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1 **Alley cropping agroforestry systems: reservoirs for weeds or refugia for plant diversity?**

2

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26 Alley cropping agroforestry is a land use practice in which arable crops are grown between
27 tree rows. In such agroforestry systems, non-crop herbaceous vegetation develops on the tree
28 rows, resulting in understory vegetation strips (UVS). UVS are perceived both as reservoirs
29 for weeds and opportunities for biodiversity conservation. The purpose of this study was to
30 assess the contribution of UVS to (i) plant spillover and (ii) plant diversity conservation,
31 depending on their functional structure and the farming system. Vegetation surveys were
32 carried out in May 2017 in South-Western France over 16 winter cereal fields (8 alley
33 cropping agroforestry systems and 8 pure crop controls), half under conventional farming and
34 half under organic farming. Using data on plant functional traits related to dispersal strategies
35 and response to agricultural disturbances, we explained the mechanisms involved in plant
36 spillover between habitats. The study revealed that very few species were able to disperse far
37 into crop alleys, except perennial species producing rhizomes and stolons whose spread has
38 been favored by tillage. The presence of UVS in agroforestry fields did not increase weed-
39 crop ratio (i.e. weed coverage / weed and crop coverage) in adjacent crop alleys. On the other
40 hand, UVS harbored richer and more abundant floras (with high proportions of species rarely
41 found in arable habitats) compared to crop alleys and pure crop controls, especially under
42 conventional farming. The functional approach provided insights for weed management in
43 alley cropping agroforestry systems in order to optimize plant diversity conservation without
44 increasing weed-crop ratio. This study showed the relevance of using the functional approach
45 to understand the mechanisms behind plant spillover in cropping systems that integrate semi-
46 natural habitats.

47

48 **Keywords:** temperate region, semi-natural habitat, understory vegetation strip, hemerophobic
49 species, spillover, functional trait

50

51

52 **1. Introduction**

53

54 The post-war agricultural intensification has led to worldwide losses of biodiversity
55 due to the increase of both agrochemicals' application and croplands, to the detriment of
56 semi-natural habitats such as woodlots, grasslands, hedges and field boundaries (Stoate et al.,
57 2001). Since then, many studies have demonstrated that semi-natural habitats provide food
58 resources, reproduction and overwintering sites and refuges from agricultural disturbances for
59 many organisms. For example, Aavik and Liira (2010) showed that field boundaries are home
60 to hemerophobic plant species, i.e. species sensitive to tillage and/or herbicides, as opposed to
61 agrotolerant species. Such species have a high conservation value as they are declining in the
62 context of intensive agriculture (Aavik et al., 2008). Beneficial arthropods such as pollinators
63 and natural enemies of pests also depend on the presence of semi-natural habitats to complete
64 their life cycle (Pfiffner and Luka, 2000; Hass et al., 2018). On the other hand, it has been
65 shown that non-crop habitats could host weeds, pathogens and pests (Norris and Kogan, 2000;
66 Wisler and Norris, 2005). If the presence of nearby semi-natural habitats impacts the
67 functioning of agroecosystem, the spillover of organisms between semi-natural and arable
68 habitats is also of major importance and can be positive or negative for crop production
69 (Blitzer et al., 2012). Indeed, in the case of arthropods, the higher the spillover of beneficial
70 arthropods towards arable fields is, the better pest control and crop pollination can be
71 achieved (Woodcock et al., 2016). On the other hand, pests coming from alternative host
72 plants in adjacent habitats could disperse towards the arable fields, potentially causing crop
73 yield losses (e.g. Johnson, 1950). In the case of spontaneous plants, which are at the basis of
74 agroecosystem food web, their spillover in arable fields could promote biodiversity
75 conservation, but also induce yield losses through competition with crops (Petit et al., 2011).
76 Many studies have assessed the negative effects of various adjacent habitats on crop

77 production, often suspected to supply arable fields with weeds. Overall, the abundance and
78 diversity of weed communities were enhanced up to 2.5 m and 4 m from field margins
79 (Marshall, 1989; Wilson and Aebischer, 1995 respectively), 3 m from forests (Devlaeminck et
80 al., 2005), 3.5 m from road verges (Chaudron et al., 2016) and 7 m from grasslands (Hume
81 and Archibold, 1986), thus only in crop edges in every case. Furthermore, the intensity of
82 organisms' spillover in arable fields, and hence the intensity of ecosystem processes
83 associated, depends on the nature of adjacent semi-natural habitats. Indeed, Metcalfe et al.
84 (2019) observed a higher plant spillover in fields next to grasslands or in the presence of field
85 margins, compared to fields next to woodlots, bare ground (ploughed fields or urban) or
86 without field margins. Woodcock et al. (2016) showed that the spillover of beneficial
87 arthropods was higher in fields next to wildflowers strips, compared to fields next to grass
88 strips. Conversely, some habitats can even constitute a barrier to the dispersal of organisms
89 into arable fields (e.g. Mauremooto et al., 1995; Cordeau et al., 2012). Besides, the spillover
90 of organisms between arable and semi-natural habitats is likely to be increased by small-scale
91 agriculture and landscape fragmentation, which are characterized by higher proportion of
92 edges (Blitzer et al., 2012; Mitchell et al., 2015). That could explain the higher weed diversity
93 observed in smaller fields (Gaba et al., 2010). In the same idea, Hatt et al. (2017) showed that
94 the presence of semi-natural habitats located within fields' core themselves favored the
95 spillover of organisms farther into the crops.

96

97 In temperate regions, agroforestry systems are gaining renewed interest as they can
98 provide a wide range of ecosystem services from the same area of land, such as sustainable
99 food and biomass production, soil and water protection, biodiversity conservation and carbon
100 sequestration (Jose, 2009; Quinkenstein et al., 2009; Torralba et al., 2016; Kay et al., 2019).
101 Agroforestry systems can take multiple faces given the wide range of practices they cover

102 (e.g. hedge farmland, silvoarable and silvopastoral systems), the diversity of species that can
103 be associated (herbaceous plants, shrubs, trees) and the spatial configurations conceivable (i.e.
104 playing on the area covered by the different strata and their position within fields). Such
105 plasticity allows agroforestry systems to be implemented in many regions and for multiple
106 objectives. If promoted by agricultural and environmental policies, agroforestry systems are
107 expected to help meet Europe policy objectives on greenhouse gas emissions while providing
108 multiple ecosystem services (Kay et al., 2019). Among agroforestry systems, alley cropping
109 agroforestry, in which arable crops are grown between tree rows, represent a great opportunity
110 for the reintegration of semi-natural habitats within fields. Indeed, the presence of trees rows
111 leads to increased edges amount and field fragmentation, which is expected to enhance
112 ecosystem (dys-)services flows (Mitchell et al., 2015). Further, to prevent any damage on
113 trees, farmers avoid tilling the soil close to the trees, resulting in the development of non-crop
114 herbaceous strips under the trees, hereafter called understory vegetation strips (UVS) (Figure
115 1). UVS are poorly disturbed by crop management and so are comparable to other linear
116 semi-natural habitats such as field boundaries, except that they are located within fields and
117 occupy about 3 to 13% of the available agricultural area. Given the spatial configuration and
118 the important extent of UVS, it is likely that both the intensity of plant spillover and the
119 amount of refugia for biodiversity are increased in alley cropping agroforestry compared to
120 pure crop systems. Many works have assessed the ecosystem services supplied by (semi-
121)permanent herbaceous vegetation in other systems such as pure crops (e.g. Hatt et al., 2017),
122 vineyards (e.g. Winter et al., 2018; Garcia et al., 2019) and orchards (e.g. Forey et al., 2016;
123 Cahenzli et al., 2019). However, research in temperate alley cropping agroforestry is recent
124 and has focused mainly on interactions between trees and crops. Works considering UVS are
125 still scarce, but we can mention Burgess (1999), Cardinael et al. (2015), Mézière et al. (2016),
126 Pardon et al. (2019) for example. If most farmers perceive agroforestry systems as a solution

127 to wildlife habitats conservation, others fear that UVS constitute reservoirs for weeds that
128 colonize crop alleys (Graves et al., 2017). To our knowledge, very few studies have assessed
129 the effects of alley cropping agroforestry on arable weed community structure and plant
130 diversity conservation in temperate regions. Mézière et al. (2016) showed that an alley
131 cropping agroforestry system can harbor higher plant diversity than a pure crop control,
132 without enhancing weed coverage in crop alleys. However, these results were restricted to one
133 pair of fields under conventional farming in a Mediterranean French context.

134

135 The purpose of this study was to assess the contribution of UVS (i) to plant spillover
136 into crop alleys and (ii) to plant diversity conservation in the agroecosystem, under
137 conventional vs organic farming and taking into account the functional structure of understory
138 vegetation. We hypothesized that **1)** the ability of a plant species to colonize crop alleys from
139 UVS depends on both its tolerance to agricultural disturbances and its dispersal strategies. So,
140 we would expect a species that can tolerate tillage and herbicides and that also has good
141 dispersal abilities (anemochory or vegetative dispersal) to be more likely to colonize crop
142 alleys from UVS. Further, we hypothesized that **2)** plant spillover from UVS would enhance
143 the abundance of weed flora in alley cropping agroforestry fields compared to pure crop
144 controls (hereafter called “weed reservoirs” hypothesis) and that **3)** UVS would constitute
145 refugia for plant diversity, particularly for hemerophobic species (hereafter called “plant
146 diversity refugia” hypothesis). Our final hypothesis was that **4)** the role of UVS as weed
147 reservoirs would be more important in organic farming fields given the lack of herbicide
148 treatments and mineral fertilizers, whereas their role as refugia for plant diversity would be
149 more important in conventional farming fields, where agricultural intensification drastically
150 reduces the ecological niches available for spontaneous plants (Hyvönen and Salonen, 2002;
151 Gabriel et al., 2006; Andreasen and Streibig, 2011).

152

153 **2. Materials and Methods**

154

155 *2.1. Vegetation survey*

156

157 The study was conducted in Gers and Pyrénées-Atlantiques Departments (South-Western
158 France), which is a hilly region (altitude about 300 meters) characterized by a sub-Atlantic
159 climate with hot summers and cool winters. Agricultural areas are mainly composed of clay-
160 limestone and clay-to-silt soils and annual precipitation usually varies from 700 to 900 mm.
161 Vegetation surveys were carried out in May 2017 over 16 winter cereal fields (8 pairs of alley
162 cropping agroforestry systems and pure crop controls) growing either winter wheat (*Triticum*
163 *aestivum* L.) or winter barley (*Hordeum vulgare* L.), half under conventional farming and half
164 under organic farming. Vegetation surveys in conventional farming fields were carried out at
165 least one month after the last herbicide treatment. Thus, observed flora in these fields is
166 mostly composed of species surviving herbicide treatments or emerging later. Each pair of
167 fields (alley cropping agroforestry vs pure crop control) was located within the same
168 perimeter, similar in terms of pedo-climatic conditions and surrounding land use (see Figure
169 S1 in Supplementary material). Each pair was also cultivated by the same farmer, with similar
170 crop managements over the three years preceding the study (see Table S1 in Supplementary
171 material). Three fields under organic farming also contained leguminous crops, either garden
172 pea (*Lathyrus oleraceus* Lam.) and/or common vetch (*Vicia sativa* L.) but the proportion of
173 legumes was always very low compared to cereals. For both organically and conventionally
174 farmed fields, UVS were either unmanaged ($n = 2$ fields), mown before sowing and after
175 harvest ($n = 1$ field) or sown with competitive perennial species ($n = 1$ field): *Schedonorus*
176 *arundinaceus* under organic farming, *Festuca rubra* under conventional farming. Features of

177 agroforestry fields (i.e. tree species and basic metrics) are given in Table S2 in Supplementary
178 material. In each agroforestry field, UVS were surveyed in three zones distant from 20 m.
179 Each zone was sampled with four quadrats (0.25 m²) separated by two meters each. Then, on
180 both sides of these zones, adjacent crop alleys were sampled on transects running
181 perpendicular to UVS, at three distances from UVS (0.5 m, 2 m and 8 m). For each distance,
182 we visually estimated the coverage of each species found in three quadrats (0.25 m²)
183 separated by two meters each (Figure 1), with an accuracy of $\pm 5\%$. Plants were mostly at
184 vegetative or floral stage during the survey. In total, 66 quadrats (16.5 m²) were sampled per
185 agroforestry field. This sampling design was located at around 50 m and 100 m from the two
186 nearest field boundaries to exclude their effect on weed communities. The crop alleys on
187 either side of the UVS were sampled to take into account the potential effect of slopes and
188 prevailing wind directions on seed dispersal. The same protocol was used for pure crop
189 controls with the transects placed at equivalent locations in the field in the absence of the
190 UVS, resulting in 54 quadrats (13.5 m²) sampled per pure crop control. In total, 960 quadrats
191 (240 m²) were sampled during the vegetation survey.

