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Promoting generalist predators of crop pests in alley cropping agroforestry fields: farming system matters

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Abstract

Developing agroecological practices that enhance biological control of crop pests is a major issue for the transition of agriculture towards sustainable and biodiversity-friendly systems. Agroecological infrastructures (AEI) are devoted to the support of ecosystem service providers, although they have mixed effects on natural enemies of crop pests. In temperate regions, alley cropping agroforestry involves within-field AEI, in the form of tree rows and associated understory vegetation strips. The objective of this study was to assess the potential of generalist predators (carabid beetles and cursorial spiders) to control weed seeds and invertebrate pests in alley cropping *vs* pure crop systems, under two contrasting farming systems (conventional *vs* organic). Predator surveys were carried out in May and June 2017 in South-Western France over 12 winter cereal fields. Our study revealed that the effect of alley cropping was modulated by the farming system. Under conventional farming, alley cropping had a negative effect on the activity-density and species richness of generalist predators, especially regarding carnivorous carabids whose activity-density was reduced by nearly 50%. Under organic farming, alley cropping enhanced both the activity-density and complementarity of generalist predators, with a two-fold increase in the activity-density of seed-feeding carabids (predominantly granivorous and omnivorous), potentially promoting weed seed and invertebrate pest control. Our results suggest that the effectiveness of AEI in promoting natural enemies depends on the farming system at the field scale, which affects resource availability and determines spillover intensity between habitats. AEI are often perceived as sources of natural enemies. However, sink and retention effects (*i.e.* reduced or delayed spillover into crop fields due to higher attractiveness of AEI) are overlooked and very likely to explain the mixed impacts of AEI on natural enemy communities.

Keywords: understory vegetation strip, natural enemy, agroecological infrastructure, organic farming, spillover, source-sink dynamics

1. Introduction

The conservation of natural enemies of crop pests is of fundamental importance to the sustainability of crop production (Begg et al., 2017). Generalist predators such as carabid beetles and spiders play a key role in the functioning of agroecosystems. Studies have demonstrated that carabids efficiently control various crop pests such as aphids (Collins et al., 2002), flies (Finch, 1996) and slugs (Oberholzer and Frank, 2003). Furthermore, some species are weed seed consumers and can contribute to reduce weed pressure in crop fields (Bohan et al., 2011). Spiders are also recognized as efficient regulators of phytophagous pests such as aphids, leafhoppers, beetles, and lepidopteran larvae (Michalko et al., 2019). However, as many other arthropods, these predators are suffering from agricultural intensification, *i.e.* high pesticide and fertilizer inputs, mechanization and simplification of agricultural landscapes (Prieto-Benítez and Méndez, 2011; Brooks et al., 2012).

Agroecological infrastructures (AEI) such as hedgerows, beetle banks or wildflower strips are devoted to shelter and support ecosystem service providers. AEI can be established around or even within crop fields to promote the spillover of predators with limited dispersal abilities (such as many carabid and spider species), whose abundance and diversity generally decrease when farther from AEI (Rand et al., 2006). Yet, AEI can also have negative impacts on predators. It has been shown that field boundaries, especially hedgerows, could act as a barrier to the dispersal of carabids, preventing them from colonizing crop fields (Mauremooto et al., 1995; Fernandez Garcia et al., 2000; Holland et al., 2004; Jowett et al., 2019), although we found no evidence of barrier effects for cursorial spiders. Conversely, even agrobiont spiders (*i.e.* reaching high densities in crops) do overwinter abundantly in AEI (Mestre et al., 2018). Further, if AEI are highly attractive, they might lead to reduced or delayed colonization of crop fields by carabids (Wamser et al., 2011; Jowett et al., 2019).

Although the presence of AEI nearby or within crop fields is of major importance to promote predators, farming system is also decisive. Positive effects of organic farming on predators can be explained by the absence of pesticides and synthetic fertilizers, which are harmful for many carabid and spider species (Haughton et al., 1999; Navntoft et al., 2006; Geiger et al., 2010; Li et al., 2018). Organic farming also favors the presence of a rich and abundant weed flora, which provides additional habitats and trophic resources such as seeds and pollen, but also phytophagous prey (Batáry et al., 2012). Alternative food is important both to sustain predators when pest populations are low and to mitigate intraguild predation, although it can also distract predators from main crop pests (Heij and Willenborg, 2020). It has been shown that organic farming increases the abundance and species richness of carabid communities (Djoudi et al., 2019), especially by favoring predominantly granivorous carabid species and those with a large body length (Diekötter et al., 2016; Gallé et al., 2019). Similarly, organic farming increases the activity-density[1] and species richness of spiders (Feber et al., 1998; Batáry et al., 2012), but do not affect their functional structure (considering their body size and hunting and dispersal strategies) (Gallé et al., 2019). Furthermore, although rarely investigated, the combination of AEI and organic farming seems very promising for promoting predators of crop pests. For example, some studies found a negative effect of AEI on weed seed or aphid suppression in fields under conventional farming, but a positive effect in fields under organic farming (Fischer et al., 2011; Winqvist et al., 2011).

In agroforestry systems, the association of woody vegetation (trees or shrubs) with crops and/or animals has been shown to provide various ecosystem services such as sustainable biomass production, soil and water protection, biodiversity conservation and

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[1] Pitfall trap catches depend on both population density and an organism's activity, to provide a quantity usually referred to as activity-density (Thomas et al. (1998).

carbon sequestration (Torralba et al., 2016; Kay et al., 2019). In temperate regions, alley cropping agroforestry represents a great opportunity for restoring ecosystem services. Indeed, in such systems, the absence of tillage operations on tree rows results in the formation of understory vegetation strips (UVS), covering about 3 to 13% of the available agricultural area and delimiting alleys (generally about 24 m wide) where arable crops are grown (Figure 1a). Agroforestry systems are therefore very conducive to ecological engineering and innovations (*e.g.* spatial and temporal diversification of crop *vs* non-crop habitats and their management strategies). This increased interspersion of AEI and cropped areas within fields themselves can affect ecosystem service flows (Mitchell et al., 2015). Although very few studies have focused on the ecological functions of UVS, it has been shown that they are important refugia for many plants and invertebrates (Boinot et al., 2019a; Boinot et al., 2019b; Pardon et al., 2019; D'Hervilly et al., 2020). UVS provide overwintering habitats for most spiders and for carabid species sensitive to agricultural intensification (characterized by a predominantly granivorous diet and a large body length), whereas small and carnivorous carabids overwinter mostly in crop alleys (Boinot et al., 2019b). These results suggest that alley cropping might efficiently promote spiders and predominantly granivorous carabids compared to pure crop systems, because UVS provide suitable overwintering habitats and enhanced plant and invertebrate resources within fields themselves. On the other hand, alley cropping could have detrimental effects on small and carnivorous carabids that forage and overwinter in arable habitats (Baulechner et al., 2019; Boinot et al., 2019b), either because UVS hamper their movements and/or host both competitors and predators. Nevertheless, to our knowledge no study has compared generalist predator communities between alley cropping and pure crop systems under contrasting farming systems.

Figure 1. (a) Alley cropping agroforestry system and pure crop control in the Gers department, France. (b) Predator sampling design (pitfall traps are represented by the circles).

