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

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Abstract

In the 20th C., anthropomorphic changes in land use have extensively modified natural forests in the Mediterranean region, which has led to a decline in the number of plant species and the fragmentation of their populations. A thorough understanding of the impact of changes in land use on the spatiotemporal dynamics of forest species is essential to the ecological sustainability of the natural forests in the region. In this study, we examined the spatiotemporal dynamics of *Q. faginea* forests in the Central Pre-Pyrenees, Spain, over the last 50 years. Changes in the patterns of *Q. faginea* forests were assessed using patch-landscape metrics, and the probable factors influencing these changes were identified using empirically based statistical models. Between 1957 and 2006, total patch area, mean patch size, and connectivity decreased, while patch density and edge length increased, which reflected an increase in forests fragmentation and loss, largely because of the expansion of pine plantations and croplands, and grazing pressure. Roads acted as attractors to changes in land use. We conclude that changes in the anthropomorphic use of land since 1957 have increased the fragmentation and loss of *Q. faginea* forests in the area. Any management plan for these forests must take into consideration land uses, particularly those that impinge on the fragments of *Q. faginea* forests from the surrounding matrix.

Key words: patch-landscape metrics, Bayesian Model Averaging, Adaptative Regression by Mixing with model Screening, Mediterranean forests, species gains and losses, fragmentation.

1. 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 of forests and to minimize the impact of disturbances on them (Rademacher et al. 2004). Researches 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 the 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 reduces the size of the fragments (patches) 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, the forests in European Mediterranean countries have been significantly affected by changes in human activities in the 20th C. (Barbero et al. 1990; Maltez-Mouro et al. 2009). The native forests have been modified substantially or replaced entirely (Suc 1984).

The magnitude of the changes in land use-cover and the factors that caused them are relatively well studied (Aspinall 2004; Callaway and Davis 1993; Kobayashi and Koike 2010; Rutherford et al. 2008), but the spatiotemporal dynamics of specific forest species and the forces acting at a regional spatial scale have received limited attention (Guirado et al. 2008; Vicente-Serrano et al. 2010), mainly because historical data on the distributions of species are limited.

Most studies have indicated that anthropogenic disturbances are the most important factors influencing the dynamics of oak forests in the Mediterranean region (Rodà et al. 1999). In this study, we investigated a semi-deciduous oak (*Quercus faginea*), which is distributed throughout Northern Africa and the Iberian Peninsula (Blanco et al. 1997) and is an important structural component of native plant communities in many mesic forests in Mediterranean environments (Rey Benayas et al. 2005). Although the species occurs in almost all of the provinces in Spain, its most important forests occur in the northeast (Pre-Pyrenees). *Q. faginea* is a shade-tolerant oak that can grow in a wide range of substrates, topographic locations, and climatic conditions (Jiménez et al. 1998), but it prefers base-rich soils and ombroclimates of a sub-humid type (Rivas-Martinez 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. In the 19th and the early 20th C., an increase in the human population increased 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 grazing livestock, for a growing human population. More 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 and the area they occupy has decreased.

In this study, we examined the spatiotemporal dynamics of *Q. faginea* forests (all areas where *Q. faginea* was the dominant species) in the Spanish Central Pre-Pyrenees between 1957 and 2006. The objectives were (i) to quantify changes in the spatial distribution of patches of *Q. faginea* forests between 1957 and 2006, (ii) to assess patch fragmentation, loss, and connectivity spatiotemporally, and (iii) to identify the factors responsible for the spatiotemporal changes in the *Q. faginea* forests. To quantify the changes in the spatial distribution of patches of *Q. faginea* forests and to assess patch fragmentation, loss, and connectivity that end, we used a set of patch-landscape metrics. To identify the factors responsible for the spatiotemporal changes in the *Q. faginea* forests, we used three statistical models (GAM, BMA and ARMS, see below). The study pictured an example of Mediterranean forests that are highly sensitive and vulnerable to changes as consequence of centuries of human land use changes which affected the forests resilience to different disturbances (Vicente-Serrano et al. 2010).

