COMMUNAUTÉ FRANÇAISE DE BELGIQUE

UNIVERSITÉ DE LIÈGE – GEMBLOUX AGRO-BIO TECH

Spatial diversification of agroecosystems towards biological control of insect pests: A focus on intercropping and wildflower strips

Séverin Marie Marc HATT

Dissertation originale présentée en vue de l'obtention du grade de docteur en sciences
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Abstract

Facing the limits of input-intensive agriculture, agroecology aims at thinking ways to design a sustainable agriculture that is economically viable and socially relevant. It notably invites to mobilize ecological processes within agroecosystems in order to enhance the delivery of ecosystem services towards reducing the use of external inputs – among others insecticides. For enhancing biological control of insect pests, a strategy is to spatially diversify agroecosystems at the field scale. Whereas increasing plant diversity could directly negatively affect pest development on the one hand (i.e. bottom-up effect), providing flowering features could allow the enhancement of natural enemies and their direct effect on pest populations on the other hand (i.e. top-down effect). The present thesis focused on intercropping (i.e. the cultivation of at least two crop species simultaneously in a same field) as a way to diversify crop habitat, and the sowing of wildflower strips as a non-crop feature.

A systematic analysis of the literature revealed that, in most of studies, wheat (*Triticum aestivum* L.)-based intercropping allows a reduction of insect pests on crops, without necessarily favouring their natural enemies, compared to pure-stands. Besides, the provision of flowering resources, by for instance sowing wildflower strips, can attract and support flower visiting predators and parasitoids.

Hence, in a first set of field experiments, combining the two tactics of increasing crop diversity and providing flowering resources was tested. First in China, wheat crop was associated with oilseed rape (*Brassica napus* L.), but it neither allowed reducing aphid (Hemiptera: Aphididae) abundance nor enhancing their natural enemies compared to pure stands. Instead, aphid density – independently from the treatments – affected natural enemy abundance, and interspecific relations between aphids and their natural enemies were observed. Second in Belgium, wildflower strips were sown within a wheat field, which led to a reduction of aphid density in wheat plots in between flowering features and an increase of aphidophagous hoverflies (Diptera: Syrphidae) compared to pure-stand wheat. Nevertheless, the presence of flowering strips did not affect the other natural enemies, i.e. lacewings (Neuroptera: Chrysopidae), ladybeetles (Coleoptera: Coccinellidae) and parasitoid wasps (Hymenoptera: Braconidae).

Therefore, a second set of field experiments focussed on ways to compose mixtures of wild flowers attractive to a diversity of natural enemies. Flower functional traits were considered due to their effect on insect behaviour. First, the hypothesis that mixtures with high functional diversity attract and support a high abundance and diversity of aphid flower visiting predators was tested. This hypothesis was not verified. Instead, the high density in the plots of some flower species (especially the Asteraceae *Leucanthemum vulgare* Lam.) known to be attractive to flower visitors was supposed to have overwhelmed the effect of functional diversity. Second, a methodology was developed to identify which flower traits significantly affect natural enemy abundance – in this experiment parasitoids of oilseed rape beetle pests (i.e. *Meligethes* spp. [Coleoptera: Nitidulidae] and *Ceutorhynchus* spp. [Coleoptera: Curculionidae]) – in flower mixtures. Among seven traits, visual traits (i.e. colour, ultra-violet reflectance) and the one related to food availability (i.e. corolla morphology) were found to significantly affect parasitoid abundance.

These results highlight that (i) increasing plant diversity at the field scale can – but not systematically – favour a reduction of insect pests, (ii) including flowering features can enhance some – but not all – of their natural enemies, and (iii) in order to compose flower mixes attractive to natural enemies, specific flower traits – rather than functional diversity at the mixture level – can be considered.

These results are discussed in a broader perspective. Indeed, strategies to spatially diversify crop and non-crop habitats in agroecosystems are various, as well as the ways to compose, manage and design such habitats. Also, processes at larger scales than the field may be determinant. Moreover, insects are not the only pests, and pests are not the only biotic or abiotic elements that need to be regulated in agroecosystems. Controlling multiple pests simultaneously but also enhancing the provision of multiple regulating services represent challenges for future research in agriculture.

摘要

面对集约化农业的局限性，农业生态学旨在思考如何设计一种在经济上可行和社会相关的可持续农业。农业生态学强调在农业生态系统中加强生态系统的功能以减少化学杀虫剂的使用。为了加强对害虫的生物防治，增加农业生态系统的植物多样性是常见策略之一。而植物多样性的增加一方面可能直接对害虫发展产生负面影响（即自下而上的效应），另一方面提供开花植物可以增强对天敌调控而对害虫种群产生影响（即自上而下的效应）。本研究通过作物与非寄主植物野花进行条带式间作（即在同一领域同时种植至少两种作物物种），以提高农业生态系统植物多样性，增强对害虫以及天敌的调控作用。

文献分析显示，在大多数研究中，与小麦 (*Triticum aestivum* L.) 单作相比，小麦间作可以显著减少害虫危害，但是对害虫天敌的发生无显著提高作用。此外，研究显示可以通过种植野花条带提高访花天敌和寄生蜂的数量。

第一部分田间试验，综合测试了作物间作和开花植物间作两种增加农田生态系统植物多样性的策略。首先在中国田间采用小麦与油菜 (*Brassica napus* L.) 间作，与单作相比，它既不能减少蚜虫 (Hemiptera: Aphididae) 为害，也没有增强蚜虫天敌的发生。其次在比利时田间采用小麦和野花进行条带间作，与小麦单作相比，间作田间的蚜虫发生显著降低，蚜虫的天敌食蚜蝇 (Diptera：Syrphidae) 发生量显著增加。然而，野花条带的存在并不影响其他天敌的发生量，如草蛉 (Neuroptera： Chrysopidae)，瓢虫(Coleoptera:Coccinellidae) 和寄生蜂 (Hymenoptera：Braconidae)。

第二部分田间实验，测试了间作不同野花品种和种植密度组合对天敌的吸引作用。主要考虑了开花特性对天敌昆虫行为的影响。首先，假设尽可能提高单位面积内植物的种类，以提高吸引访花天敌的丰度和多样性，但是结果不支持这个假设。相反，多品种混作反而掩盖了已知对访花天敌有吸引力的一些开花植物（特别是菊科植物 *Leucanthemum vulgare* Lam.）的功能。其次在这个实验中，开发了一种可以确定与天敌丰富度相关的花的性状的方法，测试对象为油菜甲虫的寄生蜂 [i.e. *Meligethes* spp. (Coleoptera：Nitidulidae) 和 *Ceutorhynchus* spp. (Coleoptera：Curculionidae)]。在花的七个性状中，视觉特征（即颜色和紫外反射率）和与食物可利用性（即花冠形态）可以显著影响寄生蜂的丰度。

这些结果表明：（i）田间增加植物多样性只能减少部分害虫为害，（ii）间作植物的开花特征对一部分的天敌吸引作用影响较大，（iii）开花植物的开花特征比密度对天敌的吸引作用更大。

这些结果有待进一步讨论。事实上在农业生态系统中，管理和设计作物和非寄主作物多样化的战略是很多的。此外，大规模的区域景观生态比单一的田间生态更加重要，害虫也不是农业生态系统中唯一需要监管的生物或非生物因素。同时控制多种害虫，可以提供多重监管服务是未来农业研究的挑战。

Résumé

Face aux limites de l'agriculture intensive en intrants, l'agroécologie propose un cadre pour penser la conception d'une agriculture écologiquement durable, mais aussi économiquement viable et socialement responsable. Notamment, elle invite à mobiliser les processus écologiques au sein des agroécosystèmes dans le but d'accroitre la fourniture de services écosystémiques, pour réduire l'usage des intrants externes – parmi d'autres les insecticides. Une stratégie pour favoriser la lutte biologique contre les insectes ravageurs est de diversifier spatialement les agroécosystèmes à l'échelle parcellaire. D'un côté, accroitre la diversité végétale peut directement pénaliser le développement des ravageurs (effet « bottom-up »), d'un autre côté fournir une resource florale peut favoriser le développement d'ennemis naturels et potentiellement leur action de prédation et de parasitisme sur les ravageurs (effet « top-down »). Dans ce but, la présente thèse s'intéresse aux associations de cultures (cultiver au moins deux cultures simultanément dans la même parcelle) comme un outil de diversification des habitats cultivés, et au semis de bandes de fleurs sauvages comme habitat semi-naturel.

Une analyse systématique de la littérature montre que, dans la plupart des études, les associations de cultures intégrant le blé (*Triticum aestivum* L.) permettent une réduction de l'abondance en insectes ravageurs, sans pour autant favoriser leurs ennemis naturels, en comparaison à des cultures pures. Par ailleurs, la fourniture de ressource florale, en semant par exemple des bandes de fleurs sauvages, peut attirer et maintenir des populations de prédateurs et de parasitoïdes.

D'où, un premier ensemble d'expériences consista à évaluer en champ l'effet combiné de l'accroissement de la diversité végétale et de la fourniture de ressources florales sur les populations de ravageurs et d'ennemis naturels. Dans un premier temps en Chine, du blé fut associé à du colza (*Brassica napus* L.), mais cela ne permit ni de réduire les populations de pucerons (Hemiptera : Aphididae), ni d'accroitre celles de leurs ennemis naturels, en comparaison à des parcelles en culture pure. Les ennemis naturels furent plutôt affectés par l'abondance en pucerons – indépendamment des traitements – et des relations interspécifiques entre pucerons et ennemis naturels furent observées. Dans un second temps en Belgique, des bandes de fleurs sauvages furent semées au sein d'une parcelle de blé. Une moindre abondance en pucerons et un accroissement du nombre de syrphes aphidiphages (Diptera : Syrphidae) fut observé dans la culture entre les bandes fleuries en comparaison à des parcelles en culture pure. Néanmoins, la présence de fleurs sauvages n'affecta pas les autres ennemis naturels, précisément les chrysopes (Neuroptera : Chrysopidae), les coccinelles (Coleoptera : Coccinellidae) et les parasitoïdes (Hymenoptera : Braconidae).

C’est pourquoi, un second ensemble d’expériences en champ se pencha sur la composition des mélanges fleuris et leur attractivité pour une diversité d’ennemis naturels. Les traits fonctionnels des fleurs furent considérés du fait de leur effet sur le comportement des insectes. Dans un premier temps, l’hypothèse que des mélanges fleuris ayant une diversité fonctionnelle élevée attirent et maintiennent une grande diversité et abondance de prédateurs de pucerons fut testée. Cette hypothèse ne fut pas vérifiée. Il fut supposé que la densité élevée, dans quelques unités expérimentales, de certaines espèces de fleurs (en particulier l’Asteraceae *Leucanthemum vulgare* Lam.) connues pour être particulièrement attractives, a pu prendre le dessus sur l’effet de la diversité fonctionnelle. Dans un second temps, une méthodologie fut développée dans le but d’identifier les traits fonctionnels qui effectivement affectent l’abondance des ennemis naturels – dans cette expérience les parasitoïdes des ravageurs coléoptères du colza (*Meligethes* spp. [Coleoptera : Nitidulidae] et *Ceutorhynchus* spp. [Coleoptera : Curculionidae]) – dans les mélanges fleuris. Parmi sept traits, ceux relatifs à la vision (couleur, réflectance ultra-violette) et à la disponibilité en ressource alimentaire (morphologie de la corolle) eurent un effet significatif sur l’abondance en parasitoïdes.

Ces résultats soulignent que (i) accroitre la diversité végétale à l’échelle parcellaire peut – mais non systématiquement – favoriser une diminution de l’abondance en insectes ravageurs, (ii) inclure des espèces florales peut accroitre certains – mais pas tous les – ennemis naturels, et (iii) pour composer des mélanges fleuris attractifs pour les ennemis naturels, certains traits floraux particuliers – plutôt que la diversité fonctionnelle à l’échelle du mélange – pourraient être considérés.

Ces résultats sont discutés dans une optique plus large. En effet, les stratégies de diversification des habitats cultivés et non-cultivés au sein des agroécosystèmes sont diverses, tout autant que les moyens de composer, gérer et agencer ces habitats. De plus, des processus à des échelles supérieures que celle du champ cultivé peuvent être déterminants. Enfin, les insectes ne sont pas les seuls ravageurs, et les ravageurs les seuls éléments biotiques ou abiotiques qui doivent être régulés dans les agroécosystèmes. Réguler les populations de ravageurs et offrir une diversité de services écosystémiques de manière conjointe représente un défi scientifique pour les recherches futures.

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General introduction

1. The limits of the input-intensive agriculture

In the twentieth century, food sovereignty issues encouraged country leaders to engage into the intensification of agriculture. The promoted model was an integrated system of chemical inputs (pesticides and fertilisers) with genetically uniform and high-yielding crop varieties using machineries in simplified agricultural landscapes (Evenson and Gollin, 2003). The single objective, which was increasing biomass production (Foley et al., 2005), has been reached in many countries. Globally, crop production and yield in the last 50 years have more than doubled, along with an increased use of chemical inputs and a reduced number of farmers per farmed area (Eurostat, 2015a; Matson, 1997; Tilman et al., 2002). Nevertheless, environmental and societal concerns arose.

First, direct exposure to chemical pesticides along with the residues found in the environment (soil, water) and the food chain (Arias-Estévez et al., 2008; Claeys et al., 2011) represent risks for human health (Kim et al., 2017; Mostafalou and Abdollahi, 2013). A report from the French National Institute on Health and Medical Research (INSERM), synthesising multiple studies that analyse the relation between pesticide exposure and human disease, concluded that “there is a presumption of causal link, sometime strong, between pesticide exposure and pathologies to adults like some cancers and neurodegenerative diseases” (Baldi et al., 2013).

Second, a general degradation of the environment leading to a loss of biodiversity is observed (Foley et al., 2005). The residues of pesticides that affect humans have detrimental effects on non-targeted organisms (Stanley and Preetha, 2016). Along with nitrogen and phosphorus-based fertilisers, they are responsible for the contamination and eutrophication of both aquatic and terrestrial habitats. Moreover, their production and use lead to the release of greenhouse gas emissions in the atmosphere (Tilman, 1999). In Europe, agriculture is responsible for about 10 % of the total emission of greenhouse gases (Eurostat, 2015b). These environmental degradations are emphasised by the simplification of landscapes. Landscape simplification is the result of a general trend aiming at merging and enlarging crop fields towards mechanisation of agriculture. It led to the elimination of non-crop features, and the fragmentation of the remaining ones, because of their conversion to crop lands (Tscharntke et al., 2005). Landscape simplification is partly responsible for the loss of biodiversity in agricultural areas as non-crop features are habitats for various animal and plant species. This phenomenon is increased by the systematic elimination of weeds and arthropods, considered as pests, but being food resources for herbivores and carnivores (Krebs et al., 1999; Robinson and Sutherland, 2002). Moreover, it participated in an increase of soil erosion and nutrient run-offs in agricultural areas, two phenomenons that can be limited by non-crop features surrounding fields (Foley et al., 2005).

Third, the economic viability and social relevance of intensive agriculture is questionable. In Europe at least, the number of farmers does not stop decreasing since decades (Eurostat, 2015a) despite the subsidies devoted to agriculture (i.e. 30 % of EU budget was devoted to direct payments and market-related expenditure in 2013, European Commission, 2016). Moreover, their suicide rate is among the highest when compared to other profession categories (Bossard et al., 2013).

Although increasing food production was the main goal for the twentieth century's agriculture, it has been acknowledged that today's challenge is to shift towards an environmentally sustainable agriculture that is economically viable and socially relevant (International Assessment of Agricultural Knowledge, 2009).

2. Towards a biodiversity-based agriculture

These limits of agricultural intensification based on the use of external inputs encouraged the gradual emergence of agroecology. Despite the various facets and the multiple definitions that have been proposed (Norder et al., 2016), the concept of agroecology is being developed and used for triggering the transition towards sustainable agricultural and food systems. Agroecology emerged as the meeting of agronomy and ecology disciplines in applying the theories of ecology to the design of agroecosystems (Altieri, 1999). Additionally, agroecology mobilises social sciences for incorporating the human dimension at both the farming, processing and the consumption levels, inevitably questioning the political choices needed for triggering a transition (C. Francis et al., 2003).

For designing farming systems less dependent on external inputs, the agroecological strategy proposes to (re-)introduce elements of biodiversity that have specific functions in agroecosystems, to enhance regulating processes and favour the delivery *ecosystem services* (Altieri, 1999; Costanzo and Bàrberi, 2014). Ecosystem services are "the benefits human populations derive, directly or indirectly, from ecosystem functions" (Costanza et al., 1997). Ecosystem services have been classified into four types, i.e. support, regulation, provision and culture, that are related to one another (Reid et al., 2005; W. Zhang et al., 2007). More specifically, the two final services of biomass provision and the cultural dimension often depend on an array of regulating services, themselves based on supporting services. Among this last service, the presence of those elements of biodiversity, that has specific functions in agroecosystems, is affected by the management of crop and non-crop habitats. The interactions between these organisms are at the origin of regulating processes (Figure 1). Interactions between elements of biodiversity can occur at various scales, from the organism to the landscape level and the choice of farming practices, i.e. the ways of composing, designing and managing crop and non-crop habitats, will produce effects at one or several of these levels (Médiène et al., 2011).

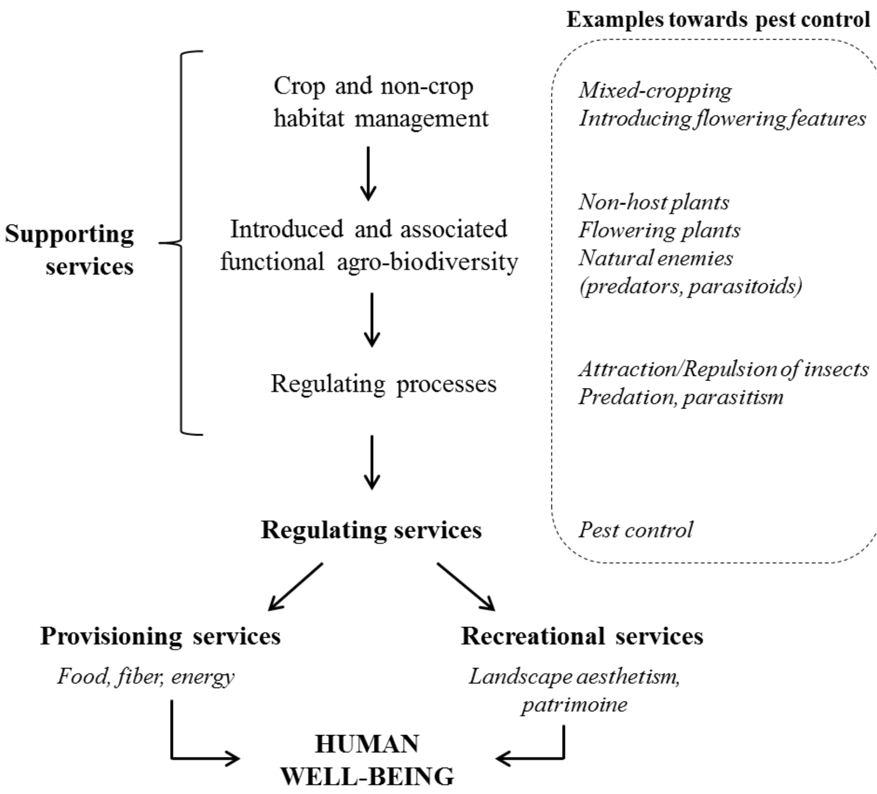


Figure 1. The concept of ecosystem services applied to the natural regulation of pests (adapted from W. Zhang et al., 2007)

3. Practices for a biological control of insect pests in agroecosystems

Pests are weeds, pathogens and insects that are responsible to crop losses (Oerke, 2006). Insect pests damage crops through direct feeding (i.e. herbivores) or by transmitting pathogens (e.g. viruses). Damages can reduce yield or aesthetic quality (in the case of fresh products) with the consequence of reducing products’ economic value on the market. In order to control them without chemical insecticides, Zehnder et al. (2007) proposed a strategy in four phases: (i) implement cultural practices that would directly negatively affect pest development; (ii) manage vegetation to enhance natural enemies and their direct effect on pest populations; (iii) deliberately introduce natural enemies; (iv) use natural insecticides and mating disruption. The agroecological approach introduced here-before aims at developping the two first phases.

The first one consists in a bottom-up control that limits the ability of pests to find and develop on their host plants, by notably preventing the temporal and spatial synchronisation of crops and pests (Médiène et al., 2011). Temporal de-synchronisation is possible by for instance rotating crops from year to year and adapting the sowing date for a given year. As for spatial de-synchronisation, it consists in complicating the search of host plants by pests. Because large and homogeneous crop fields tend to favour specialist herbivores (i.e. *concentration hypothesis* of Root, 1973), sowing mixtures of resistant varieties or mixing different plant species that host different pests would increase field heterogeneity. The non-host plant would be an introduced element of biodiversity that dis-favours pests, finally participating in their regulation (Figure 1). Mixing plants of different species can be applied through various practices: intercropping which is cultivating together two or more crops, agroforestry which is growing together crops with trees, and cover cropping which is associating crops with non-harvested plants (Malézieux et al., 2009). Apart from de-synchronisation, nutrient availability in soil also affects crop health thus crop ability to resist to pests. Therefore, fertilisation management is an additional lever to activate towards a bottom-up control of pests (Altieri and Nicholls, 2003).

The second one consists in enhancing a top-down control by natural enemies through the management of beneficial habitats. These habitats can be crop, but also non-crop areas often found at field margins. It meets the concept of *conservation biological control*, being defined as “tactics and approaches that involve the manipulation of the environment (i.e. the habitat) of natural enemies so as to enhance their survival, and/or physiological and behavioural performance, and resulting in enhanced effectiveness” (Barbosa, 1998). Within fields, increasing plant diversity (as detailed before) may offer micro-habitats that benefits a diversity of insects, among others natural enemies of pests (i.e. *enemy hypothesis* of Root, 1973). Moreover, reducing tillage frequencies may favour the survival of ground dwelling natural enemies and those over-wintering in the soil (Soane et al., 2012). As for non-crop habitats, they can benefit natural enemies by providing them an overwintering site and a shelter against adverse conditions. Indeed, they are often more stable through time than cropping features that are harvested. Moreover, they can be a source of food (e.g. nectar and pollen from flowers needed by some insect species at some stages of their development, alternative prey and hosts) due to the generally high plant diversity including flowering species and the existence of micro-habitats (Landis et al., 2000). In this context, flowering species would be elements of introduced biodiversity, and natural enemies a part of the associated biodiversity which predation and parasitism may lead to the regulation of pests (Figure 1). Non-crop habitats that can be found adjacent to fields are grassy strips potentially hosting flowering species, hedgerows that are linear woody features with grassy strips at the tree's bases, woodlots and forests.

4. Structure of the thesis

In the present thesis, intercropping is studied as a way to spatially diversify crop habitats and the sowing of wildflower strips as a way to introduce non-crop habitats in agroecosystems. It is hypothesised that these two tactics can help to biologically reduce insect pests through both a bottom-up and top-down control. The study of these practices is considered in the broad context of agroecology.

4.1. Chapter I: Towards a biodiversity-based agriculture for sustainable food systems

Through an analysis of the scientific literature, **Chapter I** aims at first clarifying the concept of agroecology (***Article 1***) in order to situate in which way spatial diversification of agroecosystems participates in the development of sustainable agricultural and food systems. In a second step, the current knowledge regarding intercropping (***Article 2***) and the sowing of wildflower strips (***Article 3***) towards biological control of insect pests is reviewed.

4.2. Chapter II: Increasing plant diversity at the field scale with the provision of flower resources for enhancing biological control

Analysing the scientific literature allowed specifying some benefits and limits of intercropping on the one hand, sowing wildflower strips on the other hand, for enhancing a bottom-up and top-down control of insect pests. Therefore, Chapter II aims at answering the following research question:

Would an increase of plant diversity with the provision of flower resources enhance a bottom-up and top-down control of insect pests?

First, pests and their natural enemies were monitored in an intercropping system including a flowering (oilseed rape *Brassica napus* L.) and a non-flowering (wheat *Triticum aestivum* L.) crop, and compared to sole crop parcels, in China (***Article 4***). Second, wildflower strips were sown within a wheat field in Belgium, pests and their natural enemies were assessed in wheat in between flowering features and compared to wheat in pure stands (***Article 5***).

4.3. Chapter III: Composing flower mixtures attractive to natural enemies: A trait-based analysis of natural enemy-flower interactions

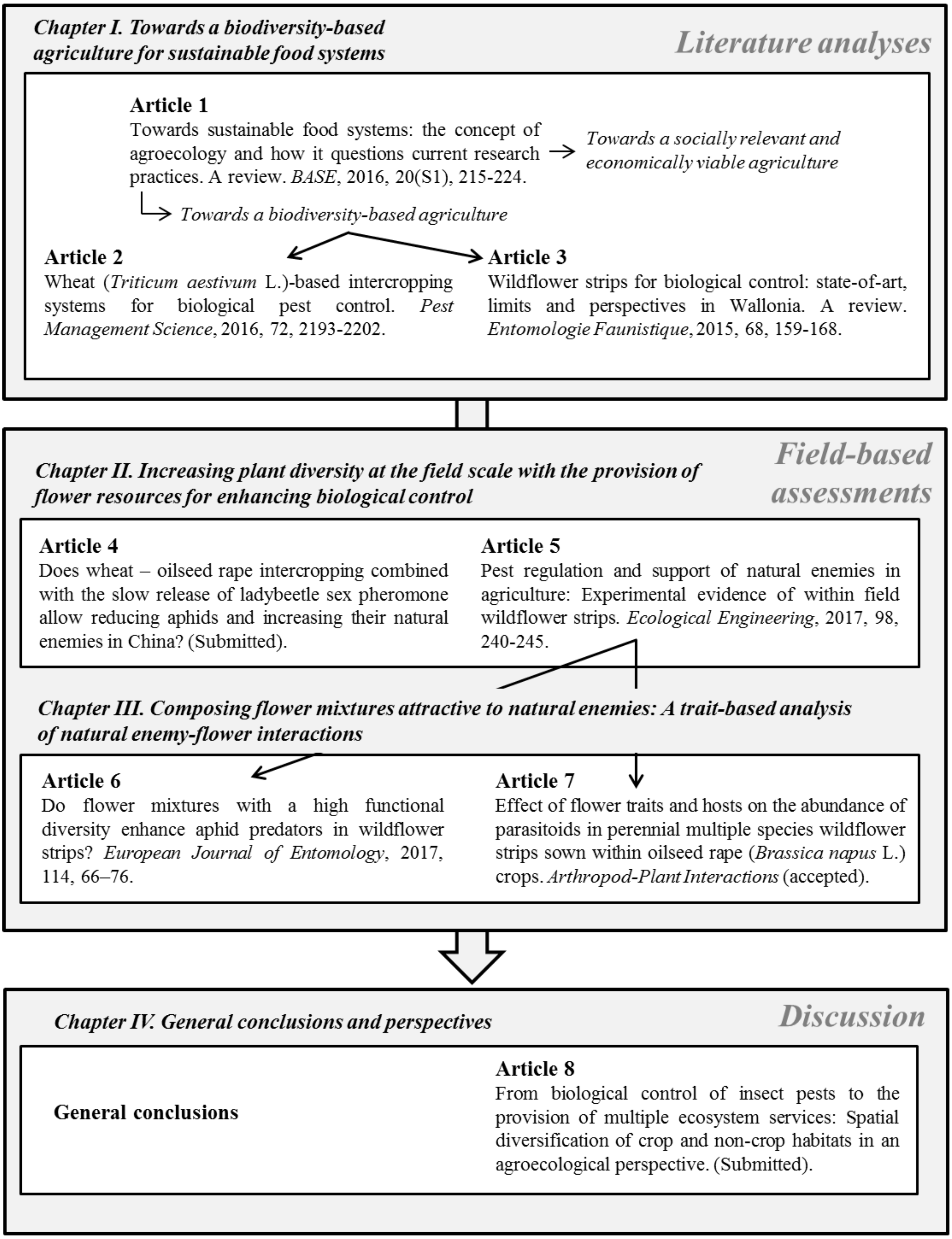
A focus was then made on wildflower strips and ways to compose flower mixtures attractive to a diversity of natural enemies. Flower traits are known to affect insect behaviour. Hence: **How knowledge on flower traits can be mobilized to compose flower mixtures attractive to natural enemies?**

First, the attractiveness to natural enemies of different mixtures with a contrasted value of functional diversity was assessed. The tested hypothesis was that mixtures with a high functional diversity support a high abundance and diversity of natural enemies (***Article 6***). Second, a methodology was developed to assess what are the specific traits that affect natural enemy behaviour in sown mixtures and whether other factors such as pest abundance could overwhelm the effect of traits (***Article 7***).

4.4. Chapter IV: General conclusions and perspectives

After concluding on the results of these field experiments, a discussion followed by perspectives (***Article 8***) is proposed in order to contextualise the results in a broad context. This last article highlights that strategies to spatially diversify agroecosystems are various, as well as the ways to compose, manage and design crop and non-crop habitats. Also, processes at larger scales than the field may be determinant. Finally, insects are not the only pests, and pests are not the only biotic or abiotic elements that need to be regulated in agroecosystems. Considering multiple regulations in agroecosystems questions the scales at which regulations are handled, as well as the responsibility of the multiple stakeholders acting in the territory.

The whole structure of the thesis is presented in Figure 2. Because the present thesis is a compilation of articles independently published (or submitted for publication), repetitions may occur in the different chapters. I apologize to those reading the whole document.



Literature analyses

Chapter I. Towards a biodiversity-based agriculture for sustainable food systems

Article 1
Towards sustainable food systems: the concept of agroecology and how it questions current research practices. A review. *BASE*, 2016, 20(S1), 215-224.

→ *Towards a socially relevant and economically viable agriculture*

→ *Towards a biodiversity-based agriculture*

Article 2
Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control. *Pest Management Science*, 2016, 72, 2193-2202.

Article 3
Wildflower strips for biological control: state-of-art, limits and perspectives in Wallonia. A review. *Entomologie Faunistique*, 2015, 68, 159-168.

Field-based assessments

Chapter II. Increasing plant diversity at the field scale with the provision of flower resources for enhancing biological control

Article 4
Does wheat – oilseed rape intercropping combined with the slow release of ladybeetle sex pheromone allow reducing aphids and increasing their natural enemies in China? (Submitted).

Article 5
Pest regulation and support of natural enemies in agriculture: Experimental evidence of within field wildflower strips. *Ecological Engineering*, 2017, 98, 240-245.

Chapter III. Composing flower mixtures attractive to natural enemies: A trait-based analysis of natural enemy-flower interactions

Article 6
Do flower mixtures with a high functional diversity enhance aphid predators in wildflower strips? *European Journal of Entomology*, 2017, 114, 66–76.

Article 7
Effect of flower traits and hosts on the abundance of parasitoids in perennial multiple species wildflower strips sown within oilseed rape (*Brassica napus* L.) crops. *Arthropod-Plant Interactions* (accepted).

Discussion

Chapter IV. General conclusions and perspectives

General conclusions

Article 8
From biological control of insect pests to the provision of multiple ecosystem services: Spatial diversification of crop and non-crop habitats in an agroecological perspective. (Submitted).

Figure 2. Structure of the thesis

Chapter I

Towards a biodiversity-based agriculture for sustainable food systems

Article 1

Towards sustainable food systems: the concept of agroecology and how it questions current research practices. A review

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Abstract

Multiple environmental and socio-economic indicators show that our current agriculture and the organization of the food system need to be revised. Agroecology has been proposed as a promising concept for achieving greater sustainability. This paper offers an overview and discussion of the concept based on existing literature and case studies, and explores the way it questions our current research approaches and education paradigms. In order to improve the sustainability of agriculture, the use of external and chemical inputs needs to be minimized. Agroecological farming practices seek to optimize ecological processes, thus minimizing the need for external inputs by providing an array of ecosystem services. Implementing such practices challenges the current structure of the food system, which has been criticized for its lack of social relevance and economic viability. An agroecological approach includes all stakeholders, from field to fork, in the discussion, design and development of future food systems. This inclusion of various disciplines and stakeholders raises issues about scientists and their research practices, as well as about the education of the next generation of scientists. Agroecology is based on the concept that agricultural practices and food systems cannot be dissociated because they belong to the same natural and socio-economic context. Clearly, agroecology is not a silver-bullet, but its principles can serve as avenues for rethinking the current approaches towards achieving greater sustainability. Adapting research approaches in line with indicators that promote inter- and transdisciplinary research is essential if progress is to be made.

Keywords: alternative agriculture, agrobiodiversity, ecosystem services, socioeconomic organization, marketing channels, interdisciplinary research, participatory approaches, innovation adoption

1. Introduction

Common practices in the food system, defined as *conventional* (Altieri, 1999; Kremen et al., 2012), are coming under increasing criticism in western Europe. Historically, conventional agriculture has led to greatly increased yields and growth in agribusiness, flooding supermarkets with processed food products. Nevertheless, issues such as climate change, pollution, the decline in numbers of farmers and in food quality are being addressed, as reported in the International Assessment of Agricultural Knowledge (2009). Voices calling for a revision of the conventional food system in order to achieve greater sustainability have become louder. Agroecology (also sometimes written *agro-ecology*) is being promoted as a promising concept in answer to this call.

Stassart et al. (2012) retraced the historical broadening of the scope of agroecology, from a focus on ecological processes in agriculture to socio-ecological processes. Agroecology first emerged in 1928 and evolved during the 20th century as the application of ecological concepts to agricultural practices, with the primary aim of reducing the use of chemical inputs and the impact of agriculture on the environment (Altieri, 1999). Agriculture is responsible for environmental pollution through, for example, greenhouse gas emissions (25 % of the total emissions worldwide; and 9 % in Wallonia, Belgium; Guns, 2008) and the use of chemicals (e.g. pesticides, growth regulators, mineral fertilizers) that are toxic to the environment

(Devine and Furlong, 2007) and human health (Baldi et al., 2013). Agroecological principles suggest that we should safeguard local ecological processes that underpin the delivery of ecosystem services (ES) crucial to agricultural activities (e.g. natural soil fertility, biological control), while maintaining the productive function of agriculture (Malézieux, 2012).

Since the start of the 21st century, agroecology has increasingly been seen as a concept dealing with both ecological and human dimensions, thus involving all stakeholders in the food chain, from production to consumption (C. Francis et al., 2003), with the aim of increasing the social responsibility and economic viability of farmers' activities. In the European Union (EU), the economic viability of farms is questionable because Common Agricultural Policy subsidies account for almost all of a farmer’s net income (86 %, 97 % and 90 % on average in Wallonia in 2011, 2012 and 2013, respectively; Service Public de Wallonie, 2014a). In addition, the large number of suicides among farmers compared with the rest of the population (in France, 20-30 % higher; Bossard et al. 2013) can be seen as a worrying trend in society. There has also been a steady decline in the number of farms and farmers over recent decades (the EU lost 2.5 million farms between 2005 and 2010; Eurostat, 2015a). These facts raise questions about both the social relevance and the economic viability of the conventional food system.

In the light of these sustainability challenges, attention has started to focus on agricultural research. The conventional agricultural system is based on the results of disciplinary and reductionist research that have been applied to a large variety of pedo-climatic conditions by changing and homogenizing these systems to meet our needs (Kremen et al., 2012). The complexity of the issues involved (i.e. environmental, economic, social and health concerns) shows that holistic and decentralized scientific approaches are needed if sustainable systems are to be developed (Louah et al., 2015; Méndez et al., 2013).

The term *agroecology* is now increasingly being used in academic publications (Bellon and Guillaume, 2012). There is a large body of work on the ecological principles of agroecology (Duru et al., 2015; Malézieux, 2012) and the socio-economic dimensions of sustainable food systems (Dumont et al., 2016; C. Francis et al., 2003; Gliessman, 2011). So far as we know, however, only a few papers (but see Stassart et al., 2012) have brought the two dimensions of agroecology together and discussed how they could be adapted to support agroecological innovation.

Based on the literature, this paper looks at how agroecology can help in planning and supporting the transition of conventional food systems towards more sustainable ones. In particular, it seeks to answer the following questions: What are the propositions of agroecology in efforts aimed at improving (i) farming practices and designs to increase environmental sustainability of agriculture and (ii) the organization of the food system in order to enhance the social and economic sustainability of agricultural product processing, distribution and consumption? (iii) How the transition towards agroecological systems challenges current research practices? This last aspect is drawn on the authors' experience of the practical issues, constraints and successes while working within the multidisciplinary research platform 'AgricultureIsLife.be' (University of Liège).

2. Agroecological practices to increase environmental sustainability

Since the Green Revolution, conventional agriculture has focused mainly on the production service (i.e. food, feed, forage, fiber and fuel products), often using practices that are highly dependent on anthropogenic external inputs (e.g. chemical fertilizers, pesticides, irrigation based on non-renewable water sources). These practices, however, override the key ecological processes (i.e. biotic and abiotic interactions) that underpin the delivery of ES crucial to the long-term performance of agriculture (e.g. natural soil fertility, biological control, water-holding capacity, resilience to extreme events) and lead instead to serious agricultural disservices (e.g. agrochemical pollution, pesticide poisoning, greenhouse gas emissions) (W. Zhang et al., 2007).

The ES framework developed through the Millennium Ecosystem Assessment (Reid et al., 2005) shows that a farming system not only provides *output services* (provisioning and cultural ES), but also receives and depends on *input services* (supporting and regulating ES), such as biological control, water purification and nutrient cycling. Through this framework, the development of environmentally sustainable agricultural practices focuses on optimizing the balance between input and output services (W. Zhang et al., 2007). Wezel et al. (2014a) noted that agroecological practices are "agricultural practices aiming to produce significant amounts of food, which valorize in the best way ecological processes and ES in integrating them as fundamental elements in the development of practices".

Within the ES framework, biodiversity comes as a key concept when setting out agroecological practices (Altieri, 1999; Duru et al., 2015; Kremen and Miles, 2012; Wezel et al., 2014a). Three levels of integration can be distinguished: planned, associated and landscape (bio)diversity. *Planned biodiversity* refers to the biodiversity intentionally introduced by the farmer into the agroecosystem (Altieri, 1999). This biodiversity includes the productive (e.g. cash crop, forage, timber, livestock) and non-productive (e.g. flowers) biota introduced into the system and managed at varying temporal (e.g. rotation, cover crops), spatial (e.g. intercropping, agroforestry, wildflower strips) and ecological (e.g. genetic diversity at the population, variety and species level) scales (Kremen and Miles, 2012). *Associated biodiversity* refers to the biodiversity unintentionally introduced into the agroecosystem (Altieri, 1999). This biodiversity relies on practices that provide favorable habitats for a diversity of above- and below-ground organisms, attracting them from the surrounding environment. It contributes indirectly to the productive function by enhancing ecological processes, which in turn can provide ES (Tscharntke et al., 2005). *Landscape diversity* level takes into account the integration of biodiversity through the structure and composition of the surrounding environment (Duru et al., 2015) and sees biodiversity as a function of its relationship with the surrounding landscape. Agroecological practices integrate these three levels of biodiversity in order to provide synergies between ecological processes and achieve multiple ES delivery within the system.

The link between the principles outlined above and the concrete implications in terms of management strategies at field, farm or landscape scale has been illustrated in detail in the literature with reference to a wide array of agroecological practices (Kremen et al., 2012; Power, 2010; Wezel et al., 2014a). For example, wildflower strips (planned biodiversity) can be sown along field margins in order to control insect pests. The flowers provide a refuge and food resources (nectar and pollen) that benefit insects (associated biodiversity) that can act as pest natural enemies (predators and parasitoids). The ecological process of biological pest control is therefore an input service benefiting farmers by enabling them to reduce their reliance on insecticides (Pfiffner et al., 2009). In terms of agricultural productivity, however, results with regard to final crop yields are still scarce (Tschumi et al., 2016a), but product quality would benefit from the reduction in pesticide residues in the food supply for the consumers.

In order to ensure the delivery of these ES, the surrounding landscape needs to be taken into account. For example, the mere presence of wildflower strips might not be efficient enough for controlling pests (Pfiffner et al., 2009) because the delivery of this ES depends on the colonization of wildflower strips by insects coming from (semi-)natural habitats in the landscape (e.g. woodlots, perennial grasslands) (Jonsson et al., 2015). The interdependence between landscape and plot scale in order to maintain ES is specific to each practice. For instance, Tamburini et al. (2016) showed that conservation tillage (defined in this paper as the non-inversion of soil, often combined with permanent vegetation cover) could be efficient for maintaining biological pest control even in simplified landscapes.

Both examples illustrate that the efficiency of a practice in the delivery of one or multiple services depends on interactions at different scales. It is therefore necessary to take account of plot management and landscape composition and the processes relevant to the different scales when planning strategies to maximize services.

Furthermore, synergies may appear between practices. It is therefore important to implement multiple agroecological practices in order to optimize ES delivery. For example, in a recent meta-analysis, Pittelkow et al. (2014) revealed that implementing no-tillage alone led to a reduction in crop yield, whereas combining no-tillage with soil cover (by crop residues or cover crops) and crop rotation could increase yield.

Finally, ES resulting from the implementation of one or multiple agroecological practices do not necessarily occur at the same scale as the practice itself or within the same time frame. For example, the implementation of agroforestry (defined as a land-use system that integrates, in the same area, woody elements with crops and/or livestock production; Torquebiau, 2000) will deliver ES at the farm scale because the deep rooting system of the tree and litterfall participates to nutrient cycling and therefore maintains soil fertility (Tsonkova et al., 2012). Other benefits arise on a wider scale through various processes; for example, research has shown that the presence of trees helps with carbon sequestration and thus contributes indirectly to climate change mitigation on a global scale (Jose and Bardhan, 2012). Farmers can therefore expect an annual agricultural income from crops and/or livestock, as well as from fruits and/or nuts from the trees and, in the longer term, from the capitalization of the timber.

Despite the potential of agroecological practices in providing ES, there are still some uncertainties. As highlighted by Wezel et al. (2014a), who outlined the advantages and drawbacks of 15 agroecological practices, their effectiveness in providing ES depends greatly on the local context. Local pedoclimatic conditions affect the ecological processes and the economic and societal environments affect the final goods. Given this context-dependent efficiency, farmers' uncertainties lack of scientific knowledge about some ecological process, possible additional costs of equipment, increase in human labor, low commercialization rate of the product, new legislation and so on (Wezel et al., 2014a). Thus, farmers need to develop tailor-made practices adapted to their local context, which often entails going through a lengthy process of trial and error.

3. Organizing the food system in order to increase social relevance and economic viability

A production system based on ecological processes instead of inputs, as described above, challenges the entire food system because it results in greater product diversity in space and time (Kremen et al., 2012). The challenge is particularly high given that the goods produced by agricultural systems are already numerous (i.e. feed, forage, fiber and fuel; Delcour et al. 2014).

With regard to food, the conventional food system, built on the model of supermarkets and controlled by a few transnational food companies, is based on logistic efficiency, product standardization and price competition (Raynolds, 2004). While product standardization became possible through the use of mechanization and external chemical inputs (Marsden and Murdoch, 2006), the need for logistic efficiency and price competitiveness led food companies – which drive the food system – to globalize their provisioning, creating competition between farmers and promoting short-term productivity (Kremen et al., 2012; Rosset and Martínez-Torres, 2012). The significant decline in the number of farmers, however, as well as the importance of EU subsidies in farmer income, are indicators of the limits of this economic model for EU agriculture.

It is in this context that the need to design sustainable food systems arose and this issue became an integral part of agroecology. C. Francis et al. (2003) proposed involving all stakeholders in building such systems: farmers, processors, retailers, consumers, scientists and politicians. As Gliessman (2011) states: “Farmers alone cannot transform the entire food system.” The approach was clarified recently through a list of 13 principles on which sustainable food systems are based. These include: environmental equity, financial independence, partnership between producers and consumers and geographic proximity (Dumont et al., 2016).

Among the multiple stakeholders, particular attention has been given to consumers. Involving and educating consumers has been seen as essential for ‘closing the loop’ in the food system (C. Francis et al., 2003). In this context, Community Supported Agriculture (CSA) networks, which have existed for decades, are seen as an advanced model for sustainable food systems (Kremen et al., 2012). They are built on direct links between farmers and consumers through direct selling at the local scale. They are economically beneficial because they create jobs on farms and assure farm incomes over the longer term (compared with conventional food systems) (Wezel et al., 2014b). Farmer incomes can also increase because there are fewer intermediaries in short-supply chain marketing. In addition, consumers know more about how their food is produced and therefore request and choose food products based on sustainability criteria (Kremen et al., 2012). Finally, developing short food supply chains to reconnect producers and consumers is seen as an essential aspect of any agroecological transition (Guzmán et al., 2013) and is one of the 13 principles of sustainable food systems listed by Dumont et al. (2016). A recent criticism of the CSA model, however, is that it does not include the stakeholders in the entire food system (Lamine, 2015a). By definition, it bypasses the intermediaries, whereas the transformation process should involve them.

There are other innovative models based on multiple stakeholder involvement. One is the French food cooperative Biocoop, a network of 345 organic shops (Lamine, 2015b). Unlike traditional supermarkets, Biocoop brings producers, shop managers, employees and consumers together in an *ethical committee*. Its role is to establish common guidelines (e.g. prices at which products are bought to producers and processors, and sold to consumers) and to ensure that the common values are respected. Biocoop's current governance has been strengthened by addressing the criticism it faced in the 1990s, when it grew considerably and developed logistical tools and management strategies that did not appear to differ much from those of the conventional food system. This illustrates the challenge facing sustainable food system initiatives of finding a balance between remaining in a highly competitive food market while conserving core values that differ significantly from those of food companies.

The challenge also lies in informing consumers of the originality of sustainable food systems, compared with the conventional system, especially because of the confusion that can arise when food companies imply, through labeling, that their products derive from sustainable systems. As Warner (2007) highlighted, labels are used in conventional food chains to persuade consumers of product quality, because food scares have become common and face-to-face relationships no longer exist. They are even seen as "initiatives to create ethical space within the marketplace" (Barham, 2002) without transforming it. *Quality* is an ambiguous term, however, its meaning changing over time (Warner, 2007). Whereas food companies try to meet the quality expectations of consumers, a sustainable food system that involves all stakeholders does not need quality labels. For example, information about synthetic pesticide use, animal welfare, production location and human working conditions (i.e. the most important quality criteria for consumers, according to Howard and Allen, 2010) can be made available through face-to-face relationships in short-supply chains; in systems such as Biocoop, these criteria are discussed by the ethical committee and made available through a charter. Transparency in the production and processing steps, as well as democratic governance (two principles of sustainable food systems; Dumont et al., 2016), allow these systems to be highly responsive to stakeholder expectations in terms of quality, which itself can vary from one location to another (Zepeda et al., 2013).

Unlike the conventional food system, these cases show that sustainable food systems can be diverse. Although they adhere to common principles, the way in which they are implemented can vary (Dumont et al., 2016) and thus attract criticism from unsatisfied stakeholders. This decentralized and therefore flexible approach, however, allows a diversity of projects to develop, each of them tailor-made to their local context.

4. Scientific practices and agricultural innovations

As is clear from the discussion above, natural, social and agricultural sciences are intrinsically intertwined in food production systems and among the stakeholders in those systems. Accompanying agroecological transition therefore throws up new challenges and opportunities for research. Agroecology questions scientists about their research topics, the methods they use and develop, and the results they produce. Rather than saying that research in conventional agriculture using a biotechnological approach is no longer relevant, this section explores more holistic approaches that scientists could use to integrate complexity and uncertainty into their research practices. Not facing these challenges would lock scientific research into a limited range of thought and action, which in turn would hamper agroecological innovation (Vanloqueren and Baret, 2009).

First, in order to foster innovation, research should draw on several disciplines, in line with the holistic and complex approach of agroecology. This movement is known as *interdisciplinary research*, which is research practice that involves several unrelated academic disciplines, each with its own contrasting research paradigm (Baveye et al., 2014). Linking together agricultural, ecological and many other disciplines leads to innovative practices that restore ecological regulating processes, which increase the flow of ES and, consequently, reduce farmers' reliance on external inputs. Adding social disciplines provides the opportunity to study the conditions and processes of learning and change, as well as the interdependencies between the diversity of stakeholders in the food system (Lamine, 2015a). Such research highlights, *inter alia*, the long-term processes of change in farming practices (e.g. Chantre and Cardona, 2014) or the main reasons for a system's irreversibility, also known as the *lock-in effect* (e.g. Stassart and Jamar 2008 on the Belgian Blue commodity system and Vanloqueren and Baret 2009 on genetic engineering). These examples illustrate how this level of understanding facilitates the development of innovative food systems.

Second, the ambition of agroecology to include all stakeholders in the whole food system leads to their iterative involvement in the research process. This research movement is known as *transdisciplinary*, defined as participatory research focused on developing practical knowledge in pursuit of worthwhile human objectives (Baveye et al., 2014), whatever the origin of the science involved and the source of knowledge implied. This approach is sometimes also referred to as *action-oriented* or *participatory* research, although there are distinctions between the terms and their interpretation varies among authors (Baveye et al., 2014; Méndez et al., 2013; Scholz and Steiner, 2015).

Such research practices are increasingly being acknowledged as beneficial in many ways. They create research that is relevant to a local context, which is necessary with the agroecological approach as the studied systems are highly context-dependent (Altieri, 1999; Lyon et al., 2011). They also create opportunities for collective social learning by facilitating an exchange of information among stakeholders with differing values, views and mental frameworks (Duru et al., 2015; Vilsmaier et al., 2015). Above all, they address the gap between theoretical scientific questions and everyday problems faced by local stakeholders (Duru et al., 2015), which facilitates the adoption of research outcomes. This enhances the likelihood of innovations being taken up (Biggs et al., 2011; Duru et al., 2011) and empowers participants (Méndez et al., 2013). This type of research has been successful in many transitions to agroecological-based systems, including the transition from a conventional to an organic beef production chain in Wallonia that required overcoming several cognitive, logistical and commercial lock-ins (Stassart et al., 2008). Another example is illustrated by Cuéllar-Padilla and Calle-Collado (2011), who empowered farmers and supported them in the transition towards organic farming at a time when they had lost control over their marketing processes to transnational intermediaries. Transdisciplinary research is also useful in improving current management, as shown by Duru et al. (2011), who developed an assessment tool with – and for – farmers for the management of permanent grasslands that took account of the wide range of ES provided by such ecosystems. In essence, integrating various knowledge systems (i.e. scientific and practical) enables the contextual socio-ecological complexity to be taken into account while accompanying agroecological transition and developing appropriate tailor-made innovations.

It should be noted that, currently, there is still a debate about the organization of agroecology as a discipline *per se* or as an inter- or transdisciplinary practice. This debate is similar to the one about sustainability sciences: Do we need to build one overarching scientific discipline that will address the whole spectrum of sustainability issues – or agroecological issues – or is a dynamic contribution through the expression of various knowledge outputs preferable (Dalgaard et al., 2003)? Beyond this epistemological issue, it is argued that, in practice, agroecology requires a variety of sources of information and therefore that inter- and transdisciplinarity practices are complementary ways of learning (Chantre and Cardona, 2014). Indeed, the meta-level of analysis promoted by inter-and transdisciplinarity requires a certain level of disciplinary expertise to build upon.

Despite much evidence of the opportunities for research to adopt an inter- and transdisciplinary approach, challenges remain for scientists when applying these principles in practice. In order to ensure socially robust innovations, time needs to be invested from the outset of the research in setting common research objectives to address a commonly defined problem (Méndez et al., 2013). This time investment can differ between social and natural sciences, because they produce knowledge at different rates. True co-leadership between science and practice is required, where both knowledge systems are rendered visible and integrated in order to achieve greater symmetry between the two (Scholz and Steiner, 2015). Throughout the whole project, regular feedback and discussions need to take place among all stakeholders in order to redirect research or its methodology, if necessary, so as to achieve the objectives of both scientists and practitioners (Cuéllar-Padilla and Calle-Collado, 2011). In essence, communication is essential in order to learn from each other, build a climate of trust and ensure socially robust outcomes (Méndez et al., 2013).

This communication can, however, be hampered because of the variety of stakeholders involved, and hence the variety of (sometimes confronting) worldviews and knowledge systems. Each stakeholder sees a farming system from a different angle, depending on the plurality of the system's elements and context. With regard to scientists' worldviews, Bawden (1997) defined three research positions: technocentric, ecocentric and holocentric. Whereas the technocentric position promotes technical solutions, the ecocentric one seeks to manage ecological processes and the holocentric one integrates human processes and their interactions within the natural environment. Disciplines and knowledge systems also have their own traditions, methods, language and frameworks, which can prove difficult to coordinate and hamper discussions (Dalgaard et al., 2003; Vilsmaier et al., 2015). In addition, knowledge is influenced by one's experiences (referred as 'grounded knowledge', Ashwood et al., 2014), which further challenges coordination.

Given the challenges of implementing inter- and trans-disciplinary research, we argue that such shift in a researcher's position needs to be supported. A more fundamental and methodological type of research is needed, one that develops methodologies that are readily applicable in inter- and transdisciplinary research, such as World Café, Delphi surveys and Citizen juries (Elliott et al., 2005). More importantly, educational programs have a role to play in fostering and conveying these new methods and training scientists in these new approaches. Some academic agroecological programs are based on learning-by-doing pedagogy (Francis et al., 2013; Lieblein et al., 2007), with the students' learning taking place *in situ* (e.g. farm, rural development organization) and being open-ended (i.e. searching for solutions not already known by professors). Theoretical and methodological approaches from natural and social sciences are progressively introduced to the students, who have to integrate demands from the stakeholders. In this way, students are trained in inter- and transdisciplinary practices to give them the ability to coordinate distinct grounded knowledge through a reflexive process. The contrast with conventional agricultural education systems is obvious: agroecological programs enable students to reconnect with actual conditions in the field, something that has been lost in agricultural academic institutions. They also focus on the system as a whole with a holistic perspective, rather than focusing on narrow segments of the food system (Louah et al., 2015). We believe that there is a need for a thorough reform in agricultural academic institutions where, currently, agroecological approaches play a minor role (DeLonge et al., 2016).

Repositioning the researcher raises further questions about current academic mindsets and institutions. The process of including stakeholders within the definition of the research issue, reflection and action, and of integrating various disciplines, is time-consuming, produces practical knowledge relevant to a specific local area (Cerf, 2011) and leads to multiple research leaders, multiple data owners and multiple author articles. All this ill suits the classical scientific working climate, with its academic performance benchmarks of personal fast accumulation of publication (Cowling et al., 2008; Daily and Ehrlich, 1999; Dalgaard et al., 2003). Adapting current research context in order to integrate inter- and transdisciplinary research approaches into the development of agroecological innovations is a major challenge, but one that urgently needs to be addressed.

5. Towards tailor-made solutions rather than recipes

The term agroecology is now widely used, but its meaning differs depending on who is using it. Too often, agroecology is presented with only one of its two major components considered: agricultural practices and food system organization. In addition, some research projects claim to use the concept of agroecology, and yet ignore the holistic approach. In this paper we argue that, within agroecology, agricultural practices and food system organization cannot be dissociated from each other because they are both needed in order to achieve sustainability from field to fork. We also argue that inter- and transdisciplinary approaches are needed in order to address the issues of sustainability.

