Land use and climate effects on forest distribution over space and time. A case study at the Eurosiberian-Mediterranean boundary

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Complete List of Authors:	Álvarez-Martínez, Jose Manuel; University of León, Biodiversidad y Gestión Ambiental; National Museum of Natural Sciences, CSIC, Ecología Evolutiva Suárez Seoane, Susana; University of León, Biodiversidad y Gestión Ambiental de Luis Calabuig, Estanisao; University of León, Biodiversidad y Gestión Ambiental
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Land use and climate effects on forest distribution over space and time. A case study at the Eurosiberian-Mediterranean boundary

Jose Manuel Álvarez-Martínez[ab*], Susana Suárez-Seoane[a] and Estanislao de Luis Calabuig[a]

[a] Área de Ecología, Departamento de Biodiversidad y Gestión Ambiental, Facultad de Ciencias Biológicas y Ambientales, Universidad de León, Campus de Vegazana s/n, 24071 León, Spain

[b] Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006 Madrid, Spain

*Corresponding author. jm.alvarez@unileon.es

Abstract

1. In Mediterranean mountainous areas, forests have expanded during recent decades because traditional management practices have been abandoned or reduced. However, understanding the ecological mechanism behind landscape change is a complex task since the effects of land use change may be influenced (reinforced or constrained) by other factors as climate.

2. We used orthorrectified aerial photographs for monitoring changes in forest distribution in a set of 20 head-water basins (located in a mountainous protected area at the Eurosiberian-Mediterranean limit) during the second half of the 20th century (years 1956, 1974, 1983, 1990 and 2004). In particular, we evaluated the combined effects of both land use history (comparing natural *vs.* anthropic basins) and microclimate (comparing shaded *vs.* sunny aspects) for assessing gain/loss rates and spatial distribution shifts of forests. Finally, in the stated scenarios of land use history and microclimate, we accomplished a spatially explicit approach (MaxEnt and BIOMOD techniques) for modelling forest expansion on the basis of topography, soil properties and mesoclimatic variables.

3. In average, forest cover increased from 10.72% in 1956 to 27.67% in 2004. The rate of expansion was significantly higher in natural basins and, particularly, in shaded slopes during recent decades. In all cases, the mean elevation of new forest patches increased during the study period, being this trend more evident on natural sunny slopes. The performance of the models and the magnitude of the effects varied across land use history, microclimatic conditions and biogeographic origin of forests. The main drivers of forest expansion were temperature and precipitation in late spring and beginning of summer and soil properties.

4. *Synthesis*. The mixed approach developed in this work, combining monitoring and modeling, contributed to the understanding of forest dynamics in cultural systems, indicating that ecological succession is not a homogeneous process, but varies spatially due to human and abiotic constraints since historical times.

Keywords: Monitoring; Forest Expansion; Land Use Change; Spatial Modelling; Vegetation shifts.

1. Introduction

Mountainous territories of Northern Hemisphere, with a long history of human occupation, have undergone important changes in traditional management practices during recent decades (Lepart and Debussche 1992; MacDonald et al. 2000). Socio-economic adjustments, as those linked to the EU Common Agricultural Policy (CAP), have led to a dramatic rural exodus and subsequent abandonment of agricultural land, a cessation of coppicing and a reduction of grazing in natural communities (Debussche et al. 2001; Benayas et al. 2007). As a consequence, natural vegetation regeneration processes have being reactivated (Peñuelas and Boada 2003; Vicente-Serrano et al. 2004), causing a widespread forest expansion (MacDonald et al. 2000; Capitanio and Carcaillet 2008). In abandoned agricultural lands, the process of secondary ecological succession exhibits a predictable sequence of change, with different species successively gaining and losing predominance (Suárez-Seoane et al. 2002; Roder et al. 2008). A few years after abandonment, shrub vegetation develops, including both light demanding species as well as seedlings of shade tolerant trees. Later, trees develop to form a close canopy and early stage species disappear (Calvo et al. 1999). Nevertheless, regeneration patterns may vary spatially depending on land use history (e.g. recurrent fire events or grazing pressure, involving soil erosion and fertility depletion, may prevent forest expansion) and climate (e.g. warmer temperatures, implying higher evapotranspiration and soil water scarcity, may drive to altitudinal or latitudinal forest shifts) (Randall and Pickett 1994; Peñuelas et al. 2007a; Gimeno et al. 2012). The evaluation of the spatially-explicit interactions between both factors is essential to understand distribution shifts since the way in which land use history modify landscape patterns may be influenced (reinforced or constrained) by climate or *viceversa*. Nevertheless, although there is a substantial body of literature on the impacts of either climate or land use history on species distribution (Verburg et al. 2002, 2006; Thuiller 2003; Araújo et al. 2005), the assessment of their interactions still remain unsolved (Dale et al. 2000). In this sense, spatial modelling approaches can be useful tools to better understanding the mechanisms behind past-to-present distributional shifts at different scales (Verburg et al. 2002). However, to achieve a comprehensive knowledge of the complex reality, modelling techniques should be combined with powerful series of data collected by monitoring (Thuiller et al. 2008). Otherwise, the magnitude of uncertainties could be so great that it could lead stakeholders to question the overall usefulness of predictions for solving management problems (Pearson et al. 2006; Araújo and New 2007; Hanspach et al. 2010).

During recent decades, an increasing number of spatially-explicit monitoring and modelling methodologies have been developed. Many of these methods are based on remote sensing (RS) techniques (Treitz and Rogan 2004), that provide regional data at different temporal scales with low collection effort. However, although RS has been presented as an easy tool for deriving land cover inventories, most of easily available satellite images have a relatively coarse spatio-temporal resolution and resulting maps are often plagued of error and uncertainty due to misclassification and landscape complexity (Lewis et al. 2000; Liu et al. 2007; Álvarez-Martínez et al. 2010; Morán-Ordóñez et al. 2012). In this framework, historical aerial photographs, available in Spain since 1956, are important sources of geographic data useful for assessing long-term distribution patterns of vegetation at decade timescales (Carmel and Kadmon 1998). Photo-interpretation, as well as image classification, can be seen as a simplification of landscape complexity associated to a certain degree of confusion

(Álvarez-Martínez et al. 2010). However, the spatial resolution of the orthophotos allows for developing highly reliable land cover maps (e.g. at local scale even small shrubs can be identified). In any case, whatever the origin of the information, spatially-explicit time-series of land cover data allow for applying modelling exercises (Serra et al. 2008, Álvarez-Martínez et al. 2011) which enable scientists, landscape managers and policy makers to design large-scale conservation strategies aimed to preserve some of the unique characteristics of landscapes under global change (Kates et al. 2001).

La Sierra de Ancares is a Spanish Natural Park located in the Cantabrian Mountains (Fig. 1), covering approximately 100000 ha. Elevation ranges from 600 to 2200 meters a.s.l. and relief is moderate to steep. Climate is Atlantic, with a mean annual precipitation of 1300 mm and a mean temperature of 8°C, but it shows Mediterranean characteristics at lower elevations and latitudes (Rivas-Martínez and Rivas-Saenz 1996-2009; Ninyerola et al. 2005). During the 20th century, a non-significant trend of slight warming and rainfall quantity and variability was detected from a long time-series of data provided by the Spanish Meteorological Institute (www.aemet.es) (Fig. 2; own unpublished data). This region constitutes the south-westernmost distribution limit of several species of Eurosiberian trees, including beeches (*Fagus sylvatica*), oaks (*Quercus petraea, Q. robur*) and birches (*Betula* spp). At lower latitudes and elevations, especially in areas receiving higher insolation, the vegetation is typically Mediterranean, with dominance of *Quercus pyrenaica*. A history of over-exploitation through cultivation and grazing, coppicing for charcoal or wood extraction for building and heating resulted in the contraction and fragmentation of the original forest cover (Gil-Sánchez and Torre-Antón 2007). Conversely, during recent decades, rural depopulation and decrease in human pressure have resulted in the disappearance of traditional management practices. Although deliberate burning still occurs in some areas, land abandonment is allowing for vegetation recovery in old fields, as described in many Mediterranean mountain areas (Poyatos 2003; Pueyo and Beguería 2007).