The objective of this study was to assess the potential of generalist predator communities to control weed seeds and invertebrate pests in alley cropping *vs* pure crop systems, under conventional *vs* organic farming. We hypothesized that **1)** predominantly granivorous carabids and cursorial spiders are favored by alley cropping, whereas carnivorous carabids, especially small ones that are adapted to highly disturbed habitats, are negatively impacted by alley cropping. Further, we expected that **2)** the effect of alley cropping is modulated by the farming system. Under conventional farming, alley cropping has an overall negative impact on the predator community that is composed predominantly of species adapted to highly disturbed habitats (*i.e.* small and carnivorous carabids), whereas alley cropping under organic farming strongly favors more sensitive species (*i.e.* larger species and granivorous carabids), by providing both undisturbed habitats under the trees and abundant trophic resources in crop alleys. Consequently, we expected **3)** higher activity-density, larger mean body size and enhanced complementarity (*i.e.* diversity of diet and body size) of predator communities in more complex systems (*i.e.* alley cropping under organic farming), which is likely to result in better biological control of weed seeds and invertebrate pests.

2. Material and Methods

2.1. Study site

The study was conducted in the Gers department (South-Western France), a hilly region (200-400 m altitude) where agricultural areas are dominated by clay-limestone and clay to silt soils.

Climate is sub-Atlantic (hot summers and cool winters) and annual precipitation usually varies from 700 to 900 mm. From a previous study assessing the effect of alley cropping on plant communities (Boinot et al., 2019a), vegetation surveys were carried out in May 2017 in fields growing either winter wheat (*Triticum aestivum* L.) or winter barley (*Hordeum vulgare* L.), half under conventional farming and half under organic farming (*i.e.* generally more diverse crop rotations, without pesticides and inorganic fertilizers). 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 (less than 15%). The same fields were used for predator sampling in May and June 2017, except that two pairs of fields were excluded from the analyses because the alley cropping plot and its pure crop control were more than three km apart, thus not located in the same landscape context. Indeed, carabids and cursorial spiders respond to landscape variables at a lower scale, generally within a 500 m or 1 km radius around fields (*e.g.* Schmidt et al., 2008; Wamser et al., 2011). This resulted in six pairs of fields (alley cropping *vs* pure crop control), half under conventional farming and half under organic farming, located within the same perimeter, similar in terms of pedo-climatic conditions and surrounding land use. Although there is a great diversity of farming systems along a gradient from conventional to organic farming (Puech et al., 2014), all farmers in our study performed shallow tillage without mouldboard ploughing. Under conventional farming, all farmers used herbicides with a wide spectrum of action and similar treatment frequency indices (*i.e.* the sum of the ratio of the applied dose to the recommended dose of all the treatments applied in a year). No insecticide was employed. Each pair of fields was cultivated by the same farmer, with similar crop management over the three years preceding the study (see Table S1 in Supplementary material). Features of alley cropping systems (*i.e.* tree species and basic metrics) are given in Table 1.

Table 1. Description of alley cropping agroforestry fields.

2.2. Predator sampling

Carabid beetles and cursorial spiders were sampled with pitfall traps (depth: 16 cm, diameter: 6.2 cm, exposure time: 48h), on three different sampling periods in May and June 2017. In each alley cropping field, pitfall traps were positioned along three transects 20 m apart and running perpendicularly to tree rows (Figure 1b). These transects were located in field cores, at around 50 m and 100 m from the two nearest field boundaries. Each transect comprised pairs of pitfall traps (10 m apart) located in UVS and in adjacent crop alleys, at two distances from UVS (2 m and 8 m). During field work, the content of each pair of pitfall traps was collected in the same plastic bag and considered as one sampling unit. The same protocol was used for pure crop controls with the transects placed at equivalent locations in the field in the absence of UVS. This resulted in a dataset of 162 pairs of pitfall traps sampled over three periods (pure crops: $n = 72$, crop alleys: $n = 72$, UVS: $n = 18$).

2.3. Biological control potential of predator communities

To estimate the potential of common generalist predators to control weed seeds and invertebrate pests, we measured the activity-density and species richness of carabids (granivorous, omnivorous, carnivorous) and cursorial spiders in pure crop controls and alley cropping systems (crop alleys *vs* UVS) under conventional *vs* organic farming. Further, we measured the activity-density, species richness, community-weighted mean (CWM) and functional divergence (FDvar) of body length and diet of the total predator community. CWM corresponds to the average of trait values weighted by the relative abundance of each species. FDvar is a relevant metric for assessing complementarity between species (Woodcock et al., 2019), which has been shown to enhance pest suppression (Dainese et al., 2017; Greenop et al., 2018). It varies from 0 to 1; FDvar is low if species and/or abundances are clustered around the mean body length value (*i.e.* low complementarity), whereas it is high if they are clustered towards one or both margins of the trait distribution (*i.e.* high complementarity). Formulas are given in Table A1 in Appendix A. Information on the diet and body length of carabid beetles were collected in databases (Hedde et al., 2012; Homburg et al., 2014) and through a search in scientific literature (references are given in Supplementary Material). Information on the body length of spiders was collected from the BETSI database (Hedde et al., 2012).

2.4. Data analysis

Data from the three sampling periods were summed per pitfall trap to analyze the global effect of cropping and farming systems. To assess hypotheses 1 and 2, we used generalized linear mixed effects models (GLMMs) and compared the activity-density and species richness of each functional group (*i.e.* granivorous, omnivorous, carnivorous carabids and cursorial spiders) between pure crop controls and alley cropping systems (crop alleys *vs* UVS) under conventional *vs* organic farming. To assess hypothesis 3, we used GLMMs to compare the activity-density, species richness, CWM and FDvar of body length and diet of predator communities in pure crop controls, crop alleys and UVS under conventional *vs* organic farming. Field pairs were included as a random effect on the intercept to take into account the spatial auto-correlation between pitfall traps located within the same perimeter. When GLMMs revealed significant interactions between farming system (conventional *vs* organic farming) and habitats (pure crop, crop alleys, UVS), least-square means were used to compare habitats under conventional *vs* organic farming separately. Activity-density and species richness were assumed to follow a Poisson distribution, CWM Body length was assumed to follow a Gaussian distribution and variables varying from 0 to 1 (CWM Diet, FDvar Diet, FDvar Body length) were assumed to follow a Beta distribution. When the latter included 0 and/or 1 value(s), the transformation (FDvar × (N − 1) + 0.5) / N was employed following Zuur et al. (2013), where N is the sample size. We used the package lme4 for fitting Gaussian LMMs (Bates et al., 2015) and the package glmmTMB (Brooks et al., 2017) for fitting Poisson and Beta GLMMs, with the link functions log and logit respectively. When Poisson GLMMs revealed under- or over-dispersion, Conway-Maxwell-Poisson GLMMs were fitted instead as suggested by (Lynch et al., 2014). The package lsmeans was used for least-square means post-hoc comparisons (Lenth, 2016). All analyses were performed using the statistical software R 5.1 (R Core Team, 2018).

3. Results

A considerably high number of carabids and cursorial spiders were sampled during the survey (Table 2).

Table 2. Total number of individuals and species sampled per functional group during the whole survey.