We have shown, first, that there are practices based on ecological processes that allow the use of external inputs to be reduced and thus increase the environmental sustainability of farming. Second, we have shown that stakeholders in the food system are able to organize themselves in order to safeguard their activities and guarantee the social relevance and economic viability of the practices. It is clear, however, that challenges remain and therefore none of the existing examples should be taken as copy-paste solutions. Agroecology is not about ‘one-size-fits-all’ solutions or clear-cut recipes (Lyon et al., 2011). Rather, it suggests taking into account the natural and socio-economic environment where the food is produced and calls for the development of innovations within this precise context. We have shown that contextualizing innovation processes can require working across different scales, combining a variety of methods and drawing on various kinds of knowledge because the challenges are often complex. Agroecology therefore requires the involvement of multiple disciplines and stakeholders within the research process. With this research approach, researchers need to adapt the way in which they address the problem: the choice of the methods to use and the scales to work at will depend on the problem they need to address. Similarly, farmers facing problems with crops or livestock need to adapt their practices according to the specific conditions of their farming context (Lyon et al., 2011).

Overall, in order to re-organize the food system and develop innovations through research, agroecology proposes that is necessary first to step back and observe the complexity of local conditions before applying general solutions. Contextualization means there can be no silver-bullet; every problem requires a tailor-made solution adapted to its specific socio-ecological context. This is why there are numerous examples of agroecological innovations, as well as their shortcomings. These tailor-made solutions, however, are an appropriate way of achieving sustainability in agriculture and in the organization of the food system.

Article 2

Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control. A review

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Abstract

Wheat (*Triticum aestivum* L.) is one of the most cultivated crops in temperate climates. As its pests are mainly controlled with insecticides which are harmful to the environment and human health, alternative practices such as intercropping have been studied for their potential to promote biological control. Based on the published literature, this study aimed to review the effect of wheat-based intercropping systems on insect pests and their natural enemies. Fifty original research papers were obtained from a systematic search of the peer-reviewed literature. Results from a vote-counting analysis indicated that, in the majority of studies, pest abundance was significantly reduced in intercropping systems compared with pure stands. However, the occurrence of their natural enemies as well as predation and parasitism rates were not significantly increased. The country where the studies took place, the type of intercropping, and the crop that was studied in the association had significant effects on these results. These findings show that intercropping is a viable practice to decrease insecticide use in wheat production systems. Nevertheless, other practices could be combined with intercropping to favour natural enemies and enhance pest control.

Keywords: sustainable agriculture, crop diversity, conservation biological control, predators, parasitoids, yield

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most important crops worldwide (ranked fifth in terms of production according to FAOSTAT (http://faostat3.fao.org/browse/Q/QC/E)). Therefore, finding alternative methods to improve its sustainable production is a major challenge for today's agriculture. Conventional farming practices contributed to increase yields during the 20th century, but are today contested for their negative impact on the environment (Gibbons et al., 2015; Krebs et al., 1999) and human health (Baldi et al., 2013). Industrialized monoculture systems [i.e. in the present paper, 'monocultures' are considered as 'pure stands'], which are highly dependent on the use of external inputs such as agrochemicals (i.e. synthetized fertilizers, chemical pesticides, growth regulators), favoured the simplification of agroecosystems (Kremen et al., 2012; Malézieux, 2012).

In contrast, promoting elements of biodiversity, which support ecological processes, may allow agricultural systems to benefit from various ecosystem services, including nutrient cycling, soil structuration and pest control (Altieri and Rosset, 1996; W. Zhang et al., 2007). One of the *agrobiodiversity strategies* to improve the sustainability of wheat production (reviewed by Costanzo and Bàrberi, 2014) is to increase plant species diversity at the field scale though intercropping designs (Hauggaard-Nielsen et al., 2001; Malézieux et al., 2009; Poggio, 2005). Intercropping is defined as the cultivation of at least two plant species simultaneously in the same field (Andrews and Kassam, 1976; Anil et al., 1998; Ofori and Stern, 1987), but which are not necessarily sown and/or harvested at the same time (Lithourgidis et al., 2011a).

Andrews and Kassam (1976) categorised intercropping into four principle types based on the spatial and temporal overlap of plant species: (1) mixed intercropping - two or more crops mixed with no distinct row arrangement; (2) row intercropping - two or more crops grown in separate alternate rows (when plant species are alternated within the same row it is considered as within-row intercropping); (3) strip intercropping - several rows of a crop (strip) alternated with several rows of one or more other crops; (4) relay intercropping - two or more crops grown in relay, but with the growth cycles overlapping to some degree. Choosing a type of intercropping may depend on the associated crops and their valuation after harvest, in addition to the knowledge of the famer and the level of mechanisation used.

Intercropping systems tend to produce higher yields compared to monocultures and reduce the impact of agriculture on the environment. Specifically, intercropping may improve soil conservation, fertility and crop quality, while possibly reducing the incidence of weeds, disease and insect pests (Aziz et al., 2015; Bedoussac et al., 2015; Lithourgidis et al., 2011a). Focusing on pests, as stated in the *resource concentration hypothesis* from Root (1973) specialist herbivores are more likely to find their host plants when they are concentrated in dense or pure stands. Moreover, according to the *enemy hypothesis* from Root (1973) the suppression of herbivores by their natural enemies (i.e. predators and parasitoids) is expected to be more efficient in diversified crop habitats compared to simplified ones, as they may be more abundant in environments offering a greater diversity of prey/host species and microhabitats to exploit.

Although the effect of intercropping on pests and natural enemies have been largely covered in the literature (Andow, 1991; Dassou and Tixier, 2016; Langellotto and Denno, 2004; Letourneau et al., 2011; Risch, 1983; Tonhasca and Byrne, 1994), most comprehensive reviews are very generalists. As wheat is one of the most important crops worldwide, understanding the potential of wheat-based intercropping systems for biological control may be of crucial importance. More specifically, this study aimed at answering the following questions: (i) Are pests reduced and natural enemies favoured in wheat-based intercropping systems compared to pure stands? (ii) Is there a correlation between biological control and yield in wheat-based intercropping systems? (iii) Where and when were these systems studied? (iv) What are the technical characteristics of wheat-based intercropping systems (i.e. types of intercropping and plant species associated with wheat)? Overall, this study is expected to give valuable information about the potential of intercropping as a tool to reduce insecticide use in wheat production.

2. Experimental methods

2.1 A systematic research of the literature

To locate scientific literature related to the effect of wheat-based intercropping on pests and/or natural enemies, all terms potentially related to intercropping, wheat, pests and natural enemies were listed. These terms were then included in a single query, as follows: (intercrop* OR "crop association" OR "crop combination" OR "combined crop" OR "associated crop"

OR "crop mix" OR "mixed crop" OR "mixed cropping" OR “row cropping” OR “relay cropping” OR “strip cropping”) AND (wheat OR "triticum aestivum") AND (pest* OR herbivor* OR "natural enemy" OR predator* OR parasit*). The composed terms were put between quotation marks so that the entire term was considered. For some of them, an asterisk was used to include all words that have a common core. The first step of this research was completed on 26 June 2015 by introducing the query in the search engine from the University of Liège (ULg - Belgium) e-bouquet. The search engine includes several e-journals and databases such as Scopus (Elsevier), AGRIS, CAB Abstracts and ProQuest (for the list of all databases included, please refer to Annex 1 [of the published paper]). Thereafter, the search query was adapted to each database, as some of them use a specific query language.

The obtained references were then selected based on the abstracts of the published papers. The abstracts had to meet four criteria to be retained for further analysis. First, they had to be research papers from peer-reviewed journals. Review and meta-analysis papers were not considered, as they are based on other studies. Second, the abstracts had to focus on intercropping. As stated in the Introduction, intercropping was defined as the cultivation of at least two plant species simultaneously in the same field, without necessarily being sown and/or harvested at the same time. Wheat had to be included in the intercropping and associated plant species had to be harvestable and consumable (human consumption, animal feeding, energy production and fibres). Ornamental, grassy or woody species were excluded. Third, insect pests and/or natural enemies (i.e. predators and parasitoids) had to be assessed by the studies and the effect of biological control had to be specified through direct (e.g. predation or parasitism rate) or indirect (e.g. abundance) indicators. Finally, the intercropping had to be compared to a pure stand control treatment. When the abstract was not available, the paper was excluded from the review. When the information contained in the abstract was not sufficiently precise to respond to criteria, the full paper was analysed. The paper was excluded from analyses if it was not obtainable.

Selected papers were then analysed in greater depth to determine the country where the study took place, the plant species associated with wheat, the type of intercropping and the effect of intercropping on yield, insect pests and/or natural enemies. Concerning insects, the effect was considered to be negative, positive or neutral when their populations declined, increased or no significant difference was detected, respectively between treatments. Furthermore, an increase in the predation or parasitism rate was considered to be a positive effect on natural enemies. In fact, both indicators allow determining the top-down impact of predators or parasitoids on their herbivorous prey or hosts. Therefore, we considered that higher predation or parasitism rates mean higher pressure on pests, which is positive for biological control. In the event that a single paper showed positive, negative and neutral effects on different insect populations, crops and intercropping designs (i.e. strip, relay, mixed), all instances were considered, hereafter termed ‘responses’.

2.2 Vote-counting method

The analysis of the selected papers was performed following the vote-counting method, which considers the number of tests supporting a theoretical relationship (i.e. in our case, if pests are reduced and natural enemies favoured in intercropping systems, compared with pure stands). Despite a wide use of this method for analysing results of numerous different studies (Connell, 1983; Denno et al., 1995; Garratt et al., 2011; Haaland et al., 2011; Root et al., 2003), vote-counting has been criticized and meta-analysis promoted (Letourneau et al., 2011; Tonhasca and Byrne, 1994). Indeed, vote-counting presents some limits that were reviewed by Combs et al. (2011). However, vote-counting allows the analysis of a large amount of papers for which the precise data are not always available. It is the case for several papers retrieved from the literature search, which still provide valuable findings that are worth to be considered.

2.3 Statistical analyses

In order to perform statistical analyses, a score was given to each response. The score ‘1’ was given when a positive effect on biological control was recorded (i.e. lower abundance of pests, higher abundance of predators or parasitoids, higher parasitism or predation rates, higher yield). The score ‘0’ was given when no effect or a negative effect was recorded. The Exact Bernouilli test ($P < 0.05$) was used to assess whether the frequency of responses where intercropping had a positive effect on biological control compared to pure stands differed from that expected by chance. Generalized linear models (GLMs) with binomial error (logit-link function) were fitted to assess whether (i) the country where the study took place, (ii) the type of intercropping, and (iii) the crop species that was studied had effects on the responses. These variables as well as every possible interaction were tested using a likelihood-ratio test ($P < 0.05$). Finally, the Pearson correlation between the effect of intercropping on pests, natural enemies and yield was tested ($P < 0.05$). The analyses were performed using R software (R Core Team, 2013).

3. Results

3.1 Countries and evolution through time

Out of 445 papers that were examined, 50 papers met the stated criteria. Thirty-nine of these papers were found using the search engine of the ULg. Eleven additional papers meeting the criteria were found by adapting the query to each database.

Four regions of the world are represented by the 50 studies. Twenty three were carried in China, 12 in Central and Southern Asia (i.e. India, Pakistan, Bangladesh and Iran), and 11 in North America (i.e. United States of America, Canada). Four papers refer to experiments carried in Western Europe (i.e. France, Denmark, Belgium and Germany) (Figure 3). The oldest paper found was published in 1987 in China (Figure 4). Since this year, one to two papers were published every year on average throughout the world. However, the number of publications increased from 2009 with 40 % of them published since this date. The first paper published in Europe was in Germany in 2006.

3.2 Plants associated with wheat and types of intercropping

Thirteen plant species were recorded in association with wheat (Table 1). The main species included cotton (*Gossypium* sp.), oilseed rape (*Brassica napus* L.) and pea (*Pisum sativum* L.). Different kinds of intercropping with wheat were implemented depending on the species used (Table 1). Strip cropping is the most common type, representing almost half of the studies, followed by relay cropping. Relay cropping was used when cotton, field bean (*Phaseolus vulgaris* L.), sorghum (*Sorghum bicolor* L.) or soybean (*Glycine max* (L.) Merr.) were associated with wheat. Mixed cropping was the least reported type. Pea, oilseed rape and faba bean (*Vicia faba* L.) were found mixed with wheat in this system.

3.3 Pests and their natural enemies

Forty-nine (98 %), twenty-four (48 %) and fourteen (28 %) papers assessed the effect of intercropping systems, compared to pure stands, on pests, predators and parasitoids respectively.

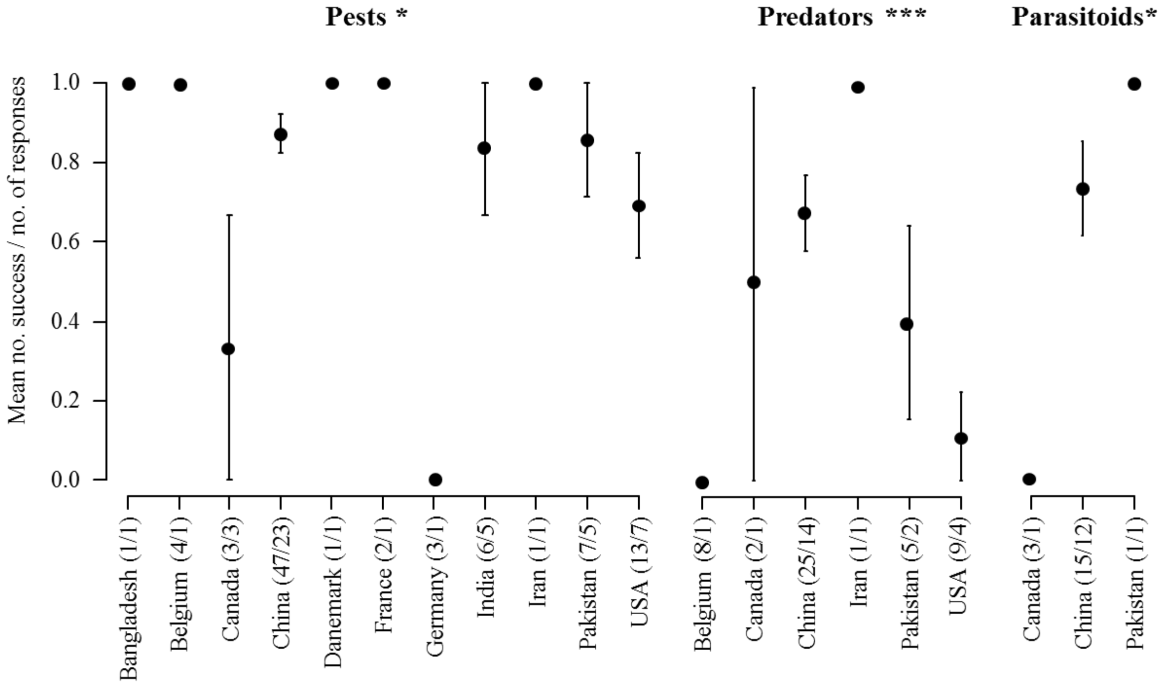

Figure 3. Mean (± SE) number of responses reporting a positive effect of wheat-based intercropping on biological control (i.e. decrease in pest and increase in natural enemy populations) on the total number of responses according to the countries where the studies took place. The ratio given in brackets corresponds to the number of responses/number of papers. Likelihood ratio tests on GLMs. * $P < 0.05$; *** $P < 0.001$.

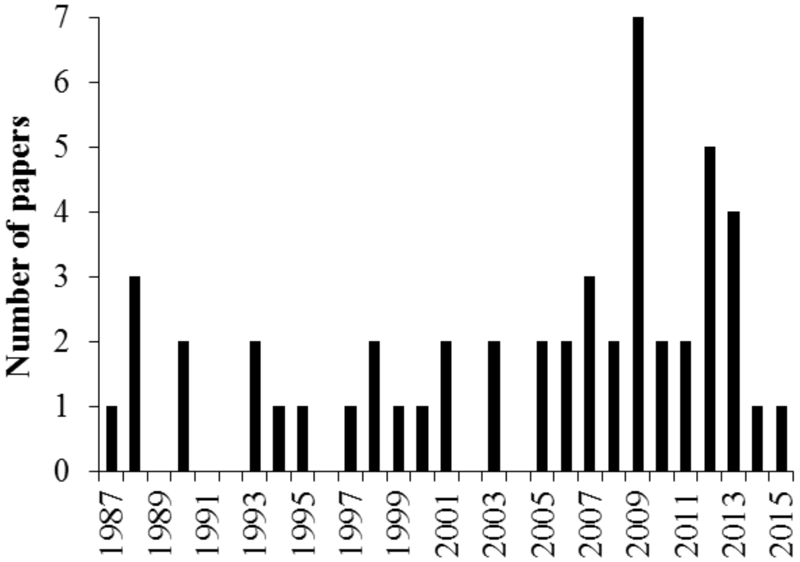

Figure 4. Evolution through time of the number of papers published on the effect of wheat-based intercropping on pests and their natural enemies.

Table 1. Plant species associated to wheat based on the type of intercropping.

Type of intercropping	Crops associated with wheat	No. of papers	References
Strip cropping	Alfalfa (*Medicago sativa* L.)	4	Fathi et al., 2013; K. Z. Ma et al., 2007; Saeed et al., 2013; Skelton and Barrett, 2005
	Garlic (*Allium sativum* L.)	2	Wang et al., 2008; Zhou et al., 2013a
	Mung bean (*Vigna radiata* (L.) Wilczek)	2	Xie et al., 2012a, 2012b
	Oilseed rape (*Brassica napus* L.)	7	Dong et al., 2012; Hummel et al., 2012; Sarwar, 2011; Sherawat et al., 2012; Wang et al., 2011, 2008; W. L. Wang et al., 2009
	Pea (*Pisum sativum* L.)	4	Ehsan-Ul-Haq and Van Emden, 2003; Zhou et al., 2013b, 2009a, 2009b
	Chili pepper (*Capsicum frutescens* L.)	1	Chen et al., 1995
Relay cropping	Cotton (*Gossypium* sp.)	10	Chen et al., 1994, 1998; Ma et al., 2006; X. M. Ma et al., 2007; Mu et al., 1993; Parajulee et al., 1997; Parajulee and Slosser, 1999; Wang and Zhao, 1993; W. Wang et al., 2009; Zhao et al., 1987
	Field bean (*Phaseolus vulgaris* L.)	1	Tingey and Lamont, 1988
	Sorghum (*Sorghum bicolor* L.)	1	Phoofolo et al., 2010
	Soybean (*Glycine max* (L.) Merr.)	2	Hammond and Jeffers, 1990; Miklasiewicz and Hammond, 2001
Mixed cropping	Oilseed rape (*Brassica napus* L.)	4	Hummel et al., 2010, 2009a, 2009b; Paulsen et al., 2006
	Bean (*Vicia faba* L.)	1	Hansen et al., 2008
Strip and mixed cropping	Pea (*Pisum sativum* L.)	2	Lopes et al., 2015; Ndzana et al., 2014
Non specified	Chickpea (*Cicer arietinum* L.)	3	Das, 1998; Hossain, 2003; Mehto et al., 1988
	Cotton (*Gossypium* sp.)	2	Xia et al., 2000; Zhang, 1990
	Bean (*Vicia faba* L.)	1	Yang et al., 2009
	Mustard (*Sinapis alba* L.)	3	Ansari et al., 2007; Mishra et al., 2001; Tiwari et al., 2005
	Sugarcane (*Saccharum officinarum* L.)	1	Masih et al., 1988

Among them, twelve (24 %) considered both predators and parasitoids. Wheat-based intercropping systems significantly decreased pest populations compared to pure stands ($P < 0.001$), while no significant effects were observed for predators ($P = 0.480$) and parasitoids ($P = 0.359$) (Figure 5).

Responses from pests and natural enemies varied significantly between countries where studies took place (Table 2). All responses obtained for pests in Bangladesh, Belgium, Denmark, France and Iran reported a decrease of their populations, while the opposite was observed in the only study that was carried in Germany. Variable responses were obtained in other countries, especially in the three Canadian studies (Figure 3). As for natural enemies, the study that was carried in Iran was the only that reported an increase in predator populations or predation rate, while the opposite was observed in Belgium. As for pests, variable responses were observed in other countries. Similar results were obtained for parasitoids. The study from Pakistan was the only one reporting an increase in parasitoid abundance or parasitism rate, while a decrease was obtained in the single study from Canada.

Both pest and natural enemy responses were significantly affected by the type of intercropping (Table 2). Pest populations were always reduced in strip cropping, which also favoured predators and parasitoids more often than relay and mixed cropping. The latter reduced pests in half of the cases and never induced an increase of natural enemy populations, as well as predation and parasitism rates (Figure 6).

Table 2. Effect of wheat-based intercropping on pests and natural enemies according to the countries where the studies took place, the type of intercropping and the crop of primary interest. Likelihood-ratio tests on GLMs; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. '-' indicates that it was not possible to perform the analysis.

	Pests			**Predators**			**Parasitoids**		
Predictor variables	**df**	**χ^2**	**p-value**	**df**	**χ^2**	**p-value**	**df**	**χ^2**	**p-value**
Country	10	19.47	0.035 *	5	21.47	< 0.001 ***	2	7.61	0.0223 *
Type of intercropping[a]	2	18.39	< 0.001 ***	2	6.20	0.045 *	2	7.85	0.020 *
Crop	11	27.63	0.004 **	5	8.46	0.133	2	7.85	0.020 *
Crop*Type of intercropping[a]	–	–	–	–	–	–	–	–	–
Crop*Country	–	–	–	1	1.29	0.255	–	–	–
Country*Type of intercropping[a]	–	–	–	1	2.15	0.142	–	–	–

[a] papers where the intercropping design was not defined were not considered in the analysis

Finally, such variability of responses was also observed for pests and parasitoids, but not for predators, when considering the crop species that was studied in the wheat-based intercropping system (Table 2; see Table 3 for details and associated references). Pests were reduced on the majority of crops, but rarely on oilseed rape (Figure 7). Variable responses were obtained for other crops, especially sorghum, sugarcane (*Saccharum officinarum* L.) and mustard (*Sinapis alba* L.). Predators were not favoured on alfalfa (*Medicago sativa* L.), pea and sorghum, and a beneficial effect was recorded on cotton and wheat in only half of the cases (Figure 7). The only study where oilseed rape was considered reported two opposite effects. As for parasitoids, all responses obtained with oilseed rape corresponded to a decrease of populations or parasitism rates, while more than a half of them were beneficial for biological control on cotton and wheat (Figure 7).

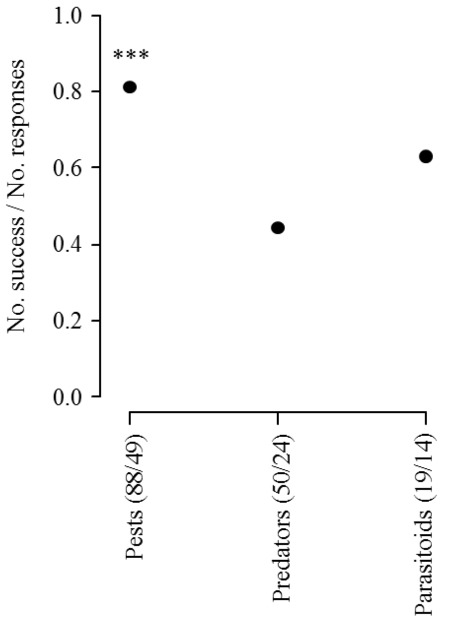

Figure 5. Ratio of the number of responses reporting a positive effect of wheat-based intercropping on biological control (i.e. decrease in pest and increase in natural enemy populations) on the total number of responses. The ratio given in brackets corresponds to the number of responses/number of papers. Exact Bernouilli test. *** P < 0.001.

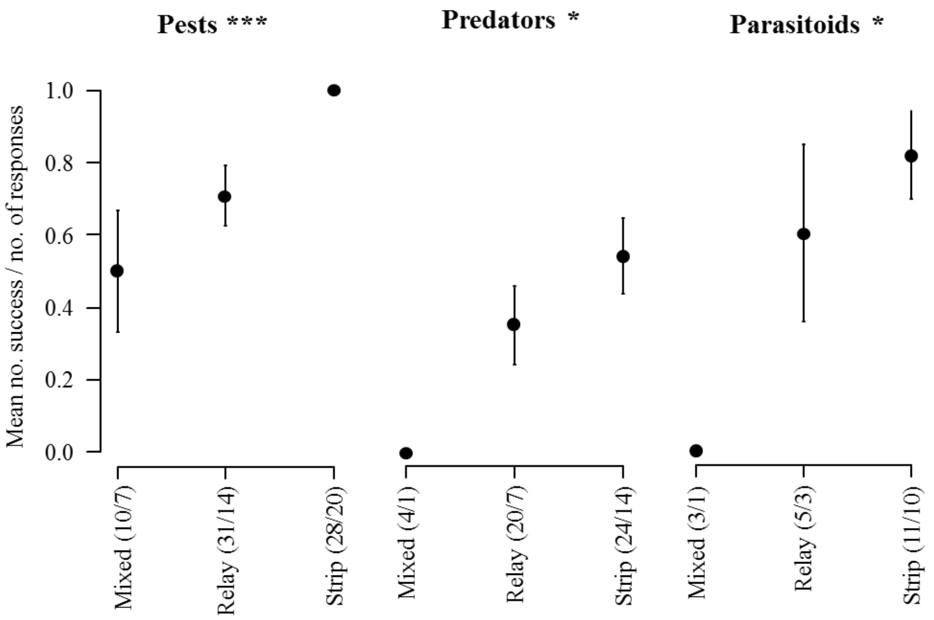

Figure 6. Mean (± SE) number of responses reporting a positive effect of wheat-based intercropping on biological control (i.e. decrease in pest and increase in natural enemy populations) on the total number of responses according to the type of wheat-based intercropping. The ratio given in brackets corresponds to the number of responses/number of papers. Likelihood ratio tests on GLMs. * P < 0.05; *** P < 0.001.

3.4 Crop yield

The effect of intercropping on yield was assessed in only 10 of the 50 papers. Six papers reported significant higher yield in intercropping systems compared to pure stands, while a single one showed the opposite. Two of them reported no significant differences. Additionally, one paper reported a significant higher yield in intercropping compared to pure stand in the first year and no significant differences in the following one. No significant correlation was found between pest reduction and yield increase ($\varphi = 0.45$, $P = 0.145$). However, higher yield was positively correlated with an increase of predator populations and predation rate ($\varphi = 0.77$, $P = 0.024$). This positive correlation was even stronger when predator and parasitoid data were analysed together ($\varphi = 0.81$, $P = 0.002$). However, not enough data were available to test such a correlation for parasitoids alone.

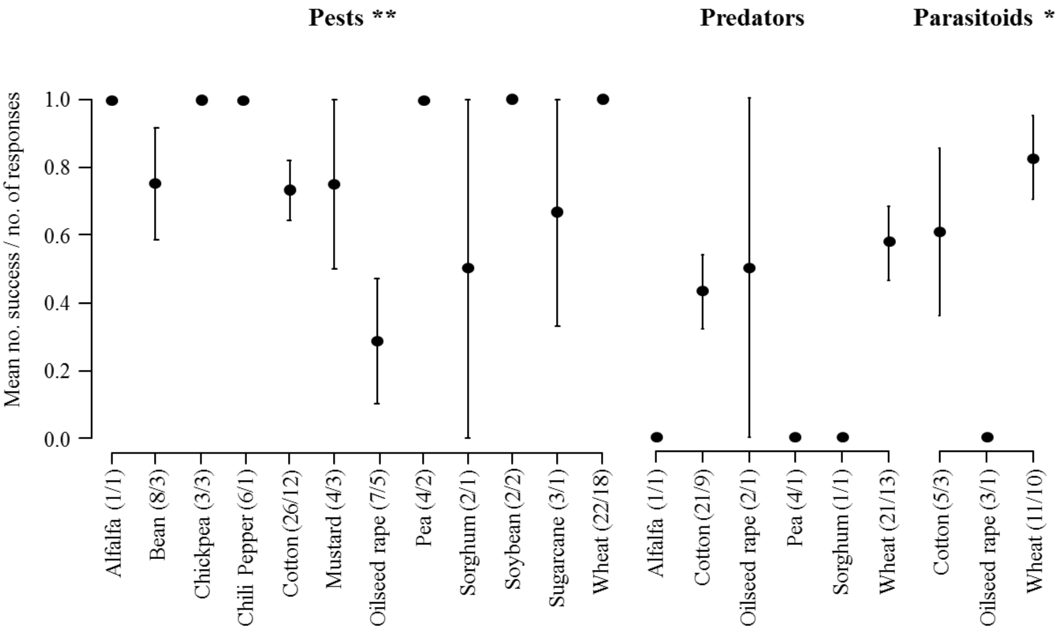

Figure 7. Mean (±SE) number of responses reporting a positive effect of wheat-based intercropping on biological control (i.e. decrease in pest and increase in natural enemy populations) on the total number of responses according to the crop species that was studied. The ratio given in brackets corresponds to the number of responses/number of papers. Likelihood ratio tests on GLMs. * $P < 0.05$; ** $P < 0.01$.

4. Discussion

4.1 Effect on pest biological control and implication for yield

4.1.1 Insect pests and natural enemies

Wheat-based intercropping systems almost systematically have a positive effect on pest control. In fact, the number of responses reporting a decrease of their populations was significantly higher than those showing the opposite. This finding is consistent with most studies addressing the effect of plant diversity on herbivores (Andow, 1991; Letourneau et al., 2011). Most of the mechanisms explaining how plant diversity promotes pest regulation, called associational resistance (Tahvanainen and Root, 1972), were compiled by Poveda et al. (2008) and Barbosa et al. (2009). For example, pest ability to locate host plant odours may be disrupted when they are masked by volatiles from non-host plants (Tahvanainen and Root, 1972). Moreover, host plant odours may be altered when exposed to volatiles from

Table 3. Effect on pests, predators and parasitoids according to the plant species that was studied in the intercropping.

Crop	**Effect**			**No. of papers**	**References**
	(-)	**(O)**	**(+)**		
Pest abundance					
Bean	♦			1	Hansen et al., 2008
	♦		♦	1	Tingey and Lamont, 1988
Chickpea	♦			3	Das, 1998; Hossain, 2003; Mehto et al., 1988
Chili pepper	♦			1	Chen et al., 1995
Cotton	♦			10	Chen et al., 1994, 1998; Ma et al., 2006; X. M. Ma et al., 2007; Mu et al., 1993; Parajulee et al., 1997; Parajulee and Slosser, 1999; W. Wang et al., 2009; Zhang, 1990; Zhao et al., 1987
	♦		♦	2	Wang and Zhao, 1993; Xia et al., 2000
Mustard	♦			2	Ansari et al., 2007; Tiwari et al., 2005
		♦		1	Mishra et al., 2001
Oilseed rape		♦		3	Hummel et al., 2009a, 2009b; Paulsen et al., 2006
	♦			2	Hummel et al., 2010; Sarwar, 2011
Pea	♦			1	Ndzana et al., 2014
Sorghum	♦	♦		1	Phoofolo et al., 2010
Soybean	♦			2	Hammond and Jeffers, 1990; Miklasiewicz and Hammond, 2001
Sugarcane	♦	♦		1	Masih et al., 1988
Wheat	♦			15	Dong et al., 2012; Ehsan-Ul-Haq and Van Emden, 2003; Fathi et al., 2013; K. Z. Ma et al., 2007; Saeed et al., 2013; Sherawat et al., 2012; Wang et al., 2011, 2008; W. L. Wang et al., 2009; Xie et al., 2012a, 2012b, Zhou et al., 2013b, 2013a, 2009a, 2009b
Wheat and alfalfa	♦			1	Skelton and Barrett, 2005
Wheat and bean	♦			1	Yang et al., 2009
Wheat and pea	♦			1	Lopes et al., 2015

Continuation of Table 3

Predator abundance and predation rate

Cotton			♦	5	X. M. Ma et al., 2007; Parajulee et al., 1997; Wang and Zhao, 1993; Xia et al., 2000; Zhang, 1990
		♦		2	Chen et al., 1994; Parajulee and Slosser, 1999
		♦	♦	2	Ma et al., 2006; W. Wang et al., 2009
Oilseed rape	♦		♦	1	Hummel et al., 2012
Sorghum		♦		1	Phoofolo et al., 2010
Wheat			♦	8	Dong et al., 2012; Fathi et al., 2013; Wang et al., 2011; W. L. Wang et al., 2009; Xie et al., 2012a; Zhou et al., 2009a, 2013b, 2013a
		♦	♦	2	Sherawat et al., 2012; Wang et al., 2008
		♦		1	Saeed et al., 2013
Wheat and alfalfa	♦			1	Skelton and Barrett, 2005
Wheat and pea	♦			1	Lopes et al., 2015

Parasitoid abundance and parasitism rate

Cotton		♦		1	Chen et al., 1994
			♦	2	Ma et al., 2006; X. M. Ma et al., 2007
Oilseed rape	♦	♦		1	Hummel et al., 2010
Wheat		♦		1	Dong et al., 2012
		♦	♦	1	Wang et al., 2008
			♦	8	Ehsan-Ul-Haq and Van Emden, 2003; K. Z. Ma et al., 2007; Wang et al., 2011; W. L. Wang et al., 2009; Xie et al., 2012a; Zhou et al., 2009a, 2013b, 2013a

neighbouring insect-infested (Ton et al., 2007) and non-infested (Ninkovic et al., 2013) plants, but also after absorbing certain root exudates from adjacent non-host plants (Finch and Collier, 2000). In some cases, competition between associated plants may alter the quality of host plants, which become less attractive for pests (Theunissen, 1994). Pests may also be more attracted to associated non-host plant species and remain on these plants without infesting the main crop (Vandermeer, 1989). Alternatively, certain plants have repellent odours (Uvah and Coaker, 1984). Other mechanisms may also affect the visual location of host plants, such as greener and/or taller non-host plants, which may camouflage the host plant (Finch and Collier, 2000) or even lead to its physical obstruction (Perrin and Phillips, 1978).

Furthermore, natural enemies may exercise a top-down control on pests. However, the number of responses reporting a beneficial effect of intercropping on predators and parasitoids was not significantly higher than the one reporting the opposite. This result is not consistent with the enemy hypothesis of Root. Several explanations have been put forward by the authors of the analysed papers to explain that. For instance, according to Hummel et al. (2012) who found that canola-wheat intercropping did not increase ground beetle (Coleoptera: Carabidae) populations compared to pure stands, intercropping may have altered microhabitat conditions (i.e. soil moisture, temperature and light penetration through the canopy), making the environment less suitable for some species. The same authors also found that the parasitism rates of the root maggot *Delia radicum* (L.) puparia decreased with increasing proportions of wheat in a canola-wheat intercropping system. Since *Delia* spp. caused less damage in intercropping systems compared to pure stands, it was hypothesised that the amount of volatiles emitted by infested canola plants, which attract the adult parasitoid *Aleochara bilineata* Gyll., were limited by intercropping. A similar hypothesis was proposed by Lopes et al. (2015) to explain why adult ladybeetles and hoverflies were significantly more attracted by pure stands of pea and wheat, respectively, which were significantly more infested by aphids compared to mixed and strip cropping systems. Moreover, some practical aspects may explain that natural enemies were rarely favoured in intercropping systems. In relay-intercropping for instance, whereas this system may allow natural enemies to maintain though time, a lack of temporal overlap between the several crops may cause a dissipation of the natural enemies (Parajulee and Slosser, 1999). Also, the use of insecticides in experiments could have negatively affected natural enemies resulting in no differences between treatments (Chen et al., 1994). Landis et al. (2000) reported that plant diversity should benefit natural enemies partly because it may provide pollen and nectar that are alternative non-host food sources. However, a particular attention must be paid on the crop phenological and physiological characteristics that may affect natural enemies. Despite several flowering crops may produce such food sources (e.g. oilseed rape, alfalfa or faba bean with extra floral nectar), the flower architecture must be adapted to insect mouth parts (Campbell et al., 2012) and the resources must be available when they are needed (Colley and Luna, 2000). These aspects may explain why simply associating crops do not necessarily favour natural enemies.

4.1.2 Crop yield

There was no significant correlation between pest reduction and yield increase. This result is consistent with Letourneau et al. (2011) who also found that beneficial effects of plant diversity on pest reduction are not systematically translated in higher yield. One reason is that the type of intercropping also influences other agronomic aspects, such as plant density and competition for resources. Yield may particularly be affected in substitutive designs like mixed intercropping, as they imply lower crop densities when compared to pure stands, but also higher competition for water, light and nutriments between associated plants (Letourneau et al., 2011). However, according to Bedoussac et al. (2015), yield of all associated crops considered together is almost systematically higher compared to the one of each crop grown in pure stands. In our study, not enough data were obtained to fully address this question. However, we might hypothesize that minimizing the competition between intercropped plants can be achieved in relay and strip intercropping, which are also the most efficient for controlling pests and favouring natural enemies. The positive correlation between the beneficial effect of intercropping on natural enemies and higher yield may encourage following this direction. Furthermore, as noted by Letourneau et al. (2011), it would be interesting to determine whether eventual yield losses due to intercropping are compensated by environmental benefits and input cost reduction (in our case insecticides) in future studies.

4.2 Adopting intercropping for pest control: constraints and opportunities

4.2.1 A well-established practice in Asia that is beginning to take hold in Europe

Most studies addressing the effect of wheat-based intercropping on pests and/or natural enemies were carried out in China. Despite the fact that intercropping has been practiced in

Chinese agriculture for over 1000 years (Knörzer et al., 2009), there has been a strong decline in the use of this method on the North China Plain over the last 20 years (Feike et al., 2012). In fact, with the decrease of rural labourers and increase in farmer's income, farmers have invested in mechanisation, adopting intensive production methods. As noted by Feike et al. (2012), one of the ways to overcome this issue is to replace the traditional labour-intensive row intercropping system by strip intercropping, which can be more easily adapted to mechanisation. Therefore, it is not surprising that many studies carried out in China have focused on this type of intercropping.

In contrast, studies remain rare on intercropping as a tool to biologically control pests in Europe. This may be because this practice needs technical adaptations (see section 4.2.2) to be implemented, which are not compatible with the conventional agriculture model that has been practiced in Europe for the last 30 years (Malézieux, 2012). In fact, for farmers, developing intercropping systems requires new skills and tools (Malézieux et al., 2009). In addition, these systems must satisfy the ecological, economic and social constraints on their farms (Malézieux, 2012). However, the growing focus on low-input farming practices in academic environments (Doré et al., 2011; Malézieux, 2012; Wezel et al., 2014a) and at the political level (De Schutter, 2010; Guillou et al., 2013) may explain the recent development of research on intercropping in Europe.

4.2.2 Adopting intercropping needs technical adaptations

Management and technical issues are central for developing intercropping systems. Indeed, phenological and spatial constraints of crop species must be taken into account to select viable combinations. Competition for resources (i.e. light, water, nutrient) (Thorsted et al., 2006), as well as allelopathic effects (Khan et al., 2002), may limit whether associations work. Appropriate machines are also needed to sow, harvest and separate grains in mixed cropping (Lithourgidis et al., 2011a). However, the management of strip and relay intercropping systems may be facilitated, as two or more crops may be separately managed. Also, the size of the strips and the ratio between the associated crops can be adapted depending on farmer production objectives and agronomic constraints (i.e. in the selected studies, the width of the strips went from few crop rows to at least 5 m and the ratio between crops was from 1 to 4). This may explain why the majority of studies focused on these two systems. Among the crops associated in relay, the combination of wheat with cotton is widely practiced in China (L.

Zhang et al., 2007). As well described by Zhang et al. (2008), "the cotton is sown in April, approximately seven weeks before the harvest date of wheat. Strips are left open in the wheat crop at sowing (October/November) to provide space for the cotton plants during their seedling stage (April, May and June). After the wheat harvest in June, cotton plants can exploit the full space, above-ground as well as below-ground." As for mixed intercropping, wheat was only found associated with pea and oilseed rape. Wheat-pea mixtures are known to provide many benefits. For instance, wheat benefits from the symbiotic nitrogen fixation of peas, allowing to reduce fertilizer inputs (Ghaley et al., 2005; Pelzer et al., 2012). Some experiments have been published on the effects of wheat-pea mixtures, but not necessarily on the aspect of pest control (Ghaley et al., 2005; Lithourgidis et al., 2011b; Pelzer et al., 2012). In comparison, studies on the effects of mixing wheat and oilseed rape seemed to be a rarer combination, at least based on the publication record.

4.2.3 Combining crops of primary importance to favour the adoption of intercropping

Intercropping systems involve cultivating two or more crops in the same place at the same time. However, one crop is often seen as more important than the other crops for economic reasons (Lithourgidis et al., 2011a). This issue may explain why intercropping was studied to mitigate pests and favour natural enemies for just one of the associated crops in most studies. Cotton, sugarcane and soybean are well-known important cash crops that are exported worldwide (FAOSTAT (http://faostat.fao.org/site/342/default.aspx)). A particular crop may also be of special economic and cultural importance in some regions, such as chili pepper (*Capsicum frutescens* L.) in China (Lu et al., 2011) or the oilseed rape variety Canola in Canada (Raymer, 2002).

Wheat is an essential food crop in northern China and central Asia (Carter and Zhong, 1999; Morgounov et al., 2007), as it is in Europe and North America (FAOSTAT (http://faostat3.fao.org/browse/Q/*/E)). However, wheat is rarely considered as the main crop in intercropping systems in Europe and North America. Because conventional farming practices applied to wheat production already tend to achieve high yields, producing wheat under intercropping systems may not be seen as needed for economic and food security reasons. However, it is necessary for agriculture to shift toward more ecological food production in Western countries. Developing intercropping systems that are beneficial for crops of primary importance may favour such a transition.

4.3 Needs for further research

This study shows that wheat-based intercropping systems allow reducing pest occurrence on crops, while natural enemies are not favoured in such systems when compared to pure stands. However these results varied significantly depending on the countries where the study took place, the type of intercropping and the crops studied. In Europe, more research is needed to better assess the potential of wheat-based intercropping for pest control. Despite some limiting factors, mixed intercropping deserves to be further studied, as it may also provide some benefits.

Because predators and parasitoids are not significantly favoured in intercropping systems, these latter could be combined with other practices known to efficiently support natural enemies within fields. For instance, some volatiles known to attract natural enemies can be released in fields. Wang et al. (2011) showed that the abundance of ladybeetles and parasitism rate were higher when methyl salicylate was released in wheat-oilseed rape intercropping fields, compared to each treatment applied separately. Moreover, infrastructures such as woodlots, hedgerows and wildflower strips could be settled in farming areas as they are known to provide habitats sustaining natural enemies that prey on and parasitize pests in adjacent fields (Colignon et al., 2002; Haaland et al., 2011; Morandin et al., 2014). Among other factors, the regulation of pests by natural enemies depends on their presence in the surrounding landscape (Fahrig et al., 2015). The conservation of natural enemies and their attraction in intercropping fields could be a way to improve the biological control of pests.

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Article 3

Wildflower strips for biological control: state-of-art, limits and perspectives in Wallonia. A review

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Abstract

Managing field margins takes part of the Agri-Environmental Measures supported by the European Union in Wallonia. Among possible infrastructures, wildflower strips are known to conserve a wide diversity of insects, including natural enemies that can be mobilized to biologically control pests. However, the efficiency of pest control is not guaranteed. It depends mainly on the ability of flowers to attract natural enemies at the right time and to keep them in this environment while favoring their migration into adjacent crops. Addressing the issue of the composition of the floral mixtures may optimize their capacity to enhance biological control. In this context, this review paper puts forward the interest of considering functional traits of flowers and presents the concept of *functional diversity*. Furthermore, sown perennial wildflower strips should be maintained by regular mowing. However, mowing affects both insect and plant populations due to a momentary destruction of the habitat. An appropriate management of field margins is therefore needed to optimize the pest control service provided.

Keywords: natural enemies, insect pests, functional trait diversity, mowing regime, ecosystem services

1. Introduction

Insect pests cause damages on crops and lead to yield losses. In order to control them, the use of chemical insecticides has been generalized in fields of western countries from 1950s (Devine and Furlong, 2007). Nevertheless, there is ample evidence of their harmful effects on the environment (Devine and Furlong, 2007; Gibbons et al., 2015) and human health (Baldi et al., 2013). Moreover, resistances pests develop to them limit their efficiency (Thieme et al., 2010). This calls for a reduction of their use and the development of alternative methods, such as *biological control*.

Biological control is defined as “the utilization of natural enemies to reduce the damage caused by noxious organisms” (Debach, 1991). In practice, there are three methods (Debach, 1991). *Classical biological control* consists in the release and establishment of natural enemies exotic to the environment where they are introduced. *Augmentative biological control* tends to increase the abundance of endogenous natural enemies by releasing individuals multiplied in laboratories, or in attracting them with semiochemical signals. Finally, *conservation biological control* aims at maintaining natural enemies that are already established in the environment by managing appropriate habitats. The present paper focuses on this last method.

In the Walloon Region of Belgium, 43 % of land area is dedicated to agriculture, among which 40 % is devoted to crop cultivation (Service Public de Wallonie, 2014b). Additionally, the Walloon landscape is composed of semi-natural elements such as forest edges, hedgerows, isolated trees and managed field margins, for instance sown with wildflowers in strips. Interactions between crop and non-crop habitats are numerous (Cremer et al., 2010; Hance et al., 2010) and may be valorised by promoting the delivery of ecosystem services (Jacobs et al., 2013). Hence, studying and designing farming practices involving semi-natural elements towards biological control of insect pests is promising.

In this context, this review paper aims at (i) exploring in which way managing non-crop habitats could enhance biological control through the conservation of insect predators and parasitoids (i.e. called natural enemies). (ii) Especially, a focus is done on wildflower strips: what are their benefits but also their limits for conservation biological control? Finally, perspectives for research are discussed, such as (iii) using functional flower traits for optimizing the composition of mixtures and (iv) adapting mowing regime for maintaining both insect populations and flower species.

2. Semi-natural elements for biodiversity conservation: which benefits for biological control?

2.1 Semi-natural habitats, providers of ecosystem services

Semi-natural elements at field margins are various: forest edges, hedgerows, wildflowers and grass strips. Their ability of providing ecosystem services is acknowledged: increasing soil fertility, reducing erosion and nutrient run-offs, enhancing insect conservation (W. Zhang et al., 2007). The provision of such services may offer a purpose to the conservation of biodiversity. In Belgium especially, at least 40 % of species are extinct or declining and habitats favouring their survival are rare (Dufrêne, 2013).

Insect conservation and biological control are among other ecosystem services. Semi-natural habitats in agricultural landscapes are known to host a higher diversity of insect species than adjacent fields (Nicholls and Altieri, 2013; Schneider et al., 2014; Thomas and Marshall, 1999). Wallonia is no exception, where insect diversity, but also density, is higher in field margins and forest edges than in crop fields (Colignon et al., 2002). Some of these insect species are natural enemies of pests, being predators (e.g. families: *Anthocoridae* [Hemiptera], *Syrphidae* [Diptera], *Elateridae* [Coleoptera], *Stapylinidae* [Coleoptera], *Tenthredinidae* [Hymenoptera]) or parasitoids (e.g. families: *Aphidiidae* [Hymenoptera], *Ichneumonidae* [Hymenoptera]) (Colignon et al., 2002).

2.2 From insect diversity to biological control

Conservation biological control is based on the presence of natural enemies at field margins. Nevertheless, favouring natural enemies does not necessarily lead to an increased control of pests. Understanding the processes of predation and parasitism is needed for managing biological control (Alhmedi et al., 2011; Macfadyen et al., 2009). Species identity and diversity are determinant in such processes. Indeed, two mechanisms may be involved: (i) the *complementarity effect* between species which affects the share of food resources, and (ii) the *sampling effect* suggesting that a diversified population of predators increases the chance to contain key species with a high predatory rate (Loreau et al., 2001). Regarding the complementarity effect for instance, it was reported that three species of natural enemies simultaneously (*Harmonia axyridis* (Pallas), *Nabis* sp., et *Aphidius ervi* (Haliday)) are more efficient in controlling two species of aphids (*Acyrthosiphon pisum* (Harris) et *Aphis craccivora* (Koch)) than the sum of each of them alone (Cardinale et al., 2003). As for the sampling effect, Straub and Snyder (2006) showed that the only presence of species from the genera Coccinella (Coleoptera) allowed a reduction of aphids *Myzus persicae* (Sulzer) while an increase of predatory species diversity had no effects. Moreover, inter- and intra-guild predation may favour some species (Gardiner et al., 2011) as well as their spread in fields (Alhmedi et al., 2006). This phenomenon may limit natural enemy diversity in agricultural landscape and favour some key species able to control pests.

Additionally, pest control implies that natural enemies found at field margins are present within crop parcels simultaneously with pests. For instance, in order that hoverfly larvae (Diptera: Syrphidae) control aphids, it is needed that (i) hoverfly adults, feeding on pollen and nectar from flowers at field margins, oviposit on crops and that (ii) oviposition occurs early enough when pest infestation starts (F. Francis et al., 2003). Similar conditions are needed for a successful pest control by other natural enemies, such as aphidophagous ladybeetles (Coleoptera: Coccinellidae) (Francis et al., 2001a).

From theory to practice, farmers may be interested by the potential benefits of semi-natural habitats, among others wildflower strips. But to what extent can flowering margins host insects and favour biological control in adjacent crops?

3. Despite their ability to host insects, do wildflower strips enhance pest biological control?

3.1 Wildflower strips: a practice with various facets

Among the variety of semi-natural habitats mentioned here-before, benefits of sown wildflower strips for biodiversity conservation are acknowledged (Haaland et al., 2011) and their ability of enhancing biological control is promising (Pfiffner and Wyss, 2004). Their implementation and management within fields or at margins is subsidised through the Agri-Environmental Schemes (AES) of the European Union (EU) (in Wallonia, Measures 3 and 9 encourage the development of grassy and flowered margins - GIREA and DDR/DGARNE/SPW, 2013). Nevertheless, sown strips may be various. For instance, mixtures are often composed by wild flowers and grass species but the proportion between them can vary, as well as the species diversity, sowing method and management. One reason is that mixture characteristics depend on the policies of each EU country subsidizing their implementation (Haaland et al., 2011). Such a variety of mixture composition and management is also found in research, where some study monospecific flower mixtures (Carrié et al., 2012) while others compare plurispecific mixtures and more generally diverse types of vegetated margins (Denys and Tscharntke, 2002; Thomas and Marshall, 1999). However, these studies share the common objective of better understanding in what extent flowering margins can affect insect diversity in agricultural landscapes and whether they could allow a reduction of pests.

3.2 Wildflower strips host a large diversity of insect

According to numerous studies, sown wildflower strips host a higher diversity and abundance of insects than adjacent crop fields (Denys and Tscharntke, 2002; Haaland et al., 2011; Pfiffner and Wyss, 2004). A reason is the ability of wildflower strips to provide to insects (i) food resources such as nectar and pollen, and (ii) habitats for overwintering and reproduction, thanks to their structure complexity and low disturbance (compared to crop fields) especially in terms of pesticide applications (Balzan and Moonen, 2014; Horton et al., 2003; Jonsson et al., 2008; Landis et al., 2000; Marshall and Moonen, 2002; Médiène et al., 2011). Natural enemies are part of this diversity of insects. Some are predators, considered as generalists (e.g. carabids [Coleoptera: Carabidae] and spiders [Araneae]) while others are more specialists (e.g. larvae of hoverflies, lacewings [Neuroptera: Chrysopidae], ladybeetles) (Alhmedi et al., 2011; Pfiffner and Wyss, 2004) ; some are parasitoids (e.g. belonging to the super-families of Cynipoidea, Ichneumonoidea, Chalcidoidea, Proctotrupoidea) (Jervis et al., 1993). Concerning predators, in addition to the benefits already mentioned, wildflower strips may host alternative prey, hence offering complementary food resource (Balzan and Moonen, 2014). As for parasitoids, the potential presence of a large diversity of insects increases their chance to find the hosts they need for their reproduction (Marino and Landis, 1996).

3.3 A diversity of natural enemies to control insect pests

As specified here-before, natural enemies developing in wildflower strips must move to the adjacent crops for preying or parasitizing pests. Alhmedi et al. (2009) reported in Wallonia that aphid predators *H. axyridis* and *Coccinella septempunctata* (Linnaeus) (Coleoptera: Coccinellidae) and the parastoid *A. ervi* (for which aphids are its main host) were first observed in nettle (*Urtica dioica* L.) strips and later in adjacent wheat (*Triticum aestivum* L.) and pea (*Pisum sativum* L.) crops. As for their efficiency to control pests and damages, it was reported that (i) parasitism rate was higher (Lee and Heimpel, 2005) and (ii) damage rate was lower (Balzan and Moonen, 2014) in fields adjacent to wildflower strips compared to parcels without managed margins. Consequently, the efficiency of parasitoids to control pests and reduce damages is increased at a reduced distance from flowering margins.

Nevertheless, the enhancement of conservation biological control by the sowing of wildflower strips is not systematic. Indeed, it may have a physical and/or temporal incompatibility between natural enemies and flower resources or a time gap between the occurrence of natural enemies and the presence of pests (Pfiffner et al., 2009). Hence, it is needed that the sown floral resource is available to targeted insects when they need it (Colley and Luna, 2000). It implies compatibility between flower and insect morphology and phenology. Moreover, natural enemies attracted by wild flowers must move to the adjacent crops to control pests (Alhmedi et al., 2009). These two conditions invite to think flower mixtures in terms of functionality for natural enemies.

4. Composing flowering mixtures: the benefits of functional diversity

4.1 Considering flower functional traits instead of species identity

Mixtures sown to implement wildflower strips are often described through the species composing them (Balzan and Moonen, 2014; Carrié et al., 2012; Pfiffner et al., 2009). Nevertheless, some studies highlight that considering functional diversity (FD) of mixtures, instead of their species diversity, would be interesting (Altieri, 1999; Landis et al., 2000; Moonen and Bàrberi, 2008). They propose to ignore species identity and instead focus on their characteristics described through their traits. These traits are “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation" (Violle et al., 2007). Once a plant is considered in the context of the environment in which it grows, its traits may affect ecological processes. Consequently, these traits are termed as *functional* (Díaz and Cabido, 2001).

Plant traits can be various. Some affect insect behaviour in attracting, or conversely repulsing them (Cook et al., 2007). They may be grouped in three categories: chemical, architectural, and phenological traits. Among them, organic volatile compounds (e.g. terpenoids) emitted by some plants are known to affect insect behaviour. The release of such volatiles, after for instance an attack of herbivores (Pickett et al., 2003), can attract natural enemies (Francis et al., 2004) and/or repulse potential new pests (Verheggen et al., 2013). As for architectural traits, corolla morphology (width and depth) affects the availability of pollen and nectar for flower visitors (Patt et al., 1997). Moreover, plant height, growth type (i.e. erect or supine), organization of leaves or stem height affect insects, especially carabids that are sensitive to the structure of vegetation (Brose, 2003). Plant height also affects flying species searching for nectar and pollen such as hoverflies (Wratten et al., 2003). Finally, flower colours are determinant in the attraction of visitors (Cowgill, 1989). Among phenological traits, the onset of blooming and blooming duration affect the availability of food source for pollen and nectar feeders. These various traits are generally determinant in plant-insect interactions (Elzinga et al., 2007), whether these lasts are natural enemies, prey or alternative hosts.

4.2 From studying the effect of a single trait to the calculation of functional diversity at the mixture level

Several studies focused on a single trait by assessing the effect of different values on insect behaviour, for instance different colours of flowers (Begum et al., 2004) or various morphologies of corolla (Campbell et al., 2012). Recently, Balzan et al. (2014) composed mixtures with a contrasting diversity of values for a single trait. Nevertheless to our knowledge, few other studies considered several values of one trait in mixtures. Such an approach implies to understand the concepts of *functional redundancy* and *functional complementarity*.

