

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

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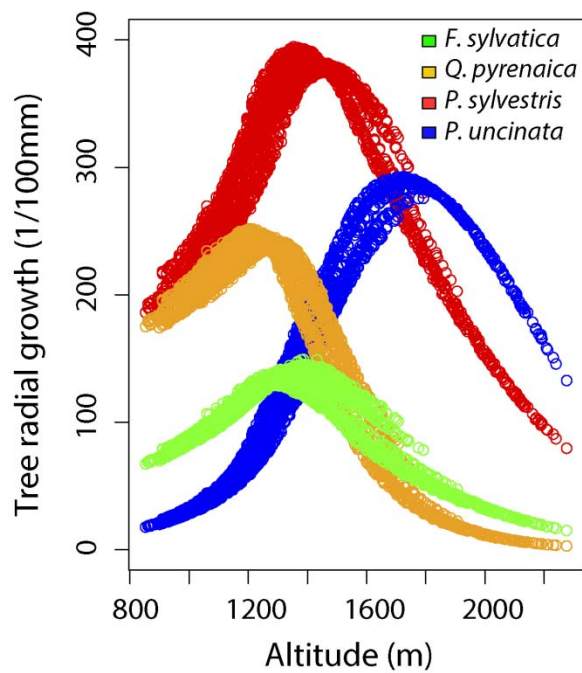
11 Abstract:

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

24 species distribution is limited, and their application may serve as a tool for adaptive  
25 management in forests subjected to climate change.

26 Graphical abstract:

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29

### 30 **Highlights**

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

35

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

37 1. Introduction:

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

50 Mediterranean forests are a living example of these processes, where the abandonment of  
51 agricultural land has also led to an expansion of shrubland and woodland cover  
52 (Debussche et al. 1999; Romero-Calcerrada and Perry 2004; San Roman Sanz et al.  
53 2013). In this respect, Moncayo Natural Park, located in Spain, exhibits numerous  
54 characteristics of a typical area where once traditional local activities have progressively  
55 ceased. Traditionally, the forest was intensively used by the local population mainly for  
56 logging activities (i.e., charcoal making and firewood) and cattle exploitation (Martínez  
57 del Castillo et al. 2015); therefore, the structure of forest was maintained as a meadow  
58 with old isolated trees or small stands mixed with open air grass zones. At the beginning  
59 of the 20<sup>th</sup> century, the involvement of the Spanish government in forest policies through  
60 reforestation led to intensive plantations (Ortigosa et al. 1990), with the aim of restoring  
61 degraded landscapes and increasing hydrological control, but the reforestations in some

62 cases were regarded as excessive (García Pérez and Groome 2000). In the case of  
63 Moncayo, two pine species were introduced to reforest the scarce vegetation mountain  
64 slopes, occupying the natural distribution area of beech and oaks (Pellicer 2000). Later,  
65 in 1978, the area was protected as a Natural Park to preserve the special ecological values  
66 of this mountain.

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

80 Tree secondary growth can be used as an indicator of tree health and general performance;  
81 this dynamic process is influenced by a complex interaction of tree physiology which, in  
82 turn, is controlled by environmental conditions (Fonti et al. 2010). Indeed, phenotypic  
83 plasticity in secondary growth allows trees to adapt to specific environmental conditions  
84 and is crucial for them to withstand environmental changes during their lifetime (Vitasse  
85 et al. 2010; Gricar et al. 2015). Therefore, knowledge of the variability of tree growth

86 across the climatic gradients of the species distribution area may be helpful to assess  
87 forest conservation and to identify optimal zones of forest expansion.

