

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., Tscharntke, 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: Link to publication record in Queen's University Belfast Research Portal

Publisher rights

Copyright 2020 Wiley. This work is made available online in accordance with the publisher's policies. Please refer to any applicable terms of use of the publisher.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Open Access

This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: http://go.qub.ac.uk/oa-feedback

- 1 Agriculture intensification reduces plant taxonomic and functional diversity across European
- 2 arable systems.
- 3 Running headline: Intensification reduces plant diversity
- 4 Carlos P. Carmona¹, Irene Guerrero², Begoña Peco³, Manuel B. Morales³, Juan J. Oñate³, Tomas
- 5 Pärt⁴, Teja Tscharntke⁵, J. Liira¹, T. Aavik¹, Mark Emmerson⁶, Frank Berendse⁷, Piotr Ceryngier⁸,
- 6 Vincent Bretagnolle^{9,10}, Wolfgang W. Weisser¹¹, Jan Bengtsson¹²
- ⁷ ¹Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, Tartu, 51005, Estonia.
- 8 ²INEA Agricultural Engineering School, Comillas Pontifical University, Valladolid, Spain.
- ³Terrestrial Ecology Group (TEG), Department of Ecology, Research Center on Biodiversity and
- 10 Global Change, Autónoma University of Madrid. C/ Darwin 2, 28049, Madrid. Spain.
- ⁴ The Swedish University of Agricultural Sciences, Dept of Ecology, Box 7002, SE-745007 Uppsala,
- 12 Sweden.
- ⁵Agroecology, Department of Crop Sciences, University of Göttingen, Germany.
- ⁶Institute for Global Food Security, School of Biological Sciences, 19 Chlorine Gardens, Belfast, BT9
 5DL, Northern Ireland, UK.
- ⁷ Department of Environmental Sciences, Wageningen University, PO Box 47, 6700AA Wageningen,
 The Netherlands.
- ⁸ Institute of Biological Sciences, Cardinal Stefan Wyszyński University, Wóycickiego 1/3, 01-938
 Warsaw, Poland.
- ⁹Centre d'Etudes Biologiques de Chizé, UMR 7372, CNRS and Université La Rochelle, F-79360
 Beauvoir-sur-Niort, France.
- 22 ¹⁰LTSER « Zone Atelier Plaine & Val de Sèvre », CNRS, 79360, Beauvoir sur Niort, France
- 23 ¹¹Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, School
- of Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2,
- 25 85354 Freising, Germany.
- ¹²Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-700 07,
- 27 Uppsala, Sweden.
- 28

29 Corresponding author: Carlos Perez Carmona; Institute of Ecology and Earth Sciences, University
30 of Tartu, Lai 40, Tartu, 51005, Estonia; email: perezcarmonacarlos@gmail.com

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.

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

3

5

6

7

4 Abstract

 Agricultural intensification is one of the main drivers of species loss worldwide, but there is still a lack of information about its effect on functional diversity of arable 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.

4. Maintaining the diversity of Europe's arable weed communities requires some simple
 management interventions, for example, reducing the high intensity of field-level
 agricultural management across Europe, which could be complemented by
 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 Shrubb, 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 agricultural disturbance activities (Billeter et al., 2007a). For example, plant diversity can 61 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, & Tscharntke, 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 commom 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), and occupying an area not exceeding 1 km^2 . These farms were situated in regions between 30 125 126 x 30 and 50 x 50 km^2 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 rippening 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 $2 \times 2 \text{ m}^2$ 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 at the sampling point level (since we consider the sampling point as representative of the 151 152 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 fields, and included measures of yield and inputs of nitrogen fertilizer and herbicides. We 158 159 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

structure that were quantified within a radius of 500 m around each sampling point, thesewere: 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 othogonal 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

We collected functional traits for the species found in the vegetation surveys from the TRY 177 178 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 Bello et al., 2010; Peco, Navarro, Carmona, Medina, & Marques, 2017; Valencia et al., 183 184 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 infomation, 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 probablity 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 function from the R package 'vegan'; Oksanen et al., 2018). We estimated 500 null values of 228 229 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

We examined the relationship between the assemblage level metrics (species richness, 237 238 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 reponses 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, Johnson, & Schielzeth, 2017). Conditional R² reflects the variance explained by the entire 251 model, including both fixed and random effects, whereas marginal R² reflects the variance 252 253 explained only by the fixed effects, i.e. intensity at the field and landscape levels.