According to Díaz and Cabido (2001), "two or more species are considered redundant with respect to an ecosystem process when the disappearance of one or more of those species does not affect that ecosystem process in a significant way". Because trait values affect ecological processes, mixtures composed with species having similar values for a certain trait will present a high functional redundancy. Additionally, functional complementarity between two species occurs when they contribute together, but differently, to an ecological process. Hence, functional complementarity within a flower mixture will increase along with the diversity of trait values between species.

The level of functional redundancy and complementarity within a mixture may affect its attractiveness to insects as well as its ability to feed them and provide them a shelter. These aspects are reflected in the calculation of FD that measures the diversity of values from a variety of traits among species composing a mixture. This value of FD is thus an index allowing comparing them. However, such a comparison is only valid in the case of equal species richness between mixtures. Because wildflower strips are often composed of several species, and that insects are sensitive to these species because of plant traits, it remains needed to assess whether a functionally diverse mixture affects the diversity of attracted insects. A hypothesis is that a functionally diverse mixture affects the behaviour of a broad diversity of insect species. However, it still needs to be verified.

5. Wildflower strips are managed but what is the effect of mowing on insect diversity?

Sown wildflower strips are often composed of perennial species and their composition evolves through time. Hence, it is needed to address the issue of their management and the consequences on insect populations.

5.1 The diversity of plants composing an ecosystem is dynamic

Plant species are classified in three categories based on their establishment ability in their environment: (i) competitive species that do not sustain stresses and disturbances, (ii) those being stress-tolerant and favoured in stable environments and (iii) ruderals adapted to stresses and disturbances (Grime, 1977). Understanding these strategies is needed for analysing plant successions in a given ecosystem. In agroecosystems, ruderal species are favoured because agricultural fields are often productive (because fertile) and disturbed. Nevertheless, when within field operations are reduced, stability increases while productivity decreases favouring firstly competitive species, secondly the development of stress-tolerant ones. This process is notably responsible for the closing of landscape in abandoned agricultural lands (Brossard et al., 1993). Indeed, although ruderals are mainly annual species, competitive and stress-tolerant are diverse, comprising shrubs and trees (Grime, 1977). Therefore, an appropriate management of perennial wildflower strips by mowing is needed in order to maintain species diversity (Piqueray et al., 2013).

5.2 Mowing maintains flower mixture diversity but briefly disturbs the environment

Mowing wildflower strips is needed, hence is a common practice. Nevertheless, mowing regimes (i.e. frequency and time) may vary. Haaland et al. (2011) reported that, from a country to another, mowing regime is ruled by AES. Several studies showed that mowing reduces diversity and abundance of insects in flower mixtures on the short term (Baines et al., 1998; Horton et al., 2003; Jervis et al., 2004; Olson and Wäckers, 2007). Indeed, it suppresses their board and lodging (Horton et al., 2003). Nevertheless, if strips were not mown, the decrease of plant diversity would also have a negative effect on insect diversity, especially on the long term. A compromise to this dilemma has been adopted in Wallonia, by mowing only a part of a strip each year and thus maintaining a refugee zone for insects. From a year to another, this refugee zone moves in order to progressively mow the whole strip and avoid the establishment of unwanted woody plants.

Consequences of mowing on trophic relations between insects have been poorly studied to our knowledge. As mentioned here-before, there are no systematic causal links between an increased diversity of insects and the establishment of trophic relations. Conversely, we may hypothesize that a reduction of species diversity limits the chances of trophic relations to establish, especially when considering natural enemy species identity more than their diversity, as suggested earlier (Straub and Snyder, 2006).

Insofar wildflower strips are mown in order to maintain their plant species diversity, cutting frequency and time may be determinant in mixture development. Moreover, because it briefly and partially disturbs the environment, frequency and time may affect insect diversity and their trophic relations.

6. Conclusion

This literature review highlights that wildflower strips sown at field margins for conserving insect diversity in agricultural landscapes has been studied, among them natural enemies that are able to biologically control pests. It must be recalled that in this context, pest control is intrinsically linked to insect conservation. Moreover, the ecological benefits of wildflower strips have been acknowledged in Wallonia through the agri-environmental policies. Nevertheless, sowing wildflower strips does not systematically lead to an increased biological control of pests in adjacent crops. Hence, considering mixture functionality, i.e. their ability to attract, feed and provide a shelter to insects for in the end enhancing parasitism and predation, is needed in order to optimize flowering margin composition. Additionally, assessing the effect of mowing on insect populations and mixture composition would allow establishing adapted practices. Finally, sowing wildflower strips may provide additional benefits not specified in the present paper: enhancement of pollination, nutrient capture or forage provision; as many ecosystem services that may be valuable for farmers and society as a whole.

Acknowledgments

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Chapter II

Increasing plant diversity at the field scale with the provision of flower resources for enhancing biological control

Introduction to Chapter II

The analysis of the scientific literature (***Chapter 2*** and ***Chapter 3***) shows that implementing intercropping and sowing flowering strips can provide complementary benefits for enhancing biological control of insect pests. Whereas intercropping increases crop habitat heterogeneity and in turn negatively affects pest abundance without especially supporting natural enemies, flowering features can notably offer missing resources, i.e. non-prey food (nectar, pollen) that are needed for some natural enemies. Conversely, simply introducing flowering plants at field margins does not increase crop habitat heterogeneity. Hence, **would increasing plant diversity with the provision of flower resources within field enhance simultaneously a bottom-up and a top-down control of insect pests?**

This strategy was tested in two different agricultural contexts. ***Article 2*** shows that intercropping as a tool for biological control is little developed in European countries while it is a common practice in China. Knörzer et al. (2009) recalled that intercropping has been practiced in China for more than a thousand years and that the benefits of mixing crops are being rediscovered in the light of the sustainability challenges agriculture faces. In this context, the tested tactic was to settle an intercropping system where one of the associated crops was a flowering species – namely oilseed rape, associated with wheat – able to offer floral food resources to insect pest natural enemies, in addition to the interest of intercropping in increasing cropping habitat heterogeneity. Moreover, semiochemical molecules were released in order to test whether it could strengthen the attraction of natural enemies, namely ladybeetle sex pheromone to attract coccinellids (***Article 4***).

In contrast, the introduction and management of wildflower strips is encouraged and financially supported in Belgium by the European Union through the agri-environmental policy (GIREA and DDR/DGARNE/SPW, 2013). Although such wildflower strips are today mainly managed for insect conservation (Haaland et al., 2011), their presence in Belgian agricultural landscapes makes them a potential tool for biological control, as discussed in ***Article 3***. Therefore, the tested tactic was to sow wildflower strips within a wheat field, in order to reduce the crop parcel size – hence increasing the field heterogeneity – in addition to provide a habitat and non-prey food to natural enemies (***Article 5***).

Article 4

Does wheat – oilseed rape intercropping combined with the slow release of ladybeetle sex pheromone allow reducing aphids and increasing their natural enemies in China?

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Abstract

Intercropping (i.e. cultivating at least two plant species simultaneously in the same field), as well as releasing semiochemicals, can allow repelling pests and/or attracting their natural enemies, hence be used as biological control tactics. The aim of the present study was to test their combination in field. Among semiochemicals, the sex pheromone of ladybeetles was recently identified and no conclusive results of its use in fields were reported so far. Among plant species to intercrop, oilseed rape (associated with wheat) was chosen because some natural enemies can benefit from the flower resources it provides. In a field trial conducted in Langfang (Hebei, China), four treatments repeated three times were compared: (i) the combination of wheat-oilseed rape intercropping with the release of ladybeetle sex pheromone, (ii) wheat-oilseed rape intercropping solely, (iii) pure stand wheat and (iv) pure-stand oilseed rape. Wheat and oilseed rape aphids, as well as their natural enemies (i.e. ladybeetles, hoverflies, lacewings, parasitoids), were observed on plants and pan-trapped over nine weeks from April to June 2016. Aphid abundance was not affected by the treatments. Treatments only affected adult ladybeetles in traps, being significantly less abundant in pure-stand oilseed rape than in the other treatments. Aphid abundance significantly affected natural enemy density in the field: ladybeetles were negatively related to aphids, while a positive relation was observed between aphids and all the other natural enemies. Principal Coordinate

Analyses followed by correlation tests performed at the species level showed that within a same family, species of natural enemies had different behaviour regarding aphid species and crops. The positive and negative correlations between individuals at the species level rather than the effect of treatments are discussed.

Keywords: biological control, *Triticum aestivum* L., *Brassica napus* L., mixed cropping, semiochemical, ladybeetle, parasitoid

1. Introduction

Aphids are common agricultural pests, damaging crops through direct feeding and by transmitting viruses (Van Emden and Harrington, 2007). Chemical insecticides are commonly used to control them but finding alternative approaches is an issue today. Indeed, evidence shows that chemical insecticides are harmful for human health and the environment (Devine and Furlong, 2007; Mostafalou and Abdollahi, 2013), while their efficiency is challenged by the resistances pests develop to them (Foster et al., 2007). Several strategies exist (Zehnder et al., 2007), among which increasing plant diversity. According to Root (1973), specialist herbivores are more likely to find their host plant when crops are concentrated in dense or pure stands (i.e. *resource concentration hypothesis*). Conversely, spatial diversification of cropping systems can disrupt the ability of pests to locate their host plant, increase pest mortality or repel them (Poveda et al., 2008). Moreover, chance of pests to be suppressed by their natural enemies increases in diversified systems. Indeed, the development of natural enemies can be favoured by the higher diversity of prey, hosts and microhabitats found in complex systems (i.e. *natural enemy hypothesis*). Intercropping is one practice of spatial diversification, defined as the cultivation of at least two plant species simultaneously in the same field, without necessarily being sown and/or harvested at the same time (Lithourgidis et al., 2011b).

Another tactic is to release semiochemicals (i.e. “natural signal chemicals mediating changes in behaviour and development”, Khan et al., 2008) to attract natural enemies and/or repel pests. Such semiochemicals are numerous in the environment. Some are produced by plants, e.g. herbivore induced plant volatiles (HIPV) when plants are attacked by herbivores (Kessler and Baldwin, 2001), others by insects, e.g. sex or alarm pheromones (Fassotte et al., 2016; Vandermoten et al., 2012). Once identified as pest repellent and/or natural enemy attractant, they can be synthesised and released in fields for enhancing biological control (Cui et al., 2012; Nakashima et al., 2016; Rodriguez-Saona et al., 2011).

In China, intercropping is a common practice (Knörzer et al., 2009). Lopes et al. (2016), who reviewed 50 studies on wheat (*Triticum aestivum* L.)-based intercropping systems for biological control, reported that almost half of the studies were conducted in China. Moreover, they showed that overall, pests are reduced in intercropping systems, but their natural enemies are not necessarily enhanced, contradicting the enemy hypothesis of Root (1973). In order to attract natural enemies, two tactics can be tested. First, flowering plants can be introduced. Indeed, flowers can attract and support a diversity of natural enemies that need floral resource (i.e. pollen, nectar) at some of their development stage (Lu et al., 2014). Studies showed that implementing wildflower strips (Hatt et al., 2017a) or companion plants (Balmer et al., 2014) within crop fields can increase the presence of some natural enemies and reduce pest density and damages. In intercropping systems, one of the combined crops can be a flowering species, e.g. oilseed rape (*Brassica napus* L.) known to be visited by insects such as hoverflies (Diptera: Syrphidae) (Jauker and Wolters, 2008). Second, intercropping can be combined with the release of semiochemicals attractant to natural enemies. Wang et al. (2011) reported a positive effect of wheat-oilseed rape intercropping combined with the release of methyl-salicylate (i.e. a HIPV) on the suppression of the wheat aphid *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae), the increase of ladybeetles (Coleoptera: Coccinellidae) and parasitism rate. Fassotte et al. (2014) identified the sex pheromone of the ladybeetle *Harmonia axyridis* (Pallas), which is a main aphid predator native to China (Brown et al., 2011). The sex pheromone is emitted by females to attract males. In laboratory conditions, Fassotte et al. (2014) reported that a synthetic blend composed after the identified compounds significantly attracts ladybeetle males. In field conditions, an experiment was conducted in Belgium to test the attractiveness of this semiochemical, nevertheless the results were not conclusive because of a general lack of ladybeetles in the fields that year (Fassotte, 2016). By testing again in fields the ability of ladybeetle sex pheromone to attract aphid predators, the aim of this study is to assess whether intercropping a flowering with a non-flowering crop, combined with the release of the sex pheromone of ladybeetles, allows increasing the abundance of aphid natural enemies and decreasing aphid density compared to pure stands and intercropping solely.

2. Material and methods

2.1 Field set up

The experiment was conducted at the Langfang experimental station of the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Hebei Province of China (39° 30’ N, 116° 37’ E). Four treatments, repeated three times in a totally randomised design, were compared (Figure 8): (i) the combination of wheat-oilseed rape intercropping with the release of ladybeetle sex pheromone, (ii) wheat-oilseed rape intercropping solely, (iii) pure stand wheat and (iv) pure-stand oilseed rape. Intercropping plots were composed of three strips of wheat separated by two strips of oilseed rape, each strip being 2 m × 6 m. The size of one plot was thus 10 m × 6 m. The twelve plots were sown at a distance of six and two meters from one another and soil was kept bare between them. Wheat (variety Zhongmai 175) was sown on 13 October 2015 and oilseed rape (variety Qinyou 2) on 15 October 2015. Possibly due to a late sowing in autumn combined with an exceptionally cold winter (see section 2.2 Weather condition), oilseed rape seedlings did not survive wintering, and it was sown again on 29 March 2016 (same variety). The field was surrounded by a two meter wide strip of wheat (same variety) in order to limit the interactions with the surrounding fields (sown with rice (*Oryza sp.*), cotton (*Gossypium sp.*) and a fallow). No pesticides were used in the whole experimental area. The field was regularly irrigated.

2.2 Weather condition

Weather data were retrieved from the meteorological station of the Langfang experimental station. Means of hourly temperature (°C), humidity (%) and rain (mm) were calculated for each month. Temperature varied from -6.5 °C in January 2016, with the minimum reaching -18.5°C that month, to 24.7°C in June 2016 with the maximum reaching 36.8°C (Figure 9a). Rains were very scarce while humidity varied from 71.9 % on average in November 2015 to 34.9 % on average in March 2016 (Figure 9b).

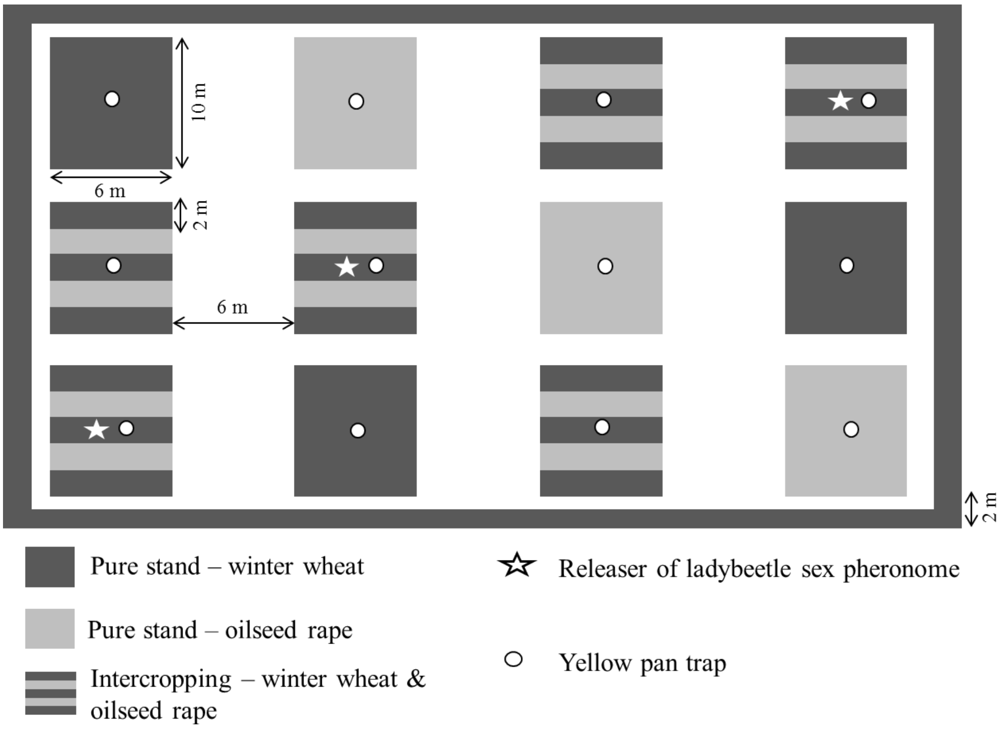

Figure 8. Experimental design (Article 4).

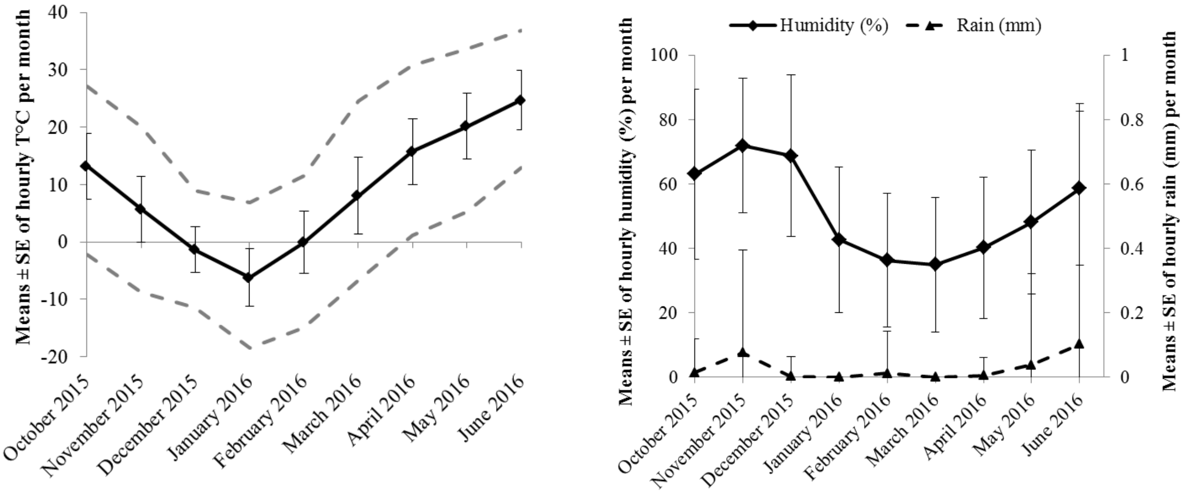

Figure 9. Weather conditions measured at the Langfang experimental station (Hebei, China) from October 2015 to June 2016: (a) monthly means ± SE of hourly temperatures (°C) with monthly minimums and maximums (grey dotted lines); (b) monthly means ± SE of hourly air humidity (%) and rain (mm).

2.3 Sex pheromone of ladybeetles and semiochemical dispensers

The synthesised pheromone of ladybeetles was prepared based on the compounds identified by Fassotte et al. (2014). Only α-bulnesene was not included because it is not available on the market. However, previous tests showed that the absence of α-bulnesene in the synthesised blend does not affect ladybeetle attraction in laboratory (Fassotte, 2016). 10 mL of solution was prepared in *n*-hexane and was constituted of β-caryophyllene (549 µL; purity: 97 %; extracted from *Nepeta cataria* L. as described by Fassotte et al., 2014), α-humulene (60 µL; purity: 98 %; Sigma-Aldrich, Bornem, Belgium), methyl eugenol (13 µL; purity: 99 %; Sigma-Aldrich, Bornem, Belgium) and β-elemene (9,5 µL; purity: 98 %; Isobionics, Geleen, The Netherlands).

A single dispenser was stuck inside an iron box with holes that protected the dispenser from the rain while allowing the diffusion of the volatiles. The box was fixed to a 1 m high stick placed near the yellow trap (Figure 8) in the intercropping with semiochemical release plots. Every three weeks, 50 µL of the solution was loaded inside a rubber septum. After solvent evaporation (one to two minutes), a second rubber septum was placed on top of the other to seal the dispenser. According to Fassotte (2016), the dispenser can release volatiles attractive to ladybeetles during 30 days.

2.4 Insect monitoring

Aphids and their natural enemies were observed (i.e. apterous and alate aphids, ladybeetle, hoverfly [Diptera: Syrphidae] and lacewing [Neuroptera: Chrysopidae] larvae) and pan-trapped (alate aphids, ladybeetle, hoverfly, lacewing and parasitoid [Hymenoptera] adults) during nine weeks from 5 April to 7 June 2016 (crops were harvested one week later). For observations, 20 oilseed rape plants and/or 20 wheat tillers (five plants and/or tillers at four distinct points randomly chosen in each plot) were observed (from top to down, both face of leaves, also the ear in the case of wheat) in each plot once a week. No distinction was made between larval stages and between species. As for trapping, one yellow pan trap (Flora®, 27 cm diameter and 10 cm depth) was installed in the middle of each plot. They were positioned at vegetation height, and filled with water containing a few drops of detergent (dish-washing liquid) to reduce the surface tension of water. Their position was adjusted during the growing season to follow crop growth. Traps were emptied and refilled every seven days, and the trapped insects were conserved in 70 % ethanol. Wheat and oilseed rape aphids, adults of aphidophagous hoverflies, lacewings, ladybeetles, and parasitoids were identified to the species.

2.5 Statistical analyses

The effect of treatments on the abundance of trapped and observed aphids was tested by fitting generalised linear mixed effect models (GLMM) (R function ‘glmer’, package ‘lme4’; Bates et al., 2014) with Poisson error distribution (log-link function). Treatments (for wheat aphids: intercropping with semiochemicals, intercropping solely, pure-stand wheat; for oilseed rape aphids: intercropping with semiochemicals, intercropping solely, pure-stand oilseed rape) were considered as fixed factors and the plots as random ones, as trappings and observations were done in the same plots for nine consecutive times. Concerning natural enemies (hoverfly, ladybeetle, lacewing and parasitoid adults trapped; hoverfly, ladybeetle and lacewing larvae observed), the effects of treatments and the density of aphids on their abundance were assessed by also fitting GLMMs with Poisson error distribution. Treatments, aphid abundance and their interaction were included as fixed factors, and the plots as random ones. For every model, data overdispersion was tested and occurred for all of them, excepted for trapped hoverflies. For models showing data overdispersion, generalised linear models with negative binomial error distribution were fitted instead (R function ‘glm.nb’, package ‘MASS’, Venables and Ripley, 2002), as suggested by Ver Hoef and Boveng (2007). For every selected model, the effects of fixed factors on insect abundance were tested using a likelihood-ratio test ($P < 0.05$). When treatments significantly affected insect abundance, means of abundance were compared using a post-hoc test of Tukey ($P < 0.05$, package ‘multcomp’, function ‘glht’, Hothorn et al., 2008). Finally, the relationships between aphid and their natural enemy species were investigated by building a Bray-Curtis dissimilarity matrix used in Principal Coordinate Analyses (PCoA) (R function ‘cmdscale’, package ‘vegan’, Oksanen et al., 2015). These relations, independently from the different treatments, were tested by using Pearson correlation tests ($P < 0.05$). All analyses were performed using R program (R Core Team, 2013).

Table 4. Abundance and diversity of aphids and natural enemies trapped in the different treatments.

	Intercropping + Semiochemical	**Intercropping**	**Oilseed rape**	**Wheat**	**Total**	**%**
Aphids (Aphididae)	**207**	**214**	**552**	**129**	**1102**	
Myzus persicae	87	77	552	-	716	65
Rhopalosiphum padi	95	96	-	93	284	25.8
Sitobion avenae	17	20	-	19	56	5.1
Metopolophium dirhodum	6	16	-	14	36	3.2
Schizaphis graminum	2	5	-	3	10	0.9
Lacewings (Chrysopidae)	**3**	**0**	**1**	**2**	**6**	
Chrysoperla carnea	3	0	1	2	6	100
Ladybeetles (Coccinellidae)	**65**	**56**	**19**	**63**	**203**	
Harmonia axyridis	26	33	7	30	96	47.3
Propylea 14 punctata	36	19	2	26	83	40.9
Coccinella 7 punctata	1	4	6	3	14	6.9
Hippodamia variegata	2	0	3	2	7	3.4
Adalia decempuctata	0	0	0	1	1	0.5
Chilocorus renipustalatus	0	0	1	0	1	0.5
Oenopia conglobata	0	0	0	1	1	0.5
Hoverflies (Syrphidae)	**5**	**9**	**9**	**6**	**29**	
Eupeodes corollae	3	4	7	3	17	58.7
Episyrphus balteatus	2	4	2	2	10	34.5
Melanostoma mellinum	0	0	0	1	1	3.4
Sphaerophoria scripta	0	1	0	0	1	3.4
Parasitoids (Braconidae)	**76**	**67**	**101**	**55**	**299**	
Aphidius gifuensis	38	40	58	43	179	59.9
Diaeretiella rapae	4	2	33	2	41	13.7
Aphidius funebris	18	14	2	0	34	11.4
Aphidius rhopalosiphi	5	5	4	6	20	6.7
Aphidius uzbekistanicus	6	4	2	3	15	5
Aphidius colemani	2	0	1	0	3	1
Ephredus plagiator	1	0	1	0	2	0.7
Trioxys auctus	1	1	0	0	2	0.7
Aphidius avenae	0	1	0	0	1	0.3
Aphidius ervi	1	0	0	0	1	0.3
Lysiphlebus fabarum	0	0	0	1	1	0.3

'-' indicates that these aphid species have not been considered in the treatments in which the pure-stand crop was not a host plant.

3. Results

Ladybeetles and parasitoids were the most abundant natural enemies, respectively seven and ten times more trapped than hoverflies. More specifically, *H. axyridis* and *Propylea 14 punctata* (Linnaeus) (Coleoptera: Coccinellidae) constituted together 88.8 % of ladybeetle individuals when *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae), *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Braconidae) and *Aphidius funebris* (Mackauer) (Hymenoptera: Braconidae) represented 85 % of parasitoids. As for hoverflies, *Eupeodes corollae* (Fabricius) (Diptera: Syrphidae) and *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae) were the most abundant species while *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) was the only species of lacewings trapped (Table 4). A very few density of lacewings in traps, and hoverfly and lacewing larvae on crops were found. Consequently, no statistical analyses were performed for these groups.

Abundance of aphids was not affected by the treatments (wheat aphids trapped: df = 2; χ^2 = 0.79; P = 0.675; wheat aphids observed: df = 2; χ^2 = 0.01; P = 0.995; oilseed rape aphids trapped: df = 2; χ^2 = 1.95; P = 0.378; oilseed rape aphids observed: df = 2; χ^2 = 0.19; P = 0.911). Concerning natural enemies, only adult ladybeetles in traps were significantly affected by the treatments (Table 5). They were significantly less abundant in pure-stand oilseed rape than in intercropping combined with the release of their sex pheromone (z-value = 2.91; P = 0.018), pure-stand wheat (z-value = 0.35; P = 0.045), and in a lesser extent than in intercropping solely (z-value = 0.34; P = 0.065).

Moreover, natural enemies were all significantly affected by aphid abundance (Table 5). A positive linear relation was found between aphids and hoverfly adults, parasitoids and ladybeetle larvae. Only ladybeetle adults were negatively related to aphids in traps. The PCoA plot of predators and aphids (Figure 10a) shows that the most abundant ladybeetle species *H. axyridis* and *P. 14 punctata* (Table 4) were mostly found in plots other than pure-stand oilseed rape, along with wheat aphid species. More specifically, the abundance of *H. axyridis* was significantly positively correlated with the abundance of *Rhopalosiphum padi* (Linnaeus) (Hemiptera: Aphididae) (cor = 0.97; P = 0.029) and of *S. avenae* (cor = 0.99; P = 0.007), while it was significantly negatively correlated with the abundance of *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) (cor = -0.96; P = 0.029). Concerning parasitoids (Figure 10b), the PCoA plot shows that *A. gifuensis* individuals were found in every treatment. Their abundance was significantly negatively correlated with the one of *R. padi* (cor = -098; P = 0.022). Conversely *D. rapae* individuals were mainly found in pure-stand oilseed rape plots (Figure 10b) and were positively correlated with the abundance of *M. persicae* (cor = 0.99; P = 0.008). Moreover, its abundance was negatively correlated with the one of the wheat aphids *R. padi* (cor = -0.99; P = 0.003) and *S. avenae* (cor = -0.99; P = 0.003). Similar relations were observed for the hoverfly *E. corollae* (Figure 10a), which abundance was positively correlated with the one of *M. persicae* (cor = 0.97; P = 0.028) and negatively correlated with the one of *R. padi* (cor = -0.96; P = 0.039) (Figure 10a).

Table 5. Effects of treatments (see material and methods) and aphid abundance, as well as their interaction, on natural enemy abundance. Signs of estimates were retrieved from the selected models when aphid abundance had a significant effect. Degree of freedom (df), χ^2-values, and p-values were obtained from the likelihood-ratio tests performed on the selected models. * P < 0.05; ** P < 0.01.

	df	χ^2	p-value	Estimate
Hoverfly adults (trapped)				
Treatment	3	1.23	0.745	
Aphid	1	4.9	0.027 *	(+)
Treatment:Aphid	3	5.76	0.127	
Ladybeetle adults (trapped)				
Treatment	3	9.14	0.027 *	
Aphid	1	4.44	0.035 *	(-)
Treatment:Aphid	3	4.16	0.244	
Parasitoid adults (trapped)				
Treatment	3	0.25	0.968	
Aphid	1	5.93	0.015 *	(+)
Treatment:Aphid	3	0.2	0.978	
Ladybeetle larvae (observed on wheat)				
Treatment	2	1.87	0.392	
Wheat aphid	1	8.35	0.004 **	(+)
Treatment:Aphid	2	0.35	0.841	
Ladybeetle larvae (observed on oilseed rape)				
Treatment	2	3.85	0.146	
Oilseed rape aphid	1	10.5	0.001 **	(+)
Treatment:Aphid	2	4.82	0.09	

4. Discussion

The present results contradict our hypotheses. Firstly, we expected a reduced abundance of aphids in intercropping treatments because crop diversification can complicate the ability of aphids to find their host plants; the associated crop possibly creating physical and chemical barriers (Poveda et al., 2008). Secondly, we expected the release of ladybeetle sex pheromone to favour the abundance of predatory coccinellids. Thirdly, natural enemies could have benefited from crop diversification, as proposed by the enemy hypothesis of Root (1973), especially because one of the crops (oilseed rape) was a flowering species offering floral food resources. Although previous experiments showed that crop diversification and the release of semiochemicals (Cui et al., 2012; Lopes et al., 2016; Zhu and Park, 2005) – as well as their combination (Wang et al., 2011) – are promising for reducing pest abundance and favouring natural enemies, it was not the case here. Instead, the abundance of aphids was the strongest driver affecting the number of natural enemies.

Several olfactory cues from aphids, or released by plants when being attacked by aphids, help natural enemies to locate their prey and hosts. This can explain the positive effect of aphid abundance on most of natural enemies. For instance, methyl-salicylate is a HIPV emitted by plants when attacked by herbivores that attracts pest natural enemies (Rodriguez-Saona et al., 2011). Endangered aphids also produce alarm pheromones, e.g. E-β-farnesene, that are used by predators and parasitoids to locate their prey and hosts (Francis et al., 2004; Micha and Wyss, 1996). Volatiles from honeydew can also guide natural enemies to aphids (Leroy et al., 2011).

The negative relation from GLMM between ladybeetle adults and aphids may thus seem surprising. However, the PCoA plot (Figure 10a) and the results from the correlation tests show that this negative relation was mainly between the most abundant ladybeetle species (*H. axyridis*) and oilseed rape aphids (*M. persicae*) in pure-stand oilseed rape. Conversely, a positive relation between ladybeetles and wheat aphids was observed in treatments including wheat (Figure 10a). Brassicaceae plants, such as oilseed rape, produce glucosinolates that are allelochemicals known to influence the interactions between the host plant, aphids and predators (Bruce, 2014). Whereas aphids can benefit from glucosinolates, these compounds can negatively affect their predators. Francis et al. (2001) indeed reported a better development of *M. persicae* on oilseed rape compared to the control plant (i.e. broad bean *Vicia faba* L. in this study), while fewer adult ladybeetles could develop when feeding on *M. persicae* on oilseed rape than on broad bean. Glucosinolates and their derivatives can be toxic for insects, but some herbivores can sequester them and being detrimental for generalist natural enemies such as ladybeetles (Bruce, 2014). This could explain the negative correlation between *H. axyridis* and *M. persicae* in our study, and that ladybeetles seemed to search for wheat aphids instead. These same allelochemicals can explain the positive relation between *M. persicae* and the parasitoid *D. rapae* in oilseed rape plots and the negative correlation with wheat aphids. Indeed, some glucosinolate derivative volatiles are emitted by Brassicaceae plants when attacked by aphids and are used by more specialised natural enemies such as *D. rapae* to locate their hosts (Pope et al., 2008). Although *D. rapae* can also parasitize wheat aphids, Brassicaceae's HIPV were reported being strong attractant for *D. rapae*

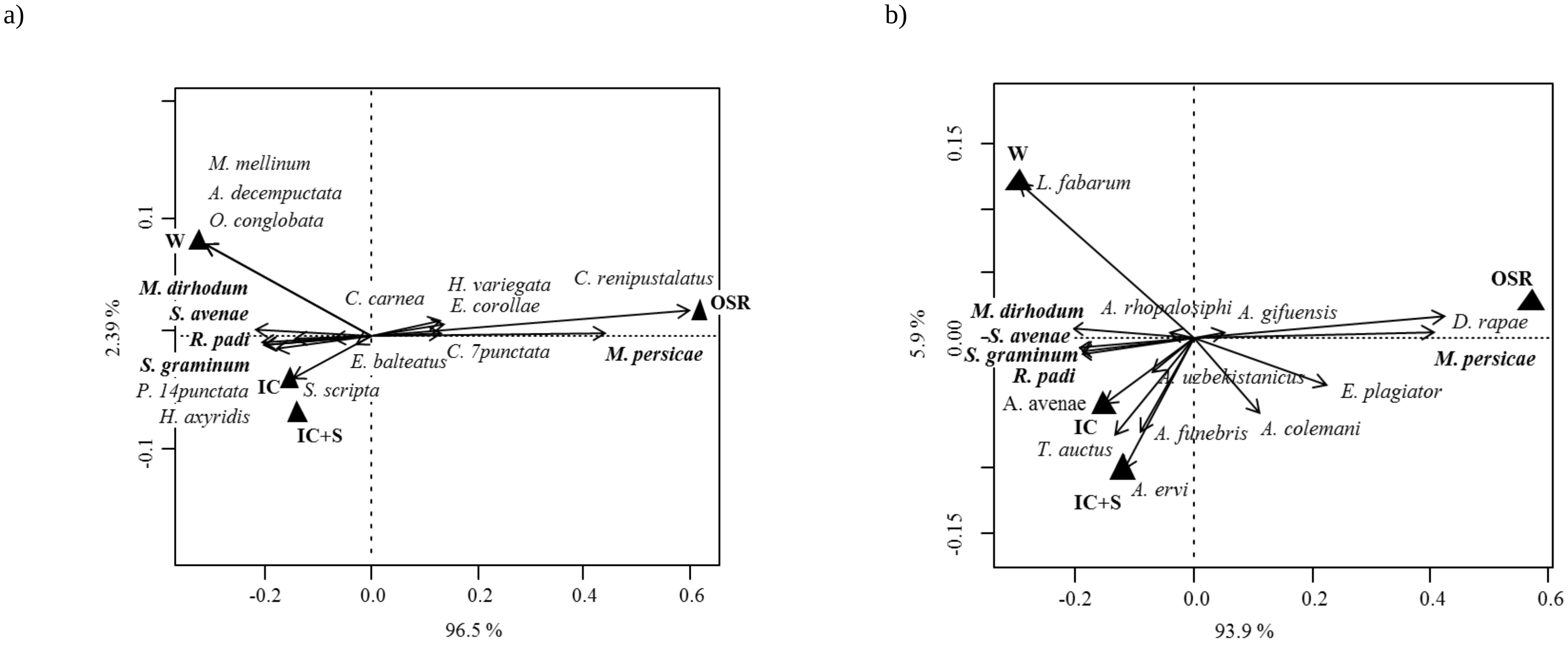

Figure 10. Principal Coordinate Analyses of (a) aphids and their predators (ladybeetles, hoverflies and lacewings) and (b) aphids and their parasitoid wasps, pan-trapped during nine weeks in the different treatments (IC+S: wheat-oilseed rape intercropping combined with the slow release of the ladybeetle sex pheromone; IC: wheat-oilseed rape intercropping; W: pure-stand wheat; OSR: pure-stand oilseed rape). In bold are the aphid species. The variance explained by each axis is given.

(Reed et al., 1995). In the present study, these processes seem to have been stronger in attracting or repulsing natural enemies than the arrangement of crops and the slow release of ladybeetle sex pheromone.

This study is the first to report the effect of releasing the synthesised sex pheromone of ladybeetles to attract *Coccinellidae* in fields. Nevertheless, this experiment has been conducted in one region over a single year. Therefore, further research is needed to confirm the present observations. Moreover, different type of diffusion method could be used, e.g. alginate beads (Heuskin et al., 2012) or paraffin oil (Verheggen et al., 2008), possibly affecting the effect of insects (Xu et al., 2017). Concerning intercropping, an unexpected slow growth of oilseed rape occurred, possibly due to a too late re-sowing in spring (29 March 2016, when it stopped freezing at night, Figure 9a). This slow growth may explain why oilseed rape did not disrupt wheat aphid search of their host plants. Conversely, we would have expected wheat to affect oilseed rape aphids as tillers were taller, hence hiding oilseed rape plants (Poveda et al., 2008). Instead, oilseed rape was attractive enough to aphids, allowing a fast development of apterous individuals. This slow growth of oilseed rape was also responsible for the non-flowering of the crops, which were expected to offer floral resources favourable to several natural enemies. This may explain the little abundance of hoverflies and lacewings trapped. Indeed, at the adult stage, hoverflies exclusively – and lacewings partially – feed on nectar and pollen, being their source of sugar and proteins, respectively (Wäckers and Van Rijn, 2012). Moreover, ladybeetles and parasitoids that were more abundant in the present study, could also have benefited from such flower resources (Wäckers and Van Rijn, 2012). In various agro-ecological contexts, recent results support the benefits flowering features bring for enhancing biological control of insect pests (Blaauw and Isaacs, 2015; Gurr et al., 2016; Tschumi et al., 2016b; Uyttenbroeck et al., 2016).

The non-effect of intercropping and its combination with the release of semiochemicals shows that some strategies, for which positive results were previously reported (Lopes et al., 2016; Wang et al., 2011), may not always be successful in enhancing biological control. It suggests that depending upon a limited number of tactics may be at risk. Hence, several complementary tactics could be used and combined. For instance, reducing tillage can benefit ground dwelling natural enemies (e.g. *Carabidae*) and those that overwinter in the soil (e.g. some parasitoids) (Stinner and House, 1990). Moreover, perennial habitats such as wildflower strips or hedgerows could be implemented and managed at field margins or within fields to support natural enemies that would migrate from habitats to crops (Holland et al., 2016).

Some studies assessed the interest, and potential interactions, of applying two of these strategies for enhancing biological control (Rusch et al., 2013a; Tamburini et al., 2016). Further research studying complex systems that combine multiple tactics for biologically controlling pests are needed in the future.

Acknowledgments

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Article 5

Pest regulation and support of natural enemies in agriculture: Experimental evidence of within field wildflower strips

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Abstract

Restoring ecosystem services in agriculture is vital to reach a sustainable food production. More specifically, developing farming practices which enhance biological pest control is a main issue for today's agriculture. The aim of this study was to assess whether the two strategies of complicating the search of host plants by pests by increasing plant diversity, and of supporting their natural enemies by managing habitats, could be combined simultaneously at the field scale to restore biological pest control and reduce chemical insecticide use. In Gembloux (Belgium), wildflower strips (WFS) were sown within wheat crops in which pests (i.e. aphids), their predators (i.e. aphidophagous hoverflies, lacewings and ladybeetles) and parasitoid wasps were monitored for 10 weeks in the period of May through July 2015 as indicators of the ES of pest control. Aphids were significantly reduced and adult hoverflies favoured in wheat in between WFS, compared to monoculture [i.e. pure stand] wheat plots. No significant differences were observed for adult lacewings, ladybeetles and parasitoids. In all treatments, very few lacewing and ladybeetle larvae were observed on wheat tillers. The abundance of hoverfly larvae was positively correlated with the aphid density on tillers in between WFS, showing that increasing food provisions by multiplying habitats within fields, and not only along margins, can help supporting aphidophagous hoverflies in crops. By enhancing the ecosystem services of biological pest control, this study shows that increasing both plant diversity and managing habitats for natural enemies may reduce aphid populations, hence insecticide use. Future research should continue this vein of work by quantifying the link between agricultural practices and the delivery of ecosystem services in order to guide future measures of agricultural policies.

Keywords: agroecological engineering, conservation biological control, plant diversity, aphids, predators, parasitoids

1. Introduction

The intensification of agriculture in Europe, which was characterised by an increased use of external inputs (i.e. improved seeds, chemical fertilisers and pesticides), has led to a simplification of agricultural ecosystems, environmental damages and health issues (Robinson and Sutherland, 2002). This acknowledgement goes beyond scientific concerns, as attested by, among other, the European Biodiversity Strategy which clearly states the need to “increase the contribution of agriculture to maintaining and enhancing biodiversity” (Target 3). More specifically, the spread of large monoculture [i.e. in the present paper, ‘monocultures’ are considered as ‘pure stands’] fields and the loss of natural habitats have increased the risk of pest outbreaks (Altieri and Nicholls, 2004) and led to a reduction of biodiversity imperilling the provision of ecosystem services (ES) (Flynn et al., 2009). Moreover, the harmful effects on human health and the environment of chemical insecticides used to control agricultural insect pests have been largely proved (Baldi et al., 2013; Devine and Furlong, 2007). The ever-tighter regulation on pesticides (Skevas et al., 2013) and the call from consumers for healthier food (Howard and Allen, 2010) encourage the development of innovative agroecological practices that would restore ES, which may allow farmers to reduce their reliance on these inputs. Among other strategies (Zehnder et al., 2007), two may be of particular interest: (i) complicate the search of host plants by pests, and (ii) provide habitats supporting pest natural enemies that may exercise predation and parasitism.

According to the *resource concentration hypothesis* of Root (1973), it is more difficult for specialist herbivores to find their host plant in diversified fields than in monoculture. In practice, intercropping and agroforestry systems (i.e. cultivating simultaneously several crops or crop and trees, respectively) are known to increase plant diversity at the field scale

(Malézieux et al., 2009). Previous studies showed that, when applied in wheat fields, aphids (Hemiptera: Aphididae) were systematically less abundant in these systems compared to pure stands (Lopes et al., 2016; Muhammad et al., 2005). However, these studies reported inconsistent results regarding natural enemy support. One reason can be that through these systems, adult natural enemies – which exclusively (e.g. hoverflies [Diptera: Syrphidae]) or partly (e.g. ladybeetles [Coleoptera: Coccinellidae], lacewings [Neuroptera: Chrysopidae], parasitoid wasps [Hymenoptera]) depend on non-prey food (Wäckers and Van Rijn, 2012) – do not find the resources they need, such as proteins, various sugars, amino-acids, mineral ions, alkaloids (Lundgren, 2009a). These resources can be made available through managing appropriate infrastructures in agricultural landscapes. For instance, wildflower strips (WFS) are known to be habitats for pest natural enemies (Haaland et al., 2011) as they potentially provide them the needed resources through nectar and pollen (Lu et al., 2014). Moreover, they may support additional prey for predators and hosts for parasitoids and be a shelter from adverse conditions (Landis et al., 2000). Several studies assessed the potential of sowing WFS along field margins to favour natural enemies and enhance pest control in the adjacent fields. Some recently showed a positive effect on pest reduction (Balzan and Moonen, 2014; Tschumi et al., 2016a, 2016b) but previous ones recall that it may not be systematic (Hickman and Wratten, 1996; Pfiffner et al., 2009).

In the light of these results, the aim of this study was to assess whether the two strategies of complicating the search of host plant by pests and of supporting natural enemies could be combined simultaneously to restore biological pest control and reduce chemical insecticide use. To our knowledge, flowering habitats are almost always sown in strips at field margins. Only Sutherland et al. (2001) investigated whether WFS sown as one large patch or several smaller ones within fields better support hoverflies. However, the effect was assessed in the patches only, and not in the adjacent crops. In the present study, we tested whether sowing multiple WFS within fields could allow reducing pests by an increase of plant diversity and the support of natural enemies.

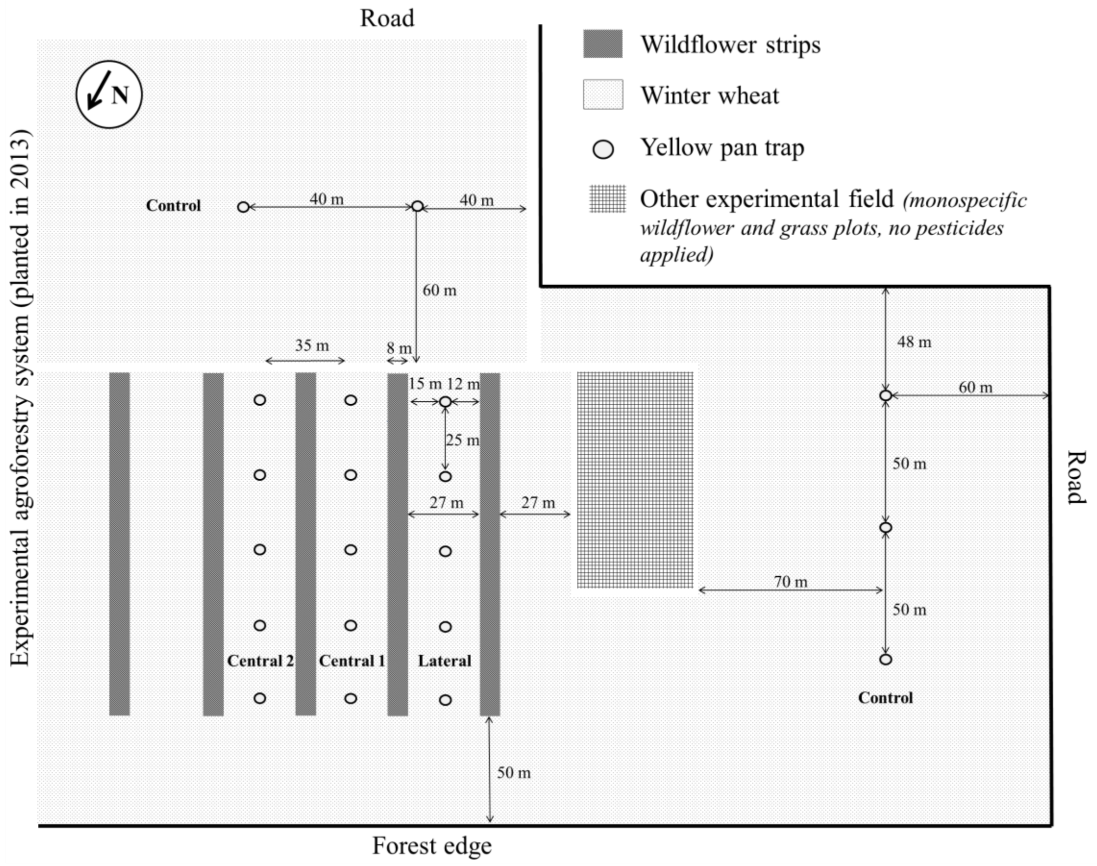

Figure 11. Experimental design (Article 5).

2. Material and methods

2.1 Field set up

This study was conducted at the experimental farm of Gembloux Agro-Bio Tech (University of Liège), Namur Province of Belgium (50°34’03’’N; 4°42’27’’E). In this region, a deep and loamy soil allows high crop productivity and the landscape is characterised by large crop fields and few non-crop habitats (in this region, 50-70 % of the surface is dedicated to agriculture while 9 % are wooded areas, respectively the highest and the lowest level in Wallonia, Service Public de Wallonie, 2014c). On a surface of 9 ha, five replicated WFS (125 m × 8 m) were sown at a distance of 27 m from each other (the field was surrounded by roads, a two-year old agroforestry system and a woodlot which edge was perpendicular to the WFS and the control plots, Figure 11). Each WFS was composed of 17 perennial wildflower species and three grass species commonly found in Belgian grasslands (see Uyttenbroeck et al., 2015 for the list of the flower species and details on the sowing protocol) and available on the market (seeds were obtained from ECOSEM, Belgium). Based on this design, four treatments were considered related to the location of wheat plots: (i) plots surrounding the WFS were considered as the treatment 'control'; (ii) the plots between the two first WFS were termed 'lateral' treatment and from west to east, the plots with two and three WFS on each side were termed (iii) 'central 1' and (iv) 'central 2' treatment, respectively. WFS were sown the 6th June 2013 and mown twice each year. The winter wheat (variety 'Edgar') was sown the 23rd October 2014. No insecticides and no herbicides were used in the whole experimental area.

2.2 Insect monitoring

As indicators of the ES of pest control, winged wheat aphids and their adult natural enemies were trapped for 10 weeks from 12 May to 29 July 2015 in wheat plots (excepting one week between the 30th June and 7th July which corresponded to the WFS mowing). Five yellow pan traps (Flora®, 27 cm diameter and 10 cm depth) were installed on a fibreglass stick in each treatment (Figure 11). Traps were placed at a distance of 12 to 15 m from WFS and separated from one to another by 25 m. They were positioned at vegetation height, and filled with water containing a few drops of detergent (dish-washing liquid) to reduce the surface tension of water. Their position was adjusted during the growing season to follow wheat growth. Traps were emptied and refilled every seven days, and the trapped insects conserved in 70 % ethanol. Wheat aphids, adult hoverflies, lacewings and ladybeetles, whose larvae are aphidophagous, were identified to the species level following Taylor (1981), van Veen (2010), San Martin (2004) and Roy et al. (2013) respectively. Keys from Tomanović et al. (2003) and Rakhshani et al. (2008) were used to identify parasitoid wasps of wheat aphids to the species level. Moreover, aphids and larvae of hoverflies, lacewings and ladybeetles were counted on wheat tillers during the same period. Around each traps, 20 tillers were randomly chosen every week. Rainy days were avoided and no distinction between larval stages was made.

2.3 Statistical analyses

Generalised linear mixed effect models (package 'lme4', function 'glmer', Bates et al., 2014) with Poisson error distribution (log-link function) were fitted to test whether the location of wheat plots with respect to WFS (i.e. treatments) affected the density of aphids and their natural enemies, both trapped and observed. The four treatments were analysed as fixed effects and trapping or observation dates (10 dates) were included as random effects as measurements were repeated each time in the same plot. Replications (five replications per treatment) were also included as random effects, nested into the effect of dates, in order to integrate their dependent relationship (i.e. pseudo-replications). The effect of the wheat plot location on insect abundance was tested using a likelihood-ratio test ($P < 0.05$) and means were compared between the different treatments using a post-hoc test of Tukey ($P < 0.05$, package ‘multcomp’, function ‘glht’, Hothorn et al., 2008). After a $\log(x+1)$ transformation, the linear relation between observed aphids and both adult predators and larvae (i.e. abundance of each predators at each observation point, pooled from all observation dates) was tested through a linear regression ($P < 0.05$). The statistical analyses were performed using R Core Team (2013).

3. Results

The presence of WFS significantly affected the aphids observed (df = 3; $\chi^2 = 93.1$; $P < 0.001$) and trapped (df = 3; $\chi^2 = 13.9$; $P = 0.003$) as well as hoverfly larvae observed (df = 3; $\chi^2 = 16.1$; $P = 0.001$) and adults trapped (df = 3; $\chi^2 = 16.3$; $P < 0.001$). These results suggest that combining the strategies of increasing plant diversity and managing habitats allows regulating pest abundance and supporting natural enemies. However, this pattern was not observed for the trapped ladybeetles (df = 3; $\chi^2 = 4.15$; $P = 0.246$), lacewings (df = 3; $\chi^2 = 7.06$; $P = 0.07$) and parasitoids (df = 3; $\chi^2 = 5.41$; $P = 0.144$).

Significantly less winged aphids were trapped in the two central wheat plots compared to the control (Figure 12a). Apterous aphids were also significantly less abundant on wheat tillers of the second central plot compared to the other treatments (Figure 12b). As for natural enemies, significantly more hoverfly adults were trapped in the two central wheat plots compared to the control (Figure 12c) and their larvae were significantly more abundant on tillers of the lateral plot compared to the control and the second central plot (Figure 12d).

Hoverflies were by far the most predominant group (Table 6). Roughly ten times less lacewings, ladybeetles and parasitoid wasps were identified. A total of 67 hoverfly larvae, but almost none of ladybeetles and lacewings, were observed on wheat tillers. Aphids (both trapped and observed) as well as hoverfly larvae peaked simultaneously between the 23rd and 30th June, and hoverfly adults peaked the 15th July. The abundance of their larvae was positively correlated with the number of aphids on wheat tillers in between WFS (i.e. in all treatments except the control) ($R^2 = 0.38$; $P = 0.015$; $y = -1.264 + 0.998x$) while it was not the case for the adults ($R^2 < 0.01$; $P = 0.89$). The linear relation between aphids and adult ladybeetles, lacewings and parasitoids was not tested as these natural enemies were not affected by the treatments. No statistical analyses were performed on their larvae as very few of them were observed.

