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## **Tree diversity does not always improve resistance of forest ecosystems to drought**

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### ► **To cite this version:**

Charlotte Grossiord, André Granier, Sophia Ratcliffe, Olivier Bouriaud, Helge Bruelheide, et al.. Tree diversity does not always improve resistance of forest ecosystems to drought. Proceedings of the National Academy of Sciences of the United States of America, 2014, 111 (41), pp.14812-14815. 10.1073/pnas.1411970111 . hal-01190150

**HAL Id: hal-01190150**

**<https://hal.science/hal-01190150>**

Submitted on 1 Sep 2015

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1 *Classification:* Biological Sciences (Major), Ecology (Minor)

2

3 **Tree diversity does not always improve resistance of forest ecosystems to**  
4 **drought**

5

6 **Short title:** Diversity and drought resistance

7

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31 **Keywords:** biodiversity, climate change, forest ecosystems, ecology

32 **Significance statement**

33 In the context of climate change, expected drier and warmer environmental conditions will  
34 have drastic consequences on forest functions and services and may bring about important  
35 drought-induced die-off events. Biodiversity promotes forest ecosystem performance and  
36 resistance to insect pests and diseases, but whether or not diverse forests are also better  
37 adapted to deal with drought stress remains unknown. Within our study network of 160 forest  
38 stands across Europe, we found that mixed species forests are less exposed to drought stress  
39 in some regions only. Therefore, managing forest ecosystems for high tree species diversity  
40 does not necessarily assure improved resistance to the more severe and frequent drought  
41 events predicted for the future.

42

43 **Abstract**

44 Climate models predict an increase in the intensity and frequency of drought episodes in the  
45 Northern Hemisphere. Among terrestrial ecosystems, forests will be profoundly impacted by  
46 drier climatic conditions with drastic consequences for the functions and services they supply.  
47 Simultaneously, biodiversity is known to support a wide range of forest ecosystem functions  
48 and services. However, whether biodiversity also improves the resistance of these ecosystems  
49 to drought remains unclear. We compared soil drought exposure levels in a total of 160 forest  
50 stands within five major forest types across Europe along a gradient of tree species diversity.  
51 We assessed soil drought exposure in each forest stand by calculating the stand-level increase  
52 in carbon isotope composition of late wood from a wet to a dry year ( $\Delta\delta^{13}C_s$ ).  $\Delta\delta^{13}C_s$   
53 exhibited a negative linear relationship with tree species diversity in two forest types,  
54 suggesting that species interactions in these forests diminished the drought exposure of the  
55 ecosystem. However, the other three forest types were unaffected by tree species diversity. We

56 conclude that higher diversity enhances resistance to drought events only in drought-prone  
57 environments. Managing forest ecosystems for high tree species diversity does not necessarily  
58 assure improved adaptability to the more severe and frequent drought events predicted for the  
59 future.

60 \body

61 Biodiversity plays an important role in ecosystem functioning by promoting a wide range of  
62 functions and services (1-3). This beneficial effect of biodiversity is determined by  
63 mechanistic processes directly under the influence of species interactions: complementarity  
64 among species for resource use through ecological niche partitioning and/or facilitation  
65 processes increase ecosystem performance because resources are better shared among  
66 neighboring species and are thus potentially more available (4). Previous studies have  
67 demonstrated that, apart from enhancing performance, diverse terrestrial ecosystems may also  
68 be more resilient and more resistant to biotic stresses such as insect pests or diseases (5, 6).  
69 However, it remains unclear whether higher biodiversity also leads to improved resistance of  
70 terrestrial ecosystems to the more frequent droughts expected in temperate regions (7). The  
71 rare case studies published so far have shown contrasting results. Two reported that species in  
72 more diverse ecosystems could be more resistant to drought stress (8, 9) while another  
73 suggested that enhanced biodiversity could trigger higher exposure to drought (10).  
74 Improving our understanding of how species diversity influences the resistance of terrestrial  
75 ecosystems to a fluctuating climate is crucial.