254

255 Results

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

259 Species richness

Agricultural intensity had a strong influence on species richness (marginal R²=0.29). In particular, field-level intensity markedly reduced species richness, with a three-fold reduction in the number of species observed in the assemblages from the least-intensified to the mostintensified fields (poisson regression $\beta_{\text{Field}} \pm \text{SE} = -0.38 \pm 0.03$; p<0.001; Fig. 2). Intensity at the landscape level had a much smaller but still highly significant negative effect ($\beta_{\text{Landscape}} =$ -0.08±.03; p=0.002; Fig. 2) reducing observed species richness. We did not observe a 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. However, it explained low amounts of variation in all cases (marginal R^2 was between 0.01 269 and 0.02), with the random effects explaining a much larger proportion (conditional R^2 270 271 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 $R^2 = 0.23$), decreasing with intensity at the field ($\beta_{Field} = -103.14 \pm 8.98$; p<0.001) and at the 282 landscape scale ($\beta_{\text{Landscape}} = -23.60 \pm 8.49$; p=0.006; Fig. 3). However, after removing the 283 284 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 intensity on this variable were very small (marginal $R^2 = 0.01$; Fig. S2). Agricultural intensity 287 had a moderate effect on functional evenness (marginal $R^2=0.08$; Fig. 3), so that functional 288 289 eveness 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
- 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 low marginal R² values; Figs 3 and 4), due to the high levels of functional redundancy among 303 304 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 interventions in agricultural landscapes (Emmerson et al., 2016; Petit et al., 2016; Tscharntke 314 315 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
- 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,

2010), and the plots considered in this study where relatively far from field edges. Further,

331 whereas other studies emcompass factors related to field management, but acting at landscape

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

elements (Billeter et al., 2007b).

335 Our results show that the two considered aspects of intensification had different effects on 336 vegetative (SLA and plan 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 and high supplies of nutrients (Westoby, 1998). Although some studies have reported no 344 345 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 occuring 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 futher 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

416 **References**

- 417 Aavik, T., & Liira, J. (2010). Quantifying the effect of organic farming, field boundary type
- and landscape structure on the vegetation of field boundaries. *Agriculture, Ecosystems and Environment*, *135*(3), 178–186. doi: 10.1016/j.agee.2009.09.005
- 420 Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G., & Violle, C. (2011). When and
- 421 how should intraspecific variability be considered in trait-based plant ecology?
- 422 *Perspectives in Plant Ecology, Evolution and Systematics, 13*(3), 217–225. doi:
- 423 10.1016/j.ppees.2011.04.003

- 424 Barton, K. (2016). MuMIn: Multi-Model Inference. Retrieved April 1, 2018, from
- 425 https://cran.r-project.org/package=MuMIn
- 426 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects
- 427 Models Using **Ime4**. *Journal of Statistical Software*, 67(1), 1–48. doi:

428 10.18637/jss.v067.i01

- 429 Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., ... Edwards, P. J.
- 430 (2007a). Indicators for biodiversity in agricultural landscapes: a pan-European study.
- 431 *Journal of Applied Ecology*, 45(1), 141–150. doi: 10.1111/j.1365-2664.2007.01393.x
- 432 Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., ... Edwards, P. J.
- 433 (2007b). Indicators for biodiversity in agricultural landscapes: a pan-European study.
- 434 *Journal of Applied Ecology*, 45(1), 141–150. doi: 10.1111/j.1365-2664.2007.01393.x
- 435 Brooks, D. R., Storkey, J., Clark, S. J., Firbank, L. G., Petit, S., & Woiwod, I. P. (2012).
- 436 Trophic links between functional groups of arable plants and beetles are stable at a
- 437 national scale. Journal of Animal Ecology, 81(1), 4–13. doi: 10.1111/j.1365-
- 438 2656.2011.01897.x
- Butler, S. J., Mattison, E. H. A., Glithero, N. J., Robinson, L. J., Atkinson, P. W., Gillings, S.,
 ... Norris, K. (2010). Resource availability and the persistence of seed-eating bird
 populations in agricultural landscapes : a mechanistic modelling approach. *Journal of*
- 442 *Applied Ecology*, 47(1), 67–75. doi: 10.1111/j.1365-2664.2009.01750.x
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: functional
 diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087. doi: 10.1111/j.1365-2664.2011.02048.x
- 446 Carmona, C. P. (2019). TPD: methods for measuring functional diversity based on Trait
 447 Probability Density.
- 448 Carmona, C. P., Bello, F., Mason, N. W. H., & Lepš, J. (2019). Trait probability density (
- 449 TPD): measuring functional diversity across scales based on TPD with R. *Ecology*,
 450 *100*(12), e02876. doi: 10.1002/ecy.2876
- 451 Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2016). Traits Without Borders :
 452 Integrating Functional Diversity Across Scales. *Trends in Ecology & Evolution*, *31*(5),
 453 382–394. doi: 10.1016/j.tree.2016.02.003
- 454 Carmona, C. P., Guerrero, I., Morales, M. B., Oñate, J. J., & Peco, B. (2017). Assessing
- 455 vulnerability of functional diversity to species loss: a case study in Mediterranean
 456 agricultural systems. *Functional Ecology*, *31*(2). doi: 10.1111/1365-2435.12709
- 457 Carmona, C. P., Guerrero, I., Peco, B, Morales, M. B., Oñate, J. J., Pärt, T., Tscharntke, T.,

- 458 Liira, J., Aavik, T., Emmerson, M., Berendese, F., Ceryngier, P., Bretagnolle, V.,
- 459 Weisser, W. W., & Bengtsson, J. (2020), Agricultural intensification reduces plant
- 460 taxonomic and functional diversity across European arable systems., v2, Dryad,

461 Dataset, https://doi.org/10.5061/dryad.2rbnzs7k5

- 462 Carmona, C. P., Mason, N. W. H., Azcárate, F. M., & Peco, B. (2015). Inter-annual
- 463 fluctuations in rainfall shift the functional structure of Mediterranean grasslands across
- 464 gradients of productivity and disturbance. *Journal of Vegetation Science*, 26(3), 538–
- 465 551. doi: 10.1111/jvs.12260
- 466 Carmona, C. P., Rota, C., Azcárate, F. M., & Peco, B. (2015). More for less: Sampling
 467 strategies of plant functional traits across local environmental gradients. *Functional*468 *Ecology*, 29(4), 579–588. doi: 10.1111/1365-2435.12366
- 469 Chamberlain, D. E., Fuller, R. J., Bunce, R. G. H., Duckworth, J. C., & Shrubb, M. (2000).
- 470 Changes in the abundance of farmland birds in relation to the timing of agricultural
- 471 intensification in England and Wales. *Journal of Applied Ecology*, *37*(5), 771–788. doi:
 472 10.1046/j.1365-2664.2000.00548.x
- 473 Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., ...
 474 Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of
 475 plant functional traits worldwide. *Australian Journal of Botany*, 335–380.
- 476 Damgaard, C. (2019). A Critique of the Space-for-Time Substitution Practice in Community
- 477 Ecology. *Trends in Ecology and Evolution*, Vol. 34, pp. 416–421. doi:
- 478 10.1016/j.tree.2019.01.013
- 479 Damschen, E. I., Brudvig, L. A., Burt, M. A., Fletcher, R. J., Haddad, N. M., Levey, D. J., ...
 480 Tewksbury, J. J. (2019). Ongoing accumulation of plant diversity through habitat
- 481 connectivity in an 18-year experiment. *Science*, *365*(6460), 1478–1480. doi:
- 482 10.1126/science.aax8992
- 483 de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., ...
- Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and
 services via functional traits. *Biodiversity and Conservation*, *19*, 2873–2893. doi:
- 486 10.1007/s10531-010-9850-9
- 487 Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D.
 488 (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. doi:
- 489 10.1038/nature16489
- 490 Donald, P. F., Sanderson, F. J., Burfield, I. J., & van Bommel, F. P. J. (2006). Further
- 491 evidence of continent-wide impacts of agricultural intensification on European farmland

