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Agriculture intensification reduces plant taxonomic and functional diversity across European arable systems

Carmona, C. P., Guerrero, I., Peco, B., Morales, M. B., Oñate, J. J., Pärt, T., Tschardtke, T., Liira, J., Aavik, T., Emmerson, M., Berendse, F., Ceryngier, P., Bretagnolle, V., Weisser, W. W., & Bengtsson, J. (2020). Agriculture intensification reduces plant taxonomic and functional diversity across European arable systems. *Functional Ecology*, 34(7), 1448-1460. <https://doi.org/10.1111/1365-2435.13608>

Published in:
Functional Ecology

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
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1 **Agriculture intensification reduces plant taxonomic and functional diversity across European**
2 **arable systems.**

3 **Running headline:** Intensification reduces plant diversity

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31 **Acknowledgements**

32 We thank the European Science Foundation and the connected national science foundations for
33 funding the presented study through the Eurodiversity AGRIPOPEs programme. Financial support
34 was provided by the Estonian Research Council (projects PSG293, MOBJD13 and IUT 20-31), the
35 European Union through the European Regional Development Fund (Centre of Excellence
36 EcolChange), the Spanish MINECO (project CGL2014-53789-R, IJCI-2016-30516), and the Madrid
37 Regional Government (projects REMEDINAL-3 and Remedinal TE). The study has been supported
38 by the TRY initiative on plant traits (<http://www.try-db.org>). The TRY initiative and database is
39 hosted, developed and maintained by J. Kattge and G. Bönisch (Max Planck Institute for
40 Biogeochemistry for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Jena, Germany).
41 TRY is currently supported by DIVERSITAS/Future Earth and the German Centre.

42 43 **Authors' contributions**

44 CPC, IG, BP, MBM and JO conceived and initiated the study; MBM, JO, IG, TP, TT, JL, TA, ME,
45 FB, PC, VB, WW and JB coordinated data collection from their study regions and/or directly
46 collected data; CPC analysed the data; CPC, IG, BP, MBM and JO and wrote the paper, with inputs
47 from all authors.

48 **Data availability statement**

49 Data will be deposited in Dryad upon acceptance of the manuscript.

1 **Agricultural intensification reduces plant taxonomic and functional diversity across**
2 **European arable systems.**

3
4 **Abstract**

- 5 1. Agricultural intensification is one of the main drivers of species loss worldwide, but
6 there is still a lack of information about its effect on functional diversity of arable
7 weed communities.
- 8 2. Using a large scale pan European study including 786 fields within 261 farms from
9 eight countries, we analysed differences in the taxonomic and functional diversity of
10 arable weeds assemblages across different levels of agricultural intensification. We
11 estimated weed species frequency in each field, and collected species' traits
12 (vegetative height, specific leaf area and seed mass) from the TRY plant trait
13 database. With this information we estimated taxonomic (species richness), functional
14 composition (community weighted means) and functional diversity (functional
15 richness, evenness, divergence and redundancy). We used indicators of agricultural
16 management intensity at the individual field scale (e.g. yield, inputs of nitrogen
17 fertilizer and herbicides, frequency of mechanical weed control practices) and at the
18 landscape scale surrounding the field (i.e. number of crop types, mean field size and
19 proportion of arable land cover within a radius of 500m from the sampling points).
- 20 3. The effects of agricultural intensification on species and functional richness at the
21 field scale were stronger than those of intensification at the landscape scale, and we
22 did not observe evidence of interacting effects between the two scales. Overall,
23 assemblages in more intensified areas had fewer species, a higher prevalence of
24 species with ruderal strategies (low stature, high leaf area, light seeds), and lower
25 functional redundancy.
- 26 4. Maintaining the diversity of Europe's arable weed communities requires some simple
27 management interventions, for example, reducing the high intensity of field-level
28 agricultural management across Europe, which could be complemented by
29 interventions that increase landscape complexity.

30 **Keywords:** agricultural intensification; arable plants; functional diversity; landscape;
31 dispersal; species richness; weeds

32 **Introduction**

33 Agriculture is the most widespread land use in Europe, occupying roughly 40% of total land
34 area of the EU-28 (Eurostat, 2018) and harbouring a large part of the continent's biodiversity
35 (Emmerson et al., 2016). Intensification of agricultural management over recent decades has
36 substantially increased crop yields, but the associated environmental costs have been a
37 significant cause for concern for some time (Chamberlain, Fuller, Bunce, Duckworth, &
38 Shrubbs, 2000; Matson, Parton, Power, & Swift, 1997). Consequently, land use change and
39 agricultural intensification are the principal drivers of species loss worldwide (Green,
40 Cornell, Scharlemann, & Balmford, 2005; Tilman et al., 2001). Agricultural intensification
41 can also affect which species are present in assemblages depending on their traits, therefore
42 changing functional diversity (Cadotte, Carscadden, & Mirotchnick, 2011; Flynn et al.,
43 2009). The loss of diversity can in turn affect the structure and functioning of ecosystems,
44 potentially threatening the provision of ecosystem services that sustain our livelihoods (de
45 Bello et al., 2010; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). In this
46 context, arable weeds are particularly important for ecosystem services delivered by pest
47 control agents or pollinators (Brooks et al., 2012; Ebeling, Klein, Weisser, & Tscharntke,
48 2012; Scherber et al., 2010), providing the resource base in trophic and mutualistic networks
49 in arable systems. As a result, they determine to a high degree the diversity and composition
50 of the associated biota, i.e. insects, birds, and mammals (Butler et al., 2010; Eraud et al.,
51 2015; Evans, Pocock, Brooks, & Memmott, 2011).

52 Increases in yields in agricultural production associated with intensification result from
53 changes occurring at two main scales (Emmerson et al., 2016): (i) at the level of the
54 individual field (where practices such as use of high-yielding crop varieties, mechanization,
55 irrigation, and pesticide and fertilizer application directly affect plant communities) (Donald,
56 Sanderson, Burfield, & van Bommel, 2006; Geiger et al., 2010); and (ii) at the level of the
57 surrounding landscape (processes that lead to smaller species pools and less connectivity,
58 reducing colonization probability) (Sirami et al., 2019; Tscharntke et al., 2012). Different
59 taxonomic groups are likely to respond to different scales of intensification, because species
60 vary in many ways, including mobility, range size, dispersal ability and sensitivity to
61 agricultural disturbance activities (Billeter et al., 2007a). For example, plant diversity can
62 respond more to local management than to landscape complexity (Aavik & Liira, 2010;
63 Guerrero, Carmona, Morales, Oñate, & Peco, 2014), while the opposite can occur for mobile
64 vertebrates (Gonthier et al., 2014).

