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1 **Assessing non-intended effects of farming practices on field margin**
2 **vegetation with a functional approach**

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23 **Abstract (320 words)**

24 To assess the unwanted side effects of farming practices on non-target plants, we used a
25 nationwide survey of the vegetation of arable field margin strips. The vegetation was
26 surveyed during two years (2013, 2014) in 430 field margins distributed over all agricultural
27 regions of France. We used two complementary multivariate, trait-based approaches to
28 examine how ten plant traits were related to ten environmental variables describing abiotic
29 conditions, landscape factors, field margin management and in-field practices. Generalized
30 additive mixed models were also developed to assess how the same environmental variables
31 correlated with species richness, functional diversity and relative richness of agrotolerant
32 versus hemerophobic species. Traits responded primarily to an environmental gradient of
33 landscape diversity and field margin management. For instance, narrow field margin strips,
34 frequent management and presence of a ditch favoured annual plants, small size at maturity
35 and perennial plants, respectively. The second environmental gradient affecting plant traits
36 was related to field size and intensity of in-field farming practices. On this gradient, fertilizer
37 drift appeared to have a much stronger effect on plant trait composition of field margin strips
38 than herbicide drift. The relationship between species richness, or functional diversity, and
39 environment was consistent with the trait-based approach: the two former variables were
40 negatively correlated with agriculture intensification (e.g. field size). However, this analysis
41 also highlighted new covariates, such as a negative relationship between frequency of
42 herbicide use and species richness. Some of the observed patterns seemed to be driven by
43 differential responses of agrotolerant versus hemerophobic species, with the latter being more
44 species-rich under organic than under conventional farming. Despite efforts to reduce
45 nitrogen inputs since the 2000s, our results shows that N-fertilization still has significant non-
46 intended effects on field margin vegetation. More generally, increasing the width of field
47 margin strips, keeping or restoring semi-natural elements (ditches, hedges) in the field

48 boundary, and lowering the number of management events may promote grassland plant
49 species more typical of semi-natural habitats.

50 **Keywords:** Agrotolerant species ; Field margin width ; Agricultural land use intensity;
51 Nitrogen fertilizer ; Pesticide drift; Plant diversity

52

53

54

55 **1. Introduction**

56 During the second half of the twentieth century, the conjunction of mechanization, landscape
57 simplification and widespread use of chemical inputs has resulted in dramatic changes in the
58 environmental conditions of arable landscapes (Stoate et al., 2001). This is associated with
59 both a loss of non-crop habitats (Robinson and Sutherland, 2002) and a massive decline in
60 abundance and diversity of biotas associated with arable fields (Benton et al., 2002; Donald et
61 al. 2001; Fried et al., 2009). In many agricultural landscapes, field boundaries have become
62 the last remnants of semi-natural habitats and their functional role as refugia for a high level
63 of botanical diversity and for supporting a diverse fauna has been increasingly recognized
64 (Marshall and Moonen, 2002). However, the quality of this habitat may also be lowered by
65 intensive agriculture, particularly due to leaked or misplaced fertilisers and herbicides in the
66 adjacent arable land (Boutin and Jobin, 1998; de Snoo and van der Poll, 1999; Kleijn and
67 Verbeek, 2000). Assessing the effects of farming practices on non-target organisms is crucial
68 to guide farmers towards better practices, and also as a part of official post registration
69 monitoring of pesticides. However, detecting such effects requires disentangling the role of
70 agricultural practices, landscape and local abiotic environmental conditions (e.g. soil type).

71 Previous studies have shown that the vegetation of field boundaries is influenced by
72 the combination of both environmental conditions and management practices. Several studies
73 found that the plant community composition of field boundaries varies primarily with
74 landscape structure (proportion and diversity of non-arable habitat patches at the landscape
75 level) and spatial variables (Aavik et al., 2008; Aavik and Liira, 2010; Tarmi et al., 2009).
76 Local habitat structure (boundary width, presence of ditches and hedgerows) and boundary
77 management were also shown to be important factors, while the influence of farming in the
78 adjacent field was less clear (Tarmi et al., 2009). Conversely, Bassa et al. (2011) found
79 significant differences between broad management type (organic versus conventional), with

80 fewer effects of landscape structure. Similarly, Petersen et al. (2006) highlighted a rapid effect
81 of conversion to organic farming in field boundaries of dairy farms, with fewer nitrogen-
82 demanding or ruderal species and more stress-tolerant species. Kleijn and Verbeek (2000)
83 also found a strong effect of in-field fertilisation on species richness of the boundary
84 vegetation, while boundary management and use of herbicides in the boundary had no effects.
85 Comparing unsprayed and sprayed ditches, de Snoo and van der Poll (1999) found a
86 significant effect of herbicide drift only on dicotyledonous species of adjacent winter wheat
87 field boundaries. Some of these previous results, and a vast literature in plant ecology
88 (reviewed e.g. in Garnier and Navas 2012), suggest that the impacts of both agricultural
89 practices and the landscape on the community composition of field margins depend on some
90 key functional traits, particularly response traits sensu Lavorel and Garnier (2002). Therefore,
91 the use of trait-based approaches may offer opportunities for a deeper mechanistic
92 understanding of the impacts of environmental factors, including management practices, on
93 the vegetation of field margins.

94 Despite the growing number of studies, there have been few attempts so far to
95 characterize the composition of plant functional traits in field margin communities, and its
96 environmental correlates (but see Alignier and Baudry, 2015; Alignier, 2018; Chaudron et al.,
97 2018). Here we use trait-based approaches to examine which environmental variables best
98 explain the assembly of field margin plant communities, using a nationwide standardized
99 monitoring scheme designed to detect the non-intended effects of in-field practices,
100 particularly the use of synthetic inputs, on biodiversity. The following questions were
101 addressed: (1) Are the links between environmental conditions, in-field management practices
102 and plant traits in field margins consistent with expectations derived from ecological
103 knowledge in more natural settings (see below for the details of such expectations)? (2) Are
104 there any trait syndromes associated with gradients of management practices and/or land-use

105 intensity? (3) What factors influence plant species richness and plant functional diversity in
106 field margins?

107

108 **2. Methods**

109 *2.1. Vegetation survey*

110 The “500 ENI” network is a long-term survey initiated by the French Ministry of Agriculture.
111 It is designed to detect and document nationally any significant changes in wild flora and
112 fauna (birds, beetles, and earthworms) of agricultural landscapes that could be associated with
113 non-intended effects of agricultural practices, especially fertilization and pesticides (Andrade
114 et al., *in prep.*). For this purpose, 500 fields distributed over all agricultural regions of France
115 (including Corsica) were chosen to be representative of the main crop productions, using a
116 stratified sampling within each administrative region. The survey focuses on three types of
117 production systems: annual crops (wheat or maize as the main crop production), vineyards
118 and market gardening centred on lettuce production. Here, we worked with a subset of 430
119 field margins (out of 500), chosen as those for which comprehensive floristic data were
120 available in both 2013 and 2014 (see Figure 1 for a distribution map).

121 Three main areas are recognized in field margins (Greaves & Marshall, 1987; Marshall &
122 Moonen, 2002): *crop edge*, *field margin strip* and *field boundary*. The area surveyed in the
123 “500-ENI” program excludes the crop edge (sometimes called *conservation headland*) which
124 is located in the first 1-6 meters *within* the crop. It also excludes the *cultivated strip*, outside
125 the last row of crop, which is an area with mostly bare soil usually colonized by weed species
126 from the field. The area of interest is the *field margin strip* (sensu Marshall & Moonen, 2002,
127 hereafter *field margin*), which is the uncultivated herbaceous vegetation area between the
128 cultivated strip and another patch in the landscape. The latter can be a field boundary

129 embodied by a ditch and/or a hedge, or other land covers such as a road, a track, other fields
130 or grassland-type vegetation (see below).

131 Wild plant species were identified in ten 1m² quadrats located in the field margin. The ten
132 quadrats were divided into two sets of five contiguous quadrats of 0.25*2 m² separated by 30
133 m. The quadrats were placed in the centre of the field margin (i.e. equidistant from the field
134 and the adjacent land cover). Their position was maintained in the same field margin across
135 the two years but their exact location may slightly differ from year to year. Only presence-
136 absence of plant species was recorded in the ten quadrats, so that the abundance of each
137 species was characterized by a frequency of occurrence (0-10) in each field margin. Surveys
138 were performed at the peak of flowering, which is from late April to early August depending
139 on locations (50% of the observations were made between June 6th and July 11th). In order to
140 avoid the issue of differences in rare species detection among observers, and because trait data
141 are not available for all species, we focused on species observed in more than 1% of the
142 surveyed margins, i.e. 186 of 331 species observed in total, representing 94.9% of the total
143 abundance (number of quadrats). All subsequent analyses were performed on this subset of
144 species.