76 More frequent and intense droughts will greatly affect the carbon and water cycles of the  
77 terrestrial biosphere (11), in particular in forested ecosystems (12). Many societies around the  
78 world rely on forests for essential services such as wood production, hunting or watershed  
79 protection. We therefore urgently need to improve our knowledge of the physiological  
80 response of these ecosystems to drier climatic conditions in order to propose new climate-  
81 smart management options. Forests, though influenced by local environmental conditions,  
82 play a major role in the global carbon and water balance as they release into and assimilate  
83 from the atmosphere huge amounts of CO<sub>2</sub> while losing water vapour through transpiration.  
84 Tree species are known to vary widely in the ecological strategies they use to deal with  
85 drought stress. It could therefore be expected that in highly diverse forests composed of tree

86 species with contrasting functional traits, limited water resources could be better partitioned  
87 among the neighboring species as a result of complementarity and facilitation processes (4).  
88 Such forests should be more resistant to deal with drought stress since the trees should be able  
89 to maintain better access to diminishing water resources as the drought progresses. In  
90 contrast, if the interacting species in a diverse forest have similar functional traits (i.e.  
91 functional redundancy), ecological niche overlap (13) may lead to more stressful conditions  
92 during drought than in pure stands due to lower water availability for each species.

93 Carbon isotope composition in C<sub>3</sub> plant tissues ( $\delta^{13}\text{C}$ ) provides an integrated record of the  
94 ratio of intercellular to atmospheric CO<sub>2</sub> concentrations during the period when the carbon  
95 was fixed, and thus reflects the balance between net CO<sub>2</sub> assimilation and stomatal  
96 conductance (14). Plants typically react towards drought stress by closing their stomata and  
97 reducing carbon assimilation rates. However, leaf stomatal conductance is affected to a  
98 greater extent than assimilation, causing a concomitant increase in  $\delta^{13}\text{C}$  (14, 15). Therefore,  
99 under soil drought conditions,  $\delta^{13}\text{C}$  from organic material has been widely accepted as an  
100 indicator of the intensity of drought exposure in plants (16, 17) (*SI Appendix*). If  
101 complementarity for water use is occurring among species,  $\delta^{13}\text{C}$  values should increase less  
102 between wet and dry soil conditions with increasing tree species diversity (i.e. a negative  
103 relationship). Inversely, if tree species occupy redundant ecological niches,  $\delta^{13}\text{C}$  values should  
104 either have a similar or higher increase between wet and dry conditions with increasing tree  
105 species diversity (i.e. a null or positive relationship).

106 In a previous study, we analyzed the influence of drought on the relationship between tree  
107 species diversity and the increase in stand-level carbon isotope composition between a wet  
108 and dry year ( $\Delta\delta^{13}\text{C}_s$ ) in boreal forests (10). Species diverse forests were shown to be more  
109 affected by drought stress than less diverse ones (i.e. a positive relationship between  $\Delta\delta^{13}\text{C}_s$   
110 and tree species diversity). In the present study, we have extended our research to five major

111 forest types across Europe which extends from northern hemi-boreal forests to southern  
112 Mediterranean forests. Our objective was to test whether the relationship between  $\Delta\delta^{13}\text{C}_s$  and  
113 tree species diversity would be consistent across a large range of climatic and edaphic  
114 conditions. At each of the five study sites, we selected a set of representative canopy trees in  
115 21 to 42 forest stands varying in tree species diversity. For each site, we used a water balance  
116 modeling approach to select one year within the last 14 years with high drought stress and one  
117 “reference” year when no drought occurred (*SI Appendix*, Fig. S1 and S2). We measured the  
118  $\delta^{13}\text{C}$  in the tree rings of the selected canopy trees and calculated  $\Delta\delta^{13}\text{C}_s$  for each stand.

119

## 120 **Results**

121 Within a given forest type, there was a large variability among species in  $\Delta\delta^{13}\text{C}$  values (*SI*  
122 *Appendix*, Fig. S3), pointing out that drought response highly varied across tree species.  
123 Nevertheless, whatever the forest type,  $\Delta\delta^{13}\text{C}$  always displayed positive values (*SI Appendix*,  
124 Fig. S3), which is consistent with the considerable literature on the impact of drought on tree-  
125 or species-level  $\delta^{13}\text{C}$  (16, 17). This result confirmed that the tree rings selected for the targeted  
126 dry year coincided with years when all tree species clearly suffered from a severe and long-  
127 lasting water shortage.

