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

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

1. Introduction

The post-war agricultural intensification has led to worldwide losses of biodiversity due to the increase of both agrochemicals' application and croplands, to the detriment of semi-natural habitats such as woodlots, grasslands, hedges and field boundaries (Stoate et al., 2001). Since then, many studies have demonstrated that semi-natural habitats provide food resources, reproduction and overwintering sites and refuges from agricultural disturbances for many organisms. For example, Aavik and Liira (2010) showed that field boundaries are home to hemerophobic plant species, i.e. species sensitive to tillage and/or herbicides, as opposed to agrotolerant species. Such species have a high conservation value as they are declining in the context of intensive agriculture (Aavik et al., 2008). Beneficial arthropods such as pollinators and natural enemies of pests also depend on the presence of semi-natural habitats to complete their life cycle (Pfiffner and Luka, 2000; Hass et al., 2018). On the other hand, it has been shown that non-crop habitats could host weeds, pathogens and pests (Norris and Kogan, 2000; Wisler and Norris, 2005). If the presence of nearby semi-natural habitats impacts the functioning of agroecosystem, the spillover of organisms between semi-natural and arable habitats is also of major importance and can be positive or negative for crop production (Blitzer et al., 2012). Indeed, in the case of arthropods, the higher the spillover of beneficial arthropods towards arable fields is, the better pest control and crop pollination can be achieved (Woodcock et al., 2016). On the other hand, pests coming from alternative host plants in adjacent habitats could disperse towards the arable fields, potentially causing crop yield losses (e.g. Johnson, 1950). In the case of spontaneous plants, which are at the basis of agroecosystem food web, their spillover in arable fields could promote biodiversity conservation, but also induce yield losses through competition with crops (Petit et al., 2011). Many studies have assessed the negative effects of various adjacent habitats on crop production, often suspected to supply arable fields with weeds. Overall, the abundance and diversity of weed communities were enhanced up to 2.5 m and 4 m from field margins (Marshall, 1989; Wilson and Aebischer, 1995 respectively), 3 m from forests (Devlaeminck et al., 2005), 3.5 m from road verges (Chaudron et al., 2016) and 7 m from grasslands (Hume and Archibold, 1986), thus only in crop edges in every case. Furthermore, the intensity of organisms' spillover in arable fields, and hence the intensity of ecosystem processes associated, depends on the nature of adjacent semi-natural habitats. Indeed, Metcalfe et al. (2019) observed a higher plant spillover in fields next to grasslands or in the presence of field margins, compared to fields next to woodlots, bare ground (ploughed fields or urban) or without field margins. Woodcock et al. (2016) showed that the spillover of beneficial arthropods was higher in fields next to wildflowers strips, compared to fields next to grass strips. Conversely, some habitats can even constitute a barrier to the dispersal of organisms into arable fields (e.g. Mauremooto et al., 1995; Cordeau et al., 2012). Besides, the spillover of organisms between arable and semi-natural habitats is likely to be increased by small-scale agriculture and landscape fragmentation, which are characterized by higher proportion of edges (Blitzer et al., 2012; Mitchell et al., 2015). That could explain the higher weed diversity observed in smaller fields (Gaba et al., 2010). In the same idea, Hatt et al. (2017) showed that the presence of semi-natural habitats located within fields' core themselves favored the spillover of organisms farther into the crops.

In temperate regions, agroforestry systems are gaining renewed interest as they can provide a wide range of ecosystem services from the same area of land, such as sustainable food and biomass production, soil and water protection, biodiversity conservation and carbon sequestration (Jose, 2009; Quinkenstein et al., 2009; Torralba et al., 2016; Kay et al., 2019). Agroforestry systems can take multiple faces given the wide range of practices they cover (e.g. hedge farmland, silvoarable and silvopastoral systems), the diversity of species that can be associated (herbaceous plants, shrubs, trees) and the spatial configurations conceivable (i.e. playing on the area covered by the different strata and their position within fields). Such plasticity allows agroforestry systems to be implemented in many regions and for multiple objectives. If promoted by agricultural and environmental policies, agroforestry systems are expected to help meet Europe policy objectives on greenhouse gas emissions while providing multiple ecosystem services (Kay et al., 2019). Among agroforestry systems, alley cropping agroforestry, in which arable crops are grown between tree rows, represent a great opportunity for the reintegration of semi-natural habitats within fields. Indeed, the presence of trees rows leads to increased edges amount and field fragmentation, which is expected to enhance ecosystem (dys-)services flows (Mitchell et al., 2015). Further, to prevent any damage on trees, farmers avoid tilling the soil close to the trees, resulting in the development of non-crop herbaceous strips under the trees, hereafter called understory vegetation strips (UVS) (Figure 1). UVS are poorly disturbed by crop management and so are comparable to other linear semi-natural habitats such as field boundaries, except that they are located within fields and occupy about 3 to 13% of the available agricultural area. Given the spatial configuration and the important extent of UVS, it is likely that both the intensity of plant spillover and the amount of refugia for biodiversity are increased in alley cropping agroforestry compared to pure crop systems. Many works have assessed the ecosystem services supplied by (semi-)permanent herbaceous vegetation in other systems such as pure crops (e.g. Hatt et al., 2017), vineyards (e.g. Winter et al., 2018; Garcia et al., 2019) and orchards (e.g. Forey et al., 2016; Cahenzli et al., 2019). However, research in temperate alley cropping agroforestry is recent and has focused mainly on interactions between trees and crops. Works considering UVS are still scarce, but we can mention Burgess (1999), Cardinael et al. (2015), Mézière et al. (2016), Pardon et al. (2019) for example. If most farmers perceive agroforestry systems as a solution to wildlife habitats conservation, others fear that UVS constitute reservoirs for weeds that colonize crop alleys (Graves et al., 2017). To our knowledge, very few studies have assessed the effects of alley cropping agroforestry on arable weed community structure and plant diversity conservation in temperate regions. Mézière et al. (2016) showed that an alley cropping agroforestry system can harbor higher plant diversity than a pure crop control, without enhancing weed coverage in crop alleys. However, these results were restricted to one pair of fields under conventional farming in a Mediterranean French context.

