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RESEARCH PAPER

Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees

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ABSTRACT

Aim To assess the spatial patterns of forest expansion (encroachment and densification) for mountain pine (*Pinus uncinata* Ram.) during the last 50 years at a whole mountain range scale by the study of different topographic and socio-economic potential drivers in the current context of global change.

Location The study area includes the whole distributional area of mountain pine in the Catalan Pyrenees (north-east Spain). This represents more than 80 municipalities, covering a total area of 6018 km^2.

Methods Forest cover was obtained by image reclassification of more than 200 pairs of aerial photographs taken in 1956 and 2006. Encroachment and densification were determined according to changes in forest cover, and were expressed as binary variables on a 150×150 m cell-size grid. We then used logistic regression to analyse the effects of several topographic and socio-economic variables on forest expansion.

Results In the period analysed, mountain pine increased its surface coverage by 8898 ha (an increase of more than 16%). Mean canopy cover rose from 31.0% in 1956 to 55.6% in 2006. Most of the expansion was found on north-facing slopes and at low altitudes. Socio-economic factors arose as major factors in mountain pine expansion, as encroachment rates were higher in municipalities with greater population losses or weaker primary sector development.

Main conclusions The spatial patterns of mountain pine expansion showed a good match with the main patterns of land-use change in the Pyrenees, suggesting that land-use changes have played a more important role than climate in driving forest dynamics at a landscape scale over the period studied. Further studies on forest expansion at a regional scale should incorporate patterns of land-use changes to correctly interpret drivers of forest encroachment and densification.

Keywords

Canopy cover, densification, encroachment, global warming, image reclassification, land-use changes, mountain pine, Pyrenees.

INTRODUCTION

Despite the high rates of deforestation measured world-wide, forest cover in most developed countries is on the increase (Coop & Givnish, 2007; Gellrich & Zimmermann, 2007; Gellrich *et al.*, 2007a). Although this increase is mainly caused by the encroachment of forest into open areas, there has also been an increase in canopy cover of pre-existing forests, either through enhanced growth of pre-existing individuals or the recruitment of new ones (densification) (Poyatos *et al.*, 2003; Gehrig-Fasel *et al.*, 2007). Forest expansion (including both encroachment and densification) does not occur homogenously at the local scale, as it is determined by both natural and cultural factors, such as local recent livestock pressure (Dirnböck *et al.*, 2003; Lasanta-Martínez *et al.*, 2005; Coop & Givnish, 2007), topographic factors (Poyatos *et al.*, 2003; Gellrich & Zimmermann, 2007) and locally dominant ecological and socio-economic conditions, among others (Debussche *et al.*, 1999). However, these drivers usually act at different scales: for example, the decision to abandon a farm depends on socio-economic factors, and

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subsequent changes in land cover will be modulated by ecological processes, which in turn are associated with environmental and climatic conditions (Rutherford *et al*., 2008). Therefore, researchers have studied land-cover change at a wide range of spatial scales, from small plots to entire mountain ranges. Local-scale approaches based on the study of plots usually employ dendrochronological methods (Camarero & Gutiérrez, 2007; Chauchard *et al*., 2007), while at larger spatial scales, land-cover changes have mainly been assessed by comparison of aerial photographs (Miller, 1999; Coop & Givnish, 2007; Gellrich *et al*., 2008). Lastly, changes in large areas (covering thousands of square kilometres) have mainly been analysed using remote-sensing techniques (Gellrich & Zimmermann, 2007; Millington *et al*., 2007). Although attempts have been made to integrate these scales (Jump *et al*., 2006; Lasanta & Vicente-Serrano, 2007; Gellrich *et al*., 2008; Rutherford *et al*., 2008), this is still one of the major challenges facing the study of forest expansion, as a holistic view is required in order to better understand the drivers underlying these processes.

Many European mountain areas have recorded a significant increase in temperatures since the 1940s (Diaz & Bradley, 1997). Mountain ecosystems, especially areas located at high altitude, are considered particularly vulnerable to climate change (Dirnböck *et al*., 2003; Camarero *et al*., 2006). Forest encroachment in these systems has often been attributed to global warming, which may favour conditions for tree recruitment and growth near or beyond the tree line (MacDonald *et al*., 1998; Peñuelas & Boada, 2003; Camarero & Gutiérrez, 2004; Camarero *et al*., 2006; Batllori & Gutiérrez, 2008). Nevertheless, over the last century European mountain systems have suffered not only global warming but also major demographic, economic and organizational changes (García-Ruiz *et al*., 1996; Hofgaard, 1997; Dirnböck *et al*., 2003). Therefore, land-use changes must be considered as a major potential factor driving forest expansion, especially in areas exposed to significant human influence, such as the north Mediterranean Basin (Dale, 1997; Sala *et al*., 2001; Chauchard *et al*., 2007; Gehrig-Fasel *et al*., 2007; Millington *et al*., 2007; Gellrich *et al*., 2007b).