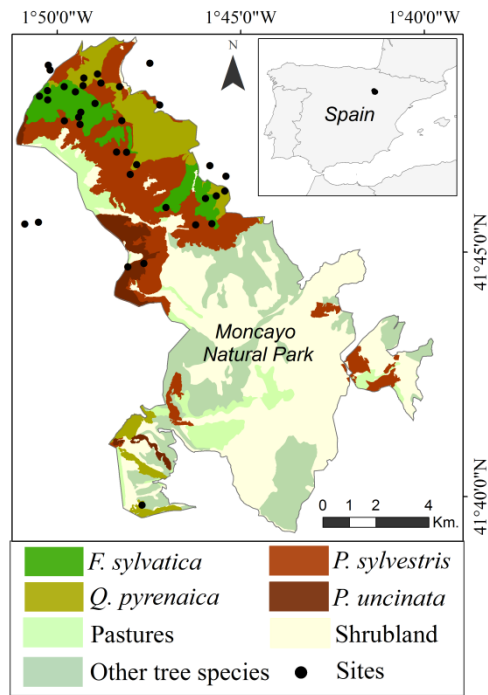
88 Here, we present a novel approach to characterize the optimal zones of forest growth and  
89 potential expansion through growth suitability maps resulting from the combination of a  
90 dense tree-ring network of the main forest species of Moncayo Natural Park and a high-  
91 resolution climate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

## 97 2. Materials and methods

### 98 2.1. Study site

99 Moncayo Natural Park is located in the Iberian range, in the northeast of the Iberian  
100 Peninsula, Spain (centroid at 41° 44' 55" N, 1° 46' 10" W). The Natural Park has an  
101 extension of 11.144 ha and the elevation range varies from 850 to 2.314 m a.s.l. (Figure  
102 1). This area belongs to the Mediterranean biogeographical region, with mild winters and  
103 seasonal precipitation regimes. However, the north slopes of the mountain intercept  
104 humid air masses, favoring the presence of different vegetation communities adapted to  
105 more cold and humid climates. Thus, the north part of the Park is covered by typically  
106 Northern European species, such as Scots pine (*Pinus sylvestris* L.), European beech  
107 (*Fagus sylvatica* L.), or mountain pine (*Pinus uncinata* Mill.), and by a forest of Pyrenean  
108 oak (*Quercus pyrenaica* Willd.). There is a presence of other tree species adapted to moist  
109 environments, such as holly (*Ilex aquifolium* L.), birch (*Betula pendula* Roth.), and rowan  
110 or mountain ash (*Sorbus aucuparia* L.). By contrast, in the south part of the Park, there

111 are no large forested areas, and species are more typically Mediterranean, such as holm  
112 oak (*Quercus ilex* L.), black pine (*Pinus nigra* Arnold) or shrubs of rosemary (*Rosmarinus*  
113 *officinalis* L.), thyme (*Thymus vulgaris* L.), or genista (*Genista scorpius* L.).



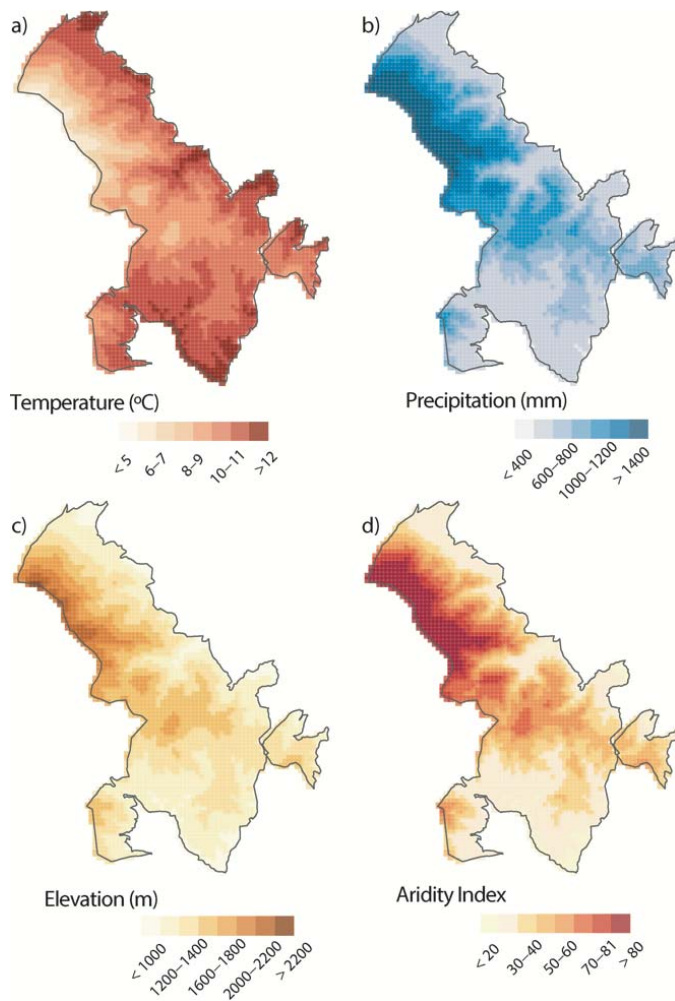
115 Figure 1. Location map of Moncayo Natural Park. The spatial distribution of the main  
116 forest species and other vegetation categories and the location of the study sites are  
117 represented as black dots.

