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1       **Elevation modulates the phenotypic responses to light of four co-**  
2                                   **occurring Pyrenean forest tree species**

3  
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10  
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26 **Abstract (max. 200 words):**

27 *Context:* Understanding the phenotypic responses of mountain tree species to different  
28 levels of local irradiance can be of critical importance for elucidating their capacity to  
29 relocate above their current distributional limit in response to environmental changes.

30 *Aim(s):* To evaluate whether the response of different co-occurring forest tree species to  
31 local irradiance varies when they are growing at various elevations or beyond their  
32 current distributional limit.

33 *Methods:* Seedlings of four tree species (*Betula pendula* Roth., *Pinus sylvestris* L.,  
34 *Abies alba* Mill. and *Pinus uncinata* Ram. ex DC.) were planted under different  
35 irradiance levels (forest understory vs natural gaps) and at various elevation (montane-  
36 subalpine ecotone and subalpine belt). After four growing seasons, 48 plants per species  
37 were excavated to assess allocational (biomass distribution) and morphological (specific  
38 leaf area) traits. Midday leaf water potential was recorded during a period of intense  
39 drought.

40 *Results:* The subalpine species (*A. alba* and *P. uncinata*) increased their allocation to the  
41 root system at low elevation and under dense canopy. We observed constant or higher  
42 SLA in all species when they develop in the subalpine belt. *B. pendula* was affected  
43 more severely by drought at low elevations and under shade than in open microsites.

44 *Conclusion:* We found marked species-specific phenotypic variability of tree seedlings  
45 to increasing irradiance, with these responses modulated by the elevation at which the  
46 trees were growing.

47 **Keywords:** phenotypic variability, elevation gradients, light responses, allocation,  
48 specific leaf area, mountain forests

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51

52 **Introduction**

53 Forest ecotones have been widely used to study the response of vegetation to changes in  
54 climate (Hufkens et al. 2009). Most research on forest ecotone dynamics has focused on  
55 treeline areas, where the limit of the forest is generally defined by temperature and thus  
56 easier to detect and monitor (Kupfer and Cairns 1996; Camarero et al. 2002, 2006).

57 Increasing attention has recently been devoted to the dynamics of transition areas  
58 between different tree populations (Berger et al. 2007; Benavides et al. 2013; Dinca et  
59 al. 2017). In the montane-subalpine ecotone, for example, not only has upward  
60 displacement of montane species been observed to track climate warming (Peñuelas and  
61 Boada 2003; Lenoir et al. 2008) but also downslope movements of the subalpine species  
62 into the montane belt (Hättenschwiler and Körner 1995; Lenoir et al. 2008; Bodin et al.  
63 2013). These different responses are the consequence of critical interactions between  
64 changing climate and a number of factors operating at various organizational levels and  
65 spatio-temporal scales. Some of these factors relate to the physical environment (e.g.  
66 topographic variables, edaphic characteristics) or to the influence of biotic agents (pests  
67 and pathogens, browsers) (Van der Putten et al. 2010; Ameztegui and Coll 2015).

68 Others are intrinsic to the species and populations, such as their capacity to adapt to  
69 changes via demographic processes (e.g. seed production, dispersion, survival-growth  
70 trade-offs), (Lloret et al. 2012; Benavides et al. 2015) or their ability to compete for  
71 resources (Loehle 2000, 2003; MacArthur 1984). In these cases, differences among  
72 coexisting species in their phenotypic responses to the various limiting factors can be  
73 decisive factors in the dynamics of transitional areas (Bradshaw 1965; Lloret et al.  
74 2012; Ameztegui et al. 2015).

75 In the Pyrenean range, where forests have experienced significant densification and  
76 canopy closure in the last decades (Ameztegui et al. 2010), the capacity of species to

77 adjust their morphology and physiology to light will be a determinant for future  
78 demographical processes in the area (Ameztegui and Coll 2011). It is well-known that  
79 the response of species to light varies throughout the developmental stages of plants  
80 (Delagrangé et al. 2004) and that this response is modulated by the availability of other  
81 primary resources, such as water (Sánchez-Gómez et al. 2006) or nutrients (Vernay et  
82 al. 2018). There is much less knowledge on whether the capacity of species to modify  
83 their form and function in response to light is maintained when they grow at the limits  
84 of, or even beyond, their current distributional ranges. However, this process - i.e., the  
85 interplay between simultaneous phenotypic responses to light and climate - can be of  
86 critical importance in defining potential displacements of mountain species in response  
87 to environmental changes (Bodin et al. 2013).

88 In this study, we set up a field experiment in the Pyrenees in which the four most  
89 widespread species coexisting in the montane-subalpine ecotone of the area (*Pinus*  
90 *sylvestris* L., *Pinus uncinata* Ram. ex DC., *Abies alba* Mill. and *Betula pendula* Roth.)  
91 were planted across a gradient of local irradiance levels, and at two different elevations:  
92 the ecotone between the montane and the subalpine belt (around 1,600 m), and at the  
93 core of the subalpine belt (around 2,000 m). We focused our study on the early stages of  
94 plant development as these are the most vulnerable to climate alterations (Matías et al.  
95 2011). Our specific objectives were: (i) to examine the variation in phenotypic  
96 responses to light at plant and organ level among the co-existing species at the ecotone  
97 level, (ii) to examine whether these responses changed or were maintained when the  
98 species develop above the ecotone and, finally (iii) to analyze how the water responses  
99 of plants to an extreme drought event were modulated by light and elevation. We  
100 hypothesized that there would be marked species-specific differences in the phenotypic  
101 responses to light, with the shade-tolerant species (*A. alba*) showing less variability than

102 the shade-intolerant ones. We also expected that these responses would be affected by  
103 the elevation (through the combined effect of temperature stress and drought) and that  
104 the species mainly distributed in the montane belt (i.e *B. pendula* and *P. sylvestris*)  
105 would be more affected by increased elevation than the ones distributed naturally at  
106 both altitudes (*A. alba* and *P. uncinata*).

107

## 108 **Material and methods**

### 109 *Study area and species*

110 The study included the four most common tree species in the Catalan Pyrenees: Scots  
111 pine (*P. sylvestris*), mountain pine (*P. uncinata*), silver fir (*A. alba*) and silver birch (*B.*  
112 *pendula*). Two of these (*P. uncinata* and *A. alba*) are characteristic of the subalpine belt  
113 and can be dominant at elevations above 1,600-1,800 m. *P. uncinata* is a shade-  
114 intolerant conifer that reaches its southern distributional limit in the Pyrenees and is  
115 restricted to the subalpine belt (between 1,600 and 2,300 m), constituting most of the  
116 Pyrenean treeline. Silver fir (*A. alba*) is usually restricted to humid sites on north-  
117 facing, shady slopes between 1,400 and 2,000 m, where the risk of summer water deficit  
118 is lower. In contrast, *P. sylvestris* and *B. pendula* are more typical in the montane belt,  
119 and are rarely found above 2,000 m. *P. sylvestris* is a shade-intolerant species that  
120 dominates the montane belt of the Pyrenees, whereas *B. pendula* is a shade-intolerant  
121 pioneer species that usually colonizes disturbed areas between 1,000 and 1,800 m, but  
122 only rarely constitutes the dominant species in the forest. These four species differ  
123 widely in their ecological requirements, and range from most (rank = 5) to least (rank =  
124 1) shade tolerant following the ranking system developed by Niinemets and Valladares  
125 (2006): *A. alba* ( $4.6 \pm 0.06$ ; mean  $\pm$  SE), *B. pendula* ( $2.03 \pm 0.09$ ), *P. sylvestris* ( $1.67 \pm$   
126  $0.33$ ), and *P. uncinata* (1.2). Moreover, the drought tolerance ranking order according to

127 the same authors would be: *P. sylvestris* ( $4.34 \pm 0.47$ ); *P. uncinata* (3.88), *B. pendula*  
128 ( $1.85 \pm 0.21$ ) and *A. alba* ( $1.81 \pm 0.28$ ). Despite their different ecological requirements,  
129 these four species are able to coexist in a strip between 1,500 and 1,800 m. constituting  
130 the montane-subalpine ecotone.