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

2. Materials and Methods

2.1. Vegetation survey

The study was conducted in Gers and Pyrénées-Atlantiques Departments (South-Western France), which is a hilly region (altitude about 300 meters) characterized by a sub-Atlantic climate with hot summers and cool winters. Agricultural areas are mainly composed of clay-limestone and clay-to-silt soils and annual precipitation usually varies from 700 to 900 mm. Vegetation surveys were carried out in May 2017 over 16 winter cereal fields (8 pairs of alley cropping agroforestry systems and pure crop controls) growing either winter wheat (*Triticum aestivum* L.) or winter barley (*Hordeum vulgare* L.), half under conventional farming and half under organic farming. Vegetation surveys in conventional farming fields were carried out at least one month after the last herbicide treatment. Thus, observed flora in these fields is mostly composed of species surviving herbicide treatments or emerging later. Each pair of fields (alley cropping agroforestry vs pure crop control) was located within the same perimeter, similar in terms of pedo-climatic conditions and surrounding land use (see Figure S1 in Supplementary material). Each pair was also cultivated by the same farmer, with similar crop managements over the three years preceding the study (see Table S1 in Supplementary material). Three fields under organic farming also contained leguminous crops, either garden pea (*Lathyrus oleraceus* Lam.) and/or common vetch (*Vicia sativa* L.) but the proportion of legumes was always very low compared to cereals. For both organically and conventionally farmed fields, UVS were either unmanaged (n = 2 fields), mown before sowing and after harvest (n = 1 field) or sown with competitive perennial species (n = 1 field): *Schedonorus arundinaceus* under organic farming, *Festuca rubra* under conventional farming. Features of agroforestry fields (i.e. tree species and basic metrics) are given in Table S2 in Supplementary material. In each agroforestry field, UVS were surveyed in three zones distant from 20 m. Each zone was sampled with four quadrats (0.25 m²) separated by two meters each. Then, on both sides of these zones, adjacent crop alleys were sampled on transects running perpendicular to UVS, at three distances from UVS (0.5 m, 2 m and 8 m). For each distance, we visually estimated the coverage of each species found in three quadrats (0.25 m²) separated by two meters each (Figure 1), with an accuracy of ± 5%. Plants were mostly at vegetative or floral stage during the survey. In total, 66 quadrats (16.5 m²) were sampled per agroforestry field. This sampling design was located at around 50 m and 100 m from the two nearest field boundaries to exclude their effect on weed communities. The crop alleys on either side of the UVS were sampled to take into account the potential effect of slopes and prevailing wind directions on seed dispersal. The same protocol was used for pure crop controls with the transects placed at equivalent locations in the field in the absence of the UVS, resulting in 54 quadrats (13.5 m²) sampled per pure crop control. In total, 960 quadrats (240 m²) were sampled during the vegetation survey.

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

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

Functional traits related to dispersal strategies and tolerance to agricultural disturbances were collected from databases and reference books of French flora (Table 1), along with Raunkiaer life forms. If an individual was identified to the genus only, the mean attributes of congeneric species found in the survey and predominant in the region were used (Association Botanique Gersoise, 2003).

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

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)

[a]Flowering onset was coded from 1 (January) to 12 (December).

[b]Emergence onset was coded from 1 (October) to 12 (September) since winter cereals were sown in October-November. Data were collected from observations at SupAgro Dijon and based on expert opinion.

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

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

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

2.3. Data analysis

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

RLQ and fourth-corner analysis following Dray et al., (2014). RLQ analysis aims to identify the main co-structures between traits (Q-table) and environmental variations (R-table) considering species abundances (L-table), while fourth-corner analysis provide tests for the correlations between each trait and each environmental variable. By combining RLQ and fourth-corner analysis we could test the correlations (i) between each trait and combination of environmental variables obtained from RLQ axes, and (ii) between each environmental variable and trait syndromes obtained from RLQ axes. First, a combination of RLQ and fourth-corner analysis was performed on the plant communities *located in the UVS* to analyze their taxonomic and functional structures in response to different management practices. We only considered dominant species, occurring in at least 5 quadrats (i.e. whose frequency of occurrence was superior to 5%), because rare species may unduly influence the results (Kenkel et al., 2002). Dominant species represented 90% of the total coverage observed in UVS. The Q-table contained 23 species described by 9 functional traits related to dispersal ability and tolerance to disturbances, along with Raunkiaer life forms. The R-table contained 96 quadrats characterized by farming system (conventional vs organic), the age of UVS and its management (i.e. sowing and mowing considered as binomial variables). Finally, the L-table contained the coverage of each species within each quadrat. Second, a combination of RLQ and fourth-corner analysis was performed on the plant communities *located in the crop alleys* to assess which life strategies were dispersing from UVS towards crop alleys. Because hypothesis 1 concerns plant species' ability to colonize crop alleys from UVS, this analysis was restricted to the same set of species that were dominant in UVS, therefore eliminating rare species and arable weed species persisting mostly in the seedbank of crop alleys (the relative coverage of these two groups can be seen in Figure S2 in Supplementary material). Again, we considered only species occurring in at least 5 quadrats in the crop alleys (i.e. whose frequency of occurrence was superior to 1%). The Q-table contained 18 species described by the same functional traits as the first analysis, along with Raunkiaer life forms. In this second analysis, the R-table contained 432 quadrats characterized by the farming system, the distance from UVS (0.5 m, 2 m, 8 m) and the direction from UVS (east or west). For both analyses, Monte-Carlo tests were used to assess the global link between traits and environment tables by comparing the observed total inertia (i.e. the sum of eigenvalues of RLQ axes) to a null distribution obtained from 999 random permutations of species and quadrats. Then, fourth-corner analysis was used to test the significance of correlations between each trait and each environmental variable, by comparing each bivariate correlation with its null distribution obtained from 49 999 random permutations of species and quadrats. The false discovery rate method was used to adjust p-values for multiple comparisons (Benjamini and Hochberg, 1995). Finally, we combined RLQ and fourth-corner analysis (49 999 permutations). Seed mass was very skewed and was therefore log-transformed as suggested by Kenkel et al. (2002). RLQ and fourth-corner analysis were performed using the package ade4 (Dray and Dufour, 2007).

