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## Tree species richness induces strong intraspecific variability of beech (*Fagus sylvatica*) leaf traits and alleviates edaphic stress

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1 Tree species richness induces strong intraspecific variability of beech (*Fagus sylvatica*) leaf  
2 traits and alleviates edaphic stress

3

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14

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16

17 **Running head:** Stand composition and stress impact beech leaf traits

18

19 **Key-words:** biotic interactions; forest management; functional trait; intraspecific variation;  
20 stand composition; stress gradient hypothesis.

21

22 **Abbreviations:** LDMC= Leaf Dry Matter Content; LMA = Leaf Mass per Area; LogRR= Log  
23 Response Ratio; SGH=Stress Gradient Hypothesis

24

25

26 **Abstract**

27

28 Manipulating stand composition is an important management tool that foresters can use to  
29 affect the nature of forests and ecosystem processes. In mixed stands, interspecific  
30 interactions among trees can cause changes in tree performance. Nevertheless, these  
31 interactions are context dependent (cf. Stress Gradient Hypothesis, SGH). We thus  
32 investigated how intraspecific functional changes in leaf trait (19 traits) of European beech  
33 (*Fagus sylvatica*) were influenced by stand composition. We compared pure beech stands  
34 with four mixed stands containing from one to three additional tree species along a gradient  
35 of edaphic stress. First, we demonstrated that stand composition induced strong intraspecific  
36 leaf trait variation in beech for LDMC, LMA, phenolic compounds, leaf pH and magnesium  
37 concentration, suggesting higher nutrient acquisition by more diverse stands. Nevertheless,  
38 these results were modulated by edaphic stress. Mixed stands only conferred an advantage  
39 in relatively-stressed sites (luvisol and leptosol). Besides, the addition of oak to beech stands  
40 had unexpected negative effects in sites with less severe stress (cambisol) as indicated by  
41 the null or positive LogRR of LMA, LDMC and phenolics. This study found that stand  
42 composition is an important though often-overlooked driver of intraspecific variability in leaf  
43 quality, and potentially reflects changes in beech tree physiology and productivity. Our  
44 results also suggest that positive interactions prevail in sites with stressful conditions. Such  
45 validation of the SGH is rare in natural or managed mature forests. Lastly, we strongly  
46 recommend that forest managers consider stand composition and abiotic factors when  
47 implementing forest growth models to improve their yield predictions.

48

## 49 **Introduction**

50

51 Mixed forest stands are considered more robust than forest monocultures and thus have  
52 strategic value when implementing sustainable forest management (Vila et al. 2007; Knoke  
53 and Seifert 2008; Sardin et al. 2008). They are recognized as more resistant against wind,  
54 snow and insect attacks than forest monocultures, thus they decrease financial risks for  
55 foresters (Jactel and Brockerhoff 2007; Merlin et al. 2015). Additionally, forest productivity in  
56 mixed stands might be high compared to pure stands (Kelty and Larson 1992; Pretzsch et al.  
57 2010; Vallet and Perot 2011).

58 The two main mechanisms potentially inducing higher productivity in mixed compared to pure  
59 forest stands are niche partitioning and positive interactions, *i.e.* complementarity and  
60 facilitation respectively (Loreau and Hector 2001). Niche partitioning (or niche  
61 complementarity) involves more effective and less competitive use of forest resources  
62 among species with distinct functional traits, such as water uptake at different periods of the  
63 year or from different depths in the soil profile. Facilitation occurs when a species increases  
64 resource availability or decreases harsh environmental conditions for another species  
65 (Bertness and Callaway 1994) resulting in higher resource use efficiency for the benefactor  
66 species. A common facilitation effect in forest stands is a higher rate of litter decomposition,  
67 and thus faster nutrient cycling induced when broadleaf species are mixed with coniferous  
68 trees compared with a monoculture (Prescott et al. 2000). These two mechanisms are not  
69 mutually exclusive and competitive interactions among species are also dependant on the  
70 environmental conditions (Cescatti and Piutti 1998).

71 Nevertheless, the positive effects of mixed forest stands on forest productivity (*i.e.* above-  
72 ground biomass production) and timber quality are far from being universal (Pretzsch 2005;  
73 Pretzsch and Schütze 2009; Richards et al. 2010). For example, Paquette and Messier  
74 (2011) demonstrated that tree biodiversity was less important for productivity in temperate  
75 forests growing in a stable and productive environment (high competitive exclusion), than in  
76 boreal forests where the environment is more stressful. More recently, Toigo et al. (2015),

77 reported that along site productivity gradients tree mixtures had a more positive effect on  
78 sites with low productivity than on sites with high productivity. Such results are consistent  
79 with the stress-gradient hypothesis (SGH). According to this theory, facilitation dominates  
80 under high-stress whereas competition prevails in the absence of resource limitation  
81 (Callaway and Walker 1997).