131 The study area was located in the northern slopes of the *Serra del Cadí*, a mountain  
132 range located in the Catalan Pyrenees (NE Spain, Figure 1). In this area, we established  
133 a total of 24 experimental plots at two elevations with contrasting climate: 12 at the  
134 ecotone between the montane and the subalpine belt (around 1,600 m) and 12 at the core  
135 of the subalpine belt (around 2,000 m). The *ecotone* plots were located at the *P.*  
136 *sylvestris* – *P. uncinata* transition zone and characterized by a mean annual temperature  
137 and precipitation of 7.4 °C and 992 mm (Ninyerola *et al.* 2000), whereas the *subalpine*  
138 plots were located upwards in the same valley and under comparable aspect and soil  
139 conditions, but colder and wetter climate (annual temperature: 4.9 °C, annual  
140 precipitation: 1118 mm). These plots were established close to the optimum elevation  
141 distribution of *P. uncinata* in the Pyrenees and displayed a colder and wetter climate  
142 (Table 1). Ground vegetation in both areas was dominated by shrubby species such as  
143 box (*Buxus sempervirens* L.) and common juniper (*Juniperus communis* L.).

#### 144 145 *Experimental design*

146 We planted 144 two-year old seedlings of each of the four studied species during late  
147 spring 2008. Due to the presence of wild ungulates and livestock in the study sites, we  
148 protected the plants from herbivore damage by an individual protector (90 cm height, 33  
149 cm diameter) with a mesh net of 20 x 20 cm (Nortène, Lille, France). Prior to planting,  
150 the seedlings were grown in a local nursery of the Catalan Forest Service (Pobla de  
151 Lillet) from local seed sources (i.e. seed source, nursery and plantation area were all  
152 located within the same provenance (Alía *et al.* 2005)). We distributed seedlings of each

153 species into 12 plots per elevation, with half planted in the forest understory and the  
154 other half in naturally-occurring gaps, to ensure enough variability in light conditions  
155 (which were measured at the individual level, see next section). Seedlings were  
156 randomly distributed within each plot, carefully planted to minimize alteration of the  
157 micro-environment, and placed at a minimum of one meter apart from each other to  
158 avoid any interaction among them. Each experimental plot measured between 40 and 50  
159 m<sup>2</sup>, and consisted of a plantation of 24 seedlings (6 per species).

160

#### 161 *Climate, local irradiance and plant water status*

162 We characterized climate at the two sites via two meteorological stations (one per site),  
163 where air temperature at a height of 1 m, below-ground soil temperature (at 10 cm  
164 depth) and precipitation were continuously measured using ECH2O sensors (Decagon  
165 Devices, Pullman, WA, USA). Throughout the study, the seedlings planted at high  
166 elevation (subalpine sites) were exposed to lower mean temperatures, more  
167 precipitation, a higher Thornthwaite index and a 20% shorter growing period than the  
168 seedlings at lower elevation (Table 1). During the summer of the last year, a rather  
169 warm and dry period (with 60% less precipitation than the average for the last 10 years,  
170 Fig. 2) exposed the vegetation to a significant drought stress that was visually  
171 appreciable, even in the adult stand, that showed brownish color in the leaves.  
172 During the fourth growing season, we randomly selected 48 plants per species (2 per  
173 plot). We measured local irradiance (percentage of transmitted photosynthetic photon  
174 flux density, %PPFD) in July for each plant using two Li-190SA quantum sensors (Li-  
175 COR, Lincoln, NE, USA). The measurements were conducted on completely overcast  
176 days using the sensors in paired mode, i.e. we placed one of the sensors at the top of  
177 each plant and the other in an adjacent open area (see Parent and Messier (1996) for a



178 full description of the method). This allowed us to have quantitative, measured values of  
179 local irradiance for each individual plant. We also sampled two fresh leaves of the year  
180 per plant (needle fascicles in the case of pines) during the summer. Leaves were  
181 collected from the outer part of the seedling, one from the upper third of the plant and  
182 the other from the middle third, and stored in moist paper in sealed plastic bags in a  
183 cooler, until scanning them in the laboratory within 24 hours. We used the CI-202  
184 Portable Laser Area Meter (CID Bio-Science Inc., WA, USA), to obtain individual leaf  
185 area measurements. Leaves were then oven-dried (60 °C, 2 days) and weighed, and we  
186 computed specific leaf area (SLA) as the ratio between leaf area and oven-dry mass  
187 ( $\text{cm}^2 \text{g}^{-1}$ ).

188 During a particularly dry period occurring at the end of the fourth growing season, we  
189 measured midday leaf water potential ( $\Psi_{\text{midday}}$ ) *in situ* on the 48 plants using a pressure  
190 chamber (Solfranc Technologies, Vila-Seca, Spain). Following recommendations by  
191 Pérez-Harguindeguy *et al.* (2013), we collected leaves directly exposed to direct sun to  
192 minimize variation due to sunflecks.

#### 193 *Plant biomass and leaf traits*

195 Before planting, we randomly selected 30 plants per species and each plant was  
196 separated into leaves, stems and roots in the laboratory. The roots were washed by  
197 placing them under running water over a fine mesh sieve and finger-massaging as  
198 needed to remove all the particles (Pérez-Harguindeguy *et al.* 2013). We then manually  
199 removed any big soil particles retained by the sieve. The parts were weighed to the  
200 nearest 0.1 mg after oven-drying (60 °C, 2 days), and total biomass, leaf, stem and root  
201 biomass, and the root-to-shoot ratio (RSR) calculated.

202 At the end of the fourth growing season (late October), the 48 plants per species  
203 previously used for leaf water potential measurements were harvested, and we

204 calculated total biomass, leaf, stem and root biomass, and the root-to-shoot ratio (RSR)  
205 as indicated above. Since at the time of excavation some birch plants had lost a part of  
206 their leaves, we did not compute leaf biomass at that time.