To assess the hypotheses n°2, 3, and 4, we used generalized linear mixed effects models (random intercept GLMMs). Transects and fields were included as random effects on the intercept, with transects nested within fields. These models take into account the spatial auto-correlation between quadrats located in a same transect or a same field. For the "weed reservoirs" hypothesis (n°2), we compared total weed coverage, crop coverage and weed-crop ratio per quadrat (response variables) between crop alleys (i.e. the cropped part of the agroforestry system) and pure crop controls under conventional vs organic farming, over 16 fields. For the "plant diversity refugia" hypothesis (n°3), we compared total coverage, species richness and evenness of agrotolerant and hemerophobic communities per quadrat (response variables) between UVS, crop alleys and pure crop controls, under conventional vs organic farming. In this analysis, the two fields with sown UVS and their pure crop controls were removed because sown species had high coverage and reduced the development of other species within UVS. They were therefore not relevant for comparing diversity indices. Moreover, given that they were hemerophobic species, it would lead to an overestimation of the total coverage of hemerophobic species within UVS. This resulted in a dataset of 12 fields and 720 quadrats. Evenness was computed using the index of Williams (1977) based on the species proportions p_1, …, p_S and species richness S in each quadrat, as suggested by Kvålseth (2015):

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

On the agroforestry dataset, other GLMMs were performed to investigate the effect of the distance from UVS (natural logarithms + 1) on all variables, under organic vs conventional farming. All GLMMs revealed a strong effect of farming system and in some cases interactions with other explanatory variables (Table 2). Therefore, each model was performed on organic farming fields and conventional ones separately to facilitate the comparison between habitats (UVS, crop alleys, pure crop controls). Species richness was assumed to follow a Poisson distribution and all other variables (proportions between 0 and 1) were assumed to follow a Beta distribution. When proportional variables included 0 and/or 1 value(s), the transformation (Y × (N − 1) + 0.5) / N was employed following Zuur et al. (2013), where Y is the response variable and N is the sample size. If a variable was bound between a and b, it was rescaled to lie between 0 and 1 by the transformation (Y − a) / (b − a). This was the case for the total coverage of agrotolerant and hemerophobic communities (corresponding to the summed coverage of all agrotolerant or hemerophobic species present within each quadrat), whose maximum values were greater than 1. We used the package glmmTMB (Brooks et al., 2017) for fitting Poisson and Beta GLMMs, with the link functions log and logit respectively. Poisson GLMMs revealed under-dispersion, therefore Conway-Maxwell-Poisson GLMMs were fitted instead as suggested by Lynch et al. (2014). All analyses were performed using the statistical software R 5.1 (R Core Team, 2018).

3. Results

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

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

A Monte-Carlo permutation test revealed no significant link between traits and environment tables (P_{max} = 0.342). Fourth-corner analysis revealed that animal-dispersed species are significantly and positively associated with unmown UVS (r = 0.240, P_{adj} = 0.0021, Figure 2a). The combination of RLQ and fourth-corner revealed that RLQ axis 1 was negatively correlated with the age of UVS and sowing or no mowing management (Figure 2b). RLQ axis 1 was positively correlated with mowing or no sowing management. Older quadrats, whatever they were unmown or sown, contained significantly more animal-dispersed species whereas mown and unsown quadrats contained more barochorous species. The second RLQ axis significantly separated quadrats according to the farming system but this variable had no significant effect on the functional structure of plant communities within UVS.

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

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

The first two axes of the RLQ accounted for 99.2% of the total inertia (84.5 and 14.7% respectively, Figure 3a). The first two RLQ axes accounted for most of the variance explained by separate analyses of environmental variables (97.5% for the analysis of the R-table) and species traits (80.5% for the analysis of the Q-table). Coefficients of environmental variables and traits (illustrated in Figure 3b and Figure 3c) are given in Table S4 in Supplementary Material, along with their basic statistics. Monte-Carlo permutation test revealed a significant link between traits and environment tables (P_{max} = 0.003). Fourth-corner analysis revealed no significant correlation between individual pairs of traits and environmental variables (Figure 4a). Testing the link between RLQ axes and traits or environment (Figure 4b) showed that RLQ axis 1 was negatively correlated with conventional farming, direction from UVS (west) and distance from UVS (2 m). RLQ axis 1 was positively correlated with organic farming, direction from UVS (east) and distance from UVS (0.5 m). The species that were dominant in UVS and also found in crop alleys of organic fields were perennial species characterized by relatively high seed mass and plant height, later emergence and flowering. On the other hand, UVS species found in crop alleys of conventional fields were much fewer and characterized by large emergence and flowering ranges, along with a short life cycle (therophyte species with high SLA). The second RLQ axis clearly separated quadrats at 0.5 m from those at 2 m and 8 m. The vast majority of species dominant in UVS were found at 0.5 m from UVS, their occurrences and abundances decreasing at 2 m and 8 m. They were mostly animal-dispersed species without runners. Conversely, *Convolvulus arvensis* and *Potentilla reptans* scored negatively on RLQ axis 2 (Figure 3a). These are barochorous species dispersing by means of runners. They emerge later and have relatively larger flowering ranges.

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

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

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

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

3.4. Comparison of plant diversity between habitats

Coverage and species richness of agrotolerant and hemerophobic communities were lower in conventional fields than in organic ones (Table 2). On the one hand, in conventional fields all diversity variables were very low and similar between pure crop controls and crop alleys, except species richness of hemerophobic communities that was slightly higher in crop alleys (Figures 6a, 6b, 6c). By contrast, UVS supported a richer and more abundant flora than cropped areas, containing both agrotolerant and hemerophobic species (Figures 6a, 6b). On the other hand, in organic fields the coverage of both agrotolerant and hemerophobic communities was higher in the UVS (Figure 6a). Species richness of both agrotolerant and hemerophobic communities was similar between pure crop controls, crop alleys and UVS (Figure 6b). Evenness of agrotolerant and hemerophobic communities was higher in cropped areas (pure crop controls and crop alleys) than in UVS (Figure 6c). Evenness of hemerophobic communities was even higher in crop alleys than in pure crop controls (Figure 6c). The effect of the distance from UVS on plant diversity was significant only in conventional fields (see Table S6 in Supplementary Material). Furthermore, only hemerophobic communities were impacted by the distance from UVS. Indeed, the coverage and species richness of hemerophobic communities decreased when farther from UVS, while theses variables remained constant regarding agrotolerant communities (see Figures S5a, S5b in Supplementary Material).

