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1 **Species choice and N fertilization influence yield gains through complementarity and**  
2 **selection effects in cereal-legume intercrops**

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11 Key words: cereal-legume intercropping, biodiversity effect, complementarity effect, selection effect

12 **Abstract**

13 Maintaining yield when reducing inputs is one prime objective of sustainable agriculture. In this  
14 context, cereal-legume intercropping is a practice that can achieve increased yield under low-input  
15 conditions through the complementary use of abiotic resources and facilitation mechanisms. Many  
16 management options exist to design cereal-legume intercropping systems, among which the choice of  
17 the species intercropped and the level of nitrogen (N) fertilization are essential.

18 In this study, we collected the results of 35 field experiments across Europe of cereal-grain legume  
19 intercrops that combined various intercropped species and N fertilization levels. We first assessed the  
20 intensity of the biodiversity effect and its components in unfertilized intercrops. Then, we focused on a  
21 subset of systems to analyze how N fertilization influenced biodiversity effects on three intercrops  
22 (durum wheat / pea, soft wheat / pea and durum wheat / faba bean). The biodiversity effect represents  
23 the gap between observed and expected yield of a mixture. The complementarity effect is the  
24 performance of mixtures relative to the performance of the component monocultures. The selection  
25 effect captures the extent to which a species with a high monoculture yield dominate a mixture at the  
26 expense of the other intercropped species.

27 Our results confirmed an overall positive biodiversity effect under unfertilized conditions and various  
28 climate conditions ( $0.86 \pm 0.04$  t.ha<sup>-1</sup>). Complementarity effect was the main driver as it represented  
29 76% of the biodiversity effect, confirming intercropping as a useful practice in low-input systems. N  
30 fertilization lowered the complementarity effect in durum wheat / pea intercrops, did not influence these  
31 effects in soft wheat / pea intercrops and increased only the selection effect in durum wheat / faba bean  
32 intercrops. These results highlight the need for a sufficiently competitive legume in intercrops when N  
33 fertilizers are applied in order to avoid too much disruption of plant-plant interactions.

## 34 **Introduction**

35 From 1960-2000, the use of fertilizers, irrigation and pesticides mitigated effects of climatic hazards,  
36 soil heterogeneity and pest pressure, and had a large and positive impact on crop yield (Tilman et al.  
37 2002). More recently, especially in Europe, the growing trend of reducing inputs in agricultural systems,  
38 due to environmental and social concerns, and the climatic uncertainty caused by climate change have  
39 increased the variability in cropping conditions compared to that of the intensive agriculture practiced  
40 in the late 20<sup>th</sup> century. To reduce the negative consequences of climatic uncertainty and continue to  
41 produce enough food while reducing the use of inputs (Sadras and Denison 2016), a promising avenue  
42 is to favor functional complementarity of abiotic resource use and biological regulations between plants  
43 by designing innovative agricultural practices and systems (Duru et al. 2015). This can be achieved by  
44 selecting relevant plant phenotypes (Lynch 2019) and/or using positive biodiversity effects through  
45 plant mixtures, also known as the biodiversity-ecosystem function (BEF) effects (Brooker et al. 2021).

46 Positive BEF effects on ecosystem services have been widely studied in natural communities (Cardinale  
47 et al. 2012), and interest in using them in cropping systems has increased in the past several years (Gurr  
48 et al. 2016; Martin-Guay et al. 2018; Brooker et al. 2021). Analyzing the diversity-productivity  
49 relationship enables the effect of biodiversity on primary production of a given system to be estimated  
50 and can divide it into complementarity and selection effects (Loreau and Hector 2001). The former  
51 measures the effect due to niche complementarity and/or facilitation, while the latter measures the effect  
52 due to the dominance of a given species that fits well with the growth environment. Thus, BEF effects  
53 should be viewed as resulting from particularly positive specific interactions rather than explaining  
54 underlying processes themselves (Maier 2012). As Brooker et al. (2021) highlight, a collaboration gap  
55 between BEF scientists and crop scientists has led to a poor understanding of “the operation of positive  
56 diversity effects in intensive agricultural systems” and thus of how to enhance them.

57 In agricultural systems, plant diversity can be promoted by a range of intercropping practices (i.e.,  
58 combining at least two crop species in the same field for most of their growing periods), which may  
59 improve crop yield (Li et al. 2020a). Several mechanisms can, for example, improve nitrogen (N)  
60 acquisition by the intercrops, including complementary distribution of roots in soil volumes (Postma  
61 and Lynch 2012), use of distinct forms of N in soils (McKane et al. 2002) and fixation of atmospheric  
62 N<sub>2</sub> by one species in the intercrop (Jensen et al. 2020). In a context of input reduction, the use of N<sub>2</sub>-  
63 fixing legumes is particularly promising. In Europe, this has been widely demonstrated in low-input  
64 cereal-legume intercrops, with an increase in total yield and cereal grain quality compared to those of  
65 sole crops (Bedoussac et al. 2015). However, supplying too much N fertilizer can cause the cereal to  
66 dominate the legume, which decreases positive plant-plant interactions in intercropping systems (Pelzer  
67 et al. 2012). Thus, the extent to which N fertilization can be used without compromising BEF effects in  
68 such systems remains unclear. More particularly, while recent meta-analyses and reviews generally  
69 agree upon positive BEF effects when multiple experiments are assessed, the results of individual

70 experiments have high variability (Bedoussac et al. 2015; Gurr et al. 2016; Raseduzzaman and Jensen  
71 2017; Martin-Guay et al. 2018). Few recent studies underline a positive effect on intercrops' yield, via  
72 temporal niche differentiation (Yu et al. 2016; Dong et al. 2018; Li et al. 2020b).