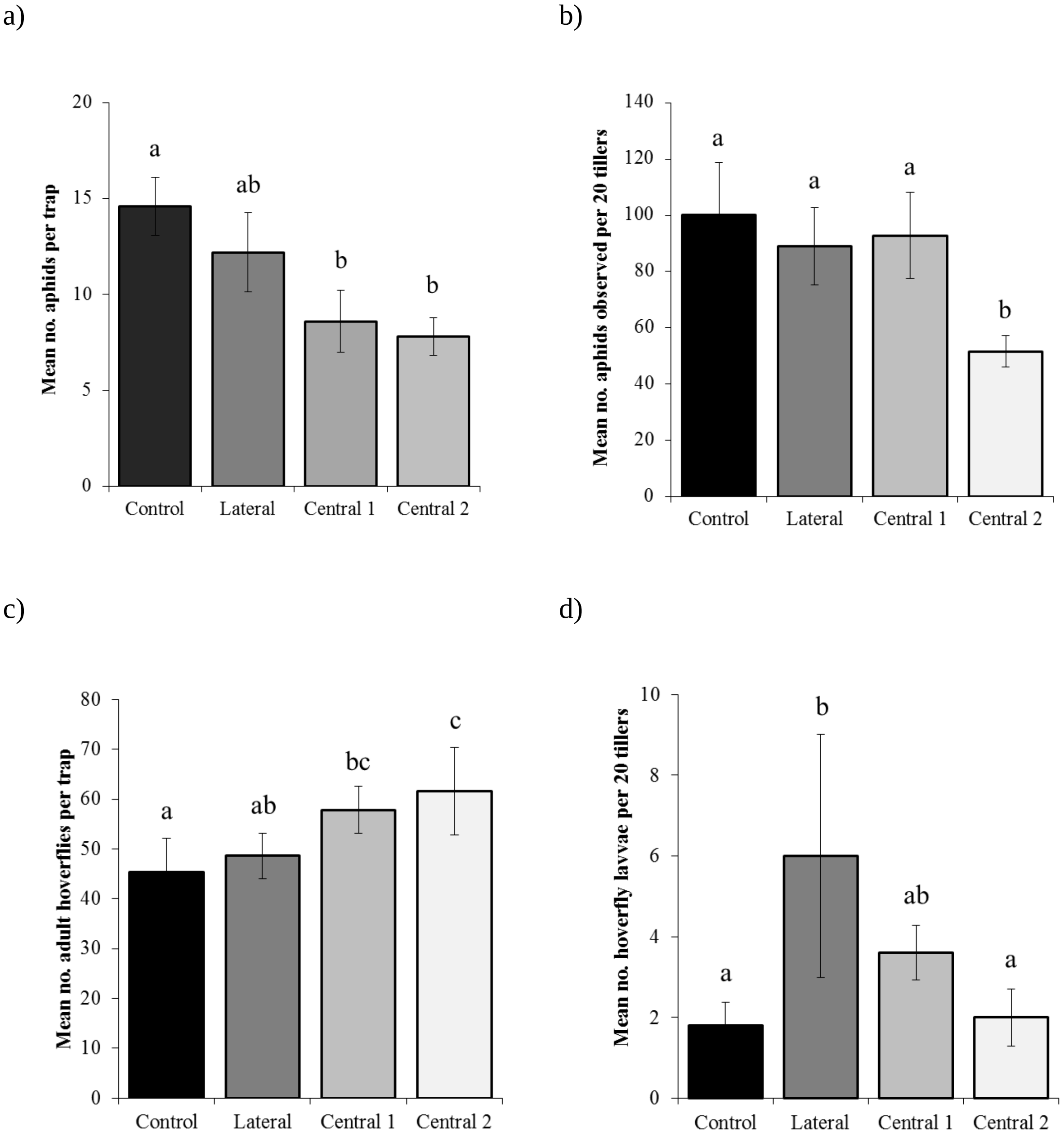

Figure 12. Effect of wheat location treatment on aphids (a) trapped and (b) observed on tillers, (c) adult hoverflies trapped and (d) hoverfly larvae observed on tillers. The letters indicate the significant differences ($P < 0.05$) of means using a post-hoc test of Tukey.

Table 6. Abundance and diversity of aphids and natural enemies trapped in the different treatments.

		Wheat between flower strips				
	Control	**Lateral**	**Central 1**	**Central 2**	**Total**	**%**
Aphid (Aphididae)	**73**	**61**	**43**	**39**	**216**	
Metopolophium dirhodum	5	11	6	7	29	13.4
Rhopalosiphum padi	61	42	26	30	159	73.6
Sitobion avenae	7	8	11	2	28	13.0
Hoverflies (Syrphidae)	**226**	**243**	**289**	**308**	**1066**	
Episyrphus balteatus	135	162	168	172	637	59.8
Eupeodes corollae	7	8	6	8	29	2.7
Melanostoma mellinum	28	19	28	40	115	10.8
Scaeva pyrastri	0	1	3	0	4	0.4
Sphaerophoria scripta	54	51	83	87	275	25.8
Syrphus ribesii	2	1	0	1	4	0.4
Syrphus vitripennis	0	1	1	0	2	0.2
Lacewings (Chrysopidae)	**31**	**33**	**34**	**17**	**115**	
Chrysoperla carnae	31	33	34	17	115	100.0
Ladybeetles (Coccinelidae)	**26**	**37**	**39**	**31**	**133**	
Coccinella 7 punctata	21	22	25	22	90	67.7
Harmonia 4 punctata	0	2	0	0	2	1.5
Harmonia axyridis	1	2	4	1	8	6.0
Hippodamia variegata	0	1	1	0	2	1.5
Propylea 14 punctata	4	10	9	8	31	23.3
Parasitoid wasps (Braconidae)	**41**	**53**	**51**	**34**	**179**	
Aphidius eadyi	8	6	4	4	22	14.0
Aphidius ervi	2	4	7	0	13	8.3
Aphidius matricariae	0	0	0	1	1	0.6
Aphidius rhopalosiphi	1	2	7	2	12	7.6
Aphidius salicis	0	1	0	0	1	0.6
Aphidius urticae	3	5	7	3	18	11.5
Aphidius uzbekistanicus	8	19	12	6	45	28.7
Diaeretiella rapae	0	1	0	0	1	0.6
Ephredus plagiator	11	6	5	8	30	19.1
Praon volucre	8	8	9	9	34	21.7
Trioxys auctus	0	1	0	1	2	1.3

4. Discussion

Increasing plant diversity at the field scale by sowing WFS within wheat fields allows regulating pests as the abundance of winged aphids and potentially apterous ones can be reduced when compared to wheat grown in monoculture. As expected, our results on winged aphids follow the resource concentration hypothesis of Root (1973). Poveda et al. (2008) reviewed the several mechanisms that may increase pest control in diversified cropping systems, compared to simplified ones. In our case, it is known that aphids use visual cues (i.e. colours, contrast between target and background, target shape) when searching for their host plants. WFS may have masked wheat plants, while also creating a physical barrier of non-host plants. Moreover, aphids use olfactory cues (i.e. plant volatiles, other aphid pheromones) to find their host plants (Döring, 2014). WFS may have released volatiles that acted as odour-masking substances confusing aphids in their host plant search. However, the density of apterous aphids was not significantly different between the control and two out of the three wheat plots in between WFS, showing that few winged aphids can still allow the development of important populations on plants. We hypothesise that, because WFS were sown every 27 m., wheat plots were still large enough to allow apterous aphids to spread and develop. In other diversified systems such as strip-intercropping, crop strips are rarely that wide (rarely more than 5 m.), hence giving few opportunities for apterous aphids to spread from plant to plant (Lopes et al., 2015).

When plant diversification comes with the management of flowering habitats, it can additionally allow supporting pest natural enemies. In the present study, significantly more adult hoverflies were trapped in both central wheat plots compared to the control ones. However, this was not observed for parasitoids, ladybeetles and lacewings. These results are surprising regarding their dependence on sugar and/or protein sources provided by nectar and/or pollen (Lundgren, 2009a). To our knowledge, the present study is the first assessing the abundance of aphid parasitoids in wheat crop adjacent to WFS. As for predators, Tschumi et al. (2015) also reported no effect of WFS on ladybeetles in wheat crops while lacewing abundance was increased. However, in our study, few individuals were trapped and almost no predatory larvae were observed in all treatments, indicating that they were generally few abundant in the field in 2015. Concerning adult hoverflies, they are also highly dependent on flower resources as all of them feed on nectar and pollen (Wäckers and Van Rijn, 2012). Nectar is their source of energy, while pollen provides them proteins. Their availability increases hoverfly longevity (Van Rijn et al., 2013) and fecundity (Laubertie et al., 2012), respectively. The presence of Apiaceae as well as some Asteraceae (e.g. *Achillea millefolium* L., *Leucanthenum vulgare* Lam.) in the WFS may have supported them (Carrié et al., 2012; Wäckers and Van Rijn, 2012). Several studies showed that managed habitats providing floral resources benefits hoverfly populations (Haenke et al., 2009; Jönsson et al., 2015; Sutherland et al., 2001). However few assessed the effect on adjacent crops, compared to fields without WFS. Hickman and Wratten (1996) found inconsistent results between years while more recently, Tschumi et al. (2016b) found no differences of adult hoverfly abundance in crops adjacent to WFS, compared to control fields. We hypothesise that sowing WFS at field margins solely may not be enough to support hoverfly populations into adjacent crops. The present study suggests that increasing food provisions by multiplying habitats within fields, and not only along margins, can help support their presence in crops.

Even if hoverfly adults were found more abundant in the central wheat plots, their larvae were mainly observed on the lateral one. Their abundance was positively correlated with the density of aphids on tillers in plots in between WFS. Furthermore, their abundance peak was observed one to two weeks later than aphids' one. As hoverfly larvae feed on aphids, adult search for oviposition sites is guided by prey abundance on plants (Tenhumberg and Poehling, 1995). Cues such as aphid pheromones (namely (E)-β-farnesene) and plant secondary metabolites (such as (Z)-3-hexenol) released by plants when attacked by aphids are strong drivers for hoverfly adults to locate prey for their larvae (Verheggen et al., 2008). Whereas wheat control plots were more infested by aphids than the one in between WFS, few hoverfly larvae were observed on tillers. This indicates that hoverfly adults were first attracted by WFS in order to fulfil their need of proteins and energy, and then oviposited on adjacent wheat tillers if they were infested by aphids, which is consistent with the description given by Almohamad et al. (2009) on hoverfly behaviour.

As this study was conducted over a single season in one field, further research is needed in order to confirm the preliminary results obtained, that both increasing plant diversity and managing flowering natural habitats within fields enhance the ES of biological pest control by simultaneously creating barriers to pests while providing food resources and living sites for natural enemies. Moreover, longer term experiments are needed in order to assess whether such observations are valid on a variety of crops in a context of crop rotation as pests – and so their natural enemies – change with the rotating crops (which is actually a practice in itself for controlling pests - Oerke, 2006). Additionally, we can wonder whether the "barrier effect" provided by the increased plant diversity have a similar effect on other pests than aphids, and if perennial WFS can support natural enemies of a variety of pests.

Nevertheless, the present results are in the continuity of previous research (among others, Balzan and Moonen, 2014; Tschumi et al., 2016a, 2016b), showing that implementing WFS in agricultural landscapes can benefit farmer's activities. In Europe, it can even be subsidised though the agri-environmental schemes of the Common Agricultural Policy (Haaland et al., 2011). However, the present agri-environmental policies were developed in order to "reduce environmental risks associated with modern farming on the one hand, and preserve nature and cultivated landscapes on the other hand", using subsidies in order to compensate a loss of productivity farmers may face (European Commission, 2005). Our study shows that WFS introduced within fields could no longer be presented as a loss but as a potential for farmers to reduce their reliance on pesticides thanks to an increased pest regulation. Shifting toward measures that acknowledge the increased ES provision may encourage farmers to adopt diversified practices that will benefit their production (Ekroos et al., 2014). While biological diversification of farming systems is widely acknowledged to support critical ES to agriculture (Kremen and Miles, 2012), research remain to be done to quantify the link between specific agricultural practices and the delivery of ES. The present study fits within this recent vein of work by providing an estimation of the potential of within field flowering habitats on pest regulation and support of natural enemies.

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Chapter III

Composing flower mixtures attractive to natural enemies: A trait-based analysis of natural enemy-flower interactions

Introduction to Chapter III

Article 4 and ***Article 5*** show contrasted benefits of increasing plant diversity with the provision of flowers for enhancing biological control of insect pests. In the case of intercropping, success understandably depends on the expected growth of both plants. ***Article 4*** highlights that any failure in the management of crops can jeopardize the enhancement of biological control. Contrastingly, sowing wildflower strips within fields seems promising. Nevertheless, ***Article 5*** highlights that simply sowing flowering features does not necessarily support a large diversity of natural enemies. Hence, ***Chapter III*** aims at exploring ways to optimize flower mixture composition in order to enhance the conservation of natural enemies.

Flower traits (i.e. "any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation", Violle et al. 2007) are known to affect flower visiting insects. Traits can be visual (e.g. colour, ultra-violet reflectance), phenological (e.g. date of the onset of blooming, blooming duration) or also structural (e.g. height, corolla type) characteristics of plants. One trait can be derived in various values (e.g. the different colours of the panel). Hence, **how knowledge on flower traits can be mobilized to compose flower mixtures attractive to natural enemies?**

First, the *functional diversity* index was used. At the flower mixture level, it indicates the diversity of values for a selection of traits among the flower species composing the mixture. Because flower visiting insects are sensitive to different values for a certain trait (Campbell et al., 2012; Lunau, 2014), a high functional diversity at the mixture level enhances the functional complementarity of flower species composing the mixture. In this context, ***Article 6*** explores whether flower mixtures with high functional diversity support a high abundance and diversity of natural enemies in wildflower strips.

Second, understanding insect-flower interactions would help composing mixtures exposing attractive values for some traits known to be determinant in the attraction of visitors. So far, the effect of flower traits on insects has been mainly studied in relatively controlled conditions (e.g. Vattala et al., 2006), through modelling (Bianchi and Wäckers, 2008) or using monospecific plots of flowers (e.g. Sivinski et al., 2011). Nevertheless, little is known about the attraction of flower traits once flower species are mixed in fields. In this context, ***Article 7*** explores what are the attractive traits to natural enemies and whether other factors, like pest abundance, could counter-balance the effects of traits.

Article 6

Do flower mixtures with high functional diversity enhance aphid predators in wildflower strips?

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Abstract

Among the semi-natural elements in agricultural landscapes, wildflower strips sown at field margins or within fields are potential habitats for the natural enemies of insect pests. As insects are sensitive to a variety of flower traits, we hypothesized that mixtures with high functional diversity attract and support a higher abundance and species richness of aphid flower visiting predators than mixtures with low functional diversity. During a field experiment, repeated over two years (2014 and 2015) in Gembloux (Belgium), aphid predators (i.e. lacewings, ladybeetles and hoverflies) were pan-trapped in five sown flower mixtures (including a control mixture, with three replicates of each mixture) of low to high functional diversity based on seven traits (i.e. flower colour, ultra-violet reflectance and pattern, start and duration of flowering, height and flower class, primarily based on corolla morphology). In both years, the species of flowering plants in the sown mixtures (i.e. sown and spontaneous flowers) were listed, and the realized functional diversity in each plot calculated. Over the two years, a high functional diversity was not associated with high abundance and richness of aphid predators. Moreover, ladybeetles, which made up the majority of the predators trapped, were more abundant in mixtures with very low or intermediate functional diversity at sowing, especially in 2014. We hypothesize that certain flowers, which were abundant in certain mixtures (and not in those exhibiting the highest functional diversity), attracted predators and were sufficiently abundant to support them. Our results present novel information that could be used for developing flower mixtures that provide effective ecosystem services, such as pest control.

Keywords: agri-environmental measure, conservation biological control, wildflower strips, functional diversity, Rao's index, syrphidae, coccinellidae, chrysopidae

1. Introduction

Wildflower strips (WFS) are one of several types of habitats used by insects in agricultural landscapes (Holland et al., 2016). There is extensive evidence that, when sown at field margins, WFS support a higher abundance and diversity of insects compared to adjacent crops (reviewed by Haaland et al. 2011). Indeed, WFS provide insects with floral food (such as nectar and pollen), as well as alternative prey and hosts for insect predators and parasitoids, respectively. WFS also provide insects with overwintering sites and shelters against adverse conditions, such as pesticide spraying (Landis et al., 2000). For these reasons, subsidizing the sowing of WFS is part of the agri-environmental policy in the European Union (EU) and some other countries in Europe. Indeed, within the EU, part of the direct payments is conditional on farmers implementing various ecological measures, including the maintenance of *ecological focus areas*, such as field margins (i.e. *greening of direct payment* in Pillar 1, Hodge et al. 2015). Moreover, agri-environmental schemes (Pillar 2), which may be adopted by farmers on a voluntary basis, were developed to "reduc[e] environmental risks associated with modern farming on the one hand, and preserve nature and cultivated landscapes on the other hand" (European Commission, 2005). More recently, there have been calls to diversify agri-environmental schemes to include measures enhancing ecosystem services, in addition to approaches that purely aim to support biodiversity (Ekroos et al., 2014; McKenzie et al., 2013). Among other ecosystem services (W. Zhang et al., 2007), the natural regulation of insect pests is of particular interest when considering the damaging effects of insecticides on human health and the environment (Baldi et al., 2013; Devine and Furlong, 2007) and the resistance of pests to insecticides (Foster et al., 2007) .

Conservation biological control is defined as “the use of tactics and approaches that involve the manipulation of the environment (i.e. the habitat) of natural enemies so as to enhance their survival, and/or physiological and behavioural performance, and resulting in enhanced effectiveness” (Barbosa, 1998). When applied to WFS, such manipulations consist of sowing mixtures that support natural enemies. Yet, enhancing natural enemies through habitat management might not necessarily lead to pest control. In addition to the five hypotheses proposed by Tscharntke et al. (2016), the resources and shelter provided by WFS might retain natural enemies, limiting their ability to control pests in adjacent crops (Rand et al., 2006). Moreover, simply sowing flowers might not generate a higher abundance of key beneficial species in strips, and reduce the abundance of pests in adjacent crops (Uyttenbroeck et al., 2016). One explanation is that some natural enemies might not be attracted to the species of flowers that are sown, or, if they are, might not find the resources that they need (Wäckers, 2004). Therefore, several studies have explored the effects of specific flower species on insect behaviour in order to select the species that effectively attract and support the beneficial ones (Carrié et al., 2012; Fiedler and Landis, 2007a; Tooker et al., 2006; Van Rijn and Wäckers, 2010). However, the *functional traits* of flowers must be assessed in order to understand why some flower species are suitable for insects, and why some are not.

Traits are defined as “any morphological, physiological or phenological feature measurable at the individual level” (Violle et al., 2007). When traits are considered in the environment in which a plant grows, they may affect ecological processes, and are qualified as functional (Díaz and Cabido, 2001). Several studies have explored the effect of flower traits on the behaviour of natural enemies using laboratory experiments, monospecific plots in fields or plants in pots (Fiedler and Landis, 2007b; Miller et al., 2013; Mondor and Warren, 2000; Schaller and Nentwig, 2000; Van Rijn and Wäckers, 2016). The shape of the corolla is another flower trait, which determines how insects access the food provided by flowers. This trait has been extensively studied because many natural enemies need pollen and nectar at certain stages in their development (Lu et al., 2014; Van Rijn and Wäckers, 2016). Other morphological traits, such as colour and ultra-violet (UV) reflectance, are involved in host plant recognition and, thus, flower attractiveness (Campbell et al., 2010; Chittka et al., 1994), while plant height might affect their flight (Wratten et al., 2003). Finally, phenological traits, such as the month of the onset and duration of flowering, might be important, because the food provided by flowers must be available when the insects need it (Colley and Luna, 2000). The extensive literature available on how flower traits affect natural enemy behaviour highlights that different insect species respond differently to the same trait. Therefore, it is hypothesized that mixing flower species with different values for these traits, generating a high functional diversity (FD) at the mixture level, will attract and support a high diversity and abundance of insects. Previous studies showed that plant mixtures with high FD benefit both natural enemies and pollinators (Balzan et al., 2014; Campbell et al., 2012; Fontaine et al., 2006). However, the high FD in these studies was based on an increased diversity in types of corolla, which determines the availability of food resources. Because insects are sensitive to several other flower traits, the present study aimed to explore whether a high FD in flower mixtures based on a multiplicity of traits enhances their use by flower visiting aphid predators. Our results are expected to provide baseline information for developing effective WFS mixtures for use in agricultural landscapes.

2. Material and methods

2.1 Study design

Field experiments were conducted during the 2014 and 2015 growing seasons in a 9 ha field of the experimental farm belonging to Gembloux Agro-Bio Tech (University of Liège), Namur Province, Belgium (50° 34′ 03″ N; 4° 42′ 27″ E). The field was characterized by a loamy soil that drains naturally (Service Public de Wallonie, 2014d). Before starting this experiment, the field was managed conventionally (i.e. synthesised fertilisers and pesticides were applied), and winter wheat was grown the previous year. No particular soil treatments were implemented before the experiment. A forest (i.e. l'Escaille natural reserve) is present on the north-west side of the field, while a young agroforestry system (planted in 2013) is present on the north-east side. Five WFS (125 m × 8 m) were sown in 2013. Each strip was divided into five equally sized plots (25 m × 8 m), i.e. a total of 25 plots. These plots were sown with five different flower mixtures in a Latin square design. Three out of the five strips were assessed due to logistic constraints and work force limitation (Figure 13). Four of the five mixtures contained seven flower species and three grass species (*Festuca rubra* L., *Agrostis* spp. and *Poa pratensis* L.). The fifth mixture (control, C) only contained the three grass species (Table 7). All flowering plants are native perennial species that are commonly found in Belgian grasslands (benefits of such species, compared to exotic and/or annual species are reviewed by Fiedler and Landis, 2007b), are typically used in agri-environmental schemes in Wallonia, Belgium, and are available commercially (seeds were obtained from ECOSEM, Belgium). Flower species (0.5 kg.ha^{-1} of each, see Table 7) and grass species (*F. rubra*: 11.5 kg.ha^{-1}; *Agrostis* spp.: 5 kg.ha^{-1}; *P. pratensis*: 5 kg.ha^{-1}) were sown on 6th June 2013. Equal seed masses of the flower species were sown so that the species were similarly abundant. Species with lower seed mass are expected to suffer a greater mortality and, thus, might need more seeds compared to species with higher seed mass in order to obtain the same abundance (Turnbull et al., 1999). Each year, WFS were mown at the end of June and September. Adjacent to WFS, oilseed rape (*Brassica napus* L.) was grown from September 2013 to June 2014, while winter wheat (*Triticum aestivum* L.) was grown from October 2014 to July 2015.

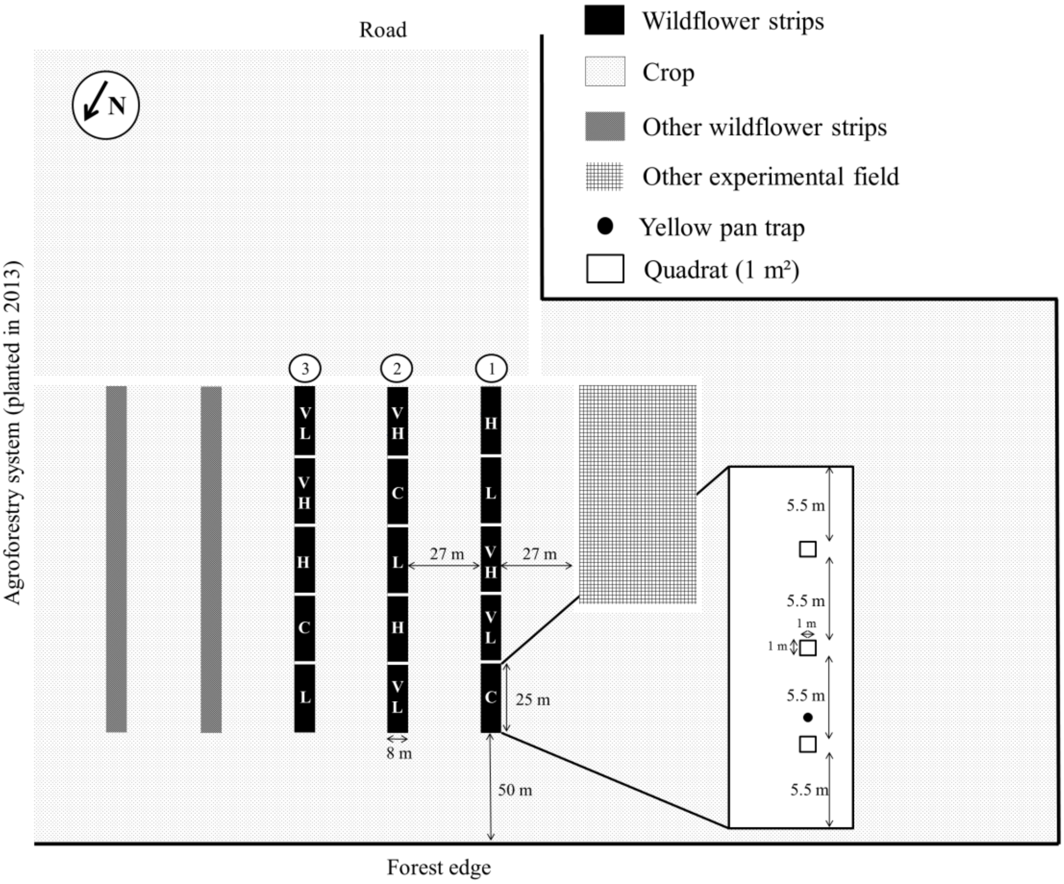

Figure 13. Experimental field design (Article 6). C (control), VL (very low), L (low), H (high), and VH (very high) are the five flower mixtures sown described in terms of their functional diversity at sowing.

2.2 Sown functional diversity

The four flower mixtures (the fifth one being the control) were chosen based on their FD values using Rao's quadratic index (Botta-Dukát, 2005). To create the mixtures, 20 flower species were chosen and described based on seven of their functional traits that were retrieved from Lambinon et al. (2008) and the TRY database (Kattge et al., 2011) (Table S 1). The seven traits were chosen based on their potential effect on flower visitors. First, visual cues are known to be decisive for insects when selecting a plant (Campbell et al., 2010). Hence, the following traits were considered: (i) flower colour, (ii) UV reflectance of the peripheral part of the flower, and (iii) whether the UV reflectance of the internal flower part differed from that of the external part (also called "UV pattern"). Second, flowering phenology determines whether floral resources are available when target insects need them (Colley and Luna, 2000). Therefore, (iv) the month of the onset of flowering and (v) the duration of flowering were chosen. Third, (vi) vegetation height was included, because it might affect insect flight (Wratten et al., 2003). Fourth, (vii) flower class after Müller (1881) was used, because it provides a measure of the the availability of nectar for insects that visit flowers, which determines whether WFS are able to support natural enemies (Van Rijn and Wäckers, 2016). All of the possible combinations of mixtures of seven species were listed, and their FD value was calculated (R function 'divc', package 'ade4'; Dray and Dufour 2007). Combinations with the lowest and the highest FD were selected, as well as those with a value closest to the 33rd and the 67th percentile of the range. As a result, four mixtures were generated with contrasting FD, termed very low (VL), low (L), high (H) and very high (VH) (Table 7).

2.3 Realized functional diversity

To evaluate the effect of the realized FD of the mixtures on flower visiting aphid predators, the effective composition of the flower mixtures was assessed each year. In three 1 m × 1 m permanent quadrats in each plot (Figure 13), flower species were recorded and their relative cover estimated on 18–19 June 2014 and 19–23 June 2015 (before mowing). The nomenclature of Lambinon et al. (2004) was followed. Based on the species of flowers listed (both sown and spontaneous), their traits and their relative cover in the quadrats, the realized FD of the mixture in each plot was calculated.

Table 7. Flower mixtures sown in June 2013, constituting a gradient of functional diversity based on Rao's index: control (C), very low (VL), low (L), high (H), very high (VH). All flowering species were perennial species that are commonly found in Belgian grasslands and used in agri-environmental schemes in Wallonia, Belgium.

Family	**Species**	**Mixtures**				
		C	**VL**	**L**	**H**	**VH**
	Functional diversity (Rao's index):	*0*	*0.08*	*0.11*	*0.15*	*0.19*
	Flowering species					
Apiaceae	*Anthriscus sylvestris*		x		x	x
Apiaceae	*Heracleum sphondylium*		x			
Asteraceae	*Achillea millefolium*		x	x	x	x
Asteraceae	*Crepis biennis*			x		
Asteraceae	*Hypochaeris radicata*			x		
Asteraceae	*Leontodon hispidus*			x	x	
Asteraceae	*Leucanthemum vulgare*		x		x	
Dipsacaceae	*Knautia arvensis*		x	x		
Fabaceae	*Lotus corniculatus*					x
Fabaceae	*Medicago lupulina*					x
Fabaceae	*Trifolium pratense*		x			
Geraniaceae	*Geranium pyrenaicum*				x	
Lamiaceae	*Origanum vulgare*				x	
Lamiaceae	*Prunella vulgaris*				x	x
Lythraceae	*Lythrum salicaria*			x		x
Malvaceae	*Malva moschata*					x
Rubiaceae	*Galium verum*		x	x		
	Grass species					
Poaceae	*Agrostis* spp.	x	x	x	x	x
Poaceae	*Festuca rubra*	x	x	x	x	x
Poaceae	*Poa pratensis*	x	x	x	x	x

2.4 Monitoring of insect species

Flower visiting predators were trapped from 7 May to 25 June 2014 and from 12 May to 30 June 2015 (i.e. for seven weeks in both years). In each plot, a yellow pan trap (Flora®, 27 cm diameter and 10 cm depth) was installed on a fiberglass stick and positioned at vegetation height. Its position was adjusted during the growing season to follow plant growth. Traps were filled with water containing a few drops of detergent (dish-washing liquid) to reduce the surface tension of the water. The traps were emptied and refilled every seven days, and the trapped insects were conserved in 70 % ethanol. Aphidophagous ladybeetles (Coleoptera: Coccinellidae), as well as lacewings (Neuroptera: Chrysopidae) and hoverflies (Diptera: Syrphidae), the larvae of which prey on aphids, were identified to species using identification keys in Roy et al. (2013), San Martin (2004) and van Veen (2010), respectively. Because the adults of these predatory families are all highly mobile and able to traverse agricultural landscapes (Almohamad et al., 2009; Evans, 2003; Villenave et al., 2006), their dispersion through the different plots was comparable.

2.5 Statistical analyses

First, the linear relation between the sown and realized FD in each plot was tested for both years by using Pearson's correlation ($P < 0.05$).

Second, the effects of the sown mixtures on insect abundance (response variables: all predators pooled, and lacewings, ladybeetles, hoverflies individually) and total predator species richness (species of the three predator families pooled) were assessed by fitting generalised linear mixed effect models (R function 'glmer', package 'lme4'; Bates et al., 2014) with Poisson error distribution (log-link function). Mixtures (C, VL, L, H, VH), years (2014, 2015) and their interaction were included as fixed factors, and the plots included as random effects, as measures were repeated on seven consecutive occasions in the same plots each year. For every model, data over-dispersion was tested and found to occur for the summed predator, ladybeetle and hoverfly abundance. For these variables, generalised linear models with negative binomial error distribution were fitted (R function 'glm.nb', package 'MASS', Venables and Ripley 2002), as suggested by Ver Hoef and Boveng (2007). The effects of fixed factors in every model were tested using likelihood-ratio tests ($P < 0.05$). When their interaction was significant, analyses were performed for each year separately.

Third, the effects of the realized FD on insect abundance (response variables: all predators pooled, and lacewings, ladybeetles, hoverflies individually) and total predator species richness (numbers of species of the three predator families pooled) were assessed for each year separately, as each year each plot potentially had a different value of FD, by fitting generalised linear mixed effect models. FD values were included as fixed factors and plots were included as random factors. Data over-dispersion was tested and found to occur for the summed predator, ladybeetle and hoverfly abundance in 2014. Thus, generalised linear models with negative binomial error distribution were fitted instead. The effects of realized FD in every model were tested using likelihood-ratio tests ($P < 0.05$). All analyses were done using R program (R Core Team, 2013).

3. Results

3.1 Flower cover, species and functional diversity

Twenty-one and 20 flower species were recorded in the quadrats in 2014 and 2015, respectively (Table 8), out of which eight species in both years were not sown. Among these spontaneous species, *Cirsium arvense* (L.) Scop. and *Sinapis alba* L. had the highest cover in plots in 2014, whereas in 2015 it was *C. arvense* and *Rumex obtusifolius* L. (Table 8). The cover of all other spontaneous species never on average exceeded 3 % of the quadrat surface in each plot. Conversely, three of the sown species, *Anthriscus sylvestris* (L.) Hoffm., *Heracleum sphondylium* L. and *Lythrum salicaria* L., were not recorded in either year, with *Origanum vulgare* L. also not recorded in 2015.

The values of the realized FD in 2014 and 2015 are given in Table 8. Except for the C plots, the values of the realized FD were lower than those of the sown mixtures. No significant correlations were found between the sown and realized FD in both 2014 (df = 13; r = 0.48; P = 0.071) and 2015 (df = 13; r = 0.22; P = 0.423).

3.2 Aphid predator abundance and diversity

Predators were significantly more abundant in 2014 than 2015 (i.e. 161 and 51 individuals trapped respectively, Table 9 and Table 10). Ladybeetles were the most abundant predators in both years, especially in 2014, followed by hoverflies and lacewings (total abundance is presented in Table 9). Equal species richness was recorded for ladybeetles and hoverflies in 2014 (i.e. four species); however, hoverfly species richness was higher in 2015 (i.e. five and three species respectively, Table 9). During this two year experiment, only one species of lacewing was recorded.

3.3 Effect of sown mixtures and realized functional diversity on aphid predators

Only ladybeetle abundance was significantly associated with the mixtures sown (Table 10). As the interaction between mixture and year effects was also significant, annual analyses showed that mixtures had a nearly significant effect in 2014 (df = 4; χ^2 = 9.4; P = 0.052) and a significant effect in 2015 (df = 4; χ^2 = 12.4; P = 0.014). The mixtures had no significant effect on the sums of predators, lacewings and hoverflies and their species richness (Table 10). In 2014, ladybeetles were the most numerous in VL, L and H mixtures, whereas they were the least abundant in L and VH mixtures in 2015 (Figure 14). Neither insect abundance (i.e. sum of predators, as well as every family separately) nor their species richness was significantly affected by the realized FD in either 2014 or 2015 (Table 11).

4. Discussion

Our study indicates that a high abundance and richness of flower visiting aphid predators is not necessarily associated with a high FD of flower mixtures. Only ladybeetles, which made up the majority of the predators trapped in both years, were affected by the sown mixtures. Ladybeetles were mostly trapped in plots where the FD of the mixture was very low or intermediate at sowing, especially in 2014.

A surprisingly low number of predators was trapped. In the case of hoverflies, we trapped on average 30 times more per week per trap in the crops growing adjacent to the WFS in 2015 (Hatt et al., 2017a) while Tschumi et al. (2016b) trapped on average 20 times more per week per trap in WFS adjacent to potato crops in June and July in Switzerland. A reason for this might be that hoverfly abundance often peaks in July in such regions, as was the case in 2015 in adjacent crops (Hatt et al., 2017a). In the present experiment, insects were trapped in the WFS only up to the end of June. As for ladybeetles, a slightly higher number than recorded in these previous studies was trapped in 2014, but three times less was recorded in 2015. Indeed, insect abundance differed in the two years of the study. The higher abundance of predators, especially ladybeetles, in 2014 might be due to the early summer in that year, favouring greater insect occurrence in early spring compared to 2015. In addition, other studies conducted in the same region report a very low density of ladybeetles in 2015, indicating that their abundance was low that year in the region of Gembloux (Fassotte, 2016; Hatt et al., 2017a). Similar annual variability in ladybeetle abundance is reported in Belgium (Vandereycken et al., 2013).

The results recorded for the effect of FD contradicted our hypothesis. We expected the abundance and richness of natural enemies to be positively associated with FD, because these predators have different nutritional requirements and might react differently to different flower traits at different times. However, our findings are consistent with Balzan et al. (2016a, 2014), who report that FD had no effect on the abundance of flower visiting natural enemies.

Table 8. Realized functional diversity (FD, Rao's index) and mean cover (%) of each flower species in each plot (C: Control, VL: very low, L: low, H: high, VH: very high; the numbers are the number of replicates of each mixture sown; see Figure 13), based on the three 1 m² quadrats in each plot in 2014 and 2015. Flower cover was assessed at the end of June each year.

	C1	**C2**	**C3**	**VL1**	**VL2**	**VL3**	**L1**	**L2**	**L3**	**H1**	**H2**	**H3**	**VH1**	**VH2**	**VH3**
2014															
Realized FD (Rao's index)	0.075	0.053	0.012	0.006	0.006	0.006	0.044	0.046	0.048	0.093	0.020	0.058	0.055	0.115	0.112
Flower cover (%)															
Achillea millefolium	0.67	0	0.67	9.67	11.67	4.67	5	14.33	12.67	1	15	9.67	8.33	3.67	1.33
Aethusa cynapium	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0
Capsella bursa-pastoris	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cichorium intybus	0	0	0	0.67	0	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	1	5.33	0.33	0	0	0.67	0.67	0	0.67	0	0	0	0	0	0.67
Conyza canadensis	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0
Crepis biennis	0	0	0	0	0	0	6	1.33	3.67	0	0	0	0.67	0	0
Galium verum	0.33	0	0	2	2	3.33	1.33	1	3.33	0	0.33	0	0	0	0
Geranium pyrenaicum	0	0	0	0	0	0	0.33	0	0	4.67	0.33	0.67	0	0	0
Hypochaeris radicata	0.67	0	0	0	0	0	11.33	13	20	0	0.33	0	0	0	0
Knautia arvensis	0	0	0	0	0	0.33	0.33	0	0.33	0	0	0	0	0	0
Leontodon hispidus	0	0	0	0	0	0	0	1	1.67	0	0	0	0	0	0
Leucanthemum vulgare	0.67	0	0	56.67	56.67	63.33	0	1	2	3.67	38.33	45	0	1	3
Lotus corniculatus	0	0	0	0	0	0	0	0	0	0	0	0	33.33	1.33	0.67
Malva moschata	0	0	0	0	0.33	0	0	0	0	0	0	1.33	2.33	1.33	4.33
Matricaria recutita	1	0.33	0.33	1	0	0	0	0	0	0.33	0	0	2.67	0	1.67
Medicago lupulina	0	0	0	0	0	0	0	0	0	0	0	0	2.33	1	1.33
Origanum vulgare	0	0	0	0	0	0	0	0	0	0	0.67	0	0	0	0
Prunella vulgaris	0	0	0	0	0	0	0	0	0	0	1.67	8	1.33	2	1
Sinapis alba	1.33	1.33	0	0	0	0	0	0	0	0	0	0	0	5	0
Trifolium repense	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0

Continuation of Table 8

2015															
Realized FD (Rao's index)	0.096	0.000	0.036	0.008	0.011	0.005	0.057	0.051	0.059	0.059	0.018	0.026	0.075	0.041	0.069
Flower cover (%)															
Achillea millefolium	1	0	1.33	9.67	20	8.67	13.67	24	20.33	5.33	33.33	22.67	20	38.33	27.67
Silene latifolia	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0
Cirsium arvense	1.67	10.67	0.67	0	0	2	1.33	0	0.67	1	0.33	0.33	1	2	0.67
Crepis biennis	0	0	0	0	0	0	0.67	0.67	0	0	0	0	0	0	0
Galium verum	0.33	0	0.33	2.33	3.33	1.67	1.33	1	4	0	0	0	0.33	0	0
Geranium pyrenaicum	0	0	0	0	0	0	0.67	0	0	5.33	0.33	0	0	0	0
Hypochaeris radicata	0.33	0	0	0	0.33	0	3.33	22.33	8	0	0.33	0	0	0	0
Knautia arvensis	0	0	0	0	0	0.33	0.33	0	0	0	0	0	0	0	0
Leontodon hispidus	0	0	0	0	0	0	1	2.67	8.33	0	1.33	1	0	0	0
Leucanthemum vulgare	1.67	0	0	71.67	80	96	0	1.33	8	19.33	68.33	51.67	0	0.33	6.67
Lotus corniculatus	0	0	0	0	0	0	0	0	0	0	0	0	0.67	0	0
Malva moschata	0	0	0	0	0	0	0	0	0.67	0	0.33	0.33	1.67	1.33	4.33
Malva sylvestris	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0
Medicago lupulina	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0
Plantago major	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunella vulgaris	1.33	0	0	0.33	0.67	0	0	0	0	0	1.67	2.67	2	2	1.67
Rumex obtusifolius	0	0	0	3.33	0	0	0	1.33	0	0	0	0	10.33	0.67	0
Rumex crispus	2	0	0	0	0	0	0	0	0	0	0	0	0.67	0	0
Sonchus sp.	0	0	0	0.33	0	0	0.67	0	0	0	0	0	0	0	0
Trifolium sp.	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0.67	0

Table 9. Summed abundance of every aphid predator species trapped in each mixture (over a seven-week period from May to June in both years, three repetitions per mixture, one yellow pan-trap per repetition, which was emptied and refilled every week).

	2014						**2015**						**2014-2015**
	C	**VL**	**L**	**H**	**VH**	**Total**	**C**	**VL**	**L**	**H**	**VH**	**Total**	**Total**
Lacewings (Chrysopidae)	**4**	**5**	**3**	**2**	**1**	**15**	**1**	**2**	**3**	**2**	**1**	**9**	**24**
Chrysoperla carnae	4	5	3	2	1	15	1	2	3	2	1	9	24
Ladybeetles (Coccinellidae)	**15**	**31**	**23**	**30**	**14**	**113**	**5**	**6**	**-**	**9**	**3**	**23**	**136**
Coccinella 7 punctata	-	8	3	4	-	15	1	4	-	3	1	9	24
Harmonia 4 punctata	-	-	-	-	-	-	-	-	-	1	-	1	1
Harmonia axyridis	7	11	9	12	8	47	-	-	-	-	-	-	47
Propylea 14 punctata	9	12	10	14	5	50	4	2	-	5	2	13	63
Tytthaspis 16 punctata	-	-	1	-	1	2	-	-	-	-	-	-	2
Hoverflies (Syrphidae)	**6**	**6**	**9**	**6**	**6**	**33**	**6**	**1**	**2**	**6**	**4**	**19**	**52**
Episyrphus balteatus	5	5	8	4	4	26	1	1	-	-	3	5	31
Eupeodes corollae	-	1	1	-	1	3	1	-	2	1	-	4	7
Melanostoma mellinum	-	-	-	2	-	2	-	-	-	2	-	2	4
Platycheirus manicatus	-	-	-	-	-	-	-	-	-	1	-	1	1
Sphaerophoria scripta	-	-	-	-	-	-	4	-	-	2	1	7	7
Syrphus ribesii	-	-	-	-	1	1	-	-	-	-	-	-	1
Total	**25**	**42**	**35**	**38**	**21**	**161**	**12**	**9**	**5**	**17**	**8**	**51**	**212**

‘-’ indicates that no individuals of these species were trapped

Table 10. Effect of mixtures sown (C, VL, L, H, VH) and years (2014, 2015), and their interaction, on the abundance and species richness of predators. Signs of estimates were retrieved from the selected models when significant, “(-)” means that the values for 2015 were lower than those for 2014. Degree of freedom (df), χ^2- and p-values were obtained from the likelihood ratio tests performed on the selected model. * P < 0.05; *** P < 0.001.

	Estimate	**df**	**χ^2**	**p-value**
Abundance				
Predators				
Mixture		4	7.75	0.101
Year	(-)	1	45.6	< 0.001 ***
Mixture:Year		4	6.18	0.186
Lacewings				
Mixture		4	3.41	0.476
Year		1	1.52	0.212
Mixture:Year		4	1.74	0.784
Ladybeetles				
Mixture		4	12.2	0.016 *
Year	(-)	1	55.3	< 0.001 ***
Mixture:Year		4	9.82	0.044 *
Hoverflies				
Mixture		4	1.12	0.891
Year		1	1.99	0.158
Mixture:Year		4	2.74	0.602
Species richness				
Predators				
Mixture		4	7.12	0.13
Year	(-)	1	33.7	< 0.001 ***
Mixture:Year		4	5.67	0.225

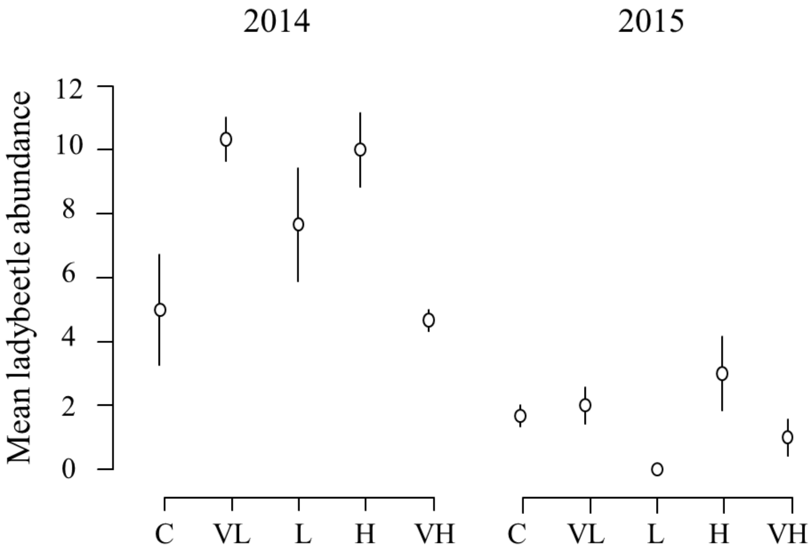

Figure 14. Mean (summed abundance recorded during seven weeks of trapping each year divided by the three repetitions ± SEM) ladybeetle abundance in each mixture sown, based on their functional diversity at sowing: control (C), very low (VL), low (L), high (H), very high (VH).

Table 11. Effect of realized functional diversity (Rao's index) on predator abundance and species richness of predators in 2014 and 2015. Signs of estimates were retrieved from the selected models. Degree of freedom (df), χ^2- and p-values were obtained from the likelihood ratio tests performed on the selected models.

	2014				**2015**			
	Estimate	**df**	**χ^2**	**p-value**	**Estimate**	**df**	**χ^2**	**p-value**
Abundance								
Predators	(-)	1	2.78	0.096	(-)	1	0.04	0.846
Lacewings	(-)	1	2.18	0.14	(-)	1	0.12	0.73
Ladybeetles	(-)	1	2.93	0.089	(-)	1	1.7	0.192
Hoverflies	(-)	1	<0.01	1	(+)	1	2.09	0.148
Diversity								
Species richness	(-)	1	2.75	0.097	(-)	1	0.63	0.428

Furthermore, these authors report that mixtures with intermediary FD support a higher natural enemy richness. Balzan et al. (2016a, 2014) increased FD by increasing the diversity of flower corolla types, which determines the ability of natural enemies to benefit from flower nectar (Van Rijn and Wäckers, 2016; Vattala et al., 2006). Insect abundance and diversity recorded in this study, however is not associated with FD based on seven traits. Balzan et al. (2016a, 2014) suggest that the presence of certain species of plants, particularly those attractive to natural enemies (i.e. *Apiaceae* spp. in their case), might mask the effect of FD on flower visitors. This might also have affected our results, especially as some flowering species covered a large surface area in some plots, whereas others that were sown were not even recorded (Table 8).

An explanation for the unequal establishment of different species of plants, despite similar seed weights being sown, may be the competition for space and resources that might have resulted in the establishment of the most competitive species. In our experiment, the Asteraceae *Leucanthemum vulgare* Lam. was the most abundant species in VL and H mixtures (Table 8). The high abundance of this species, compared to others, may account for the lower than expected values of realized FD in H and the low values in VL plots. However, most of the predators trapped, especially ladybeetles, were trapped in the H and VL plots. *L. vulgare* is typically visited by hoverflies, ladybeetles and lacewings (Carrié et al., 2012; Ricci et al., 2005; Wäckers and Van Rijn, 2012), because it is a rich source of nectar and pollen (Brodie et al., 2015). This resource might be of particular benefit to ladybeetles, for which pollen is one its most nutritious non-prey food sources, enabling them to complete their development and survive when prey are scarce (Berkvens et al., 2008; Lundgren, 2009b).

Adult hoverflies exclusively feed on flowers, with pollen providing a source of proteins that directly influence their fecundity, while nectar is a source of sugars, providing energy and increasing their longevity and foraging capacity (Laubertie et al., 2012; Van Rijn et al., 2013). Thus, any flower that was abundant in the mixtures and produced nectar (i.e. flowers with shallow florets, because hoverflies have a short proboscis; Van Rijn and Wäckers, 2016) and pollen are likely to be attractive. For instance, the Asteraceae, *Achillea millefolium* L., is typically visited by hoverflies (Carrié et al., 2012; Salveter, 1998; Tooker et al., 2006) and enhances their longevity (Van Rijn and Wäckers, 2016). In our study, *A. millefolium* was present in every flower mixture, and was quite abundant in most plots (Table 8). The presence of this species might have resulted in hoverflies being equally distributed across the different treatments. Moreover, ladybeetles and hoverflies are sensitive to colour, especially yellow

(Mondor and Warren, 2000; Sutherland et al., 1999). Hoverflies are also sensitive to flowers with a contrasting UV-pattern (Koski and Ashman, 2014). Some species with these traits might have been attractive. For instance, *Hypochaeris radicata* L. was quite abundant in L mixtures, especially in 2014, and might have attracted hoverflies, resulting in their being slightly (but not significantly) more numerous in plots with these than other mixtures.

Lacewings were less abundant than other predators in both years. They might also have benefited from a large variety of flowers in the strips, as they are considered to be opportunistic (Villenave et al., 2006). In addition, some spontaneous weeds, such as *C. arvense* and *R. obtusifolius* (the most abundant spontaneous plants listed in several plots), might have attracted predators, as they often host aphids that are prey for ladybeetle adults and the larvae of all three predators studied (Salveter, 1998). This phenomenon might also explain why some individuals were trapped in the control plots, even when few floral resources were available but with the values of the functional traits differed enough to result in higher than expected values of realized FD.

The presence of prey in adjacent crops might also have attracted natural enemies out of the flower strips, potentially explaining their generally low abundance in the mixtures. Indeed, hoverfly adults for instance search for aphid colonies in which to lay their eggs after having fed on flowers (Almohamad et al., 2009). While further analyses are needed to confirm such a hypothesis, a higher abundance of natural enemies in adjacent crops than in WFS, would enhance biological pest control. Despite the higher FD of VH mixtures at sowing, and to some extent in 2014 and 2015 (Table 8), the low attraction of the WFS to natural enemies might also be explained by the limited establishment of some of the species sown. The cover of sown flower species in the quadrats was low (except for *A. millefolium*, which was also abundant in other mixtures) and, some sown species, like *Lythrum salicaria* L., were not even recorded in the quadrats (Table 8). Moreover, some of the plant species that established successfully could *a priori* not provide food for hoverflies, ladybeetles or lacewings, because of their flower morphology. This is the case for plants of both Fabaceae and Malvaceae, which have a corolla that is too deep for e.g. hoverflies to access their nectar (Wäckers and Van Rijn, 2012).

The non-significant correlations between the sown and realized FD indicate that it is difficult to obtain a certain realized FD by sowing flower mixtures. This may be due to various factors such as the presence of spontaneous species, the better development of the most productive and competitive, and the non-development of some sown species. Considering the optimal growing conditions (e.g. exposure to sun, humidity, soil disturbance) for the different species on the one hand, and better balancing of the number of seeds between the different species by also considering their productivity and competitiveness (and not only considering their weight as in this study) on the other hand, may result in more diversified mixtures. Moreover, rather than relying on mixture FD, sowing flower species that are known to support natural enemies might enhance their presence in WFS, and even favour pest control in adjacent crops. This is the *pick and mix* approach developed by Wäckers and Van Rijn (2012) and successfully tested in the field by Tschumi et al. (2016b, 2015, 2014). Nevertheless, WFS have to provide multiple ecosystem services, including pollination, and participate in the conservation of insect species that are endangered in agricultural landscapes (Batáry et al., 2015; Ekroos et al., 2014). Within this context, a higher diversity of arthropods could potentially occur in flower mixtures with a high FD. Indeed, Balzan et al. (2014) report that the abundance of wild bees (Hymenoptera) increases with FD. Depending on the objectives assigned to WFS (i.e. enhancing pest control, pollination, conservation, or all of these combined), different strategies could be used when formulating flower mixtures.

Within an agricultural context, sowing WFS is proposed to enhance biodiversity conservation and ecosystem services, with doubts being raised about whether they will be a source of pests infesting adjacent crops (Frank, 1998; Hatt et al., 2015; Tscharntke et al., 2016). Moreover, it is worth establishing the threshold at which increasing the mixture of FD also improves its attraction for predators and shelters pests. For instance, aphids use visual and olfactory cues to locate host plants (Döring, 2014). Thus, increasing plant functional diversity might increase the chance of including more colours, UV patterns and odours that are attractive to aphids. It is also possible, a higher diversity of trait values might confuse aphids. For instance, when a high diversity of colours is present, the attractive ones might be masked. In parallel, if a large variety of odours is present, it might not be possible to distinguish attractive cues. This effect of diversified plant systems was first theorised by Root (1973) in the *resource concentration hypothesis*. This suggests that diversified cropping systems (e.g. intercropping), or, in the present case, diversified flower strips, might be less attractive to pests than monospecific systems (Letourneau et al., 2011; Lopes et al., 2016).

The present study investigated an array of traits; however, the selection was not exhaustive. Other traits could have been chosen; for instance, traits related to the abundance and quality of nectar and pollen (rather than just availability, as used here in the context of “flower type” based on the classification of Müller, 1881) or the profile of semiochemical volatiles emitted by flowers. Indeed, flower visiting insects, particularly aphid predators, respond to nectar and pollen abundance and quality, as well as odour (Adedipe and Park, 2010; Laubertie et al., 2006, 2012). Thus, it is necessary to screen a variety of flower species for these traits and establish their ability to attract and support aphid predators, in order to advance our knowledge in this field of research. As the value of the FD being tested depends on the chosen traits, further field-based research assessing different mixtures based on several other traits should be implemented, with the objective of enhancing the ability of WFS to deliver multiple ecosystem services in agriculture.

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Supplementary materials

Table S 1. Traits of each flower species considered to constitute the mixtures. Traits were retrieved from Lambinon et al. (2008) and the TRY database (Kattge et al., 2011).

Flower species	**Colour**	**UV periphery (%)**	**UV pattern**	**Blooming start**	**Blooming duration (month)**	**Max. height (cm)**	**Flower type (Müller 1881)**
Achillea millefolium	White	3.5	No	June	6	45	Associations with totally hidden nectar
Anthriscus sylvestris	White	3.5	No	May	2	120	Open nectaries
Crepis biennis	Yellow	33.5	Yes	June	3	120	Associations with totally hidden nectar
Galium verum	Yellow	3.5	No	May	5	80	Open nectaries
Geranium pyrenaicum	Violet	76	Yes	May	5	60	Totally hidden nectar
Heracleum sphondylium	White	3.5	No	June	3	150	Open nectaries
Hypericum perforatum	Yellow	53	Yes	July	3	60	Pollen flowers
Hypochaeris radicata	Yellow	33.5	Yes	June	4	60	Associations with totally hidden nectar
Knautia arvensis	Violet	3.5	No	June	4	60	Associations with totally hidden nectar
Leontodon hispidus	Yellow	53	Yes	June	5	40	Associations with totally hidden nectar
Leucanthemum vulgare	White	3.5	No	May	4	60	Associations with totally hidden nectar
Lotus corniculatus	Yellow	3.5	No	May	5	30	Bee flowers
Lythrum salicaria	Violet	76	Yes	June	4	150	Totally hidden nectar
Malva moschata	Violet	53	Yes	July	3	80	Totally hidden nectar
Medicago lupulina	Yellow	3.5	No	April	7	50	Hymenoptera flowers
Origanum vulgare	Violet	11.5	No	July	3	80	Totally hidden nectar
Prunella vulgaris	Violet	76	Yes	July	3	50	Hymenoptera flowers
Ranunculus acris	Yellow	21.5	Yes	May	5	90	Partly hidden nectar
Silene latifolia	White	21.5	Yes	May	6	90	Moth flowers
Trifolium pratense	Violet	3.5	No	May	6	50	Bee flowers

Article 7

Effect of flower traits and hosts on the abundance of parasitoids in perennial multiple species wildflower strips sown within oilseed rape (*Brassica napus* L.) crops

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Abstract

Reducing the use of insecticides is an important issue for agriculture today. Sowing wildflower strips along field margins or within crops represents a promising tool to support natural enemy populations in agricultural landscapes and, thus, enhance conservation biological control. However, it is important to sow appropriate flower species that attract natural enemies efficiently. The presence of prey and hosts may also guide natural enemies to wildflower strips, potentially preventing them from migrating into adjacent crops. Here, we assessed how seven flower traits, along with the abundance of pollen beetles (*Meligethes* spp., Coleoptera: Nitidulidae) and true weevils (*Ceutorhynchus* spp., Coleoptera: Curculionidae), affect the density of parasitoids of these two coleopterans in wildflower strips sown in an oilseed rape field in Gembloux (Belgium). Only flower traits, not host (i.e. pollen beetles and true weevils) abundance, significantly affected the density of parasitoids. Flower colour, ultra-violet reflectance and nectar availability were the main drivers affecting parasitoids. These results demonstrate how parasitoids of oilseed rape pests react to flower cues under field conditions. Similar analyses on the pests and natural enemies of other crops are expected to help to develop perennial flower mixtures able to enhance biological control throughout a rotation system.