In order to integrate the different scales at which forest expansion acts and segregate climate change from land-use change as drivers of forest expansion, we performed the analysis on mountain pine (*Pinus uncinata* Ram.), a species that grows in the subalpine belt of the central and eastern Pyrenees, where it constitutes most of the tree lines. We employed a multi-scale approach comparing hundreds of pairs of aerial photographs. Though this technique is widely used for assessing forest encroachment (Poyatos *et al*., 2003; Coop & Givnish, 2007; Gellrich *et al*., 2008), it has rarely been employed for regional-scale studies. Furthermore, the densification process has been extensively studied along the tree line from a dendroecological, climate-related standpoint (Szeicz & MacDonald, 1995; MacDonald *et al*., 1998; Camarero & Gutiérrez, 2004; Batllori & Gutiérrez, 2008) but has never, to our knowledge, been quantified at the landscape scale, despite reports establishing its important role in the context of land-cover change (Poyatos *et al*., 2003; Gehrig-Fasel *et al*., 2007; Lasanta & Vicente-Serrano, 2007).

The main objectives of this study were: (1) to assess spatial patterns of mountain pine encroachment and densification in the eastern Pyrenees at both local and regional scales, and (2) to infer the main factors driving these processes. Our main hypothesis is that if climate change is the main driver of mountain pine expansion, encroachment and densification will be more evident at high altitudes, near the tree line. In contrast, if the primary drivers are changes in land use, then spatial patterns of expansion should match reported spatial patterns of land-use change.

MATERIALS AND METHODS

Study area

Location and description of the study area

The Pyrenees is a mountain range that spreads from east to west along the border between France and Spain, with an extent of more than 50,000 km^2. The study area is located south-east of the axial zone of the range, and includes the 83 municipalities of Catalonia with current presence of mountain pine, thus covering a total area of 6018 km^2 (Fig. 1). The abrupt terrain of the study area, with altitude ranging from 500 to more than 3000 m a.s.l., in conjunction with the proximity of Mediterranean Sea creates significant climatic variation. Thus, the highest areas are representative of a mountain climate (mean annual temperature below 3 °C, precipitation over 1400 mm), while the valley bottoms present much more temperate conditions (mean annual temperature over 12 °C, precipitation below 700 mm), and show some traits of a mediterranean climate in the eastern zone. Vegetation is also strongly influenced by this double altitude–mediterranean gradient. With valley bottoms supporting most conventional human activities, the montane belt (600–1600 m a.s.l.) being dominated by beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) in humid areas, while Scots pine (*Pinus sylvestris* L.) dominates the drier areas. The alpine belt (over 2300 m a.s.l.) is highly conditioned by cold temperatures and only supports herbaceous vegetation, while the subalpine belt (1600–2300 m a.s.l.) is dominated by mountain pine (*P. uncinata* Ram.), which can grow in all kinds of soils and forms most of the central and eastern Pyrenean tree lines.

Climatic and land-use changes in the Pyrenees

Over the last 50 years, the Pyrenees have gone through major changes in land organization (García-Ruiz, 1988; García-Ruiz & Lasanta, 1990). Until the mid 20th century, all the resources needed by the local population had to be obtained locally, and thus landscapes were highly influenced by human activities (Lasanta, 2002; Lasanta & Vicente-Serrano, 2007). Since then, strong depopulation trends in rural areas have led to much farmland being abandoned, while the crisis affecting the transhumance system has led to a sharp decline in livestock (García-Ruiz, 1988; Domínguez, 2001). Therefore, human-driven pressure concentrated on the most productive areas, especially