3.1. Activity-density and species richness of generalist predators

Independently from the farming system (conventional *vs* organic farming), alley cropping had a clear negative effect on the activity-density and species richness of carnivorous carabids, which were much lower both in crop alleys and UVS as opposed to pure crop controls (Table 3, Figure 2). This result was largely driven by the reduced activity-density of small and dominant carabids such as *Anchomenus dorsalis* and Trechinii species, especially under conventional farming, but also by the reduced activity-density of the large *Carabus auratus* under organic farming (Figure A1 in Appendix A). Other functional groups responded differently to alley cropping depending on the farming system. Granivorous carabids tended to have lower activity-density in crop alleys than in pure crop controls under conventional farming, but higher activity-density and species richness in crop alleys and UVS under organic farming (Table 3, Figures 2a, 2b). Under conventional farming, granivorous carabids were mostly represented by *Harpalus dimidiatus*, whereas some species benefited from the combination of alley cropping and organic farming, such as *Harpalus affinis*, *Harpalus pygmaeus* and *Amara* spp. (Figure A1 in Appendix A). Omnivorous carabids had lower activity-density only in UVS under conventional farming, whereas their activity-density strongly increased in crop alleys under organic farming compared to pure crop controls (Table 3, Figure 2a), especially for *Poecilus cupreus* and *Brachinus crepitans* (Figure A1 in Appendix A). Cursorial spiders had lower activity-density in crop alleys than in pure crop controls under conventional farming, but similar activity-density between all habitats under organic farming (Table 3, Figure 2a). Consequently, activity-density of the total predator community was much lower in crop alleys and UVS as opposed to pure crop controls under conventional farming (Table 3, Figure 2a). Species richness of the predator community was even reduced in crop alleys under conventional farming (Table 3, Figure 2b). On the other hand, activity-density of the predator community was higher in crop alleys than in pure crop controls under organic farming (Table 3, Figure 2a).

Table 3. Results of GLMMs comparing activity-density, species richness and functional structure of predator communities between pure crop (reference level), crop alleys and understory vegetation strips (UVS), under conventional farming (reference level) *vs* organic farming. When GLMMs revealed significant interactions between habitats and farming system, least-square means were used to compare habitats under conventional *vs* organic farming separately (see Table S2 in Supplementary material for detailed outputs). CMP = Conway-Maxwell Poisson. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Figure 2. Mean and standard deviation of **(a)** activity-density and **(b)** species richness of each functional group and total predator community. Stars at the top of barplots are based on the p-values of least-square means post-hoc comparisons, when there was a significant interaction between habitats and farming systems. Stars indicate significant difference between pure crop controls (reference level) *vs* crop alleys and understory vegetation strips (UVS). See Table S2 in Supplementary material for detailed outputs. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

3.2. Functional structure of generalist predator communities

CWM Diet of predator community was close to 1 (*i.e.* towards carnivorous diet) and similar between all habitats under conventional farming, whereas it was lower in crop alleys and UVS as opposed to pure crop controls under organic farming (Table 3, Figure 3a). Although FDvar Diet tended to be higher in alley cropping, especially under organic farming (Figure 3c), no significant effect was detected (Table 3). CWM Body length was significantly higher in crop alleys than in pure crop controls (Table 3, Figure 3b), but the difference was small (+0.6 mm on average per trap). FDvar Body length was higher in crop alleys than in pure crop controls under conventional farming, but lower in crop alleys under organic farming (Table 3, Figure 3d).

Figure 3. Functional structure of total predator community. **(a)** Community-weighted mean (CWM) of diet (granivorous: 0, omnivorous: 0.5 and carnivorous: 1), **(b)** CWM of body length, **(c)** Functional divergence (FDvar) of body length and **(d)** FDvar of body length (low complementarity: 0, high complementarity: 1). Stars at the top of boxplots are based on p-values of least-square means post-hoc comparisons, when there was a significant interaction between habitats and farming systems. Stars indicate significant difference between pure crop controls (reference level) *vs* crop alleys and understory vegetation strips (UVS). See Table S2 in Supplementary material for detailed outputs. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

4. Discussion

Our study on the distribution of generalist predators in alley cropping agroforestry *vs* pure crop systems revealed that the effect of alley cropping was modulated by the farming system. Under conventional farming, alley cropping had a negative effect on the activity-density and species richness of generalist predators, especially regarding carnivorous carabids whose activity-density was reduced by nearly 50%. Under organic farming, alley cropping enhanced both the activity-density and complementarity of generalist predators, with a two-fold increase in the activity-density of seed-feeding carabids (predominantly granivorous and omnivorous).

4.1. Negative effects of alley cropping agroforestry on generalist predators under conventional farming

We confirmed that the activity-density and species richness of carnivorous carabids were clearly reduced by alley cropping, independently from the farming system (hypothesis 1). This was especially true for small species such as *Anchomenus dorsalis* and Trechinii species, and corroborates previous studies showing that carnivorous species, particularly small ones, thrive in disturbed and open habitats (Navntoft et al., 2006; Hanson et al., 2016; Baulechner et al., 2019). In alley cropping systems, UVS seem to act as a sink (*i.e.* unfavorable habitat) or a barrier hampering their movements, as their activity-density was even lower in UVS than in crop alleys, which is in line with the results of Richard et al. (2019). Moreover, Boinot et al. (2019b) showed that small and carnivorous carabids spent the winter in crop alleys, whereas larger carabids were found mostly in UVS. Therefore, small and carnivorous species might have suffered from both competition with other predators and intraguild predation in alley cropping systems. The reduction of such predatory species may result in lower biological control in alley cropping systems, especially regarding small crop pests such as aphids, on which they mostly feed (Rusch et al., 2015).

However, alley cropping alone was not enough to promote predominantly seed-feeding carabids (granivorous and omnivorous) and cursorial spiders in crop alleys. The presence of overwintering habitats and trophic resources in UVS might not have compensated for the very poor weed flora observed in fields under conventional farming (Boinot et al., 2019a). Indeed, previous studies have shown that organic farming favors seed-feeding carabids and spiders (Feber et al., 1998; Batáry et al., 2012; Diekötter et al., 2016), presumably because of the presence of a rich and abundant weed flora that provides additional habitats (*e.g.* hunting and hiding structures) and trophic resources such as seeds, but also phytophagous and detritivore prey. Probably, these predators also directly suffered from herbicide and synthetic fertilizer applications in the conventional farming fields surveyed (Haughton et al., 1999; Navntoft et al., 2006; Geiger et al., 2010; Li et al., 2018).

Conversely to our expectations, granivorous carabids (mostly represented by *Harpalus dimidiatus*) and cursorial spiders were even less active in crop alleys than in pure crop controls under conventional farming. In alley cropping systems, they probably foraged in UVS where plant and invertebrate resources are more abundant and diversified than in crop alleys (Boinot et al., 2019a; Boinot et al., 2019b), resulting in a retention effect. This result is consistent with those from Wamser et al. (2011), who showed that high availability of overwintering habitats in the landscape reduces or delays the spillover of carabid beetles in fields under conventional farming. Similarly, Boetzl et al. (2019) found that the percentage of granivorous carabids in oilseed rape under conventional farming decreased by nearly 50% when adjacent to AEI. This could be explained by the spillover of some carnivorous species from AEI towards crop fields, but also by the retention of granivorous carabids outside crop fields due to higher food supply in adjacent AEI. Finally, Schoeny et al. (2019) also found low spider spillover from flower strips towards melon crops, presumably because of low attractiveness of the crop and/or high attractiveness of the field margins, which would provide suitable microclimate, shelters and prey.

