Modeling tree-growth: Assessing climate suitability of temperate forests growing in Moncayo Natural Park (Spain)

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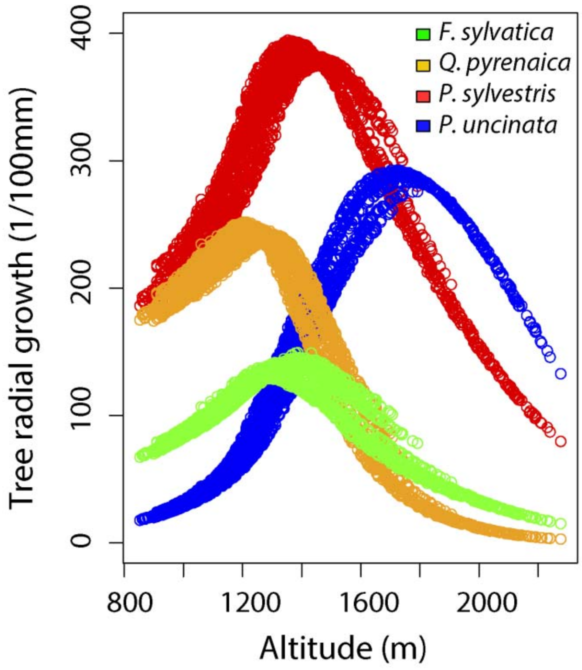
Declarations of interest: none

Abstract:

In the past few decades, temperate forests have been negatively altered by numerous anthropogenic activities and by the impact of ongoing climate change. These changes may require management actions to help preserve some forest tree species. In this sense, highly-detailed knowledge of tree growth and survival across territorial and climatic gradients will be important for forest conservation. We developed a novel approach to determine the optimal zones of forest growth and expansion through climate suitability maps, using a dense tree-ring network of four forest species in Moncayo Natural Park and high-resolution climate data. Our results showed that the mixed-effects models developed using climate data and tree size were able to predict between 65 and 80% of growth variability along the climatic gradient. All studied species were influenced by climate, and the relationship between growth and climate significantly differed along the prevailing climate gradient. Moreover, the suitability maps showed that the current species distribution is limited, and their application may serve as a tool for adaptive management in forests subjected to climate change.

Graphical abstract:



Highlights

- Climate influences species growth differently across altitudinal gradients;
- Mixed-effects models can accurately predict tree growth;
- Suitability maps are useful for designing forest management actions;
- Tree species could potentially extend their range.

Keywords: Forest management; dendroecology; forest expansion; GLMMs; climate.

1. Introduction:

In recent decades, forests have been altered by the effects of climate change. The effects of variation in climate conditions affect forests by changing the frequency and severity of natural hazards, such as fires, droughts, windstorms, late frost events, or insects and pathogen infestations (Dale et al. 2001). Those changes are also produced as a consequence of the interaction of numerous factors not related to natural disturbances: for instance, human activities shape forest systems, influencing their compositions, structure, and distribution (Dale et al. 2001). These activities include the intensification of forestry and agriculture, urban development, tourism, and intense recreational use, which increasingly threaten forested landscapes (Romero-Calcerrada and Perry 2004). Furthermore, the prompt abandonment of traditional activities, such as grazing, silviculture, and the demographic recession in rural areas, are causing imbalances in forest ecosystems.

Mediterranean forests are a living example of these processes, where the abandonment of agricultural land has also led to an expansion of shrubland and woodland cover (Debussche et al. 1999; Romero-Calcerrada and Perry 2004; San Roman Sanz et al. 2013). In this respect, Moncayo Natural Park, located in Spain, exhibits numerous characteristics of a typical area where once traditional local activities have progressively ceased. Traditionally, the forest was intensively used by the local population mainly for logging activities (i.e., charcoal making and firewood) and cattle exploitation (Martínez del Castillo et al. 2015); therefore, the structure of forest was maintained as a meadow with old isolated trees or small stands mixed with open air grass zones. At the beginning of the 20th century, the involvement of the Spanish government in forest policies through reforestation led to intensive plantations (Ortigosa et al. 1990), with the aim of restoring degraded landscapes and increasing hydrological control, but the reforestations in some cases were regarded as excessive (García Pérez and Groome 2000). In the case of Moncayo, two pine species were introduced to reforest the scarce vegetation mountain slopes, occupying the natural distribution area of beech and oaks (Pellicer 2000). Later, in 1978, the area was protected as a Natural Park to preserve the special ecological values of this mountain.

All these changes in land use caused important modifications to forest cover and species distribution, which implies the need for a management strategy for forest adaptation and to ensure the preservation of the ecological values of the Natural Park, considering the different temporal scales over which ecological mechanisms and rapid environmental changes act (Vilà-Cabrera et al. 2018). This also implies that the spatial distribution of the forest species does not correspond with its potential distribution. In addition, accurately assessing the potential distribution is complex, since species distribution modeling and ecological niche modeling studies usually estimate species climate requirements by conventional analyses of only their current distributions (Booth 2017). This could be especially problematic in geographically isolated populations located at the rear edge of their distribution and adapted to local environmental conditions. These facts further highlight the need for holistic management plans based on predictions of species' performance in their natural distribution and beyond.

Tree secondary growth can be used as an indicator of tree health and general performance; this dynamic process is influenced by a complex interaction of tree physiology which, in turn, is controlled by environmental conditions (Fonti et al. 2010). Indeed, phenotypic plasticity in secondary growth allows trees to adapt to specific environmental conditions and is crucial for them to withstand environmental changes during their lifetime (Vitasse et al. 2010; Gricar et al. 2015). Therefore, knowledge of the variability of tree growth across the climatic gradients of the species distribution area may be helpful to assess forest conservation and to identify optimal zones of forest expansion.

