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1 **Application of Loreau & Hector's (2001) partitioning method to complex**  
2 **functional traits**

3

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13

14 **RUNNING TITLE**

15 Complex traits in B-EF studies

16

17 **AUTHORSHIP**

18 CG and DB elaborated the adaptation of the method to complex functional traits. DB, AG<sup>1</sup>,  
19 AG<sup>2</sup> and MSL designed the experimental study. DB, MP and AG<sup>1</sup> performed the experimental  
20 work. CG, DB, AG<sup>1</sup> and AG<sup>2</sup> analyzed the results. CG and DB wrote the first draft of this  
21 manuscript and all authors substantially contributed to revisions.

22

23

24 **Key words**

25 Biodiversity effect, BIOTREE, carbon isotope composition, complementarity effect,  
26 FunDivEUROPE, method, selection effect, water use efficiency

27

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29

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33

34 **Tweetable abstract:**

35 We applied Loreau and Hector's (2001) method to calculate biodiversity effects of complex  
36 functional traits.

37 **Abstract**

38 1- In 2001, Loreau & Hector proposed a method to calculate the effect of biodiversity on  
39 ecosystem-level properties that distinguished selection effects from complementarity effects.  
40 The approach was designed, and has been widely used, for the study of yield in mixed-species  
41 situations taking into account the relative abundance of each species in ecosystem-level yield.  
42 However, complex functional traits commonly used to integrate ecosystem-level properties  
43 cannot be analyzed like yield data because the weighted contribution of each species is not  
44 determined by its relative abundance.

45 2- We adapted the original method by clearly identifying ecologically meaningful weighting  
46 coefficients to represent species specific contributions to ecosystem function.

47 3- We applied the adapted method of analysis to tree foliar carbon isotope composition in an  
48 experimental plantation in order to test the influence of species richness on plot water use  
49 efficiency ( $WUE_{plot}$ ). The appropriate weights for the  $WUE_{plot}$  of each species are leaf  $CO_2$   
50 assimilation rate.

51 4- We observed a large range of  $WUE_{plot}$  and biodiversity effects among plots. The absence of  
52 a significant selection effect on  $WUE_{plot}$  indicated that the overall net biodiversity effect was  
53 primarily driven by a complementarity effect. The net biodiversity and complementarity  
54 effects were mostly negative, suggesting that interspecific interactions resulted in a decrease  
55 in the ratio between carbon acquisition and transpiration at the ecosystem level.

56 5- The application of the method to complex components of ecosystem functioning provides  
57 important new insights for the practical and conceptual aspects of functional biodiversity  
58 research.

59

## 60 INTRODUCTION

61 The loss of biodiversity occurring in most natural environments worldwide has sparked an  
62 interest among the scientific community in the relationship between biodiversity and  
63 ecosystem functioning (Hooper *et al.* 2012). More than twenty years of ecological studies  
64 have led to a consensus that ecosystem performance is highly dependent on species richness  
65 and on species functional characteristics (Loreau *et al.* 2001; Hooper *et al.* 2005; Zhang *et al.*  
66 2012). However, the mechanisms underlying biodiversity-function relationships have been  
67 hotly debated. Two major groups of mechanisms were initially proposed to explain positive  
68 effects of biodiversity: (1) a sampling or selection effect which arises, as species richness  
69 increases, from the increasingly probable occurrence of one or several species that strongly  
70 contribute to the ecosystem function observed (Aarssen 1997; Huston 1997; Tilman 1997),  
71 and (2) a complementarity effect driven either by niche differentiation among species, which  
72 tends to increase the efficiency with which coexisting species use the available resources or to  
73 facilitation or other mutualistic interactions among species (Tilman *et al.* 1997; Loreau 1998).  
74 Recently, the combination of evenness, richness, and life-history variations were also  
75 successfully linked to the mechanisms producing positive biodiversity effects (Zhang *et al.*  
76 2012).

77 To quantitatively evaluate this biodiversity - ecosystem functioning relationship and partition  
78 the underlying mechanisms, Loreau & Hector (2001) proposed a convenient method to  
79 calculate the influence of species mixture on ecosystem productivity: the net biodiversity  
80 effect on the yield ( $\Delta Y$ ) of a given mixture can be calculated as the difference between the  
81 observed total yield in the mixture ( $Y_O$ ) and the expected total yield in the mixture ( $Y_E$ ) under  
82 the null hypothesis that intra- and inter-specific interactions are identical. The original method  
83 was extended by Fox (2005) to include trait-dependent and trait-independent complementarity  
84 effects in addition to the dominance effect (tripartite partitioning).

