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The final publication is available at:

<https://doi.org/10.1007/s10021-017-0196-y>

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1 **Climate change could negate positive tree diversity effects on forest productivity: A**  
2 **study across five climate types in Spain and Canada**

3

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15

16 **KEYWORDS:** climate change; climate divergence from normals; forest inventory; forest  
17 productivity; water stress; heat stress; biodiversity and ecosystem functioning; functional  
18 trait diversity

19 **RUNNING HEAD:** climate change and diversity effect in forest

20 **AUTHOR CONTRIBUTIONS:** All authors participated in the study design and initial ideas;  
21 data were gathered by JV and AP; analyses were led by JV, the writing by AP, assisted by  
22 all others.

23 ABSTRACT

24

25 A positive relationship between tree diversity and forest productivity is reported for many  
26 forested biomes of the world. However, whether tree diversity is able to increase the  
27 stability of forest growth to changes in climate is still an open question. We addressed  
28 this question using 36,378 permanent forest plots from National Forest Inventories of  
29 Spain and Québec (Eastern Canada), covering five of the most important climate types  
30 where forests grow on Earth and a large temperature and precipitation gradient. The plots  
31 were used to compute forest productivity (aboveground woody biomass increment) and  
32 functional diversity (based on the functional traits of species). Divergence from normal  
33 levels of precipitation (drier or wetter than 30-yr means) and temperature (warmer or  
34 colder), were computed for each plot from monthly temperature and precipitation  
35 means. Other expected drivers of forest growth were also included. Our results show a  
36 significant impact of climate divergences on forest productivity, but not always in the  
37 expected direction. Furthermore, although functional trait diversity had a general positive  
38 impact on forest productivity under normal conditions, this effect was not maintained in  
39 stands having suffered from temperature divergence (i.e. warmer conditions). Contrary  
40 to our expectations, we found that tree diversity did not result in more stable forest's  
41 growth conditions during changes in climate. These results could have important  
42 implications for the future dynamics and management of mixed forests worldwide under  
43 climate change.

44

45 INTRODUCTION

46 Forests are among those ecosystems predicted to suffer the most from added stress  
47 impacts following global change, such as drought, insect and disease outbreaks, and  
48 invasive species, among others (Choat et al., 2012). Increases in the frequency, duration,  
49 or severity of drought or extreme temperature could alter the composition, structure, and  
50 distribution of forests in many regions, as well as their functioning and ultimately the  
51 production of services upon which humanity depends (Allen et al., 2010; Thom and Seidl,  
52 2016). In fact, some of those anticipated changes are already observed in some forest  
53 ecosystems, such as increased mortality following climate-change induced drought (Peng  
54 et al., 2011; Vayreda et al., 2012; Grimm et al., 2013).

55

56 There is considerable interest in evaluating the role of biodiversity in promoting  
57 ecosystem functions and services, and the biodiversity - ecosystem functioning (BEF)  
58 relationship has seen considerable interest, and controversy, for over two decades  
59 (Symstad et al., 2003; Reiss et al., 2009). The hypothesis that increased producer diversity  
60 leads to increased producer productivity is now accepted with high confidence for a  
61 variety of systems, although limitations and key research needs identified early are in  
62 several cases still relevant today (Hooper et al., 2005; Balvanera et al., 2014). Forests did  
63 not escape the trend, and have been under the lens of some recent large-scale  
64 observational research, testing the hypothesis that more diverse forests are more  
65 productive (Paquette and Messier, 2011; Vilà et al., 2013; Liang et al., 2016) and produce  
66 more ecosystem services (Gamfeldt et al., 2013; Ruiz-Benito et al., 2014). The

67 hypothesized effect of biodiversity on growth is linked to facilitation and competition  
68 reduction, together forming complementarity (including niche partitioning and positive  
69 feedbacks on resource supply). Diversity effects on growth would also be dependent on  
70 the identity of the species present (sampling, or selection effect) due to dominant species  
71 driving ecosystem functioning (Roscher et al., 2012). These two mechanisms have been  
72 demonstrated in many ecosystems, with complementarity often being the most  
73 important (Reich et al., 2001; Cardinale et al., 2011). However, these positive effects are  
74 not always found, and may depend on site properties such as water and nutrient  
75 availability (Forrester et al., 2013; Pretzsch et al., 2015).