73 In this study, using a database of 35 field experiments (Fig. 1) from five European countries, we first  
74 assessed the intensity of the biodiversity effect in winter and spring cereal-grain legume intercrops  
75 under unfertilized conditions. Then, focusing on a subset of three winter intercrops – durum wheat  
76 (*Triticum turgidum* L.) / pea (*Pisum sativum* L.), soft wheat (*Triticum aestivum* L.) / pea and durum  
77 wheat / faba bean (*Vicia faba* L.) – we tested the influence of two levels of N fertilization (moderate  
78 and high) on the biodiversity effect depending on the intercropped species considered.

79



80

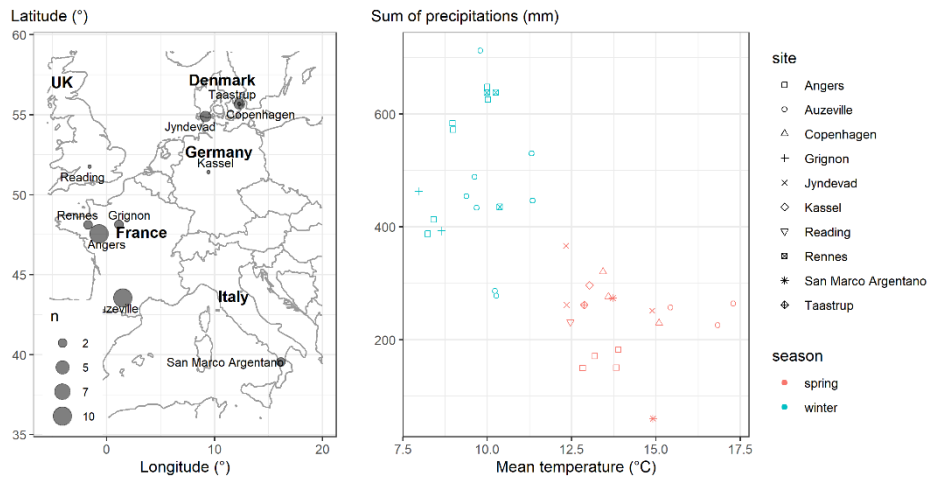
81 Fig. 1. Example of a field experiment of winter wheat / pea intercrops (and their corresponding sole  
82 crops) conducted at the ARVALIS experimental station, near Angers, France (Photograph courtesy of  
83 C. Naudin, ESA, France).

## 84 **Materials and methods**

### 85 **1. Field experiments**

86 To estimate the net biodiversity effect on intercrop productivity in a wide range of environmental  
87 conditions, we collected results from 35 factorial experiments conducted in five countries (France,  
88 Denmark, Italy, Germany, and the United Kingdom; Fig. 2A), as detailed hereafter.

89 We used the following criteria to include set of experiments in our database: (1) grain yield was  
90 measured for both species in sole- and intercropping conditions, (2) different species and genotypes  
91 were used among cereal and legumes, and (3) a given mixture was observed at least in two locations.



92

93 Fig. 2. Location and main climatic features of the experiments. Panel A displays the number of  
 94 experiments conducted at each location (different years and cropping systems). Panel B displays the  
 95 sum of precipitation (mm) as a function of mean temperature (°C) during the crop cycle, with spring  
 96 and winter crops encoded by colors, and experiment location encoded by symbols.

### 97 1.1. Environmental conditions

98 Climate conditions of each experiment were characterized using the following variables retrieved from  
 99 the NASA POWER [API](#): the sum of precipitation (mm) and mean temperature (°C) during the crop  
 100 cycle (from sowing to harvest dates). The experiments were separated into two groups: winter crops,  
 101 which had higher precipitation (280-712 mm) and lower mean temperature (6.8-11.3°C) during the crop  
 102 cycle, and spring crops, which had lower precipitation (60-366 mm) and higher mean temperature (12.3-  
 103 17.3°C) (Fig. 2B).

### 104 1.2. Agricultural management

105 All experiments included cereal-grain legume intercrops of two annual crop species and their  
 106 corresponding sole crops for which grain yield ( $t \cdot ha^{-1}$ ) was measured at harvest. Cereals and legumes  
 107 were each represented by three species: barley (*Hordeum vulgare* L.), durum wheat and soft wheat for  
 108 the cereals and faba bean, lentil (*Lens culinaris* L.) and pea for the legumes (Table 1). In the database,  
 109 39% and 61% of the intercrops were spring or winter crops, respectively. Intercropped species were  
 110 sown and harvested at the same time. The sowing dates ranged from March 11 to May 3 for spring  
 111 crops and from October 25 to December 15 for winter crops. The harvest dates for all crops ranged from  
 112 June 6 to August 23.

113 Table 1. Description of the 35 cereal-legume experiments analyzed in this study. The *Type* column defines if the experiment is carried on conventional (C) or  
 114 organic (O) farming.