145

146 *2.2. Environmental data*

147 Ten environmental variables were used to describe the field margins and were grouped into
148 four categories: 1) two abiotic factors, 2) three landscape factors, 3) two field margin
149 management practices and 4) three management practices within the adjacent field. (1) From
150 the coordinates of the field margin, we retrieved eight factors from the Soilgrids dataset at
151 250m resolution (Hengl et al., 2017). We performed a PCA and extracted the first two axes,
152 which represented 65% of total inertia. Axis 1 was associated with a combination of soil pH

153 and texture, opposing sandy acidic soils (positive values) to basic clay soils (negative values).
154 Axis 2 was positively associated with the level of organic matter (see Appendix A for the
155 detailed outputs of the PCA). (2) Landscape composition was described on the basis of the
156 proportion of land cover (crop, grassland, woodland, etc.) within 250 m of the field margin.
157 By summing the proportion of all non-cropped area (i.e. permanent grasslands, heaths, hedges
158 and woodland as well as water surfaces), we characterized the amount of non-arable land
159 cover, which is a well-established landscape metric for landscape complexity (Gabriel et al.,
160 2005). The size of the field adjacent to the studied margin was also considered as a landscape
161 variable. The local habitat structure immediately adjacent to the field margin (i.e. the field
162 boundary *sensu* Marshall & Moonen, 2002) was characterized by the presence/absence of
163 ditches or hedges resulting in four field boundary classes: i) ditch and hedge present, ii) ditch
164 present, iii) hedge present, iv) no ditch or hedge. This latter category corresponds to field
165 boundaries with no particular features, where the field margin is contiguous with another land
166 cover type, such as roads or tracks (68%), other fields (12%), or grassland-type vegetation
167 (16%). (3) Field margin management was characterized by the number of management
168 events; mowing was the dominant management type ($n=582$ occurrences for the two years)
169 with only few margins with use of chemicals ($n=8$) or grazing ($n=12$). Field margin width was
170 also recorded. When the surveyed arable field was adjacent to a grassland, field margin width
171 was measured up to the visible boundaries of cadastral parcels. (4) Management within the
172 field was summarized by the amount of nitrogen fertilizer input, and the Treatment Frequency
173 Index (TFI) for herbicides and insecticides. TFI is calculated as the cumulative ratio of the
174 dose applied to the recommended dose, for all treatments applied during the growing season
175 (Halberg, 1999). Finally, observation date (number of days since January 1st) and year (2013
176 or 2014) were also added as explanatory variables. The farming system (conventional versus
177 organic) in the field adjacent to the surveyed margin was also incorporated in the analyses

178 either as a supplementary variable (when in-field practices were already included) or as a
179 primary variable accounting for management practices.

180

181 *2.3. Plant trait data*

182 Seven functional traits and three indicators of ecological performance were chosen on the
183 basis of hypotheses related to potential non-intentional effects of farming practices and field
184 margin management on two main ecological axes, namely fertility (resources) and
185 disturbances (Table 1). The level of disturbances (frequency and intensity) is assumed to
186 favour short-lived species reaching small height at maturity but having rapid growth rate and
187 high seed output (ruderal strategy, e.g. Lavorel and Garnier 2002, Grime 2006). Thus,
188 disturbances such as the number of management events in the margins and herbicide drift
189 related to the intensity of herbicide use are expected to promote a higher proportion of annual
190 species, species with high Specific Leaf Area (SLA), low seed mass and short plant height.
191 The level of fertility is assumed to favour nitrophilous species, i.e. with high Ellenberg-N, tall
192 competitive plants or rapid growing species with high SLA values (e.g. Lavorel and Garnier
193 2002, Grime 2006), although trait responses to these two major environmental drivers can
194 sometimes be more complex (Douma et al. 2012). Additional hypotheses were also
195 considered. The presence of hedges can favour shade-tolerant species (low Ellenberg-L
196 values), while the presence of ditches can favour water-demanding species (high Ellenberg-H
197 values). Disturbance caused by insecticides are expected to favour selfing species and species
198 with abiotic pollination over entomogamous species, via a decrease in the abundance and
199 diversity of pollinators (Brittain and Potts 2011). Landscape diversity and proximity of semi-
200 natural habitats are expected to benefit plants with animal pollination and dispersal (e.g.
201 Steffan-Dewenter and Tschamtkke 1999). A functional diversity index can be computed on the

202 basis of these traits (see below) in addition to classical taxonomic diversity indices such as
203 species richness. Since we have included both response and effect traits (Lavorel and Garnier,
204 2002), a field margin with high functional diversity can be interpreted as supporting: i) a
205 community including species with different ecological strategies ensuring more resistance to
206 environmental changes and, ii) a community including species with different functions
207 providing a larger range of resources for species of higher trophic levels.

208 In parallel to classic plant traits, we also used an emergent classification of species on the
209 basis of their responses to agricultural disturbances. Following Aavik and Liira (2009),
210 species were classified into agrotolerant (i.e. species adapted to current disturbance regimes in
211 arable fields, under modern conventional agriculture) and hemerophobic species (i.e., species
212 that are sensitive to soil tillage and/or herbicides). Each species was classified on the basis of
213 its frequency of occurrence in arable fields using data of the Biovigilance Flore network
214 (2002-2012), which covered the same area as in the present survey, i.e. the whole of France
215 (Fried et al., 2008). The 47 species present in more than 10% of the 1440 arable fields
216 surveyed in Biovigilance Flore were considered as agrotolerant, while the hemerophobic
217 group was made of both grassland species and rare arable weeds that are not adapted to
218 current farming practices (see Appendix B).

219

220 *2.4. Data analysis*

221 To analyse the relationships between the variation in plant traits of field margins and the
222 variation in environmental factors, we followed the framework introduced by Dray et al.
223 (2014) combining the RLQ multivariate technique (an ordination analysis) and the fourth
224 corner analysis (a hypothesis testing analysis). RLQ assigns scores to species, samples, traits,
225 and environmental variables along orthogonal axes and yields a graphical summary of the
226 main structures (Dolédec et al., 1996), while the fourth corner analysis tests the multiple

227 associations between one trait and one environmental variable at a time (Dray and Legendre,
228 2008).

229 Both methods use three tables: the R-table, which consists of the 860 samples (430
230 field margins x two years) described by the ten environmental and two temporal variables, the
231 Q-table containing the 186 species described by their 10 traits and the L-table describing the
232 floristic composition of the 860 samples via the abundance of 186 species. The L-table
233 therefore links the R- and the Q-tables. For the RLQ analysis, a correspondence analysis (CA)
234 was first performed on the L-table using the raw frequency of occurrence score for each
235 species (0-10). Next, a Hill and Smith analysis (a mixed ordination method similar to PCA
236 that allows combining quantitative variables and factors; Hill and Smith, 1976) was
237 performed on the R-table (using the row scores of the CA on the L-table as canonical factor),
238 and on the Q-table (using the column scores of the CA on the L-table as canonical factor).
239 Finally, RLQ calculates two separate co-inertia analyses on the R-L and L-Q tables. RLQ
240 selects the axes that maximise the co-variance between the site scores constrained by the
241 environmental variables (the R-table) and the species scores constrained by the species traits
242 (the Q-table). A Monte-Carlo permutation ($n=999$) test was used to test the null hypothesis
243 (H_0) of absence of link between the environmental table (R) and the trait table (Q).

244 Thereafter, the fourth-corner statistic (Dray and Legendre, 2008) was used to test the
245 significance of the direct trait-environment relationships on these 860 samples (430 field
246 margins x 2 years). This method measures the link between species traits and environmental
247 variables using either (1) a Pearson correlation coefficient r for two quantitative variables, (2)
248 a Pearson Chi-square (χ^2) and G-statistic for two qualitative variables or (3) pseudo-F and a
249 Pearson correlation coefficient r for one quantitative and one qualitative variable. A
250 permutation model was applied to test the null hypothesis (H_0) that species are distributed
251 independently of their preferences for environmental conditions and of their traits (using the

252 permutation model 6 of Dray et al., 2014). We performed 49999 permutations and used the
253 false discovery rate method (Benjamini and Hochberg 1995) to adjust P values for multiple
254 testing.