76

77 Most studies addressing the potential effects of tree diversity on forest productivity have  
78 been tested under stable conditions. They show a generally positive effect of biodiversity  
79 on forest productivity, but which can vary in size and even sign among biomes or regions,  
80 at the regional level (Paquette and Messier, 2011; Vilà et al., 2013) and across the world  
81 (Liang et al., 2016). However little has been achieved regarding the potential role of  
82 biodiversity in reducing the vulnerability (or in increasing stability) of forests to changes  
83 in climate (e.g. drought events), an issue raised early in BEF literature (Hooper et al.,  
84 2005). Vulnerability to stress has been linked to the portfolio effect (insurance  
85 hypothesis), where more diverse ecosystems are thought to better cope with stress  
86 because diversification minimizes the risk of a given function (e.g. growth) to be  
87 drastically affected (Thibaut and Connolly, 2012; Isbell et al., 2015). An increased capacity  
88 to cope with stress could also be achieved through complementarity or facilitation using

89 the same mechanisms described above in stable conditions (Loreau and de Mazancourt,  
90 2013). For example a greater water-use efficiency was observed for mixtures growing in  
91 dry conditions, which could lead to the same communities being better able to face a  
92 further decrease in water availability by further increasing their efficiency (Grossiord et  
93 al., 2014b). But those mechanisms could be altered, or even reversed, if the stable  
94 conditions that favoured them and the associated assemblage of species are changed, for  
95 example following climate change.

96

97 Another important consideration in BEF literature is the importance of species identity as  
98 well as their functional traits (Hooper et al., 2005). Diversity effects are intimately linked  
99 to the functional traits of species, at the core of a mechanistic understanding of  
100 biodiversity effects (Reiss et al., 2009; Loreau and de Mazancourt, 2013), because they  
101 link species to the role they play in the ecosystem and influence processes at higher  
102 organizational levels (Díaz et al., 2004; Violle et al., 2007). Evidence is accumulating that  
103 functional trait derived metrics of diversity, such as functional trait diversity (FD) and  
104 functional identity (measured using community weighted means - CWM) are needed to  
105 better assess diversity effects (Mokany et al., 2008; Tobner et al., 2014; Paquette et al.,  
106 2015).

107

108 This study aimed to analyse: (i) how functional trait diversity, climate and recent  
109 divergence in climate with respect to normals affect forest productivity and (ii) whether  
110 more diverse forests are more stable (i.e. capable of maintaining productivity) when

111 facing stress due to either or both decreased precipitation levels and warmer conditions.  
112 We did so using data from 36,378 permanent survey plots in forests of Spain and Québec  
113 (Eastern Canada). Both datasets are of high quality, cover a large bioclimatic gradient and  
114 include repeated measures of the same trees over time, making them particularly suitable  
115 for testing these questions.

116

## 117 METHODS

118

### 119 *Forest survey datasets and estimation of net productivity*

120 The study was conducted in the forested areas of Québec (Eastern Canada) and  
121 peninsular Spain (i.e., excluding the Canary and Balearic Islands). These include five major  
122 climate types based on the Köppen-Geiger climate classification system (Kottek et al.,  
123 2006): (1) steppic (*Bsk* type), (2) dry Mediterranean (*Csa* and *Cfa* types), (3) humid  
124 Mediterranean (*Cfb* and *Csb* types) for Spain, (4) temperate (*Dfb* type) and (5) boreal (*Dfc*  
125 type) for Québec (Fig. 1).

126

127 Forest data from Québec and Spain were obtained from large forest inventory datasets.  
128 The Québec forest inventory was initiated in the 1970's and covers all public lands (up to  
129 the northern limit for timber allocations; Fig. 1A) including over 36,000 plots measured  
130 approximately every ten years (Duchesne and Ouimet, 2008). During surveys, all trees  
131 with a diameter at breast height (DBH) above 9.1 cm are numbered, species identified,  
132 and their DBH measured within 400 m<sup>2</sup> circular plots. To match with data from Spain, only

133 data from the last two sets of measurements that correspond to the third (ca. 1990-2000)  
134 and fourth (ca. 2000-2010) inventories were used.

135

136 In Spain, data were obtained from the Spanish second and third National Forest Inventory  
137 (NFI; 1986-1996 and 1997-2007, respectively). The NFI consists in a network of plots (>  
138 50,000) distributed across the forested area of Spain on a 1-km<sup>2</sup> grid (Ministerio de Medio  
139 Ambiente, 2007). The sampling method uses circular plots of which radius varies  
140 according to the DBH of the target tree: all trees with DBH  $\geq 7.5$  cm are measured within  
141 5 m of the plot center, additional trees with DBH  $\geq 12.5$  cm are measured in a circular  
142 band 5 to 10 m from the center, whereas trees with DBH  $\geq 22.5$  cm and with DBH  $\geq 42.5$   
143 are also considered within 10-15 and 15-25 m bands, respectively. As in Québec, the  
144 Spanish NFI plots are measured at an interval of approximately ten years.