<b>Intercropped species (cereal / legume)</b>	<b>Country</b>	<b>Year(s)</b>	<b>Soil water capacity (mm)</b>	<b>Soil texture (clay-silt-sand, %)</b>	<b>Type</b>	<b>N treatments (kg,ha<sup>-1</sup>)</b>	<b>Mixture design</b>	<b>Spatial arrangement</b>	<b>No genotypes (cereal / legume)</b>	<b>Relative density in intercrop (cereal / legume)</b>	<b>References</b>
Spring barley / fababean	Denmark	2001, 2002, 2003	173	24-29-47	O	0	substitutive	within row	2-1	0.5-0.5	(Gaudio et al., 2021; Hauggaard-Nielsen et al., 2008; Knudsen et al., 2004)
		2001, 2002, 2003	119	4-9-87	O	0	substitutive	within row	2-1	0.5-0.5	
Spring barley / pea	Denmark	2001, 2002, 2003	173	24-29-47	O	0	substitutive	within row	2-2	0.5-0.5	(Gaudio et al., 2021)
		2001, 2002, 2003	119	4-9-87	O	0	substitutive	within row	2-2	0.5-0.5	
		2003	173	24-29-47	O	0	substitutive, additive	alternate row	1-1	0.5-0.5, 0.5-1	
		2002	124	6-15-79	C	0	additive	alternate row	1-1	0.33-1	
		2003	124	6-15-79	C	0-130	substitutive, additive	alternate row	1-1	0.5-0.5, 0.5-1	
	France	2003, 2004	94	21-40-39	O	0	substitutive, additive	alternate row	1-1	0.5-0.5, 0.5-1	(Gaudio et al., 2021; Hauggaard-Nielsen et al., 2008, 2009; Launay et al., 2009)
	Germany	2004	176	51-29-20	O	0	substitutive, additive	alternate row	1-1	0.5-0.5, 0.5-1	
	Italy	2003, 2004	169	22-36-42	O	0	substitutive	alternate row	1-1	0.5-0.5	
United Kingdom	2003	142	49-32-19	O	0	substitutive, additive	alternate row	1-1	0.5-0.5, 0.5-1	(Gaudio et al., 2021; Hauggaard-Nielsen et al., 2008, 2009; Launay et al., 2009)	
Spring soft wheat / lentil	France	2015	135	10-8-82	O	0	substitutive, additive	within row	2-4	0.5-1, 0.33-1, 0.3-0.7, 0.17-1	
		2016	187	18-48-34	O	0	substitutive, additive	within row	2-4	0.5-1, 0.33-1.3, 0.33-1, 0.3-0.7, 0.17-1.3, 0.17-1	

Winter durum wheat / fababean	France	2010	187	18-48-34	C	0-60-80-140	substitutive, additive	alternate-, within row	1-1	0.5-0.5, 0.67-0.5, 0.67-1, 0.33-0.5	
		2011	187	18-48-34	C	0	substitutive	alternate row	1-1	0.5-0.5	
		2011	187	18-48-34	C	0-140	substitutive	alternate-, within row	1-1	0.5-0.5	
		2012	135	10-8-82	C	0	substitutive	within row	3-4	0.5-0.5	(Kammoun, 2014)
		2013	187	18-48-34	C	0	substitutive	within row	3-4	0.5-0.5	
Winter durum wheat / pea	France	2006	187	18-48-34	C	0-100-180	substitutive	alternate row	1-1	0.5-0.5	(Bedoussac and Justes, 2010a, 2010b)
		2007	135	10-8-82	C	0-60-80-140	substitutive	alternate row	4-1	0.5-0.5	
		2012	135	10-8-82	C	0	substitutive	within row	3-5	0.5-0.5	(Kammoun, 2014)
		2013	187	18-48-34	C	0-140	substitutive	within row	3-5	0.5-0.5	
		2015	135	10-8-82	C	0	substitutive, additive	within row	1-4	0.5-0.5, 0.5-1	
Winter soft wheat / fababean	France	2018	169	22-36-42	O	0	additive	within row	8-2	0.7-0.75	
Winter soft wheat / pea	France	2010	205	11-54-35	C	0-45-90-140	substitutive, additive	within row	1-1	0.5-0.5, 0.33- 0.66, 0.7-0.5	(Pelzer et al., 2016)
		2017	205	11-54-35	C	0	substitutive, additive	within row	1-2	0.5-0.5, 0.5-1, 0.15-1, 0.05-1	
		2007	83	20-38-42	C	0-30-45	substitutive	within row	1-1	0.5-0.5	(Gaudio et al., 2021; Naudin et al., 2010, 2014)
		2008	83	20-38-42	C	0-30-45-60-90	substitutive	within row	1-1	0.5-0.5	
		2017	197	19-49-32	O	0	additive	within row	8-3	0.5-0.75, 0.5-1	
		2018	169	22-36-42	O	0	additive	within row	8-3	0.5-0.75, 0.5-1	
		2006	94	21-40-39	O	0	substitutive	within row	1-1	0.5-0.5, 0.3-0.7	
		2007	94	21-40-39	O	0-30	substitutive	within row	1-1	0.5-0.5, 0.7-0.3	
		2008	94	21-40-39	O	0-35-72	substitutive	within row	1-1	0.5-0.5, 0.7-0.3	(Gaudio et al., 2021)
		2009	94	21-40-39	O	0-40	substitutive	within row	1-1	0.5-0.5, 0.7-0.3	

116 In the database, 54% of the intercrops were grown in a substitutive design (i.e., the sum of the relative  
117 sowing densities of the two species intercropped equals 1), while 46% were grown in an additive design  
118 (i.e., the sum of relative sowing densities exceeds 1). A species' relative density is its sowing density  
119 in the intercrop relative to that in its reference sole crop. Consequently, the database contained 199 sole  
120 crop experimental units and 307 intercrop experimental units (site x year x mix of genotypes x relative  
121 densities x N treatment), of which 140 were in an additive design and 167 in a substitutive design.  
122 Depending on the experiment, each experimental unit was replicated 2-8 times.

123 Additional details on experimental designs and management practices are reported in the reference  
124 publications of 33 of the 35 experiments (Knudsen et al. 2004; Corre-Hellou et al. 2006; Hauggaard-  
125 Nielsen et al. 2008, 2009; Launay et al. 2009; Bedoussac and Justes 2010a, b; Naudin et al. 2010, 2014;  
126 Pelzer et al. 2016; Tang et al. 2016; Viguier et al. 2018; Gaudio et al. 2021).

127

## 128 **2. Estimating the biodiversity effect on intercrop performance**

129 For each experimental unit, grain yield ( $t \cdot ha^{-1}$ ) was measured for each species. We calculated the  
130 biodiversity effect (BE, Loreau and Hector 2001) as the observed grain yield minus expected grain yield  
131 in intercrops (Eq. 1):

$$132 \quad BE = (YO_C + YO_L) - (YE_C + YE_L) \quad (\text{Eq. 1})$$

133 where  $YO_C$  and  $YO_L$  are the observed yield of the cereal and legume grown in intercrop, respectively,  
134 and  $YE_C$  and  $YE_L$  are the expected yield of the cereal and legume grown in intercrop, respectively.

