

THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Ecologie Fonctionnelle et Sciences Agronomiques

École doctorale GAIA

Unité de recherche UMR SYSTEM

Influence of within-field understory vegetation strips
on plant and invertebrate communities in alley
cropping agroforestry systems

—

Influence des linéaires sous-arborés sur les
communautés de plantes et invertébrés des systèmes
agroforestiers intra-parcellaires

Présentée par Sébastien Boinot

Le 19 novembre 2019

Sous la direction de Jean-Pierre Sarthou et Pierre-Éric Lauri
et l'encadrement de Delphine Mézière et Karim Barkaoui

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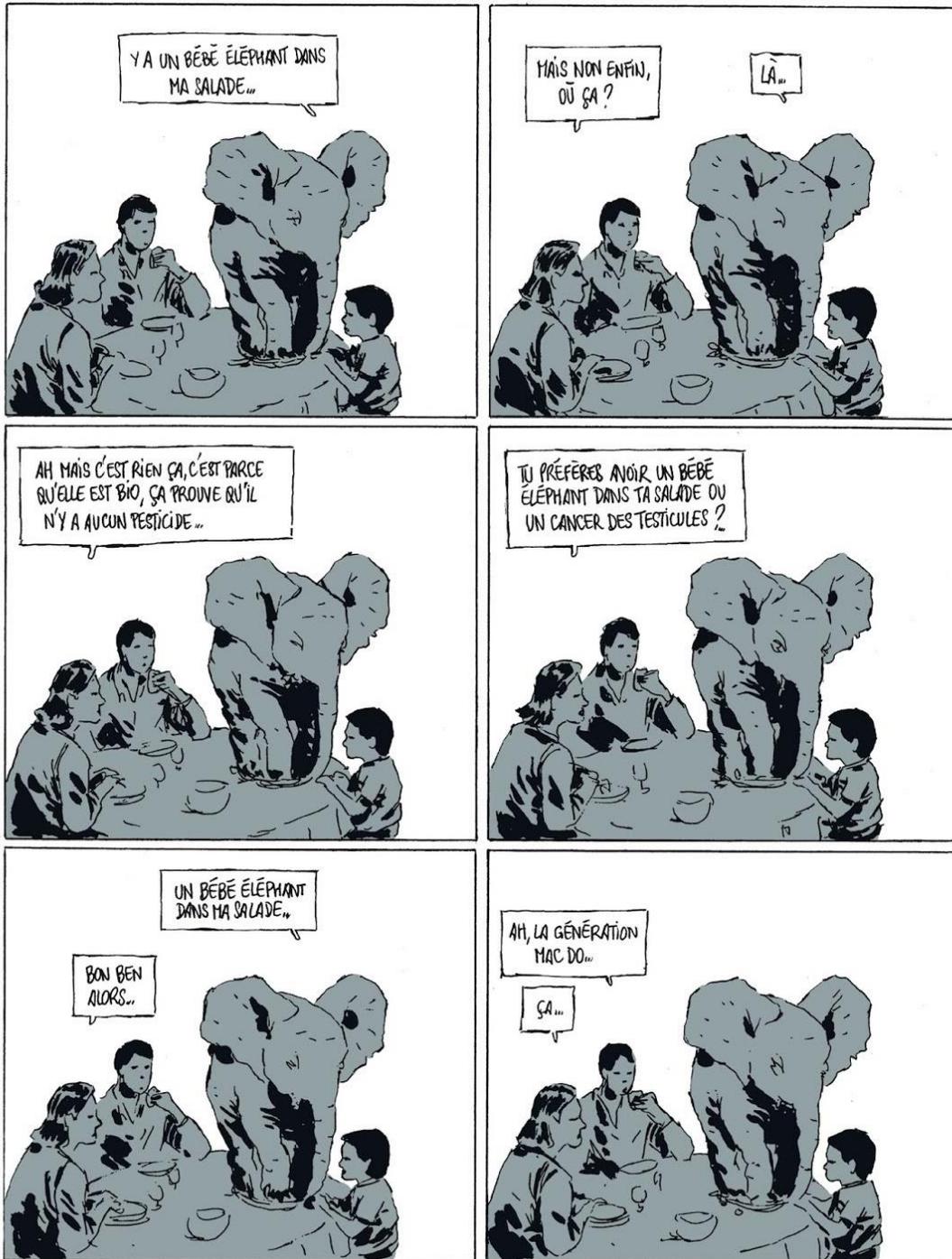
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PREFACE

This PhD thesis was carried out from October 2016 to October 2019 at the joint research unit UMR System (Tropical and Mediterranean cropping system functioning and management), Montpellier SupAgro, INRA, CIRAD, CIHEAM-IAMM. The doctoral research of Sébastien Boinot was financially supported by La Fondation de France and the experiments were funded by the European Union (AGFORWARD project: AGroFORestry that Will Advance Rural Development) and L'Agence de l'Eau Adour-Garonne (BAG'AGES project: Bassin Adour-Garonne, quelles performances des pratiques AGroécologiquES ?). Sébastien Boinot followed the program of excellence from Agreenium International Research School (EIR-A), with a three-month doctoral stay at Rothamsted Research, Harpenden, UK, under the supervision of Jonathan Storkey. This thesis was directed by Jean-Pierre Sarthou and Pierre-Eric Lauri and supervised by Delphine Mézière and Karim Barkaoui.



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Rothamsted Manor under the snow
Illustration by Chloé Malard

PUBLICATIONS

Scientific papers:

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Boinot, S., Poulmarc'h, J., Mézière, D., Lauri, P.-É., Sarthou, J.-P. (2019b). Distribution of overwintering invertebrates in temperate agroforestry systems: Implications for biodiversity conservation and biological control of crop pests. *Agriculture, Ecosystems & Environment* 285, 106630. 10.1016/j.agee.2019.106630.

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LIST OF ABBREVIATIONS

AEI	Agroecological infrastructure
CWM	Community-weighted mean
FDvar	Functional divergence
SLA	Specific Leaf Area
SNH	(Semi-)natural habitat
UVS	Understory vegetation strip

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CHAPTER 1

Introduction

1. Context

1.1. Agricultural intensification and biodiversity extinction crisis

The post-war agricultural intensification considerably increased crop production, through high pesticide and fertilizer inputs, mechanization and simplification of agricultural landscapes. However, intensive food production systems are not sustainable (e.g. [Stoate et al., 2001](#); [Pingali, 2012](#); [Emmerson et al., 2016](#)). The use of pesticides, which first helped to control crop pests, could now favors the build-up of pesticide resistance ([Thrall et al., 2011](#); [Storkey and Neve, 2018](#)). Besides, pesticides can be more detrimental to natural enemies of pests than to pests themselves, which weakens natural pest suppression and results in an even greater need for agrochemicals – the so-called pesticide treadmill ([Jonsson et al., 2015](#) and references therein). Pesticides and mineral fertilizers diffuse in the environment, causing soil, air and water pollution and threatening ecosystems health ([Sun et al., 2017](#); [Foster and Custodio, 2019](#)). The increase of cropland to the detriment of (semi-)natural habitats (SNH) such as woodlots, grasslands, peatlands, forests, hedgerows and field boundaries has led to an extinction of biodiversity worldwide ([Stoate et al., 2001](#)). Declines of diversity are especially dramatic for weeds ([Meyer et al., 2013](#)), invertebrates ([Sánchez-Bayo and Wyckhuys, 2019](#)) and farmland

birds (Donald et al., 2001). Agricultural intensification not only jeopardizes the conservation of species in itself, but also their ecological functions. For example, although weeds can sometimes compete severely with crops for water, light and nutrients, they also play a key role in the agroecosystem functioning by reducing soil erosion risks and providing food resources and habitats for higher trophic taxa (Mézière et al., 2015). Insect pollinators promoted by weed communities, such as bees and hoverflies, can in turn ensure plant pollination, including entomophilous crops (Bretagnolle and Gaba, 2015). Natural enemies of crop pests, such as spiders, carabid beetles and parasitoid wasps, contribute to reduce pest pressure and resulting crop damages (Bàrberi et al., 2010). Detritivores such as earthworms, woodlice and springtails favor nutrient cycling and soil fertility through the decomposition of organic matter (Brussaard et al., 2007). In other words, the loss of biodiversity caused by agricultural intensification results in a loss of functionality within the agroecosystem. Conversely to intensive systems, which depend on the use of agrochemical pollutants, agroecological systems seek to promote the ecological functions performed by beneficial organisms, such as pollination, biological control of crop pests and organic matter decomposition. Therefore, the fundamental objective of agroecological systems is to bring functional biodiversity back into crop fields (Figure 1.1), taking advantage of the positive functions it provides while reducing its potential negative impacts on crop production (e.g. weed-crop competition for nutrients, light and water, crop damages caused by pests).

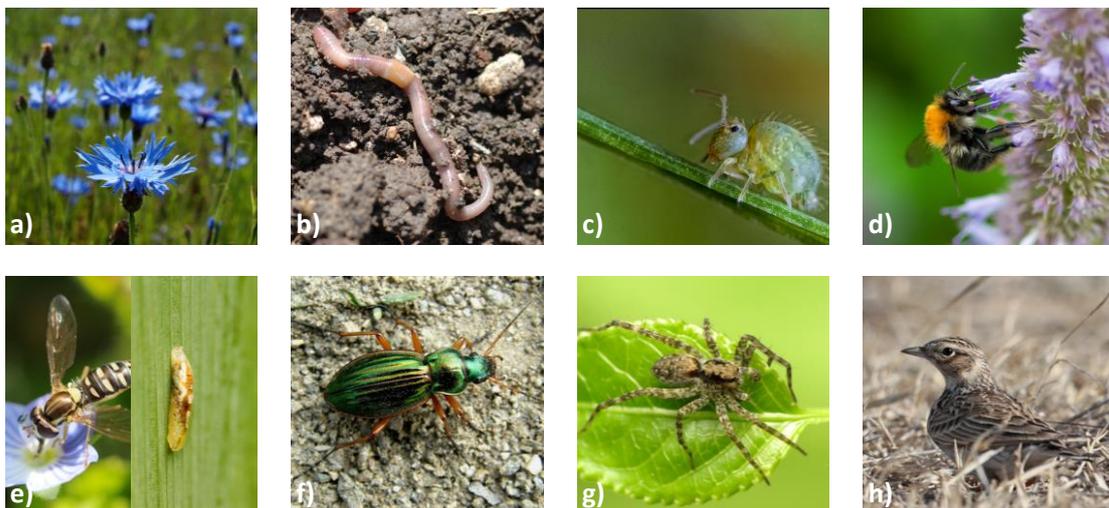


Figure 1.1. Functional biodiversity is composed of living organisms that perform ecological functions through their biological activity. For example, **a)** arable weeds provide resources and habitats for higher trophic taxa, **b)** earthworms and **c)** springtails help to decompose organic matter and favour nutrient cycling, **d)** bees and **e)** adult hoverflies ensure the pollination of entomophilous plants, **e)** hoverfly larvae, **f)** carabid beetles, **g)** spiders and **h)** birds all contribute to crop pest control. Pictures from Flickr website: © Anita, T. Stromberg, Sandra, Ferdi De gier, T. Bresson, Nikk, M. Ahmed, K. Schulz, A. Maizlish

1.2. Dispersal and distribution of living organisms in agroecosystems

Living organisms are characterized by a wide range of life strategies. Some can live in extremely disturbed habitats such as intensive crop fields, while others need more stable habitats such as grasslands, hedgerows and forests, at least at some point during their life cycle (reproduction, overwintering, estivation, feeding, etc.). Therefore, living organisms exhibit different distribution patterns across the SNH-crop interface (Figure 1.2).

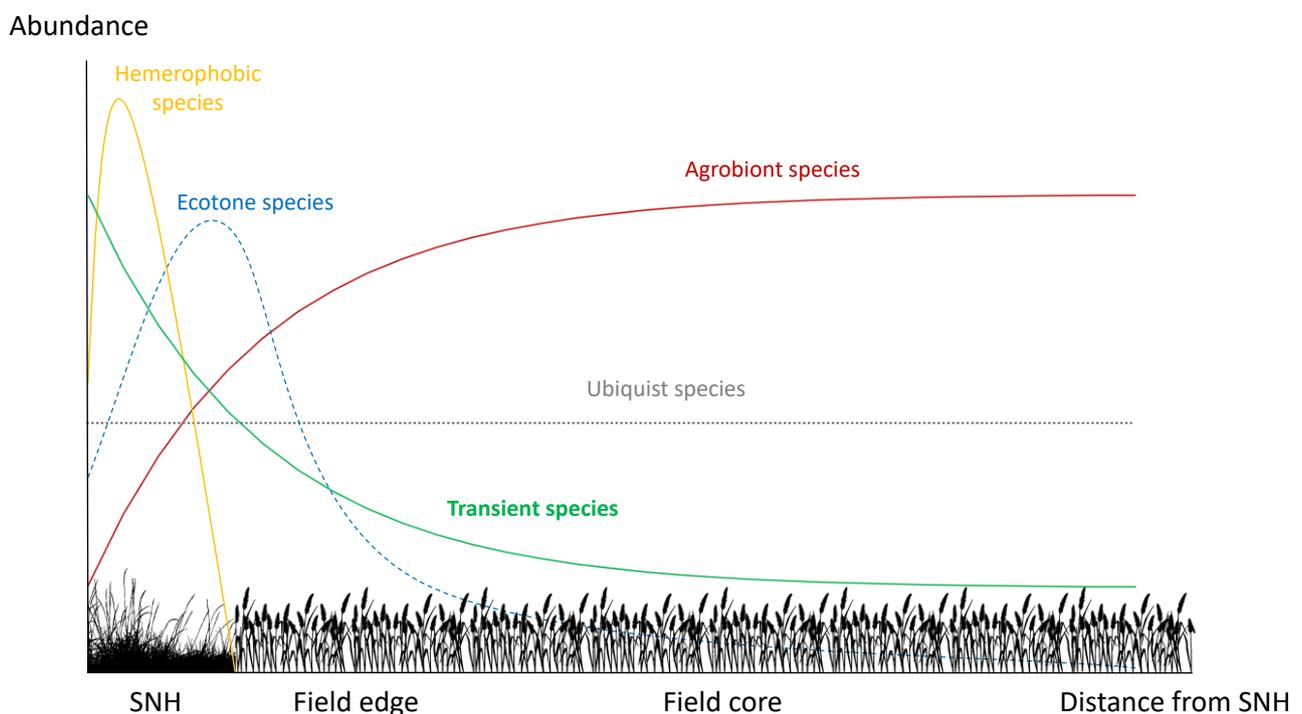


Figure 1.2. Distribution patterns of living organisms within crop fields, inspired from [Tschardt et al. \(2005\)](#). Hemerophobic species are restricted to semi-natural habitats (SNH), agrobiont species have a preference for crop fields, ecotone species are more successful at the interface of SNH and crop fields, ubiquist species have no preference for SNH or crop fields and transient species colonize crop fields from SNH. Higher abundance of transient species in the field edge (i.e. “edge-biased” distribution) results in enhanced ecosystem services and/or disservices, depending on the nature of dispersing species (e.g. competitive weeds, insect pests, pollinators, natural enemies).

Figure: © S. Boinot

The presence of SNH nearby crop fields is of major importance for the dispersal of many transient species that show “edge-biased” distribution within crop fields ([Rand et al., 2006](#); [Nguyen and Nansen, 2018](#); [Metcalf et al., 2019](#)). Indeed, their abundance decreases sharply within the field core, while it remains high near field edges that are close to SNH. The dispersal

of organisms from one habitat to another (also called “spillover” or “mass effect”) is a prerequisite for their presence, and the fulfilment of their functions, within crop fields (Blitzer et al., 2012). Spillover can have either negative or positive impacts on food production, depending on the nature of dispersing organisms (e.g. competitive weeds, invertebrate pests, pollinators, natural enemies).

1.2.1. The influence of landscape context

Plant and invertebrate communities that are found within a crop field are partly composed of species coming from surrounding habitats. Therefore, composition of within-field communities varies according to the landscape context, which is defined as the habitat composition¹ and configuration² within a certain perimeter around the crop field, depending on the dispersal distance of the considered taxa (Martin et al., 2019). Fields located in highly complex landscapes generally harbor much more diversified communities than fields located in very simple landscapes (Figure 1.3), because increased proportion of SNH and edges favor the spillover of dispersal-limited species (Tschardt et al., 2005). For instance, landscape complexity can enhance the dispersal of natural enemies of crop pests (Chaplin-Kramer et al., 2011), pollinators (Ricketts et al., 2008) and weeds (Gabriel et al., 2005) within crop fields. However, it can sometimes conversely lead to reduced or delayed colonization of crop fields (Wamser et al., 2011).

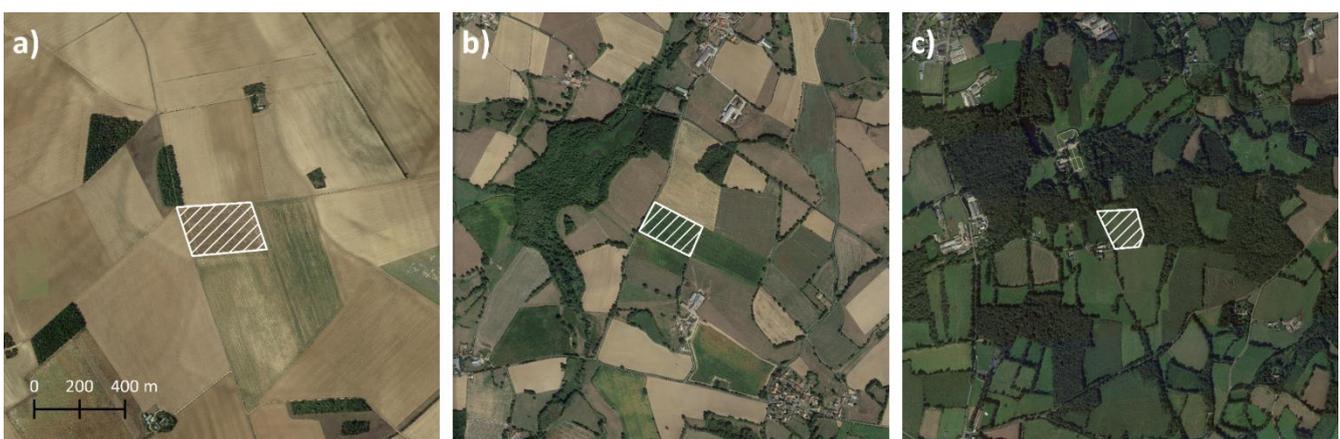


Figure 1.3. Fields located within simple (a), intermediate (b) and complex (c) landscapes. Increased landscape complexity results in both higher diversity of land-use types (especially a higher proportion of SNH) and higher density of edges. Figure: © S. Boinot

¹ Proportion of land-use types (e.g. woodland, grassland, grassland, bare ground)

² Size, shape and spatial distribution of land-use patches

1.2.2. The effect of local environment

As opposed to the landscape context, local environment is defined on a smaller scale (usually the crop field and its immediate surroundings) and is therefore intimately linked to agricultural practices occurring within the crop field. Local environment includes abiotic factors (e.g. pedoclimatic conditions) and biotic factors (e.g. predators and prey), but also the nature of immediate adjacent habitats and agroecological infrastructures (AEI) (Figure 1.4). Studies have demonstrated that local environment can be as influent, if not more, than landscape context in determining the composition of plant and invertebrate communities (e.g. Fried et al., 2008; Sarthou et al., 2014; Alignier et al., 2017; Ponisio et al., 2019).

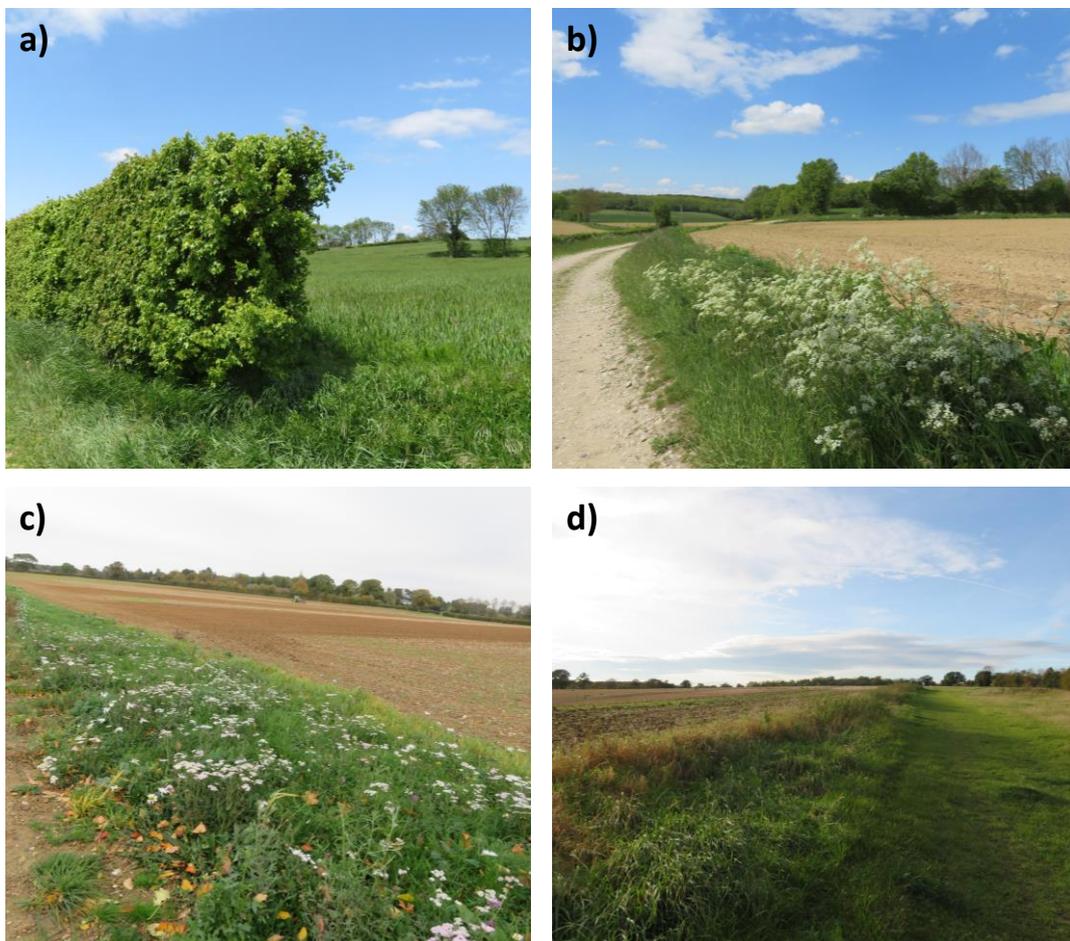


Figure 1.4. Examples of agroecological infrastructures (AEI) to promote biodiversity within crop fields. **a)** hedgerow, **b)** spontaneous field boundary, **c)** sown wildflower strip, **d)** grassy strip. Pictures: © S. Boinot

Of growing interest, AEI have been proposed to favor the spillover of beneficial invertebrates into crop fields. For instance, preserving and restoring hedgerows or sowing

grass strips and wildflower strips around crop fields have proved to be very efficient measures to improve ecosystem services such as pollination and biological control (Feltham et al., 2015; Pywell et al., 2015; van Vooren et al., 2017). Further on, to avoid the edge-biased distribution of beneficial invertebrates and promote ecosystem service flows into cropland, SNH such as beetle banks and wildflower strips can take place within crop fields themselves (Collins et al., 2002; Hatt et al., 2017). However, SNH around or within fields are also potential reservoirs for invertebrate pests and weeds (Blitzer et al., 2012; Rusch et al., 2012; Metcalfe et al., 2019), making some farmers reluctant to their presence. Moreover, as well as landscape complexity, AEI can conversely reduce or delay spillover of beneficial invertebrates into cropland by attracting them or hindering their movement (Gontijo, 2019).

1.2.3. The impact of agricultural practices

Cropping systems and crop type (i.e. cultivated species) are further major factors governing the composition of plant and invertebrate communities, with many crop-associated weeds, invertebrate pests and their natural enemies evolving together (Poggio et al., 2013; Meyer et al., 2019). Moreover, once spillover from SNH to cropland has occurred, the living organism in question has to face agricultural disturbances such as soil tillage or pesticide and fertilizer treatments, which have detrimental effects on many taxa (McLaughlin and Mineau, 1995). Indeed, crop management imposes a high selection pressure on organisms living in crop fields (Ryan et al., 2010; Thrall et al., 2011; Bourgeois et al., 2019). Only organisms that can handle agricultural disturbances can thrive in such disturbed habitats, while others depend on the presence of more stable habitats in the surroundings and need to move between each habitat (Metcalfe et al., 2019). For example, typical arable weeds that colonize the soil seed bank of crop fields generally have a short-life cycle, high reproductive output, flexible phenology and affinity for nutrient-rich environments (Bourgeois et al., 2019). They can grow and produce seeds rapidly enough to avoid soil tillage and herbicide treatments, and their important seed bank also buffers these agricultural disturbances. The same kind of successful ecological strategies are observed among invertebrates. So-called “r-strategist” characterized by small size, short life-cycle and high fecundity are generally performing better than “K-strategist” (larger, longer life-cycle and lower fecundity) in highly disturbed habitat (Thomas et al., 1992; Schirmel et al., 2016). Of particular interest, the adoption of organic farming is an efficient

way to reduce selection pressure imposed by severe agricultural disturbances, and thus enhance biodiversity into cropland (Tuck et al., 2014). In the absence of herbicides and synthetic fertilizers, fields under organic farming generally harbor highly diversified weed flora (Roschewitz et al., 2005) that provides additional habitats and resources for higher trophic taxa (Storkey and Neve, 2018). The absence of synthetic insecticides also directly favors the presence of invertebrates.

1.2.4. The interplay of landscape context, local environment and agricultural practices

Recent studies revealed that within-field biodiversity (or the resulting ecosystem services) is strongly influenced by interactions between landscape context, local environment and agricultural practices. For example, some studies showed that organic farming had higher positive effects on regulating ecosystem services when combined with a complex landscape, whereas conventional farming had higher positive effects when combined with a simple landscape (Fischer et al., 2011a; Winqvist et al., 2011; Ricci et al., 2019). Conversely, other studies showed that organic farming had higher positive effects on biodiversity in simple landscapes, whereas conventional fields reached higher diversity in complex landscapes (Roschewitz et al., 2005; Tuck et al., 2014; Flohre et al., 2011). Further, it has also been demonstrated that the effect of agricultural practices at local scale is modulated by practices at landscape scale. Indeed, within-field biodiversity tends to be higher in situations with contrasted practices, such as conventional fields in organic context or organic fields in conventional context (Rundlöf et al., 2008; Diekötter et al., 2010). In conclusion, the effectiveness of local AEI in promoting service-providing communities is likely to depend on the landscape complexity, but also on agricultural practices at both local and landscape scales (Figure 1.5).

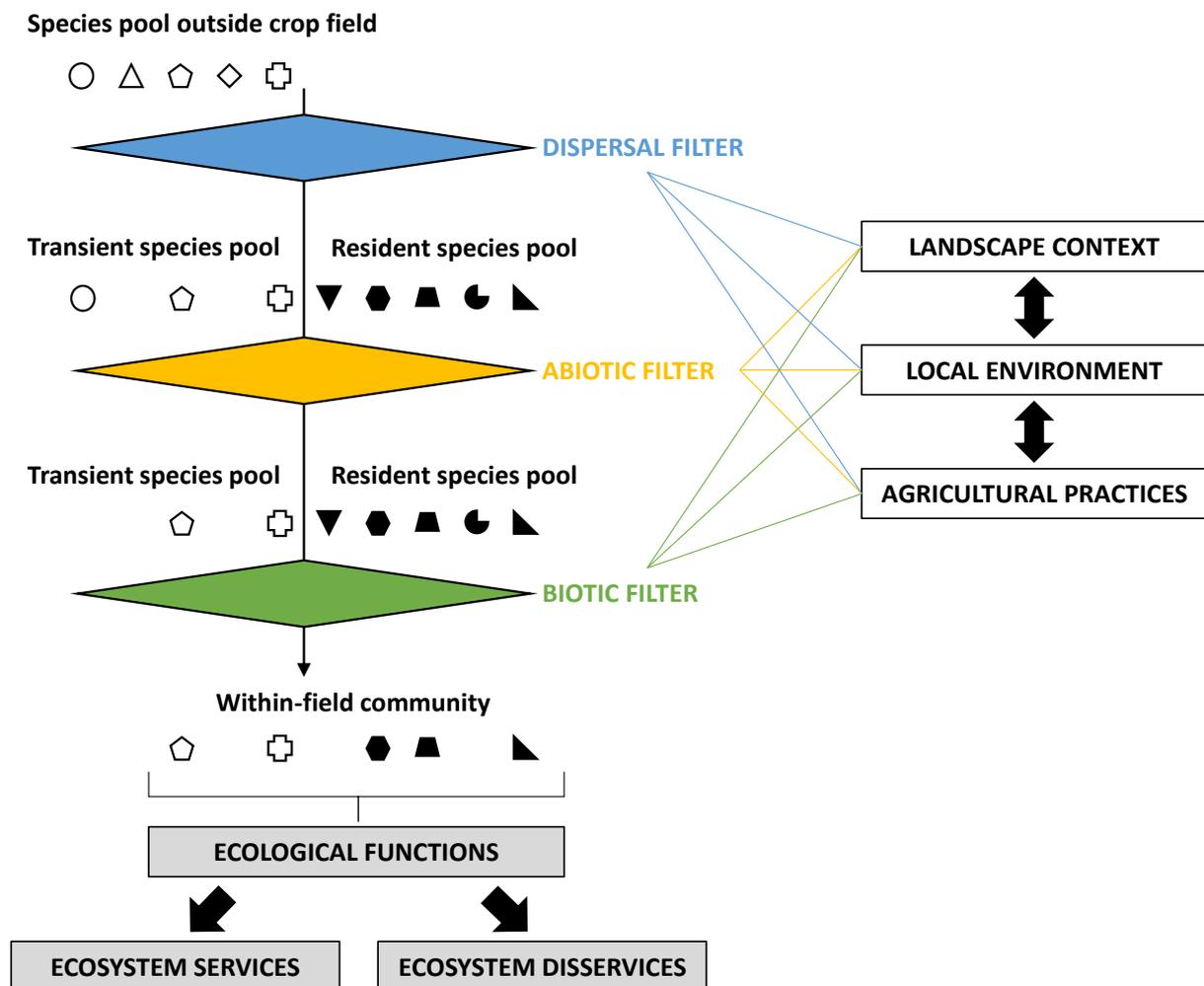


Figure 1.5. According to the community assembly theory, the composition of within-field communities is determined by a series of hierarchical filters, which govern the presence, survival and growth of individuals (Booth and Swanton, 2002). The strength of each filter is modulated by the combination of landscape context, local environment and agricultural practices. The success of each individual depends on its functional attributes related for example to dispersal strategies, tolerance to disturbances or competitiveness (Southwood, 1977). The within-field community resulting from natural and anthropogenic selection has its own functional structure, which mediates its ecological functions, leading to the delivery of ecosystem services and/or disservices. Figure: © S. Boinot

1.3. Temperate agroforestry systems: new opportunities for the conservation of semi-natural habitats

Judged as constraining obstacles and threats for crop production, trees, shrubs and associated herbaceous vegetation have been removed from agricultural landscapes during the post-war

agricultural intensification. Agroforestry, a traditional land use system integrating woody vegetation (trees or shrubs) with crop and/or animal production systems, was almost forgotten in temperate regions, replaced by agricultural and forestry development paradigms (Rigueiro-Rodríguez et al., 2009). However, temperate agroforestry systems are gaining renewed interest since the past three decades. A common objective of any agroforestry practices is to promote positive ecological interactions between the different components that are associated (i.e. trees, shrubs, crops, animals), so that agroforestry systems perform better than systems without woody vegetation, considering economic, social and environmental benefits. Indeed, agroforestry systems have been shown to provide a wide range of ecosystem services from the same area of land, such as sustainable food, timber 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., 2019b). They are also expected to be more adapted to climate change, due to the presence of trees that create favorable microclimates during cold winter or hot summers (Arenas-Corraliza et al., 2018). Temperate agroforestry systems can take multiples faces (Figure 1.6).

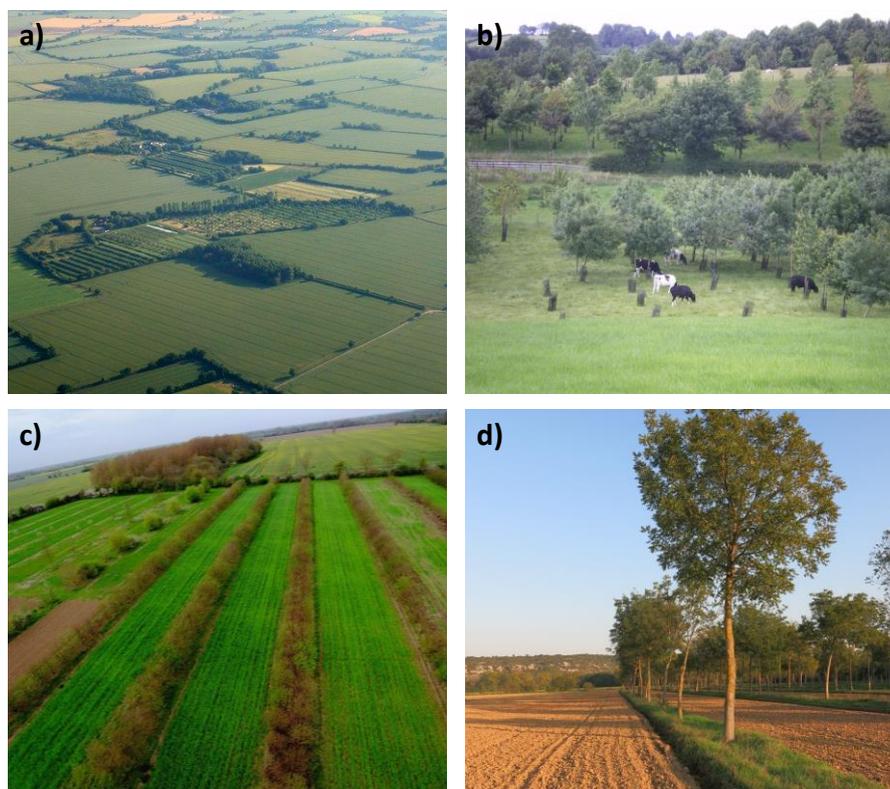


Figure 1.6. In temperate regions, agroforestry systems can have many faces, such as **a)** hedged farmland, **b)** silvopastoralism, **c)** alley cropping with coppiced wood, **d)** alley cropping with timber trees and understory vegetation strips. Pictures: ©AGFORWARD

Most common practices in Europe include silvoarable agroforestry, forest farming, riparian buffer strips, improved fallow, multipurpose trees and silvopasture (Rigueiro-Rodríguez et al., 2009). Among agroforestry systems, alley cropping agroforestry (Figure 1.6d), in which arable crops are grown between tree rows, represents a great opportunity for the reintegration of SNH within fields. Indeed, 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). UVS are poorly disturbed by crop management and so are comparable to other linear SNH providing ecosystem services, except that they are located within fields and occupy about 3 to 13% of the available agricultural area (based on the number and width of UVS per field). Given the spatial configuration and the important extent of UVS within crop fields, it is likely that both the intensity of spillover and the amount of refugia for biodiversity are increased in alley cropping agroforestry compared to pure crop systems (Figure 1.7).