255 One limit of the RLQ analysis is that it only tests for the existence of a general
256 relationship between environmental gradients and combinations of species traits, which does
257 not allow identifying precisely which environmental variable acts on which trait. Conversely,
258 the fourth-corner analysis does not account for the covariation among traits or among
259 environmental variables. Therefore we combined the two analyses by applying the fourth-
260 corner tests directly on the outputs of RLQ analysis. This latter approach consists in testing
261 the associations between individual traits and environmental gradients obtained from RLQ
262 scores, and between individual environmental variables and trait syndromes obtained from
263 RLQ scores. The detailed procedure can be found in Dray et al. (2014).

264 The centroids and ellipses of agrotolerant and hemerophobic species were also
265 projected as supplementary individuals on the RLQ axes to assess the response of these two
266 broad ecological groups on the highlighted trait-environment gradients. Similarly the
267 conventional versus organic farming systems of the fields were projected. Significant
268 differences between the median distribution of agrotolerant and hemerophobic species on the
269 RLQ axes on the one hand, and between conventional versus organic fields on the other hand,
270 were tested with a Wilcoxon test.

271 In a second part, we modelled species richness (S), relative proportion of agrotolerant
272 (S_A) vs. hemerophobic (S_H) species, and functional diversity (FD , see below for the
273 definition), three variables related to plant community diversity. This was done using
274 generalized additive mixed models (GAMMs) and the `gamm4` package (Wood and Scheipl,
275 2016) with appropriate likelihood and link function, i.e. respectively a Poisson error structure

276 with a logarithm link (species richness), a binomial error structure with a logit link
277 (proportion of agrotolerant vs. hemerophobic species) and Gaussian error with identity link
278 (functional diversity). The identity of the field margin was included as a random effect to
279 account for pseudo-replication, a common issue in ecological modelling (Hurlbert, 1984).
280 Three different models were built for the three different response variables, each including the
281 twelve variables used in the RLQ/fourth corner analysis (i.e. ten environmental variables +
282 day and year of observation) as potential explanatory variables. In addition, the spatial
283 coordinates of the field margins (latitude and longitude in meters) were used to account for
284 spatial heterogeneity that could not be properly modelled through other explanatory variables,
285 thanks to a smooth term modelling the interaction between latitude and longitude. The degree
286 of freedom of this smoother modelling spatial heterogeneity was left unconstrained (contrary
287 to other covariates, see below). Local habitat structure, number of management events and
288 year were considered as parametric coefficients, while soil pH, soil organic matter, percentage
289 of non-arable patches, field size, field margin width, N-Fertilization, TFI herbicides, TFI
290 insecticides were considered as smooth terms with a limited degree of freedom ($k=5$) to avoid
291 overfitting. Correlations for all pairs of variables included in the analyses were well below the
292 threshold of 0.7 (Burnham and Anderson, 2002; Freckleton, 2011, see Appendix C). All
293 explanatory variables (except spatial coordinates) were scaled to facilitate the estimation of
294 parameters and their interpretation (Schielzeth, 2010). Residuals were visually inspected to
295 detect trends that could bias estimates but all assumptions of GAMMs were met. Besides
296 examining the relationship with detailed in-field practices, we also compared S , S_A , S_H and FD
297 between conventional and organic field margins with Wilcoxon tests.

298 Functional diversity was computed using the package BAT (Cardoso et al., 2015) and
299 the functional diversity index introduced by Cardoso et al. (2014), which is the total branch
300 length of a functional tree linking all species present. We used the Hill and Smith analysis

301 previously performed for the RLQ analysis on the Q table (traits). The first two axes were
302 conserved and a functional tree was built on the basis of the Euclidean distance between
303 species in the trait multivariate space and Ward's clustering algorithm. Low functional
304 diversity characterizes communities composed of closely related species in the trait functional
305 space, while high functional diversity is indicative of communities with species occupying
306 distinct and distant positions in the trait multivariate space.

307

308 **3. Results**

309 3.1. Impact of environmental conditions and management practices on functional composition

310 The first two axes of the RLQ accounted for 75.1% of the total inertia (61.2 and 13.9%
311 respectively, Figure 2). The Permutation tests indicated that the environment influences the
312 distribution of species with fixed traits (Model 2, $P < 0.001$ based on 999 permutations) and
313 that the traits influence the composition of species assemblages found in samples with given
314 environmental conditions (Model 4, $P < 0.001$ based on 999 permutations). The first two RLQ
315 axes accounted for most of the variance of the corresponding axes in the separate analyses of
316 environmental descriptors (85.1% for the Hill and Smith analysis of the R-table) and species
317 traits (76.8% for the Hill and Smith analysis of the Q-table), which demonstrates the strength
318 of the link between environmental filters (including management practices) and plant species
319 traits in field margins.

320 The first RLQ axis discriminated sites according to a double gradient, related to
321 landscape diversity and soil resources (Figure 2, Table 2). The proportion of non-arable land,
322 the presence of a ditch, or both a ditch and a hedge within 5 m from the field margins as well
323 as margin width were negatively correlated with axis 1. Soil pH and clay textures were
324 positively correlated with axis 1. The second axis discriminated sites according to an
325 agricultural intensification gradient with positive loadings associated with high herbicides

326 use, high nitrogen fertilization level and large field size together with a high number of
327 management events in the field margin (Figure 2, Table 2). Soil organic matter was also
328 positively correlated with this second axis. Regarding species traits, the first axis was best
329 correlated with traits related to the competition/disturbance trade-off: perennial, shade-
330 tolerant species with high requirement for soil moisture (Ellenberg-H) were preferentially
331 associated with negative loadings and opposed to annuals, drought tolerant and light-
332 demanding (Ellenberg-L) species. On the second axis, species with rapid resource acquisition
333 syndrome were on positive loadings associated with short height at maturity, early flowering,
334 high SLA and high Ellenberg indicator values for nitrogen, while species with opposed
335 features, pollinated by insects and dispersed by animals were on negative loadings.

336 When applying the fourth corner analysis, among the 208 possible combinations of
337 bivariate associations between traits and environmental variables, 42 were found significant
338 (significance level $\alpha=0.05$, Figure 3a). When P values were adjusted for multiple testing, 13
339 associations remained significant (Figure 3b). Annuals were negatively associated with
340 margin width ($r=0.053$, $P_{adj}=0.030$), and observation date ($r=-0.158$, $P_{adj}=0.010$), while
341 perennials showed the opposite association, and were also associated with field margins with
342 ditches ($F=4807$, $P_{adj}=0.030$). Plant height at maturity was negatively correlated with the
343 number of field margin management events ($r=-0.068$, $P_{adj}=0.010$), positively associated
344 with the presence of ditches ($r=0.091$, $P_{adj}=0.010$) and negatively associated with margins
345 with no hedge or ditch beside ($r=-0.073$, $P_{adj}=0.010$). Ellenberg indicator values for light was
346 positively associated with margin with no hedge or ditch ($r=0.072$, $P_{adj}=0.030$), and
347 negatively related to soil organic matter content ($r=-0.083$, $P_{adj}=0.010$). Ellenberg indicator
348 values for soil moisture was negatively associated with soil pH ($r=-0.123$, $P_{adj}=0.010$) and
349 positively correlated with date of observation ($r=0.100$, $P_{adj}=0.030$). Finally, Ellenberg

350 indicator values for nitrogen was positively correlated with the level of N fertilization ($r=$
351 0.062 , $P_{adj} = 0.029$).

352 Testing directly the link between RLQ axes and traits or environment (Figure 4)
353 showed that RLQ axis 1 was negatively correlated with soil organic matter, high proportion of
354 non-arable habitats in the landscape, field margin width, presence of ditches, or ditches and
355 hedges and date of observation. RLQ axis 1 was positively associated with soil pH, number of
356 management events on the margin, and absence of ditches or hedges. Species associated with
357 these regularly managed, narrow field margins on high soil pH in arable-dominated
358 landscapes were heliophilous and drought resistant annuals, while shade-tolerant,
359 hygrophilous perennials were associated with large field margins on soil with elevated
360 organic matter and presence of ditches and/or hedges in more diversified landscapes. The
361 second RLQ axis significantly opposed sites according to soil organic matter, field size,
362 number of field margin management events and level of N-fertilization. Communities found
363 in field margins with little management, adjacent to small-sized fields with low N-fertilization
364 input and low organic matter content contained oligotrophic species as well as a higher
365 proportion of insect-pollinated and animal-dispersed plants.