85 Loreau & Hector's method has been widely used and so far more than 100 peer-reviewed  
86 papers analyzing the relationships between species richness and ecosystem functioning in  
87 highly diverse biomes have been published. Even though the method has proven to be very  
88 popular, existing studies have focused on a limited number of ecosystem functions, mostly on  
89 standing biomass.

90 One explanation for this limited application could stem from the fact that some ecological  
91 functions in mixed species stands cannot be treated at the ecosystem level in the same way as  
92 observed yield. For complex functional properties, ecosystem-level values correspond to the  
93 mean value of the species present in the community weighted by the contribution of each  
94 species to the given function; this weighted contribution can be totally different from the  
95 relative abundance of these species in terms of frequency or biomass, which the original  
96 method does not imply. These complex functions include, among others, any measurement  
97 related to the efficiency of individuals to acquire and use resources (e.g. water use efficiency,  
98 photosynthesis efficiency, nutrient use efficiency), whatever the ecosystem (plant or aquatic  
99 ecosystems, bacterial communities...). The isotope composition of organic or mineral  
100 elements in biological material or the density of any gas flux (e.g. sap flow density, density of  
101 CO<sub>2</sub> respiration) are also examples of such complex functional traits.

102 In this paper, we extend Loreau & Hector's (2001) method to complex functional traits by  
103 clearly identifying ecologically meaningful weighting coefficients which represent species  
104 specific contributions to ecosystem functioning. We illustrate the usefulness of the adapted  
105 equations for leaf carbon isotope composition. More precisely, we analyze the effect of  
106 species richness on foliar carbon isotope composition ( $\delta^{13}\text{C}$ ) at the ecosystem level in a  
107 temperate mixed-species tree plantation. Foliar  $\delta^{13}\text{C}$  is a convenient proxy for time-integrated  
108 intrinsic water use efficiency ( $WUE_{int}$ ) (Farquhar *et al.* 1982) and reflects the trade-off  
109 between CO<sub>2</sub> acquisition and stomatal regulation of transpiration at the leaf level. Foliar  $\delta^{13}\text{C}$

110 and  $WUE_{int}$  can only be obtained at the individual level and ecosystem-level  $\delta^{13}C$  cannot be  
111 calculated by simply taking into account the summed contribution of the individuals in terms  
112 of biomass or frequency. Instead, the proportional amount of  $CO_2$  assimilated by each species  
113 in the plot needs to be considered to correctly weight each species' contribution to ecosystem-  
114 level functioning.

115

## 116 **APPLICATION OF LOREAU & HECTOR'S (2001) METHOD TO COMPLEX** 117 **FUNCTIONAL TRAITS**

118 According to Loreau & Hector (2001), the net biodiversity effect on the yield ( $\Delta Y$ ) of a given  
119 mixture of species is the difference between the observed total yield in the mixture ( $Y_O$ ) and  
120 the expected total yield in the mixture ( $Y_E$ ) calculated as the sum of the products between the  
121 yield of the different species in their corresponding monocultures and the proportion of the  
122 species in the mixture (defined in terms of individual frequency or biomass):

123

124 , Eqn 1

125

126 where  $N$  is the number of species in the mixture,  $Y_{Os}$  and  $Y_{Es}$  denote the observed and expected  
127 yield of species  $s$  in the mixture,  $M_s$  is yield of species  $s$  in the monoculture,  $RY_{Os}$  is the  
128 observed relative yield of species  $s$  in the mixture, and  $RY_{Es}$  is the expected relative yield of  
129 species  $s$  in the mixture.  $RY_{Os}$  is calculated as the ratio of the observed yield of species  $s$  in the  
130 mixture and the yield of species  $s$  in the monoculture, whereas  $RY_{Es}$  is simply the proportion  
131 of species  $s$  seeded or planted in the mixture.