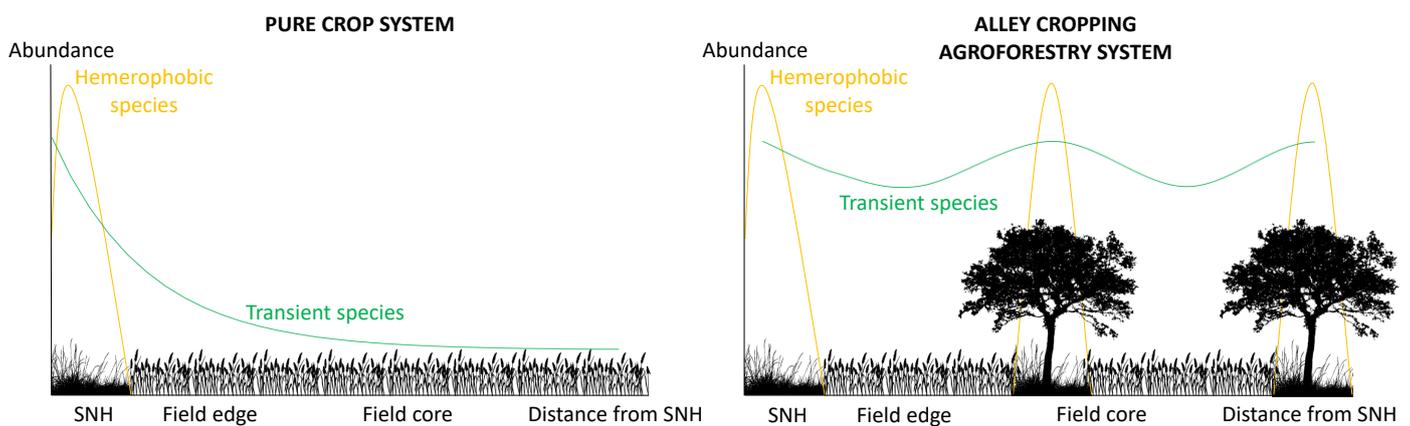


Figure 1.7. Expected changes in species distribution in alley cropping agroforestry systems, as opposed to pure crop systems. Permanent and less disturbed habitats (i.e. trees and UVS) are expected to offer refugia from agricultural disturbances for hemerophobic species. These habitats are also expected to promote spillover in crop alleys, which could result in enhanced ecosystem service and/or disservice flows depending on the nature of transient species (e.g. competitive weeds, insect pests, pollinators, natural enemies). Figure: © S. Boinot

This could result in enhanced ecosystem services and/or disservices, depending on the nature of favored species (e.g. competitive weeds, invertebrate pests, pollinators, natural enemies). 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). Research in temperate alley cropping agroforestry is recent and has focused mainly on interactions between trees and crops. To our knowledge, no study has assessed the effect of temperate agroforestry systems on biodiversity under contrasted farming systems (e.g. conventional vs organic). However, recent studies have assessed how UVS can affect soil organic carbon storage (Cardinael et al., 2015) or biodiversity, including small mammals (Klaa et al., 2005), weeds (Mézière et al., 2016; Carrier et al., 2019), invertebrates (Cardinael et al., 2019; Pardon et al., 2019b; Richard et al., 2019), arbuscular mycorrhizal fungi (Battie-Laclau et al., 2019) or soil microbial communities (Guillot et al., 2019).

2. Objectives

Conversion from a traditional pure crop system to an alley cropping agroforestry system represents a huge step for farmers. Not only do they have to deal with trees, but also with the spontaneous vegetation within their fields. If some farmers perceive these new components as opportunities for biodiversity conservation, others fear an increase of weed and invertebrate pest pressure (Graves et al., 2017). Although this survey was performed in England, it is a good reflection how what agroforestry consultants can observe in France. Besides, recent surveys revealed that the adoption of agroforestry systems might be mainly limited because of a strong cognitive lock-in among farmers, who are more influenced by the opinion of their colleagues rather than those of society and environmentalists (Sereke et al., 2016; Louah et al., 2017). This could partly explain why agroforestry systems still remain marginal in temperate regions, although the European Union has recently recognized the economic, ecological and social advantages of agroforestry in its rural development policy (Rigueiro-Rodríguez et al., 2009). The production and transmission of agroecological knowledge could help to justify and promote the adoption of agroforestry systems. To date, we do not know to what extent temperate agroforestry systems favor biodiversity conservation, neither how they affect natural enemies of crop pests and biological control, which is one of the major levers for the transition to sustainable and wildlife-friendly systems (Gontijo, 2019).

The objective of this PhD thesis is to describe the response of plant and invertebrate communities to alley cropping agroforestry systems and assess both the positive and negative effects of understory vegetation strips (UVS) on biodiversity conservation and biological control of crop pests.

To reach this goal, we sampled plant and invertebrate communities in the field core of alley cropping agroforestry systems (i.e. crop alleys and UVS) and adjacent pure crop controls with similar crop management, pedoclimatic conditions and landscape context. We described both the taxonomic and functional structures of communities to better understand their responses to agroforestry systems and, for invertebrates, their potential effects on biological control.

The PhD thesis is divided into three studies (Figure 1.8):

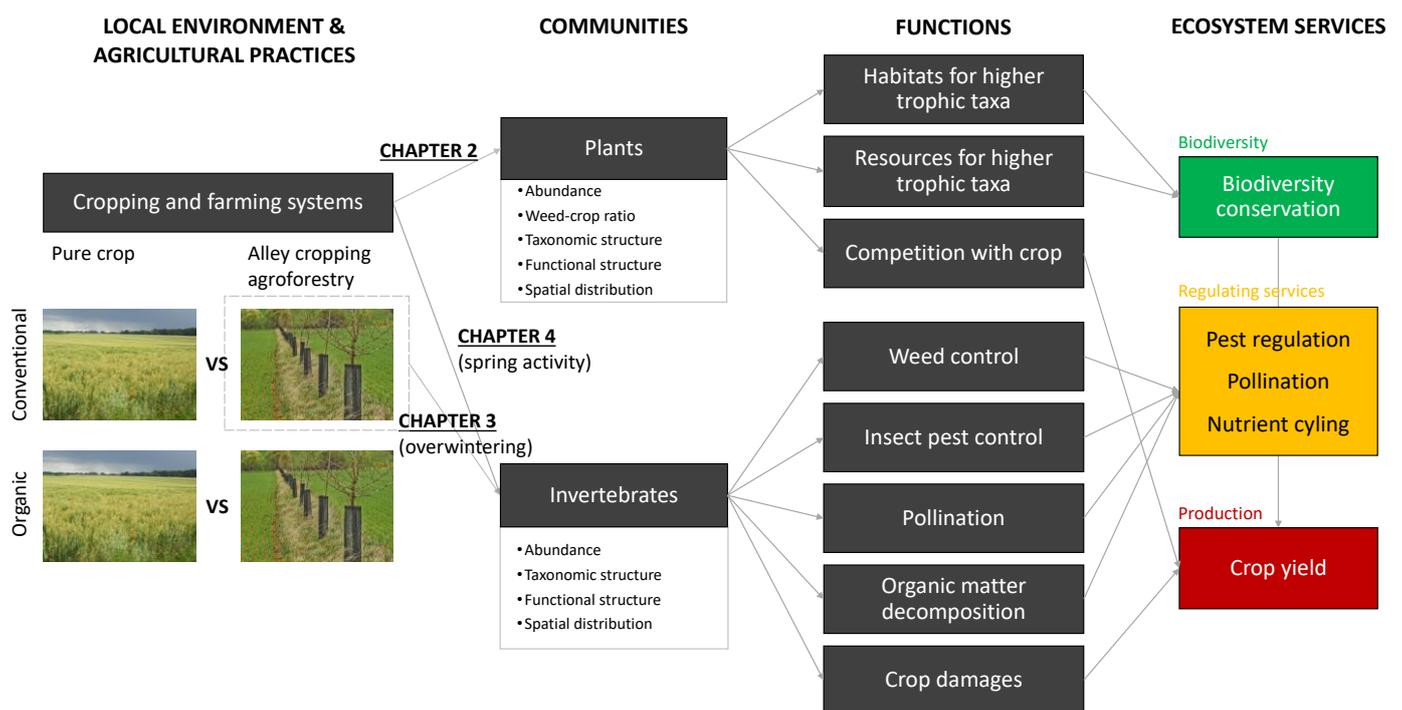


Figure 1.8. Position of each thesis chapter. Regulating ecosystem services have not been measured but assessed through the taxonomic and functional structures of plant and invertebrate communities. Arrows mean “an effect on”.

- Chapter 2: assessing the contribution of UVS (i) to plant spillover in crop alleys and (ii) to plant diversity conservation in the agroecosystem, depending on the farming system (conventional vs organic) and the functional structure of understory plant communities.

- Chapter 3: investigating the importance of UVS associated to tree rows in promoting successful overwintering of invertebrates within agroforestry fields, as opposed to crop alleys that are disturbed by soil tillage.
- Chapter 4: assessing the potential of common ground-dwelling predators to control weeds and invertebrate pests in alley cropping agroforestry vs pure crop control, under conventional vs organic farming.

3. Materials and methods

3.1. Study sites

3.1.1. Production field network

Given that agroforestry systems remain marginal in France, a first challenge was to find several couples of alley cropping agroforestry fields and pure crop controls similar in terms of crop management (i.e. tillage, pesticides, fertilizers, crop type, crop rotation) and landscape context, so that we were in measure of assessing the intrinsic effect of agroforestry systems on plant and invertebrate communities. A second challenge was to find agroforestry fields with contrasted flora within UVS, so that the conclusions we draw from our studies are more generalizable. Therefore, a survey was conducted among 39 agroforestry farmers from the Gers and Pyrénées-Atlantiques departments (South-Western France), where agroforestry practice is becoming more and more popular, especially because of soil erosion problems. This is a hilly region (altitude about 300 meters) characterized by a sub-Atlantic climate with hot summers and cool winters (Cfb climate according to the Köppe-Geiger classification) (Peel et al., 2007). Agricultural areas are mainly composed of clay-limestone and clay-to-silt soils and annual precipitation usually varies from 700 to 900 mm. Through this survey, we selected eight pairs of fields (agroforestry vs pure crop) growing either winter wheat (*Triticum aestivum* L.) or winter barley (*Hordeum vulgare* L.), half under conventional farming and half under organic farming (Figure 1.9).



Figure 1.9. Map of the agroforestry fields (in green) and their pure crop controls (in yellow) surveyed in May and June 2017 in Gers and Pyrénées-Atlantiques departments. Regarding pairs n° 4 and n°8, the agroforestry field and its pure crop control were distant from 3.7 km and 4.2 km respectively. Figure: © S. Boinot

Each pair of fields was located within the same perimeter, with similar pedoclimatic conditions and surrounding land use. Each pair of fields was also cultivated by the same farmer, with similar crop managements over the three years preceding the study (Table A.1 in Appendix A). No insecticides were used and no-plough tillage was performed by all farmers. 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 A.2 in Appendix A. The agroforestry systems studied here were relatively young (between 2 and 11 years).

3.1.2. Experimental site

A second site was used for the study of invertebrate overwintering, which required very frequent round trips from the research center to the experimentation field. Invertebrate sampling took place from February to June 2018 in seven agroforestry fields from Restinclières

estate (South France, Hérault department), which is characterized by a Mediterranean climate with mild winters and warm summers (Csa climate according to the Köppe-Geiger classification from [Peel et al., 2007](#)) ([Figure 1.10](#)). Trees were planted in 1995 on rows spaced 13 m apart (a list of tree species associated to sampled UVS can be found in [Table A.3](#) in Appendix A, along with the field area covered by UVS). Each field was cultivated by the same farmer, growing winter barley and winter wheat. A ploughing tillage was performed in October 2017, followed by one herbicide treatment (Allié® for broadleaf weeds) and fertilization (ammo nitrates 90U) in February-March 2018. No insecticides were used and UVS, on average two meters wide, were composed of spontaneous vegetation rarely managed (one crush every five to six years, mostly to remove the ash shrubs). Milk thistles (*Sylibum Marianum*) are also removed manually.



Figure 1.10. Map of the agroforestry fields surveyed from February to June 2018 in Restinclières estate, for the study on overwintering invertebrates. Figure: © S. Boinot

3.2. Plant and invertebrate sampling

3.2.1. Production field network

Plants were sampled in alley cropping agroforestry fields (crop alleys and UVS) and pure crop controls in May 2017 in Gers and Pyrénées-Atlantiques departments. In each agroforestry field, UVS were surveyed in three zones distant from 20 m. Each zone was sampled with four 0.25 m² quadrats ([Figure 1.11a](#)) 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, with an accuracy of $\pm 5\%$. 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 consider 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.

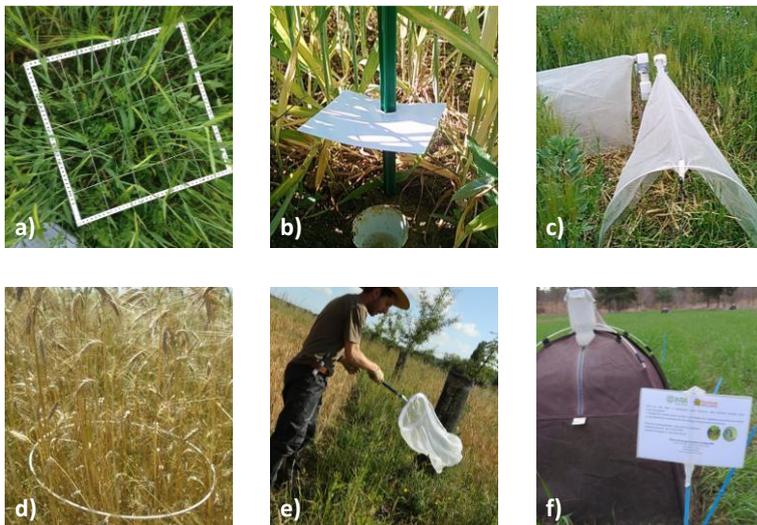


Figure 1.11. Plant and invertebrate sampling methods. **a)** quadrat for plants, **b)** pitfall trap for ground-dwellers (carabid beetles and cursorial spiders), **c)** cornet trap for flying invertebrates (e.g. hoverflies, wild bees, ladybirds), **d)** hoop for grain aphids, parasitoid wasps and hoverfly pupae, **e)** sweep net for hoverflies and wild bees, **f)** emergence trap for overwintering invertebrates. Pictures: © J. Poulmarc’h, D. Mézière, S. Boinot, A. Chabert

The same fields were used for invertebrate sampling in May and June 2017, with different sampling protocols depending on the taxa. Ground-dwelling invertebrates (carabid beetles and cursorial spiders) were sampled with pitfall traps (Figure 1.11b), on three sampling periods in spring 2017 (03/05 - 05/05, 10/05 - 12/05, 05/06 - 07/06). In each agroforestry field, pitfall traps were positioned along three transects distant from 20 m and running perpendicularly to tree rows. These transects were located in the field core, at around 50 m and 100 m from the two nearest field boundaries to exclude their effect on ground-dwelling predators. Each transect was composed by pairs of pitfall traps (distant from 4 m) located in UVS and in both 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 a 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 180 pairs of pitfall traps sampled on three periods. Datasets resulting from the following protocols have not been analyzed yet. Flying invertebrates (e.g. hoverflies, wild bees, ladybirds) were sampled with two cornet traps per field (Sarthou, 2009) (Figure 1.11c), set up during three weeks in one crop alley at nine meters from the sampled UVS (and equivalent location in pure crop controls). Further, grain aphids (*Sitobion avenae*), parasitoid wasps and hoverflies were sampled separately during two distinct periods: peak population growth for aphids and parasitoid wasps, and wheat or barley maturity for hoverflies, to assess the level of biological control. We used a hoop to sample wheat or barley ears (Figure 1.11d), on which we counted aphids and distinguished healthy individuals from mummies (parasitized by wasps). During the second sampling period, we counted hoverfly pupae of *Sphaerophoria scripta* (a specialist predator), whose larvae undergo metamorphosis on the beards of cereals after feeding on 150 aphids on average (Chabert and Sarthou, 2017). Finally, hoverflies and wild bees were also caught with sweep net (Figure 1.11e) on 10m transect in UVS (3 repetitions of 15 minutes), to assess the effect of different plant communities on pollinator activity. All sampling protocols are summarized in Figure 1.12.

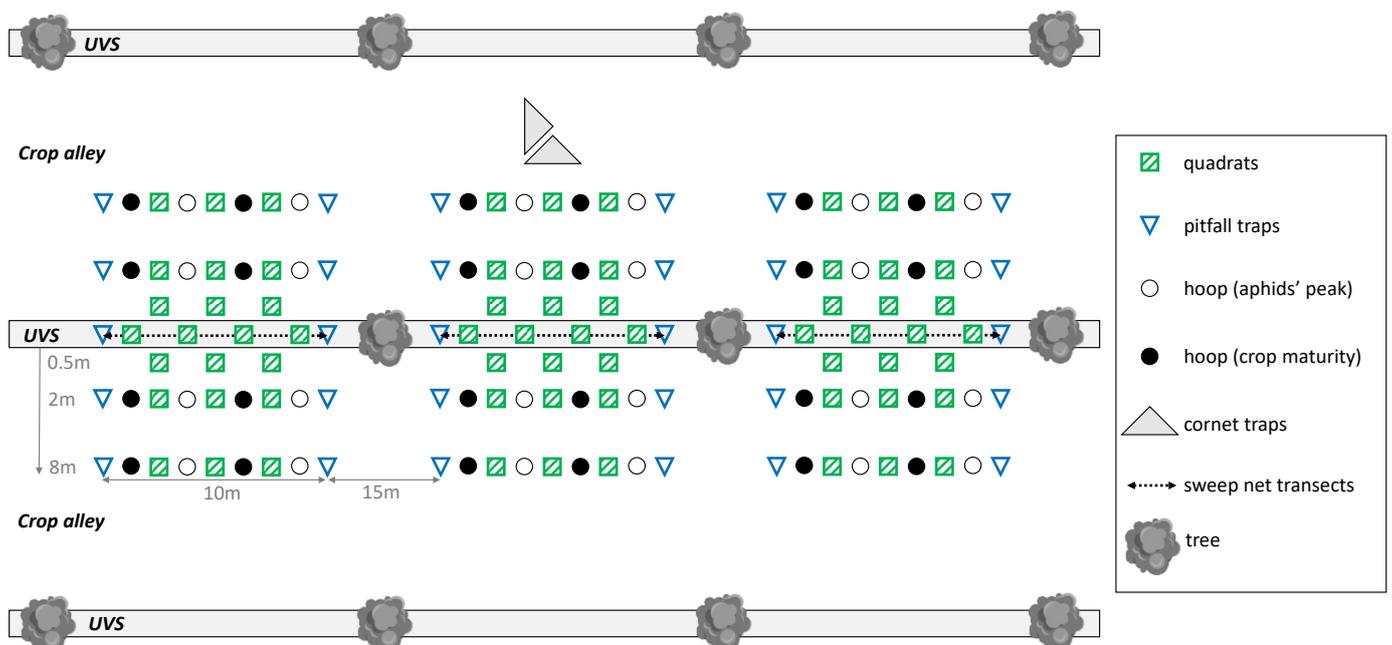


Figure 1.12. Sampling protocols in agroforestry fields in Gers and Pyrénées-Atlantiques departments. The same protocol was used for pure crop controls with the transects placed at equivalent locations in the field in the absence of the understory vegetation strips (UVS).

3.2.2. Experimental site

In Restinclières estate, overwintering invertebrates were sampled from February 16th to June 15th 2018 within 0.36 m² emergence traps buried up to 10 cm into the ground ([Figure 1.11f](#)). Per field, five emergence traps were set up in one UVS and compared to five emergence traps in the adjacent crop alley. Due to damage caused by boars, the dataset was restricted to a total of 51 emergence traps, which were undamaged during the whole experiment (n = 26 in UVS and n = 25 in crop alleys). Each emergence trap contained an aerial trap for flying and climbing invertebrates and a pitfall trap at ground level for ground-dwellers. Traps were filled with propylene glycol and collected every two weeks. All individuals (both adults and larvae) were identified. Families of dominant crop pests and beneficial invertebrates were also recorded. Carabid beetles were identified to the species level. Circulating carabid beetles were also sampled with pitfall traps next to emergence traps but species identification remains to be done.

3.3. Functional trait database

We used functional approaches to better describe both the response of plant and invertebrate communities to agroforestry farming and their effects on ecosystem (dis-)services (e.g. biodiversity conservation, biological control, pollination, organic matter decomposition, yield loss). Lists of selected plant and carabid traits along with their interpretations and sources can be found in [Table 1.1](#) and [Table 1.2](#) respectively.

Table 1.1. Plant 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 / 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)

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

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

Table 1.2. Carabid functional traits related to sensitivity to agricultural disturbances and ecological functions, along with their sources.

Traits	Sensitivity to agricultural disturbances / Ecological functions	Sources
Body length (mm)	<p>Large species, characterized by lower reproductive output and longer growth time, are less tolerant to agricultural intensification such as soil tillage. Smaller carabids are unaffected, or even positively influenced by agricultural intensification (Winqvist et al., 2014; da Silva et al., 2017).</p> <p>The ratio between predator and prey body sizes is often considered as a good predictor of predator-prey dynamics (Rusch et al., 2015). The amount and range of prey consumed increase with increasing carabids body length (Rouabah et al., 2014).</p>	<p>Thiele, 1977; Ribera et al., 1999; Ribera et al., 2001; Woodcock et al., 2010; Jaskuła and Soszyńska-Maj, 2011; Petit et al., 2011; Hedde et al., 2012; Pilon et al., 2013; Birkhofer et al., 2014;</p>
Diet	<p>Predominantly granivorous species are more impacted by local agricultural intensification than carnivorous species because of reduced weed cover and thus reduced resources. Carnivorous species usually hunt prey over larger scales and are more impacted by landscape composition and configuration (Vanbergen et al., 2010; Winqvist et al., 2014; Baulechner et al., 2019).</p> <p>Carnivorous species are important predators of crop pests and granivorous species are weed seed consumers (Kromp, 1999; Bohan et al., 2011).</p>	<p>Homburg et al., 2014; Marrec et al., 2015; Talarico et al., 2016; Hanson et al., 2017</p>
Overwintering stage	<p>Species that hibernate in both larval and adult stages are predominantly found in arable soils whereas species that hibernate in adult stage are often found in field boundaries and need to recolonize field core after emergence (Holland et al., 2009).</p> <p>Overwintering larvae in arable fields could favor early (thus more effective) regulation of crop pests (Holland et al., 2009).</p>	

CHAPTER 2

Alley cropping agroforestry systems: Reservoirs for weeds or refugia for plant diversity?

« Plants tagged as weeds belong to every botanical group from simple algae to rainforest trees. But they have at least one behavioural quality in common. Weeds thrive in the company of humans. They aren't parasites, because they can exist without us, but we are their natural ecological partners, the species alongside which they do best. They relish the things we do to the soil: clearing forests, digging, farming, dumping nutrient-rich rubbish. They flourish in arable fields, battlefields, parking lots, herbaceous borders. They exploit our transport systems, our cooking adventures, our obsession with packaging. [...] We've had a symbiotic relationship with many of them, a partnership from which we benefit as much as the plants. [...] Weeds made the first vegetables, the first home medicines, the first dyes. »

Richard Mabey

Weeds: The Story of Outlaw Plants

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Abstract

1. 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.
2. 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.
3. 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.
4. 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.
5. 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 SNH.

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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 SNH such as woodlots, grasslands, hedges and field boundaries (Stoate et al., 2001). Since then, many studies have demonstrated that SNH 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 SNH 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 SNH 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 SNH. 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 SNH 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 SNH 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., 2019b](#)). 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 established 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., 2019b](#)). Among agroforestry systems, alley cropping agroforestry, in which arable crops are grown between tree rows, represents a great opportunity for the reintegration of SNH within fields. Indeed, the presence of trees rows leads to increased edges amount and field fragmentation, which is expected to enhance ecosystem (dis-)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 2.1](#)). UVS are poorly disturbed by crop management and so are comparable to other linear SNH 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. \(2019b\)](#) 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 pedoclimatic conditions and surrounding land use (Figure 1.9). Each pair was also cultivated by the same farmer, with similar crop managements over the three years preceding the study (Table A.1 in Appendix A). 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 A.2 in Appendix A. 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 2.1), with an accuracy of $\pm 5\%$. 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.

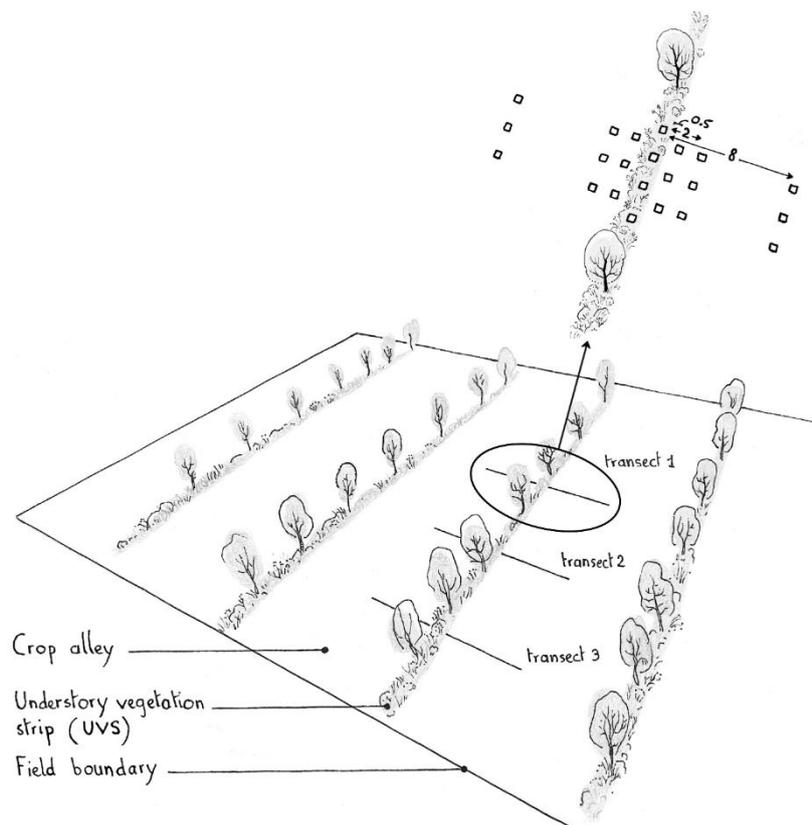


Figure 2.1. The principal compartments of alley cropping agroforestry systems and the sampling protocol used for the vegetation survey. Picture: © C. Malard

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 1.1](#)) 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 Gerçoise, 2003](#)).

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](#)) :

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

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 B.1](#) in Appendix B) 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 seed bank of crop alleys (the relative coverage of these two groups can be seen in [Figure B.1](#) in Appendix B). 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, \dots, 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 2.1). 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 $(Y \times (N - 1) + 0.5) / N$ 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* spp., *Avena* spp., *Lolium* spp. and *Convolvulus arvensis*. A list of all species recorded along with their occurrences in each habitat is given in Table B.1 in Appendix B.

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 2.2a](#)). 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 2.2b](#)). 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.

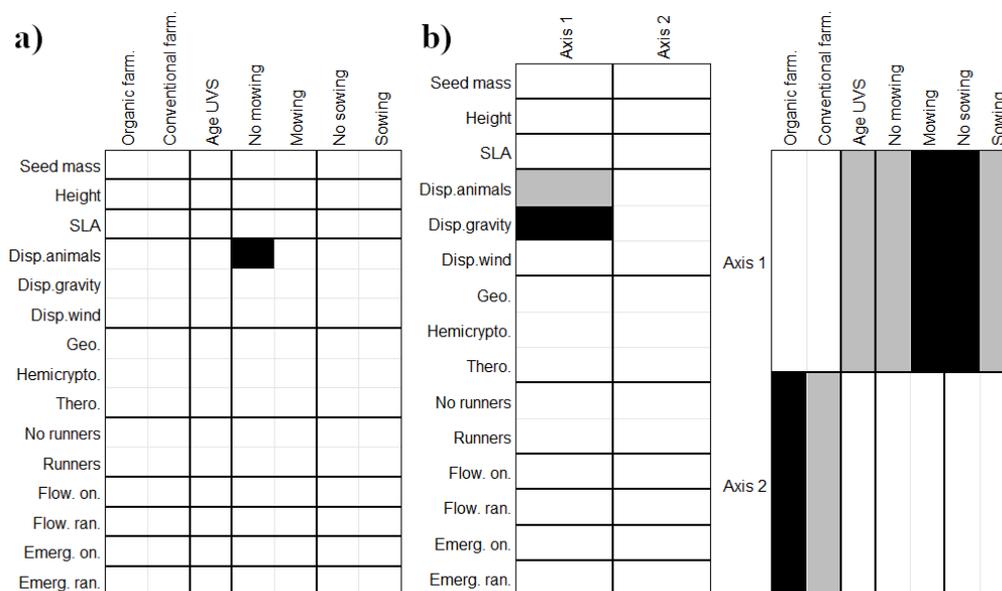


Figure 2.2. (a) Results of the fourth-corner analysis performed on dominant species of plant communities located in the understory vegetation strips (UVS). (b) Results of the fourth-corner analysis testing the link between RLQ axes and traits and environmental variables. Black cells correspond to positive significant relationships while grey 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 2.4a](#)). 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 2.4b](#) and [Figure 2.4c](#)) are given in [Table B.3](#) in Appendix B, 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 2.3a](#)). Testing the link between RLQ axes and traits or environment ([Figure 2.3b](#)) 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 2.4a](#)). These are barochorous species dispersing by means of runners. They emerge later and have relatively larger flowering ranges.

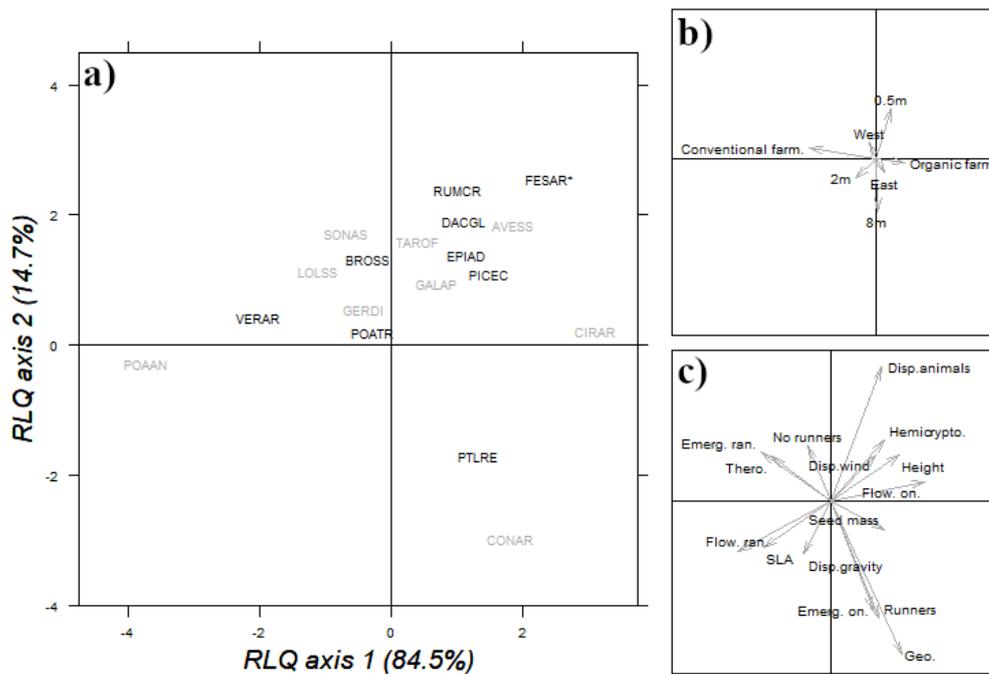


Figure 2.4. RLQ analysis performed on plant communities *located in the crop alleys*. Results are given on the first two axes for **(a)** species' scores, **(b)** environmental variables' loadings, and **(c)** traits' loadings. Only species that were dominant in the understory vegetation strips were considered, therefore eliminating rare species and arable weed species persisting mostly in the seed bank 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 B.1](#) in Appendix B.