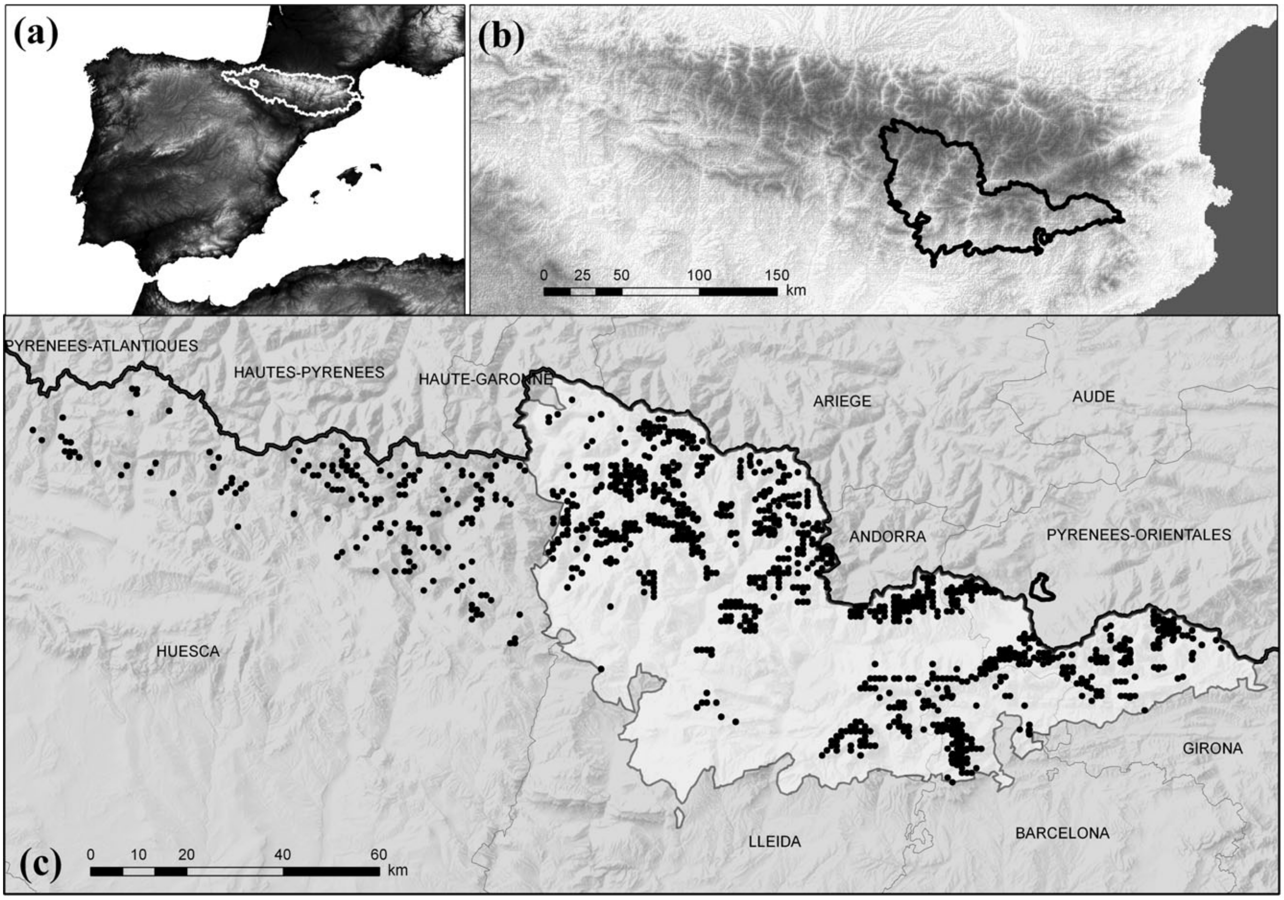

Figure 1 Location of study area showing: (a) Pyrenees mountain range; (b) study area inside the Pyrenees; (c) current distribution of mountain pine (black dots) in the Spanish Pyrenees and in the study area (white shaded) according to the Third National Forest Inventory (Dirección General para la Biodiversidad, 2007).

valley bottoms, while the hillslopes were exposed to a high risk of abandonment (García-Ruiz, 1988; García-Ruiz & Lasanta, 1990). Along with these land-use changes, climate in the Pyrenees has also changed during the last century, with annual mean temperature and annual mean minimum temperature increasing by 0.83 °C and 2.11 °C, respectively (Bucher & Dessens, 1991). These temperature increases are similar to those measured in other European mountain ranges, including the Alps (Dirnböck *et al*., 2003).

Data preparation and determination of forest cover

To investigate changes in mountain pine distribution and canopy cover, we conducted a GIS analysis by comparing more than 200 pairs of aerial photographs taken in 1956 and 2006 and covering the whole surface of the study area. The 1956 grey-scale photographs (resolution of 1 m) were georeferenced and orthorectified. For each 1956 photo, at least 15 ground control points were identified, and a digital elevation model (DEM) was added in order to incorporate altitude coordinates. Each 1956 and 2006 image was semi-automatically reclassified into a binary raster with 'tree' and 'non-tree' values, and with a resolution of 1 m (Fig. 2), and all the 1956 and 2006 reclassified images were stitched into mosaics. A 150 × 150 m sampling grid was created covering the whole 6018 km^2 study area, as this cell size (2.25 ha) matches the minimum area considered in the map of habitats of Catalonia (MHCat) (ICC, 2004). For each cell of the sampling grid, canopy cover in 1956 and 2006 was determined as the ratio between the number of 'tree' pixels and the total number of pixels in the cell, expressed as a percentage. A threshold of 10% canopy cover was used to distinguish 'forested' from 'not-forested' cells. This threshold is also used in the Spanish National Forest Inventory (Dirección General para la Biodiversidad, 2007).