65 Despite their adaptations to the particular selection pressures in agricultural fields
66 (Sutherland, 2004), the diversity of arable weeds has been strongly affected by
67 intensification. The effects of intensification on arable weeds are most noticeable at the
68 individual field scale, where a range of management practices focus on reducing their
69 presence and potential impacts on crop yield (Emmerson et al., 2016; Storkey, Meyer, Still,
70 & Leuschner, 2012). The effectiveness of some of these actions has been called into question,
71 since they are more effective at removing rare plant species than at reducing the densities of
72 competitively dominant and abundant ones (Petit et al., 2016). Here, landscape complexity
73 can play a significant role in maintaining species diversity in arable fields, providing an
74 abundant source of seeds from ruderal habitats and field edges (Gabriel, Thies, & Tschardtke,
75 2005). Beyond reducing species richness, management intensity does not affect all arable
76 weed species in the same way. Some species with specific traits or trait combinations are
77 better able to cope with high management intensities (Guerrero et al., 2014). Previous studies
78 have shown lower diversity of functional traits in arable weed assemblages from more
79 intensively managed fields, suggesting that intensification is associated to biotic
80 homogenization (Guerrero et al., 2014; Hevia et al., 2016). This biotic homogenization is
81 further compounded by the loss of functional redundancy along the intensity gradient, with
82 more intensified areas hosting assemblages that are more vulnerable to species losses
83 (Carmona, Guerrero, Morales, Oñate, & Peco, 2017).

84 Differences in climatic conditions and the size and composition of species pools can
85 further complicate the study of intensification effects on diversity. Species identity,
86 community composition, trophic complexity and trait diversity might all differ
87 biogeographically and therefore the effects of agricultural management intensity might differ
88 across biogeographical regions. Despite the urgent need for regional- and landscape-scale
89 (large scale) studies that encompass a larger variety of conditions, most of our understanding
90 about the effects of agricultural management intensity on plant diversity comes from studies
91 performed at field scales (local scales). The few studies analysing the effects of land use
92 change at continental or global scales come from meta-analyses that do not focus exclusively
93 on agricultural management intensity, rather they provide insights from a synthesis of studies
94 with a variety of experimental designs (Laliberté et al., 2010; Martin et al., 2019). In this
95 sense, coordinated efforts across different countries with common sampling methods are
96 much needed, providing important details of the effects of agricultural intensification on
97 taxonomic and functional diversity (Emmerson et al., 2016).

98 In this paper, we examine the effects of agricultural intensification, at the local field and
99 landscape level (in a radius of 500 m), on the diversity of arable weeds assemblages in fields
100 of cereal-dominated agroecosystems. We analyse a large-scale dataset originally collected
101 using standardized methods (see Emmerson et al., 2016 for a detailed description of the
102 project), and including nine study areas from eight European countries providing strong
103 gradients in agricultural intensity and environment both within- and between-regions. Within
104 these regions we selected fields that differ in the values of agricultural management variables
105 that are commonly used as proxies for agricultural intensification. This space-by-time
106 substitution enabled a characterisation of differences in the impacts of intensification on local
107 diversity between biogeographical regions. In the present study, we aim to (1) identify the
108 relevant scale (individual field or landscape scale) at which agricultural intensification is
109 most strongly associated with local arable weeds diversity; (2) evaluate whether taxonomic
110 and functional diversity respond in similar ways to intensification; (3) investigate how
111 intensification promotes certain functional trait values, leading to changes in the functional
112 diversity and composition of assemblages; and (4) characterize the type of arable weeds
113 communities favoured by current intensification trends.

114

115 **Material and Methods**

116 *Study areas, farms and fields*

117 Fieldwork was performed in cereal farms in nine study areas (Sweden, Estonia, Poland,
118 eastern and western Germany, the Netherlands, Ireland, France and Spain). In each study
119 area, 30 farms separated by at least one km were selected, and considered to be representative
120 of a gradient of regional agricultural intensification. Given the diversity of agricultural
121 management practices and the scale of management units in the different countries involved
122 in the study, individual farms were considered the ecological unit under study, and for the
123 purposes of the study each was recognised as a set of one or more fields, separated by a
124 distance of not more than 1 km, which were cultivated by the same farmer (owned or leased),
125 and occupying an area not exceeding 1 km². These farms were situated in regions between 30
126 x 30 and 50 x 50 km² in area, in order to limit within-region variation in the size of species
127 pools and β -diversity, and to avoid an excessive heterogeneity of landscapes and soil types
128 within each study area. Farms were selected so that the range of cereal productivity in the
129 sample was as large as possible, based on information obtained from the farmers on cereal

130 yields in the 3 years preceding the study, and with a representative and even distribution
131 across the gradient of productivity in each area. Only cereal crops were sampled on each farm
132 (mainly winter wheat: 80% of the fields; if wheat was not available on the farm, winter barely
133 was used). Sampled fields were never smaller than 1 ha in size nor irrigated. Sampling took
134 place from June to July 2007, and was synchronized using the phenological stages of winter
135 wheat in each study area (i.e. always during the flowering to milk ripening period within
136 each study area). To further avoid phenological effects, the sequence of farm sampling was
137 randomized over the yield gradient within each study area.

138 For each farm, five sampling points distributed over a maximum of five arable fields were
139 selected for plant sampling. When there were fewer than five fields available, the points were
140 stratified in proportion to size of sampled fields. Sampling points were laid parallel to grassy
141 (never woody) field borders and at 10 m distances from the border towards the field centre.
142 Weeds were sampled in three 2 x 2 m² quadrats per sampling point, placed parallel to the
143 field edge and separated five meters from each other.

144

145 *Vegetation sampling and agricultural management information*

146 We identified the weed species (i.e. all vascular plant species except the crops) present in
147 each sampling quadrat. Then, we pooled the three quadrats within each sampling point,
148 obtaining the frequency of presence of each species in each sampling point. A four-point
149 scale of local-abundance was used ranking sampling locations from 0 (absent) to 3 (present in
150 the three quadrats). Following Guerrero et al. (2014), all subsequent analyses were performed
151 at the sampling point level (since we consider the sampling point as representative of the
152 local community of arable weeds, for brevity we will refer to them as 'assemblages' from
153 now on).

