perry 1998), which has led to a reduction in the amount of area occupied by species and landscape diversity (Lasanta et al. 2009). Consequently, it is imperative to include anthropogenic factors when investigating the underlying causes of a species' distribution.

Q. faginea was the subject of this study because it is sensitive to abiotic and anthropogenic factors. It is a winter-deciduous tree that usually does not exceed high-shrub stature because of anthropogenic disturbances or environmental limitations (Maltez-Mouro et al. 2009). In many mesic forests in Mediterranean environments, *Q. faginea* is an important structural component of native plant communities because it provides habitat for a wide diversity of plant and animal communities and, therefore, is of great interest for ecosystem conservation (Rey Benayas et al. 2005). Despite its interest and its importance in rural populations as a source of several resources (e.g., timber and acorns), this species has been relatively little studied. The objective of this study was to quantify the effects of abiotic and anthropogenic factors on the distribution of *Q. faginea* forests in the Spanish Central Pyrenees.

Methods

Study area and species

The study was conducted in the Spanish Central Pyrenees between 42.47 N and 42.14 N, and between 0.32 W and 0.10 E (Fig. 1), an area that encompasses a wide elevation range (500-3000 m a.s.l.). The 4394-km^2 area included about 325 villages and had clear rural character. In the area, the climate is quite variable, with oceanic characteristics in the western portion and a Mediterranean influence in the easternmost portion (Lasanta 2002). Mean annual rainfall is >800 mm year $^{-1}$ at the lowest elevations and, above 1500 m, annual precipitation is >1500 mm year $^{-1}$ (Vicente-Serrano et al. 2004). Throughout the area, intra-annual variability is very high, and the rainy season extends from October to June. At the lowest elevations, mean annual temperature varies between 9 ºC and 11 ºC and, at the highest elevations (≥1500 m), it is 6 ºC. The relief of the study area occurs in three parallel bands that have a NW-SE orientation (Vicente-Serrano et al. 2004); specifically, they are the Axial Pyrenees (2500-300 m a.s.l.), the Eocene flysch areas (800-2500 m a.s.l.), and the Ebro Depression (400-800 m a.s.l.), which forms a wide valley. The landscape is a mosaic of natural and semi-natural forests, shrublands, grasslands, agricultural fields, and urban areas.

In the Central Pyrenees, *Q. faginea* is one of the most abundant tree species and it occurs naturally, it is not artificially reforested. The communities in which it occurs form a transition between conifer-sclerophyllous forests of *Q. ilex* and *Pinus halepensis* and high mountain forests of *P. sylvestris*, *P. nigra*, *Fagus sylvatica,* and *Abies alba* (Sancho et al. 1998; Loidi and Herrera 1990). The ease with which *Q. faginea* hybridizes with congeners; e.g. *Q. pubescens*, has led to numerous hybridogenic populations within the study area, which has made it difficult to identify individuals (Himrane et al. 2004; Loidi and Herrera 1990); therefore, we treated those hybrids (mainly *Q. subpyrenaica*) within *Q. faginea* species.

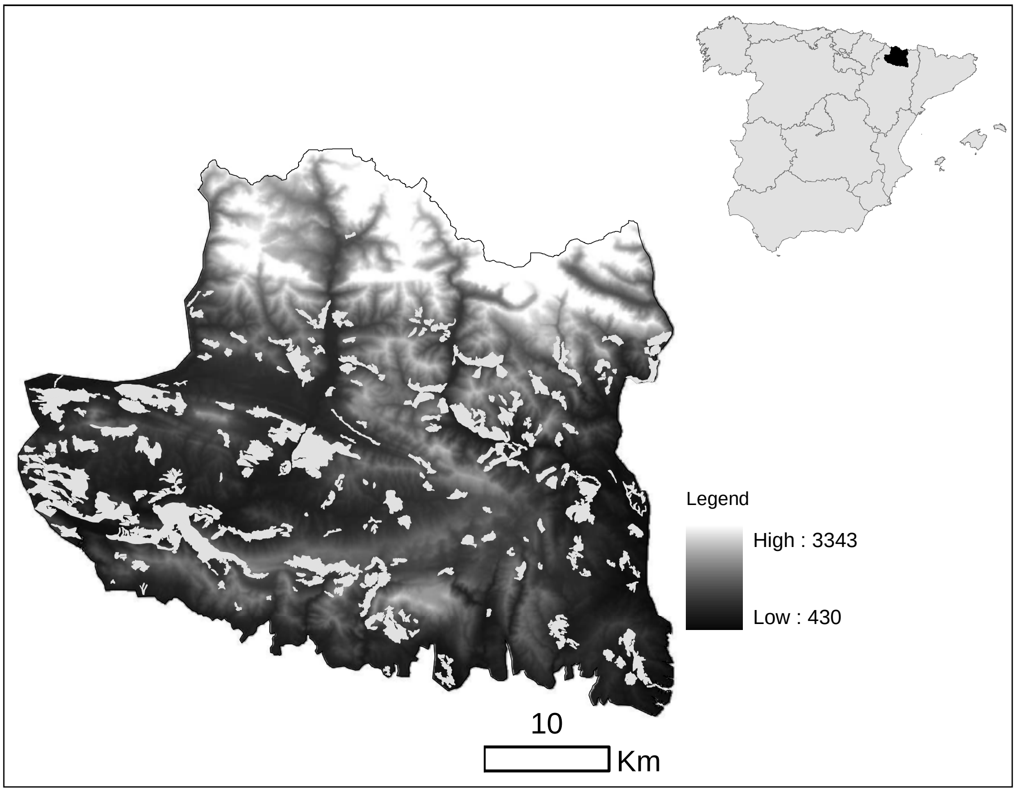

Fig. 1 Up right corner map shows the location of the study area within Spain. Central map shows the Digital Elevation Model of the study area; the grey scale indicates the elevation range (m) above sea level. Shady areas indicate patches of *Q. faginea*.

Distribution of Quercus faginea

A distribution map of *Q. faginea* in the Spanish Central Pyrenees was derived from the Third Spanish National Forest Inventory map (IFN3) (MMA 2007). In the IFN3 map, the three principal tree species were considered for each patch and classified as either the first-, second-, or third-most dominant tree species based on an visual estimate in the field of the proportional coverage of each species in the patch. All patches, in which *Q. faginea* was among the three most dominant species, were used to create the distribution map of this species within the study area. Overall, the contribution of *Q. faginea* to patches varied from 20% (in the patches where *Q. faginea* was the third most dominant species) to 90% (in the patches where it was the most dominant species). The distribution map was imported into a GIS for further processing, including correcting the edges of patches and the removal for each patch of the areas where *Q. faginea* was absent. This process was done by visual inspection of ortho-rectified, 0.5-m-resolution aerial photographs (1:30 000) from the Spanish National Plan of Aerial Orthophotographs (IGN 2006). The accuracy of the final map (96%) was quantified by sampling 200 random points and calculating confusion matrices (Congalton 1991). Data sampling was based on 20-m^2 grid layers that included all of the dependent and independent variables, from within which 2000 pixels were chosen randomly (among them 900 records of *Q. faginea* occurrences) using the ArcGIS extension, Hawth's Analysis Tools 3.27. A distance of 400 m was used as a minimum threshold in selecting sampling (see ‘‘Statistical analysis’’, below), which prevented spatial-autocorrelation in the data (Legendre 1993). To avoid non-representative sampling, each patch (polygon) of *Q. faginea* was represented by a minimum of five records of occurrence.

Abiotic data

The explanatory variables were chosen based on previous studies (Austin 2007; Guisan and Zimmermann 2000; Purves et al. 2007) and the approach we used relies on the combination of abiotic variables that might have a direct or indirect influence on *Q. faginea* (Corcuera et al. 2004; Lansac et al. 1994; Mediavilla and

Escudero 2004) and anthropogenic variables that reflect the anthropogenic disturbances. Following Coudun et al. (2006), we selected abiotic variables that have an influence on (1) biophysical processes (elevation, slope, terrain curvature, and lithology), (2) frost conditions (number of frost days per year and mean monthly minimum temperature), (3) drought (water balance and mean monthly maximum temperature), (4) primary production (insolation). We expected that most of the *Q. faginea* would occur at 500-900 m a.s.l., in areas that had a sizable positive water balance, and moderate temperatures.

The topographic variables, elevation (m a.s.l.), slope (degrees), terrain curvature (concavity/convexity), and insolation (Wh/m^2) were derived from a Digital Elevation Model of Aragón (CITA 2009) at a 20-m resolution using ArcGIS 9.2 (ESRI 2006). The data for climatic variables, obtained from the Climatic Atlas of Aragon (DMA 2007) at 100-m resolution, were averaged over the period 1971-2000 and included water balance (mm), number of frost days per year, and mean monthly maximum and minimum temperatures (ºC). The elaboration process of the climatic maps was based on the combination of local and global methods of interpolation. Topographic (latitude, longitude and insolation) and geographic variables (distance to rivers and Cantabrian Sea,) were used as independent variables to explain the spatial variability in the climatic factors. The following equation was used to predict the values of the climatic variable in areas without information:

$$z(x) = b_0 + b_1P_1 + b_2P_2 + \ldots + b_nP_n$$

Where z is the predicted value at point x, $b_0, \ldots, b_n$ are the coefficients of the regression, and $P_1, \ldots, P_n$ are the values of the set of independent variables at point x.

Measures of water balance were obtained by subtracting potential evapotranspiration estimated using the Hargreaves Equation (Hargreaves 1975) from mean annual precipitation. The climatic maps were downscaled from the original grid (100-m^2) to a 20-m^2 using nearest-neighborhood interpolation. The lithological map was derived from the geological map of Aragón (CITA 2007) and included two classes: flysch-limestones rocks and other types of rock.

Anthropogenic data (land-use variables)

In our study, we assessed several land-use variables that might have influenced the spatial distribution of *Q. faginea*, which included the distance to the nearest village, an index of exposure to human activities near villages (i.e., in the study area the villages are located in the valley bottoms or in flat areas near croplands, which allows them to be a good indicators of human activities), and to determine whether *Q. faginea* was influenced by the wood harvesting associated with mining, the distance to the nearest mine was quantified. In addition, to assess the extent to which livestock activities affected the distribution of *Q. faginea*, we included the explanatory variables: cost distance to pastures and cost distance to livestock roads (see below). Extensive reforestation with pine plantations in the area within the last 50 yr might have influenced the distribution of *Q. faginea*; therefore, the distance to the nearest pine plantation was included in the analyses. We expected that *Q. faginea* would be more common away from villages, mines, pastures, livestock roads, and pine plantations.

A map of the villages was derived from a map of the settlements in Aragon (CHE 2009) and a map of the mines in the area was derived from a map of the CORINE Land Cover 2000 5th Level Project (IGN 2002). Raster layers were created based on the Euclidean distances to the nearest village and mine within each pixel. The cost distance to pastures and cost distance to livestock roads were calculated based on a map of the CORINE Land Cover 2000 5th Level Project (IGN 2002) and a livestock road map of Aragón (DMA 2010), respectively. The cost-distance function calculates the least accumulative cost for moving from the source pixel (in this case, pasture or livestock road) to each of the other pixels using slope as a cost layer. Up to a slope of 35º, cost distance significantly positively correlated with slope; beyond that steepness, areas are effectively inaccessible (maximum cost) to livestock and men. To identify a variable that best reflected the effect of pine plantations on *Q. faginea* forests, we created a map of the pine plantations (*P. sylvestris* and *P. nigra*) in the study area based on the Third Spanish National Forest Inventory map (IFN3; MMA 2007) and calculated the Euclidean distance to the nearest plantation for each pixel using ArcGIS 9.2 (ESRI 2006).

Statistical analysis

First, collinearity was checked in the potential predictor variables using the Pearson's correlation coefficient. Water balance was highly positively correlated with elevation ($r_{pearson}$= 0.89) and highly negatively associated with mean monthly minimum temperature ($r_{pearson}$= -0.88) and mean monthly maximum temperature ($r_{pearson}$= -0.87). From the four variables, only water balance that was retained, because (1) it was highly correlated with the response variable compared to the other three variables, and (2) the three drooped variables were reflected well by water balance ($|r|_{pearson} \geq 0.87$). Contrary to the four variables, the other predictor variables were weakly correlated (for all other variables $|r|_{pearson} < 0.35$). The final set of potential explanatory variables included lithology, slope, terrain curvature, water balance, insolation, number of frost days per year, distance to the nearest plantation, distance to the nearest village, distance to the nearest mine, cost distance to livestock roads, and cost distance to pastures. Spatial autocorrelation was evaluated in the *Q. faginea* distribution map (pixels of 20-m) using the row-standardized Moran's *I* Test (Cliff and Ord 1973). Spatial autocorrelation decreased monotonically above a lag of 15 map pixels (~300 m); therefore, 400 m was used as the minimum threshold in selecting sampling (Millington et al. 2007).

To model the responses of *Q. faginea* to abiotic and anthropogenic factors, we used Bayesian Model Averaging (Madigan and Raftery 1994), which incorporates model selection and parameter estimation uncertainties into inference and prediction (Hoeting et al. 1999; Raftery et al. 1997) and produces more accurate predictions than methods that select a single best model (Thomson et al. 2007; Wintle et al. 2003). We used the function ''bic.glm'' in the ''BMA'' package (Raftery et al. 2009) in R (R Development Core Team 2009), which performs BMA for GLM (binomial error distribution and a logit link function). The function uses the Bayesian Information Criterion (BIC) to compare models, and a "leaps and bounds" algorithm to identify the most probable models (Raftery et al. 1997; Thomson et al. 2007). In BMA, the posterior probability that a variable has a non-zero coefficient in the predictor model Pr (βvs. ≠ 0) is used as a measure of the influence of that variable on the response. Explanatory variables that had high values of Pr (βvs. ≠ 0) contributed most to the final model and those that had low values of Pr (βvs. ≠ 0) were included in least probable models, only (Nally et al. 2008; Thomson et al.

2007). Explanatory variables that had values of Pr (βvs. ≠ 0) > 0.75 were identified as ‘‘key factors’’ (Nally et al. 2008; Viallefont et al. 2001).

More than one key factor was identified in our analysis; therefore, to determine relative importance of each key factor, we used Hierarchical Partitioning (HP) in the ‘‘hier.part’’ package in R (Walsh and Nally 2008). HP estimated the "independent" contribution of each "key factor" to the total variance explained by the model (Chevan and Sutherland 1991; Nally et al. 2008). Log-Likelihood goodness of fit measure was used. A logistic model was most appropriate because the dependent variable was binary (presence or absence). Note that hierarchical partitioning, as currently implemented in the "hier.part" package, assumes a monotonic relationship between the dependent and the explanatory variables (Luoto et al. 2006). To assess the nature of the relationship between the dependent variable and each one of the key factors (i.e., linear or nonlinear) we used univariate Generalized Additive Models (univariate GAMs); the smoothed function was plotted for each univariate GAM. The linear and quadratic terms were used in the HP analysis for those key factors that showed a nonlinear relationship with the dependent variable.

Results

"Key factors" influencing the distribution of Q. faginea

BMA identified the factors that had the most effect on the distribution of *Q. faginea* in the Spanish Central Pyrenees. Among the 11 explanatory variables included in the model, the following six were identified as key factors: three abiotic variables (lithology, slope, and water balance) and three anthropogenic variables (cost distance to pastures, cost distance to livestock roads, and distance to nearest plantation). BMA suggested that insolation, terrain curvature, number of frost days per year, distance to the nearest village, and distance to the nearest mine did not have a statistically significant effect on the distribution of *Q. faginea* in the region [Pr (βvs. ≠ 0) < 0.25].

All of the key factors had a high probability of being included in the final model [Pr (βvs. ≠ 0) > 0.94], which reflected their strong relationship with the occurrence of *Q. faginea*. Water balance and cost distance to the livestock roads were negatively correlated with the occurrence of *Q. faginea* because the posterior means (PM+SD) of the coefficients associated with each variable were negative

(Table 1); i.e., the probability of occurrence of *Q. faginea* increased with a decrease in the water balance, and in accessible areas from livestock roads. Slope, lithology, distance to the nearest plantation, and cost distance to pastures had a positive effect on the likelihood that *Q. faginea* was present (Table 1), which indicated that the probability that *Q. faginea* was present increased with an increase in the slope (the cross tabulation between slope and the *Q. faginea* distribution maps indicated that almost all (> 90%) of the areas occupied by *Q. faginea* had a slope between 5º and 30º. This result indicated also that the probability that *Q. faginea* was present was higher in lithological zones that were formed by flysch-limestone rocks than it was in other zones. The probability of occurrence increased with an increase in the distance to the nearest plantation, and cost distance to pastures, which indicated that *Q. faginea* was more likely to be found away from pine plantations and in unreachable areas from pastures, than in other sites.

Table 1 Bayesian Averaging Model (BMA) and hierarchical partitioning (HP) used for identifying the most important factors that affecting the distribution of *Q. faginea* over the Spanish Central Pyrenees. Pr (βvs. ≠ 0) is the posterior probability that a variable had a non-zero coefficient, and (PM+SD) is the posterior means and standard deviation of the coefficients associated with each variable

Variables	BMA		HP (%)
	Pr (βvs. ≠ 0)	PM+ SD	
Lithology	**100%**	**0.136±0.087**	**17.431**
Slope	**100%**	**0.4104±0.009**	**16.003**
Curvature	03.45%	0.007±0.004	0
Water balance	**100%**	**-0.511±0.011**	**33.661**
Insolation	21.20%	-0.023±0.021	0
Number of frosts days	06.05%	0.041±0.025	0
Cost distance to pastures	**100%**	**0.072±0.004**	**10.103**
Cost distance to livestock roads	**99.76%**	**-0.011±0.008**	**08.093**
Distance to nearest mine	14.10%	-0.012±0.027	0
Distance to nearest village	07.50%	-0.026±0.231	0
Distance to the nearest plantation	**94.70%**	**0.106±0.120**	**14.709**

Independent explained variance

HP analysis (Table 1) suggested that the abiotic factors explained > 67% of the total independent variance, which reflects the importance of those factors on the distribution of *Q. faginea*. Water balance (33.66%), lithology (17.43 %), and slope (16.00 %) made the greatest independent contributions. Anthropogenic factors explained about 33% of the total independent variance, with distance to the nearest plantation (14.70%) and cost distance to pastures (10.10 %) making the greatest contribution. Those two variables had a negative effect on the probability of *Q. faginea* presence. Cost distance to livestock had a lowest contribution (08.09%) to the total independent explained variance.

Discussion

Effects of abiotic factors

In large part, abiotic factors, particularly climate, lithology and slope, explained the spatial distribution of *Q. faginea* in the Spanish Central Pyrenees; precipitation and soil water recharge can have a significant effect on the establishment of *Q. faginea* plants (Corcuera et al. 2004), and a high soil water recharge favors the growth of *Q. faginea* (Corcuera et al. 2004). Our study indicated that water balance and the occurrence of *Q. faginea* were negatively correlated because of a particularity of the Central Pyrenees, where water balance increases with an increase in elevation and where temperatures are very low values in winter. Water balance was strongly correlated with elevation and mean monthly minimum temperatures (see statistical analysis). The cross tabulation between elevation and *Q. faginea* distribution maps indicated that, in the Central Pyrenees, all of the areas occupied by this species were between 450 m and 1500 m a.s.l.. The species does not occur above 1500 m because freezing temperatures hinder the establishment and growth of seedlings. As in our study, Sánchez de Dios et al. (2006) found that *Q. faginea* forests on the Iberian Peninsula were associated with continental areas that have low precipitation. The phenology of *Q. faginea* is similar to that of species that produce roots that can access deep water reserves (Castro and Montserrat 1998). In the Central Pyrenees, the probability of *Q. faginea* occurrence was high in areas that were characterized lithologically by flysch-limestone rocks and were rich in calcium carbonate, which generates calcareous soils that are suited to the establishment and growth of this species (Ceballos and Torre 1979; Sancho et al. 1998). In addition, the results showed that the probability of *Q. faginea* occurrence increases with a raise in slope values; the cross tabulation between slope and the

Q. faginea distribution maps revealed that *Q. faginea* occupied areas that had a slope between 5º and 30º. In the Central Pyrenees those areas were mainly occupied by croplands, grasslands, and abandoned fields. Particularly, in grasslands and abandoned fields the high radiation and low water availability during summer, and herbaceous plants competition (i.e. herbaceous plants are strong competitor for resources, particularly water) limit the establishment of *Q. faginea* seedling (Rey Benayas et al. 2005), and therefore, prevent this specie from spreading in those areas.

Effects of anthropogenic factors

In the Central Pyrenees, anthropogenic factors appear to have played a secondary role in influencing the spatial distribution of *Q. faginea*, acting to restrain the expansion of this species. In particular, livestock grazing and introduced plantations have affected negatively the distribution of *Q. faginea* in the region. Elsewhere, the probability that *Q. faginea* was present was lowest in areas near pine plantations, which indicates that native forests can be severely affected by introduced species, particularly those that are fast growing and have strong dispersal abilities (Teixido et al. 2010). In the Central Pyrenees *Q. faginea* forests were extensively deforested to increase the amount of croplands and pastures (Lasanta 1989), but latter reforested with pine plantations (Amo et al 2007). Currently these plantations occupy areas that were previously covered by *Q. faginea* forests. In addition, the introduced species are characterized as fast growing and have dispersal ability, which allows them to be great competitors to *Q. faginea*, i.e., creating a competition that prevents *Q. faginea* from spreading in those plantations. This study showed that *Q. faginea* was less likely to occur in areas close to pastures that were accessible to livestock. In areas that experience livestock overgrazing, the regeneration of tree populations is practically impossible (Barbero et al. 1990). Livestock eliminates seedlings, which diminishes recruitment and, consequently, hinders species regeneration (Cierjacks and Hensen 2004). In some areas of the Central Pyrenees, *Q. faginea* forests were used in a “dehesas” system (Barbero et al. 1990; Montserrat 1990); i.e., a silvo-pastoral system that had sparse *Q. faginea* and perennial grass layers. In these particular ecosystems, the high grazing pressure increases the acorns consumption and creates abiotic conditions unfavorable for seedling establishment (Pulido and Díaz 2005, Plieninger 2006) which hamper the regeneration of *Q. faginea* and therefore lead to its disappearance from those sites*.* Between 1200-1500 m a.s.l., *Q. faginea* forests were harvested and summer livestock pastures were created (Lasanta et al. 2005). Conversely, *Q. faginea* seemed to be favored in accessible areas from livestock roads, which is probably a consequence of silvicultural practices (thinning, pruning) used by the forestry service alongside the livestock roads, which helped to maintain the health of *Q. faginea* stands near livestock roads. BMA suggested that distance to the nearest village did not affect the likelihood of *Q. faginea* occurrence, which means that the spatial distribution of this species was not directly affected by the human activities, concentrated around villages, probably because of the important decrease in the anthropogenic pressure on the territory (e.g. the abandonment of agricultural fields) as consequence of human exodus that occurred in the region during the second half of the 20th C.

Conclusions

This study has demonstrated that abiotic variables operating on a broad scale; e.g., lithology and climate were the main factors influencing the distribution of *Q. faginea* in the Spanish Central Pyrenees, and anthropogenic factors, particularly the recent addition of plantations and previous livestock pressure, affected negatively the distribution of *Q. faginea* in the study area. Much attention has been focused on the role of abiotic variables as main factors influencing the distributions of terrestrial tree species; however, our study showed that anthropomorphic changes in land use can affect the distribution of tree species, especially in the Mediterranean region, where natural ecosystems underwent substantial modifications caused by changes in the anthropomorphic use of land.

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CAPITULO 2

Spatio-temporal dynamics of *Quercus faginea* forests in the Spanish Central Pre-Pyrenees

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Abstract

Anthropomorphic changes in land use have extensively modified natural forests in the European countries over the twentieth century. This yielded a decline in the number of plant species and fragmentation of their populations. Understanding of the impact of land use changes on the spatio-temporal dynamics of forest species is essential to the ecological sustainability of the natural forests in the region. In this study, we examined the spatio-temporal dynamics of *Quercus faginea* forests in the Central Pre-Pyrenees (Spain) over period from 1957 to 2006. Gains and losses in *Q. faginea* forests were quantified by means of construction of matrix of changes. Patch fragmentation, isolation, and irregularity were assessed using a set of standard landscape metrics. Also, the probable factors influencing these changes were identified employing three statistical models. The univariate generalized additive model (GAM) was used to explore the nature of the relationship between the response and predictor variables. The Bayesian model averaging (BMA) and the adaptative regression mixed with model screening (ARMS) were employed to identify the most important factors affecting changes in *Q. faginea* forests. The results of this research revealed substantial changes in the spatial patterns of *Q. faginea* forests in the Central Pre-Pyrenees over the last 50 years. These changes have been clearly reflected in noteworthy increase of fragmentation, isolation degrees, and patch irregularity. Changes in the spatial patterns of *Q. faginea* forests were particularly driven by the vast introduction of pine plantations and the former deforestation, associated with increasing the amount of croplands and pastures. In addition, roads acted as attractors for changes in land use and deforestation, which influenced strongly the spatial variability in *Q. faginea* forests. Therefore, the long-term sustainability of these forests largely depends on the landscape conservation, where this species occurs. Moreover, an improvement in the integrity and connectivity of the remaining patches of native *Q. faginea* forests is still demanded.

Keywords: Landscape metrics, Bayesian model averaging, Adaptative regression by mixing with model screening, Land use changes, Species gains and losses, Fragmentation.

Introduction

In forest management, there is great interest in gearing objectives and strategies to the dynamics of natural forests (Rademacher et al. 2004). Forest management strives to use natural processes within forests to optimize the environmental services and minimize the impact of disturbances on them (Rademacher et al. 2004). Researchers have shown that changes in land use are the primary causes of disturbances in natural forests (Ewers et al. 2006; Freitas et al. 2010; Kobayashi and Koike 2010; Rhemtulla et al. 2009). The effects of changes in land use can vary depending on environmental conditions such as site conditions, slope, and aspect (Gracia et al. 2002). The type and intensity of changes in land use influence the extent of habitat loss, degradation and fragmentation, with natural vegetation patches embedded within an anthropogenic matrix (Pueyo and Alados 2007). Habitat fragmentation involves reduction of patch size and increases the isolation among them. Consequently, local populations become restricted to small, isolated habitat patches and vulnerable to extinction (Sawchik et al. 2002). In particular, Europe's countryside has undergone significant land use changes throughout its history (Plieninger and Schaar 2008). The rate and magnitude of these changes have greatly accelerated during the second half of the twentieth century. (Barbero et al. 1990; Maltez–Mouro et al. 2009). These rapid changes have modified substantially the natural forests (Suc 1984).

The magnitude of changes in land use cover and their driving factors are relatively well studied (Aspinall 2004; Callaway and Davis 1993; Kobayashi and Koike 2010; Rutherford et al. 2008). Nonetheless, due to limitations in historical data on the distribution of forest species, their spatiotemporal dynamics and the forces acting at a regional spatial scale have received limited attention (Guirado et al. 2008; Vicente-Serrano et al. 2010).

Most studies have indicated that anthropogenic disturbances are the most important factors influencing the dynamics of oak forests in the Iberian Peninsula (Rodà et al. 1999). Among the oak forests, the semi-deciduous oak (*Quercus faginea*) is common in mature communities of the Eurosiberian-Mediterranean transitional belt (Villar-Salvador et al. 1997). In Spain, this species is present in most parts of the country and its most valuable forests occur in the northeast (Pre-Pyrenees). *Q. faginea* is a shade-tolerant oak that grows in a wide range of substrates, topographic locations, and climatic conditions (Sancho et al. 1998), but it prefers base-rich soils and ombroclimates of a sub-humid type (Rivas-Martínez 1987). Since antiquity, the *Q. faginea* forests of the Central Pre-Pyrenees have undergone severely intensive harvesting as a source of timber and fuel wood (Sancho et al. 1998). In the nineteenth and the early twentieth centuries, an increase in the human population amplified the need for arable lands and pastures. *Q. faginea* forests were harvested to increase the amount of arable lands available for the production of food, including the grazing of livestock for supporting the growth of human population (Kouba et al. 2010). Recently, the proliferation of conifer plantations, especially *Pinus sylvestris* and *P. nigra*, has drastically changed the structure and composition of forests (Amo et al. 2008) to the detriment of *Q. faginea* and other indigenous forest species. Populations of *Q. faginea* have become fragmented and isolated, accompanied by a decrease of the area they occupy.

In this study, we examined the spatiotemporal dynamics of *Q. faginea* forests in the Spanish Central Pre-Pyrenees between 1957 and 2006. The objectives were (1) to quantify gains and losses in *Q. faginea* forests between 1957 and 2006, (2) to assess patch fragmentation, isolation, and dynamic of patch irregularity, and (3) to identify the factors affecting changes in the *Q. faginea* forests. To quantify gains and losses in *Q. faginea* forests, we constricted a matrix of changes. To assess patch fragmentation, isolation, and dynamic of patch irregularity, we used a set of standard landscape metrics. To identify the factors affecting changes in *Q. faginea* forests, we used three statistical models (GAM, BMA, and ARMS, see below). The study pictured an example of Iberian forests that are highly sensitive and vulnerable to changes as consequence of centuries of human land use changes which affected forests resilience to different disturbance levels (Vicente-Serrano et al. 2010).

Materials and methods

Study area

This study occurred within a 1,363 km2 area of the Central Pre-Pyrenees, Spain, between 42.32 N to 42.11 N and 0.31 W to 0.04 W, with elevation varying widely (from 500 m in the inner depression to >2,000 m at the highest peaks).

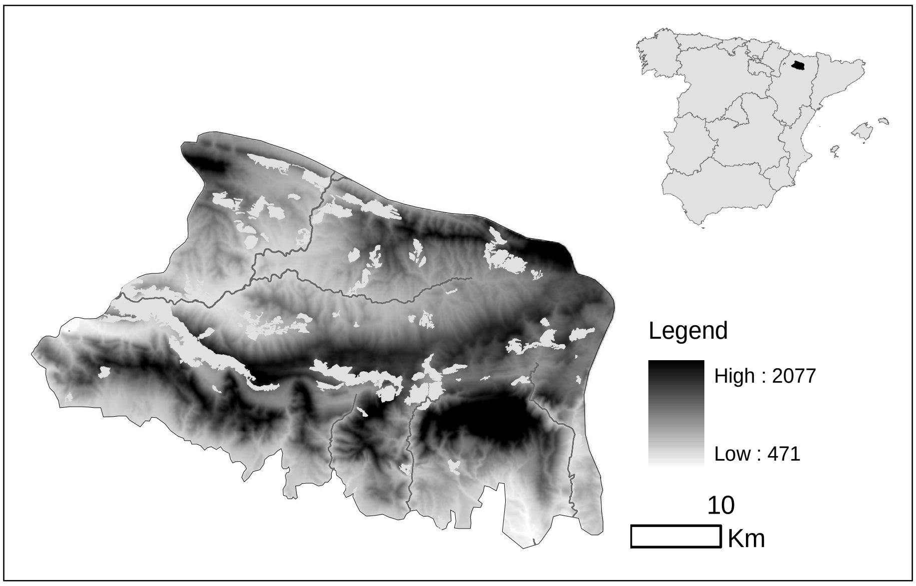

Fig. 1 The location of the study area in the Central Pre-Pyrenees, north of the Aragón Autonomous Community, within Spain. White areas in the central map represent the *Q. faginea* patches in 2006. The legend refers to elevation in meters (a. m. s. l.), dark colors indicate the most elevated areas. Lines show the main rivers in the study area

The area is located in a climate transition zone between Atlantic and Mediterranean. In the inner depression, mean annual precipitation is 500 mm, but it is higher elsewhere and, above 1,500 m it is > 1,000 mm. The rainfall is highly seasonal and the rainy season occurs between October and June. At the lowest elevations, mean annual temperature varies between 9 ºC and 11 ºC while at the highest elevations (≥ 1, 500 m), it is 6 ºC. In the cold season (November-April), the 0 ºC isotherm occurs at 1,650 m (Lasanta–Martínez et al. 2005). The lithological substrate of the area is dominated by conglomerate, limestone, marl, and sandstone. Moreover, there is a variety of land covers and uses including natural woodlands of *P. sylvestris*, *P. nigra*, *Fagus sylvatica*, *Q. ilex*, and *Q. faginea*, shrublands of *Q. coccifera* and *Buxus sempervirens*, artificial plantations of *P. sylvestris* and *P. nigra*, mono-cultural farmland (i.e., arable farmland), pastures (xeric pastures and subalpine pastures), urban areas, and abandoned farmland. The study area had an abundant shrub understory (e.g., *Acer monspessulanum*, *Genista hispanica*, *Amelanchier ovalis*, *Genista scorpius*, and *Carex halleriana*) and is typical of a rural area having a fragmented forest. The area contained a mosaic of low-density housing developments close to patches of forest and cropland. In the second half of twentieth century, major changes in land use occurred in the area (Lasanta–Martínez et al. 2005) because of agricultural mechanization and intensification, the introduction of pine plantations which have led to forest fragmentation, and the abandonment of cropland and pastures which has led to forest regrowth (Lasanta–Martínez et al. 2005; Vicente–Serrano et al. 2010).