82 Over this last decade, ecologists have invested tremendously in trait-based approaches that  
83 capture the essential attributes of species life-history strategies. This perspective argues that  
84 the assessment of traits' dispersion among species (i.e. interspecific trait variability within a  
85 plant community) allows the mechanisms behind species coexistence to be elucidated (Mc  
86 Gill et al. 2006; Adler et al. 2013) and their effects on ecosystem functioning to be forecast  
87 (Lavorel 2013). In this context, the role of the intraspecific variability of plant traits has largely  
88 been neglected (Albert et al. 2011; Jackson et al. 2013). In forest ecosystems, tree functional  
89 traits are variable and this variability is driven both by genetic and ecological factors (e.g.  
90 Bresson et al. 2011; Robson et al. 2012). This variation might be as important as inter-  
91 specific variation (Pluess and Weber 2012). Furthermore, some studies have demonstrated  
92 that intraspecific trait variation might also have significant effects on ecosystem functioning  
93 such as nutrient (nitrogen and carbon) cycles through changes in leaf decomposition (Lecerf  
94 and Chauvet 2008; Grigulis et al. 2013). In forest ecosystems subject to intense land use and  
95 to strong competition between trees, the functional-trait attributes of a given timber tree  
96 species are likely to be influenced by management decisions such as tree density, stand  
97 composition, soil fertility and the combination of these factors. The intraspecific variations  
98 induced by these biotic interactions might in turn affect tree productivity and ecosystem  
99 processes e.g. nutrient cycles (Trap et al. 2013a). Some interspecific variations in simple  
100 traits have been recognized to strongly impact forestry outcomes. For example, Leaf Mass  
101 Area (LMA), a morphological trait, is negatively correlated with the photosynthetic rate, and  
102 the potential relative growth rate is positively correlated with litter decomposition rate (Poorter  
103 et al. 2009). Leaf carbon allocation to fibres (i.e. hemicelluloses, cellulose and lignin) is a  
104 chemical functional trait also strongly linked to litter decomposition, since cellulose and lignin

105 have negative effects on litter decomposition rate and therefore nutrient turnover  
106 (Haettenschwiler et al. 2011; Freschet et al. 2012; Trap et al. 2013b). In this ecological,  
107 economic and scientific context, there is an important need to better understand both intra-  
108 and inter-specific variation in leaf traits, to further our understanding of ecosystem functioning  
109 in relation to local environmental characteristics.

110

111 The aim of this study was thus to characterize the functional changes in leaf traits of  
112 European beech (*Fagus sylvatica* L.) induced by mixed stands, i.e. tree species biotic  
113 interactions. Beech is the most abundant broad-leaved tree species in Europe with high  
114 economic value for forestry. The total area of beech-dominated forests in Europe is  
115 estimated to cover ca 14–15 Mha (excluding the Caucasian mountains). Beech occurs on a  
116 wide range of soils including acid podzols and calcareous rendzic leptosols, but they grow  
117 best on well-drained cambisols and luvisols and do not tolerate waterlogging or severe  
118 drought (Brunet et al. 2010). In our study, we compared pure beech stands with four mixed  
119 stands containing from one to three additional tree species. These stands were studied on  
120 three different types of soils (cambisol, luvisol and leptosol), representing a gradient of  
121 decreasing soil water holding capacity and rooting depth, in order to test the SGH. Nineteen  
122 beech leaf traits were studied, including LMA, LDMC, stomatal density and chemical traits  
123 (fibres, phenolic compounds, nutrients and pH). We hypothesised that (1) stand composition  
124 strongly impacts beech leaf traits; (2) the beneficial effects of mixed stands on *Fagus*  
125 *sylvatica* increase with stand diversity, and (3) this positive effect of mixed stands increases  
126 with the increasing severity of edaphic constraints (SGH).

127

## 128 **Materials and Methods**

### 129 **Study sites and soil properties**

130 This study was performed in eight beech (*Fagus sylvatica* L.) forests (Appendix 1) all located  
131 in Upper-Normandy (north-western France). These forests were Bord-Louviers (49°15'N,  
132 1°09'E, 100 m a.s.l.), Brotonne forest (49°26'N, 0°43'E, 100 m a.s.l.), Eawy (49°44'N, 1°18'E,

133 200 m a.s.l.), Eu (49°52'N, 1°36'E, 180 m a.s.l.), La Londe-Rouvray (49°20'N, 0°59'E, 90 m  
134 a.s.l.), Lyons (49°26'N, 1°37'E, 200 m a.s.l.), Roumare forest (49°25'N, 0°59'E, 100 m a.s.l.)  
135 and Forêt Verte (49°30'N, 1°06'E, 120 m a.s.l.). All stands are managed as even-aged fully-  
136 grown forests (60 to 85 years old, see Appendix 1) by the French Forestry Service (ONF)  
137 and derive from natural regeneration. The climate is temperate oceanic with mean annual  
138 precipitation about 800 mm and mean annual temperature about 10°C (Brethes 1984).

139

140 For this study, three different soil types randomly located in the eight beech forests were  
141 selected. The three soils were (i) eutric Cambisol located on 80 cm or more of colluvic parent  
142 material (mainly loess) in dry valley bottoms, (ii) endogleyic dystic Luvisol developed on  
143 loess parent material (50 - 80 cm deep) located on a plateau, and (iii) rendzic Leptosol  
144 located on chalky slopes, with less than 50cm-thick loess parent material (FAO 2006). These  
145 three soil types were chosen in order to test the effect of a gradient in maximum soil water  
146 holding capacity (WHC) and rooting depth (DR). From the Upper-Normandy reference base  
147 for soils (Brethes, 1984), we selected four soil description profiles, present in the studied  
148 forests, for each soil type. For each profile, the WHC was estimated using the "textural  
149 method" (Baize 2000 based on Jamagne et al. 1977) and, the rooting depth (DR) was noted.  
150 According to these values, the three soils that we selected represented a gradient of  
151 increasing edaphic stress with Cambisol < Luvisol < Leptosol (see Table 1 for DR and WHC  
152 values). Other soil chemical characteristics were measured and are provided in Table 1.