132 For complex functional properties where the contribution of each species to a given  
133 ecosystem-level function is not simply proportionate to the frequency of these species or their



158 species in the mixture does not give the proportional contribution of each species to total plot  
159 sapflow density. Rather, sapwood area (the cross-sectional, water conducting area in the  
160 trunk) of each tree is the correct weighting coefficient and should be used as the quantity  $W_{oi}$   
161 in equation 2.

162 The goal of Loreau & Hector's (2001) method is to partition  $\Delta Y$  into two effects generated by  
163 species interactions in mixtures: selection effects ( $SE$ ) and complementarity effects ( $CE$ ).  $SE$   
164 arises from interspecific competition leading to the dominance of a given species with  
165 particular functional traits.  $CE$  reflects the degree to which niche differences and facilitation  
166 outweigh interference competition and other negative species interactions (Loreau *et al.*  
167 2012). As when calculating  $\Delta Y$ , partitioning the effects of complex functions into  $SE$  and  $CE$   
168 must also take  $W_{oi}$  into account. The equation to calculate  $CE$  can be rewritten as:

169

170 , Eqn 3

171

172 and the equation for  $SE$  is:

173

174 . Eqn 4

175

176 As our approach is intended to be a generalisation of the original method and can be applied  
177 to complex functions which are not directly related to yield, changes in species contribution  
178 with time are not taken into account in equation 4. The selection effect thus here stresses the  
179 dominance of a one or more species for the considered complex ecosystem function at a given  
180 time.

181

182 **APPLICATION OF THE MODIFIED EQUATIONS TO ECOSYSTEM-LEVEL**  
183 **CARBON ISOTOPE COMPOSITION**

184 A positive effect of species mixture on forest ecosystem productivity (Paquette & Messier  
185 2011; Zhang *et al.* 2012) and transpiration (Forrester *et al.* 2010; Kunert *et al.* 2012) has  
186 previously been reported. Complementarity effects (*CE*) and selection effects (*SE*) for these  
187 ecosystem-level parameters were highlighted with Loreau & Hector's (2001) method, thus  
188 making it possible to explain differences in ecosystem functioning among species richness  
189 levels. Promoting a mixture of tree species to enhance the ratio of ecosystem-level  
190 productivity to transpiration (i.e. high water use efficiency) has been advocated for sustainable  
191 forest management (McCarthy *et al.* 2011), of particular importance in a context of climate  
192 change. To further investigate this relationship, we applied the widely used carbon isotope  
193 approach (Farquhar *et al.* 1982) to study the impact of tree species mixtures on ecosystem-  
194 level water use efficiency ( $WUE_{plot}$ ) in a temperate mixed plantation.

195 At leaf level, intrinsic water use efficiency ( $WUE_{int}$ ) represents the ratio between  
196 photosynthetic assimilation of  $CO_2$  by the leaf ( $A$ ) and stomatal conductance for water vapor  
197 ( $g_s$ ) and depends on the molar fraction of  $CO_2$  in the air ( $C_a$ ) and in the leaf intercellular  
198 spaces ( $C_i$ ) following this equation:

199

200 . 
$$\text{Eqn 5}$$

201

202 During photosynthetic assimilation of  $CO_2$ , plants discriminate against molecules of  $CO_2$   
203 containing  $^{13}C$  because  $^{13}CO_2$  diffuses more slowly from the atmosphere to the site of  
204 carboxylation (stomatal diffusion) than does  $^{12}CO_2$ .  $^{13}CO_2$  also reacts less with the primary

205 carboxylating enzyme (Rubisco) (Fig. 1). Farquhar *et al.* (1982) showed that foliar carbon  
206 isotope composition ( $\delta^{13}C$ , ‰) is strongly negatively correlated with  $WUE_{int}$  following this  
207 simplified equation:

208

209 ,                      Eqn 6

210

211 where  $\delta^{13}C_{air}$  is the carbon isotope composition of the air and  $a$  and  $b$  are factors  
212 characterising the discrimination against  $^{13}CO_2$  during stomatal diffusion and carboxylation,  
213 respectively. Therefore,  $\delta^{13}C$  provides a convenient time-integrated estimate of  $WUE_{int}$ . Values  
214 for  $\delta^{13}C$  are obtained at the individual tree level by sampling representative subsets of leaves  
215 or needles, but individual values cannot simply be added to represent ecosystem-level carbon  
216 isotope composition ( $\delta^{13}C_{plot}$ ). Instead, the contribution of a single tree to the carbon isotope  
217 composition of the whole population depends on tree-specific  $CO_2$  assimilation rates that  
218 control carbon isotope fractionation during photosynthesis (Lloyd & Farquhar 1994).  
219 Consequently, when  $\delta^{13}C$  values are scaled up from tree or species level to ecosystem level,  
220 tree or species  $\delta^{13}C$  values should be weighted by these assimilation rates (Fig. 2). Since direct  
221 measurements of  $CO_2$  assimilation rates cannot easily be made for each tree in the field, we  
222 used a convenient proxy for canopy-level, species  $CO_2$  assimilation. In a given environment,  
223 the quantum yield for reduction of end electron acceptors at the PSI acceptor side is strongly  
224 positively correlated with time-integrated leaf  $CO_2$  exchanges (Genty *et al.* 1989). Thus, the  
225 proportions of the measured quantum yield of species  $i$  can therefore be used as the weighting  
226 coefficient ( $W_{oi}$ ) for  $\delta^{13}C$  values.

227

228 Materials

229 We conducted our study at the BIOTREE tree biodiversity experimental site in Germany  
230 (Kaltenborn site, Scherer-Lorenzen *et al.* 2007), which was planted in winter 2003/2004. This  
231 plantation is located on acidic sandy soils and includes four species: *Fagus sylvatica* (L.),  
232 *Quercus petraea* (Matt.), *Picea abies* (L.) Karst. and *Pseudotsuga menziesii* (Mirb.) Franco.  
233 The plantation was designed to assure maximum above- and below-ground interactions  
234 among species at the adult stage. Therefore, in the mixed plots of 120 x 48m, each species  
235 was planted in monospecific rectangular patches of 8 x 8m, arranged in a regular pattern in  
236 order to reduce out-competition of slow growing species at an early stage and to maximize  
237 interspecific interactions along borders and corners (Scherer-Lorenzen *et al.* 2007). In  
238 summer 2011, we sampled leaves and needles from four trees per species and per plot in  
239 monocultures (n = four plots), two-species mixtures (n = six), three-species mixtures (n =  
240 four) and four-species mixtures (n = one). In each plot, we only took samples from trees at the  
241 corners of the patches. The samples were oven-dried at 60°C for 48 hours, then finely ground.  
242  $\delta^{13}\text{C}$  analysis was carried out at the Stable Isotope Facility of UC Davis, USA. The  $\delta^{13}\text{C}$  (‰)  
243 values are expressed relative to the Vienna Pee Dee Belemnite standard. The quantum yield  
244 for reduction of end electron acceptors at the PSI acceptor side was measured with a  
245 HandyPea fluorimeter (Hansatech Instruments, Pentney-Norfolk, UK) on leaves or needles in  
246 close vicinity to the ones harvested for elemental and isotope analyses following the  
247 procedure described by Strasser *et al.* (2010). This value was then used as a weighting  
248 coefficient ( $W_{oi}$ ) when calculating biodiversity effects on  $\delta^{13}\text{C}_{plot}$ . We used the non-parametric  
249 Wilcoxon test to check for complementarity, selection and net effects among mixture levels  
250 and t-tests to evaluate whether all the indices differed significantly from zero (SAS 9.3, SAS  
251 Institute, Cary, USA).

252

253 Results and Discussion

254 We found large differences in  $\Delta F$ ,  $CE$ , and  $SE$  among plots, with either positive or negative  
255 values (Fig. 3, Table 2). Positive or negative values confirmed that in this plantation,  
256 interactions among species drive  $\delta^{13}C_{plot}$ , and thus  $WUE_{plot}$ . When considering individual  
257 species richness levels, we found that both the net and complementarity effects were  
258 significantly different from zero ( $P < 0.05$ ) for the two-species mixtures; however, we found  
259 no selection effect ( $P = 0.27$ ). Furthermore, the net and complementarity effects were mostly  
260 negative, suggesting lower observed  $\delta^{13}C_{plot}$  than what would have been expected based on the  
261 monoculture values. Since  $\delta^{13}C$  and water use efficiency are positively related (Farquhar *et al.*  
262 1982), our findings point toward lower  $WUE_{plot}$  when several different species coexist. This  
263 result contrasts with previous patterns of enhanced water use efficiency found in species  
264 mixtures (Forrester *et al.* 2010; Kunert *et al.* 2012).