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

		Main terms			Interactions with farming system	
Response variables		Crop alleys	UVS	Conventional farming	Crop alleys	UVS
Potential harmfulness of weed communities	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	_
Diversity of agrotolerant communities	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
Diversity of hemerophobic communities	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)	**_**	**_**	_	_	_

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

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

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

4. Discussion

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

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

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

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

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

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

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

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

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

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

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

Hemerophobic species can grow in arable fields under organic farming, independently of the presence of UVS. Conversely, in conventional fields hemerophobic species were concentrated in UVS, their richness and abundance quickly decreasing in crop alleys. These results highlight the importance of UVS in conserving hemerophobic species associated with semi-natural habitats, which are threatened in intensive agricultural landscapes. However, no rare arable weeds were found during the survey, their conservation depending on targeted management of arable habitats, with reduced inputs of fertilizers and herbicides and moderate disturbances, rather than semi-natural habitats (Storkey and Westbury, 2007; Albrecht et al., 2016). Further studies are needed to assess the benefits – apart from conservation purposes – of promoting botanically diverse communities within arable fields, which are likely to offer different ecosystem services than those provided by arable weed communities. Interestingly, unmanaged and older UVS were dominated by animal-dispersed species, suggesting that these habitats act as ecological corridors. This result is concurrent with the study from Brudvig et al. (2009) who showed that animal-dispersed species are favored by the connectivity between habitats. Tewksbury et al. (2002) showed that corridors in fragmented landscapes are very important to facilitate plant–animal interactions such as pollination and that the beneficial effects of corridors extend beyond their area. Acting as refugia for plant diversity and ecological corridors, UVS are thus likely to benefit higher trophic taxa.

4.4. Guidelines for alley cropping agroforestry farmers

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

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

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

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

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

Our study revealed that UVS promote plant diversity conservation within cropped fields. Therefore, we expect that UVS can supply many additional ecosystem services like other farmland vegetative strips (Cresswell et al., 2019). For example, UVS could be used to provide alternative resources and overwintering habitats for pollinators, detritivores and natural enemies of crop pests and so enhance pollination, nutrient cycling and biological control. UVS could also improve soil structure and porosity, thus reducing soil erosion. To promote the delivery of multiple ecosystem services, future research should assess not only the nature of ecosystem services provided by plant communities of UVS but also the relationships between these services (i.e. trade-off, complementarity, synergy). Indeed, if management interventions are devoted to the promotion of a single or restricted number of services, it can have unintended negative consequences on other services (Bennett et al., 2009). However, an encouraging review on interactions between biological control, pollination and nutrient cycling revealed that complementary effects between these ecosystem services were the most common, followed by synergistic effects, whereas trade-offs were rarer (Garibaldi et al., 2018). These results demonstrate that promoting multiple ecosystem services with biodiversity-friendly practices is a possibility.

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

5. Conclusions

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

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Declaration of interest: none

Appendix A.

Table A1. Species classification, conservation value, and occurrence within the three 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	*Alopecurus myosuroides*	agrotolerant	3	X	X	X
APHAR	*Aphanes arvensis*	agrotolerant	3	X	X	X
ARBTH	*Arabidopsis thaliana*	hemerophobic	0	X	X	
ARREL	*Arrhenatherum elatius*	hemerophobic	3	X	X	X
ATXPA	*Atriplex patula*	agrotolerant	0		X	X
AVESS	*Avena sp*	agrotolerant	0	X	X	X
BROSS	*Bromus sp*	hemerophobic	0	X	X	X
LITAR	*Buglossoides arvensis*	hemerophobic	3		X	X
CAPBP	*Capsella bursa-pastoris*	agrotolerant	0		X	
CERGL	*Cerastium glomeratum*	hemerophobic	0	X	X	X
CHEAL	*Chenopodium album*	agrotolerant	0	X	X	X
CIRAR	*Cirsium arvense*	agrotolerant	0	X	X	X
CIRVU	*Cirsium vulgare*	hemerophobic	0	X	X	
CLVVT	*Clematis vitalba*	hemerophobic	0	X		X
CONAR	*Convolvulus arvensis*	agrotolerant	0	X	X	X
CAGSE	*Convolvulus sepium*	agrotolerant	0		X	

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

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

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

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

Supplementary material

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

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

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

Table S2. Description of agroforestry fields.