Materials and Methods

Study area

This study occurred within a 1363-km^2 area of the Central Pre-Pyrenees, Spain, between 42.2 N to 42.15 N and 0.43 W to 0.05 E, where the elevation varies widely (from 500 m in the inner depression to >2000 m at the highest peaks. The area is in a climate transition zone between Atlantic and Mediterranean (Vicente-Serrano et al. 2004). In the inner depression, mean annual precipitation is 500 mm, but it is higher elsewhere and, above 1500 m, annual precipitation is >1000 mm. The Rainfall is highly seasonal and the rainy season occurs between Oct and Jun (Vicente-Serrano et al. 2004). 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. In the cold season (November-April), the 0 ºC isotherm occurs at 1650 m (Lasanta-Martínez et al. 2005). The lithological substrate of the area is dominated by Conglomerate, limestone, marl, and sandstone, and 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. syvestris* 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 monpesulanus*, *Genista hispanica*, *Amelanchier ovalis*, *Genista scorpius*, and *Carex halleriana*) and is typical of a rural area that has 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 20th C., 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, and the abandonment of cropland and pastures, which has led to forest loss and fragmentation, as well as forest re-growth after the abandonment of croplands and pastures (Lasanta-Martínez et al. 2005; Vicente-Serrano et al. 2010).

Distribution maps of Q. faginea

To quantify gains and losses, we created maps of the distribution of *Q. faginea* in 1957 and in 2006. 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 is a period in which occurred significant changes in land use (Teixido et al. 2010).

The 2006 map was derived using the Forest Map of Spain (2004). The map was imported into a GIS and the position, size, and edge of patches were corrected using ortho-rectified, 0.5-m resolution aerial photographs from the Agrarian Plots Geographic Information Systems for 2005 and 2006, and the accuracy of the resulting map was confirmed in the field. The 1957 map was produced by visual interpretation using the aerial photographs of the United States Army from 1956 and 1957. The 1957 aerial photographs were 170 24x24-cm contact prints scale = 1:32 000. The photographs were scanned and georeferenced using the 2006 images as references with Topol 9.5, for a final resolution of approximately 0.5 m.

Based on published scientific literature (Molinillo et al. 1997; Montserrat 1990) and our interpretation of the aerial photographs, we assumed that only the patches that were occupied by shrubland in 1957 could have converted to *Q. faginea* through natural vegetation succession by 2006; therefore, the patches of shrub land 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 shrub land, and this information was included in the 2006 map. Overlaying the polygon maps from 1957 and 2006 (Fig. 1) produced two binary maps of changes, which were used to identify the factors influencing the changes in the spatial distribution of *Q. faginea* forests in the study area between 1957 and 2006. One map displayed the gains in *Q. faginea* forests (gain/no gain) and included all of the areas that were occupied by shrub land in 1957 but were converted to *Q. faginea* by 2006. The second map displayed the losses in *Q. faginea* forests (loss/no loss) and included all of the areas that were occupied by *Q. faginea* in 1957 but were converted to one of the other three types of land use (shrub land, pine plantation, and cropland) by 2006.

Quantification of changes and fragmentation analysis

To quantify the gains and losses of *Q. faginea* forests between 1957 and 2006, we used ArcGIS 9.2 (ESRI, 2006) and, to quantify temporal changes in the spatial configuration of patches of *Q. faginea* forests, we used the following set of landscape metrics (Echeverria et al. 2006; Sitzia et al. 2010; Teixido et al. 2010): (1) Total edge length (km) of all *Q. faginea* patches; (2) Mean patch size (ha); (3) Total area (ha) occupied by *Q. faginea* patches (ha); (4) Mean patch distance (m) (the average of the nearest distances between the edges of *Q. faginea* patches); (5) Number of *Q. faginea* patches. The following equation quantified the relative change (R) of each index:

$R = (A_{2006} - A_{1957}) \text{ X } 100/A_{1957}$.

Where A_{2006} and A_{1957} are the area, length, number of *Q. faginea* forests patches, or mean patch distances in 2006 and 1957, respectively.

Predictor variables

The statistical analyses included topo-climatic and land-use variables (topography, climate, and land use) that were suspected of influencing change in the *Q. faginea* forests in the area between 1957 and 2006. Elevation, slope, and aspect were obtained from the Digital Elevation Model (DEM) of Spain (resolution = 20 m). To generate values that were relative to a north-south (S_N) orientation, aspect values were converted to the cosine of aspect. 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 the north-south orientation gradient has a significant effect on photoperiodism and water availability (Pueyo and Beguería 2007).