154 We measured six indicators of agricultural management intensity both at the individual
155 field and at the surrounding landscape scales (Table 1). The indicators of agricultural
156 management intensity associated with the individual field scale were assessed by means of
157 questionnaires, undertaken in person with the farmers responsible for managing the sampled
158 fields, and included measures of yield and inputs of nitrogen fertilizer and herbicides. We
159 used digital maps created from remotely sensed images from each study area to estimate the
160 indicators of agricultural management intensity associated with the landscape scale. These
161 landscape scale measures included the size of the focal field and two measures of landscape

162 structure that were quantified within a radius of 500 m around each sampling point, these
163 were: mean arable field size and the proportion of arable land cover.

164 Given the multidimensional nature of agricultural intensification, which encompasses
165 many correlated variables, dimensionality reduction is a common way to estimate it
166 (Carmona et al., 2017; Flohre et al., 2011). Accordingly, following Guerrero et al. (2014), we
167 performed a principal component analysis (PCA) on these indicators of agricultural
168 management intensity. We retained two orthogonal axes that explained 62% of the total
169 variance (Table 1; Fig. S1). The first axis (PC1) was related to management practices at the
170 individual field level (contributed by yield, and the number of herbicide and nitrogen
171 fertilizer applications). The second axis (PC2) was related to the structure of the surrounding
172 landscape (and was defined by sampled field size, mean arable field size, and percentage
173 cover of arable crops). We used these axes to produce estimations of agricultural intensity at
174 the local field and landscape level, respectively (Table S1).

175

176 *Functional trait information and diversity estimation*

177 We collected functional traits for the species found in the vegetation surveys from the TRY
178 database (Kattge et al., 2020; Appendix S1). We chose three traits that are related to plant
179 strategy for resource capture and allocation: specific leaf area (SLA), vegetative plant height,
180 and seed mass (Westoby, 1998). These traits reflect different strategies in plant dispersal,
181 establishment, persistence and response to disturbances (Díaz et al., 2016), and are related to
182 ecosystem functions such as soil multifunctionality, decomposition rate or herbivory (de
183 Bello et al., 2010; Peco, Navarro, Carmona, Medina, & Marques, 2017; Valencia et al.,
184 2018). We estimated the average value for each trait and species after excluding outliers
185 (observations >3 sd away from the species' mean). The averages for each species and trait
186 combination were calculated first within individuals (if multiple measurements were taken
187 from a single individual), then within datasets (if multiple individuals were measured in the
188 same location) and finally within species (if multiple individuals were measured in various
189 locations). In calculations of functional structure we only considered species for which we
190 had complete trait information, and removed the assemblages when less than 80% of the
191 species in that assemblage had trait information associated with them. This left a total of 335
192 species and 1235 assemblages (i.e. sampling points) distributed in 786 fields within 261
193 farms in the nine study areas.

194 Preliminary data exploration showed that the raw data for seed mass and plant height
195 were not normally distributed, so these variables were log-transformed to attain normal
196 distributions. In each assemblage, we used species richness (estimated as the number of
197 species found in each sampling point) as an indicator of taxonomic diversity, and the average
198 trait value (community weighted mean; CWM) for each trait as an indicator of the most
199 frequent trait values, i.e. the functional composition of assemblages (Carmona, Mason,
200 Azcárate, & Peco, 2015). Further, we calculated several indicators of functional diversity in
201 each assemblage. We used for this the trait probability density (TPD) approach, which
202 estimates probabilistic functional niches of species and assemblages, which allow afterwards
203 to estimate several aspects of functional diversity (Carmona, Bello, Mason, & Lepš, 2019;
204 Carmona, de Bello, Mason, & Lepš, 2016). Since information on intraspecific trait variability
205 was not available, the center of each TPDs function was defined by the coordinates
206 corresponding to its three trait values, and the variance around it was estimated by means of a
207 fixed kernel bandwidth of 0.5 SD for each trait (following Lamanna et al., 2014).
208 Subsequently, we estimated the TPD function of each sampling point (TPDc) by calculating a
209 weighted average of the TPDs functions of the species in each assemblage, using their
210 relative frequency as a weighting factor (see Carmona et al., 2016 for further details). The
211 value of a TPDc function for each particular combination of trait values reflects the
212 probability of observing that combination in the considered assemblage.

213 We then used the R package 'TPD' (Carmona, 2019; Carmona et al., 2019) to estimate
214 several indicators of functional diversity in the assemblages, including functional richness
215 (the amount of functional space occupied by the assemblage; Fig. 1a), functional evenness
216 (the evenness in the distribution of the abundance in the functional trait space; Fig. 1b),
217 functional divergence (the degree to which the pooled abundance is distributed toward the
218 extremes of the functional volume of the assemblage; Fig. 1c), and functional redundancy
219 (the degree to which the species in an assemblage occupy the same functional space; Fig. 1d).
220 All these indices are described in detail in Carmona et al. (2019). Both functional richness
221 and functional redundancy are related to species richness (since both indices can only
222 increase as new species are added). To quantify the patterns of association between these
223 indices and to ensure independence from the taxonomic aspect of diversity, we additionally
224 performed two different corrections. In the case of functional richness, we compared the
225 observed value in each assemblage for this index with the values expected under random
226 species assembly processes; for this, we performed a matrix-swap null model, randomizing

227 species within each study area while keeping both row and column sums fixed (permatswap
228 function from the R package 'vegan'; Oksanen et al., 2018). We estimated 500 null values of
229 functional richness for each assemblage using this procedure, and then compared them with
230 the observed value using Standardized Effect Sizes (SES; Carmona et al., 2015; Micó et al.,
231 2020). In the case of functional redundancy, the upper bound of this measure in an
232 assemblage can also be calculated from species richness minus one (S-1); in order to break
233 this correlation we expressed redundancy in relative terms by dividing it by S-1 (Carmona et
234 al., 2019).