Here, we present a novel approach to characterize the optimal zones of forest growth and potential expansion through growth suitability maps resulting from the combination of a dense tree-ring network of the main forest species of Moncayo Natural Park and a high-resolution climate dataset. Our specific objectives were defined as follows: (i) to determine the climate elements which affect tree secondary growth in *Fagus sylvatica*, *Pinus sylvestris*, *Pinus uncinata*, and *Quercus pyrenaica* at the Moncayo Natural Park; (ii) to predict the potential growth of these species all across the Natural Park area; and (iii) to establish suitability zones for each species in the park as a tool to contribute to the improvement of forest management policies.

2. Materials and methods

2.1. Study site

Moncayo Natural Park is located in the Iberian range, in the northeast of the Iberian Peninsula, Spain (centroid at 41º 44’ 55” N, 1º 46’ 10” W). The Natural Park has an extension of 11.144 ha and the elevation range varies from 850 to 2.314 m a.s.l. (Figure 1). This area belongs to the Mediterranean biogeographical region, with mild winters and seasonal precipitation regimes. However, the north slopes of the mountain intercept humid air masses, favoring the presence of different vegetation communities adapted to more cold and humid climates. Thus, the north part of the Park is covered by typically Northern European species, such as Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), or mountain pine (*Pinus uncinata* Mill.), and by a forest of Pyrenean oak (*Quercus pyrenaica* Willd.). There is a presence of other tree species adapted to moist environments, such as holly (*Ilex aquifolium* L.), birch (*Betula pendula* Roth.), and rowan or mountain ash (*Sorbus aucuparia* L.). By contrast, in the south part of the Park, there are no large forested areas, and species are more typically Mediterranean, such as holm oak (*Quercus ilex* L.), black pine (*Pinus nigra* Arnold) or shrubs of rosemary (*Rosmarinus officinalis* L.), thyme (*Thymus vulgaris* L.), or genista (*Genista scorpius* L.).

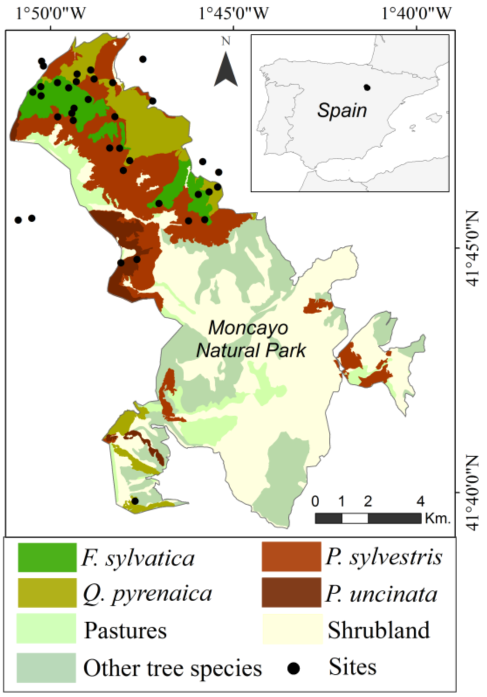


Figure 1. Location map of Moncayo Natural Park. The spatial distribution of the main forest species and other vegetation categories and the location of the study sites are represented as black dots.

2.2. Climate data

The relatively rugged orography of the Moncayo massif is a barrier to the western and northwestern fronts, resulting in frequent convective activity and consequent precipitation in high altitudes that progressively decreases with altitude.

Climate grids were generated with the *reddPrec* R package (Serrano-Notivoli et al. 2017b) based on the reconstructed stations of Serrano-Notivoli et al. (2017a). The climatic variables generated were precipitation and maximum and minimum temperature, at an annual scale for the period 1950–2012, with a spatial resolution of 200 meters (Figure 2).

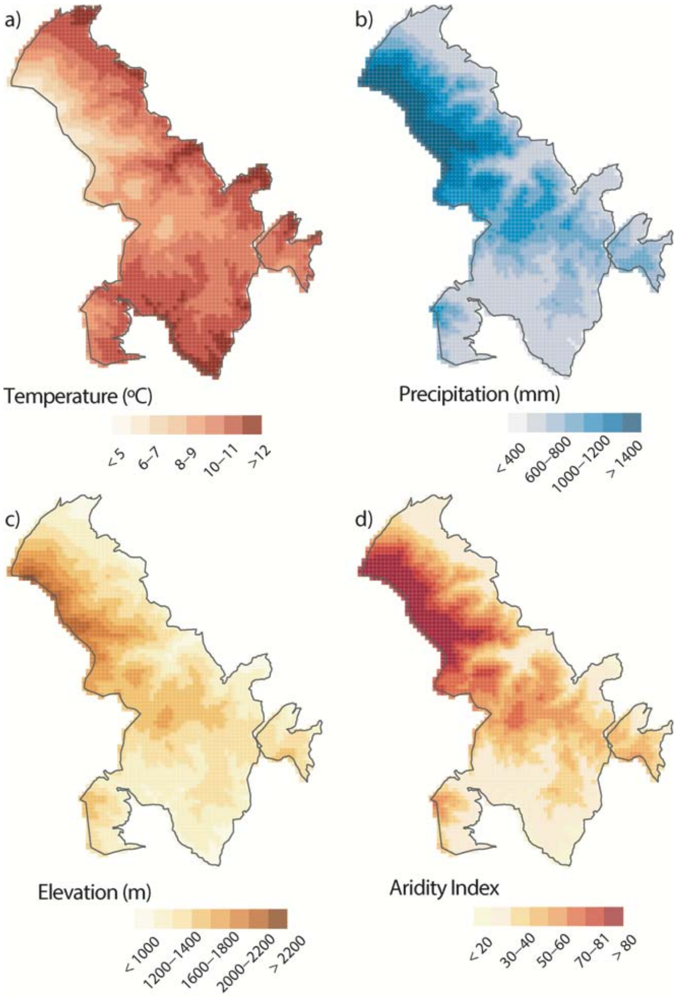


Figure 2. Grids of climate variables. a) Mean annual temperature, b) annual precipitation, c) elevation, and d) De Martonne Aridity index.