145

146 We selected pairs of plots without sign of significant disturbance (such as fire) and that  
147 had not been subjected to human interventions between the two surveys. We also  
148 excluded from the analysis plots dominated by exotic species and sparse stands with basal  
149 area  $G < 2 \text{ m}^2 \text{ ha}^{-1}$ . After selection, the total number of plots measured twice used in this  
150 study was 7,127 and 29,251 for Québec and Spain, respectively (Table 1).

151

152 For each individual pair of plots, three variables were calculated to estimate changes in  
153 aboveground woody biomass (excluding leaves) through time, i.e. net productivity: (1)  
154 *Aboveground increment due to tree growth* ( $\text{Mg ha}^{-1} \text{ y}^{-1}$ ) that is the sum of the



155 aboveground woody biomass increment of the surviving trees between the two  
156 measurement periods ( $t_1$  and  $t_2$ ) and ingrowth (i.e. recruit trees reaching the minimum  
157 DBH threshold), (2) *Aboveground biomass loss due to tree mortality*, that included those  
158 trees that were alive at  $t_1$  but were dead or had disappeared (rare; assumed to be dead)  
159 at  $t_2$ , and (3) *Net aboveground woody biomass productivity* ( $\text{Mg ha}^{-1} \text{y}^{-1}$ ) calculated as the  
160 difference between the two former variables. This last quantity forms our response  
161 variable for net productivity.

162

163 The total biomass of the trunk, bark and branches of each individual tree present in the  
164 plot was computed from DBH using species-specific allometry equations developed by  
165 Lambert et al. (2005) for Québec and by Gracia et al. (2004) and Montero et al. (2005) for  
166 Spain. For some uncommon species without published equations we used parameters  
167 and generalized equations obtained for the functional groups to which they belong (i.e.  
168 conifers, deciduous or sclerophyllous species) (see Paquette and Messier (2011) and  
169 Vayreda et al. (2012) for further details). In addition to biomass increment, we also  
170 calculated plot basal area ( $G$ ,  $\text{m}^2 \text{ha}^{-1}$ ) to account for density.

171

### 172 *Functional trait diversity indices*

173 Data on functional traits were collected from published sources for the tree species  
174 present in both regions: wood density ( $Wd$ ,  $\text{g cm}^{-3}$ ), seed mass ( $Sm$ ,  $\text{mg}$  - natural-log  
175 transformed), maximum tree height ( $H_{max}$ ,  $\text{m}$ ), and leaf mass area ( $LMA$ ,  $\text{g m}^{-2}$ ). These  
176 traits have been shown to be related to forest productivity, including the forests studied

177 here (Paquette and Messier, 2011; Ruiz-Benito et al., 2014; Paquette et al., 2015). Wood  
178 density and seed mass are closely related to life history strategies (Swenson and Enquist,  
179 2007; Chave et al., 2009; Ben-Hur et al., 2012). The same is true with maximum height  
180 which also relates to vertical stratification and the use of light (Sapijanskas et al., 2014;  
181 Kunstler et al., 2016), while leaf mass per area is related to resource acquisition (Shipley  
182 et al., 2006). Together these traits form a “plant economics spectrum” defined by trade-  
183 offs between fast and slow growing strategies (Reich, 2014) with globally consistent  
184 effects on competition among forest trees (Kunstler et al., 2016). We computed functional  
185 trait diversity using the functional dispersion index (Laliberté and Legendre, 2010) based  
186 on trait dissimilarity among species in the first three traits ( $Wd$ ,  $Sm$  and  $H_{max}$ ) as often  
187 used in the BEF literature since variation in their related strategies is posited to increase  
188 niche partitioning and complementarity. Functional identity was computed using  
189 community weighted means of trait values (CWM; Lavorel et al., 2008) for  $H_{max}$  and  $LMA$   
190 to test the hypothesis that mean trait values drive community tolerance to drought (e.g.,  
191 small trees or thick leaves that increase water-use efficiency and decrease the risks  
192 associated with water-stress). Each has been linked to different components of  
193 biodiversity effects. Complementarity effects that promote species coexistence and  
194 competition reduction are best explained by the functional trait diversity index, whereas  
195 selection effects relate to the mass ratio hypothesis, whereby ecosystem functions are  
196 driven by the traits of dominant species, and are best assessed with the functional identity  
197 of the community (CWM) (Roscher et al., 2012; Tobner et al., 2016).