The overarching objective of this work was to analyze the ecological mechanisms behind forest distribution changes over space (in a set of head-water basins located across La Sierra de Ancares) and time (during the second half of the 20th century) by developing a mixed approach based on monitoring and modelling. We explicitly evaluated the combined effects of land use history (comparing natural *vs*. anthropic basins) and microclimate (comparing shaded *vs*. sunny slope aspects) in regard to gain/loss rates and distribution shifts of forests, particularly across altitudinal gradients. Additionally, we modelled spatially forest expansion on the basis of three families of potential drivers (topography, soil and mesoclimate) for the scenarios of land use history and microclimate stated at basin scale. Finally, we evaluated the geographic transferability of the models calibrated within the basins when predicting forest expansion for the whole Natural Park (Randin *et al*., 2010). Disentangling the effects of land use and climate variability on forest distribution is of high interest from an ecological, conservation and planning perspective.

2. Materials and methods

2.1. Study area: defining a set of head-water basins

The boundaries of all head-water basins of La Sierra de Ancares were delineated using hydrological GIS tools over a Digital Elevation Model of 5-meters of spatial resolution (5-m DEM; ITACYL 2008), assuming a minimum contributing area of 100 ha (40000 pixels). In order to identify groups of basins with different land use history, we ran a Principal Component Analysis (PCA) on the basis of two variables obtained from Álvarez-Martínez et al. (2010): (i) dominant land cover (i.e. forests or heathlands) in 2004 and (ii) human management during the previous decade (i.e. recurrence of fire events larger than 1ha). Then, we selected a subset of 20 basins (Fig. 1) that maximized the differences among both variables. These basins were homogeneously distributed across the Natural Park and occupied a total area of ca 6000 ha. Ten of them were labeled as "natural basins", located in general at higher latitudes and elevations, with limited human management during last decades and mature forests in a good state of conservation covering around 50% of the total area. The other ten were labeled as "anthropic basins" and consisted of intensively human-managed basins, closer to population settlements, affected by recurrent fire events and covered by a matrix of heathlands that included some forest patches. Currently, there is no human activity in any of these 20 basins, excepting a residual grazing in some valley bottoms and subalpine pastures.

Since microclimate vary markedly between different slope aspects, each basin was subsequently split in two parts on the basis of the incoming insolation. Despite insolation drives many physical and biological processes, such as snow melt patterns, soil moisture, evapotranspiration and light available for plant photosynthesis (Hasler 1982;Valladares et al. 2008; Millington et al. 2009; Zheng et al. 2012), it has been poorly assessed as a factor contributing to plant responses against environmental change (Grace et al. 2002; Mouillot et al. 2002; Pueyo and Beguería 2007).We derived an annual incoming insolation model from the 5-m DEM to be used as a comprehensive indicator of microclimatic conditions. Output values vary spatially depending upon latitude, elevation, topography, sun angle and atmospheric effects. The highest values of insolation were assigned to sunny slopes and the lowest to shady slopes, with an averaged threshold for the 20 basins of 1.295±0.143 MWh/m^2/year. In summary, we defined a two-factor (land use history and microclimate) analysis with ten replicates for each case (Quinn and Keough 2002).

2.2. Monitoring changes in forest distribution

A total of 348 aerial photographs (scales ranging from 1:10000 to 1:30000) for the years 1956 (American flight), 1974, 1983 and 1990 were provided by the Regional Government of Castilla y León. All photos were scanned at 600 dpi, orthorectified and projected into a common UTM grid (Wrobel, 1991). Digital georeferred aerial photographs at 1:5000 scale were also obtained for 2004 from ITACYL (2008). The whole time-series was co-registered across years with a RMSE smaller than 2m. A hundred land cover maps (20 basins, five years) were then created at a detailed spatial scale by on-screen digitalization. Eight major categories were recognized, but only broadleaf forests (forests, hereinafter) were retained for further analyses. To ensure that parcel boundaries matched across the time-series, we first mapped land covers for 2004. Then, we edited these maps (deleting or adding boundary lines to the polygons) to derive land covers for the previous year (i.e. 1990) within the time-series, and so on for 1983, 1974 and 1956. To validate the 2004 land cover maps, an intensive fieldwork was carried out from 2004 to 2008, amending boundary lines and attributes when necessary. Maps were handled as GIS vector data for calculations of areas and expansion rates.

Changes in forest distribution were then spatially-explicitly analyzed through a post-classification comparison (Lambin 1999). All pair-wise combinations of maps were studied using transition matrices, which allowed an assessment of the nature, magnitude and direction of changes (Álvarez-Martínez et al. 2010). For each basin and time span, including the whole period 1956 to 2004, we quantified the following variables: (i) Percentage of area covered by forest (*FO*), calculated as the ratio between the area occupied by forest (A_F) and the total area (A_T) (Eq. 1). (ii) Percentage of forest change (FO_{CH}), estimated as the difference between forest cover in the year *t* (FO_t) and the previous year *t-1* (FO_{t-1}) (Eq. 2). (iii) Annual rates of forest change (FO_{AR}), calculated as the ratio between the percentage of forest gained or lost (FO_{CH}) and the number of years of the considered time span (*T*) (Eq. 3).

$$FO = (A_F / A_T) * 100 \qquad \text{(Eq. 1)}$$

$$FO_{CH} = FO_t - FO_{t-1} \qquad \text{(Eq. 2)}$$

$$FO_{AR} = FO_{CH} / T \qquad \text{(Eq. 3)}$$

To estimate eventual upwards altitudinal shifts of forests, we overlapped the new forest patches detected at each time span with the 5-m DEM. Since the 20 basins were located at different elevations throughout the Natural Park (Fig. 1), the average elevation of new forest patches was standardized (i.e. centered) at each time span by subtracting the average elevation of each basin.

To detect significant differences ($P<0.05$) in forest gain/loss rates and altitudinal shifts for the scenarios of land use history and microclimate, we conducted (for each time span) two-way ANOVAs with Bonferroni correction (to counteract the problem of multiple comparisons). The majority of data fulfilled both normality (Kolmogorov-Smirnov and Shaphiro-Wilk tests) and homocedasticity (Levenne test) criteria.

2.3. Modelling forest expansion

We modelled forest expansion for all possible scenarios of land use history and microclimate. To ensure a good representation of environmental heterogeneity, avoiding high spatial autocorrelation, we calibrated the models using a random sample of 6000 points that covered the set of 20 basins under study (6000ha). Sample size was defined after several tests on the effects of background sample size on model structure. A 1000 of points were positive cases corresponding to new patches of forest (i.e. those present in 2004 but not in 1956) and the remaining 5000 were background negative locations. The number of positive and background cases varied among the nine scenarios, but prevalence 1/5 (proportion of presence cases) was always guaranteed. Cramer (1999) and Hosmer and Lemeshow (2000) stated that large number of negative cases bias the model output probabilities towards zero, leading to higher omission error rates and reducing sensitivity (true predicted presences) of the analyses. Since overestimation is frequent in land cover change studies of heterogeneous and changing landscapes (Bradley and Mustard, 2005; Álvarez-Martínez *et al.*, 2010), we used in this work an unbalanced dataset towards absences. This will provide more conservative and reliable models of forest expansion (Álvarez-Martínez *et al.*, 2011). To state the purpose of the model (i.e. to predict forest expansion, but not persistence) (Pontius and Pacheco, 2004), the existing forests in 1956 were excluded from the analyses.