135 Expected yield was estimated from the yield of the species in sole crop weighted by its scaled relative  
136 density in intercrop (Eq. 2; Li et al. 2020a):

$$137 \quad YE_C = M_C \frac{RD_C}{RD_C + RD_L} \quad \text{and} \quad YE_L = M_L \frac{RD_L}{RD_C + RD_L} \quad (\text{Eq. 2})$$

138 where  $M_C$  and  $M_L$  are the yield of the cereal and legume in sole crop, respectively, and  $RD_C$  and  $RD_L$   
139 are the relative density of the cereal and legume in intercrop, respectively. Grain yield in sole crops and  
140 intercrops is calculated as the mean from each replicate of every experimental units, within each  
141 experiment.

142 As mentioned, the biodiversity effect can be divided into a selection effect (SE, Eq. 3) and a  
143 complementarity effect (CE, Eq. 4) (Loreau and Hector, 2001; Li et al. 2020a):

$$144 \quad SE = \frac{1}{2} \times \left( \left( \frac{YO_C}{M_C} - \frac{RD_C}{RD_C + RD_L} \right) - \left( \frac{YO_L}{M_L} - \frac{RD_L}{RD_C + RD_L} \right) \right) \times (M_C - M_L) \quad (\text{Eq. 3})$$



145 
$$CE = \frac{M_C + M_L}{2} \times \left( \frac{YO_C}{M_C} - \frac{RD_C}{RD_C + RD_L} + \frac{YO_L}{M_L} - \frac{RD_L}{RD_C + RD_L} \right) = M \times (LER - 1) \text{ (Eq. 4)}$$

146 These formulas, used to compute selection and complementarity effects, are only valid in bispecific  
147 mixtures.

148 The first term of Eq. 3 calculates the difference in increase or decrease in yield between the two species  
149 intercropped, while the second term calculates the difference between their sole crop yields. Thus, a  
150 positive selection effect means that the species with the higher yield in sole crop has a higher relative  
151 increase in yield in intercrop (i.e., benefits more from intercropping).

152 Into the equation for the complementarity effect (Eq. 4), we introduced the classic Land Equivalent  
153 Ratio, which is used to calculate land-use efficiency ( $LER = Y_C/M_C + Y_L/M_L$ ; Willey and Rao 1980).

154 Thus, the complementarity effect equals the Land Equivalent Ratio minus 1, multiplied by M, the mean  
155 yield in sole crops.

156

### 157 **3. Experimental design, data processing and analysis**

158 The data were curated and formatted in a database. The data were ordered, reshaped and homogenized  
159 using the collection of R packages *tidyverse* (Wickham et al. 2019).

160 The dataset was unbalanced (i.e., groups had different numbers of observations) because the  
161 experiments collected were conducted for different purposes and examined many factors (e.g., N  
162 fertilization, intercrop design) (Table 1). Thus, the influence of several of the factors on the biodiversity  
163 effect and its components could not be analyzed, especially due to the lack of certain treatments in some  
164 experiments and to the nesting of factors. For example, only 12 of the 35 experiments tested N  
165 fertilization levels, or the species effect also included site and year effects (e.g., spring barley / faba  
166 bean intercrops were grown only in Denmark, so they could not be analyzed properly). The statistical  
167 analysis performed was adjusted in response to this unbalanced structure.

168 We first investigated the overall behavior of mean biodiversity, complementarity and selection effects  
169 within the unfertilized cereal-legume intercrops in the 35 experiments, and the correlation between the  
170 biodiversity effect and each of its components. Thus, our goal was to assess the influence of N  
171 fertilization on the biodiversity effect and its components. N fertilization ranged from 0-180 kg N.ha<sup>-1</sup>,  
172 which we split into three levels: null, moderate (30-80 kg N.ha<sup>-1</sup>) and high (> 80 kg N.ha<sup>-1</sup>). A factorial  
173 design was then defined between the species intercropped and these levels of N fertilization. The subset  
174 of our database with a factorial design of species and N fertilization levels corresponded to three  
175 intercrops: durum wheat / pea, soft wheat / pea and durum wheat / faba bean (70 experimental units,  
176 among which 62 are in substitutive design, all located in France, Table 1). Durum wheat / pea and

177 durum wheat / faba bean intercrops were grown in experiments with moderate and high levels of N  
178 fertilization, while soft wheat / pea intercrops were grown only with a moderate level of N fertilization.

179 The effect of N fertilization on the biodiversity effect and its components in intercrops was assessed  
180 using the Bayesian approach. Bayesian inference is based on reallocating credible values for a parameter  
181 (posterior distribution) given prior knowledge (prior distribution) and the adequacy of the data to the  
182 model (likelihood). The Bayesian approach provides information about the probability of a hypothesis  
183 being true given the data ( $P(\text{hypothesis}|\text{data})$ ). Bayesian estimation for the difference in group means  
184 (Kruschke 2018) is an alternative to the classic Student's  $t$  test to compare the means of two groups.  
185 This method calculates a posterior distribution for the mean differences between the two groups and  
186 derives a 95% highest density interval (HDI), which is defined as the 95% most credible values of the  
187 parameter. We performed Bayesian estimation for the difference in mean values of components of the  
188 biodiversity effect between N-fertilized (moderate and high) and unfertilized treatments for each of the  
189 three intercrops. The null hypothesis ( $H_0$ ) was defined as equal mean biodiversity effect components  
190 for N-fertilized and unfertilized intercrops. We applied the following decision rule to the position of the  
191 95% HDI: reject  $H_0$  if the 95% HDI excludes 0 but do not reject  $H_0$  if it includes 0.

192 All indicator calculations and statistical analyses were performed with R software, v. 4.0.0 (R Core  
193 Team 2020). Bayesian statistical analyses were performed using the R package *BEST* (Kruschke and  
194 Meredith 2020).