192

193 **Figure 1.** The principal compartments of alley cropping agroforestry systems and the
194 sampling protocol used for the vegetation survey.

195

196 2.2. *Functional structure, potential harmfulness and diversity of plant communities*

197

198 Functional traits related to dispersal strategies and tolerance to agricultural disturbances were
199 collected from databases and reference books of French flora (Table 1), along with Raunkiaer
200 life forms. If an individual was identified to the genus only, the mean attributes of congeneric

201 species found in the survey and predominant in the region were used (Association Botanique
 202 Gersoise, 2003).

203

204 **Table 1.** List of selected functional traits related to dispersal strategies and tolerance to
 205 disturbances (see Gaba et al., 2017 and references therein) along with their sources and
 206 associated references.

207

Traits, life forms	Dispersion abilities and/or expected response to disturbances	Sources
Specific leaf area (mm ² .mg ⁻¹)	Fertilization, crop harvesting and vegetation mowing favor species with high resources acquisition capacity (high SLA).	LEDA (Kleyer et al., 2008)
Plant height at maturity (cm)	Vegetation mowing favors short species.	(Coste, 1937)
Seed mass (g)	Seed mass/number trade-off; disturbances favor species producing numerous small seeds whereas stable habitats favor competitive species producing fewer but bigger seeds.	SID (Royal Botanical Gardens Kew, 2017)
Flowering onset and range (month) ^a	Determines species ability to flower and produce seeds before crop harvest or vegetation mowing.	BaseFlor (Julve, 1998)
Emergence onset and range (month) ^b	Trade-off between escaping tillage and herbicide treatment (late emergence) and avoiding crop competition (early emergence). Successful weeds often emerge simultaneously with the crop.	Internal compilation of traits in a weed-oriented database
Raunkiaer life forms	Tillage favors therophyte species (i.e. annual species spending winter in the form of seeds) and geophyte ones (i.e. perennial species spending winter in the form of bulbs, tubers or rhizomes).	(Jauzein, 2011)
Seed dispersal strategies	Spillover of animal-dispersed plants increases in response to connectivity provided by ecological corridors. Spillover of wind-dispersed plants increases in response to higher edge-to-interior ratio of habitats.	BaseFlor (Julve, 1998)
Presence of runners (rhizomes and/or stolons)	Tillage favors the dispersal of species with runners. Once these organs are cut into fragments, they can heal and form new plants.	(Jauzein, 2011)

208 ^aFlowering onset was coded from 1 (January) to 12 (December).

209 ^bEmergence onset was coded from 1 (October) to 12 (September) since winter cereals were sown in
 210 October-November. Data were collected from observations at SupAgro Dijon and based on expert
 211 opinion.

212

213 To assess the potential harmfulness of weed communities (here defined as plant
214 communities found in crops), total weed and crop coverage (0 to 100%) were estimated
215 within each 0.25 m² quadrat. A weed-crop ratio was then computed for each quadrat and used
216 as a proxy of the competitive effects of weeds on yield loss (Lutman et al., 1996) :

217

$$218 \quad \text{weed-crop ratio} = \frac{\text{weed coverage}}{\text{weed coverage} + \text{crop coverage}}$$

219

220 To assess the diversity and conservation value of plant communities, total coverage,
221 species richness and evenness of both agrotolerant and hemerophobic communities were
222 measured within each quadrat. Following Aavik et al. (2008), each species was classified as
223 agrotolerant or hemerophobic (see Table A1 in Appendix) based on its frequency of
224 occurrence in arable fields at national scale, using data of the Biovigilance Flore network
225 2002–2012 (Fried et al., 2008). A species was considered as hemerophobic if its frequency of
226 occurrence in the sample plots of arable fields was lower than 10%. We used this
227 classification rather than functional diversity indices because (i) it provides efficient and
228 integrative indicators of diversity and conservation value of plant communities in response to
229 agricultural land use intensity, (ii) data is available for most species thanks to national scale
230 surveys, and (iii) functional diversity indices are based on a restricted number of relevant
231 traits given specific objectives (e.g. favoring beneficial arthropods, protecting soil and water
232 quality).

233

234 2.3. *Data analysis*

235

236 To assess the hypothesis n°1 (plant species' ability to colonize crop alleys from UVS depends
237 on both its tolerance to agricultural disturbances and its dispersal strategies), we combined

238 RLQ and fourth-corner analysis following Dray et al., (2014). RLQ analysis aims to identify
239 the main co-structures between traits (Q-table) and environmental variations (R-table)
240 considering species abundances (L-table), while fourth-corner analysis provide tests for the
241 correlations between each trait and each environmental variable. By combining RLQ and
242 fourth-corner analysis we could test the correlations (i) between each trait and combination of
243 environmental variables obtained from RLQ axes, and (ii) between each environmental
244 variable and trait syndromes obtained from RLQ axes. First, a combination of RLQ and
245 fourth-corner analysis was performed on the plant communities *located in the UVS* to analyze
246 their taxonomic and functional structures in response to different management practices. We
247 only considered dominant species, occurring in at least 5 quadrats (i.e. whose frequency of
248 occurrence was superior to 5%), because rare species may unduly influence the results
249 (Kenkel et al., 2002). Dominant species represented 90% of the total coverage observed in
250 UVS. The Q-table contained 23 species described by 9 functional traits related to dispersal
251 ability and tolerance to disturbances, along with Raunkiaer life forms. The R-table contained
252 96 quadrats characterized by farming system (conventional vs organic), the age of UVS and
253 its management (i.e. sowing and mowing considered as binomial variables). Finally, the L-
254 table contained the coverage of each species within each quadrat. Second, a combination of
255 RLQ and fourth-corner analysis was performed on the plant communities *located in the crop*
256 *alleys* to assess which life strategies were dispersing from UVS towards crop alleys. Because
257 hypothesis 1 concerns plant species' ability to colonize crop alleys from UVS, this analysis
258 was restricted to the same set of species that were dominant in UVS, therefore eliminating
259 rare species and arable weed species persisting mostly in the seedbank of crop alleys (the
260 relative coverage of these two groups can be seen in Figure S2 in Supplementary material).
261 Again, we considered only species occurring in at least 5 quadrats in the crop alleys (i.e.
262 whose frequency of occurrence was superior to 1%). The Q-table contained 18 species

263 described by the same functional traits as the first analysis, along with Raunkiaer life forms.
264 In this second analysis, the R-table contained 432 quadrats characterized by the farming
265 system, the distance from UVS (0.5 m, 2 m, 8 m) and the direction from UVS (east or west).
266 For both analyses, Monte-Carlo tests were used to assess the global link between traits and
267 environment tables by comparing the observed total inertia (i.e. the sum of eigenvalues of
268 RLQ axes) to a null distribution obtained from 999 random permutations of species and
269 quadrats. Then, fourth-corner analysis was used to test the significance of correlations
270 between each trait and each environmental variable, by comparing each bivariate correlation
271 with its null distribution obtained from 49 999 random permutations of species and quadrats.
272 The false discovery rate method was used to adjust p-values for multiple comparisons
273 (Benjamini and Hochberg, 1995). Finally, we combined RLQ and fourth-corner analysis
274 (49 999 permutations). Seed mass was very skewed and was therefore log-transformed as
275 suggested by Kenkel et al. (2002). RLQ and fourth-corner analysis were performed using the
276 package ade4 (Dray and Dufour, 2007).

277

278 To assess the hypotheses n°2, 3, and 4, we used generalized linear mixed effects
279 models (random intercept GLMMs). Transects and fields were included as random effects on
280 the intercept, with transects nested within fields. These models take into account the spatial
281 auto-correlation between quadrats located in a same transect or a same field. For the “weed
282 reservoirs” hypothesis (n°2), we compared total weed coverage, crop coverage and weed-crop
283 ratio per quadrat (response variables) between crop alleys (i.e. the cropped part of the
284 agroforestry system) and pure crop controls under conventional vs organic farming, over 16
285 fields. For the “plant diversity refugia” hypothesis (n°3), we compared total coverage, species
286 richness and evenness of agrotolerant and hemerophobic communities per quadrat (response
287 variables) between UVS, crop alleys and pure crop controls, under conventional vs organic

288 farming. In this analysis, the two fields with sown UVS and their pure crop controls were
289 removed because sown species had high coverage and reduced the development of other
290 species within UVS. They were therefore not relevant for comparing diversity indices.
291 Moreover, given that they were hemerophobic species, it would lead to an overestimation of
292 the total coverage of hemerophobic species within UVS. This resulted in a dataset of 12 fields
293 and 720 quadrats. Evenness was computed using the index of Williams (1977) based on the
294 species proportions p_1, \dots, p_S and species richness S in each quadrat, as suggested by Kvålseth
295 (2015):

296

$$297 \quad \text{evenness} = 1 - \left[\frac{S \sum_{i=1}^S (p_i^2 - 1)}{S - 1} \right]^{1/2}$$

298

299 On the agroforestry dataset, other GLMMs were performed to investigate the effect of the
300 distance from UVS (natural logarithms + 1) on all variables, under organic vs conventional
301 farming. All GLMMs revealed a strong effect of farming system and in some cases
302 interactions with other explanatory variables (Table 2). Therefore, each model was performed
303 on organic farming fields and conventional ones separately to facilitate the comparison
304 between habitats (UVS, crop alleys, pure crop controls). Species richness was assumed to
305 follow a Poisson distribution and all other variables (proportions between 0 and 1) were
306 assumed to follow a Beta distribution. When proportional variables included 0 and/or 1
307 value(s), the transformation $(Y \times (N - 1) + 0.5) / N$ was employed following Zuur et al.
308 (2013), where Y is the response variable and N is the sample size. If a variable was bound
309 between a and b , it was rescaled to lie between 0 and 1 by the transformation $(Y - a) / (b - a)$.
310 This was the case for the total coverage of agrotolerant and hemerophobic communities
311 (corresponding to the summed coverage of all agrotolerant or hemerophobic species present
312 within each quadrat), whose maximum values were greater than 1. We used the package

313 glmmTMB (Brooks et al., 2017) for fitting Poisson and Beta GLMMs, with the link functions
314 log and logit respectively. Poisson GLMMs revealed under-dispersion, therefore Conway-
315 Maxwell-Poisson GLMMs were fitted instead as suggested by Lynch et al. (2014). All
316 analyses were performed using the statistical software R 5.1 (R Core Team, 2018).