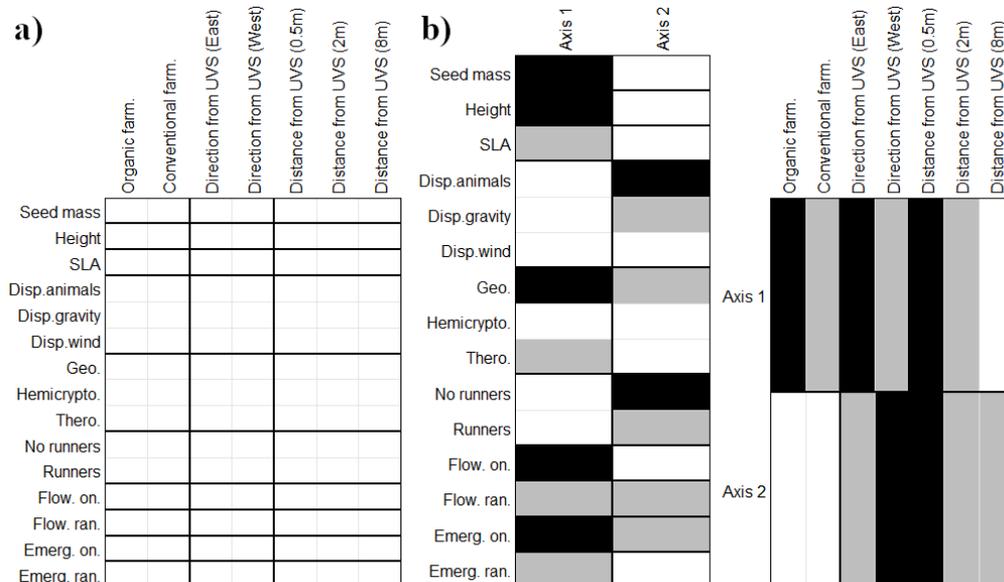


Figure 2.3. **(a)** Results of the fourth-corner analysis performed on plant communities *located in the crop alleys*, restricted to the set of species that were also dominant in the understory vegetation strips (UVS). **(b)** Results of the fourth-corner analysis testing the link between RLQ axes and traits and environmental variables. Black cells correspond to positive significant relationships while grey 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 2.1). As a consequence, weed-crop ratio was much lower in conventional fields (on average -36% per quadrat) (Table 2.1). In conventional fields, crop and weed coverage along with weed-crop ratio were similar between crop alleys and pure crop controls (Figure 2.5, Table B.4 in Appendix B). 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 2.5, Table B.4 in Appendix B). 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 B.5 and Figure B.3 in Appendix B). However, no effect of the distance from UVS was detected in organic fields.

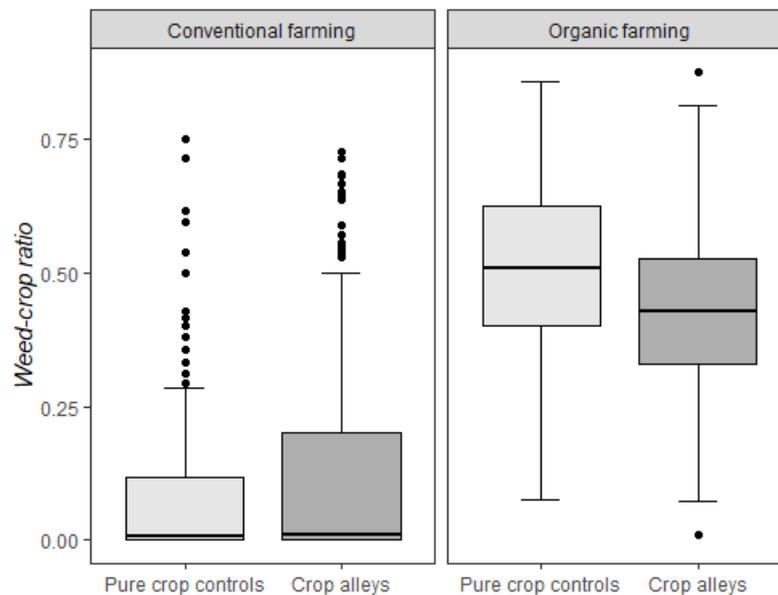


Figure 2.5. Comparison of weed-crop ratio (i.e. weed coverage / weed and crop coverage), used as a proxy for the potential harmfulness of weed communities, between pure crop controls and crop alleys, under conventional vs organic farming. See Table B.4 in Appendix B for detailed outputs of GLMMs.

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 2.1). 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 (Figure 2.6a, Figure 2.6b, Figure 2.6c). By contrast, UVS supported a richer and more abundant flora than cropped areas, containing both agrotolerant and hemerophobic species (Figure 2.6a, Figure 2.6b). On the other hand, in organic fields the coverage of both agrotolerant and hemerophobic communities was higher in the UVS (Figure 2.6a). Species richness of both agrotolerant and hemerophobic communities was similar between pure crop controls, crop alleys and UVS (Figure 2.6b). Evenness of agrotolerant and hemerophobic communities was higher in cropped areas (pure crop controls and crop alleys) than in UVS (Figure 2.6c). Evenness of hemerophobic communities was even higher in crop alleys than in pure crop controls (Figure 2.6c). The effect of the distance from UVS on plant diversity was significant only in conventional fields (see Table B.5 in Appendix B). 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 these variables remained constant regarding agrotolerant communities (see Figure B.4 in Appendix B).

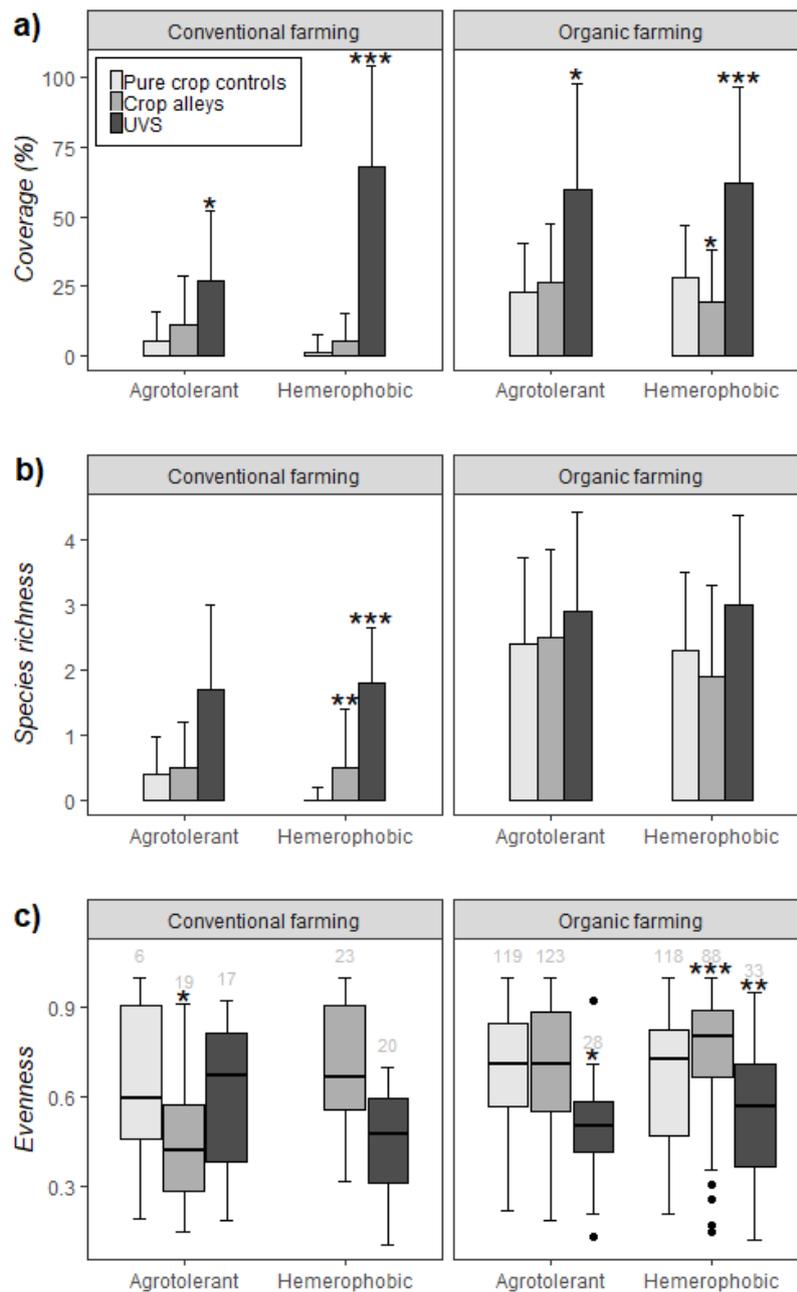


Figure 2.6. Comparison of the variables considered for the assessment of plant diversity between habitats (pure crop controls, crop alleys, understory vegetation strips). Stars indicate significant difference at 0.05 threshold based on p-values of GLMMs comparing these variables between pure crop controls (taken as reference) and agroforestry systems (crop alleys and understory vegetation strips), under conventional and organic farming. See [Table B.4](#) in Appendix B for detailed outputs of GLMMs.

Table 2.1. 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 (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

Response variables			Main terms		Interactions with farming system		
			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	$n = 282$	–	–	–	–	–

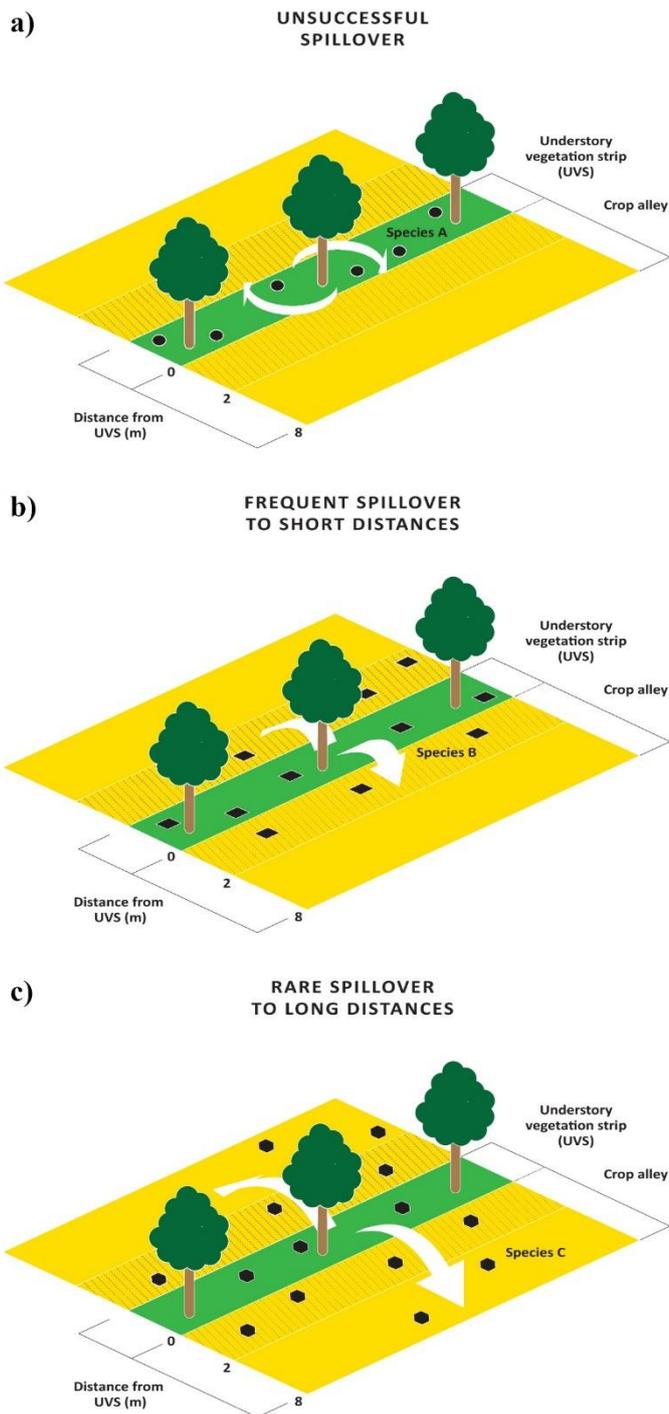


Figure 2.7. Plant spillover from UVS to crop alleys in alley cropping agroforestry systems.

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 seed bank 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 B.2 in Appendix B). 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* spp. and *Anisantha* spp., 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 SNH, 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 SNH 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 SNH ([Bischoff, 2005](#)). Moreover, agricultural disturbances reduce the ecological niches available in arable fields for plants coming from SNH ([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 SNH 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 SNH 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 SNH, 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 SNH (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 *Galium aparine*, *Avena* spp. and *Anisantha* spp., 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 B.2 in Appendix B), 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 seed bank, 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 UVS towards crop alleys had a very weak impact on the potential harmfulness of weed communities. We also revealed a high potential of UVS, 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.

CHAPTER 3

Distribution of overwintering invertebrates in temperate agroforestry systems: Implications for biodiversity conservation and biological control

« Although most insects in temperate climates spend a large proportion of their life in an overwintering stage [...] the study of insect overwintering has, in many cases, been surprisingly neglected. Perhaps this is a reflection of the fact that many entomologists, like the majority of the insects they study, spend the long cold winter months carefully insulated from the outside world »

S. R. Leather, K. F. A. Walters and J. S. Bale
The Ecology of Insect Overwintering

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Abstract

1. The dramatic decline of invertebrates at a global scale is mainly driven by habitat loss, agricultural intensification and urbanization. Alley cropping agroforestry is a land use practice in which arable crops are grown between tree rows. In such systems, understory vegetation strips (UVS) develop in the tree rows, providing habitats undisturbed by soil tillage. We investigated whether UVS are major overwintering habitats for invertebrates. We focused on carabid communities, which are dominant beneficial invertebrates in crop fields, but suffer from agricultural intensification.
2. We described carabid communities with functional traits related to sensitivity to agricultural disturbances and ecological functions (i.e. pest control). Sampling of invertebrates were carried out from February to June 2018 over seven agroforestry fields in Restinclières estate (South France), one of the oldest experimental sites in Europe.
3. The study revealed that 55% of invertebrate taxonomic groups were more abundant in UVS, whereas only 14% were more abundant in crop alleys.
4. Crop pests were overwintering mainly in crop alleys while beneficial invertebrates were more dependent on UVS.
5. Finally, UVS hosted carabids sensitive to agricultural disturbances, characterized by large body length, predominantly granivorous diet and overwintering in adult stage. On the other hand, crop alleys were home to smaller carnivorous species overwintering in both larval and adult stages, which can tolerate high levels of disturbance.
6. Environmental and agricultural policies should consider agroforestry systems, especially UVS, as valuable habitats for biodiversity conservation and biological control in agricultural landscapes.

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1. Introduction

The dramatic decline of invertebrates at a global scale is mainly driven by habitat loss and conversion to intensive agriculture and urbanization (Habel et al., 2019; Sánchez-Bayo and Wyckhuys, 2019). SNH are of major importance for the survival of invertebrates, especially by offering them resources and overwintering habitats undisturbed by soil tillage (Pywell et al., 2005; Mallinger et al., 2016). Indeed, ploughing significantly reduces the emergence of many invertebrates (Holland and Reynolds, 2003; Ganser et al., 2019). Moreover, the success of hibernation is a key factor driving the population dynamics in crops during spring and summer (Leather et al., 1993). Thus, overwintering success of invertebrates in uncropped habitats has a direct influence on the conservation of higher trophic taxa such as birds and mammals, by conditioning resource availability. The presence of suitable overwintering habitats also has an impact on the agroecosystem functioning. It can reduce crop yields if it promotes the spillover of emerging crop pests within fields, or conversely increase crop yields if it favors the dispersal of beneficial invertebrates such as pollinators and predators of crop pests (Blitzer et al., 2012). AEI are more and more established for reconciling crop production with the conservation of biodiversity and the ecosystem services it provides. For example, sown grass strips, wildflower strips and conservation headlands can take place in field margins, providing resources and overwintering habitats for invertebrates (Smith et al., 2008; Feltham et al., 2015; Ganser et al., 2019). Although these measures reduce the surface available for crop production, it can even lead to higher yields and economic profitability by promoting the dispersal of beneficial invertebrates within crops (Pywell et al., 2015), making production and biodiversity conservation compatible. However, if cropland dominates in the landscape, AEI at field edges might not be sufficient for biodiversity conservation and promotion of ecosystem service flows in cropland (Mitchell et al., 2015). Then, establishment needs to take place within fields themselves, as in the case of within-field wildflower strips that support natural enemies of crop pests (Hatt et al., 2017).

Agroforestry is a land use practice integrating woody vegetation (trees or shrubs) with crop and/or animal production systems. Such systems have been shown to provide a wide range of ecosystem services from the same area of land, such as sustainable food, timber 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., 2019b). In temperate regions, alley cropping agroforestry systems, in which arable crops are grown between tree rows, represent a great opportunity for the reintegration of SNH directly within fields. Indeed, the presence of tree rows entails the growth of understory vegetation strips (UVS) that are not disturbed by soil tillage. However, only a few studies have assessed the potential of alley cropping systems for enhancing biodiversity, most of them revealing promising results (Peng et al., 1993; Burgess, 1999; Stamps et al., 2002; Akbulut et al., 2003; Naeem et al., 2010; Smits et al., 2012; Varah et al., 2013), and even less have focused on the ecological functions of UVS. Boinot et al. (2019a) showed that UVS constitute refugia for plant diversity, harboring species that are poorly tolerant to agricultural disturbances. Recent studies revealed that abundance and diversity of woodlice and millipedes (Pardon et al., 2019b) and earthworms (Cardinael et al., 2019) were higher in UVS than in adjacent crop alleys. Yet these results were obtained in spring and to our knowledge, no study has described the distribution of overwintering invertebrates in agroforestry systems and assessed the potential of UVS in promoting successful overwintering of a wide range of invertebrates.

The objective of this study was to investigate the importance of UVS associated to tree rows in promoting successful overwintering of invertebrates within agroforestry fields, as opposed to crop alleys that are disturbed by soil tillage (in non-conservation agricultural systems). We also identified families of crop pests and beneficial invertebrates that were dominant during the survey. We gave a focus on carabid communities because (i) they suffer from agricultural intensification and can be used as bioindicators (Rainio and Niemelä, 2003; Brooks et al., 2012), (ii) they are common prey for other invertebrates, birds, micro-mammals, reptiles and amphibians (Holland, 2002; Larochelle and Larivière, 2003), (iii) they are important predators of crop pests and weed seed consumers (Kromp, 1999; Bohan et al., 2011) and (iv) knowledge on carabid communities in agroforestry systems is currently poor (but see Martin-Chave et al., 2019; Pardon et al., 2019b; Richard et al., 2019). We hypothesized that **1**) for most taxonomic groups, UVS are better overwintering habitats than crop alleys that are disturbed by soil tillage, which reduces the emergence of many invertebrates. Moreover, we hypothesized that **2**) crop pests successfully overwinter in crop alleys whereas beneficial invertebrates tend to be more dependent on UVS, because so-called “r-strategist” characterized by smaller size, shorter life-cycle and higher fecundity are

generally performing better than “K-strategist” in highly disturbed habitats (Thomas et al., 1992; Schirmel et al., 2016). Finally, we expected that **3**) UVS are overwintering refugia for carabid species that are sensitive to agricultural disturbances, which are characterized by a unique overwintering stage (adult), large size and mixed diet (Table 1.2). On the other hand, small and exclusively carnivorous carabids that overwinter at both larval and adult stages can successfully spend the winter in disturbed crop alleys.

2. Materials and methods

2.1. Study site

The study was conducted over seven agroforestry fields, in Restinclières estate (South France, Hérault department), which is characterized by a Mediterranean climate with mild winters and warm summers. Trees were planted in 1995 in rows spaced 13 m apart (a list of tree species associated to sampled UVS can be found in Table A.3 in Appendix A, along with the area covered by UVS). All fields were cultivated by the same farmer, growing winter barley and winter wheat during the study (crop rotation is composed of winter wheat, winter barley and winter pea). Between crop harvest in summer and following sowing in autumn, crop alleys were dominated by spontaneous vegetation. A ploughing tillage was performed in October 2017, followed by one herbicide treatment and fertilization in February-March 2018. No insecticides were used and UVS, on average two meters wide, were composed of spontaneous vegetation rarely managed (one crush every five to six years).

2.2. Invertebrate sampling

Overwintering invertebrates were sampled from February 16th to June 15th within 0.36 m² emergence traps buried up to 10 cm in the ground. Per field, five emergence traps at least 10 m apart were set up in one UVS and compared to five emergence traps in the adjacent crop alley (Figure 3.1). Due to damage caused by boars, the dataset was restricted to a total of 51 emergence traps, which were undamaged during the whole experiment (n = 26 in UVS and n = 25 in crop alleys). Each emergence trap contained an aerial trap for flying and climbing

invertebrates and a pitfall trap at ground level for ground-dwellers. Traps were filled with propylene glycol and collected every two weeks. All individuals found within traps (whether they were adults or larvae) were identified to the order level using the guide from [Chinery \(2012\)](#). Families of dominant crop pests and beneficial invertebrates were also recorded. Adult carabid beetles were identified to the species level using [Jeannel \(1941\)](#), [Jeannel \(1942\)](#), [Coulon et al. \(2011a\)](#) and [Coulon et al. \(2011b\)](#).



Figure 3.1. Emergence traps used for sampling overwintering invertebrates in agroforestry fields (Restinclières estate, South France, Hérault department).

2.3. Functional structure of overwintering carabid communities

We used a functional approach to describe the dominant life strategies in crop alleys vs UVS, but also to assess the nature and intensity of ecosystem services provided by carabid communities in each habitat. We described overwintering carabid communities with functional traits related to sensitivity to agricultural disturbances and ecological functions (i.e. crop pest control) ([Table 1.2](#)). Functional trait values were collected in databases ([Hedde et al., 2012](#); [Homburg et al., 2014](#)) and through an extensive research in literature ([Thiele, 1977](#); [Ribera et al., 1999](#); [Ribera et al., 2001](#); [Woodcock et al., 2010](#); [Jaskuła and Soszyńska-Maj, 2011](#); [Petit et al., 2011](#); [Pilon et al., 2013](#); [Birkhofer et al., 2014](#); [Marrec et al., 2015](#); [Talarico et al., 2016](#); [Hanson et al., 2017](#)).

Community-weighted mean (CWM) and functional divergence (FDvar) of each trait were then computed for carabid communities sampled in each emergence trap, following [Garnier and Navas \(2012\)](#) and [Schleuter et al. \(2010\)](#). Formulas are given in [Table C.1](#) in Appendix C. CWM corresponds to the average of trait values weighted by the relative abundance of each species. FDvar is an expression of the variance of trait values within a community, weighted by the relative abundance of each species. FDvar varies from 0 to 1; it is low if species and/or abundances are clustered around the mean trait value, whereas it is high if they are clustered towards one or both margins of the trait distribution. This metric is relevant for assessing to what extent functional attributes are constrained by natural or anthropogenic selection, but also for assessing complementarity between species ([Woodcock et al., 2019](#)). Regarding biological control, it is expected that predator communities characterized by different ecological strategies (i.e. non-overlapping trait distributions) control more efficiently a wide range of crop pests.

2.4. Data analysis

To assess hypotheses 1 and 2, we used generalized linear mixed effects models (GLMMs) and compared the total density of each taxonomic group per emergence trap between UVS and crop alleys. Fields were included as a random effect on the intercept to take into account the spatial auto-correlation between emergence traps located in a same field. To assess hypothesis 3, we described the functional structure of carabid communities with traits related to sensitivity to agricultural disturbances. GLMMs were used to compare CWM and FDvar of each trait between UVS and crop alleys. Density (individuals / m²) and species richness were assumed to follow a Poisson distribution, CWM of body length was assumed to follow a Gaussian distribution and all other variables (proportional CWM and FDvar varying from 0 to 1) were assumed to follow a Beta distribution. When proportional variables included 0 and/or 1 value(s), the transformation $(Y \times (N - 1) + 0.5) / N$ was employed following [Zuur et al. \(2013\)](#), where Y is the response variable and N is the sample size. We used the package lme4 for fitting Gaussian GLMMs ([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 over-dispersion, Conway-Maxwell-Poisson GLMMs were fitted instead as

suggested by Lynch et al. (2014). All figures were built using raw data. All analyses were performed using the statistical software R 5.1 (R Core Team, 2018).

3. Results

Many taxonomic groups of invertebrates were found during the survey, with huge differences in abundance and relative proportion: Homoptera ($n = 46441$, 47%), Coleoptera ($n = 13324$, 13%), Diptera ($n = 12466$, 13%), Hymenoptera ($n = 8187$, 8%), Collembola ($n = 7907$, 8%), Myriapoda ($n = 2257$, 2%), Araneae ($n = 1885$, 2%), Isopoda ($n = 1778$, 2%), Stylommatophora ($n = 1429$, 1%). There were also other groups below 1%: Acarina ($n = 785$), Dermaptera ($n = 762$), Heteroptera ($n = 528$), Orthoptera ($n = 354$), Psocoptera ($n = 323$), Blattoptera ($n = 239$), Lepidoptera ($n = 172$), Opiliones ($n = 75$), Neuroptera ($n = 21$), Pseudoscorpionida ($n = 19$), Thysanoptera ($n = 14$), Thysanura ($n = 5$), Trichoptera ($n = 4$), Megaloptera ($n = 2$). Density differences between UVS and crop alleys could not be statistically tested for Thysanura, Trichoptera and Megaloptera because too few individuals were captured. This was also the case for Apoidae family ($n = 3$). Regarding carabid beetles, a total of 1538 individuals belonging to 50 species were collected.

3.1. Overwintering invertebrates in crop alleys and understory vegetation strips

Out of the 22 invertebrate taxonomic groups found during the survey, 12 were more abundant in UVS whereas only 3 were more abundant in crop alleys (Table 3.1, Figure 3.2).

Table 3.1. Results of Conway-Maxwell-Poisson GLMMs comparing invertebrate density (individuals / m²) between crop alleys (reference level) and understory vegetation strips.

	Estimate	SE	d.f.	z-value	p-value
Coleoptera (tot.)	-0.33	0.106	47	-3.160	0.002
<i>Carabidae</i>	-0.33	0.148	47	-2.213	0.027
<i>Staphylinidae</i>	-0.76	0.182	47	-4.180	< 0.001
<i>Coccinellidae</i>	1.65	0.292	47	5.653	< 0.001
<i>Elateridae</i>	-1.39	0.362	47	-3.835	< 0.001
Diptera (tot.)	-0.27	0.158	47	-1.700	0.089
<i>Syrphidae</i>	-3.29	0.847	47	-3.885	< 0.001
Hymenoptera (tot.)	0.47	0.142	47	3.289	0.001
<i>Formicidae</i>	0.71	0.221	47	3.188	0.001
Homoptera (tot.)	-4.74	0.313	47	35.350	< 0.001
<i>Aphidae</i>	-5.17	0.313	47	-16.500	< 0.001
Neuroptera (tot.)	2.47	0.629	47	3.918	< 0.001
<i>Chrysopidae</i>	2.28	0.634	47	3.599	< 0.001
Heteroptera	3.25	0.274	47	11.857	< 0.001
Collembola	0.56	0.114	47	4.863	< 0.001
Dermoptera	-0.31	0.262	47	-1.201	0.230
Psocoptera	4.57	0.515	47	8.882	< 0.001
Orthoptera	-0.06	0.331	47	-0.182	0.856
Lepidoptera	1.59	0.236	47	6.731	< 0.001
Blattoptera	2.43	0.344	47	7.080	< 0.001
Thysanoptera	-0.18	0.467	47	-0.387	0.698
Myriapoda	-1.11	0.211	47	-5.237	< 0.001
Isopoda	0.36	0.183	47	1.984	0.047
Araneae	1.43	0.145	47	9.822	< 0.001
Opiliones	2.82	0.470	47	5.997	< 0.001
Acarina	1.49	0.279	47	5.325	< 0.001
Pseudoscorpionida	3.12	0.740	47	4.215	< 0.001
Stylommatophora (tot.)	-0.20	0.187	47	-1.094	0.274
<i>Snails</i>	1.62	0.318	47	5.106	< 0.001
<i>Slugs</i>	-1.14	0.196	47	-5.833	< 0.001

SE: standard error of the estimates, d.f.: degrees of freedom

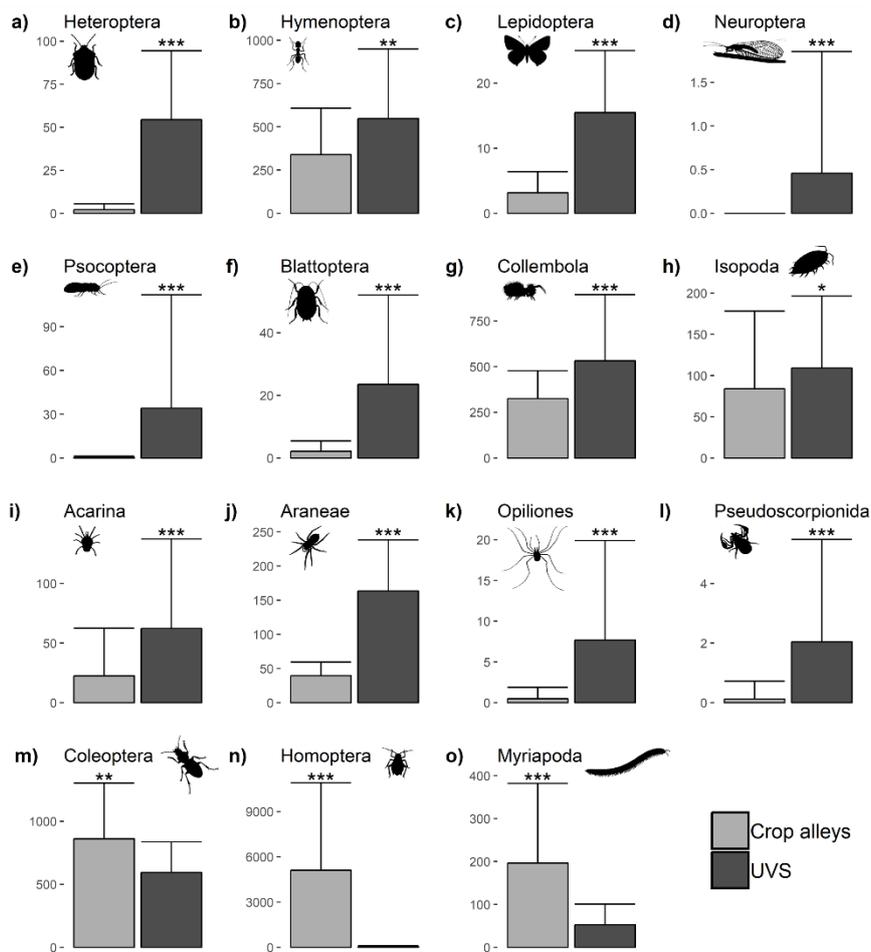


Figure 3.2. Mean and standard deviation of group density (individuals / m²) in crop alleys and understory vegetation strips (UVS). Only groups showing significant differences in density between habitats were represented (see Figure C.1 in Appendix C for other groups). Stars indicate significant difference between crop alleys and UVS at 0.05 threshold based on p-values of GLMMs (* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001).

3.2. Overwintering of crop pests vs beneficial invertebrates

Crop pests (i.e. Aphidae, Elateridae and slugs) overwintered predominantly in crop alleys (Table 3.1, Figure 3.3). On the other hand, snails were more abundant in UVS. The response was less dichotomic for the families of beneficial invertebrates considered in this study. Coccinellidae, Formicidae and Chrysopidae overwintered mostly in UVS, whereas Carabidae, Staphylinidae and Syrphidae were more abundant in crop alleys.

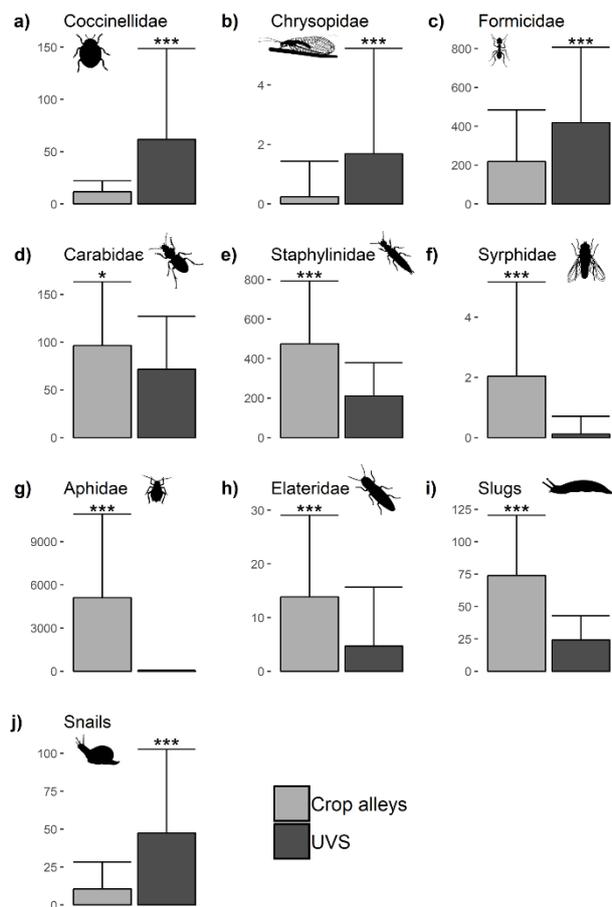


Figure 3.3. Mean and standard deviation of dominant crop pest and beneficial invertebrate density (individuals / m²) in crop alleys and understory vegetation strips (UVS). Stars indicate significant difference between crop alleys and UVS at 0.05 threshold based on p-values of GLMMs (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

3.3. Functional structure of overwintering carabid communities

There was a clear shift in the functional structure of carabid communities between habitats in agroforestry systems. UVS hosted larger carabids than crop alleys (Table 3.2, Figure 3.4). Crop alleys hosted mainly carnivorous species, such as *Trechus quadristriatus*, *Metallina lampros* and *Apotomus rufus*, whereas predominantly granivorous species, such as *Ophonus azureus*, *Parophonus mendax* and *Harpalus dimidiatus*, were clearly associated to UVS (Table 3.2, Figure 3.4, see Figure C.2 in Appendix C for the analysis of species composition). The response was more variable for omnivorous species; *Brachinus crepitans* and *Scybalicus oblongiusculus* were associated to UVS whereas *Phyla obtusa* was more abundant in crop alleys and *Pseudophonus rufipes* was found equally in both habitats. Finally, CWM and FDvar of overwintering stages were respectively close to 1 and 0 in UVS, indicating that species overwintering in adult stage were strongly dependent on the presence of UVS (Table 3.2,

Figure 3.4). On the other hand, species overwintering in both larval and adult stages were found in high abundances in crop alleys.

Table 3.2. Results of GLMMs comparing species richness and functional structure of carabid communities between crop alleys (reference level) and understory vegetation strips.