The climatic conditions varied widely, considering the area of the Natural Park. The monthly distribution of precipitation ranged from less than 20 mm in the summer months at low elevation to more than 170 mm in May or November at high altitudes, resulting in a range of annual precipitation from 387 to 1572 mm. The difference in maximum and minimum temperatures in the altitudinal range is from 6 ºC to 8 ºC warmer in low altitudes throughout the year.

A measure of aridity which integrates precipitation and temperature data has been calculated for each point of the climate grid. The aridity index (AI) proposed by De Martonne (1926) is given by the following relationship:

$$AI = \frac{P}{10 + T}$$

where P is the annual mean precipitation (in mm) and T (in °C) the annual mean air temperature. The climate types defined by AI vary from arid (0–10), semi-arid (10–20), Mediterranean (20–24), semi-humid (24–28), humid (28–35), very humid (35–55), to extremely humid (>55). The range of values of AI inside the Natural Park ranged from 17.96 to 109.84, with a mean value of 44 (Figure 2).

2.3 Field sampling and sample processing

We sampled 40 sites, distributed across the species range and along a broad elevation range, from 950 to 1900 m.a.s.l. in the Natural Park (Table 1). The sampling covers the elevation range of the four species in the study area. A total of 427 trees were sampled from 2009 to 2014, extracting from 1 core (4.91% of the cases) to 2 cores (95%) per tree. At each site, the cores were taken at DBH from 5 to 25 healthy, dominant, and mature trees, using increment borers of 40 or 50 cm length.

		Altitudinal range (m a.s.l.)	Mean annual temperature range (ºC)	Mean annual precipitation range (mm)	No. Sites	No. Trees	No. Samples	Time span (y)
Moncayo Natural Park		853 - 2276	11,8 - 4,4	387 - 1572				
F. sylvatica	Actual distribution	1115 - 1723	10,4 - 7,2	569 - 1413				
	Sampled sites	1150 - 1600	10,1 - 8,1	647 - 1274	15	150	284	1799 - 2014
P. sylvestris	Actual distribution	909 - 1834	11,4 - 6,7	448 - 1461				
	Sampled sites	1020 - 1635	10,5 - 7,9	544 - 1301	8	117	217	1919 - 2014
P. uncinata	Actual distribution	1296 - 2144	9,6 - 5,1	649 - 1546				
	Sampled sites	1765 - 1900	7,2 - 6,8	1157 - 1450	3	30	59	1935 - 2011

Q. pyrenaica	Actual distribution	909 - 1420	11,4 - 8,8	430 - 1110				
	Sampled sites	950-1550	10,8 - 9,2	464 - 929	14	130	252	1739 - 2013

Table 1. Summary of actual species distribution and sampling points by species.

In the laboratory, the cores were air-dried and mounted into wooden supports which were correctly oriented to show the transversal section after the samples were polished. The cores were scanned with a 2400 ppi resolution scanner and then cross-dated using CooRecorder v8.0 software (Larsson 2010). The ring widths of each core were measured using a LINTAB^{TM} 5 measuring device (Rinntech, Heidelberg, Germany), with a precision of 0.01 mm, and the TSAP-Win program. The quality of the dating and measuring were checked with quantitative methods with the program COFECHA, which dates the growing series against the master dating series using moving correlation analysis (Grissino-Mayer 2001). Cores including evident wood anatomical anomalies and those not successfully dated were discarded from further analysis. Finally, a total of 61,229 tree rings were dated and measured. The size of each tree (basal area) previous to each tree-ring formation was calculated for each ring, using the diameter at breast height and subtracting the tree-ring measures.

2.4 Predictive growth models

Species-specific generalized linear mixed-effects models (GLMM) using a Poisson distribution of the errors were used to describe variation in tree-ring width (TRW) as a function of climate conditions.

Model <- glmer(TRW_t~ (AI_{mean} * Climate $variables_t$) + (BA_{t-1} | Tree identity), family=poisson(link=”log”)

Total seasonal precipitation and mean seasonal maximum and minimum temperatures (from the previous summer to current autumn) were used as independent variables.

Since the importance of the different climatic elements may significantly differ across species distribution, the mean aridity index (AI_{mean}) was also included in the model as a site index reflecting the mean climatic characteristics of each study site. The interaction between the AI_{mean} and the seasonal climate variables was also considered.

To take into account variations in the TRW of each individual tree, tree identity was used as a random effect variable. In addition, given that radial growth is well known to vary as a tree becomes larger/older (Bowman et al. 2013), the basal area of the tree in the previous year of each tree-ring formation (BA) was also included in the random term. All independent variables were standardized before model constructions to guarantee a compensated weight of each variable.

Model construction was based on information for the period of 1950 to 2013 due to the common availability of both tree-ring measurements and climatic data. The models were evaluated with a chi-squared test comparing the model (full model) with a null model (constructed including only the random effects).