198

199 *Divergence from 30-year climate normals and environmental variables*

200 Climatic data for this study were obtained from Willmott and Matsuura (2001) which  
201 provides monthly temperature and precipitation means for every year for the last  
202 decades at a spatial resolution of 0.5 x 0.5 degree of latitude/longitude. We assigned  
203 mean temperature and precipitation values for each plot based on their geographical  
204 coordinates. The same source was used to assess temperature and precipitation trends  
205 between study periods. We determined for each plot the absolute temperature trend (°C)  
206 which was calculated as the difference between the mean temperature for the study  
207 period and the mean temperature for a reference period of 30 years before the first  
208 sampling period. We also calculated a relative precipitation trend (%) as the ratio of the  
209 difference in precipitations between the study period and the reference period divided  
210 by the reference period. These trends were assessed only for the summer season (mean  
211 temperature trend of June, July and August). In addition to climatic characterization, we  
212 collected for each plot the slope (°) and the depth of the organic layer (cm). Both variables  
213 were considered representative of environmental site conditions and were equally  
214 measured in Québec and Spanish surveys.

215

216 *Analyses*

217 The response variable we used to test our main hypothesis was net annual aboveground  
218 productivity based on 10-year intervals. Explanatory variables were the divergence from  
219 normal levels of precipitation (drier or wetter than 30-yr means) and temperature  
220 (warmer or colder than the past 30 years), functional trait diversity, and their interactions.

221 Appropriate confounding factors such as mean annual temperature and total  
222 precipitation, local growing conditions (slope, depth of the organic layer), and stand basal  
223 area ( $G$ ), were also included in our analysis.

224

225 For each climate type, we used general linear models (GLM) to analyze the relationship  
226 between net annual aboveground productivity, the different explanatory variables, and  
227 the interactions considered (those between climatic divergences and diversity variables)  
228 (see Table 1 for the list and mean values of all variables initially considered). A stepwise  
229 model selection was applied starting with a saturated model and removing least  
230 significant variables until no further decrease in the Bayesian Information Criterion (BIC)  
231 was observed. We considered the fit of models to be equivalent within 2 BIC units. All  
232 statistical analyses were made within the R environment (R Core Team, 2015).

233

234 We then checked for multicollinearity in the final model using variance inflation factors  
235 (VIFs) without interaction terms; all VIFs obtained were lower than 3, i.e. a low correlation  
236 (Heiberger and Holland, 2015). Furthermore for each final model, latitude and longitude  
237 were used to model the correlation structure of the errors (Venables and Ripley, 2013)  
238 using generalized least squares (function `gls` in package `nlme`) and a linear spatial  
239 correlation structure. Only in one case (boreal forests) was the model improved (increase  
240 in  $AIC \geq 84$  units) but the coefficients for all other factors were not different from the  
241 original GLM model and so only that model is shown for simplicity.  $R^2$  and VIFs of the  
242 selected model were obtained using the general linear model (function `lm` in R).

243 RESULTS

244 *Global trends among the five climate types.*

245 There was a clear geographic pattern for the distribution of net productivity according to  
246 climate. In peninsular Spain, net productivity was mainly driven by precipitation and  
247 temperature, showing an increase in productivity from the south-east (drier and warmer)  
248 to the north-northwest (wetter and colder), while in Eastern Canada net productivity was  
249 driven by temperature, decreasing from south to north (Table 1). In peninsular Spain the  
250 lowest net productivity values occurred in the steppe (semi-arid) climate, characterized  
251 by high temperatures and very low precipitation (~ 360 mm). In the dry Mediterranean  
252 climate precipitation was twice that of the steppes and temperature was similar, leading  
253 to a significant increase in net productivity. Finally, in the Humid Mediterranean climate  
254 temperature was clearly lower (by more than 4 °C) and precipitation was higher (by  
255 almost 200 mm per year), which allowed the highest net productivity of the five areas  
256 analyzed. In Eastern Canada, the geographical productivity pattern also followed a south-  
257 north gradient, but opposite to the Spanish, where net productivity decreased slightly  
258 with decreasing temperature. As expected, the largest basal areas were found in the most  
259 productive climates. There was a clear increasing gradient of organic layer depth with  
260 increasing precipitation and decreasing mean annual temperature, going from 1.4 cm  
261 deep in the steppe of Spain to 20.5 cm in the boreal forest of Québec.

262 Temperature and precipitation divergences were clearly stronger in Spain than in Québec,  
263 with a 1°C temperature increase in Spain compared to 0.3°C in Québec and a decline in  
264 precipitation between 5 and 20% in Spain compared to only 2 to 3% in Québec. Finally,

265 functional trait diversity was lowest in the steppe climate of Spain and highest in the  
266 temperate climate of Québec. Community weighted means for maximum height  
267 ( $CWM_{maxH}$ ) were very similar among climates varying from a low of 21 m in the dry  
268 Mediterranean climate to a high of 25 m in the temperate climate. The  $CWM_{LMA}$  was  
269 lowest in the temperate climate, dominated by broadleaf angiosperms, and highest in the  
270 boreal, dominated by needle-like gymnosperms (Table 1).