128 Mean site  $\Delta\delta^{13}\text{C}_s$  values were highly variable across the different forest types (Fig. 1). This  
129 can be partly explained by the large differences in the intensity of drought stress during the  
130 selected dry years across forest types (*SI Appendix*, Table S3). We found a wide variability in  
131  $\Delta\delta^{13}\text{C}_s$  among forest stands within a given forest type (Fig. 2). The observed range of values  
132 (typically around 2 ‰) suggested highly contrasting ecosystem-level carbon and water trade-  
133 offs among stands indicating highly contrasting soil water availability during the dry year.  
134 Among the confounding factors that were included in the  $\Delta\delta^{13}\text{C}_s$  statistical model



135 (competition intensity, light interception levels, microclimate and soil nutrient availability), in  
136 the hemi-boreal and mountainous beech forest types only competition intensity explained part  
137 of the large variability (*SI Appendix*, Fig. S4), the other factors being non-significant (*SI*  
138 *Appendix*, Table S4). In the temperate beech and thermophilous deciduous forest types,  
139 variations in  $\Delta\delta^{13}\text{C}_s$  were only significantly correlated with tree species diversity (Fig. 2,  
140 Table S4). Variations observed in the Mediterranean forest were not explained by tree  
141 diversity, nor by any of the confounding factors (*SI Appendix*, Table S4).

142

### 143 **Discussion**

144 The positive relationship between  $\Delta\delta^{13}\text{C}_s$  and tree species diversity that had been previously  
145 observed for boreal forests (10) indicated a higher drought exposure in the more diverse  
146 stands. This previous study suggested that drought stress could exacerbate competition for  
147 water among neighboring tree species. However, in the present study, we found evidence that  
148 such a detrimental effect of tree species diversity cannot be generalized to European forest  
149 types. Indeed, we observed either no relationship (hemi-boreal, mountainous beech,  
150 Mediterranean forests) or negative relationships (temperate beech, thermophilous deciduous  
151 forests) between  $\Delta\delta^{13}\text{C}_s$  and tree species diversity (Fig. 2).

152 The negative relationship between  $\Delta\delta^{13}\text{C}_s$  and tree species diversity that we observed for  
153 temperate beech and thermophilous deciduous forests implies that water availability was  
154 higher in diverse stands than in pure ones under drought conditions. These observations are  
155 consistent with other studies in which tree species diversity was found to reduce drought  
156 stress (8, 9). Higher water availability in more diverse stands suggests niche partitioning  
157 and/or facilitation processes among the interacting species. Below-ground partitioning may  
158 occur when species that extend their root systems towards deeper soil layers coexist with

159 others that occupy the superficial layers. Facilitation mechanisms such as hydraulic lift  
160 whereby deeper rooting tree species take up water and redistribute it via their root system to  
161 drier superficial soil layers are also known to take place in mixed forest ecosystems (18).  
162 Higher functional diversity of the fungal community could also partially improve water  
163 availability in more diverse stands (19). These underlying processes nevertheless remain  
164 speculative and future research is needed to shed light on the relative contribution of these  
165 potential processes (20).

166 For the three other forest types (hemi-boreal, mountainous beech and Mediterranean), the  
167 relationship between  $\Delta\delta^{13}\text{C}_s$  and tree species diversity was non-significant (Fig. 2), suggesting  
168 that no net resource partitioning or facilitation processes were occurring. For these three forest  
169 types, tree species diversity did not play an important role in modulating ecosystem-level  
170 response to drought stress, despite strong functional differences among species in their  
171 response to drought (*SI Appendix*, Fig. S3). Intra-specific and inter-specific interactions  
172 therefore seem to have an equal influence on the level of drought exposure in these  
173 ecosystems. The tree species that compose these forests may be “ecological equivalents” (21)  
174 that use similar competitive strategies to deal with drought stress. However, for both the hemi-  
175 boreal and mountainous beech forests, the variability among stands in  $\Delta\delta^{13}\text{C}_s$  was partly  
176 explained by competition intensity (i.e. basal area, *SI Appendix*, Fig. S4). Stands with higher  
177 basal area showed the greatest increase in  $\Delta\delta^{13}\text{C}_s$ , and thus the strongest soil water limitation.  
178 In these forest types, silvicultural practices controlling stand basal area may therefore be one  
179 management option to improve resistance to drought.