In addition, the applicability domains (AD) (Norinder et al. 2016) should be considered when discussing the predictive performance of statistical model. For each species, the predictive growth models included -as independent variables- the climate conditions occurred during the year of each tree-ring formation. As a consequence, a wide range of climate conditions contained in the dendrochronological dataset of each species defines the AD of each model.

Despite the limited actual distribution of species across the Moncayo Natural Park, dendrochronological sampling, containing tree-rings from different sites and years, include a wide range of climate conditions that allows extending the domain of the obtained models to outside their actual distribution range. The climate grid included 2801 points for which seasonal climate values were estimated for the period 1951-2012 (62 years). Whether climate conditions occurred in this set of 2801*62 situations are included in the climatic domain of the dendrochronological dataset of each species has been calculated to define the AD of each model.

Finally, a suitability index was defined and calculated for each pixel as the ratio between the mean tree-ring width predicted in each pixel and the maximum tree-ring width predicted in the whole Natural Park. Thus, suitability index values for each species could vary from 0, which indicates minimum suitability, to 1, meaning maximum suitability (i.e., a value of 0.5 indicates that the growth is half of the potential maximum growth).

3. Results

3.1. Radial growth across species

The dendrochronological network consisted in 40 sites, where a total of 812 cores were taken, ranging from 5 to 25 trees per site (Table 1). Altogether, more than 60,000 rings were dated and measured. The tree structure of the sampled trees (DBH) and the tree-ring widths varied among the species, as shown in Figure 3. The DBH ranged from 5.74 cm, recorded in *Q. pyrenaica*, to 53.72 cm, in the case of *P. sylvestris*, with mean values of 14.54 (*Q. pyrenaica*), 21.69 (*P. uncinata*), 26.55 (*F. sylvatica*), and 29.73 (*P. sylvestris*). The tree-ring width measurements varied from 0.012 to 8.87 mm. in *Q. pyrenaica*, from 0.57 to 6.45 in *P. uncinata*, from 0.085 to 11.58 in *P. sylvestris*, and from 0.01 to 8.27 in case of *F. sylvatica*. The lower mean value was 1.057 (*F. sylvatica*), followed by 1.502 (*Q. pyrenaica*) and 2.116 (*P. sylvestris*), and the higher value was 2.296 mm (*P. uncinata*).

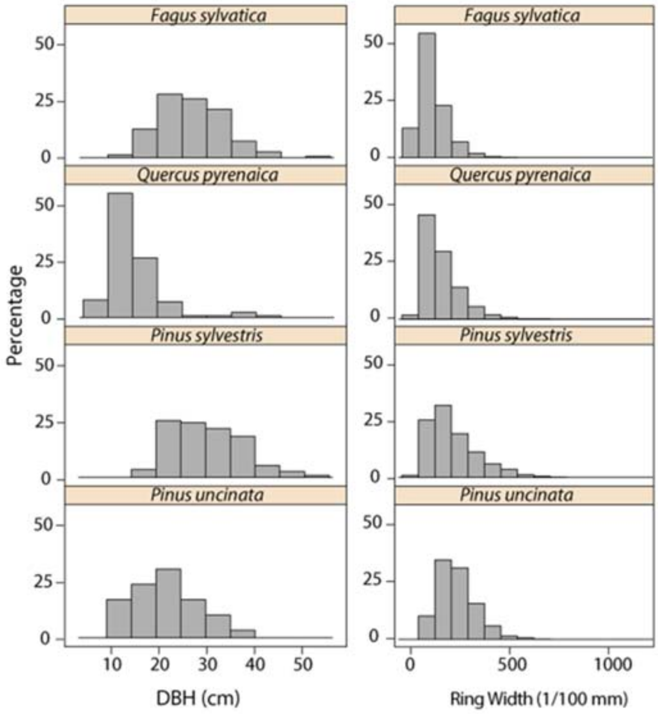


Figure 3. Histograms of the DBHs of the sampled trees and the measured tree-ring widths.

3.2. Predictive tree growth models

Predictive growth models for the analyzed species are shown in the supplementary materials (Table S1, S2, S3, and S4). Overall, most of the climatic parameters included in the models presented a significant relevance in all species. For *F. sylvatica* and *P. uncinata*, the only parameter without a significant contribution to the model was the interaction between the AI_{mean} and the maximum temperature of the previous autumn; in the case of *P. sylvestris*, it was the AI_{mean}, meaning that the spatial variation of the aridity index did not have a significant relevance in the construction of a growth model of this species. Lastly, all parameters included were significant in the *Q. pyrenaica* growth model. The models were able to explain 66% of the total variance in the case of *P. uncinata* and 73%, 75%, and 80% in the cases of *F. sylvatica*, *Q. pyrenaica*, and *P. sylvestris*, respectively.