317

318 **3. Results**

319

320 A total of 88 plant species were recorded during the whole survey. Pure crop controls
321 harbored 61 species whereas 70 species were found in crop alleys of agroforestry fields, over
322 108 m² sampled per system. In UVS, 55 species were found over 24 m² sampled. The five
323 most frequent species in UVS were *Galium aparine*, *Anisantha* sp., *Avena* sp., *Lolium* sp. and
324 *Convolvulus arvensis*. A list of all species recorded along with their occurrences in each
325 habitat is given in Table A1 in Appendix A.

326

327 *3.1. Functional structure of plant communities of understory vegetation strips under different* 328 *management practices*

329

330 A Monte-Carlo permutation test revealed no significant link between traits and environment
331 tables ($P_{max} = 0.342$). Fourth-corner analysis revealed that animal-dispersed species are
332 significantly and positively associated with unmown UVS ($r = 0.240$, $P_{adj} = 0.0021$, Figure
333 2a). The combination of RLQ and fourth-corner revealed that RLQ axis 1 was negatively
334 correlated with the age of UVS and sowing or no mowing management (Figure 2b). RLQ axis
335 1 was positively correlated with mowing or no sowing management. Older quadrats, whatever
336 they were unmown or sown, contained significantly more animal-dispersed species whereas
337 mown and unsown quadrats contained more barochorous species. The second RLQ axis

338 significantly separated quadrats according to the farming system but this variable had no
339 significant effect on the functional structure of plant communities within UVS.

340

341 **Figure 2.** (a) Results of the fourth-corner analysis performed on dominant species of plant
342 communities *located in the understory vegetation strips (UVS)*. (b) Results of the fourth-
343 corner analysis testing the link between RLQ axes and traits and environmental variables. Red
344 cells correspond to positive significant relationships while blue cells correspond to negative
345 significant relationships.

346

347 *3.2. Identification of trait syndromes enabling species to colonize crop alleys from understory*
348 *vegetation strips*

349

350 The first two axes of the RLQ accounted for 99.2% of the total inertia (84.5 and 14.7%
351 respectively, Figure 3a). The first two RLQ axes accounted for most of the variance explained
352 by separate analyses of environmental variables (97.5% for the analysis of the R-table) and
353 species traits (80.5% for the analysis of the Q-table). Coefficients of environmental variables
354 and traits (illustrated in Figure 3b and Figure 3c) are given in Table S4 in Supplementary
355 Material, along with their basic statistics. Monte-Carlo permutation test revealed a significant
356 link between traits and environment tables ($P_{max} = 0.003$). Fourth-corner analysis revealed no
357 significant correlation between individual pairs of traits and environmental variables (Figure
358 4a). Testing the link between RLQ axes and traits or environment (Figure 4b) showed that
359 RLQ axis 1 was negatively correlated with conventional farming, direction from UVS (west)
360 and distance from UVS (2 m). RLQ axis 1 was positively correlated with organic farming,
361 direction from UVS (east) and distance from UVS (0.5 m). The species that were dominant in
362 UVS and also found in crop alleys of organic fields were perennial species characterized by

363 relatively high seed mass and plant height, later emergence and flowering. On the other hand,
364 UVS species found in crop alleys of conventional fields were much fewer and characterized
365 by large emergence and flowering ranges, along with a short life cycle (therophyte species
366 with high SLA). The second RLQ axis clearly separated quadrats at 0.5 m from those at 2 m
367 and 8 m. The vast majority of species dominant in UVS were found at 0.5 m from UVS, their
368 occurrences and abundances decreasing at 2 m and 8 m. They were mostly animal-dispersed
369 species without runners. Conversely, *Convolvulus arvensis* and *Potentilla reptans* scored
370 negatively on RLQ axis 2 (Figure 3a). These are barochorous species dispersing by means of
371 runners. They emerge later and have relatively larger flowering ranges.

372

373 **Figure 3.** RLQ analysis performed on plant communities *located in the crop alleys*. Results
374 are given on the first two axes for (a) species' scores, (b) environmental variables' loadings,
375 and (c) traits' loadings. Only species that were dominant in the understory vegetation strips
376 were considered, therefore eliminating rare species and arable weed species persisting mostly
377 in the seedbank of crop alleys. Species marked with a star were sown in UVS. Grey and black
378 labels correspond to agrotolerant and hemerophobic species respectively. Codes for species
379 are given in Table A1 in Appendix.

380

381 **Figure 4.** (a) Results of the fourth-corner analysis performed on plant communities *located in*
382 *the crop alleys*, restricted to the set of species that were also dominant in the understory
383 vegetation strips (UVS). (b) Results of the fourth-corner analysis testing the link between
384 RLQ axes and traits and environmental variables. Red cells correspond to positive significant
385 relationships while blue cells correspond to negative significant relationships.

386

387 *3.3. Comparison of weed-crop ratio between alley cropping agroforestry and pure crop*
388 *controls*

389
390 Conventional fields had significantly lower total weed coverage (on average –33% per
391 quadrat) and higher crop coverage (on average +22% per quadrat) than organic ones (Table
392 2). As a consequence, weed-crop ratio was much lower in conventional fields (on average
393 –36% per quadrat) (Table 2). In conventional fields, crop and weed coverage along with
394 weed-crop ratio were similar between crop alleys and pure crop controls (Figure 5, Table S5
395 in Supplementary Material). On the other hand, in organic fields, total weed coverage was
396 significantly lower (–12%) in crop alleys compared to pure crop controls, while crop
397 coverage and weed-crop ratio were comparable between both systems (Figure 5, Table S5 in
398 Supplementary Material). The effect of the distance from UVS on weed-crop ratio was
399 significant in conventional fields. Indeed, weed coverage and weed-crop ratio decreased when
400 farther from UVS while crop coverage increased (see Table S6 and Figure S4 in
401 Supplementary Material). However, no effect of the distance from UVS was detected in
402 organic fields.

403

404 *3.4. Comparison of plant diversity between habitats*

405

406 Coverage and species richness of agrotolerant and hemerophobic communities were
407 lower in conventional fields than in organic ones (Table 2). On the one hand, in conventional
408 fields all diversity variables were very low and similar between pure crop controls and crop
409 alleys, except species richness of hemerophobic communities that was slightly higher in crop
410 alleys (Figures 6a, 6b, 6c). By contrast, UVS supported a richer and more abundant flora than
411 cropped areas, containing both agrotolerant and hemerophobic species (Figures 6a, 6b). On

412 the other hand, in organic fields the coverage of both agrotolerant and hemerophobic
413 communities was higher in the UVS (Figure 6a). Species richness of both agrotolerant and
414 hemerophobic communities was similar between pure crop controls, crop alleys and UVS
415 (Figure 6b). Evenness of agrotolerant and hemerophobic communities was higher in cropped
416 areas (pure crop controls and crop alleys) than in UVS (Figure 6c). Evenness of
417 hemerophobic communities was even higher in crop alleys than in pure crop controls (Figure
418 6c). The effect of the distance from UVS on plant diversity was significant only in
419 conventional fields (see Table S6 in Supplementary Material). Furthermore, only
420 hemerophobic communities were impacted by the distance from UVS. Indeed, the coverage
421 and species richness of hemerophobic communities decreased when farther from UVS, while
422 these variables remained constant regarding agrotolerant communities (see Figures S5a, S5b
423 in Supplementary Material).

424

425 **Table 2.** Estimates, their standard errors and p-values obtained from generalized linear
426 mixed-effects models (GLMMs). Crop alleys and understory vegetation strips (UVS) are
427 compared to pure crop controls (reference level in GLMMs). Conventional farming is
428 compared to organic farming (reference level in GLMMs). n = number of quadrats used for
429 each GLMM. In the case of evenness, only quadrats containing more than 1 species were
430 considered. No quadrats containing more than one hemerophobic species were found in pure
431 crop controls under conventional farming, therefore comparisons with agroforestry systems
432 were impossible in this case. Bold letters indicate significance difference at 0.05 threshold (*
433 $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

Response variables	Main terms			Interactions with farming system		
	Crop alleys	UVS	Conventional farming	Crop alleys	UVS	
<i>Potential harmfulness of weed communities</i>	Weed coverage (n = 863)	-0.49 ± 0.497	–	-2.84 ± 0.500 ***	0.90 ± 0.706	–
	Crop coverage (n = 863)	0.07 ± 0.424	–	2.35 ± 0.424 *	0.86 ± 0.600	–
	Weed-crop ratio (n = 863)	-0.31 ± 0.521	–	-2.84 ± 0.524 ***	0.64 ± 0.740	–
<i>Diversity of agrotolerant communities</i>	Total coverage (n = 720)	-0.00 ± 0.542	1.23 ± 0.550 *	-1.52 ± 0.544 **	0.27 ± 0.769	-0.18 ± 0.788
	Species richness (n = 720)	0.01 ± 0.618	0.15 ± 0.620	-2.31 ± 0.658 ***	0.50 ± 0.907	1.52 ± 0.909
	Evenness (n = 312)	-0.12 ± 0.390	-1.03 ± 0.422 *	0.32 ± 0.66	-1.47 ± 0.836	0.14 ± 0.829
<i>Diversity of hemerophobic communities</i>	Total coverage (n = 720)	-0.62 ± 0.275 *	1.13 ± 0.294 ***	-2.14 ± 0.279 ***	0.96 ± 0.393 **	2.53 ± 0.419 ***
	Species richness (n = 720)	-0.16 ± 0.432	0.27 ± 0.436	-4.17 ± 0.603 ***	2.64 ± 0.746 ***	3.40 ± 0.750 ***
	Evenness (n = 282)	–	–	–	–	–

434 **Figure 5.** Comparison of weed-crop ratio (i.e. weed coverage / weed and crop coverage), used
435 as a proxy for the potential harmfulness of weed communities, between pure crop controls
436 and crop alleys, under conventional vs organic farming. See Table S5 in Supplementary
437 material for detailed outputs of GLMMs.

438

439 **Figure 6.** Comparison of the variables considered for the assessment of plant diversity
440 between habitats (pure crop controls, crop alleys, understory vegetation strips). Stars indicate
441 significant difference at 0.05 threshold based on p-values of GLMMs comparing these
442 variables between pure crop controls (taken as reference) and agroforestry systems (crop
443 alleys and understory vegetation strips), under conventional and organic farming. See Table
444 S5 in Supplementary material for detailed outputs of GLMMs.

445

446 **Figure 7.** Plant spillover from UVS to crop alleys in alley cropping agroforestry systems. **a)**
447 Species A is too sensitive to agricultural disturbances, thus hardly able to grow in crop alleys,
448 **b)** Species B has low tolerance to disturbances and low dispersal abilities, it relies on regular
449 recolonization of crop alleys' edges from UVS to persist in such disturbed habitat, **c)** Species
450 C is both tolerant to agricultural disturbances and competitive in undisturbed habitats,
451 therefore able to thrive anywhere. Species C also has high dispersal abilities (vegetative
452 reproduction through runners), making spillover between habitats easier especially when soil
453 tillage is performed in crop alleys. Regarding typical arable weed species persisting mostly in
454 the soil seedbank of crop alleys, the spillover between habitats is less likely given that such
455 species are mostly barochorous (limited dispersal ability) and are hardly able to handle the
456 competitiveness of the already well established plant community in UVS.