Keywords: conservation biological control, hymenopteran wasp, flower colour, ultra-violet reflectance, nectar availability, redundancy analysis

1. Introduction

Conserving natural enemies in farming landscapes is a primary challenge for increasing the sustainability of agriculture. Indeed, natural enemies may help to biologically control pests and, thus, reduce the use of insecticides, which irrational uses have led to environmental degradation (Gibbons et al., 2015; Krebs et al., 1999) and may be harmful to human health (Baldi et al., 2013). *Conservation biological control* is defined as “the use of tactics and approaches that involve the manipulation of the environment (i.e. the habitat) of natural enemies so as to enhance their survival, and/or physiological and behavioural performance, and resulting in enhanced effectiveness” (Barbosa, 1998). These habitats include woodlots, hedgerows, and wildflower or grassy strips introduced to fields, farms and landscapes. Because these habitats are less disturbed compared to annual crop fields, they provide a range of resources for natural enemies, including food, alternative prey or hosts, shelters and overwintering sites (Landis et al., 2000).

There is clear evidence supporting that agricultural practices (i.e. mowing, pesticide use, harvesting) negatively affect natural enemy populations in fields (Colignon et al., 2001; Hanson et al., 2015; Horton et al., 2003) and, thus, the potential for biological control (Geiger et al., 2010). In most cases, wildflower strips (WFS) sown at field margins support a higher abundance and diversity of insects compared to adjacent fields (Haaland et al., 2011). Some of these insects are natural enemies of pests that are able to migrate to adjacent crops to control them, which reduces damage and potentially enhances yield and crop quality (Balzan and Moonen, 2014; Büchi, 2002; Tschumi et al., 2016a). However, these beneficial effects may not always occur (Uyttenbroeck et al., 2016). One reason is the potential incompatibility between the natural enemies and the floral resource provided (Lundgren, 2009a; Tscharntke et al., 2016). As simply sowing flowers may not necessarily support the targeted natural enemies, it is important to improve our understanding about how flowers affect their behaviour to enhance the efficiency of WFS to support these species.

Flowers may be described through their traits, which are defined as “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation” (Violle et al., 2007). Once a plant is considered in the context of the environment in which it grows, its traits may affect ecological processes. Consequently, these traits are termed as *functional* (Díaz and Cabido, 2001; Lavorel and Garnier, 2002), even though debate remains on the use of this term (Violle et al., 2007). Díaz and Cabido (2001) showed that the range and values of functional traits carried by plants are strong drivers of ecological processes. Furthermore, different insect taxa may respond differently to a specific flower trait. For example, Campbell et al. (2012) showed that for the flower trait ‘corolla length’, long corolla flowers were visited by bumblebees *Bombus* spp. Latreille (Hymenoptera: Apidae), while flowers with short corollas were visited by hoverflies (Diptera: Syrphidae) and hymenopteran parasitoids. Many studies have explored the effect of one or two traits on insect behaviour in relatively controlled experiments (Cook et al., 2013; Döring et al., 2012; Patt et al., 1997; Van Rijn and Wäckers, 2016; Vattala et al., 2006), or through modelling (Bianchi and Wäckers, 2008). In field conditions, the effect of multiple flower traits was tested by developing small monospecific plots (Fiedler and Landis, 2007b; Sivinski et al., 2011). However, no studies investigated how traits of flowers incorporated in multiple species mixtures affect natural enemies whereas such mixtures are bought and sown by farmers.

The attractiveness of WFS for natural enemies may also arise from the presence of prey and host species. They may help support natural enemy populations at field margins (Landis et al., 2000), potentially retaining them there if they are more abundant than in the adjacent field (Rand et al., 2006). Thus, it is important to assess whether the presence of prey and hosts are significant drivers of natural enemy behaviour in WFS, or whether flower traits alone are important.

Oilseed rape (OSR) *Brassica napus* L. is an important crop in Western Europe. Pollen beetles *Meligethes* spp. (Coleoptera: Nitidulidae) and true weevils *Ceutorhynchus* spp. (Coleoptera: Curculionidae) are its main pests in spring (Williams, 2010). Their natural enemies are mainly parasitoids – some being more specialists than others –, parasitising pest larvae (Nilsson, 2003; Ulber, 2003; Williams, 2003). With levels of parasitism which can exceed 50 % (Ulber et al., 2010), finding ways to support their presence at OSR field margins may allow enhancing biological control. In the present study, we analysed how WFS sown within OSR crops affected the parasitoids of these two coleopteran pests by answering the following questions: (i) what factors affect parasitoid abundance in WFS (i.e. flower traits or hosts); and (ii) which flower traits are drivers? The results are expected to provide information on potential perennial flower mixtures that would enhance biological pest control in crop rotation systems.

2. Material and methods

2.1 Field set up

This study was conducted at the experimental farm of Gembloux Agro-Bio Tech (University of Liège), Namur Province, Belgium (50° 34′ 03″ N; 4° 42′ 27″ E). In a field of about 9 ha, five replicated WFS (125 m × 8 m) were sown, separated by 27 m (Figure 15). Each WFS was divided into five equally sized plots (25 m × 8 m). In each plot, a different flower mixture was sown (mixtures A to E, Table 12). The layout resulted in a Latin square design with 25 plots. However, in the present study, only three strips (thus totally 15 plots, named 1 to 15, Figure 15) were used. Four out of the five mixtures (i.e. mixtures A to D) sown in each strip were composed of seven flower species and three grass species (*Festuca rubra* L., *Agrostis capillaris* L. and *Poa pratensis* L.), while the remaining mixture (i.e. mixture E) only contained the three grass species (Table 12). The five mixtures were originally chosen regarding their value of functional diversity using the Rao quadratic entropy index described by Botta-Dukát (2005) (mixture A had the highest value while mixture E the lowest one, see Uyttenbroeck et al., 2015 for more details). However the present study focuses on how flowers affect insect behaviour through their traits rather than through mixture functional diversity. All flowering plants were native perennial species commonly found in Belgian grasslands (benefits of such species, compared to exotic and/or annual ones were reviewed by Fiedler and Landis, 2007b), used in Agri-Environmental Schemes (AES) in Wallonia, Belgium, and available on the market (seeds were obtained from ECOSEM, Belgium). Each species was described based on seven traits (Table S 2). Visual traits were (i) flower colour (i.e. yellow, white, violet), (ii) the ultra-violet (UV) reflectance of the peripheral part of the flower (numerical value indicated as 'UV periphery') and (iii) whether the UV reflectance of the internal flower part differed to that of the external flower part (i.e. yes or no, indicated as 'UV pattern'). Phenological traits were (iv) the month of the onset of blooming (i.e. numerical value from 1 to 12 with '1' being January) and (v) the number of blooming months (numerical value). (vi) Height (numerical value) was chosen based on its effect on insect flight (Wratten et al., 2003) and (vii) flower class was delineated after Müller (1881) (indicated as 'Flower type') because it notably gives the availability of nectar for insects that visit flowers (i.e. bee flowers, hymenoptera flowers, flowers with open nectaries, flowers with partly hidden nectar, flowers with totally hidden nectar, flower associations with totally hidden nectar). For each plant species, the values on the phenological traits and plant height were obtained from Lambinon et al. (2008), while those on the visual and nectar availability traits were retrieved from the TRY database (Kattge et al., 2011). The flower mixtures were sown on 6 June 2013 and the OSR was sown on 10 September 2013. During the experimental period, the WFS were mown twice a year, at the end of June and September.

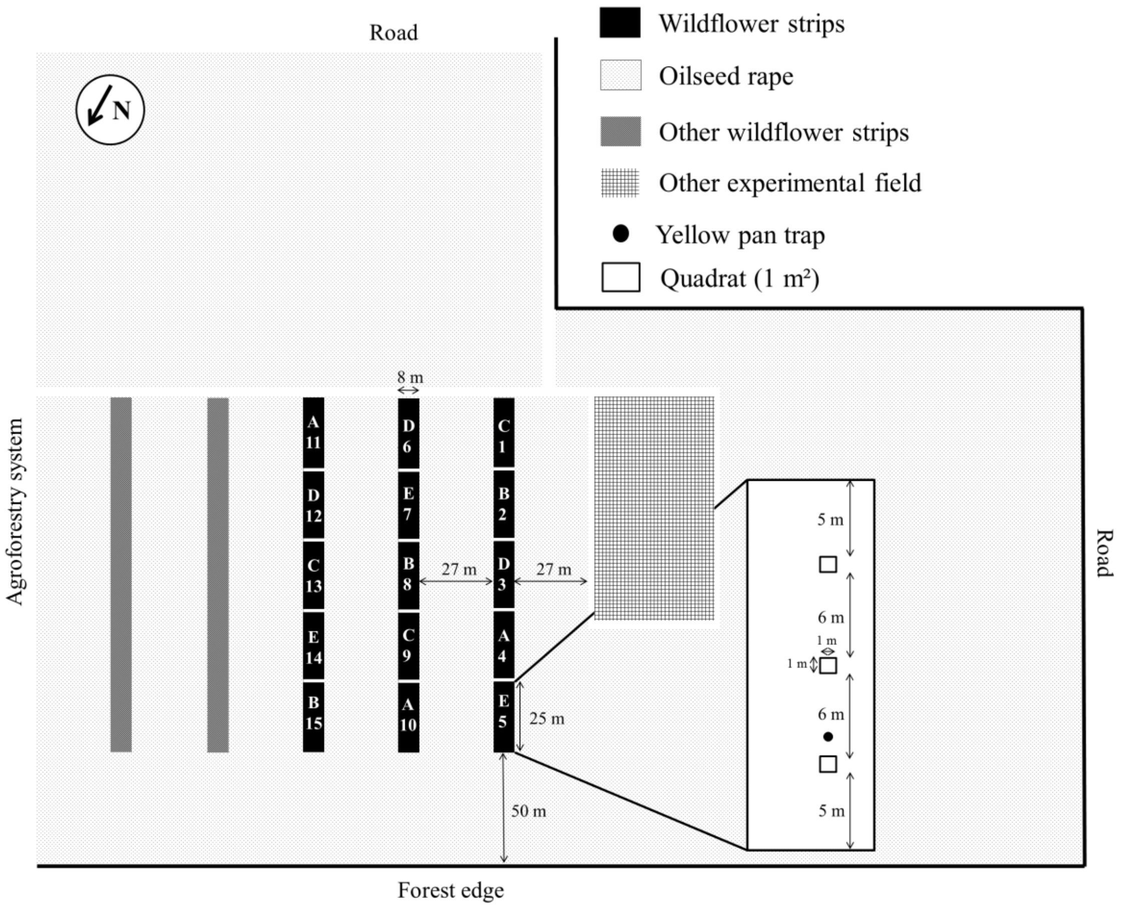

Figure 15. Field experimental design (Article 7). The composition of the wildflower mixtures originally sown (A to E) is detailed in Table 12. Each plot (1 to 15) was then considered independent in the statistical analyses.

2.2 Flower species monitoring

Flower species and their relative cover were monitored on 17 and 18 June 2014. In brief, three 1 m² permanent quadrats were laid at a distance of 6 m from one another in each plot (Figure 15). Every flower species present in the quadrats was listed and its cover assessed. Plant nomenclature of Lambinon et al. (2004) was followed. Every month, the species that bloomed were recorded by visual observations following a 20 m × 2 m transect in each plot. To address the effect of flower traits on parasitoids fully, only the flower species that were blooming when wasp abundance peaked were used for the analyses.

2.3 Insect species monitoring

OSR pests and their associated parasitoids were monitored for 11 weeks from 2 April to 25 June 2014. In brief, a yellow pan trap (Flora®, 27 cm diameter and 10 cm depth) was installed on a fibreglass stick in each plot. Traps were positioned at vegetation height, and were filled with water containing a few drops of detergent (dish-washing liquid) to reduce the surface tension of the water. Their position was adjusted during the growing season to follow plant growth. The traps were emptied and refilled every seven days during the survey period, and the trapped insects were conserved in 70 % ethanol. Pollen beetles and true weevils were identified to the genus level following Kirk-Spriggs (1996) and Morris (2008), respectively. Parasitoids were identified to the species level following Ferguson et al. (2010).

2.4 Statistical analyses

For the data analysis (performed with R Core Team 2013), each plot (i.e. plots 1 to 15) was considered unique. We assumed that the sown replicated mixtures (i.e. mixtures A to E) could have developed to form different vegetation compositions. Therefore, 15 flower plots, thus 15 flower mixtures, were considered. For each plot, the average cover of each species found (i.e. both sown and spontaneous ones) was calculated from the three quadrats (the average cover of each blooming flowering species in each plot is given in Table S 3). Then, for each plot, the Community Weight Mean (CWM, Lavorel et al. 2008; Laliberté and Legendre 2010) value was calculated for each trait based on the trait values obtained for each flowering species and their average cover in the plot (R function 'dbFD', package 'FD', Laliberté et al.

2014). For numerical trait values, a single CWM value was obtained per trait for each plot. For class trait values, a single value for each class was obtained per plot. Both CWM values and the abundance of *Meligethes* spp. and *Ceutorhynchus* spp. were used as explanatory variables (details about CWM values in each plot are given in Table S 4).

Table 12. Composition of the flower mixtures sown, record of the ones that bloomed in May and June and mean cover (% ± standard error) of each species through the different plots. Among those that bloomed, *A. cynapium, C. bursa-pastoris, M. recutita, S. alba* and *T. repens* were not sown.

Family	**Species**	**Mixtures**					**Blooming**		**Cover (%)**
		A	**B**	**C**	**D**	**E**	**May**	**June**	**Mean (±SE)**
	Flowering species								
Apiaceae	*Aethusa cynapium*						x	x	0.02 (± 0.09)
Apiaceae	*Anthriscus sylvestris*	x		x	x				0
Apiaceae	*Heracleum sphondylium*	x							0
Asteraceae	*Achillea millefolium*	x	x	x	x		x	x	6.56 (± 5.36)
Asteraceae	*Crepis biennis*		x				x	x	0.78 (± 1.74)
Asteraceae	*Hypochaeris radicata*		x				x	x	3.02 (± 6.33)
Asteraceae	*Leontodon hispidus*		x	x			x	x	0.18 (± 0.49)
Asteraceae	*Leucanthemum vulgare*	x		x			x	x	18.09 (± 25.42)
Asteraceae	*Matricaria recutita*						x	x	0.49 (± 0.79)
Brassicaceae	*Capsella bursa-pastoris*						x		0.02 (± 0.09)
Brassicaceae	*Sinapis alba*						x	x	0.51 (± 1.33)
Dipsacaceae	*Knautia arvensis*	x	x				x	x	0.07 (± 0.14)
Fabaceae	*Lotus corniculatus*				x		x	x	2.35 (± 8.57)
Fabaceae	*Medicago lupulina*				x		x		0.31 (± 0.69)
Fabaceae	*Trifolium pratense*	x							0
Fabaceae	*Trifolium repens*						x	x	0.02 (± 0.09)
Geraniaceae	*Geranium pyrenaicum*			x			x	x	0.40 (± 1.20)
Lamiaceae	*Origanum vulgare*			x					0
Lamiaceae	*Prunella vulgaris*			x	x				0
Lythraceae	*Lythrum salicaria*		x		x				0
Malvaceae	*Malva moschata*				x			x	0.64 (± 1.24)
Rubiaceae	*Galium verum*	x	x					x	0.91 (± 1.22)
	Grass species								
Poaceae	*Agrostis capillaris*	x	x	x	x	x			
Poaceae	*Festuca rubra*	x	x	x	x	x			
Poaceae	*Poa pratensis*	x	x	x	x	x			

The interactions between parasitoids and explanatory variables were analysed by considering only data when the populations of parasitoids reached their abundance peak in order to limit the random dilution effect of parasitoids in the different plots. Indeed, it was hypothesised that the effect of explanatory variables would be clearer on when parasitoid population was the highest. To do so, a forward selection of the significant explanatory variables was firstly performed, and secondly a redundancy analysis (RDA) was used. This method combines multivariate multiple linear regression and principal component analysis (Borcard et al., 2011). The matrix of the CWM values and host abundance was the ‘matrix of explanatory variables’, while the ‘matrix of centred response’ was the $\log_{10}(x+1)$ transformation of parasitoid abundance in each plot (respectively the matrices X and Y in Borcard et al. 2011). Through the forward selection process (function ‘ordistep’, package ‘vegan’, Oksanen et al. 2015), the significant variables ($P < 0.05$) affecting parasitoid abundance were identified and those with the lowest Akaike Information Criterion (AIC) at each step were selected for inclusion in the RDA model. Based on the selected model, the constrained ordination between parasitoid abundance and the selected variables was obtained using Bray-Curtis distances (function ‘capscale’, package ‘vegan’, Oksanen et al. 2015) and tested with a permutation test ($n = 1000$, $P = 0.05$). Finally, correlation circles of significant explanatory variables were plotted to visualise how they were correlated with the parasitoid species.

3. Results

3.1 Flowers

Fourteen flowering species bloomed during insect peaks, which occurred in May and June. *Leucanthemum vulgare* Lam. and *Achillea millefolium* L. were the most abundant species found in the different plots. *Capsella bursa-pastoris* (L.) Medik. and *Medicago lupulina* L. only bloomed in May, while *Galium verum* L. and *Malva moschata* L. only flowered in June. *Aethusa cynapium* L., *C. bursa-pastoris*, *Matricaria recutita* (L.) Rauschert, *Sinapis alba* L. and *Trifolium repens* L. were not sown, but grew spontaneously in the quadrats (Table 12, see also Table S 3 for details of each plot).

3.2 Parasitoids and hosts

Five parasitoid species of *Meligethes* spp. and six parasitoid species of *Ceutorhynchus* spp. were trapped, representing 254 and 193 individuals, respectively. The diversity and relative abundance of the parasitoid species are presented in Table 13. In WFS, population peaks of *Meligethes* spp. and their parasitoids in WFS occurred simultaneously on 14 and 21 May (Figure 16a). The populations of *Ceutorhynchus* spp. and their parasitoids peaked on 11 June (Figure 16b). On these dates, four parasitoid species of both *Meligethes* spp. and *Ceutorhychus* spp. were identified in WFS (Table 13). For each host, a second peak occurred at end of June. Despite parasitoids and their hosts occurred simultaneously in WFS, neither the abundance of *Meligethes* spp. nor *Ceutorhynchus* spp. affected the abundance of their related parasitoid species (Table 14, see also Figure S 1 for the abundance of hosts and parasitoids in each plot at their peaks).

3.3 Parasitoid–flower trait interactions

Instead, flower traits were the main drivers of parasitoid density in WFS. Indeed, flower colour, UV reflectance (i.e. both ‘UV Pattern’ and ‘UV Periphery’) and the availability of nectar (i.e. ‘Flower type’) were the traits that significantly affected parasitic wasps (Table 14). *Meligethes* spp. parasitoids *Blacus nigricornis* (Haeselbarth) (Hymenoptera: Braconidae), *Brachyserphus parvulus* (Nees) (Hymenoptera: Proctotrupidae) and *Phradis interstitialis* (Thomson) (Hymenoptera: Ichneumonidae) were more abundant in mixtures dominated by yellow flowers, rather than mixtures dominated by white and violet flowers. Flowers with high UV reflectance for both internal and external flower parts were also more attractive to these parasitoids. Moreover, parasitoids were less abundant in mixtures containing flowers with totally hidden nectar (Figure 17a-b, Table 14). *Tersilochus heterocerus* (Thomson) (Hymenoptera: Ichneumonidae) generally responded to the opposite flower cues compared to the other species (Figure 17a). *Ceutorhynchus* spp. parasitoids *Mesopolobus morys* (Walker) (Hymenoptera: Pteromalidae), *Trichomalus lucidus* (Walker) (Hymenoptera: Pteromalidae) and *Trichomalus perfectus* (Walker) (Hymenoptera: Pteromalidae), but not *Stenomalina gracilis* (Walker) (Hymenoptera: Pteromalidae), were significantly less abundant in mixtures containing violet flowers and flowers with totally hidden nectar (Figure 17c-d, Table 14).

Table 13. Diversity and abundance of parasitoid species trapped during the whole season and at respective peaks (i.e. *Meligethes* spp. parasitoids: 14 and 21 May; *Ceutorhynchus* spp. parasitoids: 11 June). The proportion (%) of each species among those having the same host is given.

Host	**Family, Species**	**Abundance (total)**	**%**	**Abundance (at peak)**	**%**
Meligethes spp.	**Braconidae**				
	Blacus nigricornis	230	90.5	136	90.1
	Diosphilus capito	1	0.4	0	0.0
	Ichneumonidae				
	Phradis interstitialis	14	5.5	10	6.6
	Tersilochus heterocerus	6	2.4	4	2.6
	Proctotrupidae				
	Brachyserphus parvulus	3	1.2	1	0.7
	Total	254		151	
Ceutorhynchus spp.	**Ichneumonidae**				
	Tersilochus fulvipes	1	0.5	0	0.0
	Tersilochus obscurator	1	0.5	0	0.0
	Pteromalidae				
	Mesopolobus morys	50	25.9	15	20.8
	Stenomalina gracilis	51	26.4	15	20.8
	Trichomalus lucidus	5	2.6	4	5.6
	Trichomalus perfectus	85	44.1	38	52.8
	Total	193		72	

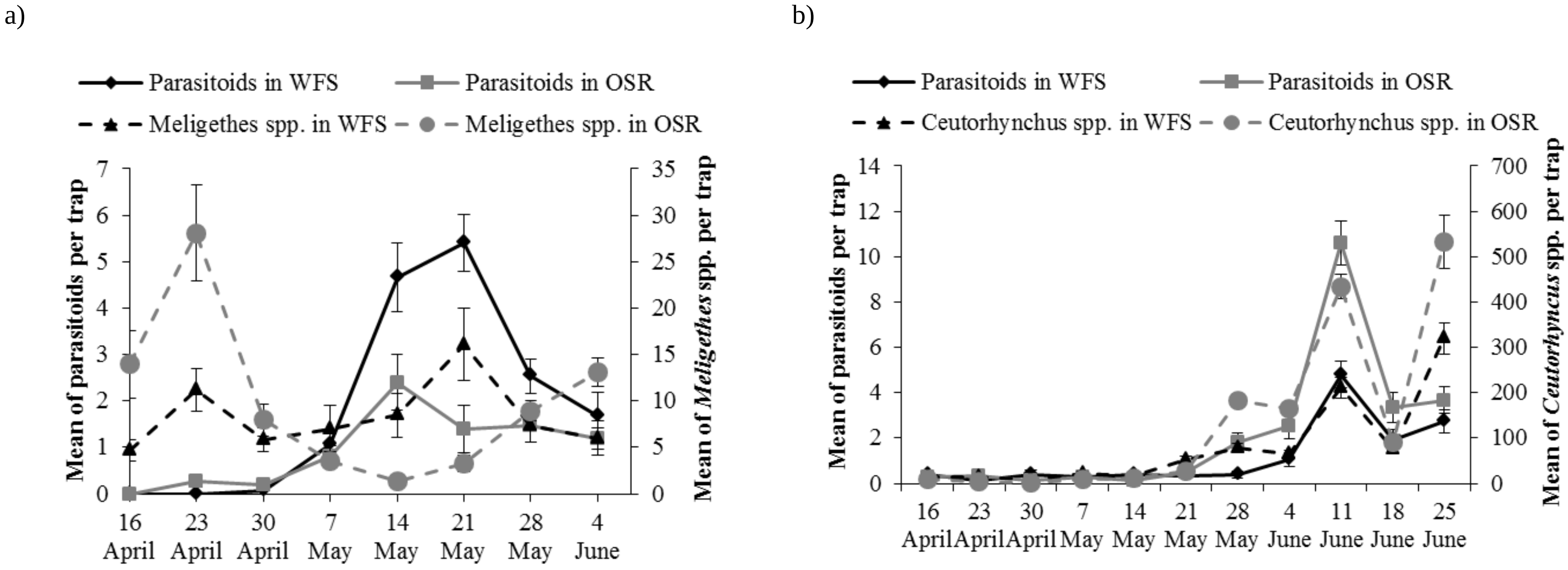

Figure 16. Mean number per trap in WFS and OSR of (a) *Meligethes* spp. and their parasitoids and (b) *Ceutorhynchus* spp. and their parasitoids along the trapping period. For *Meligethes* spp. and their parasitoids, the three last trapping weeks (from 11 to 25 June) are not included in the graph to facilitate the reading. Indeed, in the end of June, abundance of *Meligethes* spp. increased to reach, on 18 June, 1902 and 2444 individuals on average per trap in WFS and OSR, respectively, while abundance of parasitoids decreased. However at that time, crops were not sensitive to *Meligethes* spp. anymore. Details of abundance means for all trapping dates are given in Table S 5.

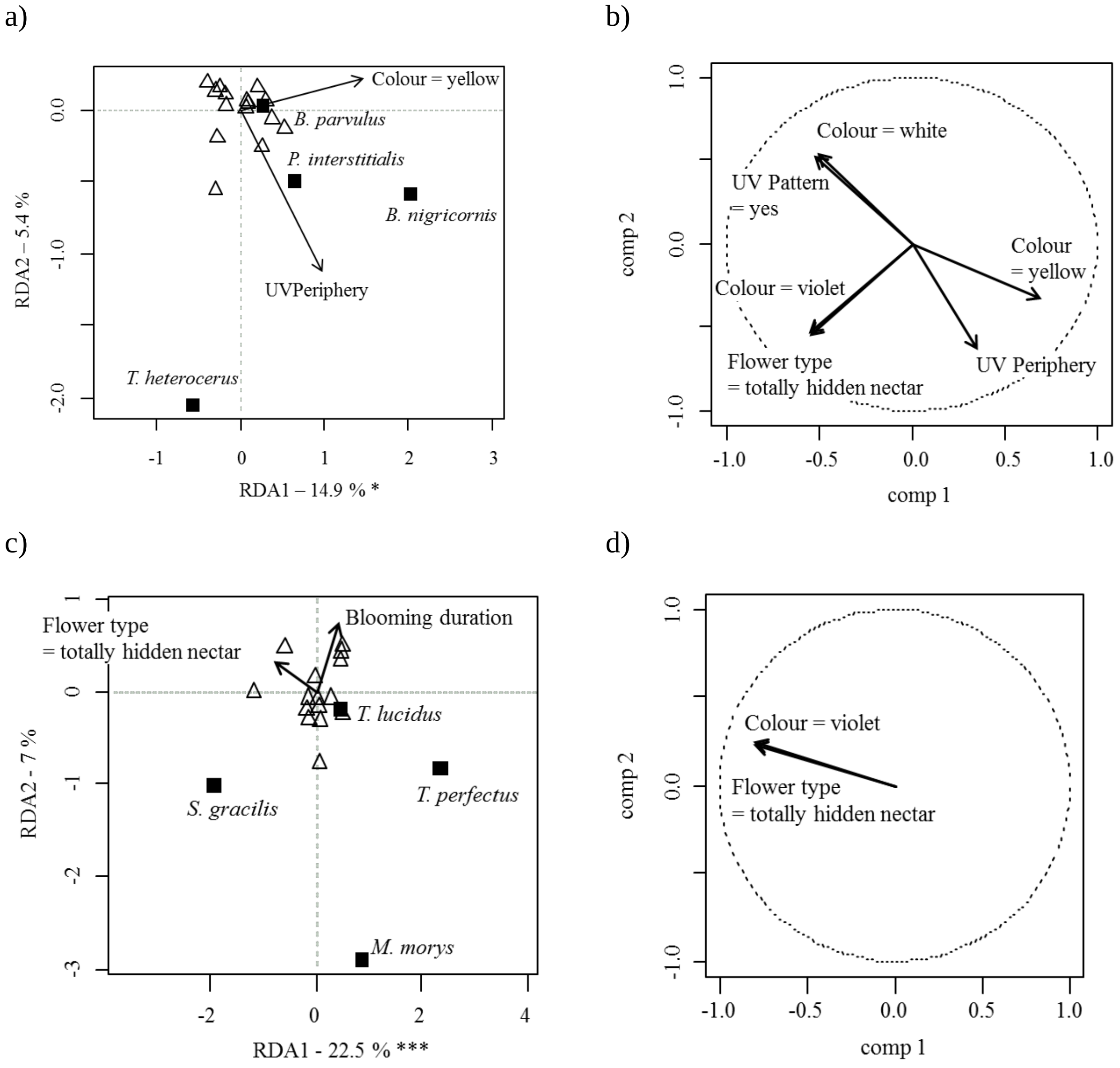

Figure 17. Factorial map of the redundancy analysis (RDA) carried out on (a) *Meligethes* spp. parasitoids and (c) *Ceutorhynchus* spp. parasitoids. The empty triangles represent the flower mixtures. The variance explained by each axis is given, as well as the effect of the selected factors (i.e. those with the $P < 0.05$ – see Table 14) on them (Permutation test: n=1000; *$P < 0.05$; ***$P < 0.001$). (b) and (d) are the respective correlation circles of the significant factors affecting the parasitoids (the significant factors are detailed in Table 14).

Table 14. Permutation test (n=1000) of the forward selection of the explanatory variables affecting *Meligethes* spp. parasitoids in May, and *Ceutorhynchus* spp. parasitoids in June. When the value of a trait is a class (i.e Colour, Flower type, UV pattern), each class is considered as an explanatory variable. When it is numerical (i.e. Blooming duration, Blooming start, Height, UV periphery), each trait is an explanatory variable. For the first two steps, the Akaike Information Criterion (AIC), F-value and p-value (* P < 0.05; ** P < 0.01) are given.

Explanatory variables		**Step 1**			**Step 2**		
Trait	**Value**	**AIC**	**F**	**p-value**	**AIC**	**F**	**p-value**
***Meligethes* spp. parasitoids**							
Flower type	Totally hidden nectar	8.512	1.76	0.010 **			
Colour	Yellow	8.025	2.24	0.020 *	8.076	2.12	0.060
Colour	Violet	8.527	1.74	0.045 *	9.690	0.68	0.745
Colour	White	8.417	1.85	0.060	8.078	2.11	0.030 *
UV Pattern	No	8.608	1.66	0.085	8.084	2.11	0.070
Flower type	Open nectaries	8.631	1.64	0.090	8.696	1.54	0.160
UV Pattern	Yes	8.608	1.66	0.115	8.084	2.11	0.040 *
Meligethes spp.	Numerical	8.730	1.55	0.150	8.521	1.70	0.095
UV Periphery	Numerical	8.909	1.37	0.210	7.914	2.27	0.025 *
Flower type	Associations with totally hidden nectar	9.259	1.04	0.400	9.043	1.23	0.295
Blooming duration	Numerical	9.427	0.88	0.505	9.447	0.88	0.530
Height	Numerical	9.507	0.81	0.595	9.386	0.94	0.460
Blooming start	Numerical	9.548	0.77	0.605	9.544	0.80	0.565
Flower type	Bee flowers	9.585	0.74	0.735	9.530	0.81	0.690
Flower type	Hymenoptera flowers	9.622	0.70	0.740	9.485	0.85	0.635
Flower type	Partly hidden nectar	9.622	0.71	0.775	9.688	0.68	0.735
***Ceutorhynchus* spp. parasitoids**							
Flower type	Totally hidden nectar	29.502	3.32	0.010 **			
Colour	Violet	29.555	3.26	0.020 *	30.506	0.82	0.550
Blooming duration	Numerical	31.194	1.58	0.130	29.647	1.58	0.165
Flower type	Associations with totally hidden nectar	31.604	1.19	0.290	30.740	0.63	0.795
Ceutorhynchus spp.	Numerical	31.774	1.03	0.360	30.074	1.20	0.245
UV Periphery	Numerical	31.806	1.00	0.400	30.341	0.97	0.405
Colour	Yellow	31.861	0.95	0.510	30.809	0.57	0.835
UV Pattern	No	32.092	0.73	0.625	30.320	0.98	0.395
Flower type	Bee flowers	32.055	0.77	0.640	30.424	0.89	0.505
UV Pattern	Yes	32.092	0.73	0.700	30.320	0.98	0.405
Height	Numerical	32.195	0.64	0.720	30.596	0.75	0.625
Blooming start	Numerical	32.205	0.63	0.755	30.544	0.79	0.630
Flower type	Open nectaries	32.304	0.54	0.835	30.647	0.70	0.660
Colour	White	32.433	0.42	0.950	30.804	0.57	0.845

4. Discussion

Meligethes spp. and *Ceutorhychus* spp. parasitoids and their respective hosts reached their abundance peaks in WFS simultaneously in May and June, respectively. Pests, but not their parasitoids, showed a second peak at the end of June. However, at that time, harvesting of OSR was imminent and crops were not sensitive to the pests anymore.

4.1 Effect of hosts on parasitoids

Despite the simultaneity of their abundance peak, the density of *Meligethes* spp. and *Ceutorhynchus* spp. in the WFS did not affect the one of parasitoids. Instead, several flower traits had a significant role. Previous studies have warned that the presence of crop pests in WFS could affect natural enemy behaviour (Carrié et al., 2012; Rand et al., 2006). However, this study is the first to assess pest abundance in WFS as a potential explanatory variable for natural enemy density. It matters as *Meligethes* spp. are polyphagous feeders (Free and Williams, 1978), thus may have settled in the WFS. *Ceutorhynchus* spp., however, are oligophagous on Brassicaceae and none of them were sown. Only *S. alba* was found flowering in June, certainly as a regrowth from previously cultivated crop. Nevertheless, even if OSR pests were trapped in the WFS, we previously indicated that they were always more attracted by the adjacent crops at their abundance peak, which shows that OSR pests did not prefer wildflower species (Hatt et al., 2015). Our results demonstrate that flower traits are stronger drivers at attracting parasitoids in WFS compared to hosts. An explanation is that parasitoids, at early stage of their adult life and before ovipositing, need energy they can find through flower nectar, which also increases their reproduction capacity (Lundgren, 2009a). The presence of attractive and suitable flowers may orient their flight when they start colonising WFS. This confirms the importance of understanding which flower traits affect parasitoid behaviour in open fields and how.

4.2 Traits affecting parasitoid abundance in WFS

The abundance of *Meligethes* spp. parasitoids was significantly affected by flower colour and UV reflectance in the WFS. Visual cues have an important role in insect–plant interactions (Begum et al., 2004; Wäckers, 1994). In the present study, yellow coloured flowers attracted more parasitic wasps compared to white and violet flowers. This result is consistent with that obtained by Jönsson (2005), who also found that yellow is a strong visual cue for pollen beetle parasitoids. The attraction to yellow is caused by the positive input from green receptors coupled with a negative input from blue receptors in the insect eye, termed the ‘green–blue colour opponent mechanism’ (Döring et al., 2009, 2012). In contrast to *Meligethes* spp. parasitoids, *Ceutorhynchus* spp. parasitoids were less sensitive to flower colour. Only violet had a significant effect, repellent to most wasps. Yellow also attracts *Meligethes* spp. (Döring et al., 2012), which partly explains why it is one of the main pest of OSR (Williams, 2010). Their parasitoids, also attracted by yellow coloured flowers, are more likely to find their hosts on such flowers. Thus, we hypothesise that flower colour is a main driver for pollen beetle parasitoids to locate their hosts. This phenomenon is not the case for *Ceutorhynchus* spp. parasitoids. Indeed, the majority of these species were not positively affected by any colour, with Williams and Cook (2010) also reporting that their parasitism rate is not affected by flower colour.

In addition to colour, flowering species with high UV reflectance for both internal and external flower parts attracted *Meligethes* spp. parasitoids. Indeed, the UV reflectance of flowers affects insect behaviour (Chittka et al., 1994; Tansey et al., 2010). Yet, it did not affect *Ceutorhynchus* spp. parasitoids. This study is the first to assess the attraction of OSR pest parasitoids to UV. However, pollen beetles have been shown to be attracted to flowers with higher UV reflectance (Döring et al., 2012), such as OSR (Ômura et al., 1999). Like the colour yellow, the attractiveness of flowers with high UV reflectance to *Meligethes* spp. parasitoids may help them to locate their hosts.

After visual cues, nectar availability, which is linked to flower morphology, also influenced insect attraction. In particular, parasitoids search for sugar resources to increase their longevity and help to increase oviposition rate of females by accelerating egg maturation (Lundgren, 2009a). In the present study, the parasitoids of both *Meligethes* spp. and *Ceutorhynchus* spp. were negatively affected by flowers with totally hidden nectar. This result is consistent with all previous studies, which showed that hymenopteran parasitoids preferentially feed on flowers that offer accessible nectar, notably those with open nectaries (Bianchi and Wäckers, 2008; Idris and Grafius, 1995; Patt et al., 1997; Vattala et al., 2006). Jervis et al. (1993) reported that Ichneumonidae and some Braconidae species are generally too large and have mouth parts that are too short, which prevents them from exploiting the nectar of flowers with narrow and tubular corolla. In contrast, Proctotrupoidea species may feed on such flowers; however, in the present study, very few individuals of this superfamily were trapped (Table 13). There is a lack of information on the interactions between Pteromalidae species and flower corolla. In the present study, they were mainly negatively affected by flowers with totally hidden nectar, as were the majority of the studied parasitoids.

4.3 Practical implications and further research

Parasitoids were trapped at their adult stage. As mentioned here-above, flower nectar is an essential resource for parasitoid longevity and reproduction capacity, thus its provision may favour their ability of controlling pests. Nectar from OSR flowers may be exploited, however, the resource must be available at the latest when pests flight on crops in order to increase parasitoid chance to find and parasite their host at the early stage of infestation. Because pollen beetles damage crops from their green bud stage, other source of nectar than those from OSR flowers must be available earlier. In the present study, OSR was even not blooming anymore when *Meligethes* spp. parasitoids occurred (i.e. in mid-May, simultaneously in WFS and OSR, Figure 16a). The present results on the effects of flower morphology, colour and UV may be used in order to select flower species – among those blooming earlier than OSR – able to attract and support *Meligethes* spp. parasitoids at field margins before OSR flourishes and pollen beetles occur on them. In the present study, the first *Meligethes* spp. individuals were trapped on 23 April in OSR, three weeks before parasitoids peaked (Figure 16a). As for *Ceutorhynchus* spp. parasitoids, they appeared in the field along with weevil adults (i.e. mid-June, simultaneously in WFS and OSR, Figure 16b). The presence of blooming flowers in WFS from which they may have benefited could have increased their longevity and foraging capacity in order to parasite weevil larvae in the following days in adjacent crops. Their simultaneous occurrence in both WFS and adjacent OSR may have favoured parasitism, thus pest control.

By focusing on the effect of flower traits on natural enemies in cropping conditions, the present study may allow improving the constitution of mixtures sown at field margins or within fields. The sowing of WFS is subsidised by several European countries through the AES policy. The AES were firstly introduced to “reduce environmental risks associated with modern farming on the one hand, and preserve nature and cultivated landscapes on the other hand” (European Commission, 2005). Today, there is a need to optimise AES to benefit from important ecosystem services, such as biological control (Ekroos et al., 2014; Haaland et al., 2011). The results of the current study indicate that yellow flowers with high UV reflectance should be sown – if only they can bloom early in spring – while those with totally hidden nectar should be excluded to attract the parasitoids of OSR pests when OSR is cultivated.

However, in cropping systems following rotations (which is actually a practice in itself to control pests as it disrupts the presence of pest host plants through time, Oerke 2006), the challenge remains to develop flower mixtures that are able to support a wide diversity of natural enemies associated with the different pests of crops that are sown adjacent to perennial WFS. It could be proposed to sow annual flowering plants adapted to each crop each year, as some previously studied (Balzan and Wäckers, 2013; Tschumi et al., 2015). Nevertheless, perennial WFS present the advantage of preserving permanent vegetation in annual cropping systems, providing an overwintering site and resources for natural enemies, thus, reducing ecological disturbance in agricultural landscapes and potentially favouring the early colonisation of crops (Rusch et al., 2013a). Previous studies have shown that increasing the range of values taken by various traits within mixtures may optimise the conservation of several arthropod functional groups that provide multiple ecosystem services (Balzan et al., 2014; Campbell et al., 2012). However, research is needed to determine whether flower mixtures with higher functional diversity support a wide range of natural enemies that are able to control different crop pests. Better knowledge on how flower cues affect different predators and parasitoids may help with the selection of appropriate perennial species for inclusion in mixtures. Similar analyses to those presented in this study, but on crops other than OSR, could provide such information. The present study provides first results, as well as a methodology, towards long term research on the development of perennial flower mixtures that are able to enhance biological control throughout a whole rotation period.

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Supplementary materials

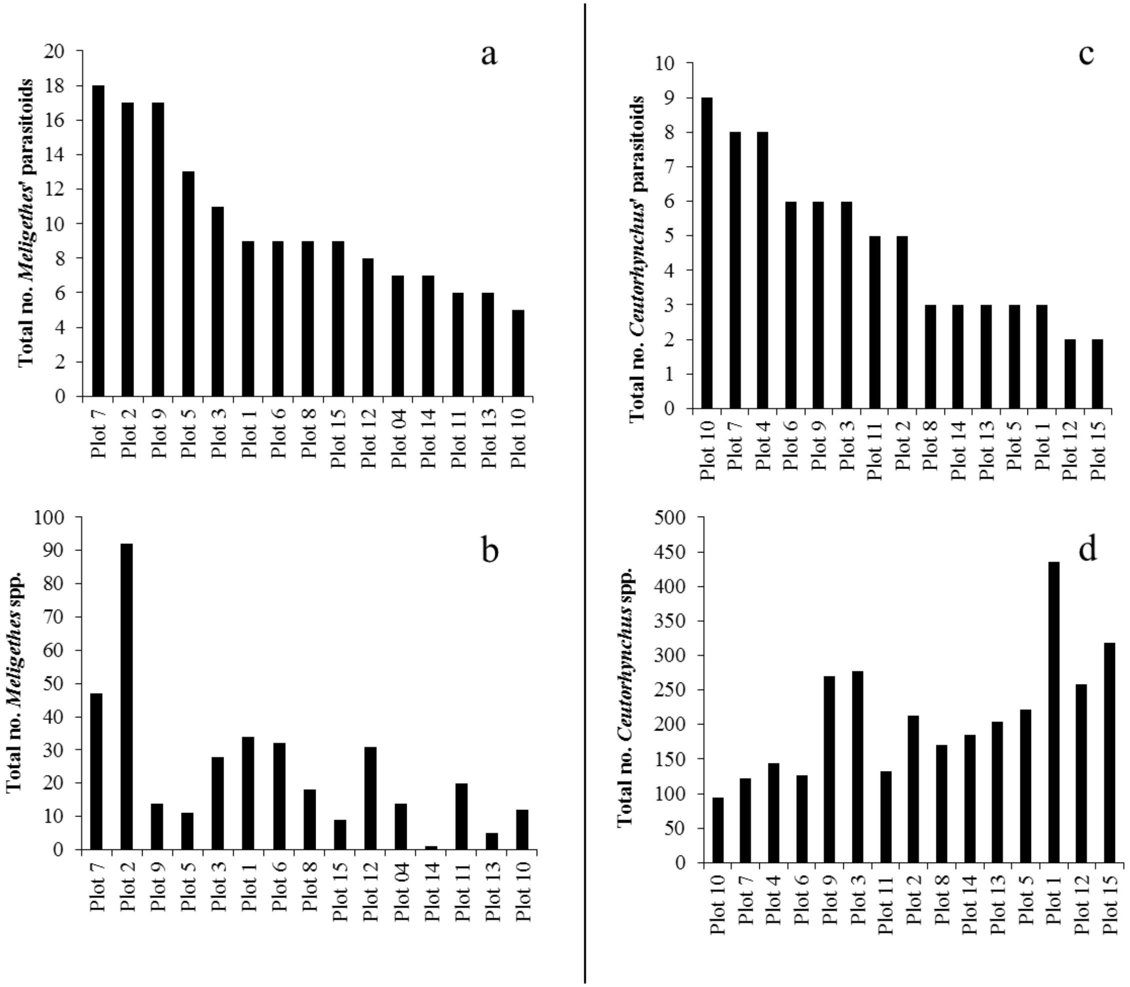

Figure S 1. Total number of a) *Meligethes* spp. and b) their parasitoids trapped at peak (14 and 21 May), as well as of c*) Ceutorhynchus* spp. and d) their parasitoids at peak (11 June) in each plot.

Table S 2. Theoretical trait values for each flower species. The values on blooming start, blooming duration and plant height were obtained from Lambinon et al. (2008), while those on colour, UV periphery, UV pattern, and the flower type were retrieved from the TRY database (Kattge et al., 2011).

Flower species	**Colour**	**UV periphery (%)**	**UV pattern**	**Blooming start**	**Blooming duration (month)**	**Height (cm)**	**Flower type (Müller 1881)**
Achillea millefolium	White	3.5	No	June	6	45	Associations with totally hidden nectar
Aethusa cynapium	White	3.5	No	June	4	80	Open nectaries
Anthriscus sylvestris	White	3.5	No	May	2	120	Open nectaries
Capsella bursa-pastoris	White	11.5	No	February	8	60	Partly hidden nectar
Crepis biennis	Yellow	33.5	Yes	June	3	120	Associations with totally hidden nectar
Galium verum	Yellow	3.5	No	May	5	80	Open nectaries
Geranium pyrenaicum	Violet	76	Yes	May	5	60	Totally hidden nectar
Heracleum sphondylium	White	3.5	No	June	3	150	Open nectaries
Hypochaeris radicata	Yellow	33.5	Yes	June	4	60	Associations with totally hidden nectar
Knautia arvensis	Violet	3.5	No	June	4	60	Associations with totally hidden nectar
Leontodon hispidus	Yellow	53	Yes	June	5	40	Associations with totally hidden nectar
Leucanthemum vulgare	White	3.5	No	May	4	60	Associations with totally hidden nectar
Lotus corniculatus	Yellow	3.5	No	May	5	30	Bee flowers
Lythrum salicaria	Violet	76	Yes	June	4	150	Totally hidden nectar
Malva moschata	Violet	53	Yes	July	3	80	Totally hidden nectar
Matricaria recutita	White	11.5	No	May	4	50	Associations with totally hidden nectar
Medicago lupulina	Yellow	3.5	No	April	7	50	Hymenoptera flowers
Origanum vulgare	Violet	11.5	No	July	3	80	Totally hidden nectar
Prunella vulgaris	Violet	76	Yes	July	3	50	Hymenoptera flowers
Sinapis alba	Yellow	53	Yes	May	4	70	Open nectaries
Trifolium pratense	Violet	3.5	No	May	6	50	Bee flowers
Trifolium repens	White	3.5	No	May	7	25	Bee flowers

Table S 3. Mean cover (%), calculated from the three quadrats in each plot, of each blooming flower species found. Sum of percentage may be less than 100 as grass cover and bare soil was also considered when assessing flower cover.

	Plot 1	**Plot 2**	**Plot 3**	**Plot 4**	**Plot 5**	**Plot 6**	**Plot 7**	**Plot 8**	**Plot 9**	**Plot 10**	**Plot 11**	**Plot 12**	**Plot 13**	**Plot 14**	**Plot 15**
Achillea millefolium	1	5	8.33	9.67	0.67	3.67	0	14.3	15	11.7	4.67	1.33	9.67	0.67	12.7
Aethusa cynapium[3]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33
Capsella bursa pastoris[1,3]	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0
Crepis biennis	0	6	0.67	0	0	0	0	1.3	0	0	0	0	0	0	3.67
Galium verum[2]	0	1.33	0	2	0.33	0	0	1	0.33	2	3.33	0	0	0	3.33
Geranium pyrenaicum	4.67	0.33	0	0	0	0	0	0	0.33	0	0	0	0.67	0	0
Hypochaeris radicata	0	11.3	0	0	0.67	0	0	13	0.33	0	0	0	0	0	20
Knautia arvensis	0	0.33	0	0	0	0	0	0	0	0	0.33	0	0	0	0.33
Leontodon hispidus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1.67
Leucanthemum vulgare	3.67	0	0	56.7	0.67	1	0	1	38.3	56.7	63.3	3	45	0	2
Lotus corniculatus	0	0	33.3	0	0	1.33	0	0	0	0	0	0.67	0	0	0
Malva moschata[2]	0	0	2.33	0	0	1.33	0	0	0	0.33	0	4.33	1.33	0	0
Matricaria recutita[3]	0.33	0	2.67	1	1	0	0.33	0	0	0	0	1.67	0	0.33	0
Medicago lupulina[1]	0	0	2.33	0	0	1	0	0	0	0	0	1.33	0	0	0
Sinapis alba[3]	0	0	0	0	1.33	5	1.33	0	0	0	0	0	0	0	0
Trifolium repense[3]	0	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0

These species only bloomed in [1]May or [2]June. [3]These species were not sown but grew spontaneously in the quadrats.

Table S 4. Community Weight Mean (CWM) calculated for each plot based on the average cover of each flower species found in the quadrats and blooming in May and June (see Table S 3), and the traits of each species (see Table S 2). CWMs of May was put into relation with *Meligethes* spp. parasitoids, while CWMs of June was linked with *Ceutorhynchus* spp. parasitoids, as these two parasitoids groups did not occurred at the same time in the wildflower strips.

MAY	**Plot 1**	**Plot 2**	**Plot 3**	**Plot 4**	**Plot 5**	**Plot 6**	**Plot 7**	**Plot 8**	**Plot 9**	**Plot 10**	**Plot 11**	**Plot 12**	**Plot 13**	**Plot 14**	**Plot 15**
Violet	0.483	0.029	0	0	0	0	0	0	0.006	0	0.005	0	0.012	0	0.008
White	0.517	0.217	0.232	1	0.571	0.405	0.200	0.500	0.988	1.000	0.995	0.750	0.988	1.000	0.369
Yellow	0	0.754	0.768	0	0.429	0.595	0.800	0.500	0.006	0	0	0.250	0	0	0.623
Bee flowers	0	0	0.704	0	0	0.135	0	0	0	0	0	0.083	0	0	0
Associations with totally hidden nectar	0.517	0.986	0.246	1	0.643	0.378	0.200	1.000	0.994	1.000	1.000	0.750	0.988	1.000	0.992
Open nectaries	0	0	0	0	0.286	0.405	0.800	0	0	0	0	0	0	0	0.008
Partly hidden nectar	0	0	0	0	0.071	0	0	0	0	0	0	0	0	0	0
Totally hidden nectar	0.483	0.014	0	0	0	0	0	0	0.006	0	0	0	0.012	0	0
Hymenoptera flowers	0	0	0.049	0	0	0.081	0	0	0	0	0	0.167	0	0	0
Blooming start	5.103	5.986	5.141	5.144	5.071	5.216	5.000	5.967	5.284	5.171	5.073	5.000	5.175	5.667	5.951
Blooming duration	4.690	4.188	5.190	4.287	4.571	5.027	4.000	4.924	4.562	4.341	4.137	4.917	4.361	5.333	4.574
Height	58.103	72.391	36.021	57.698	58.571	54.595	66.000	54.946	55.833	57.439	58.976	51.250	57.380	46.667	60.082
UV Periphery	38.776	27.159	4.373	3.619	24.214	23.568	44.700	19.136	4.133	3.500	3.500	5.167	4.373	6.167	22.988
UV Pattern = yes	0.517	0.232	0.986	1	0.571	0.595	0.200	0.500	0.988	1.000	1.000	1.000	0.988	1.000	0.377
UV Pattern = no	0.483	0.768	0.014	0	0.429	0.405	0.800	0.500	0.012	0	0	0	0.012	0	0.623

Continuation of Table S 4

JUNE	**Plot 1**	**Plot 2**	**Plot 3**	**Plot 4**	**Plot 5**	**Plot 6**	**Plot 7**	**Plot 8**	**Plot 9**	**Plot 10**	**Plot 11**	**Plot 12**	**Plot 13**	**Plot 14**	**Plot 15**
Violet	0.483	0.027	0.049	0	0	0.105	0	0	0.006	0.005	0.005	0.394	0.035	0	0.008
White	0.517	0.205	0.232	0.971	0.500	0.395	0.200	0.484	0.982	0.967	0.949	0.545	0.965	1.000	0.341
Yellow	0	0.767	0.718	0.029	0.500	0.500	0.800	0.516	0.012	0.028	0.047	0.061	0	0	0.652
Bee flowers	0	0	0.704	0	0	0.132	0	0	0	0	0	0.061	0	0	0
Associations with totally hidden nectar	0.517	0.932	0.246	0.971	0.643	0.368	0.200	0.968	0.988	0.967	0.953	0.545	0.965	1.000	0.917
Open nectaries	0	0.055	0	0.029	0.357	0.395	0.800	0.032	0.006	0.028	0.047	0	0	0	0.083
Totally hidden nectar	0.483	0.014	0.049	0	0	0.105	0	0	0.006	0.005	0	0.394	0.035	0	0
Blooming start	5.103	5.932	5.289	5.139	5.286	5.500	5	5.937	5.282	5.175	5.070	5.909	5.218	5.667	5.879
Blooming duration	4.690	4.233	4.993	4.308	4.357	4.658	4	4.926	4.564	4.354	4.177	3.909	4.329	5.333	4.606
Height	58.103	72.808	37.500	58.341	60.000	57.632	66.000	55.737	55.982	58.184	59.953	62.727	57.912	46.667	61.591
UV Periphery	38.776	25.863	6.813	3.615	23.643	28.250	44.700	18.642	4.129	3.733	3.500	24.212	5.518	6.167	21.511
UV Pattern = yes	0.483	0.726	0.063	0	0.429	0.500	0.800	0.484	0.012	0.005	0	0.394	0.035	0	0.576
UV Pattern = no	0.517	0.274	0.937	1	0.571	0.500	0.200	0.516	0.988	0.995	1.000	0.606	0.965	1.000	0.424

Table S 5. Mean per trap of pests and their related parasitoids in wildflower strips (WFS) and oilseed rape (OSR)

Meligethes spp. and their parasitoids

	Parasitoids in WFS	**Parasitoids in OSR**	***Meligethes* spp. in WFS**	***Meligethes* spp. in OSR**
16 April	0	0	4.66666667	13.9333333
23 April	0	0.26666667	11.2	28.0666667
30 April	0.06666667	0.2	5.8	7.93333333
7 May	1.06666667	0.8	7	3.46666667
14 May	4.66666667	2.4	8.46666667	1.33333333
21 May	5.4	1.4	16.0666667	3.26666667
28 May	2.53333333	1.46666667	7.4	8.93333333
4 June	1.66666667	1.2	6	13.0666667
11 June	0.46666667	1	417	956.733333
18 June	0.06666667	0.33333333	1902.06667	2444
25 June	1	0.46666667	552.866667	539.6

Ceutorhynchus spp. and their parasitoids

	Parasitoids in WFS	**Parasitoids in OSR**	***Ceutorhynchus* spp. in WFS**	***Ceutorhynchus* spp. in OSR**
16 April	0.4	0.26666667	14.4666667	8.06666667
23 April	0.13333333	0.33333333	13.4666667	4.2
30 April	0.4	0.13333333	10.1333333	2.4
7 May	0.26666667	0.26666667	22.6666667	9.46666667
14 May	0.4	0.13333333	15.8666667	11.6
21 May	0.33333333	0.46666667	52.9333333	27.6
28 May	0.4	1.8	77.9333333	183
4 June	1.06666667	2.53333333	65.4666667	164.6
11 June	4.8	10.6	211.533333	434.066667
18 June	1.93333333	3.33333333	75.6	91.8
25 June	2.73333333	3.66666667	320.133333	533.333333

Chapter IV

General conclusions and perspectives

General conclusions

The present thesis explored the strategy of increasing field heterogeneity, by increasing plant diversity through the introduction of flowering features, in order to enhance the biological control of insect pests. After reviewing the existing scientific literature (**Chapter I**), a first set of experiments (**Chapter II**) aimed at testing two different field designs: intercropping a flowering (i.e. oilseed rape) with a non-flowering (i.e. winter wheat) crop in China (***Article 4***) on the one hand, sowing wildflower strips within a wheat field in Belgium on the other hand (***Article 5***). In a second set of experiments (**Chapter III**), a focus was made on the composition of wild flower mixtures, by considering flower traits as determinant factors in the attraction of natural enemies (***Article 6*** and ***Article 7***). Contrasted results regarding our hypotheses were obtained.