Dependent variables

Encroachment (colonization)

Current distribution of mountain pine (Mp06) was obtained by intersecting the sampling grid with the MHCat, while distribution of mountain pine in 1956 (Mp56) was obtained by removing those sampling-grid cells qualified as 'not forested' in 1956. Encroachment was assessed by establishing a 200-m buffer

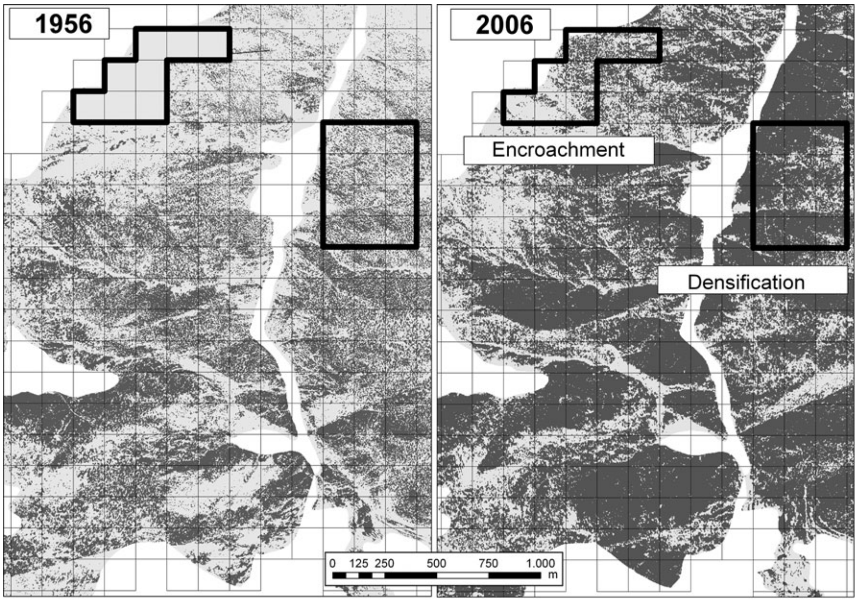

Figure 2 Example of aerial photographs from 1956 (left) and 2006 (right), reclassified into a binary variable to show mountain pine distribution. Thin solid lines correspond to the 150 × 150 m sampling grid, while thick solid lines correspond to examples of encroachment and densification processes.

around each Mp56 patch, as seed dispersion is unlikely to occur beyond this distance (Dullinger *et al*., 2004). All land-cover types where encroachment was not possible (e.g. lakes, rivers, reforested and stony areas) were excluded from the analysis. Encroachment was then assessed using a binary approach. To minimize sampling errors associated with the use of aerial photographs, we only defined as encroached those cells with no tree cover in 1956 (i.e. tree cover = 0) and with more than a 10% increase in canopy cover in the studied period (Fig. 2). Deforestation processes (areas covered by mountain pine in 1956 but not in 2006) were not taken into account, as clear-cuts and deforestation are scarce, with shelterwood, group and selection systems being the only treatments applied to mountain pine forests since the early 20th century (Gonzalez, 2008).

Densification

Forest canopy cover can increase due to growth of pre-existing individuals as well as recruitment of new ones (densification). Our focus was on densification, so in order to separate these two processes, only those cells with a 1956 canopy cover of between 10 and 40% were considered in the analysis. Cells with a canopy cover lower than 10% were considered as 'not forested' and therefore not susceptible to undergoing densification processes. Areas with canopy cover greater than 40% were also excluded, on the basis that recruitment was impossible. In fact, a mountain pine stand with a canopy cover of 40% corresponds to an average density of 600 trees ha^{-1}, which is the recommended threshold to start selection thinning (Gonzalez, 2008) and therefore wholly unsuitable for recruitment of new individuals. Furthermore, as a conservative measure aimed at ensuring that only recruitment processes were taken into account, only areas showing more than a 30% increase in canopy cover were considered as densified due to recruitment (Fig. 2).

Potential factors driving land-use changes

A set of topographic and land-use variables were selected as potential drivers of mountain pine encroachment and densification. The topographic variables included *altitude*, *slope* and *aspect*. These three variables were obtained from a digital elevation model (DEM) with a resolution of 150 m, as expansion was assessed on a 150 × 150 m grid. *Aspect* was pre-transformed into a *shade index* to more adequately reflect the variation between north and south aspects (Table 1). Thus, *shade index* increased from 0° on south aspects to 180° on north aspects, with east and west aspects given a value of 90°.

Land-use changes have affected forest expansion by two main processes: abandonment of land and reduction of livestock density (Lasanta, 2002). However, these processes cannot be directly determined, as there is no local-level information on farmland extension or livestock densities for 1956. Indirect measures or proxies based on current available indicators provide an alternative approach. *Farmland abandonment* during the second half of the 20th century is strongly tied to depopulation and to changes in economic structure (Lasanta, 2002). Therefore, the variable *population change*, defined as the ratio between population in 2001 and population in 1951, was included in the models. In addition, *population density*, defined as the total population in 2001 relative to the municipality's surface area in km^2, and *importance of primary sector*, defined as the proportion of primary-sector-dedicated employees (agriculture and stockbreeding), were used to assess differences in economic structure among municipalities (Table 1). As mentioned above, current livestock density is also a determinant of forest expansion. García-Ruiz & Lasanta (1990) observed that, at the municipality level, livestock density was highly correlated with the extension of both subalpine pastures and lowland meadows. Therefore, the influence of current livestock density on forest expansion was assessed by incorporating *proportion of*

Table 1 Covariates included in the model, indicating source, resolution and descriptive statistics.