Regarding environmental predictors, a comprehensive GIS-database on mesoclimate, topography and soil properties was created from different sources. Potentially explanatory variables were chosen according to our knowledge of the study area (Álvarez Martínez et al. 2010, 2011) and other mountain landscapes (e.g. Rao and Pant 2001), avoiding any aprioristic selection/rejection. (i) Fifty two annual and monthly mesoclimatic variables representing minimum, maximum and mean temperature and rainfall, annual rainfall variability (coefficient of variation of monthly values) and thermal amplitude (i.e. maximum difference between extreme monthly temperatures) were extracted from a climatic data set at 200 meters resolution for the Iberian Peninsula (Ninyerola et al. 2005, 2007). (ii) Three topographical variables accounting for elevation (indirectly determining temperature and rainfall), slope (accounting for water and nutrient availability in the soil) and curvature (calculated as the second derivative of the surface, indicating whether a given area is convex or concave, which is also related to solar radiation and soil moisture) were calculated from the 5-m DEM. (iii) Three variables on soil properties were derived from a soil map created *ad hoc* for the 20 head-water basins. 100 soil samples (1 kilo each), 5 for each watershed, were taken from the 20 cm top soil and analyzed for organic matter content, pH and sand percentage. To exclude short distance variability of the soil, a mixed sample was taken from 4 points in an area of approximately 100 m^2. Samples were then analyzed in the laboratory, after being air dried for a couple of days and sieved using a 2 mm sieve, to separate the mineral fraction from gravel, stones and roots. Topsoil organic matter content (SOM) was assessed by loss of the humidity on oven-dry (105 ºC) and ignition at 550 ºC for 3 hours (Howard and Howard 1990). pH was determined with a soil-to-solution ratio of 1:2 (Hendershot et al. 2007). Sand percentage was assessed with the soil density method (Benbi et al. 1996). Soil data were analyzed using regression models for establishing relationships between soil properties and physical attributes (elevation, Topographic Wetness Index TWI, land cover, fire recurrence and geological unit). Land cover and fire recurrence were obtained from satellite image classification (Álvarez-Martínez et al. 2010) and geological units from IGME (1971-2009). TWI was calculated from the 5-m DEM to assess soil moisture (Eq. 4). 75% of the samples were used as training data and the remaining 25% as validation data.

$$TWI = \ln (As / \tan \beta) \qquad \text{(Eq. 4)}$$

Where As is the contributing catchment in m^2 and ß is the slope angle in degrees (Wilson and Gallant 2000). High TWI values indicate shallow slopes and large contributing areas and, thus, a higher probability of soil water saturation.

To avoid statistical problems due to multi-collinearity (i.e. variance inflation and parameter bias; MacNally 2000; Freckleton 2011), we checked Pearson bivariate correlations among the pool of 58 predictors. The best explanatory variables (i.e. with more than 10% contribution in exploratory uni-variate Maxent models, the heuristic estimate of the relative contributions of predictors; Phillips et al. 2006) were retained from each correlated pairwise (r > 0.7; Randin et al. 2006). Then, we applied two different techniques for modelling forest expansion under each scenario of land use history and microclimate: MaxEnt (Phillips et al. 2006; Phillips and Dudick 2008) and BIOMOD (Thuiller 2003; Thuiller et al. 2009).

The maximum entropy method (MaxEnt) is one of the best performing algorithms for modelling species distribution (Elith et al. 2006), despite certain limitations (Haegeman and Loreau 2008). We ran this algorithm on the full training dataset to provide the best estimate of forest distribution for visual interpretation (full models). Then, we evaluated model performance and variable contribution through a 5-fold cross-validation on the training dataset (Verbyla and Litvaitis 1989). Both full and cross-validated models were evaluated by means of the area under the receiver operating characteristic (ROC) curve (AUC; Pontius and Schneider 2001). Continuous outputs were converted into Boolean maps of suitable/unsuitable areas for forest expansion using the "equate entropy of thresholded and original distributions" value (Phillips et al. 2006; Morán-Ordóñez et al. 2011). Spatial maps were obtained for the 20 basins and furthermore extrapolated to the whole Natural Park, for allowing a comprehensive evaluation of forest expansion patterns.

BIOMOD is a mixed method combining a range of statistical techniques for examining the species-environment relationships: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Classification Tree Analysis (CTA), Artificial

Neural Networks (ANN), Surface Range Envelope (SRE), Generalized Boosting Model (GBM), Breiman and Cutler's random forest for classification and regression (RF), Mixture Discriminant Analysis (MDA) and Multiple Adaptive Regression Splines (MARS). Models were run under default settings and parameters (Thuiller et al. 2009). Using a permutation procedure, we assessed the relative importance of each predictor across models, which is a difficult task since each model relies on different algorithms, techniques and assumptions (Triviño et al. 2011). The multi-modelling approach of BIOMOD was undertaken with the aim of provide a complementary sensitivity analysis to MaxEnt about the trend and magnitude of the most relevant variables driving forest expansion (Fang et al. 2007; Álvarez-Martínez et al. 2011; Alonso et al. 2012b).

GIS analyses were done in ArcGIS 10.1 (ESRI 2012) and Orthobase Erdas IMAGINE 8.5 (ERDAS 2001). We used IBM SPSS 19 (SPSS IBM Company 2010) and R software 2.14.2 (R Development Core Team 2011) for statistical anlyses.

3. Results

3.1. Monitoring changes in forest distribution: the effects of land use history and microclimate

Secondary succession has been the dominant process during the second half of the 20th century in the study area. On average, forests covered 10.72 ± 12.88 % of the basins in 1956, reaching 27.67 ± 24.10 % in 2004 (Table 1, Fig. 3). However, the percentage of forest differed noticeably between natural and anthropic basins. In natural basins, they occupied 20.31 ± 11.97 % in 1956, rising 47.53 ± 17.38 % in 2004, while in anthropic basins the increase was from 1.12 ± 1.57 % to 7.80 ± 6.93 %. In turn, shady slopes showed higher forest cover than sunny slopes, even when considering natural and anthropic basins independently (Table 2). Complementarily, differences in forest expansion rates increased through the study period (Table 1, Fig. 4a). Rates were always above the general trend in natural basins, while they were constantly below in anthropic basins, with significant differences for all time spans (Table 3). However, differences between slopes only become significant during the most recent decades. The interaction between climate and land use was always not significant.

For any time span, the new patches of forest were always located at higher elevations in natural basins and sunny slopes (Fig. 4b). In anthropic basins the effect was much slighter, with no major trends. However, none of these differences were significant (Table 3).

3.2. Modelling forest expansion: relevant driving forces

MaxEnt models achieved a consistently high AUC for both calibration and evaluation datasets, with values ranging from 70.8% to 91.1% (Table 4). AUC values were always higher in sunny than in shady slopes, being maximum in anthropic basins.

Table 5 shows the relative importance for modelling forest expansion of the nine predictors selected in former exploratory analyses on the initial dataset. In broad, the most relevant variables driving forest expansion were related to mesoclimate and soil properties. In natural basins, the percentage of sand of the topsoil, maximum temperature of June, annual thermal amplitude and the coefficient of variation of annual rainfall were the most contributing variables. In anthropic basins, together with temperature of June, rainfall variables (i.e. rainfall in May and December) become much more important. When comparing the most relevant drivers for different slope aspects, we found slighter differences unless we analyze independently both basin types. In natural basins, May rainfall and annual thermal amplitude were more influent in sunny slopes, whereas the maximum temperature of June and the coefficient of variation of rainfall had more relevance in shady. In turn, annual thermal amplitude was more important in anthropic shady than sunny slopes; oppositely, December rainfall and maximum temperature of June were more important in sunny. Dealing with the sign of the effects, there were more important differences between basins with different land use history than between slope aspects. Figure 5 shows, as an example, an unforeseen result: the probability of forest expansion increases with higher values of May rainfall in natural basins but deceases in anthropics. Complementarily, Fig.s 6 and 7 illustrated forest expansion suitability, as modelled with MaxEnt, for basins with different land use history and microclimatic conditions. Figure 6 showed that natural basins had larger suitability for forest expansion than anthropic basins. Figure 7 revealed a higher suitability for forest expansion in shady slopes.

Finally, Fig. 8 showed the geographic transferability of model predictions across the whole Natural Park. The northernmost and more elevated areas had a higher suitability for the expansion of Eurosiberian forests, mainly present in natural basins, while southern and lower elevations, more insolated and human-managed, were more suitable for Mediterranean sclerophyllous vegetation, dominant in anthropic basins.

4. Discussion

Forest expansion in the Cantabrian mountains have been coincident with other European mountains since the beginning of the 20th century, being mainly linked to the disappearance of traditional extensive livestock farming and agricultural systems

(Jongmann 2002; Laiolo et al. 2004; Vicente-Serrano et al. 2004; Lasanta et al. 2006; Morán-Ordóñez et al. 2011). The ongoing process of land abandonment has implied the transformation of large areas of open grasslands into heathlands and woodlands. These habitats offer new ecosystem services as sequestering carbon from the atmosphere, protecting upstream watersheds and soil formation, providing habitat for species and other social increased demands as landscape beauty (Morán-Ordóñez et al. 2013; FAO 2012). By contrast, other areas remain open because of high elevation, slope or poor soil conditions, preventing woody species from growing or reduced their spread rates.