366 The median of agrotolerant species was significantly different from the median of
367 hemerophobic species both on RLQ axis 1 and axis 2, with higher values on both axes for
368 agrotolerant species (Figure 5), i.e. agrotolerant species were associated with disturbed field
369 margins (RLQ axis 1) adjacent to fields with intensive farming practices (RLQ axis 2). The
370 position of field margins adjacent to conventional fields was not different from those adjacent
371 to organic fields on RLQ axis 1 but they were significantly higher on RLQ axis 2 (Figure 6),
372 which was expected because farming system (conventional vs. organic) recapitulates farming
373 practices encapsulated in RLQ axis 2 (N fertilization and pesticides).

374

375 3.2. Impact of environmental conditions and management practices on taxonomic and
376 functional diversity

377 In all three generalized additive mixed models (whose adjusted R^2 values were 0.34, 0.31 and
378 0.30 for species richness, relative proportion of agrotolerant species and functional diversity
379 respectively), the spatial term absorbed a lot of the deviance by delimiting areas with
380 contrasting spatial structure for the response variable (see Appendix D). In addition to these
381 spatial effects, species richness in field margins decreased linearly with increasing field size
382 (Chi sq.=12.83, $P<0.001$) and decreasing soil organic matter (Chi sq.=5.61, $P=0.018$) with
383 similar magnitude ($\beta_{Field\ size} = -0.07 \pm 0.02$ and $\beta_{Soil\ organic\ matter} = 0.06 \pm 0.028$) and responded
384 negatively to the frequency index of herbicides use, although with a lower slope ($\beta_{TFI\ herbicides}$
385 $= -0.028 \pm 0.014$, Figure 7a, Appendix E). Functional diversity was related similarly to these
386 two variables: linearly with field size ($F=12.08$, $P<0.001$) and in a slightly non-linear way
387 with soil organic matter ($F=5.91$, $P=0.030$), with slopes of similar magnitude (see Figure 7b).
388 The proportion of agrotolerant relative to hemerophobic species depended on field boundary
389 structure, with more agrotolerant species in the absence of a ditch or hedge ($z=2.32$, $P=0.020$).
390 The proportion of agrotolerant species also increased with decreasing field margin width (Chi
391 sq.=5.33, $P=0.021$) and increasing soil pH (Chi.sq=4.769, $P=0.029$), with a weaker effect for
392 field margin width than for soil pH ($\beta_{Margin\ width} = -0.065 \pm 0.03$ and $\beta_{Soil\ pH} = 0.1 \pm 0.045$,
393 Figure 7c).

394 With an average of 16.53 ± 6.38 species, organic field margins were richer than conventional
395 field margins (14.07 ± 6.61 species; Student t-test, $t = 3.690$, $P < 0.001$). This difference was
396 caused mainly by hemerophobic species whose number was significantly higher in organic
397 (9.34 ± 5.29) than in conventional (7.49 ± 4.89) field margins ($t = 3.509$, $P = 0.001$) with

398 smaller but nonetheless significant differences regarding agrotolerant species (7.19 ± 3.24 and
399 6.58 ± 3.26 respectively, Student t-test, $t = 1.841$, $P = 0.022$). Functional diversity was also
400 higher in organic ($FD = 125.83 \pm 27.69$) compared with conventional field margins
401 ($FD = 114.95 \pm 29.63$, Student t-test, $t = 4.774$, $P < 0.001$).

402

403 **4. Discussion**

404 The aim of the study was to test the relationships between plant traits and environmental and
405 management conditions in field margins, and to identify the main factors structuring field
406 margin vegetation. The first gradient discriminating field margin vegetation at the nationwide
407 level depended on field boundary “naturalness” (landscape diversity, field boundary structure,
408 margin width and number of management events). The second gradient was based on the
409 intensity of in-field management (amount of nitrogen fertilizers, field size). Field margin
410 vegetation was thus structured by two independent gradients of disturbances and fertility. We
411 showed that these gradients were associated with particular plant trait syndromes including
412 life cycle duration, plant height, mode of pollination and dispersal as well as responses to
413 light, soil moisture and nitrogen. Broad classification of species into agro-tolerant versus
414 hemerophobic species, and management practices into conventional versus organic, were also
415 distinctly distributed on the RLQ axes showing the consistency of these groupings. Species
416 richness and functional diversity were primarily correlated with landscape heterogeneity (field
417 size) and abiotic factors (soil organic matter), with species richness also decreasing with the
418 frequency index of herbicides use. The relative proportion of agrotolerant versus
419 hemerophobic species changed with soil pH and was also related to more local factors such as
420 margin width and field boundary structure.

421

422 4.1. Disturbances gradient and naturalness of field margins

423 The level of disturbances incurred by field margins via direct management appeared as the
424 main factor structuring the functional composition of the vegetation. As expected, it opposed
425 small annual agro-tolerant species in narrow, frequently managed margins to taller perennial
426 hemerophobic species in wider, less frequently managed margins. The accumulation of
427 recurring disturbances such as mowing can create bare soil for colonization and transient
428 establishment of annual species able to use resources rapidly (Kleijn, 1997).

429 In our dataset, this gradient of disturbance was also correlated with the proportion of non-
430 arable crop habitats in the landscape and with the diversity of the field boundary structure,
431 especially the presence of ditches and/or hedges. The combination of these local and
432 landscape elements creates a diversity of environmental conditions that is suitable for various
433 hemerophobic species. Hence, the above-mentioned factors generate a gradient from moist
434 and shady conditions (i.e. ditch verges with tree layer) with hygrophilous and shade-tolerant
435 species typical of wetlands such as *Lysimachia vulgaris* or *Mentha suaveolens*, to open dry
436 conditions (i.e. open road verges) with heliophilous and drought tolerant species (*Erodium*
437 *cicutarium*, *Echium plantagineum*). Our study confirms the importance of this gradient in a
438 different context (Western Europe) and at a wider spatial scale, similarly to the gradient
439 observed in a region of Estonia (Aavik et al., 2008, 2010).

440 This double gradient of boundary management intensity and naturalness was not related to a
441 gradient of species richness but it did influence the richness of agrotolerant and hemerophobic
442 species. General theory concerning diversity-area relations predicts that larger margins will
443 support richer communities. Our standardized protocol measuring species richness on 10m²
444 equidistant from the field and the adjacent habitat excludes this type of effect (that may
445 however still exist on the larger landscape level). Instead, the width of the field margin

446 determines higher buffering capacities relative to within field practices (De Cauwer et al.,
447 2006) and higher environmental quality in the interior of the margin (Aavik and Liira, 2010).
448 Thus it is not surprising that species richness on the whole was unaffected by field margin
449 width, while as expected, more agrotolerant species were observed on narrow margins which
450 reflects the higher influence of in-field management practices in this type of margins.
451 Conventional and organic field margins were not different on this gradient, which suggests
452 that some field margins of organic farms can be managed intensively (e.g., field margins next
453 to roads, managed by regional or local authorities), while conversely some conventional
454 farmers maintain margins with diversified local habitat structure.

455

456 4.2. Resource gradient associated with agricultural intensification and non-intended effects of 457 in-field practices

458 The second structuring factor was related to in-field practices (fertilization,
459 herbicides), field size and again the frequency of field margin management. It opposes small-
460 sized nitrophilous species, with early flowering and rapid acquisition resource capacity (SLA)
461 in margins of large, intensively managed crop fields, to taller, later flowering and less
462 nitrogen-demanding species with slower resource acquisition in smaller, less intensively
463 managed crop fields. Specific bivariate association between practices and species traits
464 showed that this gradient was mainly driven by the dose of in-field nitrogen fertilizers and the
465 proportion of nitrophilous species. Contrary to our expectations, we did not find any
466 particular traits associated with more intensive uses of herbicides within the field. However,
467 there was a significant negative effect of the frequency index of herbicide use within the field
468 on species richness in the field margin. This result is consistent with several fine scale
469 experiments that showed a delayed flowering onset and a reduced flower number for plants

470 exposed to herbicide drift at ~1% of the field application rate (Bohnenblust et al., 2016) or a
471 reduction of species richness in plant communities exposed to increasing doses of glyphosate
472 applied at drift levels, from 0 to 25% of the counselled rate (Pelissier et al., 2014). Decreased
473 species richness combined with an absence of effects on functional diversity or composition
474 suggests that the loss of species due to the intensity of herbicide use is not determined by the
475 ten traits used in our classification. Other traits such as plant morphology or leaf surface traits,
476 including cuticle characteristics, hairiness (e.g. density of trichomes), density of stomata or
477 cell size, may be more relevant for sensitivity to herbicides, as they are related to the wetting
478 and the penetration of foliar applied herbicides and therefore their bioavailability within the
479 plant (Gaba et al., 2017). Alternatively, opposite responses of plant traits, such as height or
480 SLA, to herbicides vs. fertilizers (Pelissier et al. 2014) may have hampered our ability to
481 detect trait-based changes in community composition.