457

458 **4. Discussion**

459

460 *4.1. How are plants able to colonize crop alleys from understory vegetation strips?*

461

462 The functional approach supported the hypothesis that the ability of a species to colonize crop
463 alleys from UVS depends both on its tolerance to tillage and herbicide and its dispersal
464 strategy. Very few species were able to colonize crop alleys from UVS, even under organic
465 farming. The only species both dominant in UVS and also found ingressing into crop alleys
466 were *Convolvulus arvensis* and *Potentilla reptans*. These are perennial species that produce
467 runners, have relatively late emergence and larger flowering ranges. Tillage in crop alleys
468 probably favored their spread over long distances, as cutting their roots or stems can promote
469 new shoots. A later emergence and larger flowering range can enable them to grow in summer
470 crops as well, making it easier to colonize fields year after year. Besides, only *Poa annua* was
471 successful in crop alleys of conventional fields after herbicide treatment. This is a ruderal
472 species flowering all year round, therefore able to escape herbicide pressure (Storkey et al.,
473 2010). This result is concurring with the results of Metcalfe et al. (2019) who showed that the
474 effects of immediate adjacent habitats on species richness were reduced after herbicide
475 treatment in fields under conventional farming.

476

477 Regarding wind-dispersed species, such as *Picris echioides* and *Sonchus asper*, we
478 expected them to be important contributors to spillover from UVS but they were not
479 dispersing far into crop alleys. Although there was no significant effect of UVS management
480 on wind-dispersed species, they tended to be found in mown UVS where they could have
481 been prevented from producing seeds (see Figure S3 in Supplementary Material). It is likely
482 that we have underestimated the dispersion of wind-dispersed species, that were uncommon in

483 UVS and probably well controlled by farmers in our experiment, which might be higher in
484 another context (no mowing and windier climate). Further, although the functional approach
485 was mostly based on categorical traits for which there is no concern of intra-specific variation,
486 the use of mean trait values collected from databases can be misleading for plastic traits such
487 as plant height and SLA, which are highly dependent on vegetation management,
488 environmental conditions and biological interactions. Interpretations regarding such traits
489 should be treated with caution. Finally, these results were restricted to no-plough tillage
490 systems and winter cereal crops – the most abundant crops in France – but problematic weeds
491 might be different in other crops and under different crop management, especially in the
492 absence of tillage. For example, Trichard et al. (2013) showed that direct drilling favored
493 perennial grass species such as *Poa trivialis*, which was found in UVS and could become
494 problematic under such no-tillage systems.

495

496 *4.2. Understory vegetation strips do not increase weed-crop ratio in crop alleys*

497

498 The vast majority of species dominant in UVS, such as *Galium aparine*, *Avena* sp. and
499 *Anisantha* sp., were abundant only in crop alleys' edges (i.e. less than 2 m from UVS), so we
500 rejected the “weed reservoirs” hypothesis. Consequently, weed-crop ratio was similar
501 between alley cropping agroforestry fields and pure crop controls, which shows the very weak
502 impact of UVS on the potential harmfulness of weed communities in crop alleys. This concurs
503 with the results of other studies assessing plant spillover from semi-natural habitats, such as
504 field margins (Smith et al., 1999), sown grass strips (Cordeau et al., 2012), forest edges
505 (Devlaeminck et al., 2005), road verges (Chaudron et al., 2016) or grasslands (Hume and
506 Archibold, 1986) towards cropland. These empirical studies showed that plant populations in
507 semi-natural habitats disperse only up to a few meters within the crops, generally less than 4

508 m. This is not surprising as most weeds have poor dispersal abilities (Benvenuti, 2007) and
509 are more likely to be distributed by farm equipment parallel to the adjacent semi-natural
510 habitat (Bischoff, 2005). Moreover, agricultural disturbances reduce the ecological niches
511 available in arable fields for plants coming from semi-natural habitats (Poggio et al., 2013 and
512 references therein), whose population retention depends on regular recolonization of the field
513 (Metcalf et al., 2019). In conclusion, plant spillover from semi-natural habitats towards
514 cropland appears to be restricted to short distances, even in very fragmented systems such as
515 alley cropping agroforestry.

516

517 Interestingly, although the weed-crop ratio was similar between alley cropping
518 agroforestry fields and pure crop controls under conventional farming, the weed-crop ratio
519 decreased when farther from UVS in agroforestry. This could be explained by the fact that
520 UVS – often forming dense covers – would constitute a barrier to weed dispersal within
521 fields, especially for species that are poorly competitive in a more stable and shadier habitat.
522 This potential function of UVS could have stronger impacts on weed communities than the
523 spillover itself. Indeed, some authors showed that grass margin strips reduced the dispersal of
524 arable weed species from semi-natural habitats to cropped fields or the other way around
525 (Cordeau et al., 2012; Marshall, 2009). This could also explain that under organic farming,
526 weed coverage was lower in crop alleys than in pure crop controls (–12% per quadrat on
527 average), whereas we expected a very high spillover given the lack of herbicide treatments
528 and mineral fertilizers. Under organic farming, the fact that weed-crop ratio was constant
529 whatever the distance from UVS can be explained by the presence of an already-established
530 and abundant flora in crop alleys, in comparison to the plants dispersing from UVS. Further
531 studies are needed to assess this role of barrier to weed dispersal.

532

533 4.3. Understory vegetation strips: an opportunity for plant diversity conservation in
534 agroecosystems

535

536 The group of hemerophobic species constitutes a more adequate indicator of environmental
537 quality in agricultural landscapes than species richness *per se*. It includes rare weeds and
538 habitat specialists, whose abundances have decreased with intensive agriculture (Aavik et al.,
539 2008).

540

541 We confirmed the “plant diversity refugia” hypothesis. In conventional fields, the
542 weed flora was very poor. By contrast, UVS were home to a rich and abundant flora
543 containing both agrotolerant and hemerophobic species, the latter in higher proportion. In
544 organic fields, both UVS and arable habitats (i.e. pure crops and crop alleys) supported rich
545 and abundant flora containing agrotolerant and hemerophobic species in similar proportions.
546 The weed flora was more even, but less abundant, than the UVS flora. The intermediate
547 values of communities’ evenness in UVS indicate that the vegetation is generally composed
548 of a few dominant species along with a set of less abundant species.

549

550 Hemerophobic species can grow in arable fields under organic farming, independently
551 of the presence of UVS. Conversely, in conventional fields hemerophobic species were
552 concentrated in UVS, their richness and abundance quickly decreasing in crop alleys. These
553 results highlight the importance of UVS in conserving hemerophobic species associated with
554 semi-natural habitats, which are threatened in intensive agricultural landscapes. However, no
555 rare arable weeds were found during the survey, their conservation depending on targeted
556 management of arable habitats, with reduced inputs of fertilizers and herbicides and moderate
557 disturbances, rather than semi-natural habitats (Storkey and Westbury, 2007; Albrecht et al.,

558 2016). Further studies are needed to assess the benefits – apart from conservation purposes –
559 of promoting botanically diverse communities within arable fields, which are likely to offer
560 different ecosystem services than those provided by arable weed communities. Interestingly,
561 unmanaged and older UVS were dominated by animal-dispersed species, suggesting that
562 these habitats act as ecological corridors. This result is concurrent with the study from
563 Brudvig et al. (2009) who showed that animal-dispersed species are favored by the
564 connectivity between habitats. Tewksbury et al. (2002) showed that corridors in fragmented
565 landscapes are very important to facilitate plant–animal interactions such as pollination and
566 that the beneficial effects of corridors extend beyond their area. Acting as refugia for plant
567 diversity and ecological corridors, UVS are thus likely to benefit higher trophic taxa.

568

569 *4.4. Guidelines for alley cropping agroforestry farmers*

570

571 This study revealed a very weak impact of plant spillover from UVS on the potential
572 harmfulness of weed communities, even under organic farming, which is good news for alley
573 cropping agroforestry farmers. We argue that the best way to avoid spillover from UVS
574 towards crop alleys is to use contrasting management practices between these two habitats, in
575 order to favor plant communities with different ecological preferences. Indeed, in this study,
576 all farmers used contrasting management between UVS (no-tillage) and crop alleys (tillage).
577 However, in no-tillage systems such as direct drilling, plant spillover could be enhanced,
578 especially because of the presence of perennial grasses. In this case, mowing the vegetation of
579 UVS could help reducing the spread of perennial grasses and favoring annual species.
580 Regarding wind-dispersed species, which could be important contributors to plant spillover in
581 windier climates, one solution to prevent them from dispersing towards crop alleys would be
582 to plant the tree rows parallel to dominant winds whenever possible. Sowing competitive

583 grass species is also a very effective way to avoid the development of problematic weed
584 species in UVS, but it is clearly reducing the overall diversity and probably depriving alley
585 cropping agroforestry systems of one of their greatest assets.

586

587 Indeed, this study revealed that UVS can be home to a rich and abundant flora,
588 including hemerophobic species who suffered from agricultural intensification. We believe
589 that plant diversity conservation in UVS can even be optimized by widening UVS, in order to
590 favor perennial species to the detriment of common arable weed species which were also
591 found in UVS (Aavik and Liira, 2010; Fried et al., 2018). This could also promote the role of
592 UVS as a barrier to weed dispersal. Further, despite the resulting loss of cropland, the
593 promotion of wildlife habitats enhances ecosystem services' flows in crops by supporting
594 pollinators and natural enemies of pests, leading to even higher crop yields than in absence of
595 such habitats (Pywell et al., 2015) . Mowing the vegetation could help enhancing plant
596 diversity by preventing the spread of competitive species often dominating unmanaged UVS
597 over time, such as *G. aparine*, *Avena* sp. and *Anisantha* sp., although it might also favor
598 potentially troublesome weeds. Indeed, the only species that were dominant in UVS and also
599 found far into crop alleys (*Convolvulus arvensis* and *Potentilla reptans*) tended to be found in
600 mown UVS (see Figure S3 in Supplementary Material), where their prostrate forms,
601 underground organs and resprouting capacities would have given them advantages over the
602 other species. Probably the mowing of UVS also created better light conditions by reducing
603 the canopy of herbaceous strata. It was shown that the abundance of *Convolvulus arvensis* can
604 be reduced by shading (using shade cloth) whereas mowing has no effect or can even lead to
605 positive response (see Orloff et al., 2018 and references therein). However, it seems that UVS
606 are unsuitable for the conservation of rare weeds for which alternative habitats (such as
607 conservation headlands) would need to be established in the landscape.

608

609 *4.5. What can we expect in older alley cropping agroforestry fields?*

610

611 The agroforestry systems studied here were relatively young (between 2 and 11 years). On the
612 one hand, it could be expected that plant spillover from UVS is higher in younger agroforestry
613 fields. Indeed, after tree plantation in a field, the vegetation of UVS is first composed of
614 typical arable weeds coming from the soil seedbank, which are adapted to agricultural
615 disturbances and therefore likely to disperse in crop alleys. Over time, hemerophobic species
616 can colonize UVS and contribute to reduce the spread of weeds. On the other hand, it could be
617 expected that plant spillover from UVS is higher for older agroforestry fields. The
618 heterogeneity of environmental conditions induced by the trees could favor the growth of
619 opportunist weeds with high plasticity to the detriment of crop varieties which remain selected
620 only in full sun conditions (Desclaux et al., 2016). For example, Boinot (2015) showed that
621 *Avena sterilis* and *Fallopia convolvulus* exhibited higher specific leaf area and lower canopy
622 height in an old agroforestry field with high shading, compared to an agroforestry field with
623 poorly developed trees. This shade-tolerance syndrome (Perronne et al., 2014) might
624 constitute a competitive advantage for weeds in agroforestry fields.