153

#### 154 **Sampling design**

155 For each of the three soil types, intraspecific variations in leaf traits of beech trees were  
156 investigated in forests representing five characteristic types of stand composition. For every  
157 forest, where present, we sampled stands of all different treatment combinations (similar age  
158 and management and composition) to obtain a balanced design. The five stand compositions  
159 were selected to represent a diversity gradient from 1 species to at least 3 species. These  
160 stand compositions were 1) pure beech (F), 2) beech with oak (FQ) (*Quercus petraea* Liebl.

161 or *Q. robur* L.), 3) beech with hornbeam (FC) (*Carpinus betulus* L.), 4) beech with oak and  
162 hornbeam (FCQ) and 5) beech with at least three other tree species (F+). In this last  
163 category, the other species were usually *Acer pseudoplatanus* L., *Fraxinus excelsior* L.,  
164 *Prunus avium* L., *C. betulus* L., *Q. robur* L., and *Q. petraea* Liebl., and occasionally *Acer*  
165 *campestre* L., *Betula pubescens* Ehrh., *Quercus pubescens* Wild., *Aesculus hippocastanum*  
166 L. and *Tilia platyphyllos* Scop (see Appendix 2 for a details of species abundance). For each  
167 of the 5 stand compositions x 3 soil types, three independent replicate stands were selected  
168 leading to an overall 45 stands. But, among the beech–oak stands only one could be found  
169 that was located on rendzinas, hence reducing the actual number of stands sampled to 43  
170 (45 - 2= 43 stands). For each replicate, approximately 50 sun leaves from the top of the  
171 canopy of equivalent age and stage of development were collected from three individual  
172 trees in May and June 2011 using a BIG SHOT (SherrillTree, USA,). In total, 129 samples of  
173 leaves were collected: 43 stands x 3 trees. In mixed stands, these three individual trees were  
174 selected so that their close neighbours corresponded to those species that occurred  
175 throughout the whole stand. Immediately after the collection, leaves were stored in a cool  
176 box with at saturating vapour-pressure, following Cornelissen et al. (2003), prior to leaf-trait  
177 measurements.

178

### 179 **Leaf traits measurements**

180 Leaf Mass Area (LMA), Leaf Dry Matter Content (LDMC) and stomatal density were  
181 measured in the 129 samples. The LMA corresponds to the oven-dry mass of the leaf  
182 divided by its fresh one-sided area expressed as g.cm<sup>-2</sup>. The LDMC is the dry mass of the  
183 leaf divided by its fresh mass. Fresh mass and leaf area of ten leaves per sampled tree were  
184 measured on the day of collection using Winfolia (Regent Instruments, Canada). These  
185 leaves were dried at 50°C to constant weight and reweighed to obtain their dry mass  
186 (Cornelissen et al., 2003). Lastly, the stomatal density was measured on a 0.25 mm<sup>2</sup> area x  
187 400 magnification with Leica Application Suite (Leica, Germany), of one leaf per sampled  
188 tree, and expressed as stomata.mm<sup>-2</sup>.



189 Leaves used for chemical analyses (fibres, phenolic compounds, minerals and pH), were  
190 dried at 25°C to a constant weight, prior to being ground to 1 mm for fibre analysis and  
191 further ground to a fine powder to obtain the most homogenous sample possible for analysis  
192 of phenolic compounds, minerals and pH (Boizot and Charpentier 2006). For fibres and  
193 mineral concentration, leaves from the three sampled trees of each replicate stand were  
194 pooled to obtain one composite sample per replicate (n=3). The fibres (i.e. hemicelluloses,  
195 cellulose, lignin) and soluble compound concentrations were measured according to the Van  
196 Soest method (1994), with a fibre extractor (Velp Scientifica, Italia). All fibre types were  
197 expressed as % total organic matter (% TOM). The total phenolic compound concentration  
198 (n=9) was determined according to Bärlocher and Graça (2005). Absorbance was read at  
199 760 nm after 2h (6715 UV/Vis. Spectrophotometer, Jenway, UK). Concentration was  
200 expressed as % TAE (tannic acid equivalent). The concentrations of potassium (K),  
201 manganese (Mn), magnesium (Mg), sodium (Na), iron (Fe), aluminium (Al) and calcium (Ca)  
202 were determined by atomic absorption spectrometry (AAS, ICE 3000 SERIES, Thermo  
203 Scientific, USA) after dry ashing for 4h at 500°C. The ash was dissolved by heating in 1 M  
204 hydrochloric acid, method according to Miller (1998). Concentrations were expressed as mg  
205 of each element per g of leaf dry mass. The leaf carbon concentration ( $C_{Tot}$ ), the leaf nitrogen  
206 concentration ( $N_{Tot}$ ) and the lignin nitrogen concentration ( $N_{Lign}$ ) were determined by gas  
207 chromatography with a CHN pyrolysis micro-analyser.  $C_{Tot}$  and  $N_{Tot}$  were expressed as mg of  
208 elements per g of leaf dry mass.  $N_{Lign}$  corresponded to the percent of total nitrogen assigned  
209 in lignin. The foliar pH was measured according to Cornelissen et al. (2006). For each  
210 sample, 200 mm<sup>3</sup> of powdered dried leaves were mixed in 1600 mm<sup>3</sup> of Milli-Q water (i.e.  
211 volume ratio 1:8) in an Eppendorf tube. After 1h of shaking and 5 min of centrifugation, pH of  
212 the supernatant was measured.