- birds, 1990-2000. Agriculture, Ecosystems and Environment, 116(3–4), 189–196. doi:
- 493 10.1016/j.agee.2006.02.007
- Ebeling, A., Klein, A.-M., Weisser, W. W., & Tscharntke, T. (2012). Multitrophic effects of
- 495 experimental changes in plant diversity on cavity-nesting bees, wasps, and their
- 496 parasitoids. *Oecologia*, *169*(2), 453–465. doi: 10.1007/s00442-011-2205-8
- 497 Emmerson, M., Morales, M. B., Oñate, J. J., Batáry, P., Berendse, F., Liira, J., ... Bengtsson,
- 498 J. (2016). How Agricultural Intensification Affects Biodiversity and Ecosystem
- 499 Services. In *Advances in Ecological Research* (Vol. 55, pp. 43–97). doi:
- 500 10.1016/bs.aecr.2016.08.005
- 501 Eraud, C., Cadet, E., Powolny, T., Gaba, S., Bretagnolle, F., & Bretagnolle, V. (2015). Weed
- 502 seeds, not grain, contribute to the diet of wintering skylarks in arable farmlands of
- 503 Western France. *European Journal of Wildlife Research*, 61(1), 151–161. doi:
- 504 10.1007/s10344-014-0888-y
- 505 Eurostat. (2018). 2018. Agriculture, forestry and fishery statistics. Luxembourg.
- Evans, D. M., Pocock, M. J. O., Brooks, J., & Memmott, J. (2011). Seeds in farmland foodwebs: Resource importance, distribution and the impacts of farm management. *Biological Conservation*, 144(12), 2941–2950. doi: 10.1016/j.biocon.2011.08.013
- 509 Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., ... Tscharntke,
- 510 T. (2011). Agricultural intensification and biodiversity partitioning in European
- landscapes comparing plants, carabids, and birds. *Ecological Applications*, 21(5), 1772–
 1781.
- Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., ...
 DeClerck, F. (2009). Loss of functional diversity under land use intensification across
 multiple taxa. *Ecology Letters*, *12*(1), 22–33. doi: 10.1111/j.1461-0248.2008.01255.x
- 516 Fried, G., Kazakou, E., & Gaba, S. (2012). Trajectories of weed communities explained by
 517 traits associated with species' response to management practices. *Agriculture*,
- 518 *Ecosystems and Environment*, 158, 147–155. doi: 10.1016/j.agee.2012.06.005
- Gaba, S., Gabriel, E., Chadœuf, J., Bonneu, F., & Bretagnolle, V. (2016). Herbicides do not
 ensure for higher wheat yield, but eliminate rare plant species. *Scientific Reports*, 6(1),
 30112. doi: 10.1038/srep30112
- 522 Gabriel, D., Sait, S. M., Hodgson, J. A., Schmutz, U., Kunin, W. E., & Benton, T. G. (2010).
- Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, *13*(7), 858–869. doi: 10.1111/j.1461-0248.2010.01481.x
- 525 Gabriel, D., Thies, C., & Tscharntke, T. (2005). Local diversity of arable weeds increases