4.2. Positive effects of alley cropping agroforestry on generalist predators under organic farming

The effect of alley cropping was modulated by the farming system, thereby confirming hypothesis 2. Indeed, although alley cropping had a negative impact on predator communities under conventional farming, it was the opposite under organic farming. First, the total activity-density of seed-feeding carabids (granivorous and omnivorous) was doubled in crop alleys of alley cropping systems as opposed to pure crop controls. This could be explained by (i) the presence of UVS that are favorable overwintering habitats for seed-feeding carabids in alley cropping systems (Boinot et al., 2019b), and (ii) a rich and abundant weed flora enhancing habitat and resource availability under organic farming, including associated phytophagous and detritivore prey (Batáry et al., 2012; Diehl et al., 2012; Boinot et al., 2019a), thereby favoring the spillover of predators associated to UVS towards crop alleys (*i.e.* source effect). Second, alley cropping no longer had a negative effect on the activity-density of cursorial spiders, which was similar in all habitats (pure crops, crop alleys, UVS). Although we expected cursorial spiders to benefit from UVS in alley cropping systems, they might have been limited by the high activity of omnivorous carabids that can feed on them (Roubinet et al., 2017).

Considering the whole community, the total activity-density of predators was higher in crop alleys than in pure crop controls. Besides, CWM Diet of predator communities was close to 1 in pure crop controls (indicating a high dominance of carnivorous diet), whereas it was getting closer to 0.5 in crop alleys (indicating a higher complementarity between predators with various diet), thereby partly confirming hypothesis 3. However, we expected higher difference in CWM and FDvar of body length between cropping systems than those observed in our study. It is likely that we did not detect a clear effect of cropping and farming systems on these variables because we focused on circulating predators during spring, which might partly come from adjacent habitats and arable fields. Indeed, using emergence traps, Boinot et al. (2019b) showed that carabids overwintering in UVS are larger than those associated with crop alleys. This result was consistent with previous studies showing that large carabids are more sensitive to agricultural disturbances (Winqvist et al., 2014; da Silva et al., 2017). Distinguishing overwintering from circulating individuals would help disentangling the effect of local and landscape factors on predator communities in arable fields (Djoudi et al., 2019).

Nevertheless, although spillover might have occurred between an alley cropping field and its adjacent pure crop control, or between AEI and arable fields, there were still very large variations of activity-density for all functional groups, in response to the different combinations of cropping and farming systems. Alley cropping combined with organic farming can enhance both the activity-density and complementarity of predator communities within fields during spring, even in relatively small fields such as those observed in the Gers department (generally less than 10 ha).

In conclusion, the combination of alley cropping and organic farming should be the best option for enhancing both weed seed and invertebrate pest control, provided that niche complementarity outweighs intraguild predation (Straub et al., 2008; Heij and Willenborg, 2020). Our results are in line with those of Caro et al. (2016) and Fusser et al. (2018), who found that AEI had stronger effect on carabid diversity when combined with organic farming. Other studies also revealed contrasting effects of AEI on weed seed or aphid suppression, depending on the local farming system and pesticide use intensity (*i.e.* positive effects under organic farming and low pesticide use intensity, negative ones under conventional farming and high pesticide use intensity) (Fischer et al., 2011; Winqvist et al., 2011; Ricci et al., 2019). All these results highlight the key role of organic farming to promote the spillover of predators from AEI towards cropped areas, most likely by increasing resource availability – a major factor driving the movement of organisms between habitats (Dunning et al., 1992; Corbett and Plant, 1993; Blitzer et al., 2012; Tscharntke et al., 2016). An alternative but not exclusive hypothesis is that increased soil organic matter under organic farming promotes predator spillover into crop fields, by improving structural habitat complexity and soil microclimate (Aldebron et al., 2020). All in all, the establishment of AEI alone cannot guarantee the restoration of biological pest control, and should therefore be coupled with within-field plant diversification, which is a key factor in promoting beneficial trophic interactions (Wan et al., 2020). More precisely, fine-grained interspersion of crop(s) and alternate vegetation, such as weeds, is of major importance for generalist predators (especially for species suffering from agricultural intensification), although this might not be the case for specialist ones (Sheehan, 1986). Plant diversification should additionally reduce pest pressure through the resource concentration hypothesis, which predicts that specialist pests are more likely to locate and remain on host plants (*i.e.* crops) occurring in large, dense, pure stands compared to species-rich environment, where host chemical cues are disrupted (Root, 1973).

4.3. Future research on biological control in alley cropping agroforestry

Since alley cropping agroforestry is a marginal farming practice in Europe, it is very challenging to find old systems, especially when looking for adjacent pure crop controls. Therefore, our results do not apply to alley cropping in general, but rather to systems in transition (less than 12 years old), where farmers performed shallow tillage without mouldboard ploughing and grew winter cereals during the study year. In this study, we focused on the presence of UVS, which was indeed the major difference between alley cropping and pure crop systems (tree canopy was never very imposing, although some trees could already reach up to seven meters). However, trees and shrubs might greatly enhance natural enemy communities by providing additional trophic resources and sites for reproduction, overwintering and estivation (Stamps and Linit, 1998), especially in older systems (> 15-20 years). Higher trophic taxa such as birds and small mammals have also been shown to benefit from the presence of tree rows and UVS in alley cropping systems (Klaa et al., 2005; Gibbs et al., 2016), and their effects on weed and invertebrate pest suppression are mixed (Tschumi et al., 2018). Besides, agroforestry farmers are currently using contrasting strategies for UVS management (*e.g.* minimalist management, maintaining bushes, mowing the vegetation, sowing plant mixtures). UVS width also varies from one alley cropping system to another and is expected to have an impact on the quality and quantity of habitats and trophic resources (Aavik and Liira, 2010; Fried et al., 2018). Ecological engineering of UVS is still in its infancy, and future research should assess how these management strategies affect biological control level in crop alleys. Although our results and those of a recent meta-analysis (Staton et al., 2019) show that natural enemies generally benefit from agroforestry, a broader food web perspective is required to describe the processes that enhance or reduce biological control of invertebrate pests and weeds in temperate agroforestry systems. Encouragingly, diversified natural enemy communities generally improve biological control through higher niche complementarity (Straub et al., 2008; Holland et al., 2012; Woodcock et al., 2016; Dainese et al., 2017; Greenop et al., 2018).

5. Conclusions

Under conventional farming, the presence of understory vegetation strips within fields has a negative effect on the activity-density and species richness of generalist predators in crops, but is still useful for biodiversity conservation. On the other hand, the combination of alley cropping agroforestry and organic farming greatly enhances both the activity-density and complementarity of generalist predators, potentially making biodiversity conservation and crop pest control compatible. Our results suggest that the establishment of other agroecological infrastructures such as wildflower strips, beetle banks or hedgerows within fields would enhance biological control by generalist predators under organic farming, although it could well be the opposite under conventional farming. We emphasize that agroecological infrastructures and agrochemicals are intrinsically antagonistic strategies to control pests; the former are dedicated to the promotion of biodiversity whereas the latter lead to the destruction of biodiversity (in sprayed areas and even beyond). This antagonism can lead to strong sink or retention effects on predatory species, depending on their life strategies and associated ecological preferences. We suggest that within-field plant diversification and fine-grained interspersion of crop(s) and alternate vegetation, such as weeds, are key to promote the positive functions of agroecological infrastructures.

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Appendix A.

Table A1. Single trait indices. *S* is total number of species, w_i is the relative abundance of species *i* and x_i is the trait value for species *i*. FDvar modified is used for variables that contain 0 values.