	Distribution	Estimate	SE	d.f.	z/t-value	p-value
Species richness	Poisson	-0.11	0.098	48	-1.155	0.248
Body length						
CWM	Gaussian	1.54	0.429	44	3.595	< 0.001
FDvar	Beta	0.08	0.249	47	0.316	0.752
Diet						
CWM	Beta	-0.52	0.241	47	-2.145	0.032
FDvar	Beta	0.29	0.176	47	1.658	0.097
Overwintering stage						
CWM	Beta	1.02	0.239	47	4.245	< 0.001
FDvar	Beta	-0.92	0.191	47	-4.841	< 0.001

SE: standard error of the estimates, d.f.: degrees of freedom

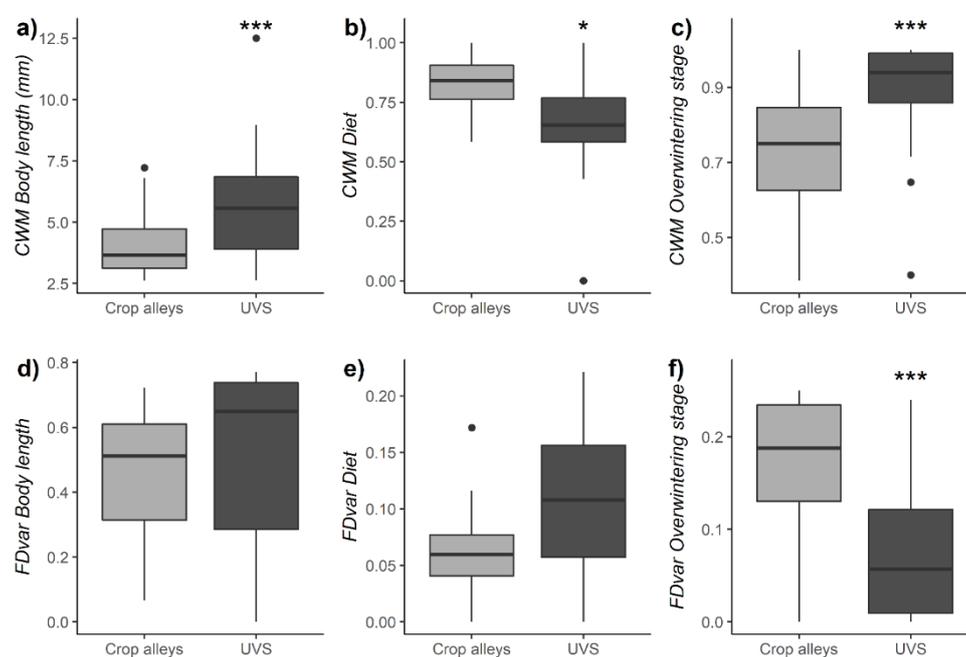


Figure 3.4. Functional structure of carabid communities overwintering in crop alleys vs understory vegetation strips (UVS). **(a)** Community-weighted mean (CWM) of body length; **(b)** CWM of diet (granivorous: 0, omnivorous: 0.5 and carnivorous: 1); **(c)** CWM of overwintering stage (overwintering in both larval and adult stages: 0, overwintering in adult stage: 1); **(d)** Functional divergence (FDvar) of body length; **(e)** FDvar of diet; **(f)** FDvar of overwintering stage. Stars indicate significant difference at 0.05 threshold based on p-values of GLMMs (* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001).

4. Discussion

Our study on the distribution of overwintering invertebrates in alley cropping agroforestry systems revealed that UVS are home to a wide range of overwintering invertebrates, as opposed to crop alleys. Crop pests overwintered predominantly in crop alleys while beneficial invertebrates were often associated to UVS. Moreover, carabid species that are sensitive to agricultural disturbances were overwintering mostly in UVS.

4.1. Understory vegetation strips provide overwintering habitats for many invertebrates

Even if UVS are surrounded by crop alleys, with potential disturbances induced by pesticide and fertilizer drifts, our results show that UVS are SNH of major importance for invertebrate conservation. Indeed, 55% of the taxonomic groups of invertebrates found during the survey were more abundant in UVS whereas only 14% were more abundant in crop alleys. This is in line with previous studies showing that SNH provide suitable habitats for overwintering invertebrates (Sotherton, 1984; Pfiffner and Luka, 2000; Pywell et al., 2005; Geiger et al., 2009; Schaffers et al., 2012; Sutter et al., 2017). Butterflies, characterized by a high degree of host-plant specialization and sensitivity to habitat degradation, are drastically declining in many European countries (van Strien et al., 2019). Lepidoptera (butterflies and moths confounded) were more abundant in UVS, indicating that this habitat has higher environmental quality than crop alleys. Detritivores (Collembola, Isopoda, some Acarina and Blattoptera) were also more abundant in UVS, which is not surprising given the permanent litter quantity available at the ground level, although Myriapoda (Diplopoda and Chilopoda confounded) were more abundant in crop alleys. All Arachnida groups found during the survey (Acarina, Araneae, Opiliones and Pseudoscorpionida) were overwintering in great majority in UVS. Araneae are not able to dig into the soil to find refuges and rely on the presence of vegetation and crevices for overwintering (Lemke and Poehling, 2002). This seems to be the case for Opiliones too, which are favored by the presence of grassy field margins in spring and autumn (Holland et al., 2016). However, Apoidae did not seem to overwinter in UVS, neither in crop alleys. They probably preferred overwintering habitats located outside the fields, such as grasslands and

scrublands, which are very diversified in Restinclières estate (Smits et al., 2012). UVS cover about 3 to 13% of the available agricultural area and thus greatly enhance the conservation of plants (Boinot et al., 2019a) and invertebrates directly within crop fields. Moreover, trees and shrubs associated to UVS were not sampled in this study, but are very likely to offer permanent overwintering habitats for invertebrates (Dix et al., 1995; Stamps and Linit, 1998). Further studies should assess to what extent improved plant and invertebrate resources in agroforestry systems favor higher trophic taxa such as threatened farmland species (Donald et al., 2001; Fischer et al., 2011b).

4.2. Crop pests and beneficial invertebrates are not equally dependent on undisturbed habitats for overwintering

Overall, beneficial invertebrates were more dependent on UVS for overwintering, considering groups composed in majority of detritivore species (Collembola, Isopoda, Acarina, Blattoptera and Myriapoda), predators (Araneae, Opiliones, Carabidae, Staphylinidae, Syrphidae, Chrysopidae, Coccinellidae) and weed controllers (predominantly granivorous carabids and harvester ants). However, Syrphidae, Carabidae and Staphylinidae were more abundant in crop alleys. We found only two species of Syrphidae: *Episyrphus balteatus* and *Sphaerophoria scripta*. Raymond et al. (2014) showed that these aphidophagous syrphid species mainly overwinter in crop fields whereas non aphidophagous species are associated to field margins. Many species of Carabidae and Staphylinidae are also major predators of aphids (Sunderland and Vickerman, 1980), which could explain their higher presence in crop alleys, where aphids were overwintering. On the other hand, lacewings (aphid predators) were found in UVS. Coccinellidae, both carnivorous species such as *Scymnus* spp. and mycophagous ones such as *Psyllobora vigintiduopunctata*, mostly overwintered in UVS in aggregated groups. Formicidae, which can control crop pests, weeds and plant diseases depending on the species (Offenberg, 2015), were also more abundant in UVS.

On the other hand, crop pests overwintered predominantly in crops, which could explain higher probability of pest outbreaks when suitable overwintering habitats for predators are missing (Bianchi et al., 2006; Rusch et al., 2016). Homoptera were much more abundant in crop alleys, a result driven by aphids that probably reproduced under the emergence traps and benefited from their protection. Elateridae and slugs were also overwintering predominantly in crop alleys. Griffiths et al. (1998) showed that slugs were more abundant in agroforestry fields than in pure crop controls, however our results suggest that this would not be due to the presence of less disturbed overwintering habitats in agroforestry fields. Slugs might rather have been favored by a more suitable microclimate in agroforestry fields. Finally, snails were the only dominant crop pest more abundant in UVS.

It is likely that species overwintering in UVS are strongly dependent on SNH for overwintering and thus poorly represented in the field core of pure crops. Indeed, many studies have shown that habitats such as hedges, wildflower strips or grassy field margins provide more suitable overwintering habitats than arable land (e.g. Pfiffner and Luka, 2000; Ganser et al., 2019). This explains why so-called “edge-effects” or “edge-biased distribution” are frequently observed among invertebrates, resulting in decreased abundance and diversity in the field core (Rand et al., 2006; Nguyen and Nansen, 2018). The great extent and spatial configuration of UVS could promote the spillover of many invertebrates between cropped and uncropped habitats, especially regarding poorly dispersive species that hardly move between field edges and field cores, such as some Carabidae species (e.g. *Amara* species, *Metallina lampros*) and spiders of the Lycosidae family (Holland et al., 1999). Then, a wide range of overwintering predators, from specialist to generalist and from ground-dwelling to aerial ones, would improve biological control in agroforestry systems through a process of complementarity and additive effects (Woodcock et al., 2016). On the other hand, if intraguild predation or competition is enhanced, this could reduce the efficiency of predator community to control crop pests, although field studies generally contradict this hypothesis (Woodcock et al., 2016). Finally, SNH have also been shown to have negative impacts on the dispersal of invertebrates, especially agrobiont ones, either by acting as a sink habitat or a physical barrier (Holland et al., 2009). Further studies are thus needed to assess the positive and negative impacts of the presence of UVS on the dispersal of a wide range of invertebrates, from emergence to the return in SNH at the end of the season or cycle.

4.3. Understorey vegetation strips are refugia for sensitive carabid species

Although Carabidae were overall more abundant in crop alleys, this varied from one species to another according to their sensitivity to agricultural disturbances. Higher density of carabid beetles in crop alleys is explained by the dominance of small carabids with higher reproductive output such as *Trechus quadristriatus*, *Metallina lampros* or *Apotomus rufus*. On the other hand, UVS hosted carabid species with higher sensitivity to agricultural disturbances (such as *Harpalus dimidiatus*, *Parophonus mendax* and *Ophonus* spp.), which are characterized by a unique overwintering stage (adult), a large body length and a predominantly granivorous diet (Holland et al., 2009; Vanbergen et al., 2010; Winqvist et al., 2014; da Silva et al., 2017; Baulechner et al., 2019). This is in line with the results of Hanson et al. (2016), who demonstrated that increasing management intensity reduces the average body size of overwintering carabid beetles and the proportion of mixed feeders. Such sensitive species probably moved to undisturbed UVS after crop harvest and/or suffered from ploughing in crop alleys, which is known to greatly reduce the emergence of many invertebrates (Holland and Reynolds, 2003; Ganser et al., 2019). Our results also confirm that overwintering stage is an important trait explaining the response of carabid beetles to agricultural disturbances. Species overwintering in both larval and adult stages are able to adapt to environmental changes by shifting their reproductive period and are also more likely to tolerate fluctuating biotic and abiotic conditions, given that they are composed of different age classes (Nolte et al., 2017).

A negative relationship was observed between the community-average value of body size of ground-dwelling predators and predation rates of aphids (Rusch et al., 2015). Presumably, smaller carnivorous species at larval stage were overwintering in crop alleys both to consume aphids and to avoid intraguild predation by larger carabids or spiders found in UVS, which hardly tolerate tillage disturbances. Indeed, many species found abundantly in crop alleys, such as *Anchomenus dorsalis*, *Metallina lampros* and *Trechus quadristriatus*, are known to feed on aphids (Sunderland and Vickerman, 1980; Sunderland et al., 1987; Hedde et al., 2012). Given their differences in terms of phenology, body length and habitat preferences, carabids that overwinter predominantly in crop alleys and those associated to UVS can be

complementary. Such complementarity could lead to enhanced biological control in agroforestry fields, whereas large carabids and mixed feeders are particularly affected by crop management in fields with high land-use intensity (Hanson et al., 2016). A successful overwintering of large carabid species within agroforestry fields could enhance the control of a wider range of prey (Rouabah et al., 2014), provided that these species do disperse towards crop alleys after emergence. Moreover, the spread of granivorous and omnivorous species that overwinter in UVS should be favored in agroforestry field core, whereas these species need to cover larger distances to recolonize pure crops after emergence from adjacent habitats. Species that consume weed seeds can help reduce weed pressure (Menalled et al., 2007; Bohan et al., 2011). Overall, these results suggest that carabid communities in agroforestry systems are likely to offer various and enhanced ecosystem services compared to those associated to crop fields or restricted to adjacent habitats, which are too far from the field core. This effect of agroforestry systems on the functional structure of carabid communities should be of particular interest in intensively cultivated agricultural landscapes, where SNH are missing.

5. Conclusions

The massive decline of invertebrates is driven by habitat loss, intensive agricultural practices and urbanization. This study revealed that UVS are home to a wide range of overwintering invertebrates in agroforestry systems, as opposed to crop alleys. Crop pests overwintered predominantly in crop alleys while beneficial invertebrates were often associated to UVS. Carabid species that are sensitive to agricultural disturbances were overwintering mostly in UVS. The presence of rich invertebrate communities within UVS could favor higher trophic taxa such as birds, mammals, reptiles and amphibians. We also expect enhanced spillover of beneficial invertebrates in agroforestry fields, due to the presence of undisturbed habitats within fields themselves, which could have strong impacts on the biological control of crop pests. To our knowledge, this is the first study to describe the distribution of overwintering invertebrate communities in alley cropping agroforestry systems, and accounting for the effects of the non-crop herbaceous strips under the tree rows. Given the context of climate change and biodiversity extinction crisis we are facing, such SNH should be used for biodiversity conservation purposes and the enhancement of ecosystem service flows in the agroecosystem.

CHAPTER 4

Ecological processes driving the spillover of ground-dwelling predators in alley cropping agroforestry fields: farming system matters

« La dévorante engeance nous affamerait, mes enfants, si d'autres ne travaillaient pour nous, d'autres doués d'une patience que rien ne lasse, d'une adresse qui déjoue toutes les ruses, d'une vigilance à qui rien n'échappe. Guetter l'ennemi, le rechercher dans ses réduits les plus cachés, le poursuivre sans relâche, l'exterminer, c'est leur unique souci, leur incessante affaire. Ils sont acharnés, impitoyables ; la faim les y pousse [...] Ils vivent de ceux qui vivent à nos dépens, ils sont les ennemis de nos ennemis. »

Jean-Henri Fabre

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Abstract

1. To promote the spillover of natural enemies within crop fields, agroecological systems rely on the presence of SNH around and/or within fields. In temperate regions, alley cropping agroforestry involves within-field natural habitats, in the form of tree rows and associated understory vegetation strips (UVS). The objective of this study was to assess the potential of common ground-dwelling predators (carabid beetles and cursorial spiders) to control weeds and invertebrate pests in alley cropping agroforestry compared to pure crop control, under two contrasted farming systems (conventional vs organic).
2. Arthropod surveys were carried out in May and June 2017 in South-Western France over 12 winter cereal fields.
3. Our study revealed that the effect of alley cropping agroforestry was modulated by the farming system. Under conventional farming, agroforestry practice had a negative effect on the activity-density of ground-dwelling predators, especially regarding carnivorous carabids whose activity-density was reduced by nearly 50%. Under organic farming, agroforestry practice enhanced both the activity-density and complementarity of ground-dwelling predators, with a two-fold increase in the activity-density of seed-feeding carabids (predominantly granivorous and omnivorous), potentially promoting weed and invertebrate pest control.
4. Our results suggest that the effectiveness of within-field agroecological infrastructures (AEI) in promoting predator spillover depends not only on the landscape context as shown by previous studies, but also on the farming system, which affects resource availability and determines spillover intensity between crop and non-crop habitats.
5. To conclude, AEI are often perceived as sources of natural enemies. Sink effect and retention (i.e. reduced or delayed spillover into crop fields due to higher attractiveness of AEI) are generally overlooked, but are likely to explain the mixed impacts of AEI on natural enemy communities.

This chapter has been submitted as a scientific article to Agricultural Systems.

1. Introduction

Agroecological systems rely on the action of natural enemies of crop pests for reducing the dependence of crop production on pesticides. 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). On the other hand, 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). Although common in agricultural landscapes, 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 the support of ecosystem service providers. At local scale, 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 SNH (Rand et al., 2006). However, AEI can also have negative impacts on predator communities. 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), although we found no evidence of barrier effect regarding spiders. Conversely, even agrobiont spider species (i.e. species reaching high densities in crops) do overwinter abundantly in SNH (Mestre et al., 2018). Further, if SNH are highly attractive, they might also lead to delayed colonization of crop fields by carabids (Wamser et al., 2011).

If the presence of AEI nearby or within crop fields is of major importance for enhancing predator communities, farming system is also decisive. Positive effects of organic farming on predator communities can be explained by the absence of pesticides and synthetic fertilizers, which are harmful practices 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 resources

such as seeds and pollen, but also phytophagous prey (Batáry et al., 2012). It has been shown that organic farming increases the abundance and species richness of carabid communities (Djouadi 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 and species richness of spiders (Feber et al., 1998; Batáry et al., 2012), but does not seem to affect their functional structure (considering their body size and hunting and dispersal strategies) (Gallé et al., 2019). Furthermore, studies at landscape scale revealed interactions between landscape complexity (i.e. proportion of SNH around fields) and farming system (i.e. conventional vs organic). Indeed, Ricci et al. (2019) showed that nearby SNH had a positive effect on aphid suppression in fields with low pesticide use intensity only, whereas they had a negative effect elsewhere. Similarly, other studies found a negative effect of landscape simplification on weed seed or aphid suppression in organic fields but a positive effect in conventional fields (Fischer et al., 2011a; Winqvist et al., 2011). The effectiveness of SNH in promoting predator spillover is mixed and little understood (Karp et al., 2018), which could actually be explained by the fact that (i) negative impacts of SNH on predators are generally overlooked, and (ii) studies are often restricted to conventional farming.

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 carbon sequestration (Torralba et al., 2016; Kay et al., 2019b). In temperate regions, alley cropping agroforestry represents a great opportunity for the reintegration of SNH within crop fields. Indeed, in such systems, the absence of tillage operations and crop sowing 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 where arable crops are grown (Figure 4.1).

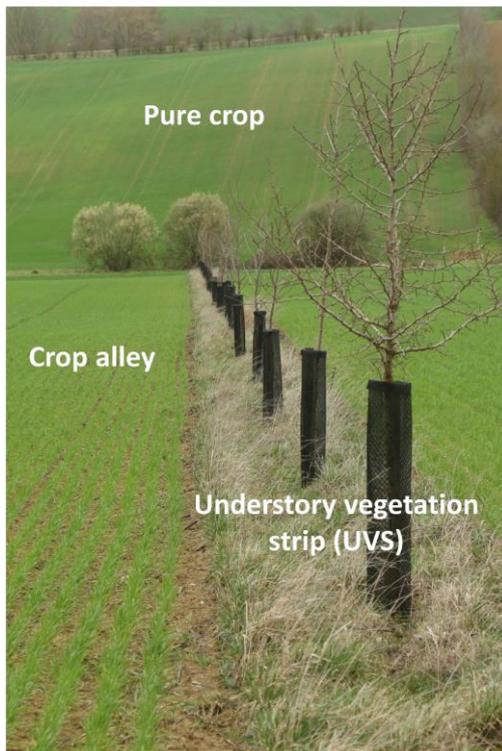


Figure 4.1. Alley cropping agroforestry system and pure crop control in the Gers department.

It has been shown that UVS are important refugia for many plants and invertebrates (Boinot et al., 2019a; Boinot et al., 2019b). 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), while small and carnivorous carabids overwinter mostly in crop alleys (Boinot et al., 2019b). These results suggest that alley cropping agroforestry systems might promote the spillover of 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 agroforestry systems 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 ground-dwelling predator communities between alley cropping agroforestry and pure crop systems.

The objective of this study was to assess the potential of ground-dwelling predator communities to control weeds and invertebrate pests in alley cropping agroforestry vs pure crop control, under conventional vs organic farming. We hypothesized that **1)** predominantly granivorous carabids and spiders are favored by alley cropping agroforestry, while carnivorous carabids, especially small ones that are adapted to highly disturbed habitats, are negatively impacted by alley cropping agroforestry. Further, we expected that **2)** the effect of alley cropping agroforestry is modulated by the farming system. Under conventional farming, agroforestry has an overall negative impact on the predator community that is composed predominantly of species adapted to highly disturbed habitats (e.g. small and carnivorous carabids), while agroforestry under organic farming strongly favors more sensitive species (i.e.

larger species and carabids with mixed diet), by providing both undisturbed habitats under the trees and abundant 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 agroforestry under organic farming), which is likely to result in a better biological control of weeds and invertebrate pests.

2. Materials 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 precipitations usually vary from 700 to 900 mm. From a previous study assessing the effect of alley cropping agroforestry 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. The same fields were used for arthropod sampling in May and June 2017, except that two pairs of fields were excluded from the analyses because the agroforestry plot and its pure crop control were distant from more than 3 km, thus not located in the same landscape context. Indeed, carabids and cursorial spiders respond to landscape variables at lower scale, generally within a 500 m or 1 km radius around fields (e.g. Schmidt et al., 2008b; Wamser et al., 2011). This resulted in six pairs of fields (alley cropping agroforestry 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 non-plough tillage. Under conventional farming, farmers used herbicides with a wide spectrum of action and similar treatment frequency indices, while 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 D.1 in Appendix D). 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. UVS were either unmanaged (n = 4 fields), mown before sowing and after harvest (n = 1 field) or sown with *Festuca rubra* (n = 1 field). Features of agroforestry fields (i.e. tree species and basic metrics) are given in [Table D.2](#) in Appendix D.

2.2. Arthropod sampling

Circulating carabid beetles and cursorial spiders were sampled with pitfall traps (height: 16 cm, diameter: 6.2 cm), on three different sampling periods in May and June 2017. In each agroforestry field, pitfall traps were positioned along three transects distant from 15 m and running perpendicularly to tree rows. These transects were located in field cores, at around 50 m and 100 m from the two nearest field boundaries (fields were too small to go farther). Each transect was composed by 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 a 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 180 pairs of pitfall traps sampled over three periods.

2.3. Biological control potential of predator communities

To estimate the potential of common ground-dwelling predators to control weeds and invertebrate pests, we measured the activity-density and species richness of carabids (granivorous, omnivorous, carnivorous) and cursorial spiders in pure crop controls and agroforestry fields (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., 2017b](#); [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 C.1 in Appendix C. 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 (Ribera et al., 1999; Purtauf et al., 2005; Woodcock et al., 2010; Petit et al., 2011; Birkhofer et al., 2014; Hanson et al., 2017). Information on the body length of spiders was collected in 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 spiders) between pure crop controls and agroforestry fields (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 a same perimeter. When GLMMs revealed significant interactions between farming system (conventional vs organic) and habitats (pure crop, crop alleys, UVS), models were then performed separately on conventional vs organic farming fields to facilitate the comparison between habitats. 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 $(FDvar \times (N - 1) + 0.5) / N$ 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). All analyses were performed using the statistical software R 5.1 (R Core Team, 2018).

3. Results

Total number of individuals and species sampled per functional group is given in (Table 4.1).

Table 4.1. 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

3.1. Effect of alley cropping agroforestry on the activity-density and species richness of ground-dwelling predators under conventional vs organic farming

Independently from the farming system (conventional vs organic), alley cropping agroforestry 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 4.2, Figure 4.2). 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 D.1 in Appendix D). Other functional groups responded differently to agroforestry practice depending on the farming system. Granivorous carabids had 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 4.2, Figure 4.2). Under conventional farming, granivorous carabids were mostly represented by *Harpalus dimidiatus*, whereas some species benefited from the combination

of agroforestry practice and organic farming, such as *Harpalus affinis*, *Harpalus pygmaeus* and *Amara* spp. (Figure D.1 in Appendix D). 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 4.2, Figure 4.2a), especially for *Poecilus cupreus* and *Brachinus crepitans* (Figure D.1 in Appendix D). 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 4.2, Figure 4.2a). Consequently, the activity-density of total predator community was much lower in crop alleys and UVS as opposed to pure crop controls under conventional farming (Table 4.2, Figure 4.2a). Species richness of predator community was even reduced in crop alleys under conventional farming (Table 4.2, Figure 4.2b). On the other hand, activity-density of predator community was higher in crop alleys than in pure crop controls under organic farming (Table 4.2, Figure 4.2a).

Table 4.2. 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 (reference level) vs organic farming. When GLMMs revealed significant interactions between habitats and farming system, models were then performed on organic farming fields and conventional ones separately to facilitate the comparison between habitats (See Table D.3 in Appendix D for detailed outputs of GLMMs). CMP = Conway-Maxwell Poisson. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

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

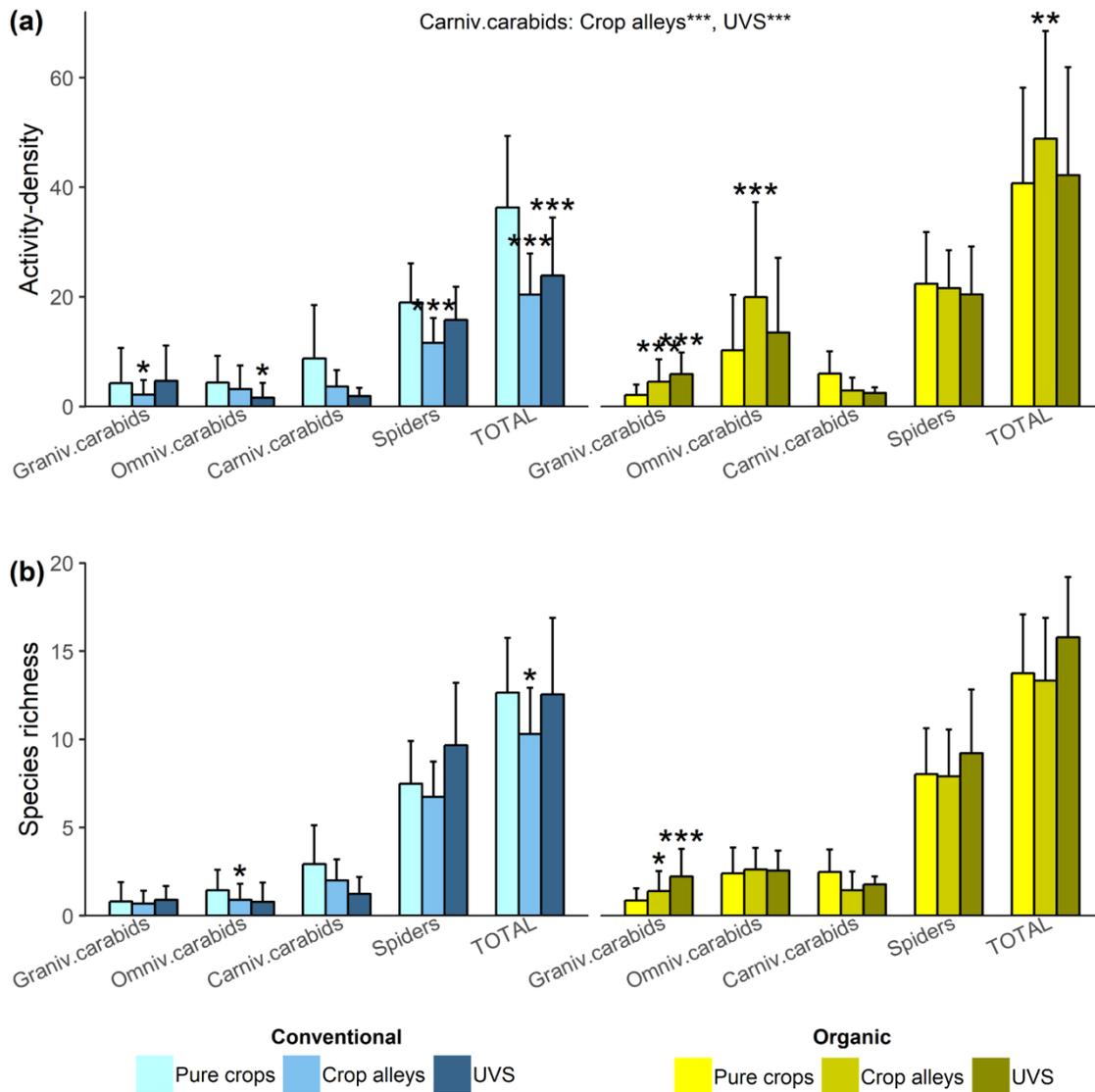


Figure 4.2. Mean and standard deviation of **(a)** activity-density and **(b)** species richness of each functional group and total predator community. Stars at the top of barplots are based on the p-values of GLMMs performed on conventional and organic farming fields separately, when there was a significant 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 D.3](#) in Appendix D for detailed outputs of GLMMs. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

3.2. Effect of alley cropping agroforestry on the functional structure of ground-dwelling predators under conventional vs organic farming

CWM Diet of predator community was close to 1 (i.e. towards carnivorous diet) and similar

between all habitats under conventional farming, while it was lower in crop alleys and UVS as opposed to pure crop controls under organic farming (Table 4.2, Figure 4.3a). Although FDvar Diet tended to be higher in agroforestry systems, especially under organic farming (Figure 4.3c), no significant effect was detected (Table 4.2). CWM Body length was significantly higher in crop alleys than in pure crop controls (Table 4.2, Figure 4.3b), 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 4.2, Figure 4.3d). A conceptual diagram of the results of this study is given (Figure 4.4).

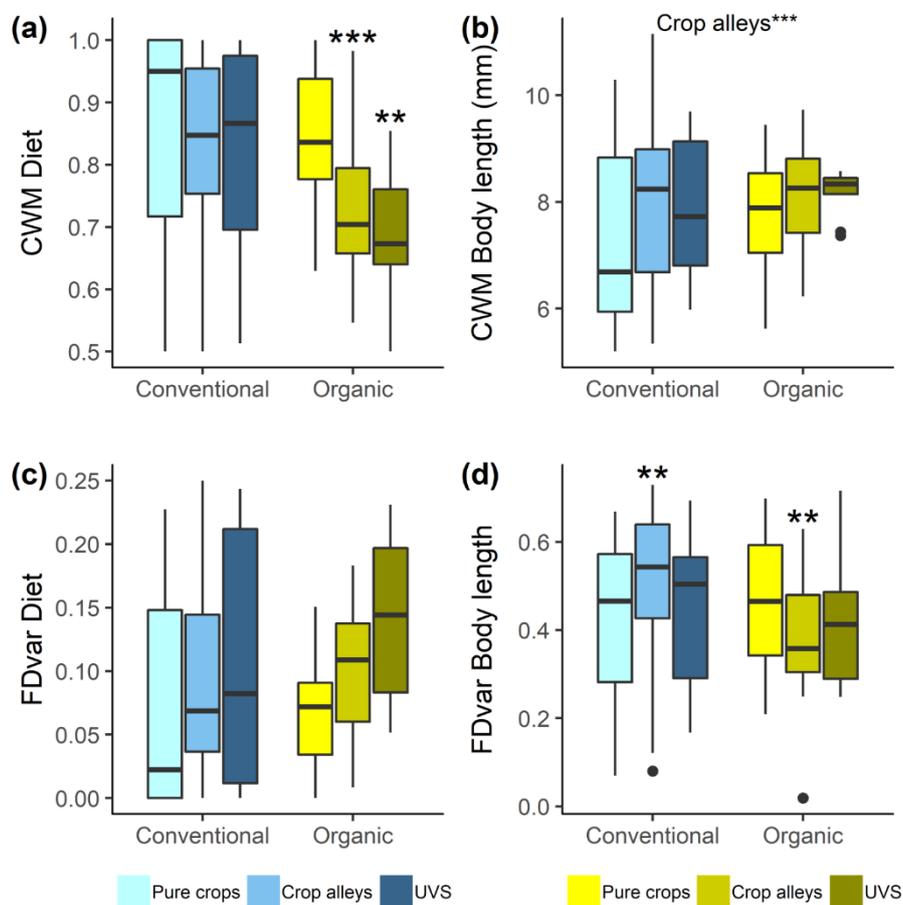


Figure 4.3. Functional structure of total predator community. **(a)** Community-weighted mean (CWM) of diet (granivorous: 0, omnivorous: 0.5 and carnivorous: 1), **(b)** CWM of body length, **(c)** Functional divergence (FDvar) of body length and **(d)** FDvar of body length (low complementarity: 0, high complementarity: 1). Stars at the top of boxplots are based on p-values of GLMMs performed on conventional and organic farming fields separately, 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 D.3 in Appendix D for detailed outputs of GLMMs. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

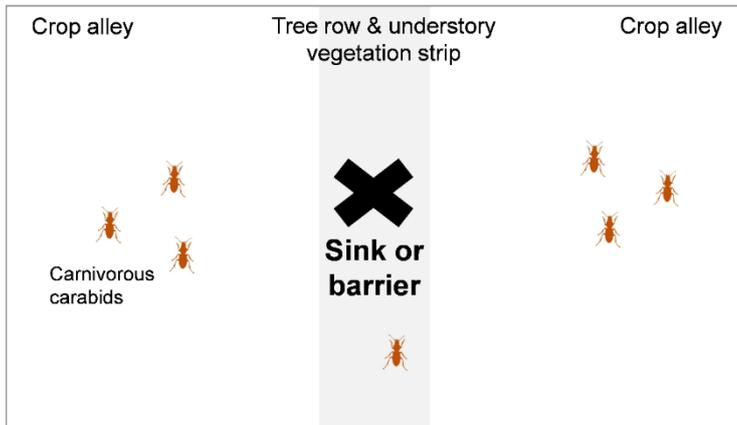
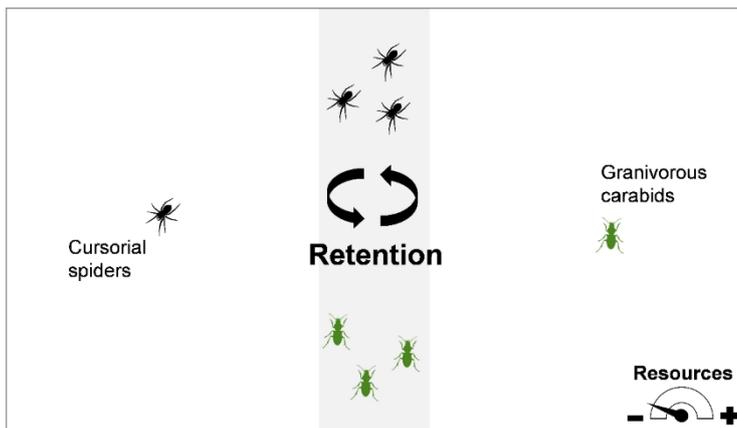
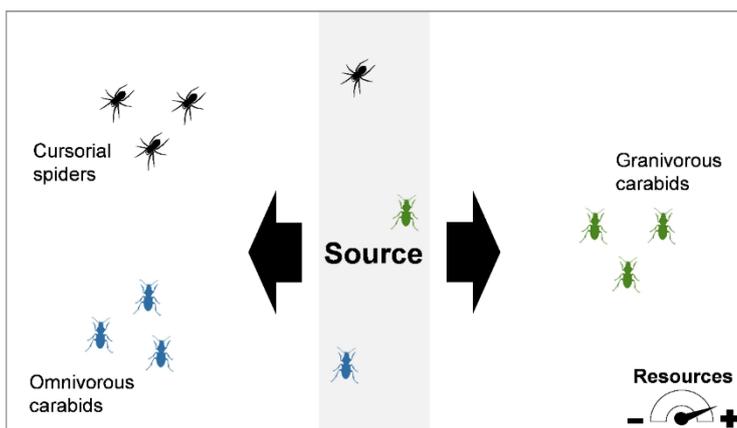
(a) agroforestry

Figure 4.4. Ecological processes driving the spillover of ground-dwelling predators between habitats in alley cropping agroforestry fields. For each case, only the relevant functional groups are represented.