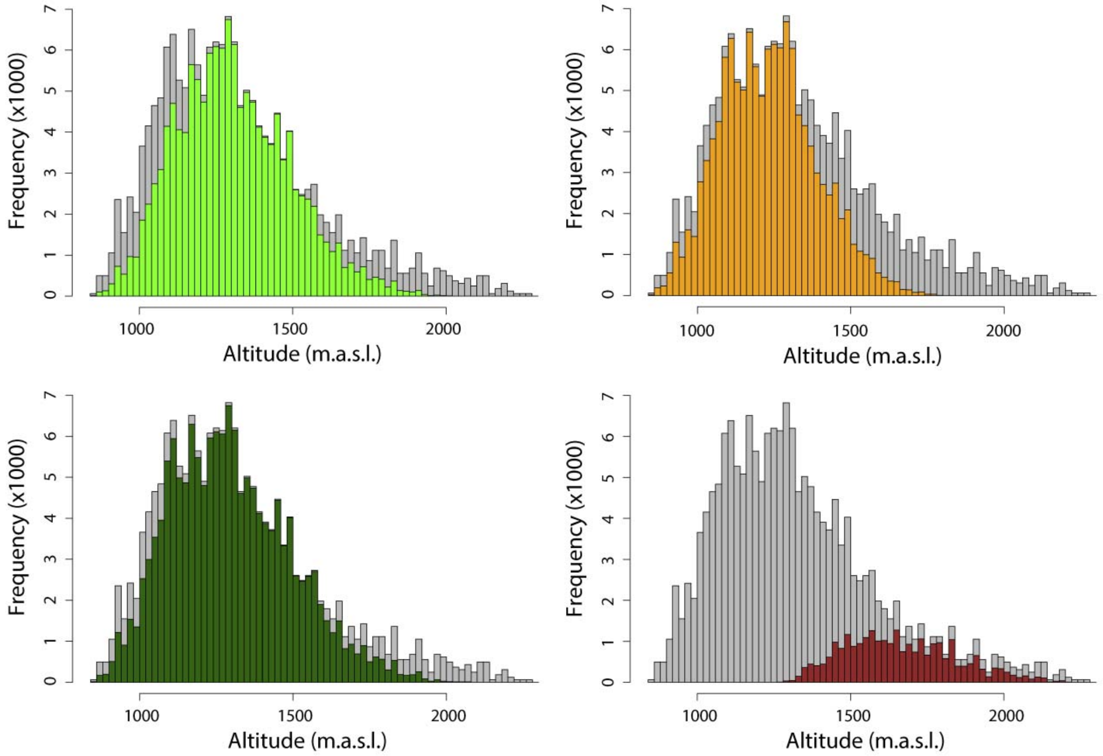


Figure 4. Applicability domains. The altitudinal distribution of the climate range of each specie (for a) *Fagus sylvatica*, b) *Quercus pyrenaica*, c) *Pinus sylvestris*, and d) *Pinus uncinata*) F. sylvatica) overlapping the climate range across Moncayo Natural Park (grey bars).

AD of each specie is shown in Figure 4. For *F. sylvatica*, AD includes a wide climate domain that is representative of most of the climate conditions occurred across the Natural Park from 1200 to 1600 m of altitude. At lower and higher altitudes, only certain climate conditions occurred during the period 1951-2012 are represented in the tree-ring network (Figure 4a). In case of *Q. pyrenaica*, the AD is representative of most of the conditions occurred at lower altitudes while it decrease progressively at altitudes higher than 1400 m (Figure 4b). Representativeness for *P. sylvestris* is wider including most of the climate conditions occurred from 1000 to 1800 m (Figure 4c). On the contrary, the dendrochronological network of *P, uncinata* shows a relatively good representativeness of climate conditions occurred at higher altitude being not representative of conditions occurred below 1350 m (Figure 4d).

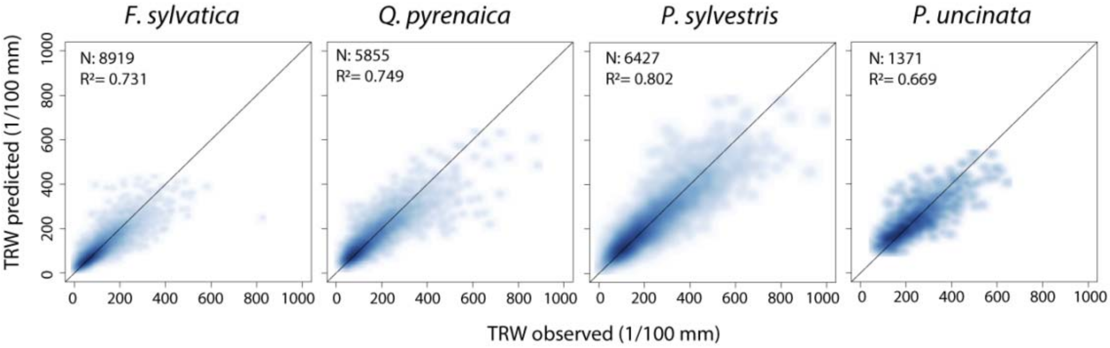


Figure 5. Tree ring width predicted using the GLMMs versus measured tree ring width. Number of observations (N) and agreement between observations and predictions are indicated (r2).

The growth predictions of the models (Figure 5) were computed for each species for all grid extensions (2801 points) and for all years with climate data (62 years). The spatial distribution of the mean TRW predicted at each point is shown in Figure 6 (left panel) and the distribution of the values across the altitudinal gradient of the Natural Park is shown in Figure 6 (upper-right panel).