265 The absence of a significant selection effect on  $WUE_{plot}$  indicates that the overall negative net  
266 biodiversity effect observed in the 2-species mixtures was primarily driven by a  
267 complementarity effect. Our interpretation is that the species coexisting in the mixed plots are  
268 in direct competition for the same resources because they still share the same ecological niche  
269 at the early establishment stage (7 years after planting, at the time of our measurements). This  
270 competition most likely caused a decrease in the ratio between carbon acquisition and  
271 transpiration at the ecosystem level in the two-species mixtures. As no overshading was  
272 observed, the competition among species is presumably occurring belowground. This  
273 assumption is consistent with the strong competition among fine roots observed by Lei *et al.*  
274 (2012) in this plantation.

275 Furthermore, we did not observe any significant effect of richness level for any of the  
276 biodiversity effects ( $P > 0.05$ ). This indicates that the number of species competing for  
277 resources does not significantly affect the difference in  $\delta^{13}C_{plot}$  between observed and expected

278 values. The  $\delta^{13}C$  value for a given species in the two-, three- and four-species mixtures did not  
279 greatly change.

280

281

## 282 **CONCLUSION**

283 Applying the version of Loreau & Hector's (2001) method to complex components of  
284 ecosystem functioning will provide important new practical applications as well as conceptual  
285 insights in functional biodiversity research. We have shown here that, with the appropriate  
286 weighting factors for specific, complex functional properties, the method can be applied to a  
287 broad range of functional properties, rather than to yield alone. In our case, we used the  
288 quantum yield for reduction of end electron acceptors at the PSI acceptor side as the  
289 weighting factor for ecosystem-level carbon isotope composition. This combination of  
290 weights and functions provides an estimate of intrinsic water use efficiency in mixed species  
291 plots. For other complex traits, the selection of the most pertinent weighting factor should  
292 make it possible to determine the contribution of each species to the studied ecosystem  
293 property. Some of the weighting factors may be difficult to measure precisely with currently  
294 available equipment, as in the case of CO<sub>2</sub> assimilation rates in our study. Nevertheless, if  
295 appropriate measurements are not easily obtainable, proxies could be found that provide the  
296 same proportional contributions; modelling approaches may be of help in this case. In the  
297 young mixed temperate plantation in our study, complementarity rather than selection effects  
298 were the substantial drivers of plot water use efficiency. As the plantation ages and taller trees  
299 with broader root systems begin to compete for light and soil resources, the complementarity  
300 effects might increase and selection effects might arise due to more frequent interspecific  
301 interactions. It will thus be interesting to follow the changes in the relative importance of

302 these two components of net biodiversity effects for a multitude of ecological processes and  
303 functions.

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315

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378

379 **Table 1.** Examples of complex functional properties used in plant ecological studies, with  
380 units and suitable corresponding weighting coefficients.

381

382

<b>Properties</b>	<b>Units</b>	<b>Weighting coefficient</b>
Sap flow density	L dm <sup>-2</sup> h <sup>-1</sup>	Sapwood area
Bark CO <sub>2</sub> efflux	μmol m <sup>-2</sup> s <sup>-1</sup>	Trunk surface
Photosynthesis	μmol m <sup>-2</sup> s <sup>-1</sup>	Leaf area
Leaf water use efficiency	μmol mol <sup>-1</sup>	Leaf CO <sub>2</sub> exchange
Carbon isotope composition	‰	Leaf CO <sub>2</sub> exchange
Plant water use efficiency	Kg L <sup>-1</sup>	Leaf area
Nutrient uptake rates	μmol g <sup>-1</sup> h <sup>-1</sup>	Root surface area

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386 **Table 2.** Mean species foliar carbon isotope composition measured in the mixed plots ( $F_{O_i}$ ,  
387 ‰), expected mean species foliar carbon isotope composition measured in the monoculture  
388 plots ( $F_{E_i}$ , ‰), and proportional weighting coefficient ( $W_{O_i}$ ) of species  $i$ , in each studied plot  
389 for the four studied species: *Fagus sylvatica* (Fs), *Pseudotsuga menziesii* (Pm), *Quercus*  
390 *petraea* (Qp) and *Picea abies* (Pa). Species richness, net biodiversity effect ( $\Delta F$ ),  
391 complementarity effect ( $CE$ ), selection effect ( $SE$ ) and calculated plot carbon isotope  
392 composition ( $F_O$ ) are shown for each plot.