235

236 *Statistical analyses*

237 We examined the relationship between the assemblage level metrics (species richness,
238 functional CWM of the three traits, functional richness, evenness, divergence and
239 redundancy) and agricultural intensity at the field and landscape levels by means of mixed
240 models (with a Poisson distribution in the case of species richness), using the 'lme4' R
241 package (Bates, Mächler, Bolker, & Walker, 2015). The models included both intensity
242 indicators (scores in the PCA axes) as explanatory variables, and field nested in farm nested
243 in study area as random factors, to account for the hierarchical study design. We explored
244 whether the responses to agricultural intensity were similar across study areas for each
245 response variable by fitting a model with random slopes for both intensity indicators as
246 random slopes within study areas and a model without these random slopes. We compared
247 these two models with different random structures by means of AIC, and kept for each
248 variable the model with the lowest AIC score (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).
249 For all selected models, we estimated conditional and marginal coefficients of determination
250 using the function `r.squaredGLMM` from the MuMIn package (Barton, 2016; Nakagawa,
251 Johnson, & Schielzeth, 2017). Conditional R^2 reflects the variance explained by the entire
252 model, including both fixed and random effects, whereas marginal R^2 reflects the variance
253 explained only by the fixed effects, i.e. intensity at the field and landscape levels.

254

255 **Results**

256 All the models including random slopes for intensification had higher AIC values than
257 the models without the random slopes (Table S2). Accordingly, all reported results
258 correspond to the models without random slopes.

259 *Species richness*

260 Agricultural intensity had a strong influence on species richness (marginal $R^2=0.29$). In
261 particular, field-level intensity markedly reduced species richness, with a three-fold reduction
262 in the number of species observed in the assemblages from the least-intensified to the most-
263 intensified fields (poisson regression $\beta_{\text{Field}} \pm \text{SE} = -0.38 \pm 0.03$; $p < 0.001$; Fig. 2). Intensity at
264 the landscape level had a much smaller but still highly significant negative effect ($\beta_{\text{Landscape}} =$
265 -0.08 ± 0.03 ; $p = 0.002$; Fig. 2) reducing observed species richness. We did not observe a
266 significant interaction between the two levels of intensification ($p = 0.19$).

267 *Functional composition*

268 Agricultural intensity significantly affected the average values of the three selected traits.
269 However, it explained low amounts of variation in all cases (marginal R^2 was between 0.01
270 and 0.02), with the random effects explaining a much larger proportion (conditional R^2
271 between 0.67 and 0.73). Similarly, the proportion of variation explained by each level of the
272 random factor differed markedly between traits, with differences between fields and between
273 farms accounting for a majority of variability in plant height (ca 25% each level), whereas
274 most of the variation in SLA and seed mass was between study areas (42% and 39%,
275 respectively). Plant height decreased with field-level intensity ($\beta_{\text{Field}} = -0.18 \pm 0.06$; $p = 0.003$),
276 whereas average SLA values generally increased ($\beta_{\text{Field}} = 0.14 \pm 0.05$; $p = 0.006$; Fig. 3).
277 However, landscape level intensity did not have any important effect on these two traits. In
278 contrast, seed mass decreased with intensification at the landscape level, but showed no
279 patterns at the field scale ($\beta_{\text{Landscape}} = -0.11 \pm 0.05$; $p = 0.016$; Fig. 3).

280 *Functional diversity*

281 As expected, functional richness followed patterns similar to species richness (marginal
282 $R^2 = 0.23$), decreasing with intensity at the field ($\beta_{\text{Field}} = -103.14 \pm 8.98$; $p < 0.001$) and at the
283 landscape scale ($\beta_{\text{Landscape}} = -23.60 \pm 8.49$; $p = 0.006$; Fig. 3). However, after removing the
284 effect of species richness by means of the null model (functional richness SES), landscape-
285 level intensity ceased to have an effect (Fig. S2). In contrast to raw functional richness,
286 functional richness SES increased with intensity at the field level, but overall the effects of
287 intensity on this variable were very small (marginal $R^2 = 0.01$; Fig. S2). Agricultural intensity
288 had a moderate effect on functional evenness (marginal $R^2 = 0.08$; Fig. 3), so that functional
289 evenness increased with intensity at the field scale ($\beta_{\text{Field}} = 0.008 \pm 0.001$; $p < 0.001$), but not at
290 the landscape scale. Similarly, functional divergence increased with intensity at the field scale

291 ($\beta_{\text{Field}} = 0.02 \pm 0.003$; $p < 0.001$) and was not significantly related to intensity at the landscape
292 scale. Functional redundancy decreased substantially with field scale intensity ($\beta_{\text{Field}} = -$
293 0.78 ± 0.06 ; $p < 0.001$; Fig. 3), but was not affected by intensity at the landscape scale. This
294 negative effect of intensification at the field scale remained significant after correcting for the
295 effect of species richness on redundancy (relative redundancy; Fig. S3).

296

297 **Discussion**

298 Our results show that agricultural intensification had consistently negative effects on the
299 diversity of arable weeds assemblages of European cereal-dominated agroecosystems and
300 that this effect was stronger at local field scales than at the landscape scale. Despite the strong
301 decline of taxonomic diversity associated with agricultural intensification (Fig. 2), we found
302 much weaker effects on the functional structure of assemblages (evidenced by the generally
303 low marginal R^2 values; Figs 3 and 4), due to the high levels of functional redundancy among
304 species that buffered the effects of species loss. Overall, intensification selected for species
305 with ruderal strategies (low stature, high SLA, light seeds; Pierce et al., 2017), so that these
306 traits were more prevalent in assemblages subject to intensification. Ultimately, this selection
307 contributes to lower functional redundancy. These results depended strongly on the level at
308 which intensification was considered: we found evidence supporting the idea that
309 intensification affects weeds diversity mostly through selection operating at the local field
310 scale. Nonetheless, intensification at the landscape scale also had a negative effect on the
311 average seed mass of weeds assemblages, suggesting that species with poor dispersal abilities
312 are selected against in very intensified landscapes.

313 The relevance of spatial scale remains vitally important for how we manage conservation
314 interventions in agricultural landscapes (Emmerson et al., 2016; Petit et al., 2016; Tschardtke
315 et al., 2005). For example, previous work suggests that the most important scale for
316 consideration depends on the mobility of the taxonomic group under study. Whereas birds
317 (Guerrero et al., 2012), carabids (Winqvist et al., 2014) or wild bees (Happe et al., 2018) are
318 primarily influenced by landscape factors, weed diversity seems to be more strongly
319 determined by field-scale factors (Carmona et al., 2017; Guerrero et al., 2014). However,
320 some recent studies have underscored the importance of the larger-scale factors for arable
321 weeds diversity, either independently or by modulating the effects of local factors (Gabriel et
322 al., 2010; Henckel, Börger, Meiss, Gaba, & Bretagnolle, 2015; Petit et al., 2016; Tuck et al.,
323 2014). Our results do not support this view, since intensification at the landscape scale had

324 little influence on local species richness, and the interaction with the field scale was not
325 significant for any of the studied variables. The contrasting results obtained from different
326 studies could be due to factors such as the position within the field of the considered samples,
327 or the different ways in which landscape level intensification was measured between studies.
328 For example, the influence of landscape scale processes is known to decrease as the distance
329 from the edge of the field increases (José-María, Armengot, Blanco-Moreno, Bassa, & Sans,
330 2010), and the plots considered in this study were relatively far from field edges. Further,
331 whereas other studies encompass factors related to field management, but acting at landscape
332 level, such as the proportion of organic fields (Petit et al., 2016), our landscape-level
333 variables measure exclusively landscape structure or complexity based on semi-natural
334 elements (Billeter et al., 2007b).