Distribution maps of Q. faginea

To study the spatio-temporal dynamic of *Q. faginea* forests, we created maps of *Q. faginea* distribution in the study area during 2006 and 1957. Those years were chosen because the interval between them is likely sufficient for the detection of significant changes in the distribution of *Q. faginea*. In addition, that interval represents a period in which significant changes in land use occurred in the Central Pyrenees (Lasanta-Martínez et al. 2005). The 2006 map was derived from the Third Spanish National Forest Inventory map (IFN3) (MMA 2007). In the IFN3 map, the three principal tree species were considered for each patch and classified as either the first, second, or third most dominant tree species based on a field visual estimate of the proportional coverage of each species in the patch. All patches, in which *Q. faginea* was among the three most dominant species, were used to create the distribution map of this species within the study area. Overall, the contribution of *Q. faginea* to patches varied from 20% (in the patches where *Q. faginea* was the third most dominant species) to 90% (in the patches where it was the most dominant species). The distribution map was imported into a GIS for further processing, including correcting the edges of patches and the removal for each patch of the areas where *Q. faginea* was absent. This process was done by visual inspection of ortho-rectified, 0.5-m-resolution aerial photographs (1:30,000) from the Spanish National Plan of Aerial Orthophotographs (IGN 2006). The accuracy of the final map (96%) was quantified by sampling 200 random points and calculating confusion matrices (Congalton 1991). The 1957 map was produced by visual interpretation of the aerial photographs of the United States Army from 1956 to 1957 provided by Spain's Centro Cartográfico y Fotográfico del Ejército del Aire. The 1957 aerial photographs were taken on panchromatic film with a scale of 1:32,000 and were obtained as 24 x 24 contact prints. A total of 170 contact prints covering the study area were scanned into digital format at a resolution of 1,000 dpi, and then geo-referenced with the software Topol 9.5, using 12 ground control points per photograph, for a final resolution of approximately 0.5 m. However, it is worthwhile indicate that the polygons defined in the 2006 map were used, as a guide, to locate the *Q. faginea* forest patches in the 1957 aerial photographs by means of the overlapping tool in GIS environment. It should be noted that a minimum mapping unit of 0.1 ha per patch was defined in both maps (Fig. 1).

Change analysis

Based on published scientific literature (Molinillo et al. 1997; Montserrat 1990) and our interpretation of the aerial photographs, we assumed that only patches that were occupied by shrubland in 1957 could have converted to *Q. faginea* through natural vegetation succession by 2006; therefore, the patches of shrubland were included in the 1957 map. By 2006, however, the patches that were occupied by *Q. faginea* in 1957 might still be *Q. faginea* or had been converted to other land uses. Visual inspection of the 1957 and 2006 photographs revealed that some patches of *Q. faginea* had been converted to croplands, pine plantations, or shrublands, and this information was included in the 2006 map. The changes in *Q. faginea* forests were mapped by overlaying maps from 1957 and 2006. Changes map was summarized by calculating change rates (probabilities of change) and the area covered by each change class (Table 1). The probabilities of change were calculated using the following formula:

$$P_{ij} = A_{j2006}/A_{i1957}$$

where P_{ij} is the probability that a section changes from class i to class j, $A_{j\,2006}$ is the area of the class j in 2006, and $A_{i\,1957}$ is the area of the class i in 1957. Three types of change were defined (1) gain (i.e., i = {shrubland} and j = {Q. faginea forest}), (2) loss (i.e., i = {Q. faginea forest} and j = {pine plantation, shrubland, cropland}), (3) remnants (no change) (i.e., i = {Q. faginea forest} and j = {Q. faginea forest}). To avoid errors arose from misregistration between two dates, only changes classes covering an area more than 0.1 ha were considered.

Fragmentation analysis

Quantification and temporal comparison of the spatial configuration of *Q. faginea* forest patches between 1957 and 2006 was conducted based on a following set of standard landscape metrics: (1) Number of *Q. faginea* patches; (2) Mean patch size (ha); (3) Total area (ha) occupied by *Q. faginea* patches; (4) Mean patch distance (m) (the average of the nearest distances between the edges of *Q. faginea* patches); (5) Total patches edge length (km) of all *Q. faginea* patches; (6) Mean perimeter-to-area ratio (the mean of the ratio of perimeter (m) to area (m^2) of all *Q. faginea* patches). Most of these metrics have been applied in diverse forest fragmentation studies (Echeverria et al. 2006; Sitzia et al. 2010; Teixido et al. 2010), and have enabled the assessment of spatial attributes in fragmented landscapes.

Number of patches was used as a proxy of patch subdivision, i.e., an increase in the number of *Q. faginea* patches means that some of them were broken up into separate patches (fragments). Mean patch size and total area, were used for the assessment of patch fragmentation and loss, a decline in these metrics involves an increase of patch fragmentation and loss. In the same way, mean patch distance was used as a measure of patch isolation, i.e., used to compare the degree of isolation among *Q. faginea* patches between 1957 and 2006. Finally, total patches edge length and mean perimeter-to-area ratio were used to assess the dynamic of irregularity of *Q. faginea* patches (i.e., patch-shape complexity).

The following equation quantified the relative change (R) of each index:

$R = (A_{2006} - A_{1957}) \times 100/A_{1957}$

Where A_{2006} and A_{1957} are the number of patches, mean patch size, total area, mean patch distance, total edge length, or mean perimeter-to-area ratio in 2006 and 1957, respectively.

Statistical analysis

Dependent and independent variables

The response variables were derived by reclassifying and dividing the changes map in two binary maps. One map displayed the gains in *Q. faginea* forests (i.e., gain/no gain) and the other one displayed the losses in *Q. faginea* forests (i.e., loss/no loss).

The predictor variables included topo-climatic and land use variables that were suspected of causing changes in the *Q. faginea* forests between 1957 and 2006. Elevation (m a.s.l.), slope (º), and insolation (WH/m^2) were derived from the Digital Elevation Model of Aragón (CITA 2009) at 20m of resolution using ArcGIS 9.2 (ESRI 2006). A map of number of frost days per year (Frost_days) was obtained from the Digital Climatic Atlas of Aragón (DMA 2007); the data in this map was averaged for the period 1971-2000. Topography can have a strong effect on the dynamics of vegetation (Carmel and Kadmon 1999), and elevation strongly influences temperature and rainfall in mountains (Barry 1992). Thus, elevation is often a proxy for climatic gradients (Gallego Fernández et al. 2004; Pueyo and Beguería 2007). Slope gradient influences hydrological and erosion processes in the soil (Florinsky et al. 2002) and insolation influences soil-vegetation, evapotranspiration and, therefore, soil water content, and it might have a significant effect on the spatial dynamic of *Q. faginea*. Number of frost days per year is postulated to have a direct influence on the establishment and distribution of plant species (Coudun et al. 2006).

The extensive pine plantations that were created in the area within the last 50 years might have influenced the distribution of *Q. faginea*; therefore, distance to the nearest pine plantation (Distance_plant) was included in the analyses and calculated in a GIS using the straight line distance function. Distance to the nearest village (Distance_village) and distance to the nearest road (Distance_road) were measures of the intensity of human activity; activity is more likely to occur close to these structures. The road map in the study area was digitized on 2006 aerial photographs. The road network map of Aragón (CITA 2010) was used to identify the roads locations (all road types of this map were considered, i.e., primary, secondary, and unpaved roads). The distance to the nearest road was quantified using the straight line distance function in the GIS. Similarly, the distance to the nearest village was derived from a map of settlements in Aragon (CHE 2009). To assess the extent to which livestock and agricultural activities affected the spatiotemporal dynamics of *Q. faginea* between 1957 and 2006, cost distance to the nearest pasture (Cosdistance_pasture) and cost distance to the nearest cropland (Cosdistance_crop) were derived from a CORINE Land Cover map and included in the analyses. Maps of the cost distance to the nearest pasture and cropland were measures of transportation costs, i.e., calculate the least accumulative cost for moving from the source pixel (in this case pasture or cropland) to each of other pixels using slope as cost layer. The cost increase with an increasing of slope values up to 35º, beyond this steepness, areas were considered inaccessible to man and livestock (Kouba et al. 2010).

All maps were subset to identical extents at a spatial resolution of 20-m. Moran's *I* correlogram (Legendre and Legendre 1998) was used to assess the spatial autocorrelations (SAC) of the dependent variables. If present in the data, SAC violate the assumption about the independence of residuals and call into question the validity of hypothesis testing (Dormann et al. 2007). Moran's *I* correlogram show a decrease from some level of SAC to a value of 0 (or below), indicating no SAC at some distance between pixels. In our study, the SAC declined monotonically above a lag of 10 pixels (~ 200 m) in the map of gain and 12 pixels (~ 240 m) in the map of loss; therefore, a length of 300 m was used as a minimum threshold in extracting pixels (Millington et al. 2007). The selected sample (i.e., extracted pixels) of the response variables values was intersected with the corresponding values of the 10 predictor variables layers and the resulting dataset was imported into R (R Development Core Team 2009) for statistical analyses.

Statistical models

To examine the effect of each predictor on each of the dependent variables, we first used generalized additive models (GAM; Hastie and Tibshirani 1990). We created a univariate GAM model for each potential predictor variable and each of the two binary dependent variables, i.e., gain/no gain and loss/no loss, and selected the best predictors from these models based on their statistical significance and explained deviance (D^2) (Rutherford et al. 2008). To determine whether the dependent variable exhibited a linear or a non-linear response to the predictor variable, the smoothed function was plotted for each univariate GAM model (Guisan and Zimmermann 2000). If the response of the dependent variable to the predictor is non-linear, the quadratic terms should be included in subsequent analyses. When there is curvature in the trend, the inclusion of the quadratic term increases the precision of the linear term estimation (Hair et al. 1998). In order to avoid the strong correlations between the linear and quadratic terms, the input variables were ''centered'' by subtracting the sample mean from all values before being squared (Schielzeth 2010).

Collinearity was detected in the predictor variables using the Pearson correlation coefficients, with a threshold of 0.8 (Menard 2002; Rutherford et al. 2008). If Pearson correlation coefficient between two independent variables exceeded 0.8, one of the variables was excluded from the analyses. The final models were generated using Bayesian model averaging (BMA; Madigan and Raftery 1994) and adaptative regression by mixing with model screening (ARMS; Yuan and Ghosh 2008), which deal with uncertainty in the selection of models and add inference about the most important predictor variables. BMA uses Bayesian information criterion (BIC) to find good candidate models for inclusion in the final model (Hoeting et al. 1999). ARMS involves the following main steps (Morfin and Makowski 2009): (1) the sample is split into a training set and a test set; (2) each model is fitted by least square or maximum likelihood; (3) a set of models is selected based on Akaike's information criterion (AIC) and Bayesian information criterion (BIC); and (4) the response values are predicted in the test set using the fitted models obtained from the training set. The models are weighted using likelihood ''likeli'' or Akaike's information criterion ''AIC''. BMA and ARMS models were fitted using the predictor variables that had significant predictive power in the univariate GAMs and were not correlated with other predictor variables. The overall fit of the BMA and the ARMS was evaluated using the received operating characteristic (ROC) curve (Hanley and McNeil 1982). The area under the curve (AUC) was calculated using fivefold cross-validation (Millington et al. 2010). BMA, ARMS, and AUC were implemented using the MMIX package (Morfin and Makowski 2009) of R software (R Development Core Team 2009), functions ''bmaBIC'', ''arms,'' and ''aucCV,'' respectively.

Results

Gains, losses, and fragmentation of Q. faginea forests

In the Central Pre-Pyrenees of Spain, the total area occupied by *Q. faginea* forests decreased by ~ 9% between 1957 and 2006. In 1957, *Q. faginea* forests covered 7% (9,149 ha) of the study area, but by 2006, they were reduced to 6% (8,336 ha) of the area. The changes matrix (Table 1) revealed that *Q. faginea* forests gained 626 ha in some areas through natural transitions from shrubland to *Q. faginea* forests and lost 1,438 ha in others. The transition to pine plantations and shrubland was the most important source of losses in *Q. faginea* forests: ~ 924 ha were converted to pine plantations and ~ 390 ha to shrubland. Moreover, the changes matrix revealed that ~ 125 ha of *Q. faginea* forests were converted to cropland.

Table 1 Changes matrix calculated for *Q. faginea* forests in the Spanish Central Pre-Pyrenees between 1957 and 2006

Change classes		P^a	Area (ha)^b	Type of change
1957	2006			
Q. faginea	*Q. faginea*	0.774	7110	No change
Q. faginea	Pine plantations	0.100	924	Loss
Q. faginea	Shrubland	0.042	390	Loss
Q. faginea	Cropland	0.013	125	Loss
Shrubland	*Q. faginea*	0.068	626	Gain

^{a}: The probability of change. ^{b}: The area covered by each change class.

In the study area, the number of patches of *Q. faginea* forests increased from 104 in 1957 to 118 in 2006 (~ 13.5%) (Table 2). In 1957, 30 patches (29%) > 100 ha contributed > 81% of the total *Q. faginea* forests. By 2006, the number of large patches (> 100 ha) was 24, while the total area occupied by these patches was ~ 70% (Fig. 2a, b). The number of small patches (< 10 ha) decreased from 34 in 1957 to 30 in 2006, but the number of medium-sized patches (10-100 ha) increased from 40 in 1975 to 64 in 2006 (Fig. 2a).

Table 2 Landscape metrics used in an analysis of the fragmentation of *Q. faginea* forests in the Spanish Central Pre-Pyrenees between 1957 and 2006

Landscape metric	1957	2006	R (%) 1957-2006
Number of patches	104	118	13.5
Mean patch size (ha)	87.7	70.6	-19.5
Total patch area (ha)	9149	8336	-8.65
Mean patch distance (m)	1087	1179.4	8.50
Total patches edge length (km)	637	660	3.60
perimeter-to-area ratio	95.5	109.5	14.65

R: is the relative change in each metric (Positive values indicate an increase, and negative values indicate a decrease).

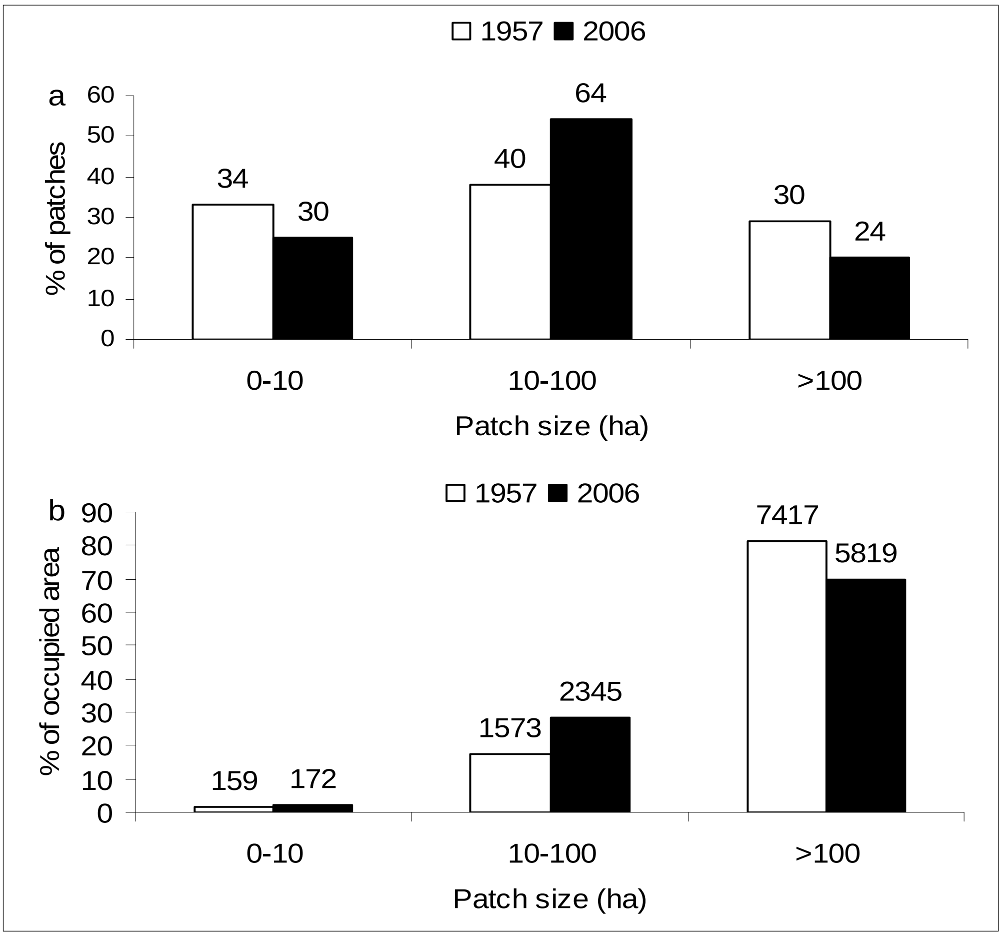

Fig. 2 Proportion (%) of (a) *Q. faginea* patches and (b) area occupied by each patch category as a function of the size of *Q. faginea* patches, between 1957 and 2006, in the Spanish Central Pre-Pyrenees. The number above each bar represents (a) the number of patches or (b) the area (ha) occupied by each patch category

In addition to the general decline in total patch area and the increase of number of patches, our results (Table 2) showed substantial changes in the spatial patterns of *Q. faginea* forests. These changes implied the reduction of mean patch size (from 87.7 ha in 1957 to 70.6 ha in 2006), the increase of mean patch distance (augmented by approximately 8.5% between 1957 and 2006), as well as the increase of total edge length and mean perimeter-to-area ratio by 3.6 and 14.65%, respectively.

Factors correlated with changes in Q. faginea forests

The univariate GAMs revealed that gains in *Q. faginea* forests were significantly ($P < 0.05$) correlated with elevation, number of frost days "Frost_days", insolation, distance to the nearest road "Distance_road", cost distance to the nearest cropland "Cosdistance_crop", distance to the nearest village "Distance_village", elevation and distance to the nearest road explained the most deviance (Table 3). Losses of *Q. faginea* forests were significantly ($P \leq 0.05$) correlated with all land use variables and slope (Table 3). All variables that were significant ($P \leq 0.05$) in the univariate GAMs were included in the BMA and ARMS, except insolation, which was excluded from the gains model because it was highly correlated with elevation (data not shown), but the latter explained more of the deviance in the univariate GAM model (Table 3).

Table 3 Univariate GAM models for each predictor variable against the two dependent variables (Gains and Losses). Variables statistically significant at $P<0.05$ are shown in bold

Variables	Gains		Losses	
	P	D^2	P	D^2
Elevation	**<0.05**	**0.26**	0.25	0.06
Slope	0.65	0.07	**<0.05**	**0.10**
Insolation	**<0.05**	**0.15**	0.11	0.02
Frost_days	**<0.05**	**0.13**	0.57	0.11
Distance_road	**<0.05**	**0.22**	**<0.05**	**0.08**
Cosdistance_crop	**<0.05**	**0.09**	**<0.05**	**0.09**
Distance_village	**<0.05**	**0.11**	**<0.05**	**0.08**
Cosdistance_pastur	0.25	0.01	**<0.05**	**0.11**
Distance_plant	0.58	0.03	**<0.05**	**0.14**

BMA and ARMS indicated that, in the gains model, elevation, "Frost_days", and "Distance_road" had high probabilities [Pr ($B_{\mathrm{vs}} \neq 0$) $\geq$ 0.90], and "Cosdistance_crop" and "Cosdistance_village," low probabilities [Pr ($B_{\mathrm{vs}} \neq 0$) $\leq$ 0.41] of being in the best-candidate model (Table 4). In the losses model, "Cosdistance_crop", "Cos- distance_pastur", "Distance_plant", "Distance_road" and slope had high probabilities [Pr ($B_{\mathrm{vs}} \neq 0$) $\geq$ 0.90] and "Distance_village" low probabilities [Pr ($B_{\mathrm{vs}} \neq 0$) $\leq$ 0.37] of being in the best-candidate model (Table 4).

Millington et al. (2010) argued that only the variables that have a great probability of being in the best-candidate model are useful; therefore, here we considered only those predictor variables that had a [Pr ($B_{vs} \neq 0$) ≥ 0.90] in both BMA and ARMS as factors that have had a significant influence on the changes in the *Q. faginea* forests.

Table 4 Bayesian Averaging Model (BMA) and Adaptative Regression by Mixing with Model Screening (ARMS) used for identifying the most important factors that affecting the gains "gains-model" and losses "losses-model" in *Q. faginea* forests over the Spanish Central Pre-Pyrenees between 1957 and 2006

Variables	BMA		ARMS	
	Mean β (±SD)	Pr ($\beta_{vs} \neq 0$)	Mean β	Pr ($\beta_{vs} \neq 0$)
Gains-model				
Elevation	**-0.046± 0.040**	**1.00**	**-0.046**	**1.00**
Frost_days	**-0.549± 0.005**	**1.00**	**-0.559**	**1.00**
Distance_road	**0.360± 0.009**	**1.00**	**0.370**	**0.92**
Cosdistance_crop	0.002± 0.006	0.38	0.001	0.40
Distance_village	0.400± 0.070	0.41	0.410	0.39
AUC.CV	0.889		0.891	
Losses-model				
Slope	**-0.002± 0.283**	**0.94**	**-0.001**	**0.98**
Distance_road	**-0.003± 0.003**	**0.93**	**-0.004**	**0.97**
Cosdistance_crop	**-0.190± 0.001**	**0.99**	**-0.302**	**0.97**
Distance_village	0.009± 0.002	0.33	0.009	0.37
Cosdistance_pastur	**-0.005± 0.050**	**1.00**	**-0.005**	**1.00**
Distance_plant	**-0.150± 0.080**	**1.00**	**-0.130**	**1.00**
AUC.CV	0.872		0.878	

Variables have a Pr ($\beta_{vs} \neq 0$) ≥ 0.9 (i.e. drivers of change) are shown in bold

Greater expansion of *Q. faginea* forests in areas distant to roads, given the significant positive relationship between "Distance_road" and *Q. faginea* forests gains in both BAM and ARMS (Table 4). Both BAM and ARMS indicated that the expansion of *Q. faginea* forests (i.e., the probability of gains) increased as elevation and number of days with frost decreased. Patches of *Q. faginea* forests close to pine plantations and those that were accessible from croplands, had the highest probability of loss, which was not unexpected because many *Q. faginea* forests had been converted to cropland and pine plantations. The probability loss of *Q. faginea* forests was high among patches that were close to roads, patches that were located in accessible areas to livestock from pastures, and those that were on gentle slopes (Table 4). Distance to the nearest village did not have a significant effect on the spatiotemporal changes in the *Q. faginea* forests.

Discussion

Spatiotemporal dynamics of Q. faginea forests

In general, the area of *Q. faginea* forests decreased by approximately 813 ha in the Spanish Central Pre-Pyrenees from 1957 to 2006. This translates to an annual rate of deforestation of -0.2% (calculated according to Puyravaud 2003) which is comparable to that estimated for other Iberian fragmented forests (e.g., Teixido et al. 2010; Plieninger 2006). The reduction in *Q. faginea* forests was caused mainly by the replacement by pine plantations (especially *P. sylvestris* and *P. nigra*) and deforestation for increasing the amount of arable lands. Many studies argued that the native plants can be severely affected by the presence of introduced species, particularly, those that are characterized as fast growing and having dispersal abilities (e.g., Echeverria et al. 2006; Teixido et al. 2010). In the study area, most pine plantations were established during the second half of the twentieth century (Amo et al. 2008) and, currently, pine plantations occupy areas that once were occupied by native *Q. faginea* forests. Furthermore, the rapid growth rate of those pines impedes *Q. faginea* to colonize more areas particularly the mesic areas (Gracia et al. 2002; Pueyo and Beguería 2007). Indeed, the *Q. faginea* forests in the Spanish Central Pre-Pyrenees were extensively deforested to increase the amount of arable land, especially for the cultivation of cereals (Lasanta-Martínez 1989). In the study area, the land was divided into small holdings and traditional forest management practices involved clear cutting for the expansion of arable lands (Lasanta-Martínez 1989). Some of the arable lands remain under cultivation, but most of them were abandoned after a few decades of exploitation. Part of abandoned lands were reforested by the Spanish forestry service, while the remainder has undergone natural re-vegetation (i.e., shrub encroachment) and transformed into shrubland (Molinillo et al. 1997; Montserrat 1990). The gains in *Q. faginea* forests that occurred in some areas were mainly due to the transition from shrub to forest as a result of natural succession.

In our study, the number of *Q. faginea* forest patches increased and mean patch size decreased, as consequence of forest fragmentation, as it has been also reported in several other studies of fragmentation in temperate forests (Echeverria et al. 2006; Staus et al. 2002) and specifically, in other Spanish regions (Teixido et al. 2010). In the Central Pre-Pyrenees, six of the large patches of *Q. faginea* forests were subdivided and converted to many medium-sized patches, which both, increased the number of patches and decreased the mean patch area. The increase of the mean patch distance means that the patches of *Q. faginea* forests become more isolated in space. Similar results have been obtained in other forest fragmentation studies of the Iberian Peninsula (Teixido et al. 2010). In our case, the increase of the isolation degree among patches of *Q. faginea* was the result of widespread deforestation which caused the neighborhoods of patches of *Q. faginea* forests to become occupied rapidly by different types of land cover type (i.e., pine plantation, cropland or shrubland); consequently, patches of *Q. faginea* forests became spatially separated and less frequently contiguous. The results showed an increase in the total edge length and mean perimeter-to-area ratio, indicating the increase of patch-shape complexity, i.e., the patches of *Q. faginea* forests become more irregular and convoluted than before. These results are in agreement with the study of García et al. (2005), who found a strong irregularity of the patches of oak forests in the Cantabrian forests. The increase of edge length and patch irregularity coupled with a decrease of mean patch size, reflect an increase in the magnitude of the edge effect, which, in addition to deforestation, might have been influenced by grazing pressure at the edge of patches (see below).

Effect of land use variables on Q. faginea forests changes

In the Central Pre-Pyrenees, land use variables had a significant elevated effect on the fragmentation and loss of *Q. faginea* forests. Similar result has been found in other studies carried out in fragmented forests (e.g., Rhemtulla et al. 2009; Teixido et al. 2010). In the Central Pre-Pyrenees, most losses occurred in areas close to pine plantations or accessible from croplands. This result was evident since many areas of *Q. faginea* forests were converted to cropland and pine plantations. The high probability of *Q. faginea* forests loss in areas located near pastures and were essentially accessible to livestock, can be related to the grazing pressure. Grazing might have a negative effect on vegetation dynamics, hinder the expansion of woody vegetation (Callaway and Davis 1993; Carmel and Kadmon 1999; Wahren et al. 1994) and can hamper the development of edge vegetation (Palik and Murphy 1990). In the study area, *Q. faginea* forests were harvested at some locations to increase the amount of arable land or used directly as ''dehesas'' system (Barbero et al. 1990; Montserrat 1990), i.e., a silvo-pastoral system with sparse *Q. faginea* and perennial grass layers. In these particular ecosystems, the high grazing pressures increase the acorns consumption and create abiotic conditions unfavorable for seedling establishment (Pulido and Díaz 2005, Plieninger 2006) which hamper the regeneration of *Q. faginea*, and therefore led to the disappearance of this species from those sites. At some areas, *Q. faginea* forests were burned to increase the amount of summer pasture (Lasanta-Martínez et al. 2005) but the reduction in the number of livestock has led to the abandonment of most pastures and, by 2006, they had been converted to pine plantations through reforestation or to shrublands through natural succession (i.e., shrub encroachment). The results of this study indicated that in the Central Pre-Pyrenees, most losses in *Q. faginea* forests occurred near roads. This finding was earlier reported in several countries, such as: New Zealand (Ewers et al. 2006), the USA (Saunders et al. 2002), and Brazil (Freitas et al. 2010), where roads were a strong predictor of cumulative forest loss and fragmentation. In the Central Pre-Pyrenees, the general road network, established relatively early (1905–1920) (Lasanta-Martínez et al. 2005) improved access to land and permitted new uses of the land, particularly, new croplands and pine plantations. Therefore, the roads were not a direct factor influencing the loss of *Q. faginea* forests, but they acted as attractors for changes in land use and deforestation. This fact influenced strongly the spatial variability in *Q. faginea* forests. Nevertheless, the expansion of *Q. faginea* forests was greater at sites far from roads, probably because these areas were inaccessible to humans and livestock. In those locations, the expansion of *Q. faginea* forests resulted from the natural transition of shrubland to forest. Apparently, the distance to the nearest village did not influence the spatiotemporal dynamics of *Q. faginea* forests, which indicates that the spatiotemporal dynamics of these forests were not affected directly by the rural activities of humans concentrated around village, more probably because of the human exodus that occurred in the region during the second half of the twentieth century.

Effect of topo-climatic variables on Q. faginea forests changes

The abiotic factors play a key role in determining vegetation dynamics in the Central Pyrenees (Barrio et al. 1997). Gracia et al. (2002) have found a strong influence of the abiotic conditions (i.e., topography) on rates and patterns of succession in the mixed forests of *P. nigra* and *Q. faginea*. In our case, the negative correlations between gains in *Q. faginea* forests and both elevation and number of frost days per year are mainly attributed to the topographical characteristics of the Central Pre-Pyrenees. In particular, the total annual number of frost days is markedly higher in highlands than in lowlands. In highlands, freezing temperatures hinder the establishment and growth of seedlings of *Q. faginea*. Accordingly, in the Central Pre-Pyrenees, *Q. faginea* forests have expanded at lowlands with relative to highlands. Currently, almost all of the areas occupied by these forests are located between 450 m and 1,500 m of altitude (Kouba et al. 2010). Furthermore, the results revealed a high probability of loss at sites with low slope. This can be explained by the earlier competition from agricultural activities. On gentle slopes, *Q. faginea* forests were harvested and the land was used for cereal cultivation (Lasanta-Martínez 1989). These developments restricted *Q. faginea* to poor soils and stony hillsides (Kouba et al. 2010). This finding suggests a difficulty in separating the possible role of abiotic factors from land use changes, as they are closely interrelated (Poyatos et al. 2003).

Implication for conservation

Forest fragmentation can have negative genetic impacts, leading to the disruption of species breeding system (Young et al. 1996) even in the wind-pollinated species (e.g., *Q. faginea* and *Fagus sylvatica*). For example, Jump and Peñuelas (2006) have found that forest habitat fragmentation in the European beech (*Fagus sylvatica*) has led to significant elevated levels of inbreeding, population divergence, and reduced genetic diversity within populations. Therefore, it is believed that the continuous loss of habitat and the increasing trend of fragmentation in *Q. faginea* forests over the next decades could have negative genetic impacts on this species. Moreover, forest fragmentation and loss might have significant ecological implications for species dependent on high-quality habitats situated in the interior regions of forest patches (Echeverria et al. 2006). Given that the *Q. faginea* forests are nowadays highly appreciated in many Mediterranean environments as a consequence of being an invaluable habitat for outstanding biodiversity of plant and animal species, they have recently been of great interest for ecosystem conservation (Rey Benayas et al. 2005, Kouba et al. 2010). A decline in the amount of *Q. faginea* forests and increasing fragmentation of *Q. faginea* patches mean less habitats are available for a multitude of mammalian, bird, insect, bryophyte, and other species associated with these forests. For instance, Díaz et al. (1996) noted that fragmentation of oak forests might significantly reduce the winter carrying capacity of acorn-eating birds, such as common cranes (*Grus grus*). Also, on their study on the Pyrenean oak forests, Amo et al. (2008) revealed that the ancient conversion of oak forests to pine plantations altered the lizard community, with a loss of two typical species of oak forests (*Psammodromus algirus* and *Lacerta lepida*). Hence, the increase of fragmentation in *Q. faginea* forests could have substantial impacts on the flora and the fauna prevailing in the remnant *Q. faginea* forests. Accordingly, maintaining large forest blocks could be of great mandatory in the region not only to prevent this species from more inbreeding and population differentiation, but also to preserve species dependent on habitats situated interior of the remnant *Q. faginea* forests.