Table A2. Functional trait values of carabid and cursorial spider species (diet; granivorous: 0, omnivorous: 0.5 and carnivorous: 1). References are given in Supplementary Material.

Figure A1. Mean activity-density of common species (*i.e.* occurring in at least five pitfall traps) in each functional group (G: granivorous carabids, O: omnivorous carabids, C: carnivorous carabids, S: cursorial spiders) under **a)** conventional farming and **b)** organic farming.

Supplementary material

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

Table S2. Results of least-square means post-hoc comparisons.

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Table 1. Description of alley cropping agroforestry fields.

Field	**Farming system**	**Age of the system (years)**	**Field size (ha)**	**Crop alley width (m)**	**UVS width (m)**	**UVS management**	**Dominant plant species in UVS**	**Tree species**
1	Conventional	10	9	25	2	Unmanaged	*Bromus* spp., *Galium aparine, Geranium columbinum*	*Acer campestre, Juglans regia, Pyrus pyraster, Prunus avium, Quercus petraea*
2	Conventional	6	12	28	1.5	Unmanaged	*Bromus* spp., *Schedonorus arundinaceus, Galium aparine*	*Juglans regia, Pyrus pyraster, Prunus avium, Quercus pubescens, Sorbus domestica*
3	Conventional	5	6	38	2	Unmanaged	*Festuca rubra* (sown), *Avena* spp., *Galium aparine*	*Acer campestre, Juglans regia, Prunus avium, Sorbus domestica, Tilia cordata*
4	Organic	2	8	26	1	Unmanaged	*Avena* spp., *Myosotis arvensis, Rubus* spp.	*Juglans regia, Prunus avium, Quercus petraea, Sorbus torminalis, Fraxinus excelsior*
5	Organic	8	3	17	1	Unmanaged	*Dactylis glomerata, Potentilla reptans, Lactuca serriola*	*Pyrus pyraster, Quercus petraea, Sorbus domestica, Sorbus torminalis, Fraxinus excelsior, Cornus sanguinea.*
6	Organic	5	6	32	2	Mown twice a year (before crop sowing/after harvest)	*Lolium* spp., *Convolvulus arvensis, Bromus* spp.	*Acer campestre, Juglans regia, Prunus avium, Sorbus domestica, Fraxinus excelsior, Ulmus campestris*

Table 2. Total number of individuals and species sampled per functional group during the whole survey.

	Total number of individuals	**Total number of species**
Carabids		
Granivorous	560	15
Omnivorous	1492	8
Carnivorous	803	25
Total	2855	48
Cursorial spiders	3006	63

Table 3. Estimates and standard errors of GLMMs comparing activity-density, species richness and functional structure of predator communities between pure crop (reference level), crop alleys and understory vegetation strips (UVS), under conventional farming (reference level) *vs* organic farming. When GLMMs revealed significant interactions between habitats and farming system, least-square means were used to compare habitats under conventional *vs* organic farming separately (see Table S2 in Supplementary material for detailed outputs). CMP = Conway-Maxwell Poisson.* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001.

	Distribution	**Main effects**			**Interactions**	
		Crop alleys	**UVS**	**Organic farming**	**Crop alleys x Organic farming**	**UVS x Organic farming**
Granivorous carabids						
Activity-density	CMP	−0.48 ± 0.247	0.05 ± 0.337	0.19 ± 0.906	**1.23** ± 0.337***	**1.04** ± 0.456*
Species richness	CMP	−0.13 ± 0.256	0.02 ± 0.372	0.16 ± 0.482	**0.68** ± 0.333*	**0.96** ± 0.456*
Omnivorous carabids						
Activity-density	CMP	−0.43 ± 0.254	**−1.25** ± 0.464**	0.82 ± 1.023	**1.20** ± 0.305***	**1.69** ± 0.536**
Species richness	CMP	**−0.45** ± 0.180*	−0.60 ± 0.325	0.62 ± 0.508	**0.55** ± 0.213**	**0.74** ± 0.371*
Carnivorous carabids						
Activity-density	CMP	**−0.73** ± 0.165***	**−1.31** ± 0.336***	−0.25 ± 0.520	0.11 ± 0.244	0.53 ± 0.461
Species richness	CMP	**−0.38** ± 0.130**	**−0.95** ± 0.281***	−0.15 ± 0.314	−0.11 ± 0.199	0.62 ± 0.366
Cursorial spiders						
Activity-density	CMP	**−0.47** ± 0.107***	−0.22 ± 0.161	0.14 ± 0.126	**0.49** ± 0.139***	0.20 ± 0.216
Species richness	CMP	−0.08 ± 0.088	0.22 ± 0.126	0.05 ± 0.125	0.12 ± 0.121	−0.03 ± 0.174
TOTAL						
Activity-density	CMP	**−0.55** ± 0.100***	**−0.47** ± 0.161**	0.07 ± 0.271	**0.78** ± 0.127***	**0.58** ± 0.205**
Species richness	CMP	**−0.18** ± 0.077*	−0.05 ± 0.115	−0.07 ± 0.137	**0.21** ± 0.104*	0.24 ± 0.155
CWM Diet	Beta	−0.11 ± 0.187	−0.32 ± 0.266	−0.37 ± 0.546	**−0.54** ± 0.249*	−0.44 ± 0.373
FDvar Diet	Beta	0.21 ± 0.163	0.33 ± 0.234	0.21 ± 0.534	0.26 ± 0.227	0.48 ± 0.323
CWM Body length	Gaussian	**0.84** ± 0.221***	0.53 ± 0.350	0.42 ± 0.999	−0.38 ± 0.313	0.01 ± 0.495
FDvar Body length	Beta	**0.41** ± 0.123***	0.02 ± 0.194	0.24 ± 0.454	**−0.76** ± 0.173***	0.17 ± 0.273

Table A1. Single trait indices. S is total number of species, w_i is the relative abundance of species i and x_i is the trait value for species i. FDvar modified is used for variables that contain 0 values.

Name	**Abbreviation**	**Formula**
Community-weighted mean	CWM	$\sum_{i=1}^{S} w_i x_i$
Functional divergence	FDvar	$\frac{2}{\pi} arctan\left[5\left(\sum_{i=1}^{S} w_i\left(\ln x_i - \overline{\ln x}\right)^2\right)\right]$ $\overline{\ln x} = \sum_{i=1}^{S} w_i \ \ln x_i$
	FDvar modified	$\sum_{i=1}^{S} w_i(x_i - \ \overline{x})^2$ $\overline{x} = CWM$

Table A2. Functional trait values of carabid and cursorial spider species (diet; granivorous: 0, omnivorous: 0.5 and carnivorous: 1). References are given in Supplementary Material.