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

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

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

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

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

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

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

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

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

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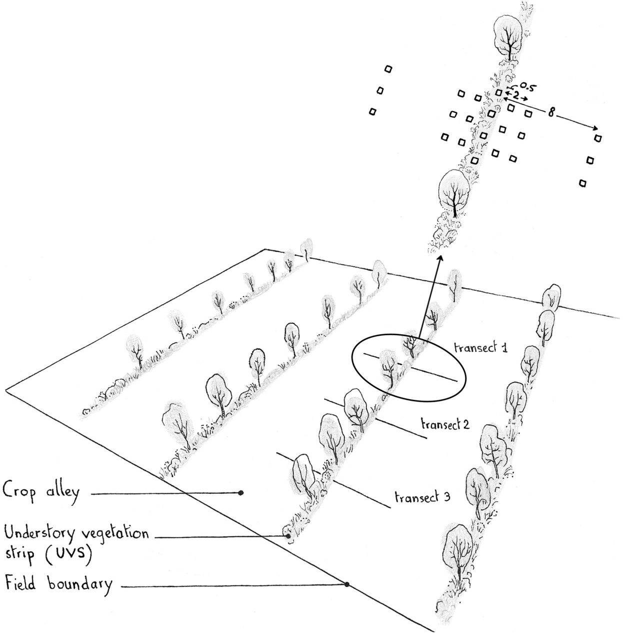
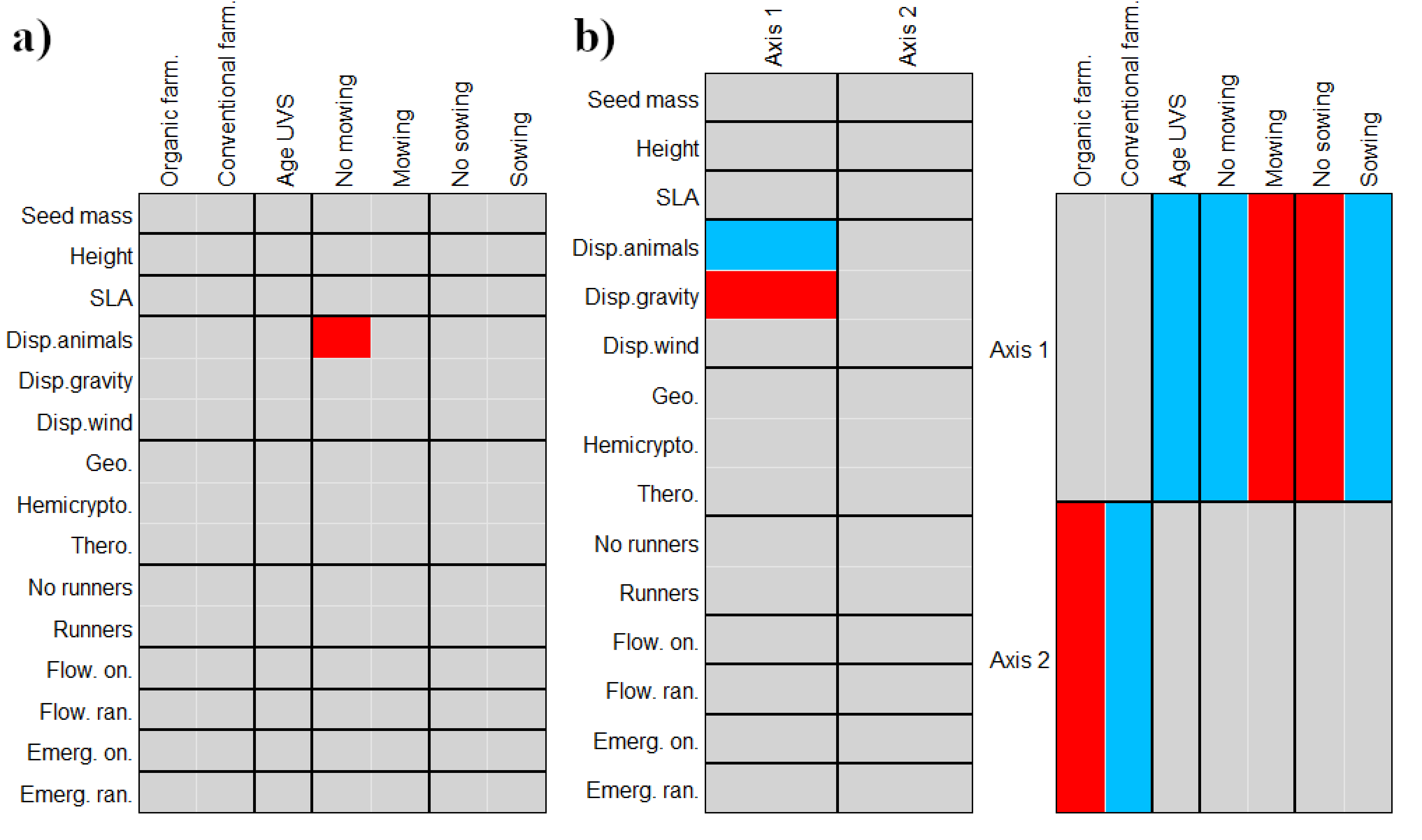
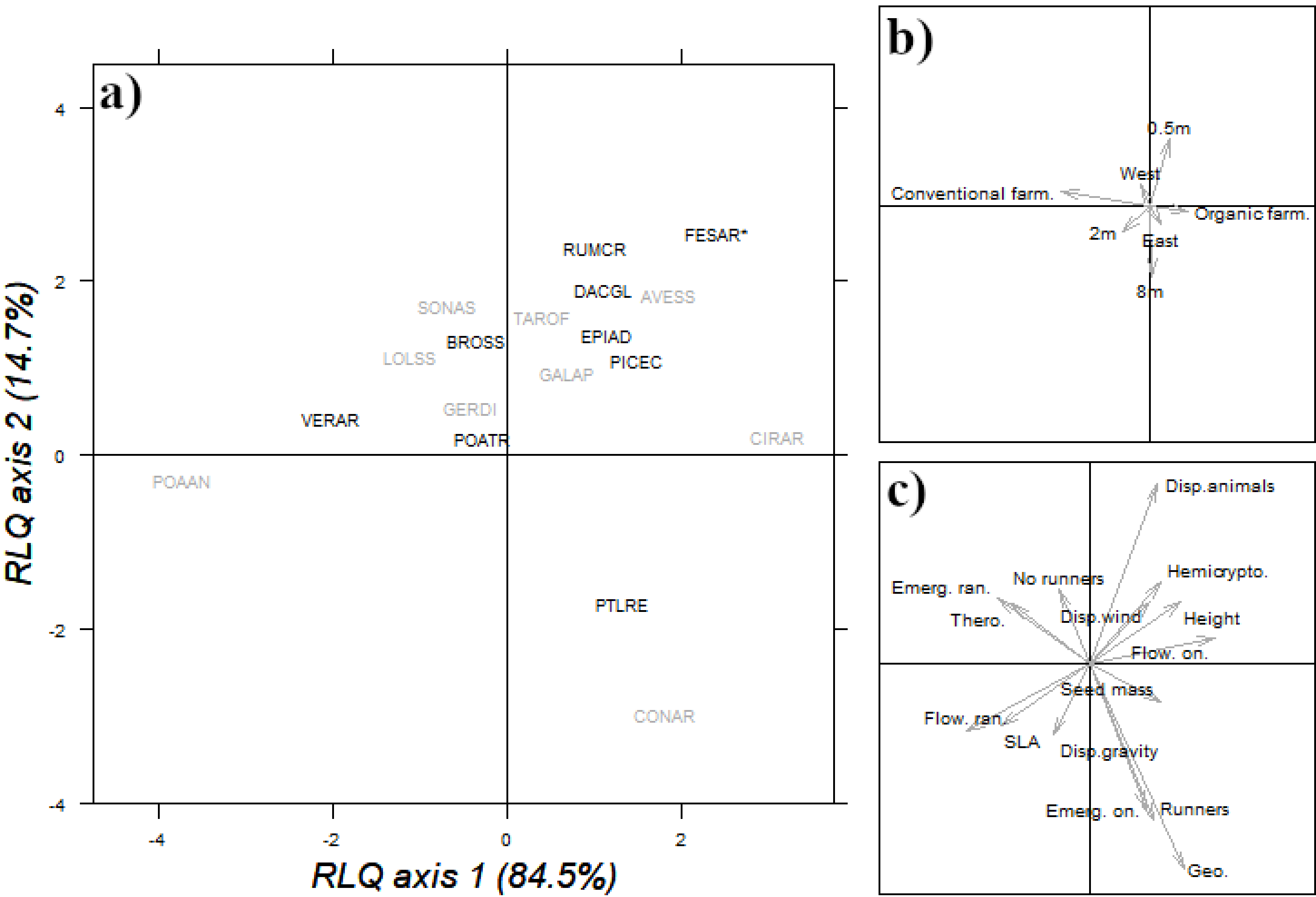


