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DOI: [10.1111/j.1466-8238.2010.00550.x](https://doi.org/10.1111/j.1466-8238.2010.00550.x)

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

Running header: Land-use changes drive *Pinus uncinata* expansion

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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 in a whole mountain-range scale by the study of different topographic and socio-economic potential drivers in the current global-change context.

Location The study area includes the whole distributional area of Mountain pine in the Catalan Pyrenees (NE Spain). This represents more than 80 municipalities, covering a total area of 6,018 km².

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 150x150m cell-size grid. We then used logistic regression to analyze the effects of several topographic and socio-economic variables on forest expansion.

Results In the period analyzed, Mountain pine increased its surface coverage by 8,898 hectares (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 of Mountain pine expansion, as encroachment rates were higher at municipalities with greater population losses or weaker primary sector development.

Main Conclusions The spatial patterns of Mountain pine expansion highly matched the main patterns of land-use change in the Pyrenees, suggesting that land-use changes have played a more determinant role than climate in driving forest dynamics at landscape scale over the period

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studied. Further studies on forest expansion at regional scale should incorporate patterns of land-use changes to correctly interpret drivers of forest encroachment and densification.

Keywords Mountain pine, Pyrenees, encroachment, densification, land-use changes, global warming, canopy cover, image reclassification

1 INTRODUCTION

2 Despite the high rates of deforestation measured worldwide, forest cover in most developed
3 countries is on the increase (Coop & Givnish, 2007; Gellrich *et al.*, 2007a; Gellrich &
4 Zimmermann, 2007). Although this increase is mainly caused by forest encroachment into open
5 areas, there has also been an increase in canopy cover of pre-existent forests, either through
6 enhanced growth of pre-existent individuals or the recruitment of new ones (densification)
7 (Poyatos *et al.*, 2003; Gehrig-Fasel *et al.*, 2007). Forest expansion (including both encroachment
8 and densification) does not occur homogeneously at the local scale, as it is determined by both
9 natural and cultural factors, such as local recent livestock pressure (Dirnböck *et al.*, 2003;
10 Lasanta-Martinez *et al.*, 2005; Coop & Givnish, 2007), topographic factors (Poyatos *et al.*,
11 2003; Gellrich & Zimmermann, 2007) and locally dominant ecological and socio-economic
12 conditions, among others (Debussche *et al.*, 1999). However, these drivers usually act at
13 different scales: for example, the decision to abandon a farmland depends on socio-economic
14 factors, and subsequent changes in land cover will be modulated by ecological processes, which
15 in turn are associated with environmental and climatic conditions (Rutherford *et al.*, 2008).
16 Therefore, researchers have studied land-cover change at a wide range of spatial scales, from
17 small plots to entire mountain ranges. Local-scale approaches based on the study of plots
18 usually employ dendrochronology methods (Camarero & Gutierrez, 2007; Chauchard *et al.*,
19 2007), while at larger spatial scales, land-cover changes have mainly been assessed by
20 comparison of aerial photographs (Miller, 1999; Coop & Givnish, 2007; Gellrich *et al.*, 2008).
21 Lastly, changes in large areas (covering thousands of square kilometres) have mainly been
22 analyzed using remote sensing techniques (Gellrich & Zimmermann, 2007; Millington *et al.*,
23 2007). Although attempts have been made to integrate these scales (Jump *et al.*, 2006; Lasanta
24 & 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, since 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 & Gutierrez, 2004; Camarero *et al.*, 2006; Batllori & Gutierrez, 2008). Nevertheless, over the last century, European mountain systems have suffered not only global warming but also major demographic, economic and organizational changes (Garcia-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 north-Mediterranean basin (Dale, 1997; Sala *et al.*, 2001; Chauchard *et al.*, 2007; Gehrig-Fasel *et al.*, 2007; Gellrich *et al.*, 2007b; Millington *et al.*, 2007).

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 dendro-ecological, climate-related standpoint (Szeicz & Macdonald, 1995; Macdonald *et al.*, 1998; Camarero & Gutierrez,

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2004; Batllori & Gutierrez, 2008) but has never, to our knowledge, been quantified at landscape scale, despite reports establishing its important role in land-cover change contexts (Poyatos *et al.*, 2003; Gehrig-Fasel *et al.*, 2007; Lasanta & Vicente-Serrano, 2007).

The main objectives of this study were (i) to assess spatial patterns of Mountain pine encroachment and densification in the Eastern Pyrenees at both local and regional scale, and (ii) 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 changes.