Conclusions

This study highlighted the impact of the anthropomorphic changes in land use on forest fragmentation and loss in a region, characterized with disruption of the structural integrity of the landscape due to the anthropogenic activities. The most important changes occurred in the spatial patterns of *Q. faginea* forests in the Central Pre-Pyrenees over the last 50 years were mainly reflected by the increase of forest fragmentation and isolation degree. These changes are particularly driven by the introduction of pine plantations and deforestation, associated with increasing the amount of croplands and pastures. These findings highlight the necessity to understand in detail the dependency between changes in human land use and degree of forest fragmentation. This could help decision-makers clarify their recommendations for land use planning and management, and also allow the facilitation of future forest landscape management and monitoring actions in this type of forests.

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CAPITULO 3

Roles of land-use and climate change on the establishment and regeneration dynamics of Mediterranean semi-deciduous oak forests

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Abstract

Long-term changes in climate and land use have significant effects on the forest dynamics in formerly managed landscapes. To quantify the relative importance of climatic and land use factors on tree establishment at regional scales, retrospective analyses are required. In this paper, we provide an historical reconstruction of the establishment of Mediterranean oak (*Quercus faginea*) forests in the 20th century within the context of substantial changes in climate and changes in land use in the Spanish Pre-Pyrenees. Since the late 1930s, *Q. faginea* became established episodically, and the highest peak occurred between 1965 and 1975. Tree establishment was negatively correlated with mean summer maximum temperature, population size of nearby villages, and the amount of livestock, but was positively correlated with annual, winter, and winter-spring precipitation. This study revealed that assessments of the effects of land use and climate changes on historical forest recruitment are vital in understanding the structure of contemporary forests.

Key words: climate change, land use changes, forest dynamics, Pre-Pyrenees, *Quercus faginea*, tree recruitment.

Introduction

Changes in land use and climate can have significant influences on tree establishment and on forest structure and dynamics in formerly managed landscapes (Barbero et al., 1990; Améztegui et al., 2010; Chauchard et al. 2010; Gimmi et al., 2010). In the Mediterranean region, the availability of water is the main factor that limits tree growth (Ogaya et al., 2003; Linares et al., 2010) and forest regeneration (Pulido and Díaz, 2005). In addition, inter-annual variability in precipitation significantly affects annual tree recruitment (Urbieta et al., 2008). However, differences in annual rainfall might not be the only climatic factor that influences forest regeneration in inland areas that have a continental Mediterranean climate because in these areas temperature and the amount of precipitation act together to dictate water availability, and low temperatures in winter cause cold stress (Larcher, 2000; Vicente-Serrano et al., 2010). Furthermore, the frequency and intensity of extreme weather events such as severe drought are expected to increase in those inland areas because of global climatic change (IPCC, 2007). In the Mediterranean region, particularly in the southern Pre-Pyrenees, where dry conditions prevail, semi-deciduous oak forests (*Quercus faginea*) occur in areas that are incur variable drought stress and, therefore, they might be especially sensitive to climate warming and increasing aridity (Alla et al., 2011).

Understanding the nature of changes in land use is important for understanding the structure and stand dynamics of contemporary forests (Améztegui et al., 2010; Gimmi et al., 2010). In general, in the mountains of Europe, anthropogenic factors have had a greater influence on the current composition and structure of many forests than have changes in climate (Olano et al., 2008; Tappeiner et al., 2008, Gimmi et al., 2010). Furthermore, the ongoing changes in the policies of the EU for agricultural and rural developmental might lead to even more pronounced changes in the mountain forests (Tappeiner et al., 2008).

In the Central Pre-Pyrenees, changes in land use (i.e., farmland abandonment and grazing cessation) have led to the expansion of forests into formerly cultivated or grazed areas (Lasanta et al. 2006; Améztegui et al., 2010). In particular, *Q. faginea* has colonized some of the abandoned lands in the Central Pre-Pyrenees through natural transitions from abandoned lands to forests (Kouba and Alados, 2012). Acorns dispersed locally by gravity or through short- or long-distance dispersal mediated by rodents (Pulido and Díaz, 2005) and birds (Gómez, 2003), respectively, are the main means by which *Q. faginea* seeds reach abandoned fields (Maltez-Mouro et al., 2008). Encroachment by *Q. faginea* into abandoned lands has led to the formation of two types of forests: (i) *Q. faginea* stands that were harvested intensively for timber and firewood for centuries and that were used as pastures (Sancho et al., 1998), and (ii) new *Q. faginea* stands that became established in the abandoned terraces, mainly during the second half of the twentieth century (Kouba and Alados, 2012). Those forests are valued highly because they provide invaluable habitat for maintaining the biodiversity of Mediterranean plant and animal species (Rey Benayas et al., 2005, Kouba et al., 2010, Kouba and Alados, 2012).

To understand how changes in land use and climate influence the dynamics of forest regeneration and how they affect tree establishment , both of these factors should be assessed simultaneously (Abrams and Copenheaver, 1999; Camarero and Gutiérrez, 2007; Chauchard et al., 2007, 2010; Copenheaver and Abrams, 2003); however, identifying the importance of changes in land use and recent climate trends on the regeneration dynamics in forests can be attained only by comparing sites that have contrasting histories and climates.

The main purpose of this study was to assess our understanding of the potential effects of changes in land use and climate on the regeneration and growth dynamics of *Q. faginea* forests. Specifically, we aimed to (i) determine whether tree recruitment in *Q. faginea* forests in the last century was affected by climatic factors (e.g., drought) or changes in land use (e.g., land abandonment), (ii) assess the importance of specific types of forest habitats (i.e., coppice stands and abandoned terraces) on tree growth and performance in *Q. faginea,* and provide a basis for the development of land-management strategies that can mitigate the effects of global warming and the abandonment of traditional land use regimes on these sub-Mediterranean forests.

Materials and methods

Study area

The study area was in Huesca Province, within the Central Pre-Pyrenees, Spain, at an elevation of 450-1950 m a.s.l. (Fig. 1). Conglomerate, limestone, marl, and sandstone developed on Eocene flysch sedimentary formations predominate the lithology.

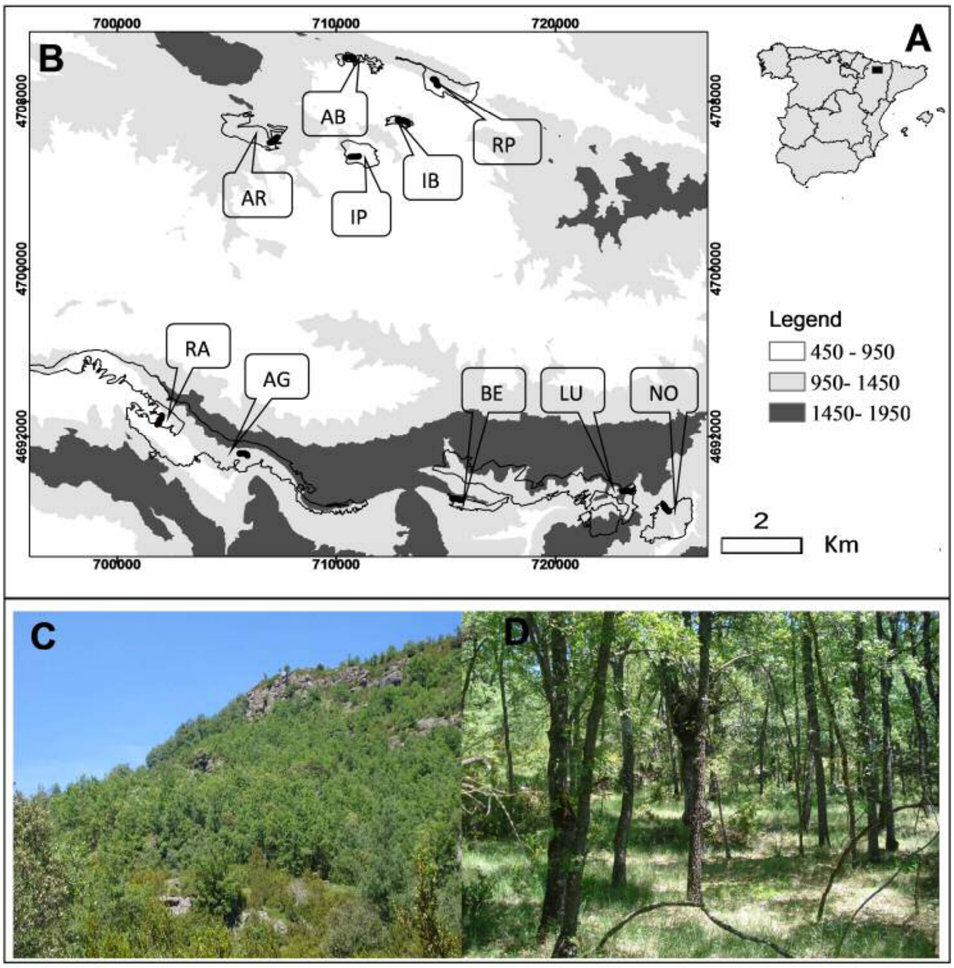

Fig. 1 Location of the study area (A) in the Central Pre-Pyrenees (northeastern Spain), topographical features of the study area (legend shows the elevation classes in meters a.s.l.), and location of the ten stands sampled (polygons indicated by black lines) (B). The dark points inside each polygon are 500-m linear transects. An example of *Q. faginea* coppice stand (C) and young *Q. faginea* stand on an abandoned terrace (D).

The climate is transitional sub-Mediterranean because it is affected by continental effects from the north in the Pyrenees and by milder Mediterranean conditions that prevail from the south; i.e., the Ebro Basin. Based on the weather data collected at the meteorological stations within the study area (see Climate trends section), the mean annual precipitation is 1317 ± 302 mm (1915-2005), but most occurs between October and Jun, and mean annual air temperature is 11.5 ± 2.8º C (1910-2005).

The area has a variety of land covers and uses types including natural forests of several species (*Pinus sylvestris*, *P. nigra* ssp. *salzmannii*, *Fagus sylvatica*, *Quercus ilex* ssp. *ballota,* and *Q. faginea*), shrublands (*Q. coccifera*, *Buxus sempervirens*, *Genista scorpius*, *Juniperus communis*), and plantations (*P. sylvestris* and mostly *P. nigra* ssp. *austriaca*), arable farmland, pastures, abandoned farmland, and urban areas. In the area, *Q. faginea* is one of the most abundant naturally occurring species and the communities in which it occurs constitute a transition zone between Mediterranean forests in which *Q. ilex* ssp. *ballota* or *P. halepensis* are predominant and mountain continental or mesic forests of *P. sylvestris*, *P. nigra* ssp. *salzmannii*, and *F. sylvatica* (Sancho et al., 1998; Loidi and Herrera, 1990).

Data collection and analysis

Based on earlier studies (Kouba et al., 2010, Kouba and Alados, 2012), we selected ten sites throughout the study area that were representative of the most common types of *Q. faginea* forests in the region. A stand dominated by *Q. faginea* was selected at each site (for details of the stands, see Table 1). Within each stand, a 500-m linear transect was established at a randomly chosen location, parallel to elevation contour lines. Each transect had sampling points (n=20) at 25 m intervals. Using the point-quarter method (Cottam and Curtis, 1956) at each point, we identified the closest adult *Q. faginea* tree in each of the four cardinal directions. Adult trees were defined as those >2 m high or that had a stem diameter at breast height (DBH) ≥ 4 cm.

To estimate tree density in each stand, we measured the distance between each sampling point and each of the four trees. A maximum distance of 5 m was designed between the sampling point and each of the four closest adult trees, and the quadrat was considered empty if there was no adult oak tree within 5 m. Absolute density of the stand was calculated using the equation proposed by Pollard (1971), which was adjusted using a corrector factor based on the number of vacant quadrats (see Warde and Petranka 1981).

Within each quadrat, the following variables were recorded for each of the four trees: diameter at breast height (DBH) (cm), tree height (m), and habitat (coppice stand or abandoned terrace). Tree-size distributions were examined by plotting the number of trees per class diameter (DBH) or tree height. In each quadrat, the ages of two of the four trees sampled (DBH ≥ 4 cm) were estimated by taking a core using a Pressler increment borer or by removing a disc using a chain saw (mean ± SE = 29 ± 0.30 trees per stand). Cores were taken or discs were cut from 290 trees at 1.3 m above ground, and another core or disc was taken from 90 of these trees at ground level; i.e., as close to the presumed root collar as possible to obtain an accurate estimate of age (Gutsell and Johnson, 2002). The discs and cores were sanded using progressively finer sandpapers until annual tree rings were clearly visible. Rings were counted under a binocular microscope at 10× magnification. The ring-porous wood of *Q. faginea* is well suited to dendroecological analyses because ring boundaries are clear and false or locally absent rings are rare (Corcuera et al., 2004).

To estimate the ages of the trees that were sampled at 1.3 m, we used the following equation:

$$\text{Age} = \text{Cst} + \text{A} \times \text{number of rings at 1.3 m height (DBH)}.$$

Cst is the constant of the regression equation and A is the coefficient of the regression. Cst and A were estimated by applying linear regression analyses to the data from the 90 trees that had cores or discs taken at ground level and at 1.3 m. We assumed that the age estimates had errors lower than 5 yr (Table 1); therefore, the analysis of tree establishment was based on age classes at 5-yr intervals. For those cores that did not contain pith (5%), we estimated the number of missing rings by fitting a geometric pith locator (a transparent plate that has concentric circles matched to the curvature of the innermost rings; Norton et al., 1987). To estimate the year in which each stem became established, we used the estimated age at the time of sampling (2010) and the presumed date of germination.

Table 1 Characteristics of ten *Q. faginea* stands sampled in the Central Pre-Pyrenees, Spain. Values are mean ± standard error

Stand characteristics	Rasal (RA)	Belsué (BE)	Abena (AB)	Ara (AR)	Lucera (LU)	Ibort (IB)	Ipies (IP)	Nocito (NO)	Arguis (AG)	Rapun (RP)
Area (ha)	114	94	73	244	1115	40	146	294	1847	217
Elevation (m a.s.l.)	868.3 ± 4.8	1158.5 ± 1.2	970.3 ± 1.5	971.1 ± 2.0	1198.0 ± 7.7	950.8 ± 2.6	852.5 ±2.3	1046.7 ± 2.1	1026.2 ± 1.9	923.31 ± 2.4
Orientation[a]	S	S	S	SE	SE	S	E	SW	S	SW
Slope (º)	9.3 ± 0.5	30.5 ± 0.4	11.7 ± 0.5	19.6 ± 0.5	16.8 ± 1.2	14.8 ± 1.1	7.8 ± 0.6	25.0 ± 0.8	11.0 ± 0.6	17.98 ± 1.4
Density (stems ha^{-1})	607 ± 0.1	1100 ± 0.1	999 ± 0.1	503 ± 0.1	867 ± 0.1	1088 ± 0.1	812 ± 0.1	983 ± 0.1	818 ± 0.1	540 ± 0.1
DBH (cm)	14.0 ± 1.4	9.0 ± 0.7	13.3 ± 1.3	7.2 ± 0.5	12.0 ± 0.8	13.3 ± 0.8	11.4 ± 0.7	12.3 ± 1.7	13.0 ± 1.4	6.8 ± 0.5
Tree height (m)	5.1 ± 0.4	4.8 ± 0.3	5.1 ± 0.3	3.4 ± 0.2	5.5 ± 0.3	6.1 ± 0.2	4.3 ± 0.3	5.5 ± 0.4	4.7 ± 0.3	3..9 ± 0.2
Nº stems per tree[b]	---	4 ± 1	2 ± 0	3 ± 0	3 ± 1	3 ± 1	4 ± 1	2 ± 1	---	3 ± 1
Age (years)	31 ± 3	40 ± 4	50 ± 2	35 ± 1	39 ± 1	63 ± 2	64 ± 2	56 ± 5	50 ± 1	69 ± 2
Radial-growth rate (mm year^{-1})	2.1 ± 0.1	1.0 ± 0.1	1.3 ± 0.1	0.9 ± 0.0	1.7 ± 0.1	1.0 ± 0.1	0.9 ± 0.0	1.3 ± 0.1	1.2 ± 0.0	0.73 ± 0.1
Height-growth rate (cm year^{-1})	17.6 ± 2.4	13.6 ± 1.1	11.9 ± 0.6	9.6 ± 0.4	16.3 ± 1.4	11.5 ± 0.7	7.1 ± 0.6	12.9 ± 0.9	10.4 ± 0.8	6.0 ± 0.3

[a] Orientation divided in four classes;S: South, SE: South East, SW: south West, E: East

[b] Calculated only for multi-stemmed trees.

Age estimates were for stems, rather than genetic individuals because, typically, *Q. faginea* produces several shoots per individual, which generally are much younger than the stumps.

To determine whether the recruitment and survival of *Q. faginea* varied significantly over time, the age-structure data were analysed using a power function (Szeicz and Macdonald, 1995) as follows:

$$\boldsymbol{y = y_0\, x^{-b}}$$

Where $\boldsymbol{y}$ is the number of individuals in an age class $\boldsymbol{x}$, $\boldsymbol{y_0}$ is the initial input into the population at time zero, and $\boldsymbol{b}$ is the mortality rate. Recruitment residuals were calculated by subtracting the predicted from the observed tree frequencies in each 5-yr age-class. The mean annual radial- and height-growth rates of the trees were calculated by dividing the stem radius (i.e., half the DBH, excluding the bark) and the tree height by the age of each stem. The diameter at 1.3 m (DBH), height, age, mean annual radial- and height-growth rates of the trees sampled in coppice stands and those sampled in abandoned terraces were compared statistically using linear mixed-effects models that included site as a random factor and habitat type as a fixed factor (Zuur et al., 2007).

Climate trends

The analysis of the effects of climate on the establishment of *Q. faginea* was restricted to the periods in which reliable monthly weather data were available. Weather data were obtained from the four meteorological stations that had the longest records and were located within the study area: Canfranc-Los Arañones (42º44'N, 0º31'W, 1160 m a.s.l., 1910-2007), Sabiñánigo (42º31'N, 0º21'W, 790 m, 1941-2007), Botaya (42º30'N, 0º40'W, 790 m,1927-2007), and Arguis (42º18'N, 0º26'W, 709 m, 1928-2007).

Precipitation data were analyzed for four periods: winter (December-February), winter-spring (December-May), summer (June-August), and the entire year. The following temperature variables were used in the analyses: mean annual temperature, mean summer maximum temperature (average of mean June-August monthly maximum temperatures), mean winter minimum temperature (average of mean December-February monthly minimum temperatures), and absolute monthly maximum and minimum temperatures. All of the climate variables were averaged for each of the 5-yr recruitment-survival age classes.

To assess the effects of climate on *Q. faginea* establishment, we calculated Spearman correlation coefficients (r_S) between the climate variables and both the observed number of trees established (Camarero and Gutiérrez, 2007; Chauchard et al., 2007) and the residuals obtained from the fitted power function (Szeicz and Macdonald, 1995). In addition, we identified significant inflections in the temporal trends in the climate variables that were significantly correlated with either the number of trees established or the residuals of the fitted model (Chauchard et al., 2010). To that end, we used the "turnpoints" function of the "pastecs" package in the R software (Ibanez et al., 2009). The statistical significance of the climate trends in each period was tested using the Mann-Kendall Tau (τ) Test ("Kendall" package in R software, McLeod, 2009).

Changes in land use

In this study, the temporal changes in the number of inhabitants in villages and the number of livestock: sheep, goats, and cattle (the grazing pressure of one head of cattle was considered equivalent to that of six sheep; see García-González and Marinas, 2008) within the study area were used as indicators for reconstructing past changes in land use and for assessing indirectly changes in grazing intensity.

Demographic data for the four municipalities encompassing the study area (Arguís, Caldearenas, Loarre, and Nueno) were obtained from the Instituto Nacional de Estadística (2011). The data from historical livestock censuses were divided in two periods (1890 until the early 1970s, and the late 1970s until the early 1990s). In the analysis of the data from the first period, we used the livestock numbers for the four villages closest to the ten stands sampled, which were provided by the Historical Archives of Huesca Province (2011).

Since the early 1970s, exodus from most of the villages in the Central Pyrenees towards cities has led to changes in the boundaries of the municipalities. Several municipalities merged in a large municipality, reducing the total number of municipalities in the study area. In the analysis of the data from the second period, we used the number of livestock in the two municipalities that encompassed the four villages near the ten sampling sites. Those data were obtained from the Provincial Service of Agriculture of Huesca Province (2011).

Inflections and trends in the land-use variables (number of inhabitants and number of livestock) were assessed in the same way as were climate variables. The effects of changes in human and livestock densities on *Q. faginea* recruitment were evaluated by comparing the number of inhabitants, livestock numbers, and both the observed number of trees established and the residuals of the fitted model for each of the 5-yr age classes by calculating Spearman correlation coefficients.

Results

Tree-size and age strictures explorations

The distribution of the diameters of all of the *Q. faginea* trees fit best a negative exponential distribution, and the most abundant class of trees had DBH between 5 and 10 cm (Fig. 2A). The most abundant class of trees was 4-6 m tall (Fig. 2B). The age distribution of the *Q. faginea* trees (Fig. 3A) indicated episodic recruitment, with highest recruitment in the late 1960s and early 1970s (Fig. 3B).

Between 1935 and the early 1970s, *Q. faginea* recruitment was greater than the recruitment predicted by a power function, and maximum differences (number of positive residuals) occurred in the late 1960s and early 1970s (Fig. 3A). Furthermore, there were three periods of either reduced recruitment or high mortality (periods in which the predicted tree frequency was much higher than the observed frequency of trees and the residuals were negative): the late 1970s, the late 1980s, and the early 1990s (Fig. 3A). In abandoned terraces, *Q. faginea* recruitment did not occur until the 1940s. More than 65% of the individuals sampled on abandoned terraces were established between 1965 and the early 1990s, and most of them recruited in the late 1960s. In coppice stands, the first recruitment peak occurred in the late 1930s, and others occurred in the late 1940s and early 1950s, in the early 1970s and early1980s (Fig. 3B).

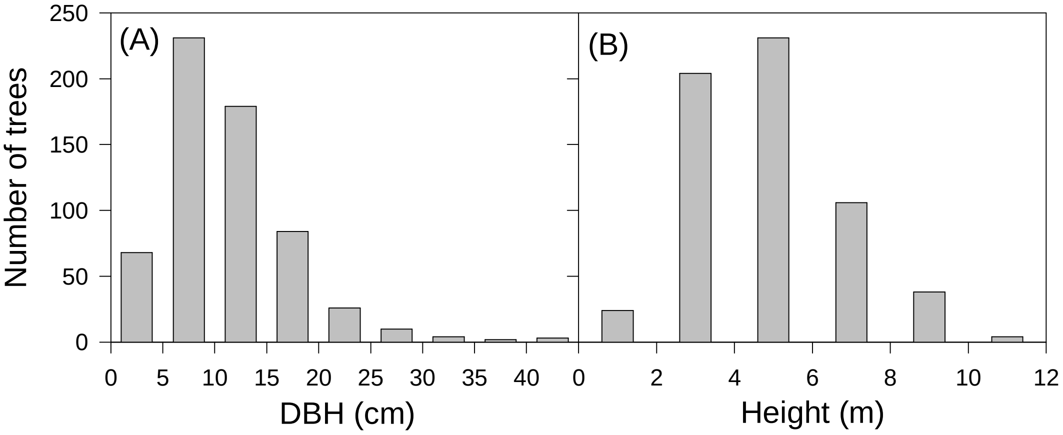

Fig. 2 Diameter at breast height (DBH) (A) and height (B) of *Q. faginea* trees at ten sampling sites in the Spanish Pre-Pyrenees.

The *Q. faginea* trees in coppice stands (mean ± SE = 54 ± 4 yr) were significantly ($p < 0.05$) older than the trees in abandoned terraces (mean ± SE = 43 ± 5 yr) (Table 2); however, the trees on abandoned terraces had mean annual radial- and height-growth rates that were significantly ($p < 0.05$) higher than those of the *Q. faginea* trees in coppice stands (Table 2). Although mean annual radial- and height-growth rates are age-dependent, in this study, the difference between the two habitats in the mean age of the trees was not large (overall mean ± SE = 48 ± 5 yr). Thus, a comparison of the rates was a valid means of detecting differences in the vigor and performance of the trees in the two habitats. In addition, the mean DBH of *Q. faginea* trees was significantly ($p <$ 0.05) greater on abandoned terraces (13.0 cm) than in coppice stands (10.6 cm) (Table 2).

Climate trends

In the Central Pre-Pyrenees, mean annual temperatures and mean summer maximum temperatures exhibited moderate inter-annual variability between 1910 and 1990 (coefficients of variation of 14.3% and 7.2%, respectively). Between 1915 and 1990, mean annual, winter, summer, and winter-spring precipitation exhibited high variability in comparison to temperature variables (coefficients of variation of 40.0%, 54.5%, 32.1%, and 40.0%, respectively).

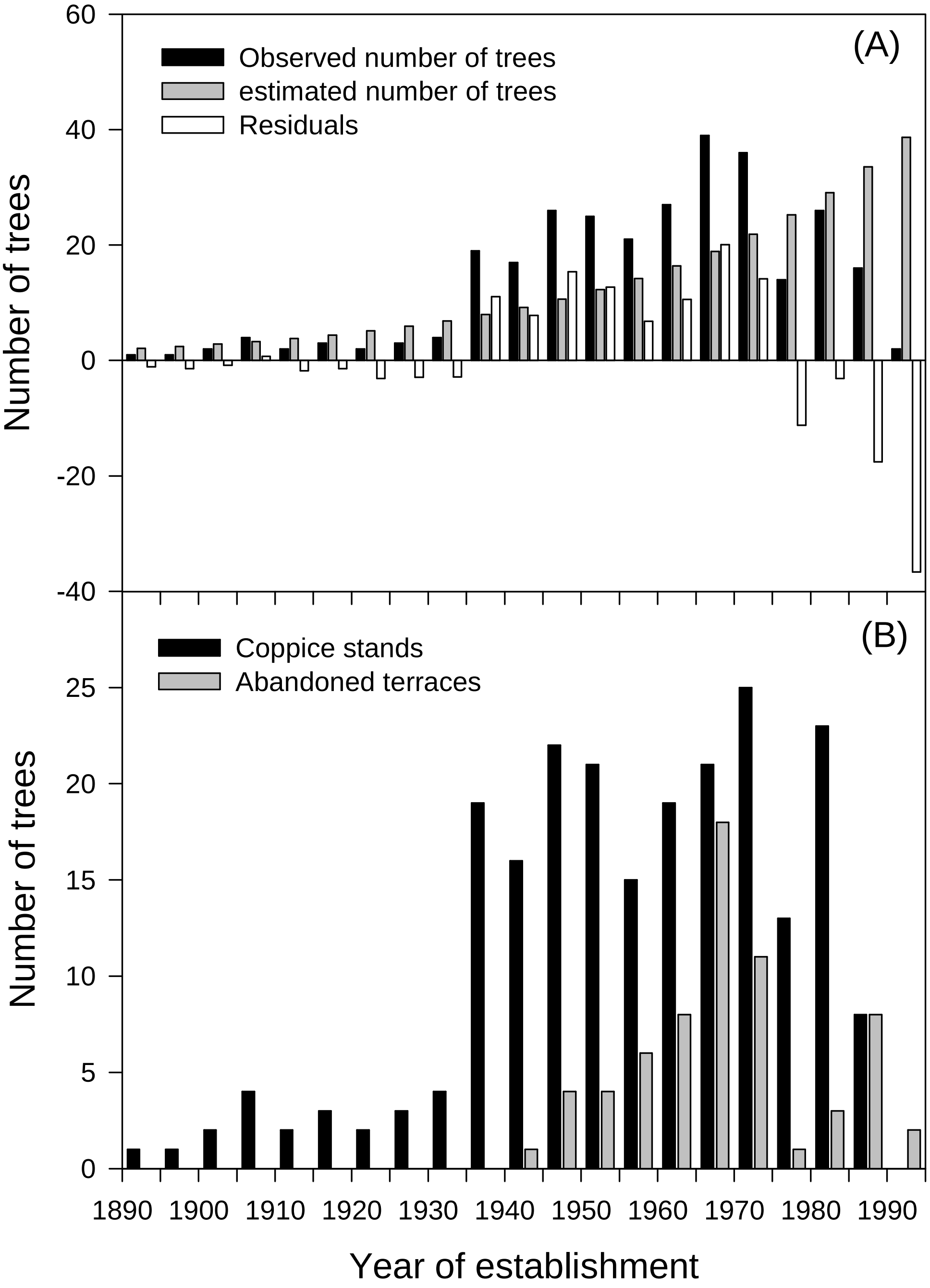

Fig. 3 Observed and estimated numbers of *Q. faginea* trees at ten sampling sites in the Spanish Pre-Pyrenees, as a function of their year of establishment (A), and the residuals that correspond to the difference between the observed and predicted number of trees. Comparative histograms between abandoned terraces and coppice stands displaying the number of trees against year of establishment (B).

Table 2 Characteristics and related statistics of linear mixed-effects models that compare the *Q. faginea* tree variables of coppice stands (C) and abandoned terraces (T) with site as a random factor. Significant (p <0.05) differences between forest and terrace are indicated in bold. Values are mean ± standard error.

Variable	Terrace (T)	Coppice stands (C)	Comparaison (T-C)	*F*	*p-value*
DBH (cm)	13.0 ± 1.0	10.6 ± 0.5	**T > C**	4.2	0.042
Height (m)	5.4 ± 0.4	4.7 ± 0.2	**T - C**	3.3	0.071
Age (years)	43 ± 5	54 ± 4	**T < C**	11	0.001
Radial-growth rate (mm yr^{-1})	1.5 ± 0.2	1.1 ± 0.1	**T > C**	11	0.001
Height-growth rate (cm yr^{-1})	13.7 ± 1.6	11.9 ± 0.9	**T > C**	5.4	0.020

In the last century, there have been five significant inflections in mean summer maximum temperature trends (Fig. 4A), with low values in 1925 (turn-point test, $p < 0.05$), 1939 ($p < 0.05$), and 1972 ($p < 0.05$), and high values in 1943 ($p < 0.01$) and 1975 ($p < 0.05$). Mean summer maximum temperature anomalies decreased significantly (Mann-Kendall test, $\tau = -0.37$, $p < 0.05$) between 1910 and 1925 (Fig. 4A), increased significantly between 1939 and 1943 ($\tau = 0.70$, $p < 0.05$), and, thereafter, decreased until 1972. Since 1975, mean summer maximum temperatures have increased significantly ($\tau = 0.52$, $p < 0.05$).

Between 1915 and 1990, seven inflections were detected in the distributions of either winter-spring or annual precipitation (Fig. 4B). Mean annual precipitation anomalies increased significantly ($p < 0.05$) between 1938 and 1943 ($\tau = 0.61$) and between 1943 and 1960 ($\tau = 0.52$). Between 1960 and 1972, mean annual rainfall was high. From 1973 until 1990, annual rainfall was markedly lower than it was at any other time in the 20th century.

Changes in land use

The human population was highest in the early 20th century (Fig. 5), declined sharply between 1920-30, and continued to decline until 1990 ($\tau = -0.96$, $p < 0.01$). The livestock numbers (Fig. 5) increased significantly ($\tau = 0.98$, p

< 0.05) between 1890 and 1910, remained high until 1930, and decreased significantly between 1930 and 1970 (τ = -0.66, p < 0.01). Between 1970 and 1990, livestock densities have increased substantially and have oscillated in the last 20 yr.