1. Conclusions on the increase of plant diversity at the field scale with the provision of flower resources for enhancing biological control

First, the success of intercropping in limiting pests and favouring natural enemies understandably depends on the growth of the associated crops. In ***Article 4***, the unexpected limited growth of oilseed rape prevented the establishment of a proper intercropping system, which could explain the non-differences in pest abundance between intercropping and pure stands. It also led to the absence of flowering features which could be responsible for the non-differences between the treatments regarding the abundance of most of natural enemies. Instead, the spread of natural enemies was determined by the abundance of pests and their interactions with crops. Enemies with preferences for oilseed rape aphids were mainly found in pure stand oilseed rape (i.e. the parasitoid *Diaeretiella rapae* (M'Intosh) correlated with the aphid *Myzus persicae* (Sulzer)) while more generalists enemies were spread all over the treatments, or even escaped oilseed rape (i.e. ladybeetles), possibly because of the glucosinolates and their derivatives produced by Brassicaceae plants. Indeed, these compounds can be concentrated by specialist herbivores, but are toxic to some generalist predators (Francis et al., 2001b). These findings recall that the abundance and species of pests – that are prey and hosts for natural enemies – is a key factor affecting the spread of natural enemies in fields (Schellhorn et al., 2014). Here, it affected natural enemies independently from crop habitat design, especially because the expected design failed to be implemented.

Pest abundance also affected natural enemy spread in ***Article 5,*** but along with the effect of field design, that was the sowing of wildflower strips within a wheat field, finally reducing parcel size and increasing heterogeneity at the field scale. Hoverfly adults were found more numerous in wheat crops in between wildflower strips than in pure stand plots, and their larvae density was positively related with aphid abundance in between wildflower strips, despite that aphids were more abundant in pure stands. Indeed, sowing several wildflower strips allowed reducing aphid density on wheat in between flowering features, especially in the centre of the system, compared to its border. Knowledge on the needs of adult hoverflies in terms of food source and on their reproductive behaviour allows making assumptions on the order of their priorities. It was hypothesised that the floral food resources attracted adults that exclusively depend on nectar and pollen for their energy and the maturation of their eggs respectively (Wäckers and Van Rijn, 2012), before they oviposited in the adjacent crops, mainly where aphids were abundant. Hence here, habitat composition and design, along with prey abundance, affected the spread of hoverfly adults and larvae. A similar behaviour was expected for aphid parasitoids, for which floral nectar is a main source of sugar increasing adult longevity and their reproductive ability (Tylianakis et al., 2004), while adults also search for aphid colonies for ovipositing. The non-effect of the presence of flowering strips on parasitoids and other predators (ladybeetles, lacewings) in this experiment invited to go further, notably in questioning the composition of the flowering strips.

2. Conclusions on the trait-based analyses for composing flower mixtures attractive to natural enemies

Flower traits were considered because of their known effect on flower visitor behaviour. It was first hypothesised that flower mixtures with a high functional diversity would attract and support a high abundance and diversity of natural enemies (***Article 6***). This hypothesis was not confirmed and the high abundance in some plots of few flower species known to be attractive to natural enemies was supposed to be a main factor that limited the effect of functional diversity. These results are consistent with previous experiments testing the same hypothesis (Balzan et al., 2014, 2016a) and continue to question the approach to use in order to compose flowering mixtures able to support a diversity of natural enemies. Flower species known to individually attract and benefit natural enemies could be mixed, as Tschumi et al. (2016b, 2015) tested. Nevertheless as those particular species are actually attractive because of their traits, continuing understanding flower-insect interactions in flower mixtures is needed. Studying mixtures in fields is of particular importance because, although flower species are often mixed when sown in fields, studies only assessed the effect of flower traits on insects in relatively controlled conditions (e.g. Vattala et al., 2006), modelling (Bianchi and Wäckers, 2008) or by using mono-specific plots (e.g. Sivinski et al., 2011).

Therefore, ***Article 7*** aimed at identifying flower traits that significantly affect natural enemies – in the present case parasitoids of oilseed rape pests – when flowers are mixed and sown in fields. It showed that visual traits (colour and ultra-violet reflectance) and the corolla morphology (which notably determines the availability of nectar and pollen for visitors) were the traits that significantly affected the behaviour of oilseed rape parasitoids. More specifically, the values of these traits found to benefit, or on the contrary not to support, the parasitoids were identified. In addition to the results obtained, the methodology developed in this experiment could be used in order to broadly assess the effect of flower traits from sown mixtures on a diversity of natural enemies.

More generally, the trait-based approach could be applied to any plant in agroecosystems. Whereas here we focussed on flower traits in flower mixtures, an original approach would be to also assess the effect of traits from the associated crops in intercropping systems in order to choose appropriate pairs of species.

3. Prey/hosts versus habitats: what does explain natural enemy abundance and diversity in agroecosystems?

Natural enemy behaviour is driven by numerous stimuli in agroecosystems (reviewed by Schellhorn et al. 2014). In the present thesis, various effects of prey/hosts on the one hand, habitats on the other hand, were observed. In ***Article 4***, aphid abundance and species were the strongest drivers explaining the spread of natural enemies in fields. On the contrary in ***Article 7***, flower traits but not host abundance affected parasitoid spread in wildflower strips. In ***Article 5***, a synergy effect of field design and aphid abundance was observed on hoverflies. Such synergies and tradeoffs between prey/hosts and habitats in the attraction and support of natural enemies represent a challenge for conceiving strategies of conservation biological control. Indeed, the attractiveness of natural enemies by pests may not necessarily lead to an effective control if pest colonization is already advanced, i.e. if pests are too abundant. Therefore, it has been proposed that an early arrival of natural enemies, i.e. when pests are still absent or in a low abundance, is a key factor for the control of insect herbivores (Macfadyen et al., 2015). Early attracting natural enemies may be possible by providing floral resources that bloom before pests colonize crops. Nevertheless, in some regions with long winter like Belgium, some pests colonize crops before that the majority of wildflower species bloom (e.g. *Meligethes* spp. on winter sown oilseed rape – ***Article 7***). Another tactic would be to implement permanent habitats adjacent to crops as overwintering sites for natural enemies. Attention should be paid to local management and the type of habitats as they both affect the abundance and diversity of overwintering natural enemies (Sarthou et al., 2014). Nevertheless, there is no guaranty that natural enemies emerging from such non-crop features migrate to adjacent crops. They may indeed be retain if for instance they find in these habitats appropriate prey or hosts (Tscharntke et al., 2016). Macfadyen et al. (2015) however reported a significant immigration of predators and parasitoids from naturally developed vegetation to crop fields. They hypothesised that the simplier structure of crop fields and the higher density of prey and hosts in crops, compared to non-crop features, favoured natural enemy immigration. But, does an increased abundance of natural enemies in crop fields effectively lead to an improved biological control of pests?

4. Assessing biological control of insect pests in agroecosystems: what is the best indicator?

In the present thesis, abundance and diversity of pests and natural enemies were the indicators used to study the effect of crop and non-crop habitat composition and design towards biological control. These chosen indicators were proxys for the ecosystem service that is the natural regulation of insect pests.

Numbering insect pests provides a direct indication of their effective presence, and in some cases may be a predictor of damages on crops (Tschumi et al., 2016a). Nevertheless, pest abundance may not be the only factor responsible for damage density. Rusch et al. (2013b) for instance reported that the crop nitrogen index was a significant factor affecting the amount of damages on oilseed rape buds. Damages may even not come from the insect pests directly, but from the pathogens they convey. Claflin et al. (2016) indeed reported an increased prevalence of viruses on crops in simplified landscape despite a non effect of landscape composition on aphid abundance. In the present thesis, damages were not evaluated, neither economic or action theresholds (i.e. abundance of insect pests from which insecticides are applied) to evaluate whether pest abundance was critical for crops. Tschumi et al. (2016b) showed that the probability of reaching action threshold was reduced from 70.0 % in control fields to 12.5 % in crops adjacent to wildflower strips. A similar assessment may have been possible here. Finally, yield could also have been associated with pest abundance in order to assess the potential effect of pest regulation on crops (see for e.g. Tschumi et al. 2016a). In ***Article 2***, we reported that 10 out of the 50 original studies reviewed assessed the effect of intercropping on crop yield and we did not find a correlation between pest reduction and yield.

As for natural enemies, abundance and diversity are indirect indicators that do not guarantee for an increase of biological control. Indeed, the only presence of natural enemies may not lead to predation and parasitism. It is especially the case for those that have a diversified diet of both prey and floral source such as ladybeetles and lacewings (Lundgren, 2009a). Concerning hoverflies and parasitoids, they would search for floral source at adult stage for their own needs while look for prey and hosts for laying their eggs (Almohamad et al., 2009; Gillespie et al., 2016). Nevertheless, a meta-analysis showed that in a majority of experiments, an increased richness of natural enemies increases pest suppression, a phenomenon explained by the complementary and sampling effects of natural enemies (Letourneau et al. 2009, a phenomenon recalled in ***Article 3***). A direct assessment of predation by natural enemies can be provided by molecular analyses through polymerase chain reaction (PCR) of predator guts (Gariepy et al., 2007). However, as specified by Lefebvre et al. (2017), a positive response of PCR informs of the effective food webs but does not quantify pest reduction. In turn, parasitism rate (of aphids by parasitoids for instance, calculated as: number of mummies / [number of aphids + number of mummies] × 100) provides a valuation of biological control by parasitoids. The combined use of these different indicators may help understanding the ecological processes involved, and their potential variability in the delivery of ecosystem services.

5. Variability in the delivery of ecosystem services: an intrinsic component of agroecological systems?

The results of the present thesis bring knowledge regarding in which ways spatial diversification of agroecosystems can participate in enhancing the natural regulation of insect pests. They also highlight the complexity of the processes involved, implying the risk that biological control may not be enhanced. Indeed, plants may fail to grow (oilseed rape in

Article 4) or some species may be more competitive than others (*Leucanthemum vulgare* Lam. and other flower species in ***Article 6***), unbalancing the planned equilibrium between the different elements of biodiversity that are sown. Climatic conditions may be a main factor affecting plant development. Whereas the strong winter in China in 2015-2016 may have negatively affected oilseed rape seedlings (***Article 4***), the lack of rain in spring 2013 in Belgium may be responsible for an inequal development of the flower species sown (***Article 6***). As for natural enemies, their abundance may vary from year to year (***Article 6***), independently from the type of habitats, limiting the potential of pest regulation the years enemies are few. Moreover, habitat diversification may favour some of them but not all (***Article 5***), while species among a group of natural enemies may have different behaviour regarding habitat composition and prey/host species (***Article 4***). These examples highlight the uncertainty of the delivery of ecosystem services because they are based on ecological processes and their intrinsic variability. This represents a deep change in regard to conventional practices that mobilise external inputs for guaranteeing reaching an expected goal (e.g. insecticides to control insect pests). It recalls that, as specified in ***Article 1***, the agroecological approach does not promote recipes but tailored-made solutions based on synergies and tradeoffs that must take into account the complexity of a farm in its ecological, social and economic environment. While agroecological farming systems, based on natural regulations, must integrate the variability of ecological processes on the one hand, the possible consequences on biomass production (i.e. the volume produced) must be integrated and anticipated at the economic level on the other hand, through for instance decentralized food systems that involve the diversity of stakeholders.

Combining crops and introducing wildflower strips are two among other practices being considered for enhancing both a bottom-up and a top-down control of insect pests. The findings of the present thesis must be included in the broader scope of spatial diversification of agroecosystems towards biological control of insect pests. Issues on the composition and design of habitats have been addressed in the present work, but their management may be an additional determinant component in the support of natural enemies. Moreover, other practices such as crop rotation, soil tillage, fertilisation or residue management may interact with habitat diversification towards the enhancement of biological pest control. Additionally, whereas experiments in the present thesis were conducted at the field level, scaling-up to the landscape level may be of significant effects because of the high mobility of insects. Finally, insects are not the only pests that trouble farmers, and pests are not the only biotic or abiotic elements of the agroecosystem that needs to be regulated. Therefore, regulating multiple pests on the one hand, and providing multiple regulating services on the other hand, represent challenges for future research. These perspectives are addressed in ***Article 8***.

Article 8

From biological control of insect pests to the provision of multiple ecosystem services: Spatial diversification of crop and non-crop habitats in an agroecological perspective

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Abstract

Spatial diversification of crop and non-crop habitats in farming systems is promising for enhancing natural regulation of insect pests. Nevertheless, results from recent syntheses show variable effects. An explanation is that at the local and landscape scales, composition, design, and management of crop and non-crop habitats are determinant in their effect on pest and natural enemy abundance and diversity. Moreover, interactions between local and landscape scale elements and practices may affect the regulations of insect pest. Hence, research is being conducted for understanding these inter-dependencies. But insects are not the only pests, and pests are not the only elements to regulate in agroecosystems. Broadening the scope would allow addressing multiple issues simultaneously, but also solving them together by enhancing synergies. Indeed, spatial diversification of crop and non-crop habitats can allow addressing the issues of weeds and pathogens, along with being beneficial to several other regulating services like pollination, soil conservation and nutrient cycling. Although calls rise to develop multifunctional landscapes that optimize the delivery of multiple ecosystem services, it still represents a scientific challenge today. Enhancing interdisciplinarity in research institutions and building inter-relations between scientists and stakeholders may help reach this goal. Despite obstacles, positive results from research based on such innovative approaches are encouraging for engaging science in this path. Hence, the aim of the present paper is to offer an update on these issues by reviewing the most recent findings, discuss these results in order to highlight needs for future research.

Keywords: agroecology, conservation biological control, crop diversity, field margin, landscape heterogeneity, natural enemy, interdisciplinarity

1. Introduction

Increasing the environmental sustainability of farming through a reduction of external input uses is a main challenge for today's agriculture. The concept of agroecology proposes to mobilise ecological processes towards the delivery of ecosystem services (Hatt et al., 2016), i.e. the benefits ecosystems can provide to human well-being (Reid et al., 2005). Chemical pesticides are among these external inputs, for which there is ample evidence of their harmful effects on human health (Mostafalou and Abdollahi, 2013) and the environment (Annett et al., 2014; Devine and Furlong, 2007). Moreover, their efficiency faces pest resistance (Heap, 2014; Thieme et al., 2010) and consumers call for healthier food (Howard and Allen, 2010). This is leading to ever tighter regulations on their use (Skevas et al., 2013). Hence, programs have been set by governments of countries in order to reduce pesticide uses (DEFRA, 2013; MAP, 2008). Nevertheless, applying pesticides remains the most common way to protect crops (Hossard et al., 2017), inviting to strengthen efforts at various levels.

One of the propositions put forwards by agroecology hinge on the conception of farming systems less sensitive to pest pressure by mobilising elements of biodiversity (Malézieux, 2012; Nicholls and Altieri, 2004). In agroecosystems, two types of biodiversity are distinguished: (i) the *planned biodiversity* refers to the one deliberately introduced by the farmer such as crop and non-crop biota (e.g. of non-crop biota: linear woody elements, woodlots, linear grassy strips, ungrazed grasslands managed at the farm level, Holland et al., 2016); (ii) the *associated biodiversity* is the one developing in relation with these crop and non-crop biota (e.g. insect herbivores, predators, pollinators) (Altieri, 1999). Both types of biodiversity are intrinsically related. *Functional agro-biodiversity* [not to be confused with the *functional diversity* index used in this thesis] has been defined as "those elements of biodiversity on the scale of agricultural fields or landscapes, which provide ecosystem services that support sustainable agricultural production and can also deliver benefits to the regional and global environment and the public at large" (ELN-FAB, 2012). Functional agrobiodiversity, though ecological processes and functions (e.g. predation, flower visits, mineralisation), allows the provision of regulating services (e.g. pest control, pollination, nutrient cycling), on which depend provisioning services (production of biomass for food, fibre and energy) but also cultural services (e.g. landscape sight, recreation sources) (W. Zhang et al., 2007). Nevertheless, enhancing agro-biodiversity may induce dis-services (e.g. plant competition, crop herbivory). Intensive agriculture optimises the provision of biomass while limiting the occurrence of these dis-services by simplifying and artificializing agroecosystems with the use of external inputs. However, these external inputs also decrease the flow of regulating services (Foley et al., 2005; Robinson and Sutherland, 2002). Hence, the challenge remains in mobilizing functional agro-biodiversity able to provide regulating services for producing resources with fewer external inputs and with a limited provision of dis-services (Power, 2010; W. Zhang et al., 2007).

Pest control is a regulating service delivered by functional agro-biodiversity (W. Zhang et al., 2007). By considering the trophic chain between organisms, two processes leading to the control of insect pests have been described: the top-down and the bottom-up processes (Gurr et al., 2003). The top-down process involves the diversity of natural enemies (i.e. the third trophic level, such as predators and parasitoids) of insect herbivores (i.e. the second trophic level). These natural enemies find in non-crop habitats a shelter against adverse conditions, overwintering sites, floral resources, prey and hosts (Landis et al., 2000). Favouring their presence towards pest control relates to *conservation biological control*, being described as “the use of tactics and approaches that involve the manipulation of the environment (i.e. the habitat) of natural enemies so as to enhance their survival, and/or physiological and behavioural performance, and resulting in enhanced effectiveness” (Barbosa, 1998). The bottom-up process involves the plants on which pests feed (i.e. the first trophic level). The tactic consists in complicating the ability of pests to locate and develop on their host plant. Because pest development is facilitated in homogeneous fields (i.e. *resource concentration hypothesis* of Root, 1973), diversifying cropping areas by mixing crops (i.e. intercropping), crop with non-crop plants (i.e. cover cropping such as rye [*Secale cereal* L.] with cereals) or trees (i.e. agroforestry) have been proposed (Altieri and Nicholls, 2004). Enhancing both a bottom-up and a top-down control of insect pests by spatially diversifying crop and non-crop habitats represents the two first phases proposed by Zehnder et al. (2007) for managing arthropod pests without chemical pesticides in a context of organic farming and is a main component of agroecological crop protection described by Deguine et al. (2016). Although they can be implemented at the farm level, they together induce a diversification at the landscape scale, influencing insects (both pests and natural enemies) that are highly mobile, easily crossing farm borders. Hence, considering the landscape scale, in addition to smaller scales, is determinant for understanding the pest regulation processes and to design pest control strategies (Tscharntke et al., 2005; Zhao et al., 2016).

These last years, studies brought novel knowledge allowing evaluating in which ways spatial diversification of agroecosystems can lead the regulation of insect pests. Efforts have been made in reviewing and synthesising through meta-analyses the numerous studies assessing the effect of spatial diversification at the local and landscape scales on the control of insect pests. Additionally, research has continued addressing specific issues, i.e. how to compose, manage and design crop and non-crop habitats at the local scale, and how managements at the local and landscape scales interact. Hence, the first aim of the present paper is to update our current knowledge by reviewing these recent findings, in order to highlight gaps and propose issues for future research.

Additionally, insects are not the only pests that trouble farmers, and pests are not the only biotic or abiotic elements of the agroecosystem that need to be regulated. Indeed, weeds and pathogens but also soil erosion or nutrient run-offs lead to crop losses (Oerke, 2006). Moreover, pollination is determinant in yield and quality of crops (Bommarco et al., 2012; Holzschuh et al., 2012). Therefore, regulating multiple pests along with favouring the provision of other regulating services is needed. Previous papers addressed this need to develop multi-functional systems (Fiedler et al., 2008; Gurr et al., 2003; Kremen and Miles, 2012; Marshall and Moonen, 2002). Recently, Landis (2017) approached the issue by focussing on levers to trigger at the landscape scale. As studies generally focus on a single regulation (as it is reviewed in the first part of the present paper), our second aim is to address the issue of multi-functional farming systems, in discussing the possible ways to compose, manage and design crop and non-crop habitats towards the provision of multiple regulating ecosystem services. After Landis (2017) who discussed ways to design agricultural landscapes, it is proposed here to address the issues at a more local scale, i.e. habitat composition and management as well as field/farm design.

Finally, such an investment of scientific research is only meaningful if it aims at participating in the development of a more sustainable agriculture. Therefore, our third aim is to address the following question: from the production of knowledge to the implementation of novel practices in fields, how to trigger change?

Because conditions of crop and non-crop habitat diversification are very different between temperate and tropical regions, the present perspectives focus on agricultural systems under temperate climate.

2. Spatial diversification towards biological control of insect pests

2.1 Does spatial diversification at local and landscape scales enhance insect pest regulation?

At the local scale (i.e. field and farm), diversifying plants in space is possible by cultivating several crops (i.e. intercropping), crop with non-crop plants (i.e. cover-cropping), or crop with trees (i.e. agroforestry) simultaneously in the same field, and by implementing non-crop habitats. In a meta-analysis, Letourneau et al. (2011) showed that spatial diversification of both crop and non-crop habitats at the local scale allows reducing insect pests and damages on crops, while increasing natural enemies and yields. More specifically, increasing plant diversity tends to enhance generalist predators, while reducing specialist pests (Dassou and Tixier, 2016). Nevertheless, when focussing on specific practices (summarized in Table 15), the effect of diversification may vary. For instance, in their review, Lopes et al. (2016) showed that diversifying crop habitat through intercropping solely allows significantly reducing pests, while not necessarily enhancing natural enemies, in wheat (*Triticum aestivum* L.)-based systems. Such a bottom-up control of pests was also analysed for cover cropping (Médiène et al., 2011). The success of this bottom up approach (inter and cover-cropping management) on pest reduction can be explained by the creation of chemical and physical barriers by the non-host plants complicating the search of host plants by pests (Poveda et al., 2008). Moreover, the non-significant increase of natural enemies could be explained by the fact that such diversified systems do not necessarily provide stable habitats with non-prey resources needed to numerous natural enemies (Lundgren, 2009a). To enhance such top down approach, habitats can be introduced at the local scale by implementing non-crop areas adjacent to fields. In a recent review, Holland et al. (2016) present the ability of a diversity of non-crop habitats in Europe to enhance conservation biological control. They reported that linear woody (i.e. hedgerows) and grassy strips (i.e. wildflower strips, beetle banks, natural regenerated strips) were those mainly studied, generally supporting natural enemies, with however a variable effect on insect pest reduction in adjacent crops. They also highlighted a lack of knowledge regarding other habitat types, such as woodlots and ungrazed pasture that might not be especially managed for biocontrol purposes, but may be abundant in agricultural landscapes.

At the landscape scale, spatial diversity is considered as the proportion of non-crop area, of natural habitat, of crop or by measuring habitat diversity using indicators such as the Shannon index and the Simpson index. Moreover, the landscape size can vary from small (250 m wide) to large (several km wide) scales (which questions where to situate the frontier between the local and the landscape scale). A meta-analysis based on studies using these indexes and considering various scale sizes, reported an overall enhancement of natural enemies when landscape complexity is increased (Chaplin-Kramer et al., 2011). This same analysis specifically highlighted that, although generalist enemies positively responded to landscape complexity, specialist ones were especially enhanced at a small scale (bellow 1 km). Nevertheless, regarding pest abundance and control, inconsistent results were obtained from different meta-analyses. In fact, Chaplin-Kramer et al. (2011) did not find any response of pests to landscape complexity while Veres et al. (2013) reported a reduction of insect pest abundance, hence an increase of their control within fields when the amount of semi-natural areas increases. Specifically on aphids (Hemiptera: Aphididae), landscape simplification (i.e. an increase proportion of cultivated land) also tends to reduce their natural control (Rusch et al., 2016). Chaplin-Kramer et al. (2011) and Veres et al. (2013) proposed explanations for the variable effects of landscape complexity on insect pests across studies. Despite the resource concentration hypothesis (Root, 1973) stating that an increased proportion of crop land should enhance insect pest abundance, large fields may also favour pest dilution, finally resulting in a reduced abundance in regard to the field size. Moreover, although non-crop habitats can enhance natural enemies and in turn pests control, landscape complexity may also complicate their search for prey or hosts. Furthermore, the use of insecticides in fields may vary across the landscape and interfere with the effect of landscape complexity by reducing pest abundance in simplified landscapes. Indeed, a positive correlation between simplified landscapes and insecticide uses was reported (Meehan et al., 2011).

The proportion of crop and non-crop areas remains the main index for measuring landscape complexity. Some studies also consider habitat diversity, assigning functions to these specific areas for insects. This refers to the *compositional heterogeneity*, that can be complemented by the *configurational heterogeneity* which evaluates the arrangement of the various types of habitats within a landscape (Fahrig et al., 2011).

Table 15. Types of crop and non-crop habitats with their functions and specificities (i.e. composition and/or management) in regards to control of insect pests.

Habitat	Type	Functions for pest control	Specificities	References
Crop habitat				
Mixing cultivated crops	Intercropping	Complicating the search of host plant for pests	Multiple crop species hosting different pests	Lopes et al., 2015; Ndzana et al., 2014
	Variety mixture	Complicating the search of host plant for pests	Multiple variety of a given species with different sensitivity to their pests	Grettenberger and Tooker, 2017
Mixing cultivated crops and trees	Agroforestry	Complicating the search of host plant for pests	Usually not managed for enhancing pest control	Muhammad et al., 2005; Stamps et al., 2009
Mixing cultivated crops and non-crops	Cover crop	Complicating the search of host plant for pests	Non-host species, usually not harvested	Dunbar et al., 2016; Irvin et al., 2016
Non-crop habitat				
Herbaceous strip	Wildflower strip	Support of flower visiting natural enemies	Rich in flowering species	Balzan et al., 2016a; Hatt et al., 2017b; Tschumi et al., 2016b
	Beetle bank	Support ground dwelling natural enemies	Vegetation structure through selected grassy species	MacLeod et al., 2004; Woodcock et al., 2008
	Natural regenerated strip	Support ground dwelling natural enemies	Herbaceous margin at low price	Rouabah et al., 2015
Herbaceous patch	Grassland, fallow	Support flower visiting and ground dwelling natural enemies	Usually not managed for enhancing pest control	Werling et al., 2014
Woody strip	Hedgerow	Support flower visiting and ground dwelling natural enemies	Multiple habitat types (tree, shrub, grass)	Dainese et al., 2017; Morandin et al., 2014
Woody patch	Woodlot	Support flower visiting and ground dwelling natural enemies	Usually not managed for enhancing pest control	Bianchi et al., 2008; Gonzáles et al., 2017

Fahrig et al. (2015) reported that between landscapes having a similar proportion of non-crop habitats, those with a higher configurational heterogeneity support a higher abundance and diversity of animal species in crop fields, among which natural enemies of insect pests. A high configurational heterogeneity increases the proportion of non-crop cover at field margins, producing long interfaces between crop and non-crop areas. Such interfaces allow natural enemies that overwinter in non-crop habitats to migrate into crops (Macfadyen et al., 2015). Nevertheless, non-crop areas can also favour pest colonization (discussed by Tscharntke et al., 2016), thus the effect of a high configurational heterogeneity on pest control remains to be assessed.

Results reviewed from these studies at both local and landscape scales show that on the one hand spatial diversification of crop and non-crop habitats can reduce insect pest abundance, but on the other hand, several factors may intervene creating variability in pest control. Therefore, research currently focus on the effect on pest control of (i) the composition and design crop and non-crop habitats, and (ii) the management of crop and non-crop habitats at both – and between – the local and landscape scales.

2.2 How composing and designing crop and non-crop habitats to enhance insect pest regulation?

Five hypotheses have been proposed to explain why the introduction of non-crop habitats may not lead to pest control in adjacent crops (Tscharntke et al., 2016). One of them is that non-crop habitats are inappropriate in composition, or configuration to provide large enough enemy populations needed for pest control. The effect of the non-crop habitat composition on insect pest control has been assessed by distinguishing the specific diversity on the one hand, the functional diversity on the other hand, of such habitats. Regarding herbaceous strips (one of the most studied non-crop habitats at the local scale, Holland et al., 2016), the ultimate aim is to constitute attractive flower mixtures able to support natural enemy needs. On the one hand, the *pick and mix approach* (Wäckers and Van Rijn, 2012) focuses on the specific diversity by assessing the effect of a diversity of flower species on natural enemies. Recent field-based experiments highlight the ability of these specific flower mixtures to enhance insect pest control and reduce crop damages in the adjacent crops, as compared to the generic flower mixture often proposed in the framework of agri-environmental policies for biodiversity conservation purpose (targeted pests were aphids on potato [*Solanum tuberosum*

L.] and leaf beetles [Coleoptera: Chrysomelidae] on winter wheat, Tschumi et al., 2016b, 2015 respectively). On the other hand, the *functional diversity approach* has been considered, with the hypothesis that mixtures with high functional diversity (i.e. constituted with flower species presenting different values for their traits, Lavorel et al., 2008) support a high diversity of natural enemies. Indeed, different natural enemies are sensitive to different values of traits (e.g. colour, nectar and pollen availability, flowering time and duration, flower volatiles) (Campbell et al., 2010; Fiedler and Landis, 2007b; Wäckers, 2004). Nevertheless, recent findings did not confirm this hypothesis (Balzan et al., 2016a; Hatt et al., 2017b). A reason is that some attractive species present in the mixtures may have overwhelmed the effect of functional diversity. Hence, introducing such attractive flower species in the strips could be efficient, meeting the pick and mix approach.

Hedgerows are another type of non-crop habitats. Their interest for supporting natural enemies has been mainly studied in orchards. Nevertheless their ability of enhancing biological pest control has been rarely assessed (Holland et al., 2016). Still, Morandin et al. (2014) reported an increased abundance of parasitoids and a reduced density of a diversity of pests (i.e. aphids, flea beetles [Coleoptera: Chrysomelidae], weevils [Coleoptera: Curculionoidea] and bugs [Hemiptera: Miridae, Pentatomidae]) in adjacent tomato (*Solanum lycopersicum* L.) fields. Similar assessment in field crops is needed. The potential of hedgerows to support natural enemies may come from the presence of flowering shrub and herbaceous species (Landis et al., 2000). On the one hand, there is a lack of knowledge on the effect of a variety of tree species on natural enemies and pest control to our knowledge. On the other hand, as the flowering cover often associated with hedgerows may be determinant (Morandin and Kremen, 2013), the advances in the composition of flower mixtures for enhancing pest control presented before may be applied to hedgerow habitats too.

The choice of flower species to compose mixtures must also be based on the optimal time lag between flower appearance, crop growth and insect pest occurrence. In a rotation scheme where crops – thus insect pests – change within and between growing seasons, sowing annual species mixtures presents the advantage of choosing species able to support the natural enemies of the targeted insect pests. For instance to regulate aphids, annual flower species from Asteraceae (e.g. *Centaurea cyanus* Hill, *Calendula arvensis* M.Bieb.) and Apiaceae (e.g. *Coriandrum sativum* L., *Daucus carota* L.) families are often considered because they are known to be visited by some of their natural enemies, among others hoverflies (Diptera: Syrphidae), ladybeetles (Coleoptera: Coccinellidae) and parasitoids (Hymenoptera:

Braconidae; Aphelinidae) (Campbell et al., 2012; Martínez-Uña et al., 2013; Wäckers and Van Rijn, 2012). However, the implementation of perennial species strips could also provide benefits, notably offering over-wintering sites to natural enemies and favouring their presence at the early stage of insect pest colonisation. Nevertheless, perennial mixtures must allow enhancing a broad variety of natural enemies, able to control the diversity of pests that will follow the rotating crops. The issue for future research is to identify perennial flowers able to support a diversity of natural enemies and conduct field-based research following a whole rotation cycle.

The arrangement between crop and non-crop habitats, but also the cropping design itself in the case of intercropping, may be determinant in the enhancement of biological control. Wildflower strips and hedgerows are often introduced at existing field margins, but could also be set within fields, resulting in dividing large fields into smaller parcels and increasing configurational heterogeneity. Successions of wheat crops and wildflower strips or trees, compared to sole wheat, was reported to reduce aphid abundance and support aphidophagous hoverflies and parasitism rate (Hatt et al., 2017a; Muhammad et al., 2005, respectively). As for intercropping, various design exist (Andrews and Kassam, 1976). In wheat-based systems, strip intercropping generally better favours pest reduction and natural enemy support than mixed or relay intercropping (Lopes et al., 2016).

These findings show that studies on spatial diversification must be accompanied by an assessment of their composition and design in term of space, but also temporality, in order to propose systems that indeed enhance biological control (Figure 18).

2.3 How managing crop and non-crop habitats to enhance insect pest regulation?

The management of habitats may also affect the ability of supporting natural enemies and enhancing pest control. Mowing of flowering strips (followed by the removal of the biomass) for instance is needed to maintain a diversity of plant species (Pfiffner and Wyss, 2004). Nevertheless, it also disturbs the habitats for insects. A reduced mowing frequency (i.e. once a year) has thus been recommended (Horton et al., 2003). Moreover, only the half of the strip width could be mown every year in order to permanently keep a vegetated area. This practice is required in the case of the *improved field margins* measure of the Swiss agri-environmental policy (Jacot et al., 2007). Nevertheless, the presence of unwanted weeds remains an issue for farmers, who often spray herbicides locally to destroy them (Haaland et al., 2011). Exploring in which way mowing regime may help reducing the occurrence of such weeds is needed. Similar issues exist for hedgerows, for which branches are cut for maintaining the aligned habitat, but where the way they are cut affects the hedge structure and finally the insect populations living in trees. Practices maintaining a significant leaf biomass on trees (e.g. hedgelaying avoiding circular saw) were reported to favour invertebrate abundance (i.e. predators but also herbivores) (Amy et al., 2015). It remains to assess whether such a management also enhances insect pest control in the adjacent crops.

The way farmers manage habitats in their farms necessarily affects the landscape complexity. Thus, it is needed to understand the existing interactions between local and landscape managements on natural enemies and insect pest control. According to the *intermediate landscape hypothesis*, introducing and managing non-crop habitats at the local scale will be more effective in enhancing biodiversity and ecosystem processes in simple landscape, compared to simple or complex ones. Indeed, "in cleared [i.e. simple] landscapes, the very few species are not a sufficient basis to result in a recognizable response to management changes [and] in complex landscapes, management does not result in a significant effect, because biodiversity is high everywhere" (Tscharntke et al., 2005). This hypothesis was confirmed in the case of wildflower strips sown at field margins for enhancing the parasitism of *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) and aphids on oilseed rape (*Brassica napus* L.) (Jonsson et al., 2015). Nevertheless, high plant diversity in wildflower strips along with a complex landscape was found to increase natural enemy diversity and reduce damages from Lepidoptera on tomato crops (Balzan et al., 2016b). Conversely, no interaction between the presence of wildflower strips and landscape complexity was found on ladybeetle abundance and aphid control in soybean (*Glycine max* (L.) Merr.) fields (Woltz et al., 2012). Finally, Sarthou et al. (2014) observed that the local habitat structure (especially of grass strips), rather than landscape complexity, affects abundance of a diversity of natural enemies at emergence (i.e. after overwintering period) while Dainese et al. (2017) reported that the increased cover of hedgerows at the landscape scale increased aphid parasitism independently from margin diversity at the local scale. This variability of results in the interaction between local and landscape scales may be explained by the diversity of natural enemies, pests and crops studied. Further research continuing evaluating the possible interactions of non-crop habitat management between local and landscape scale is needed in order to assess whether general trends could finally be drawn or if the local context will remain determinant. Performing a meta-analysis though the existing body of literature would also be particularly useful by quantify trends.

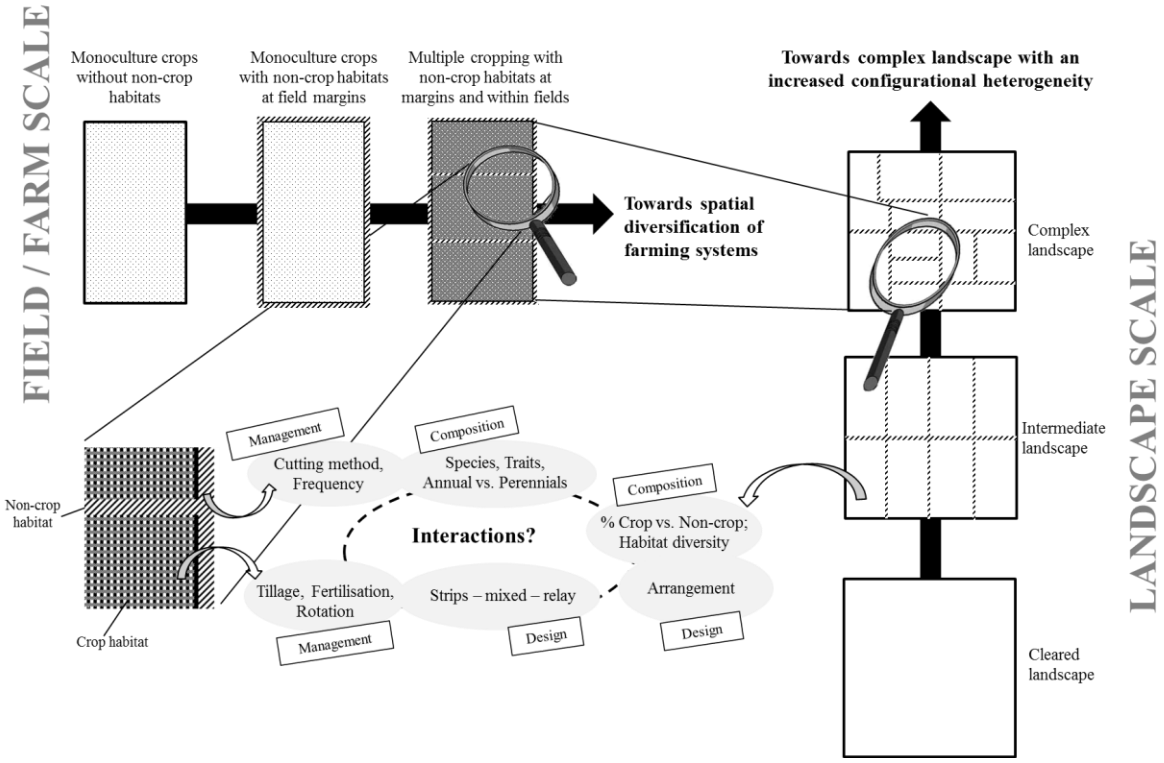

Figure 18. Current issues regarding the impact of diversification of crop and non-crop habitats on pest control: (1) composition, design, and management of the habitats at the local and landscape scales and (2) the interactions between these scales.

Interactions between crop habitat management and landscape complexity on biological control of insect pests have also drawn attention these last years. Reduced tillage at large scale for instance, in addition to a high landscape complexity, was found to enhance parasitism of pollen beetles (Coleoptera: Nitidulidae: *Meligethes aeneus* Fabricius) in oilseed rape fields (Rusch et al., 2011). Additionally, reduced tillage can mitigate the detrimental effect of landscape simplification on predation and parasitism of cereal aphids (Tamburini et al., 2016). Indeed, it is assumed that conventional tillage is harmful to ground-dwelling predators and parasitoids that overwinter into the soil (Nilsson, 2010; Soane et al., 2012). The impact of fertilisation management, on pest control, also depends on the surrounding landscape complexity. Fertilisation can indeed affect crop health, with a too low or an excessive provisioning of nitrogen weakening plants (Altieri and Nicholls, 2003). Rusch et al. (2013b) reported on oilseed rape crops that the amount of damaged buds by pollen beetles was negatively related to the nitrogen index and positively correlated with the proportion of non-crop habitats. However in this same study, the abundance of pollen beetles was not determined by the crop nitrogen status, but only by landscape complexity. Finally, crop rotation, that allows reducing pest pressure on crops by disrupting the presence of host plants through time (Oerke, 2006), was found to not interact with landscape complexity on cereal aphid parasitism (Rusch et al., 2013a).

As strong interactions are observed between the management of crop and non-crop habitats and the different scales, additional studies following this vein of research are needed. However, these results already indicate that multiple agronomic and ecological factors at various scales must be considered simultaneously. Such comprehensive approach in the study of agroecosystems would imply broadening the scope of insect pest control, towards the regulation of various pests simultaneously and the delivery of multiple ecosystem services.

3. From insect pest control to multiple ecosystem services

3.1 Towards natural regulation of multiple pests

In addition to insect pest control, managing crop and non-crop habitats may allow enhancing natural regulations of weeds and pathogens that are also commonly controlled by using chemical pesticides (Figure 19). With regards to weed control, crop area management such as cover crops leads to substitute unwanted weeds by a manageable plant species (Médiène et al., 2011). To do so, the cover crop must be sown in order to develop earlier than weeds, hence competing for resources and reducing the ability of weeds to grow. Positive results on reducing weed biomass have been reported, even if a negative effect on the main crop yield can also occur (Anderson, 2016; Pfeiffer et al., 2016). When the cover crop is a legume, a recent meta-analysis shows that the main crop yield is generally increased (thanks to the ability of legumes to fix and make available the nitrogen for the neighbouring plants) while weed biomass is decreased (Verret et al., 2017). By reducing insect pest abundance on the one hand and weeds on the other hand, cover cropping may provide a double benefit. However, assessment of such multiple benefits is still lacking. Likewise, non-crop habitats could also be involved for controlling weeds (Petit et al., 2011). Indeed, some natural enemies of insect pests enhanced by semi-natural habitats are also predators of weed seeds, e.g. the majority of carabid (Coleoptera: Carabidae) species (Lundgren, 2009a). Even if omnivorous carabids may prefer seeds rather than prey when both are available (Frank et al., 2011), enhancing their survival and activity may allow reducing both insect and weed pests. Beetle banks (i.e. a type of herbaceous strip) can be introduced in order to support carabids (MacLeod et al., 2004). Evaluating the effect of beetle banks on both insect and weed pests would be useful to identify potential synergies. Moreover, beetle banks could benefit other natural enemies. Particular attention has been devoted to the structure of beetle bank vegetation (large carabid species prefer dense but homogeneous vegetation (Brose, 2003) while smaller ones are positively correlated with heterogeneous vegetation (Rouabah et al., 2015)) but little is known about the benefits they may offer to natural enemies visiting flowers (Ramsden et al., 2015). Hence, a challenge would be to conceive herbaceous strips that optimise both the structure of the vegetation and the provision of flower resources, i.e. mixing the benefits of beetle banks and wildflower strips, in order to support ground dwelling predators along with flower visiting natural enemies, able together to reduce both weed seeds and insect pests.

For pathogens such as fungi, bacteria or viruses, landscape composition and heterogeneity can play a determinant role in their dispersion. Indeed, pathogens are vector-, soil- , or air-borne, thus landscape elements act as corridors or conversely as barriers (Plantegenest et al., 2007). At the local scale, Mundt et al. (2007) reported that, whatever the field size, mixing host and non-host plants (i.e. inter- or cover cropping) allows limiting the dispersion of the fungi *Puccinia striiformis* responsible for the strip rust on wheat. At the landscape scale, the importance of mixed cropping for limiting disease spread was confirmed through modelling (Skelsey et al., 2010). Moreover mixed cropping, by limiting the abundance of insect pests on crops, could be mobilised to control viruses hosted by insects (e.g. aphids, Katis et al., 2007). Nevertheless to our knowledge, little is known on the effect of intercropping on virus dispersion. As for non-crop habitats, by potentially enhancing top-down predation and parasitism through natural enemies, their implementation could result in a reduction of damages by viruses. However, anti-predation/parasitism behaviour of prey/hosts (e.g. flying, walking away, dropping from plant), leading to insect pest dispersion, could also favour virus spread. To this dilemma, Dáder et al. (2012) reported a temporal tradeoff: in the case of the aphid *Aphis gossypii* (Glover) facing parasitism, whereas the parasitoid *Aphidius colemani* Viereck (Heminoptera: Braconidae) favoured the dispersion of the *Cucumber mosaic virus* (CMV) and the *Cucurbit aphid-borne yellow virus* (CABYV) on the short-term, virus incidence was reduced by the control of aphid abundance on the long term. At the landscape scale, while spatial simplification tends to reduce natural enemies and pest control of aphids (Rusch et al., 2016), Claflin et al. (2016) reported that it also favours the prevalence of the

Potato virus Y (PVY) on potato crops. This last result is promising and needs future studies for confirming the interest of landscape complexity in limiting virus spread.

3.2 Towards the provision of multiple ecosystem services

In addition to enhancing the regulation a multiple pests, spatial diversification of crop and non-crop habitats may increase the provision of additional ecosystem services (Figure 19). This call for multi-functional landscapes is not new but still represents a scientific challenge (Fiedler et al., 2008; Gurr et al., 2003; Kremen and Miles, 2012; Marshall and Moonen, 2002). For instance, flowering habitats can support flower visiting natural enemies on the one hand, but also pollinators on the other hand (Blaauw and Isaacs, 2014; Nicholls and Altieri, 2013). In order to benefit both of them, flower mixtures should be adapted to the different ability of insects to feed on flower resources. Campbell et al. (2012) showed that mixtures with both long and short corolla flowers allow supporting parasitoids, hoverflies and bumble bees (Hymenoptera: Apidae: *Bombus spp.*) together, whereas parasitoids did not visit long corolla flowers and bumble bees were absent from short corolla ones. Nevertheless, Balzan et al. (2016a, 2014) did not obtain an increased diversity of both flower visiting natural enemies and pollinators with such a mixture, recalling that a high functional diversity at the mixture level does not necessarily enhance insect diversity. At the landscape scale however, the increased density of flowering features such as hedgerows showed a positive effect on pest control by parasitoids and pollination (Dainese et al., 2017). Moreover, herbaceous and woody linear habitats could also reduce soil erosion and nutrient run-offs (Borin et al., 2010). Nevertheless, buffer strips composed of only grassy species represent little interest for flower visitors, even if they can benefit ground dwelling predators (Josefsson et al., 2013). Cole et al. (2015) reported that buffer strips rich in flowering species benefit pollinators in addition to reduce erosion and runoffs. Hence, similar assessment on flower visiting natural enemies and pest control in adjacent fields is needed. Within fields, contour farming consists in sowing successively in space crops and grass strips in order to reduce soil erosion and nutrient run-offs (Panagos et al., 2015; Stevens et al., 2009). Managing these lasts for providing flower resources may allow supporting flower visitors. Moreover, intercropping that provides benefits towards pest control, can lead to an increase of nitrogen and carbon in soils when leguminous plants are combined with cereals, potentially favouring soil fertility and reducing nutrient runoffs with less fertiliser applications (Bedoussac et al., 2015; Cong et al., 2014). As for agroforestry system, a recent meta-analysis shows that the introduction of trees generally reduce soil erosion, increase soil fertility and nutrient cycling as well as biodiversity (Torralba et al., 2016). Nevertheless, the type of biodiversity, hence the functions it can exert, was not specified.

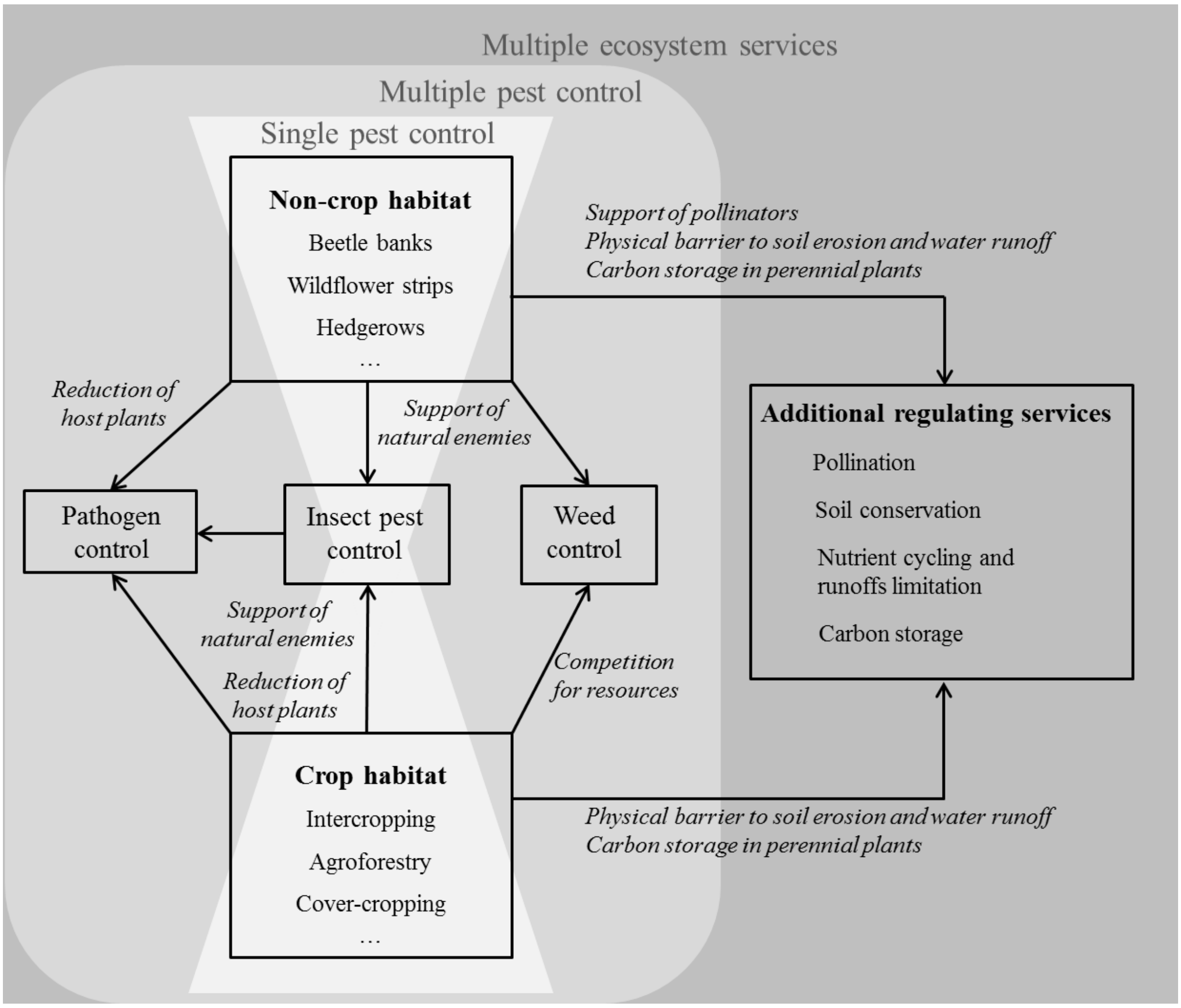

Figure 19. From the regulation of a single type of pest towards the delivery of multiple ecosystem services through the spatial diversification of crop and non-crop habitats. The processes involved are indicated in italics.

These results show that the composition, design and/or management of crop and non-crop habitats are determinant in the delivery multiple ecosystem services. Because certain habitat characteristics may optimize the production of one service, tradeoffs may occur when multi-functionality becomes the objective (Power, 2010). Nevertheless, synergies also exist. For instance, as mentioned here-before, controlling insect pests can allow reducing pathogens when the former is the vector of the later. Also, a well nutrient-balanced soil tends to reinforce plant health, hence their ability of resisting to pests (Altieri and Nicholls, 2003). Lundin et al. (2013) moreover observed a positive interaction between pollination and pest control resulting in an increased yield. These examples of synergies should encourage the implementation of multi-functional landscapes in an agroecological perspective (Figure 19). Nevertheless, field and farm-based evidence is still lacking and conducting such experiments may represent a methodological challenge. Crossing disciplinary barriers, as well as the doors of research institutions may help taking it up.

3.3 From theory to implementation, how triggering change?

At the farm level, farmers are the only managers of crop and non-crop areas. As recalled before, there is evidence that multiple cropping and the introduction of non-crop habitats can enhance the natural regulation of pests. Nevertheless, there is a variability of results among studies maintaining uncertainties, potentially explaining that implementations in farmers' fields remain rare. Indeed many farmers do not have high confidence in such pest control strategies compared to chemical treatments. For instance, in the case of flowering strips, few farmers who manage flowering borders for insect conservation in the framework of agri-environmental schemes acknowledge that these habitats can enhance biological pest control (assumption based on 18 interviews performed in Belgium in 2015, unpublished data). Although being informed of the potential benefits may be a first step to think changes, self-experiencing is known to be determinant in a transition process (Sutherland et al., 2012).

Brédart and Stassart (2017) recently reviewed the current theories used to analyse changes in farmers' practices. Transition has been described as being a succession of steps (i.e. the “triggering change cycle” of Sutherland et al. 2012), with different levels of risks (i.e. robust vs. reversible transitions, Lamine, 2011) related to gradual levels of changes (i.e. Efficiency/Substitution/Redesign framework of Hill and MacRae, 1996). Spatial diversification for enhancing the natural regulation of pests may be the final stage of a “quite slowly and step-by-step” process of changes (Lamine, 2011). The author described for instance the successive changes of a particular farmer as following: first resistant varieties were adopted and the doses of pesticides were reduced, then date of crop sowing was changed, sowing density as well as fertilizer amount were lowered, and at the latest hedges and buffer zones were created leading to a reduction of plot sizes. Spatial diversification may also be the result of changes which primarily did not aim at reducing the use of pesticides.

Vankeerberghen and Stassart (2016) for instance reported the trajectory of farmers for whom questioning soil ploughing pushed to a general reconsideration of biodiversity at the farm level, materialised by the introduction of diversified cover-crops, leading finally to a reduction of pesticide uses. It highlights the way farmers experience the potential interactions between different practices and the multiple services a single change can provide (Figure 19). Studies reporting farmer's trajectories of change show that such a succession is often not planned in advance, but rather a non-linear process with potential returns to previous stages, as well as abrupt changes of directions (Brédart and Stassart, 2017).

Farmers can innovate and engage changes individually. Nevertheless, they also often take part in farmer unions which facilitate exchanges of information. Working groups – linked or not to farmer unions – can also be organised, where farmers meet for collectively addressing an issue. According to Brédart and Stassart (2017), such working groups help farmers to "identify the levers of action that each farmer could adjust, change, and take over in the specific context of his farm". Moreover, the group may strengthen farmers in their choice and help them to confront the pressure of a professional environment that is often sceptical to changes. Reducing pesticide uses may for instance need a collective change of the conception of what is good farming, the objectives to reach and the indicators used (e.g. considering gross margin instead of absolute yield) (Lamine, 2011). Collective organisations may also attract external experts from various types of institutions (e.g. universities, non-profit organisations, governmental institutions) who bring additional knowledge and advices. Such an opening of the group may even be determinant in its ability to reach its objectives (Dolinska and d'Aquino, 2016). Indeed, farmer's activities are intrinsically linked to others such as those related to processing, marketing, distribution and consumption, but also for instance to biodiversity conservation, water provisioning, inhabiting, which make complex any process of changes (i.e. *lock-ins* theory, Vanloqueren and Baret, 2008).