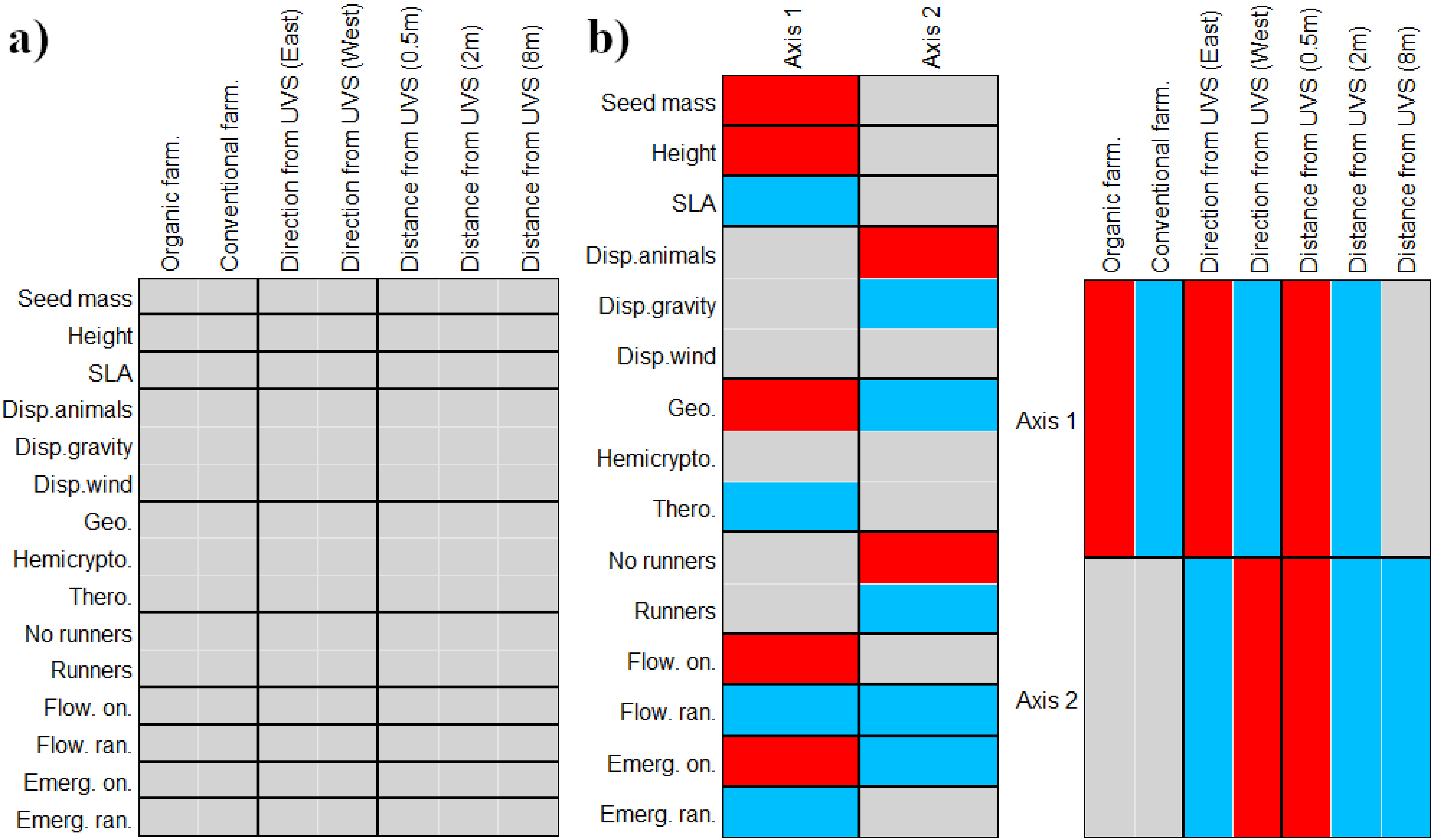
0.5
2
8
transect 1
transect 2
transect 3
Crop alley
Understory vegetation strip (UVS)
Field boundary