213

## 214 **Data analysis**

215 Data analyses were performed to test the effects of stand composition and soil type on  
216 beech leaf traits. All statistical analyses were made using R 2.10.1 (R Development Core

217 Team, 2009), and differences were considered significant at  $p < 0.05$ . We used mixed-effect  
218 models with forest treated as a random factor to test the effect of stand composition, soil and  
219 interactions. The mixed-effect models were fitted by using the *lmer* function of the *lme4*  
220 package in R (Bates and Sarkar 2006).

221 For each soil type, to compare the effect of pure stands vs. species mixtures of increasing  
222 richness, we calculated the Log Response Ratio (LogRR) for each trait that responded  
223 significantly:

$$224 \text{LogRR}_{\text{trait}} = \log_2 \frac{\text{trait attribute for a mixed stand}}{\text{trait attribute for the pure reference}}$$

225 The log-transformation produces a negative value when the attribute for a mixed stand is  
226 lower than the attribute for the pure stand. On the contrary, a positive value indicates that the  
227 attribute for the pure stand is lower than that of a mixed stand. One-sample t-tests (for  
228 parametric data) or one-sample Wilcoxon signed rank tests (for non-parametric data) were  
229 performed for each combination of stand composition and soil, and for all mixed stands of a  
230 particular soil type, in order to detect significant deviation from unity.

231

## 232 **Results**

### 233 **Overall effect of stand composition on intraspecific trait variation**

234 Among the nineteen leaf traits measured, fourteen did not exhibit any significant differences  
235 with stand composition (Table 2). Only LMA, LDMC, phenolic compounds, Mg concentration  
236 and pH responded to this factor (Fig. 1).

237 The LMA (Fig. 1, Table 3) was significantly affected by stand composition with the lowest  
238 values recorded in the most-species-rich stand (F+): in the other stands LMA values were  
239 similar. The LDMC (Fig. 1) also differed with stand composition (Table 3) following the same  
240 pattern as LMA: the highest LDMC values were attained from pure beech stands and the  
241 lowest in FCQ and F+.

242 The concentration of total phenolic compounds (Fig. 1, Table 3) was slightly higher in F and  
243 FQ stands, and decreased with increasing stand richness reaching its lowest concentration

244 in F+. Although phenolics and LDMC followed similar patterns with stand composition, the  
245 correlation between these variables was weak ( $r^2=0.28$ ). Leaf pH was significantly higher in F  
246 and FQ, intermediate in FC and F+ and lowest in FCQ (Fig. 1, Table 3). Lastly, there was an  
247 effect of stand composition on leaf Mg concentration (Fig. 1, Table 3), with the highest  
248 concentration in F+ and the lowest concentration in the mixtures that included oak (FQ,  
249 FCQ).

250

### 251 **Combined effects of soil and stand composition on intraspecific trait variation**

252 The LogRR for each soil-x-stand combination was only calculated for the traits which were  
253 influenced by stand composition (Fig. 2). On the whole, LogRR were negative – for LDMC,  
254 LMA, phenolic compounds and pH - resulting from a lower value of these traits in all mixtures  
255 compared to pure stands, and even lower values at the highest richness (F+) for phenols,  
256 LDMC and LMA.

257 For LMA, LogRR co-varied with soil type (interaction effect stand composition  $\times$  soil type,  
258 Table 3) with Cambisol producing the opposite LogRR result to Luvisol and Leptosol (Fig. 2).

259 The magnitude of LogRR and significant difference from unity increased with species  
260 richness in Leptosol and Luvisol. Among these two soils, the only mixture that produced no  
261 significant effect was FQ stands. Conversely, on Cambisol this mixture (FQ) had the highest  
262 absolute value for LMA compared to other mixed stands, but this effect was not different from  
263 unity, suggesting that there were no LMA changes on Cambisol among mixtures compared  
264 to pure stands.

265 Regarding the LogRR for LDMC (Fig. 2), only the FQ stand had a positive LogRR for  
266 Cambisol. All other soil-stand combinations exhibited negative LogRR values that further  
267 decreased as stand diversity increased for trees growing on Luvisol and Leptosol.

268 For phenolic compounds (Fig. 2), a significant effect of soil type was detected (Table 3). The  
269 LogRR for phenolic compounds was generally negative on Luvisol and on Leptosol, and was  
270 not different from unity for Cambisol. Nevertheless, for those FQ stands growing on

271 Cambisols, the LogRR was significantly positive suggesting a higher concentration of  
272 phenols in the leaves of FQ stands than leaves of F stands.

273 Regarding the pH (Fig. 2), although the logRR was significantly negative for all mixed stands  
274 of a given soil, the only significant differences from unity were recorded for the three  
275 following combinations: FC on Cambisol, and FCQ on Luvisol and Leptosol.

276 Leaf magnesium concentration was significantly affected by soil type (Table 3). The LogRR  
277 was globally positive for Luvisol and not different from unity for Cambisol and Leptosol (Fig  
278 2). The only combination of soil and mixed stands that differed from the pure stand was F+  
279 on Luvisol, with a significantly lower leaf Mg concentration in F+ than the pure stand (positive  
280 LogRR).

281 Lastly, although, the single effect of soil type on functional traits was not the aim of this study  
282 we found that Mg, K, Mn and phenolics in beech leaves were significantly affected by soil  
283 type (Tables 2 and 3).