Variable	Source	Resolution	Mean	SD	Min.	Max.	Range
Topographic							
Altitude	DEM	150 m	1984.3	256.1	1340.2	2514.9	1174.7
Slope	DEM	150 m	44.5	20.5	0.0	146.0	146.0
Shade index	DEM	150 m	70.2	45.2	0.0	180.0	180.0
Socio-economic							
Proxies for farmland abandonment							
Population change	INE	Municipality	84.5	46.6	16.0	214.0	198.0
Population density	INE	Municipality	7.7	17.5	0.7	371.0	370.3
Primary sector	IDESCAT	Municipality	13.9	8.9	0.0	53.0	53.0
Proxies for reduction of livestock density							
% meadows	IDESCAT	Municipality	1.7	3.5	0.0	29.7	28.0
% pastures	IDESCAT	Municipality	42.4	18.4	2.4	80.2	77.8

DEM, digital elevation model; INE, Spanish National Statistics Institute; IDESCAT, Catalan Statistics Institute; see text for further descriptions of the variables.

meadows and *proportion of pastures* for each municipality into the models (Table 1).

Statistical analyses

As both response variables (encroachment and densification) were represented using a binary approach, they were modelled by logistic regression. This kind of model has been extensively used to assess land-cover changes, as they are commonly expressed as discrete variables (Carmel *et al*., 2001; Serneels & Lambin, 2001; Munroe *et al*., 2004). As logistic regression is based on the assumption of independence among observations, spatial autocorrelation for both response variables was tested using Moran's I statistic. Because both response variables showed high autocorrelation, regular subsampling tools were applied. Subsampling is based on a sample-size reduction that causes distance between observations to increase, so only spatially independent data are analysed (Munroe *et al*., 2004). Semi-variograms were constructed, and the range (the distance after which semi-variance stabilizes) was determined as approximately 400 m for both datasets. Therefore, as the sample grid was 150 × 150 m, only one of each of the three points in both the x- and y-axes was sampled.

Given that most socio-economic variables were taken at the municipality level and that these factors may have an influence on both response variables, observations belonging to the same municipality may not be independent from one another (cluster-correlated data), so we followed the recommendations of Müller & Munroe (2005) and used a robust estimator based on the Huber–White or 'sandwich' estimator (Williams, 2000).

Low levels of collinearity were found among the covariates. The coefficients of determination (R^2) of one variable against all the others ranged from 0.02 to 0.59, which are in all cases below the critical value of 0.80 set by Menard (2002). All independent variables were therefore used in the models. Evidence of non-linearity between the independents and the logit of the dependent were not found for any of the models, and thus variable transformation was not required.

In order to get the most parsimonious models, a stepwise procedure was performed to remove non-significant variables. Significance of covariates was tested using the Wald statistic, and odds ratios for each covariate were estimated. Model accuracy was tested by Nagelkerke's R^2 and area under the receiver operating characteristic (ROC curve). The area under the ROC curve (AUC) gives the probability that the model will properly distinguish between presence and absence of the studied process, so predictions by chance would correspond to a value of approximately 0.5 (Gellrich *et al*., 2007a).

RESULTS

Changes in mountain pine forests

In 1956, mountain pine covered 55,196 ha, with an average canopy cover of 54.3%. By 2006, it had colonized 8898 new hectares to reach a total of 64,074 ha, i.e. a 16.1% increase in surface area. Mean canopy cover in 2006 had reached 60.9%. However, to assess this process correctly, changes in canopy cover should only be considered for the areas susceptible to densification (canopy cover lower than 40% but higher than 10% in 1956; see Methods for further detail). Taking this into account, mean canopy cover in 1956 was 31.0%, and by 2006 it had increased up to 55.6%, so canopy cover almost doubled in open mountain pine forests between 1956 and 2006.

Variables driving mountain pine encroachment and densification

Both logistic models for encroachment and densification were significant ($P < 0.001$). However, their overall explanatory power was particularly low, as indicated by Nagelkerke's pseudo-R^2, with values of 0.123 for the encroachment model and 0.101 for

Table 2 List of main parameters of both encroachment and densification logistic models.

Variable	Coefficient	Wald statistic	P	Odds ratio
Encroachment				
Intercept	1.173	13.92	< 0.001	–
Altitude	–0.001	74.04	< 0.001	0.999
Shade index	0.010	117.60	< 0.001	1.010
Population change	–0.005	28.79	< 0.001	0.995
Population density	0.008	22.32	< 0.001	1.008
Densification				
Intercept	2.170	4.50	0.038	–
Altitude	–0.001	7.92	0.006	0.999
Shade index	0.011	31.25	< 0.001	1.011

Only variables included in the model after the stepwise procedure are shown ($P < 0.05$).

the densification model, while AUC was 0.699 for the encroachment model and 0.656 for the densification model.