In the study area, the more suitable conditions of natural basins for seedling and sprouting allowed for a larger expansion of forests that in anthropic basins. Therefore, land use history controlled primarily the reforestation process at landscape scale. As found by Foster (1992), field abandonment usually proceed outward from adjacent areas to the continuous woodlots and, eventually, may affect productive tilled land in valley bottoms and slopes. This pattern of forest expansion can be related to historical factors as the kind of former woodlands (i.e. primary and secondary) present nearby and their age, as well as the timing of site abandonment. In our case, the area covered by forests at the beginning of the study period (i.e. year 1956) was higher in natural than anthropic basins, due to far fewer human disturbances as burning, agricultural practices and logging activities in the former (Foster et al. 1998; Morán-Ordóñez et al. 2011). Nevertheless, independently of historical factors and functional traits, forest expansion started in all cases from roughly the same altitudinal level (i.e. small patches close to valley bottoms; see the example of Fig. 3), but new forest patches reached higher elevations in natural than in anthropic basins. This fact could be explained in combination with climate. Altitudinal shifts in species distribution have been described for many tree species during this century as a response to changes in climatic conditions

(Huntley 1991; Grace et al. 2002; González et al. 2010). In Spain, Peñuelas and Boada (2003) monitored a 70 meter upward shift in beech forests during the last five decades. However, other studies (Peterson 1998; Peñuelas et al. 2007a) have shown certain sluggishness in the analysis of treeline upward shifts as a response to global warming. The reason could be that distribution shifts caused by climate are not easy to measure in human-dominated landscapes because of the interplay with land use and related disturbances, as fire events or agricultural activities. This may disguise pure climatic effects (Fuller et al. 1998; Vicente-Serrano et al. 2004). Therefore, the more important upward expansion of forests in natural basins, in comparison to anthropic basins, could be more related to the effect of human constraints on forest ecotones in the latter than pure climatic effects in the former. In the same way, Colombaroli et al. (2010) reconstructed local fire variability and vegetation dynamics over the last 12 000 years in in the Swiss Alps, determining that intensified land use coupled with fire occurrence since the Bronze Age (c. 4000 cal. years bp) had a larger impact on community composition near the tree line than climate change.

Regarding the effect of microclimate, the warmer and drier conditions of sunny slopes hampered forest expansion by reducing seedling survival and sprouting in spring and summer (Pigott 1993; Valladares et al. 2008). Therefore, upward expansion of forests could be a key strategy for compensating thermo-pluviometric deficits. Nevertheless, is the interplay with land use the one which may explain the more intensive upward shifts of new forest patches in sunny slopes during last decades, through the worst soil conditions in lower areas. These areas, more accessible and closer to crops of valley bottoms, should have suffered in the past more fire recurrence and farming activities, causing widespread soil erosion and fertility depletion (Stoorvogel and Smaling, 1998; Arnaez et al., 2011). Thus, the combination of more rigorous climatic conditions with poorer soils may force trees to shift upward to compensate for both negative effects with more intensity than in shady slopes. According the observed trends, we may expect larger differences in upward shifts between slope aspects during forthcoming decades due to the interplay of climate and land use. However, further research is necessary.

Other interesting factor to understand forest expansion, mainly in anthropic basins, was topography. Stepper areas, frequently excluded from grazing or harvesting activities, maintained a higher suitability for forest expansion. However, in flatter areas, whenever residual crops or cattle do not still exist, recurrent fire events for understory management and historical farming activities may have caused soil erosion and fertility depletion, preventing tree species colonization (Acácio et al. 2010). Consequently, the pattern of soil quality in anthropic basins became homogeneously poor (i.e. more sandy texture and lower organic matter content and pH). In these areas, water availability during the plant growing period depends upon precipitation and temperature, due to low water retention capability of the soil, which in turn may control actual evapotranspiration (Peñuelas et al. 2007b). Therefore, the most important variables for forest expansion in anthropic basins were climatic. By contrast, in natural basins, sand percentage and climate had an equivalent relevance for forest expansion. In this case, soil pattern may be more heterogeneous, being the best soil patches (i.e. those located at lower shady slopes) associated to greater suitability for forest expansion.

The biogeographic origin of the tree dominant species also played an important role on forests altitudinal shifts. Eurosiberian species (more abundant in natural basins) are more sensitive to hot summer droughts than Mediterranean vegetation (dominant in anthropic basins) (Moreno et al. 1990; Sardans and Peñuelas 2013). In this sense, it is remarkable the high importance for modelling forest expansion of the rainfall coefficient of variation and the temperatures during the coldest season for the former; and the relevance of temperature in spring for the latter. In this sense, some authors (e.g. Barclay and Crawford 1984; Peñuelas et al. 2007a) have found that high late-spring and summer temperatures would favor vegetation shifts, mainly in natural basins, since the production of viable seeds at high elevations fails more frequently, except in exceptionally warm years. If global temperature keep increasing in the future, more suitable conditions will appear at higher elevations, even on shady slopes, eventually involving more intensive altitudinal shifts of the forests. Therefore, according to Fig. 8, Eurosiberian forests would tend to colonize primarily higher latitudes and elevations. As explained by Sardans and Peñuelas (2013), the long-term evolutionary adaptation to drought of some species of Mediterranean plants allows them to cope with moderate increases of drought without significant losses of production and survival. However, other species have been proved to be more sensitive, decreasing their growth and increasing their mortality under moderate rising of drought. As a consequence, if climate change follows IPCC (2007) predictions, we would expect continuous vegetation shifts of Eurosiberian forests. The lower gaps, where weather conditions are warmer and drier, would be filled by Mediterranean trees (Peñuelas and Boada 2003; Peñuelas et al. 2007a, 2007b).

5. Conclusions

This study provided some clues for understanding the combined effect of climate and land use on forest expansion in mountainous landscapes. We determined that, even if abiotic constraints are relevant drivers, land use history primarily controls forest expansion rates, as well as upward altitudinal shifts. In fact, the large plant diversity that characterizes Mediterranean ecosystems is associated to the success of coexisting species with a legacy land use history, climatic and soil resources exploited differentially in space and time (Sardans and Peñuelas 2013). Therefore, these factors should not be delinked in ecological studies; otherwise biased conclusions could be achieved, misguiding policy decisions (Hanspach et al. 2010). Finally, although our results are site-specific, conclusions could be generalized to other mountainous areas, where landscape homogenization requires scientific-based planning (Lasanta et al. 2006) and locally-tailored sustainable management strategies (Scarascia-Mugnozza et al. 2000) to maintain their cultural and ecological values (Jongman 2002).

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Table 1. Annual rates of forest change ($ARCH_F$) for each basin and time span (see Fig. 1). Forest cover (FO) for 1956 and 2004, averaged forest increase rates for the whole period 1956 to 2004 and basin area are also shown.

Basin number	Basin area (ha)	% Forest cover in 1956	Annual rates of forest change (% gain/loss per year)				% Forest cover in 2004	Averaged rate of forest increase (% gain per year)
			1956 to 1974	1974 to 1983	1983 to 1990	1990 to 2004		1956 to 2004
1	293.07	20.48	0.77	1.11	1.14	0.67	61.59	0.82
2	206.94	10.46	0.32	-0.16	0.49	1.26	35.82	0.51
3	295.33	22.41	0.33	0.18	0.67	0.79	45.71	0.47
4	378.74	17.90	0.31	0.28	0.95	0.25	36.25	0.37
5	314.23	3.62	0.32	0.50	1.25	0.84	34.43	0.62
6	301.56	25.21	0.07	0.68	0.25	0.49	41.26	0.32
7	691.05	17.20	0.40	0.57	0.61	0.69	43.51	0.53
8	747.28	14.94	0.21	0.35	0.28	0.80	34.94	0.40
9	147.04	49.27	0.96	0.93	1.04	0.60	90.58	0.83
10	221.37	21.56	0.23	0.72	0.86	0.92	51.17	0.59
Natural (mean±sd)	359.66±200.58	20.31±11.97	0.39±0.27	0.52±0.37	0.75±0.35	0.73±0.27	47.53±17.38	0.54±0.17
11	277.87	0.60	0.27	0.78	0.37	0.55	22.64	0.44
12	242.89	5.15	0.16	-0.16	0.09	0.28	11.10	0.12
13	118.44	0.31	0.01	0.07	-0.07	0.06	1.44	0.02
14	182.98	2.30	0.12	-0.12	-0.13	0.07	3.52	0.02
15	301.57	0.48	0.04	0.16	0.03	0.10	4.16	0.07
16	522.29	1.18	0.03	0.04	0.21	0.62	12.26	0.16
17	322.34	0.16	0.03	-0.02	0.11	0.28	5.28	0.10
18	342.67	1.04	0.17	0.33	0.16	0.40	13.71	0.25
19	119.25	0.00	0.01	0.00	0.01	0.09	1.49	0.03
20	304.34	0.04	0.01	0.04	0.06	0.11	2.45	0.05
Anthropic (mean±sd)	273.46±119.16	1.12±1.57	0.08±0.09	0.11±0.27	0.08±0.14	0.26±0.21	7.8±6.93	0.13±0.13
All (mean±sd)	316.56±166.55	10.72±12.88	0.24±0.25	0.31±0.38	0.42±0.43	0.49±0.34	27.67±24.1	0.34±0.26

Table 2. Forest cover (%) for each slope aspect (i.e. different microclimate) in basins with different land use history. The averaged annual rate of forest increase for the whole period 1956-2004 is also shown.