207

#### 208 *Data analyses*

209 We analyzed the effect of light availability (measured for each individual plant) on plant  
210 biomass, its components, RSR, specific leaf area, and plant water status. Following the  
211 likelihood approach, we compared different models to test our hypotheses: instead of  
212 assuming an *a priori* form of the relationship between dependent variables and  
213 predictors, we tested and assessed five model formulations (linear, exponential, power,  
214 logarithmic and Michaelis–Menten; Table A1), to account for potential non-linear  
215 responses of the dependent variable to light. We compared the results across the four  
216 alternative models via the corrected Akaike information criterion ( $\Delta\text{AICc}$ , Burnham and  
217 Anderson, 2002). Each model was also compared to a null model in which there was no  
218 effect of the independent variable (light availability). The  $R^2$  of the regression between  
219 observed vs. predicted values provided a measure of the goodness-of-fit of each model,  
220 and we deemed a model to be statistically better than another one when  $\Delta\text{AICc} > 2$ .  
221 Once the best formulation for the effect of light availability was selected, we tested  
222 whether it was mediated by elevation by comparing the strength of evidence from a  
223 model in which parameters were estimated separately for ecotone and subalpine sites,  
224 against another model in which all the data were pooled together, and the first model  
225 was only retained if it was substantially supported by the data ( $\Delta\text{AICc} > 2$ ).  
226 The maximum likelihood parameter values for all models were estimated using  
227 simulated annealing (Goffe et al. 1994) and the asymptotic 2-unit support intervals were  
228 used to assess the strength of evidence for individual maximum likelihood parameter

229 estimates. All analyses were performed with R 3.2.2 software (R Core Team 2015) and  
230 the ‘likelihood’ package ver. 1.7 for R.

231

## 232 **Results**

233 *Responses to light and elevation at whole-plant level: plant biomass and allocation*

234 Total biomass at the moment of plantation ranged from 1.3 to 2.5 g·plant<sup>-1</sup> (*Abies alba*

235 and *Betula pendula*, respectively), with intermediate values for pines (*P. sylvestris*: 2.2

236 g·plant<sup>-1</sup>; *P. uncinata*: 2.1 g·plant<sup>-1</sup>). Four years after planting, total biomass ranged

237 from 3.7 to 4.7 g·plant<sup>-1</sup>, with no significant differences in average plant biomass

238 among the species. All the species increased their biomass with light availability, with

239 the exception of *A. alba* (Fig 3A). We observed no effect of elevation on the response of

240 aboveground biomass to light for *B. pendula*, *P. sylvestris* and *A. alba*. In contrast, *P.*

241 *uncinata*, showed a greater response in biomass to light at the subalpine belt (Fig. 3B,

242 Table 2). The pattern of carbon allocated to roots along the light gradient differed

243 significantly among species and elevation stages. *B. pendula* showed the highest overall

244 investment to roots and markedly increased its belowground biomass with light

245 availability, in particular at the montane sites. In contrast, *P. sylvestris* and *A. alba*

246 showed moderate to null trends, and maintained comparable root biomass under

247 different light availabilities at both stages. Finally, *P. uncinata* plants increased their

248 root biomass in response to irradiance in the subalpine sites but, interestingly, was the

249 only species that decreased root biomass with irradiance at the montane sites (Fig 3C,

250 Table 2).

251 The abovementioned differences translated into between-species and between-site

252 variations in the root-to-shoot ratio (RSR) of plants (Fig 3D). On the one hand, the two

253 species characteristic of the subalpine area (*A. alba* and *P. uncinata*) showed a decrease

254 in RSR with light at the montane areas, but a slight increase on the subalpine sites (Fig.  
255 2). On the other hand, the species that are currently found in the montane belt showed  
256 either no variations of RSR with light availability (*B. pendula*) or a decrease in RSR in  
257 response to light increases, particularly when growing in the subalpine sites.

258

259 *Responses to light and elevation at leaf level: specific leaf area and plant water status*

260 At leaf level, shading resulted in an increase in SLA on *A. alba*, *B. pendula* and *P.*  
261 *sylvestris*, but failed to affect *P. uncinata* (Table 2). Moreover, the plants of the three  
262 former species presented higher SLA values in the subalpine plots, but *P. uncinata* was  
263 again the exception (Figure 4).

264 Midday water potential values ( $\Psi_{min}$ ) in September were much higher (less negative) for  
265 both pine species (*P. sylvestris* and *P. uncinata*) than for *A. alba* and *B. pendula* (Figure  
266 5). Conifer species did not show differences in  $\Psi_{min}$  between elevation gradients, with  
267 mean values ranging from -0.63 MPa (*P. sylvestris*, montane sites) to -2.99 MPa (*A.*  
268 *alba*, montane sites). In contrast, *B. pendula* presented lower  $\Psi_{min}$  values in the montane  
269 sites than in the subalpine ones (Figure 5). Interestingly, we found  $\Psi_{min}$  in *B. pendula*  
270 plants to decrease following a power function in the shaded areas, but this pattern was  
271 only observed at the montane sites. Conversely, light availability failed to affect  $\Psi_{min}$   
272 for any of the conifer species (*P. uncinata*, *P. sylvestris* and *A. alba*).

273

## 274 **Discussion**

275 Our study revealed marked species-specific phenotypic variability of tree seedlings to  
276 increasing light (at plant- and organ-level), and showed that, in most cases, these  
277 responses were modulated by the elevation at which the species grew. The use of plants  
278 with the same origin (seed source and nursery were within the same provenance) at two

279 different elevations allowed us to assess and reveal the phenotypic component of the  
280 allocational and morphological responses of the species to the environment. This  
281 phenotypic variability can be a determinant in how young plants respond to  
282 environmental changes in the future, and is likely to drive the dynamics of transition  
283 zones such as ecotones.

284

#### 285 *Responses to light and elevation at whole-plant level*

286 The seedlings of the three light-demanding species included in this study (*B. pendula*,  
287 *P. sylvestris* and *P. uncinata*) increased both stem biomass and total plant biomass with  
288 light availability, confirming the critical role played by this factor in the demographic  
289 processes of Mediterranean mountain forests (Matías et al. 2011; Ameztegui and Coll  
290 2011). In contrast, the shade-tolerant species (*A. alba*) showed almost no variability in  
291 aboveground and belowground biomass allocation in response to light. These results are  
292 in line with a number of studies that have reported overall lower plasticity of shade-  
293 tolerant species compared to shade-intolerant ones (Sánchez-Gómez et al. 2006;  
294 Valladares et al. 2002a). Interestingly, the two species naturally developing in montane  
295 areas (*B. pendula* and *P. sylvestris*) displayed a similar increase in their stem and root  
296 biomass with light both at the montane-subalpine ecotone and at the subalpine stage.  
297 The other two species – found naturally above the ecotone (i.e. *A. alba* and *P. uncinata*)  
298 – seemed to adopt a more conservative strategy at low elevation, and showed little  
299 growth and higher root-to-shoot ratio when growing below a dense canopy (i.e. under  
300 low light availability). Despite the fact that shade adaptation usually implies the  
301 opposite allocational trend (i.e. higher carbon allocation to the aboveground organs  
302 responsible for capturing light (Mooney 1972; Sack and Grubb 2002; Van Hees and  
303 Clerkx 2003)), maintaining high root-to-shoot ratios may allow *A. alba* and *P. uncinata*

304 to better face belowground competition from the overstory under particularly intense  
305 summer drought episodes. This more conservative strategy was previously observed for  
306 these species in a nearby mountain range in relation to height growth (Ameztegui and  
307 Coll 2011), and seems to be linked to a trade-off between growth and survival. Our  
308 study suggests that Pyrenean subalpine species adopt more conservative allocational  
309 strategies under warmer, drier conditions than others in their range.