The variable *altitude* contributed significantly ($P < 0.05$) to both response variables, and the relationship was in both cases negative (Table 2), with forest expansion (i.e. encroachment or densification) more likely to occur at low altitudes. The odds of finding forest expansion were 2.7 times higher at 1500 m than at 2500 m, near the tree line. Therefore, the probability of forest encroachment varied from 0.50 at 1500 m to 0.27 at 2300 m, while the probability of densification varied between 0.80 and 0.60 for the same altitude range (Fig. 3). *Shade index* also contributed significantly and positively to both the encroachment and densification models ($P < 0.05$; Table 2). Thus, these processes were more likely to occur on northern rather than southern slopes. The odds ratios were 1.010 and 1.011 for encroachment and densification, respectively. This means that the odds of finding forest encroachment or densification were nearly six times higher on northern slopes (shade index of 180) than on southern slopes (shade index of 0). The probability of encroachment therefore varied between 0.24 on south-facing slopes and 0.65 on northern aspects, while the probability of densification varied between 0.55 and 0.90 for the same cases (Fig. 3). On the contrary, *slope* had no significant relationship with the response variable, either for the encroachment or densification models (data not shown).

None of the socio-economic variables showed significant relationships at $P < 0.05$ with the densification response variable (data not shown), meaning that either densification occurs independently of socio-economic conditions or that our proxy variables were unable to capture the ultimate driving factors for densification. However, the case was different for the encroachment model, in which *population change* and *population density* appeared to be significantly related to the observed changes in mountain pine forests ($P < 0.05$) while *importance of primary sector*, *proportion of pastures* and *proportion of meadows* were not (Table 2). The relationship between *population change* and encroachment was negative, showing that forests were more likely to encroach in municipalities with declining populations. For example, probability of encroachment was 0.45 for a municipality experiencing a 50% drop in population but only 0.25 for a municipality doubling its population (Fig. 3). On the other hand, *population density* had a significant and positive relationship with changes in forest cover ($P < 0.05$; Table 2), thus encroachment was more likely to occur in municipalities with a higher population density. The odds of finding encroachment in densely populated municipalities (200 inhabitants per hectare) were 4.6 times higher than for a municipality with only 10 inhabitants per hectare, and probabilities of encroachment varied, for the same cases, from 0.74 to 0.38 (Fig. 3). On the other hand, no significant relationship was found between encroachment and the proxies for the reduction of livestock density (data not shown).

DISCUSSION

During the last half of the 20th century there has been a significant expansion of mountain pine forests in the eastern Pyrenees. This process has not occurred in a homogeneous way, and has been strong in the low, north-facing slopes, although there is also a significant influence of some of the socio-economic indicators.

The major influence of topographic variables on encroachment processes seems to indicate an effect of site conditions in mountain pine expansion. The greatest probabilities of encroachment corresponded to low altitudes and to north-facing aspects, where neither thermal nor hydrological limitations could constrain the development of mountain pine (Thuiller *et al.*, 2003; Camarero & Gutiérrez, 2004; Batllori & Gutiérrez, 2008). Other studies conducted in mountain areas (Poyatos *et al.*, 2003; Coop & Givnish, 2007; Lasanta & Vicente-Serrano, 2007) have also reported lower encroachment rates in south-facing slopes associated with water stress. However, to correctly assess the importance and meaning of topographic variables, it is important to understand that they are not independent of patterns of land abandonment and livestock grazing in the Pyrenees, and therefore these results have to be reframed in a context of land-use changes (Poyatos *et al.*, 2003). In the mid 19th century, when the population of the Pyrenees was at its peak, farmlands spread into hillslopes, occupying higher altitudes and slopes. García-Ruiz (1988) points out that farmlands came to cover up to 30% of all land below 1600 m. However, profitability limitations meant that cultivation only rarely rose