625

626 *4.6. Taking advantage of understory vegetation strips to optimize the delivery of multiple*
627 *ecosystem services*

628

629 Our study revealed that UVS promote plant diversity conservation within cropped fields.
630 Therefore, we expect that UVS can supply many additional ecosystem services like other
631 farmland vegetative strips (Cresswell et al., 2019). For example, UVS could be used to
632 provide alternative resources and overwintering habitats for pollinators, detritivores and

633 natural enemies of crop pests and so enhance pollination, nutrient cycling and biological
634 control. UVS could also improve soil structure and porosity, thus reducing soil erosion. To
635 promote the delivery of multiple ecosystem services, future research should assess not only
636 the nature of ecosystem services provided by plant communities of UVS but also the
637 relationships between these services (i.e. trade-off, complementarity, synergy). Indeed, if
638 management interventions are devoted to the promotion of a single or restricted number of
639 services, it can have unintended negative consequences on other services (Bennett et al.,
640 2009). However, an encouraging review on interactions between biological control,
641 pollination and nutrient cycling revealed that complementary effects between these ecosystem
642 services were the most common, followed by synergistic effects, whereas trade-offs were
643 rarer (Garibaldi et al., 2018). These results demonstrate that promoting multiple ecosystem
644 services with biodiversity-friendly practices is a possibility.

645

646 The ecological engineering of UVS should focus on both the functional structure and
647 area covered by plant communities in UVS, which are expected to be the major drivers of
648 ecosystem services supported by plant communities. There is currently a wide range of UVS
649 management strategies among alley cropping agroforestry farmers, resulting in different
650 spatial configuration (i.e. UVS width, spacing between UVS) and disturbance regimes (i.e. no
651 management, mowing, crushing, mulching, plant mixtures sowing). Further experiments are
652 needed to determine what are the best UVS management strategies to promote multiple
653 ecosystem services, while reducing the risk of crop pest and weed spillover within crop alleys.
654 Taking full advantage of the presence of UVS should greatly improve the agricultural and
655 environmental performance of alley cropping agroforestry systems in temperate regions.

656

657 **5. Conclusions**

658

659 The non-crop herbaceous strip under the tree rows is a compartment often forgotten but
660 nevertheless essential to understand the provision of ecosystem services that we can expect
661 from alley cropping agroforestry. To our knowledge, our study is the first to describe plant
662 communities associated to tree rows in temperate alley cropping agroforestry systems. We
663 demonstrated that plant spillover from understory vegetation strips towards crop alleys had a
664 very weak impact on the potential harmfulness of weed communities. We also revealed a high
665 potential of understory vegetation strips, home to a rich and abundant hemerophobic flora, for
666 preserving plant diversity in agroecosystems. The originality of alley cropping agroforestry
667 systems lies in the presence of trees and non-crop herbaceous vegetation within fields
668 themselves, which should definitely be used for biodiversity conservation purposes and for
669 the enhancement of ecosystem services flows in the crops, in the perspective of reducing our
670 dependence to agrochemicals. However, even within pure crops, farmers could establish non-
671 crop habitats to take advantage from their functions, as it has been done with beetle banks and
672 wildflowers strips. We suggest that reconnecting with non-crop vegetation is a crucial step for
673 the transition towards agroecological systems, urgently needed given the context of climate
674 change and biodiversity extinction crisis we are facing.

675

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677

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687

688 **Declaration of interest:** none

689

690 **Appendix A.**

691

692 **Table A1.** Species classification, conservation value, and occurrence within the three
693 surveyed habitats.

EPPO code	Latin name	Classification ¹	Conservation value of arable weeds ²	Alley cropping agroforestry		Pure crop controls (n = 432)
				Understory vegetation strips (n = 96)	Crop alleys (n = 432)	
ALOMY	<i>Alopecurus myosuroides</i>	agrotolerant	3	X	X	X
APHAR	<i>Aphanes arvensis</i>	agrotolerant	3	X	X	X
ARBTH	<i>Arabidopsis thaliana</i>	hemerophobic	0	X	X	
ARREL	<i>Arrhenatherum elatius</i>	hemerophobic	3	X	X	X
ATXPA	<i>Atriplex patula</i>	agrotolerant	0		X	X
AVESS	<i>Avena sp</i>	agrotolerant	0	X	X	X
BROSS	<i>Bromus sp</i>	hemerophobic	0	X	X	X
LITAR	<i>Buglossoides arvensis</i>	hemerophobic	3		X	X
CAPBP	<i>Capsella bursa-pastoris</i>	agrotolerant	0		X	
CERGL	<i>Cerastium glomeratum</i>	hemerophobic	0	X	X	X
CHEAL	<i>Chenopodium album</i>	agrotolerant	0	X	X	X
CIRAR	<i>Cirsium arvense</i>	agrotolerant	0	X	X	X
CIRVU	<i>Cirsium vulgare</i>	hemerophobic	0	X	X	
CLVVT	<i>Clematis vitalba</i>	hemerophobic	0	X		X
CONAR	<i>Convolvulus arvensis</i>	agrotolerant	0	X	X	X
CAGSE	<i>Convolvulus sepium</i>	agrotolerant	0		X	

DACGL	<i>Dactylis glomerata</i>	hemerophobic	0	X	X	X
DAUCA	<i>Daucus carota</i>	hemerophobic	0		X	X
DIWSI	<i>Dipsacus fullonum</i>	hemerophobic	0	X		
AGRRE	<i>Elytrigia repens</i>	hemerophobic	0		X	X
EPIAD	<i>Epilobium tetragonum</i>	hemerophobic	0	X	X	X
EQUAR	<i>Equisetum arvense</i>	hemerophobic	0			X
ERICA	<i>Erigeron canadensis</i>	agrotolerant	0	X	X	
EPHEX	<i>Euphorbia exigua</i>	hemerophobic	0			X
POLCO	<i>Fallopia convolvulus</i>	agrotolerant	0		X	X
FESRU	<i>Festuca rubra</i>	hemerophobic	0	X		
FUMOF	<i>Fumaria officinalis</i>	agrotolerant	0		X	
GALAP	<i>Galium aparine</i>	agrotolerant	0	X	X	X
GERCO	<i>Geranium columbinum</i>	agrotolerant	0	X		
GERDI	<i>Geranium dissectum</i>	agrotolerant	0	X	X	X
PICEC	<i>Helminthotheca echioides</i>	hemerophobic	0	X	X	X
HOLLA	<i>Holcus lanatus</i>	hemerophobic	0	X	X	
HOLMO	<i>Holcus mollis</i>	hemerophobic	0	X		
HYPPE	<i>Hypericum perforatum</i>	hemerophobic	0	X	X	
IUNBU	<i>Juncus bufonius</i>	hemerophobic	0		X	
KICEL	<i>Kickxia elatine</i>	hemerophobic	0		X	X
LACSE	<i>Lactuca serriola</i>	agrotolerant	0	X	X	
LAMPU	<i>Lamium purpureum</i>	agrotolerant	0	X	X	
LAPCO	<i>Lapsana communis</i>	hemerophobic	0	X	X	X
LOLSS	<i>Lolium sp</i>	agrotolerant	0	X	X	X
ANGAR	<i>Lysimachia arvensis</i>	agrotolerant	0	X	X	X
MATMT	<i>Matricaria discoidea</i>	hemerophobic	0	X	X	X
MEDPO	<i>Medicago polymorpha</i>	hemerophobic	0			X
MYOAR	<i>Myosotis arvensis</i>	hemerophobic	0	X	X	X
PAPRH	<i>Papaver rhoeas</i>	agrotolerant	3	X	X	X
POLLA	<i>Persicaria lapathifolia</i>	agrotolerant	0			X
PHAPA	<i>Phalaris paradoxa</i>	hemerophobic	0		X	X
PICHI	<i>Picris hieracioides</i>	hemerophobic	0	X	X	X
PLALA	<i>Plantago lanceolata</i>	hemerophobic	0	X	X	X
PLAMA	<i>Plantago major</i>	hemerophobic	0		X	X
POAAN	<i>Poa annua</i>	agrotolerant	0	X	X	X
POATR	<i>Poa trivialis</i>	hemerophobic	0	X	X	X
POLAV	<i>Polygonum aviculare</i>	agrotolerant	0		X	X
PTLRE	<i>Potentilla reptans</i>	agrotolerant	0	X	X	X
RANAR	<i>Ranunculus arvensis</i>	hemerophobic	2		X	
RANBU	<i>Ranunculus bulbosus</i>	hemerophobic	0	X		X
RANRE	<i>Ranunculus repens</i>	hemerophobic	0	X	X	
RUBSS	<i>Rubus sp</i>	hemerophobic	0	X	X	X
RUMCR	<i>Rumex crispus</i>	hemerophobic	0	X	X	X
RUMOB	<i>Rumex obtusifolius</i>	hemerophobic	0		X	
SAIPR	<i>Sagina procumbens</i>	hemerophobic	0			X
FESAR	<i>Schedonorus arundinaceus</i>	hemerophobic	0	X	X	X

FESPR	<i>Schedonorus pratensis</i>	hemerophobic	0	X		
SENVU	<i>Senecio vulgaris</i>	agrotolerant	0			X
SETVI	<i>Setaria italica</i>	hemerophobic	0		X	
SHRAR	<i>Sherardia arvensis</i>	hemerophobic	0	X	X	X
SLYMA	<i>Silybum marianum</i>	hemerophobic	0			X
SINAR	<i>Sinapis arvensis</i>	agrotolerant	0	X	X	X
SONAS	<i>Sonchus asper</i>	agrotolerant	0	X	X	X
SONOL	<i>Sonchus oleraceus</i>	agrotolerant	0	X	X	X
TAROF	<i>Taraxacum officinale</i>	agrotolerant	0	X	X	X
TOIAR	<i>Torilis arvensis</i>	hemerophobic	0	X	X	
TROPS	<i>Tragopogon porrifolius</i>	hemerophobic	0	X		
TROPR	<i>Tragopogon pratensis</i>	hemerophobic	0	X		X
TRFAR	<i>Trifolium arvense</i>	hemerophobic	0		X	
TRFPR	<i>Trifolium pratense</i>	hemerophobic	0		X	X
VLLLO	<i>Valerianella locusta</i>	hemerophobic	0			X
VEBOF	<i>Verbena officinalis</i>	hemerophobic	0	X	X	X
VERAR	<i>Veronica arvensis</i>	hemerophobic	0	X	X	X
VERPE	<i>Veronica persica</i>	agrotolerant	0		X	X
VERPO	<i>Veronica polita</i>	hemerophobic	0	X	X	X
VICBI	<i>Vicia bithynica</i>	hemerophobic	0		X	X
VICHY	<i>Vicia hybrida</i>	hemerophobic	0		X	
VLPMY	<i>Vulpia myuros</i>	hemerophobic	0	X	X	

694 ¹ Following Aavik et al. (2008), each species was classified as agrotolerant or hemerophobic
695 based on its frequency of occurrence in arable fields at national scale, using data of the
696 Biovigilance Flore network 2002–2012 (Fried et al., 2008). A species was considered as
697 hemerophobic if its frequency of occurrence in the sample plots of arable fields was lower
698 than 10%.