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Plot	Richness level	Species	$F_{O_i}$	$F_{E_i}$	$W_{O_i}$	$\Delta F$	$CE$	$SE$	$F_O$
3	2	Fs	-28.46	-28.82	0.46	0.26	0.26	$3.11 \times 10^{-3}$	-26.99
		Pm	-25.74	-25.91	0.54				
6	2	Qp	-27.43	-26.60	0.50	-0.48	-0.47	$-5.91 \times 10^{-3}$	-26.64
		Pa	-25.84	-25.72	0.50				
7	2	Pm	-26.36	-25.91	0.51	-0.52	-0.52	$-7.38 \times 10^{-4}$	-26.77
		Qp	-27.19	-26.60	0.49				
10	2	Pm	-26.13	-25.91	0.58	-0.30	-0.30	$2.14 \times 10^{-4}$	-26.13
		Pa	-26.15	-25.72	0.42				
12	2	Fs	-28.99	-28.82	0.41	-0.52	-0.53	$1.59 \times 10^{-2}$	-28.02
		Qp	-27.36	-26.60	0.59				
16	2	Fs	-28.58	-28.82	0.36	-0.26	-0.28	$2.54 \times 10^{-2}$	-27.11
		Pa	-26.26	-25.72	0.64				
4	3	Fs	-28.60	-28.82	0.25	-0.22	-0.24	$1.61 \times 10^{-2}$	-27.06
		Qp	-26.73	-26.60	0.39				
		Pa	-26.35	-25.72	0.36				
5	3	Fs	-28.57	-28.82	0.29	0.15	0.15	$-5.72 \times 10^{-4}$	-26.84
		Pm	-25.57	-25.91	0.36				
		Qp	-26.75	-26.60	0.35				
9	3	Fs	-28.82	-28.82	0.27	-0.07	-0.07	$3.58 \times 10^{-3}$	-26.70
		Pm	-25.70	-25.91	0.34				
		Pa	-26.09	-25.72	0.39				

15	3	Pm	-26.25	-25.91	0.38				
		Qp	-27.20	-26.60	0.30	-0.47	-0.47	$2.54 \times 10^{-2}$	-27.11
		Pa	-26.23	-25.72	0.31				
8	4	Fs	-28.92	-28.82	0.18				
		Pm	-25.24	-25.91	0.25				
		Qp	-26.95	-26.60	0.30	-0.03	-0.02	$-3.15 \times 10^{-3}$	-26.61
		Pa	-26.00	-25.72	0.27				

395

396 **Figure legends:**

397 **Figure 1:** Schematic representation of the processes involved in leaf carbon isotope  
398 discrimination during photosynthesis. The carbon isotope composition ( $\delta^{13}\text{C}$ ) of total leaf  
399 organic matter is determined by the carbon isotope composition of  $\text{CO}_2$  in the air ( $\delta^{13}\text{C}_{\text{air}}$ ) and  
400 the  $\text{CO}_2$  concentration in the air ( $C_a$ ) and in the leaf intercellular spaces ( $C_i$ ). Discrimination  
401 processes against  $^{13}\text{CO}_2$  occur during photosynthetic  $\text{CO}_2$  assimilation ( $A$ ) when  $\text{CO}_2$  passes  
402 through the stomata ( $g_s$ ) from the outside air (fractionation factor  $a$ ) and during the  
403 carboxylation process by the Rubisco enzyme inside the chloroplasts (fractionation factor  $b$ ).  
404 The plain arrow represents  $A$  and the dotted arrow represents the transpiration flux.