#### 195 **4. Definition of references for fertilized legumes**

196 A common assumption when calculating indicators to compare the performance of intercrops to that of  
197 sole crops is that N is not a limiting resource for legumes and does not influence their yield (e.g., Pelzer  
198 et al. 2012). To test this hypothesis, we performed Bayesian estimation for the difference in group means  
199 between N-fertilized and unfertilized legume sole crops. The database contained only three experiments  
200 (i.e., 11 experimental units) in which legume sole crops were N-fertilized, because the experiments we  
201 collected were designed to conform to agronomic practices of farmers, who rarely fertilize legume sole  
202 crops (Magrini et al. 2016). The Bayesian estimation confirmed that N fertilization had no significant  
203 influence on the yield of legume sole crops. Given this result and the lack of data on N-fertilized legume  
204 sole crops, we used the unfertilized legume sole crops as a reference when calculating the biodiversity  
205 effect and its components in all experimental units.

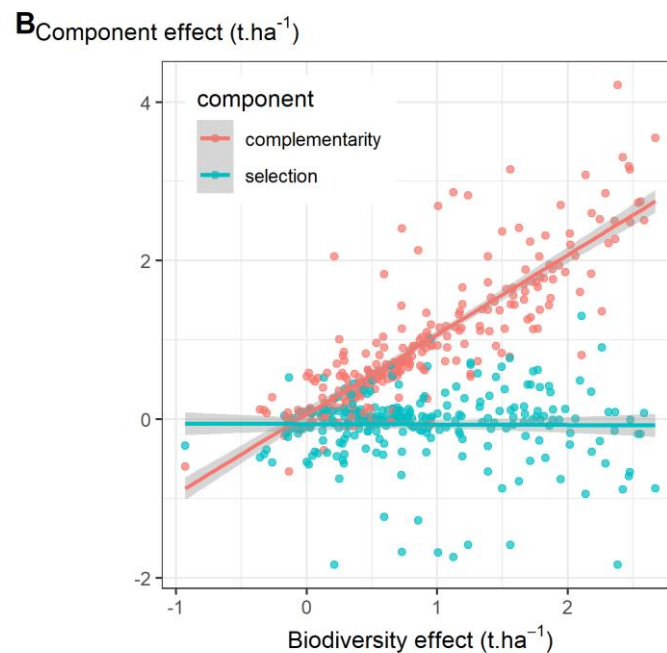
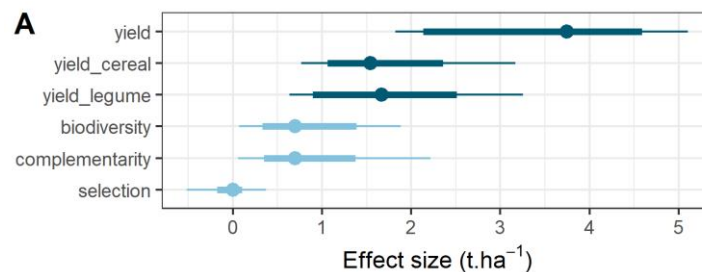
206

## 207 **Results and discussion**

208 **1. Distribution of the biodiversity effect and its components in unfertilized intercrops**

209 On the whole dataset, the mean ( $\pm 1$  standard error) yield gain in unfertilized intercrops equaled  $0.86 \pm$   
210  $0.04 \text{ t.ha}^{-1}$  ( $1.04 \pm 0.01 \text{ t.ha}^{-1}$  for additive designs and  $0.68 \pm 0.00 \text{ t.ha}^{-1}$  for substitutive designs) for a  
211 mean total intercrop yield of  $3.54 \pm 0.08 \text{ t.ha}^{-1}$  (Fig. 3A). These results highlight an increase in the yield  
212 of cereal-legume intercrops in most experimental units under unfertilized conditions compared to those  
213 of the corresponding sole crops, which agrees with results of several studies (Pelzer et al. 2012, 2014;  
214 Yu et al. 2016) and confirms the ability of intercropping to increase grain yield in low-input farming  
215 systems (Bedoussac et al. 2015).

216 However, the increase in yield observed was influenced by the cropping conditions used as references  
217 to calculate the biodiversity effect. The unfertilized cereal sole crops used as references had lower grain  
218 yield ( $3.2 \pm 0.08 \text{ t.ha}^{-1}$ , all cereals pooled) than cereals grown under conventional farming conditions,  
219 which are always N fertilized (i.e., a mean grain yield of  $6.1 \text{ t.ha}^{-1}$  for the cereals of interest in the five  
220 European countries considered for the period covered by the experiments (Food and Agriculture  
221 Organization of the United Nations; <http://faostat.fao.org/>). Thus, the low yield observed for the  
222 unfertilized cereal sole crops contributed greatly to the positive biodiversity effect estimated (Garnier  
223 et al. 1997).



225 Fig. 3. **(A)** Distribution of unfertilized cereal-legume intercrop yield and biodiversity effect ( $\text{t}\cdot\text{ha}^{-1}$ ).  
226 Points represent the median, broad lines represent the interquartile range, and thin lines represent the  
227 [0.1, 0.9] quantile interval. **(B)** Correlation between biodiversity effect ( $\text{t}\cdot\text{ha}^{-1}$ ) and complementarity  
228 effect ( $\text{t}\cdot\text{ha}^{-1}$ ) or selection effect ( $\text{t}\cdot\text{ha}^{-1}$ ) in unfertilized cereal-legume intercrops. Grey zones represent  
229 the 95% confidence interval for the linear regressions. Data used: whole dataset ( $n = 263$ )