699 ² Conservation value of arable weeds according to the Archeophyt Weed National Red Lists
700 (Aboucaya et al., 2000); 1: species in real danger of extinction, 2: species that are thought to
701 have experienced significant regression but are nevertheless still common in some regions, 3:
702 species that are at best stable in at least some regions.

703

704 **Supplementary material**

705

706 Supplementary material may be found in the online version of this article:

707 **Figure S1.** Map of the agroforestry fields and their pure crop controls.

708 **Table S1.** Crop management for each pair of agroforestry fields and pure crop controls.

709 **Table S2.** Description of agroforestry fields.

710 **Figure S2.** Mean and standard deviation of the coverage of species dominant in UVS
711 (kept in the spillover analysis) vs arable weed species persisting mostly in the seedbank
712 (excluded from the analysis).

713 **Figure S3.** RLQ analysis performed on plant communities located in the understory
714 vegetation strips.

715 **Table S3.** Abbreviations, units, basic statistics and RLQ axis loadings of environmental
716 variables and traits considered in the RLQ analysis of plant communities *located in the*
717 *understory vegetation strips (UVS)*.

718 **Table S4.** Abbreviations, units, basic statistics and RLQ axis loadings of environmental
719 variables and traits considered in the RLQ analysis of plant communities *located in the crop*
720 *alleys* and restricted to species that were also dominant in the understory vegetation strips
721 (UVS).

722 **Table S5.** Regression parameters, standard errors and p-values of generalized mixed-
723 effects models (GLMMs) performed on organic and conventional fields separately.

724 **Table S6.** Regression parameters, standard errors and p-values of generalized mixed-
725 effects models (GLMMs) assessing the effect of the distance from understory vegetation
726 strips (UVS) on potential harmfulness and diversity of communities *in the crop alleys*.

727 **Figure S4.** Effect of distance from understory vegetation strips (UVS) on the weed-crop
728 ratio (weed coverage / weed and crop coverage).

729 **Figure S5.** Effect of distance from understory vegetation strips (UVS) on the variables
730 considered for the assessment of communities' diversity.

731 **Table S7.** Total species richness observed across all fields, per habitat and under
732 conventional vs organic farming.