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 French and Spanish border, with an extension of more than 50,000 km². The study area is located southeast 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 6,018 km² (Fig. 1). The abrupt terrain of the study area, with altitude ranging from 500 to more than 3,000 m a.s.l., in conjunction with the proximity of Mediterranean Sea creates significant climatic variation. Thus, the highest areas are representative of mountain climate (mean annual temperature below 3°C, precipitation over 1400 mm), while the valley bottoms present much temperate conditions (mean annual temperature over 12°C, precipitations below 700 mm), and show some traits of mediterraneity in the eastern zone. Vegetation is also strongly influenced by this double altitude-mediterraneity gradient. With valley bottoms supporting most conventional human activities, the montane belt (600-1600 m a.s.l.) is dominated by beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) in humid areas, while Scots pine (*Pinus sylvestris* L.) dominates the dryer ones. 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 (*Pinus uncinata* Ram.), which can grow in all kinds of soils and forms most of the central and eastern Pyrenean tree lines.

PLEASE INSERT HERE FIGURE 1

Climatic and land-use changes in the Pyrenees

Over the last 50 years, the Pyrenees have gone through major changes in land-organisation (Garcia-Ruiz, 1988; Garcia-Ruiz & Lasanta, 1990). Until the mid-20th century, all the resources needed by local societies 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 led to many farmlands being abandoned, while the crisis affecting the transhumance system led to a sharp decline in livestock (Garcia-Ruiz, 1988; Domínguez, 2001). Therefore, human-driven pressure concentrated on the most productive areas, especially valley bottoms, while the hillslopes were exposed to high risk of abandonment (Garcia-Ruiz, 1988; Garcia-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 (with a resolution of 1 m)) were geo-referenced 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 meter (Fig. 2), and all the 1956 and 2006 reclassified images were stitched into mosaics. A 150x150 m sampling grid was created covering the whole 6,018 km² study area, as this cell size

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(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 were determined as the ratio between the amount of ‘tree’ pixels and the total number of pixels in the cell, expressed as 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 (Direccion General Para La Biodiversidad, 2007).

PLEASE INSERT HERE FIGURE 2

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 meters buffer 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 to 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 on Mountain pine forests since the early 20th century (Gonzalez, 2008).

Densification

Forest canopy cover can increase due to growth of pre-existent 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 undergo 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 assuring 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 meters, as expansion was assessed on a 150x150 m grid. *Aspect* was pre-transformed into a *shade index* to more adequately reflect variation between north and south aspects (Table 1). Thus, shade index increased from 0° at south aspects to 180° at north aspects, with east and west aspects given a value of 90°.

Land-use changes have affected forest expansion by two main processes: land abandonment 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 in relation the municipality's surface area in square kilometers; 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. Garcia-Ruiz & Lasanta (1990) observed that, at municipality level, livestock density was highly correlated with the extension of both subalpine pastures and lowland meadows. Therefore, influence of current livestock density on forest expansion was assessed by incorporating *proportion of meadows* and *proportion of pastures* for each municipality into the models (Table 1).

PLEASE INSERT HERE TABLE 1

Statistical analyses

As both response variables (encroachment and densification) were represented using a binary approach, they were modeled 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). Since logistic regression is based on the assumption of independence among observations, spatial autocorrelation for both response variables was tested using Moran's *I* statistic. Since 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-

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independent data are analyzed (Munroe *et al.*, 2004). Semivariograms were constructed, and the range (the distance after which semivariance stabilizes) was determined as approximately 400 m for both datasets. Therefore, as the sample grid was 150x150 m, only one of each three points in both the *x* and *y* axis was sampled.

Given that most socio-economic variables were taken at 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 Muller & Munroe (2005) and used a robust estimator based on the Huber-White or ‘sandwich’ estimator (Williams, 2000).

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13

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

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

13

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 8,898 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 has 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 considerably low, as indicated by Nagelkerke's pseudo- R^2 , with values of 0.123 for the encroachment model and 0.101 for 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 meters than at 2500 meters, near the tree line. Therefore, the probability of forest encroachment varied from 0.50 at 1500 meters to 0.27 at 2300 meters, 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

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northern rather than southern slopes. Odds-ratio was 1.010 and 1.011 for encroachment and densification, respectively. This means that the odds of finding forest encroachment or densification were nearly 6 times higher on northern slopes (shade index of 180) than on southern slopes (shade index of 0). Probability of encroachment therefore varied between 0.24 on south-facing slopes and 0.65 on northern aspects, while 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 neither for the encroachment nor densification models (data not shown).

PLEASE INSERT HERE TABLE 2

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 higher population density. The odds of finding encroachment in dense-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).

PLEASE INSERT HERE FIGURE 3

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 hydric limitations could condition the development of Mountain pine (Thuiller *et al.*, 2003; Camarero & Gutierrez, 2004; Batllori & Gutierrez, 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. Garcia-Ruiz (1988) points out that farmlands came to cover up to 30% of all land below 1600 meters. However, profitability limitations meant that cultivation only rarely rose above these altitudes.