A set of climatic variables were derived from the Digital Climatic Atlas of Aragón (2007). The data in the climate maps were averaged for the period 1977-2000 and included annual potential radiation and the number of frost days per year (Frost_days). Annual potential radiation (radiation) influences soil-vegetation evapo-transpiration and, therefore, soil water content, and it might have a significant effect on the distribution of *Q. faginea*. Frost conditions affect negatively the establishment and growth of *Q. faginea* seedlings and saplings.

The extensive pine plantations that were created in the area within the last 50 year (Amo et al. 2008) 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 settlement (Distance_settle) 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 distance to the nearest road was derived from the National Vector Map of Spain using the straight line distance function in the GIS. Similarly, the distance to the nearest settlement was derived from a map of the settlements of Aragon. To assess the extent to which livestock and agricultural activities affected the spatiotemporal dynamics of *Q. faginea* between 1957 and 2006, distance to the nearest pasture (Cosdistance_pasture) and distance to the nearest cropland (Cosdistance_crop) were included in the analyses. Maps of the distances to the nearest pasture and cropland were measures of transportation costs and were derived from a CORINE Land Cover map.

All of the maps of the dependent and predictor variables were subset to identical extents at a spatial resolution of 20 m. Moran's I Test assessed the spatial autocorrelations of the dependent variables (Cliff and Ord 1973). Spatial autocorrelations declined monotonically above a lag of 10 pixels (~200 m) in the map of gains and 12 pixels (~240 m) in the map of losses; therefore, 300 m was used as the minimum distance between extracted pixels (Millington et al. 2007). A randomly selected sample of the values of the response variables was intersected with the corresponding values of the 10 predictor variables and the resulting dataset was imported into R (R Development Core Team 2009) for the statistical analyses.

Statistical models

To examine the influence of the predictor variables on the gains and losses of *Q. faginea* forests, we created a univariate GAM model for each potential predictor variable and each of the two binary dependent variables i.e., gain and 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 estimate of the linear term (Hair et al. 1998). In our study, 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 the 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 8.65% between 1957 and 2006. In 1957, *Q. faginea* forests covered 7% (9149 ha) of the study area, but by 2006, these forests covered 6% (8336 ha) of the area. The transition matrix revealed that the *Q. faginea* forests gained 626 ha in some areas through natural transitions from shrub land to *Q. faginea* forests and lost 1438 ha in others. The transition to pine plantations and shrub land was the most important source of the losses to *Q. faginea* forests: ~924 ha were converted to pine plantations and ~ 390 ha were converted to shrubland. The transition analysis revealed also that ~ 125 ha of *Q. faginea* forests were converted to cropland.

In the study area, the number of patches of *Q. faginea* forests increased from 104 in 1957 to 118 in 2006 (~13.5%) (Table1). In 1957, 30 patches (29%) >100 ha contributed >81% of the total *Q. faginea* forests. By 2006, the number of the large patches (> 100 ha) was 24, and 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). The losses of *Q. faginea* forests were the result of the loss of four small patches and the fragmentation and reduction in the size of six large patches, which fragmented and became medium-sized patches. The gains of *Q. faginea* forests resulted from the expansion of some medium-sized patches (Fig. 2b). Between 1957 and 2006, the mean distance between patches increased by approximately 8.5%, which reflected a reduction in the connectivity among patches of *Q. faginea* forests, and edge length increased (Table 1), which indicated that the shape of the patches of *Q. faginea* forests became more irregular. Mean patch size decreased from 87.7 ha in 1957 to 70.6 ha in 2006 and, coupled with increases in total edge length and the number of patches, reflected an increase in the edge effect in patches of *Q. faginea* forests.

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”, radiation, distance to the nearest road “Distance_road”, distance to the nearest cropland “Cosdistance_crop”, distance to the nearest settlement “Distance_settle”, and elevation and distance to the nearest road explained the most deviance (Table 2). The losses of *Q. faginea* forests was significantly ($P<0.05$) correlated with each of the land-use variables and slope (Table 2). All of the variables that were significant ($P\leq0.05$) in the univariate GAMs were included in the BMA and ARMS, except radiation, 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 2).