284

## 285 **Discussion**

286

287

288

### 289 **Stand composition induces strong intraspecific trait variation**

290 Intraspecific trait variation has already been shown to be related to environmental  
291 heterogeneity and genetic variability (Albert et al. 2010a). In our study, beeches were  
292 sampled from natural regeneration in stands covering a large area, and although no genetic  
293 tests were performed, we can assume that intraspecific variability was not genetically driven  
294 but related to neighbouring tree species, i.e. stand composition. We found that the variability  
295 in beech functional traits across stands of differing composition was high, with some traits  
296 showing particularly large variations resulting from high plasticity of form and function among  
297 populations. For example, the variation in LMA for beech ranged from 0.046 to 0.081 g.cm<sup>-2</sup>  
298 on Luvisol depending on tree species assemblages. Intraspecific variation in beech traits has

299 also been studied at large geographical scales by Sánchez-Gómez et al. (2013), where it  
300 was lower than in our study. These authors examined six European beech provenances in a  
301 glasshouse experiment including Spanish, German, Italian and Sweden beech populations,  
302 where the LMA of seedlings ranged from 0.049 to 0.055 g.cm<sup>-2</sup> and from 0.056 to 0.066  
303 g.cm<sup>-2</sup> in a control treatment and water deficit treatment respectively (Sánchez-Gómez et al.  
304 2013). Thus, stand composition is far from being a negligible factor, although this source of  
305 trait variation has never been estimated in forests. Similar studies on other tree species  
306 and/or biogeographical contexts must be done to compare the importance of these  
307 intraspecific variations. Our results support the hypothesis of Bussotti et al. (2015) who  
308 suggested that genetic and phenotypic variability of European trees might be higher within  
309 than among populations (i.e. higher within a given site than among sites). Recently, the role  
310 of forest age as a potential driver of intraspecific litter trait variability (litter nutrient and fibre  
311 content) has been also reported for beech in the same forests as this current study (Trap et  
312 al. 2013a). These results are in agreement with the growing consensus that within-species  
313 variation in functional traits is not negligible (Albert et al. 2010b; de Bello et al. 2011; Fajardo  
314 and Piper 2011) and that we need to better identify factors influencing this intraspecific  
315 variation in order to highlight mechanisms behind plant species co-occurrence and its  
316 consequences for ecosystem functioning and productivity.

317

### 318 **Stand composition impacts beech strategy**

319

320 Our analysis revealed a general trend for increasing resource acquisition with an increasing  
321 number of neighbouring species:  $F < FQ < FC = FCQ < F+$ . Indeed, both LMA and LDMC  
322 significantly decreased along the gradient of tree richness. Higher LMA and LDMC may be  
323 related to nutrient deficiency (especially N and P, Reich *et al.*, 1992; Wright *et al.*, 2004;),  
324 drought (Sanchez-Gomez et al. 2013), or high irradiance (ref). In this study, sampled beech  
325 leaves were always taken from equivalent locations from all stands, i.e. sun leaves located at  
326 the top of the canopy. Thus, the differences in LMA and LDMC at the leaf level could not be

327 related to differences in solar radiation but rather to differences in edaphic resource  
328 availability (water and/or nutrient availability) attributable to facilitation or complementary  
329 effects. Nevertheless, it is conceivable that changes in beech architecture between pure and  
330 mixed stands (see Bayer et al. 2013 and the review by Ishii and Asano 2010) could alter the  
331 profile of canopy light absorbance improving complementarity of light use and tree  
332 photosynthetic light use efficiency, and consequently tree competitiveness. Leaf nitrogen  
333 content (NTOT) which is also a central tenet of the leaf economic spectrum (Wright et al.  
334 2004) also tended to be higher in F+, although the difference was not statistically significant  
335 ( $p = 0.13$ ).

336 Phenolic compound concentration was lower in beech leaves growing in F+ than in the other  
337 stands. Phenolic compounds are generally believed to be key components of the oxidative  
338 defences of plants against pathogens and herbivores (but see Bussotti et al. 1998). Tree  
339 diversity is known to reduce herbivory by forest insects (Jactel and Brockerhoff 2007,  
340 Castagneyrol et al. (2014)). Bussotti et al. (1998) noted that an increase in phenolic content  
341 is often associated with the thickened cell walls (as would increase LMA, and LDMC).  
342 Nevertheless, the correlation between phenolics and LMA or LDMC in our samples was  
343 weak (respectively  $r=0.403$  and  $r=0.053$ ).

344 Magnesium concentration was highest in F+ suggesting a high potential photosynthetic rate  
345 in these stands. Mg makes up part of the chlorophyll molecule and is essential for  
346 photosynthesis (Bottrill et al. 1970). When leaf [Mg] is low, chlorophyll production is reduced.  
347 On the other hand, [Mg] was lowest in the presence of oak (FQ and FCQ), which must be  
348 due to a combination of the higher nutrient demand (Mellert and Goettlein, 2012) and a  
349 negative effect of oak on [Mg] compared with beech (Nickmans et al., 2015).

350 The pH of beech leaves was also significantly affected by stand composition. pH has recently  
351 been suggested as a functional trait with useful predictive power associated with  
352 biogeochemical properties and processes in ecosystems (Cornelissen et al. 2006) but its use  
353 is not yet widespread. A high green-leaf pH is supposed to reflect high concentrations of  
354 metal cations (calcium, magnesium, potassium), whereas low leaf pH corresponds to high

355 concentrations of organic acids and C-rich secondary metabolites (chemical-defence  
356 compounds) such as tannins. Nevertheless, leaf pH and phenolic concentrations in our  
357 samples were uncorrelated ( $r=0.11$ ).