In this context, inter-relations between scientists and farmers have been encouraged (MacMillan and Benton, 2014) and conceptualised by scientists as *participatory approaches* (also called transdisciplinarity, collaborative, iterative, action research, Cerf, 2011; Méndez et al., 2013). While farmers experiment, observe and evaluate innovations themselves and progressively engage into the transition process individually and collectively, interactions with scientists allow these lasts to consider farmer's constraints and opportunities as well as wishes and objectives in their studies. Such approach, based on theories and practical experiences, creates a novel type of knowledge that incorporates farmer's constraints.

Moreover, scientists may accompany farmers in their interactions with the other stakeholders. Role-playing games could for instance be used to make stakeholders realise the issues and initiate collective management (such as in Souchère et al., 2010 in the case of run-off management at the landscape level). More generally, workshop meetings and field visits with stakeholders, including researchers, would allow on-site observations and group discussions, to finally build scenarios (Geertsema et al., 2016). Despite a rising interest for participatory approaches, they still represent a challenge for scientists and stakeholders as it asks to use methodologies that change current research practices and would disrupt entrenched farmer's and stakeholder's habits (Cerf, 2011). Scientists especially would need to broaden their research scope. Indeed, the economic, social and political dimensions fully intervene in farmer decision-making (Cullen et al., 2008; Griffiths et al., 2008), in addition to the ecological and agronomic issues that are multiple and inter-dependant (Doré et al., 2011). Therefore, enhancing interdisciplinarity (i.e. practices that involve several unrelated disciplines, each with its own contrasting paradigm, Baveye et al., 2014) at the academic level is essential for addressing complex issues related to agricultural sustainability.

Some successful projects, in both tropical and temperate climate countries, addressing spatial diversification for pest management are encouraging. For instance, in several Southeast Asian countries, flowering strips were introduced at rice (*Oryza sativa* L.)-field boarders to enhance rice pest natural enemies. Field schools were organised to allow farmers and researchers to interact while mass media and entertainment programs were involved to spread information (Westphal et al., 2015). In The Netherlands, the management of already existing ecological landscape elements in the Hoeksche Waard region was adapted so that they also enhance pest control in adjacent fields. While scientists brought knowledge on the effect of semi-natural habitats on natural enemies and pest control, stakeholders (i.e. farmers, nature and landscape conservationists, water managers, and politicians) worked together in order to build strategies with compromises that meet everyone's interests (Steingröver et al., 2010). Whereas the power of pressure groups or lobbies with narrow interests is often accused to prevent transitions towards sustainability (Vanloqueren and Baret, 2009), it is in the core of participatory approaches to enhance a "democratic process […] in the pursuit of practical solutions to issues of pressing concerns for people, and more generally the flourishing of individual persons and their communities" (Reason and Bradbury, 2001). Hence, participatory approach may be a promising way to trigger changes.

Table 16. Summary of future research needs towards the enhancement of biological control of insect pests, the simultaneous regulation of multiple pests and the provision of multiple ecosystem services through the spatial diversification of crop and non-crop habitats.

Practice	Object to study	Research questions
Towards biological control of insect pests		
Sowing wildflower strips	Composition	Which perennial flower species would allow supporting the diversity of natural enemies able to control the diversity of pests that occur over a whole rotation cycle?
	Management	Can mowing regime help reducing the occurrence of unwanted weeds in mixtures?
Planting hedgerows	Composition	Which tree species are able to support natural enemies and enhance insect pest control in adjacent fields?
	Design	What is the effect of planting hedgerows on insect pest control of adjacent field crops?
	Management	Which cutting regime of trees does favour insect pest control in adjacent crops?
Introducing non-crop habitats at the landscape scale	Design	Does a high configurational heterogeneity of landscape enhance insect pest control?
Towards the simultaneous regulation of multiple pests		
Cover cropping	Composition, Design, Management	Can cover cropping reduce both weeds and insect pests simultaneously?
Sowing beetle banks	Composition, Design, Management	Would the enhancement of carabids lead to the control of both weeds and insect pests?
	Composition	Could flowering species be introduced in beetle banks for enhancing both carabids and flower visiting natural enemies?
Intercropping	Composition, Design, Management	Can intercropping allow the control of both pathogens and insect pests by limiting the spread of diseases, but also virus vectors?
Towards the provision of multiple ecosystem services		
Sowing wildflower strips	Composition	How composing mixtures that enhance both natural enemies and pollinators?
Sowing buffer strips	Composition, Design, Management	Could buffer strip both support natural enemies and limit nutrient run-offs as well as soil erosion?
Contour farming	Composition, Design, Management	Could contour farming both support natural enemies, pollinators and limit nutrient run-offs as well as soil erosion?
Agroforestry	Composition, Design, Management	Could agroforestry both support natural enemies, pollinators and limit nutrient run-offs as well as soil erosion?

4. Conclusion

There is ample evidence that spatial diversification of crop and non-crop habitats at both the local and landscape scales can enhance natural regulations of insect pest. Nevertheless, an increased control of insect pests may not be systematic as it may depend on the composition, design and management of crop and non-crop habitats, as well as interactions between local and landscape scale practices. Strengthening efforts to better understand these interactions and the related variability of the regulations provided is thus needed (Table 16). But insects are not the only pests and spatial diversification could be beneficial regarding other services. Hence, addressing regulation processes with a global approach would allow mobilising existing synergies towards multiple benefits (Table 16). In this context, broadening the scopes of research is needed to trigger transition in fields but represent challenges that can be addressed by enhancing interdisciplinarity in research institutions, and inter-relations between scientists, farmers and other stakeholders in territories. Considering such an entanglement of processes is the approach proposed by agroecology towards a sustainable agriculture.

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References

Adedipe, F., Park, Y.-L., 2010. Visual and olfactory preference of Harmonia axyridis (Coleoptera: Coccinellidae) adults to various companion plants. Journal of Asia-Pacific Entomology 13, 316–323. doi:10.1016/j.aspen.2010.07.004

Alhmedi, A., Haubruge, E., Bodson, B., Francis, F., 2006. Inter- and intra-guild interactions related to aphids in nettle (Urtica dioica L.) strips closed to field crops. Communications in Agricultural and Applied Biological Sciences 71, 413–423.

Alhmedi, A., Haubruge, E., D'Hoedt, S., Francis, F., 2011. Quantitative food webs of herbivore and related beneficial community in non-crop and crop habitats. Biological Control 58, 103–112. doi:10.1016/j.biocontrol.2011.04.005

Alhmedi, A., Haubruge, E., Francis, F., 2009. Effect of stinging nettle habitats on aphidophagous predators and parasitoids in wheat and green pea fields with special attention to the invader Harmonia axyridis Pallas (Coleoptera: Coccinellidae). Entomological Science 12, 349–358. doi:10.1111/j.1479-8298.2009.00342.x

Almohamad, R., Verheggen, F., Haubruge, É., 2009. Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. Biotechnology, Agronomy, Society, Environment 13, 467–481.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems & Environment 74, 19–31. doi:10.1016/S0167-8809(99)00028-6

Altieri, M.A., Nicholls, C.I., 2004. Biodiversity and pest management in agroecosystems, 2nd ed. Haworth Press, New York, USA.

Altieri, M.A., Nicholls, C.I., 2003. Soil fertility management and insect pests: harmonizing soil and plant health in agroecosystems. Soil and Tillage Research 72, 203–211. doi:10.1016/S0167-1987(03)00089-8

Altieri, M.A., Rosset, P., 1996. Agroecology and the conversion of large-scale conventional systems to sustainable management. International Journal of Environmental Studies 50, 165–185. doi:10.1080/00207239608711055

Amy, S.R., Heard, M.S., Hartley, S.E., George, C.T., Pywell, R.F., Staley, J.T., 2015. Hedgerow rejuvenation management affects invertebrate communities through changes to habitat structure. Basic and Applied Ecology 16, 443–451. doi:10.1016/j.baae.2015.04.002

Anderson, R.L., 2016. Suppressing weed growth after wheat harvest with underseeded red clover in organic farming. Renewable Agriculture and Food Systems 31, 185–190. doi:10.1017/S1742170515000022

Andow, D.A., 1991. Vegetational diversity and arthropod population response. Annual Review of Entomology 36, 561–586. doi:10.1146/annurev.en.36.010191.003021

Andrews, D.J., Kassam, A.H., 1976. The importance of multiple cropping in increasing world food supplies, in: Papendick, R.I., Sanchez, P.A., Triplett, G.B. (Eds.), Multiple Cropping, ASA Special Publication. Madison, WI, USA, pp. 1–10.

Anil, L., Park, J., Phipps, R.H., Miller, F.A., 1998. Temperate intercropping of cereals for forage: a review of the potential for growth and utilization with particular reference to the UK. Grass and Forage Science 53, 301–317. doi:10.1046/j.1365-2494.1998.00144.x

Annett, R., Habibi, H.R., Hontela, A., 2014. Impact of glyphosate and glyphosate-based herbicides on the freshwater environment. Journal of Applied Toxicology 34, 458 – 479. doi:10.1002/jat.2997

Ansari, N.A., Mishra, V.A., Madhvi, P., Srivastava, G.P., Tewari, J.P., 2007. Role of intercropping on population build-up of Lipaphis pseudobrassicae (L.) on mustard. Flora and Fauna 13, 41–42.

Arias-Estévez, M., López-Periago, E., Martínez-Carballo, E., ́Simal-Gándara, J., Mejuto, J.-C., García-Río, L., 2008. The mobility and degradation of pesticides in soils and the pollution of groundwater resources. Agriculture, Ecosystems & Environment 123, 247–260. doi:10.1016/j.agee.2007.07.011

Ashwood, L., Harden, N., Bell, M.M., Bland, W., 2014. Linked and situated: grounded knowledge. Rural Sociol 79, 427–452. doi:10.1111/ruso.12042

Aziz, M., Mahmood, A., Asif, M., Ali, A., 2015. Wheat-based intercropping: a review. The Journal of Animal & Plant Sciences 25, 896–907.

Baines, M., Hambler, C., Johnson, P.J., Macdonald, D.W., Smith, H., 1998. The effects of arable field margin management on the abundance and species richness of Araneae (spiders). Ecography 21, 74–86. doi:10.1111/j.1600-0587.1998.tb00395.x

Baldi, I., Cordier, S., Coumoul, X., Elbaz, A., Gamet-Payrastre, L., Le Bailly, P., Multigner, L., Rahmani, R., Spinosi, J., Van Maele-Fabry, G., 2013. Pesticides: effets sur la santé. INSERM, Institut national de la santé et de la recherche médicale, Paris.

Balmer, O., Géneau, C.E., Belz, E., Weishaupt, B., Förderer, G., Moos, S., Ditner, N., Juric, I., Luka, H., 2014. Wildflower companion plants increase pest parasitation and yield in cabbage fields: Experimental demonstration and call for caution. Biological Control 76, 19–27. doi:10.1016/j.biocontrol.2014.04.008

Balzan, M.V., Bocci, G., Moonen, A.-C., 2016a. Utilisation of plant functional diversity in wildflower strips for the delivery of multiple agroecosystem services. Entomologia Experimentalis et Applicata 158, 319. doi:10.1111/eea.12403

Balzan, M.V., Bocci, G., Moonen, A.-C., 2016b. Landscape complexity and field margin vegetation diversity enhance natural enemies and reduce herbivory by Lepidoptera pests on tomato crop. BioControl 61, 141–154. doi:10.1007/s10526-015-9711-2

Balzan, M.V., Bocci, G., Moonen, A.-C., 2014. Augmenting flower trait diversity in wildflower strips to optimise the conservation of arthropod functional groups for multiple agroecosystem services. Journal of Insect Conservation 18, 713–728. doi:10.1007/s10841-014-9680-2

Balzan, M.V., Moonen, A.-C., 2014. Field margin vegetation enhances biological control and crop damage suppression from multiple pests in organic tomato fields. Entomol Exp Appl 150, 45–65. doi:10.1111/eea.12142

Balzan, M.V., Wäckers, F.L., 2013. Flowers to selectively enhance the fitness of a host-feeding parasitoid: adult feeding by Tuta absoluta and its parasitoid Necremnus artynes. Biological Control 67, 21–31. doi:10.1016/j.biocontrol.2013.06.006

Barbosa, P.A., 1998. Conservation Biological Control. Academic Press, San Diego, USA.

Barbosa, P.A., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., Szendrei, Z., 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. Annual Review of Ecology, Evolution, and Systematics 40, 1–20. doi:10.1146/annurev.ecolsys.110308.120242

Barham, E., 2002. Towards a theory of values-based labeling. Agriculture and Human Values 19, 349–360. doi:10.1023/A:1021152403919

Batáry, P., Dicks, L.V., Kleijn, D., Sunderland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conservation Biology 29, 1006–1016. doi:10.1111/cobi.12536

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package.

Baveye, P.C., Palfreyman, J., Otten, W., 2014. Research efforts involving several disciplines: adherence to a clear nomenclature is needed. Water, Air & Soil Pollution 225, 1997. doi:10.1007/s11270-014-1997-7

Bawden, R., 1997. The community challenge: the learning response. Presented at the 29th Annual International Meeting of the Community Development Society, Athens Georgia.

Bedoussac, L., Journet, E.-P., Hauggaard-Nielsen, H., Naudin, C., Corre-Hellou, G., Jensen, E.S., Prieur, L., Justes, E., 2015. Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. Agronomy for Sustainable Development 35, 911–935. doi:10.1007/s13593-014-0277-7

Begum, M., Gurr, G.M., Wratten, S.D., Nicol, H.I., 2004. Flower color affects tri-trophic-level biocontrol interactions. Biological Control 30, 584–590. doi:10.1016/j.biocontrol.2004.03.005

Bellon, S., Guillaume, O., 2012. L’agroécologie en France, l’institutionnalisation d’utopies., in: Goulet, F., Magda, D., Girard, N., Hernandez, V. (Eds.), L’agroécologie En Argentine et En France - Regards Croisés. L’Harmattan, Paris, France, pp. 55–90.

Berkvens, N., Bonte, J., Berkvens, D., Deforce, K., Tirry, L., De Clercq, P., 2008. Pollen as an alternative food for Harmonia axyridis. BioControl 53, 201–210. doi:10.1007/s10526-007-9128-7

Bianchi, F.J.J.A., Goedhart, P.W., Baveco, J.M., 2008. Enhanced pest control in cabbage crops near forest in The Netherlands. Landscape Ecology 23, 595–602. doi:10.1007/s10980-008-9219-6

Bianchi, F.J.J.A., Wäckers, F., 2008. Effects of flower attractiveness and nectar availability in field margins on biological control by parasitoids. Biological Control 46, 400–408. doi:10.1016/j.biocontrol.2008.04.010

Biggs, D., Abel, N., Knight, A.T., Leitsch, A., Langston, A., Ban, N.C., 2011. The implementation crisis in conservation planning: could “mental models” help? Conservation Letters 4, 169–183. doi:10.1111/j.1755-263X.2011.00170.x

Blaauw, B.R., Isaacs, R., 2015. Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. Biological Control 91, 94–103. doi:10.1016/j.biocontrol.2015.08.003

Blaauw, B.R., Isaacs, R., 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. J Appl Ecol 51, 890–898. doi:10.1111/1365-2664.12257

Bommarco, R., Marini, L., Vaissière, B., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia 169, 1025–1032. doi:10.1007/s00442-012-2271-6

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical ecology with R. Springer, New York, USA.

Borin, M., Passoni, M., Thiene, M., Tempesta, T., 2010. Multiple functions of buffer strips in farming areas. European Journal of Agronomy 32, 103–111. doi:10.1016/j.eja.2009.05.003

Bossard, C., Santin, G., Guseva Canu, I., 2013. Surveillance de la mortalité par suicide des agriculteurs exploitants: premiers résultats. Saint-Maurice: Institut de veille sanitaire.

Botta-Dukát, Z., 2005. Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science 16, 533–540. doi:10.1111/j.1654-1103.2005.tb02393.x

Brédart, D., Stassart, P.M., 2017. When farmers learn through dialog with their practices: A proposal for a theory of action for agricultural trajectories. Journal of Rural Studies 53, 1–13. doi:10.1016/j.jrurstud.2017.04.009

Brodie, B.S., Smith, M.A., Lawrence, J., Gries, G., 2015. Effects of floral scent, color and pollen on foraging decisions and oocyte development of common green bottle flies. PLoS ONE 10, e0145055. doi:10.1371/journal.pone.0145055

Brose, U., 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia 135, 407–413. doi:10.1007/s00442-003-1222-7

Brossard, T., Joly, D., Pierret, P., 1993. Déprise agricole et fermeture des paysage. Mappemonde 3, 17–21.

Brown, P.M.J., Thomas, C.E., Lombaert, E., Jeffries, D.L., Estoup, A., Lawson Handley, L.-J., 2011. The global spread of Harmonia axyridis (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion. BioControl 56, 623–641. doi:10.1007/s10526-011-9379-1

Bruce, T.. J.A., 2014. Glucosinolates in oilseed rape: secondary metabolites that influence interactions with herbivores and their natural enemies. Annals of Applied Biology 164, 348–353. doi:10.1111/aab.12128

Büchi, R., 2002. Mortality of pollen beetle (Meligethes spp.) larvae due to predators and parasitoids in rape fields and the effect of conservation strips. Agriculture, Ecosystems & Environment 90, 255–263. doi:10.1016/S0167-8809(01)00213-4

Campbell, A.J., Biesmeijer, J.C., Varma, V., Wäckers, F.L., 2012. Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity. Basic and Applied Ecology 13, 363–370. doi:10.1016/j.baae.2012.04.003

Campbell, D.R., Bischoff, M., Lord, J.M., Robertson, A.W., 2010. Flower color influences insect visitation in alpine New Zealand. Ecology 91, 2638–2649. doi:10.1890/09-0941.1

Cardinale, B.J., Harvey, C.T., Gross, K., Ives, A.R., 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. Ecology Letters 6, 857–865. doi:10.1046/j.1461-0248.2003.00508.x

Carrié, R.J.G., George, D.R., Wäckers, F.L., 2012. Selection of floral resources to optimise conservation of agriculturally-functional insect groups. J Insect Conserv 16, 635–640. doi:10.1007/s10841-012-9508-x

Carter, C.A., Zhong, F., 1999. Rural wheat consumption in China. American Journal of Agricultural Economics 81, 582–592. doi:10.2307/1244017

Cerf, M., 2011. Is participatory research a scientific practice? Journal of Rural Studies 27, 414–418. doi:10.1016/j.jrurstud.2011.10.004

Chantre, E., Cardona, A., 2014. Trajectories of French field crop farmers moving toward sustainable farming practices: change, learning, and links with the advisory services. Agroecology and Sustainable Food Systems 38, 573–602. doi:10.1080/21683565.2013.876483

Chaplin-Kramer, R., O'Rourke, M., Blitzer, E.J., Kremen, 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters 14, 922–932. doi:10.1111/j.1461-0248.2011.01642.x

Chen, P.-R., Zhang, Z.-Q., Wang, K., Wang, X.-Y., Xu, W.-L., Gao, Z.-L., 1994. Allothrombium pulvinum Ewing (Acari, Trombidiidae), an important early season natural enemy of Aphis gossypii Glover (Hom., Aphididae) in cotton. Journal of Applied Entomology 117, 113–121. doi:10.1111/j.1439-0418.1994.tb00716.x

Chen, Z.J., Wu, G.J., Zhang, M., 1995. Study on the efficacies of wheat-pepper interplantation to evade aphid damage and alleviate virus disease. Acta Phytophylacica Sinica 22, 343–347.

Chen, Z.J., Wu, G.J., Zhang, S.L., 1998. Integrated pest management in cotton field of wheat interplanting with cotton. Acta Agricultural Boreali-Occidentalis Sinica 7, 27–31.

Chittka, L., Shmida, A., Troje, N., Menzel, R., 1994. Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. Vision Research 34, 1489–1508. doi:10.1016/0042-6989(94)90151-1

Claeys, W.L., Schmit, J.-F., Bragard, C., Maghuin-Rogister, G., Pussemier, L., Schiffers, B., 2011. Exposure of several Belgian consumer groups to pesticide residues through fresh fruit and vegetable consumption. Food Control 22, 508–516. doi:10.1016/j.foodcont.2010.09.037

Claflin, S.B., Jones, L.E., Thaler, J.S., Power, A.G., 2016. Crop-dominated landscapes have higher vector-borne plant virus prevalence. Journal of Applied Ecology in press. doi:10.1111/1365-2664.12831

Cole, L.J., Brocklehurst, S., Robertson, D., Harrisson, W., McCracken, D.I., 2015. Riparian buffer strips: Their role in the conservation of insect pollinators in intensive grassland systems. Agriculture, Ecosystems & Environment 211, 207–220. doi:10.1016/j.agee.2015.06.012

Colignon, P., Gaspar, C., Haubruge, E., Francis, F., 2002. Impact of close habitat on the entomological diversity and abundance in carrot open fields. Mededelingen van de

Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen (Rijksuniversiteit te Gent) 67, 481–486.

Colignon, P., Hastir, P., Gaspar, C., Francis, F., 2001. Effects of insecticide treatments on insect density and diversity in vegetable open fields. Mededelingen van de Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen (Rijksuniversiteit te Gent) 66, 403–411.

Colley, M.R., Luna, J.M., 2000. Relative Attractiveness of Potential Beneficial Insectary Plants to Aphidophagous Hoverflies (Diptera: Syrphidae). Environmental Entomology 29, 1054–1059. doi:10.1603/0046-225X-29.5.1054

Combs, J.G., Ketchen, D.J., Crook, T.R., Roth, P.L., 2011. Assessing cumulative evidence within 'macro' research: why meta-analysis should be preferred over vote counting. Journal of Management Studies 48, 178–197. doi:10.1111/j.1467-6486.2009.00899.x

Cong, W.-F., Hoffland, E., Li, L., Six, J., Sun, J.-H., Bao, X.-G., Zhang, F.-S., van der Werf, W., 2014. Intercropping enhances soil carbon and nitrogen. Global Change Biology 21, 1715–1726. doi:10.1111/gcb.12738

Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist 122, 661–696. doi:10.1086/284165

Cook, S.M., Khan, Z.R., Pickett, J.A., 2007. The Use of Push-Pull Strategies in Integrated Pest Management. Annual Review of Entomology 52, 375–400. doi:10.1146/annurev.ento.52.110405.091407

Cook, S.M., Skellern, M.P., Döring, T.F., Pickett, J.A., 2013. Red oilseed rape? The potential for manipulation of petal colour in control strategies for the pollen beetle (Meligethes aeneus). Arthropod-Plant Interactions 7, 249–258. doi:10.1007/s11829-013-9252-5

Costanza, R., D'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260.

Costanzo, A., Bàrberi, P., 2014. Functional agrobiodiversity and agroecosystem services in sustainable wheat production. Agronomy for Sustainable Development 34, 327–348. doi:10.1007/s13593-013-0178-1

Cowgill, S., 1989. The role of non-crop habitats on hoverfly (Diptera: Syrphidae) foraging on arable land. Proceedings of the Brighton Crop Protection conference 1103–1108.

Cowling, R.M., Egoh, B., Knight, A.T., O'Farrell, P.J., Reyers, B., Rouget, M., Roux, D.J., Welz, A., Wilhelm-Rechman, A., 2008. An operational model for mainstreaming ecosystem services for implementation. Proceedings of the National Academy of Sciences 105, 9483–9488. doi:10.1073/pnas.0706559105

Cremer, S., Branquart, E., Ledant, J.-P., Luxen, P., 2010. Les lisières agroforestières. Agrinature.

Cuéllar-Padilla, M., Calle-Collado, Á., 2011. Can we find solutions with people? Participatory action research with small organic producers in Andalusia. Journal of Rural Studies 27, 372–383. doi:10.1016/j.jrurstud.2011.08.004

Cui, L.L., Francis, F., Heuskin, S., Lognay, G., Liu, Y.J., Dong, J., Chen, J.L., Song, X.-M., Liu, Y., 2012. The functional significance of E-b-Farnesene: Does it influence the populations of aphid natural enemies in the fields? Biological Control 60, 108–112. doi:10.1016/j.biocontrol.2011.11.006

Cullen, R., Warner, K.D., Jonsson, M., Wratten, S.D., 2008. Economics and adoption of conservation biological control. Biological Control 45, 272–280. doi:10.1016/j.biocontrol.2008.01.016

Dáder, B., Moreno, A., Viñuela, E., Fereres, A., 2012. Spatio-temporal dynamics of viruses are differentially affected by parasitoids depending on the mode of transmission. Viruses 4, 3069–3089. doi:10.3390/v4113069

Daily, G.C., Ehrlich, P.R., 1999. Managing Earth’s ecosystems: An interdisciplinary challenge. Ecosystems 2, 277–280. doi:10.1007/s100219900075

Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M., Marini, L., 2017. High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. Journal of Applied Ecology 54, 380–388. doi:10.1111/1365-2664.12747

Dalgaard, T., Hutchings, N.J., Porter, J.R., 2003. Agroecology, scaling and interdisciplinarity. Agriculture, Ecosystems & Environment 100, 39–51. doi:10.1016/S0167-8809(03)00152-X

Das, S.B., 1998. Impact of intercropping on Helicoverpa armigera (Hub.): incidence and crop yield of chickpea in West Nimar Valley of Madhya Pradesh. Insect Environ 4, 84–85.

Dassou, A.G., Tixier, P., 2016. Response of pest control by generalist predators to local-scale plant diversity: a meta-analysis. Ecology and Evolution 6, 1143–1153. doi:10.1002/ece3.1917

De Schutter, O., 2010. Agroecology and the right to food (No. A/HRC/16/49). United Nations - Human Right Council, New York.

Debach, P., 1991. Biological control by natural enemies, 2e éd. ed. Cambridge University Press, Cambridge.

DEFRA, 2013. UK National Action Plan for the sustainable use of pesticides (plant protection products). https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/221034/pb13894-nap-pesticides-20130226.pdf (accessed 2.16.17).

Deguine, J.-P., Gloanec, C., Laurent, P., Ratnadass, A., Aubertot, J.-N., 2016. Protection agroécologique des cultures, Quae. ed.

Delcour, A., Van Stappen, F., Gheysens, S., Decruyenaere, V., Stilmant, D., Burny, P., Rabier, F., Louppe, H., Goffart, J.-P., 2014. État des lieux des flux céréaliers en Wallonie selon différentes filières d’utilisation. Biotechnology, Agronomy, Society, Environment 18, 181–192.

DeLonge, M.S., Miles, A., Carlisle, L., 2016. Investing in the transition to sustainable agriculture. Environmental Science & Policy 55, 266–273. doi:10.1016/j.envsci.2015.09.013

Denno, R.F., McClure, M.S., Ott, J.R., 1995. Interspecifific interactions in phytophagous insects: competition reexamined and resurrected. Annual Review of Entomology 40, 297–331. doi:10.1146/annurev.en.40.010195.001501

Denys, C., Tscharntke, T., 2002. Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. Oecologia 130, 315–324. doi:10.1007/s004420100796

Devine, G.J., Furlong, M.J., 2007. Insecticide use: Contexts and ecological consequences. Agric Hum Values 24, 281–306. doi:10.1007/s10460-007-9067-z

Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16, 646–655. doi:10.1016/S0169-5347(01)02283-2

Dolinska, A., d'Aquino, P., 2016. Farmers as agents in innovation systems. Empowering farmers for innovation through communities of practice. Agricultural Systems 142, 122–130. doi:10.1016/j.agsy.2015.11.009

Dong, J., Liu, Y.J., Li, P.L., Lin, F.J., Chen, J.L., Liu, Y., 2012. Ecological effects of wheat-oilseed rape intercropping combined with methyl salicylate release on Sitobion avenae and its main natural enemies. Ying yong sheng tai xue bao= The journal of applied ecology 23, 2843–2848.

Doré, T., Makowski, D., Malézieux, E., Munier-Jolain, N., Tchamitchian, M., Tittonell, P., 2011. Facing up to the paradigm of ecological intensification in agronomy: Revisiting methods, concepts and knowledge. European Journal of Agronomy 34, 197–210. doi:10.1016/j.eja.2011.02.006

Döring, T.F., 2014. How aphids find their host plants, and how they don't. Annals of Applied Biology 165, 3–26. doi:10.1111/aab.12142

Döring, T.F., Archetti, M., Hardie, J., 2009. Autumn leaves seen through herbivore eyes. Proceedings of the Royal Society of London Series B, Biological Sciences 276, 121–127. doi:10.1098/rspb.2008.0858

Döring, T.F., Skellern, M., Watts, N., Cook, S.M., 2012. Colour choice behaviour in the pollen beetle Meligethes aeneus (Coleoptera: Nitidulidae). Physiological Entomology 37, 360–368. doi:10.1111/j.1365-3032.2012.00850.x

Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22, 1–20. doi:10.18637/jss.v022.i04

Dufrêne, M., 2013. Relevance of an Ecosystem Services Approach in Southern Belgium, in: Jacobs, S., Dendoncker, N., Keune, H. (Eds.), Ecosystem Services - Local Issues, Global Practices. Elsevier, Boston, pp. 341–345.

Dumont, A.M., Vanloqueren, G., Stassart, P.M., Baret, P.V., 2016. Clarifying the socio-economic dimensions of agroecology: between principles and practices. Agroecology and Sustainable Food Systems 40, 24–47. doi:10.1080/21683565.2015.1089967

Dunbar, M.W., O'Neal, M.E., Gassmann, A.J., 2016. Increased risk of insect injury to corn following rye cover crop. Journal of Economic Entomology 109, 1691–1697. doi:10.1093/jee/tow101

Duru, M., Cruz, P., Jouany, C., Theau, J.P., 2011. Combiner des recherches en agroécologie et des dispositifs participatifs pour construire des outils d'évaluation des prairies permanentes. Cahiers Agricultures 20, 223–234. doi:10.1684/agr.2011.0486

Duru, M., Therond, O., Martin, G., Martin-Clouaire, R., Magne, M.-A., Justes, E., Journet, E.-P., Aubertot, J.-N., Savary, S., Bergez, J.-E., Sarthou, J.P., 2015. How to implement biodiversity-based agriculture to enhance ecosystem services: a review. Agronomy for Sustainable Development 35, 1259–1281. doi:10.1007/s13593-015-0306-1

Ehsan-Ul-Haq, Van Emden, H.F., 2003. Effects of intercropping wheat and peas on the growth and development of Metopolophium dirhodum and Aphidius rhopalosiphi (A glasshouse simulation). Pakistan Journal of Zoology 35, 271–275.

Ekroos, J., Olsson, O., Rundlöf, M., Wätzold, F., Smith, H.G., 2014. Optimizing agri-environment schemes for biodiversity, ecosystem services or both? Biological Conservation 172, 65–71. doi:10.1016/j.biocon.2014.02.013

Elliott, J., Heesterbeek, S., Lukensmeyer, C., Slocum, N., 2005. Participatory methods toolkit - A practitioner's manual. King Baudouin Foundation & Flemish Institute for Science and Technology Assessment (viWTA), Belgium.

ELN-FAB, 2012. Functional agrobiodiversity, Nature serving Europe's farmers. ECNC-European Centre for Nature Conservation, Tilburg, the Netherlands.

Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E., Bernasconi, G., 2007. Time after time: flowering phenology and biotic interactions. Trends in Ecology & Evolution 22, 432–439. doi:10.1016/j.tree.2007.05.006

European Commission, 2016. Myths and facts: Most of the EU budget goes to farmers! http://ec.europa.eu/budget/explained/myths/myths_en.cfm (accessed 2.28.17).

European Commission, 2005. Agri-environment measures. Overview on general principles, types of measures and application. European Commission, Directorate General for Agriculture and Rural Development.

Eurostat, 2015a. Agriculture, forestry and fishery statistics - 2014 edition. http://ec.europa.eu/eurostat/documents/3217494/6639628/KS-FK-14-001-EN-N.pdf/8d6e9dbe-de89-49f5-8182-f340a320c4bd (accessed 11.2.15).

Eurostat, 2015b. Agriculture - greenhouse gas emission statistics. http://ec.europa.eu/eurostat/statistics-explained/index.php/Agriculture_-_greenhouse_gas_emission_statistics (accessed 2.28.17).

Evans, E.W., 2003. Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. European Journal of Entomology 100, 1–10. doi:10.14411/eje.2003.001

Evenson, R.E., Gollin, D., 2003. Assessing the impact of the Green Revolution, 1960 to 2000. Science 300, 758–762. doi:10.1126/science.1078710

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14, 101–112. doi:10.1111/j.1461-0248.2010.01559.x

Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Freemark Lindsay, K., Mitchell, S., Tischendorf, L., 2015. Farmlands with smaller crop fields have higher within-field biodiversity. Agriculture, Ecosystems & Environment 200, 219–234. doi:10.1016/j.agee.2014.11.018

Fassotte, B., 2016. Sexual attraction in lady beetles: fundamentals and applications. University of Liège - Gembloux Agro-Bio Tech, Gembloux, Belgique.

Fassotte, B., Fischer, C., Durieux, D., Lognay, G., Haubruge, E., Francis, F., Verheggen, F.J., 2014. First evidence of a volatile sex pheromone in lady beetles. PLoS ONE 9, e115011. doi:10.1371/journal.pone. 0115011

Fassotte, B., Francis, F., Verheggen, F., 2016. The scent of love: how important are semiochemicals in the sexual behavior of lady beetles? Journal of Pest Science 89, 347–358. doi:10.1007/s10340-016-0735-x

Fathi, S.A.A., Nouri-Ganbalani, G., Belali-Mashkour, E., 2013. Evaluation of two wheat cropping systems for enhancing biological control of the wheat thrips, Haplothrips tritici (Thys.: Phlaeothripidae). Journal of Entomological Society of Iran 33, 49–85.

Feike, T., Doluschitz, R., Chen, Q., Graeff-Hönninger, S., Claupein, W., 2012. How to overcome the slow death of intercropping in the north China plain. Sustainability 4, 2550–2565. doi:10.3390/su4102550

Ferguson, A.W., Williams, I.H., Castle, L.M., Skellern, M.P., 2010. Key parasitoids of the pests of oilseed rape in Europe: A guide to their identification, in: Williams, I.H. (Ed.), Biocontrol-Based Integrated Management of Oilseed Rape Pests. Springer, The Netherlands, pp. 77–114.

Fiedler, A.K., Landis, D.A., 2007a. Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. Environmental Entomology 36, 751–765. doi:10.1093/ee/36.4.751

Fiedler, A.K., Landis, D.A., 2007b. Plant characteristics associated with natural enemy abundance at Michigan native plants. Environmental Entomology 36, 878–886. doi:10.1093/ee/36.4.878

Fiedler, A.K., Landis, D.A., Wratten, S.D., 2008. Maximizing ecosystem services from conservation biological control: The role of habitat management. Biological Control, Conservation Biological Control 45, 254–271. doi:10.1016/j.biocontrol.2007.12.009

Finch, S., Collier, R.H., 2000. Host-plant selection by insects - a theory based on “appropriate/inappropriate landings” by pest insects of cruciferous plants. Entomologia Experimentalis et Applicata 96, 91–102. doi:10.1046/j.1570-7458.2000.00684.x

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12, 22–33. doi:10.1111/j.1461-0248.2008.01255.x

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574. doi:10.1126/science.1111772

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities. PLoS Biol 4, 129–135. doi:10.1371/journal.pbio.0040001

Foster, S.P., Devine, G.J., Devonshire, A.L., 2007. Insecticide resistance, in: Van Emden, H.F., Harrington, R. (Eds.), Aphids as Crop Pests. Cambridge, Massachusetts, pp. 261–286.

Francis, C., Breland, T.A., Østergaard, E., Lieblein, G., Morse, S., 2013. Phenomenon-based learning in agroecology: a prerequisite for transdisciplinarity and responsible action. Agroecology and Sustainable Food Systems 37, 60–75. doi:10.1080/10440046.2012.717905

Francis, C., Lieblein, G., Gliessman, S., Breland, T.A., Creamer, N., Harwood, R., Salomonsson, L., Helenius, J., Rickerl, D., Salvador, R., Wiedenhoeft, M., Simmons, S., Allen, P., Altieri, M., Flora, C., Poincelot, R., 2003. Agroecology: The Ecology of Food Systems. Journal of Sustainable Agriculture 22, 99–118. doi:10.1300/J064v22n03_10

Francis, F., Colignon, P., Gaspar, C., Haubruge, E., 2003. Evaluation de la présence des Syrphidae en cultures maraîchères et relation avec les populations aphidiennes. Presented at the 5ème Conférence Internationale Francophone d’Entomologie, Montréal, p. 149.

Francis, F., Colignon, P., Haubruge, E., Gaspar, C., 2001a. Evaluation of aphidophagous ladybird populations in a vegetable crop and implications as biological agents. Mededelingen van de Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen (Rijksuniversiteit te Gent) 66, 333–340.

Francis, F., Haubruge, É., Hastir, P., Gaspar, C., 2001b. Effect of aphid host plant on development and reproduction of the third trophic level, the predator Adalia bipunctata (Coleoptera: Coccinellidae). Environmental Entomology 30, 947–952. doi:10.1603/0046-225X-30.5.947

Francis, F., Lognay, G., Haubruge, E., 2004. Olfactory responses to aphid and host plant volatile releases: (E)-β-farnesene an effective kairomone for the predator Adalia bipunctata. J Chem Ecol 30, 741–755. doi:10.1023/B:JOEC.0000028429.13413.a2

Frank, S.D., Shrewsbury, P.M., Denno, R.F., 2011. Plant versus prey resources: Influence on omnivore behavior and herbivore suppression. Biological Control 57, 229–235. doi:10.1016/j.biocontrol.2011.03.004

Frank, T., 1998. The role of different slug species in damage to oilseed rape bordering on sown wildflower strips. Annals of Applied Biology 133, 483–493. doi:10.1111/j.1744-7348.1998.tb05845.x

Free, J.B., Williams, I.H., 1978. The responses of the pollen beetle, Meligethes aeneus, and the seed weevil, Ceuthorhynchus assimilis, to oil-seed rape, Brassica napus, and other plants. Journal of Applied Ecology 15, 761–774. doi:10.2307/2402773

Gardiner, M.M., O’Neal, M.E., Landis, D.A., 2011. Intraguild Predation and Native Lady Beetle Decline. PLoS ONE 6, e23576. doi:10.1371/journal.pone.0023576

Gariepy, T.D., Kuhlmann, U., Gillott, C., Erlandson, M., 2007. Parasitoids, predators and PCR: the use of diagnostic molecular markers in biological control of Arthropods. Journal of Applied Entomology 131, 225–240. doi:10.1111/j.1439-0418.2007.01145.x

Garratt, M.P.D., Wright, D.J., Leather, S.R., 2011. The effects of farming system and fertilisers on pests and natural enemies: A synthesis of current research. Agriculture, Ecosystems & Environment 141, 261–270. doi:10.1016/j.agee.2011.03.014

Geertsema, W., Rossing, W.A.H., Landis, D.A., Bianchi, F.J.J.A., Van Rijn, P.C.J., Schaminée, J.H.J., Tscharntke, T., van der Werf, W., 2016. Actionable knowledge for ecological intensification of agriculture. Frontiers in Ecology and the Environment 14, 209–216. doi:10.1002/fee.1258

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantgenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology 11, 97–105. doi:10.1016/j.baae.2009.12.001

Ghaley, B.B., Hauggaard-Nielsen, H., Høgh-Jensen, H., Jensen, E.S., 2005. Intercropping of wheat and pea as influenced by nitrogen fertilization. Nutrient Cycling in Agroecosystems 73, 201–212. doi:10.1007/s10705-005-2475-9

Gibbons, D., Morrissey, C., Mineau, P., 2015. A review of the direct and indirect effects of neonicotinoids and fipronil on vertebrate wildlife. Environ Sci Pollut Res 22, 103–118. doi:10.1007/s11356-014-3180-5

Gillespie, M.A.K., Gurr, G.M., Wratten, S.D., 2016. Beyond nectar provision: the other resource requirements of parasitoid biological control agents. Entomologia Experimentalis et Applicata 159, 207–221. doi:10.1111/eea.12424

GIREA, DDR/DGARNE/SPW, 2013. MAE en Wallonie: 11 Méthodes, 13 Questions-Réponses d'évaluation. https://www.natagriwal.be/sites/default/files/kcfinder/files/Autres_doc/MAE%20en%2013%20questions_janv_2013.pdf (accessed 7.3.14).

Gliessman, S., 2011. Transforming food systems to sustainability with agroecology. Journal of Sustainable Agriculture 35, 823–825. doi:10.1080/10440046.2011.611585

Gonzáles, E., Salvo, A., Valladares, G., 2017. Arthropod communities and biological control in soybean fields: Forest cover at landscape scale is more influential than forest proximity. Agriculture, Ecosystems & Environment 239, 359–367. doi:10.1016/j.agee.2017.02.002

Grettenberger, I.M., Tooker, J.F., 2017. Variety mixtures of wheat influence aphid populations and attract an aphid predator. Arthropod-Plant Interactions 11, 133–146. doi:10.1007/s11829-016-9477-1

Griffiths, G.J.K., Holland, J.M., Bailey, A., Thomas, M.B., 2008. Efficacy and economics of shelter habitats for conservation biological control. Biological Control 45, 200–209. doi:10.1016/j.biocontrol.2007.09.002

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111, 1169–1194. doi:10.1086/283244

Guillou, M., Guyomard, H., Huyghe, C., Peyraud, J.-L., 2013. Vers des agricultures doublement performantes pour concilier compétitivité et respect de l'environnement.

Guns, A., 2008. Emissions de gaz à effet de serre et de gaz acidifiants du secteur agricole en Région wallonne. Presented at the Carrefour des productions animales, CRA-W & FUSAGx, Gembloux, Belgique, pp. 14–19.

Gurr, G.M., Lu, Z.-X., Zheng, X.-S., Xu, H.-X., Zhu, P.-Y., Chen, G.-H., Yao, X.-M., Cheng, J.-A., Zhu, Z.-R., Catindig, J.L., Villareal, S., Chien, H.V., Cuong, L.Q., Channoo, C., Chengwattana, N., Lan, L.P., Hai, L.H., Chaiwong, J., Nicol, H.I., Perovic, D.J., Wratten, S.D., Heong, K.-L., 2016. Multi-country evidence that crop diversification promotes ecological intensification of agriculture. Nature Plants 2, 16014. doi:10.1038/nplants.2016.14

Gurr, G.M., Wratten, S.D., Luna, J.M., 2003. Multi-function agricultural biodiversity: pest management and other benefits. Basic and Applied Ecology 4, 107–116. doi:10.1078/1439-1791-00122

Guzmán, G., López, D., Román, L., Alonso, A., 2013. Participatory action research in agroecology: building local organic food networks in Spain. Agroecology and Sustainable Food Systems 37, 127–146. doi:10.1080/10440046.2012.718997

Haaland, C., Naisbit, R.E., Bersier, L.-F., 2011. Sown wildflower strips for insect conservation: a review. Insect Conservation and Diversity 4, 60–80. doi:10.1111/j.1752-4598.2010.00098.x

Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T., Thies, C., 2009. Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. Journal of Applied Ecology 46, 1106–1114. doi:10.1111/j.1365-2664.2009.01685.x

Hammond, R.B., Jeffers, D.L., 1990. Potato leafhopper (Homoptera: Cicadellidae) populations on soybean relay intercropped into winter wheat. Environmental Entomology 19, 1810–1819. doi:10.1093/ee/19.6.1810

Hance, T., Demeter, S., Le Roi, A., Mahy, G., Rouxhet, S., Thirion, M., Mulders, C., 2010. Agriculture et biodiversité, Hors Série. ed. Agrinature.

Hansen, L.M., Lorentsen, L., Boelt, B., 2008. How to reduce the incidence of black bean aphids (Aphis fabae Scop.) attacking organic growing field beans (Vicia faba L.) by growing partially resistant bean varieties and by intercropping field beans with cereals. Acta Agriculturae Scandinavica, Section B — Soil & Plant Science 58, 359–364. doi:10.1080/09064710701788844

Hanson, H.I., Smith, H.G., Hedlund, K., 2015. Agricultural management reduces emergence of pollen beetle parasitoids. Agriculture, Ecosystems & Environment 205, 9–14. doi:10.1016/j.agee.2015.03.001

Hatt, S., Artru, S., Brédart, D., Lassois, L., Francis, F., Haubruge, E., Garré, S., Stassart, P.M., Dufrêne, M., Monty, A., Boeraeve, F., 2016. Towards sustainable food systems: the position of agroecology and how it questions current research practices (Review). Biotechnology, Agronomy, Society, Environment 20, 215–224.

Hatt, S., Lopes, T., Boeraeve, F., Chen, J., Francis, F., 2017a. Pest regulation and support of natural enemies in agriculture: experimental evidence of within field wildflower strips. Ecological Engineering 98, 240–245. doi:10.1016/j.ecoleng.2016.10.080

Hatt, S., Uyttenbroeck, R., Lopes, T., Mouchon, P., Chen, J., Piqueray, J., Monty, A., Francis, F., 2017b. Do flower mixtures with high functional diversity enhance aphid predators in wildflower strips? European Journal of Entomology 114, 66–76. doi:10.14411/eje.2017.010

Hatt, S., Uyttenbroeck, R., Lopes, T., Paul, A., Danthine, S., Bodson, B., Piqueray, J., Monty, A., Francis, F., 2015. Do wildflower strips favor insect pest populations at field margins? Agriculture and Agricultural Science Procedia 6, 30–37. doi:10.1016/j.aaspro.2015.08.034

Hauggaard-Nielsen, H., Ambus, P., Jensen, E.S., 2001. Interspecific competition, N use and interference with weeds in pea-barley intercropping. Field Crops Research 70, 101–109. doi:10.1016/S0378-4290(01)00126-5

Heap, I., 2014. Herbicide Resistant Weeds, in: Pimentel, D., Peshin, R. (Eds.), Integrated Pest Management, Pesticide Problems. Springer New York, pp. 281–301.

Heuskin, S., Lorge, S., Godin, B., Leroy, P., Frère, I., Verheggen, F.J., Haubruge, E., Wathelet, J.-P., Mestdagh, M., Hance, T., Lognay, G., 2012. Optimisation of a semiochemical slow-release alginate formulation attractive towards Aphidius ervi Haliday parasitoids. Pest Management Science 68, 127–136. doi:10.1002/ps.2234

Hickman, J.M., Wratten, S.D., 1996. Use of Phacelia tanacetifolia strips to enhance biological control of aphids by hoverfly larvae in cereal fields. Journal of Economic Entomology 89, 832–840. doi:10.1093/jee/89.4.832

Hill, S.B., MacRae, R.J., 1996. Conceptual framework for the transition from conventional to sustainable agriculture. Journal of Sustainable Agriculture 7, 81–87. doi:10.1300/J064v07n01_07

Hodge, I., Hauck, J., Bonn, A., 2015. The alignment of agricultural and nature conservation policies in the European Union. Conservation Biology 29, 996–1005. doi:10.1111/cobi.12531

Holland, J.M., Bianchi, F.J.J.A., Entling, M.H., Moonen, A.C., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. Pest Management Science 72, 1638–1651. doi:10.1002/ps.4318

Holzschuh, A., Dudenhöffer, J.-H., Tscharntke, T., 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. Biological Conservation 153, 101–107. doi:10.1016/j.biocon.2012.04.032

Horton, D.R., Broers, D.A., Lewis, R.R., Granatstein, D., Zack, R.S., Unruh, T.R., Moldenke, A.R., Brown, J.J., 2003. Effects of mowing frequency on densities of natural enemies in three Pacific Northwest pear orchards. Entomologia Experimentalis et Applicata 106, 135–145. doi:10.1046/j.1570-7458.2003.00018.x

Hossain, M.A., 2003. Management of chickpea pod borer, Helicoverpa armigera (Hubner) through intercroppings and insecticide spraying. Thai Journal of Agricultural Science 36, 51–56.

Hossard, L., Guichard, L., Pelosi, C., Makowski, D., 2017. Lack of evidence for a decrease in synthetic pesticide use on the main arable crops in France. Science of The Total Environment 575, 152–161. doi:10.1016/j.scitotenv.2016.10.008

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical Journal 50, 346–363. doi:10.1002/bimj.200810425

Howard, P.H., Allen, P., 2010. Beyond organic and Fair Trade? An analysis of ecolabel preferences in the United States. Rural Sociology 75, 244–269. doi:10.1111/j.1549-0831.2009.00009.x

Hummel, J.D., Dosdall, L.M., Clayton, G.W., Harker, K.N., O'Donovan, J.T., 2012. Ground beetle (Coleoptera: Carabidae) diversity, activity density, and community structure in a diversified agroecosystem. Environmental Entomology 41, 72–80. doi:0.1603/EN11072

Hummel, J.D., Dosdall, L.M., Clayton, G.W., Harker, K.N., O'Donovan, J.T., 2010. Responses of the parasitoids of Delia radicum (Diptera: Anthomyiidae) to the vegetational diversity of intercrops. Biological Control 55, 151–158. doi:10.1016/j.biocontrol.2010.08.004

Hummel, J.D., Dosdall, L.M., Clayton, G.W., Harker, K.N., O'Donovan, J.T., 2009a. Effects of canola wheat intercrops on Delia spp. (Diptera: Anthomyiidae) oviposition, larval feeding damage, and adult abundance. Journal of Economic Entomology 102, 219–228. doi:10.1603/029.102.0131

Hummel, J.D., Dosdall, L.M., Clayton, G.W., Turkington, T.K., Lupwayi, N.Z., Harker, K.N., O'Donovan, J.T., 2009b. Canola-wheat intercrops for improved agronomic performance and integrated pest management. Agronomy Journal 101, 1190–1197. doi:10.2134/agronj2009.0032

Idris, A.B., Grafius, E., 1995. Wildflowers as nectar sources for Diadegma insulare (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). Environmental Entomology 24, 1726–1735. doi:10.1093/ee/24.6.1726

International Assessment of Agricultural Knowledge, 2009. Agriculture at a crossroads. Island Press, Washington, DC.

Irvin, N.A., Bistline-East, A., Hoddle, M.S., 2016. The effect of an irrigated buckwheat cover crop on grape vine productivity, and beneficial insect and grape pest abundance in southern California. Biological Control 93, 72–83. doi:10.1016/j.biocontrol.2015.11.009

Jacobs, S., Dendoncker, N., Keune, H., 2013. Ecosystem Services: Global Issues, Local Practices. Elsevier.

Jacot, K., Eggenschwiler, L., Junge, X., Luka, H., Bosshard, A., 2007. Improved field margins for a higher biodiversity in agricultural landscapes. Aspects of Applied Biology 81, 277 – 283.

Jauker, F., Wolters, V., 2008. Hoverflies are efficient pollinators of oilseed rape. Oecologia 156, 819–823. doi:10.1007/s00442-008-1034-x

Jervis, M.A., Kidd, N.A.C., Fitton, M.G., Huddleston, T., Dawah, H.A., 1993. Flower-visiting by hymenopteran parasitoids. Journal of Natural History 27, 67–105. doi:10.1080/00222939300770051

Jervis, M.A., Lee, J.C., Heimpel, G.E., 2004. Use of behavioural and life-history studies to understand the effects of habitat manipulation, in: Gurr, G.M., Wratten, S.D., Altieri, M.A. (Eds.), Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods. CSIRO Publishing, Collingwood, Australia, pp. 65–100.

Jönsson, A.M., Ekroos, J., Dänhardt, J., Andersson, G.K.S., Olsson, O., Smith, H.G., 2015. Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the wider landscape. Biological Conservation 184, 51–58. doi:10.1016/j.biocon.2014.12.027

Jönsson, M., 2005. Responses to oilseed rape and cotton volatiles in insect herbivores and parasitoids (Doctoral thesis). Swedish University of Agricultural Sciences, Alnarp, Sweden.

Jonsson, M., Straub, C.S., Didham, R.K., Buckley, H.L., Case, B.S., Hale, R.J., Gratton, C., Wratten, S.D., 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. Journal of Applied Ecology 52, 1274–1282. doi:10.1111/1365-2664.12489

Jonsson, M., Wratten, S.D., Landis, D.A., Gurr, G.M., 2008. Recent advances in conservation biological control of arthropods by arthropods. Biological Control 45, 172–175. doi:10.1016/j.biocontrol.2008.01.006

Jose, S., Bardhan, S., 2012. Agroforestry for biomass production and carbon sequestration: an overview. Agroforestry Systems 86, 105–111. doi:10.1007/s10457-012-9573-x

Josefsson, J., Berg, Å., Hiron, M., Pärt, T., Eggers, S., 2013. Grass buffer strips benefit invertebrate and breeding skylark numbers in a heterogeneous agricultural landscape. Agriculture, Ecosystems & Environment 18, 101–107. doi:10.1016/j.agee.2013.09.018

Katis, N.I., Tsitsipis, J.A., Stevens, M.H.H., Powell, G., 2007. Transmission of plant viruses, in: Van Emden, H.F., Harrington, R. (Eds.), Aphids as Crop Pests. CABI, Cambridge, Massachusetts, pp. 353–390.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin Iii, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E., Wirth, C., 2011. TRY – a global database of plant traits. Global Change Biology 17, 2905–2935. doi:10.1111/j.1365-2486.2011.02451.x

Kessler, A., Baldwin, I.T., 2001. Defensive function of herbivore-induced plant volatile emissions in nature. Science 291, 2141–2144. doi:10.1126/science.291.5511.2141

Khan, Z.R., Hassanali, A., Overholt, W., Khamis, T.M., Hooper, A.M., Pickett, J.A., Wadhams, L.J., Woodcock, C.M., 2002. Control of witchweed Striga hermonthica by intercropping with Desmodium sp. and the mechanism defined as allelopathic. Journal of Chemical Ecology 28, 1871–1885. doi:10.1023/A:1020525521180

Khan, Z.R., James, D.G., Midega, C.A.O., Pickett, J.A., 2008. Chemical ecology and conservation biological control. Biological Control 45, 210–224. doi:10.1016/j.biocontrol.2007.11.009

Kim, K.-H., Kabir, E., Jahan, S.A., 2017. Exposure to pesticides and the associated human health effects. Science of The Total Environment 575, 525–535. doi:10.1016/j.scitotenv.2016.09.009

Kirk-Spriggs, A.H., 1996. Pollen beetles: Coleoptera: Kateretidae and Nitidulidae: Meligethinae., RES Handbooks for the Identification of British Insects. Royal Entomological Society, London, UK.

Knörzer, H., Graeff-Hönninger, S., Guo, B., Wang, P., Claupein, W., 2009. The rediscovery of intercropping in China: a traditional cropping system for future Chinese agriculture – A Review, in: Lichtfouse, E. (Ed.), Climate Change, Intercropping, Pest Control and Beneficial Microorganisms, Sustainable Agriculture Reviews. Springer Netherlands, pp. 13–44.

Koski, M.H., Ashman, T.-L., 2014. Dissecting pollinator responses to a ubiquitous ultraviolet floral pattern in the wild. Functional Ecology 28, 868–877. doi:10.1111/1365-2435.12242

Krebs, J.R., Wilson, J.D., Bradbury, R.B., Siriwardena, G.M., 1999. The second Silent Spring? Nature 400, 611–612. doi:10.1038/23127

Kremen, C., Iles, A., Bacon, C., 2012. Diversified farming systems: an agroecological, systems-based alternative to modern industrial agriculture. Ecology and Society 17, 44. doi:10.5751/ ES-05103-170444

Kremen, C., Miles, A., 2012. Ecosystem services in biologically diversified versus conventional farming systems: Benefits, externalities, and trade-offs. Ecology and Society 17, 40. doi:10.5751/ES-05035-170440

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. doi:10.1890/08-2244.1

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package, R package.