335 Our results show that the two considered aspects of intensification had different effects on
336 vegetative (SLA and plant height) and regenerative (seed mass) traits. Field level
337 intensification seemed to select for phenotypes characterized by smaller stature and higher
338 SLA. Plants with low height are better able to cope with physical disturbance associated with
339 tillage (Rota, Manzano, Carmona, Malo, & Peco, 2017; Westoby, 1998), whereas high SLA
340 values are associated with higher relative growth rates (Shipley, 2006). Together, these traits
341 allow plants to complete their life cycles quickly, hence reducing competition with the crop
342 vegetation (Guerrero et al., 2014), and being able to complete their full life cycle before
343 harvest. Further, herbaceous species with high SLA are better adapted to shade conditions
344 and high supplies of nutrients (Westoby, 1998). Although some studies have reported no
345 relationship between intensification and these traits (Fried, Kazakou, & Gaba, 2012; Guerrero
346 et al., 2014), both smaller stature and higher SLA are frequently found in response to
347 agricultural intensification (Kazakou et al., 2016; Solé-Senan, Juárez-Escario, Robleño,
348 Conesa, & Recasens, 2017), in agreement with the expectation that this process selects for
349 ruderal strategies. In this line, it is important to remark that higher N availability is associated
350 to higher SLA values due to the effect of intraspecific variability (He, Chen, Zhao,
351 Cornelissen, & Chu, 2018), so that local measurements should be preferable to assess the
352 effect of intensification on functional diversity. However, the relative importance of
353 considering local trait values, which is critical at local scales (Carmona, Rota, Azcárate, &
354 Peco, 2015), decreases as spatial scale increases (Albert, Grassein, Schurr, Vieilledent, &
355 Violle, 2011), as is the case of the present study. The fact that species rankings considering
356 traits from databases and local measurements are similar (Kazakou et al. 2014), suggests that
357 our results should be robust to this effect.

358 Conclusions

359 Because of the loss of landscape complexity in intensively managed landscapes, arable weeds
360 assemblages become more isolated and disconnected from seed sources (e.g. grasslands,
361 fallows and field borders) and tend to have lower propagule pressure. Consequently, the
362 negative effect of landscape level intensification on species richness observed in this study is
363 likely to be due to this isolation effect (Damschen et al., 2019). In the present study, average
364 seed mass decreased with intensification at the landscape scale, probably due to the higher
365 dispersal ability of species with small seeds. Small seeds tend to disperse further (Cornelissen
366 et al., 2003), and tend to persist longer in the soil seed bank (Hernández Plaza, Navarrete, &
367 González-Andejar, 2015). Additionally, given equivalent reproductive investment, plants
368 with small seeds produce more seeds (Jakobsson & Eriksson, 2000). For these reasons, plants
369 with smaller seeds might have a dispersion advantage in intensively managed landscapes and
370 might persist longer in the assemblages. Similar patterns have been observed in other habitats
371 (reviewed in Vellend, 2016), but this is, to the best of our knowledge, the first observation in
372 agricultural landscapes.

373 The reduction in species richness associated with intensification was accompanied by a
374 similar reduction in the functional space occupied by these arable weeds assemblages. The
375 species-rich assemblages at the least intensified end of the gradient had lower functional
376 evenness and divergence than the assemblages from more intensified fields. This means that
377 the distribution of trait values in the more diverse assemblages tended to be more clumped
378 (see Fig. 1). This interpretation was further confirmed by the observed reduction in functional
379 redundancy with intensification. Overall, we found clear evidence showing that agricultural
380 intensification acts by selecting against (or at least reducing the abundance of) functionally
381 redundant species. This in turn implies that the functional structure of these systems can
382 resist, relatively well, the loss of species associated with agricultural intensification (Carmona
383 et al., 2017). However, the observed reductions in redundancy were higher than expected for
384 similar levels of species loss (Fig. S3), which suggests that functionally unique species are
385 more sensitive to intensification than species with more commonly occurring trait values. The
386 extirpation of more unique species could have profound impacts if they are also important for
387 ecosystem functioning, as found in other systems (Mouillot et al., 2013). Overall, lower
388 functional redundancy due to intensification is likely to increase the vulnerability of these
389 systems to other impacts, such as climate change (Rader, Bartomeus, Tylianakis, & Laliberté,
390 2014) or biological invasions (Galland et al., 2019; Loiola et al., 2018).

391 European arable weeds communities are threatened by agricultural intensification (Weisser et
392 al., 2017). Their decline weakens fundamental ecosystem functions (Knops et al., 1999), thus
393 compromising the provision of key ecosystem services, and even the profitability of certain
394 productive activities associated with agriculture (Emmerson et al., 2016; Gaba, Gabriel,
395 Chadœuf, Bonneu, & Bretagnolle, 2016). Our results highlight the need to extensify field-
396 level agricultural management throughout Europe, i.e. reduction of input amounts and
397 frequency of ploughing and other mechanical operations, and longer rotation cycles that
398 incorporate fallow periods. Arable weeds communities would also benefit from the
399 promotion of higher landscape complexity, which could be achieved through maintaining or
400 developing extensive use of some cereal fields (e.g. by promoting organic agriculture or by
401 using fallows), and would support species with poor dispersal abilities. Although dynamic
402 interpretations should be made carefully when using space-for-time substitution studies
403 (Damgaard, 2019), the use of data collected following a standardized protocol across a
404 continental scale, and the selection of fields with relatively homogenous characteristics (crop
405 type, climate, soils) within study areas, make the results of this study particularly valuable.
406 Our study provides expectations about the changes in farmland plant community structure
407 and functional composition in the face of increasing agriculture intensification across Europe
408 (see Table 2). This knowledge could be used to guide and inform management interventions
409 at the appropriate spatial scales aimed at preventing further species loss and mitigating
410 potential impacts on ecosystem services linked to global change processes.