Microclimate (Slope aspect)	Land use history	% Forest cover (FO) (mean±SD)					Annual rate of forest increase (% gain per year)
		1956	1974	1983	1990	2004	1956 - 2004
Sunny slopes	Natural	5.27±4.37	8.23±6.23	10.28±7.93	12.04±9.36	16.31±10.81	0.22±0.17
	Anthropic	0.30±0.43	0.62±0.93	1.15±1.64	1.19±1.72	1.99±2.48	0.03±0.05
	All	2.79±3.95	4.43±5.83	5.71±7.28	6.62±8.6	9.15±10.6	0.13±0.15
Shady slopes	Natural	15.05±9.17	19.16±10.28	21.77±10.7	25.29±10.36	31.30±9.18	0.32±0.1
	Anthropic	0.82±1.25	2.00±2.16	2.48±2.52	3.03±3.03	5.82±4.66	0.10±0.09
	All	7.94±9.69	10.58±11.39	12.12±12.46	14.16±13.62	18.56±14.87	0.21±0.15

Table 3. Results of two-way ANOVA with Bonferroni correction for comparing: a) forest increase rates and b) average elevation occupied by new forest patches, in natural-anthropic basins and sunny-shady slopes, as well as their interaction, for each time span. Significant differences are shown in bold. The averaged elevation of new forest patches for each basin and time span was standardized by subtracting the average elevation of each basin before running the statistical tests.

	1956 to 1974		1974 to 1983		1983 to 1990		1990 to 2004		1956 to 2004	
	F-test	*P value*	F-test	*P value*	F-test	*P value*	F-test	*P value*	F-test	*P value*
a) Forest increase rates										
Land use history (natural *vs* anthropic basins)	18.64	***0.00***	12.67	***0.00***	27.6	***0.00***	19.4	***0.00***	35.59	***0.00***
Microclimate (sunny *vs* shady slopes)	2.44	*0.13*	0.24	*0.63*	6.47	***0.02***	5.99	***0.02***	6.07	***0.02***
Interaction microclimate * land use	0.05	*0.82*	0.36	*0.55*	1.92	*0.18*	0.03	*0.87*	0.3	*0.59*
b) Average elevation of new forest patches										
Land use history (natural *vs* anthropic basins)	1.04	*0.32*	0.22	*0.64*	0.93	*0.34*	1.64	*0.21*	0.23	*0.63*
Microclimate (sunny *vs* shady slopes)	3.76	*0.06*	1.76	*0.19*	1.32	*0.26*	1.54	*0.22*	1.8	*0.19*
Interaction microclimate * land use	0.04	*0.84*	1.23	*0.28*	0.1	*0.75*	0.34	*0.56*	0.2	*0.65*

Table 4. AUC values of full and 5-folder cross-validated (5CV) MaxEnt models.

Land use history	Natural			Antrhopic			All		
Microclimate (slope)	Both	Sunny	Shady	Both	Sunny	Shady	Both	Sunny	Shady
Full Models	75.40	81.50	70.80	87.90	91.10	83.30	80.40	86.20	77.10
5 CV	75.44	81.16	71.40	83.44	85.31	75.36	80.31	84.97	76.73

Table 5. Relative importance of environmental predictors for forest expansion in four scenarios of forest expansion: natural and anthropic basins split into sunny and shady slopes. MaxEnt models show also the sign of the effect for each variable within the environmental range of variability of study area: (+) Positive effect, (-) Negative effect. Variable codes: Terrain slope (Slope), terrain curvature (Curv), Topographic Wetness Index (TWI), percentage of sand in the topsoil (Sand), rainfall in May (RainMay), rainfall in December (RainDec), coefficient of variation of rainfall (RainCV), maximum temperature of June (TmaxJun), annual thermal amplitude (TAmpl). For MaxEnt we show the relative contribution of each variable, averaged from 5-fold cross validation; for BIOMOD the averaged value ± standard deviation of variable importance obtained from the nine algorithms. For visualization help, dark grey boxes indicate predictor relative importance >20% and light grey boxes 15-20 %.

	Natural basins					
	Sunny slopes			Shady slopes		
	MaxEnt		BIOMOD	MaxEnt		BIOMOD
Slope	-	4.0	4.2 ± 1.8	-	2.6	1.9 ± 1.5
Curv	-	0.7	1.1 ± 2.6	+	0.1	0.5 ± 0.3
TWI	+	0.6	1.2 ± 1.9	+	0.0	0.4 ± 0.5
Sand	-	24.9	21.8 ± 3.6	-	24.6	17.4 ± 7.5
RainMay	+	15.3	16.8 ± 3.8	+	10.1	14.3 ± 7.7
RainDec	-	1.7	5.7 ± 3.8	-	2.0	9.8 ± 3.6
RainCV	-	16.5	6.9 ± 4.7	-	23.2	14.4 ± 9.3
TmaxJun	+	13.1	22.5 ± 5.9	+	27.1	28.8 ± 5.4
TAmpl	-	23.3	19.9 ± 6.0	-	10.4	12.5 ± 2.6

	Anthropic basins					
	Sunny slopes			Shady slopes		
	MaxEnt		BIOMOD	MaxEnt		BIOMOD
Slope	+	9.2	3.7 ± 3.8	+	11.3	8.9 ± 9.1
Curv	-	0.0	0.2 ± 0.2	-	2.0	2.1 ± 3.0
TWI	+	0.8	1.1 ± 1.3	+	6.0	3.1 ± 2.3
Sand	-	9.2	15.9 ± 6.3	-	9.7	11.9 ± 3.2
RainMay	-	22.4	36.2 ± 14.3	-	25.3	24.1 ± 10.8
RainDec	+	22.5	12.5 ± 5.6	+	7.1	10.3 ± 5.3
RainCV	-	6.8	9.9 ± 6.1	-	9.0	12.3 ± 5.8
TmaxJun	+	21.5	16.5 ± 12.9	+	13.1	17.9 ± 7.4
TAmpl	-	7.7	3.1 ± 4.1	-	16.6	9.4 ± 3.6

Figure 1. Set of 20 head-water basins selected as study area in the Natural Park of La Sierra de Ancares (Cantabrian Mountains, Spain).

Figure 2. Climatic trends in La Sierra de Ancares during the 20th century (data provided by the Spanish Meteorological Institute; own elaboration). (a) Monthly temperatures from 1991 to 2006 (grey bars indicate data gaps), (b) annual rainfall and (c) variation coefficient of precipitation from 1974 to 2006.

Figure 3. An example of two land cover map series for: (a) a natural basin (number 9, Fig. 1) and (b) an anthropic basin (number 16, Fig. 1).

Figure 4. (a) Annual rates of forest expansion. (b) Averaged elevation of new forest patches for each time span, land use history and microclimate (i.e. slope aspect).

Figure 5. Variable responses (i.e. May rainfall) to forest expansion in MaxEnt models calibrated with data from both basins and slopes.

Figure 6. MaxEnt model outputs of forest expansion, calibrated with data from both basins and slopes, in: (a) a natural (number 5, Fig. 1) and (b) an anthropic basin (number 18, Fig. 1). Current forest cover of the year 2004, derived from satellite imagery in Álvarez-Martínez et al. (2010) is also shown.