405

406 **Figure 2:** Comparison of the factors taken into account to calculate the observed trait at plot  
407 level for yield ( $Y_o$ ) and carbon isotope composition ( $F_o$ ). For yield, the observed biomass of  
408 each species  $i$  in the mixture ( $B_{oi}$ ) and the proportion of each species in the mixture ( $p_i$ ) are  
409 taken into account to calculate  $Y_o$ . For carbon isotope composition,  $F_o$  is dependent on the  
410 observed carbon isotope composition of species  $i$  in the mixture ( $\delta^{13}\text{C}_{oi}$ , i.e.  $F_{oi}$ ) and the  
411 corresponding  $\text{CO}_2$  assimilation rate during photosynthesis ( $A_i$ ) representing the species-  
412 specific contribution to plot level carbon isotope composition. Letters on the trees denote  
413 different species.

414

415 **Figure 3:** Application of the adapted method to plot carbon isotope composition ( $\delta^{13}\text{C}_{\text{plot}}$ ).  
416 Net, complementarity and selection effects calculated for  $\delta^{13}\text{C}_{\text{plot}}$  for the different richness  
417 levels. Asterisks denote significant differences from zero for each effect (t-test, \*,  $P < 0.05$ ).

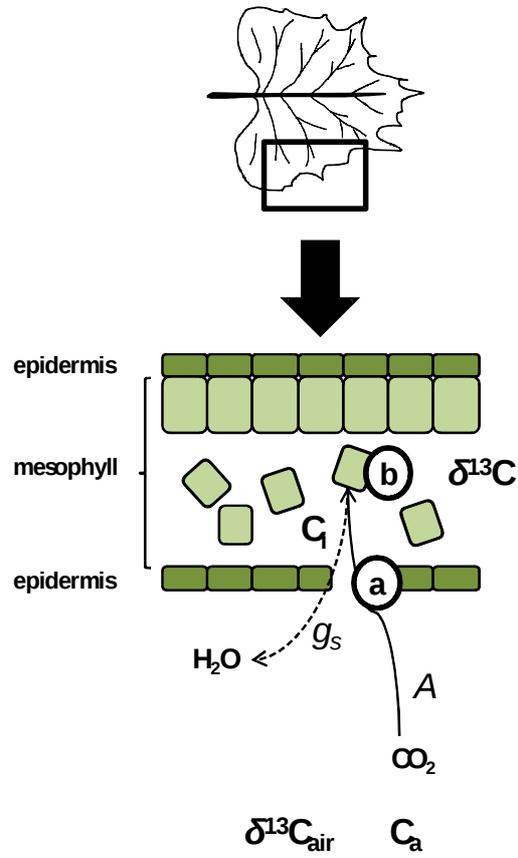
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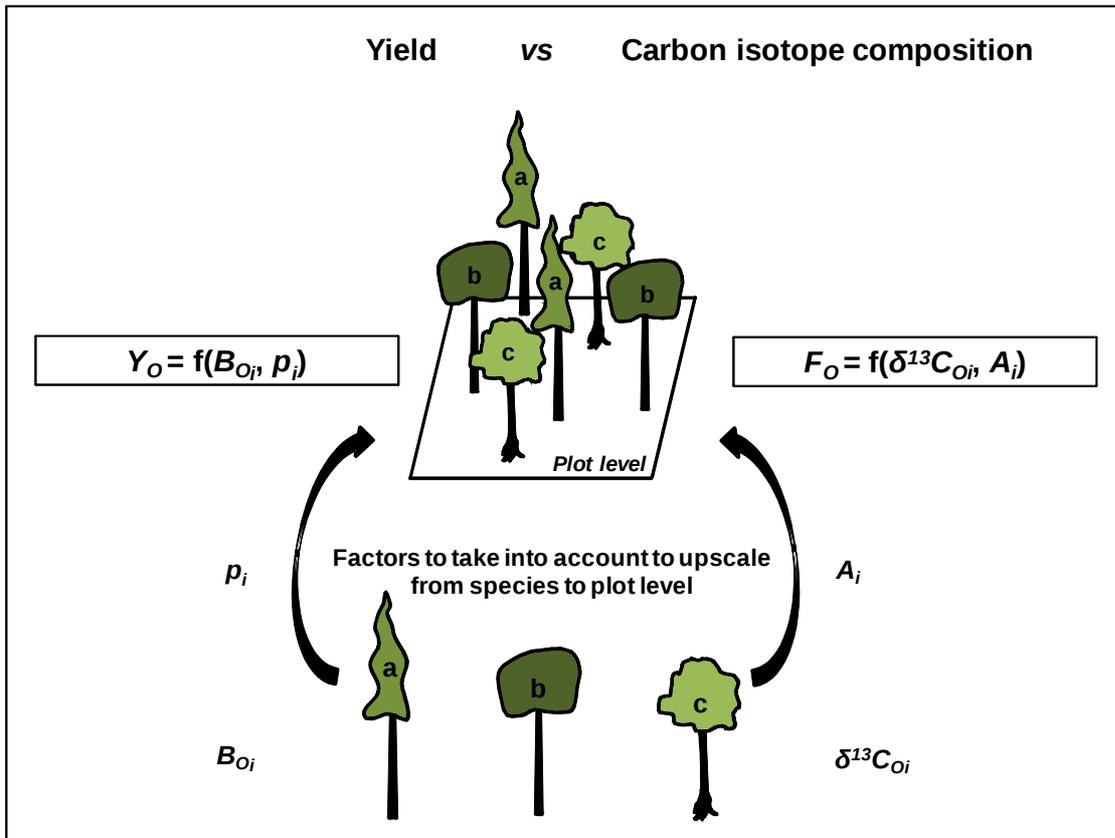
Figure 1