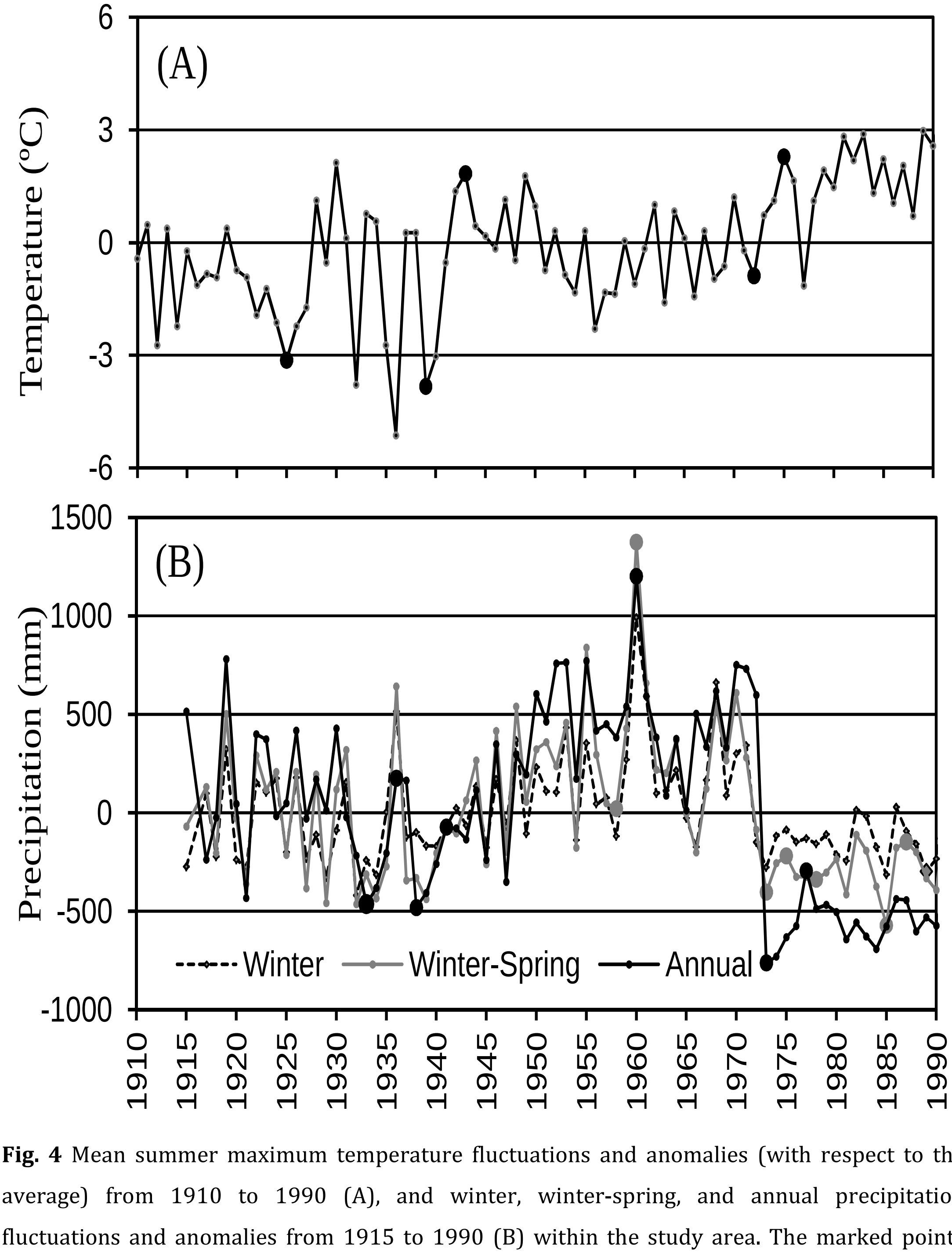

Fig. 4 Mean summer maximum temperature fluctuations and anomalies (with respect to the average) from 1910 to 1990 (A), and winter, winter-spring, and annual precipitation fluctuations and anomalies from 1915 to 1990 (B) within the study area. The marked points indicate significant ($p \leq 0.05$) inflections in temperature or precipitation, which were identified using the "turnpoints" function.

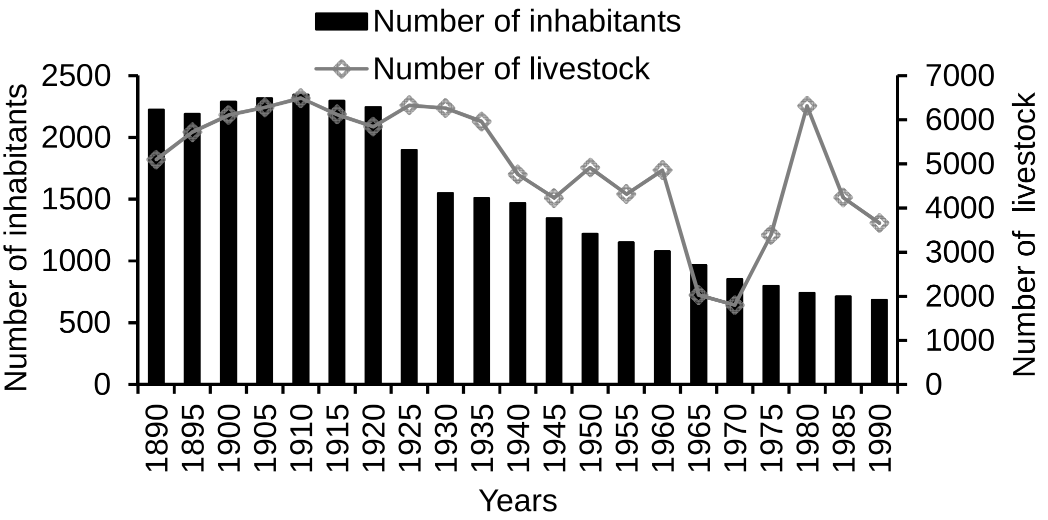

Fig. 5 Changes in the size of the human population and the amount of livestock (cattle, sheep, and goats) in the study area, between 1890 and 1990.

Table 3 Spearman correlation coefficients (r_S) and related probability levels (*p-value*) calculated between weather and land-use variables *vs.* established trees. Calculations were performed using the observed number of established trees and the residuals of fitted power functions.

Variable	Observed	*p-value*	Residuals	*p-value*
Weather variables				
Mean summer maximum Temperature	–	–	-0.54	0.025
Annual precipitation	–	–	0.61	0.004
Winter precipitation	0.5	0.048	0.63	0.009
Winter-spring precipitation	–	–	0.62	0.010
Land use variables				
Local population size	-0.72	0.009	–	–
Number of livestock	-0.82	0.000	-0.75	0.001

Factors influencing Q. faginea recruitment

All of the climate and land use variables that were significantly correlated with either the recruitment residuals of the fitted power function or the numbers of trees established were considered to have affected the recruitment history of *Q. faginea* forests. Correlation analyses indicated that the residuals of the power function fitted to the observed number of trees established were significantly negatively correlated with mean summer maximum temperatures and the number of livestock, and significantly positively correlated with annual, winter, and winter-spring precipitation (Table 3). The number of trees established and winter precipitation were significantly positively correlated. In addition, the number of trees established was significantly negatively correlated with the numbers of inhabitants and the amount of livestock within the study area (Table 3).

Discussion

Dynamics of Q. faginea forests

The negative exponential distribution of the diameters of the *Q. faginea* trees and the episodic recruitment revealed by this study reflect uneven-aged forests (Smith et al., 1997). The comparison of the age-class distributions of trees in coppice stands and those in young stands established on abandoned terraces can provide insights into the dynamics of forest development on abandoned lands. The colonization of the abandoned terraces by *Q. faginea* began in the 1940s; however, more than 65% of the *Q. faginea* trees present on those abandoned terraces in 2010 became established after 1965. Before *Q. faginea* began colonizing the abandoned terraces, shrubs (e.g., *B. sempervirens*, *G. scorpius*) were occupied them, which indicates that they were abandoned long before 1965 (Montserrat, 1990; Capitanio and Carcaillet, 2008; Kouba and Alados, 2012).

The mean annual radial- and height-growth rates of the *Q. faginea* trees on the abandoned terraces were higher and the stems were thicker than were those of the trees in coppice stands; probably, because the abandoned terraces and farmlands in the study area are on relatively flat lands and some are in valley bottoms where the soils have the highest amounts of nutrients and water, which might have enhanced tree growth (Lasanta et al., 2000). After abandonment, herbaceous plants and shrubs colonized the terraces before becoming forested by *Q. faginea.* The process of secondary succession involves significant changes in habitat and microclimate at local scales, including a reduction in runoff and an improvement in soil infiltration, which enhances soil conservation (Molinillo, 1997, Lasata et al., 2000), an increase in litter accumulation, which generates a large amount of organic-matter because of leaf decomposition (Maltez-Mouro et al., 2005), and the accumulation of minerals in the flatlands, which increases soil nutrient contents (Maltez-Mouro et al., 2005). Those changes helped to improve soil fertility (Lasanta et al., 2000). In other studies, *Q. faginea* trees had the highest growth rates and stands had the highest densities on the shallowest slopes, which had the highest soil fertility (Maltez-Mouro et al., 2005).

Effects of climate on Q. faginea recruitment

The recent reductions in annual precipitation and increases in summer temperatures in the last 20 yr have had a significant effect on *Q. faginea* recruitment. The positive correlations between *Q. faginea* recruitment and annual, winter, and winter-spring precipitation reflect how inter-annual variability in precipitation has affected *Q. faginea* recruitment. Mean maximum summer temperature and *Q. faginea* recruitment were negatively correlated, which suggests that most of the recruitment occurred in years that had cool summers, and oak seedlings experienced high mortality in years that had hot, dry summers (see also Rey Benayas et al., 2005).

The establishment of *Q. faginea* was very low in the late 1970s, late 1980s, and early 1990s and high in the late 1960s and early 1970s. Periods of low recruitment coincided with hot summers and low precipitation in winter and spring, which caused the most severe droughts in the region during the 20th century (Vicente-Serrano, 2006) and might have caused high mortality among *Q. faginea* recruits. In the Mediterranean Basin, the weather in summer is one of the main factors that influence recruitment (i.e., seed germination, seedling emergence and survival) in oak species (Pulido and Díaz, 2005; Urbieta et al., 2008). Harsh conditions such as hot and dry summers are major causes of seedling mortality in *Q. faginea* and other Mediterranean oak species (Valladares et al., 2000; Esteso-Martínez et al., 2006; Maltez-Mouro et al., 2008). Sufficient precipitation in winter and spring, and cool summer temperatures in the 1960s and early 1970s, especially between 1970 and 1972, might have produced the recruitment pulses that occurred between 1965 and 1975. The amount of moisture available in the soil has a strong influence on the survival of *Q. faginea* seedlings, which usually germinate in early spring (Esteso-Martínez et al., 2006; Maltez-Mouro et al., 2007). In our study, high precipitation in winter and spring increased soil moisture, which can increase seedling survival if the subsequent summer is not exceptionally hot and dry. Other studies revealed also that low water availability reduces the growth of *Q. faginea* (Rey Benayas et al., 2005).

Effects of human and livestock populations on Q. faginea recruitment

The first expansion of *Q. faginea* into the study area occurred in the late 1930s, when local human populations declined, which might have reduced anthropogenic pressures on the territory in the area. Furthermore, the high *Q. faginea* recruitment in the late 1960s and early 1970s coincided with an increase in the recruitment rate of *Q. faginea* on the abandoned terraces and the decline in the local human population that had begun about 40 yr earlier.

The negative correlation between *Q. faginea* recruitment and the number of livestock suggests that grazing pressure had a significant negative effect on the establishment of *Q. faginea*, particularly between 1890 and 1930. In addition, the first peak in *Q. faginea* recruitment occurred when grazing pressure began to decline, and the highest recruitment peaks occurred in late 1960s and early 1970s, which coincided with the lowest numbers of livestock. Livestock overgrazing constrains the regeneration of tree species (Barbero et al., 1990; Carmel and Kadmon 1999). Livestock eliminate seedlings, which diminishes recruitment and, consequently, hinders forest regeneration (Cierjacks and Hensen, 2004; Callaway and Davis 1993; Wahren et al. 1994). The increase in the number of livestock that began in the 1970s was not accompanied by an increase in grazing pressure because of significant changes in livestock husbandry in the Central Pre-Pyrenees (García-Ruiz et al., 1996). Since the 1970s, the number of livestock grazing freely in the mountain grasslands and rangelands of the study area in summer has decreased sharply (Molinillo et al., 1997; Lasanta et al., 2006).

Conclusions

In the 20th Century, changes in land use and climate have strongly influenced the dynamics of *Q. faginea* forests in the Central Pre-Pyrenees. The history of recruitment in those forests involved the following stages: (i) before 1935, the establishment of *Q. faginea* was restricted mainly to coppice stands because of extensive farmland cultivation on the mountain terraces and livestock overgrazing; (ii) between 1935 and the early 1960s, reductions in human land use and livestock pressure favored *Q. faginea* recruitment and expansion; (iii) in the late 1960s and early 1970s, the encroachment of abandoned terraces by *Q. faginea* was enhanced by favorable climatic conditions; and (iv) since 1975, *Q. faginea* recruitment has been stressed by drought (insufficient amount of rainfall in winter and spring, and high temperature in summer). high rates of tree growth and recruitment in this species should be maintained by using improved management of the forests based on drought alerts and mitigation adaptive systems (e.g., preventive thinning in very dense forests) and by the enhancement and regulation of *Q. faginea* colonization in formerly cultivated and grazed lands (e.g., selection of vigorous or reproductive trees in encroached abandoned terraces).

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Pirineos (accepted)

CAPITULO 4

La expansión del quejigo (*Quercus faginea*) en el Prepirineo Aragonés durante la segunda mitad del siglo XX

The expansion of Quercus faginea in the Aragón's Pre-Pyrenees over the second half of the twentieth century

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Resumen

Se investigó la expansión de Quercus faginea Lam. (quejigo) debida a la disminución de la presión antrópica en siete municipios del Prepirineo Aragonés durante la segunda mitad del siglo XX. La emigración rural que ha ocurrido en esta zona a partir de los años sesenta ha producido un abandono masivo de las tierras agrícolas junto con la disminución de la presión pastoral. Como resultado algunos de los campos abandonados han sido colonizados por el quejigo, sobre todo en los municipios con una disminución notable en el número de agricultores y cabezas de ganado. Se espera que, con la continua disminución de la presión humana en el territorio, los quejigares colonicen nuevas áreas en los próximos años como resultado de la sucesión secundaria.

Palabras clave: Montes bajos. Terrazas abandonadas. Bosques segundarios. Población y ganado. Presión humana en el territorio.

ABSTRACT.-The expansion of Quercus faginea Lam. -due to a decrease in human pressure- was investigated in seven municipalities of the Aragón's Pre-Pyrenees over the second half of the twentieth century. The rural emigration that occurred in this area since 1960s has generated a massive abandonment of agricultural lands and a *decrease in livestock pressure. As a result, some abandoned fields have been colonized by Q. faginea; specially, in the municipalities that have known a marked decrease in the numbers of farmers and livestock. With the continued decrease of human pressure in the territory, it is expected that Q. faginea will colonize new areas during the next years as a result of secondary succession.*

Key words: Coppices. Abandoned terraces. Secondary forests. Population and livestock. Human pressure in the territory.

Introducción

Desde hace miles de años la cuenca mediterránea está sometida a cambios constantes en los usos de suelo (Quezel & Barbero*,* 1990; Hoùerou, 1981), habiendo dominado la deforestación para aumentar la superficie de las tierras cultivadas y los pastos (Barbero *et al.,* 1990). Durante la segunda parte del siglo veinte, sin embargo, esta dinámica ha variado debido a cambios socioeconómicos (Margaris *et al.,* 1996; Lasanta & Vicente-Serrano, 2007). Mientras que en los países de la parte sur de la cuenca mediterránea la deforestación y la presión sobre las tierras continúa, en los países euro-mediterráneos se han abandonado muchos campos de cultivo y se ha reducido la presión pastoral (MacDonald *et al.,* 2000). Estos cambios en el uso del suelo han provocado en estos últimos países un cambio significativo en el paisaje, en particular la regeneración natural de la vegetación en los campos abandonados (Margaris *et al.,* 1996; MacDonald *et al.,* 2000).

En el Prepirineo Aragonés las zonas rurales han experimentado cambios socioeconómicos profundos, con un gran despoblamiento, muy especialmente entre las décadas sesenta y ochenta. Ello ha supuesto el abandono de importantes superficies anteriormente cultivadas, la disminución de la presión pastoral y cambios en las fuentes de alimentación del ganado (García-Ruiz & Lasanta, 1990; Lasanta *et al.,* 2010). Estos cambios han afectado a la dinámica de los ecosistemas, desencadenándose un proceso de revegetación con avance del bosque y de los matorrales como consecuencia de la sucesión secundaria (Lasanta *et al.,* 2000, 2010; Vicente-Serrano *et al.,* 2000).

Algunos estudios previos han argumentado que los campos abandonados solo llegan a ser totalmente recubiertos con matorral o bosque en las áreas donde la sucesión no ha sido interrumpida por las actividades humanas, principalmente el pastoreo y la agricultura (Lasanta *et al.,* 2010). Otros estudios recientes han documentado la instalación de nuevas masas de *Quercus faginea* Lam. (quejigo) en el Prepirineo Aragonés (Kouba & Alados, 2012; Kouba *et al.,* 2012), especialmente en las terrazas abandonadas, durante la segunda parte del siglo XX como resultado de la sucesión (Kouba *et al.,* 2012). Aunque los bosques de quejigo tienen un papel relevante en la conservación de la diversidad biológica (Kouba *et al.,* 2011; Maltez-Mouro *et al.,* 2009; Rey Benayas *et al.,* 2005), pocos trabajos han tratado de estudiar la dinámica de los quejigares del Prepirineo Aragonés. Este trabajo parte de la hipótesis de que existe una relación entre los cambios socioeconómicos que han ocurrido en el Prepirineo Aragonés durante la segunda mitad del siglo veinte y la expansión del quejigo. Particularmente, queremos saber si la colonización del quejigo de algunas zonas del Prepirineo es realmente el resultado de la reducción de la presión antrópica en el territorio como consecuencia del abandono de las tierras agrícolas y la disminución de la presión pastoral.

Materiales y métodos

Situación geográfica y descripción de la zona de estudio

Se ha seleccionado un área de 1363 km^2 en el Prepirineo Aragonés que incluye siete municipios: Jaca, Sabiñánigo, Arguis, Nueno, Caldearinas, Loarre y Las Piñas de Riglos (Figura 1). El área se caracteriza por una gran variación altitudinal, desde los 500 m en las Sierras Interiores a los 2000 m en las zonas más altas. El clima es sub-Mediterráneo con influencia continental en la parte norte y con influencia Mediterránea en la parte Sur. La precipitación media anual es de 1317 mm y la temperatura media anual es de 11,5 ºC (Kouba et al., 2012). Las precipitaciones presentan fuerte variación estacional y el periodo con mayor pluviosidad ocurre entre octubre y junio (Lasanta et al., 2000). El sustrato litológico está dominado por rocas areniscas, lutitas, margas y calizas. La cobertura vegetal es muy variada e incluye pinares de *P. sylvestris*, *P. nigra* (naturales o repoblados), *Fagus sylvatica*, *Q. ilex*, y *Q. faginea*. Los bosques de quejigo se extienden principalmente en las zonas del flysch y rocas detríticas eoceno-oligocenas de la depresión media pirenaica (800-2000 m). También existen matorrales dominados por *Q. coccifera* y *Buxus sempervirens,* pastizales, campos abandonados y terrenos agrícolas.

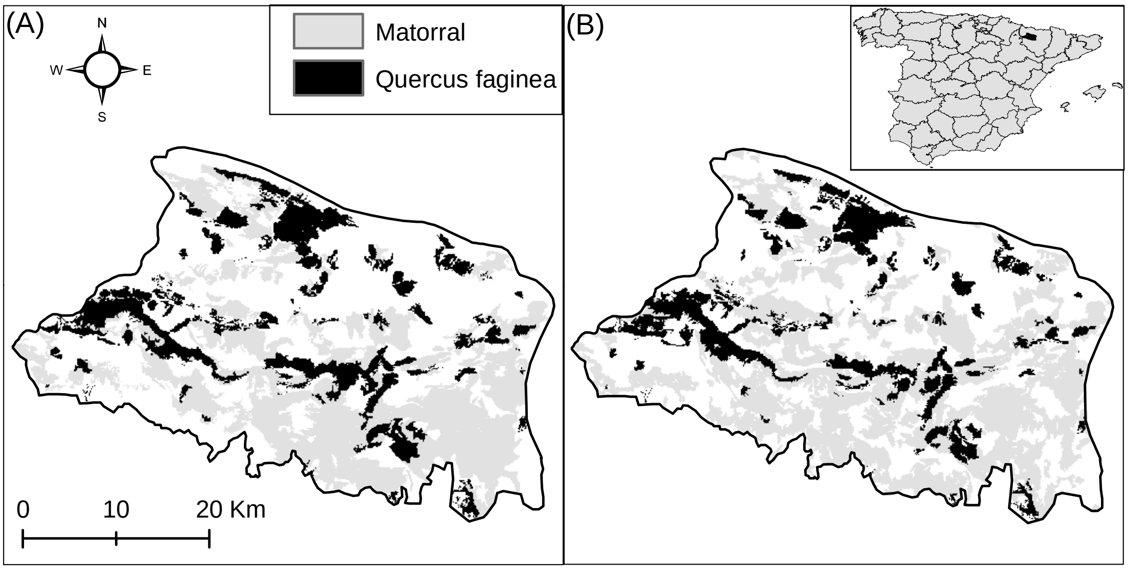

Figura 1: Mapas de distribución de masas forestales de *Q. faginea* y de matorral en el área de estudio en los años (A) 1957 y (B) 2006.

Figure 1: *Distribution maps of Q. faginea stands and shrublands in the study area during (A) 1957 and (B) 2006.*

Identificación y cuantificación de los cambios en la superficie ocupada por los bosques de quejigo entre 1957-2006

En primer lugar se han elaborado los mapas de distribución de *Q. faginea* en los años 1957 y 2006 (Figura 1). El mapa de distribución en 1957 se ha elaborado mediante la interpretación visual de las fotos aéreas del año 1957 proporcionados por el Centro Cartográfico y Fotográfico del Ejército del Aire. Basándonos en los trabajos publicados (Molinillo *et al.*, 1997; Monserrat, 1990) y en nuestra propia inspección de las fotos aéreas, hemos asumido que sólo las zonas que eran ocupadas por matorral en 1957 podrían haberse transformado en manchas de *Q. faginea* en 2006, por lo que las manchas de matorral se han incluido en el mapa de 1957. El mapa de distribución en 2006 fue elaborado a partir del tercer Inventario Nacional Forestal (IFN3; MMA, 2007). Para ello se seleccionaron las manchas de bosque en las que el quejigo era una de las tres especies arbóreas más abundantes. Las manchas de distribución de la vegetación fueron corregidas con la ayuda de las fotos aéreas orto-rectificadas a escala 1:30000 del Plan Nacional de Ortofotografía Aérea (PNOA, 2006). Debido a que *Q. faginea* se hibrida con *Q. pubescens*, haciendo difícil la identificación de individuos (Himrane *et al.,* 2004; Loidi & Herrera, 1990), hemos incluido los híbridos (principalmente *Q. subpyrenaica*) con *Q. faginea*. Hay que señalar que hemos usado una unidad mínima cartografiable (UMC) de 0,1 ha por mancha en ambos mapas. Los cambios en la superficie ocupada por *Q. faginea* se obtuvieron a partir de la superposición de los mapas de 1957 y de 2006. El siguiente paso fue cuantificar las ganancias en la superficie ocupada por *Q. faginea* en cada uno de los siete municipios de la zona de estudio, mediante la superposición del mapa de las ganancias con el mapa de los límites administrativos de los municipios. Es importante señalar aunque el área de estudio no incluye la totalidad de los términos municipales implicados, envuelve la mayor parte de los bosques de quejigo en estos municipios.

Caracterización de las zonas con presencia de quejigo y definición de los indicadores socioeconómicos

Las características de las zonas con presencia de *Q. faginea* se relacionan con variables climáticas que pueden influir directa o indirectamente en *Q. faginea* y con variables antrópicas que reflejan las perturbaciones causadas por las actividades humanas (Kouba et al., 2011). La variable climática es el balance hídrico (mm), que refleja las condiciones de sequía en la zona de estudio, esta variable se obtuvo del Atlas Climático de Aragón (DMA, 2007) con una resolución de 100-m, para el periodo 1971-2000. Las variables antrópicas que se incluyen son: la distancia a la repoblación de pinar más próxima y la distancia de coste a pastizales (Kouba et al., 2011). Estas variables se han usado para saber si las extensivas reforestaciones con pinos durante los últimos 50 años y el pastoreo han influenciado a la distribución espacial de *Q. faginea*. La distancia a las repoblaciones de pinares se realizó calculando la distancia euclidiana entre cada pixel y la reforestación más próxima. La distancia de coste es una combinación de la distancia entre dos puntos y la pendiente que los separa.

Los cambios en el número de habitantes (1960-2006), el número de agricultores (1970-2006) y el número de cabezas de ganado (1970-2006) se han usado como indicadores de los cambios socioeconómicos en la zona de estudio. Dichos cambios se han calculado por cada municipio de la zona de estudio usando los datos de evolución de la población humana y los censos de población obtenidos del Instituto Aragonés de Estadística (IAE) y el Instituto Nacional de Estadística (INE), respectivamente, así como los datos de ganado (ovino, bovino, y caprino) obtenidos del IAE y el Servicio Provincial de Agricultura de Huesca. Hay que señalar que para el cálculo del número total de cabezas de ganado se ha considerado que una vaca es equivalente a seis ovejas (García-González and Marinas, 2008).

Análisis de los datos

Para definir las características de las zonas con presencia de *Q. faginea* se ha usado el mapa de distribución de *Q. faginea* en 2006 para extraer aleatoriamente 1000 puntos, la mitad con presencia y la otra mitad con ausencia de *Q. faginea*. Para asegurar la representatividad de la muestra, cada mancha de *Q. faginea* se ha representado por cinco puntos o más. El valor de cada variable en cada punto se obtuvo usando la función "*simple*" del software ArcGIS 10.1 (ESRI, 2013). La base de datos resultante fue importada al software estadístico R (R Development Core, 2013). Para examinar las diferencias entre las zonas con presencia y las con ausencia de *Q. faginea* se ha usado la prueba de Wilcoxon.

Las relaciones entre el cambio en el número de habitantes, agricultores y cabezas de gado y el cambio en la superficie ocupada por *Q. faginea* han sido examinadas mediante coeficientes de correlación de Spearman.

Resultados

La mayor parte de los bosques de *Q. faginea* del Prepirineo están situados en zonas que se caracterizan por un balance hídrico negativo e inferior a las zonas sin *Q. faginea* (Figura 2a). Una gran parte de los bosques de *Q. faginea* del Prepirineo están relativamente alejados de las repoblaciones de pinos, con un intervalo de distancia de 1 a 6 km y un promedio de 2,5 km (Figura 2b). Las zonas con presencia de *Q. faginea* parecen ser de muy difícil acceso desde los pastos; en otras palabras, son zonas inaccesibles al ganado (Figura 2c).

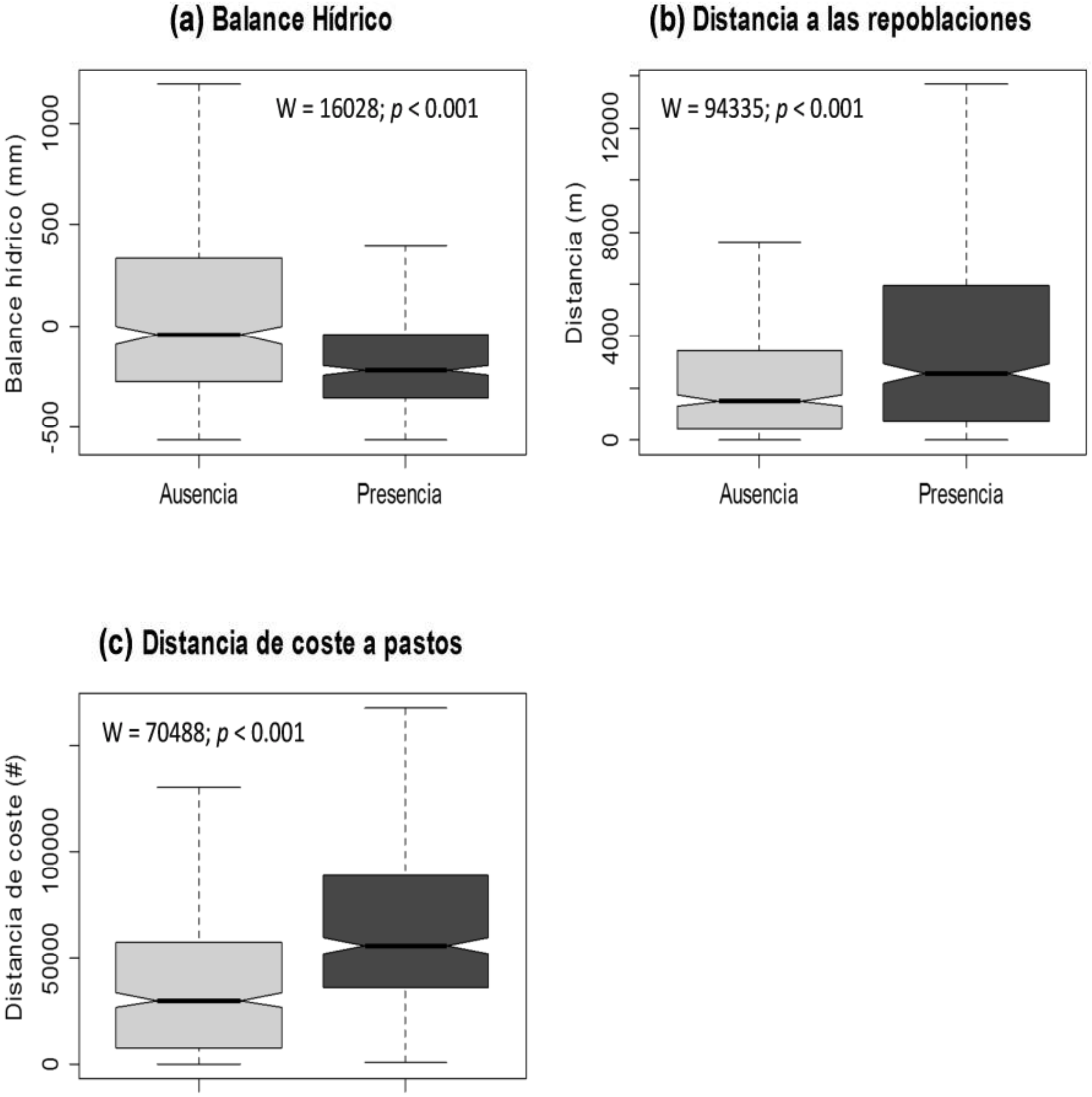

Figura 2: Comparación de las áreas con presencia y con ausencia de *Q. faginea*. El valor de la prueba de Wilcoxon (W) y el nivel de significación estadística (*p*) son mostrados por cada variable.