Figure 7. (a) Sunny and shady slopes of the anthropic basin number 4 (Fig. 1). (b) MaxEnt models of habitat suitability for forest expansion, calibrated using data from both land use history and slopes. Maps show a strong relationship between shady slopes and high suitability for forest expansion.

Figure 8. Suitability maps of forest expansion in La Sierra de Ancares Natural Park, extrapolated from MaxEnt models calibrated with: (a) natural basins, both slopes, and (b) anthropic basins, both slopes.

Figure 1.

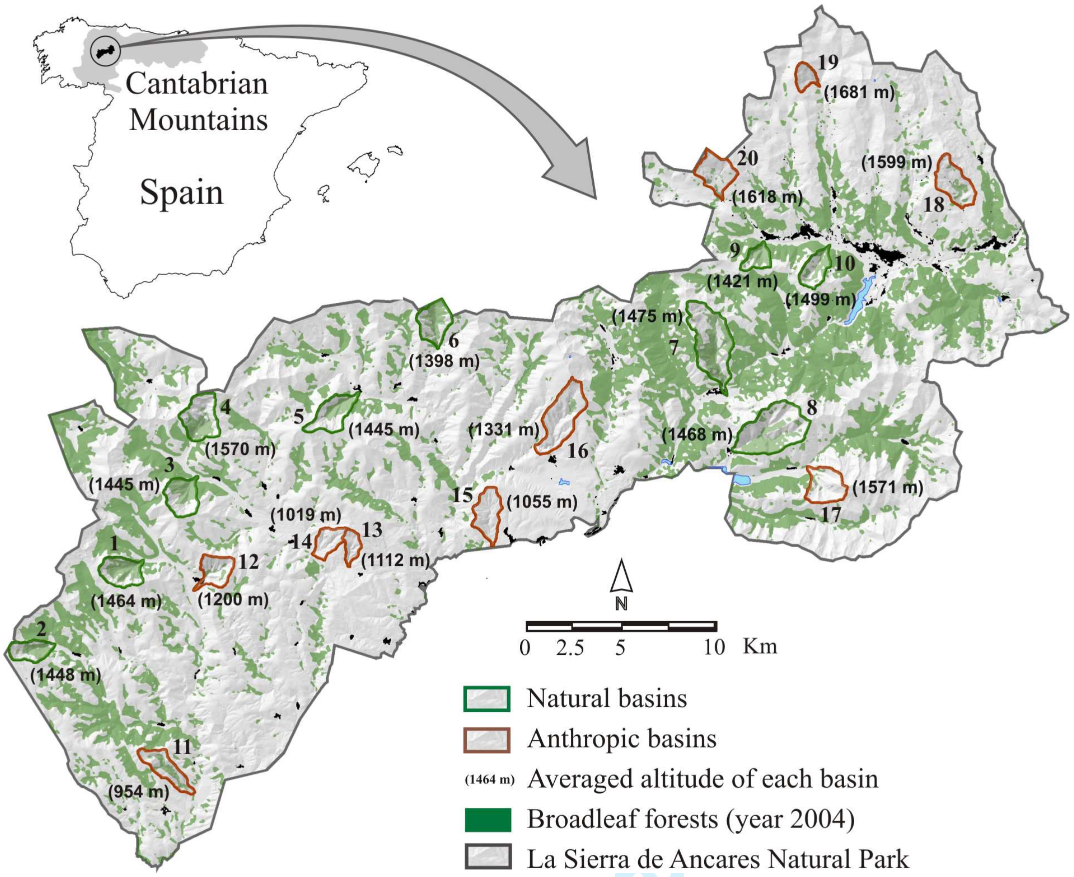

Cantabrian
Mountains
Spain
19
(1681 m)
20
(1618 m)
(1599 m)
18
9
(1421 m)
10
(1499 m)
(1475 m)
7
6
(1398 m)
4
(1570 m)
5
(1445 m)
(1331 m)
16
(1468 m)
8
3
(1445 m)
(1571 m)
17
15
(1055 m)
(1019 m)
13
14
(1112 m)
1
12
(1464 m)
(1200 m)
2
(1448 m)
11
(954 m)
N
0 2.5 5 10 Km
Natural basins
Anthropic basins
(1464 m) Averaged altitude of each basin
Broadleaf forests (year 2004)
La Sierra de Ancares Natural Park

Figure 2.

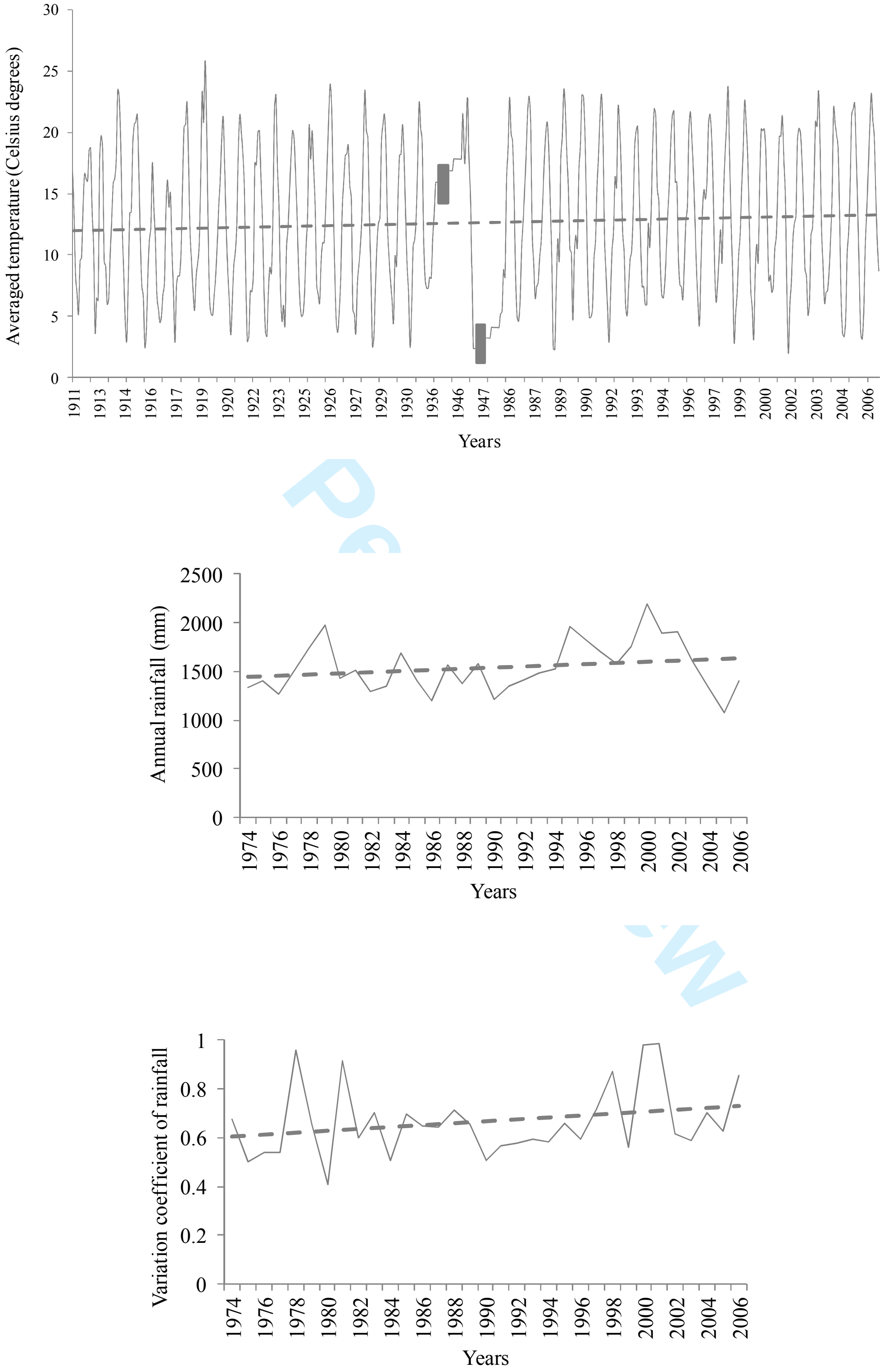

a)
30
25
20
15
10
5
0
Averaged temperature (Celsius degrees)
1911 1913 1914 1916 1917 1919 1920 1922 1923 1925 1926 1927 1929 1930 1936 1946 1947 1986 1987 1989 1990 1992 1993 1994 1996 1997 1999 2000 2002 2003 2004 2006
Years
b)
2500
2000
1500
1000
500
0
Annual rainfall (mm)
1974 1976 1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006
Years
c)
1
0.8
0.6
0.4
0.2
0
Variation coefficient of rainfall
1974 1976 1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006
Years

Figure 3.