358

359 Globally our results suggest that intraspecific competition might be higher than interspecific  
360 competition for beech. Consequently, mixed stands are more favourable for beech whatever  
361 the soil type, and the identity of neighbouring species is of primary importance in determining  
362 the extent to which beech improves its nutrient acquisition.

363

364

### 365 **Edaphic stress modulates the effect of stand composition (SGH)**

366

367 According to the stress-gradient hypothesis (SGH), facilitation dominates under high-stress  
368 whereas competition is claimed to prevail at low resources limitation (Callaway and Walker  
369 1997). Thus, benefits of species-mixing are predicted in neutral and harsh environments, but  
370 negative effects are expected in favourable environments. Most of the literature on the SGH  
371 is based on herbaceous systems, and its validation in forest ecosystems is still relatively  
372 scarce and recent e.g. (Pretzsch et al. 2013; del Rio et al. 2014; Toigo et al. 2015). Our study  
373 offers the opportunity to test this hypothesis since we studied a gradient of decreasing soil  
374 water holding capacity and rooting depth with stress increasing from  
375 Cambisol<Luvisol<Leptosol. Among variables significantly affected by stand composition,  
376  $\log RR_{LMA}$ ,  $\log RR_{LDMC}$  and  $\log RR_{phenolics}$  presented a coherent pattern with the SGH. In low  
377 stress conditions (Cambisol), the mixture conferred no great advantage since the LogRR was  
378 around zero. With an increasing level of stress, there was a clear positive effect of the  
379 mixture (whatever the assemblage) compared to pure stands. This effect was particularly  
380 large for F+ (in terms of intensity and significance). Thus, the responses to increasing tree  
381 richness detected in our study actually corroborate the stress-gradient hypothesis outlined by  
382 Callaway and Walker (1997). Lastly, other studies report similar changes in leaves traits

383 collected from beech trees in conditions of natural soil and climatic water stress (Bussotti et  
384 al. 1995; Bussotti et al. 1998; Nardini et al. 2012) that support the finding that soil water  
385 stress was the main constraint differentiating our soils.

386

387 Several different mechanisms could explain these positive interactions for beech in the  
388 context of water stress (see Pretzsch et al. 2014 for a complete review) in addition to a  
389 decrease in competition intensity. For instance, in woody plants ‘hydraulic redistribution’ is  
390 the passive transfer at night of water through roots from the wetter often deeper soil layers to  
391 the drier layers (Caldwell et al. 1998; Prieto et al. 2012). Zapater et al. (2011) demonstrated  
392 that oak trees (*Q. petraea*) used water from deeper soil layers than beech trees and that  
393 there was evidence for hydraulic lift by oaks benefitting young beech. In our study, such a  
394 positive effect of oaks under stressed conditions was not demonstrated since there was no  
395 advantage for beech (F) of growth with oak (FQ). Beech water uptake is achieved utilizing  
396 ectomycorrhizae (EM) that acquire soil nutrients and water from finer soil pores than can be  
397 accessed by the root hairs of fine roots. Thus, mixtures of these two tree species may  
398 increase mycorrhizal diversity resulting in improved exploration and exploitation of soil  
399 nutrient stocks especially in poor soils. Moreover, under increasing drought stress, changes  
400 in soil condition might impact ectomycorrhizal community composition and function (Pretzsch  
401 et al. 2014). Nevertheless, we lack direct evidence for such an increase in EM diversity, and  
402 in a mixed central European forest, Lang et al. (2011) failed to demonstrated a higher  
403 diversity of EM in mixed stands.

404

#### 405 **Conclusion**

406 Our study reveals that management decisions such as selecting stand composition, and the  
407 combination of these decisions with factors like soil fertility, might strongly influence  
408 functional trait attributes for a given timber tree species and consequently ecosystem  
409 function and services. Currently, the mixture of beech and oak is of considerable importance  
410 in Europe and will probably become even more important under climate change (Pretzsch et



411 al. 2013) since the climate is predicted to become drier and warmer. Our results suggest that  
412 in sites with potential water stress, mixing beeches with oaks can slightly improve soil  
413 exploration and/or exploitation of soil nutrients in comparison with pure stands of beech (i.e.  
414 negative LogRR). Nevertheless, oak addition could have unexpected negative effects on  
415 beech stands in sites with low water stress, and there oak is far from being the best partner  
416 for beech (positive LogRR). Thus, decisions about mixing species must be made with due  
417 consideration for environmental constraints (i.e. stress level). In this study, we only  
418 investigated leaf quality but Pretzsch et al. (2013) also found complementary and similar  
419 results for the productivity of oak-beech mixtures along a gradient of nutrient availability.  
420 Likewise, productivity was enhanced in mixed stands on poor sites, and was slightly reduced  
421 in rich sites. According to our results, we recommend mixing species that have different  
422 ecological strategies. Beech and oak are both strong competitors and late successional  
423 species with low litter quality. These two species are thus too similar to be ideal for mixing. It  
424 would be better to mix beech with other tree species such as for example hornbeam, ash,  
425 maple or lime-trees, in order to foster complementarity effects and to reduce competition  
426 within stands.

427

428

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434

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638

639 **TABLES**

640

641 **Table 1.** Physico-chemical characteristics of the three soils types (mean and standard  
642 deviation in brackets, n=15).