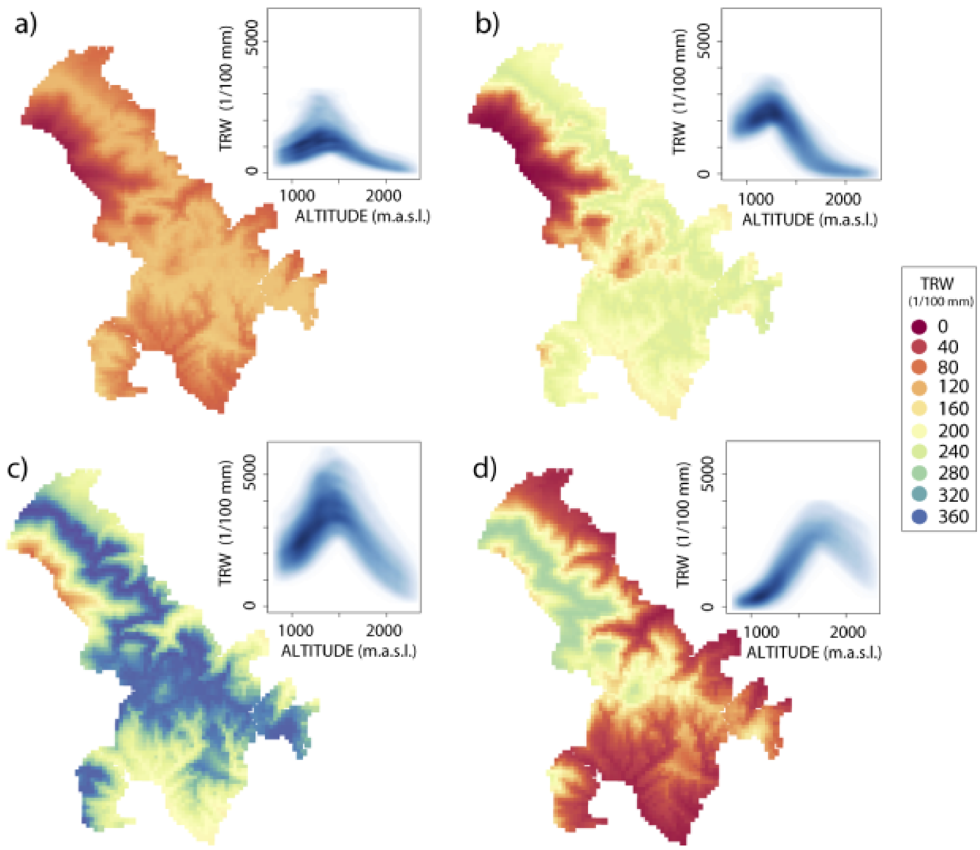


Figure 6. Growth predictions developed by GLMM models for a) *Fagus sylvatica*, b) *Quercus pyrenaica*, c) *Pinus sylvestris*, and d) *Pinus uncinata*. Maps represent the mean annual growth predictions for the period 1951–2012 and graphs include the variability through the years across the NMP.

The maximal predicted growth of *F. sylvatica* was reached at 1337 meters. The predicted growth rapidly increased from 1000 m a.s.l. to the peak, slowly decreasing at higher altitudes. There was a higher variability in predicted growth between 1100 and 1600 m due to the different climate conditions among sites with a similar altitude across the park. Overall, the growth rates in this species were lower compared to those of the others. *Q. pyrenaica* growth reached its maximum at 1240 m a.s.l., which is higher than the mean altitude where the species is present (1118 m). At high altitudes, growth progressively decreases as the climate conditions change, reaching near-zero values of ring width over 2000 m. By contrast, *P. sylvestris* showed a high variability in their growth predictions, with this variability being rather constant along the altitudinal gradient. The maximum growth is predicted at 1430, almost 100 meters higher than the actual mean altitude of the species. Lastly, *P. uncinata* growth predictions reached minimum values at lower altitudes, which include most of the Natural Park, especially in the south and a maximum growth at 1760 m. For all the four analyzed species, the higher growth rates predicted are located within the applicability domains (AD) of predictive models which support their reliability. On the contrary, predicted growth of *P. uncinata* and *Q. pyrenaica* at lower and higher altitudes respectively, should be interpreted with special caution since represents extrapolations of the constructed models out to their AD.

Climate suitability defined by growth models was applied to the Natural Park cover for all species (Figure 7). Overall, inside the actual distribution of the species, the suitability index was high: *F. sylvatica* is present in 155 pixels, of which 81.6% scored more than 0.8 of suitability and only 4.4% less than 0.5. *Q. pyrenaica* achieved the best match between the actual distribution and the suitability index, at over 145 pixels, where 99.3% scored more than 0.8 and none less than 0.5. *P. sylvestris* was the most extended species, with a presence in 432 pixels and 78.9% with a high suitability (>0.8) and none with suitability below the average value. *P. uncinata* was present in 121 pixels, with 89.3% over 0.8 and with 5.79% under 0.5 in the suitability index.