Code	Latin name	Diet	Body length (mm)
Carabids			
Acin.pici	*Acinopus picipes*	0	14.5
Acup.meri	*Acupalpus meridianus*	1	3.625
Agon.muel	*Agonum muelleri*	0.5	7.5
Amar.sp	*Amara* spp.	0	7.5
Anch.dors	*Anchomenus dorsalis*	1	6.5
Anis.bino	*Anisodactylus binotatus*	0	10.5
Asap.stie	*Asaphidion stierlini*	1	3.5
Badi.bull	*Badister bullatus*	1	5.25
Bemb.sp	*Bembidion* spp.	1	NA
Brac.crep	*Brachinus crepitans*	0.5	8.25
Brac.expl	*Brachinus explodens*	1	5.75
Cala.fusc	*Calathus fuscipes*	0.5	12.5
Call.luna	*Callistus lunatus*	1	6
Cara.aura	*Carabus auratus*	1	23.5
Cara.purp	*Carabus purpurascens*	0.5	28.5
Chla.chry	*Chlaenius chrysocephalus*	1	8.5
Cici.camp	*Cicindela campestris*	1	12.75
Cyli.germ	*Cylindera germanica*	1	9.5
Deme.atri	*Demetrias atricapillus*	1	5
Diac.germ	*Diachromus germanus*	0	8.75
Harp.affi	*Harpalus affinis*	0	10.25
Harp.cupr	*Harpalus cupreus*	0	12.75
Harp.dimi	*Harpalus dimidiatus*	0	12.5
Harp.dist	*Harpalus distinguendus*	0.5	9.5
Harp.obli	*Harpalus oblitus*	0	10
Harp.pygm	*Harpalus pygmaeus*	0	6.125
Harp.smar	*Harpalus smaragdinus*	0	9.5
Harp.tene	*Harpalus tenebrosus*	0	9
Leis.fulv	*Leistus fulvibarbis*	1	7.5
Lori.pili	*Loricera pilicornis*	1	7.25
Meta.lamp	*Metallina lampros*	1	3.125
Meta.prop	*Metallina properans*	1	3.5

Micr.sp	*Microlestes* spp.	1	2.5
Nebr.brev	*Nebria brevicollis*	1	11.5
Nebr.sali	*Nebria salina*	1	11
Noti.bigu	*Notiophilus biguttatus*	1	4.875
Noti.quad	*Notiophilus quadripunctatus*	1	4.625
Opho.ardo	*Ophonus ardosiacus*	0	12
Opho.azur	*Ophonus azureus*	0	7.75
Paro.mend	*Parophonus mendax*	0	7.75
Phil.bigu	*Philochthus biguttatus*	1	3.625
Phil.gutt	*Philochthus guttula*	1	2.875
Poec.cupr	*Poecilus cupreus*	0.5	11
Pseu.rufi	*Pseudoophonus rufipes*	0.5	13.5
Pter.madi	*Pterostichus madidus*	0.5	16.5
Sten.skri	*Stenolophus skrimshiranus*	0.5	5.875
Stom.pumi	*Stomis pumicatus*	1	7
Synt.obsc	*Syntomus obscuroguttatus*	1	2.875
Trec.sp	*Trechinii* spp.	1	3.55
Zabr.tene	*Zabrus tenebrioides*	0	15
Cursorial spiders			
Agra.line	*Agraecina lineata*	1	6.1
Agro.lusa	*Agroeca lusatica*	1	5.3
Alop.albo	*Alopecosa albofasciata*	1	9.8
Alop.cune	*Alopecosa cuneata*	1	7.3
Alop.pulv	*Alopecosa pulverulenta*	1	8.5
Arct.peri	*Arctosa perita*	1	7
Aulo.albi	*Aulonia albimana*	1	4.1
Chal.nigr	*Chalcoscirtus nigritus*	1	3.5
Civi.civi	*Civizelotes civicus*	1	4.4
Dipl.grae	*Diplocephalus graecus*	1	1.9
Dras.lapi	*Drassodes lapidosus*	1	10.8
Dras.pube	*Drassodes pubescens*	1	7.1
Dras.lute	*Drassyllus lutetianus*	1	5.7
Dras.pumi	*Drassyllus pumilus*	1	3.8
Dras.pusi	*Drassyllus pusillus*	1	4.4
Dras.prae	*Drassyllus praeficus*	1	6.2

Dysd.eryt	*Dysdera erythrina*	1	9.3
Erig.dent	*Erigone dentipalpis*	1	2.3
Hapl.dalm	*Haplodrassus dalmatensis*	1	5.4
Hapl.sign	*Haplodrassus signifer*	1	7.3
Hogn.radi	*Hogna radiata*	1	16
Lasi.hirs	*Lasiargus hirsutus*	1	2.6
Liop.flav	*Liophrurillus flavitarsis*	1	5
Merm.tril	*Mermessus trilobatus*	1	1.9
Mica.albo	*Micaria albovittata*	1	5.3
Mica.puli	*Micaria pulicaria*	1	3.6
Micr.aper	*Micrargus apertus*	1	1.9
Nomi.exor	*Nomisia exornata*	1	5.9
Oedo.apic	*Oedothorax apicatus*	1	2.6
Ozyp.simp	*Ozyptila simplex*	1	3.5
Pard.agre	*Pardosa agrestis*	1	4.8
Pard.hort	*Pardosa hortensis*	1	5.2
Pard.nigr	*Pardosa nigriceps*	1	5.4
Pard.palu	*Pardosa palustris*	1	6
Pard.prat	*Pardosa prativaga*	1	6.1
Pard.prox	*Pardosa proxima*	1	6.7
Pard.pull	*Pardosa pullata*	1	4.8
Pard.salt	*Pardosa saltans*	1	5.8
Pard.vitt	*Pardosa vittata*	1	6.2
Pele.para	*Pelecopsis parallela*	1	1.5
Phle.bres	*Phlegra bresnieri*	1	5
Phru.fest	*Phrurolithus festivus*	1	2.7
Phru.nigr	*Phrurolithus nigrinus*	1	2.8
Poca.junc	*Pocadicnemis juncea*	1	1.9
Seta.carm	*Setaphis carmeli*	1	4
Sibi.auro	*Sibianor aurocinctus*	1	3.4
Tala.aper	*Talavera aperta*	1	2.5
Than.atra	*Thanatus atratus*	1	4.6
Tibe.oblo	*Tibellus oblongus*	1	7.6
Trac.fusc	*Trachyzelotes fuscipes*	1	4.6
Trac.pede	*Trachyzelotes pedestris*	1	6.6
Troc.hisp	*Trochosa hispanica*	1	10.5

Troc.robu	*Trochosa robusta*	1	14
Walc.capi	*Walckenaeria capito*	1	2.7
Xyst.acer	*Xysticus acerbus*	1	6.5
Xyst.cris	*Xysticus cristatus*	1	5.6
Xyst.koch	*Xysticus kochi*	1	6.6
Zelo.atro	*Zelotes atrocaeruleus*	1	6.9
Zelo.latr	*Zelotes latreillei*	1	6.7
Zelo.petr	*Zelotes petrensis*	1	5.8
Zoda.ital	*Zodarion italicum*	1	2.7
Pard.sp	*Pardosa* spp.	1	5.7
Xyst.sp	*Xysticus* spp.	1	6
Zelo.sp	*Zelotes* spp.	1	6.5