## 118 2.2. Climate data

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

122 Climate grids were generated with the *reddPrec* R package (Serrano-Notivoli et al.  
123 2017b) based on the reconstructed stations of Serrano-Notivoli et al. (2017a). The  
124 climatic variables generated were precipitation and maximum and minimum temperature,

125 at an annual scale for the period 1950–2012, with a spatial resolution of 200 meters  
126 (Figure 2).



127

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

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

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

$$139 \quad AI = \frac{P}{10 + T}$$

140 where P is the annual mean precipitation (in mm) and T (in °C) the annual mean air  
 141 temperature. The climate types defined by AI vary from arid (0–10), semi-arid (10–20),  
 142 Mediterranean (20–24), semi-humid (24–28), humid (28–35), very humid (35–55), to  
 143 extremely humid (>55). The range of values of AI inside the Natural Park ranged from  
 144 17.96 to 109.84, with a mean value of 44 (Figure 2).

### 145 2.3 Field sampling and sample processing

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

		Altitudinal range a.s.l.)	Mean annual temperature range (°C)	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				
<i>F. sylvatica</i>	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
<i>P. sylvestris</i>	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
<i>P. uncinata</i>	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



<i>Q. pyrenaica</i>	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	

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

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

#### 166 2.4 Predictive growth models

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

```
170 Model <- glmer(TRWt ~ (AImean * Climate variablest) + (BAt-1 | Tree identity),
171 family=poisson(link="log"))
```

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

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

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

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

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

194 Despite the limited actual distribution of species across the Moncayo Natural Park,  
195 dendrochronological sampling, containing tree-rings from different sites and years,  
196 include a wide range of climate conditions that allows extending the domain of the  
197 obtained models to outside their actual distribution range. The climate grid included 2801  
198 points for which seasonal climate values were estimated for the period 1951-2012 (62

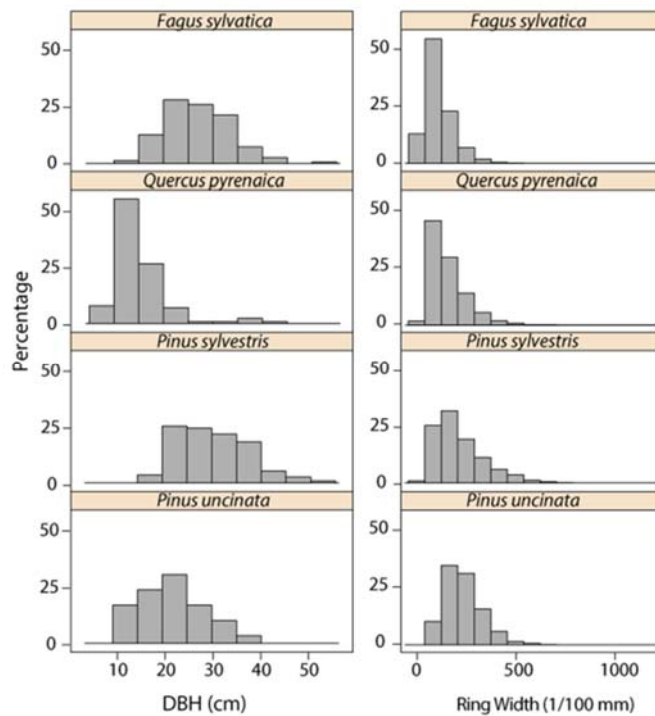
199 years). Whether climate conditions occurred in this set of 2801\*62 situations are included  
200 in the climatic domain of the dendrochronological dataset of each species has been  
201 calculated to define the AD of each model.