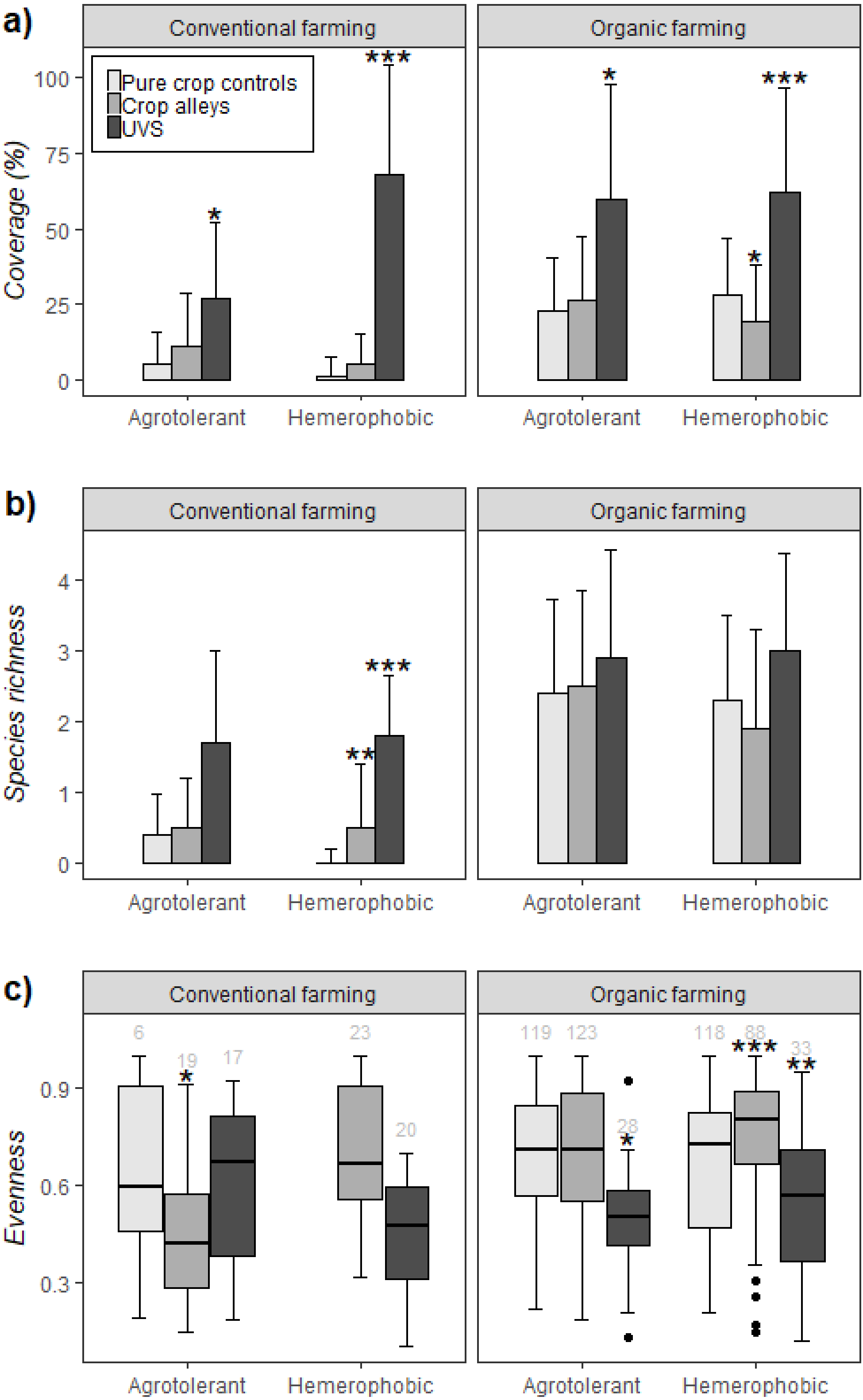
a)
Organic farm.
Conventional farm.
Age UVS
No mowing
Mowing
No sowing
Sowing
Seed mass
Height
SLA
Disp.animals
Disp.gravity
Disp.wind
Geo.
Hemicrypto.
Thero.
No runners
Runners
Flow. on.
Flow. ran.
Emerg. on.
Emerg. ran.
b)
Axis 1
Axis 2
Seed mass
Height
SLA
Disp.animals
Disp.gravity
Disp.wind
Geo.
Hemicrypto.
Thero.
No runners
Runners
Flow. on.
Flow. ran.
Emerg. on.
Emerg. ran.
Organic farm.
Conventional farm.
Age UVS
No mowing
Mowing
No sowing
Sowing
Axis 1
Axis 2