310

### 311 *Responses to light and elevation at leaf level*

312 At leaf level, all the species except *P. uncinata* showed the expected increase in SLA  
313 with decreasing light availability (Poorter et al. 2010), which is related to the need to  
314 maximize light capture under shade conditions (Planchais and Sinoquet 1998; Curt et al.  
315 2005). In fact, in agreement with Poorter et al. (2012), our results showed generally  
316 higher phenotypic variability at organ level rather than at whole plant level (allocation  
317 traits), particularly in the case of *A. alba*, the most shade tolerant species (see also  
318 Robakowski et al. 2003). *P. uncinata* seedlings responded differently from the others  
319 and upheld constant SLA values along the light gradient (except *P. sylvestris* growing in  
320 the montane sites). Although the light gradient in *P. uncinata* was somewhat  
321 discontinuous (with only one plot clearly exposed to the sun), this species was also the  
322 only one showing no SLA variation between the elevation stages included. A previous  
323 study revealed little or no variation in the growth and survival of this species along  
324 elevation gradients (Ameztegui and Coll 2013) proving its ability to develop well at  
325 both elevation stages. Although no variation of this leaf trait with elevation has already  
326 been reported in conifers (Read et al. 2014), we unexpectedly found higher SLA values  
327 in the other three studied species when growing at the highest elevation, especially  
328 under low light conditions. These findings did not agree with most published literature

329 on the topic, which generally report thicker leaves at high elevation or in a response to  
330 low temperatures (see for example Körner et al. 1989; Cordell et al. 1998; Poorter et al.  
331 2010; Bresson et al. 2011). Our results can be explained by the particular gradient of  
332 summer drought that is found in Mediterranean mountains. As postulated by Pescador et  
333 al. (2015), who found comparable responses to ours in Mediterranean mountain  
334 grasslands, drought stress markedly decreases with altitude in these systems.  
335 Accordingly, under such conditions, changes in allocational and morphological plant  
336 traits within an elevation gradient might not only be mediated by temperature stress, but  
337 by the combined effect of both forces. Higher stress in terms of water availability in the  
338 lower part of our elevation gradient might partly explain the lower SLA we found for  
339 most of the studied species.

340 At leaf level, the three conifers (*A. alba*, *P. sylvestris* and *P. uncinata*) were able to  
341 maintain constant midday water potential during the studied drought period, regardless  
342 of the light conditions and the elevation stage at which they developed. The marked  
343 isohydric character of these species (they close stomata early during drought to avoid  
344 cavitation losses at the expense of carbon assimilation) is probably at the root of this  
345 result, and might also explain the poor growth experienced by *A. alba* and *P. uncinata*  
346 at the lower elevation, where water stress periods during the summer are more frequent  
347 (Ameztegui and Coll 2013). Although leaf water potential of *B. pendula* did not vary  
348 with light in the subalpine stage, it decreased significantly in the shade at the ecotone  
349 level. Higher soil depletion in the understory compared to the gaps, due to competition  
350 from mature trees may be the cause of this trend (Valladares et al. 2002b), together with  
351 the well-known low drought tolerance of birch (Niinemets and Valladares 2006), and  
352 the reported inability of the species (contrary to *A. alba* and *P. uncinata*) to allocate  
353 more C to roots in shade conditions.

354

355 *Conclusion*

356 In this study, we found evidence that elevation variation strongly modified species-  
357 specific phenotypic responses to light. The effects from elevation mostly occurred at  
358 organ level (SLA) for the montane species, but at whole-plant level (allocation traits)  
359 for the subalpine species (*A. alba* and *P. uncinata*). The latter showed a conservative  
360 strategy in the absence of light when climatic conditions were warmer and drier than  
361 those in their current range, as is expected to happen in the future. Considering the  
362 progressive canopy closure that the Pyrenean forests have experienced in the last few  
363 decades, the conservative strategy may increase their survival rates, but is likely to put  
364 them at a competitive disadvantage against ecologically similar species from the  
365 montane belt such as Scots pine (Ameztegui et al. 2015).

366 We also observed constant or higher SLA in the studied species when they grow at high  
367 elevation, a result that differs from most published literature and may be related to the  
368 particular climate of Mediterranean mountains. Finally, we found little effect from light  
369 and elevation on the water status of the seedlings during a drought event, although the  
370 most drought-intolerant species seemed to be more affected by dry conditions in shade  
371 than in open microsites. As mentioned in Valladares et al. (2000), caution is needed  
372 when interpreting and extrapolating the observed patterns of phenotypic variability to  
373 other species and environments in studies conducted with a limited number of these.  
374 Further studies involving more species and mountain ranges would be needed to  
375 confirm the reported trends.

376



377 **References**

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513 **Table 1.** Main abiotic and biotic characteristics of the studied stands.

	<b>Montane-subalpine ecotone plots</b>	<b>Subalpine plots</b>
Latitude (N) / Longitude (E)	42°19'/1°43'	42°18'/1°42'
Elevation (m a.s.l.)	1550	1955
Aspect/slope (%)	NE/39	NE/53
Bedrock	Limestone	Limestone
Mean annual/summer temperature (°C)	7.4/14.8	4.9/11.7
Total annual/summer precipitation (mm)	992/271	1118/327
Length of the growing season (days)	194	147
Mean summer maximum temperature (°C)	21.0	17.3
Mean winter minimum temperature (°C)	-3.4	-4.6
Dominant species	<i>Pinus sylvestris</i> , <i>Betula pendula</i>	<i>Pinus uncinata</i> , <i>Abies alba</i>

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517 **Table 2.** Akaike Information Criterion (AIC) of the models predicting biomass  
 518 allocation, specific leaf area and water potential as a function of light availability for  
 519 seedlings of four tree species planted at two elevations.  
 520

Species	<i>Pinus uncinata</i>		<i>Abies alba</i>		<i>Pinus sylvestris</i>		<i>Betula pendula</i>	
	Model	AIC	Model	AIC	Model	AIC	Model	AIC
Plant Biomass (g)	Pow*	103.8	Null	137.4	MM	145.5	Lin	163.7
		(-26.6)		(0)		(-23.3)		(-25.0)
Stem Biomass (g)	Pow*	67.29	Lin	64.4	MM	97.7	MM	103.7
		(-24.1)		(-9.9)		(-34.1)		(-24.3)
Root Biomass (g)	Lin*	50.65	Null	89.4	MM	93.3	Lgt*	109.1
		(-27.2)		(0)		(-6.8)		(-27.1)
Root:Shoot Ratio	Lin*	69.1	Pow*	84.4	Pow*	43.7	Null	76.0
		(-16.8)		(-7.0)		(-12.7)		(0)
SLA (cm <sup>2</sup> g <sup>-1</sup> )	Null	315.8	Lgt*	378.1	Lgt*	337.9	Pow*	478.4
		(0)		(-8.3)		(-26.2)		(-12.3)
Water Potential (MPa)	Null	315.5	Null	283.7	Null	315.5	Pow*	318.8
		(0)		(0)		(0)		(-10.8)

521  
 522 For each species, only the best model (i.e., the one with stronger empirical support) is provided, and the  
 523 value in brackets is the decrease in AIC compared to the null model (assuming no effect of light  
 524 availability on the dependent variable). Models flagged with an asterisk indicate stronger empirical  
 525 support for a model with separate data for both elevations than for pooled data, i.e. an elevation effect.  
 526 Models are: null: null; Lin: linear; Pow: power; Lgt: logarithmic; MM: Michaelis-Menten. The detailed  
 527 equations for each model and the estimated parameters can be found in and Table A1 (Online Appendix).  
 528  
 529

530 **Captions of figures**

531

532

533 **Fig. 1.** Situation of the study area, showing the location of the Cadí-Moixeró Natural  
534 Park and the ecotone and subalpine plots within the park.