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

### 207 3. Results

#### 208 3.1. Radial growth across species

209 The dendrochronological network consisted in 40 sites, where a total of 812 cores were  
210 taken, ranging from 5 to 25 trees per site (Table 1). Altogether, more than 60,000 rings  
211 were dated and measured. The tree structure of the sampled trees (DBH) and the tree-ring  
212 widths varied among the species, as shown in Figure 3. The DBH ranged from 5.74 cm,  
213 recorded in *Q. pyrenaica*, to 53.72 cm, in the case of *P. sylvestris*, with mean values of  
214 14.54 (*Q. pyrenaica*), 21.69 (*P. uncinata*), 26.55 (*F. sylvatica*), and 29.73 (*P. sylvestris*).  
215 The tree-ring width measurements varied from 0.012 to 8.87 mm. in *Q. pyrenaica*, from  
216 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  
217 case of *F. sylvatica*. The lower mean value was 1.057 (*F. sylvatica*), followed by 1.502  
218 (*Q. pyrenaica*) and 2.116 (*P. sylvestris*), and the higher value was 2.296 mm (*P.*  
219 *uncinata*).

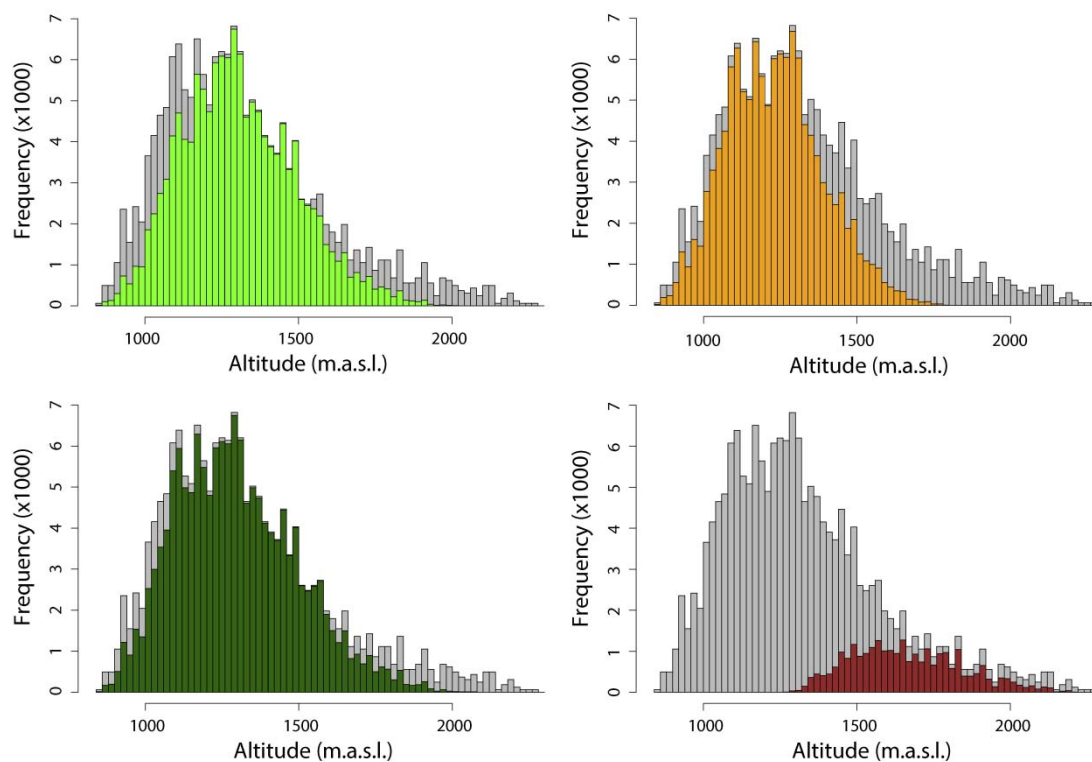


220

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

222 3.2. Predictive tree growth models

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



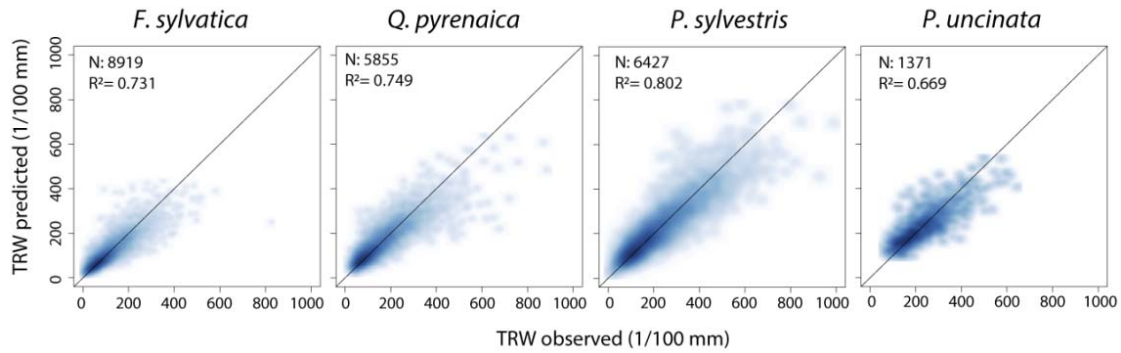
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235 Figure 4. Applicability domains. The altitudinal distribution of the climate range of each  
 236 specie (for a) *Fagus sylvatica*, b) *Quercus pyrenaica*, c) *Pinus sylvestris*, and d) *Pinus*  
 237 *uncinata*) F. *sylvatica*) overlapping the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

239 AD of each specie is shown in Figure 4. For *F. sylvatica*, AD includes a wide climate  
 240 domain that is representative of most of the climate conditions occurred across the Natural  
 241 Park from 1200 to 1600 m of altitude. At lower and higher altitudes, only certain climate  
 242 conditions occurred during the period 1951-2012 are represented in the tree-ring network  
 243 (Figure 4a). In case of *Q. pyrenaica*, the AD is representative of most of the conditions  
 244 occurred at lower altitudes while it decrease progressively at altitudes higher than 1400  
 245 m (Figure 4b). Representativeness for *P. sylvestris* is wider including most of the climate  
 246 conditions occurred from 1000 to 1800 m (Figure 4c). On the contrary, the  
 247 dendrochronological network of *P. uncinata* shows a relatively good representativeness

248 of climate conditions occurred at higher altitude being not representative of conditions  
249 occurred below 1350 m (Figure 4d).