230

231 The biodiversity effect was strongly and positively correlated with the complementarity effect ( $r = 0.86$ ,  
232  $p < 10^{-15}$ ), but it was not correlated with the selection effect ( $r = -0.01$ ,  $p = 0.87$ ) (Fig. 3B). Thus, the  
233 complementarity effect was the main driver of the yield gain in unfertilized cereal-legume intercrops,  
234 meaning that positive plant-plant interactions (i.e., facilitation and / or niche complementarity) rather  
235 than the dominance of one of the species increased intercrop yields (Pelzer et al. 2012). However,  
236 caution is needed when distinguishing complementarity causes (e.g., niche partitioning, facilitation) of  
237 the resulting complementarity effect (Barry et al. 2019). To quantify the relative importance of these  
238 processes, specific measurements would be needed, such as symbiotic  $\text{N}_2$  fixation to reflect differences  
239 in N use between cereals and legumes, or a lodging score to quantify mechanical facilitation (e.g.,  
240 Podgórska-Lesiak and Sobkowicz 2013). As Brooker et al. (2021) highlight, explicitly distinguishing  
241 facilitation and niche partitioning would help when applying new analytical and conceptual frameworks  
242 to design intercrops. Nevertheless, differences in N use in cereal-legume intercrops is a well-known  
243 process in which the more competitive cereal usually takes disproportionately more soil mineral N than  
244 the legume, which is forced to compensate by increasing symbiotic  $\text{N}_2$  fixation (Rodriguez et al. 2020).  
245 In a low-input context, this complementarity of N use enables cereals in intercrops to have higher grain  
246 yield and quality than cereals in sole crops.

247 The complementarity effect contributed 76% of the biodiversity effect when the latter was positive (i.e.,  
248 in 94% of the experimental units), but it contributed only 36% when the latter was negative (i.e., in 6%  
249 of the experimental units). In the few cases in which we observed a yield loss in intercrops, the relative  
250 contributions of complementarity and selection were reversed:  $-0.05 \pm 0.02$  and  $-0.16 \pm 0.02 \text{ t}\cdot\text{ha}^{-1}$ ,  
251 respectively. In these cases, the total yield of intercrops were lower than those of corresponding sole  
252 crops because the competition between cereals and legumes exceeded the complementarity effect (also  
253 reported by Pelzer et al. (2016) for soft wheat / pea intercrops and Baxevanos et al. (2017) for oat / pea  
254 intercrops).

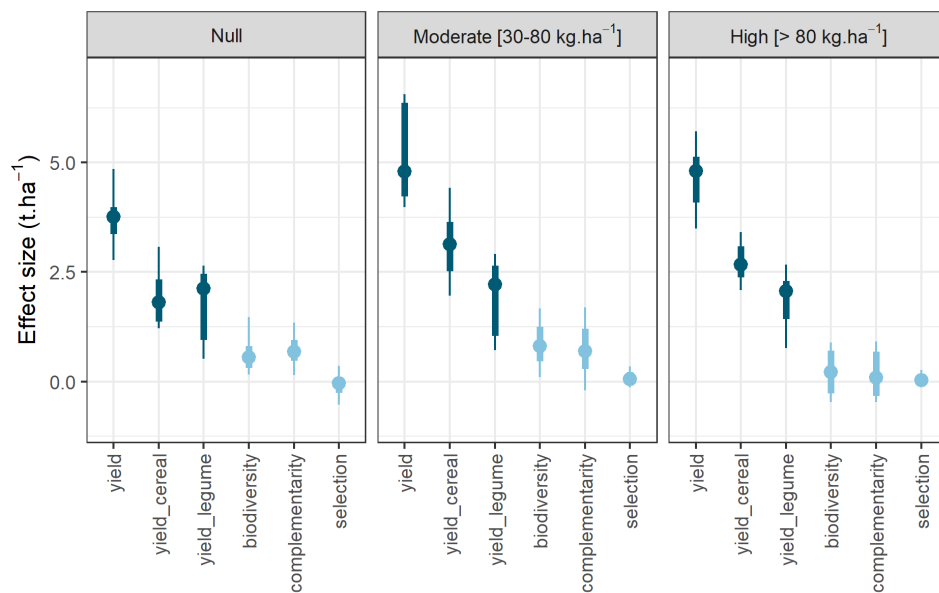
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256

## 257 **2. Influence of N fertilization on the biodiversity effect and its components**

258 The biodiversity effect and its components were altered by N fertilization, which is a key practice in  
259 agricultural systems. While the biodiversity effect was positive in 100% of the unfertilized experimental  
260 units of the data subset considered (i.e., factorial designs of species and N fertilization levels), the

261 percentage of experimental units with a positive biodiversity effect decreased with N fertilization (i.e.,  
 262 92% and 67% of the experimental units under moderately and highly N-fertilized conditions,  
 263 respectively) (Fig. 4). Overall, the total intercrop yield increased with N fertilization ( $4.16 \pm 0.18$ ,  $5.09$   
 264  $\pm 0.24$  and  $4.62 \pm 0.21$  t.ha<sup>-1</sup> under unfertilized, moderately and highly N-fertilized conditions  
 265 respectively); specifically, mean grain yield decreased for legumes ( $2.23 \pm 0.12$ ,  $1.88 \pm 0.19$  and  $1.84$   
 266  $\pm 0.16$  t.ha<sup>-1</sup> under unfertilized, moderately and highly N-fertilized conditions respectively) but  
 267 increased for cereals ( $1.93 \pm 0.20$ ,  $3.21 \pm 0.23$  and  $2.78 \pm 0.15$  t.ha<sup>-1</sup> under unfertilized, moderately and  
 268 highly N-fertilized conditions respectively) with N fertilization (Fig. 4). The same pattern was observed  
 269 for the complementarity effect, which was positive in 96%, 83% and 56% of the experimental units  
 270 under unfertilized, moderately and highly N-fertilized conditions, respectively. Conversely, the  
 271 percentage of experimental units with a positive selection effect increased with N fertilization: 25%,  
 272 71% and 61% of the experimental units, under unfertilized, moderately and highly N-fertilized  
 273 conditions, respectively. Thus, N fertilization tends to decrease positive plant-plant interactions within  
 274 cereal-legume intercrops by acting on the balance between the two intercropped species to the benefit  
 275 of the cereal (Pelzer et al. 2012).  
 276