(a) Sink or barrier effect: UVS act as a barrier or a sink for dominant carnivorous carabids established within crop fields, which have been shown to overwinter and forage in open and disturbed habitats,

(b) agroforestry + conventional farming

(b) Retention effect: under conventional farming, UVS are too attractive as opposed to crop alleys (higher food supply and more favourable microclimate), therefore the spillover of predominantly granivorous carabids and cursorial spiders in crop alleys is limited or delayed,

(c) agroforestry + organic farming

(c) Source effect: under organic farming, UVS act as a source of seed-feeding carabids and spiders, which have been shown to rely on this habitat for overwintering and whose spillover in crop alleys is probably favoured by a rich weed flora and associated phytophagous and detritivore prey.

4. Discussion

4.1. Negative effect of alley cropping agroforestry on predator communities under conventional farming

We confirmed that the activity-density and species richness of carnivorous carabids were clearly reduced by alley cropping agroforestry, independently from the farming system (hypothesis 1). This was especially true for small species such as *Anchomenus dorsalis* and Trechini 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 agroforestry fields, UVS seem to act as a sink 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, while larger carabids and spiders were found mostly in UVS. Therefore, small and carnivorous species might also have suffered from both competition with other predators and intraguild predation in agroforestry fields. The reduction of such predator species may result in lower biological control in agroforestry fields, especially regarding small crop pests such as aphids, on which they mostly feed (Rusch et al., 2015).

On the other hand, alley cropping agroforestry alone was not enough for promoting predominantly granivorous carabids and spiders in crop alleys. The presence of overwintering habitats and 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 granivorous 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 and associated resources such as phytophagous and detritivore prey. Probably, granivorous carabids and spiders also directly suffered from herbicide and synthetic fertilizer applications in the conventional farming systems 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 spiders were even less

active in crop alleys than in pure crop controls under conventional farming. In agroforestry fields, they rather seemed to stay 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 negative retention effect. Indeed, the spillover of natural enemies between habitats is largely driven by resource availability in each habitat (Dunning et al., 1992; Corbett and Plant, 1993; Blitzer et al., 2012; Tschardt et al., 2016). This result is also 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 conventionally managed fields. Similarly, Boetzl et al., 2019b 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 predatory species from AEI towards crop fields, but also by retention of predominantly 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. Alley cropping agroforestry enhances predator activity-density and complementarity under organic farming

The effect of alley cropping agroforestry was modulated by the farming system, thereby confirming hypothesis 2. Indeed, although alley cropping agroforestry had a negative impact on predator communities under conventional farming, it was the opposite under organic farming. First, alley cropping agroforestry no longer had a negative effect on the activity-density of cursorial spiders, which was similar in all habitats (pure crops, crop alleys, UVS). Second, the total activity-density of seed-feeding carabids was doubled in crop alleys of agroforestry fields as opposed to pure crop controls. This could be explained by (i) the presence of UVS that are favorable overwintering habitats for spiders and seed-feeding carabids in agroforestry fields (Boinot et al., 2019b), and (ii) a rich and abundant weed flora enhancing resource availability under organic farming (including associated phytophagous and detritivore prey) (Boinot et al., 2019a; Batáry et al., 2012), thereby favoring the spillover of ground-dwellers associated to UVS towards crop alleys (i.e. source effect). Indeed, Diehl et

al. (2012) showed that the presence of weeds in organic wheat fields fosters carabid activity-density and species richness via both resource and structure-mediated effects. Besides, the higher activity-density of seed feeding carabids could partly explain the results of Boinot et al. (2019a), who observed lower total weed coverage (-12% on average per quadrat) in agroforestry fields as opposed to pure crop controls under organic farming. In conclusion, the combination of alley cropping agroforestry and organic farming seems to be the best option for enhancing both weed and invertebrate pest control. These results are in line with those of Caro et al. (2016), who found that AEI had stronger effect on carabid diversity when combined with organic farming. Fusser et al. (2018) also found that carabid species richness increased with the amount of SNH in the surrounding landscape, but only in organic fields. Finally, studies at landscape scale revealed contrasted effects of SNH on weed seed or aphid suppression, depending on local farming system and pesticide use intensity (i.e. positive effects under organic farming and low pesticide use intensity, no effects or negative ones under conventional farming and high pesticide use intensity) (Fischer et al., 2011a; Winqvist et al., 2011; Ricci et al., 2019).

Under organic farming, 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 CWM Body length because we focused on circulating arthropods 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 to 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 agroforestry field and its adjacent pure crop control, or between SNH 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. Agroforestry systems combined with organic farming can enhance both the activity-density and complementarity of predator communities within fields during spring, even in relatively small fields (generally less than 10 ha) such as those observed in the Gers department.

4.3. Future researches on biological control in alley cropping agroforestry systems

Agroforestry farmers are currently using contrasted strategies for UVS management (e.g. minimalist management, maintaining bushes, mowing the vegetation, sowing plant mixtures). UVS width is also varying from one agroforestry field to another and is expected to have an impact on the quantity of habitats and resources, but also on the composition of plant communities (Aavik and Liira, 2010; Fried et al., 2018). Future researches should assess how these management strategies affect biological control level in crop alleys. Besides, trees and shrubs were not considered in this study, but might greatly enhance natural enemy communities by providing additional resources and sites for reproduction, overwintering and estivation (Stamps and Linit, 1998). 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 agroforestry systems (Klaa et al., 2005; Gibbs et al., 2016), but their effects on weed and invertebrate pest suppression are mixed (Tschumi et al., 2018). Our results and those of a recent meta-analysis (Staton et al., 2019) show that natural enemy generally benefit from agroforestry. Diversified natural enemy communities could greatly improve biological control through higher niche complementarity (Straub et al., 2008; Holland et al., 2012; Woodcock et al., 2016; Dainese et al., 2017b; Greenop et al., 2018). We conclude that 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.

5. Conclusions

Under conventional farming, the presence of UVS within fields has a negative effect on the activity-density of ground-dwelling predators in crops, but is still useful for biodiversity conservation. On the other hand, the combination of agroforestry practice and organic farming enhances both the activity-density and complementarity of ground-dwelling predators, making biodiversity conservation and biological control compatible. Our results suggest that the establishment of other AEI such as wildflower strips, beetle banks or hedgerows within fields themselves would enhance biological control by ground-dwelling predators under organic farming, when it could well be the opposite under conventional farming. Particular attention must be paid to sink and retention effects induced by AEI, which are very likely to explain their mixed impacts on natural enemy communities.

CHAPTER 5

Discussion



1. Summary of results

The objective of this PhD thesis was to describe the response of plant and invertebrate communities to alley cropping agroforestry systems under conventional vs organic farming and assess the positive or negative effects of understory vegetation strips (UVS) on biodiversity conservation and biological control of crop pests.

1.1. Biodiversity conservation

Vegetation surveys were carried out in May 2017 in South-Western France over 16 winter cereal fields (eight alley cropping agroforestry systems and eight pure crop controls), half under conventional farming and half under organic farming. No-plough tillage was performed in all fields. Each pair of fields (agroforestry vs pure crop) was cultivated by the same farmer, with similar crop managements. As opposed to cropped areas, UVS were home to a rich and abundant hemerophobic flora (i.e. species sensitive to agricultural disturbances), especially under conventional farming. These results highlight the potential of UVS for preserving plant diversity in agroecosystems.

Sampling of overwintering invertebrates were carried out from February to June 2018 over seven agroforestry fields growing winter cereals in Restinclières estate (South France), where crop alleys were ploughed before sowing. No insecticide was used, and crop alleys were dominated by spontaneous vegetation between crop harvest in summer and sowing in following autumn. The study revealed that 55% of invertebrate taxonomic groups were more abundant in UVS, whereas only 14% were more abundant in crop alleys. Furthermore, carabid species that are sensitive to agricultural disturbances (characterized by large body length, predominantly granivorous diet and overwintering in adult stage only) were overwintering mostly in UVS. All in all, these results show that UVS can be considered as areas of conservation as they harbor a high diversity of plants and invertebrates, which should also favor higher trophic taxa such as birds, mammals, reptiles and amphibians.

1.2. Biological control of crop pests

Our study on the distribution of overwintering invertebrates in agroforestry systems revealed that spiders were mostly spending the winter period in UVS rather than in crop alleys. Moreover, UVS hosted larger carabids and those with mixed diet, whereas crop alleys were dominated by small and carnivorous species.

In spring, ground-dwelling predators (carabids and cursorial spiders) were sampled in the same fields as those used for vegetation surveys. Two pairs of fields were excluded from the analyses because the agroforestry plot and its associated pure crop control were too distant from each other. This resulted in six pairs of fields (alley cropping agroforestry vs pure crop control, half under conventional farming and half under organic farming) located within the same perimeter, with similar pedoclimatic conditions and surrounding land use. Our study revealed that the effect of alley cropping agroforestry was modulated by the farming system. Under conventional farming, agroforestry practice had a negative effect on the activity of ground-dwelling predators in crops through two mechanisms: (i) UVS acted as a barrier or a sink for carnivorous carabids, whose activity-density was reduced by nearly 50% in crop alleys, and (ii) spillover of cursorial spiders and granivorous carabids was reduced presumably because of low resource availability in crop alleys (retention effect). On the other hand, under organic farming, UVS acted as a source of granivorous carabids and spiders, whose spillover in crop alleys was probably favored by a rich and abundant weed flora and associated resources. Under organic farming, agroforestry practice enhanced both the activity and complementarity of ground-dwelling predators, with a two-fold increase in the activity of seed-feeding carabids.

The results of these two studies conducted on different sites are complementary and consistent. By offering overwintering habitats, UVS promote the spillover of seed-feeding carabids and cursorial spiders in crops, which is likely to result in enhanced weed and invertebrate pest control. This is especially true under organic farming, whereas retention effect occurs under conventional farming. On the other hand, UVS appear to have a strong negative effect on dominant carnivorous carabids, which forage and overwinter in crops,

either by hampering their movements or by favoring competitors and intraguild predators. This could conversely have detrimental effect on the biological control of crop pests.

2. Limits of the study

2.1. Validity domain of the results

Given that agroforestry systems remain marginal in France, it was challenging to find several pairs of alley cropping agroforestry fields and pure crop controls similar in terms of crop management (i.e. tillage, pesticides, fertilizers, crop type, crop rotation) and landscape context, so that we were able to assess the intrinsic effect of agroforestry systems on plant and invertebrate communities. For each study, our results were obtained on a low number of fields ($n = 16$, $n = 7$ and $n = 12$ for chapters 2, 3 and 4 respectively) in specific pedoclimatic conditions. We could expect to find different plant and invertebrate life strategies elsewhere, whose response to agroforestry practice might have been different from what we observed in our study. For example, anemochorous plant species did not seem to spillover much from UVS to crop alleys, but they could be more abundant and problematic in windier regions than the Gers department. Furthermore, our results are restricted to winter cereal fields in which farmers performed soil tillage. However, in no-tillage systems such as direct drilling, we could expect higher plant spillover in crop alleys because of the presence of perennial grasses such as *Poa trivialis* in UVS, which have been shown to be favored by the absence of tillage (Trichard et al., 2013). Besides, crop type (i.e. cultivated species) is also an important variable driving the species composition of communities, with many crop-associated weeds, invertebrate pests and their natural enemies evolving together (Poggio et al., 2013; Meyer et al., 2019). Results might thus differ in other common arable crops such as rapeseed, sunflowers or peas. Finally, we were not able to assess how the effect of agroforestry systems on plant and invertebrate communities is modulated by landscape complexity or by farming practices at landscape scale, which are known to affect the distribution of living organisms within crop fields (Chaplin-Kramer et al., 2011; Alignier et al., 2017; Ricci et al., 2019).

2.2. Describing communities vs measuring ecosystem services

Given the significant number of protocols set up during our study (vegetation quadrat, pitfall trap, cornet trap, hoop, sweep net, emergence trap) and the work it requires in the laboratory, we were not able to both describe plant and invertebrate communities and measure associated ecosystem services directly within fields. As knowledge on plant and invertebrate communities in alley cropping agroforestry is currently poor, the most logical option was to describe the taxonomic and functional structures of communities, both to understand their response to alley cropping agroforestry practice and to assess the ecosystem services they are likely to offer. Based on our results, future studies should measure and compare biological control level between agroforestry systems and pure crops, under contrasted farming systems. For example, a common protocol is to use sentinel prey affixed to cards exposed on the ground or in the vegetation and to measure the number of consumed prey within a few days (Boetzi et al., 2019a). These predation cards can even be placed in exclusion cages of different mesh sizes to assess the contribution of different predators such as small vs large invertebrates or birds (e.g. Holland et al., 2012). Ideally, this protocol should be coupled with invertebrate predator sampling (e.g. pitfall traps located next to the predation cards) so that one can analyze the relationships between taxonomic and functional structures of predator communities and the level of biological control.

3. Perspectives

3.1. Ecological engineering of UVS for ecosystem service delivery

Our study revealed that UVS promote plant and invertebrate diversity conservation within crop fields. Therefore, we expect that UVS can supply many additional ecosystem services as other farmland vegetative strips do (Cresswell et al., 2019). For example, UVS can be used to provide alternative resources and overwintering or refuge habitats for pollinators, detritivores and natural enemies of crop pests and so enhance pollination, nutrient cycling and biological

control. Besides, UVS could reduce soil erosion and improve water infiltration through both vegetation barrier effect (reduction of water flow velocity) and increased soil structure and porosity. The ongoing project SALSA (Systèmes Agroforestiers et Linéaires Sous-Arborés) funded by the French National Institute of Agricultural Research (INRA) should bring insights to these questions. To promote the delivery of various ecosystem services, future researches 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). Their results demonstrate that promoting various ecosystem services with biodiversity-friendly practices is a possibility. Besides, 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). To take full advantage of the presence of UVS in agroforestry fields, we need to determine what are the best management strategies of UVS to promote multiple ecosystem services while reducing the risk of invertebrate pest and weed spillover within crop alleys (Figure 5.1). Functional approaches might be very useful to answer these questions, as they allow to understand (i) how plant traits are affected by different management strategies (e.g. Navas, 2012; Gaba et al., 2014; Gaba et al., 2017), (ii) how plant traits in turn affect ecosystem services (e.g. Navas, 2012; Lavorel, 2013; Storkey et al., 2015; Gaba et al., 2017; Bàrberi et al., 2018), and (iii) how plant traits correlate with each other, thus assessing trade-off, complementarity or synergy between ecosystem services (e.g. Lavorel and Grigulis, 2012; Martin and Isaac, 2015). This information could help choosing the best management strategies and/or developing seed mixes to reach target ecosystem services (e.g. Laughlin, 2014; Cresswell et al., 2019; Hatt et al., 2019).

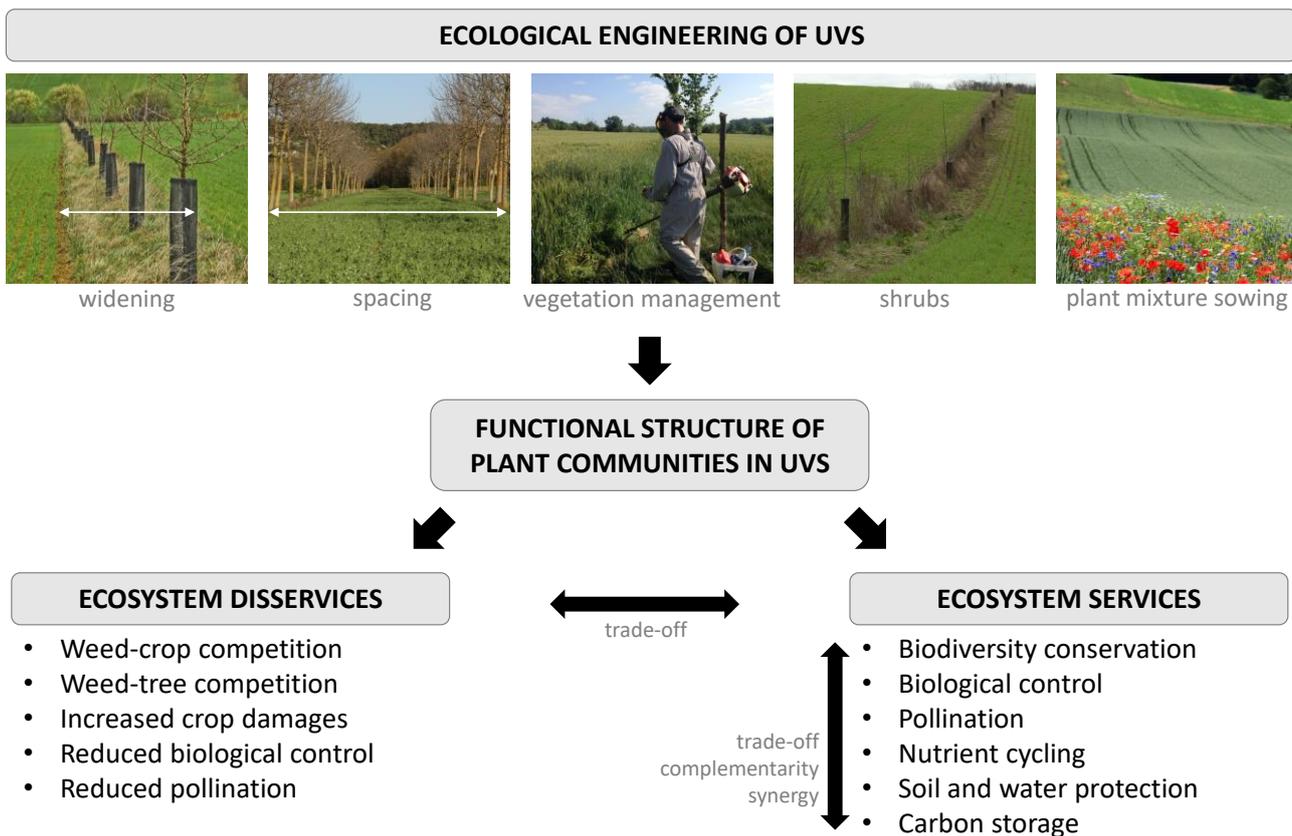


Figure 5.1. The ecological engineering of UVS, through its impact on the functional structure of plant communities in UVS, is likely to affect the delivery of ecosystem (dis-)services in crop alleys. Pictures: © J. Poulmarc’h, L. De Waal, D. Mézière, S. Boinot, M. Tschumi

3.1.1. Woody components

The purpose of this PhD thesis was to describe the ecosystem services provided by UVS, which were until very recently overlooked in agroforestry research. Trees and shrubs were not considered in our study, but are likely to promote both biodiversity conservation and biological control in agroforestry fields. Indeed, trees offer overwintering micro-habitats for invertebrates (Dix et al., 1995). Moreover, given that trees have longer lifespan, are larger and more complex in their architecture than herbaceous plants, they generally host a higher diversity of invertebrates (Stamps and Linit, 1998). Woody habitats provide important resources for pollinators, especially for bees (Donkersley, 2019; Kay et al., 2019a), which are drastically declining in Europe (Potts et al., 2010; Powney et al., 2019). Trees also provide additional services for invertebrates, such as sites for mating, hiding, resting or estivating. Akbulut et al. (2003) showed that the tree canopy of agroforestry systems had higher invertebrate diversity than the crop alleys (either corn, green bean or zucchini) from mid-summer to early autumn. Moreover, as hypothesized by Stamps and Linit (1998), the

combination of trees and crops in agroforestry systems should provide greater invertebrate niche diversity in both time and space, both for herbivores and their predators, thus decreasing the probability of pest outbreaks. Trees and hedgerows also favor higher trophic taxa suffering from agricultural intensification such as birds (Gibbs et al., 2016) and bats (Froidevaux et al., 2019), which can contribute to crop pest suppression (Kross et al., 2016; Russo et al., 2018). Hedgerows have the potential to enhance biodiversity conservation, pollination, biological control, carbon storage, nutrient cycling and water infiltration (Dainese et al., 2017a; van Vooren et al., 2017; van den Berge et al., 2018; van Vooren et al., 2018; Holden et al., 2019). Future researches should address the contribution of trees and shrubs to biodiversity conservation and associated ecosystem (dis-)services in agroforestry fields. As in the case of UVS, tree rows can be established and managed in a variety of ways (Figure 5.2), which are likely to affect the fauna by conditioning not only the quantity and diversity of resources and micro-habitats, but also their spatial and temporal distributions.

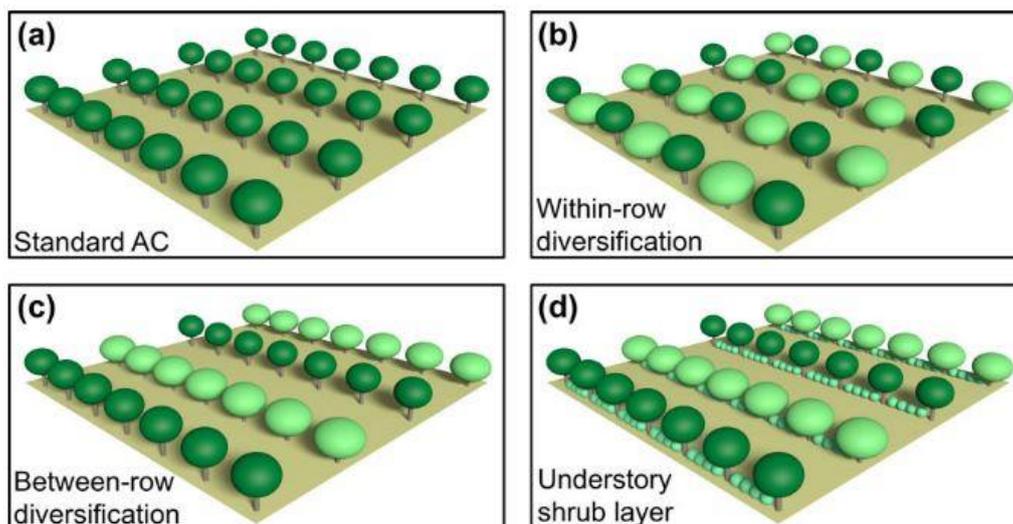


Figure 5.2. Conceptual diagram depicting practical designs for the within-row diversification in alley cropping agroforestry systems (AC), from Wolz et al. (2018). Higher diversity and complementarity of resources and shelters are expected to favor beneficial invertebrates and higher trophic taxa such as birds and bats.

3.1.2. UVS widening

One of the most simple and cost-effective ways to promote ecosystem service delivery from spontaneous plant communities in agroforestry fields could well be the widening of UVS, from 1-2 m to 5-6 m for example (Cauwer et al., 2006; Marshall et al., 2006; Aavik and Liira, 2010).

First, it has been shown that increasing field boundary width favors hemerophobic species relative to common arable weed species (Aavik and Liira, 2010; Fried et al., 2018), and also tends to increase species richness (Tarmi et al., 2009), presumably because of higher environmental quality inside the boundary (Cauwer et al., 2006). This could help prevent weed spillover in crop alleys and favor the potential role of UVS as a barrier to weed dispersal. The reduction of fast-growing competitive grasses due to lessened soil eutrophication could enhance the abundance and diversity of species, and consequently of inflorescences (David et al., 2019), thereby offering resources for many pollinators and natural enemies. Second, increased area of SNH within fields would directly enhance resource availability and offer additional refuges from agricultural disturbances for sensitive species, including many beneficial invertebrates. Pywell et al. (2015) showed that despite the resulting loss of cropland (3 or 8 % in their study), the promotion of wildlife habitats enhances ecosystem service flows in crops by supporting pollinators and natural enemies of pests, leading to even higher crop production than in absence of such habitats. Third, wider boundaries reduce soil erosion and water pollution by efficiently intercepting pesticide residues, nitrogen, phosphorus and soil sediments (Patty et al., 1997; Schmitt et al., 1999; van Vooren et al., 2017). Fourth, widening UVS could directly increase soil carbon storage (Cardinael et al., 2015) and surface albedo compared to disturbed soils (Davin et al., 2014; Carrer et al., 2018), which would contribute to mitigating climate change if established at large scale. Finally, using crop alley margins for other purposes than crop production might be more appropriate as it has been shown that yield losses are highest in field margins adjacent to woody elements, presumably because of shading (Raatz et al., 2019). This holds true for alley cropping agroforestry, where decreased crop yield and altered crop quality were observed near the oldest tree rows (Pardon et al., 2018; Pardon et al., 2019a), probably because of higher competition for light, water and nutrients but also as a consequence of crop variety selection in full sun conditions (Desclaux et al., 2016). What would be the best spatial configuration (i.e. area occupied by crop alleys vs UVS in agroforestry fields) for a good balance between crop production and ecosystem service delivery remains to be studied.

3.1.3. Vegetation mowing

Under nutrient-rich conditions, mowing (or cutting) the vegetation is another solution to

reduce the dominance of tall and competitive species and maintain species richness and abundant flower provision (Tarmi et al., 2011; Jakobsson et al., 2018; Kirmer et al., 2018; Tälle et al., 2018; Piqueray et al., 2019). Mowing should be coupled with biomass removal to enhance species richness, because high amount of litter generally hinders seedling germination and establishment (Tarmi et al., 2011; Kirmer et al., 2018; Tälle et al., 2018; Piqueray et al., 2019). Besides, increased biomass uptake through multiple mowing is likely to reduce soil nutrient stocks, thereby creating more suitable conditions for the maintenance of non-weedy species (Cauwer et al., 2008; Piqueray et al., 2019) and also favoring water quality protection (Tarmi et al., 2009). However, frequent mowing might prevent the seed set of lower-growing species, thus threatening their long-term survival, and mowing early may have negative effects on species with late seed-setting (Tälle et al., 2018 and references therein). Mowing performed by machines leads to homogeneous habitat structure, temporarily depleting resources, affecting micro-climate conditions and causing direct animal mortality (Noordijk et al., 2010; Cizek et al., 2012). Late mowing also destroys overwintering structures for invertebrates and removes winter trophic resources and nesting sites for farmland birds (Kirmer et al., 2018 and references therein). By contrast, many forbs are able to regenerate quickly after early mowing, thus prolonging the flowering period until early autumn (Humbert et al., 2012; Kirmer et al., 2018; Piqueray et al., 2019). All in all, mowing once or twice a year (late June and September) with biomass removal seems to be an intermediate disturbance regime that maintains plant and invertebrate species richness (Noordijk et al., 2010; Uchida and Ushimaru, 2014; Kirmer et al., 2018; Piqueray et al., 2019). However, this strategy should be coupled with rotational management, i.e. maintaining unmown refuge zones under the form of patches or strips (Schmidt et al., 2008a; Cizek et al., 2012; Bonari et al., 2017; Piqueray et al., 2019). In case of a second mowing, the refuge zone of the first mowing must be maintained or enlarged to keep a safe overwintering zone. Unmown refuges can be moved annually to avoid species richness decrease due to management abandonment and soil eutrophication (Piqueray et al., 2019). Besides, frequent operations with tractor mowers are likely to have negative impacts on ground-dwelling organisms (Humbert et al., 2010), thus manual tools should be used whenever possible. Finally, what time of the day is more appropriate for mowing (i.e. reducing direct animal mortality) should be investigated. For example, mowing in early mornings should probably be avoided as many invertebrates are still inactive and hidden in the vegetation by that time of the day.

3.1.4. Various management strategies

Although sowing wildflower strips can greatly enhance ecosystem services such as pollination and biological control (Feltham et al., 2015; Tschumi et al., 2016; Hatt et al., 2017; Pollier et al., 2018), it might be difficult to maintain target sown species over time. Once the trees are grown, re-sowing next to the tree rows becomes a complicated task. Sowing competitive grasses 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. On the other hand, the three management strategies described above (i.e. maintaining shrubs under the trees, widening UVS, mowing the vegetation) can more easily be used by agroforestry farmers to promote the delivery of ecosystem services such as pollination, biological control, nutrient cycling, soil and water quality protection. Given that herbaceous strips and hedgerows have been shown to support different living organisms and provide various ecosystem services (Schirmel et al., 2016; Holland et al., 2014; Holland et al., 2016; van Vooren et al., 2017; van Vooren et al., 2018), using various management strategies to promote a diversity of habitats in agroforestry systems might be of particular interest. Besides, alternating management strategies between each UVS could also prevent the dispersal of weeds and invertebrate pests that would be favored by one habitat but disadvantaged by the other.

3.2. Emerging research issues

3.2.1. Are UVS a barrier to weed dispersal in crop alleys?

During our study, we answered an important question for agroforestry farmers: are UVS a reservoir for weeds? We demonstrated that very few species found in UVS were able to disperse far into crop alleys, except perennial species producing runners, whose spread has probably been favored by tillage. Consequently, the presence of UVS in agroforestry fields did not increase weed-crop ratio (i.e. weed coverage / weed and crop coverage, used as a proxy for weed competition) in adjacent crop alleys. This shows the very weak impact of plant spillover from UVS on the potential harmfulness of arable weed communities, even under organic farming.

Our study has raised a new question, less intuitive and to the exact opposite of our first point of view: are UVS a sink habitat for weeds? In other words, are UVS a barrier to weed dispersal within crop alleys? Indeed, 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 fields. This could be explained by the fact that UVS – often forming dense covers – would constitute a sink habitat for weeds, especially for species that are poorly competitive in a more stable and shadier habitat. Then, this potential function of UVS could have stronger impacts on weed communities than the spillover in crop alleys itself. Indeed, some authors showed that grass margin strips reduced the dispersal of arable weed species from SNH to crop fields or the other way around (Cordeau et al., 2012; Marshall, 2009). Similarly, Alignier et al. (2017) found that larger fields were characterized by higher weed density, biomass and seed rain, and explained this result by the fact that large fields constitute higher productive habitats, with less overall influence of edge effect (e.g. light competition). Such barrier or sink effects 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 high spillover from UVS given the lack of herbicide treatments and mineral fertilizers that favor herbicide tolerant and nitrophilous species, respectively.

Two mechanisms could actually explain how UVS can act as a barrier to weed dispersal. First, as said above, arable weeds that spillover from crop alleys to UVS are adapted to agricultural disturbances and are likely to suffer from competition with other plants in (or near to) a stable habitat such as UVS. This could be especially true for species with high dispersal abilities such as anemochorous and zoochorous species or those spreading by means of runners, but less likely for barochorous species that would hardly move from crop alleys towards UVS. Second, horizontal dispersal by agricultural machines and secondary weed dispersal over the ground are interrupted by the presence of UVS at regular intervals, which might affect all species independently from their dispersal strategies. This would lead to reduced habitat area (restriction to crop alleys vs large open field), with fewer opportunities to grow and potentially increased intra- and inter-specific competition. Consequently, we could expect a reduced population growth for dominant arable weeds that usually colonize the whole field, which would free up space for less common species (Figure 5.3). This would

support the results of Boinot (2015), who found that the total abundance of weeds was lower in an agroforestry field compared to a pure crop, which was explained by reduced abundance of the most frequent weed species observed, such as *Papaver rhoeas*, *Fumaria officinalis*, *Fallopia convolvulus* and *Polygonum aviculare*.