- 526 with landscape complexity. *Perspectives in Plant Ecology, Evolution and Systematics*,
- 527 7(2), 85–93. doi: 10.1016/j.ppees.2005.04.001
- 528 Galland, T., Adeux, G., Dvořáková, H., E-Vojtkó, A., Orbán, I., Lussu, M., ... Götzenberger,
- 529 L. (2019). Colonization resistance and establishment success along gradients of
- 530 functional and phylogenetic diversity in experimental plant communities. *Journal of*
- 531 *Ecology*, *107*(5), 2090–2104. doi: 10.1111/1365-2745.13246
- 532 Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B., ...
- 533 Inchausti, P. (2010). Persistent negative effects of pesticides on biodiversity and
- biological control potential on European farmland. *Basic and Applied Ecology*, 11(2),
- 535 97–105. doi: 10.1016/j.baae.2009.12.001
- 536 Gonthier, D. J., Ennis, K. K., Farinas, S., Hsieh, H.-Y., Iverson, A. L., Batary, P., ...
- 537 Perfecto, I. (2014). Biodiversity conservation in agriculture requires a multi-scale
- 538 approach. Proceedings of the Royal Society B: Biological Sciences, 281(1791),
- 539 20141358–20141358. doi: 10.1098/rspb.2014.1358
- 540 Green, R. E., Cornell, S. J., Scharlemann, J. P. W., & Balmford, A. (2005). Farming and the
 541 Fate of Wild Nature. *Science*, *307*(5709).
- 542 Guerrero, I., Carmona, C. P., Morales, M. B., Oñate, J. J., & Peco, B. (2014). Non-linear
- 543 responses of functional diversity and redundancy to agricultural intensification at the
- 544 field scale in Mediterranean arable plant communities. *Agriculture, Ecosystems &*
- 545 *Environment*, 195, 36–43. doi: 10.1016/j.agee.2014.05.021
- 546 Guerrero, I., Morales, M. B., Oñate, J. J., Geiger, F., Berendse, F., Snoo, G. de, ...
- 547 Tscharntke, T. (2012). Response of ground-nesting farmland birds to agricultural
- 548 intensification across Europe: Landscape and field level management factors. *Biological*
- 549 *Conservation*, 152, 74–80. doi: 10.1016/j.biocon.2012.04.001
- 550 Happe, A. K., Riesch, F., Rösch, V., Gallé, R., Tscharntke, T., & Batáry, P. (2018). Small-
- scale agricultural landscapes and organic management support wild bee communities of
- 552 cereal field boundaries. *Agriculture, Ecosystems and Environment, 254, 92–98.* doi:
- 553 10.1016/j.agee.2017.11.019
- He, D., Chen, Y., Zhao, K., Cornelissen, J. H. C., & Chu, C. (2018). Intra- and interspecific
 trait variations reveal functional relationships between specific leaf area and soil niche
 within a subtropical forest. *Annals of Botany*, *121*(6), 1173–1182.
- Henckel, L., Börger, L., Meiss, H., Gaba, S., & Bretagnolle, V. (2015). Organic fields sustain
 weed metacommunity dynamics in farmland landscapes. *Proceedings of the Royal*
- 559 Society of London B: Biological Sciences, 282(1808).

- 560 Hernández Plaza, E., Navarrete, L., & González-Andújar, J. L. (2015). Intensity of soil
- 561 disturbance shapes response trait diversity of weed communities: The long-term effects
- of different tillage systems. *Agriculture, Ecosystems and Environment, 207, 101–108.*doi: 10.1016/j.agee.2015.03.031
- 564 Hevia, V., Carmona, C. P., Azcárate, F. M., Torralba, M., Alcorlo, P., Ariño, R., ...
- 565 González, J. A. (2016). Effects of land use on taxonomic and functional diversity: a
- 566 cross-taxon analysis in a Mediterranean landscape. *Oecologia*, 181(4). doi:

567 10.1007/s00442-015-3512-2

- Jakobsson, A., & Eriksson, O. (2000). A comparative study of seed number, seed size,
 seedling size and recruitment in grassland plants. *Oikos*, 88(3), 494–502. doi:
 10.1034/j.1600-0706.2000.880304.x
- 571 José-María, L., Armengot, L., Blanco-Moreno, J. M., Bassa, M., & Sans, F. X. (2010).
- 572 Effects of agricultural intensification on plant diversity in Mediterranean dryland cereal
- 573 fields. Journal of Applied Ecology, 47(4), 832–840. doi: 10.1111/j.1365-
- 574 2664.2010.01822.x
- Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., ... Wirth, C. (2020).
 TRY plant trait database enhanced coverage and open access. *Global Change Biology*,
 26(1), 119–188. doi: 10.1111/gcb.14904
- Kazakou, E., Fried, G., Richarte, J., Gimenez, O., Violle, C., & Metay, A. (2016). A plant
 trait-based response-and-effect framework to assess vineyard inter-row soil
- 580 management. *Botany Letters*, *163*(4), 373–388. doi: 10.1080/23818107.2016.1232205
- 581 Knops, J. M. H., Tilman, D., Haddad, N. M., Naeem, S., Mitchell, C. E., Haarstad, J., ...
- 582 Groth, J. (1999). Effects of plant species richness on invasion dynamics, disease
- 583 outbreaks, insect abundances and diversity. *Ecology Letters*, 2(5), 286–293. doi:
- 584 10.1046/j.1461-0248.1999.00083.x
- 585 Laliberté, E., Wells, J. A., Declerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., ...
- 586 Mayfield, M. M. (2010). Land-use intensification reduces functional redundancy and 587 response diversity in plant communities. *Ecology Letters*, *13*(1), 76–86. doi:
- 588 10.1111/j.1461-0248.2009.01403.x
- Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., Šímová, I., ... Enquist, B. J.
- 590 (2014). Functional trait space and the latitudinal diversity gradient. *Proceedings of the*
- 591 National Academy of Sciences, 111(38), 13745–13750. doi: 10.1073/pnas.1317722111
- 592 Loiola, P. P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C. P., Pyšek, P., &
- 593 Lososová, Z. (2018). Invaders among locals: alien species decrease phylogenetic and

- 594 functional diversity while increasing dissimilarity among native community members.
- 595 *Journal of Ecology*. doi: 10.1111/1365-2745.12986
- 596 Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., ... Steffan-
- 597 Dewenter, I. (2019). The interplay of landscape composition and configuration: new
- 598 pathways to manage functional biodiversity and agroecosystem services across Europe.
- 599 *Ecology Letters*, 22(7), 1083–1094. doi: 10.1111/ele.13265
- Matson, P. A., Parton, W. J., Power, A. G., & Swift, M. J. (1997). Agricultural Intensification
 and Ecosystem Properties. *Science*, 277(5325), 504–509.
- Micó, E., Ramilo, P., Thorn, S., Müller, J., Galante, E., & Carmona, C. P. (2020). Contrasting
 functional structure of saproxylic beetle assemblages associated to different
- 604 microhabitats. Scientific Reports, 10(1), 1520. doi: 10.1038/s41598-020-58408-6
- Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., ...
- 606Thuiller, W. (2013). Rare species support vulnerable functions in high-diversity
- 607 ecosystems. *PLoS Biology*, *11*(5), e1001569. doi: 10.1371/journal.pbio.1001569
- 608 Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R609 2 and intra-class correlation coefficient from generalized linear mixed-effects models
- 610 revisited and expanded. *Journal of The Royal Society Interface*, *14*(134), 20170213. doi:
 611 10.1098/rsif.2017.0213
- 612 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., ...
- 613 Wagner, H. (2018). *vegan: Community Ecology Package*.
- 614 Peco, B., Navarro, E., Carmona, C. P., Medina, N. G., & Marques, M. J. (2017). Effects of
- 615 grazing abandonment on soil multifunctionality: The role of plant functional traits.
- 616 Agriculture, Ecosystems & Environment, 249(April), 215–225. doi:
- 617 10.1016/j.agee.2017.08.013
- 618 Petit, S., Gaba, S., Grison, A. L., Meiss, H., Simmoneau, B., Munier-Jolain, N., &
- 619 Bretagnolle, V. (2016). Landscape scale management affects weed richness but not
- 620 weed abundance in winter wheat fields. *Agriculture, Ecosystems and Environment, 223,*
- 621 41–47. doi: 10.1016/j.agee.2016.02.031
- 622 Pierce, S., Negreiros, D., Cerabolini, B. E. L., Kattge, J., Díaz, S., Kleyer, M., ... Tampucci,
- 623 D. (2017). A global method for calculating plant <scp>CSR</scp> ecological strategies
- 624 applied across biomes world-wide. *Functional Ecology*, *31*(2), 444–457. doi:
- 625 10.1111/1365-2435.12722
- Rader, R., Bartomeus, I., Tylianakis, J. M., & Laliberté, E. (2014). The winners and losers of
 land use intensification: Pollinator community disassembly is non-random and alters