180 Environmental conditions are highly variable along the North-South gradient considered in  
181 this study and could account for the inconsistency of the response among the different forest  
182 types. Negative relationships occurred in the temperate beech and thermophilous deciduous  
183 forests, the two sites that showed the highest mean drought stress intensity and the highest

184 drought stress frequency over the past 14 years (*SI Appendix*, Table S3). In contrast, drought  
185 events in the boreal and hemi-boreal forests were moderate and rather rare (*SI Appendix*,  
186 Table S3), and these are the sites where we observed positive relationships (10) or no effect of  
187 species interaction. Thus, overall, the global pattern we found seems consistent with the  
188 “stress-gradient hypothesis” (22, 23), though our study was not designed to test this  
189 hypothesis. This hypothesis indeed suggests that facilitation and complementarity processes  
190 should occur more frequently and should be more important under drier conditions while  
191 competition should dominate under favorable ones. The Mediterranean forest was also  
192 characterized by high drought stress intensity and frequency (*SI Appendix*, Table S3), but we  
193 found no effect of species interactions. We suspect that the very shallow soils found at this site  
194 prevented any chance for the establishment of below-ground complementarity processes such  
195 as root stratification.

196 We conclude that higher tree species diversity offers a greater resistance to drought events in  
197 some forest types, but that this pattern cannot be generalized to all forest ecosystems. Forest  
198 response is likely to be context-dependent. Local tree species associations are probably  
199 interacting with local environmental conditions and this would explain the complexity of the  
200 relationship between biodiversity and forest resistance to drought stress we observed across  
201 Europe. Managing forest ecosystems for high tree species diversity does not necessarily  
202 assure improved resistance to the more severe and frequent drought events predicted for the  
203 future.

204

## 205 **Materials and methods**

206 **Experimental sites.** The sites used in this study are included in a permanent network of  
207 stands established in 2011-2012 in existing mature forests in five European countries  
208 (Germany, Poland, Romania, Italy, Spain) within the framework of the FP7-FunDivEurope

209 project (24). The study areas include highly variable climatic conditions and host Europe's  
210 most important broadleaved and coniferous tree species (*SI Appendix*). In each site 21 to 42  
211 forest stands (30 m × 30 m) were selected for a total of 160 stands covering a gradient of tree  
212 species diversity, from pure to the local maximum of between three and five species per stand  
213 (*SI Appendix*). Each level of tree species diversity was replicated approximately ten times, but  
214 with different species compositions: the experimental set-up was not designed to separate the  
215 effect of the presence of particular species or particular combinations of species from the  
216 effect of tree species diversity. To minimize confounding factors among stands within a given  
217 site, stands were selected for similar developmental stage, soil characteristics, slope, altitude,  
218 past management practises, or canopy structure characteristics (24). This focuses the study on  
219 rather average site conditions and is not suited to assess the influence of species diversity  
220 across a wider range of environmental factors. With this design we aimed, however, to  
221 eliminate other local factors that could have affected ecosystem functioning as much as tree  
222 species diversity. Nevertheless, some variability among stands within a given site could not be  
223 avoided and stand characteristics were included in the statistical analyses as confounding  
224 factors. A detailed description of stand selection and characteristics can be found in *SI*  
225 *Appendix* and (24). To characterize each stand's tree species diversity, we calculated the  
226 Shannon diversity index of each stand with species basal area as a surrogate for abundance in  
227 the equation (*SI Appendix*).

228

229 **Selection of target years.** In order to select a year with non-limiting soil water conditions  
230 during the growing season and a year with severe soil drought during the growing season, we  
231 used the water balance model BILJOU (25) to estimate the daily relative extractable water in  
232 the soil (REW, unitless) for each site during the period from 1997 to 2010 (*SI Appendix*, Fig.

233 S1). Based on REW, a water stress index (25) was calculated and used to select the two years  
234 (*SI Appendix*, Fig. S2).

235

236 **Wood sample preparation and analyses.** We selected a subsample of dominant and co-  
237 dominant trees per species and per stand to avoid confounding factors related to light  
238 interception (*SI Appendix*). For each tree, we extracted one wood core at breast height and  
239 carefully extracted the latewood for each selected year. Latewood sections from a given  
240 species, a given year and a given stand were bulked and analyzed for  $\delta^{13}\text{C}$  with a mass  
241 spectrometer. By selecting only the latewood, whose  $\delta^{13}\text{C}$  mainly characterizes the  
242 functioning of the trees during the second part of the growing season, we avoided potential  
243 effects related to the remobilization of stored photosynthates from the previous growing  
244 season (26) or to a favorable spring climate.