271

#### 272 *Stand density, soil and climatic factors affecting net productivity*

273 Variance explained by the models was always higher than 50%, ranging from 52% in the  
274 temperate to 72% of the humid Mediterranean climates (Table 2). The effect of basal area  
275 was always strong, with a positive effect on net productivity, especially in the Spanish  
276 climates (Table 2). Climatic variables (average temperature and annual precipitation) had  
277 a significant effect everywhere except in the steppes of southern Spain. In all other  
278 climate types, annual precipitation had a positive effect on net productivity. On the other  
279 hand, mean temperature had a positive effect on net productivity in the boreal,  
280 temperate and humid Mediterranean climates, while in the dry Mediterranean it was  
281 negative. In all climates, slope had a negative effect on net productivity, while the depth  
282 of the organic layer had a positive effect in the Mediterranean climates and a negative  
283 effect in the temperate and boreal climates.

284

285 *Divergence from 30-year climate normals and diversity metrics affecting net productivity*  
286 The direct effect of recent changes in precipitation or temperatures with respect to the  
287 previous 30 years was not strong (Table 2). Thermal divergence showed a positive effect  
288 on net productivity in the dry Mediterranean and temperate climates, and negative in the  
289 humid Mediterranean. The effect of the precipitation divergence was significant and  
290 positive for the humid Mediterranean climate, and negative for the Boreal climate.

291

292 Functional trait diversity showed a positive effect on net productivity in all climates except  
293 in the steppes, where it was not significant (Table 2). The variables relating to functional  
294 identity, measured through community-level weighted means (CWM), showed different  
295 patterns in the five climates. CWM for maximum height had a positive effect in  
296 intermediate climates and no effect in the extreme climates of both regions. The effect of  
297 mean LMA on net productivity went from positive in Peninsular Spain (but no effect in the  
298 steppe climate) to negative in Québec, indicating that conifers with high LMA in Spain and  
299 broadleaves with low LMA in Eastern Canada were the most productive.

300

301 *Effects of functional trait diversity in mitigating climatic divergence effects on net tree*  
302 *productivity*

303 In order for diversity to show a mitigation effect on net tree aboveground productivity,  
304 our GLM model should indicate a significant functional diversity\*divergence interaction.  
305 There was no significant effect for the interaction between functional trait diversity and  
306 the precipitation divergence (Table 2). However, some significant interactions were found

307 between functional diversity and the temperature divergence for three climates. In all  
308 cases, net productivity in the more diverse plots was negatively affected by the  
309 divergence in temperature (Fig. 2). We recall that this divergence (increased temperature)  
310 had in two cases a mean positive impact on net productivity (i.e. it was not stressful), so  
311 what these significant interactions actually show is that more diverse forests were more  
312 productive on average, except where temperatures had increased through recent  
313 warming, whereas the same increase in temperature had a positive impact in less diverse  
314 plots. In the humid Mediterranean, the effect was similar except that diversity had no  
315 effect where temperature had increased, causing lower productivity throughout (Fig. 2).

316

## 317 DISCUSSION

318

### 319 *The effect of climate on growth*

320 Our study supports previous findings of positive effects of tree diversity on forest  
321 productivity (Vilà et al., 2007; Lei et al., 2009; Paquette and Messier, 2011; Gamfeldt et  
322 al., 2013; Vilà et al., 2013; Ruiz-Benito et al., 2014; Liang et al., 2016). As expected, the  
323 net productivity pattern was also conditioned by climate; from warmer to colder climates  
324 in Québec, and from hot and dry to cooler and more humid conditions in Spain. Where  
325 significant, increased temperature had a positive impact on net productivity, except in  
326 the humid Mediterranean (Table 2). This was expected for Québec forests where a longer  
327 season and increased temperatures, combined with sufficient water supplies, would  
328 improve growing conditions (Grimm et al., 2013). In contrast, the result obtained for dry  
329 Mediterranean areas is difficult to explain. Within this climate, forest productivity was



330 found to be the lowest in the warmest areas (Table 2) but, contrary to expected, forests  
331 responded positively to temperature increases. This could be explained by the wide  
332 average period we used to compute divergence (~10 years) which could hide changes in  
333 growth associated to temperature variations occurring over shorter periods. Only in the  
334 humid Mediterranean did we find a significant negative effect of reduced precipitation as  
335 predicted, as well as from increased temperature. During the summer, these forests are  
336 normally able to cope with warm conditions because of a sufficient water supply.  
337 However, decreases in pluviometry and increased temperature lead to water stress,  
338 reduced growth and possibly increased mortality (Vayreda et al., 2012) (Table 2). The  
339 opposite effect was found in boreal forests, where recent increases in precipitations  
340 caused declines in productivity. These systems do not suffer from lack in precipitations;  
341 rather they grow in soils that are often waterlogged – due to poor drainage, limited  
342 evapotranspiration and a short growing season – so an increase in precipitation would  
343 worsen growing conditions and increase mortality where water may accumulate. We  
344 expected the reverse response for water-limited steppes and dry Mediterranean forests  
345 (i.e. the same as in the humid Mediterranean). However variations in precipitation levels  
346 did not affect net productivity in these climates, meaning either that the forests were  
347 already well equipped to face variations in precipitations (Vayreda et al., 2012), that  
348 precipitations did not vary much within those areas through time or, on the contrary, that  
349 normal variation in climate over the previous 30 years were on average larger than the  
350 divergence computed over 10 years.