482 The effect of nitrogen fertilizer input to the crop on the richness or composition of the
483 vegetation of field margin has been reported previously (e.g., Kleijn and Verbeek, 2000 ;
484 Pélissier et al., 2014) and this drift was also confirmed in our study. In addition to earlier
485 studies, the fourth corner test in our study demonstrates the direct link between the abundance
486 of high-nitrogen demanding species (species with high Ellenberg-N values) in the field
487 margin and the amount of nitrogen fertilizer applied within the field. This suggests a strong
488 shift in species composition following higher resource supply. However, contrary to other
489 studies, the high levels of fertilization were not associated with a decrease in species richness.
490 The expected negative relationship between fertility and species richness (Tilman, 1993) is
491 attributable both to increased living biomass and litter accumulation that reduce light to very
492 low levels and thus inhibit germination and/or survival of seedlings, and decrease rates of
493 establishment of new species (Foster and Gross, 1998). The same processes are at play in
494 arable field margins where higher nutrient application levels on the field generally increases

495 field margin biomass (Kleijn, 1996). However, disturbances created by field margin direct
496 management can maintain gaps with less competitive annual species. Overall, the larger area
497 covered by our study (the whole of metropolitan France) compared to previous field boundary
498 studies, showed that species richness depends primarily on the natural soil trophic gradient,
499 which opposes species rich communities on organic-rich acidic soils, versus poorer
500 communities on organic-poor basic clay soils (Manhoudt et al., 2007).

501 Species depending on animals for their reproduction (obligate entomogamous species)
502 or for their dispersal (zoochorous species) were associated with smaller less intensively
503 managed fields in landscapes with a high proportion of non-arable habitats. Several processes
504 may be at play, which are difficult to disentangle. Small fields mean higher configurational
505 heterogeneity of landscapes (Fahrig et al., 2011) with more numerous linear elements that can
506 act as corridors needed for the stability of some animal populations (Marshall and Moonen,
507 2002; Molina et al., 2014). The higher proportion of non-arable habitats has also been shown
508 to favor animal diversity in agricultural landscapes (Weibull et al., 2000) through dispersal
509 from these habitats to field margins. More generally, the negative link of plants depending on
510 animals with RLQ axis 2 suggests that the absence of these species could be a consequence of
511 agricultural intensification. According to the fourth corner analysis none of the within field
512 practices of the contemporary years (dose of nitrogen fertilizer, intensity of herbicides or
513 insecticides use) were related to the presence of this group of species. However, the strong
514 link of dispersal and pollination modes with RLQ axis 2 (related to agricultural
515 intensification) might suggest that the presence/absence of entomogamous and animal-
516 dispersed species is rather a result of the interactions of cumulative management practices
517 over several years and their interactions with large scale factors (field size, landscape,
518 Roschewitz et al., 2005).

519 Relative proportion of agrotolerant and hemerophobic species could not be directly related to
520 one of these agricultural intensification factors. However, the distribution of agrotolerant
521 species was clearly more associated with positive values of RLQ axis 2 which means a
522 response to a combination of high input of agrochemicals (fertilizer, herbicides) and large
523 field size. Our general result on this agricultural intensification axis is consistent with
524 previous studies showing that among agrochemicals, the effect of fertilizers on plant
525 community composition in field margins is always stronger than the effect of herbicides
526 (Kleijn and Snoeiijing, 1997).

527

528 4.3. Implications for management of biodiversity in field margins

529 It is recognized that species richness is not necessarily the most suitable indicator of healthy
530 field margins because some species are known to respond positively to disturbances and/or
531 excess of nitrogen fertilizers. Following that idea, Aavik and Liira (2009) introduced a
532 classification in two groups, agrotolerant species and hemerophobic species, on the basis of
533 their capacity to persist in arable fields with modern cultivation practices (i.e., present in more
534 than 10% of the agricultural fields of the studied region). With our trait-based approach that
535 links directly environmental conditions and plant traits, we can confirm the utility of this
536 broad classification and characterize the functional profile of species associated with
537 undisturbed field margins adjacent to low input fields. Our RLQ axes reflect two independent
538 dimensions of field margin disturbances (axis 1) and agricultural intensification (axis 2). The
539 position of agrotolerant and hemerophobic species on these two axes is consistent with what
540 was expected. Therefore one can identify factors promoting hemerophobic species. On the
541 whole, their presence increases with field margin width, presence of semi-natural elements
542 such as ditches and hedges, high proportion of non-arable land, small field size, low number

543 of management events and low amounts of nitrogen fertilizer input. Associated traits include
544 species with a perennial life cycle, a high stature at maturity, low nitrogen requirements,
545 pollination by insects and dispersion by animals. As found in previous studies (e.g. Bengtsson
546 et al. 2005 for a review), organic field margins have higher species richness than conventional
547 field margins. Interestingly, the higher species richness in organic field margins is due, at
548 75%, to a higher number of hemerophobic species. Differences on the RLQ trait-environment
549 multivariate space showed that organic field margins differed from conventional field margins
550 on the agricultural intensification axis with fewer nitrogen-demanding species, more insect-
551 pollinated species and more animal-dispersed species.

552

553 **Conclusions**

554 With the aim of detecting non-intended effects of agrochemicals on non-targeted plants, our
555 study highlighted that the composition and the diversity of vegetation in arable field margins
556 were primarily driven by the direct field margin management and by landscape factors.
557 However, among farming practices, distinct non-intended effects of fertilization and
558 herbicides were highlighted. The level of nitrogen fertilizers had the strongest effects on the
559 functional composition of field margin vegetation with a change toward more nutrient-
560 demanding species, while the intensity of herbicides use was related to a slight decrease in
561 species richness with no effects on functional composition or diversity. A better
562 understanding of the effect of herbicide drift on non-target plant communities will require a
563 finer characterization of herbicides modes of action, as well as data on species traits related to
564 herbicides sensitivity, which will be the aim of further analyses.

565

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Table 1. List of selected traits with their abbreviations, units, and the management practices likely to affect these traits based on ecological mechanisms: Dist. = Disturbance, Res. = Resources.

Traits	Ecological mechanisms	Expected responses in field margin strips
Life form (annual/perennial)	Dist.	Field margin strip management frequency favours annuals; Field margin strip width favour perennials; herbicide drift favours agrotolerant (annual) species.
Plant height at maturity (cm)	Dist. (+Res.)	Field margin strip management frequency favours short species Plant height increases with resources (fertile soils, N Fertilisation)
Seed mass (mg)	Dist., Res.	Seed size/number trade-off : disturbed field margins favour species producing numerous small seeds (ruderal strategy) while stable field margins favour species producing fewer seeds each with higher seed mass (competitive strategy)
Specific Leaf Area, SLA (mm².mg⁻¹)	Res.(+Dist.)	N fertilization, Soil fertility (Organic matter), and Field margin strip management frequency favour species with high resource acquisition capacity (high SLA)
Flowering onset (month)	Dist. (+Res.)	Field margin strip management frequency favours early flowering species
Ellenberg-N (EIV-N)	Res. (soil N)	High N fertilization, fertile soils favour nitrogen-demanding species (high EIV-N) or tall competitive species.
Ellenberg-H (EIV-H)	Res. (water availability)	Presence of ditches favours hygrophilous species (high EIV-H)
Ellenberg-L (EIV-L)	Res. (Light availability)	Presence of hedges favours shade-tolerant species (low EIV-L)
Mode of pollination Mode of dispersal	Biotic interactions, Landscape	Plants dependent on animal for reproduction and dispersion may be less frequent in simplified landscapes (openfield) , pollinated plants may also decrease with insecticide use .