411

412 **Data availability statement**

413 Data have been deposited in the Dryad Digital Repository,
414 <https://doi.org/10.5061/dryad.2rbnzs7k5> (Carmona et al. 2020).

415

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688

689 Table 1. Description of the different agricultural management intensity variables at the field
 690 and landscape level used in the study, and their loadings in the selected PCA axes.

Variable		Description	PC1 (field)	PC2 (landscape)
Field-level	Yield	Cereal grain obtained in focal field (tons/ha)	0.86	0.02
	Amount of herbicide	Total amount of herbicide active ingredients applied on focal field (g/ha)	0.75	0.19
	N Fertilizer	Total amount of nitrogen applied on focal field (kg/ha)	0.86	-0.08
Landscape-level	Mean field size	Mean size of fields with arable crops within a 500 m radius circle centred on focal field (ha)	-0.01	0.84
	Percentage cover of arable crops	Percentage area of arable crops within a 500 m radius circle centred on focal field	-0.03	0.61
	Focal field size	Size of each surveyed plot's focal field (ha)	0.16	0.75

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692

693 Table 2. Summary of the expected effects of agricultural intensification across Europe on
 694 taxonomic diversity, functional composition (community weighted means) and functional
 695 diversity considered in this study.

	Field-level	Landscape-level
TAXONOMIC DIVERSITY		
Species richness	Communities with fewer species	Communities with fewer species
FUNCTIONAL COMPOSITION		
Plant height	Shorter plants with reduced dispersal ability	–
SLA	Faster growing plants (more vulnerable to predators and parasites)	–
Seed mass	–	Light-seeded plants with high dispersal but lower seedling survival
FUNCTIONAL DIVERSITY		
Richness	Communities with reduced variation in functional trait values	Communities with reduced variation in functional trait values
Evenness	Communities where all trait values are more evenly represented	–
Divergence	Communities where the most abundant species have different trait values	–
Redundancy	Communities with fewer plants of similar trait values	–

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698 Fig. 1. Illustration of the selected indices of functional structure. In the TPD framework, the
699 functional structure of an assemblage is expressed as a probability distribution (TPDc) whose
700 value in each point in the functional space reflects the relative abundance of the
701 corresponding trait in the assemblage. For simplicity, all examples are shown in a single
702 dimension (1 trait), although in the analyses we have considered a three dimensional
703 functional space. Functional richness (a) indicates the amount of functional space occupied
704 by assemblages; assemblages with higher functional richness (community 2) display a larger
705 variety of trait values. Functional evenness (b) reflects the uniformity in the occupation of the
706 functional space by an assemblage; assemblages with higher functional evenness (community
707 1) are more similar to an imaginary assemblage occupying the same functional space in a
708 perfectly even way (which are depicted by discontinuous lines). Functional divergence (c)
709 indicates the degree to which the trait abundances in the assemblages are distributed toward
710 the extremes of the part of the functional space they occupy; assemblages with lower
711 functional divergence (assemblage 1) have a higher concentration of traits close to the center
712 of gravity of the assemblage in the trait space. Functional redundancy (d) reflects how much
713 different species (indicated by different colors in the figure) occupy the same functional
714 space. This is estimated by dividing the functional space in a large number of cells (N) and
715 then averaging the number of species (M) that are found within each cell, using the
716 abundance of the total distribution (TPDc) as weighting factor. In the example, the functional
717 space of the assemblage is occupied by an average of 3.87 species; after subtracting 1 from
718 that, functional redundancy expresses the average number of species that could be removed
719 from the assemblage without reducing its functional richness. For formal definitions of these
720 indices see (Carmona et al., 2019, 2016).

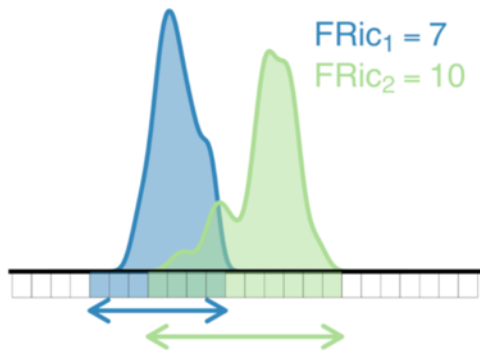
721 Fig. 2. Partial regression plots showing the effects of agricultural intensification at the field
722 (left) and landscape (right) levels on weed species richness (mean prediction and 95%
723 confidence intervals), modelled using a generalized mixed model with Poisson distribution.
724 R^2_{Marg} indicates the proportion of variance explained by the fixed effects (field and landscape
725 level management intensity and their interaction), and R^2_{Cond} includes both fixed and random
726 effects. Colors indicate the study area to which each point belongs (EST: Estonia, FR;
727 France; Go: Germany (Göttingen); IRL: Ireland; JE: Germany (Jena); NL: Netherlands; PL:
728 Poland; SP: Spain; SWE: Sweden).

729 Fig. 3. Partial regression plots showing the effects of agricultural intensification at the field
730 (left) and landscape (right) levels on functional composition modelled using linear mixed
731 models. Functional composition is represented by the community weighted mean of plant

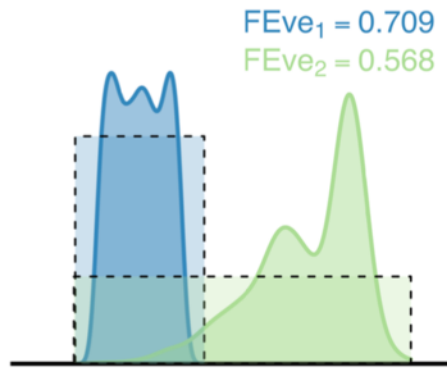
732 height, specific leaf area (SLA) and seed mass. R^2_{Marg} indicates the proportion of variance
733 explained by the fixed effects (field and landscape level management intensity and their
734 interaction), and R^2_{Cond} includes both fixed and random effects. Colors indicate the study area
735 to which each point belongs (EST: Estonia, FR: France; Go: Germany (Göttingen); IRL:
736 Ireland; JE: Germany (Jena); NL: Netherlands; PL: Poland; SP: Spain; SWE: Sweden).