535

536 **Fig. 2.** Evolution of precipitation and monthly average of the maximum temperatures in  
537 the study area over the 4-year study period (2008–2011). Dashed lines and shaded areas  
538 indicate mean  $\pm$  SD during the last 10 years, whereas solid lines indicate measured  
539 values. Data are from the Prat d’Aguiló meteorological station (2,138 m a.s.l.), located  
540 less than 1 km from the high-elevation site. The grey box indicates the extreme drought  
541 event and high temperatures during early September 2011 (see text for further details).  
542 The arrow indicates the day when measurements of leaf water potential were made.

543

544 **Fig. 3.** Predicted variation in plant biomass, stem and root mass fraction and in root-to-  
545 shoot ratio as a function of light availability and elevation for seedlings of the 4 studied  
546 species. Black lines and dots correspond to predicted and observed values, respectively,  
547 for seedlings in the montane-subalpine ecotone, whereas grey lines and dots correspond  
548 to predicted and observed values in the subalpine belt. When no effect of elevation was  
549 predicted, data were pooled together and the predicted values are presented in grey.  
550 Horizontal lines indicate lack of effect of light availability for that species, and are  
551 shown for comparative purposes. Dashed lines represent average values of the response  
552 variable at the moment of plantation.

553

554 **Fig. 4.** Predicted variation in specific leaf area (SLA) as a function of light availability  
555 and elevation for seedlings of the 4 studied species. Black lines and dots correspond to  
556 predicted and observed values, respectively, for seedlings in the montane-subalpine

557 ecotone, whereas grey lines and dots correspond to predicted and observed values in the  
558 subalpine belt. When no effect of elevation was predicted, data were pooled together  
559 and the predicted values are presented in grey. Horizontal lines indicate lack of effect of  
560 light availability for that species, and are shown for comparative purposes. Fitted  
561 models and parameter values can be found in Table 2 and Table A1 (Online Appendix),  
562 respectively.

563 **Fig. 5.** Predicted variation in water potential (MPa) as a function of light availability  
564 and elevation for seedlings of the 4 studied species. Black lines and dots correspond to  
565 predicted and observed values for seedlings in the montane-subalpine ecotone, whereas  
566 grey lines and dots correspond to predicted and observed values in the subalpine belt.  
567 When no effect of elevation was predicted, data were pooled together and the predicted  
568 values are presented in grey. Horizontal lines indicate lack of effect of light availability  
569 for that species, and are shown for comparative purposes. Fitted models and parameter  
570 values can be found in Table 2 and Table A1 (Online Appendix), respectively.

571

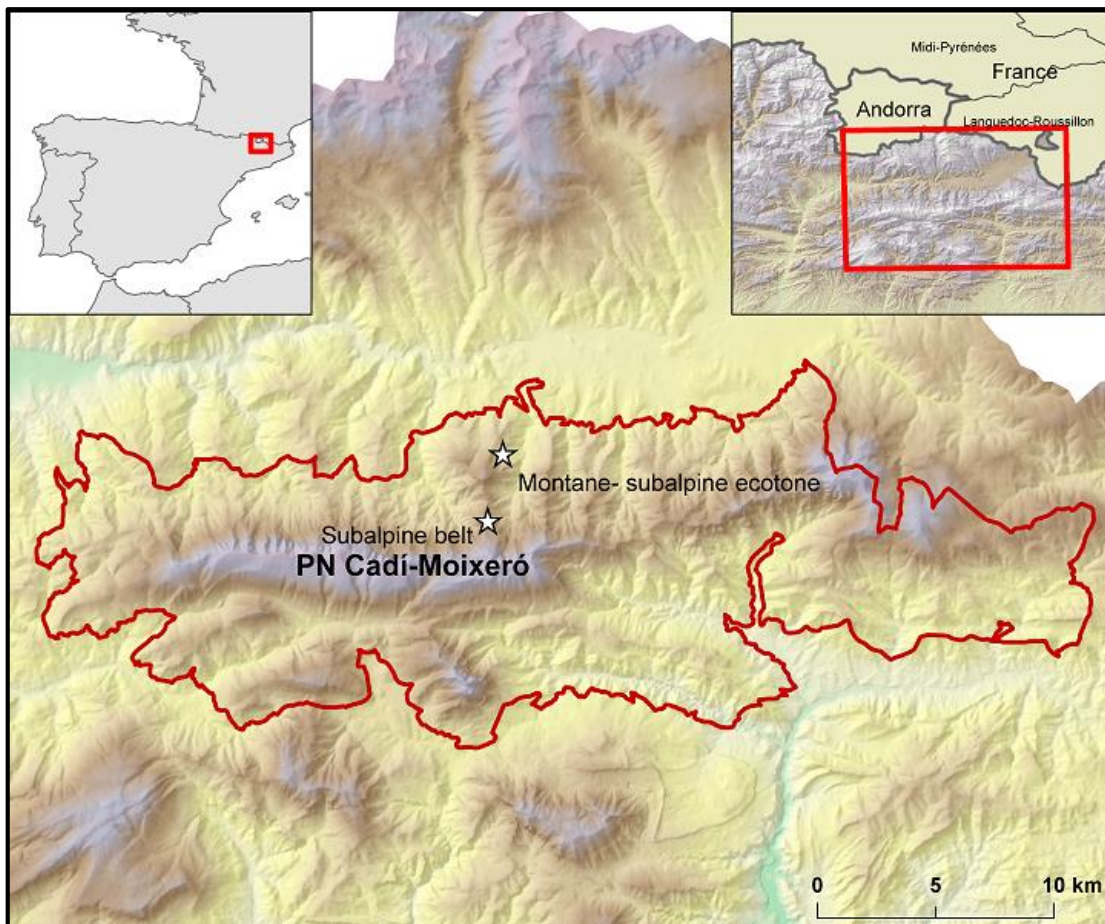
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573 **Figures**