733

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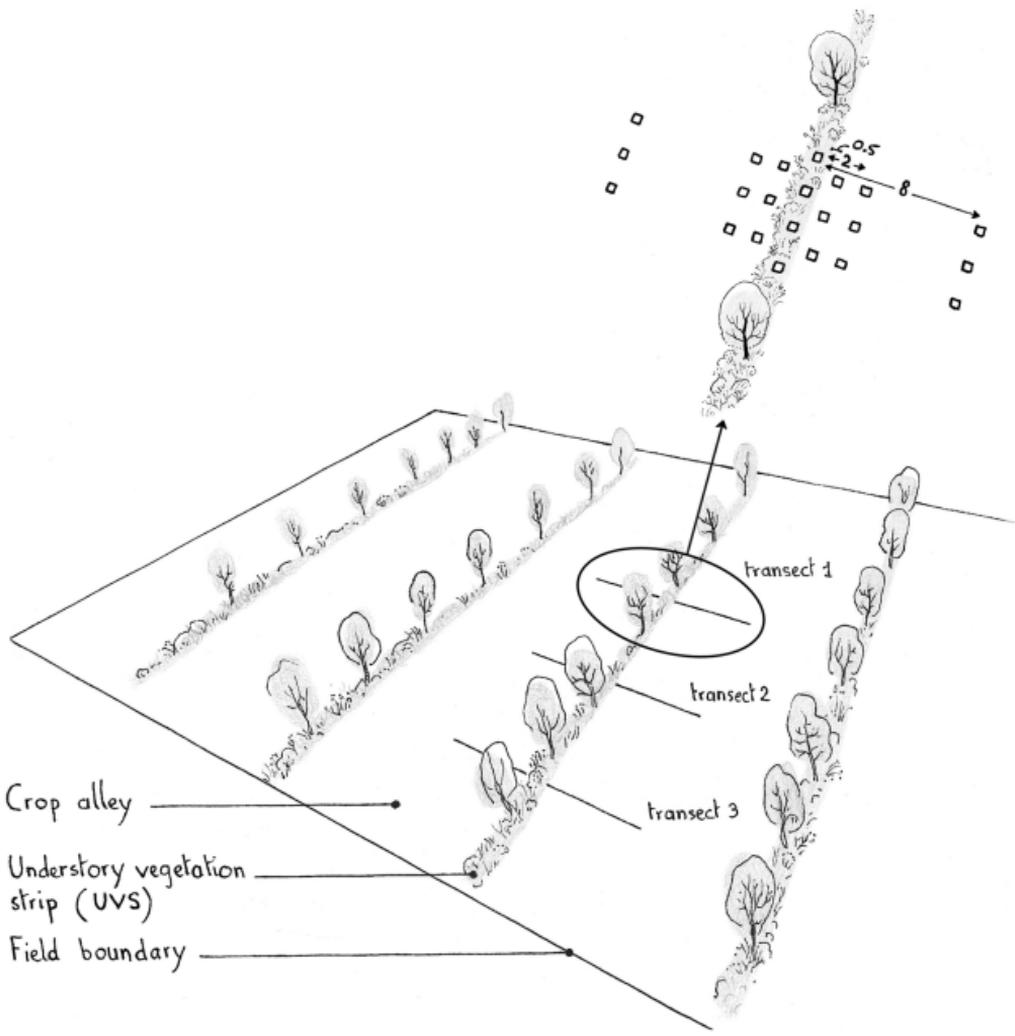
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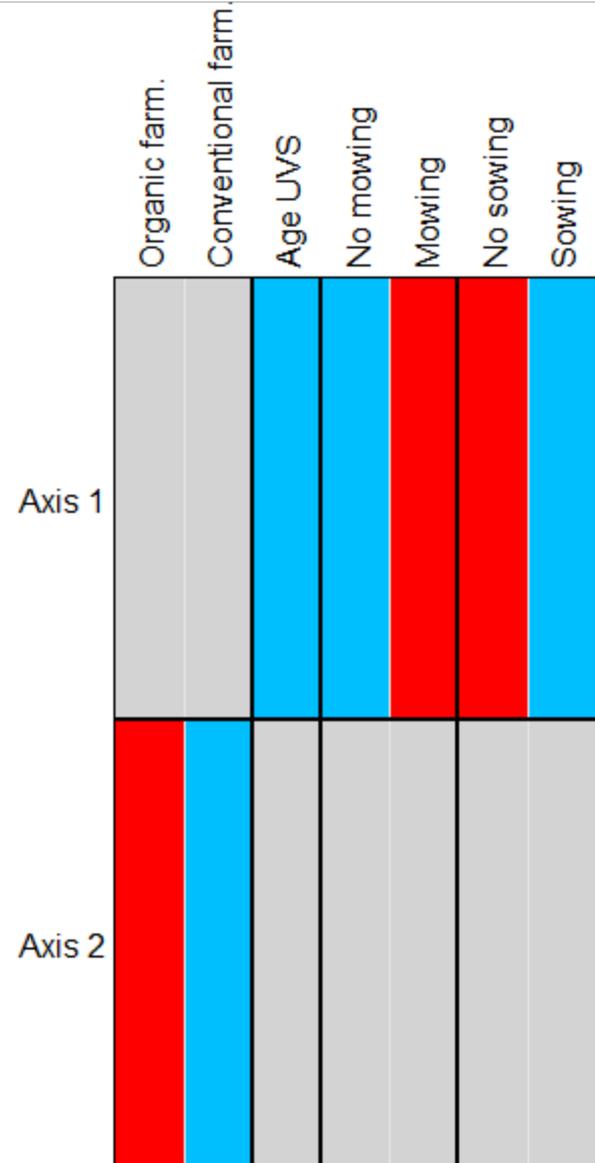
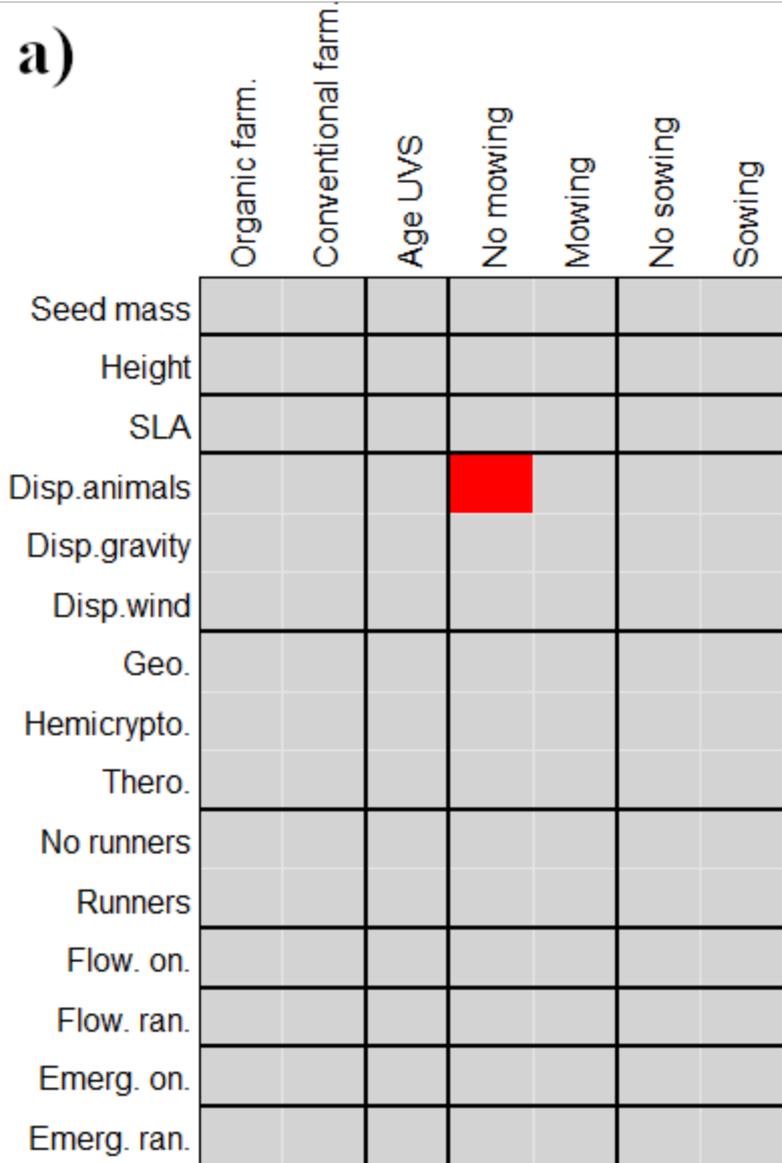
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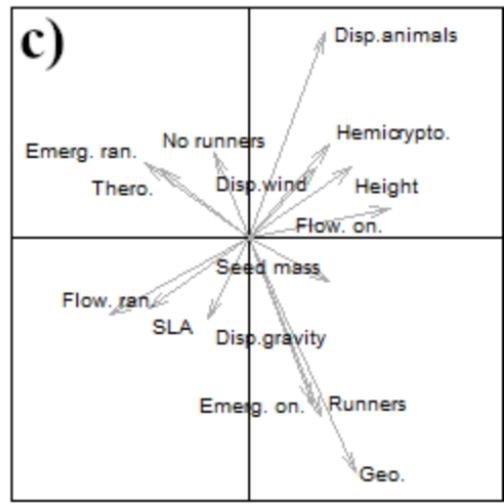
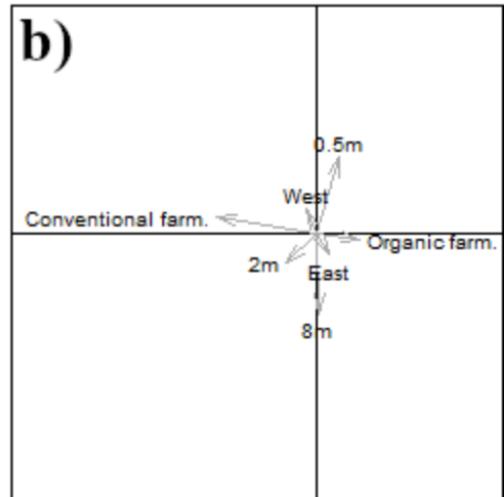
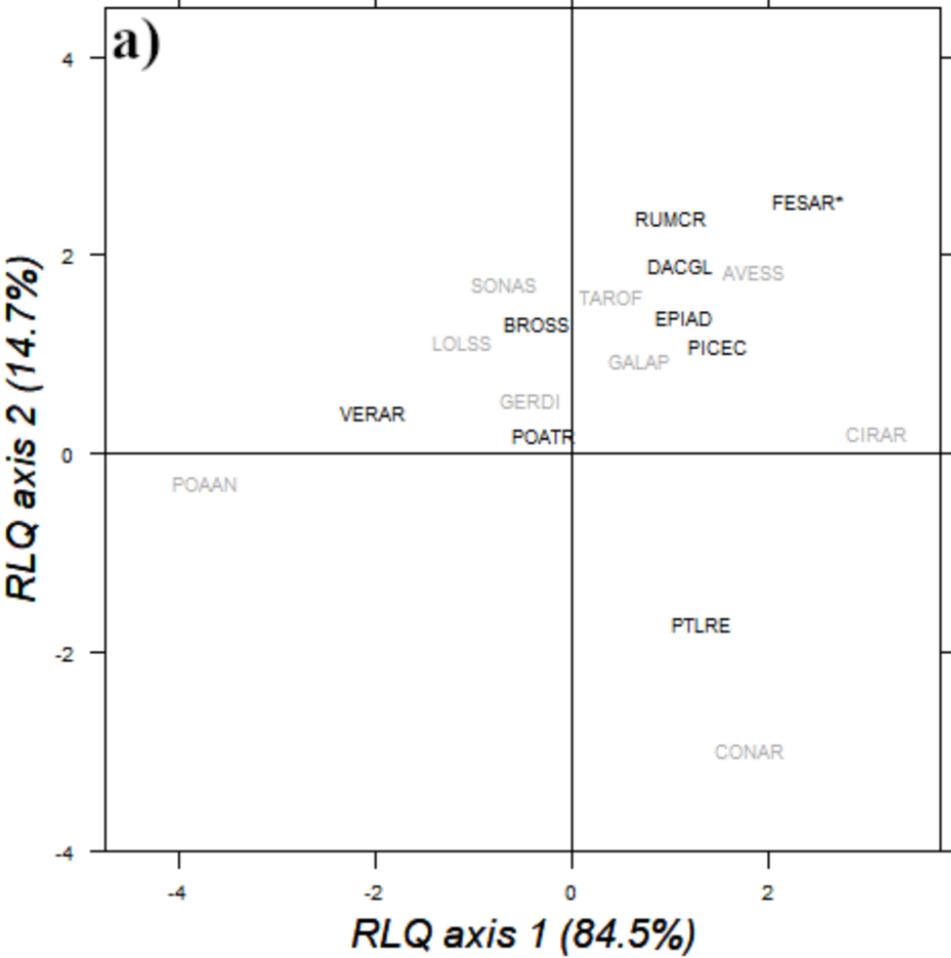
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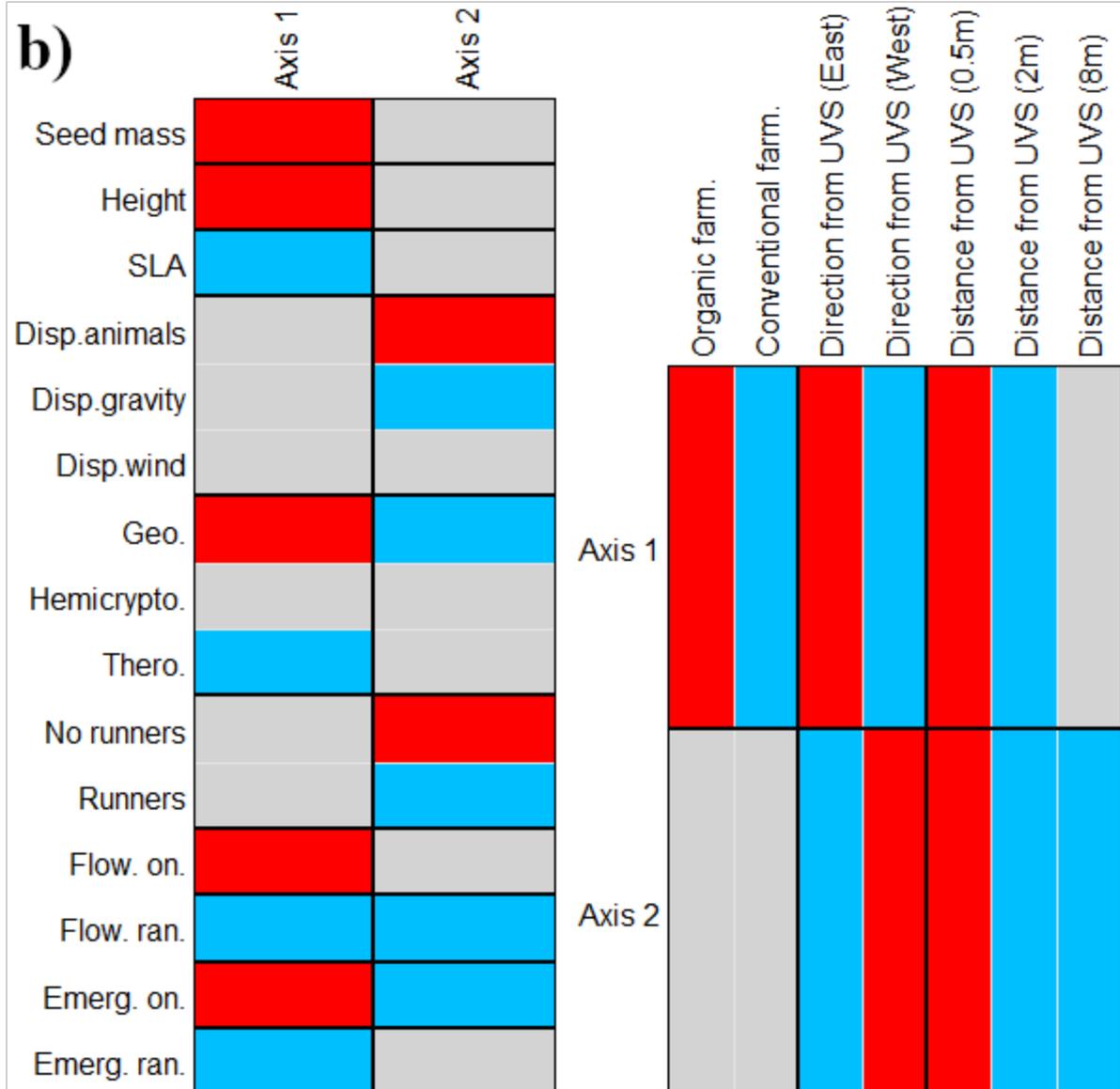
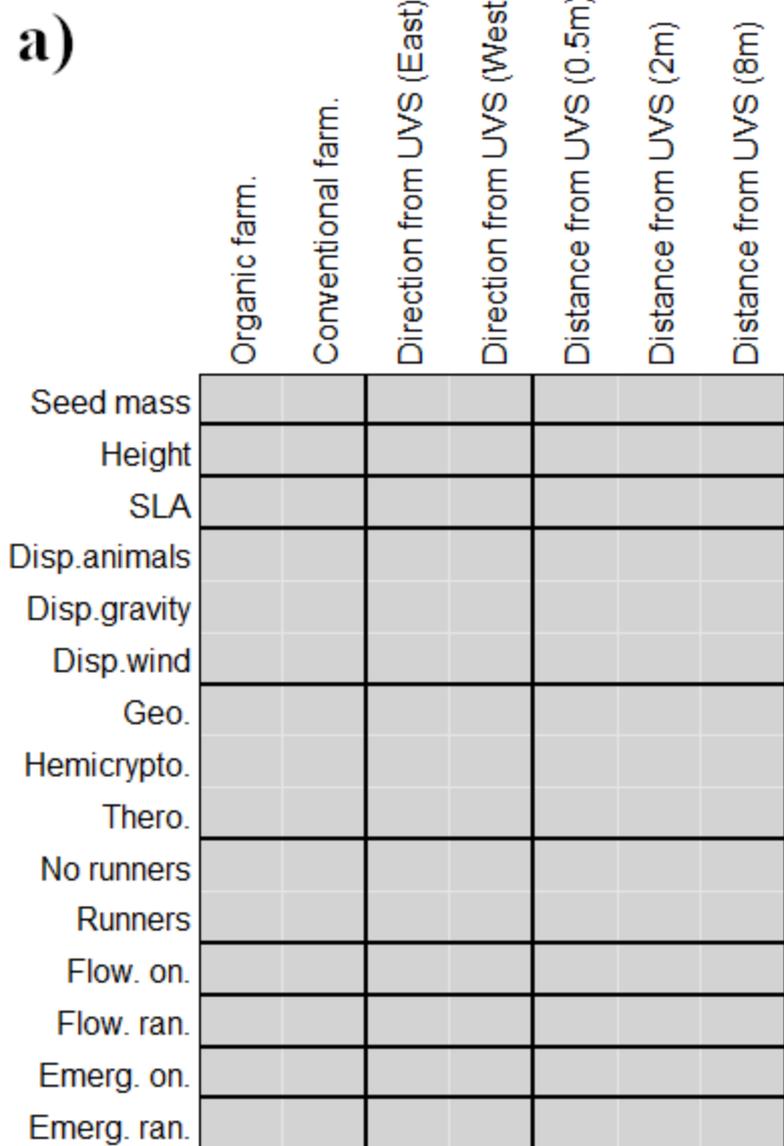
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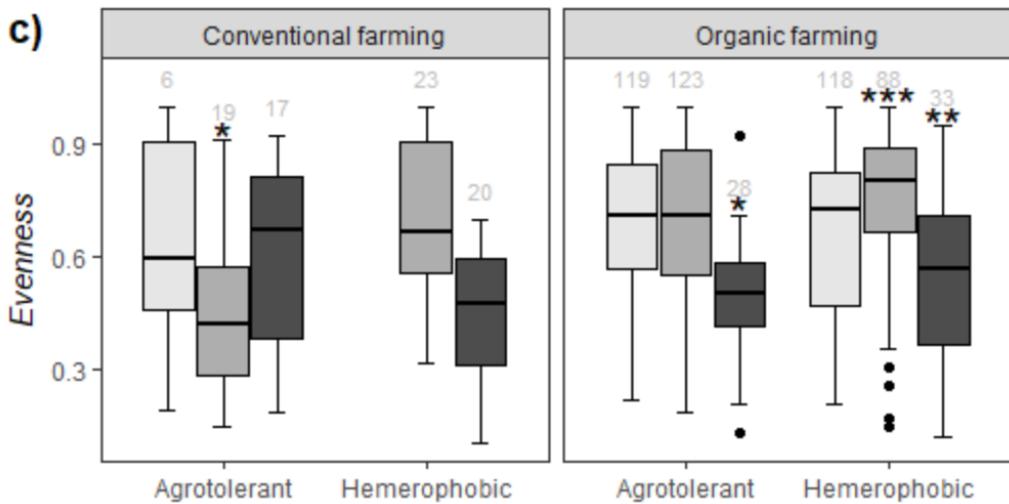
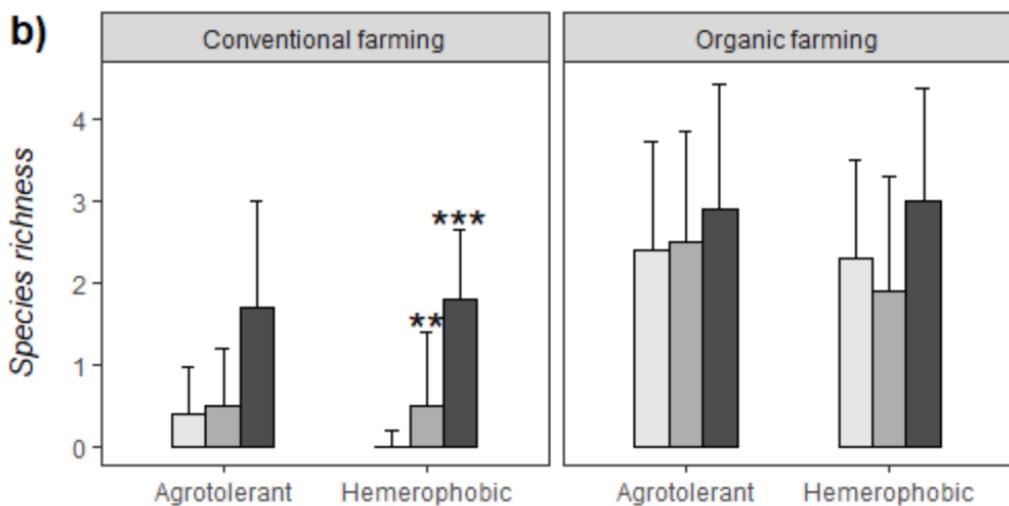
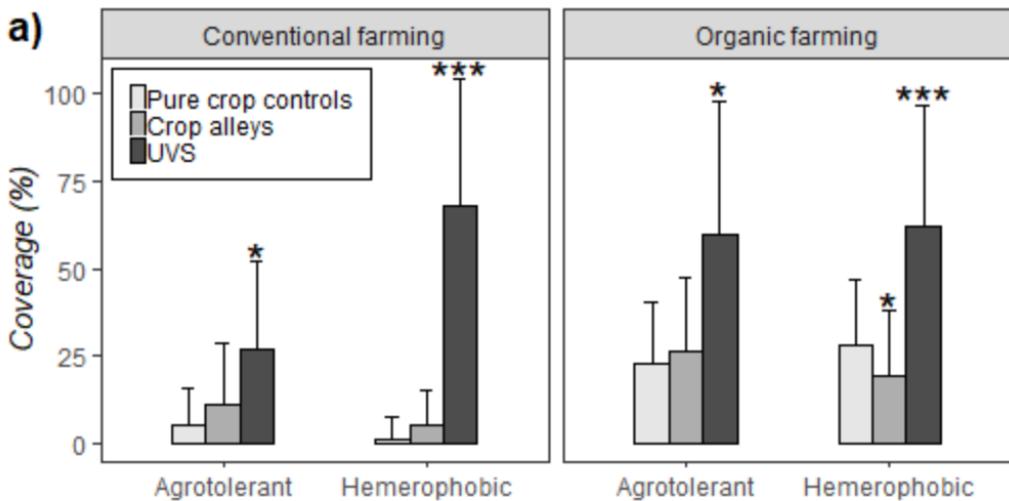
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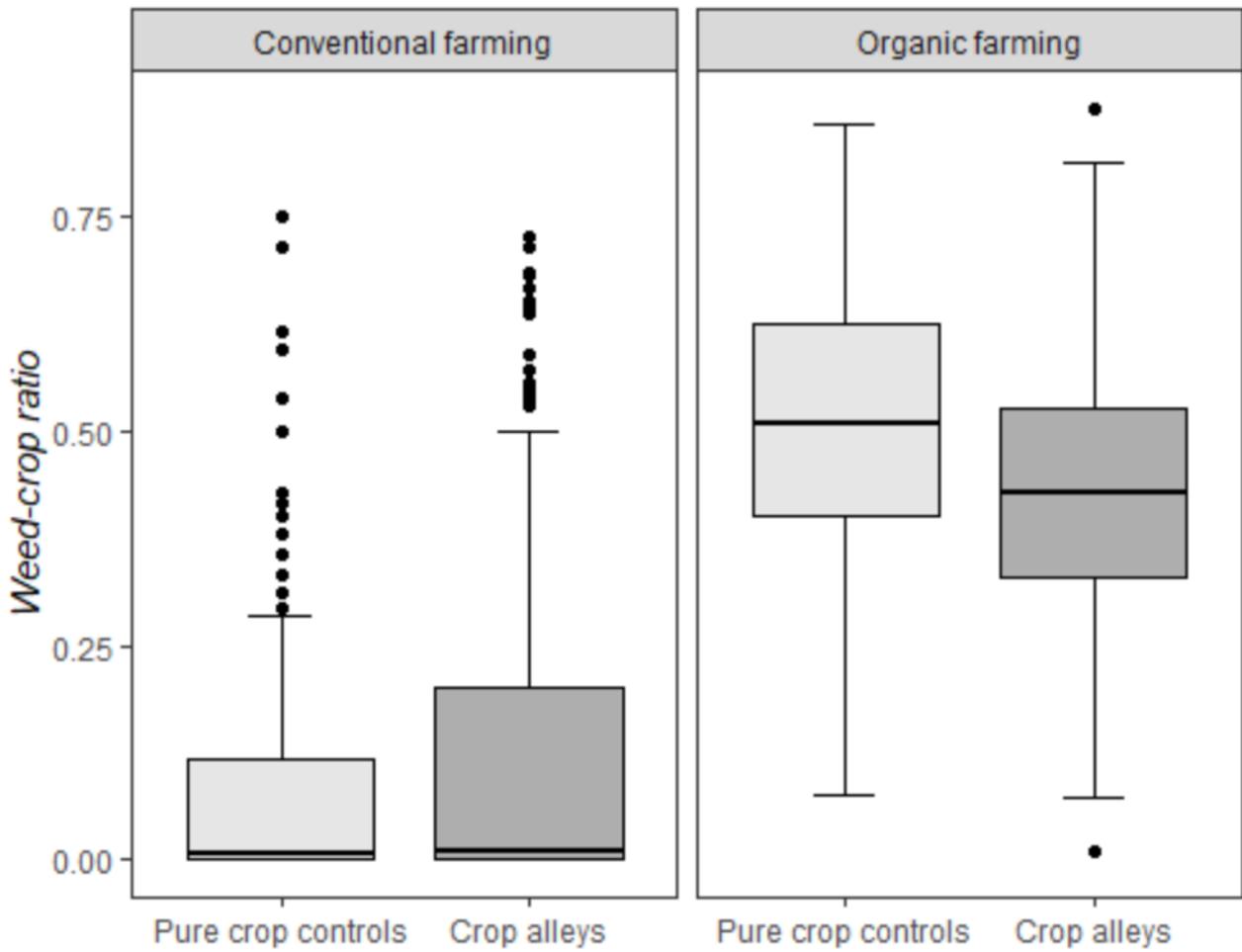