737 Fig. 4. Partial regression plots showing the effects of agricultural intensification at the field
738 (left) and landscape (right) levels on different indicators of the functional diversity of arable
739 weeds assemblages (functional richness, evenness, divergence and redundancy) modelled
740 using linear mixed models. R^2_{Marg} indicates the proportion of variance explained by the fixed
741 effects (field and landscape level management intensity and their interaction), and R^2_{Cond}
742 includes both fixed and random effects. Colors indicate the study area to which each point
743 belongs (EST: Estonia, FR: France; Go: Germany (Göttingen); IRL: Ireland; JE: Germany
744 (Jena); NL: Netherlands; PL: Poland; SP: Spain; SWE: Sweden).

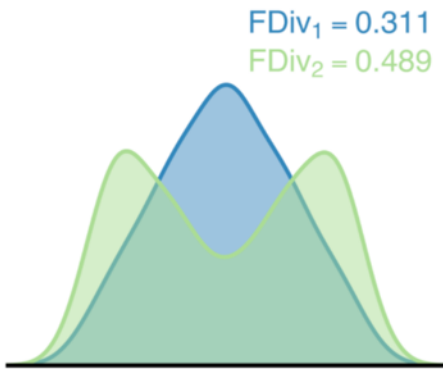
a) Functional richness



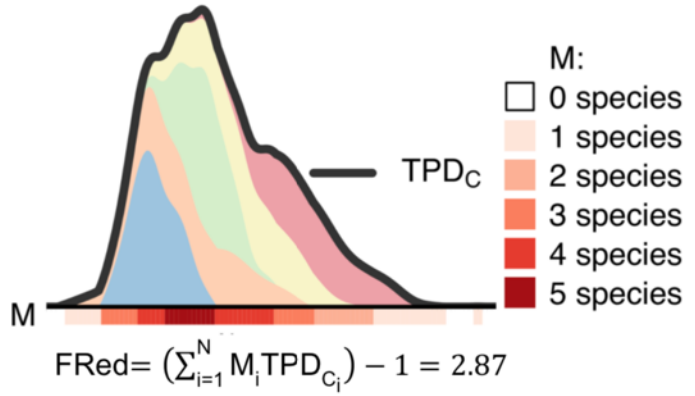
b) Functional evenness



c) Functional divergence

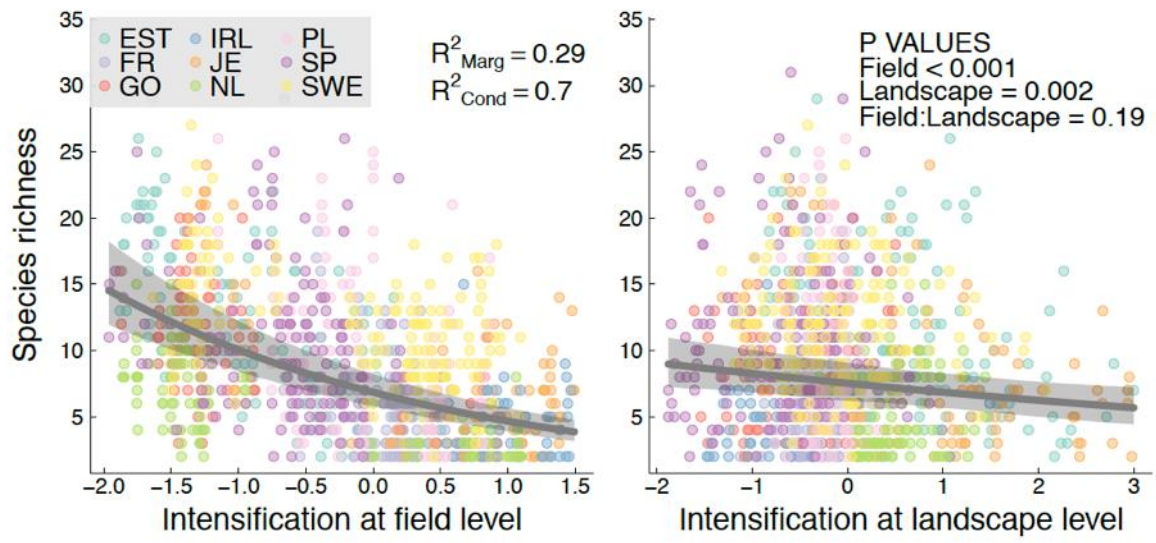


d) Functional redundancy



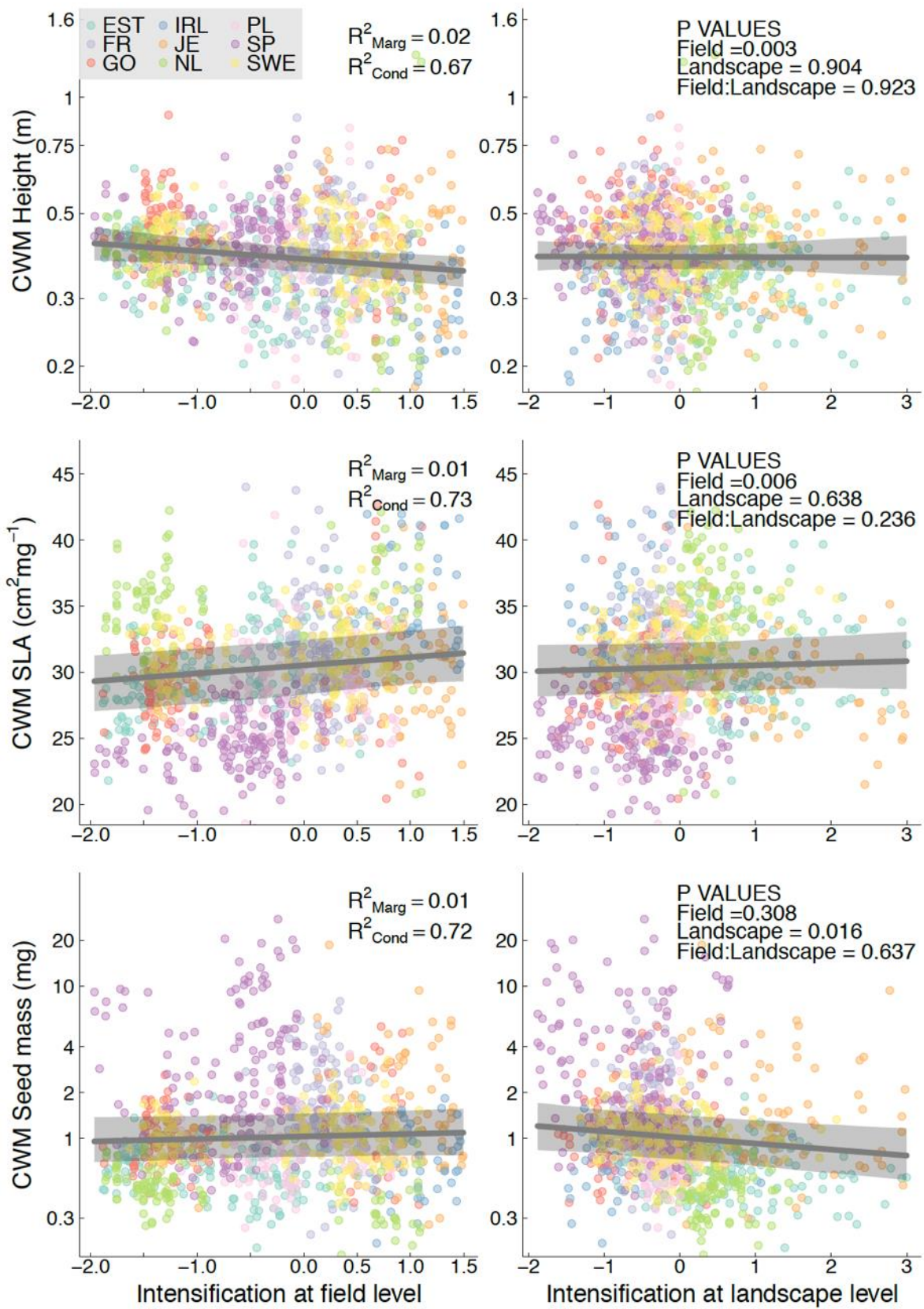
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746 Fig. 1