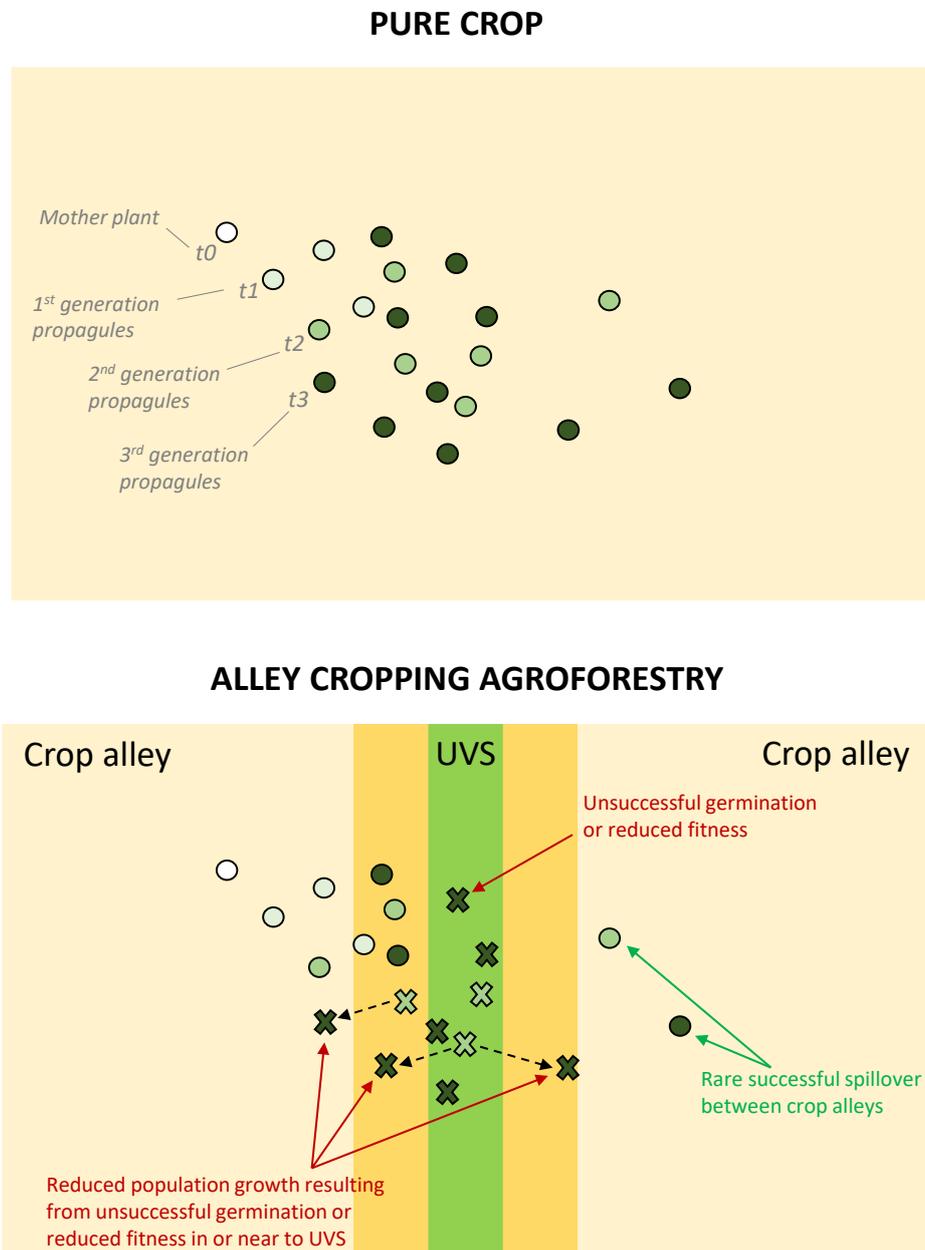


Figure 5.3. Illustration of the barrier effect potentially provided by UVS, which would act as a sink for weeds, and its expected impact on weed population growth and spatial distribution. **a)** In pure crops, any propagule from a mother plant will have to face competition with crop and other arable weeds. **b)** In agroforestry fields, propagules that end up in UVS will have to face competition with species already well established and better adapted to less disturbed habitat. Therefore, it is likely that these propagules will not germinate, or will give new individuals with lower fitness. This should result in reduced weed population growth, especially for dominant species that usually colonize the whole field. Figure: © S. Boinot

To assess the role of barrier to weed dispersal provided by UVS, one would ideally estimate (i) the percentage of arable weed propagules dispersing in UVS vs crop alleys, and (ii) the success of establishment within UVS vs crop alleys. The latter can easily be estimated through the measure of presence-absence or coverage in each habitat. However, tracking propagules is a complicated task, especially if we are to survey many individuals from various troublesome weed species. Indirect measurement of seed dispersal with seed traps (so-called “Eulerian methods”) provides a reliable estimate of seed rain at a given location (Lemke et al., 2009). However, such protocol is mostly used for anemochorous species and does not provide information on the distance or location of the source. Seed traps also stop the dispersal process, whereas secondary dispersal is an important mechanism (Higgins et al., 2003). Some protocols allow for a direct measurement of propagule dispersal by animals (including humans and their agricultural machinery) or secondary wind dispersal over the ground, by tracking them from a start point to a final point where germination might occur (so-called “Langrangian methods”). Such protocols include magnet locators, radioactive marking, wire tin-tagging, thread-marking and color marking. In particular, combining fluorescent color marking with the use of UV torches seems to be a promising way to measure weed seed dispersal (Lemke et al., 2009). Another approach, the characterization of weed seed bank in UVS vs crop alleys with soil samples, would reveal if UVS contain a high proportion of troublesome weed propagules, but would not indicate if such propagules come from mother plants in crop alleys, neither if collected seeds would have germinated or not in UVS. Finally, none of these protocols is adequate for tracking vegetative individuals dispersing by means of runners (i.e. rhizomes and/or stolons). One indirect alternative would be to compare the spatio-temporal distribution of some common weeds with different dispersal strategies (i.e. barochorous, anemochorous, zoochorous, runners) in agroforestry fields and pure crop controls. This would only require recording the presence-absence of some weed species on the whole of each field over a few years, using a systematic sampling. Then, mapping weed species distribution could be done with SADIE (Spatial Analysis by Distance Indices) or MAPCOMP (MAP COMParison) for example, which are used for spatial analysis of count data (Lavigne et al., 2010; Trichard et al., 2014; Martín et al., 2015; Winder et al., 2019). Reduction in presence and patch size along with restriction to some crop alleys would constitute evidences for a barrier effect provided by UVS in alley cropping agroforestry fields.

3.2.2. Increased niche complementarity or intraguild predation between natural enemies of crop pests in agroforestry systems?

Two major mechanisms affect the level of biological control of crop pests: niche complementarity and intraguild predation (Straub et al., 2008). Niche complementarity is a result of resource partitioning and/or facilitation (Hooper et al., 2005). Resource partitioning occurs when natural enemy species differ in how, where, and when they attack prey. Without resource partitioning, there would be strong resource competition and functional redundancy between natural enemies. Facilitation occurs when a natural enemy species enables a second species to attack more prey than it would if hunting alone. For example, Woodcock et al. (2016) showed that aphid control was higher in the presence of both ground-active and canopy-active natural enemies. This could be explained by an avoidance behavior of aphids that drop from the plants when attacked by canopy-active predators, which makes them more accessible to ground-active predators. On the other hand, intraguild predation occurs when a top predator (intraguild predator) consumes an intermediate predator (intraguild prey) with which it competes for a common resource (crop pest). Given the “enemy hypothesis”, which states that natural enemies are more abundant in complex versus simple plant systems, we could expect higher abundance and diversity of both aerial and epigeal natural enemies in alley cropping agroforestry systems under organic farming. Indeed, the combination of tree rows, UVS and crop alleys within agroforestry fields is likely to increase the complementarity and temporal continuity of resources for natural enemies, while providing refugia from agricultural disturbance. However, the spillover of specialist natural enemies such as hoverflies within crop alleys could conversely be reduced, because prey or hosts may be more difficult to locate due to chemical cue disruption from multiple plant species (Stamps and Linit, 1998).

To what extent diverse natural enemy communities would result in higher niche complementarity or intraguild predation in agroforestry systems remains to be studied, although field studies tend to confirm the niche complementarity hypothesis (Straub et al., 2008; Holland et al., 2012; Woodcock et al., 2016). A recent meta-analysis also revealed that functional diversity (based on habitat domain, diet breadth and hunting strategy) positively affects prey suppression by invertebrate predators (Greenop et al., 2018). Complex-structured

vegetation tends to reduce intraguild predation by reducing encounter rates between predators and by providing refuges for intraguild prey (Finke and Denno, 2002; Janssen et al., 2007). Yet, Roubinet et al. (2017) showed that carabids had higher detection frequencies for most common spider families in organically compared to conventionally managed fields, a result attributed to the observed trend of higher activity-density of Lycosidae (ground-dwellers) in organically managed fields. Besides, the profusion of resources provided by complex plant systems may either reduce the impact of generalist predators on pest populations, because they are diverted from main crop pests, or increase it, as it helps them survive periods of low pest availability (Roubinet et al., 2017). Furthermore, earthworms and higher trophic taxa such as insectivorous birds and small mammals benefit from the presence of tree rows in alley cropping agroforestry systems (Cardinael et al., 2019; Klaa et al., 2005; Gibbs et al., 2016), but their effect on pest suppression remains unclear. Some earthworm species could contribute to weed control by feeding on weed seeds (Eisenhauer et al., 2009; Eisenhauer et al., 2010). Birds have been shown to control pest populations (Kross et al., 2016), but also to disrupt biological control by feeding on invertebrate natural enemies (Grass et al., 2017). Small mammals consume weed seeds (Fischer et al., 2011a; Fischer and Türke, 2016) and could feed on invertebrate pests, but they can also be agricultural pests of various crops (Brown et al., 2007) and could feed on invertebrate natural enemies as well. We expect that a higher availability in extraguild prey in agroforestry systems (Boinot et al., 2019b) would reduce intraguild predation by vertebrates, as opposed to simplified agroecosystems (Grass et al., 2017). To simultaneously quantify crop pest vs intraguild predation, traditional sampling of invertebrate communities should be coupled with molecular gut content analysis, which gives DNA detection frequencies; the proportion of positively tested predators for a given prey (Roubinet et al., 2017). To measure the effect of higher trophic taxa such as birds and small mammals, exclusion experiments could be used (Fischer et al., 2011a; Grass et al., 2017). A broad food web perspective would greatly improve our understanding of the complex trophic interactions that are likely to occur in alley cropping agroforestry fields, and the processes that enhance or reduce biological control of crop pests (Figure 5.4).

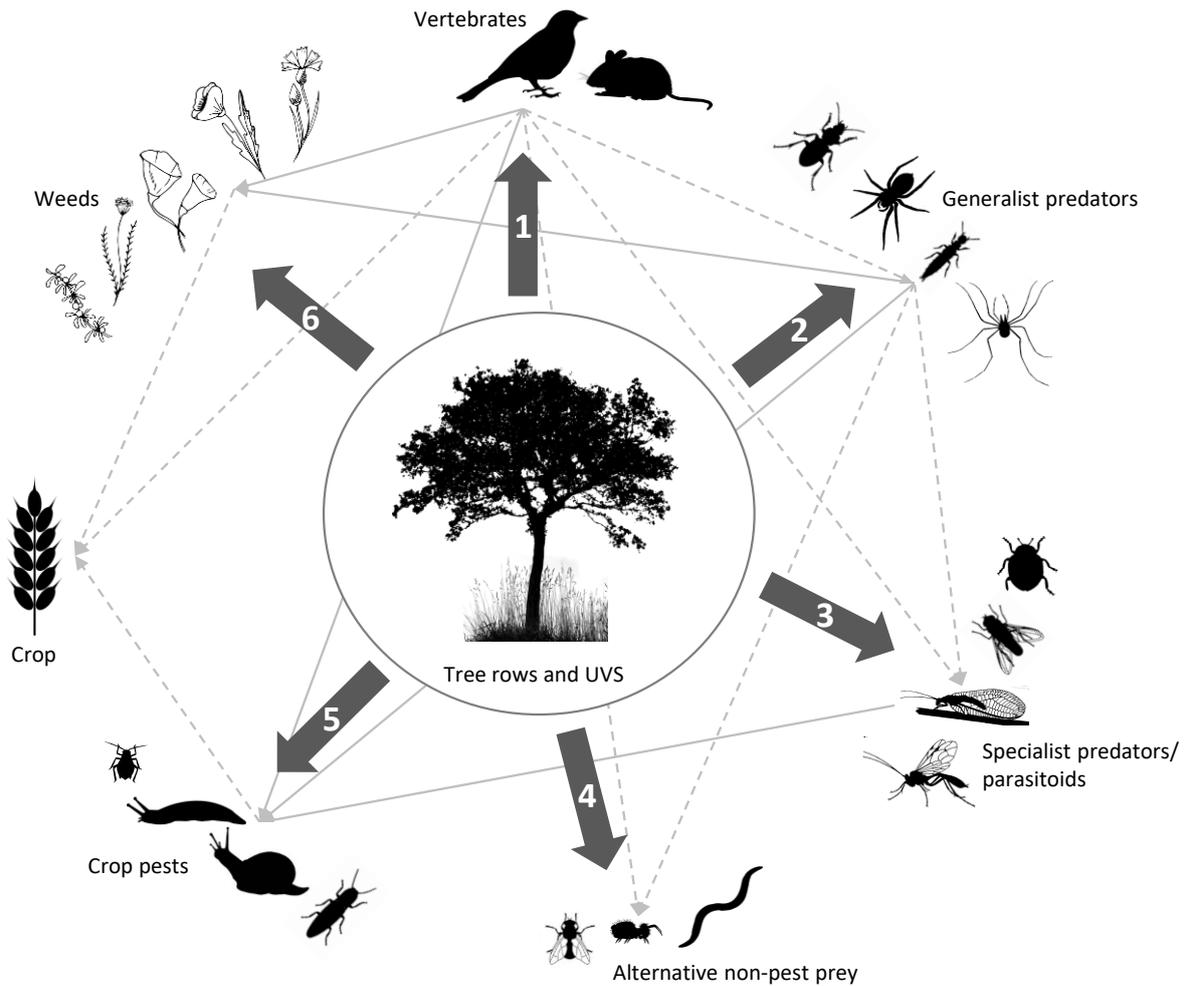


Figure 5.4. Conceptual framework for future researches in biological control of invertebrate pests and weeds in alley cropping agroforestry systems, with winter cereals as model crops. Solid and dashed lines indicate interactions that would enhance or reduce the level of biological control, respectively.

1. Source effect, enhanced or disrupted biological control?
2. Source vs sink effect, barrier to dispersal, reduced/delayed colonization, niche complementarity vs intraguild predation?
3. Source vs sink effect, chemical cue disruption, niche complementarity vs intraguild predation?
4. Source effect, alternative extraguild prey favoring or distracting predators, reducing intraguild predation by vertebrates?
5. Source vs sink effect, barrier to dispersal, resource dilution effect?
6. Source vs sink effect, barrier to dispersal?

Figure: © S. Boinot

4. Conclusion

This PhD thesis confirmed that alley cropping agroforestry is a valuable land use system for biodiversity conservation, providing refugia from agricultural disturbances for plants and invertebrates. Further studies are needed to draw any conclusion regarding the biological control of crop pests, although our results clearly suggest that agroforestry combined with organic farming enhances weed and invertebrate pest suppression by ground-dwelling predators (cursorial spiders and carabid beetles). Our results also provide reassuring answers for farmers, as we demonstrated that UVS hardly constitute a reservoir for dominant weeds or invertebrate pest that would disperse in crop alleys and induce yield losses. To conclude on a personal note, I really enjoyed working on this rich and complex system that is alley cropping agroforestry and I hope that I will have opportunities to continue in this highly stimulating research area. In agroforestry, many processes, concepts and theories from ecology (e.g. life strategies and functional traits, spillover and source-sink dynamics, ecological interactions) are of major importance and can be used to design agroecological systems. Considering biotic interactions, research in temperate agroforestry is still in its infancy, but I have clearly noticed the increase in the publication of articles and the emergence of research projects in Europe since I started in 2015, and this is only the beginning. I hope that the articles published during my PhD thesis, and this manuscript, will contribute to promote the adoption of agroforestry systems among farmers and motivate more agroecologists to get involved in agroforestry research.

APPENDIX A

Table A.1. Crop management for each pair of agroforestry fields and pure crop controls surveyed in the Gers and Pyrénées-Atlantiques departments in May and June 2017.

Farming system	Farmer	Cropping system	Cumulated treatment frequency index from sowing 2014 to harvest 2017 ¹	Maximum tillage depth 2016-2017 (cm)	Crop harvested in 2016	Intercrop 2016-2017	Crop harvested in 2017
Conventional	1	Agroforestry	5.1	15	sunflower	none	wheat
		Pure crop	5.1	15	sunflower	none	wheat
	2	Agroforestry	5.8	15	sunflower	none	wheat
		Pure crop	5.2	15	sunflower	none	wheat
	3	Agroforestry	5.7	4	field bean	field bean	wheat
		Pure crop	4.3	25	sunflower	none	wheat
	4	Agroforestry	6	20	wheat	none	barley
		Pure crop	6	20	wheat	none	barley
Organic	5	Agroforestry	0	20	sunflower	none	wheat
		Pure crop	0	20	sunflower	none	wheat
	6	Agroforestry	0	5	soybean	none	barley, garden pea, vetch
		Pure crop	0	15	wheat	spontaneous vegetation	barley
	7	Agroforestry	1.7	5	barley, garden pea	none	barley, garden pea
		Pure crop	1.7	5	barley, garden pea	none	barley, garden pea
	8	Agroforestry	0	10	clover, trefoil	clover, trefoil	wheat
		Pure crop	0	10	clover, trefoil, alfalfa	clover, trefoil, alfalfa	wheat

¹Under conventional farming, all farmers used herbicides with a wide spectrum of action (grass and broadleaf weeds). Farmer n°7 was under conventional farming in 2014-2015.

Table A.2. Description of agroforestry fields surveyed in the Gers and Pyrénées-Atlantiques departments in May and June 2017.

Farmer	Age of the system (years)	Crop alleys' width (m)	UVS' width (m)	UVS mowing	UVS sowing	Tree species found in transects
1	10	25	2	0	0	<i>Acer campestre</i> , <i>Juglans regia</i> , <i>Pyrus pyraster</i> , <i>Prunus avium</i> , <i>Quercus petraea</i>
2	6	28	1.5	0	0	<i>Juglans regia</i> , <i>Pyrus pyraster</i> , <i>Prunus avium</i> , <i>Quercus pubescens</i> , <i>Sorbus domestica</i>
3	5	38	2	0	1	<i>Acer campestre</i> , <i>Juglans regia</i> , <i>Prunus avium</i> , <i>Sorbus domestica</i> , <i>Tilia cordata</i>
4	5	22	1.5	1	0	<i>Juglans regia</i> , <i>Pyrus pyraster</i> , <i>Prunus avium</i> , <i>Quercus petraea</i> , <i>Sorbus domestica</i> , <i>Sorbus torminalis</i> , <i>Fraxinus excelsior</i> , <i>Salix sp.</i>
5	2	26	1	0	0	<i>Juglans regia</i> , <i>Prunus avium</i> , <i>Quercus petraea</i> , <i>Sorbus torminalis</i> , <i>Fraxinus excelsior</i>
6	8	17	1	0	0	<i>Pyrus pyraster</i> , <i>Quercus petraea</i> , <i>Sorbus domestica</i> , <i>Sorbus torminalis</i> , <i>Fraxinus excelsior</i> , <i>Cornus sanguinea</i> .
7	5	32	2	1	0	<i>Acer campestre</i> , <i>Juglans regia</i> , <i>Prunus avium</i> , <i>Sorbus domestica</i> , <i>Fraxinus excelsior</i> , <i>Ulmus campestris</i>
8	11	22	1	0	1	<i>Acer campestre</i> , <i>Juglans regia</i> , <i>Prunus avium</i> , <i>Quercus pubescens</i> , <i>Fraxinus excelsior</i>

Table A.3. Trees species associated to sampled UVS and area covered by UVS in agroforestry fields from Restinclières estate.

	Field area covered by UVS (%)	Tree species
Field N°1 (A2)	13	<i>Juglans x Regia x Nigra</i>
Field N°2 (A3)	13	<i>Juglans x Regia x Nigra</i>
Field N°3 (A5)	11	<i>Alnus cordata, Celtis spp., Fraxinus angustifolia, Acer platanoides</i>
Field N°4 (A6)	12	<i>Celtis spp., Sorbus domestica, Prunus avium, Pyrus communis</i>
Field N°5 (A8a)	11	<i>Pyrus communis, Prunus avium, Fraxinus ornus, Juglans nigra</i>
Field N°6 (A8b)	11	<i>Prunus mahaleb, Tilia tomentosa, Malus domestica, Ostrya carpinifolia</i>
Field N°7 (A9)	10	<i>Juglans regia, Acer monspessulanum, Cupressus sempervirens</i>

APPENDIX B

Table B.1. Species classification, conservation value, and occurrence within the three surveyed habitats.

EPPO code	Latin name	Classification ¹	Conservation value ²	Alley cropping agroforestry		Pure crops (n = 432)
				UVS (n = 96)	Crop alleys (n = 432)	
ALOMY	<i>Alopecurus myosuroides</i>	A	3	X	X	X
APHAR	<i>Aphanes arvensis</i>	A	3	X	X	X
ARBTH	<i>Arabidopsis thaliana</i>	H	0	X	X	
ARREL	<i>Arrhenatherum elatius</i>	H	3	X	X	X
ATXPA	<i>Atriplex patula</i>	A	0		X	X
AVESS	<i>Avena</i> spp.	A	0	X	X	X
BROSS	<i>Bromus</i> spp.	H	0	X	X	X
LITAR	<i>Buglossoides arvensis</i>	H	3		X	X
CAPBP	<i>Capsella bursa-pastoris</i>	A	0		X	
CERGL	<i>Cerastium glomeratum</i>	H	0	X	X	X
CHEAL	<i>Chenopodium album</i>	A	0	X	X	X
CIRAR	<i>Cirsium arvense</i>	A	0	X	X	X
CIRVU	<i>Cirsium vulgare</i>	H	0	X	X	
CLVVT	<i>Clematis vitalba</i>	H	0	X		X
CONAR	<i>Convolvulus arvensis</i>	A	0	X	X	X
CAGSE	<i>Convolvulus sepium</i>	A	0		X	
DACGL	<i>Dactylis glomerata</i>	H	0	X	X	X
DAUCA	<i>Daucus carota</i>	H	0		X	X
DIWSI	<i>Dipsacus fullonum</i>	H	0	X		
AGRRE	<i>Elytrigia repens</i>	H	0		X	X
EPIAD	<i>Epilobium tetragonum</i>	H	0	X	X	X
EQUAR	<i>Equisetum arvense</i>	H	0			X
ERICA	<i>Erigeron canadensis</i>	A	0	X	X	
EPHEX	<i>Euphorbia exigua</i>	H	0			X
POLCO	<i>Fallopia convolvulus</i>	A	0		X	X
FESRU	<i>Festuca rubra</i>	H	0	X		
FUMOF	<i>Fumaria officinalis</i>	A	0		X	
GALAP	<i>Galium aparine</i>	A	0	X	X	X
GERCO	<i>Geranium columbinum</i>	A	0	X		
GERDI	<i>Geranium dissectum</i>	A	0	X	X	X
PICEC	<i>Helminthotheca echioides</i>	H	0	X	X	X
HOLLA	<i>Holcus lanatus</i>	H	0	X	X	
HOLMO	<i>Holcus mollis</i>	H	0	X		
HYPPE	<i>Hypericum perforatum</i>	H	0	X	X	
IUNBU	<i>Juncus bufonius</i>	H	0		X	
KICEL	<i>Kickxia elatine</i>	H	0		X	X
LACSE	<i>Lactuca serriola</i>	A	0	X	X	
LAMPU	<i>Lamium purpureum</i>	A	0	X	X	
LAPCO	<i>Lapsana communis</i>	H	0	X	X	X

LOLSS	<i>Lolium</i> spp.	A	0	X	X	X
ANGAR	<i>Lysimachia arvensis</i>	A	0	X	X	X
MATMT	<i>Matricaria discoidea</i>	H	0	X	X	X
MEDPO	<i>Medicago polymorpha</i>	H	0			X
MYOAR	<i>Myosotis arvensis</i>	H	0	X	X	X
PAPRH	<i>Papaver rhoeas</i>	A	3	X	X	X
POLLA	<i>Persicaria lapathifolia</i>	A	0			X
PHAPA	<i>Phalaris paradoxa</i>	H	0		X	X
PICHI	<i>Picris hieracioides</i>	H	0	X	X	X
PLALA	<i>Plantago lanceolata</i>	H	0	X	X	X
PLAMA	<i>Plantago major</i>	H	0		X	X
POAAN	<i>Poa annua</i>	A	0	X	X	X
POATR	<i>Poa trivialis</i>	H	0	X	X	X
POLAV	<i>Polygonum aviculare</i>	A	0		X	X
PTLRE	<i>Potentilla reptans</i>	A	0	X	X	X
RANAR	<i>Ranunculus arvensis</i>	H	2		X	
RANBU	<i>Ranunculus bulbosus</i>	H	0	X		X
RANRE	<i>Ranunculus repens</i>	H	0	X	X	
RUBSS	<i>Rubus</i> spp.	H	0	X	X	X
RUMCR	<i>Rumex crispus</i>	H	0	X	X	X
RUMOB	<i>Rumex obtusifolius</i>	H	0		X	
SAIPR	<i>Sagina procumbens</i>	H	0			X
FESAR	<i>Schedonorus arundinaceus</i>	H	0	X	X	X
FESPR	<i>Schedonorus pratensis</i>	H	0	X		
SENVU	<i>Senecio vulgaris</i>	A	0			X
SETVI	<i>Setaria italica</i>	H	0		X	
SHRAR	<i>Sherardia arvensis</i>	H	0	X	X	X
SLYMA	<i>Silybum marianum</i>	H	0			X
SINAR	<i>Sinapis arvensis</i>	A	0	X	X	X
SONAS	<i>Sonchus asper</i>	A	0	X	X	X
SONOL	<i>Sonchus oleraceus</i>	A	0	X	X	X
TAROF	<i>Taraxacum officinale</i>	A	0	X	X	X
TOIAR	<i>Torilis arvensis</i>	H	0	X	X	
TROPS	<i>Tragopogon porrifolius</i>	H	0	X		
TROPR	<i>Tragopogon pratensis</i>	H	0	X		X
TRFAR	<i>Trifolium arvense</i>	H	0		X	
TRFPR	<i>Trifolium pratense</i>	H	0		X	X
VLLLO	<i>Valerianella locusta</i>	H	0			X
VEBOF	<i>Verbena officinalis</i>	H	0	X	X	X
VERAR	<i>Veronica arvensis</i>	H	0	X	X	X
VERPE	<i>Veronica persica</i>	A	0		X	X
VERPO	<i>Veronica polita</i>	H	0	X	X	X
VICBI	<i>Vicia bithynica</i>	H	0		X	X
VICHY	<i>Vicia hybrida</i>	H	0		X	
VLPMY	<i>Vulpia myuros</i>	H	0	X	X	

¹Following [Aavik et al. \(2008\)](#), each species was classified as agrotolerant (A) or hemerophobic (H) 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%.

²Conservation 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.

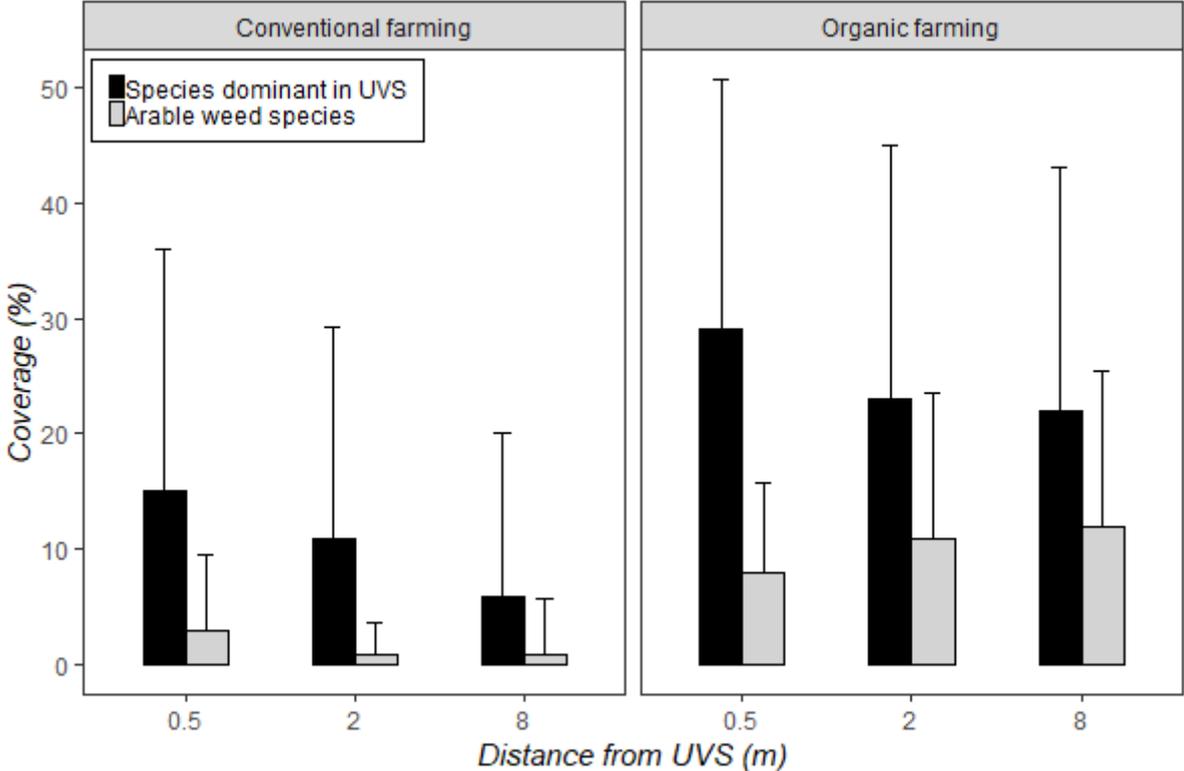


Figure B.1. Mean and standard deviation of the coverage of species dominant in understory vegetation strips (kept in the spillover analysis) vs arable weed species persisting mostly in the seed bank (excluded from the analysis).

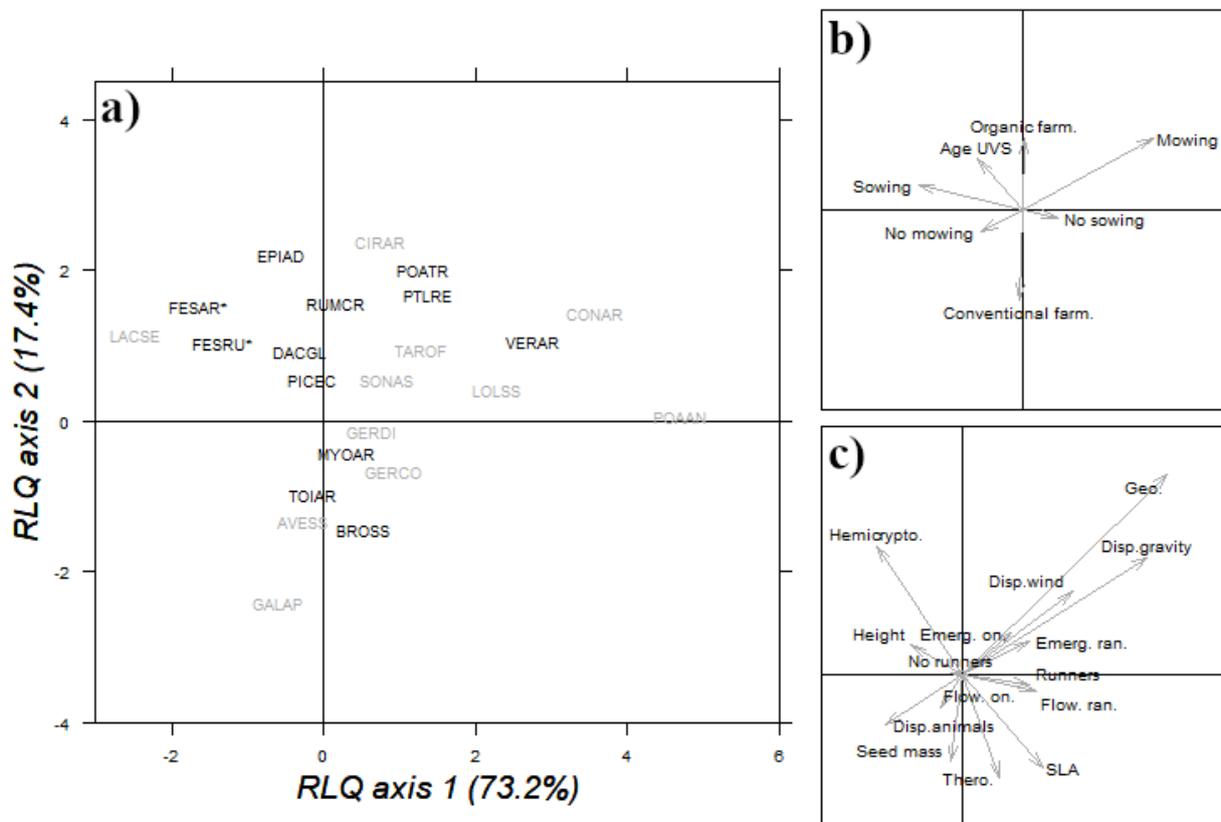


Figure B.2. RLQ analysis performed on plant communities located in the understory vegetation strips (UVS). Results are given on the first two axes for a) species' scores, b) environmental variables' loadings, and c) traits' loadings. Only dominant species were considered (occurring in at least 5 quadrats), representing 90% of the total plant coverage in UVS. Species marked with a star were sown. Grey and black labels correspond to agrotolerant and hemerophobic species respectively. Codes for species are given in [Table B.1](#) in Appendix B.

Table B.2. 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)*.