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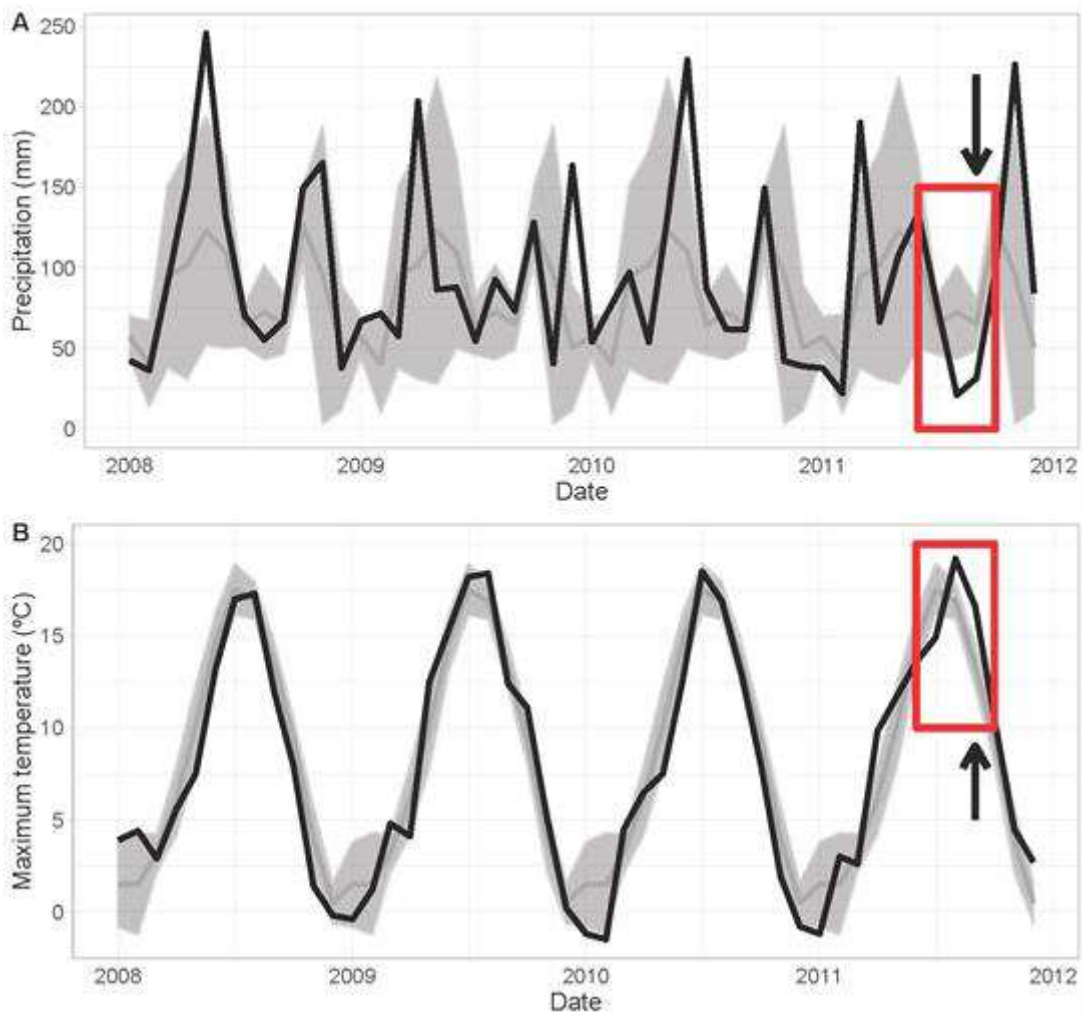
575 **Fig. 1**

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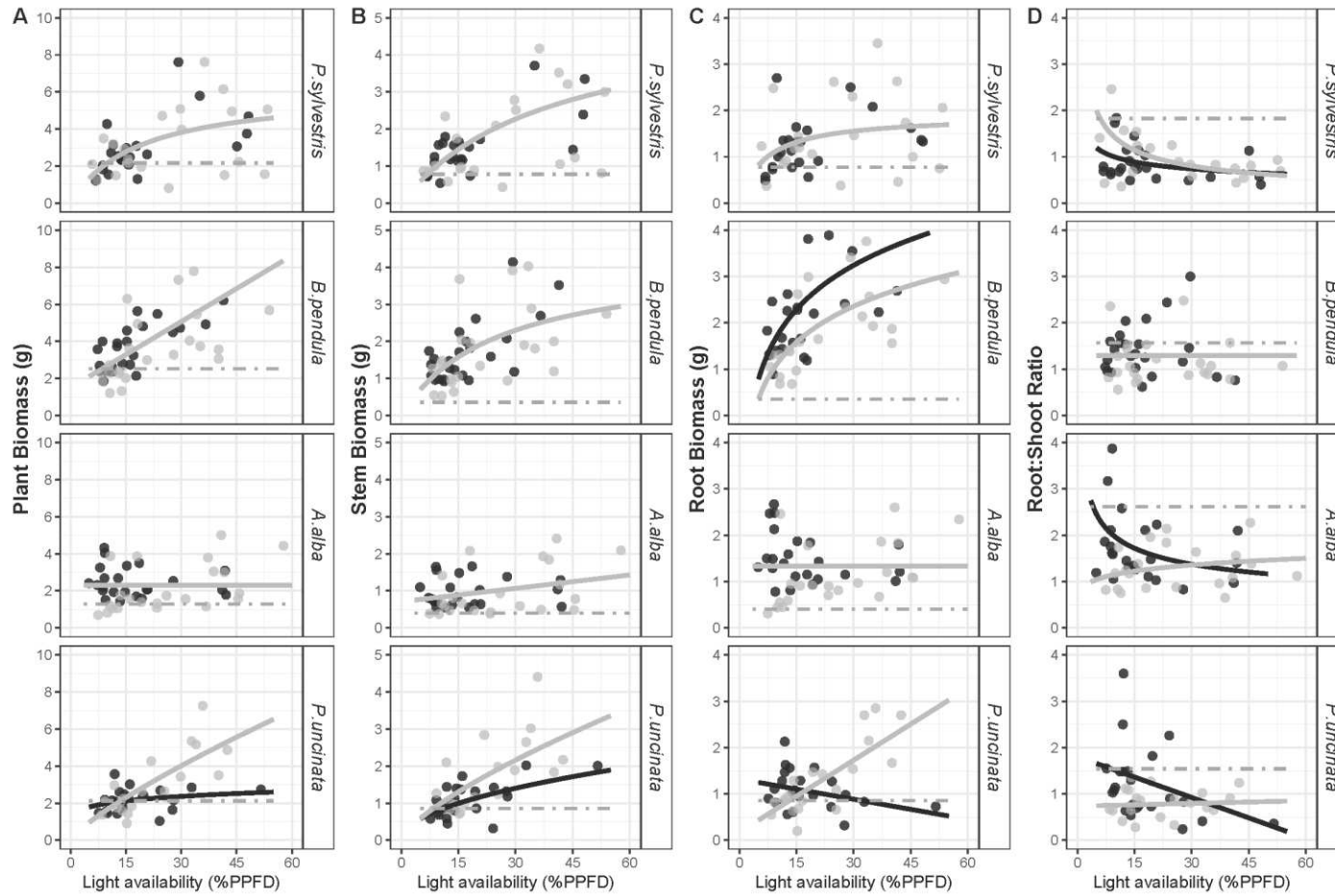
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579 **Fig. 2**  
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585 **Fig. 3**  
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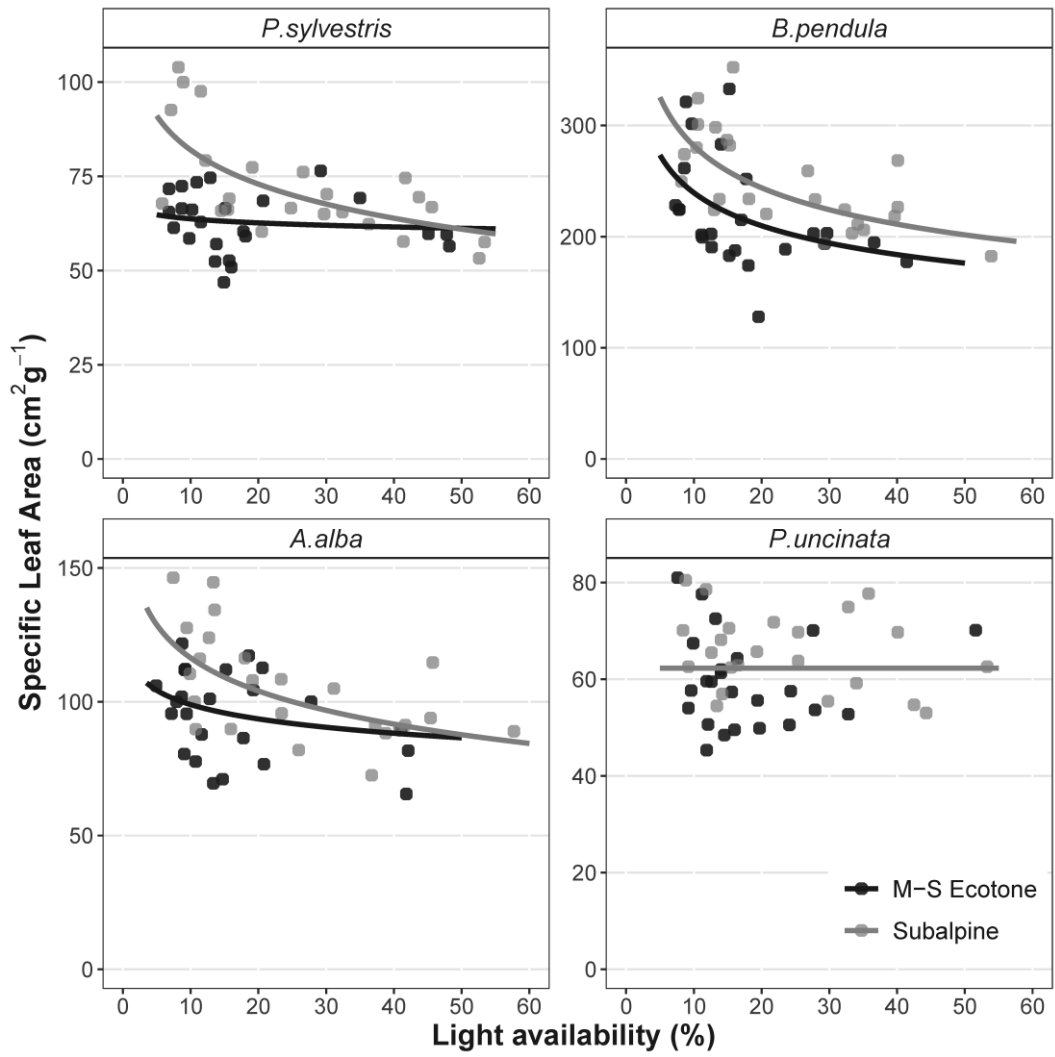