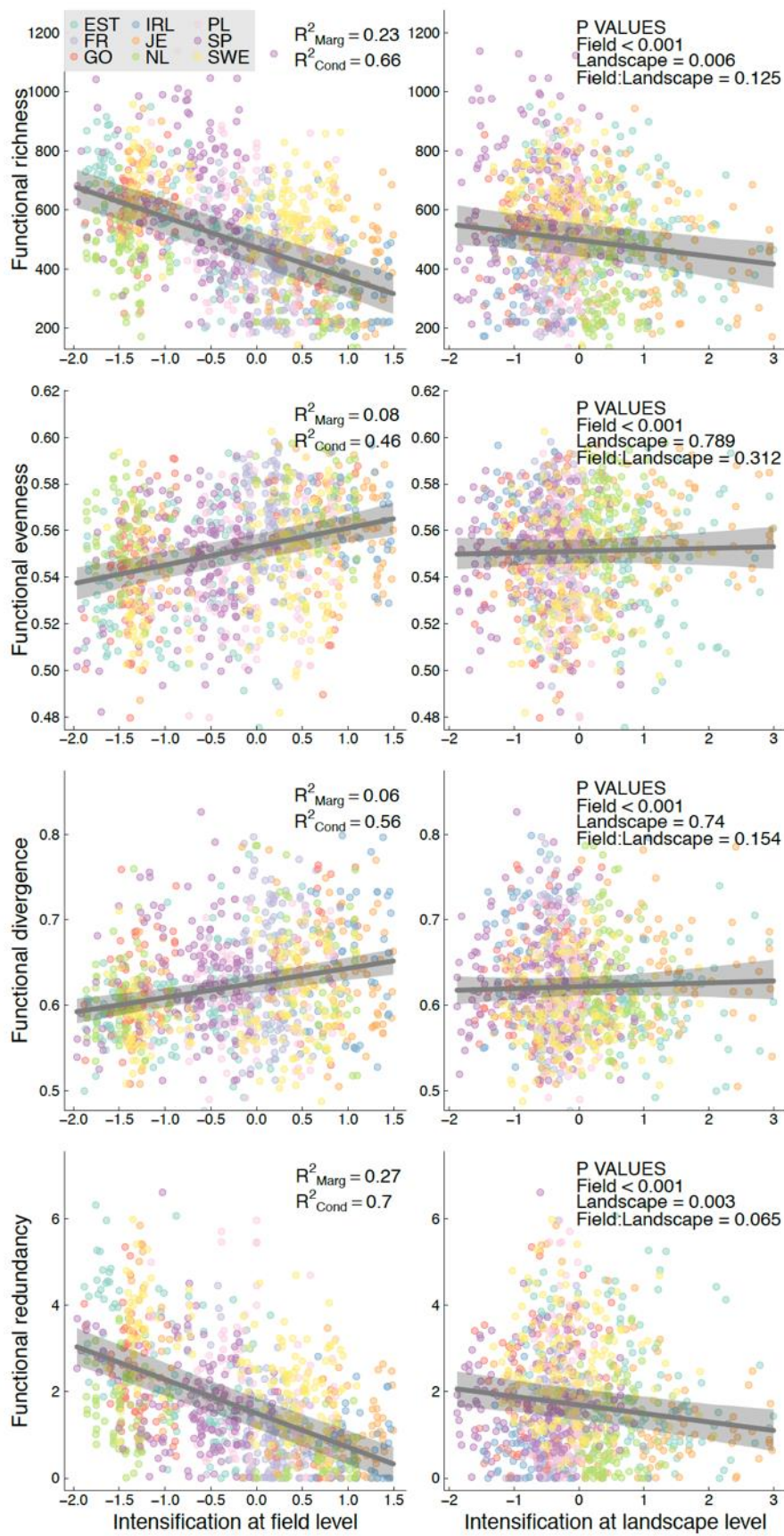
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748 Fig. 2



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750 Fig. 3.



751

752 Fig. 4.

753 **Supporting information**

754 **Appendix S1.** References for individual datasets included in the TRY database from which
755 trait information was used.

756 **Table S1.** Mean and standard deviation of agricultural intensification values at the field and
757 landscape levels for each study area.

758 **Table S2.** Comparisons of models considering and not considering random slopes for the
759 study areas.

760 **Fig. S1.** Biplot of the principal components analysis (PCA).

761 **Fig. S2.** Partial regression plots showing the effects of agricultural intensification at the field
762 and landscape levels on functional richness SES.

763 **Fig. S3.** Partial regression plots showing the effects of agricultural intensification at the field
764 and landscape levels on relative functional redundancy (functional redundancy after
765 removing the effect of species richness).