- 628 functional diversity. *Diversity and Distributions*, 20(8), 908–917. doi:
- 629 10.1111/ddi.12221
- Rota, C., Manzano, P., Carmona, C. P., Malo, J. E., & Peco, B. (2017). Plant community
- assembly in Mediterranean grasslands: understanding the interplay between grazing and
 spatio-temporal water availability. *Journal of Vegetation Science*, 28(1), 149–159. doi:
- 633 10.1111/jvs.12470
- 634 Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., ...
- Tscharntke, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions
 in a biodiversity experiment. *Nature*, 468(7323), 553–556. doi: 10.1038/nature09492
- 637 Shipley, B. (2006). Net assimilation rate, specific leaf area and leaf mass ratio: Which is most
 638 closely correlated with relative growth rate? A meta-analysis. *Functional Ecology*,
- 639 20(4), 565–574. doi: 10.1111/j.1365-2435.2006.01135.x
- 640 Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., ... Fahrig, L. (2019).
- 641 Increasing crop heterogeneity enhances multitrophic diversity across agricultural
- regions. *Proceedings of the National Academy of Sciences*, *116*(33), 16442–16447. doi:
 10.1073/pnas.1906419116
- 644 Solé-Senan, X. O., Juárez-Escario, A., Robleño, I., Conesa, J. A., & Recasens, J. (2017).
- 645 Using the response-effect trait framework to disentangle the effects of agricultural
- 646 intensification on the provision of ecosystem services by Mediterranean arable plants.
- 647 *Agriculture, Ecosystems and Environment, 247, 255–264. doi:*
- 648 10.1016/j.agee.2017.07.005
- Storkey, J., Meyer, S., Still, K. S., & Leuschner, C. (2012). The impact of agricultural
 intensification and land-use change on the European arable flora. *Proceedings of the*
- 651 *Royal Society B: Biological Sciences*, 279(1732), 1421–1429. doi:
- 652 10.1098/rspb.2011.1686
- Sutherland, S. (2004). What makes a weed a weed: life history traits of native and exotic
 plants in the USA. *Oecologia*, *141*(1), 24–39. doi: 10.1007/s00442-004-1628-x
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., ...
- 656 Swackhamer, D. (2001). Forecasting Agriculturally Driven Global Environmental
 657 Change. *Science*, 292(5515).
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005).
- Landscape perspectives on agricultural intensification and biodiversity †" ecosystem
- 660 service management. *Ecology Letters*, 8(8), 857–874. doi: 10.1111/j.1461-
- 661 0248.2005.00782.x

- 662 Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., ...
- 663 Westphal, C. (2012, August). Landscape moderation of biodiversity patterns and
- 664 processes eight hypotheses. *Biological Reviews*, Vol. 87, pp. 661–685. doi:

665 10.1111/j.1469-185X.2011.00216.x

- Tuck, S. L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L. A., & Bengtsson, J. (2014).
 Land-use intensity and the effects of organic farming on biodiversity: a hierarchical
 meta-analysis. *Journal of Applied Ecology*, *51*(3), 746–755. doi: 10.1111/13652664.12219
- Valencia, E., Gross, N., Quero, J. L., Carmona, C. P., Ochoa, V., Gozalo, B., ... Maestre, F.
 T. (2018). Cascading effects from plants to soil microorganisms explain how plant
 species richness and simulated climate change affect soil multifunctionality. *Global*

673 *Change Biology*. doi: 10.1111/gcb.14440

- 674 Vellend, M. (2016). The Theory of Ecological Communities. doi: 10.1515/9781400883790
- 675 Weisser, W. W., Roscher, C., Meyer, S. T., Ebeling, A., Luo, G., Allan, E., ... Eisenhauer, N.
- 676 (2017). Biodiversity effects on ecosystem functioning in a 15-year grassland
 677 experiment: Patterns, mechanisms, and open questions. *Basic and Applied Ecology*, 23,
 678 1–73. doi: 10.1016/j.baae.2017.06.002
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199, 213–227.
- 681 Winqvist, C., Bengtsson, J., Öckinger, E., Aavik, T., Berendse, F., Clement, L. W., ...
- Bommarco, R. (2014). Species' traits influence ground beetle responses to farm and
- landscape level agricultural intensification in Europe. *Journal of Insect Conservation*, *18*(5), 837–846. doi: 10.1007/s10841-014-9690-0
- 685 Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). Mixed Effects
- 686 Models and Extensions in Ecology with R. In *Springer* (1st ed.). New York, USA:
- 687 Springer-Verlag New York.

689	Table 1. Description of the	e different agricultural	management intensity	variables at the field
-----	-----------------------------	--------------------------	----------------------	------------------------

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

and landscape level used in the study, and their loadings in the selected PCA axes.

- 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				
	Shorter plants with reduced				
Plant neight	dispersal ability	_			
	Faster growing plants (more				
SLA	vulnerable to predators and	_			
	parasites)				
		Light-seeded plants with high			
Seed mass	_	dispersal but lower seedling			
		survival			
FUNCTIONAL DI		L DIVERSITY			
Diskasaa	Communities with reduced	Communities with reduced			
Richness	variation in functional trait values	variation in functional trait values			
	Communities where all trait values				
Evenness	are more evenly represented	_			
	Communities where the most				
Divergence	abundant species have different	_			
	trait values				
Dodurdore	Communities with fewer plants of				
Keaundancy	similar trait values	-			

698 Fig. 1. Illustration of the selected indices of functional structure. In the TPD framewok, 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

125 level management intensity and their interaction), and R^{2}_{Cond} includes both fixed and random

reaction of the field of the fi

727 France; Go: Germany (Göttingen); IRL: Ireland; JE: Germany (Jena); NL: Netherlands; PL:

728 Poland; SP: Spain; SWE: Sweden).

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

models. Functional composition is represented by the community weighted mean of plant

- 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 mnagement intensity and their
- interaction), and R^{2}_{Cond} includes both fixed and random effects. Colors indicate the study area
- 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).
- 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
- via using linear mixed models. R^{2}_{Marg} indicates the proportion of variance explained by the fixed
- refrects (field and landscape level management intensity and their interaction), and R^{2}_{Cond}
- 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).









750 Fig. 3.



752 Fig. 4.

753 Supporting information

- Appendix S1. References for individual datasets included in the TRY database from which
 trait information was used.
- **Table S1**. Mean and standard deviation of agricultural intensification values at the field and
 landscape levels for each study area.
- **Table S2**. Comparisons of models considering and not considering random slopes for thestudy areas.
- 760 **Fig. S1**. Biplot of the principal components analysis (PCA).
- Fig. S2. Partial regression plots showing the effects of agricultural intensification at the fieldand landscape levels on functional richness SES.
- 763 Fig. S3. Partial regression plots showing the effects of agricultural intensification at the field
- and landscape levels on relative functional redundancy (functional redundancy after
- removing the effect of species richness).