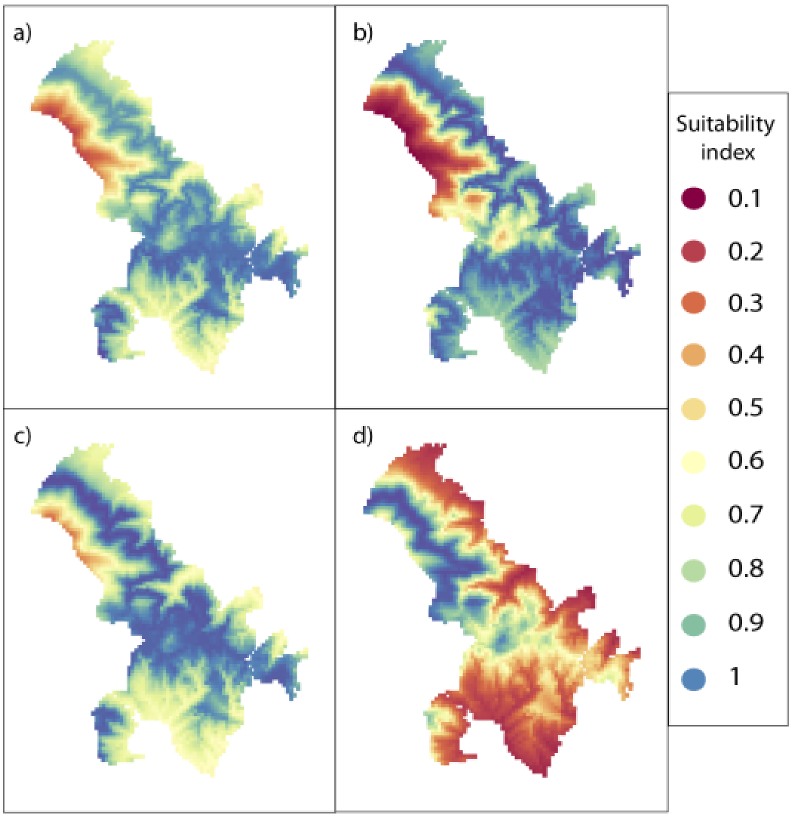


Figure 7. Climate suitability maps ranged from 1 (maximum suitability) to 0 (minimum suitability) for a) *Fagus sylvatica*, b) *Quercus pyrenaica*, c) *Pinus sylvestris*, and d) *Pinus uncinata*.

Furthermore, the suitability maps showed zones where the species are not present at this moment, but which were highly suitable for them. Considering the whole study area, consisting in 2801 pixels, the *F. sylvatica* suitability was high in large areas over the territory. Specifically, its suitability reached 0.9 in 525 pixels, and 0.8 in 1133 pixels—in other words, 40% of the territory—in contrast to the actual presence in just 5.5% of the park. *Q. pyrenaica* counted 223 pixels with more than 0.9 suitability points and without species presence, especially in low-elevation zones. *P. sylvestris* showed a high suitability index, although *F. sylvatica* and *Q. pyrenaica* were more suitable in 79 and in 108 pixels, respectively, leaving only 71 pixels where the most suitable species was *P. sylvestris*. Lastly, although *P. uncinata* is restricted to high-elevation zones occupying the majority of the suitable zone, the higher values of suitability were located at 1762 m a.s.l., higher than the mean of its actual distribution.

4. Discussion

4.1. Modeling climate suitability

The use of mixed-effects models applied to TRW, including climatic components and tree size as independent variables, has been proven to have the potential to predict the growth variability of species across the Natural Park. Indeed, between 65 and 80% of the variability was explained by the models, depending on the species. Other abiotic variables can interact with tree growth, such as topography, aspect, soil associations, or current management (Parresol et al. 2017; Vennetier et al. 2018), and certainly may improve the accuracy of the models, but those variables are difficult to extrapolate over the territory and would introduce uncertainties into the growth models.

The proposed models are based on easily available variables (i.e., the high resolution gridded climate dataset and tree-ring width measurements) and allow predicting a species' growth all over its distribution and in other zones where the species is not present. Like every forecasting model, these predictions are subject to uncertainties especially in areas or years where climate conditions are outside the applicability domain (AD) of species specific species. Alternative modeling approaches as classical species distribution models or ecological niche modeling are not free of such inherent limitation but fail also to integrate biological information as included in our approach (Booth 2017; Walentowski et al. 2017) that may help to obtain a more realistic approximation of species growth patterns.

Applicability domains (AC) represents the climate domains where models may exhibit sufficient predictive performance for training samples (dendrochronological network) and thus for new samples. In addition, for a different combination of seasonal climate conditions located inside the AD, their growth estimates are also expected to be as reliable as those in the training sample. However, if they are outside the AD, reliability of their estimates decrease and interpretation of predicted growth patterns should be interpreted with caution. This can be especially the case of *P. uncinata* model apply to low elevation sites and *Q. pyrenaica* model apply to high elevation areas.

Despite inherent limitations related to the applicability of obtained models all across the Natural Park, we apply them to the full climate grid. Then, for each grid pixel and for each species, the mean of the predicted TRW for all years was calculated as a general growth forecast. In addition, to guarantee the comparison between species and study sites, the tree-ring width was predicted for a theoretical tree with a common basal area of 252.91 cm2 (equivalent to 17.97 cm of diameter at breast height), which is the mean basal area of all analyzed trees before each tree ring formation.

4.2. Climate-smart plastic behavior of tree species

Climatic variability is a key explanatory element of the different patterns of forest growth and its distribution around the world (Vicente-Serrano et al. 2013). The ability of forests to respond to changes in climate through genetic adaptations or phenotypic plasticity will play a decisive role in species distribution conditioning their expansion, recession, or even extinction (Matesanz et al. 2010; De Luis et al. 2013; Gentili et al. 2015).

In the case of the Moncayo Natural Park, all the studied species are in their distribution limits; therefore, their growth is likely to be constrained by the climate. *F. sylvatica* is a widespread European species, reaching at this point its southernmost forest stands. This late-successional and highly-competitive species is known to be sensitive to drought and high temperatures (Zimmermann et al. 2015; Bolte et al. 2016), both in the southernmost or xeric limits (Rozas et al. 2015) and in the core of their distribution in central Europe (Babst et al. 2013). Particularly in our study site, the growth of *F. sylvatica* is limited by an extremely short growing period: i.e., between 2 and 3 months, the shortest xylogenesis period reported in the literature (Martínez del Castillo et al. 2016). Our results confirm that growth is influenced by climate; previous and current summer conditions play an important role in this influence, and the combination of all climatic factors explains 73% of the within-tree-total growth variability. The importance of the mean value of the aridity index and its interaction with all other climatic variables in the models is indicative of the plasticity and adaptation of the species; the climatic stressors for tree growth vary across the prevailing climate.