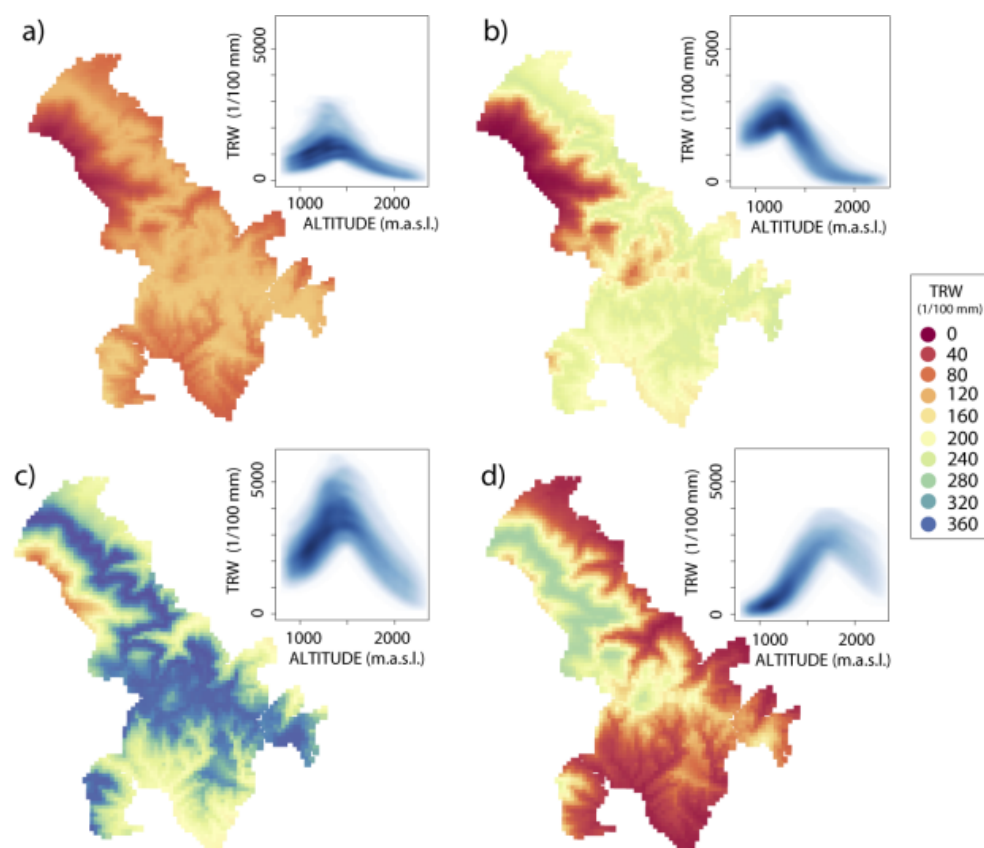
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251

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

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



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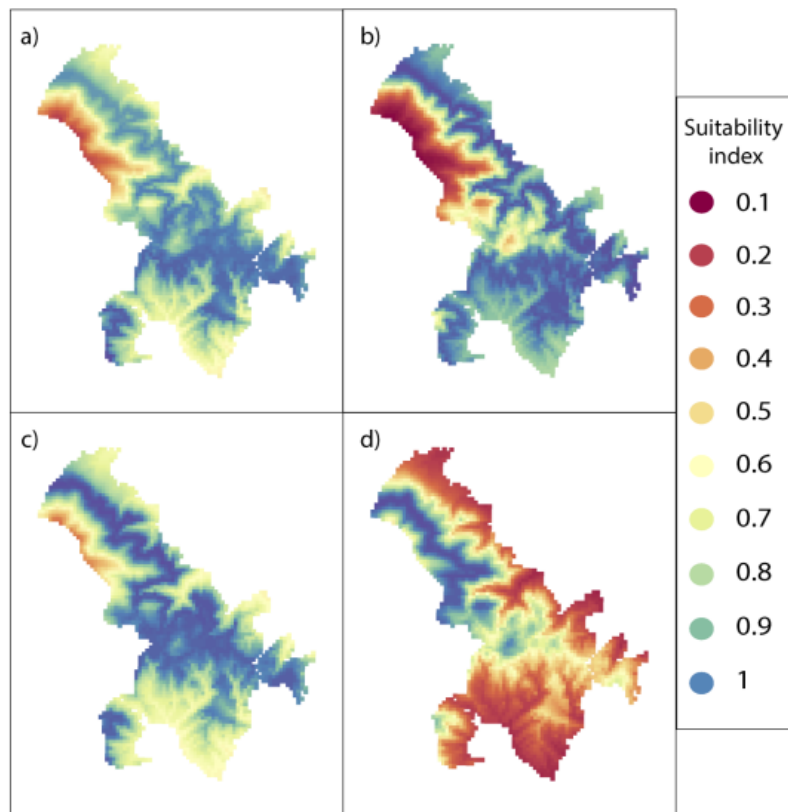
261 Figure 6. Growth predictions developed by GLMM models for a) *Fagus sylvatica*, b)  
 262 *Quercus pyrenaica*, c) *Pinus sylvestris*, and d) *Pinus uncinata*. Maps represent the mean  
 263 annual growth predictions for the period 1951–2012 and graphs include the variability  
 264 through the years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