Figure 2: *The comparison between the areas with presence and those with absence of Q. faginea. The value of Wilcoxon test (W) and its significance level (p) are shown for each variable.*

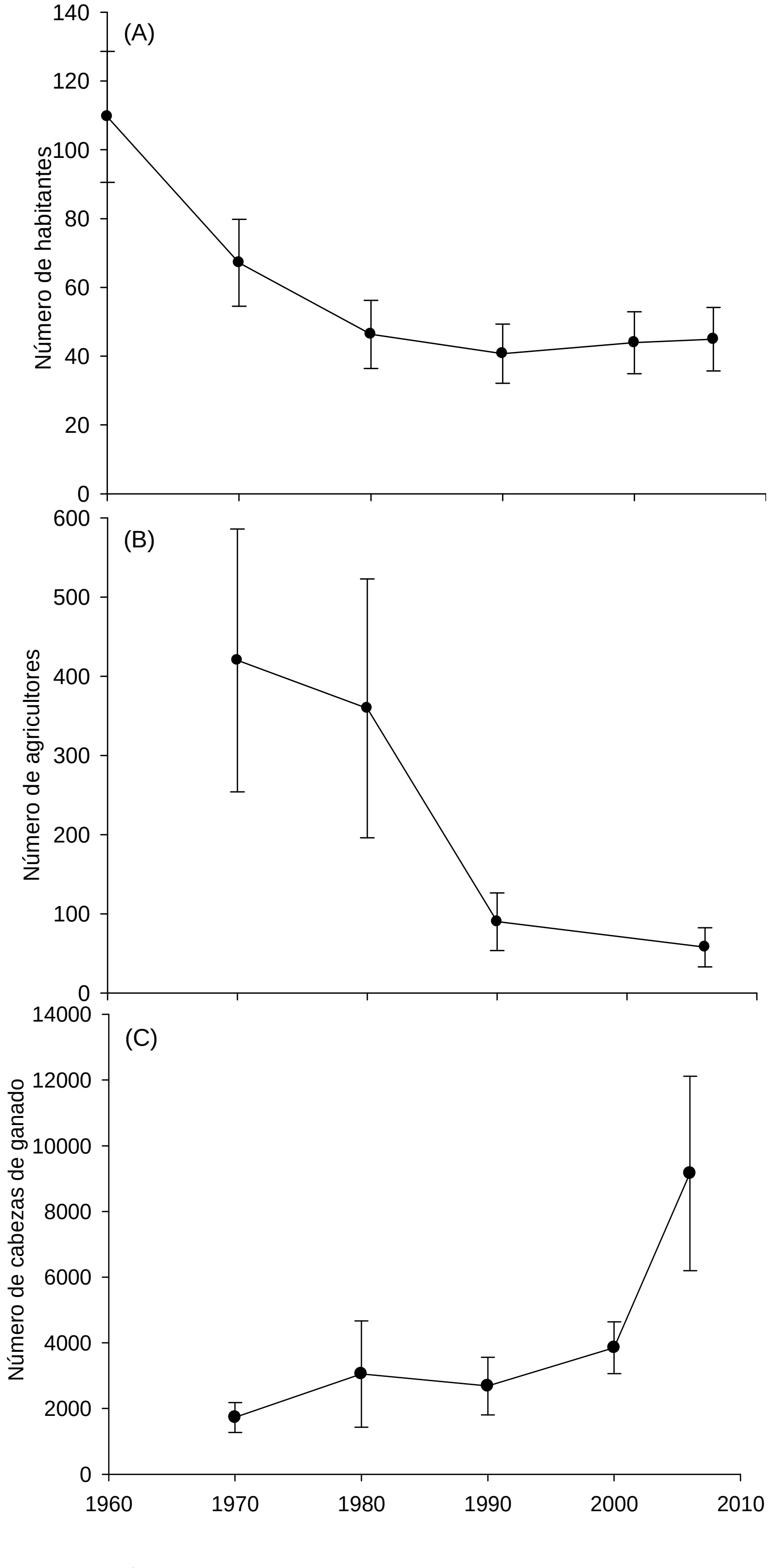

Figura 3: Cambios en el número de (A) habitantes, (B) agricultores, y (C) cabezas de ganado en los municipios de la zona de estudio (media ± error estándar) entre 1960 y 2006.

Figure 3: *Changes in the number of (A) inhabitants, (B) farmers, and (C) livestock in the municipalities of the study area (mean ± standard error) between 1960 and 2006.*

Se ha producido un decremento de la población humana y del número de agricultores en los municipios de la zona de estudio durante el periodo (1960-2006) (Figura 3A, B). Sin embargo, el número de cabezas de ganado ha aumentado durante el periodo 1960-2006 (Figura 3C). Existe una relación negativa entre la expansión de *Q. faginea* y los cambios en el número de habitantes (Figura 4), número de agricultores (Figura 5) y número de cabezas de ganado (Figura 6) en los municipios de la zona de estudio.

Discusión

El hecho de que *Q. faginea* se encuentre en zonas con un balance de agua negativo se debe a que, en la zona de estudio, este aumenta con la altitud, donde a su vez disminuyen ampliamente las temperaturas, impidiendo el establecimiento y crecimiento de las plántulas de *Q. faginea* (Kouba *et al.,* 2011). Así, el área de distribución del *Q. faginea* en la zona de estudio se encuentra entre las cotas 450 m a 1500 m (Kouba *et al.,* 2011).

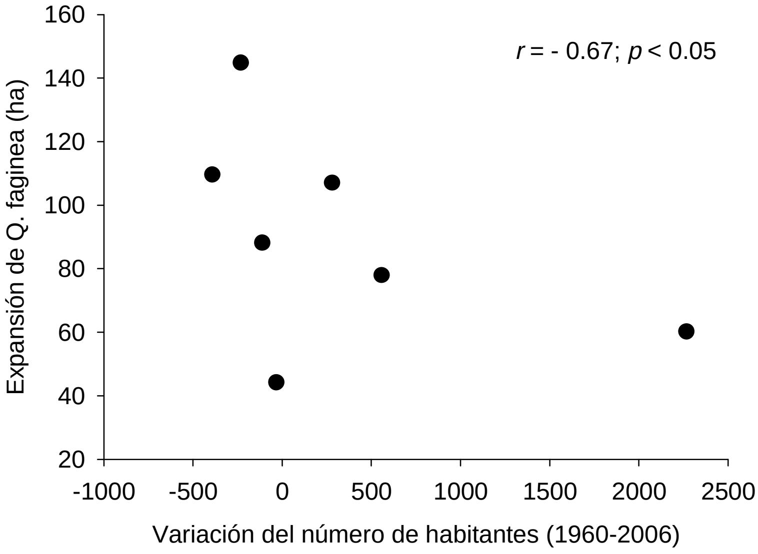

Figura 4: Relación entre la expansión de *Q. faginea* y el cambio en el número de habitantes entre 1970 y 2006 en los municipios de la zona de estudio. El valor del coeficiente de correlación de Spearman (*r*) y el nivel de significación estadística (*p*) son mostrados.

Figure 4: *Relationship between the expansion of Q. faginea and changes in the number of inhabitants during the period 1970-2006 in the municipalities of the study area. The value of Spearman correlation coefficient (r) and its significance level (p) are shown.*

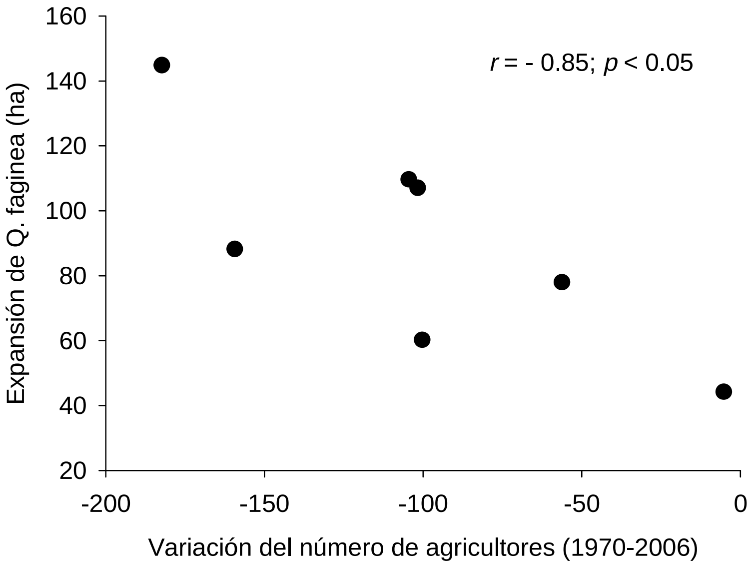

Figure 5: Relación entre la expansión de *Q. faginea* y la variación en el número de agricultores entre 1970 y 2006 en los municipios de la zona de estudio. El valor del coeficiente de correlación de Spearman (*r*) y el nivel de significación estadística (*p*) son mostrados.

Figure 5: *Relationship between the expansion of Q. faginea and changes in the number of farmers during the period 1970-2006 in the municipalities of the study area. The value of Spearman correlation coefficient (r) and its significance level (p) are shown.*

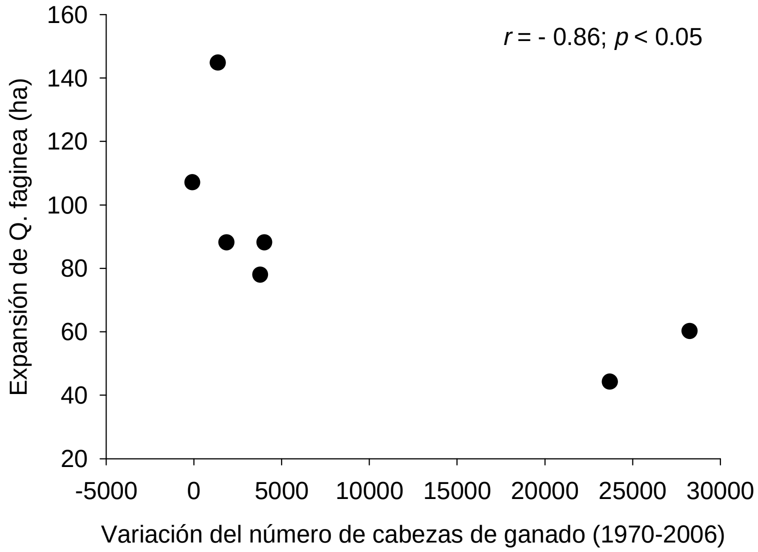

Figure 6: Relación entre la expansión de *Q. faginea* y el cambio en el número de cabezas de ganado entre 1970 y 2006 en los municipios de la zona de estudio. El valor del coeficiente de correlación de Spearman (*r*) y el nivel de significación estadística (*p*) son mostrados.

Figure 6: *Relationship between the expansion of Q. faginea and changes in the number of farmers during the period 1970-2006 in the municipalities of the study area. The value of Spearman correlation coefficient (r) and its significance level (p) are shown.*

Los resultados mostraron que los quejigares del Prepirineo Aragonés están situados lejos de las plantaciones de pinos y en áreas que son inaccesibles al ganado. Ello implica que los bosques nativos pueden ser influenciados negativamente por las plantaciones de crecimiento rápido (Teixido et al., 2010). Estudios previos han argumentado que en el Prepirineo, los quejigares fueron primero desforestados para aumentar las áreas de cultivo y pastos (Lasanta, 1989; Sancho et al., 1998), y éstas fueron posteriormente reforestadas con plantaciones de pinos (Amo et al., 2007; Kouba et al., 2011). Igualmente, la antigua presión de pastoreo afectó negativamente a la distribución de *Q. faginea*, siendo la presencia de éstos menos frecuente cerca de los pastos. Otros autores han apuntado la dificultad de regeneración de las poblaciones de árboles ante la presión del pastoreo, al eliminar las plántulas el ganado (Barbero et al., 1990). Cuando la presión del pastoreo es elevada, el consumo de las bellotas dificulta el establecimiento de las plántulas (Plieninger, 2006) impidiendo la regeneración del *Q. faginea*.

En la zona de estudio los bosques de *Q. faginea* han ganado mayor superficie en los municipios con un gran despoblamiento humano y, sobre todo, con una disminución notable en el número de agricultores, lo que indica un abandono de los campos agrícolas. Como es el caso en todo el Pirineo, estos pueblos han tenido una elevada migración de la gente hacia las ciudades grandes como Zaragoza en búsqueda de trabajo y mejores condiciones de vida (García-Ruiz & Lasanta, 1990). Este despoblamiento de las zonas rurales ha reducido notablemente la presión antrópica en el territorio incluyendo el abandono de las tierras agrícolas, lo que ha permitido la revegetación de los campos abandonados. Particularmente, Kouba *et al.* (2012) han argumentado que la expansión de *Q. faginea* fue el resultado de una colonización de las terrazas abandonadas por esta especie esencialmente a finales de los años 1960s y principios de los años 1970s. Los mismos autores han señalado que esa colonización coincide con unas condiciones climáticas muy adecuadas.

La relación negativa entre la expansión de *Q. faginea* y el número de cabezas de ganado significa que esta especie se ha expandido principalmente en los municipios que han conocido una disminución de la presión pastoral. El incremento en el número de cabezas de ganado que se inició en los años 1970s no ha sido acompañado por un aumento de la presión pastoral debido a los cambios en los métodos de manejo del ganado, con un aumento en el número de animales que se crían en establos y granjas y diferentes fuentes de alimentación del ganado (García-Ruiz *et al.,* 1996; Lasanta *et al.,* 2010; Kouba *et al.,* 2012). Muchos autores han argumentado que, desde los años 1970s, el número de cabezas de ganado que pasta libremente en los pastos y las montañas de la zona de estudio durante el verano ha bajado notablemente (Molinillo *et al.,* 1997; Lasanta *et al.,* 2006).

Conclusiones

Estudios previos han encontrado una disminución en la superficie total ocupada por los bosques de *Q. faginea* en el Prepirineo durante la segunda mitad del siglo veinte (Kouba & Alados, 2012). Sin embargo, este estudio ha mostrado que *Q. faginea* ha colonizado algunas áreas en los municipios con un gran despoblamiento y una reducción marcada de la presión pastoral, la cual es debida a los cambios en los métodos de crianza y alimentación del ganado. El éxodo rural ha producido un abandono de tierras agrícolas y la disminución de la presión pastoral, que han favorecido la expansión de *Q. faginea* en algunas zonas del Prepirineo Aragonés, principalmente en las terrazas abandonadas (Kouba *et al.,* 2012) durante la segunda mitad del siglo veinte.

Se postula que, con la tendencia observada de descenso de la presión humana en el territorio, *Q. faginea* colonizará nuevas zonas durante las próximas décadas, principalmente en los campos abandonados. Pero, ¿pueden estos bosques que están instalando en las tierras abandonadas jugar un papel tan importante como los bosques primarios en conservar la biodiversidad? La respuesta a esta pregunta puede ser el tema de una futura investigación.

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CAPITULO 5

Plant β-diversity in human-altered forest ecosystems: The importance of the structural, spatial, and topographical characteristics of stands in patterning plant species assemblages

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Abstract

An understanding of spatial patterns of plant species diversity and the factors that govern and generate those patterns is critical for the development of appropriate biodiversity management in forest ecosystems. We studied the spatial organization of plants species in human-modified and managed oak forests (primarily, *Quercus faginea*) in the Central Pre-Pyrenees, Spain. To test whether plant community assemblages varied non-randomly across the spatial scales, we used multiplicative diversity partitioning based on a nested hierarchical design of three increasingly coarser spatial scales (transect, stand, region). To quantify the importance of environmental factors in patterning plant community assemblages and identify the determinants of plant diversity patterns, we used canonical ordination. We observed a high contribution of β-diversity to total γ-diversity and found β-diversity to be higher and α-diversity to be lower than expected by random distributions of individuals at different spatial scales. Environmental variables that are strongly influenced by historical land use such as mean stand age, the abundance of the dominant tree species (*Q. faginea*), the age structure of stand, stand size, and the topographical conditions (i.e., slope) were the main factors that explained the compositional variation in plant communities. The results indicate that (1) the structural, spatial, and topographical characteristics of the forest stands have the greatest effect on diversity patterns, (2) forests in landscapes that have different land use histories are environmentally heterogeneous and, therefore, can experience high levels of compositional differentiation, even at local scales (e.g., within the same stand). Maintaining habitat heterogeneity at multiple spatial scales should be considered in the development of management plans for enhancing plant diversity and related functions in human-altered forests.

Key words: secondary forests, community assembly, forest structure, compositional dissimilarity, beta diversity, species turnover.

Introduction

Most studies of forest ecosystems focused on α-diversity, i.e., the diversity within a specific site; however, recent studies that have partitioned diversity into hierarchical components have shown that much of the floral diversity is due to differentiation in species composition among sites (β-diversity; Arroyo-Rodríguez et al., 2013; Chandy, Gibson, & Robertson, 2006; Gossner et al., 2013). An understanding of how diversity components, particularly, β-diversity, vary spatially, and the factors that are responsible for the patterns observed is essential for understanding how species diversity is organized and maintained (Condit et al. 2002; Arroyo-Rodríguez et al. 2013). Particularly, in human-modified and managed forests, the structural, spatial, and topographical characteristics of the forest stands, which are strongly influenced by historical land use-type and intensity, might have a significant role in shaping plant diversity patterns (Flinn and Vellend 2005; Hermy and Verheyen 2007; Berhane et al. 2013). Recent studies have found that forest stands in landscapes that have different land use histories manifest a high environmental heterogeneity, which can lead to high levels of compositional differentiation (i.e., β-diversity) even at fine scales (e.g. Arroyo-

Rodríguez et al. 2013). The floristic differentiation can drive successional trajectories and potentially affect the maintenance of biodiversity in such altered forests (Chazdon et al. 2009; Melo et al. 2013; Arroyo-Rodríguez et al. 2013).

For centuries, the oak forests (mainly, *Quercus faginea*) in the western Mediterranean region have been harvested intensively for timber and firewood, and clearcut for agriculture (Sancho et al. 1998), which has reduced them to coppice stands that have different management histories; i.e., different coppicing intensities and time since coppicing ceased (Sancho et al. 1998). In the late 19th and 20th centuries, however, changes in socioeconomic structures and production systems resulted in the abandonment of the poorest arable lands and their subsequent afforestation (Sciama et al. 2009). In particular, in the Central Pyrenees, Spain, the encroachment of some abandoned farmlands by *Q. faginea* has led to new, secondary growth *Q. faginea*-dominated stands (Kouba et al. 2012). Probably, the biodiversity that can be observed in these human-modified and managed forests (i.e., either the formerly managed or the new secondary growth forests) does not have value for conservation, per se, because it usually is deprived of any conservation status. Often, however, such islets of habitats are considered biodiversity “refuges”, which allows them to recover many components of the original biodiversity (Chazdon 2008), and provide important ecosystem services such as control of climate and erosion. Therefore, the assessment of plant diversity patterns across multiple spatial scales and the factors that govern and generate those patterns is required to accurately evaluate the impact of historical man-induced disturbances on the spatial dissimilarities in species composition (β-diversity) and to gain a better understanding of the mechanisms that contribute to the maintenance of species diversity in such human-modified and managed forests.

Although the use of multi-scale analyses to analyze the spatial patterns of faunal diversity has increased, very few studies have used this approach to assess the hierarchical organization of plant species diversity, particularly β-diversity, at multiple spatial scales in forest ecosystems (but see Chandy et al. 2006; Chávez and Macdonald 2012; Arroyo-Rodríguez et al. 2013). In this study, we used multiplicative diversity partitioning to understand how plant species diversity changes across three spatial scales (transect, stand, and entire region) as well as to identify the spatial scales at which nonrandom processes have had the greatest effect. To identify the environmental factors that might have patterned plant species diversity in human-modified and managed oak forests, we used constrained ordination analysis (RDA). We hypothesized that (H1) plant community assemblages vary non-randomly across the spatial scales, (H2) β-diversity components contribute more to γ-diversity than do α-diversity components because of high habitat heterogeneity, and (H3) the structural, spatial, and topographical characteristics of the forest stands, which are largely the result of historical land use, are the main factors that structure the compositional variation in plant communities in these human-modified and managed forests.

Methods

Study area

The study was conducted within a 1363-km^2 area at an elevation of 450-1950 m a.s.l. in the Central Pre-Pyrenees, Spain (between 42.32 N to 42.11 N, and 0.31 W to 0.04 W) (Fig. 1). The lithology is mostly conglomerate, limestone, marl, and sandstone developed on Eocene flysch sedimentary formations (Kouba and Alados 2011). The climate is transitional sub-Mediterranean; i.e., influenced by continental effects from the Pyrenees to the north and by milder Mediterranean conditions that prevail from the south (i.e., the Ebro Basin). In the study area, mean annual precipitation is 1317 ± 302 mm (1915-2005) (Kouba et al. 2012) and mean annual air temperature is 11.5 ± 2.8º C (1910-2005) (Kouba et al. 2012).

The area has a variety of land-use/cover types including natural forests of *Pinus sylvestris*, *P. nigra*, *Fagus sylvatica*, *Q. ilex*, and *Q. faginea*, shrublands of *Q. coccifera* and *Buxus sempervirens*, artificial plantations of *P. sylvestris* and *P. nigra*, arable farmland, pastures (xeric pastures and subalpine pastures), urban areas, and abandoned farmland. In the second half of the twentieth century, major changes in land use occurred in the area (Lasanta et al. 2005) because of agricultural mechanization and intensification, the introduction of pine plantations, and the abandonment of croplands and pastures, which has led to forest regrowth (Lasanta et al. 2005; Vicente-Serrano et al. 2010). In the area, *Q. faginea* is one of the most abundant naturally occurring species and the communities in which it occurs constitute a transition zone between Mediterranean forests in which *Q. ilex* ssp.

ballota or *P. halepensis* are predominant, and mountain continental or mesic forests of *P. sylvestris*, *P. nigra* ssp. *salzmannii*, and *F. sylvatica* (Loidi and Herrera 1998; Sancho et al. 1998). The overstorey canopy of those semi-deciduous oak stands is dominated by *Q. faginea* interspersed with some scattered pines (*Pinus sylvestris* and *P. nigra*) and evergreen oak (*Q. ilex* subsp. *ballota*). The understory is composed of shrubs (*Q. coccifera*, *B. sempervirens*, *Genista scorpius*, *Juniperus communis*), forbs (*Aphyllanthes monspeliensis*, *Arenaria montana*, *Achillea millefolium*), and graminoids (*Brachypodium pinnatum*, *Carex halleriana*, *Festuca rubra*, *Carex flacca*, *Bromus erectus*).

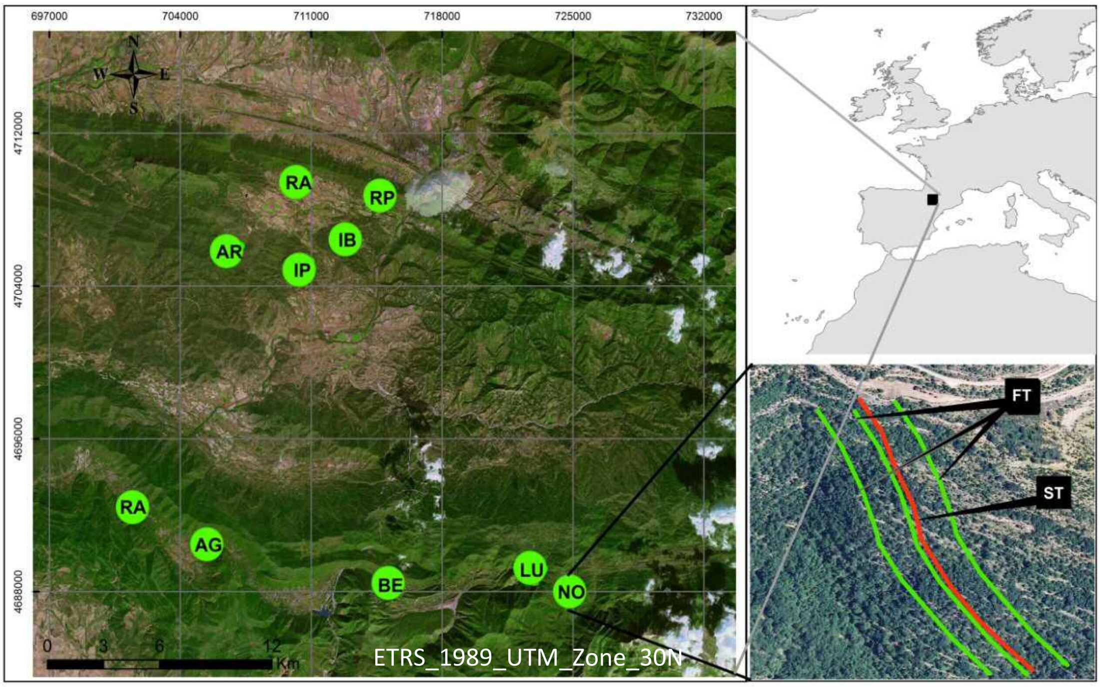

Fig. 1 Location of the study area within Europe (upper right panel), and the locations of the ten *Q. faginea* forest stands sampled in the Central Pre-Pyrenees, Spain (left panel). The location of the three floristic transects (FT) and the forest structural transect (ST) within each stand (lower right panel). AB = Abena, AG = Arguis, AR = Ara, BE = Belsué, IB = Ibort, IP = Ipies, LU = Lucera, NO = Nocito, RA = Rasal, RP = Rapun

Stand selection and surveys

Based on the distribution maps of *Q. faginea* in the study area in 1957 and 2006 (Kouba and Alados 2011) and dendrochronological data that reflect the historical dynamics of *Q. faginea* stands in the study area (Kouba et al. 2012), ten *Q. faginea*-

Table 1 Characteristics of ten oak stands within a 1363-km^2 area in the Central Pre-Pyrenees, Spain. Values are mean ± standard error. ELEVAT = elevation, ORIENT = orientation (S = South, SE = South East, SW = South West, E = East), SLOP = slope, STSIZE = stand size, SHPCOMP = shape complexity, DENSITY = density, QFAB = *Q. faginea* abundance, DBH = diameter at breast height, TREHEIGHT = tree height, AGE = mean stand tree age, CVAGE = Coefficient of Variation of age of stand, FORTYPE = Forest type (SF = secondary forest, CS = abandoned coppice stand)

Stand characteristics/stand locations	Rasal (RA)	Belsué (BE)	Abena (AB)	Ara (AR)	Lucera (LU)	Ibort (IB)	Ipies (IP)	Nocito (NO)	Arguis (AG)	Rapun (RP)
Topography										
ELEVAT (m a.s.l.)	868.3 ± 4.8	1158.5 ± 1.20	970.3 ± 1.50	971.1 ± 2.00	1198.0 ± 7.70	950.8 ± 2.60	852.5 ±2.30	1046.7 ± 2.10	1026.2 ± 1.90	923.3 ± 2.40
ORIENT	S	S	S	SE	SE	S	E	SW	S	SW
SLOP (º)	9.3 ± 0.50	30.5 ± 0.40	11.7 ± 0.50	19.6 ± 0.50	16.8 ± 1.20	14.8 ± 1.10	7.8 ± 0.60	25.0 ± 0.80	11.0 ± 0.60	17.98 ± 1.40
Spatial attributes										
STSIZE (ha)[a]	114	94	73	244	1115	40	146	294	1847	217
SHPCOMP (perimeter/area)[a]	126.41	119.60	77.49	164.23	244.28	103.17	268.11	267.27	232.38	204.62
Forest structure										
DENSITY (stems ha-1)	607 ± 0.20	1100 ± 0.10	999 ± 0.10	503 ± 0.30	867 ± 0.10	1088 ± 0.10	812 ± 0.10	983 ± 0.10	818 ± 0.10	540 ± 0.10
QFAB (Tree/Transect)	239±43	362±15	339±18	133±32	173±14	426±7	193±8	389±28	381±13	212±18
DBH (cm)	14.00 ± 1.40	9.0 ± 0.70	13.3 ± 1.30	7.2 ± 0.50	12.0 ± 0.80	13.3 ± 0.80	11.4 ± 0.70	12.3 ± 1.70	13.0 ± 1.40	6.8 ± 0.50
TREHEIGHT (m)	5.10 ± 0.40	4.8 ± 0.30	5.1 ± 0.30	3.4 ± 0.20	5.5 ± 0.30	6.1 ± 0.20	4.3 ± 0.30	5.5 ± 0.41	4.7 ± 0.33	3.9 ± 0.25
AGE (years)	31 ± 3	40 ± 4	50 ± 2	35 ± 1	39 ± 1	63 ± 2	64 ± 2	56 ± 5	50 ± 1	69 ± 2
CVAGE (%)d	31	43	19	17	12	17	15	47	10	9
FORTYPE	SF	CS	SF	CS	CS	CS	CS	SF	CS	CS

[a] Calculated based on the distribution map of *Q. faginea* forests in the study area (for more details, see Kouba et al. 2011)

dominated stands that differed in their structural, spatial, and topographical characteristics were selected within the study area (see Table 1, Fig. 1). Primarily, the stands were surrounded by farmland, pine plantations, abandoned land, and grasslands (see Fig. 1).

In 2009 and 2010, during the period of peak growth (May and June), the vascular plant species were surveyed in the ten stands. Within each stand, three 500-m linear transects (30 transects in total) were established (hereafter, floristic transects). To estimate plant abundance and richness within each transect, we used the Point-Intercept Method (Goodall 1952), which involves recording, at 40-cm intervals, the identity of all individuals that are in contact with a vertical nail (Alados et al. 2009). We recorded all of the vascular plants that touched the nail and any overstorey species (including *Q. faginea*) that was above the nail. The abundance of each species in each transect was estimated as the number of individuals (of this species) recorded along the transect. Plant species that could not be identified with certainty in the field were collected, pressed, and brought to the laboratory for identification by botanical experts. Species that have traits that make them difficult to distinguish were only identified to the genera level. Plant nomenclature followed *Flora Ibérica* (Castroviejo et al. 1986-2012).

Plant growth forms represent broad patterns of variation among correlated plant traits that are more related to ecosystem functions, e.g. nutrient use efficiency, protection against abiotic and biotic hazards, and competitive strength (Lavorel et al. 1997; Dorrepaal 2007), and, therefore, are expected to differ in their responses to environmental factors. Accordingly, plant species were grouped based on growth forms: woody (tree and shrubs), graminoids, or forbs.

In this study, the relative abundance of *Q. faginea* (QFAB) in each floristic transect was included in the analyses as surrogate for the amount of canopy cover (%). To quantify the structural properties of each stand (Table 1) a 500-m linear transect (hereafter, forest structure transect) was established within each stand (n =10) and the forest was sampled using the Point-quarter Method (Cottam and Curtis 1956). Each forest structure transect was placed close to the central floristic transect within each stand. Sampling points (n = 20) were at 25-m intervals along each of the transects. At each sampling point, we identified the closest adult *Q. faginea* tree in each of the four cardinal directions within a maximum distance of 5-

m from the sampling point (Kouba et al. 2012). Adult trees were defined as those > 2 m high or that had a stem diameter at breast height (DBH) ≥ 4 cm. The following measurements were recorded: diameter at breast height (DBH) (cm), tree height (m), and age (for details about age estimation, see Kouba et al. 2012). Those data were used to estimate the following variables for each stand: density (DENSITY), mean diameter at breast height (DBH), mean tree height (TREHEIGHT), mean age (AGE), and coefficient of variation of tree age (CVAGE). Furthermore, forest type (FORTYPE; secondary growth stands vs. abandoned coppice stands) was recorded for each stand based on visual observation on the field (see Table 1).

To quantify the spatial attributes of each stand (Table 1), we measured stand size (STSIZE) and shape complexity (SHPCOMP) using a digitized *Q. faginea* distribution map, the 'Patch Analyst' extension in ArcGIS 10.1 (ESRI 2013), the Third National Forest Inventory map (IFN3; MAGMARA, 2013), and orthorectified aerial photographs taken in 2006 (CINTA 2013). In addition, the mean elevation (ELEVAT), mean slope (SLOP), and orientation (ORIENT) of each stand were derived from a Digital Elevation Model (CINTA 2013).