Table 2. List of management practices and selected traits with their abbreviations, units, basic statistics and their coordinates on the first two RLQ axes.

Environmental Variables	Mean (Min-Max) or counts	RLQ axis 1	RLQ axis 2
Soil			
Soil pH and texture gradient (soil pH)	6.89 (5.39-7.83)	0.501	0.248
Soil organic matter (soil OM) (ppm)	19.08 (5.71-53.29)	-0.322	0.486
Landscape			
Non-arable land [%]	16.68 (0-90.16)	-0.253	-0.218
Field size [ha]	7.47 (0.005-40)	-0.112	0.391
Boundary type			
Ditch	<i>n</i> = 46	-0.812	-1.169
Ditch and hedge	<i>n</i> = 12	-1.012	0.738
Hedge	<i>n</i> = 49	-0.036	0.250
Other boundary type	<i>n</i> = 323	0.170	0.118
Field Margin			
Margin width [m]	3.13 (1-10)	-0.141	0.029
Number of management events (N. Mgt events)	1.18 (1-3)	0.171	0.311
In-field farming practices			
Nitrogen fertilizer input in field (N Fertilizer) [kg.ha ⁻¹ .year ⁻¹]	119.17 (0-500)	-0.083	0.397
TFI Herbicides (TFI Herbi)	0.94 (0-3)	-0.037	0.156
TFI Insecticides (TFI Insec)	0.21 (0-3.90)	0.078	0.059
Temporal variables			
Date (number of days since January 1st)	175 (116-276)	-0.607	0.165
Year 2013	<i>n</i> = 430	0.101	0.024
Year 2014	<i>n</i> = 430	-0.102	-0.024
Traits			
Lifeform			
<i>Annual</i>	<i>n</i> =84	0.915	-0.281
<i>Perennial</i>	<i>n</i> =102	-0.388	0.119
Plant height [cm]	122.18 (20-3000)	-0.170	-0.493
Seed mass [mg]	5.09 (0.02-193.6)	0.225	-0.313
Specific Leaf Area (SLA) [mm ² .mg ⁻¹]	26.19 (6.50-53.68)	0.096	0.194
Flowering onset (Flow. On.)	5.11 (1-9)	-0.138	-0.375
Pollination mode (Polli.)			
<i>Entomogamous</i>	<i>n</i> =60	-0.247	-0.646
<i>Other (wind, water, autogamous)</i>	<i>n</i> =126	0.064	0.170
Mode of dispersal (Disp.)			
<i>By animals</i>	<i>n</i> =77	-0.242	-0.689
<i>By other means</i>	<i>n</i> =109	0.143	0.407
Ellenberg indicator values for Light (EIV-L)	7.20 (4-9)	0.422	-0.057
Ellenberg indicator values for soil moisture (EIV-H)	4.78 (1-8)	-0.554	0.154
Ellenberg indicator values for nitrogen (EIV-N)	6.24 (1-9)	-0.026	0.172

Figure captions

Figure 1. Distribution map of the 430 field margins surveyed in France. Colors correspond to the different production systems: wheat (black), maize (red), market gardening centred on lettuce production (green) and vineyards (blue). The black lines represent the limit of departments, a French administrative unit dividing metropolitan France into 95 units.

Figure 2. Results of the first two axes of the RLQ analysis: (a) scores of species, (b) coefficients for environmental variables, and (c) traits. The values of d give the grid size. Codes for variables and traits are given in Tables 1 and 2; codes for species in Appendix B.

Figure 3. Results of the fourth-corner tests. a) Significant ($P < 0.05$) positive associations are represented by red cells, and significant negative associations by blue cells. Nonsignificant associations are in grey. Black lines separate different variables; white lines separate different modalities for categorical variables. b) The same associations when P values were adjusted for multiple comparisons using the false discovery rate procedure. Codes for traits and variables are given in Tables 1 and 2.

Figure 4. a) Fourth-corner tests between the first two RLQ axes for environmental gradients (AxcR1/AxcR2) and traits. (b) Fourth-corner tests between the first two RLQ axes for trait syndromes (AxQ1 and AxQ2) and environmental variables. Positive significant associations are represented by red cells, and negative significant associations by blue cells.

Figure 5. a) Projection of agrotolerant versus hemerophobic species as supplementary variables in the RLQ analysis. The value of d gives the grid size. Comparison of the distribution of agrotolerant versus hemerophobic species on b) RLQ axis 1 and c) RLQ axis 2. The values of Wilcoxon test statistic W and the associated P -values are provided on the graphs.

Figure 6. a) Projection of organic versus conventional field margin strips as supplementary variables in the RLQ analysis. The value of d gives the grid size. Comparison of the distribution of organic (org.) versus conventional (conv.) field margin strips on b) RLQ axis 1 and c) RLQ axis 2. The values of Wilcoxon test statistic W and the associated P -values are provided on the graphs.

Figure 7. Scaled response of a) species richness, b) functional diversity and c) proportion of agrotolerant species to significant continuous variables identified in Generalized Additive Mixed Models (see Appendix E). TFI herbicides = Treatment frequency index of herbicides.

Figure 1.

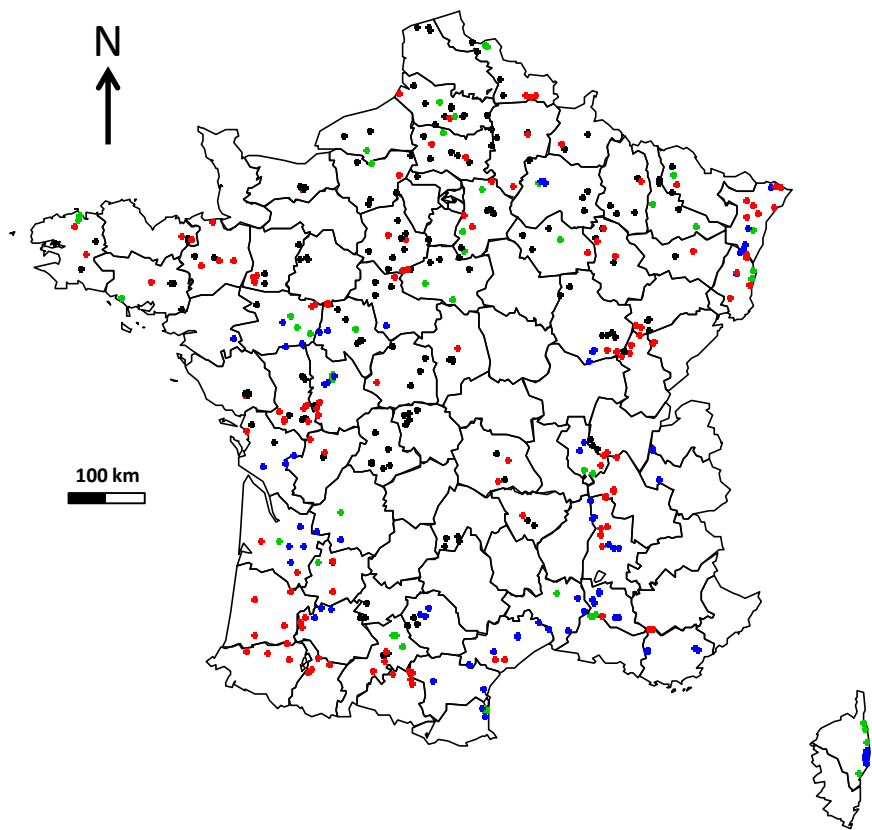


Figure 2.