265 The maximal predicted growth of *F. sylvatica* was reached at 1337 meters. The predicted  
 266 growth rapidly increased from 1000 m a.s.l. to the peak, slowly decreasing at higher  
 267 altitudes. There was a higher variability in predicted growth between 1100 and 1600 m  
 268 due to the different climate conditions among sites with a similar altitude across the park.  
 269 Overall, the growth rates in this species were lower compared to those of the others. *Q.*  
 270 *pyrenaica* growth reached its maximum at 1240 m a.s.l., which is higher than the mean  
 271 altitude where the species is present (1118 m). At high altitudes, growth progressively  
 272 decreases as the climate conditions change, reaching near-zero values of ring width over  
 273 2000 m. By contrast, *P. sylvestris* showed a high variability in their growth predictions,

274 with this variability being rather constant along the altitudinal gradient. The maximum  
275 growth is predicted at 1430, almost 100 meters higher than the actual mean altitude of the  
276 species. Lastly, *P. uncinata* growth predictions reached minimum values at lower  
277 altitudes, which include most of the Natural Park, especially in the south and a maximum  
278 growth at 1760 m. For all the four analyzed species, the higher growth rates predicted are  
279 located within the applicability domains (AD) of predictive models which support their  
280 reliability. On the contrary, predicted growth of *P. uncinata* and *Q. pyrenaica* at lower  
281 and higher altitudes respectively, should be interpreted with special caution since  
282 represents extrapolations of the constructed models out to their AD.

283 Climate suitability defined by growth models was applied to the Natural Park cover for  
284 all species (Figure 7). Overall, inside the actual distribution of the species, the suitability  
285 index was high: *F. sylvatica* is present in 155 pixels, of which 81.6% scored more than  
286 0.8 of suitability and only 4.4% less than 0.5. *Q. pyrenaica* achieved the best match  
287 between the actual distribution and the suitability index, at over 145 pixels, where 99.3%  
288 scored more than 0.8 and none less than 0.5. *P. sylvestris* was the most extended species,  
289 with a presence in 432 pixels and 78.9% with a high suitability (>0.8) and none with  
290 suitability below the average value. *P. uncinata* was present in 121 pixels, with 89.3%  
291 over 0.8 and with 5.79% under 0.5 in the suitability index.





292

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

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

306 of the suitable zone, the higher values of suitability were located at 1762 m a.s.l., higher  
307 than the mean of its actual distribution.

## 308 4. Discussion

### 309 4.1. Modeling climate suitability

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

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

328 Applicability domains (AC) represents the climate domains where models may exhibit  
329 sufficient predictive performance for training samples (dendrochronological network)

330 and thus for new samples. In addition, for a different combination of seasonal climate  
331 conditions located inside the AD, their growth estimates are also expected to be as reliable  
332 as those in the training sample. However, if they are outside the AD, reliability of their  
333 estimates decrease and interpretation of predicted growth patterns should be interpreted  
334 with caution. This can be especially the case of *P. uncinata* model apply to low elevation  
335 sites and *Q. pyrenaica* model apply to high elevation areas.

336 Despite inherent limitations related to the applicability of obtained models all across the  
337 Natural Park, we apply them to the full climate grid. Then, for each grid pixel and for  
338 each species, the mean of the predicted TRW for all years was calculated as a general  
339 growth forecast. In addition, to guarantee the comparison between species and study sites,  
340 the tree-ring width was predicted for a theoretical tree with a common basal area of 252.91  
341 cm<sup>2</sup> (equivalent to 17.97 cm of diameter at breast height), which is the mean basal area  
342 of all analyzed trees before each tree ring formation.