Q. pyrenaica is a deciduous transitional sub-Mediterranean oak, of a character that is between Mediterranean and mesic, which finds its western edge in this region. One of the main physiological adaptations of this species is the duration of the growing season (i.e., about six months), delaying the early phenological phases to avoid late-frost events (Souto-Herrero et al. 2018). Although this species is more tolerant to both winter frost and summer drought than other *Q.* species, water stress in late spring and summer are the main constraints for xylem production (Pérez-de-Lis 2016). The combined climatic variability in the region explains 75% of the growth variability. The model shows predictions of zero growth in high elevations, constraining the possible distribution limit of the species.

The main climatic threat and stressor to *P. sylvestris,* which is one of the most widely distributed tree species over Europe in this region, is water availability, which is important throughout most of the year, as pines have a long growth period, reaching up to seven months of xylogenesis (Martínez del Castillo et al. 2016, 2018a). This species presents great variability in its growth predictions all over the Natural Park, showing its plastic behavior. On the other hand, *P. uncinata* presents less coverage over Europe and is usually limited to hilly mountains. This species has been widely used for climate reconstructions, and its growth and wood density is closely related to temperature (Büntgen et al. 2010; Konter et al. 2014) and drought (Tejedor et al. 2016), in accordance with the limited growth predictions in lower elevations and drought-prone environments with higher temperatures. Although both species showed a remarkable climate sensitivity, the explained variability of growth derived from climate varied between these two pine species, at 80% in *P. sylvestris* and 67% in *P. uncinata*.

In all studied species, the importance of the climatic variables significantly differs along the prevailing climate of each zone (e.g., a specific climatic variable can affect growth in one way in warm zones, but not in cool zones, or even affect it in the opposite way). This can be explained by the plastic behavior of tree species throughout the altitudinal gradient to specific climate conditions; overall, in higher altitudes, temperatures become more important than precipitation (Martínez del Castillo et al. 2018b). Such genetic adaptations, phenotypic plasticity, or both have been studied in other extensive analyses (Richter et al. 2012; De Luis et al. 2013) and have to be considered as an important matter in growth predictions over climate change scenarios.

4.3. Climate suitability for forest management

The definition of a suitability model for forest species has been developed for management purposes since the 1980s (Tikkanen et al. 2007). Other studies dealing with the calculation of a habitat suitability index include diverse information, but they are usually incomplete, because they do not incorporate all underlying mechanisms of variation (Elith et al. 2002). Nonetheless, the climate effect is clear and present in all modeling. Therefore, assessing the climate suitability of tree species is the necessary first approach for both species modeling and management actions designed as assisted migration (Koralewski et al. 2015). In addition, the spatialization of the suitability index through the cartography of suitability—covering all of the Natural Park area—provides useful and important information for managers, such as the identification of areas where one species can be substituted by others, or favorable edges for species expansion. In this case, the potential growth is used as an integrative variable of population fitness over the territory.

Specifically, the suitability maps indicated large areas of potential expansion for all species, balanced overall by altitude. *Q. pyrenaica* showed great potential in low-elevation zones below 1100 m.a.s.l., while, for *P. uncinata*, higher performance was forecasted in high altitudes, with values even higher than its actual distribution. *F. sylvatica* and *P. sylvestris* shared their highest suitability zone in the mid-range of the altitudinal gradient of the Natural Park where the species are present, but also in the central part of the Park, which is currently under-forested. These two species are growing in the same altitudinal range, competing in their expansion. In this sense, previous research proved that *F. sylvatica* may partially substitute *P. sylvestris* areas (Martínez del Castillo et al. 2015), in accordance with recent global studies that revealed a consistent directional substitution of Pinaceae by Fagaceae worldwide (Alfaro Reyna et al. 2018) or studies showing the drought-related vulnerability of *P. sylvestris* (José Vidal-Macua et al. 2017; Sánchez-Salguero et al. 2017)

The comparison between the actual distribution of these four species in this Natural Park and the suitability maps revealed that *F. sylvatica* and *P. uncinata* are growing, in some cases, in zones with a low level of suitability, while the other two species grow in more suitable zones; therefore, the first two species may not reach their potential distribution in the Natural Park and may be favored.

5. Conclusions:

This study shows a novel methodology to assess the climatic suitability of forest species based on models that integrate tree growth with climate. As a case study, we addressed the climatic suitability of four tree species which are protected in Moncayo Natural Park, in Spain. Among the investigated species, *F. sylvatica* showed a plastic behavior limited by its short growing season, but with possibilities of expansion over new zones, since it is growing in middle-suitable areas. The potential presence of *Q. pyrenaica* is limited at higher altitudes, in accordance with its climatic constraints, and it is already occupying the most suitable zones within the Moncayo Natural Park. However, potential expansion areas already exist at lower elevation zones. *P. sylvestris* share their most suitable climatic zone with *F. sylvatica*, and the promotion of one of these species may be at the expense of the other. *F. sylvatica* is an autochthone species that showed great potential to substitute the reforested *P. sylvestris* in large zones of its actual distribution. Finally, *P. uncinata* could be expanded in higher zones, where conditions are cooler and moister.

Overall, the studied species showed a certain level of climatic plasticity, and the models showed that their actual distribution is limited compared to the potential distribution given by the suitability cartography. In this sense, the proposed methodology and the application of the suitability maps may be a key element in policy-making related to adaptive management actions in forests subjected to climate change impacts.

Acknowledgments

The study was funded by DGA-La Caixa (project GA-LC-031/2010) and by the Spanish Ministry of Economy and competitiveness (projects CGL2012-31668 and CGL2015-69985-R). E. Martinez del Castillo benefited from a PhD grant (no. BES-2013-064453) funded by the Spanish Ministry of Economy and competitiveness. The authors thank the staff of Moncayo Natural Park (Gob. Aragón) for their help in the field work. We would like to thank anonymous reviewers for their helpful comments.

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