BMA and ARMS indicated that, in the gains model, elevation, “Frost_days”, and “Distance_road” had high probabilities [Pr ($\beta_{vs} \neq 0$) ≥0.90], and “Cosdistance_crop” and “Cosdistance_settle,” low probabilities [Pr ($\beta_{vs} \neq 0$) ≤0.41] of being in the best-candidate model (Table 3). In the losses model, “Cosdistance_crop”, “Cosdistance_pastur”, “Distance_plant”, “Distance_road” and slope had high probabilities [Pr ($\beta_{vs} \neq 0$) ≥0.90] and “Distance_settle” low probabilities [Pr ($\beta_{vs} \neq 0$) ≤0.37] of being in the best-candidate model (Table 3). 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 ($\beta_{vs} \neq 0$) ≥0.90] in both BMA and ARMS as factors that have had a significant influence on the changes in the *Q. faginea* forests.

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 3). Both BAM and ARMS indicated that the expansion of *Q. faginea* forests (i.e., the probability of gains) increased as elevation (a.s.l.) and number of days with frost decreased. Patches of *Q. faginea* forests close to croplands or pine plantations 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 pastures and roads, and those that were on shallow slopes (Table 3). Distance to the nearest settlement did not have a significant effect on the spatiotemporal changes in the *Q. faginea* forests.

Discussion

Spatiotemporal dynamics of Q. faginea forests

In this study, we modeled the changes that occurred in the distribution of *Q. faginea* forests at the level of patches (polygons) in the Spanish Central Pre-Pyrenees between 1957 and 2006. As in other studies (Echeverria et al. 2006; Teixido et al. 2010), patch-level landscape spatial indices were useful in examining variability and changes in the distribution of *Q. faginea* forests over time.

In general, the area under study experienced a significant (8.65%) reduction in *Q. faginea* forests in the last 50 yr, primarily because of the creation of pine plantations (especially *P. sylvestris* and *P. negra*) and deforestation for increasing the amount of arable land. Most of the pine plantations in the region were established during the second half of the 20th C. (Amo et al. 2008) and, currently, pine plantations dominate most of the areas neighbouring isolated patches of native *Q. faginea* forests. Native plants can be severely affected by the presence of introduced species, particularly, those that are characterized as fast growing and having dispersal abilities (Echeverria et al. 2006; Teixido et al. 2010). 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. Some of the abandoned lands were reforested by the Spanish forestry service, while the remainder has undergone natural re-vegetation and been transformed into shrub land (Molinillo et al. 1997; Montserrat 1990). In some areas, the *Q. faginea* forests expanded through the natural succession from shrub to forest.

In our study, the number of patches and total edge length increased as consequence of forest fragmentation. In temperate forests in Chile, fragmentation increased patch density and total edge length (Echeverria et al. 2006). In our study, the substantial increase in patch density was associated with an increase in the number of medium-sized (10-100 ha) patches (Fig. 2a). The reduction in the connectivity of patches of *Q. faginea* forests was the result of an increase in 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 shrub land); consequently, patches of *Q. faginea* forests became spatially separated and less frequently contiguous. The disruption of patch connectivity can have significant effects on the distribution and persistence of populations and, therefore, persistence of species (Zebisch et al. 2004). Between 1957 and 2006, there was an increase in the edge effect in patches of *Q. faginea* forests, which, in addition to deforestation, might have been influenced by grazing patterns (see below).