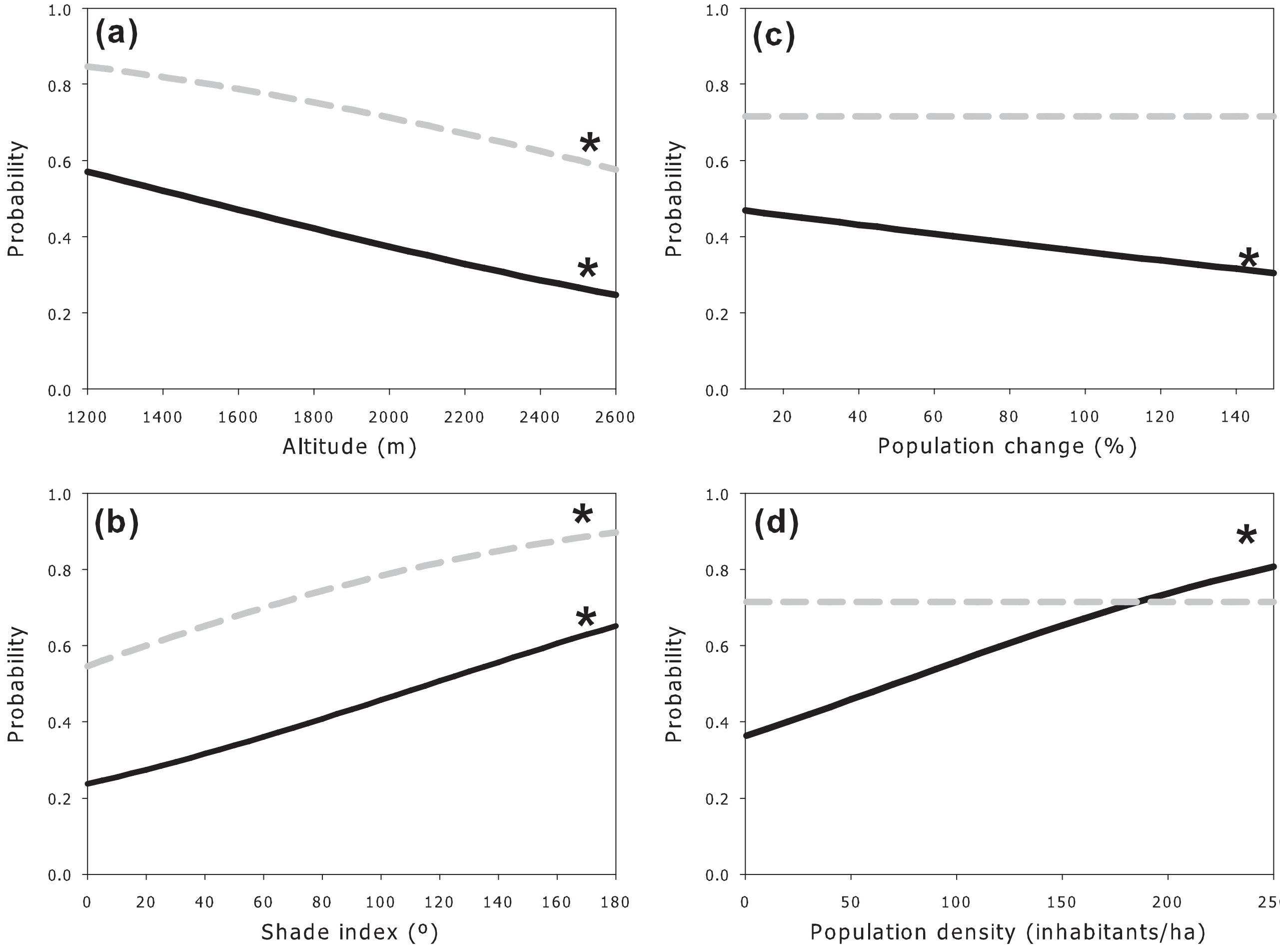

Figure 3 Effect of (a) altitude, (b) shade index, (c) population change and (d) population density on the probability of encroachment (black solid line) and densification (grey dashed line), according to developed models (Table 2). Variables other than the one on the *x*-axis are equal to their mean value in the modelling data (Table 1). Significant relationships are indicated by an asterisk (*) above the curve.

above these altitudes. Along with the important changes in land organization during the 20th century, agriculture concentrated in the valley bottoms, leaving most hillslopes abandoned, especially those situated at higher altitudes (Poyatos *et al.*, 2003). As only 10% of the mountain pine stands are located on altitudes below 1600 m, areas with higher abandonment rates would correspond to the lowest altitudes in the study area. Aspect is also not independent of land abandonment patterns, as farmlands were primarily located on south-facing slopes, with better conditions for cultivation. Therefore, after the maximum expansion of farmlands, those located on north-facing aspects were the first to be abandoned. Furthermore, the south-facing slopes had been cultivated for thousands of years, causing a loss of fertility that could limit or delay forest encroachment especially in the highest and steepest areas, where no soil conservation techniques or fertilization were implemented (García-Ruiz, 1988; García-Ruiz *et al.*, 1996; Lasanta & Vicente-Serrano, 2007). Patterns of livestock grazing are also related to topographic variables, especially altitude. When transhumance was still practised, livestock grazed subalpine grasslands during the summer and moved to the Ebro Valley in the winter (García-ruiz *et al.*, 1996; Domínguez, 2001), while low- and mid-range forests and scrublands were grazed in the intermediate periods, accounting for 17% of the total livestock food sources in the central Pyrenees (García-Ruiz *et al.*, 1996; Lasanta, 2002). More recent farming practices only use summer grasslands, while autumn, winter and spring food is obtained from lowland meadows, and forest and scrublands account for only 2% of the total food supply (Domínguez, 2001). Therefore, there has been a significant reduction in livestock density on low- and mid-range lands, which have almost disappeared as grazing areas, while grazing in subalpine summer pastures, although at a lower livestock density, remains important.