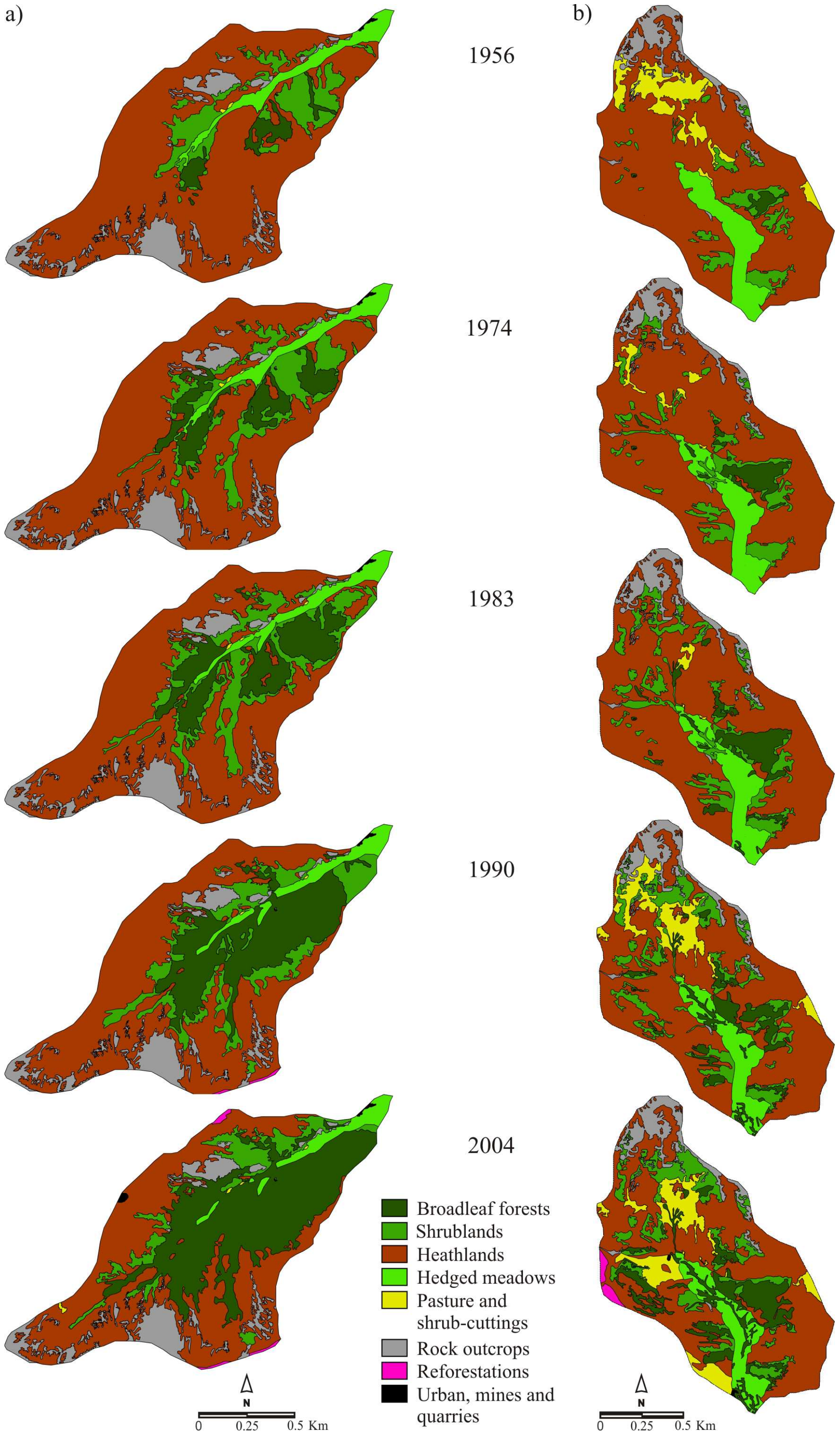

a)
b)
1956
1974
1983
1990
2004
Broadleaf forests
Shrublands
Heathlands
Hedged meadows
Pasture and shrub-cuttings
Rock outcrops
Reforestations
Urban, mines and quarries
N
0 0.25 0.5 Km
N
0 0.25 0.5 Km

Figure 4.

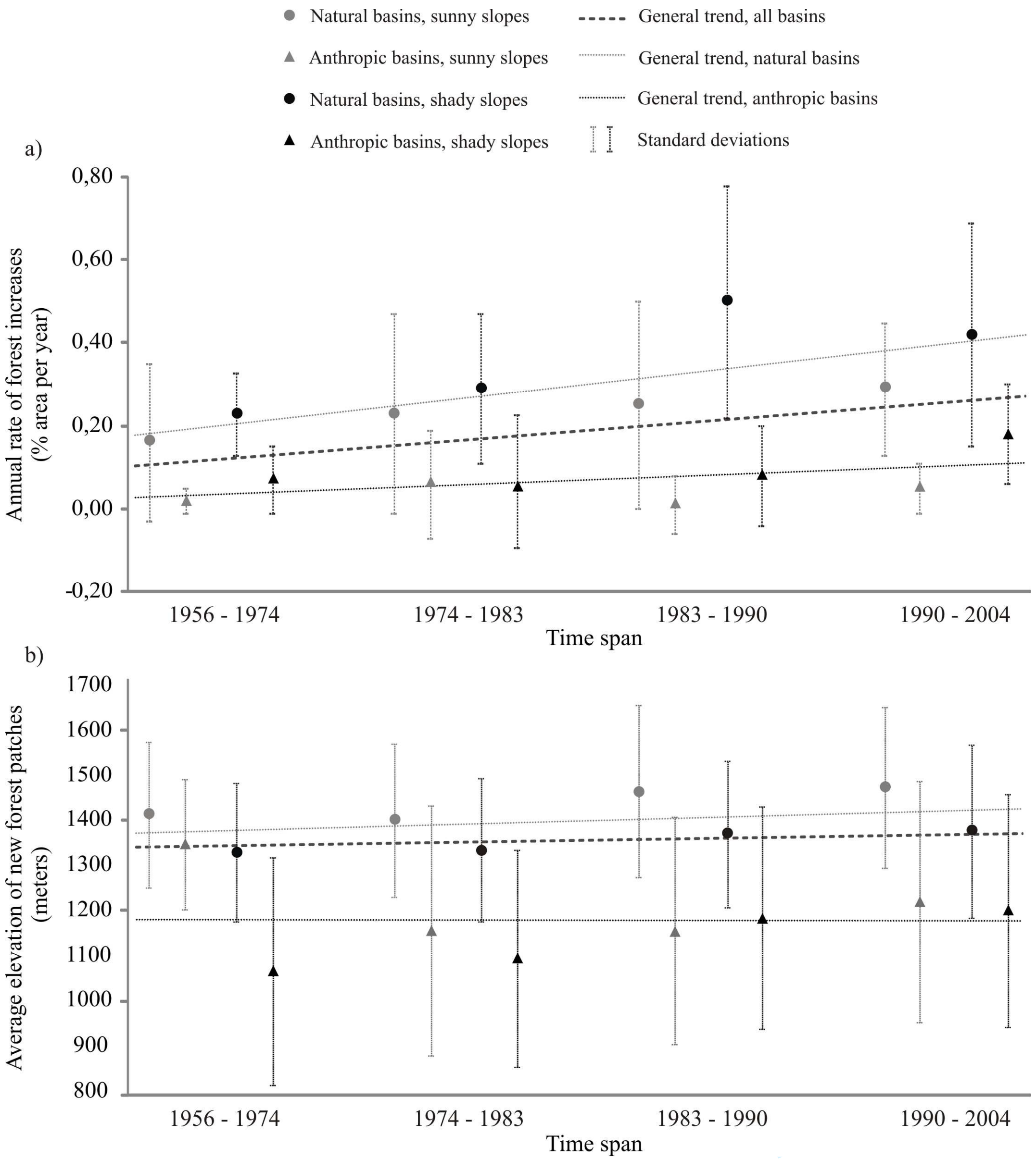

Natural basins, sunny slopes
Anthropic basins, sunny slopes
Natural basins, shady slopes
Anthropic basins, shady slopes
General trend, all basins
General trend, natural basins
General trend, anthropic basins
Standard deviations
a)
Annual rate of forest increases (% area per year)
0,80
0,60
0,40
0,20
0,00
-0,20
1956 - 1974
1974 - 1983
1983 - 1990
1990 - 2004
Time span
b)
Average elevation of new forest patches (meters)
1700
1600
1500
1400
1300
1200
1100
1000
900
800
1956 - 1974
1974 - 1983
1983 - 1990
1990 - 2004
Time span

Figure 5.