Factors that influence changes in Q. faginea forests

In the Central Pre-Pyrenees, land use had a significant effect on the loss of *Q. faginea* forests and other studies have demonstrated the negative effect of land use changes on forest dynamics (Rhemtulla et al. 2009; Teixido et al. 2010). In the Central Pre-Pyrenees, most of the losses occurred in areas close to pine plantations or croplands because many areas of *Q. faginea* forest were converted to cropland and pine plantations. The high probability of the loss of *Q. faginea* forests near pastures can be interpreted by the grazing pressure. Grazing had a significant effect on the distribution of vegetation in Mediterranean ecosystems (Carmel and Kadmon 1999). Grazing can have a negative effect on vegetation dynamics and 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, the *Q. faginea* forests were harvested 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. 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 of these pastures and, by 2006, they had been converted to pine plantations through reforestation or to shrub lands through natural succession. In the Central Pre-Pyrenees, losses of *Q. faginea* forests were more likely near roads than elsewhere, which has been reported in, for example, New Zealand (Ewers et al. 2006), the USA (Saunders et al. 2002), and Brazil (Freitas et al. 2010), where road network density was a strong predictor of cumulative forest loss and fragmentation. In the Central Pre-Pyrenees, the general road network was established relatively early (1905-1920) (Lasanta-Martínez et al. 2005), which improved access to land and permitted new uses of the land, specifically, new croplands and pine plantations. In our study, then, 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, which influenced strongly the spatial variability in *Q. faginea* forests. The probability of loss at sites that had a low slope was high because of earlier competition from agricultural activities. The *Q. faginea* forests on low slopes were harvested and the land was used for cereal cultivation (Lasanta-Martínez 1989), which restricted *Q. faginea* to poor soils and stony hillsides. The negative correlations between the gains in *Q. faginea* forests and elevation and number of frost days per year were a consequence of the study area; there are more days with frost in the highlands than there are in the lowlands. In the highlands, freezing temperatures inhibit the establishment and growth of seedlings and saplings, which is an obstacle for the dispersal of *Q. faginea*. The expansion of *Q. faginea* forests was greater at sites far from roads, probably because these sites were inaccessible to humans and livestock. In those areas, the expansion of *Q. faginea* forests resulted from a natural transition from shrub land to forest. Evidently, the distance to the nearest settlement did not influence the spatiotemporal dynamics of *Q. faginea* forests, which indicates that the spatiotemporal dynamics of these forests were not influenced directly by the rural activities of humans concentrated around settlements, because of the human exodus that occurred in the region during the second half of the 20th C.

Conclusions

This study used patch-level landscape spatial indices and empirically based statistical models to quantify the spatiotemporal dynamics of *Q. faginea* forests in the Spanish Central Pre-Pyrenees by comparing the spatial distribution of *Q. faginea* in 1957 and 2006, and identified the most important factors influencing changes in the distribution of *Q. faginea*. The analysis indicated significant changes in the distribution of patches of *Q. faginea* forests, which were reflected in significant changes in the size, density, edge length, connectivity, and total patch area. Although the size of some medium-sized patches of *Q. faginea* forests at sites inaccessible to humans and livestock increased between 1957 and 2006, the most significant changes in the distribution of *Q. faginea* involved forests fragmentation and loss that were directly related to the expansion of pine plantations and croplands, and grazing pressure. In addition, roads acted as attractors of changes in land use. The long-term preservation of these forests depends on the sustainability of the landscape where this species occurs, which requires an improvement in the integrity and the connectivity of the fragments of native *Q. faginea* forests that remain.

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Tables

Table1. Landscape metrics used in an analysis of the fragmentation of *Q. faginea* forests in the Spanish Central Pre-Pyrenees between 1957 and 2006. R is the relative change in each metric.

Landscape metric	1957	2006	R (%) 1957-2006
Total patches edge length (km)	637	660	3.60
Mean patch size (ha)	87.7	70.6	-19.5
Total patch area (ha)	91489	8336	-8.65
Mean patch distance (m)	1087	1179.4	8.50
Number of patches	104	118	13.5

Table 2. 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**
Radiation	**<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_settle	**<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**
S_N	0.47	0.02	0.64	0.10

Table 3. 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.

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_settle	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_settle	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	

Figures

Figure 1: Map of transitions from/to *Q. faginea* forests (i.e. gains and losses) in the Spanish Central Pre-Pyrenees, between 1957 and 2006.

Figure 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, in the Spanish Central Pre-Pyrenees, between 1957 and 2006. The number above each bar represents (a) the number of patches or (b) the proportion (%) of the area occupied by each patch category.