Along with the important changes on land-organisation during the 20th century, agriculture concentrated in the valley-bottoms, leaving most hillslopes abandoned, especially those situated on higher altitudes (Poyatos *et al.*, 2003). Since only 10% of the Mountain pine stands are located on altitudes below 1,600 m, areas with higher abandon rate would correspond to the lowest altitudes in the study area. Aspect is also not independent of land abandonment patterns, since 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 highest and steepest areas, where no soil conservation techniques or fertilization were implemented (Garcia-Ruiz, 1988; Garcia-Ruiz *et al.*, 1996; Lasanta & Vicente-Serrano, 2007). Patterns of livestock grazing are also related to topographic variables, especially altitude. When transhumance was still practiced, livestock grazed subalpine grasslands during the summer and moved to the Ebro valley in the winter (Garcia-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 Central Pyrenees (Garcia-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 only account for 2% of the total food supply (Domínguez, 2001). Therefore, there has been a significant reduction in livestock density on low and mid-range land, which have almost disappeared as grazing areas, while grazing in subalpine summer pastures, although at lower livestock density, remains important.

Mountain pine encroachment was also significantly affected by patterns of farmland abandonment on the municipality level, as indicated by its relationship with the analyzed proxies. However, it was not the case for proxies of livestock density. 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, 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 compete 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; Gellrich *et al.*, 2008). Surprisingly, the variable *primary sector* showed a non-significant relationship with encroachment probability. This is likely 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)

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1 highlighted the importance of part-time farms in determining forest encroachment in the Alps.
2 Therefore, the lack of significance for primary sector activity could be due to these part-time
3 farmers, who are not included in the agrarian census.

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

22 To recap, over the last 50 years, alpine forests in the Eastern Pyrenees have undergone
23 significant encroachment and densification. On a regional scale, these patterns are highly related
24 to patterns of farmland abandonment. Forest has colonized most of the abandoned fields, and

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DOI: [10.1111/j.1466-8238.2010.00550.x](https://doi.org/10.1111/j.1466-8238.2010.00550.x)

1 therefore forest encroachment has been more important at low and medium altitudes than close
2 to the tree line, indicating that land-use changes have a greater influence on forest expansion
3 than climate changes. However, this does not mean climate has no influence on forest dynamics,
4 as the response of forest-grassland ecotones to climate changes depends on several factors,
5 including autoecological characteristics, phenotypic plasticity and availability of regeneration
6 niches, among others (Camarero & Gutierrez, 1999; Holtmeier & Broll, 2005). Therefore,
7 influence of climate change is not necessarily reflected as tree line displacements, as changes in
8 stand density and recruitment or in growth form are more likely to occur (Szeicz & Macdonald,
9 1995; Camarero *et al.*, 2000; Camarero & Gutierrez, 2004; Gehrig-Fasel *et al.*, 2007; Batllori &
10 Gutierrez, 2008). In fact, Camarero & Gutierrez (1999; 2004) studying a Mountain pine stand in
11 the Pyrenees, found significant changes in recruitment and tree growth inside the stand, despite
12 a reduced or even null altitudinal rise of the tree line. However, even considering the influence
13 of climate on tree line dynamics, our results indicate that, in the Pyrenees, land-use changes are
14 the main drivers of recent Mountain pine encroachment at regional scale. Therefore, future
15 research on tree line dynamics in the Pyrenees should explicitly consider the influence of land-
16 use changes in order to correctly estimate the net contribution of climate-change associated
17 processes.

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ACKNOWLEDGEMENTS

This research was primarily supported by the Spanish Ministry of Science and Innovation via the Consolider-Ingenio Montes project (CSD2008-00040) and the DINAMIX project (AGL2009-13270-C02). It was also supported by a Ramon y Cajal contract to Drs. L.Coll and L.Brotons, and a doctoral grant to the first author (AP2007-01663). Additional funding came from the *Departament de Medi Ambient* of the Regional Catalan government. The authors thank the Department of Geography of the Universitat Autònoma de Barcelona for kindly providing access to aerial photographs, and Dr. Gonzalez-Olabarria for valuable input on drafting the manuscript.

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1 TABLES

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

Variable	Source	Resolution	Mean	Std. Dev.	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							
<i>Proxies for farmland abandonment</i>							
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
Imp. Primary Sector	IDESCAT	Municipality	13.9	8.9	0.0	53.0	53.0
<i>Proxies for reduction of livestock density</i>							
% 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

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Table 2 List of main parameters of both encroachment and densification logistic models. Only variables included in the model after stepwise procedure are showed (p<0.05).

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
Pop. 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

1 FIGURES

2

Figure 1 Location of study area showing (a) Pyrenees mountain range; (b) study area inside the Pyrenees; (c) current distribution of Mountain pine in Spanish Pyrenees and in study area (white shaded) according to Third National Forest Inventory (Direccion General Para La Biodiversidad, 2007).

Figure 2 Example of 1956 (left) and 2006 (right) aerial photographs, reclassified into a binary variable to show Mountain pine distribution. Thin solid lines correspond to 150x150 m sampling grid, while thick solid lines correspond to examples of encroachment and densification processes.

Figure 3 Effect of altitude (a), shade index (b) population change (c) and population density (d) 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 modeling data (Table 1). Significant relationships are indicated by an asterisk (*) above the curve.