Figure 1

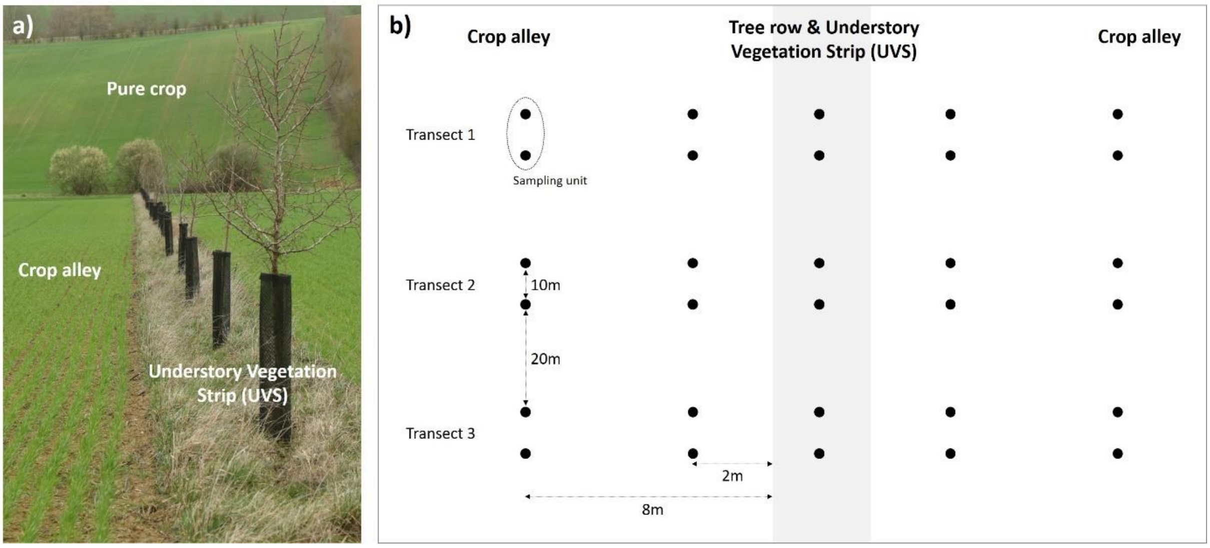

a)
Pure crop
Crop alley
Understory Vegetation Strip (UVS)
b)
Crop alley
Tree row & Understory Vegetation Strip (UVS)
Crop alley
Transect 1
Sampling unit
Transect 2
10m
20m
Transect 3
2m
8m

Figure 2

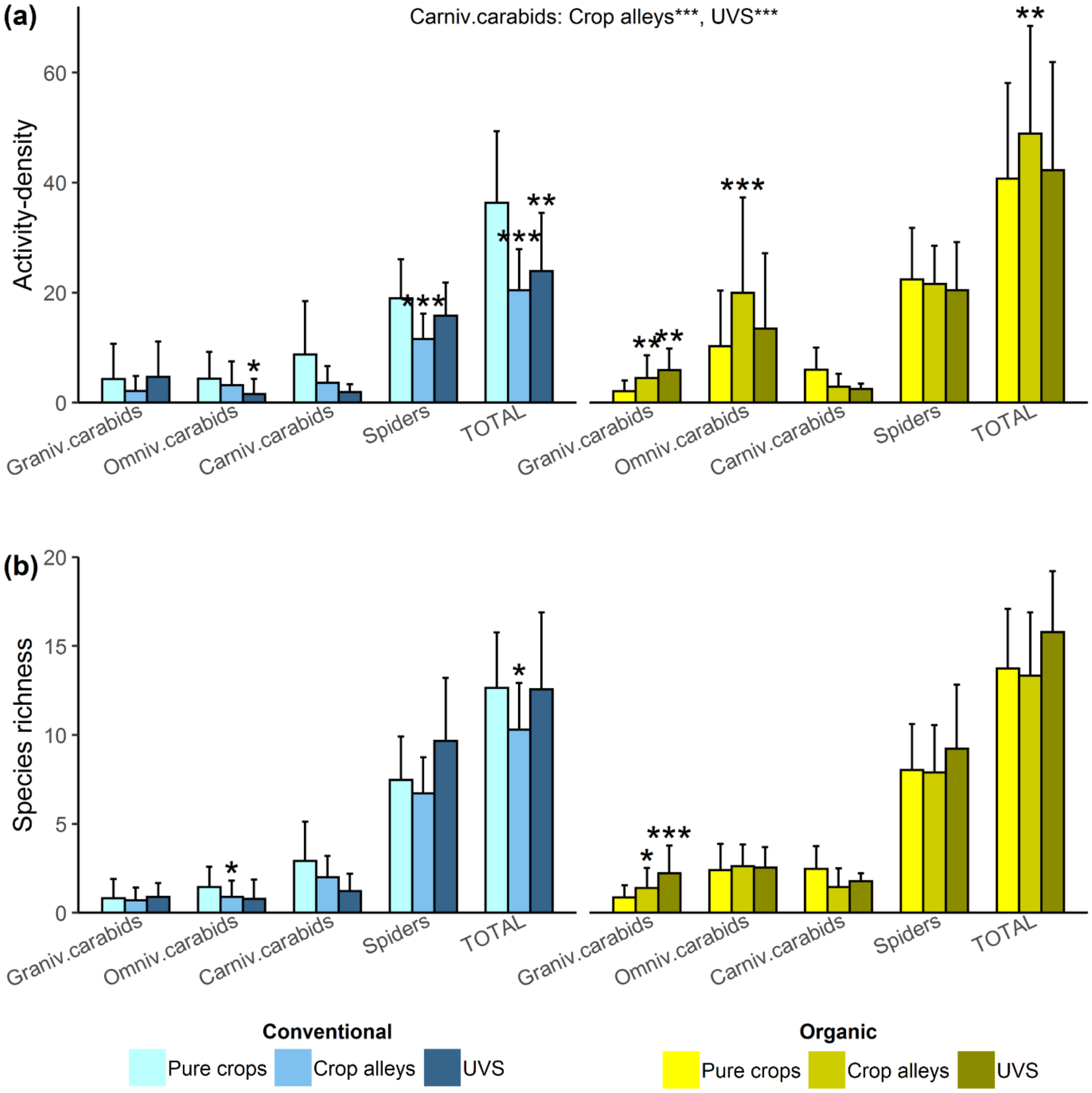

(a)
Carniv.carabids: Crop alleys***, UVS***
Activity-density
0
20
40
60
*
***
**
***
**
**
***
**
Graniv.carabids
Omniv.carabids
Carniv.carabids
Spiders
TOTAL
(b)
Species richness
0
5
10
15
20
*
*
*
***
Conventional
Pure crops
Crop alleys
UVS
Organic
Pure crops
Crop alleys
UVS