277  
 278 Fig. 4. Distribution of cereal-legume intercrop yield, cereal and legume yield (t.ha<sup>-1</sup>) and the biodiversity  
 279 effect (t.ha<sup>-1</sup>) as a function of nitrogen fertilization level. Points represent the median, broad lines  
 280 represent the interquartile range, and thin lines represent the [0.1, 0.9] quantile interval. Data used:  
 281 Experiments with a factorial design of species and N fertilization levels (n = 82)

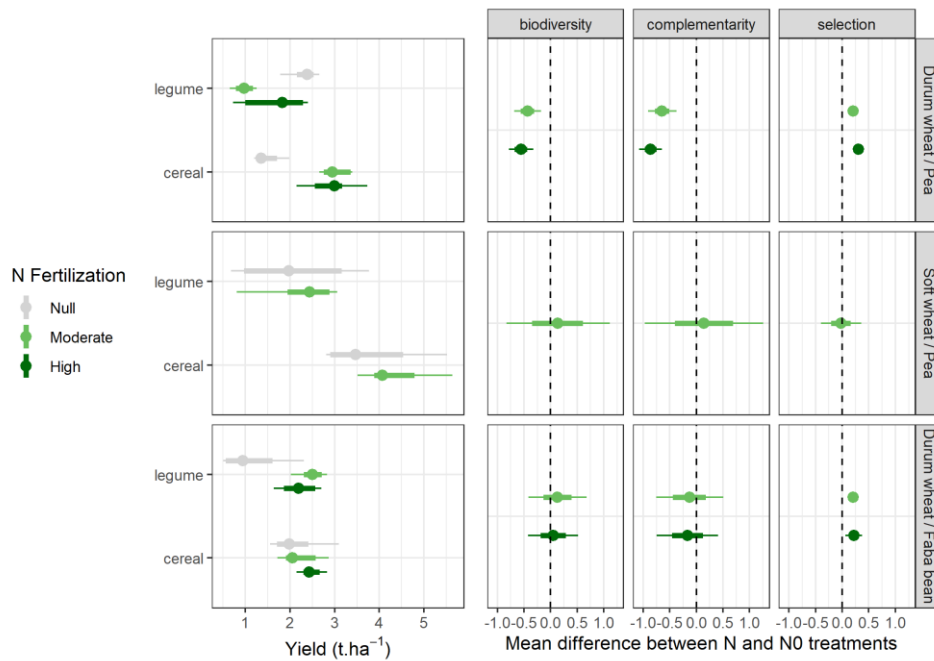
282  
 283 The effect of N fertilization on the biodiversity effect and its components depended on the species  
 284 intercropped (Fig. 5). In durum wheat / pea intercrops, even moderate N fertilization decreased the  
 285 biodiversity effect significantly by 66% compared to that under unfertilized conditions. This moderate

286 N fertilization increased the selection effect significantly by 0.21 t.ha<sup>-1</sup> (99.1% of the posterior values  
287 for the difference in group means between N-fertilized and unfertilized conditions were positive), while  
288 the complementarity effect decreased by 0.65 t.ha<sup>-1</sup> (99.1% of the posterior values for the difference in  
289 means were negative). These effects were emphasized under highly N-fertilized conditions (Fig. 5).  
290 When focusing on the yield of both species intercropped, N fertilization disadvantaged the legume,  
291 since pea yield decreased by a mean of 37% under N-fertilized conditions compared to that under  
292 unfertilized conditions, while the opposite was observed for durum wheat, whose yield increased by a  
293 mean of 94%. These results could explain the shift in complementarity and selection effects for durum  
294 wheat / pea intercrops between N-fertilized and unfertilized conditions. This behavior is usually  
295 highlighted in existing literature related to cereal-legume intercrops (e.g., Naudin et al. 2010). Under  
296 N-fertilized conditions, selection effect increases because durum wheat has a competitive advantage  
297 over the legume (Mariotti et al. 2009; Duchene et al. 2017). Our results showed, however, that choosing  
298 a different cereal or legume species can change this effect.

299 When soft wheat replaced durum wheat in wheat / pea intercrops, N fertilization did not influence the  
300 biodiversity effect or its components (Fig. 5). Because the cereal and legume yields tended to increase  
301 slightly with N fertilization, the latter did not disrupt the balance between the two species (Table 2).  
302 Based on the soil and climate conditions considered, the level of N fertilization (45 kg N.ha<sup>-1</sup>) was  
303 probably too low, compared to usual N fertilization rates in conventional agriculture, to increase the  
304 yield of one or both species significantly, unlike that of durum wheat / pea intercrops (60-140 kg N.ha<sup>-1</sup>).  
305

306 Finally, in durum wheat / faba bean intercrops, N fertilization did not influence the biodiversity effect  
307 or its complementarity effect, but it did increase the selection effect significantly by 0.3 t.ha<sup>-1</sup> and 0.2  
308 t.ha<sup>-1</sup> under moderately and highly N-fertilized conditions, respectively (95.5% and 95.2% of posterior  
309 values for the difference in group means were positive, respectively) (Fig. 5). This increase was due to  
310 an increase in durum wheat yield, since faba bean yield changed little in intercrops as N fertilization  
311 increased. This behavior contrasts with that of pea yield when intercropped with durum wheat: pea yield  
312 decreased as N fertilization increased. Height and biomass differences between two intercropped  
313 species have been shown to influence their yields (Gaudio et al. 2021). Since the faba bean is taller and  
314 larger than the pea (Guinet et al. 2018), it showed greater competitive ability (but whether aboveground  
315 for light capture or belowground for nutrient and water acquisition remains to be tested), which explains  
316 the lack of shift in the biodiversity effect observed in durum wheat / faba bean intercrops.