#### 343 4.2. Climate-smart plastic behavior of tree species

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

349 In the case of the Moncayo Natural Park, all the studied species are in their distribution  
350 limits; therefore, their growth is likely to be constrained by the climate. *F. sylvatica* is a  
351 widespread European species, reaching at this point its southernmost forest stands. This  
352 late-successional and highly-competitive species is known to be sensitive to drought and  
353 high temperatures (Zimmermann et al. 2015; Bolte et al. 2016), both in the southernmost

354 or xeric limits (Rozas et al. 2015) and in the core of their distribution in central Europe  
355 (Babst et al. 2013). Particularly in our study site, the growth of *F. sylvatica* is limited by  
356 an extremely short growing period: i.e., between 2 and 3 months, the shortest xylogenesis  
357 period reported in the literature (Martínez del Castillo et al. 2016). Our results confirm  
358 that growth is influenced by climate; previous and current summer conditions play an  
359 important role in this influence, and the combination of all climatic factors explains 73%  
360 of the within-tree-total growth variability. The importance of the mean value of the aridity  
361 index and its interaction with all other climatic variables in the models is indicative of the  
362 plasticity and adaptation of the species; the climatic stressors for tree growth vary across  
363 the prevailing climate.

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

374 The main climatic threat and stressor to *P. sylvestris*, which is one of the most widely  
375 distributed tree species over Europe in this region, is water availability, which is important  
376 throughout most of the year, as pines have a long growth period, reaching up to seven  
377 months of xylogenesis (Martínez del Castillo et al. 2016, 2018a). This species presents  
378 great variability in its growth predictions all over the Natural Park, showing its plastic

379 behavior. On the other hand, *P. uncinata* presents less coverage over Europe and is  
380 usually limited to hilly mountains. This species has been widely used for climate  
381 reconstructions, and its growth and wood density is closely related to temperature  
382 (Büntgen et al. 2010; Konter et al. 2014) and drought (Tejedor et al. 2016), in accordance  
383 with the limited growth predictions in lower elevations and drought-prone environments  
384 with higher temperatures. Although both species showed a remarkable climate sensitivity,  
385 the explained variability of growth derived from climate varied between these two pine  
386 species, at 80% in *P. sylvestris* and 67% in *P. uncinata*.

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

#### 396 4.3. Climate suitability for forest management

397 The definition of a suitability model for forest species has been developed for  
398 management purposes since the 1980s (Tikkanen et al. 2007). Other studies dealing with  
399 the calculation of a habitat suitability index include diverse information, but they are  
400 usually incomplete, because they do not incorporate all underlying mechanisms of  
401 variation (Elith et al. 2002). Nonetheless, the climate effect is clear and present in all  
402 modeling. Therefore, assessing the climate suitability of tree species is the necessary first  
403 approach for both species modeling and management actions designed as assisted

404 migration (Koralewski et al. 2015). In addition, the spatialization of the suitability index  
405 through the cartography of suitability—covering all of the Natural Park area—provides  
406 useful and important information for managers, such as the identification of areas where  
407 one species can be substituted by others, or favorable edges for species expansion. In this  
408 case, the potential growth is used as an integrative variable of population fitness over the  
409 territory.

410 Specifically, the suitability maps indicated large areas of potential expansion for all  
411 species, balanced overall by altitude. *Q. pyrenaica* showed great potential in low-  
412 elevation zones below 1100 m.a.s.l., while, for *P. uncinata*, higher performance was  
413 forecasted in high altitudes, with values even higher than its actual distribution. *F.*  
414 *sylvatica* and *P. sylvestris* shared their highest suitability zone in the mid-range of the  
415 altitudinal gradient of the Natural Park where the species are present, but also in the  
416 central part of the Park, which is currently under-forested. These two species are growing  
417 in the same altitudinal range, competing in their expansion. In this sense, previous  
418 research proved that *F. sylvatica* may partially substitute *P. sylvestris* areas (Martínez del  
419 Castillo et al. 2015), in accordance with recent global studies that revealed a consistent  
420 directional substitution of Pinaceae by Fagaceae worldwide (Alfaro Reyna et al. 2018) or  
421 studies showing the drought-related vulnerability of *P. sylvestris* (José Vidal-Macua et al.  
422 2017; Sánchez-Salguero et al. 2017)

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

428 5. Conclusions:

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

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

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