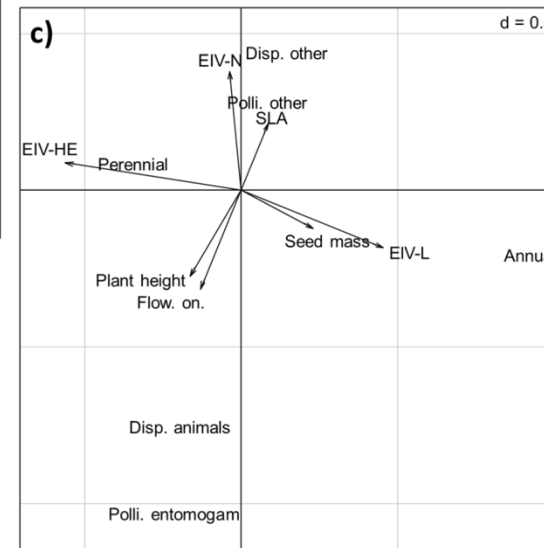
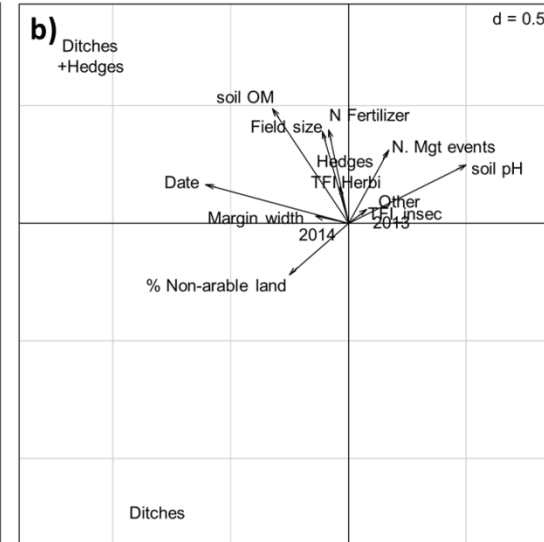
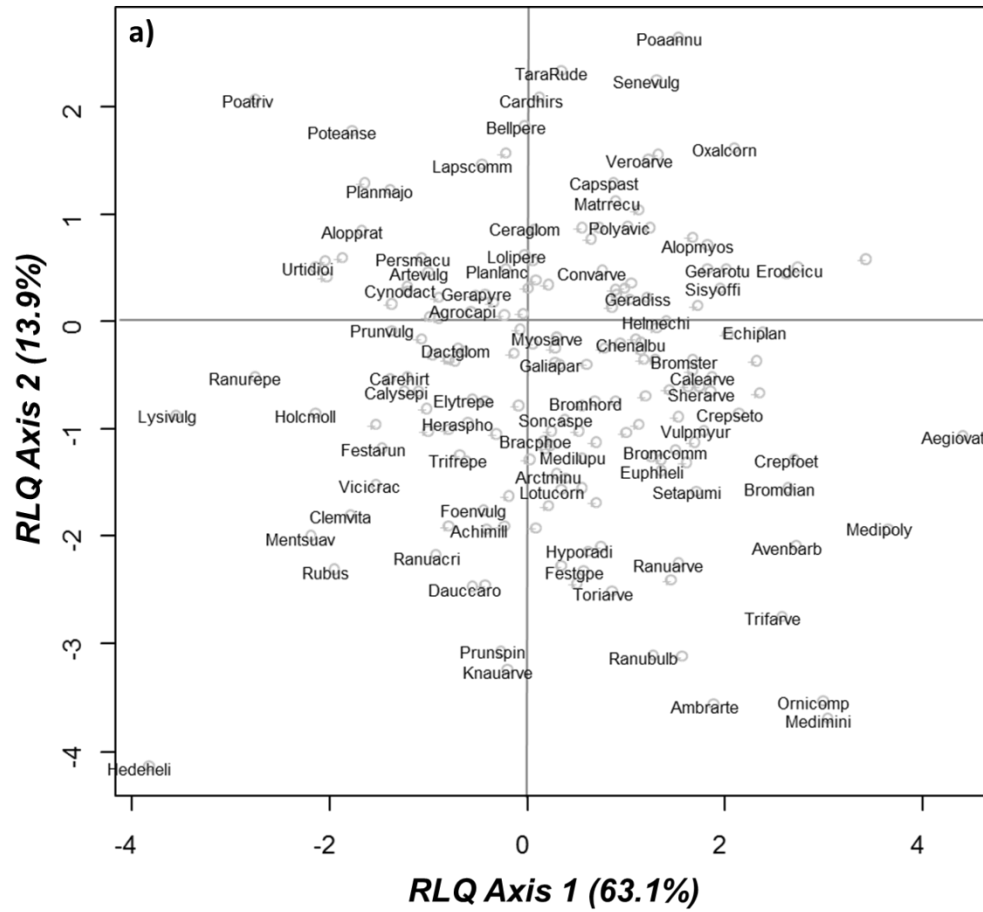


Figure 3.

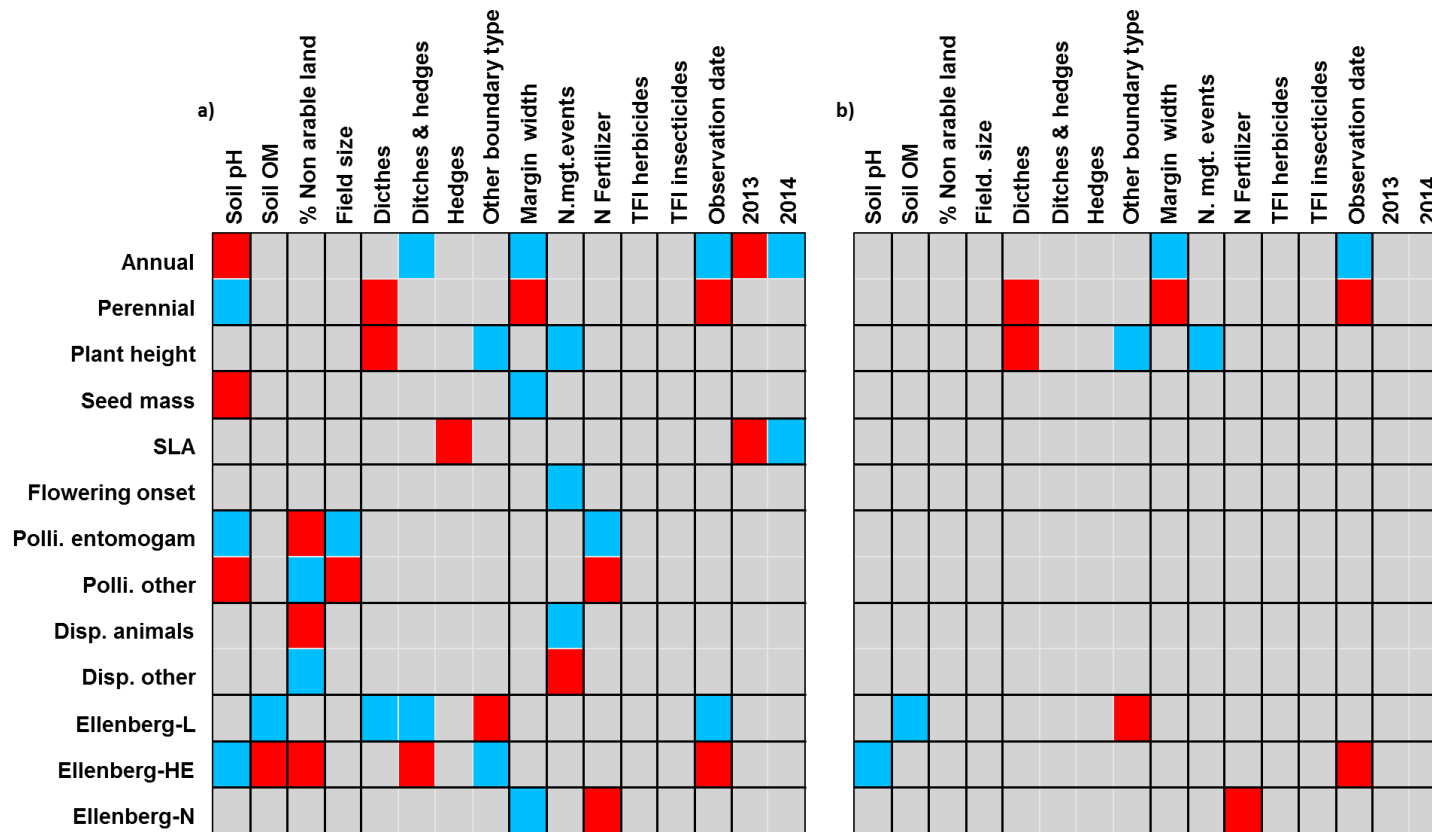


Figure 4.