Variables (abbreviation)	Units	Mean (Min–Max) or counts	RLQ Axis 1	RLQ Axis 2
Environmental variables				
Farming system				
<i>Conventional</i>		<i>n</i> = 48	–0.03	–0.578
<i>Organic</i>		<i>n</i> = 48	0.024	0.459
UVS management				
<i>Mowing</i>		<i>n</i> = 24	1.706	0.46
<i>No mowing</i>		<i>n</i> = 72	–0.531	–0.143
<i>Sowing</i>		<i>n</i> = 24	–1.359	0.153
<i>No sowing</i>		<i>n</i> = 72	0.459	–0.052
Age of UVS	years	6.5 (2 – 11)	–0.579	0.325
Numerical traits				
Seed mass	g	3.52 (0.1 – 29.73)	–0.076	–0.287
Plant height	cm	82.74 (20 – 200)	–0.344	0.096
Specific leaf area (SLA)	mm ² .mg ⁻¹	25.77 (15.4 – 36.43)	0.537	–0.307
Flowering onset (Flow. on.)	months	5.17 (1 – 7)	–0.146	–0.108
Flowering range (Flow. ran.)	months	4.74 (2 – 12)	0.49	–0.053
Emergence onset (Emerg. on.)	months	1.65 (1 – 7)	0.331	0.139
Emergence range (Emerg. ran.)	months	6.91 (3 – 12)	0.456	0.11
Categorical traits				
Raunkiaer life forms				
<i>Therophyte (Thero)</i>		<i>n</i> = 12	0.253	–0.337
<i>Geophyte (Geo)</i>		<i>n</i> = 2	1.373	0.656
<i>Hemicryptophyte (Hemicrypto)</i>		<i>n</i> = 9	–0.57	0.421
Seed dispersal				
<i>Wind</i>		<i>n</i> = 7	0.742	0.272
<i>Animals</i>		<i>n</i> = 8	–0.512	–0.164
<i>Gravity</i>		<i>n</i> = 8	1.238	0.384
Presence of runners				
<i>Runners</i>		<i>n</i> = 6	0.444	–0.034
<i>No runners</i>		<i>n</i> = 17	–0.074	0.006

Table B.3. 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)

Variables (abbreviation)	Units	Mean (Min–Max) or counts	RLQ Axis 1	RLQ Axis 2
Environmental variables				
Farming system				
<i>Conventional</i>		<i>n</i> = 216	–1.933	0.127
<i>Organic</i>		<i>n</i> = 216	0.826	–0.054
Direction from UVS				
<i>East</i>		<i>n</i> = 216	0.204	–0.174
<i>West</i>		<i>n</i> = 216	–0.221	0.188
Distance from UVS				
<i>0.5 m</i>		<i>n</i> = 144	0.426	0.602
<i>2 m</i>		<i>n</i> = 144	–0.589	–0.24
<i>3 m</i>		<i>n</i> = 144	0.041	–0.638
Numerical traits				
Seed mass	g	4.04 (0.1 – 29.73)	0.204	–0.045
Plant height	cm	81.83 (20 – 150)	0.262	0.073
Specific leaf area (SLA)	mm ² .mg ^{–1}	26.21 (15.4 – 36.43)	–0.256	–0.073
Flowering onset (Flow. on.)	months	5.17 (1 – 7)	0.358	0.031
Flowering range (Flow. ran.)	months	5 (3 – 12)	–0.351	–0.079
Emergence onset (Emerg. on.)	months	1.67 (1 – 7)	0.16	–0.172
Emergence range (Emerg. ran.)	months	7.67 (3 – 12)	–0.262	0.078
Categorical traits				
Raunkiaer life forms				
<i>Therophyte (Thero)</i>		<i>n</i> = 8	–0.222	0.071
<i>Geophyte (Geo)</i>		<i>n</i> = 2	0.269	–0.244
<i>Hemicryptophyte (Hemicrypto)</i>		<i>n</i> = 8	0.203	0.097
Seed dispersal				
<i>Wind</i>		<i>n</i> = 6	0.173	0.074
<i>Animals</i>		<i>n</i> = 5	0.194	0.214
<i>Gravity</i>		<i>n</i> = 7	–0.105	–0.085
Presence of runners				
<i>Runners</i>		<i>n</i> = 5	0.181	–0.187
<i>No runners</i>		<i>n</i> = 13	–0.086	0.088

Table B.4. Regression parameters, standard errors and p-values of generalized mixed-effects models (GLMMs) performed on organic and conventional fields separately. Crop alleys and understory vegetation strips (in the case of variables assessing plant diversity) are compared to pure crop controls (reference level in GLMMs) for each response variable. Weed-crop ratio refers to the relative weed coverage ratio (i.e. weed coverage / weed and crop coverage).

			Organic farming		Conventional farming	
			Crop alleys	UVS	Crop alleys	UVS
<i>Potential harmfulness of weed communities</i>	Weed coverage (%)	<i>n</i> = 863	-0.50 ± 0.255 0.050	–	0.38 ± 0.620 0.546	–
	Crop coverage (%)	<i>n</i> = 863	0.07 ± 0.160 0.664	–	0.55 ± 0.550 0.316	–
	Weed-crop ratio	<i>n</i> = 863	-0.32 ± 0.222 0.148	–	0.30 ± 0.635 0.638	–
<i>Diversity of agrotolerant communities</i>	Total coverage (%)	<i>n</i> = 720	-0.01 ± 0.555 0.987	1.27 ± 0.561 0.023	0.27 ± 0.521 0.610	1.10 ± 0.544 0.043
	Species richness	<i>n</i> = 720	0.02 ± 0.235 0.948	0.15 ± 0.242 0.524	0.82 ± 1.173 0.483	1.99 ± 1.174 0.091
	Evenness	<i>n</i> = 312	-0.13 ± 0.454 0.768	-1.05 ± 0.481 0.029	-1.08 ± 0.445 0.015	-0.58 ± 0.448 0.196
<i>Diversity of hemerophobic communities</i>	Total coverage (%)	<i>n</i> = 720	-0.57 ± 0.263 0.028	1.24 ± 0.285 <0.001	0.35 ± 0.321 0.279	3.79 ± 0.342 <0.001
	Species richness	<i>n</i> = 720	-0.16 ± 0.187 0.397	0.28 ± 0.196 0.159	2.98 ± 1.166 0.011	4.20 ± 1.166 <0.001
	Evenness	<i>n</i> = 282	0.55 ± 0.159 0.001	-0.54 ± 0.201 0.008	–	–

Table B.5. 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* (performed on organic and conventional fields separately). Weed-crop ratio refers to the relative weed coverage ratio (i.e. weed coverage / weed and crop coverage).

		Distance from UVS (log-scaled+1)	
		Organic farming	Conventional farming
<i>Potential harmfulness of weed communities</i>	Weed coverage (%) (n = 863)	-0.22 ± 0.133 0.095	-1.18 ± 0.184 <0.001
	Crop coverage (%) (n = 863)	0.14 ± 0.100 0.176	0.69 ± 0.147 <0.001
	Weed-crop ratio	-0.21 ± 0.117 0.068	-1.34 ± 0.175 <0.001
<i>Diversity of agrotolerant communities</i>	Total coverage (%) (n = 720)	-0.04 ± 0.196 0.849	-0.42 ± 0.215 0.054
	Species richness (n = 720)	-0.00 ± 0.109 0.976	-0.36 ± 0.189 0.058
	Evenness (n = 312)	-0.37 ± 0.249 0.136	-1.21 ± 0.560 0.031
<i>Diversity of hemerophobic communities</i>	Total coverage (%) (n = 720)	-0.35 ± 0.244 0.146	-1.31 ± 0.264 <0.001
	Species richness (n = 720)	0.05 ± 0.156 0.725	-2.44 ± 0.386 <0.001
	Evenness (n = 282)	-0.36 ± 0.324 0.244	2.83 ± 1.201 0.019

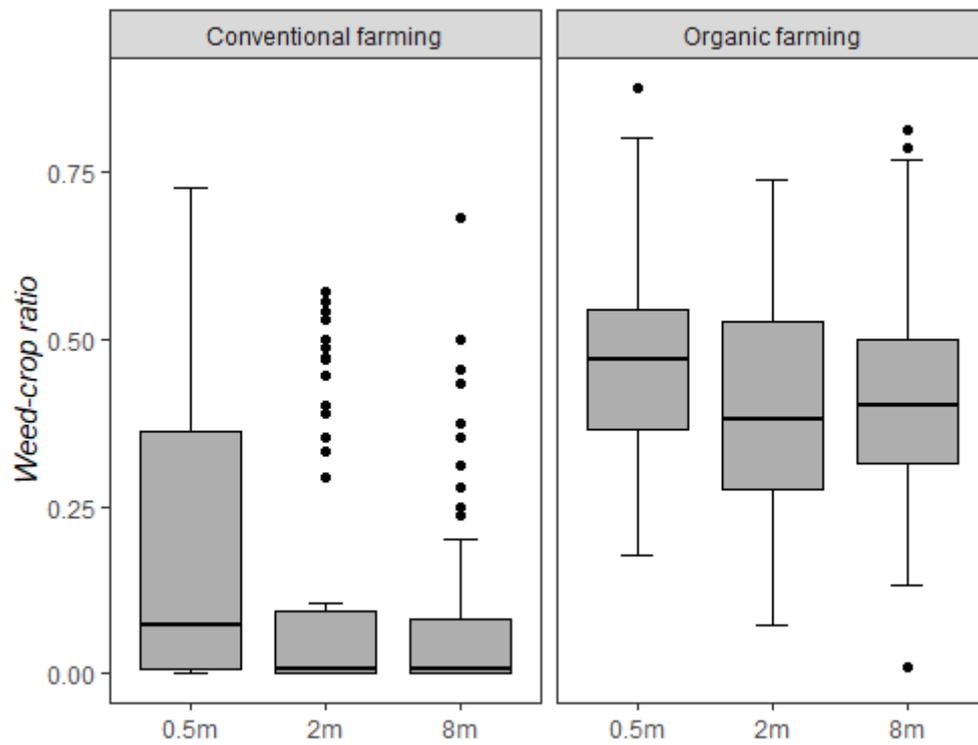


Figure B.3. Effect of distance from understory vegetation strips (UVS) on weed-crop ratio (weed coverage / weed and crop coverage).

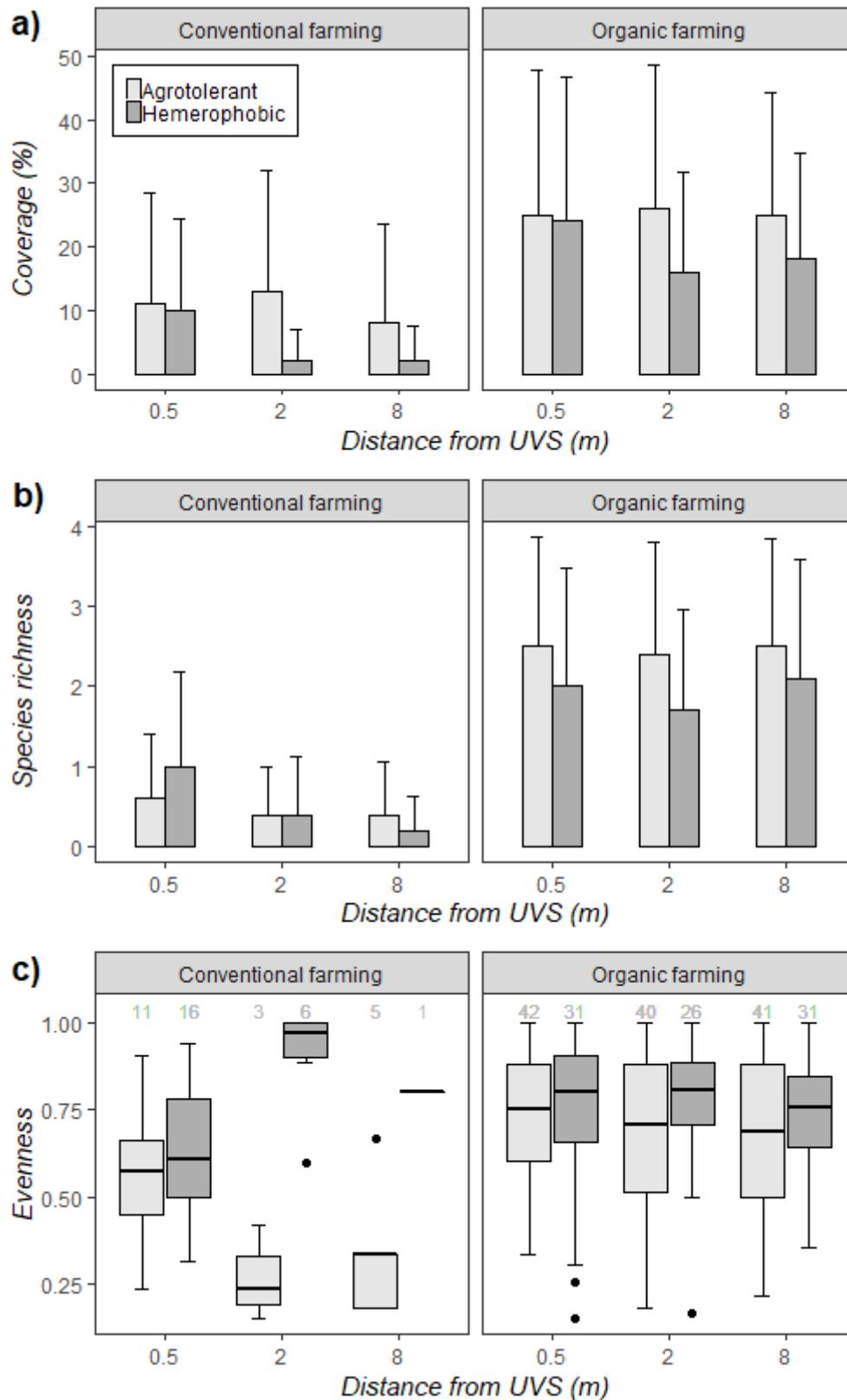


Figure B.4. Effect of distance from understory vegetation strips (UVS) on the variables considered for the assessment of communities' diversity.

Table B.6. Total species richness observed across all fields, per habitat (UVS = understory vegetation strips) and under each farming system. n = number of quadrats in each case.

	Conventional farming			Organic farming		
	Pure crop controls (n = 216)	Crop alleys (n = 216)	UVS (n = 48)	Pure crop controls (n = 216)	Crop alleys (n = 216)	UVS (n = 48)
Agrotolerant communities	8	10	13	20	25	17
Hemerophobic communities	4	12	15	35	38	26
Total	12	22	28	55	63	43

APPENDIX C

Table C.1. 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	$\frac{2}{\pi} \arctan \left[5 \left(\sum_{i=1}^S w_i (\ln x_i - \overline{\ln x})^2 \right) \right]$
		$\overline{\ln x} = \sum_{i=1}^S w_i \ln x_i$
	FDvar modified	$\sum_{i=1}^S w_i (x_i - \bar{x})^2$
		$\bar{x} = CWM$

Table C.2. Functional trait values of carabid species (**diet**; granivorous: 0, omnivorous: 0.5 and carnivorous: 1 / **overwintering stage**; overwintering in both larval and adult stages: 0, overwintering in adult stage: 1).

Latin name	Diet	Body length	Overwintering stage
<i>Acinopus picipes</i>	0	14.5	0
<i>Acupalpus meridianus</i>	1	3.6	1
<i>Anchomenus dorsalis</i>	1	6.5	1
<i>Apotomus rufus</i>	1	4	NA
<i>Badister bullatus</i>	1	5.3	0
<i>Brachinus crepitans</i>	0.5	8.3	1
<i>Brachynidius sclopeta</i>	1	5.6	1
<i>Calathus cinctus</i>	1	7.5	0
<i>Calathus fuscipes</i>	0.5	12.5	0
<i>Carterus fulvipes</i>	0.5	10.5	NA
<i>Demetrias atricapillus</i>	1	5	1
<i>Dinodes decipiens</i>	NA	11.5	1
<i>Dixus capito</i>	0	12.5	1
<i>Harpalus dimidiatus</i>	0	12.5	1
<i>Harpalus oblitus</i>	0	10	1
<i>Harpalus serripes</i>	0	11	NA
<i>Metallina lampros</i>	1	3.1	1
<i>Metoponus laticollis</i>	0	9.5	1
<i>Metoponus spp.</i>	NA	NA	NA
<i>Microlestes abeillei</i>	1	2.6	1
<i>Microlestes fissuralis</i>	1	2.5	1
<i>Microlestes fulvibasis</i>	1	2.5	1
<i>Microlestes minutulus</i>	1	2.7	1
<i>Microlestes negrita</i>	1	2	1
<i>Nebria brevicollis</i>	1	11.5	0
<i>Ocys harpaloides</i>	NA	NA	NA
<i>Ocys quinquestriatus</i>	1	4	NA
<i>Olisthopus fuscatus</i>	NA	5.5	NA
<i>Ophonus azureus</i>	0	7.8	1
<i>Ophonus sabulicola</i>	0	15	1
<i>Ophonus subquadratus</i>	0	7.3	1
<i>Paradromius linearis</i>	1	4.5	1
<i>Paroponus maculicornis</i>	0	6.3	1
<i>Paroponus mendax</i>	0	7.8	1
<i>Philorhizus crucifer confusus</i>	NA	2.5	1
<i>Philorhizus quadrisignatus</i>	NA	3.5	1
<i>Phyla obtusa</i>	0.5	2.5	1
<i>Poecilus cupreus</i>	0.5	11	1
<i>Poecilus sericeus</i>	1	12.8	1
<i>Pseudoophonus rufipes</i>	0.5	13.5	0
<i>Scybalicus oblongiusculus</i>	0.5	11.5	0
<i>Syntomus obscuroguttatus</i>	1	2.9	1

<i>Tachyura</i> spp.	NA	NA	NA
<i>Trechus aubei</i>	NA	NA	NA
<i>Trechus austriacus</i>	1	3.5	0
<i>Trechus fulvus</i>	1	4.5	0
<i>Trechus obtusus</i>	1	3.6	0
<i>Trechus quadristriatus</i>	1	3.6	0
<i>Trechus</i> spp.	1	3.6	0
<i>Zuphium olens</i>	NA	9	NA

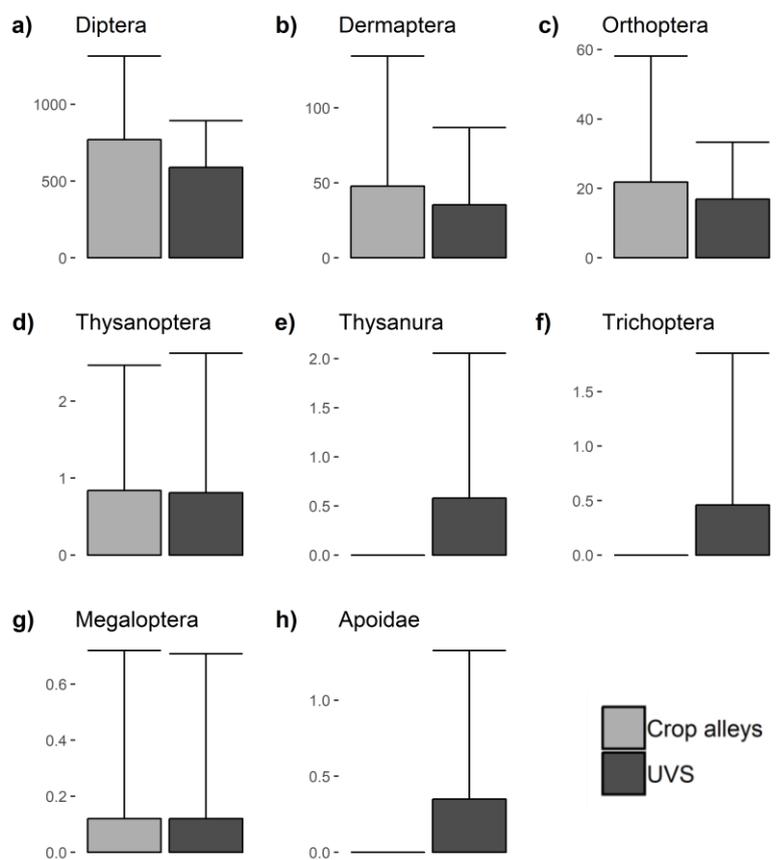


Figure C.1. Mean and standard deviation of density (individuals / m²) for taxonomic groups equally abundant in crop alleys vs UVS.

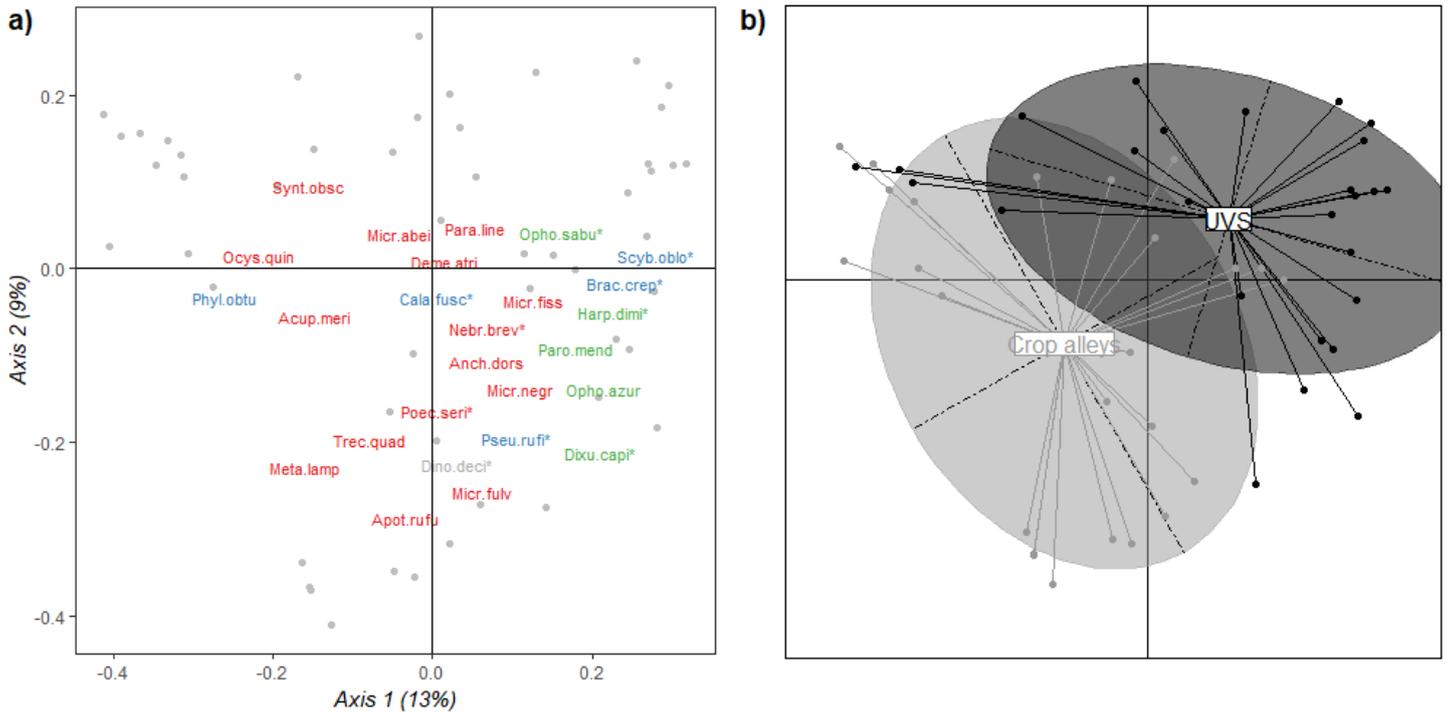


Figure C.2. Principal Coordinates Analysis (PCoA) based on Bray-Curtis distances used to compare carabid species composition between crop alleys and understory vegetation strips (UVS) (Borcard et al., 2011). For this multivariate analysis we only considered dominant species, occurring in more than three emergence traps, because rare species may unduly influence the results (Kenkel et al., 2002). **(a)** Emergence trap scores (grey circles) on the first two axes based on Bray-Curtis distances, and projection of species following Borcard et al. (2011). Green, blue and red labels correspond to predominantly granivorous, omnivorous and carnivorous species, respectively. Species marked with a star are larger carabids ($\geq 8\text{mm}$). **(b)** Ellipses with a 95% confidence interval used to indicate the relative position for habitat clusters. A PERMANOVA test revealed a significant effect of habitat (crop alleys vs UVS) on species composition ($p\text{-value} = 0.001$).

APPENDIX D

Table D.1. Crop management for each pair of agroforestry fields and pure crop controls.

Farming system	Farmer	Cropping system	Cumulated treatment frequency index from sowing 2014 to harvest 2017 ¹	Maximum tillage depth 2016-2017 (cm)	Crop harvested in 2016	Intercrop 2016-2017	Crop harvested in 2017
Conventional	1	Agroforestry	5.1	15	sunflower	none	wheat
		Pure crop	5.1	15	sunflower	none	wheat
	2	Agroforestry	5.8	15	sunflower	none	wheat
		Pure crop	5.2	15	sunflower	none	wheat
	3	Agroforestry	5.7	4	field bean	field bean	wheat
		Pure crop	4.3	25	sunflower	none	wheat
Organic	4	Agroforestry	0	20	sunflower	none	wheat
		Pure crop	0	20	sunflower	none	wheat
	5	Agroforestry	0	5	soybean	none	barley, garden pea, vetch
		Pure crop	0	15	wheat	spontaneous vegetation	barley
	6	Agroforestry	1.7	5	barley, garden pea	none	barley, garden pea
		Pure crop	1.7	5	barley, garden pea	none	barley, garden pea

¹Under conventional farming, all farmers used herbicides with a wide spectrum of action (grass and broadleaf weeds). Farmer n°6 was under conventional farming in 2014-2015.

Table D.2. Description of agroforestry fields.

Farmer	Age of the system (years)	Crop alleys' width (m)	UVS' width (m)	UVS mowing	UVS sowing	Tree species found in transects
1	10	25	2	0	0	<i>Acer campestre, Juglans regia, Pyrus pyraster, Prunus avium, Quercus petraea</i>
2	6	28	1.5	0	0	<i>Juglans regia, Pyrus pyraster, Prunus avium, Quercus pubescens, Sorbus domestica</i>
3	5	38	2	0	1	<i>Acer campestre, Juglans regia, Prunus avium, Sorbus domestica, Tilia cordata</i>
4	2	26	1	0	0	<i>Juglans regia, Prunus avium, Quercus petraea, Sorbus torminalis, Fraxinus excelsior</i>
5	8	17	1	0	0	<i>Pyrus pyraster, Quercus petraea, Sorbus domestica, Sorbus torminalis, Fraxinus excelsior, Cornus sanguinea.</i>
6	5	32	2	1	0	<i>Acer campestre, Juglans regia, Prunus avium, Sorbus domestica, Fraxinus excelsior, Ulmus campestris</i>

Table D.3. Results of GLMMs performed on organic farming fields and conventional ones separately to compare activity-density, species richness and functional structure of predator communities between pure crop (reference level), crop alleys and understory vegetation strips (UVS). CMP = Conway-Maxwell Poisson. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

		Distribution	Conventional		Organic	
			Crop alleys	UVS	Crop alleys	UVS
Granivorous carabids						
Activity-density	CMP		$-0.48 \pm 0.245^*$	-0.04 ± 0.331	$0.77 \pm 0.232^{***}$	$1.10 \pm 0.315^{***}$
Species richness	Poisson		-0.13 ± 0.260	0.02 ± 0.377	$0.54 \pm 0.228^*$	$0.99 \pm 0.286^{***}$
Omnivorous carabids						
Activity-density	CMP		-0.53 ± 0.346	$-1.36 \pm 0.546^*$	$0.76 \pm 0.158^{***}$	0.43 ± 0.255
Species richness	CMP		$-0.46 \pm 0.188^*$	-0.62 ± 0.341	0.10 ± 0.110	0.14 ± 0.172
Cursorial spiders						
Activity-density	CMP		$-0.47 \pm 0.097^{***}$	-0.22 ± 0.146	0.02 ± 0.095	-0.02 ± 0.154
TOTAL						
Activity-density	CMP		$-0.55 \pm 0.087^{***}$	$-0.47 \pm 0.140^{***}$	$0.24 \pm 0.087^{**}$	0.11 ± 0.141
Species richness	CMP		$-0.18 \pm 0.073^*$	-0.05 ± 0.110	0.02 ± 0.073	0.19 ± 0.109
CWM Diet	Beta		-0.11 ± 0.189	-0.30 ± 0.272	$-0.65 \pm 0.147^{***}$	$-0.77 \pm 0.234^{**}$
FDvar Body length	Beta		$0.41 \pm 0.126^{**}$	0.02 ± 0.198	$-0.35 \pm 0.119^{**}$	-0.15 ± 0.187

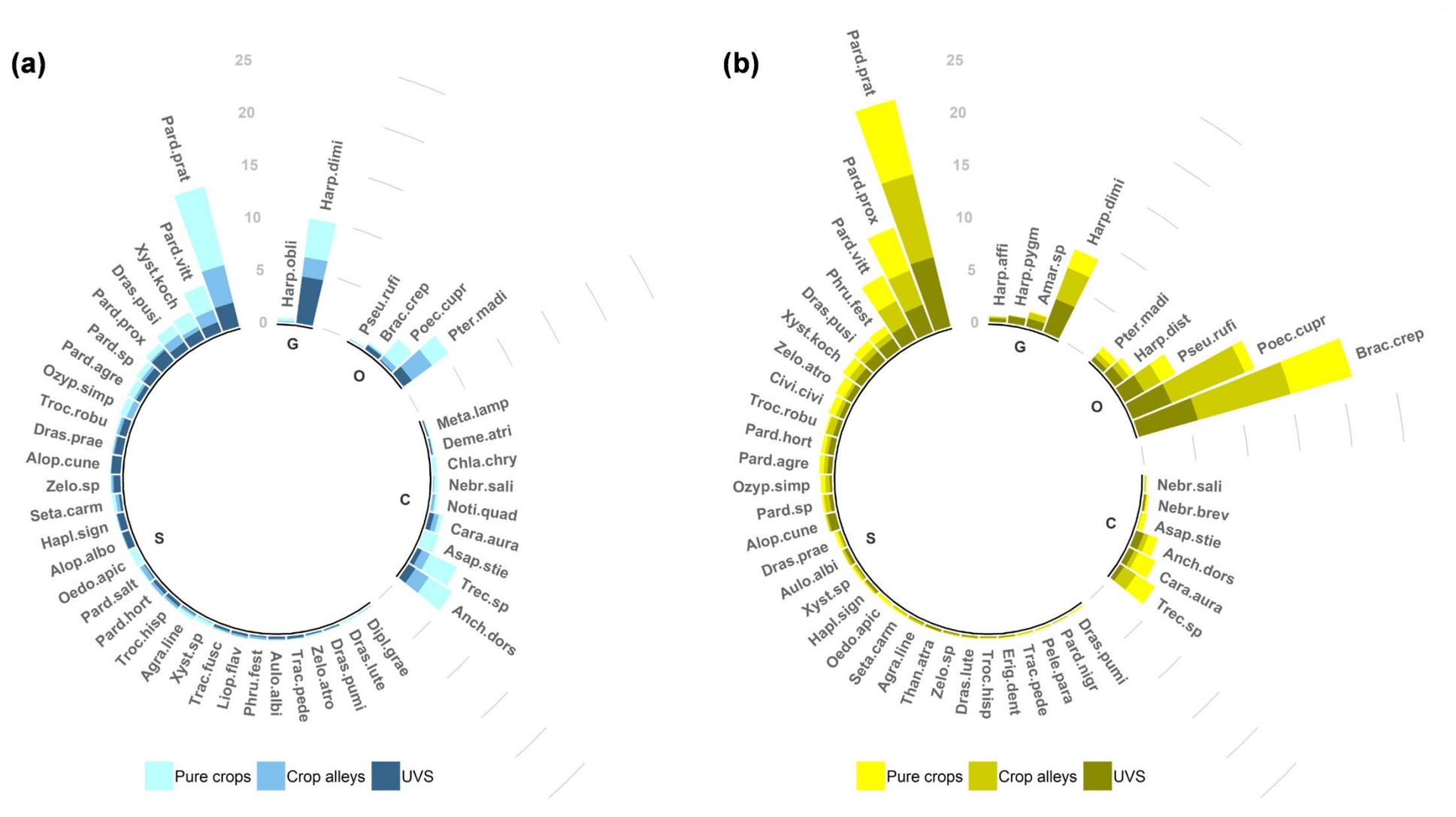


Figure D.1. Mean activity-density of common species (i.e. occurring in at least five pitfall traps) in each functional group (**G**: granivorous carabids, **O**: omnivorous carabids, **C**: carnivorous carabids, **S**: cursorial spiders) under **a)** conventional farming and **b)** organic farming.

Table D.4. Functional trait values of carabid and cursorial spider species (diet; granivorous: 0, omnivorous: 0.5 and carnivorous: 1).