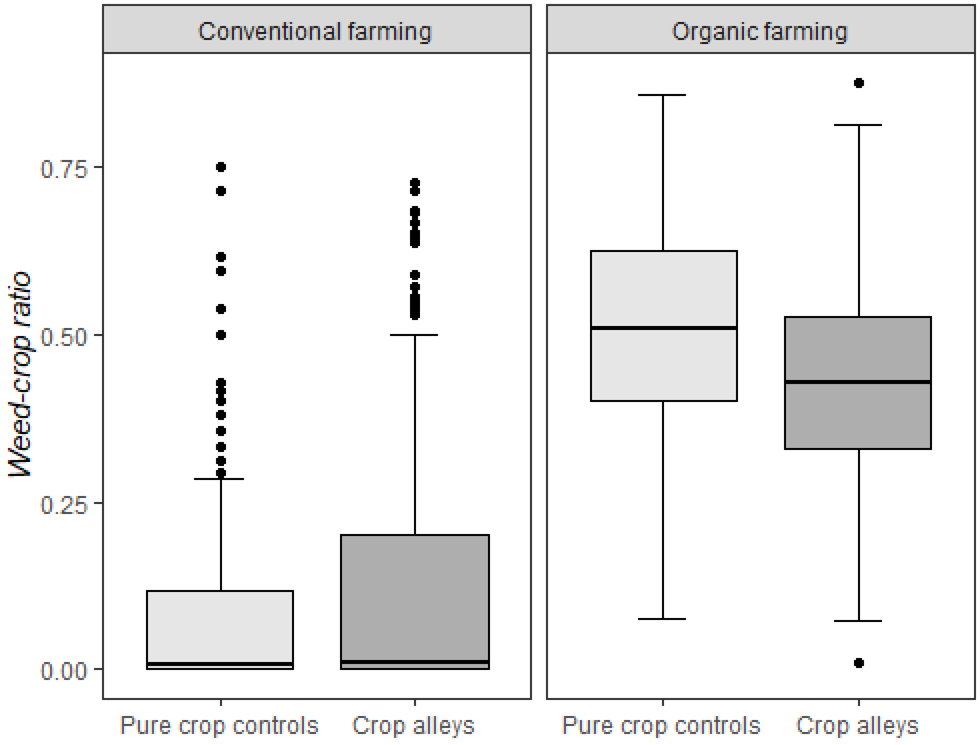


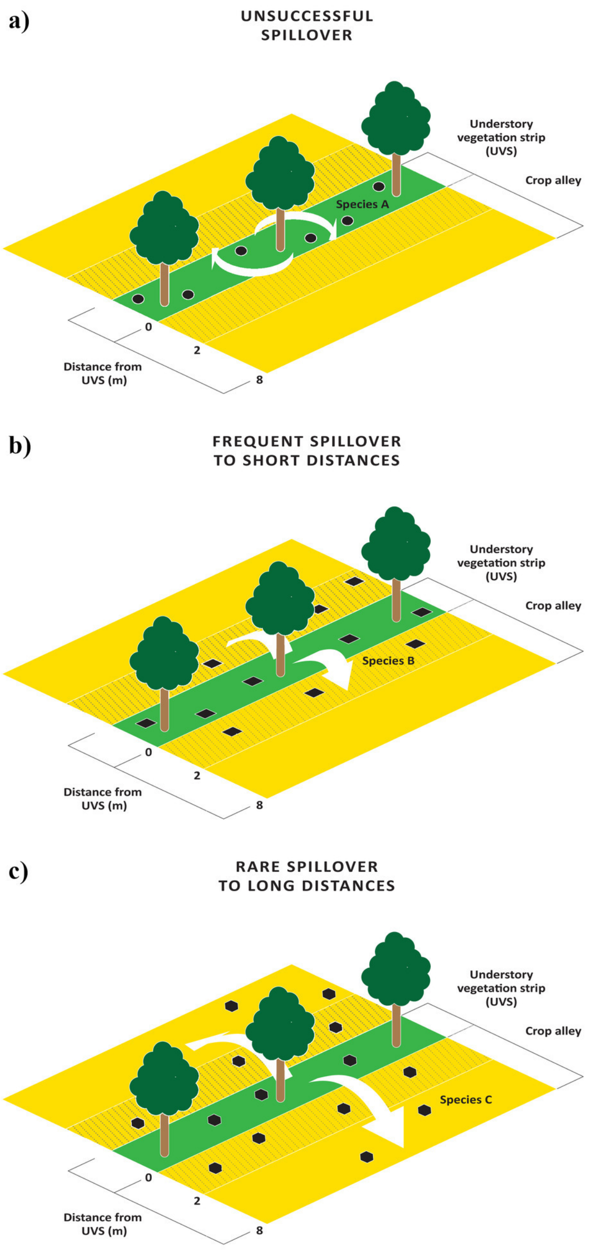
a)
b)
c)
RLQ axis 1 (84.5%)
RLQ axis 2 (14.7%)
-4
-2
0
2
4
FESAR*
RUMCR
DACGL
AVESS
SONAS
TAROF
EPIAD
BROSS
LOLSS
PICEC
GALAP
GERDI
VERAR
POATR
CIRAR
POAAN
PTLRE
CONAR
0.5m
West
Conventional farm.
Organic farm.
2m
East
8m
Disp.animals
Hemicrypto.
Emerg. ran.
No runners
Height
Thero.
Disp.wind
Flow. on.
Seed mass
Flow. ran.
SLA
Disp.gravity
Emerg. on.
Runners
Geo.



a)
Organic farm.
Conventional farm.
Direction from UVS (East)
Direction from UVS (West)
Distance from UVS (0.5m)
Distance from UVS (2m)
Distance from UVS (8m)
Seed mass
Height
SLA
Disp.animals
Disp.gravity
Disp.wind
Geo.
Hemicrypto.
Thero.
No runners
Runners
Flow. on.
Flow. ran.
Emerg. on.
Emerg. ran.
b)
Axis 1
Axis 2
Seed mass
Height
SLA
Disp.animals
Disp.gravity
Disp.wind
Geo.
Hemicrypto.
Thero.
No runners
Runners
Flow. on.
Flow. ran.
Emerg. on.
Emerg. ran.
Organic farm.
Conventional farm.
Direction from UVS (East)
Direction from UVS (West)
Distance from UVS (0.5m)
Distance from UVS (2m)
Distance from UVS (8m)
Axis 1
Axis 2


a)
Conventional farming
Organic farming
Pure crop controls
Crop alleys
UVS
Coverage (%)
100
75
50
25
0
*
***
*
*
***
Agrotolerant
Hemerophobic
b)
Conventional farming
Organic farming
Species richness
4
3
2
1
0
***
**
Agrotolerant
Hemerophobic
c)
Conventional farming
Organic farming
Evenness
0.9
0.6
0.3
6
19
17
23
20
119
123
28
118
88
33
*
*
***
**
Agrotolerant
Hemerophobic


Conventional farming
Organic farming
Weed-crop ratio
0.75
0.50
0.25
0.00
Pure crop controls
Crop alleys
Pure crop controls
Crop alleys



a)
UNSUCCESSFUL SPILLOVER
Understory vegetation strip (UVS)
Crop alley
Species A
0
2
8
Distance from UVS (m)
b)
FREQUENT SPILLOVER TO SHORT DISTANCES
Understory vegetation strip (UVS)
Crop alley
Species B
0
2
8
Distance from UVS (m)
c)
RARE SPILLOVER TO LONG DISTANCES
Understory vegetation strip (UVS)
Crop alley
Species C
0
2
8
Distance from UVS (m)