	AxcR1	AxcR2		AxcQ1	AxcQ2
Annual	Red	Grey	Soil pH	Red	Grey
Perennial	Blue	Grey	Soil OM	Blue	Red
Plant height	Grey	Grey	% non-arable land	Grey	Grey
Seed mass	Grey	Grey	Field size	Grey	Red
SLA	Grey	Grey	Ditches	Blue	Grey
Flowering onset	Grey	Grey	Ditches & hedges	Blue	Grey
Polli. Entomogam	Grey	Blue	Hedges	Grey	Grey
Polli. Other	Grey	Red	Other boundary type	Red	Grey
Disp. Animals	Grey	Blue	Margin width	Blue	Grey
Disp. Other	Grey	Red	N. mgt. events	Red	Red
Ellenberg-L	Red	Grey	N Fertilizer	Grey	Red
Ellenberg-HE	Blue	Grey	TFI Herbicides	Grey	Grey
Ellenberg-N	Grey	Red	TFI Insecticides	Grey	Grey
			Observation date	Blue	Grey
			2013	Grey	Grey
			2014	Grey	Grey

Figure 5.

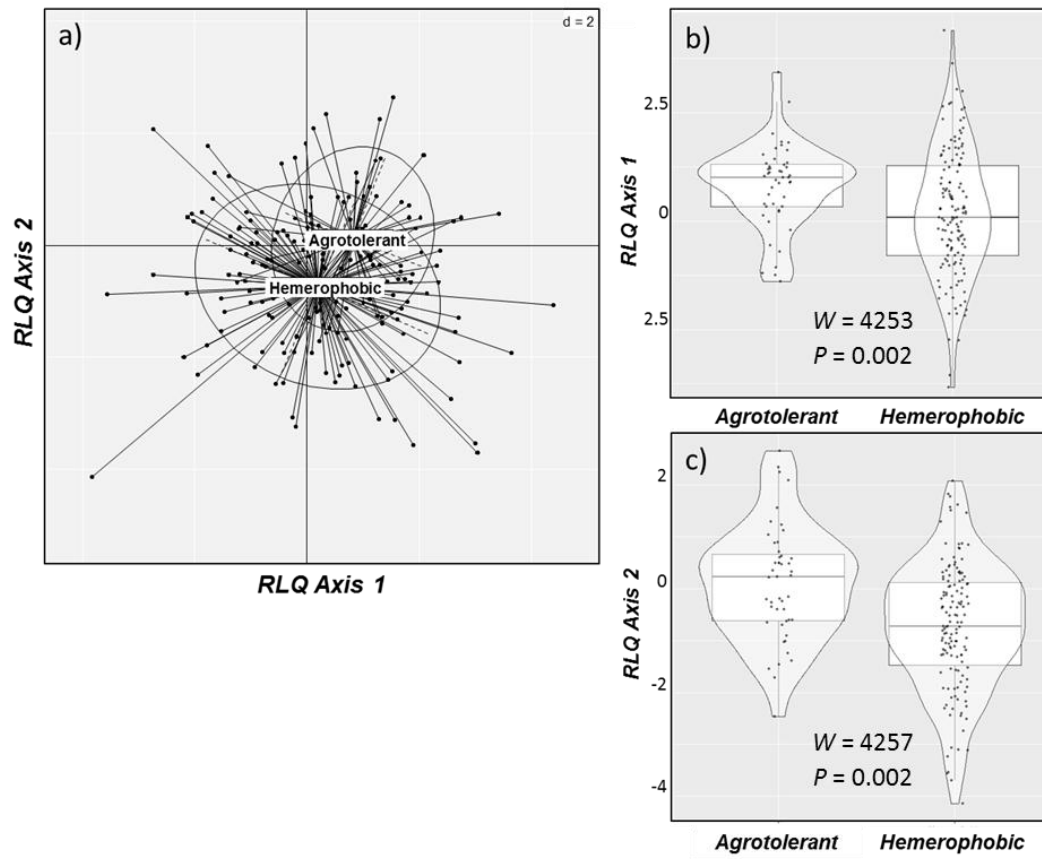


Figure 6.

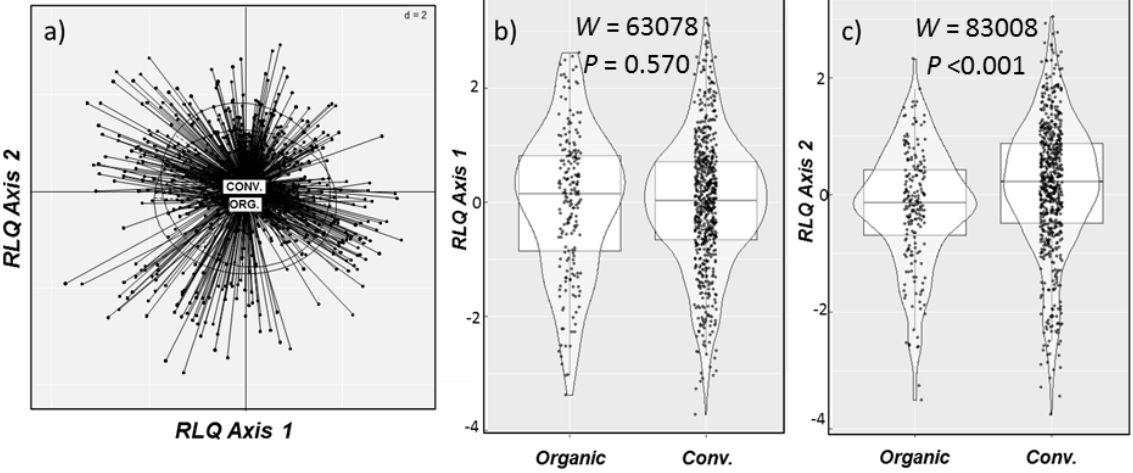
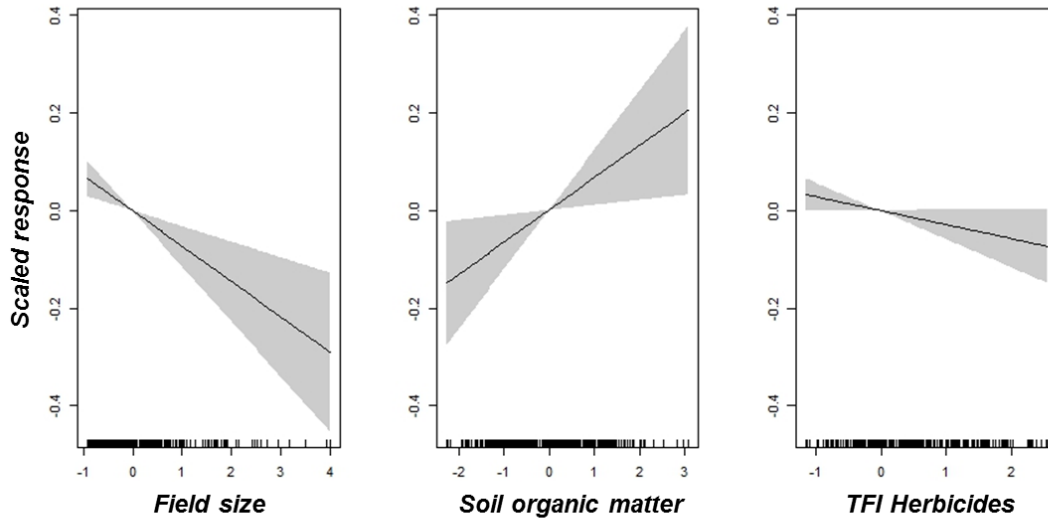
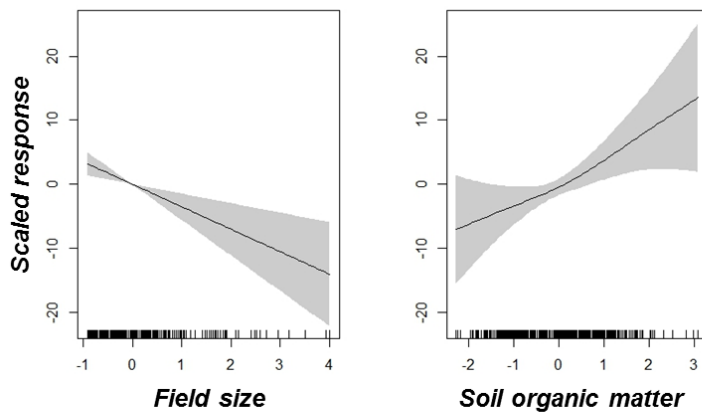


Figure 7.

a) Species richness



b) Functional diversity



c) Relative proportion of agrotolerant/hemierophobous species