Partitioning of biodiversity

To assess plant diversity patterns across multiple spatial scales, we used multiplicative partitioning because of the advantages of the Hill Number (${}^{q}D$) and q-metric (see below): ${}^{q}D_{\gamma} = {}^{q}D_{\beta} \times {}^{q}D_{\alpha}$ (Whittaker 1972; Jost 2006, 2007, 2010). Diversity is quantified using the Hill Number (${}^{q}D$), which has the property to be invariant to changes in absolute numbers; if all species double in abundance, ${}^{q}D$ remains unchanged. It measures variation in relative, rather than absolute abundance, and it follows the replication principle: Combining two sets of non-overlapping species that have the same abundance distributions doubles the value of ${}^{q}D$ (Jost 2006; Scheiner 2012). To quantify diversity patterns based on various weightings for rare and abundant species, we used the q-metric, which reflects the sensitivity of the diversity index to the relative frequencies of species. The analyses included two q-values: (1) $q = 0$ reflects species richness, which is not sensitive to species abundance and, therefore, assigns disproportionate weight to rare species (Jost 2006), and (2) $q = 0.999$ (and not $q = 1$, which would require division by zero) is equivalent to the exponential of Shannon entropy; here, species are weighted in proportion to their frequency in the sampled community and, therefore, it can be interpreted as the number of 'typical species' in the community (Chao et al. 2012).

We used a nested hierarchical design of three increasingly coarser spatial scales: individual assemblages at the transect level, pooled assemblages within a stand, and a single, pooled assemblage across the entire region (Fig. 2).

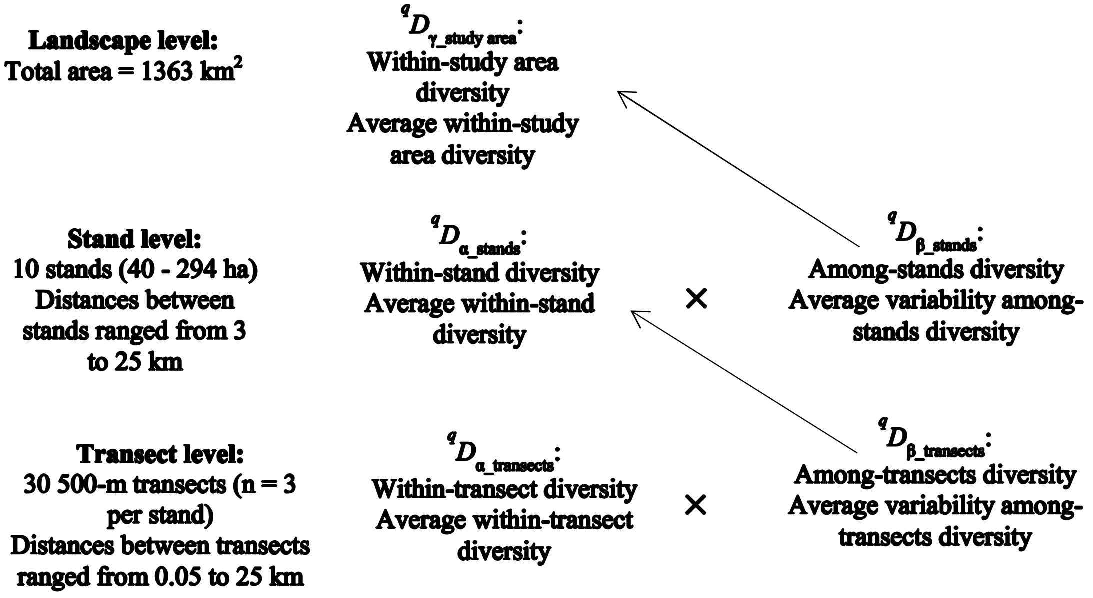

Fig. 2 Hierarchical levels in the multiplicative partitioning of plant species diversity in ten oak forest stands in the Central Pre-Pyrenees, Spain

The design allowed $^qD_\gamma$ diversity to be decomposed into within transect ($^qD_{\alpha\_transects}$), among transects ($^qD_{\beta\_transects}$), within stand ($^qD_{\alpha\_stands}$), and among stands ($^qD_{\beta\_stands}$) components (Fig. 2). To test for significant differences in the spatial partitioning of diversity, the expected values of the measures of diversity were calculated using individual-based randomizations (10^4 permutations; Crist et al. 2003), which evaluated whether the α and β components of diversity differed significantly from a random distribution of individuals among samples (Crist et al. 2003). Those analyses were performed using the 'vegan' package (Oksanen et al. 2013) implemented in the R software (R Development Core Team 2013).

To test whether differences in species richness might have biased the observed spatial diversity pattern, we additively partitioned β-diversity into the two components of spatial turnover and nestedness using the method suggested by Baselga (2010). We performed this analysis using the 'betapart' package (function ‘*beta.sample*’) (Baselga and Orme 2012) within the R software (R Development Core Team 2013).

Partitioning the variation in plant communities in response to environmental factors

To identify the environmental variables that explained a significant amount of the variation in species composition, we used Canonical Redundancy Analyses (RDA). The matrices of species abundance were transformed using Hellinger’s Transformation (Legendre and Gallagher 2001). The explanatory variables included in the finale RDA models were selected based on forward stepwise procedure, which provided an estimate of the best set of non-redundant variables for predicting species composition and a ranking of the relative importance of the individual explanatory variables.

The spatial autocorrelation of the residuals of the RDA models was tested using a multi-scale ordination (MSO; Borcard et al. 2011; Legendre and Legendre 2012). Initial analyses indicated significant spatial autocorrelation in the residuals of the RDA models and a scale-dependent relationship between the species data and the explanatory variables. To address those problems, the following three steps were followed: (i) the Hellinger-transformed species data matrices and the explanatory variables were detrended along the Y Cartesian geographic coordinates (i.e., the coordinates of transect-central points), which supported the assumption of stationarity in the computation of confidence intervals in the MSO variograms (Legendre and Legendre 2012). (ii) The sampling design was spatially nested; therefore, the function ‘*create.MEM.model’* (Borcard et al. 2011; Declerck et al. 2011) was used to construct a staggered spatial matrix of Moran’s eigenvector maps (MEM), and (iii) partial canonical redundancy analyses (partial RDAs) were performed using the detrended data and included the computed MEMs as covariables, which controlled for the effects of spatial structure (i.e., excluded the compositional variation caused by spatial structure; Borcard et al. 2011; Legendre and Legendre 2012).

Results

In the survey of the 10 oak stands in the Central Pre-Pyrenees, Spain, we identified 238 vascular plant species. On average, the floristic transects contained

64 species (range = 43-98). Twenty-one (9%) of the species contributed 80% of the total plant coverage by abundance, and *B. sempervirens* was the most abundant species in all of the stands (Fig. 3). Most of the species were forbs (159 species), followed by woody plants (54 species) and graminoids (25 species). Among rare species (i.e., species that had a relative abundance <0.01% and occurred in <5% of the transects; see Appendix 1), 75 % were forbs, 7 % were graminoids, and 18 % were woody species.

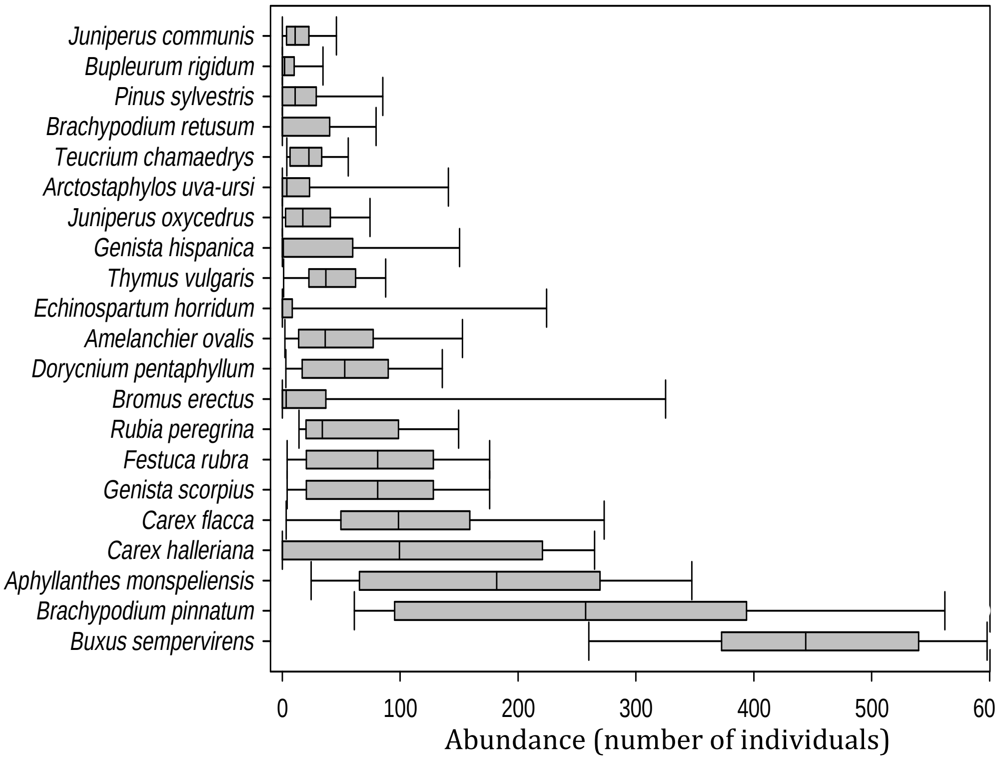

Fig. 3 The abundances of common species (expressed as median values) in ten *Q. faginea* forest stands (n = 30 transects) in the Central Pre-Pyrenees, Spain. Boxes indicate the 25th and 75th percentiles, and whiskers indicate the 5th and 95th percentiles

Patterns of diversity across spatial scales

In general, beta diversity components (${}^{q}D_{\beta\_\text{transects}}$ and ${}^{q}D_{\beta\_\text{stands}}$) made up a large proportion of overall diversity (Fig. 4). At all spatial scales, and independently of the value of q, beta diversity was significantly higher, and alpha diversity was significantly lower than expected based on a random distribution of individuals (Table 2). Beta diversity and the deviations from random distributions were higher

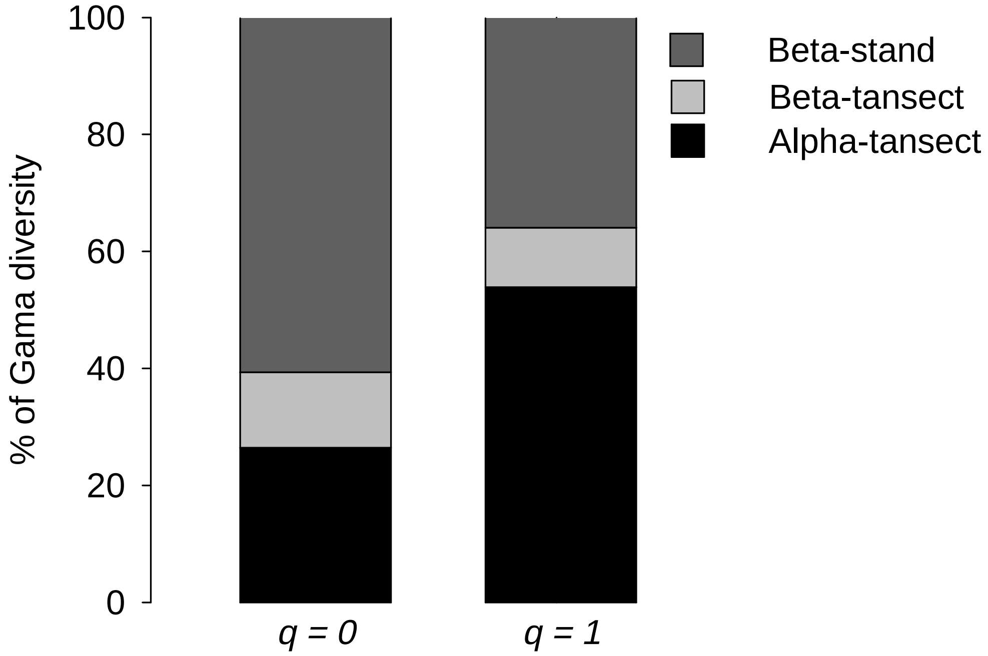

Fig. 4 The contributions of the alpha and beta components of diversity to total gamma diversity for two values of *q* (0 and 1) assessed using multiplicative diversity partitioning of plant species within ten oak forest stands in the Central Pre-Pyrenees, Spain. Apha-transect = within-transect diversity (${}^{q}D_{\alpha\_\text{transects}}$), Beta-transect = among-transects beta diversity (${}^{q}D_{\beta\_\text{transects}}$), and Beta-stand = among-stands beta diversity (${}^{q}D_{\beta\_\text{stands}}$)

Table 2 Hierarchical multiplicative partitioning of the alpha (${}^{q}D_{\alpha}$) and beta (${}^{q}D_{\beta}$) components of overall diversity (${}^{q}D_{\gamma}$) in ten *Q. faginea* forest stands in the Central Pre-Pyrenees, Spain. Diversity was quantified using the Hill Index (${}^{q}D$), with q = 0 (all species are given equal weight) or q = 1 (greater weight is given to common species). Deviations from null distributions (numbers within brackets) are expressed by dividing the observed values by the expected values. The p-values were obtained by comparing the observed values with the values generated by 10^4 randomizations

	q = 0			*q* = 1		
	Observed	Expected	p-value	Observed	Expected	p-value
${}^{q}D_{\alpha\_\text{transects}}$	62.88 (0.52)	120.09	<0.01	17.31 (0.57)	30.27	<0.01
${}^{q}D_{\alpha\_\text{stands}}$	93.70 (0.58)	159.73	<0.01	20.58 (0.65)	31.49	<0.01
${}^{q}D_{\beta\_\text{transects}}$	1.49 (1.12)	1.33	<0.01	1.18 (1.13)	1.04	<0.01
${}^{q}D_{\beta\_\text{stands}}$	2.54 (1.82)	1.39	<0.01	1.56 (1.52)	1.02	<0.01
${}^{q}D\,{}^{q}D_{\gamma\_\text{study area}}$	238	238	-	32.12	32.12	-

among stands than among transects for the two values of *q* (0 and 1). The two components of beta diversity (${}^{q}D_{\beta\_\text{transects}}$ and ${}^{q}D_{\beta\_\text{stands}}$) declined with increasing values of *q* (Table 2), which reflected the lower emphasis given to rare species as *q* increases.

The partitioning of beta-diversity into two components, spatial turnover and nestedness, revealed that overall spatial turnover accounted for > 96% of total beta diversity, which suggests that bias caused by differences in species richness among transects was negligible.

Partitioning the variation in plant communities in response to environmental factors

The environmental variables measured in this study explained a significant amount of the variation in the composition of forbs and woody species (Table 3), but not the composition of graminoids. Collectively, AGE (10.6%), QFAB (8.9), CVAGE (13.3), and SLOP (11.4) explained 44.2% of the variation in the composition of forbs species (Table 3).

Table 3 Redundancy analysis of the environmental variables that explained a significant amount of the variation in species composition of forbs and woody species (significant relationships are shown). "R^2_{adj}Cum" is the cumulative adjusted R^2 of the model; the values within brackets indicate the variance (%) explained by each explanatory variable, "R^2_{adj}" is the total explained variance (%) in each model. AGE = Mean stand age, CVAGE = Coefficient of variation of tree age, STSIZE = Stand size, SLOP = slope, QFAB = *Q. faginea* abundance

Species group	Variables	R^2_{adj}Cum	F	p-value
Forbs (R^2_{adj} = 44.2)	AGE	0.10 (10.6)	2.65	0.01
	QFAB	0.19 (08.9)	2.41	0.02
	CVAGE	0.33 (13.3)	3.28	0.00
	SLOP	0.44 (11.4)	3.11	0.01
Woody (R^2_{adj} = 43.8)	STSIZE	0.12 (11.7)	2.65	0.01
	QFAB	0.23 (11.4)	2.67	0.01
	AGE	0.34 (11.5)	2.77	0.01
	CVAGE	0.44 (9.2)	2.46	0.02

Most of the forbs were common in young and uneven-aged stands, although there were some exceptions, such as *Aphyllanthes monspeliensis* (APHMON) and *Bupleurum rigidum* (BUGRA), which were related to lower *Q. faginea* abundance and higher stand age, respectively, and the perennial species *Hepatica nobilis* (HEPAT) and *Q. faginea* abundance were correlated (Fig. 5).

For woody species, STSIZE (11.7%), QFAB (11.4), AGE (11.5), and CVAGE (9.2) explained 43.8% of the variation in species composition (Table 3). The long-lived shrub *B. sempervirens* (BUXSEM) was positively correlated with *Q. faginea* abundance, *Genista scorpius* (GENSCO), *Thymus vulgaris* (THYVUL), and *Echinospartum horridum* (ECHIOR) were prevalent in uneven-aged stands, and others, i.e., *Juniperus oxycedrus* (JUNOXY) and *P. sylvestris* (PINSIL), were related to lower *Q. faginea* abundance. *Cytisophyllum sessilifolium* (CYTSES), *Amelanchier ovalis* (AMEOVA), and *Arctostaphylos uva-ursi* (ARCUVA) predominated in old stands (Fig. 5).

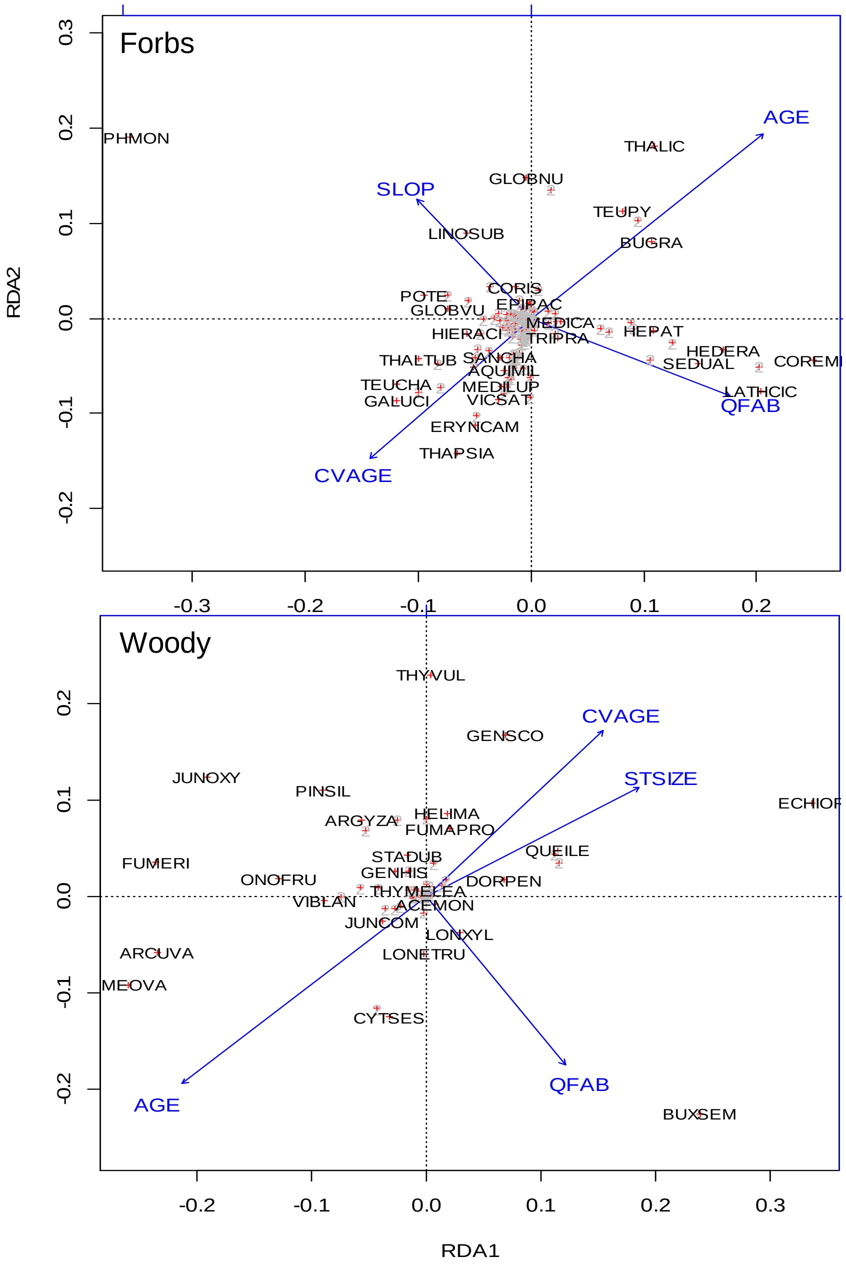

Fig. 5 Ordination plots of the significant environmental variables and the composition of forbs and woody species within ten oak forest stands in the Central Pre-Pyrenees, Spain. Arrows indicate the direction of increasing values of significant environment variables. AGE = mean stand tree age,

CVAGE = coefficient of variation of stand age, STSIZE = stand size, SLOP = slope, QFAB = *Q. faginea* abundance. The letter codes indicate the locations of plant species that had a correlation of ≥0.25 to the ordination axes. Species presented are: Forbs (APHMON: *Aphyllanthes monspeliensis*, GLOBNU: *Globularia nudicaulis*, THALIC: *Thalictrum alpinum*, LINOSUB: *Linum suffruticosum*, TEUPY: *Teucrium pyrenaicum*, BUGRA: *Bupleurum rigidum*, CORIS: *Coris monspeliensis*, POTE: *Polygala monspeliaca*, GLOBVU: *Globularia vulgaris*, EPIPAC: *Epipactis sp.*, MEDICA: *Medicago minima*, HIERACI: *Hieracium pilosella*, TRIPRA: *Trifolium pretense*, HEPAT: *Hepatica nobilis*, THALTUB: *Thalictrum tuberosum*, SANCHA: *Santolina chamaecyparissus*, HEDERA: *Hedera helix*, AQUIMIL: *Achillea millefolium*, SEDUAL: *Sedum album*, COREME: *Coronilla emerus*, TEUCHA: *Teucrium chamaedrys*, MEDILUP: *Medicago lupulina*, LATHCIC: *Lathyrus cicero*, GALUCI: *Galium lucidum*, VICSAT: *Vicia sativa*, ERYNCAM: *Eryngium campestre*, THAPSIA: *Thapsia villosa*); Woody (THYVUL: *Thymus vulgaris*, GENSCO: *Genista scorpius*, JUNOXY: *Juniperus oxycedrus*, PINSIL: *Pinus sylvestris*, HELIMA: *Helianthemum marifolium*, ARGYZA: *Argyrolobium zanonii*, FUMAPRO: *Fumana procumbens*, ECHIOR: *Echinospartum horridum*, FUMERI: *Fumana ericifolia*, STADUB: *Staehelina dubia*, QUEILE: *Quercus ilex*, ONOFRU: *Ononis fruticosa*, GENHIS. *Genista hispanica*, DORPEN: *Dorycnium pentaphyllum*, THYMELEA: *Thymelaea pubescens*, VIBLAN: *Viburnum lantana*, ACEMON: *Acer monpessulanum*, JUNCOM: *Juniperus communis*, LONXYL: *Lonicera xylosteum*, ARCUVA: *Arctostaphylos uva-ursi*, LONETRU: *Lonicera etrusca*, AMEOVA: *Amelanchier ovalis*, CYTSES: *Cytisophyllum sessilifolium*, BUXSEM. *Buxus sempervirens*).

Discussion

Our study is one of the first to assess plant spatial diversity patterns and identify the factors that govern the structuring of plant species composition in human-modified and managed forests. The high contribution of β-diversity to total γ-diversity with β-diversity being significantly higher than expected by chance at all spatial scales, independent of the value of *q*, suggests that changes in species composition, rather than variation in species abundances, are primarily responsible for the spatial diversity patterns, which has been observed elsewhere (Devictor et al. 2010; Gossner et al. 2013). Furthermore, the results underscore the need to consider β-diversity at all spatial levels including fine spatial scales when making management plans.

In our study, among stands β-diversity was highest when all species were weighted equally (*q = 0*), which corresponds to a stronger influence of rare species (i.e., species with small populations). Thus, rare species appeared to have a heterogeneous distribution in the human-altered oak forests; probably, because their habitats had a clumped distribution (Gossner et al. 2013, Arroyo-Rodríguez et al. 2013). The high turnover of rare species among stands reflected a high level of interspecific competition (competition exclusion) at this spatial scale, which reduced sharply the abundance of rare species (most were forbs).

High environmental heterogeneity caused by differences in stand history and successional stage might have led to the high level of compositional differentiation among stands observed in our study. Indeed, the constrained ordination showed that the structural, spatial, and topographical characteristics of the forest stands explained a high proportion of the compositional variation. Stand age, the age structure distribution, *Q. faginea* abundance, stand size, and site conditions (i.e., slope) explained most of the spatial variation in composition, particularly, of forbs and woody species. Other studies have shown that forest structure (e.g., stand age, canopy cover), forest spatial attributes (e.g., patch size), and topographical conditions can have important roles in structuring the composition of plant communities in many types of forests worldwide (e.g., Aavik et al. 2009; Vockenhuber et al. 2011; Lomba et al. 2011), mainly, by controlling the availability of resources, particularly light and soil nutrients, and habitat conditions, particularly substrate, temperature, and pH (Härdtle et al. 2003; Aubert et al. 2004; Hart and Chen 2006).

At the finest spatial scale, among transects, the compositional differentiation was higher than expected, based on either rare or typical species, which reflects a degree of microhabitat heterogeneity within the same stand (Chávez and Macdonald 2012). The within-stand dissimilarity in canopy cover (differences in *Q. faginea* abundance among the transects) might be responsible for the microhabitat heterogeneity; i.e., heterogeneity can result from the creation of gaps in the canopy, which might increase the resources available at forest floor and, therefore, provide conditions for the development of species that have different resource requirements (Hart and Chen 2006; Fahey and Puettmann 2007; Chávez and Macdonald 2012), which can lead to relatively high rates of species turnover within the same stand.

Conclusions

The results of our study clearly demonstrate the importance of β-diversity components; in particular, among-stands and among-transects β-diversity, for overall diversity. Furthermore, the study has shown the importance of environment factors, particularly, those associated with historical land use-type and intensity in structuring β-diversity at multiple spatial scales. The approach used in the study has limitations because factors such as plant establishment and dispersion strategies might have had a significant effect on β-diversity in the human-modified and managed oak forests. That said, our study suggests that the maintenance of habitat heterogeneity at multiple spatial scales should be included in management plans designed to enhance plant diversity and related functions in human-altered forests. Furthermore, the use of silvicultural techniques that enhance canopy complexity might increase microhabitat diversity on the forest floor, which can increase within-stand species turnover and, in turn, augment plant diversity at fine scales.

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Appendix 1: The codes, scientific names, growth forms, abundance, and frequency (i.e., number of transects in which the species occurred) of the documented plant species in ten *Q. faginea* forest stands in the Central Pre-Pyrenees, Spain. Species are listed based on their abundance (lowest to highest)

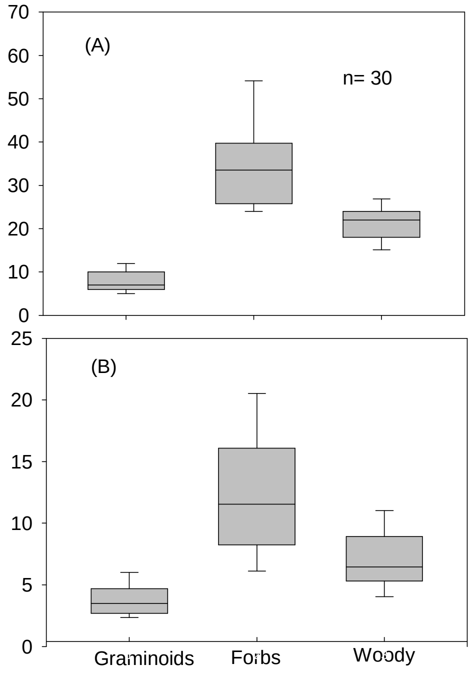
Code	Species scientific name	Growth form	Abundance (%)	Frequency (nº of transects)
ANVUL	*Anthyllis vulneraria*	Forb	0.001	1
ARATUR	*Arabis turrita*	Forb	0.001	1
ASPERULA	*Asperula aristata*	Forb	0.001	1
BROTEC	*Bromus tectorum*	Graminoid	0.001	1
CEPHARUB	*Cephalanthera rubra*	Forb	0.001	1
CLEVIT	*Clematis vitalba*	Woody	0.001	1
CROCNEV	*Crocus nevadensis*	Forb	0.001	1
DIANTPUN	*Dianthus pungens*	Forb	0.001	1
ECHIUM	*Echium vulgare*	Forb	0.001	1
ERYSIRUS	*Erysimum ruscinonense*	Forb	0.001	1
HELHAPE	*Helianthemum apenninum*	Forb	0.001	1
HIPCOM	*Hippocrepis comosa*	Woody	0.001	1
HYACINHIS	*Hyacinthoides hispanica*	Forb	0.001	1
LATHSPHA	*Lathyrus sphaericus*	Forb	0.001	1
LATHYSAX	*Lathyrus saxatilis*	Forb	0.001	1
NARCISS	*Narcissus sp.*	Forb	0.001	1
OPHRYS	*Ophrys sp.*	Forb	0.001	1
ORCHUS	*Orchis ustulata*	Forb	0.001	1
PLAMED	*Plantago media*	Forb	0.001	1
PRUNVU	*Prunella vulgaris*	Forb	0.001	1
RESEDA	*Reseda lutea*	Forb	0.001	1
SALVER	*Salvia verbenaca*	Forb	0.001	1
TAMUCOM	*Tamus communis*	Forb	0.001	1
VALERI	*Valerianella sp.*	Forb	0.001	1
VULUNI	*Vulpia unilateralis*	Graminoid	0.001	1
ALLIUM1	*Allium sp.*	Forb	0.003	1
AVENBRO	*Avenula bromoides*	Graminoid	0.003	1
CENTNIG	*Centaurea nigra*	Forb	0.003	1
LINUCAM	*Linum campanulatum*	Forb	0.003	1
PRUMA	*Prunus mahaleb*	Woody	0.003	1
SORARI	*Sorbus aria*	Woody	0.003	1
ARENAR	*Arenaria leptoclados*	Forb	0.003	2
CAMPANULA	*Campanula sp.*	Forb	0.003	2
CONOPOD	*Conopodium sp.*	Forb	0.003	2
HELLFOE	*Helleborus foetidus*	Forb	0.003	2
LONPERI	*Lonicera periclymenum*	Woody	0.003	2
PLATBIF	*Platanthera bifolia*	Forb	0.003	2
GENIS	*Genista cinerea*	Woody	0.004	1
GEUSYLV	*Geum sylvaticum*	Forb	0.004	1
LATHAPH	*Lathyrus aphaca*	Forb	0.004	1
MEREMON	*Merendera montana*	Forb	0.004	1
VERBA	*Verbascum lychnitis*	Forb	0.004	1
BISCUTE	*Biscutella valentina*	Forb	0.004	2
LINVIS	*Linum viscosum*	Forb	0.004	2
VERORSI	*Veronica orsiniana*	Forb	0.004	2
THYMPUB	*Thymelaea pubescens*	Woody	0.004	3
CEPHALEU	*Cephalaria leucantha*	Forb	0.006	1
CRUCAN	*Crucianella angustifolia*	Forb	0.006	1
PRUNHYS	*Prunella hyssopifolia*	Forb	0.006	1
ALYSALY	*Alyssum alyssoides*	Forb	0.006	2
BRASYL	*Brachypodium sylvaticum*	Graminoid	0.006	2
GERAROB	*Geranium robertianum*	Forb	0.006	2
ORCHY	*Orchis sp.*	Forb	0.006	3
TARAXA	*Taraxacum sp.*	Forb	0.006	3
BERVU	*Berberis vulgaris*	Woody	0.007	2
SORBUS	*Sorbus sp.*	Woody	0.007	2
ORIVUL	*Origanum vulgare*	Forb	0.007	3
ARRHENATALB	*Arrhenatherum album*	Graminoid	0.009	2
DIGIPUR	*Digitalis purpurea*	Forb	0.009	2
PRUNELLA	*Prunella sp.*	Forb	0.009	2
SIBERHIR	*Sideritis hirsuta*	Woody	0.009	2
TRIPRA	*Trifolium pratense*	Forb	0.009	2