643 **Required parameters are missing or incorrect.**

644 **Table 2.** Intraspecific variation in those beech leaf traits not significantly affected by  
645 stand composition (mean of leaf traits and standard deviation in brackets). F = pure  
646 beech stand, FQ = beech-oak stands, FC = beech-hornbeam stands, FCQ = beech-  
647 hornbeam-oak stands, F+ = stands with beech and three or more others species.  
648 Stand composition effect and soil type effect were tested by mixed-model ANOVA.  
649 Stand composition x soil interactions were always non-significant and were not  
650 reported in this table. The significance level was  $p = 0.05$  (with  $n=3$ , except for  
651 stomatal density  $n=9$ ).

652 ***Required parameters are missing or incorrect.***

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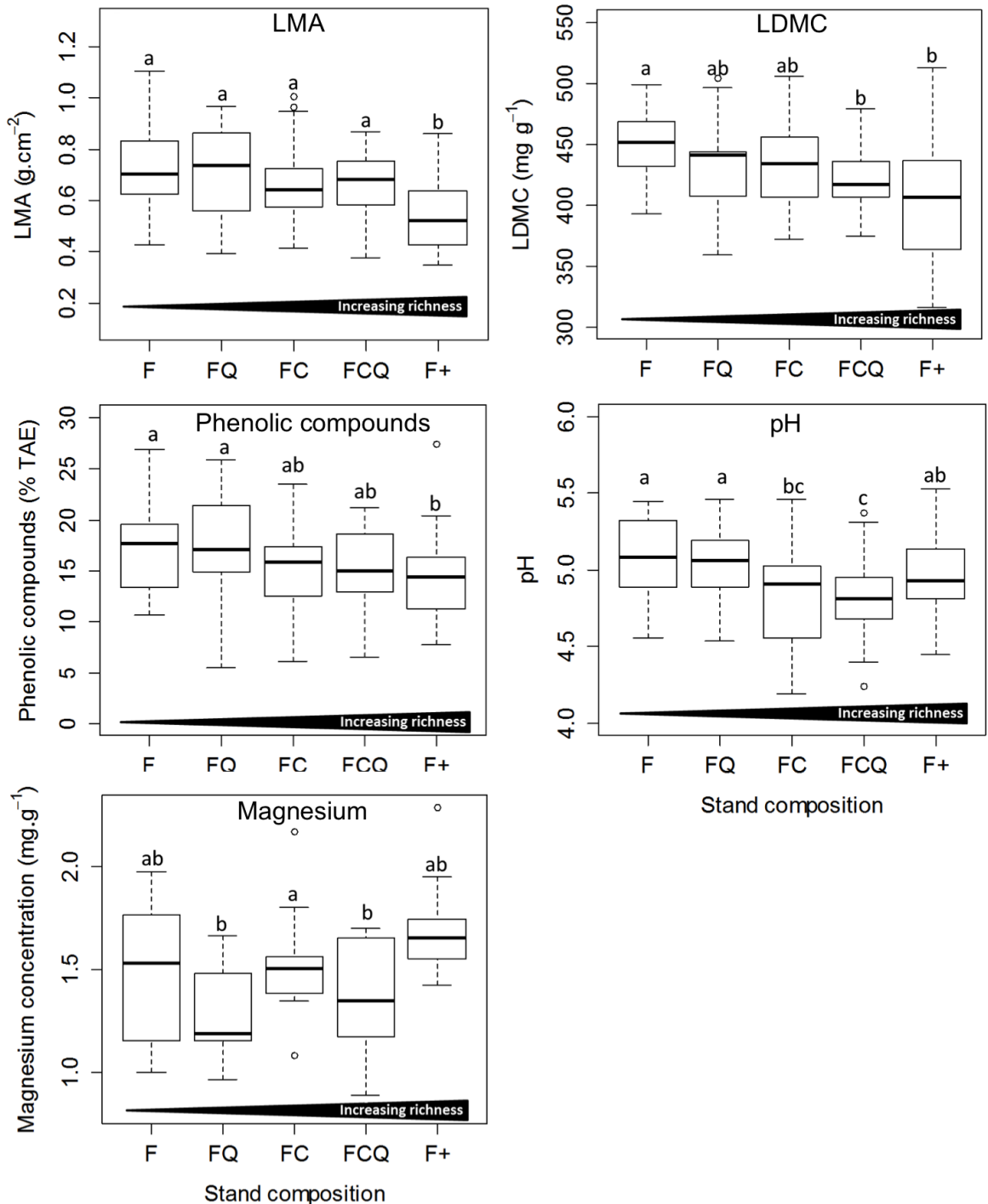
654 **Table 3.** Effect of stand composition, soil type and interaction of these two factors on 5  
655 beech leaf traits tested by mixed-model ANOVA. The significance level was  $p = 0.05$ .

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658 FIGURES Required parameters are missing or

659 incorrect.