Figure 3

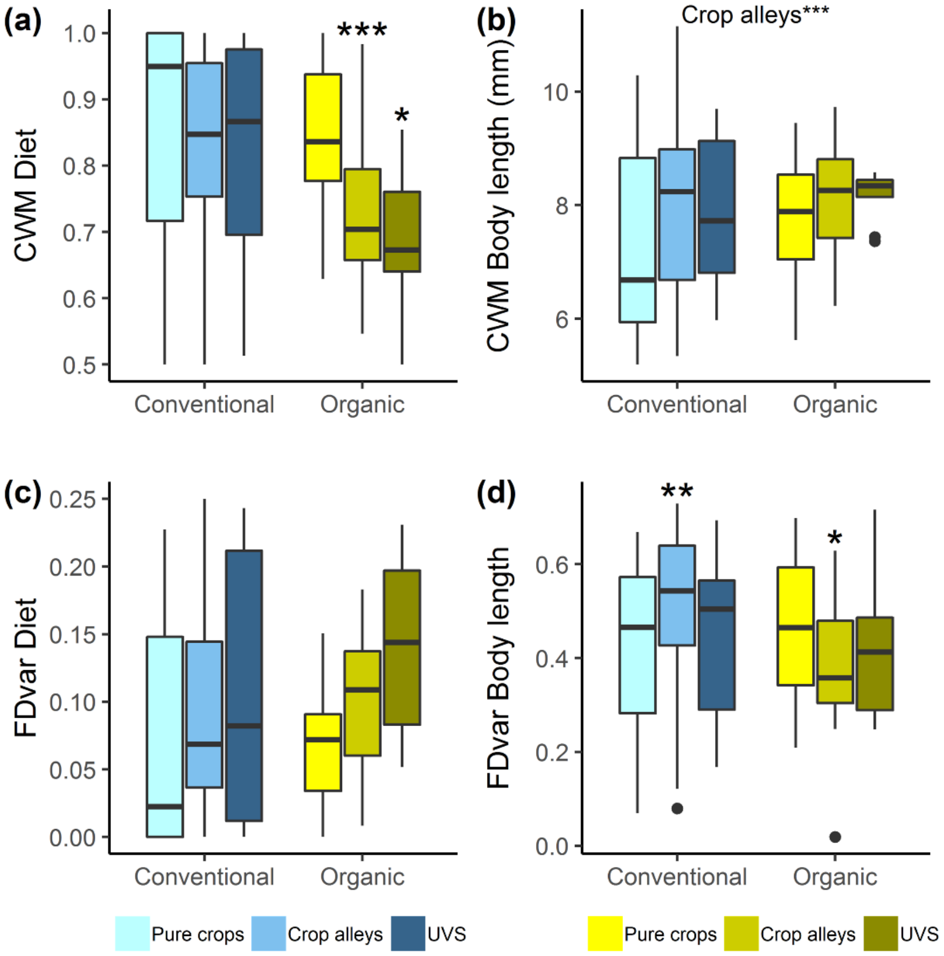
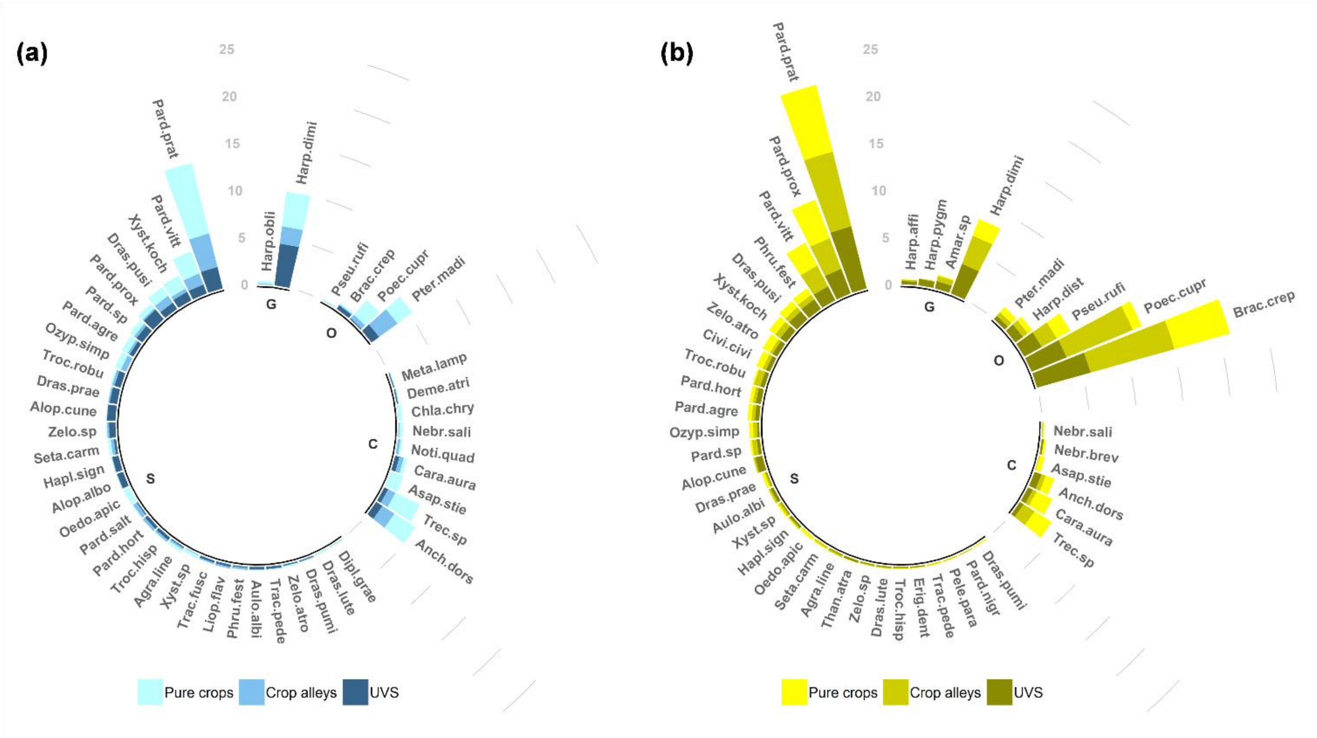

(a)
CWM Diet
1.0
0.9
0.8
0.7
0.6
0.5
***
*
Conventional
Organic
(b)
Crop alleys***
CWM Body length (mm)
10
8
6
Conventional
Organic
(c)
FDvar Diet
0.25
0.20
0.15
0.10
0.05
0.00
Conventional
Organic
(d)
FDvar Body length
**
*
0.6
0.4
0.2
0.0
Conventional
Organic
Pure crops
Crop alleys
UVS
Pure crops
Crop alleys
UVS

Figure A1


(a)
25
20
15
10
5
0
Pard.prat
Harp.obli
Harp.dimi
G
Pseu.rufi
Brac.crep
Poec.cupr
Pter.madi
O
Meta.lamp
Deme.atri
Chla.chry
Nebr.sali
Noti.quad
C
Cara.aura
Asap.stie
Trec.sp
Anch.dors
Dipl.grae
Dras.lute
Dras.pumi
Zelo.atro
Trac.pede
Aulo.albi
Phru.fest
Liop.flav
Trac.fusc
Xyst.sp
Agra.line
Troc.hisp
Pard.hort
Pard.salt
Oedo.apic
Alop.albo
Hapl.sign
Seta.carm
Zelo.sp
Alop.cune
Dras.prae
Troc.robu
Ozyp.simp
Pard.agre
Pard.sp
Pard.prox
Dras.pusi
Xyst.koch
Pard.vitt
S
Pure crops
Crop alleys
UVS
(b)
25
20
15
10
5
0
Pard.prat
Pard.prox
Pard.vitt
Phru.fest
Dras.pusi
Xyst.koch
Zelo.atro
Civi.civi
Troc.robu
Pard.hort
Pard.agre
Ozyp.simp
Pard.sp
Alop.cune
Dras.prae
Aulo.albi
Xyst.sp
Hapl.sign
Oedo.apic
Seta.carm
Agra.line
Than.atra
Zelo.sp
Dras.lute
Troc.hisp
Erig.dent
Trac.pede
Pele.para
Pard.nigr
Dras.pumi
S
Harp.affi
Harp.pygm
Amar.sp
Harp.dimi
G
Pter.madi
Harp.dist
Pseu.rufi
Poec.cupr
Brac.crep
O
Nebr.sali
Nebr.brev
Asap.stie
Anch.dors
Cara.aura
Trec.sp
C
Pure crops
Crop alleys
UVS