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589 **Fig. 4**

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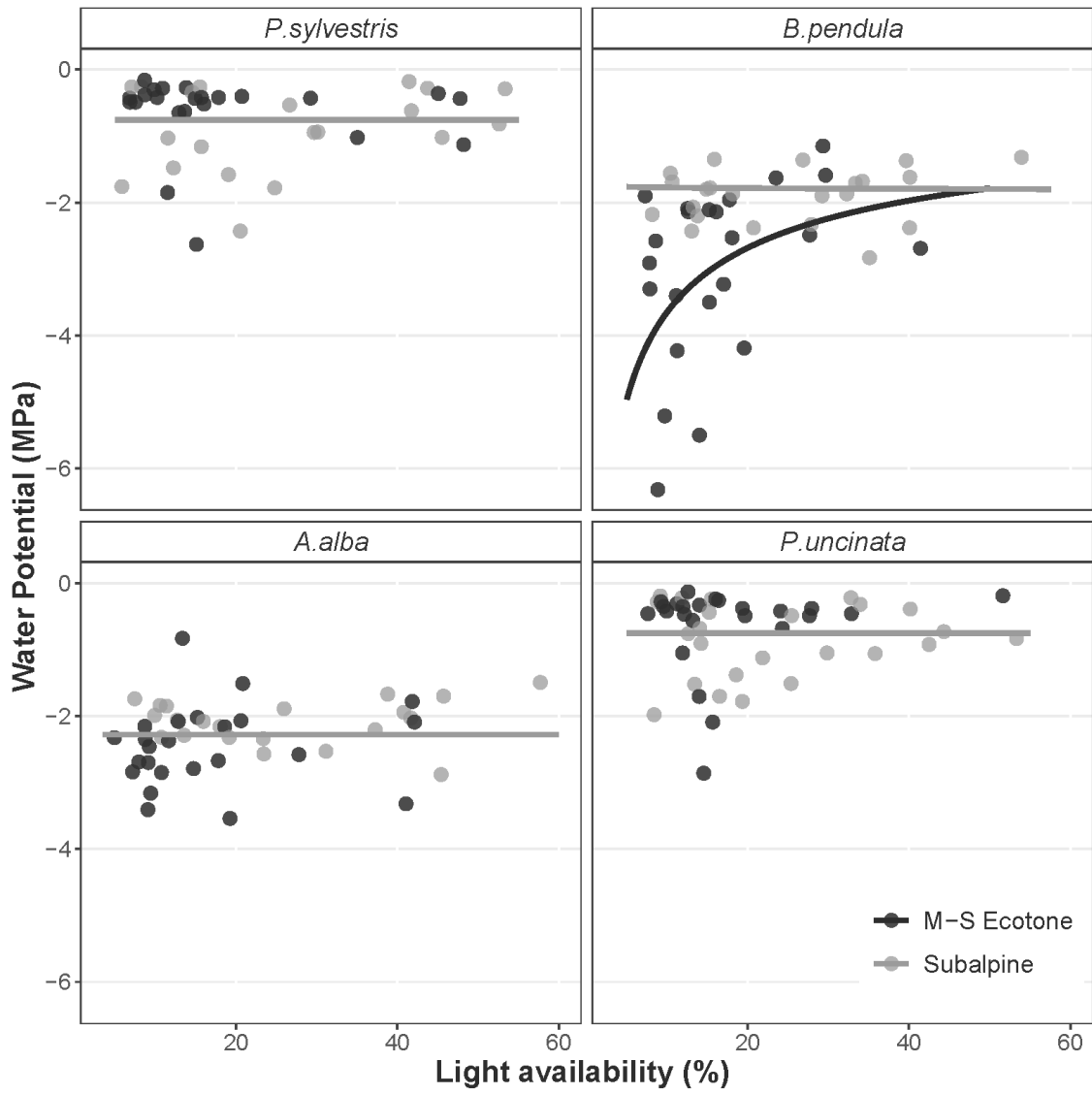


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593 **Fig. 5**

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**Table A1.** Estimates of equation parameters and 2-unit support intervals (in parentheses) for models of biomass allocation, specific leaf area and water potential as a function of light availability shown in Table 2. Parameter estimates are given only for the best model (Lin: linear, Pow: power; Lgt: logarithmic, MM: Michaelis-Menten) for all the data pooled together (a, b) and separated between montane-subalpine ecotone (ae, be) and subalpine (as, bs) stands. Parameter estimates in bold indicate the strongest empirical support for pooled data or for separated data, i.e. an altitudinal effect