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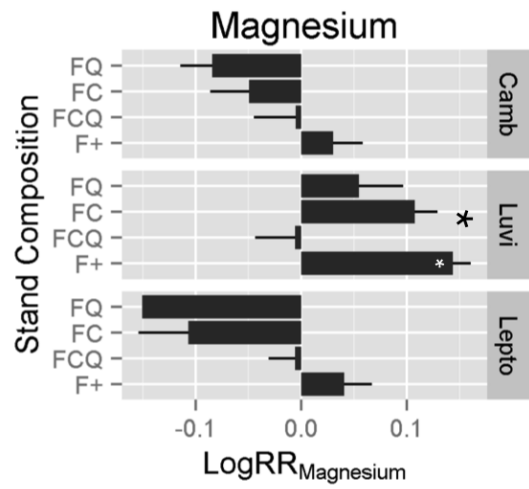
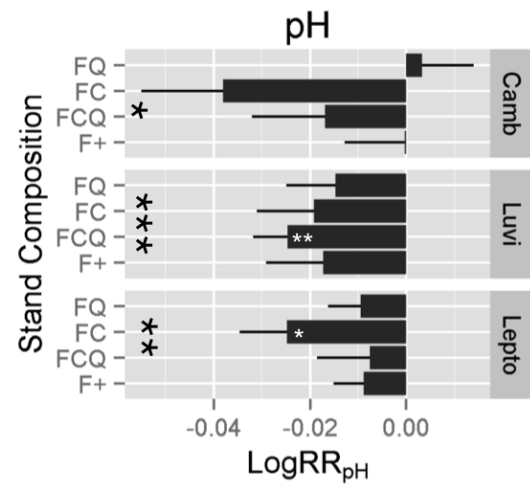
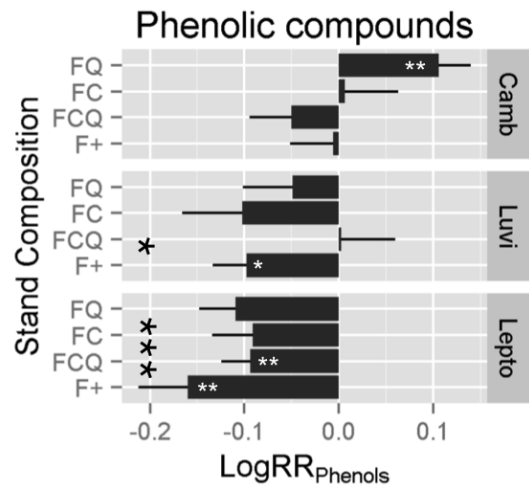
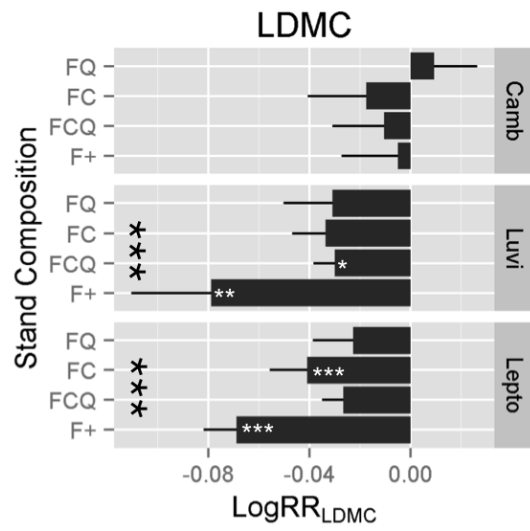
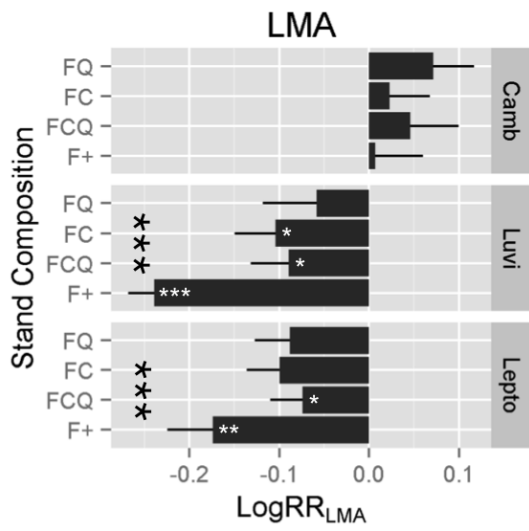
661 **Fig. 1** Intraspecific variation of beech leaf traits according to stand composition irrespective

662 of soil type: (A) Leaf Mass per Area (LMA), (B) Leaf Dry Matter Content (LDMC), (C)

663 phenolic compounds concentration, (D) pH, and (E) Magnesium (Mg) concentration. The

664 letters represent differences between compositions at significance level of  $p = 0.05$  (Mixed-  
665 model ANOVA). F = pure beeches, FQ = beeches with oaks, FC = beeches with hornbeams,  
666 FCQ = beeches with hornbeams and oaks, F+ = beeches with three or more other species.  
667 Box-and-whisker plots show the medians (n=9, except for Mg n=3).

668 Required parameters are missing or  
669 incorrect.





671 **Fig. 2** Log Response Ratio for (A) Leaf Mass per Area (LMA) , (B) Leaf Dry Matter Content  
672 (LDMC), (B) phenolic compounds, (C) pH, and (D) magnesium (Mg) concentration in the  
673 three different soils (Cambisol, Luvisol, and Leptosol) and stand compositions. Negative  
674 values correspond to a lower trait attributes in mixed stands than in pure stands; positive  
675 values to a higher trait attribute than in pure stands. Abbreviations of the four different mixed  
676 stand compositions (FQ, FC, FCQ and F+) are described in legend of Fig.1. Error bars show  
677 standard errors. Small white asterisks indicate significant differences from unity (one-sample  
678 t test, n=9 except for Mg n=3) for a unique combination of mixed stand and soil. Black  
679 asterisks indicate significant differences from unity (one-sample t test, n=36 except for Mg  
680 n=12) for all mixed stand of a given soil; \* $p<0.05$ , \*\*  $p<0.005$  and \*\*\* $p<0.001$ .

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