351

352 *Recent climatic divergences and the effects of functional trait diversity*

353 Our working hypothesis was that more diverse forests can better cope (i.e., their net  
354 productivity would be less affected) with recently induced increasing levels of drought or  
355 higher temperatures, than less diverse forests. The interactions found between  
356 temperature divergences and diversity were on the opposite direction of our hypothesis.  
357 While in most cases an increase in temperature did not affect negatively tree net  
358 productivity, only the forests with the lowest diversity were either less affected, or  
359 actually able to maintain or even increase net productivity with increasing temperature  
360 (Fig. 2). In contrast, those forest stands with higher functional trait diversity responded in  
361 the opposite direction, showing in all cases pronounced reduction in growth with  
362 increasing temperature. This result suggests that the hypothesized positive effect of  
363 diversity on net productivity might not occur with increasing climatic divergences; i.e. the  
364 current benefit of growing together in a stable climate may not hold when conditions  
365 change (Grossiord et al., 2014b). Indeed, some recent studies suggest that when facing  
366 climatic divergences, species mixtures that were favouring complementarity effects may  
367 start competing for resources and negate the diversity effects found under the previous  
368 stable conditions (Jucker et al., 2014). This could be the result of the higher transpiration  
369 induced by mixed tree species compared to monoculture (Kunert et al., 2012). However,  
370 others have found the opposite (Lebourgeois et al., 2013), with some finding positive  
371 effects of diversity only during dry (vs wet) years (Grossiord et al., 2013; Grossiord et al.,  
372 2014a), or only in drought-prone environments (Grossiord et al., 2014b). Interestingly  
373 however, Grossiord et al. (2014a) reported a positive effect of diversity in dry years via an

374 increase of the water use efficiency, which incidentally did not provide any buffering  
375 against the observed reduction in productivity (increments in basal area), as we also  
376 found. This suggests that resources are better accessed and exploited in mixtures which  
377 may then lead to detrimental biodiversity effects where soil water can be more  
378 intensively exhausted during droughts by the more efficient mixtures (Grossiord et al.,  
379 2014a). Our results reported only aboveground growth and it is possible that mixtures  
380 invested more belowground with increasing temperature divergence to better cope with  
381 the possible increasing evapotranspiration. This is supported by results from a controlled  
382 experiment where tree mixtures were found to allocate proportionally less belowground  
383 than monospecific stands under optimal growing conditions (Archambault, 2016).

384

385 In summary, our study found a general positive effect of tree diversity on stand  
386 productivity under stable conditions, and showed different responses of forests to  
387 temperature and precipitation divergences depending on the considered climatic zone.  
388 However, and contrary to our expectations, we found an overall negative effect of tree  
389 diversity on the capacity of the stands to maintain productivity when faced with climatic  
390 divergences. Further research is required to assess the underlying mechanisms behind  
391 these unexpected patterns.

392

### 393 ACKNOWLEDGMENTS

394 This research was supported by the NEWFORESTS program and the project EST\_RES  
395 (AGL2015-70425-R) funded by the Spanish Ministry of Science and Innovation. We wish

396 to thank the *Ministère des Forêts, de la Faune et des Parcs du Québec* (Canada) and the

397 Spanish National Forest Inventory for providing the data from permanent forest plots.

398

399

400 LITTERATURE CITED

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591 TABLE LEGENDS

592 Table 1. Species composition and values of the different variables in the five climate  
593 types analyzed.

594 Table 2. GLM model results for factors and interactions explaining net aboveground tree  
595 productivity in forests of the five climates studied. \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; n.s. not  
596 significant.

597

598 FIGURE LEGENDS

599

600 Figure 1. Distribution of sampled plots and climates (in different colors) covered in (b)  
601 Québec and (c) Spain. Note that in Québec, sampling covers the land up to the limit of  
602 the exploitable forest (ca. latitude 52°).

603 Figure 2. 3D changes in net aboveground productivity (production;  $\text{Mg ha}^{-1} \text{yr}^{-1}$ ) in  
604 relation to functional trait diversity and temperature trends as found in some biomes.