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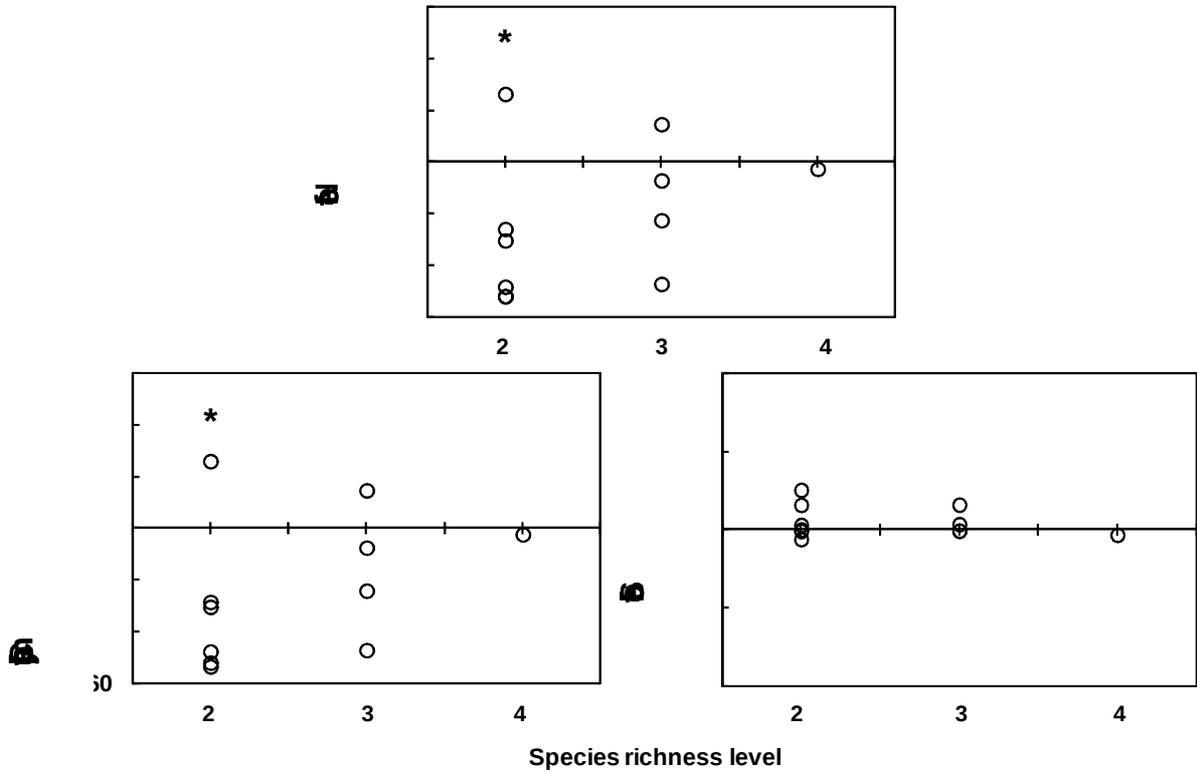
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Figure 2



426  
427

Figure 3



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