Code	Latin name	Diet	Body length (mm)
Carabids			
Acin.pici	<i>Acinopus picipes</i>	0	14.5
Acup.meri	<i>Acupalpus meridianus</i>	1	3.625
Agon.muel	<i>Agonum muelleri</i>	0.5	7.5
Amar.sp	<i>Amara</i> spp.	0	7.5
Anch.dors	<i>Anchomenus dorsalis</i>	1	6.5
Anis.bino	<i>Anisodactylus binotatus</i>	0	10.5
Asap.stie	<i>Asaphidion stierlini</i>	1	3.5
Badi.bull	<i>Badister bullatus</i>	1	5.25
Bemb.sp	<i>Bembidion</i> spp.	1	NA
Brac.crep	<i>Brachinus crepitans</i>	0.5	8.25
Brac.expl	<i>Brachinus explodens</i>	1	5.75
Cala.fusc	<i>Calathus fuscipes</i>	0.5	12.5
Call.luna	<i>Callistus lunatus</i>	1	6
Cara.aura	<i>Carabus auratus</i>	1	23.5
Cara.purp	<i>Carabus purpurascens</i>	0.5	28.5
Chla.chry	<i>Chlaenius chrysocephalus</i>	1	8.5
Cici.camp	<i>Cicindela campestris</i>	1	12.75
Cyli.germ	<i>Cylindera germanica</i>	1	9.5
Deme.atri	<i>Demetrias atricapillus</i>	1	5
Diac.germ	<i>Diachromus germanus</i>	0	8.75
Harp.affi	<i>Harpalus affinis</i>	0	10.25
Harp.cupr	<i>Harpalus cupreus</i>	0	12.75
Harp.dimi	<i>Harpalus dimidiatus</i>	0	12.5
Harp.dist	<i>Harpalus distinguendus</i>	0.5	9.5
Harp.obli	<i>Harpalus oblitus</i>	0	10
Harp.pygm	<i>Harpalus pygmaeus</i>	0	6.125
Harp.smar	<i>Harpalus smaragdinus</i>	0	9.5
Harp.tene	<i>Harpalus tenebrosus</i>	0	9
Leis.fulv	<i>Leistus fulvibarbis</i>	1	7.5
Lori.pili	<i>Loricera pilicornis</i>	1	7.25
Meta.lamp	<i>Metallina lampros</i>	1	3.125
Meta.prop	<i>Metallina properans</i>	1	3.5
Micr.sp	<i>Microlestes</i> spp.	1	2.5
Nebr.brev	<i>Nebria brevicollis</i>	1	11.5
Nebr.sali	<i>Nebria salina</i>	1	11
Noti.bigu	<i>Notiophilus biguttatus</i>	1	4.875
Noti.quad	<i>Notiophilus quadripunctatus</i>	1	4.625
Opho.ardo	<i>Ophonus ardosiacus</i>	0	12
Opho.azur	<i>Ophonus azureus</i>	0	7.75
Paro.mend	<i>Parophonus mendax</i>	0	7.75

Phil.bigu	<i>Philochthus biguttatus</i>	1	3.625
Phil.gutt	<i>Philochthus guttula</i>	1	2.875
Poec.cupr	<i>Poecilus cupreus</i>	0.5	11
Pseu.rufi	<i>Pseudoophonus rufipes</i>	0.5	13.5
Pter.madi	<i>Pterostichus madidus</i>	0.5	16.5
Sten.skri	<i>Stenolophus skrimshiranus</i>	0.5	5.875
Stom.pumi	<i>Stomis pumicatus</i>	1	7
Synt.obsc	<i>Syntomus obscuroguttatus</i>	1	2.875
Trec.sp	<i>Trechinii</i> spp.	1	3.55
Zabr.tene	<i>Zabrus tenebrioides</i>	0	15

Cursorial spiders

Agra.line	<i>Agraecina lineata</i>	1	6.1
Agro.lusa	<i>Agroeca lusatica</i>	1	5.3
Alop.albo	<i>Alopecosa albofasciata</i>	1	9.8
Alop.cune	<i>Alopecosa cuneata</i>	1	7.3
Alop.pulv	<i>Alopecosa pulverulenta</i>	1	8.5
Arct.peri	<i>Arctosa perita</i>	1	7
Aulo.albi	<i>Aulonia albimana</i>	1	4.1
Chal.nigr	<i>Chalcoscirtus nigrinus</i>	1	3.5
Civi.civi	<i>Civizelotes civicus</i>	1	4.4
Dipl.grae	<i>Diplocephalus graecus</i>	1	1.9
Dras.lapi	<i>Drassodes lapidosus</i>	1	10.8
Dras.pube	<i>Drassodes pubescens</i>	1	7.1
Dras.lute	<i>Drassyllus lutetianus</i>	1	5.7
Dras.pumi	<i>Drassyllus pumilus</i>	1	3.8
Dras.pusi	<i>Drassyllus pusillus</i>	1	4.4
Dras.prae	<i>Drassyllus praeficus</i>	1	6.2
Dysd.eryt	<i>Dysdera erythrina</i>	1	9.3
Erig.dent	<i>Erigone dentipalpis</i>	1	2.3
Hapl.dalm	<i>Haplodrassus dalmatensis</i>	1	5.4
Hapl.sign	<i>Haplodrassus signifer</i>	1	7.3
Hogn.radi	<i>Hogna radiata</i>	1	16
Lasi.hirs	<i>Lasiargus hirsutus</i>	1	2.6
Liop.flav	<i>Liophrurillus flavitarsis</i>	1	5
Merm.tril	<i>Mermessus trilobatus</i>	1	1.9
Mica.albo	<i>Micaria albovittata</i>	1	5.3
Mica.puli	<i>Micaria pulicaria</i>	1	3.6
Micr.aper	<i>Micrargus apertus</i>	1	1.9
Nomi.exor	<i>Nomisia exornata</i>	1	5.9
Oedo.apic	<i>Oedothorax apicatus</i>	1	2.6
Ozyp.simp	<i>Ozyptila simplex</i>	1	3.5
Pard.agre	<i>Pardosa agrestis</i>	1	4.8
Pard.hort	<i>Pardosa hortensis</i>	1	5.2
Pard.nigr	<i>Pardosa nigriceps</i>	1	5.4

Pard.palu	<i>Pardosa palustris</i>	1	6
Pard.prat	<i>Pardosa prativaga</i>	1	6.1
Pard.prox	<i>Pardosa proxima</i>	1	6.7
Pard.pull	<i>Pardosa pullata</i>	1	4.8
Pard.salt	<i>Pardosa saltans</i>	1	5.8
Pard.vitt	<i>Pardosa vittata</i>	1	6.2
Pele.para	<i>Pelecopsis parallela</i>	1	1.5
Phle.bres	<i>Phlegra bresnieri</i>	1	5
Phru.fest	<i>Phrurolithus festivus</i>	1	2.7
Phru.nigr	<i>Phrurolithus nigrinus</i>	1	2.8
Poca.junc	<i>Pocadicnemis juncea</i>	1	1.9
Seta.carm	<i>Setaphis carmeli</i>	1	4
Sibi.auro	<i>Sibianor aurocinctus</i>	1	3.4
Tala.aper	<i>Talavera aperta</i>	1	2.5
Than.atra	<i>Thanatus atratus</i>	1	4.6
Tibe.oblo	<i>Tibellus oblongus</i>	1	7.6
Trac.fusc	<i>Trachyzelotes fuscipes</i>	1	4.6
Trac.pede	<i>Trachyzelotes pedestris</i>	1	6.6
Troc.hisp	<i>Trochosa hispanica</i>	1	10.5
Troc.robu	<i>Trochosa robusta</i>	1	14
Walc.capi	<i>Walckenaeria capito</i>	1	2.7
Xyst.acer	<i>Xysticus acerbus</i>	1	6.5
Xyst.cris	<i>Xysticus cristatus</i>	1	5.6
Xyst.koch	<i>Xysticus kochi</i>	1	6.6
Zelo.atro	<i>Zelotes atrocaeruleus</i>	1	6.9
Zelo.latr	<i>Zelotes latreillei</i>	1	6.7
Zelo.petr	<i>Zelotes petrensis</i>	1	5.8
Zoda.ital	<i>Zodarion italicum</i>	1	2.7
Pard.sp	<i>Pardosa</i> spp.	1	5.7
Xyst.sp	<i>Xysticus</i> spp.	1	6
Zelo.sp	<i>Zelotes</i> spp.	1	6.5

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Résumé de la thèse

Chapitre 1 : Introduction

L'intensification agricole d'après-guerre a permis d'augmenter la productivité des systèmes, à travers la sélection génétique, l'utilisation de pesticides et de fertilisants minéraux, la mécanisation et la simplification des paysages agricoles. Cependant, de tels systèmes de production intensifs ne sont pas durables. L'utilisation de pesticides peut favoriser le développement de résistances et entraîne leur dispersion dans l'air, l'eau et le sol, menaçant ainsi la santé des écosystèmes dont font partie les humains. De plus, les pesticides peuvent s'avérer plus néfastes pour les ennemis naturels de ravageurs, que pour les ravageurs eux-mêmes, ce qui fragilise le contrôle biologique de ces derniers et résulte en un besoin accru en pesticides. Enfin, la destruction des habitats semi-naturels (tels que les forêts, haies, prairies, tourbières, bords de champs, etc.) au profit des surfaces cultivées a engendré un déclin massif de la biodiversité. Les systèmes agroécologiques ont pour objectif de favoriser la biodiversité fonctionnelle dans les champs, tirant profit des fonctions positives qu'elle peut offrir (*e.g.* décomposition de la matière organique, pollinisation, contrôle biologique des ravageurs) tout en limitant ses impacts négatifs potentiels sur la production (*e.g.* compétition entre cultures et adventices, dommages causés par les ravageurs).

La biodiversité d'une parcelle cultivée dépend de la composition et configuration du paysage alentour (*i.e.* proportion, taille, forme et distribution des différents habitats), de facteurs locaux abiotiques (conditions pédoclimatiques) et biotiques (*e.g.* prédateurs, proies) mais aussi de la présence d'infrastructures agroécologiques à proximité, voire à l'intérieur de la parcelle (*e.g.* haies, bandes enherbées semées, mélanges fleuris). Enfin, la biodiversité non cultivée est aussi largement impactée par les pratiques agricoles appliquées dans la parcelle, notamment par les perturbations physiques ou chimiques (telles que le travail du sol et les produits phytosanitaires), mais aussi par le choix des espèces cultivées (auxquelles sont associés différents cortèges d'adventices, ravageurs et ennemis naturels par exemple).

Certaines espèces sont très bien adaptées aux perturbations agricoles et sont même favorisées dans les milieux perturbés. En revanche, beaucoup d'espèces ont besoin d'habitats plus stables pour boucler leur cycle de vie. Les infrastructures agroécologiques sont destinées à favoriser les organismes vivants (notamment les espèces sensibles aux perturbations) et leur dispersion dans les champs, où ils pourront accomplir leurs diverses fonctions (e.g. pollinisation, contrôle biologique).

Les systèmes agroforestiers tempérés bénéficient d'un regain d'intérêt depuis ces trois dernières décennies. Un objectif commun à toute pratique agroforestière est de promouvoir des interactions écologiques positives entre les différentes composantes du système qui sont associées (*i.e.* arbres, arbustes, cultures annuelles, animaux), de sorte que les systèmes agroforestiers soient économiquement, socialement et environnementalement plus performants que les systèmes sans composante ligneuse. Il a été montré que les systèmes agroforestiers offrent une large gamme de services écosystémiques tels que la production plus durable de biomasse, une meilleure protection des sols et des eaux et une conservation accrue de la biodiversité. Les systèmes agroforestiers sont aussi probablement mieux adaptés au changement climatique grâce à la présence des arbres, qui pourraient créer un microclimat plus favorable aux cultures sous-jacentes et à la biodiversité en hiver et en été.

Parmi ces systèmes, l'agroforesterie intra-parcellaire, qui consiste à associer arbres et grandes cultures dans une même parcelle, représente une grande opportunité pour la réintégration des habitats semi-naturels dans les champs. En l'absence de travail du sol et de semis de culture sous les arbres, des bandes de végétation non cultivées se forment, que l'on appelle linéaires sous-arborés (LSA). Étant donné l'implantation des LSA à intervalles réguliers dans la parcelle, et la surface qu'ils occupent, il est probable que la dispersion des organismes et la quantité de refuges pour la biodiversité soient augmentées en agroforesterie intra-parcellaire, en comparaison de témoins agricoles. Cela pourrait résulter en une augmentation des services et/ou dis-services écosystémiques en fonction de la nature des espèces favorisées (adventices compétitives, ravageurs ou auxiliaires de culture). Cependant, nous manquons de connaissances concernant l'impact de l'agroforesterie tempérée sur la conservation de la biodiversité et sur le contrôle biologique des ravageurs, qui représentent des leviers majeurs de la transition vers des systèmes durables et respectueux de l'environnement. Par ailleurs, la majeure partie des études sur le sujet sont restreintes à l'agriculture conventionnelle. L'objectif de cette thèse est (i) de décrire la réponse des communautés de plantes et invertébrés aux systèmes agroforestiers, en interaction avec le mode de production (agriculture conventionnelle vs biologique) (chapitres 2 et 4) et (ii) d'évaluer les effets positifs et négatifs des LSA sur la conservation de la biodiversité et le contrôle biologique des ravageurs (chapitres 2, 3 et 4).

Chapitre 2 : Les systèmes agroforestiers intra-parcellaires : réservoirs à adventices ou refuges pour la diversité végétale ?

Les LSA sont souvent perçus comme des réservoirs à adventices, susceptibles de coloniser les allées cultivées et engendrer des pertes de rendement, mais aussi comme des refuges favorisant la conservation de la biodiversité. Nous avons évalué la contribution des LSA à (i) la dispersion des adventices dans les allées cultivées, et (ii) la conservation de la diversité végétale en agroforesterie. Des relevés de flore ont été réalisés en mai 2017 dans les départements du Gers et des Pyrénées-Atlantiques, sur 16 parcelles de céréales d'hiver avec travail du sol sans labour, pour moitié en agriculture conventionnelle (quatre parcelles agroforestières et quatre témoins agricoles) et pour moitié en agriculture biologique (idem). Les espèces végétales ont été classées selon leur sensibilité aux perturbations agricoles, et considérées comme « agrotolérantes » (adaptées) ou « hémérophobes » (sensibles), sur la base de leur fréquence d'occurrence dans les champs cultivés issue d'une base de données nationale. Les espèces hémérophobes sont celles qui présentent des fréquences d'occurrence dans les champs inférieures à 10%. De plus, les traits fonctionnels des plantes liés à leur tolérance aux perturbations agricoles et à leur stratégie de dispersion ont été récupérés dans des bases de données, afin d'évaluer par quels mécanismes les plantes étaient capables de disperser ou non depuis les LSA vers les allées cultivées.

L'étude révéla que très peu d'espèces sont capables de disperser loin dans les allées cultivées, excepté certaines espèces pérennes capables de reproduction végétative, dont la dispersion a sans doute été favorisée par le travail du sol. C'est le cas du liseron des champs (*Convolvulus arvensis*) et de la potentille rampante (*Potentilla reptans*). En effet, une fois coupés, les fragments végétatifs peuvent former de nouveaux plants. Par conséquent, la compétition par les adventices (estimée par le recouvrement relatif des adventices par rapport à celui de la culture) était similaire entre systèmes agroforestiers et témoins agricoles. En revanche, les LSA abritaient une flore riche et abondante, avec de fortes proportions en espèces hémérophobes, en comparaison des allées cultivées et témoins agricoles. Les refuges offerts par les LSA étaient particulièrement importants en agriculture conventionnelle, où les traitements herbicides limitent grandement le développement des plantes. Ces résultats montrent que l'agroforesterie permet d'augmenter la diversité végétale au sein des parcelles (principalement dans les LSA), sans pour autant augmenter la compétition par les adventices dans les allées cultivées adjacentes aux LSA.

Chapitre 3 : Distribution des invertébrés hivernants dans les systèmes agroforestiers intra-parcellaires : implications pour la conservation de la biodiversité et le contrôle biologique

Le déclin massif des invertébrés à l'échelle mondiale est principalement causé par la destruction des habitats (semi-)naturels, l'intensification agricole et l'urbanisation. Les habitats semi-naturels sont particulièrement importants pour les invertébrés car ils leur servent de sites permanents d'alimentation, de reproduction, d'hivernation et de refuges lors des travaux agricoles. Par ailleurs, le succès de l'hivernation des invertébrés régit directement la dynamique des populations observées au printemps dans les parcelles, affectant donc la conservation de la biodiversité et le contrôle biologique des ravageurs. Or, les milieux cultivés, très souvent perturbés par le travail du sol et/ou par les traitements phytosanitaires, ne sont généralement pas propices à l'hivernation des invertébrés. Nous avons donc évalué si les LSA constituaient des sites d'hivernation importants pour les invertébrés dans les systèmes agroforestiers intra-parcellaires, en comparaison des allées cultivées qui sont perturbées par le travail du sol. Nous nous sommes concentrés sur les carabes, qui sont des prédateurs généralistes communs des milieux agricoles, mais en déclin à cause de l'intensification agricole. Ces coléoptères peuvent se nourrir de différents ravageurs tels que les pucerons ou les limaces par exemple, et peuvent aussi pour certaines espèces consommer des graines adventices. Nous avons décrit les communautés de carabes par des traits fonctionnels liés à leur sensibilité aux perturbations agricoles mais aussi à leur fonction (*i.e.* régulation des adventices et ravageurs). Nous avons échantillonné les invertébrés hivernants à l'aide de tentes à émergence de février à juin 2018 sur sept parcelles agroforestières (céréales d'hiver avec labour), au domaine de Restinclières dans le sud de la France.

L'étude révéla que les LSA sont d'importants sites d'hivernation pour les invertébrés. En effet, 55% des groupes taxonomiques observés étaient plus abondants dans les LSA que dans les allées cultivées, tandis que 14% étaient plus abondants dans les allées. Par ailleurs, les ravageurs de culture dominants (pucerons, limaces, taupins) hivernaient principalement dans les allées cultivées, tandis que les invertébrés fournissant des services (décomposeurs de matière organique, ennemis naturels de ravageurs, consommateurs de graines adventices, pollinisateurs) dépendaient plus souvent de la présence des LSA pour passer l'hiver. Les carabes étaient plus abondants dans les allées cultivées (toutes espèces confondues) mais cela variait grandement d'une espèce à l'autre en fonction de sa sensibilité aux perturbations agricoles. Dans les allées cultivées se trouvaient en majorité les carabes strictement carnivores, de petite taille et hivernant à l'état adulte et/ou larvaire, qui préfèrent les milieux perturbés. En revanche, les espèces sensibles (carabes principalement granivores, de grande taille et hivernant à l'état adulte uniquement) dépendaient très fortement des LSA. En conclusion, ces résultats suggèrent que l'agroforesterie permet, grâce à la présence des LSA,

d'augmenter la conservation de la diversité en invertébrés sans pour autant favoriser l'hivernation des ravageurs dominants. La dispersion des invertébrés bénéfiques serait aussi facilitée en comparaison des témoins agricoles, grâce à la présence de sites d'hivernation favorables au sein même des parcelles.

Chapitre 4 : Dispersion des prédateurs généralistes dans les systèmes agroforestiers: rôle déterminant du mode de production

Afin de promouvoir la dispersion des ennemis naturels de ravageurs dans les champs, les systèmes agroécologiques reposent notamment sur la présence d'habitats semi-naturels autour, voire à l'intérieur des parcelles. L'agriculture biologique permet aussi de favoriser la biodiversité, par la réduction de l'utilisation de produits phytosanitaires mais aussi par la présence d'une flore adventice riche et abondante, offrant des micro-habitats et des ressources (pollen, nectar, graines, détritivores et phytophages associés) aux invertébrés. Nous avons évalué le potentiel de régulation des adventices et ravageurs par les communautés de prédateurs généralistes (carabes et araignées coureuses) dans les systèmes agroforestiers comparés aux témoins agricoles et selon le mode de production (agriculture conventionnelle vs biologique). Nous avons effectué des relevés de carabes et araignées à l'aide de pièges Barber en mai et juin 2017 dans le département du Gers, sur 12 parcelles de céréales d'hiver avec un travail du sol sans labour (pour moitié en agriculture conventionnelle et pour moitié en agriculture biologique, avec trois couples de parcelles agroforestières et témoins agricoles dans chaque cas).

L'étude révéla que l'effet de l'agroforesterie sur les communautés de prédateurs généralistes est modulé par le mode de production. En agriculture conventionnelle, l'agroforesterie avait un impact négatif sur les communautés de prédateurs, qui peut s'expliquer par deux mécanismes. Premièrement, les LSA peuvent défavoriser ou gêner le déplacement des prédateurs dominants établis dans les champs, qui hivernent et chassent dans les milieux perturbés et ouverts (effet « puits » des LSA). C'est le cas des carabes strictement carnivores (en particulier ceux de petite taille), dont l'activité-densité était réduite de 50% en moyenne dans les allées cultivées, en comparaison des témoins agricoles. De plus, la dispersion des carabes granivores et araignées, qui hivernent dans les LSA, est limitée par la faible quantité et diversité de ressources dans les allées (effet « rétention » des LSA). En agriculture biologique, l'agroforesterie impactait positivement les communautés de prédateurs généralistes, en augmentant l'activité-densité et la complémentarité des prédateurs, et donc potentiellement le contrôle biologique des adventices et ravageurs (effet « source » des LSA). En particulier, combiner agroforesterie et agriculture biologique favorisait très largement les carabes majoritairement granivores et omnivores, qui consomment des graines adventices. Ces résultats suggèrent que l'efficacité des infrastructures

agroécologiques pour favoriser les prédateurs généralistes dépend non seulement du contexte paysager, comme démontré par de précédentes études, mais aussi du mode de production, qui affecte la disponibilité en ressources et détermine l'intensité de dispersion des prédateurs entre habitats semi-naturels et cultivés. Ainsi, si les infrastructures agroécologiques sont souvent perçues comme des sources d'ennemis naturels de ravageurs, leurs effets sur les communautés de prédateurs sont potentiellement mitigés par leurs effets de « puits » ou de « rétention », notamment en agriculture conventionnelle.

Chapitre 5 : Discussion

Les résultats de cette thèse, restreints aux céréales d'hiver avec travail du sol, montrent que les LSA sont des habitats précieux pour la conservation de la biodiversité car ils abritent une forte diversité de plantes et d'invertébrés, ce qui devrait aussi favoriser des niveaux trophiques supérieurs tels que les oiseaux, mammifères, reptiles et amphibiens. Par ailleurs, les LSA ne semblent guère constituer une source d'adventices ni favoriser l'hivernation des ravageurs dominants. Il est encore difficile de tirer des conclusions concernant le contrôle biologique des ravageurs, bien que nos résultats suggèrent un effet positif des systèmes agroforestiers. En offrant des sites d'hivernation, les LSA peuvent favoriser la dispersion des carabes majoritairement granivores et des araignées coureuses dans les allées cultivées, ce qui devrait résulter en un contrôle biologique accru des adventices et ravageurs. Ceci est particulièrement vrai en agriculture biologique, tandis que des effets négatifs de « rétention » se produisent en agriculture conventionnelle. L'agroforesterie semble aussi impacter négativement les carabes strictement carnivores, en particulier ceux de petite taille qui hivernent et chassent dans les milieux ouverts et perturbés. Cette thèse, dont les résultats ont été obtenus sur des céréales d'hiver avec travail du sol superficiel, a permis de combler un manque de connaissances sur la biodiversité en agroforesterie tempérée et de fournir des pistes de gestion des infrastructures agroécologiques, implantées pour favoriser la biodiversité et réduire l'utilisation de produits phytosanitaires.

5.1. Optimiser la fourniture de services écosystémiques par les LSA

En agroforesterie, trois leviers semblent prometteurs afin d'améliorer la fourniture de services écosystémiques tels que la pollinisation, le contrôle biologique des ravageurs, la protection des eaux et des sols et le stockage de carbone par les LSA : maintenir des arbustes entre les arbres de haut-jet, élargir les LSA, faucher partiellement la végétation. Les arbres et arbustes n'ont pas été étudiés au cours de cette thèse, bien qu'ils permettent très certainement de favoriser la conservation de la biodiversité et le contrôle biologique des ravageurs. En effet, les ligneux offrent des micro-habitats aux invertébrés, servant à la reproduction, au repos, à l'estivation ou encore leur permettant d'échapper aux prédateurs. Les ligneux peuvent aussi représenter une source de nourriture importante pour les pollinisateurs (pollen, nectar) mais

aussi pour les prédateurs (proies invertébrées associées aux ligneux mais aussi pollen et nectar floral ou extra-floral). Les arbres et haies favorisent aussi les oiseaux et chauve-souris, qui peuvent contribuer au contrôle biologique. La combinaison de ligneux et de cultures devrait fournir une plus grande diversité de niches écologiques dans le temps et dans l'espace pour les invertébrés, permettant ainsi de réduire les probabilités de colonisation par les ravageurs. Enfin, les haies sont des éléments incontournables des paysages agricoles car elles favorisent la conservation de la biodiversité, la pollinisation, le contrôle biologique des ravageurs, le stockage de carbone, le cycle des nutriments ou encore la protection des sols et des eaux.

L'élargissement des LSA diminuerait directement la surface de production agricole mais pourrait en contrepartie offrir de nombreux services. Des études sur les bords de champs ont montré que des bandes de végétation plus larges tendent à abriter plus d'espèces végétales, mais aussi à favoriser les espèces végétales sensibles aux perturbations agricoles en comparaison des adventices communes des champs, ce qui s'expliquerait par une meilleure qualité environnementale à l'intérieur des larges bandes de végétation. Ceci permettrait de diminuer le risque de colonisation des allées cultivées par des adventices provenant des LSA. Par ailleurs, la réduction de l'eutrophisation du sol dans les bandes larges permettrait de réduire la dominance des graminées compétitives à croissance rapide, ce qui augmenterait l'abondance et la diversité des espèces mellifères et favoriserait de nombreuses espèces de pollinisateurs et d'ennemis naturels de ravageurs. L'augmentation de la proportion d'habitats peu perturbés au sein de la parcelle augmenterait la disponibilité en ressources et la présence de refuges pour les invertébrés bénéfiques. Une étude a montré que malgré la perte de surface de production (3 à 8% dans cette étude), maintenir des infrastructures agroécologiques augmente les services de pollinisation et de contrôle biologique des ravageurs dans les cultures adjacentes, résultant en une production agricole globale plus élevée qu'en l'absence de ces habitats. De plus, les bandes de végétation plus larges interceptent efficacement les résidus de pesticides, l'azote, le phosphore et les sédiments, préservant ainsi la qualité des sols et des eaux. Elargir les LSA pourrait aussi augmenter le stockage de carbone et l'albédo de surface dans les parcelles de grandes cultures, ce qui pourrait contribuer à l'atténuation du changement climatique, si les LSA étaient implantés à plus large échelle. Enfin, il semble plus approprié d'utiliser la surface à proximité des rangées d'arbres à d'autres fins que la production agricole, étant donné que les pertes de rendement et de qualité de la culture sont plus fortes à proximité des rangées d'arbres âgés, probablement à cause de l'ombrage. Il reste à déterminer quelles configurations spatiales (i.e. surface occupée par les allées cultivées vs LSA) offrent un bon équilibre entre production agricole et fourniture de services écosystémiques.

Enfin, dans les milieux riches en nutriments, faucher la végétation permet de réduire la dominance des espèces compétitives et de grande taille, augmentant ainsi la richesse en espèces et la provision de fleurs pour les invertébrés. Il est important de retirer la biomasse après fauche pour favoriser la croissance des espèces, car une trop grande quantité de litière au sol peut empêcher la germination des graines. De plus, une fauche répétée avec retrait de biomasse permet de réduire le stock de nutriments dans le sol, créant des conditions

favorables aux espèces moins rudérales et favorisant la protection de la qualité des eaux (via le prélèvement des polluants par les plantes compétitives fauchées). Beaucoup d'espèces dicotylédones sont capables de se régénérer rapidement après la fauche, prolongeant ainsi la provision de fleurs jusqu'au début de l'automne. Cependant, une fauche trop fréquente peut empêcher le développement des plantes à croissance plus lente, tandis qu'une fauche trop précoce peut affecter les espèces à grenaison tardive. De plus, la fauche effectuée par les machines forme des habitats très homogènes, épuisant temporairement les ressources, affectant le microclimat et tuant de nombreuses espèces animales. La fauche tardive détruit les structures végétales servant de sites d'hivernation pour certains invertébrés et les sites de nidification pour les oiseaux des champs. Dans l'ensemble, faucher une à deux fois par an avec retrait de la biomasse semble constituer un régime de perturbations intermédiaire maintenant une forte richesse en plantes et invertébrés. Cependant, il est recommandé de préserver des zones refuges non fauchées, sous la forme de patches ou de bandes. Ces zones refuges peuvent être déplacées d'année en année afin d'éviter le déclin de la richesse en espèces dû aux graminées compétitives, qui dominent rapidement dans des conditions riches en nutriments. Les opérations fréquentes avec une faucheuse montée sur tracteur peuvent avoir un impact négatif sur les organismes du sol, c'est pourquoi il est conseillé d'utiliser des outils manuels autant que possible. Enfin, quelle période de l'année, mais aussi de la journée, est la plus appropriée pour faucher reste à étudier. La fauche en début de matinée devrait probablement être évitée car beaucoup d'invertébrés sont inactifs et cachés dans la végétation à ce moment de la journée. Pour conclure, ces trois leviers de gestion des LSA (maintenir des arbustes, élargir les LSA, faucher partiellement la végétation) pourraient être combinés sur une même parcelle afin de favoriser une diversité d'habitats, chacun abritant des cortèges d'espèces végétales et animales qui leur sont propres et offrant différents services écosystémiques.

5.2. Questions de recherches émergentes

Durant cette thèse, nous avons répondu à une question importante pour les agriculteurs agroforestiers : les LSA sont-ils des réservoirs à adventices ? Nous avons démontré que peu d'espèces sont capables de bien se développer à la fois dans les LSA et dans les allées cultivées avec travail du sol superficiel. Ce résultat soulève une nouvelle question, moins intuitive et à l'exact opposé de notre premier point de vue : les LSA sont-ils une barrière à la dispersion des adventices ? Certains auteurs ont montré que les bandes enherbées semées peuvent en effet réduire la dispersion des adventices depuis les habitats semi-naturels vers les champs ou inversement. Ceci s'explique par le fait que les adventices typiques des champs cultivés sont adaptées aux perturbations agricoles, et ne pourraient persister sans elles. Ces espèces adventices sont incapables de s'installer dans les bandes enherbées semées, qui sont dominées par des graminées compétitives dans les milieux plus stables. De même, il a été montré que les champs de plus grande taille abritent des communautés adventices plus abondantes. Il est donc probable que les habitats semi-naturels, dont font partie les LSA,

affectent la dynamique des populations adventices en constituant des habitats « puits », dans lesquels les adventices des champs ne sont guère performantes. Deux mécanismes pourraient expliquer le rôle de barrière à la dispersion des adventices assuré par les LSA. Premièrement, les adventices qui dispersent depuis les allées vers les LSA pourraient souffrir de la compétition imposée par d'autres plantes déjà bien établies à l'intérieur (ou à proximité) des LSA. Ceci est vraisemblable pour les espèces adventices à forte capacité de dispersion (anémochore, zoochore, végétative). De plus, la dispersion horizontale au niveau du sol, via les machines agricoles ou le vent, serait interrompue par la présence des LSA à intervalles réguliers (affectant également les espèces barochores). Ceci résulterait en une surface d'habitat réduite pour les adventices, avec moins d'opportunités de s'établir et une compétition intra- et interspécifique potentiellement accrue.

Une autre question reste en suspens concernant le contrôle biologique des ravageurs : l'agroforesterie augmente-t-elle la complémentarité de niches ou la prédation intraguilde entre ennemis naturels de ravageurs ? Dans le cas de complémentarité de niches entre prédateurs, le contrôle biologique des ravageurs est efficace car les espèces prédatrices diffèrent par la façon, l'endroit et le moment où elles attaquent les ravageurs. En revanche, la prédation intraguilde diminue le contrôle biologique des ravageurs car une espèce prédatrice (*i.e.* prédateur intraguilde) peut s'attaquer à un autre prédateur (*i.e.* proie intraguilde), avec lequel elle est en compétition pour une ressource (*i.e.* ravageur de culture). Des études ont confirmé l'hypothèse de complémentarité de niches entre prédateurs, montrant qu'une diversité de prédateurs aboutit à un contrôle biologique accru des ravageurs. En agroforesterie et en agriculture biologique, la complexité structurale de la végétation pourrait offrir des niches écologiques pour une diversité de prédateurs et réduire ainsi les risques de rencontres entre prédateurs (*i.e.* prédation intraguilde). Les plantes favorisent également des proies alternatives (*e.g.* phytophages et décomposeurs de matière organique) qui peuvent aider les prédateurs à survivre en période de faible disponibilité en ravageurs, mais qui pourraient aussi détourner les prédateurs des ravageurs dominants. Par ailleurs, il a été montré que la présence d'arbres et de LSA en agroforesterie favorise les oiseaux et micromammifères, dont l'effet sur le contrôle biologique des adventices et invertébrés ravageurs reste plus ou moins obscur. En effet, les oiseaux et micromammifères peuvent aider à la régulation des adventices en consommant des graines, et peuvent aussi bien s'attaquer aux invertébrés ravageurs qu'aux prédateurs. Il apparaît nécessaire de tenir compte de l'ensemble des réseaux trophiques afin de décrire les interactions complexes se produisant certainement dans les systèmes agroforestiers et comprendre les processus écologiques réduisant ou augmentant le contrôle biologique des ravageurs.

Abstract: The current intensive food production is one of the main causes of biodiversity extinction worldwide. Alley cropping agroforestry, in which arable crops are grown between tree rows, represents a great opportunity for the reintegration of semi-natural habitats within fields. Tree rows are associated with non-crop vegetation, hereafter called understory vegetation strips (UVS). Given the spatial configuration and the important extent of UVS within crop fields, it is likely that both the dispersal of living organisms and the amount of refugia for biodiversity are increased in alley cropping agroforestry compared to pure crop systems. This could result in enhanced ecosystem services and/or disservices, depending on the nature of favored species (e.g. competitive weeds, invertebrate pests, natural enemies). The objective of this PhD thesis was to describe the response of plant and invertebrate communities to alley cropping agroforestry and farming systems (conventional vs organic) and assess both the positive and negative effects of UVS on biodiversity conservation and biological control of weeds and crop pests. A production field network was used to sample plant and invertebrate communities in alley cropping agroforestry systems and pure crop controls, while an experimental site was used to study invertebrate overwintering in agroforestry systems. We described both the taxonomic and functional structures of communities to better understand their responses to agroforestry systems and, for invertebrates, their potential effects on biological control. Our studies confirmed that UVS are valuable habitats for plant and invertebrate diversity conservation. UVS do not appear to be a source of troublesome weeds or to favor the overwintering of dominant pests, but greatly affect the spillover of ground-dwelling predators in negative or positive ways depending on the farming system. The results obtained from this PhD thesis fill a knowledge gap about the biodiversity of temperate agroforestry systems and provide insights for the management of agroecological infrastructures, which are established to favor functional biodiversity and reduce the use of agrochemicals.

Résumé : Le système de production agricole actuel est l'une des causes principales d'extinction globale de la biodiversité. L'agroforesterie intra-parcellaire, qui consiste à associer arbres et grandes cultures sur une même parcelle, représente une grande opportunité pour la réintégration des habitats semi-naturels dans les champs. Les rangées d'arbres sont associées à des bandes de végétation non cultivées, que l'on appelle linéaires sous-arborés (LSA). Étant donné la configuration spatiale et la surface occupée par les LSA, il est probable que la dispersion des organismes et la quantité de refuges pour la biodiversité soient augmentées en agroforesterie intra-parcellaire, en comparaison de témoins agricoles. Cela pourrait résulter en une augmentation des services et/ou dis-services écosystémiques en fonction de la nature des espèces favorisées (adventices compétitives, ravageurs ou auxiliaires de culture). L'objectif de cette thèse était de décrire la réponse des communautés de plantes et invertébrés aux systèmes agroforestiers et au mode de production (agriculture conventionnelle vs biologique) et d'évaluer les effets positifs et négatifs des LSA sur la conservation de la biodiversité et le contrôle biologique des ravageurs et adventices. Les communautés de plantes et invertébrés des systèmes agroforestiers et des témoins agricoles ont été échantillonnées sur un réseau de parcelles, tandis qu'un site expérimental servit à l'étude de l'hivernation des invertébrés en agroforesterie. Nous avons décrit la structure taxonomique et fonctionnelle des communautés pour comprendre leurs réponses aux systèmes agroforestiers et, pour les invertébrés, leurs potentiels effets sur le contrôle biologique. Nos études ont confirmé que les LSA sont des habitats favorables au maintien de la biodiversité dans les champs. Les LSA ne semblent guère constituer une source d'adventices ni favoriser l'hivernation des ravageurs dominants, mais affectent grandement la dispersion des prédateurs généralistes, de façon positive ou négative selon le mode de production. Les résultats obtenus au cours de cette thèse comblent un manque de connaissances sur la biodiversité des systèmes agroforestiers tempérés et fournissent des pistes de gestion des infrastructures agroécologiques, qui sont implantées afin de favoriser la biodiversité fonctionnelle et réduire l'utilisation de produits phytosanitaires.