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606

Table 1. Species composition and values of the different variables in the five climate types analyzed.

	<b>Steppe (semi-arid) (BSk)</b>	<b>Dry Mediterranean (Csa + Cfa)</b>	<b>Humid Mediterranean (Cfb+ Csb)</b>	<b>Temperate (Dfb)</b>	<b>Boreal (Dfc)</b>
<b>Most abundant tree species</b>	<i>Pinus halepensis</i> <i>Quercus ilex</i>	<i>Quercus ilex</i> <i>Pinus halepensis</i> <i>Pinus pinaster</i> <i>Quercus suber</i>	<i>Pinus sylvestris</i> <i>Quercus ilex</i> <i>Pinus nigra</i> <i>Pinus pinaster</i>	<i>Acer saccharum</i> <i>Abies balsamea</i> <i>Acer rubrum</i> <i>Betula</i> <i>alleghaniensis</i>	<i>Picea mariana</i> <i>Abies balsamea</i> <i>Betula papyrifera</i> <i>Populus</i> <i>tremuloides</i>
<b>Net productivity (Mg ha<sup>-1</sup> yr<sup>-1</sup>)</b>	0.87 ± 0.75	1.43 ± 1.59	2.86 ± 2.62	1.97 ± 0.14	1.77 ± 0.13
<b>Basal area (G; m<sup>2</sup> ha<sup>-1</sup>)</b>	8.0 ± 5.7	10.9 ± 8.8	18.5 ± 12.8	22.8 ± 8.7	18.2 ± 9.4
<b>Annual precipitation (mm)</b>	361 ± 48	668 ± 174	827 ± 300	1015 ± 109	993 ± 166
<b>Mean annual temperature (°C)</b>	14.3 ± 1.4	14.5 ± 1.6	10.4 ± 1.6	2.7 ± 1.3	-0.8 ± 1.5
<b>Slope (°)</b>	18.8 ± 9.7	16.0 ± 10.2	18.9 ± 11.2	12.7 ± 11.0	12.2 ± 11.4
<b>Organic layer depth (cm)</b>	1.35 ± 1.10	1.78 ± 1.55	2.86 ± 2.26	12.1 ± 18.1	20.5 ± 20.7
<b>Temperature trend (°C)</b>	0.83 ± 0.28	1.11 ± 0.41	1.11 ± 0.42	0.31 ± 0.31	0.31 ± 0.27
<b>Precipitation trend (%)</b>	-9.2 ± 13.2	-20.5 ± 16.8	-4.5 ± 7.3	-1.7 ± 7.7	-3.3 ± 6.0
<b>Species richness</b>	1.13 ± 0.4	1.52 ± 0.83	1.88 ± 1.09	4.91 ± 2.03	2.52 ± 1.27
<b>Functional trait diversity</b>	0.11 ± 0.35	0.36 ± 0.56	0.57 ± 0.63	0.90 ± 0.33	0.46 ± 0.28
<b>CWM<sub>maxH</sub></b>	23.2 ± 1.42	20.9 ± 3.01	23.2 ± 4.43	25.1 ± 3.87	21.5 ± 1.84
<b>CWM<sub>LMA</sub></b>	227.9 ± 27.4	206.7 ± 76.7	190.9 ± 86.3	136.0 ± 67.9	240.25 ± 60.9
<b>N plots</b>	1,603	12,585	15,063	4,486	2,641



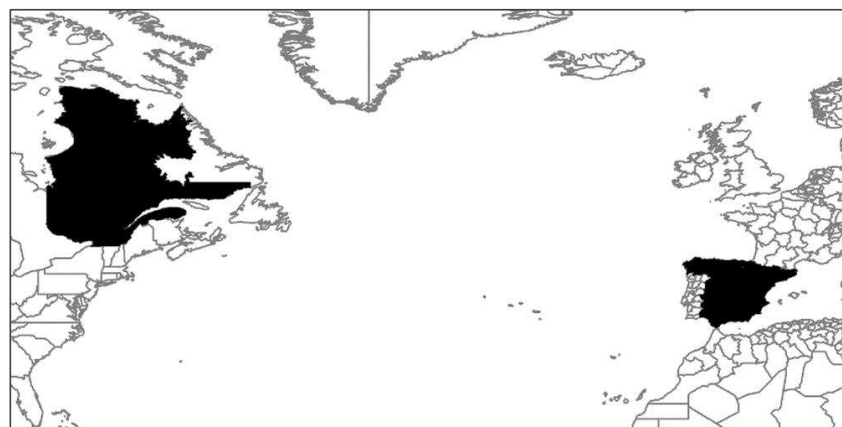
Table 2. GLM model results for factors and interactions explaining net aboveground tree productivity in forests of the five climates studied. \*\*\*p<0.001; \*\*p<0.01; n.s. not significant.