Figure 1

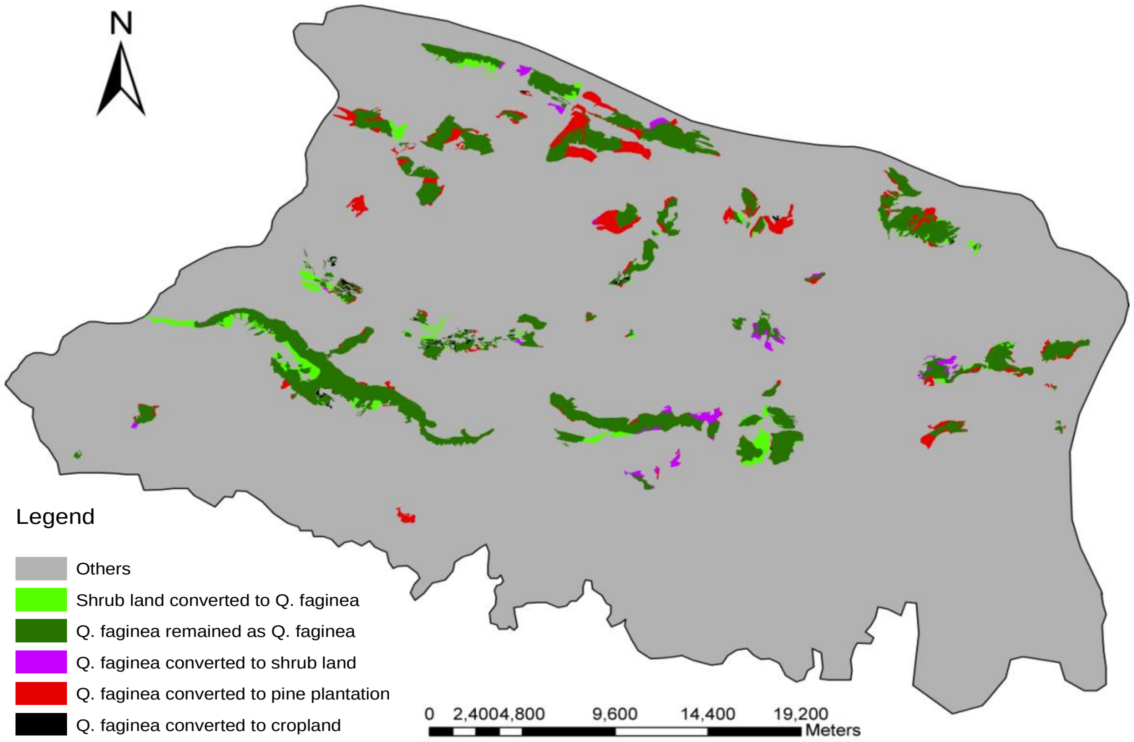
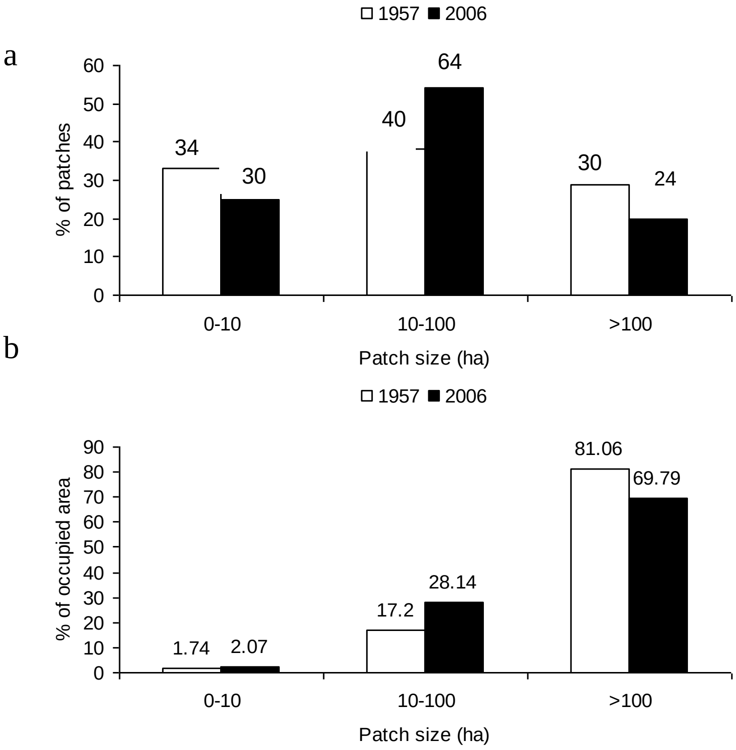

N
Legend
Others
Shrub land converted to Q. faginea
Q. faginea remained as Q. faginea
Q. faginea converted to shrub land
Q. faginea converted to pine plantation
Q. faginea converted to cropland
0
2,400
4,800
9,600
14,400
19,200
Meters

Figure 2


a
☐ 1957 ■ 2006
% of patches
60
50
40
30
20
10
0
34
30
40
64
30
24
0-10
10-100
>100
Patch size (ha)
b
☐ 1957 ■ 2006
% of occupied area
90
80
70
60
50
40
30
20
10
0
1.74
2.07
17.2
28.14
81.06
69.79
0-10
10-100
>100
Patch size (ha)