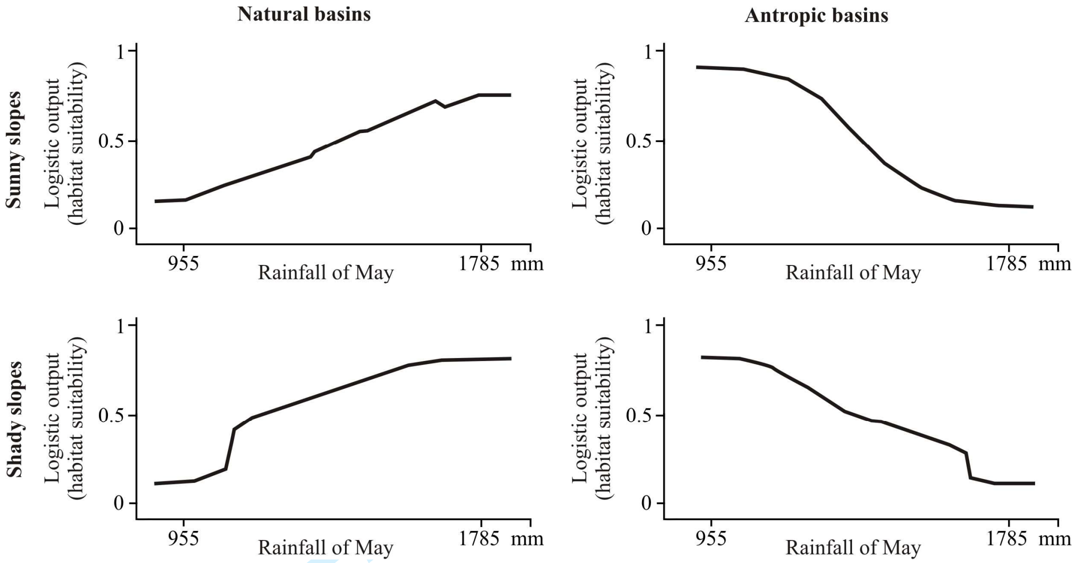

Natural basins
Antropic basins
Sunny slopes
Shady slopes
Logistic output
(habitat suitability)
1
0.5
0
955
1785 mm
Rainfall of May

Figure 6.

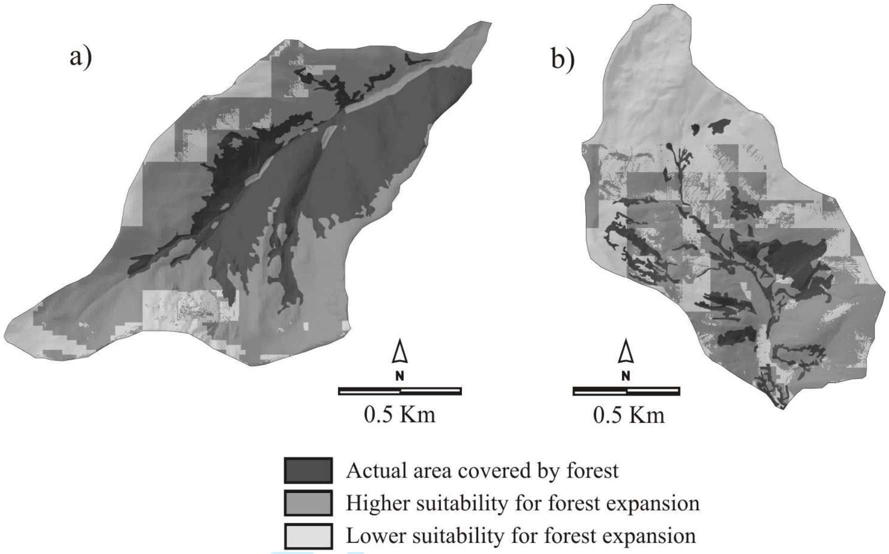

a)
b)
N
0.5 Km
N
0.5 Km
Actual area covered by forest
Higher suitability for forest expansion
Lower suitability for forest expansion

Figure 7.

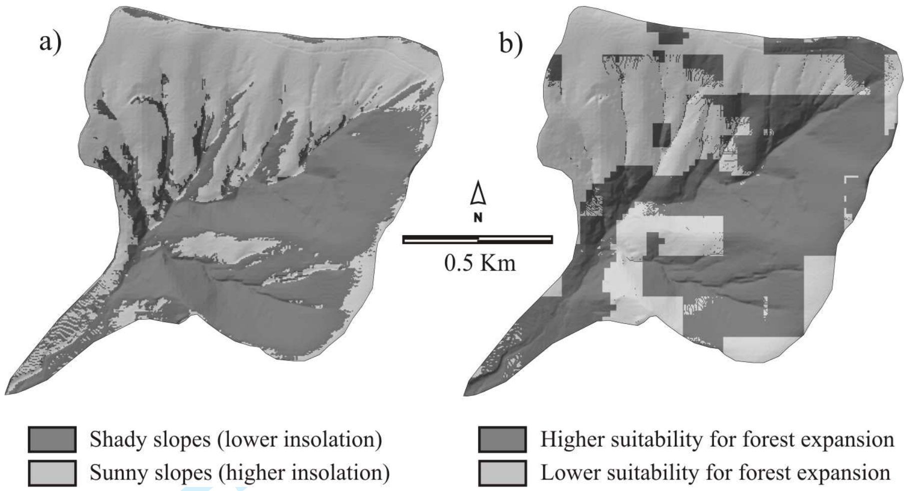
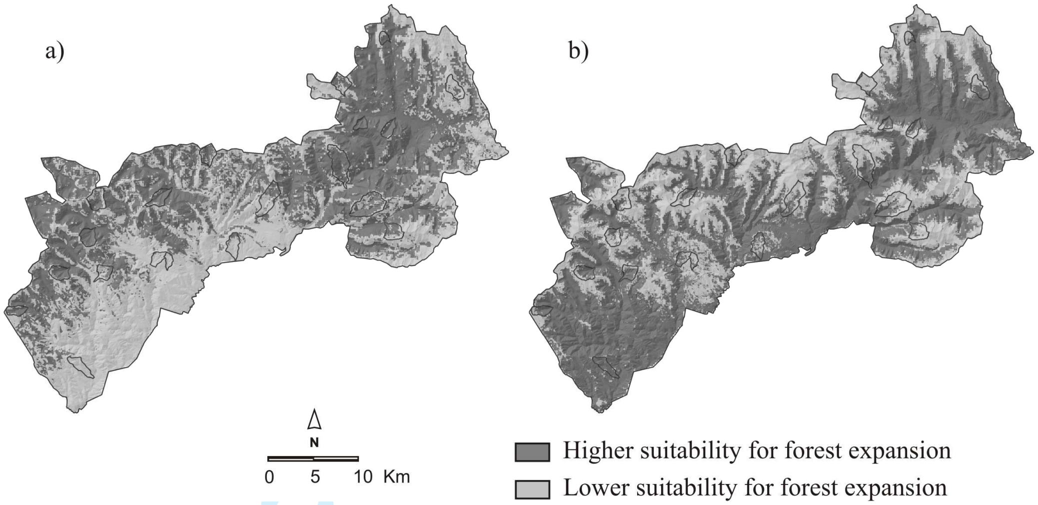

a)
b)
N
0.5 Km
Shady slopes (lower insolation)
Sunny slopes (higher insolation)
Higher suitability for forest expansion
Lower suitability for forest expansion

Figure 8.


a)
b)
N
0
5
10 Km
Higher suitability for forest expansion
Lower suitability for forest expansion