	Steppe (semi-arid) (BSk)		Dry Mediterranean (Csa + Cfa)		Humid Mediterranean (Cfb+ Csb)		Temperate (Dfb)		Boreal (Dfc)	
	t-value	Sign.	t-value	Sign.	t-value	Sign.	t-value	Sign.	t-value	Sign.
<b>(Intercept)</b>	-47.7	***	-32.8	***	-47.5	***	33.3	***	59.9	***
<b>Basal area</b>	46.3	***	101.0	***	145.6	***	46.6	***	38.5	***
<b>Annual Precipitation</b>			4.3	***	13.3	***	5.2	***	5.8	***
<b>Mean annual Temperature</b>			-8.6	***	12.3	***	10.7	***	17.3	***
<b>Slope</b>	-4.5	***	-3.0	**	-11.6	***	-4.8	***	-2.8	**
<b>Organic layer depth</b>	2.6	**	12.1	***	10.0	***	-8.8	***	-5.8	***
<b>Temperature trend (TT)</b>			7.7	***	-4.0	**	4.0	***	0.7	n.s.
<b>Precipitation trend (PT)</b>					7.1	***			-8.8	***
<b>Functional diversity (FDis)</b>			12.8	***	10.42	***	3.8	***	4.6	***
<b>CWM<sub>maxH</sub></b>			21.2	***	22.1	***	7.5	***		
<b>CWM<sub>LMA</sub></b>			6.8	***	3.7	***	-12.3	***	-16.7	***
<b>TT x FDis</b>					-6.2	***	-4.7	***	-3.4	***
<b>PT x FDis</b>										
<b>d.f.</b>	1,599		12,502		15,017		4,381		2,587	
<b>R<sup>2</sup></b>	0.60		0.64		0.71		0.52		0.69	
<b>BIC</b>	2,590		23,422		24,953		-13,669		-9,291	

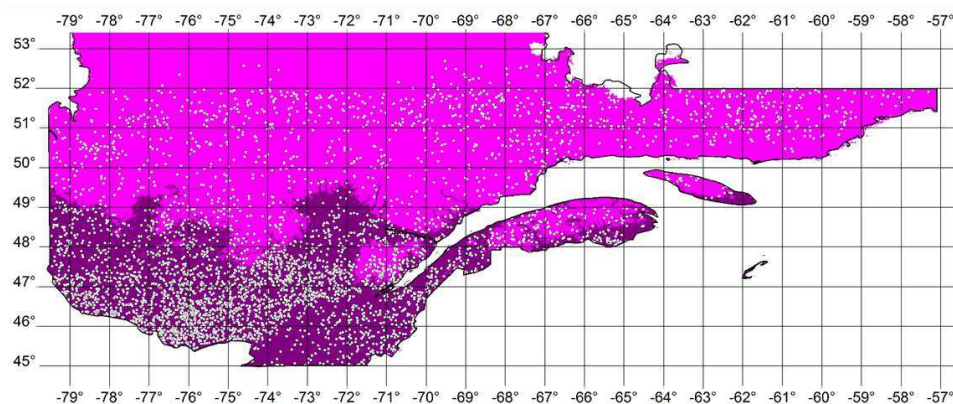
Note: Only significant effects are shown except where involved in a significant interaction (one instance).

Figure 1. Distribution of sampled plots and climates (in different colors) covered in (b) Québec and (c) Spain. Note that in Québec, sampling covers the land up to the limit of the exploitable forest (ca. latitude 52°).

(a)



(b)



(c)

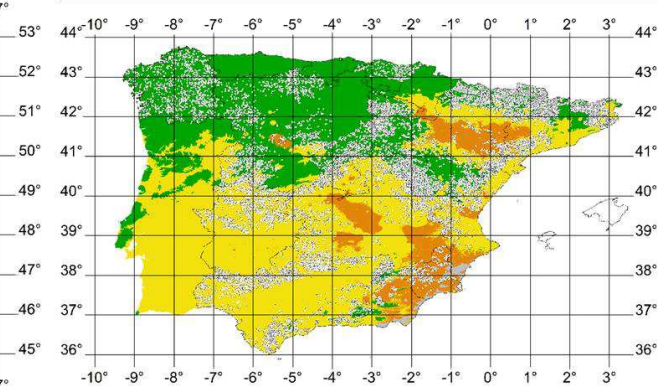


Figure 2. 3D changes in net aboveground productivity (production; Mg ha<sup>-1</sup> yr<sup>-1</sup>) in relation to functional trait diversity and temperature trends as found in some biomes.