317



318

319 Fig. 5. Distribution of cereal and legume yields ( $\text{t.ha}^{-1}$ ) in three cereal-grain legume intercrops (durum  
 320 wheat / pea, soft wheat / pea and durum wheat / faba bean) as a function of nitrogen (N) fertilization  
 321 level: null, moderate ( $30\text{-}80 \text{ kg N.ha}^{-1}$ ) and high ( $> 80 \text{ kg N.ha}^{-1}$ ). For the three intercrops, posterior  
 322 distributions of the difference in mean of the biodiversity effect between the two N-fertilized (moderate  
 323 and high) and unfertilized (N0) treatments is illustrated ( $\text{t.ha}^{-1}$ ), with dashed lines representing the null  
 324 value of the posterior difference in means. Points represent the median, broad lines represent the  
 325 interquartile range, and thin lines represent the [0.1, 0.9] quantile interval. Data used: Experiments with  
 326 a factorial design of species and N fertilization levels ( $n = 82$ ).

327

328

329

### 330 3. Pathway to applications

331 Because cereal-legume intercrops are used mainly to decrease the use of agricultural inputs, most are  
 332 managed without synthetic inputs. In this way, our study confirmed an increase in productivity under a  
 333 wide range of unfertilized cropping conditions, with a balance between the two species intercropped  
 334 (i.e., no species clearly dominated), although the increase depends on the species intercropped (Cheriere  
 335 et al. 2020). N fertilization can disrupt this balance, shifting positive plant-plant interactions to a  
 336 dominance of the cereal at the expense of the legume (e.g., in durum wheat / pea intercrops). This shift  
 337 appeared at moderate N fertilization levels and even led to lower productivity of intercrops than that of  
 338 sole crops at the high N fertilization levels applied to wheat sole crops in conventional agriculture ( $>$   
 339  $100 \text{ kg N.ha}^{-1}$ ).

340 It would thus be interesting to identify the level of moderate N fertilization that provides benefits from  
341 positive effects of intercropping and positive plant-plant interactions, while increasing the total yield  
342 by increasing the cereal yield, as farmers often perform in winter intercrops (Verret et al. 2020). Because  
343 this N level is likely to differ among species, future research should focus on the interaction between N  
344 fertilization and the intercrop species chosen. For instance, recent meta-analysis (Li et al. 2020b) shows  
345 high advantages of N fertilization on mixtures including maize (*Zea mays* L.).

346 In our study, only one combination of species x N fertilization had a positive interaction on yield (i.e.,  
347 durum wheat / faba bean intercrops): cereal yield increased and legume yield remained the same, while  
348 in durum wheat / pea intercrops, legume yield decreased. Thus, our results suggest that the legume  
349 chosen can be a management mechanism, with the idea that the legume should be sufficiently  
350 competitive to counterbalance the increased competition from the N-fertilized cereal (Duchene et al.  
351 2017). Probably, it is the balance of competition between the two components rather than  
352 competitiveness of the legume that matters. However, we also observed that the cereal yield stagnated  
353 if the N fertilization level was not sufficient (e.g., soft wheat / pea intercrops). Thus, the optimal N  
354 fertilization level should depend on the proportion of legume biomass in the intercrop (Naudin et al.  
355 2010). As highlighted by other studies, the species chosen are a relevant mechanism for controlling  
356 intercrops' yield (Cheriere et al. 2020) and suitability for the cropping environment in which they grow  
357 (Baxevanos et al. 2017). Finally, it is worthwhile to recall that many barriers to adoption of intercrops  
358 in Europe exist, beyond the scope of this article, such as. technical and economical ones (Bonke et al.  
359 2020). Different possibilities (e.g., better communication of scientific results, breeding adapted to  
360 intercrops) exist to overcome these barriers (Meynard et al. 2018) and allow intercrops to be more  
361 widely cultivated.

## 362 **Conclusion**

363 This study highlights that the complementarity between intercropped species is the main driver of the  
364 positive biodiversity effect on the performance of cereal-legume intercrops under diverse cropping  
365 conditions. If the biodiversity effect depended instead mainly on the selection effect (i.e., if one  
366 intercropped species strongly dominated), growing the dominant species alone would be more practical  
367 agronomically, which would shift the balance towards sole crops.

368 While multiple meta-analyses and reviews highlighted the overall yield gain in intercrops, analysis and  
369 tools to derive specific management recommendations for farmers from this general knowledge are still  
370 lacking (Brooker et al. 2021). We argue that it may be counterproductive to emphasize that biodiversity  
371 has this broad beneficial effect while the specific positive interactions between pairs of species and even  
372 more so, cultivars, remain to be identified (Maier 2012).

373 The key question remains how to secure complementarity while intensifying or increasing productivity.  
374 When focusing on the response of complementarity processes to N fertilization, we found that behavior



375 differed depending on the species chosen. We highlighted that N fertilization does not always depress  
376 complementarity processes as long as the legume species can also benefit from it. Therefore, such shifts  
377 in balance need to be understood through the prism of community ecology to develop the use of  
378 intercrops in a wider range of agricultural systems besides low-input agriculture.

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- 390 • Conflicts of interest/Competing interests (include appropriate disclosures): The authors declare that  
391 they have no conflict of interest
- 392 • Ethics approval (include appropriate approvals or waivers): the study was performed in accordance  
393 with the ethical standards as laid down in the 1964 Declaration of Helsinki and its later amendments  
394 or comparable ethical standards
- 395 • Consent to participate (include appropriate statements): not appropriate
- 396 • Consent for publication (include appropriate statements): not appropriate
- 397 • Availability of data and material (data transparency): the datasets generated during and/or analyzed  
398 during the current study are available from the corresponding author on reasonable request.
- 399 • Code availability (software application or custom code): not applicable
- 400 • Authors' contributions (include appropriate statements): “Funding acquisition: PC, NH, NG; data  
401 collection and formatting: NG, RM, PC; data analysis: RM, NH; writing original draft: RM, NG,  
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403

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