Mountain pine encroachment was also significantly affected by patterns of farmland abandonment at the municipality level, as indicated by its relationship with the analysed proxies. However, it was not the case for proxies of livestock density. The probability of encroachment was higher in municipalities experiencing greater population losses and in municipalities with higher population density. These findings reflect two extreme cases of changes in population structure in the Pyrenees. On one hand, small villages, where the economy was highly dependent on agriculture and stockbreeding, suffered strong depopulation over the 20th century, as traditional activities lost profitability (Molina, 2002; Gellrich *et al*., 2008). In these municipalities, the rate of land abandonment (and associated forest encroachment) is highly related to depopulation (Lasanta, 1990). On the other hand, the biggest villages had developed a trade and industry network, so instead of losing population they actually recruited part of the exodus from the smaller villages (Lasanta, 1990; Molina, 2002). Furthermore, the 1970s marked the growth of tourism as an important economic sector in the Pyrenees. Most of the tourist facilities were located in the most populated villages in each valley, where tourists could find the services they demanded (Molina, 2002), further consolidating the population differences between small and big villages. However, in these municipalities, a greater population density does not necessarily correspond to a greater pressure on the territory, as their economy is not based on primary sectors. In fact, most of the tourist facilities (apartments, camp sites and hotels) were sited on valley bottoms, where they directly competed for space with meadows and farmlands, causing opportunity costs for agriculture and stockbreeding to increase, and therefore contributing to land abandonment. Lasanta (2002) found a positive and significant correlation between tourist development and rates of farmland abandonment and livestock density decline in several municipalities in the Pyrenees, while other authors report correlations between high population densities and rates of forest encroachment (Gellrich *et al*., 2007a, 2008). Surprisingly, the variable *primary sector* showed a non-significant relationship with encroachment probability. This is probably related to the increasing number of part-time farms (i.e. where the farmer is not exclusively dedicated to agriculture or stockbreeding) established in the area over the last few decades. Gellrich *et al*. (2007a) highlighted the importance of part-time farms in determining forest encroachment in the Alps. Therefore, the lack of significance for primary sector activity could be due to these part-time farmers, who are not included in the agrarian census.

Unlike encroachment, densification was not significantly influenced by any of the socio-economic covariates. According to Poyatos *et al*. (2003), forest densification reflects the decreasing use of fuelwood and timber as a result of population decline and the shift towards other energy sources and materials. However, mountain pine timber has never been extensively used as fuelwood in the Pyrenees, where other species, such as beech or oak, were preferred due to their better properties and proximity to village centres. Nevertheless, densification is significantly related to altitude and, above all, to aspect. This could imply that climatic conditions may limit this process, either by temperature constraints at higher altitudes or by drought conditions on south-facing slopes. In any case, our analysis of mountain pine densification focuses exclusively on the period 1956–2006. However, land abandonment, and hence forest encroachment, had started before 1956. Indeed, Lasanta (2002) points out that most of the non-permanent and low-fertility farmlands had already been abandoned by 1936. Thus, many of these areas could have undergone encroachment processes in the following years, and therefore by 1956 would present low canopy cover susceptible to densification in the following years. Hence, patterns of densification may depend on encroachment patterns prior to 1956. Our results agree with this premise as densification processes were found to be more important in north-facing exposures and low altitudes (between 1200 and 1600 m), home to the first farmlands to be abandoned during the first half of the century (García-Ruiz, 1988; Poyatos *et al*., 2003).

To recap, over the last 50 years, subalpine forests in the eastern Pyrenees have undergone significant encroachment and densification. On a regional scale, these patterns are highly related to patterns of farmland abandonment. Forest has colonized most of the abandoned fields, and therefore forest encroachment has been more important at low and medium altitudes than close to the tree line, indicating that land-use changes have a greater influence on forest expansion than climate changes. However, this does not mean that climate has no influence on forest dynamics, as the response of forest–grassland ecotones to climate changes depends on several factors, including autoecological characteristics, phenotypic plasticity and availability of regeneration niches, among others (Camarero & Gutiérrez, 1999; Holtmeier & Broll, 2005). Therefore, the influence of climate change is not necessarily reflected as tree line displacement, as changes in stand density and recruitment or in growth form are more likely to occur (Szeicz & MacDonald, 1995; Camarero *et al*., 2000; Camarero & Gutiérrez, 2004; Gehrig-Fasel *et al*., 2007; Batllori & Gutiérrez, 2008). In fact, Camarero & Gutiérrez (1999, 2004) studying a mountain pine stand in the Pyrenees, found significant changes in recruitment and tree growth inside the stand, despite a reduced or even null altitudinal rise of the tree line. However, even considering the influence of climate on tree line dynamics, our results indicate that, in the Pyrenees, land-use changes are the main drivers of recent mountain pine encroachment at regional scale. Therefore, future research on tree line dynamics in the Pyrenees should explicitly consider the influence of land-use changes in order to correctly estimate the net contribution of processes associated with climate change.

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