Code	Species scientific name	Growth form	Abundance (%)	Frequency (nº of transects)
MELICI	*Melica ciliata*	Graminoid	0.009	3
CENTALB	*Centaurea alba*	Forb	0.010	2
HELVIO	*Helianthemum violaceum*	Forb	0.010	2
CIRSITUB	*Cirsium tuberosum*	Forb	0.010	3
BLAKPER	*Blakstonia perfoliata*	Forb	0.010	6
DIANT	*Dianthus benearnensis*	Forb	0.010	6
POLYMONS	*Polygala monspeliaca*	Forb	0.012	2
ARENASER	*Arenaria serpyllifolia*	Forb	0.012	4
LEUCA	*Leucanthemum pallens*	Forb	0.012	4
LEUCANTEMUN	*Leucanthemun sp.*	Forb	0.012	4
EUCHA	*Euphorbia characias*	Forb	0.012	5
CREPVIS	*Crepis vesicaria*	Forb	0.013	2
PINNIG	*Pinus nigra*	Woody	0.013	2
SORAUC	*Sorbus aucuparia*	Woody	0.013	3
SILEVU	*Silene vulgaris*	Forb	0.013	4
ARABIS	*Arabis sp.*	Forb	0.013	5
RANUREP	*Ranunculus repens*	Forb	0.015	2
CHEIRINT	*Cheirolophus intybaceus*	Woody	0.015	4
PAROKAP	*Paronychia kapela*	Forb	0.015	4
HELISTO	*Helichrysum stoechas*	Woody	0.015	5
PRUNLAC	*Prunella laciniata*	Forb	0.015	5
FI	*Festuca indigesta*	Graminoid	0.016	2
INUMON	*Inula montana*	Forb	0.016	3
EPIPAC	*Epipactis sp.*	Forb	0.016	7
GERADIS	*Geranium dissectum*	Forb	0.018	3
ONOSP	*Ononis spinosa*	Forb	0.018	3
SCABAT	*Scabiosa atropurpurea*	Forb	0.018	4
CLINOVU	*Clinopodium vulgare*	Forb	0.018	5
BRIZA	*Briza media*	Graminoid	0.018	6
HIEMURO	*Hieracium murorum*	Forb	0.018	6
PHLEPRA	*Phleum pratense*	Forb	0.019	2
THYFONT	*Thymus fontqueri*	Forb	0.019	2
CEPHALARIS	*Cephalaria sp.*	Forb	0.019	4
TRAPOG	*Tragopogon sp.*	Forb	0.019	4
VICSEPI	*Vicia sepium*	Forb	0.019	7
BRADIS	*Brachypodium distachyon*	Graminoid	0.021	3
CORSCO	*Coronilla scorpioides*	Forb	0.021	3
TRINIGLA	*Trinia glauca*	Forb	0.021	6
ACEMON	*Acer monpessulanum*	Woody	0.022	3
HYPEPER	*Hypericum perforatum*	Forb	0.022	4
TRIFOL	*Trifolium sp.*	Forb	0.022	5
ONONIS	*Ononis sp.*	Forb	0.024	5
HELINUM	*Helianthemum nummularium*	Woody	0.024	7
SCABIOSA	*Scabiosa columbaria*	Forb	0.024	7
TEUCAP	*Teucrium capitatum*	Forb	0.024	11
AGROCA	*Agrostis capillaris*	Graminoid	0.025	1
LATHYLIN	*Lathyrus linifolius*	Forb	0.025	2
LONETRU	*Lonicera etrusca*	Woody	0.025	2
VICILATH	*Vicia lathyroides*	Forb	0.025	2
VICCRA	*Vicia cracca*	Forb	0.027	3
MEDI	*Medicago sativa*	Forb	0.027	4
STIPERIO	*Stipa eriocaulis*	Graminoid	0.027	4
AREMON	*Arenaria montana*	Forb	0.027	6
QUECO	*Quercus coccifera*	Woody	0.028	4
CEPHALB	*Cephalanthera alba*	Forb	0.028	5
ERYGIU	*Eryngium bourgatii*	Forb	0.028	6
PRIMULA	*Primula sp.*	Forb	0.028	6
ASTRAMON	*Astragalus monspessulanus*	Forb	0.028	7
ACHMIL	*Achillea millefolium*	Forb	0.030	1
PLANTAG	*Plantago sp.*	Forb	0.030	2
XERINA	*Xeranthemum inapertum*	Forb	0.030	3
CORSAN	*Cornus sanguinea*	Woody	0.031	4
STACHREC	*Stachys recta*	Forb	0.031	4
RANUNC	*Ranunculus sp.*	Forb	0.031	5
SANCHA	*Santolina chamaecyparissus*	Forb	0.031	7
ASPCY	*Asperula cynanchica*	Forb	0.031	8
ASTRA	*Astragalus sp.*	Forb	0.033	5
PLANLAN	*Plantago lanceolata*	Forb	0.034	3
GALVER	*Galium verum*	Forb	0.036	4
HELHIR	*Helianthemum hirtum*	Woody	0.036	5
LOTUSCOR	*Lotus corniculatus*	Forb	0.036	6
CONVCANT	*Convolvulus cantabrica*	Forb	0.039	6

Code	Species scientific name	Growth form	Abundance (%)	Frequency (nº of transects)
ARISTOPIS	*Aristolochia pistolochia*	Forb	0.039	13
COLUTARB	*Colutea arborescens*	Woody	0.040	3
LINUNAR	*Linum narbonense*	Forb	0.043	10
POLYCAL	*Polygala calcarea*	Forb	0.045	6
VIBLAN	*Viburnum lantana*	Woody	0.046	6
CRUCIATA	*Cruciata glabra*	Forb	0.048	4
LONXYL	*Lonicera xylosteum*	Woody	0.048	8
MEDILUP	*Medicago lupulina*	Forb	0.049	3
LATHYFIL	*Lathyrus filiformis*	Forb	0.051	7
CATACA	*Catananche caerulea*	Forb	0.052	7
THYMPRA	*Thymus praecox*	Forb	0.054	7
LEUZEA	*Leuzea conifera*	Forb	0.054	12
RHAALA	*Rhamnus alaternus*	Woody	0.057	3
LAVANG	*Lavandula angustifolia*	Woody	0.057	6
SCA	*Scabiosa sp.*	Forb	0.057	11
VICSAT	*Vicia sativa*	Forb	0.061	3
LAVAND	*Lavandula latifolia*	Woody	0.064	11
TANACOR	*Tanacetum corymbosum*	Forb	0.067	18
SEDUAL	*Sedum album*	Forb	0.070	5
SAPOCY	*Saponaria ocymoides*	Forb	0.075	11
SCORZO	*Scorzonera aristata*	Forb	0.078	10
LITFRU	*Lithodora fruticosa*	Woody	0.084	8
ANTHELI	*Anthericum liliago*	Forb	0.087	6
KNAUTIA	*Knautia arvensis*	Forb	0.091	9
RHASAX	*Rhamnus saxatilis*	Woody	0.093	10
SANGUIMI	*Sanguisorba minor*	Forb	0.094	16
JUNPHO	*Juniperus phoenicea*	Woody	0.105	5
POTENEU	*Potentilla neumanniana*	Forb	0.108	7
SEDUSE	*Sedum sediforme*	Forb	0.108	18
THESDIV	*Thesium divaricatum*	Forb	0.111	17
CORIS	*Coris monspeliensis*	Forb	0.115	16
POA	*Poa angustifolia*	Graminoid	0.118	12
VIO	*Viola sp.*	Forb	0.120	7
HEDERA	*Hedera helix*	Forb	0.124	3
ERYNCAM	*Eryngium campestre*	Forb	0.127	7
STADUB	*Staehelina dubia*	Woody	0.127	18
POLYGAL	*Polygala alpestris*	Forb	0.132	15
ARRHENAT	*Arrhenatherum elatius*	Graminoid	0.139	11
GLOBVU	*Globularia vulgaris*	Forb	0.141	10
LATHCIC	*Lathyrus cicera*	Forb	0.145	7
MEDICA	*Medicago minima*	Forb	0.145	10
THAPSIA	*Thapsia villosa*	Forb	0.156	8
GALIUM	*Galium sp.*	Forb	0.162	12
CERASPUM	*Cerastium pumilum*	Forb	0.165	2
VICINCA	*Vicia incana*	Forb	0.166	8
ONONAT	*Ononis natrix*	Forb	0.178	11
LINOSUB	*Linum suffruticosum*	Forb	0.184	21
CYTSES	*Cytisophyllum sessilifolium*	Woody	0.185	10
HEPAT	*Hepatica nobilis*	Forb	0.191	11
EUPHSE	*Euphorbia serrata*	Forb	0.200	18
COREME	*Coronilla emerus*	Forb	0.206	10
BUPLE	*Bupleurum ranunculoides*	Forb	0.217	5
FUMAPRO	*Fumana procumbens*	Woody	0.230	9
VIOLA	*Viola alba*	Forb	0.232	26
LIGVUL	*Ligustrum vulgare*	Woody	0.236	13
FGL	*Festuca glauca*	Graminoid	0.262	3
DACT	*Dactylis glomerata*	Graminoid	0.271	13
HIERACI	*Hieracium pilosella*	Forb	0.271	25
ONOBRY	*Onobrychis viciifolia*	Forb	0.278	17
POTE	*Potentilla sp.*	Forb	0.281	23
THALTUB	*Thalictrum tuberosum*	Forb	0.283	10
RUBUS	*Rubus sp.*	Woody	0.284	18
HIPPO	*Hippocrepis ciliata*	Forb	0.287	27
AVENULA	*Avenula pratensis*	Graminoid	0.319	14
PRUSPI	*Prunus spinosa*	Woody	0.347	15
QUEILE	*Quercus ilex*	Woody	0.350	13
ROSA	*Rosa sp.*	Woody	0.365	24
TEUPY	*Teucrium pyrenaicum*	Forb	0.375	16
GALUCI	*Galium lucidum*	Forb	0.407	15
ARGYZA	*Argyrolobium zanonii*	Woody	0.407	24
HELIMA	*Helianthemum marifolium*	Woody	0.414	23
GALEST	*Galium estebanii*	Forb	0.437	21

Code	Species scientific name	Growth form	Abundance (%)	Frequency (nº of transects)
FUMERI	*Fumana ericifolia*	Woody	0.459	13
BRAPH	*Brachypodium phoenicoides*	Graminoid	0.468	4
PSBI	*Psoralea bituminosa*	Forb	0.470	22
CRAMON	*Crataegus monogyna*	Woody	0.471	27
CORMIN	*Coronilla minima*	Woody	0.495	18
KOELERVAL	*Koeleria vallesiana*	Graminoid	0.510	26
ONOFRU	*Ononis fruticosa*	Woody	0.536	10
THALIC	*Thalictrum alpinum*	Forb	0.540	20
CARDUS	*Carduus sp.*	Forb	0.554	2
GLOBNU	*Globularia nudicaulis*	Forb	0.576	14
JUNCOM	*Juniperus communis*	Woody	0.706	26
BUGRA	*Bupleurum rigidum*	Forb	0.742	17
PINSIL	*Pinus sylvestris*	Woody	1.016	18
BRARE	*Brachypodium retusum*	Graminoid	1.035	13
TEUCHA	*Teucrium chamaedrys*	Forb	1.162	30
ARCUVA	*Arctostaphylos uva-ursi*	Woody	1.200	16
JUNOXY	*Juniperus oxycedrus*	Woody	1.248	25
CAREX	*Carex sp.*	Graminoid	1.536	10
GENHIS	*Genista hispanica*	Woody	1.750	17
THYVUL	*Thymus vulgaris*	Woody	1.984	28
ECHIOR	*Echinospartum horridum*	Woody	2.017	13
AMEOVA	*Amelanchier ovalis*	Woody	2.338	29
DORPEN	*Dorycnium pentaphyllum*	Woody	2.536	29
BROMERE	*Bromus erectus*	Graminoid	2.557	17
RUBPER	*Rubia peregrina*	Forb	3.424	30
CAREXFLA	*Carex flacca*	Graminoid	3.539	19
FR	*Festuca rubra*	Graminoid	3.673	30
GENSCO	*Genista scorpius*	Woody	4.132	30
CAREXHAL	*Carex halleriana*	Graminoid	5.215	19
APHMON	*Aphyllanthes monspeliensis*	Forb	7.839	30
BRAPIN	*Brachypodium pinnatum*	Graminoid	11.700	30
BUXSEM	*Buxus sempervirens*	Woody	19.664	30

Appendix 2: species richness (Hill Index with exponent q = 0) (A) and exponential of Shannon entropy (Hill index with exponent q = 1) (B) for plant ecological groups found in the *Q. faginea* forest stands in the Central Pre-Pyrenees, Spain. Boxes depict the 25th and 75th percentiles, and whiskers represent the 5th and 95th percentiles



Ecosystems (under review)

CAPITULO 6

The importance of historical land use in shaping contemporary patterns of plant community in Mediterranean forests

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Abstract

Although plant diversity and the compositional differences between primarily old growth forests and secondary growth forests, and between managed and unmanaged forests have been well studied, few studies have compared formerly managed forests and secondary growth forests, particularly, in Mediterranean environments. This study compared the plant diversity and composition of abandoned coppices and secondary growth stands in oak forests (primarily, *Quercus faginea*) in the Central Pre-Pyrenees, Spain. In addition, plant diversity and composition were assessed based on stand age (young vs. old) and the age structure of the stand (even-aged vs. uneven-aged). Furthermore, we examined the effect of canopy cover (%) on the variation of plant diversity and composition. The findings revealed a significant compositional differentiation between stands and a significant effect of canopy cover on species composition. The compositional variation is due to differences in the richness and evenness of plant species of different habitat preferences (i.e. early-, mid-, and late-successional species). Historical land management has led to increasing compositional divergences among oak stands and the loss of forest specialists.

Key words: Species composition, Evenness, Richness, Secondary forests, Managed forests, Plant diversity.

Introduction

Most of today's unmanaged Mediterranean forests were once under intensive management (Barbero *et al.* 1990; Bengtsson *et al.* 2000; Vanbergen *et al.* 2005). Since antiquity, those forests have been subject to extensive clearance, and the rate of loss accelerated in the 18th and 19th centuries (Paillet *et al.* 2010). In Euro-Mediterranean countries in particular, many of the previously spread forests were coppiced for timber and firewood, which created coppices that differed in their management intensity and time since coppicing had ceased. In the late 19th and 20th centuries, however, changes in socioeconomic structures and production systems resulted in the abandonment and subsequent afforestation of the poorest arable lands (Mather, Fairbairn & Needle 1999; Verheyen *et al.* 1999; Sciama *et al.* 2009). In many regions, several phases of abandonment and forest encroachment occurred, which created a complex pattern of forest stands that are at different phases of succession (Flinn & Vellend 2005; Hermy & Verheyen 2007; Matuszkiewicz *et al.* 2013). In Spain, as in many other European countries, the largest increase in forest cover on abandoned lands that had been used for agriculture occurred in the second half of the 20th century (Lasanta *et al.* 2009). In such human-modified or formerly managed forests, the characteristics of the stands are strongly influenced by prior land use type and intensity in the case of secondary forest stands (Gehring, Denich & Vlek 2005; Carson & Schnitzer 2008) and historical management type in the case of abandoned coppice stands (Smith *et al.* 2008; Duguid & Ashton 2013). Furthermore, the historical logging and agriculture might have affected the diversity and composition of the plant communities in these forests (Flinn & Vellend 2005; Hermy & Verheyen 2007; Berhane, Totland & Moe 2013). Understanding the long-term consequences of past land-use is critical, not only to inform conservation biologists about existing plant communities, but also to predict the response of the communities to future disturbance and environmental change.

There is an extensive literature on plant diversity and compositional differences between primarily old growth forests and secondary growth forests (e.g. Sciama *et al.* 2009; Baeten *et al.* 2010; De Frenne *et al.* 2010; Matuszkiewicz *et al.* 2013) as well as between managed and unmanaged forests (e.g. Halpern, 1995; Okland, Rydgren & Halvorsen, 2003; Paillet et al., 2010). Comparative studies of formerly managed forests and secondary growth forests in Mediterranean environments are rare. Studies have emphasized the importance of anthropogenic disturbances in fostering the establishment of early-successional species to the disadvantage of forest specialists (Seiwa *et al.* 2012). In a recent review, Duguid & Ashton (2013) found that type of forest management (even-aged vs. uneven-aged) had no clear pattern predicting plant diversity response; however, other studies found that uneven-aged stands had the capacity to maintain high plant diversity (e.g. Smith *et al.* 2008).

Our study was conducted in mountain oak forests in the Central Pre-Pyrenees that included secondary growth stands and formerly managed stands that differed in their structural properties. The main objective was to investigate the effects of the previous forest management and agricultural land use on contemporary forest plant communities. Specifically, we addressed the following questions: Do stands at different successional stages and that had different land use histories differ in their species composition? Do species richness and evenness, of early-, mid-, and late-successional species differ among stands at different successional stages or differ in their land use history?

Methods

Study area

The study was conducted within a 1363-km^2 area in the Central Pre-Pyrenees, Spain, (between 42.32 N and 42.11 N, and 0.31 W and 0.04 W) (Fig. 1). The lithology is mostly conglomerate, limestone, marl, and sandstone developed on Eocene flysch sedimentary formations. The climate is transitional sub-Mediterranean; i.e., influenced by continental effects from the north and by milder Mediterranean conditions that prevail from the south (i.e., the Ebro Basin). The mean annual precipitation is 1317 ± 302 mm (1915-2005) and mean annual temperature is 11.5 ± 2.8º C (1910-2005) (Kouba et al. 2012).

The oak forests (mainly *Quercus faginea*) of the Central Pre-Pyrenees are a mosaic of stands that differ in their structure and history. Based on historical land use, those semi-deciduous oak forests were two types: abandoned coppice stands (coppices that differed in historical coppicing intensities and time since management abandonment) and secondary growth stands (most of which were established on abandoned farmlands, primarily, in the second half of the 20th century; Kouba & Alados 2012). The overstorey canopy of those semi-deciduous oak stands was mostly *Q. faginea* interspersed with some scattered pines (*Pinus sylvestris* and *P. nigra*) and evergreen oak (*Q. ilex* subsp. *ballota*). The understory comprised shrubs (*Q. coccifera*, *Buxus sempervirens*, *Genista scorpius*, *Juniperus communis*), forbs (*Aphyllanthes monspeliensis*, *Arenaria montana*, *Achillea millefolium*), and graminoids (*Brachypodium pinnatum*, *Carex halleriana*, *Festuca rubra*, *Carex flacca*, *Bromus erectus*).

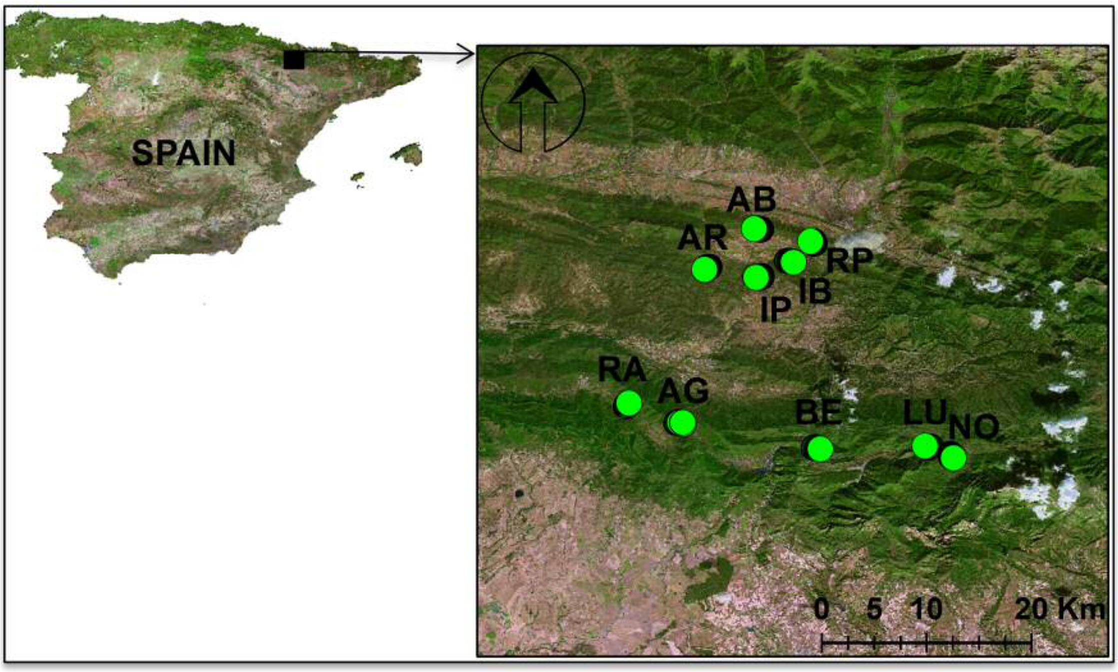

Fig. 1 Geographical setting of the study area in Spain (left panel), and the locations of the sampled stands (right panel) in the Central Pre-Pyrenees.

Data collection

Within the study area, ten *Q. faginea*-dominated stands that were at different successional stages and had different land-use histories were selected based on historical land-use data (see Kouba & Alados 2012; Kouba *et al.* 2012, Table 1). In 2009 and 2010, during the period of peak growth (May and June), the vascular plant species were surveyed in the ten stands. Within each stand, three 500-m linear transects (30 transects in total) were established (hereafter, floristic transects). To estimate plant abundance and richness within each transect, we used the Point-Intercept Method (Goodall 1952), which involves recording, at 40-cm intervals, the identity of all individuals that are in contact with a vertical nail (Alados *et al.* 2009). We recorded all of the vascular plants that touched the nail and any overstorey species (including *Q. faginea*) that was above the nail. Plant species that could not be identified with certainty in the field were collected, pressed, and brought to the laboratory for identification by botanists. Species that have traits that make them difficult to distinguish were identified to genus, only. Plant nomenclature followed *Flora Ibérica* (Castroviejo *et al.* 1986-2012). In each transect, canopy cover (CANCOV) was estimated based on the relative abundance (%) of woody species (include trees and large shrubs) that were ≥ 1.5 m tall. For each stand, we estimated the age of ~ 40 trees (for details on age estimations, see Kouba *et al.* 2012), calculated mean tree-age and the coefficient of variation of tree-age. Two binary variables were derived from the age data: AGE (young vs. old stands) and CVAGE (even-aged vs. uneven-aged stands). Forest type (FORTYPE; secondary growth stands vs. abandoned coppice stands) of each stand was based on observations in the field (see Table 1).

Table 1 Characteristics of the sampled *Q. faginea* stands. Stand characteristics include forest type (FORTYPE), mean stand tree age (AGE), coefficient of variation of stand age (CVAGE), and canopy cover (CANCOV). SF: secondary growth stand, CS: abandoned coppice stand, EA: even-aged stand, UEA: uneven-aged stand.

Abbreviation	Location	FORTYPE	AGE (year)	CVAGE (%)	CANCOV (%)[a]
AB	Abena	SF	Old (50)	EA (19)	47.7, 49.3, 48.4
AR	Ara	CS	Young (35)	EA (17)	39.8, 29.3, 29.6
AG	Arguis	CS	Old (50)	EA (10)	38.9, 47.1, 45.4
BE	Belsué	CS	Young (40)	UEA (43)	43.9, 47.2, 41.0
IB	Ibort	CS	Old (63)	EA (17)	75.4, 68.6, 63.6
IP	Ipies	CS	Old (64)	EA (15)	08.3, 15.9, 39.9
LU	Lucera	CS	Young (39)	EA (12)	53.5, 45.6, 60.9
NO	Nocito	SF	Old (56)	UEA (47)	50.4, 36.6, 44.4
RP	Rapun	CS	Old (69)	EA (9)	44.6, 46.6, 49.6
RA	Rasal	SF	Young (31)	UEA (31)	46.0, 41.2, 29.3

[a] Canopy cover (CANCOV) is reported for the three transects of each stand

Grouping of species by successional status

Ecological groups can help to explain the mechanisms that underlie the tree species-plant diversity relationship (Barbier, Gosselin & Balandier 2008). In our study, species were clustered within one of three ecological groups based on species habitat preference and successional status (Ramovs & Roberts 2005; Seiwa *et al.* 2012): Early-successional species (ES), are defined as a shade-intolerant pioneer species that reach maximum abundance in open-canopy and disturbed areas; Intermediate-successional species (IS; i.e., species that occupy young to mature, open- or closed-canopy forests, but not excessively disturbed habitats); and late-successional species (LS; i.e., shade-tolerant species that reach maximum abundance in mature, closed-canopy, forest interiors).

Statistical analyses

To assess the effects of the explanatory variables (AGE, CVAGE, FORTYPE, and CANCOV) on species composition, we used a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001), which is a multivariate, nonparametric analogue of the univariate analysis of variance (MANOVA). PERMANOVA was run on the species abundance data (all species included) using Bray-Curtis distance measure, and 9999 permutations. To identify patterns in the compositional variation among stand types (i.e., young vs. old, even-aged vs. uneven-aged, secondary growth vs. abandoned coppice stands), we used unconstrained ordination, non-metrical multidimensional scaling (NMDS). In addition, to test whether there was a gradient, canopy cover was plotted as a smooth surface in an ordination diagram.

Differences in species richness and species evenness among stand types (i.e., young vs. old, even-aged vs. uneven-aged, secondary growth vs. abandoned coppice stands) and the relationship between these two measures of diversity and canopy cover were analyzed using ANCOVA, both for all species combined and for each ecological group. To account for spatial dependencies, stand location was included as a random factor. Normality and homogeneity of variance were tested by examining the residuals versus the fitted plots and the normal *q*-*q* plots of the models. The appropriate transformations were used when required.

Indicator species analyses were used to assess the strength of the association between plant species and the following forest classes that resulted from the interaction AGE × CVAGE × FORTYP: old even-aged secondary growth stands (old_even_sf), old even-aged coppice stands (old_even_cs), old uneven-aged secondary growth stands (old_uneven_sf), young even-aged coppice stands (young_even_cs), young uneven-aged secondary growth stands (young_uneven_sf), and young uneven-aged coppice stands (young_uneven_cs). The indicator species of each forest class were identified based on the indicator value (IndVal; Dufrene & Legendre 1997), which was calculated using the Multilevel Pattern Analysis Method (De Cáceres, Legendre & Moretti 2010).

All of the statistical analyses were performed using R software (R Development Core Team 2013) packages. The PERMANOVA and the NMDS were performed using the '*vegan*' package (Oksanen *et al.* 2012), the ANCOVA was performed using the '*nlme*' package (Pinheiro *et al.* 2013), and the Indicator Species Analysis was performed using the '*indicspecies*' package (De Cáceres & Legendre 2009).

Results

Species frequency and abundance

In all sampled oak stands most (56%) of the 238 vascular plant species recorded were ES species, followed by IS species (26%), and LS species (18%). *Genista scorpius* (ES), *Teucrium chamaedrys* (ES), *Thymus vulgaris* (ES), *Buxus sempervirens* (IS), *Festuca rubra* (IS), *Amelanchier ovalis* (IS), *Aphyllanthes monspeliensis* (IS), *Brachypodium pinnatum* (IS), and *Rubia peregrina* (LS) were the most frequent species (found in all transects). *Buxus sempervirens* (19.17%), *Brachypodium pinnatum* (13.38), *Aphyllanthes monspeliensis* (8.93%), *Carex halleriana* (5.95%, IS), *Genista scorpius* (4.50%), *Carex flacca* (4.10%, IS), and *Festuca rubra* (3.61%) were the most abundant species, which comprising 60% of all individuals recorded.

Factors that affected plant community composition

The PERMANOVA revealed that stand types (i.e., young vs. old, even-aged vs. uneven-aged, secondary growth vs. abandoned coppice stands) differed significantly in their plant species composition. In addition, the canopy cover significantly influenced the composition of the plant communities.

Table 2 Non-parametric MANOVA test for the effects of stand age (AGE), age structure of stand (CVAGE), forest type (FORTYPE), and canopy cover (CANCOV) on the composition of plant species found in ten *Q. faginea* forest stands. R^2 is the variance explained by each variable.

	F	R^2	*P*
AGE	2.6	0.072	<0.001
CVAGE	2.6	0.071	0.004
FORTYPE	3.8	0.152	<0.001
CANCOV	7.6	0.110	<0.001

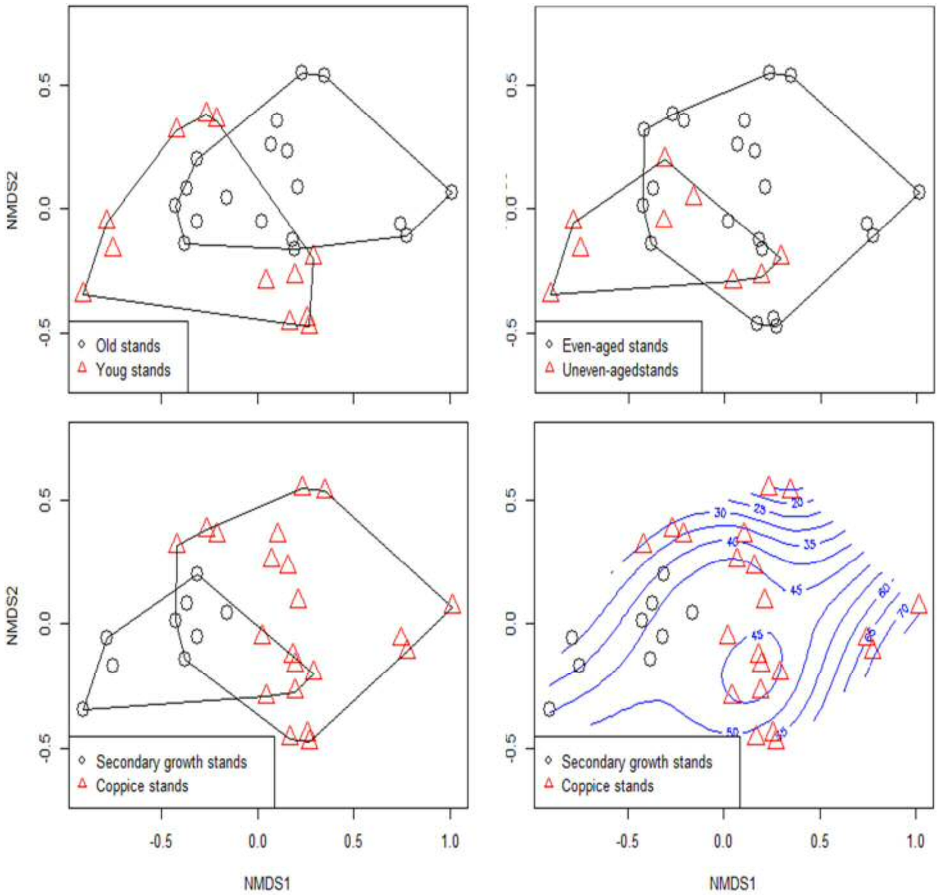

Fig. 2 Nonparametric multidimensional scaling (NMDS) ordinations (final stress: 0.18) showing the grouping of floristic transects by stand types: young vs. old stands, even aged vs. uneven aged stands, secondary forest stands vs. abandoned coppice stands. The canopy cover is plotted in the ordination diagram as smooth surface (below right plot).

The explanatory variables explained almost 40% of the variation in species composition (Table 2). “FORTYPE” explained the largest proportion (15.2%) of the variation in species composition, followed by “CANCOV”, which explained 11% of the variance. “AGE” and “CVAGE” each explained ~ 7% of the variance. The NMDS analysis revealed the grouping of transects by stand type in the ordination space (Fig. 2).

Factors that affected the richness and evenness of plant species of different habitat preference

Table 3 ANCOVA test for the effects of explanatory variables on plant species diversity (richness and evenness) for all vascular plant species (AS) and by their habitat preference (ES: early successional species; IS: intermediate successional species; LS: late successional species). Significant effects (P < 0.05) are shown in bold. R^2 is the variance explained by each significant explanatory variable.