245

246 **Stand-level carbon isotope composition.** We calculated the stand-level  $\delta^{13}\text{C}$  for each year  
247 using species-level  $\delta^{13}\text{C}$ , with the sum of basal area of each species in each stand as the  
248 weighting factor for the contribution of each species (*SI Appendix*).  $\Delta\delta^{13}\text{C}_S$  was then defined  
249 as the increase in stand-level  $\delta^{13}\text{C}$  between the dry and the wet conditions and therefore  
250 characterizes the ecosystem-level physiological response to soil drought.

251

252 **Characterization of confounding factors.** The following stand characteristics were  
253 measured in order to take them into account in the statistical model: leaf area index (i.e. light  
254 regimes), soil C/N (i.e. nutrient availability), stand basal area (competition intensity) and  
255 altitude (local climatic conditions).

256

257 **Data analyses.** For each site, linear mixed models were used to determine the fixed effects of  
258 the Shannon diversity index and the confounding factors on  $\Delta\delta^{13}\text{C}_s$  (*SI Appendix*, Table S4).  
259 Interactions between the Shannon index and the confounding factors were initially integrated  
260 into the model but then were removed because none were significant.

261

## 262 **Footnotes**

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264

265 Author contributions: DB, AG<sup>a</sup>, and AG<sup>l,m</sup> designed the research; OB, HB, EC, LF, MP, M S-L  
266 and FV selected the sites; CG, DB, AG<sup>a</sup>, AG<sup>m,n</sup>, MP and SMD performed research; CG, DB,  
267 AG<sup>a</sup> and AG<sup>l,m</sup> analyzed the data. All authors contributed to the writing of the paper. DB and  
268 AG<sup>m,n</sup> contributed to the supervision of the work in a similar manner and share a similar  
269 position (latest) as co-authors.

270

271 The authors declare no conflict of interest.

272 This article contains supporting information online.

273

274 **ACKNOWLEDGMENTS.** We are especially grateful to Bogdan Jaroszewicz, Filippo  
275 Bussotti, Timo Domish and all the site technicians for establishing the study stands and for  
276 their logistical help. We thank Daniel Avăcăriței, Iulian Dănilă, Gabriel Duduman and Ionuț  
277 Bărnoaia for their help with the wood core sampling. We also thank Francois Geremia for the  
278 wood sample preparation and Pierre Montpied for his advice on statistical analyses. We thank  
279 the technical Isotope Platform of INRA Nancy and the Isotope Facility of UC Davis for the  
280 carbon isotope analyses. Two anonymous reviewers significantly contributed to the  
281 improvement of a previous manuscript. The research leading to these results received funding

282 from the European Union Seventh Framework Programme (FP7/2007-2013) under grant  
283 agreement n° 265171. This research was conducted in the framework of the Laboratory of  
284 Excellence ARBRE (ANR-12- LABXARBRE-01) supported by the French National Research  
285 Agency. AG<sup>m,n</sup> acknowledges financial support from the DFG (GE 1090/8-1). EC  
286 acknowledges financial support from the Polish Ministry of Science and Higher Education.  
287

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353 **Figure legends**

354 **Figure 1:** Intensity of the physiological response to drought stress during the targeted dry  
355 year. Mean  $\pm$  SE of the increase in stand-level carbon isotope composition ( $\Delta\delta^{13}\text{C}_s$ , ‰)  
356 between the dry year and the year without water stress are shown for all stands with all tree  
357 species diversity levels for a given forest type. The increase in  $\Delta\delta^{13}\text{C}_s$  between dry and wet  
358 conditions characterizes the intensity of drought stress to which the ecosystems were  
359 subjected.

360

361 **Figure 2:** Increase in stand-level carbon isotope composition in relation to tree species  
362 diversity for each forest type. Relationship between the increase in stand-level carbon isotope  
363 composition ( $\Delta\delta^{13}\text{C}_s$ , ‰) and the Shannon diversity index for the hemi-boreal, mountainous  
364 beech, temperate beech, thermophilous deciduous and Mediterranean forest types. Solid lines  
365 show the statistically significant relationships ( $P < 0.05$ ). Corresponding equations,  $R^2$  and  $P$ -  
366 values are given for each significant relationship.

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