Variable	Model	a	b	ae	be	as	bs
<i>Pinus uncinata</i>							
Plant Biomass	Lin	0.814 (0.554 – 1.154)	0.155 (0.137 – 0.176)	<b>1.887 (1.627 – 2.367)</b>	<b>0.066 (0.049 – 0.094)</b>	<b>0.569 (0.243 – 1.168)</b>	<b>0.181 (0.161 – 0.217)</b>
Stem Biomass	Pow	0.183 (0.167 – 0.203)	0.680 (0.647 – 0.714)	<b>0.254 (0.221 – 0.289)</b>	<b>0.513 (0.462 – 0.558)</b>	<b>0.246 (0.211 – 0.278)</b>	<b>0.637 (0.591 – 0.677)</b>
Root Biomass	Lin	0.633 (0.527 – 0.766)	0.027 (0.021 – 0.035)	<b>1.337 (1.217 – 1.477)</b>	<b>-0.014 (-0.018 – -0.008)</b>	<b>0.175 (0.087 – 0.355)</b>	<b>0.48 (0.042 – 0.058)</b>
Root-Shoot Ratio	Lin	1.272 (1.159 – 1.412)	-0.012 (-0.016 – -0.006)	<b>1.867 (1.767 – 2.047)</b>	<b>-0.031 (-0.033 – -0.024)</b>	<b>0.642 (0.550 – 0.809)</b>	<b>0.0049 (0.0014 – 0.0127)</b>
Specific Leaf Area	Null	<b>62.50 (60.48 – 65.11)</b>	-	59.46 (56.86 – 63.24)	-	65.46 (62.13 – 69.43)	-
Hydric Potential	Null	<b>7.532 (6.531 – 8.806)</b>	-	7.444 (6.094 – 9.442)	-	7.650 (6.373 – 9.649)	-
<i>Abies alba</i>							
Plant Biomass	Lgt	<b>2.411 (2.043 – 2.860)</b>	<b>0.397 (0.269 – 0.557)</b>	4.587 (4.050 – 5.125)	-0.378 (-0.580 – -0.177)	-0.914 (-1.385 – -0.252)	1.437 (1.282 – 1.657)
Stem Biomass	Lin	0.692 (0.592 – 0.819)	0.0123 (0.008 – 0.019)	<b>0.867 (0.759 – 1.064)</b>	<b>0.0001 (-0.0047 – 0.0111)</b>	<b>0.540 (0.395 – 0.736)</b>	<b>0.019 (0.013 – 0.027)</b>
Root Biomass	Null	<b>1.330 (1.200 – 1.503)</b>	-	1.400 (1.206 – 1.653)	-	1.251 (1.071 – 1.491)	-
Root-Shoot Ratio	Pow	2.678 (2.424 – 2.958)	-0.199 (-0.234 – -0.160)	<b>3.607 (3.207 – 4.207)</b>	<b>-0.285 (-0.331 – -0.223)</b>	<b>0.726 (0.631 – 0.833)</b>	<b>0.186 (0.140 – 0.229)</b>
Specific Leaf Area	Lgt	130.50 (126.45 – 134.45)	-10.89 (-12.43 – -9.27)	<b>122.93 (118.88 – 128.86)</b>	<b>-10.28 (-12.26 – -7.87)</b>	<b>162.03 (157.97 – 167.94)</b>	<b>-19.33 (-21.11 – 16.92)</b>
Hydric Potential	Null	<b>23.963 (22.286 – 25.958)</b>	-	23.699 (21.457 – 26.642)	-	24.426 (21.689 – 27.399)	-
<i>Pinus sylvestris</i>							
Plant Biomass	Pow	<b>0.546 (0.495 – 0.612)</b>	<b>0.707 (0.672 – 0.741)</b>	0.395 (0.351 – 0.471)	0.795 (0.755 – 0.855)	0.722 (0.655 – 0.889)	0.622 (0.589 – 0.688)
Stem Biomass	Pow	<b>0.202 (0.182 – 0.224)</b>	<b>0.718 (0.683 – 0.752)</b>	0.172 (0.154 – 0.208)	0.770 (0.730 – 0.837)	0.220 (0.191 – 0.262)	0.680 (0.640 – 0.733)
Root Biomass	Lgt	<b>0.403 (0.271 – 0.575)</b>	<b>0.326 (0.279 – 0.389)</b>	0.296 (0.127 – 0.519)	0.341 (0.277 – 0.421)	0.554 (0.394 – 0.894)	0.292 (0.240 – 0.410)
Root-Shoot Ratio	Pow	<b>2.738 (2.483 – 3.048)</b>	<b>-0.382 (-0.420 – -0.342)</b>	2.075 (1.792 – 2.379)	-0.313 (-0.366 – 0.257)	4.161 (3.719 – 4.927)	-0.497 (-0.540 – -0.437)
Specific Leaf Area	Lgt	91.605 (88.671 – 94.503)	-8.102 (-9.206 – -7.046)	<b>67.594 (64.905 – 70.257)</b>	<b>-1.624 (-2.822 – -0.512)</b>	<b>120.74 (117.50 – 123.92)</b>	<b>-15.69 (-16.869 – -14.375)</b>
Hydric Potential	Lgt	21.682 (20.814 – 22.983)	-4.357 (-4.690 – -3.862)	<b>-2.016 (-3.135 – -0.147)</b>	<b>3.258 (2.826 – 3.956)</b>	<b>31.064 (29.821 – 33.368)</b>	<b>-6.786 (-7.196 – -6.051)</b>
<i>Betula pendula</i>							
Plant Biomass	Pow	<b>0.767 (0.699 – 0.842)</b>	<b>0.575 (0.543 – 0.606)</b>	0.711 (0.624 – 0.798)	0.631 (0.585 – 0.671)	0.48 (0.471 – 0.613)	0.668 (0.621 – 0.701)
Stem Biomass	Pow	<b>0.328 (0.301 – 0.368)</b>	<b>0.571 (0.539 – 0.611)</b>	0.309 (0.269 – 0.359)	0.591 (0.545 – 0.643)	0.342 (0.292 – 0.396)	0.564 (0.513 – 0.610)
Root Biomass	Lgt	-0.935 (-1.114 – -0.715)	1.057 (0.997 – 1.137)	<b>-1.403 (-1.682 – -1.124)</b>	<b>1.366 (1.266 – 1.466)</b>	<b>-1.475 (-1.633 – -1.167)</b>	<b>1.110 (1.059 – 1.210)</b>
Root-Shoot Ratio	Null	<b>1.295 (1.175 – 1.435)</b>	-	1.396 (1.236 – 1.616)	-	1.191 (1.031 – 1.383)	-
Specific Leaf Area	Pow	390.03 (374.43 – 409.25)	-0.181 (-0.120 – -0.160)	<b>378.08 (357.32 – 404.88)</b>	<b>-0.198 (-0.222 – -0.171)</b>	<b>483.47 (457.67 – 521.53)</b>	<b>-0.229 (-0.250 – -0.200)</b>
Hydric Potential	Pow	85.036 (78.134 – 93.818)	-0.436 (-0.472 – 0.396)	<b>95.209 (85.113 – 108.05)</b>	<b>-0.423 (-0.471 – -0.370)</b>	<b>18.798 (16.794 – 21.193)</b>	<b>-0.013 (-0.052 – 0.027)</b>

Equations for the different models in the table are:

Null: null model  $y = a + \varepsilon$

Lin: lineal model  $y = (a + b \cdot x) + \varepsilon$

Pow: power model  $y = a \cdot x^b + \varepsilon$

MM: Michaelis-Menten model  $y = \frac{a \cdot x}{a/b + x} + \varepsilon$

Lgt: logarithmic model  $y = a + b \cdot \ln(x) + \varepsilon$