		Richness			Evenness		
		R^2	F	P	R^2	F	P
AS	AGE	**0.150**	**12.8**	**<0.001**	-	0.08	0.770
	CVAGE	**0.107**	**9.2**	**0.006**	-	0.01	0.980
	FORTYPE	**0.291**	**25.0**	**<0.001**	-	0.00	0.459
	CANCOV	**0.160**	**13.7**	**<0.001**	**0.324**	**11.61**	**0.004**
ES	AGE	**0.150**	**16.04**	**<0.001**	-	2.68	0.123
	CVAGE	**0.146**	**15.60**	**<0.001**	-	3.25	0.091
	FORTYPE	**0.326**	**34.72**	**<0.001**	-	0.00	0.985
	CANCOV	**0.156**	**16.98**	**<0.001**	**0.291**	**11.88**	**0.003**
IS	AGE	-	0.17	0.904		0.09	0.764
	CVAGE	**0.122**	**5.35**	**0.029**		0.01	0.981
	FORTYPE	**0.197**	**8.61**	**0.007**		1.04	0.316
	CANCOV	**0.150**	**6.53**	**0.017**	**0.324**	**10.11**	**0.002**
LS	AGE	-	0.4	0.538	-	0.97	0.340
	CVAGE	-	0.0	0.962	**0.293**	**10.2**	**0.003**
	FORTYPE	-	1.6	0.219	-	1.03	0.322
	CANCOV	-	0.7	0.412	-	0.21	0.648

All four of the explanatory variables explained a significant amount of the variation in species richness and, collectively, they explained >70% of the total variance (Table 3). Based on the variance explained by each variable, “FORTYP” was the most important variable followed by “CANCOV”, “AGE”, and “CVAGE” (Table 3). Secondary growth stands that had been established in abandoned terraces, young stands, and uneven-aged stands had the highest species richness (Fig. 3), and “CANCOV” were negatively correlated (Fig. 4). The same trends in species richness were apparent among ES and IS species (Table 3; Figs. 3 and 4), although the effect of “AGE” among IS species was not statistically significant

(Table 3). None of the explanatory variables had a significant effect on the richness among LS species (Table 3). Among ES and IS species, evenness was affected by "CANCOV" and, among LS species, "CVAGE" had a significant effect on species evenness (Table 3). Species evenness was positively correlated with extent of canopy cover among ES species, but negatively correlated with extent of canopy cover among IS species (Fig. 4). Species evenness among LS species was significantly higher in even-aged stands than it was in uneven-aged stands (Fig. 3).

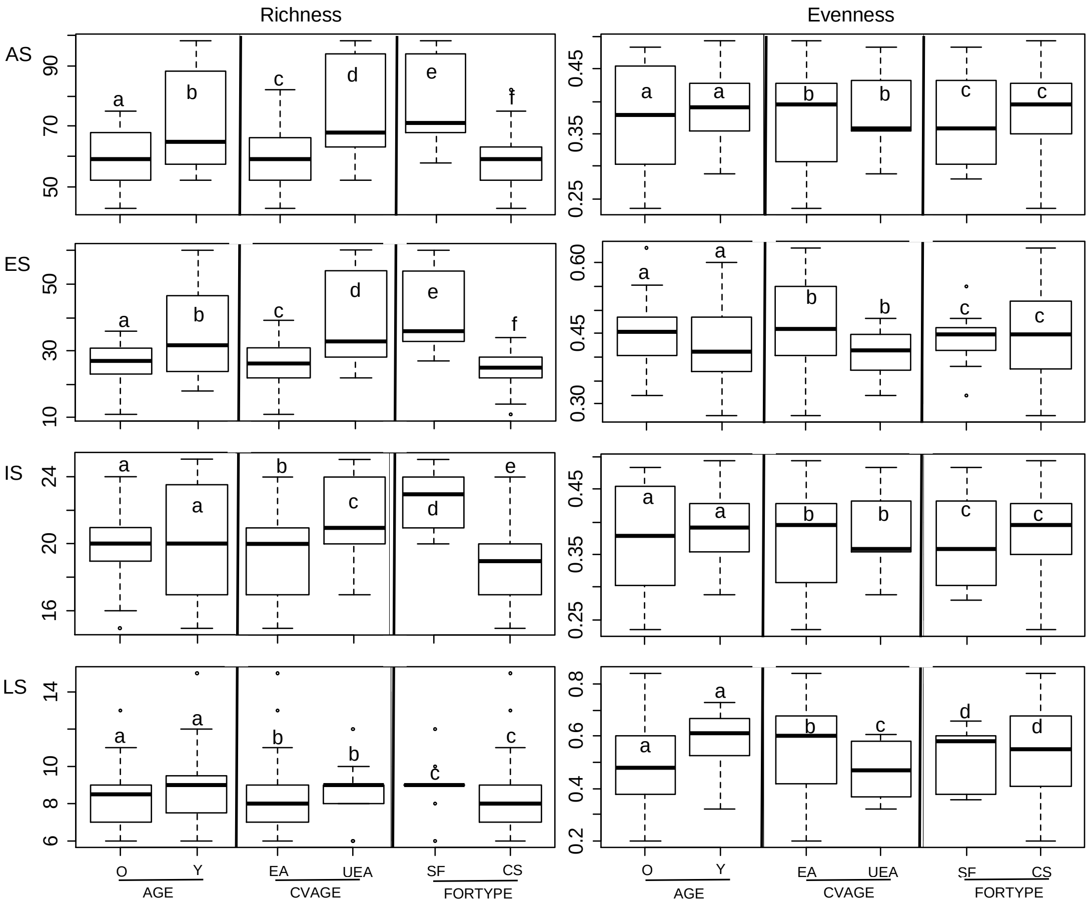

Fig. 3 Richness and evenness of all vascular plant species (AS) and species by successional status (ES: early successional species; IS: intermediate successional species; LS: late successional species) as influenced by stand age (O: old stands; Y: young stands), age structure of stand (EA: even-aged stands; UEA: Uneven-aged stands), and forest type (SF: secondary forest stands; CS: coppice stands). Boxes with same letter were not significantly different based on ANCOVA.

Indicator species and forest classes

Overall, 69 species were significant ($p < 0.05$) indicator species and most (39 pecies) were indicative of young uneven-aged coppice stands (Table 4). Fewer significant indicator species were found in old even-aged coppice stands (1), old even-aged secondary growth stands (6), old uneven-aged secondary growth stands (7), young even-aged coppice stands (4), and young uneven-aged secondary growth stands (12). ES indicator species occurred in almost all of the forest classes, but most were in young uneven-aged abandoned coppice stands. IS indicator species occurred in all forest classes, except old even-aged abandoned coppice stands. A few LS species were significant indicator species, and most occurred in old-uneven-aged secondary forest stands and young-uneven-aged coppice stands.

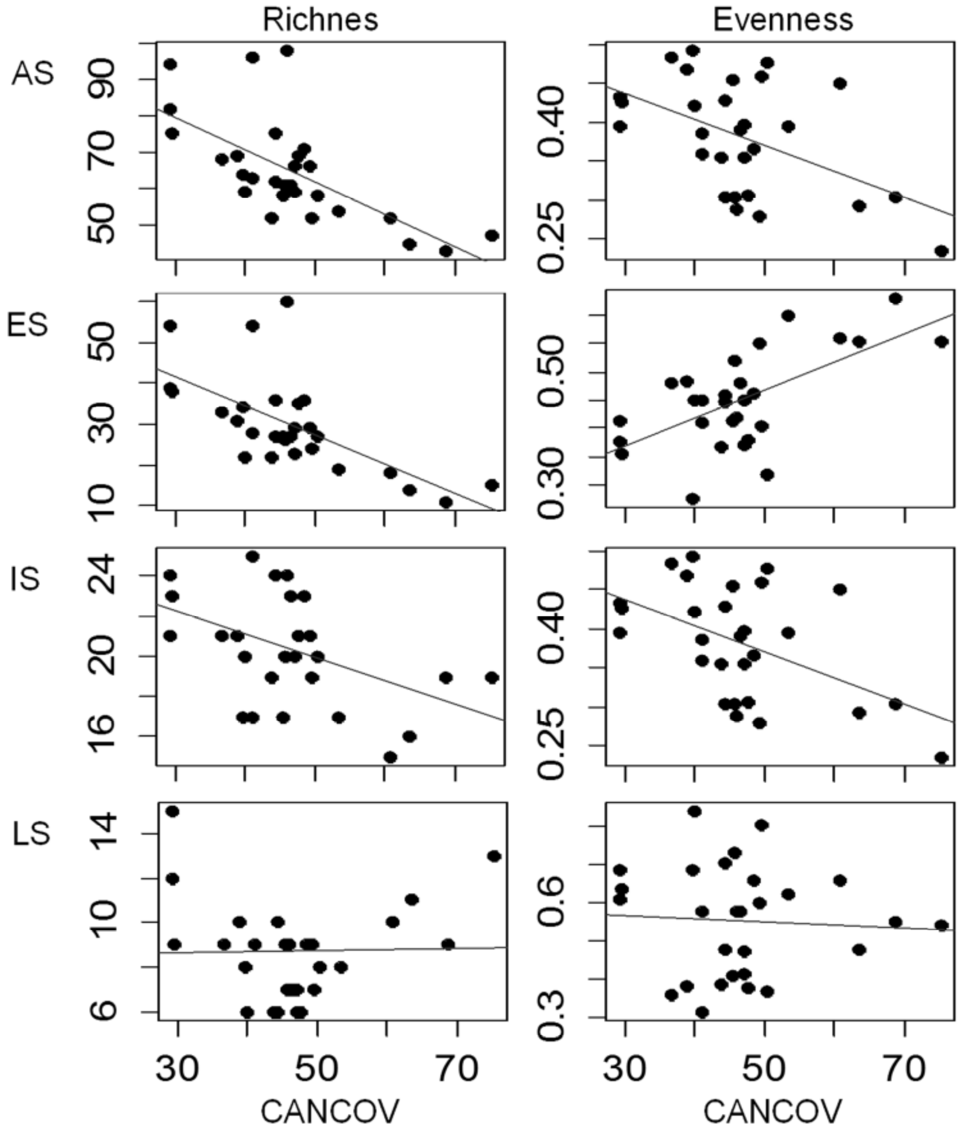

Fig. 4 Canopy cover (CANCOV) and the richness and evenness of all vascular species (AS), early successional species (ES), intermediate successional species (IS), and late successional species (LS).

Discussion

Our study has demonstrated the importance of previous agricultural land use and forest management type in the development of plant species assemblages and the richness and evenness of plant species of different habitat preference. Thus, human-induced disturbances can have a strong influence on plant communities in forest ecosystems, which has been reported in other studies (e.g., Flinn & Vellend 2005; Hermy & Verheyen 2007; Baeten *et al.* 2010).

In our study, the small number of ES species in old oak stands was the main reason for the differences in the plant species composition of young and old stands. Similarly, the absence of a substantial proportion of the ES and IS species in coppice stands and even-aged stands was responsible for the dissimilarities in plant community composition between secondary growth/ coppice stands and even-aged/uneven-aged stands. In addition, the changes in the relative abundance of LS species found in this study might have contributed to the compositional differences between even-aged and uneven-aged stands.

Overall species richness was significantly higher in secondary growth stands than it was in abandoned coppice stands, because of the greater number of ES and IS species in the secondary growth stands. The persistence of old-field species in stands that develop in abandoned fields might have contributed to the high total richness in these stands (Flinn & Vellend 2005). The secondary growth stands in our study area were established on formerly abandoned terraces that were on relatively flat land, and some were in valley bottoms where the soils have large amounts of nutrients and water (Lasanta *et al.* 2000; Kouba *et al.* 2012). Those conditions strongly favor shade intolerant, ruderal, and competitive species (Paillet *et al.* 2010), which can increase total richness.

The large number of early-successional colonizers was responsible for the high species richness in young oak stands. ES species are the first to colonize previously disrupted or damaged ecosystems (Hermy & Verheyen 2007; Schmiedinger *et al.* 2012). In our study, the disappearance (i.e., competition exclusion) of early seral plant species in the transition from one successional stage to another might have been responsible for the comparatively low overall species richness in old (> 50 yr) stands. The richness of ES and IS species was higher in uneven-aged stands than it was in even-aged stands because of the high resource availability caused by the development of gaps in the canopy of uneven-aged stands (Duguid & Ashton 2013), which can provide conditions that favor the establishment of ES and IS species (Fahey & Puettmann 2007). In contrast, in even-aged stands, the structure of the overstorey canopy, the amount of interspecific competition, and the resources available on the forest floor changes more dramatically and phases of development move through time more uniformly than they do in uneven-aged stands, which might reduce the richness of shad-intolerant species (Oliver & Larson 1996), most of which are ES and IS species.

Overall richness and the richness of ES and IS species were negatively correlated with the extent of the canopy cover and many studies have demonstrated the negative effect of canopy closure on shade-intolerant species (e.g., Hart & Chen 2006; Vockenhuber *et al.* 2011). The reduction in the availability of light as a forest canopy closes can reduce species richness and limit the growth and survival of many species that became established during the stand initiation stage, and allow only late-succession specialist species to persist (Hart & Chen 2006; Breugel, Bongers & Martínez-Ramos 2007). Furthermore, in our study, the competitor shrub *Buxus sempervirens* might out competed other shade-intolerant species by reducing the amount of resources (i.e., light, soil nutrients, and water) in the understory. The explanatory variables did not explain a significant amount of the variation in the richness of LS species, which indicates that stand types did not differ significantly in the number of LS species; perhaps because only a few of the least abundant late-successional specialists occurred in the oak stands in our study. These findings are similar to those of Seiwa *et al.* (2012), who found that forest stands that differed in management intensity did not differ in the number of late-successional species.

The extent of canopy cover was positively correlated with ES species evenness, perhaps because canopy closure increases interspecific competition which can lead to the exclusion of rare species and increase the mortality rate among highly abundant ES species. Probably, the reduction in sunlight caused by canopy closure contributed to a reduction in the evenness of IS species (competition exclusion).

In our study, the evenness of LS species was highest in even-aged stands, which have a more homogeneous structure and are more uniformly limiting in shade and microhabitats than are uneven-aged stands (Bartels & Chen 2010; Duguid &

Ashton 2013). Under those conditions, interspecific competition inhibits the establishment of shad-intolerant species but favors the establishment of LS species that can thrive in these environments (Messier, Parent & Bergeron 1998; Hart & Chen 2006; Bartemucci, Messier & Canham 2006; Szeicz & Macdonald 1995), which can increase the abundance of uncommon LS species, thereby, increasing species evenness. Other studies have suggested that facilitation or release from inhibition by preceding successional species, or intrinsic characteristics such as arrival time, growth rate, and the absence of direct interaction with early species might lead to the establishment of LS species (Carson & Schnitzer 2008).

In our study, the old oak stands harbored a considerably small share of forest specialists, which suggests that the historical land management has led to the loss of such specialist species. Furthermore, in addition to harboring many indicator species, uneven-aged stands had the capacity to maintain plant diversity and permitted the species of different habitat preference to co-exist.

Table 4 Multilevel Pattern Analysis of the relationship between plant species and forest classes in ten *Q. faginea* forest stands in the Central Pyrenees, Spain. Forest classes included old-even-aged secondary forest stands (sold_even_sf), old-even-aged coppice stands (old_even_cs), old-uneven-aged secondary forest stands (old_uneven_sf), young-even-aged coppice stands (young_even_cs), young-uneven-aged secondary forest stands (young_uneven_sf), and young-uneven-aged coppice stands (young_uneven_cs). Only species that had a significant indicator value (p < 0.05) are included in the table. ES: early-successional species, IS: intermediate-successional species, LS: late-successional species.

Forest type/ indicator species	Indicator value	p-vales	Successional status
old_even_sf			
Rhamnus saxatilis	0.818	0.018	IS
Berberis vulgaris	0.816	0.028	IS
Thymus praecox	0.811	0.013	IS
Polygala calcarea	0.764	0.023	ES
Linum narbonense	0.724	0.04	IS
Dorycnium pentaphyllum	0.585	0.024	IS
old_even_cs			
Lathyrus filiformis	0.764	0.02	ES
old_uneven_sf			
Viburnum lantana	0.951	0.001	IS
Globularia nudicaulis	0.874	0.015	ES
Polygala alpestris	0.805	0.004	ES
Carex flacca	0.8	0.018	IS
Cornus sanguinea	0.786	0.024	LS
Rubia peregrina	0.748	0.001	LS
Cheirolophus intybaceus	0.73	0.05	ES
young_even_cs			

Forest type/ indicator species	Indicator value	p-vales	Successional status
Echinospartum horridum	0.988	0.001	IS
Paronychia kapela	0.816	0.006	ES
Hieracium murorum	0.73	0.013	LS
Rosa sp.	0.646	0.039	IS
young_uneven_sf			
Rhamnus alaternus	1	0.001	IS
Stipa eriocaulis	0.894	0.003	ES
Juniperus phoenicea	0.886	0.004	IS
Lithodora fruticosa	0.819	0.018	ES
Bupleurum ranunculoides	0.813	0.008	ES
Cytisophyllum sessilifolium	0.805	0.002	LS
Quercus coccifera	0.793	0.013	IS
Thalictrum alpinum	0.774	0.001	IS
Teucrium pyrenaicum	0.743	0.032	IS
Trinia glauca	0.707	0.032	IS
Amelanchier ovalis	0.7	0.001	IS
Juniperus oxycedrus	0.649	0.032	IS
young_uneven_cs			
Brachypodium distachyon	1	0.002	ES
Coronilla scorpioides	1	0.002	ES
Plantago lanceolata	1	0.002	ES
Xeranthemum inapertum	1	0.002	ES
Medicago sativa	0.993	0.002	ES
Thapsia villosa	0.969	0.001	ES
Stachys recta	0.93	0.005	IS
Prunella laciniata	0.918	0.007	IS
Dactylis glomerata	0.904	0.01	ES
Arrhenatherum elatius	0.878	0.01	ES
Convolvulus cantabrica	0.844	0.009	ES
Prunus spinosa	0.824	0.009	IS
Alyssum alyssoides	0.816	0.031	ES
Arenaria leptoclados	0.816	0.031	ES
Brachypodium sylvaticum	0.816	0.031	LS
Centaurea alba	0.816	0.032	ES
Crepis vesicaria	0.816	0.031	ES
Lathyrus linifolius	0.816	0.032	LS
Phleum pratense	0.816	0.031	IS
Ranunculus repens	0.816	0.031	LS
Sideritis hirsuta	0.816	0.024	ES
Veronica orsiniana	0.816	0.031	ES
Vicia sativa	0.806	0.028	ES
Vicia cracca	0.805	0.044	ES
Medicago lupulina	0.804	0.022	ES
Potentilla neumanniana	0.8	0.027	ES
Melica ciliata	0.797	0.014	ES
Eryngium campestre	0.789	0.015	ES
Galium verum	0.789	0.033	ES
Silene vulgaris	0.776	0.017	ES
Hypericum perforatum	0.766	0.048	ES
Achillea millefolium	0.756	0.034	ES
Santolina chamaecyparissus	0.756	0.049	ES
Poa angustifolia	0.732	0.028	ES
Helianthemum marifolium	0.717	0.018	ES
Galium lucidum	0.644	0.035	ES
Hippocrepis ciliata	0.642	0.021	ES
Teucrium chamaedrys	0.632	0.004	ES
Thymus vulgaris	0.611	0.006	ES

Conclusions

Our study identified the consequences of historical “land management” practices on present day Mediterranean forests by comparing species assemblages and the diversity of plant species of different habitat preference, between stands that have had different land use histories, and that are at different successional stages. Plant species composition differed significantly among stands primarily, because of differences in the richness and evenness of early-, mid-, and late-successional species among the studied oak stands.

Although our findings support the suggestion that the recolonization by forest specialists can be difficult, even if the stand is left unmanaged for a long time, the uneven-aged stands permitted the species of different habitat preference to co-exist, which reflects their capacity to maintain plant diversity.

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Discusión general y conclusiones

Discusión general

El objetivo de esta tesis doctoral es contribuir al conocimiento de los procesos que influyen en la distribución de los bosques de *Quercus faginea* y su relación con la ordenación del territorio. En concreto en esta tesis doctoral se ha analizado el efecto de los factores abióticos y el uso antrópico en la distribución de *Q. faginea*, se ha examinado la dinámica espaciotemporal de los bosques de *Q. faginea* durante el periodo entre 1957 y 2006. También se ha evaluado el papel del cambio del uso del suelo y el cambio climático en el establecimiento y la dinámica re-generacional de los bosques de *Q. faginea*, y se ha analizado la relación entre la expansión de *Q. faginea* observada en algunos campos abandonados y los cambios socioeconómicos en siete municipios del Prepirineo Central durante la segunda mitad del siglo XX. Por último se ha estudiado la organización de la diversidad florística a múltiples escalas espaciales así como el efecto del uso histórico del suelo en las comunidades vegetales (diversidad y composición florística) en los bosques de *Q. faginea* del Prepirineo Central.

En general muchos estudios han destacado la importancia de las variables abióticas como por ejemplo el clima, topografía, las condiciones del suelo y la litología (Araújo & Pearson, 2005; Raxworthy et al., 2007; Coudun et al., 2006; Gastón et al., 2009) en la distribución espacial de las especies. Esta tesis (capítulo1) ha mostrado que la distribución de *Q. faginea* en el Pirineo Central está afectada en gran parte por las variables abióticas, particularmente el clima (heladas), la litología, y la topografía (las pendientes de las laderas). En particular, los resultados han mostrado que en el Pirineo Central los bosques de *Q. faginea* ocupan áreas situadas entre 450-m y 1500-m, esta especie no puede subir a los picos del Pirineo a causa de las heladas que constituyen un obstáculo para el establecimiento y el crecimiento de las nuevas plántulas. Las variables asociadas con las actividades antrópicas, particularmente el sobre-pastoreo y las plantaciones de pino han afectado negativamente a la distribución de *Q. faginea* en el Pirineo Central. En esta zona los bosques de *Q. faginea* han sido deforestados para aumentar la superficie de las tierras agrícolas y los pastos (Lasanta, 1989), pero después, debido al abandono de las zonas rurales, estas tierras han sido repobladas por pinos (Amo et al., 2007). Además en algunas zonas los bosques de *Q. faginea* han sido usado como dehesas (Benito, 2005). En estos ecosistemas particulares el sobre-pastoreo impide la instalación de nuevas plántulas y por lo tanto conduce con el tiempo a la desaparición de la especies (Plieninger, 2006).

Numerosas investigaciones han mostrado que el cambio del uso de suelo es la causa principal de las perturbaciones en los bosques (Ewers et al., 2006; Freitas et al., 2010). Particularmente en Europa, las zonas rurales han sufrido un cambio significativo en el uso de suelo a lo largo de su historia, y estos cambios se han acelerado de una manera marcada durante la segunda mitad del siglo XX (Plieninger & Schaar, 2008; Barbero et al., 1990). Estos cambios rápidos en el uso del suelo han modificado substancialmente los bosques naturales (Suc, 1984). En este sentido, esta tesis (capitulo 2) ha demostrado que los cambios en el uso de suelo que han ocurrido durante la segunda mitad del siglo XX (entre 1957 y 2006) en el Prepirineo Central han incrementado considerablemente la fragmentación (aumento en el número total de las manchas y decremento en el tamaño medio de las manchas de *Q. faginea*), el grado de aislamiento (incremento en la distancia media entre las manchas de *Q. fagine*), y la complejidad de las manchas de *Q. faginea* (incremento en la longitud total de los bordes de manchas y la tasa “perímetro/área de la mancha”). Estos cambios en los patrones espaciales en los bosques de *Q. faginea* se asocian particularmente a las plantaciones de pinos introducidas en la zona y la antigua deforestación asociada con el aumento de las tierras agrícolas. Además de modificar los patrones espaciales de las manchas, los cambios en el uso del suelo han reducido la superficie total ocupada por los bosques de *Q. faginea*.

Por otro lado, el cambio climático junto con el cambio del uso del suelo pueden influenciar significativamente en el establecimiento de los árboles en particular, y la dinámica de las masas forestales en general, sobre todo en las zonas que se han sometido a una fuerte explotación (Améztegui et al., 2010; Chauchard et al., 2010; Gimmi et al., 2010). Esta tesis (capitulo 3) ha mostrado que los cambios en el uso del suelo junto con el cambio climático que han ocurrido durante el siglo XX influenciaron fuertemente el reclutamiento anual de nuevos individuos, de modo que los periodos con unas condiciones climáticas favorables y una baja presión antrópica se caracterizaron por una alta tasa de reclutamiento de nuevos individuos y viceversa. En general la historia del reclutamiento en los bosques de *Q. faginea* del Prepirineo Central incluye las siguientes fases: (i) antes de 1935, a causa de la explotación extensiva de las tierras agrícolas, particularmente en las terrazas establecidas en las zonas montañosas, el establecimiento de *Q. faginea* se limitó a las masas del monte bajo; (ii) entre 1935 y los principios de 1960s, el abandono de las tierras agrícolas junto con la reducción de la presión ganadera han favorecido el reclutamiento de nuevos individuos y la expansión de *Q. faginea*, (iii) a finales de 1960s y principio de 1970s, las condiciones favorables climáticas (abundantes precipitación en el invierno y la primavera, y temperaturas frescas en el verano) han provocado un aumento en el reclutamiento de *Q. faginea* en las terrazas abandonadas, y (iv) a partir de 1975, el reclutamiento de *Q. faginea* se ha visto limitado por las condiciones de sequía (insuficientes lluvias durante el invierno y primavera y altas temperaturas en el verano). Además, esta tesis (capitulo 4) ha mostrado que la expansión de *Q. faginea* durante la segunda mitad del siglo XX es mayor en los municipios con una reducción marcada en el número de agricultores lo que ha generalizado un abandono masivo de las tierras agrícolas y los pastos.

El estudio de la diversidad vegetal y la composición florística en los bosques alterados por el hombre, como es el caso de la mayoría de los bosques en los países desarrollados, es un tema muy importante ya que estos bosques constituyen un refugio a muchas especies (plantas y animales) lo que les permite jugar un papel importante en la conservación de la biodiversidad (Barbier et al., 2008; D'Amato et al., 2009). El estudio de la organización espacial de la diversidad florística (capitulo 5) ha revelado que la mayor parte de la diversidad florística (diversidad gama) en las masas de *Q. faginea* del Prepirineo Central es el resultado de la diferenciación florística entre las masas, dicho de otra manera, es resultado de la diversidad beta entre las masas de *Q. faginea*. El mismo estudio ha mostrado que esta misma diversidad -diversidad beta- está estructurada en gran parte por unos factores que están determinados por el uso histórico de la masa forestal como por ejemplo la edad media de la masa de *Q. faginea*, la distribución de la edad de los árboles de *Q. faginea* en cada masa forestal, y la abundancia de *Q. faginea*. En general estos resultados sugieren que los planes de gestión diseñados para mejorar la diversidad florística en los bosques alterados por el hombre deben tener en cuenta la heterogeneidad del hábitat por su influencia en la diversidad florística en estos bosques.

Por último, muchos de las investigaciones que han estudiado el efecto del uso histórico del suelo en la diversidad y la composición florística en los bosques han argumentado que las perturbaciones antrópicas afectan esencialmente a la composición florística de los bosque, favoreciendo el establecimiento de las especies ruderales y pioneras (especies adaptadas a las zonas perturbadas) en el detrimento de las especies especialistas a los bosques (e.j. Baeten *et al.* 2010; De Frenne *et al.* 2010; Matuszkiewicz *et al.* 2013; Paillet et al., 2010). En este sentido los resultados del estudio del efecto del uso histórico del suelo en la composición florística en los bosque de *Q. faginea* (capitulo 6) han revelado diferencias significativas en cuanto a la composición florística entre masas de *Q. faginea* con diferentes (i) edades (viejas vs. jóvenes), (ii) tipos de bosque (bosque secundario vs. monte bajo), e (iii) intensidades en la gestión histórica. Estas diferencias en la composición florística son debidas principalmente a diferencias en riqueza y equitabilidad “evenness” de especies que desarrollan en diferentes estadios sucesionales: especies de la fase inicial de la sucesión vegetal, especies de la fase intermedia de la sucesión vegetal, y especies de la fase final de la sucesión vegetal. Los resultados de este estudio (capitulo 6) han revelado también que las masas viejas de *Q. faginea* albergan pocas especies que son consideradas como especies especialistas de los bosques. Ello respalda la idea de que la recolonización de los bosques alterados por especies especialistas es muy difícil incluso cuando las masas forestales se dejan sin ningún tipo de gestión por mucho tiempo. Sin embargo, este estudio ha mostrado la capacidad de las masas irregulares (masas con diferentes clases de edad) en conservar la diversidad florística porque permiten coexistir a especies con diferentes preferencias de hábitat

En general los resultados presentados en esta tesis y las discusiones de los capítulos pueden tener unas aplicaciones muy amplias para los lectores y científicos. Algunos de los nuevos conocimientos generados en esta tesis pueden también ser usados bajo otras consideraciones, por lo tanto pueden ser útiles para los estadísticos, ecólogos o forestales que trabajan en otras zonas de estudio.

Conclusiones

A- En relación a la distribución espacial de *Q. faginea*:

La distribución espacial de Q. faginea en el Pirineo Central ha sido afectada principalmente por los factores abióticos. Los factores antrópicos han jugado un papel secundario en la distribución espacial de Q. faginea, pero han actuado como frenadores de la expansión de esta especie.

B- En relación a la evolución espaciotemporal de *Q. faginea* entre 1957 y 2006.

Aunque Q. faginea se ha expandido en algunas zonas del área de estudio entre 1957 y 2006, los cambios en el uso del suelo han causado una reducción en la superficie total ocupada por los bosques de Q. faginea. Así, el grado de fragmentación, aislamiento, y complejidad de las manchas de Q. faginea han aumentado entre 1957 y 2006. La reducción en la superficie total y los cambios en la configuración espacial de las manchas de Q. faginea fueron causados principalmente por el reemplazamiento de estos bosques por las plantaciones de pino (especialmente P. nigra y P. syvestris) y las deforestaciones para aumentar la superficie de las tierras agrícolas.

C- En relación al establecimiento y la dinámica de las masas de *Q. faginea.*

1. Los cambios en el uso de suelo y el cambio climático han influenciado fuertemente la dinámica de los bosques de Q. faginea del Prepirineo Central durante el siglo veinte. Debido a esta influencia el reclutamiento de los nuevos individuos ha sido episódico. En general había periodos con altas tasas de reclutamiento como por ejemplo el periodo entre 1965 y 1975 y otras con bajas tasas de reclutamiento (1975-1980, 1985-1995). Los periodos con altas tasas de reclutamiento coinciden con unas condiciones climáticas más favorables (mayor precipitación durante el invierno y *primavera y temperaturas moderadas en el verano) y baja presión antrópica en el territorio.*

2. El crecimiento anual (crecimiento secundario y apical) es mayor entre los individuos establecidos en las terrazas abandonadas en comparación con los individuos establecidos en los montes bajos. Este efecto es debido a que las terrazas abandonadas están en las partes bajas de las laderas o en los fondos de valles, que se caracterizan por unos suelos profundos y contienen una gran cantidad de nutrientes, lo que mejora el crecimientos de los árboles.

D- En relación con la expansión de *Q. faginea* en los campos abandonados.

La emigración rural que ha ocurrido en el Prepirineo Aragonés a partir de los años sesenta ha producido un abandono masivo de las tierras agrícolas junto con la disminución de la presión pastoral. Como resultado algunos de los campos abandonados han sido colonizados por Q. faginea, sobre todo en los municipios con una disminución notable en el número de agricultores.

E- En relación con la organización de la diversidad a múltiples escalas espaciales en los bosques de *Q. faginea*.

Una gran parte de la diversidad florística en los bosques de Q. faginea del Pripirineo Central (diversidad gama) es el resultado de la diversidad beta, la diversidad florística generada entre las masas de Q. faginea. Esta misma diversidad -diversidad beta- está estructurada en gran parte por las características estructurales, espaciales, y topográficas de las masas de Q. faginea.

F- En relación al efecto del uso histórico del suelo en la diversidad y la composición de los bosques de *Q. faginea*.

En los bosques de Q. faginea del Prepirineo Central, las masas con diferentes historias de gestión y que están en distintos estadios de sucesión (jóvenes vs. viejos) han experimentado una gran variación en la composición florística. Esta diferencia en la *composición florística es debida principalmente a diferencias en riqueza y equitabilidad "evenness" de especies que se desarrollan en diferentes estadios sucesionales: especies de la fase inicial de la sucesión vegetal, especies de la fase intermedia de la sucesión vegetal, y especies de la fase final de la sucesión vegetal.*

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