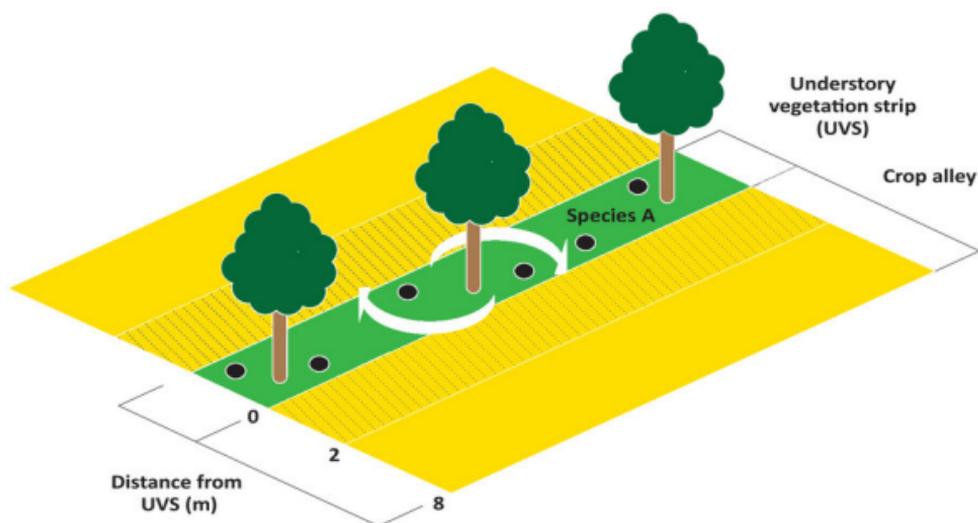
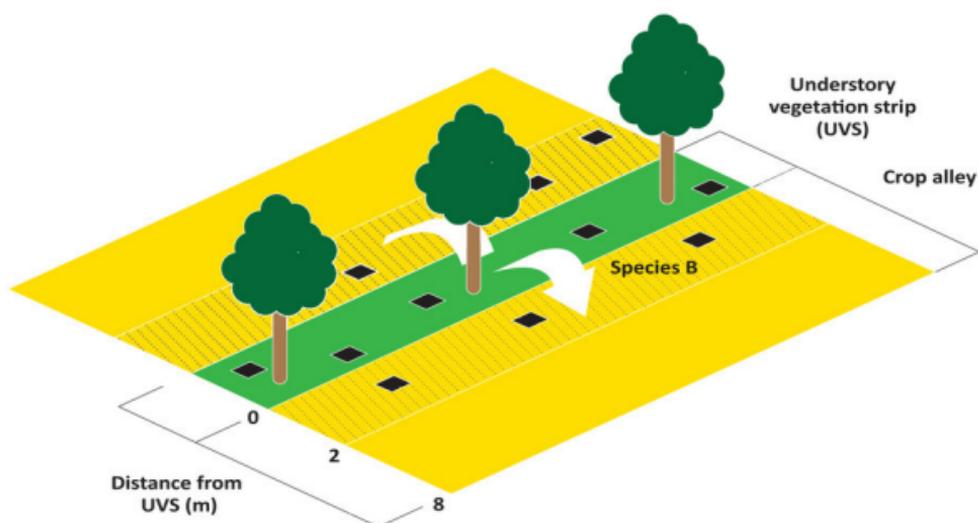










a)**UNSUCCESSFUL SPILLOVER****b)****FREQUENT SPILLOVER TO SHORT DISTANCES****c)****RARE SPILLOVER TO LONG DISTANCES**