Lambinon, J., De Langhe, J.-E., Delvosalle, L., Duvigneaud, J., 2008. Flora van België, het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden. Nationale Plantentuin van België, Meise.

Lambinon, J., Delvosalle, L., Duvigneaud, J., 2004. Nouvelle flore de Belgique, du Grand-Duché de Luxembourg, du Nord de la France et des régions voisines., 5th ed. Jardin Botanique National de Belgique, Meise.

Lamine, C., 2015a. Sustainability and resilience in agrifood systems: reconnecting agriculture, food and the environment. Sociol Ruralis 55, 41–61. doi:10.1111/soru.12061

Lamine, C., 2015b. Full case study report: Biocoop-France, HealthyGrowth - From niche to volume with integrity and trust.

Lamine, C., 2011. Transition pathways towards a robust ecologization of agriculture and the need for system redesign. Cases from organic farming and IPM. Journal of Rural Studies 27, 209–219. doi:10.1016/j.jrurstud.2011.02.001

Landis, D.A., 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. Basic and Applied Ecology 18, 1–12. doi:10.1016/j.baae.2016.07.005

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45, 175–201. doi:10.1146/annurev.ento.45.1.175

Langellotto, G.A., Denno, R.F., 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139, 1–10. doi:10.1007/s00442-004-1497-3

Laubertie, E.A., Wratten, S.D., Hemptinne, J.-L., 2012. The contribution of potential beneficial insectary plant species to adult hoverfly (Diptera: Syrphidae) fitness. Biological Control 61, 1–6. doi:10.1016/j.biocontrol.2011.12.010

Laubertie, E.A., Wratten, S.D., Sedcole, J.R., 2006. The role of odour and visual cues in the pan-trap catching of hoverflies (Diptera: Syrphidae). Annals of Applied Biology 148, 173–178. doi:10.1111/j.1744-7348.2006.00046.x

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16, 545–556. doi:10.1046/j.1365-2435.2002.00664.x

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field–methodology matters! Functional Ecology 22, 134–147. doi:10.1111/j.1365-2435.2007.01339.x

Lee, J.C., Heimpel, G.E., 2005. Impact of flowering buckwheat on Lepidopteran cabbage pests and their parasitoids at two spatial scales. Biological Control, Working at the interface of art and science: how best to select an agent for classical biological control? 34, 290–301. doi:10.1016/j.biocontrol.2005.06.002

Lefebvre, M., Franck, P., Olivares, J., Ricard, J.-M., Mandrin, J.-F., Lavigne, C., 2017. Spider predation on rosy apple aphid in conventional, organic and insecticide-free orchards and its impact on aphid populations. Biological Control 104, 57–65. doi:10.1016/j.biocontrol.2016.10.009

Leroy, P.D., Sabri, A., Heuskin, S., Thonart, P., Lognay, G., Verheggen, F.J., Francis, F., Brostaux, Y., Felton, G.W., Haubruge, É., 2011. Microorganisms from aphid honeydew attract and enhance the efficacy of natural enemies. Nature Communications 2, 348. doi:10.1038/ncomms1347

Letourneau, D.K., Armbrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar, S., Galindo, V., Gutiérrez, C., López, S.D., Mejía, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M., Trujillo, A.R., 2011. Does plant diversity benefit agroecosystems? A synthetic review. Ecological Applications 21, 9–21. doi:10.1890/09-2026.1

Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G., Moreno, C.R., 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 40, 573–592.

Lieblein, G., Breland, T.A., Østergard, E., Salomonsson, L., Francis, C., 2007. Educational perspectives in agroecology: steps on a dual learning ladder toward responsible action. NACTA Journal 51, 37–44.

Lithourgidis, A.S., Dordas, C.A., Damalas, C.A., Vlachostergios, D.N., 2011a. Annual intercrops: an alternative pathway for sustainable agriculture. Australian Journal of Crop Science 5, 396–410.

Lithourgidis, A.S., Vlachostergios, D.N., Dordas, C.A., Damalas, C.A., 2011b. Dry matter yield, nitrogen content, and competition in pea–cereal intercropping systems. European Journal of Agronomy 34, 287–294. doi:10.1016/j.eja.2011.02.007

Lopes, T., Bodson, B., Francis, F., 2015. Associations of wheat with pea can reduce aphid infestations. Neotropical Entomology 44, 286–293. doi:10.1007/s13744-015-0282-9

Lopes, T., Hatt, S., Xu, Q., Chen, J., Liu, Y., Francis, F., 2016. Wheat (Triticum aestivum L.)-based intercropping systems for biological pest control: a review. Pest Management Science 72, 2193–2202. doi:10.1002/ps.4332

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808. doi:10.1126/science.1064088

Louah, L., Visser, M., Baltazar, S., Delobel, V., 2015. Changements de postures du chercheur, de l’agriculteur et de l’enseignant pour l’innovation agroécologique paysanne. Pour 226, 5–10.

Lu, M., Yuan, B., Zeng, M., Chen, J., 2011. Antioxidant capacity and major phenolic compounds of spices commonly consumed in China. Food Research International 44, 530–536. doi:10.1016/j.foodres.2010.10.055

Lu, Z.-X., Zhu, P.-Y., Gurr, G.M., Zheng, X.-S., Read, D.M.Y., Heong, K.-L., Yang, Y.-J., Xu, H.-X., 2014. Mechanisms for flowering plants to benefit arthropod natural enemies of insect pests: Prospects for enhanced use in agriculture. Insect Science 21, 1–12. doi:10.1111/1744-7917.12000

Lunau, K., 2014. Visual ecology of flies with particular reference to colour vision and colour preferences. Journal of Comparative Physiology A 200, 497–512. doi:10.1007/s00359-014-0895-1

Lundgren, J.G., 2009a. Relationships of natural enemies and non-prey foods, Progress in Biological Control. ed. Springer, The Netherlands.

Lundgren, J.G., 2009b. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. Biological Control 51, 294–305. doi:10.1016/j.biocontrol.2009.05.016

Lundin, O., Smith, H.G., Rundlöf, M., Bommarco, R., 2013. When ecosystem services interact: crop pollination benefits depend on the level of pest control. Proceedings of the Royal Society B 280, 20122243. doi:10.1098/rspb.2012.2243

Lyon, A., Bell, M.M., Gratton, C., Jackson, R., 2011. Farming without a recipe: Wisconsin graziers and new directions for agricultural science. Journal of Rural Studies, Subjecting the Objective– Participation, Sustainability and Agroecological Research 27, 384–393. doi:10.1016/j.jrurstud.2011.04.002

Ma, K.Z., Hao, S.G., Zhao, H.Y., Kang, L., 2007. Strip cropping wheat and alfalfa to improve the biological control of the wheat aphid Macrosiphum avenae by the mite Allothrombium ovatum. Agriculture, Ecosystems & Environment 119, 49–52. doi:10.1016/j.agee.2006.06.009

Ma, X.M., Liu, X.X., Zhang, Q.W., Zhao, J.Z., Cai, Q.N., Ma, Y.A., Chen, D.M., 2006. Assessment of cotton aphids, Aphis gossypii, and their natural enemies on aphid-resistant and aphid-susceptible wheat varieties in a wheat–cotton relay intercropping system. Entomologia Experimentalis et Applicata 121, 235–241. doi:10.1111/j.1570-8703.2006.00484.x

Ma, X.M., Zhang, H., Liu, X.X., 2007. Economic profit of intercropping of wheat and transgenic Bt cotton and its effect on cotton aphids and natural enemies. Acta Phytophylacica Sinica 34, 167–172.

Macfadyen, S., Gibson, R., Polaszek, A., Morris, R.J., Craze, P.G., Planqué, R., Symondson, W.O.C., Memmott, J., 2009. Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? Ecology Letters 12, 229–238. doi:10.1111/j.1461-0248.2008.01279.x

Macfadyen, S., Hopkinson, J., Parry, H., Neave, M.J., Bianchi, F.J.J.A., Zalucki, M.P., Schellhorn, N., 2015. Early-season movement dynamics of phytophagous pest and natural enemies across a native vegetation-crop ecotone. Agriculture, Ecosystems & Environment 200, 110–118. doi:10.1016/j.agee.2014.11.012

MacLeod, A., Wratten, S.D., Sotherton, N.W., Thomas, M.B., 2004. ‘Beetle banks’ as refuges for beneficial arthropods in farmland: long-term changes in predator communities and habitat. Agricultural and Forest Entomology 6, 147–154. doi:10.1111/j.1461-9563.2004.00215.x

MacMillan, T., Benton, T.G., 2014. Agriculture: Engage farmers in research. Nature 509, 25–27. doi:10.1038/509025a

Malézieux, E., 2012. Designing cropping systems from nature. Agron. Sustain. Dev. 32, 15–29. doi:10.1007/s13593-011-0027-z

Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., De Tourdonnet, S., Valantin-Morison, M., 2009. Mixing plant species in cropping systems: concepts, tools and models. Agronomy for Sustainable Development 29, 43–62. doi:10.1051/agro:2007057

MAP, 2008. Ecophyto 2018. http://agriculture.gouv.fr/ecophyto-english (accessed 2.16.17).

Marino, P.C., Landis, D.A., 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. Ecological Applications 6, 276–284. doi:10.2307/2269571

Marsden, T., Murdoch, J., 2006. Between the local and the global: confronting complexity in the contemporary agri-food sector. Elservier JAI, Amsterdam.

Marshall, E.J.., Moonen, A.., 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agriculture, Ecosystems & Environment 89, 5–21. doi:10.1016/S0167-8809(01)00315-2

Martínez-Uña, A., Martín, J.M., Fernández-Quintanilla, C., Dorado, J., 2013. Provisioning floral resources to attract aphidophagous hoverflies (Diptera: Syrphidae) useful for pest management in Central Spain. Journal of Economic Entomology 106, 2327–2335. doi:10.1603/EC13180

Masih, R., Hashmi, A.A., Khan, N.A., 1988. Effect of different intercroppings on incidence of insect pests of sugarcane. Pakistan Journal of Agricultural Research 9, 469–472.

Matson, P.A., 1997. Agricultural Intensification and Ecosystem Properties. Science 277, 504–509. doi:10.1126/science.277.5325.504

McKenzie, A.J., Emery, S.B., Franks, J.R., Whittingham, M.J., 2013. Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? Journal of Applied Ecology 50, 1274–1280. doi:10.1111/1365-2664.12122

Médiène, S., Valantin-Morison, M., Sarthou, J.-P., Tourdonnet, S. de, Gosme, M., Bertrand, M., Roger-Estrade, J., Aubertot, J.-N., Rusch, A., Motisi, N., Pelosi, C., Doré, T., 2011. Agroecosystem management and biotic interactions: a review. Agronomy Sust. Developm. 31, 491–514. doi:10.1007/s13593-011-0009-1

Meehan, T.D., Werling, B.P., Landis, D.A., Gratton, C., 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. Proceedings of the National Academy of Sciences 108, 11500–11505. doi:10.1073/pnas.1100751108

Mehto, D.N., Singh, K.M., Singh, R.N., 1988. Influence of intercropping on succession and population build up of insect pests in chickpea, Cicer arietinum Linn. Indian Journal of Entomology 50, 257–275.

Méndez, V.E., Bacon, C.M., Cohen, R., 2013. Agroecology as a transdisciplinary, participatory, and action-oriented approach. Agroecology and Sustainable Food Systems 37, 3–18. doi:10.1080/10440046.2012.736926

Micha, S.G., Wyss, U., 1996. Aphid alarm pheromone (E)-b-farnesene: a host finding kairomone for the aphid primary parasitoid Aphidius uzbekistanicus (Hymenoptera: Aphidiinae). Chemoecology 7, 132–139. doi:10.1007/BF01245965

Miklasiewicz, T.J., Hammond, R.B., 2001. Density of potato leafhopper (Homoptera: Cicadellidae) in response to soybean-wheat cropping systems. Environmental Entomology 30, 204–214. doi:10.1603/0046-225X-30.2.204

Miller, N., Al Dobai, S., Legaspi, J., Sivinski, J., 2013. Estimating attraction of Syrphidae (Diptera) to flowering plants with interception traps. Biocontrol Science and Technology 23, 1040–1052. doi:10.1080/09583157.2013.813907

Mishra, S.K., Kanwat, P.M., Sharma, J.K., 2001. Effect of dates of sowing and intercropping on the seed yield and incidence of mustard aphid, Lipaphis erysimi (Kalt.). Annals of Agricultural Research 22, 445–446.

Mondor, E.B., Warren, J.L., 2000. Unconditioned and conditioned responses to colour in the predatory coccinellid, Harmonia axyridis (Coleoptera: Coccinellidae). European Journal of Entomology 97, 463–467. doi:10.14411/eje.2000.071

Moonen, A.-C., Bàrberi, P., 2008. Functional biodiversity: An agroecosystem approach. Agriculture, Ecosystems & Environment 127, 7–21. doi:10.1016/j.agee.2008.02.013

Morandin, L.A., Kremen, C., 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecological Applications 23, 829–839. doi:10.1890/12-1051.1

Morandin, L.A., Long, R.F., Kremen, C., 2014. Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. Agriculture, Ecosystems & Environment 189, 164–170. doi:10.1016/j.agee.2014.03.030

Morgounov, A., Ferney Gómez-Becerra, H., Abugalieva, A., Dzhunusova, M., Yessimbekova, M., Muminjanov, H., Zelenskiy, Y., Ozturk, L., Cakmak, I., 2007.

Iron and zinc grain density in common wheat grown in Central Asia. Euphytica 155, 193–203. doi:10.1007/s10681-006-9321-2

Morris, M.G., 2008. True Weevils (Part II): (Coleoptera: Curculionidae, Ceutorhynchinae), RES Handbooks for the Identification of British Insects. Royal Entomological Society, London, UK.

Mostafalou, S., Abdollahi, M., 2013. Pesticides and human chronic diseases: Evidences, mechanisms, and perspectives. Toxicology and Applied Pharmacology 268, 157–177. doi:10.1016/j.taap.2013.01.025

Mu, J.Y., Li, Z.H., Mu, S.M., 1993. Control index of Aphis gossypii Glover and comprehensive control of main insect pests on cotton interplanted with wheat. Journal of Shandong Agricultural Sciences 33–36.

Muhammad, N., Compton, S., Incoll, L.D., Akram, W., Lee, J.-J., 2005. Interaction of English grain aphid, Sitobion avenae (F.) and their natural enemies to an agro-forestry environment. Journal of Asia-Pacific Entomology 8, 175–183. doi:10.1016/S1226-8615(08)60089-8

Müller, H., 1881. Alpenblumen, ihre Befruchtung durch Insekten und ihre Anpassungen an dieselben. Leipzig.

Mundt, C.C., Sackett, K.E., Wallace, L.D., 2007. Landscape heterogeneity and disease spread: experimental approaches with a plant pathogen. Journal of the Royal Society Interface 963–972, 963–972. doi:10.1098/rsif.2007.1114

Nakashima, Y., Ida, T.Y., Powell, W., Pickett, J.A., Birkett, M.A., Taki, H., Takabayashi, J., 2016. Field evaluation of synthetic aphid sex pheromone in enhancing suppression of aphid abundance by their natural enemies. BioControl 61, 485–496. doi:10.1007/s10526-016-9734-3

Ndzana, R.A., Magro, A., Bedoussac, L., Justes, E., Journet, E.-P., Hemptinne, J.-L., 2014. Is there an associational resistance of winter pea–durum wheat intercrops towards Acyrthosiphon pisum Harris? J. Appl. Entomol. 138, 577–585. doi:10.1111/jen.12119

Nicholls, C.I., Altieri, M.A., 2013. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. Agron. Sustain. Dev. 33, 257–274. doi:10.1007/s13593-012-0092-y

Nicholls, C.I., Altieri, M.A., 2004. Agroecological bases of ecological engineering for pest management, in: Gurr, G.M., Wratten, S.D., Altieri, M.A. (Eds.), Ecological Engineering for Pest Management. Advances in Habitat Manipulation for Arthropods. CSIRO Publishing, Collingwood, Australia, pp. 33–54.

Nilsson, C., 2010. Impact of soil tillage on parasitoids of oilseed rape pests, in: Williams, I.H. (Ed.), Biocontrol-Based Integrated Management of Oilseed Rape Pests. Springer, The Netherlands, pp. 305–311.

Nilsson, C., 2003. Parasitoids of the pollen beetles, in: Alford, D.V. (Ed.), Biocontrol of Oilseed Rape Pests. Blackwell, Oxford, UK, pp. 73–86.

Ninkovic, V., Dahlin, I., Vucetic, A., Petrovic-Obradovic, O., Glinwood, R., Webster, B., 2013. Volatile exchange between undamaged plants - a new mechanism effecting insect orientation in intercropping. PLoS one 8, 1–9. doi:10.1371/journal.pone.0069431

Norder, L.A., Lamine, C., Bellon, S., Brandenburg, A., 2016. Agroecology: polysemy, pluralism and controversies. Ambiente & Sociedade 19, 1–20. doi:10.1590/1809-4422ASOC129711V1932016

Oerke, E.C., 2006. Crop losses to pests. Journal of Agricultural Science 144, 31–43. doi:10.1017/S0021859605005708

Ofori, F., Stern, W.R., 1987. Cereal-legume intercropping systems. Advances in Agronomy 41, 41–90. doi:10.1016/S0065-2113(08)60802-0

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. Vegan: Community Ecology Package. R package, R package.

Olson, D.M., Wäckers, F.L., 2007. Management of field margins to maximize multiple ecological services. Journal of Applied Ecology 44, 13–21. doi:10.1111/j.1365-2664.2006.01241.x

Ômura, H., Honda, K., Hayashi, N., 1999. Chemical and chromatic bases for preferential visiting by the cabbage butterfly, Pieris rapae, to rape flowers. Journal of Chemical Ecology 25, 1895–1906. doi:10.1023/A:1020990018111

Panagos, P., Borrelli, P., Meusburger, K., van der Zanden, E.H., Poesen, J., Alewell, C., 2015. Modelling the effect of support practices (P-factor) on the reduction of soil erosion by water at European scale. Environmental Science & Policy 51, 23–34. doi:10.1016/j.envsci.2015.03.012

Parajulee, M., Montandon, R., Slosser, J.E., 1997. Relay intercropping to enhance abundance of insect predators of cotton aphid (Aphis gossypii Glover) in Texas cotton. International Journal of Pest Management 43, 227–232. doi:10.1080/096708797228726

Parajulee, M., Slosser, J.E., 1999. Evaluation of potential relay strip crops for predator enhancement in Texas cotton. International Journal of Pest Management 45, 275–286. doi:10.1080/096708799227680

Patt, J.M., Hamilton, G.C., Lashomb, J.H., 1997. Foraging success of parasitoid wasps on flowers: interplay of insect morphology, floral architecture and searching behavior. Entomologia Experimentalis et Applicata 83, 21–30. doi:10.1046/j.1570-7458.1997.00153.x

Paulsen, H.M., Schochow, M., Ulber, B., Kühne, S., Rahmann, G., 2006. Mixed cropping systems for biological control of weeds and pests in organic oilseed crops. Aspects of Applied Biology 79, 215–220.

Pelzer, E., Bazot, M., Makowski, D., Corre-Hellou, G., Naudin, C., Al Rifaï, M., Baranger, E., Bedoussac, L., Biarnès, V., Boucheny, P., Carrouée, B., Dorvillez, D., Foissy, D., Gaillard, B., Guichard, L., Mansard, M.-C., Omon, B., Prieur, L., Yvergniaux, M., Justes, E., Jeuffroy, H., 2012. Pea–wheat intercrops in low-input conditions combine high economic performances and low environmental impacts. European Journal of Agronomy 40, 39–53. doi:10.1016/j.eja.2012.01.010

Perrin, R.M., Phillips, M.L., 1978. Some effects of mixed cropping on the population dynamics of insect pests. Entomologia Experimentalis et Applicata 24, 585–593. doi:10.1111/j.1570-7458.1978.tb02820.x

Petit, S., Boursault, A., Le Guilloux, M., Munier-Jolain, N., Reboud, X., 2011. Weeds in agricultural landscapes. A review. Agronomy for Sustainable Development 31, 309–317. doi:10.1051/agro/2010020

Pfeiffer, A., Silva, E., Colquhoun, J., 2016. Living mulch cover crops for weed control in small-scale applications. Renewable Agriculture and Food Systems 31, 309–317. doi:10.1017/S1742170515000253

Pfiffner, L., Luka, H., Schlatter, C., Juen, A., Traugott, M., 2009. Impact of wildflower strips on biological control of cabbage lepidopterans. Agriculture, Ecosystems & Environment 129, 310–314. doi:10.1016/j.agee.2008.10.003

Pfiffner, L., Wyss, E., 2004. Use of sown wildflower strips to enhance natural enemies of agricultural pests, in: Gurr, G.M., Wratten, S.D., Altieri, M.A. (Eds.), Ecological Engineering for Pest Management. CABI-Publishing, Collingwood, Australia, pp. 167–188.

Phoofolo, M.W., Giles, K.L., Elliott, N.C., 2010. Effects of relay-intercropping sorghum with winter wheat, alfalfa, and cotton on lady beetle (Coleoptera: Coccinellidae) abundance and species composition. Environmental Entomology 39, 763–774. doi:10.1603/EN09122

Pickett, J.A., Rasmussen, H.B., Woodcock, C.M., Matthes, M., Napier, J.A., 2003. Plant stress signalling: understanding and exploiting plant-plant interactions. Biochemical Society Transactions 31, 123–127. doi:10.1042/BST0310123

Piqueray, J., Gilliaux, V., Mahy, G., 2013. Appui scientifique à la mise en oeuvre et à l’entretien des méthodes agro-environnementales bandes de parcelles aménagées (MAE 9). Service Public de Wallonie, Direction générale de l’Agriculture des Ressources naturelles et de l’Environnement.

Pittelkow, C.M., Liang, X., Linquist, B.A., van Groenigen, K.J., Lee, J., Lundy, M.E., van Gestel, N., Six, J., Venterea, R.T., van Kessel, C., 2014. Productivity limits and potentials of the principles of conservation agriculture. Nature 517, 365–368. doi:10.1038/nature13809

Plantegenest, M., Le May, C., Fabre, F., 2007. Landscape epidemiology of plant diseases. Journal of Royal Society Interface 4, 963–972. doi:10.1098/rsif.2007.1114

Poggio, S.L., 2005. Structure of weed communities occurring in monoculture and intercropping of field pea and barley. Agriculture, Ecosystems & Environment 109, 48–58. doi:doi:10.1016/j.agee.2005.02.019

Pope, T.W., Kissen, R., Grant, M., Pickett, J.A., Rossiter, J.T., Powell, G., 2008. Comparative innate responses of the aphid parasitoid Diaeretiella rapae to alkenyl glucosinolate derived isothiocyanates, nitriles, and epithionitriles. Journal of Chemical Ecology 34, 1302–1310. doi:10.1007/s10886-008-9531-2

Poveda, K., Gómez, M.I., Martínez, E., 2008. Diversification practices: their effect on pest regulation and production. Revista Colombiana de Entomologia 34, 131–144.

Power, A.G., 2010. Ecosystem services and agriculture: tradeoffs and synergies. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 2959–2971. doi:10.1098/rstb.2010.0143

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rakhshani, E., Talebi, A.A., Starỳ, P., Tomanović, Ž., Kavallieratos, N.G., Manzari, S., 2008. A review of Aphidius Nees (Hymenoptera: Braconidae: Aphidiinae) in Iran: host associations, distribution and taxonomic notes. Zootaxa 1767, 37–54. doi:10.5281/zenodo.182039

Ramsden, M.W., Menéndez, R., Leather, S.R., Wäckers, F., 2015. Optimizing field margins for biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. Agriculture, Ecosystems & Environment 199, 94–104. doi:10.1016/j.agee.2014.08.024

Rand, T.A., Tylianakis, J.M., Tscharntke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecology Letters 9, 603–614. doi:10.1111/j.1461-0248.2006.00911.x

Raymer, P.L., 2002. Canola: An emerging oilseed crop, in: Janick, J., Whipkey, A. (Eds.), Trends in New Crops and New Uses. ASHS Press, Alexandria, VA, pp. 122–126.

Raynolds, L.T., 2004. The globalization of organic agro-food networks. World Development 32, 725–743. doi:10.1016/j.worlddev.2003.11.008

Reason, P., Bradbury, H., 2001. Introduction: inquiry and participation in search of a world worthy of human inspiration, in: Reason, P., Bradbury, H. (Eds.), Handbook of Action-Research. Sage Publications, London, UK, pp. 1–13.

Reed, H.C., Tan, S.H., Haapanen, K., Killmon, M., Reed, D.K., Elliott, N.C., 1995. Olfactory responses of the parasitoid Diaeretiella rapae (Hymenoptera: Aphidiidae) to odour of plants, aphids, and plant-aphid complexes. Journal of Chemical Ecology 21, 407–418. doi:10.1007/BF02036738

Reid, W., Mooney, H., Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being: general synthesis : a report of the Millennium Ecosystem Assessment. Island Press, Washington, DC.

Ricci, C., Ponti, L., Pires, A., 2005. Migratory flight and pre-diapause feeding of Coccinella septempunctata (Coleoptera) adults in agricultural and mountain ecosystems of Central Italy. European Journal of Entomology 102, 531–538. doi:10.14411/eje.2005.076

Risch, S.J., 1983. Intercropping as cultural pest control: prospects and limitations. Environmental Management 7, 9–14. doi:10.1007/BF01867035

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39, 157–176. doi:10.1046/j.1365-2664.2002.00695.x

Rodriguez-Saona, C., Kaplan, I., Braasch, J., Chinnasamy, D., Williams, L., 2011. Field responses of predaceous arthropods to methyl salicylate: A meta-analysis and case study in cranberries. Biological Control 59, 294–303. doi:10.1016/j.biocontrol.2011.06.017

Root, R.B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). Ecological Monographs 43, 95–124. doi:10.2307/1942161

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60.

Rosset, P.M., Martínez-Torres, M.E., 2012. Rural social movements and agroecology: context, theory, and process. Ecology and Society 17, 17. doi:10.5751/ES-05000-170317

Rouabah, A., Villerd, J., Amiaud, B., Plantureux, S., Lasserre-Joulin, F., 2015. Response of carabid beetles diversity and size distribution to the vegetation structure within differently managed field margins. Agriculture, Ecosystems & Environment 200, 21–32. doi:10.1016/j.agee.2014.10.011

Roy, H.E., Brown, P.M.J., Comont, R.F., Poland, R.L., Sloggett, J.J., 2013. Ladybirds, Naturalists' Handbook. Pelagic Publishing, Exeter.

Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G., Ekbom, B., 2013a. Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. Journal of Applied Ecology 50, 345–354. doi:10.1111/1365-2664.12055

Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J.M., Landis, D.A., Thies, C., Tscharntke, T., Weisser, W.W., Winqvist, C., Woltz, M., Bommarco, R., 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. Agriculture, Ecosystems & Environment 221, 198–204. doi:10.1016/j.agee.2016.01.039

Rusch, A., Valantin-Morison, M., Sarthou, J.-P., Roger-Estrade, J., 2013b. Effect of crop management and landscape context on insect pest populations and crop damage. Agriculture, Ecosystems & Environment 166, 118– 125. doi:10.1016/j.agee.2011.05.004

Rusch, A., Valantin-Morison, M., Sarthou, J.-P., Roger-Estrade, J., 2011. Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. Landscape Ecology 26, 473–486. doi:10.1007/s10980-011-9573-7

Saeed, Q., Zaka, M., Saeed, S., Bakhtawar, M., 2013. Lucerne as trap crop in wheat for development of predators population against wheat aphids (Aphididae: Homoptera). Pakistan Journal of Zoology 45, 193–196.

Salveter, R., 1998. The influence of sown herb strips and spontaneous weeds on the larval stages of aphidophagous hoverflies (Dipt., Syrphidae). Journal of Applied Entomology 122, 103–114. doi:10.1111/j.1439-0418.1998.tb01470.x

San Martin, G., 2004. Clé de détermination des Chrysopidae de Belgique. Jeune et Nature asbl, Wavre.

Sarthou, J.-P., Badoz, A., Vaissière, B., Chevallier, A., Rusch, A., 2014. Local more than landscape parameters structure natural enemycommunities during their overwintering in semi-natural habitats. Agriculture, Ecosystems & Environment 194, 17–28. doi:10.1016/j.agee.2014.04.018

Sarwar, M., 2011. Effects of wheat and barley intercropping ecosystem on the prevalence of aphid (Hemiptera: Aphididae) population in canola (Brassica napus L.) crop. Biological Diversity and Conservation 4, 11–16.

Schaller, M., Nentwig, W., 2000. Olfactory orientation of the seven-spot ladybird beetle, Coccinella septempuctata (Colleoptera: Coccinellidae): Attraction of adults to plants and conspecific females. European Journal of Entomology 97, 155–159. doi:10.14411/eje.2000.029

Schellhorn, N., Bianchi, F.J.J.A., Hsu, C.L., 2014. Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. Annual Review of Entomology 59, 559–581. doi:10.1146/annurev-ento-011613-161952

Schneider, M.K., Lüscher, G., Jeanneret, P., Arndorfer, M., Ammari, Y., Bailey, D., Balázs, K., Báldi, A., Choisis, J.-P., Dennis, P., Eiter, S., Fjellstad, W., Fraser, M.D., Frank, T., Friedel, J.K., Garchi, S., Geijzendorffer, I.R., Gomiero, T., Gonzalez-Bornay, G., Hector, A., Jerkovich, G., Jongman, R.H.G., Kakudidi, E., Kainz, M., Kovács-Hostyánszki, A., Moreno, G., Nkwiine, C., Opio, J., Oschatz, M.-L., Paoletti, M.G., Pointereau, P., Pulido, F.J., Sarthou, J.-P., Siebrecht, N., Sommaggio, D., Turnbull, L.A., Wolfrum, S., Herzog, F., 2014. Gains to species diversity in organically farmed fields are not propagated at the farm level. Nat Commun 5, 4151. doi:10.1038/ncomms5151

Scholz, R.W., Steiner, G., 2015. Transdisciplinarity at the crossroads. Sustainability Science 10, 521–526. doi:10.1007/s11625-015-0338-0

Service Public de Wallonie, 2014a. Evolution de l'économie agricole et horticole de la Wallonie 2012-2013. http://agriculture.wallonie.be/apps/spip_wolwin/IMG/pdf/rapport2012.pdf (accessed 3.2.14).

Service Public de Wallonie, 2014b. L'agriculture wallone en chiffres. http://agriculture.wallonie.be/apps/spip_wolwin/IMG/pdf/L_agriculture_wallonne_en_chiffres_2011.pdf (accessed 2.20.15).

Service Public de Wallonie, 2014c. Environmental Outlook for Wallonia, SPW Editions. ed, Bilan et perspectives. Jambes - Namur.

Service Public de Wallonie, 2014d. Cartes des Sols de Wallonie. http://geoapps.wallonie.be/CigaleInter/#CTX=CNSW#BBOX=172556.38064514095,175228.67765640165,139464.25249213536,140017.23276476256 (accessed 11.28.16).

Sherawat, S.M., Butt, A., Tahir, H.M., 2012. Effect of brassica strips on the population of aphids and arthropod predators in wheat ecosystem. Pakistan Journal of Zoology 44, 173–179.

Sivinski, J., Wahl, D., Holler, T., Al Dobai, S., Sivinski, R., 2011. Conserving natural enemies with flowering plants: Estimating floral attractiveness to parasitic Hymenoptera and attraction's relationship to flower and plant morphology. Biological Control 58, 208–214. doi:10.1016/j.biocontrol.2011.05.002

Skelsey, P., Rossing, W.A.H., Kessel, G.J.T., van der Werf, W., 2010. Invasion of Phytophthora infestans at the landscape level: How do spatial scale and weather modulate the consequences of spatial heterogeneity in host resistance? Phytopathology 100, 1146–1161. doi:10.1002/ps.4145

Skelton, L.E., Barrett, G.W., 2005. A comparison of conventional and alternative agroecosystems using alfalfa (Medicago sativa) and winter wheat (Triticum aestivum). Renewable Agriculture and Food Systems 20, 38–47. doi: 10.1079/RAF200478

Skevas, T., Oude Lansink, A.G.J.M., Stefanou, S.E., 2013. Designing the emerging EU pesticide policy: A literature review. NJAS - Wageningen Journal of Life Sciences 64–65, 95–103. doi:10.1016/j.njas.2012.09.001

Soane, B.D., Ball, B.C., Arvidsson, J., Basch, G., Moreno, F., Roger-Estrade, J., 2012. No-till in northern, western and south-western Europe: A review of problems and opportunities for crop production and the environment. Soil & Tillage Research 118, 66–87. doi:10.1016/j.still.2011.10.015

Souchère, V., Millair, L., Escheverria, J., Bousquet, F., Le Page, C., Etienne, M., 2010. Co-constructing with stakeholders a role-playing game to initiate collective management of erosive runoff risks at the watershed scale. Environmental Modelling and Software 25, 1359–1370. doi:10.1016/j.envsoft.2009.03.002

Stamps, W.T., McGraw, R.L., Godsey, L., Woods, T.L., 2009. The ecology and economics of insect pest management in nut tree alley cropping systems in the Midwestern United States. Agriculture, Ecosystems & Environment 131, 4–8. doi:10.1016/j.agee.2008.06.012

Stanley, J., Preetha, G., 2016. Pesticide toxicity to non-target organisms. Exposure, toxicity and risk assessment methodologies. Springer Nature, Dordrecht.

Stassart, P.M., Baret, P., Grégoire, J.-C., Hance, T., Mormont, M., Reheul, D., Stilmant, D., Vanloqueren, G., Visser, M., 2012. L’agroécologie: trajectoire et potentiel pour une transition vers des systèmes alimentaires durables, in: Van Dam, D., Nizet, J., Streith, M., Stassart, P.M. (Eds.), Agroéocologie: Entre Pratiques et Sciences Sociales. Educagri éditions, Dijon, France, pp. 25–51.

Stassart, P.M., Jamar, D., 2008. Steak up to the horns! The conventionalization of organic stock farming: knowledge lock-in in the agrifood chain. GeoJournal 73, 31–44. doi:10.1007/s10708-008-9176-2

Stassart, P.M., Mormont, M., Jamar, D., 2008. Recherche intervention pour la transition vers le développement durable. Économie rurale 306, 8–22.

Steingröver, E.G., Geertsema, W., van Wingerden, W.K.R.E., 2010. Designing agricultural landscapes for natural pest control: a transdisciplinary approach in the Hoeksche Waard (The Netherlands). Landscape Ecology 25, 825–838. doi:10.1007/s10980-010-9489-7

Stevens, C.J., Quinton, J.N., Bailey, A.P., Deasy, C., Silgram, M., Jackson, 2009. The effects of minimal tillage, contour cultivation and in-field vegetative barriers on soil erosion and phosphorus loss. Soil and Tillage Research 106, 145–151. doi:10.1016/j.still.2009.04.009

Stinner, B.R., House, G.J., 1990. Arthropods and other invertebrates in conservation-tillage agriculture. Annual Review of Entomology 35, 299–318. doi:10.1146/annurev.en.35.010190.001503

Straub, C.S., Snyder, W.E., 2006. Species Identity Dominates the Relationship between Predator Biodiversity and Herbivore Suppression. Ecology 87, 277–282. doi:10.2307/20068940

Sutherland, J.P., Sullivan, M.S., Poppy, G.M., 2001. Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. Agricultural and Forest Entomology 3, 57–64. doi:10.1046/j.1461-9563.2001.00090.x

Sutherland, J.P., Sullivan, M.S., Poppy, G.M., 1999. The influence of floral character on the foraging behaviour of the hoverfly, Episyrphus balteatus. Entomologia Experimentalis et Applicata 93, 157–164. doi:10.1046/j.1570-7458.1999.00574.x

Sutherland, L.-A., Burton, R.J.F., Ingram, J., Blackstock, K., Slee, B., Gotts, N., 2012. Triggering change: Towards a conceptualisation of major change processes in farm decision-making. Journal of Environmental Management 104, 142–151. doi:10.1016/j.jenvman.2012.03.013

Tahvanainen, J.O., Root, R.B., 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, Phyllotreta crucifera (Coleoptera: Chrysomelidae). Oecologia 10, 321–346. doi:10.1007/BF00345736

Tamburini, G., De Simone, S., Sigura, M., Boscutti, F., Marini, L., 2016. Conservation tillage mitigates the negative effect of landscape simplification on biological control. Journal of Applied Ecology 53, 233–241. doi:10.1111/1365-2664.12544

Tansey, J.A., Dosdall, L.M., Keddie, B.A., Noble, S.D., 2010. Contributions of visual cues to cabbage seedpod weevil, Ceutorhynchus obstrictus (Marsham) (Coleoptera: Curculionidae), resistance in novel host genotypes. Crop Protection 29, 476–481. doi:10.1016/j.cropro.2009.11.005

Taylor, L.R., 1981. Euraphid 1980: aphid forecasting and pathogens & a handbook for aphid identification. Rothamsted Experimental Station, Harpenden.

Tenhumberg, B., Poehling, H.-M., 1995. Syrphids as natural enemies of cereal aphids in Germany: Aspects of their biology and efficacy in different years and regions. Agriculture, Ecosystems & Environment 52, 39–43. doi:10.1016/0167-8809(94)09007-T

Theunissen, J., 1994. Intercropping in field vegetable crops: pest management by agrosystem diversification, an overview. Pesticide Science 42, 65–68. doi:10.1002/ps.2780420111

Thieme, T., Heimbach, U., Müller, A., 2010. Chemical Control of Insect Pests and Insecticide Resistance in Oilseed Rape, in: Williams, I.H. (Ed.), Biocontrol-Based Integrated Management of Oilseed Rape Pests. Springer Netherlands, pp. 313–335.

Thomas, C.F.., Marshall, E.J.., 1999. Arthropod abundance and diversity in differently vegetated margins of arable fields. Agriculture, Ecosystems & Environment 72, 131–144. doi:10.1016/S0167-8809(98)00169-8

Thorsted, M.D., Weiner, J., Olesen, J.E., 2006. Above- and below-ground competition between intercropped winter wheat Triticum aestivum and white clover Trifolium repens. Journal of Applied Ecology 43, 237–245. doi:10.1111/j.1365-2664.2006.01131.x

Tilman, D., 1999. Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. Proceedings of the National Academy of Sciences 96, 5995–6000. doi:10.1073/pnas.96.11.5995

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418, 671–677. doi:10.1038/nature01014

Tingey, W.M., Lamont, W.J., 1988. Insect abundance in field beans altered by intercropping. Bulletin of Entomological Research 78, 527–535. doi:10.1017/S0007485300013274

Tiwari, M., Singh, C.P., Goel, R., 2005. Effect of intercropping on the population, dynamics of insect pests and yield of mustard. Shashpa 12, 106–110.

Tomanović, Ž., Kavallieratos, N.G., Starȳ, P., Athanassiou, C.G., Žikić, V., Petrović-Obradović, O., Sarlis, G.P., 2003. Aphidius Nees aphid parasitoids (Hymenoptera, Braconidae, Aphidiinae) in Serbia and Montenegro: tritrophic associations and key. Acta entomologica serbica 8, 15–39.

Ton, J., D'Alessandro, M., Jourdie, V., Jakab, G., Karlen, D., Held, M., Mauch-Mani, B., Turlings, T.C., 2007. Priming by airborne signals boosts direct and indirect resistance in maize. The Plant Journal 49, 16–26. doi:10.1111/j.1365-313X.2006.02935.x

Tonhasca, A., Byrne, D.N., 1994. The effects of crop diversification on herbivorous insects: a meta-analysis approach. Ecological Entomology 19, 239–244. doi:10.1111/j.1365-2311.1994.tb00415.x

Tooker, J.F., Hauser, M., Hanks, L.M., 2006. Floral host plants of Syrphidae and Tachinidae (Diptera) of central Illinois. Annals of the Entomological Society of America 99, 96–112. doi:10.1603/0013-8746(2006)099[0096:FHPOSA]2.0.CO;2

Torquebiau, E.F., 2000. A renewed perspective on agroforestry concepts and classification. Comptes Rendus de l'Academie des Sciences-Series III-Sciences de la Vie 323, 1009–1017. doi:10.1016/S0764-4469(00)01239-7

Torralba, M., Fagerholm, N., Burgess, P.J., Moreno, G., Plieninger, T., 2016. Do European agroforestry systems enhance biodiversity and ecosystem services? A meta-analysis. Agriculture, Ecosystems & Environment 230, 150–161. doi:10.1016/j.agee.2016.06.002

Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A.R., Jonsson, M., Larsen, A., Martin, E.A., Martínez-Salinas, A., Meehan, T.D., O'Rourke, M., Poveda, K., Rosenheim, J.A., Rusch, A., Schellhorn, N., Wanger, T.C., Wratten, S.D., Zhang, W., 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. Biological Conservation 204, 449–458. doi:10.1016/j.biocon.2016.10.001

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecology Letters 8, 857–874. doi:10.1111/j.1461-0248.2005.00782.x

Tschumi, M., Albrecht, M., Bärtschi, C., Collatz, J., Entling, M.H., Jacot, K., 2016a. Perennial, species-rich wildflower strips enhance pest control and crop yield. Agriculture, Ecosystems & Environment 220, 97–103. doi:10.1016/j.agee.2016.01.001

Tschumi, M., Albrecht, M., Collatz, J., Dubsky, V., Entling, M.H., Najar-Rodriguez, A.J., Jacot, K., 2016b. Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. Journal of Applied Ecology 53, 1169–1176. doi:10.1111/1365-2664.12653

Tschumi, M., Albrecht, M., Entling, M.H., Jacot, K., 2015. High effectiveness of tailored flower strips in reducing pests and crop plant damage. Proceedings of the Royal Society B 282, 20151369. doi:10.1098/rspb.2015.1369

Tschumi, M., Albrecht, M., Entling, M.H., Jacot, K., 2014. Targeted flower strips effectively promote natural enemies of aphids. IOBC/wprs Bulletin 100, 131–135. doi:10.13140/2.1.4382.0488

Tsonkova, P., Böhm, C., Quinkenstein, A., Freese, D., 2012. Ecological benefits provided by alley cropping systems for production of woody biomass in the temperate region: a review. Agroforestry Systems 85, 133–152. doi:10.1007/s10457-012-9494-8

Turnbull, L.A., Rees, M., Crawley, M.J., 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. Journal of Ecology 87, 899–912. doi:10.1046/j.1365-2745.1999.00405.x

Tylianakis, J.M., Didham, R.K., Wratten, S.D., 2004. Improved fitness of aphid parasitoids receiving resource subsidies. Ecology 85, 658–666. doi:10.1890/03-0222

Ulber, B., 2003. Parasitoids of Ceutorhynchid stem weevils, in: Alford, D.V. (Ed.), Biocontrol of Oilseed Rape Pests. Blackwell, Oxford, UK, pp. 87–96.

Ulber, B., Williams, I.H., Luik, A., Klukowski, Z., Nilsson, C., 2010. Parasitoids of oilseed rape pests in Europe: Key species for conservation biocontrol, in: Williams, I.H. (Ed.), Biocontrol-Based Integrated Management of Oilseed Rape Pests. Springer, The Netherlands, pp. 45–76.

Uvah, I.I.I., Coaker, T.H., 1984. Effect of mixed cropping on some insect pests of carrots and onions. Entomologia experimentalis et applicata 36, 159–167. doi:10.1111/j.1570-7458.1984.tb03422.x

Uyttenbroeck, R., Hatt, S., Paul, A., Boeraeve, F., Piqueray, J., Francis, F., Danthine, S., Fréderich, M., Dufrêne, M., Bodson, B., Monty, A., 2016. Pros and cons of flowers strips for farmers: a review. Biotechnology, Agronomy, Society, Environment 20, 225–235.

Uyttenbroeck, R., Hatt, S., Piqueray, J., Paul, A., Bodson, B., Francis, F., Monty, A., 2015. Creating perennial flower strips: think functional! Agriculture and Agricultural Science Procedia 6, 95–101. doi:10.1016/j.aaspro.2015.08.044

Van Emden, H.F., Harrington, R. (Eds.), 2007. Aphids as crop pests. CABI, Cambridge, Massachusetts.

Van Rijn, P.C.J., Kooijman, J., Wäckers, F.L., 2013. The contribution of floral resources and honeydew to the performance of predatory hoverflies (Diptera: Syrphidae). Biological Control 67, 32–38. doi:10.1016/j.biocontrol.2013.06.014

Van Rijn, P.C.J., Wäckers, F.L., 2016. Nectar accessibility determines fitness, flower choice and abundance of hoverflies that provide natural pest control. Journal of Applied Ecology 53, 925–933. doi:10.1111/1365-2664.12605

Van Rijn, P.C.J., Wäckers, F.L., 2010. The suitability of field margin flowers as food source for zoophagous hoverflies. IOBC/wprs Bulletin 56, 125–128.

van Veen, M.P., 2010. Hoverflies of Northwest Europe: identification keys to the Syrphidae. KNNV Publishing, Zeist.

Vandereycken, A., Durieux, D., Joie, E., Sloggett, J.J., Haubruge, É., Verheggen, F.J., 2013. Is the multicolored Asian ladybeetle, Harmonia axyridis, the most abundant natural enemy to aphids in agroecosystems? Journal of Insect Science 13, 1–14. doi:10.1673/031.013.15801

Vandermeer, J., 1989. The ecology of intercropping. Cambridge University Press, New York, USA.

Vandermoten, S., Mescher, M., Francis, F., Haubruge, É., Verheggen, F.J., 2012. Aphid alarm pheromone: An overview of current knowledge on biosynthesis and functions. Insect Biochemistry and Molecular Biology 42, 155–163. doi:10.1016/j.ibmb.2011.11.008

Vankeerberghen, A., Stassart, P.M., 2016. The transition to conservation agriculture: an insularization process towards sustainability. International Journal of Agricultural Sustainability 14, 392–407. doi:10.1080/14735903.2016.1141561

Vanloqueren, G., Baret, P., 2008. Why are ecological, low-input, multi-resistant wheat cultivars slow to develop commercially? A Belgian agricultural ‘lock-in’ case study. Ecological Economics 66, 436–446. doi:10.1016/j.ecolecon.2007.10.007

Vanloqueren, G., Baret, P.V., 2009. How agricultural research systems shape a technological regime that develops genetic engineering but locks out agroecological innovations. Research Policy 38, 971–983. doi:10.1016/j.respol.2009.02.008

Vattala, H.D., Wratten, S.D., Vattala, C.B., Phillips, F.L., Wäckers, F.L., 2006. The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. Biological Control 39, 179–185. doi:10.1016/j.biocontrol.2006.06.003

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4th Edition. ed. Springer, New York, USA.

Ver Hoef, J.M., Boveng, P.L., 2007. Quasi-Poisson vs. Negative binomial regression: how should we model overdispersed count data? Ecology 88, 2766–2772. doi:10.1890/07-0043.1

Veres, A., Petit, S., Conord, C., Lavigne, C., 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. Agriculture, Ecosystems & Environment 166, 110–117. doi:10.1016/j.agee.2011.05.027

Verheggen, F., Arnaud, L., Bartram, S., Gohy, M., Haubruge, E., 2008. Aphid and plant volatiles induce oviposition in an aphidophagous hoverfly. Journal of Chemical Ecology 34, 301–307. doi:10.1007/s10886-008-9434-2

Verheggen, F., Haubruge, E., De Moraes, C., Mescher, M., 2013. Aphid responses to volatile cues from turnip plants (Brassica rapa) infested with phloem-feeding and chewing herbivores. Arthropod-Plant Interactions 7, 567–577. doi:0.1007/s11829-013-9272-1

Verret, V., Gardarin, A., Pelzer, E., Médiène, S., Makowski, D., Valantin-Morison, M., 2017. Can legume companion plants control weeds without decreasing crop yield? A meta-analysis. Field Crops Research 204, 158–168. doi:10.1016/j.fcr.2017.01.010

Villenave, J., Deutsch, B., Lodé, T., Rat-Morris, E., 2006. Pollen preference of the Chrysoperla species (Neuroptera: Chrysopidae) occurring in the crop environment in western France. European Journal of Entomology 103, 771–777. doi:10.14411/eje.2006.104

Vilsmaier, U., Engbers, M., Luthardt, P., Maas-Deipenbrock, R.M., Wunderlich, S., Scholz, R.W., 2015. Case-based mutual learning sessions: knowledge integration and transfer in transdisciplinary processes. Sustainability Science 10, 563–580. doi:10.1007/s11625-015-0335-3

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. doi:10.1111/j.0030-1299.2007.15559.x

Wäckers, F., 2004. Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. Biological Control 29, 307–314. doi:10.1016/j.biocontrol.2003.08.005

Wäckers, F.L., 1994. The effect of food deprivation on the innate visual and olfactory preferences in the parasitoid Cotesia rubecula. Journal of Insect Physiology 40, 641–649. doi:10.1016/0022-1910(94)90091-4

Wäckers, F.L., Van Rijn, P.C.J., 2012. Pick and mix: selecting flowering plants to meet the requirements of target biological control insects, in: Gurr, G.M., Wratten, S.D., Snyder, W.E., Read, D.M.Y. (Eds.), Biodiversity and Insect Pests: Key Issues for Sustainable Management. John Wiley & Sons, Ltd, Chichester, UK, pp. 139– 165.

Wang, G., Cui, L.L., Dong, J., Francis, F., Liu, Y., Tooker, J., 2011. Combining intercropping with semiochemical releases: optimization of alternative control of Sitobion avenae in wheat crops in China. Entomologia Experimentalis et Applicata 140, 189–195. doi:10.1111/j.1570-7458.2011.01150.x

Wang, H.Z., Zhao, H.L., 1993. The ecological effects of cotton interplanted in wheat field on cotton pests. Acta Phytophylacica Sinica 20, 163–167.

Wang, W., Yao, J., Li, H.B., Zhang, Y., Wang, D., Ma, G.L., 2009. Occurrence of predators in different cotton fields in south Xinjiang. Chinese Journal of Plant Protection 5, 10.

Wang, W.L., Liu, Y., Chen, J.L., Ji, X.L., Zhou, H.B., Wang, G., 2009. Impact of intercropping aphid-resistant wheat cultivars with oilseed rape on wheat aphid (Sitobion avenae) and its natural enemies. Acta Ecologica Sinica 29, 186–191. doi:doi:10.1016/j.chnaes.2009.07.009

Wang, W.L., Liu, Y., Ji, X.L., Wang, G., Zhou, H.B., 2008. Effects of wheat-oilseed rape or wheat-garlic intercropping on the population dynamics of Sitobion avenae and its main natural enemies. Ying yong sheng tai xue bao = The journal of applied ecology 19, 1331–1336.

Warner, K.D., 2007. The quality of sustainability: agroecological partnerships and the geographic branding of California winegrapes. Journal of Rural Studies 23, 142–155. doi:10.1016/j.jrurstud.2006.09.009

Werling, B.P., Dickson, T.L., Isaacs, R., Gaines, H., Gratton, C., Gross, K.L., Liere, H., Malmstrom, C.M., Meehan, T.D., Ruan, L., Robertson, B.A., Robertson, G.P., Schmidt, T.M., Schrotenboer, A.C., Teal, T.K., Wilson, J.K., Landis, D.A., 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. Proceedings of the National Academy of Sciences 111, 1652–1657. doi:10.1073/pnas.1309492111

Westphal, C., Vidal, S., Horgan, F.G., Gurr, G.M., Escalada, M., Chien, H.V., Tscharntke, T., Heong, K.-L., Settele, J., 2015. Promoting multiple ecosystem services with flower strips and participatory approaches in rice production landscapes. Basic and Applied Ecology 16, 681–689. doi:10.1016/j.baae.2015.10.004

Wezel, A., Casagrande, M., Celette, F., Vian, J.-F., Ferrer, A., Peigné, J., 2014a. Agroecological practices for sustainable agriculture. A review. Agronomy for Sustainable Development 34, 1–20. doi:10.1007/s13593-013-0180-7

Wezel, A., Fleury, P., David, C., Mundler, P., 2014b. The food system approach in agroecology supported by natural and social sciences, in: Benkeblia, N. (Ed.), Agroecology, Ecosystems and Sustainability. CRC Press / Taylor and Francis Group, pp. 181–199.

Williams, I.H., 2010. The major insect pests of oilseed rape in Europe and their management: an overview, in: Williams, I.H. (Ed.), Biocontrol-Based Integrated Management of Oilseed Rape Pests. Springer, The Netherlands, pp. 1–43.

Williams, I.H., 2003. Parasitoids of the cabbage seed weevil, in: Alford, D.V. (Ed.), Biocontrol of Oilseed Rape Pests. Blackwell, Oxford, UK, pp. 97–112.

Williams, I.H., Cook, S.M., 2010. Crop location by oilseed rape pests and host location by their parasitoids, in: Williams, I.H. (Ed.), Biocontrol-Based Integrated Management of Oilseed Rape Pests. Springer, The Netherlands, pp. 215–244.

Woltz, J.M., Isaacs, R., Landis, D.A., 2012. Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. Agriculture, Ecosystems & Environment 152, 40–49. doi:10.1016/j.agee.2012.02.008

Woodcock, B.A., Westbury, D.B., Tscheulin, T., Harrison-Cripps, J., Harris, S.J., Ramsey, A.J., Brown, V.K., Potts, S.G., 2008. Effects of seed mixture and management on beetle assemblages of arable field margins. Agriculture, Ecosystems & Environment 125, 246–254. doi:10.1016/j.agee.2008.01.004

Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R., Tylianakis, J.M., 2003. Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. Oecologia 134, 605–611. doi:10.1007/s00442-002-1128-9

Xia, J.Y., Wang, C.Y., Cui, S.Z., 2000. Comparative studies on life tables of cotton bollworm (Helicoverpa armigera) in different cotton cropping systems. Acta Gossypii Sinica 12, 281–287.

Xie, H.C., Chen, J.L., Cheng, D.F., Zhou, H.B., Sun, J.R., Liu, Y., Francis, F., 2012a. Impact of wheat-mung bean intercropping on English grain aphid (Hemiptera: Aphididae) populations and its natural enemy. Journal of Economic Entomology 105, 854–859. doi:10.1603/EC11214

Xie, H.C., Chen, J.L., Cheng, D.F., Zhou, H.B., Sun, J.R., Liu, Y., Francis, F., 2012b. The function of ecological regulation to aphids in the wheat intercropping field. Chinese Journal of Plant Protection 1, 12.

Xu, Q., Hatt, S., Lopes, T., Yong, Z., Bodson, B., Chen, J., Francis, F., 2017. A push-pull strategy to control aphids combines intercropping with semiochemical releases. Journal of Pest Science In press.

Yang, J.C., Liu, J.J., An, Z.Y., Zhu, Y.Y., Li, C.Y., Chen, X.D., Lu, Y.E., Li, H.Y., Dian, L.F., 2009. Analyses on effect of interplanting on diseases and pests control and yield increase of wheat and faba bean. Journal of Yunnan Agricultural University 24, 340–348.

Zehnder, G., Gurr, G.M., Kühne, S., Wade, M.R., Wratten, S.D., Wyss, E., 2007. Arthropod pest management in organic crops. Annual Review of Entomology 52, 57–80. doi:10.1146/annurev.ento.52.110405.091337

Zepeda, L., Sirieix, L., Pizarro, A., Corderre, F., Rodier, F., 2013. A conceptual framework for analyzing consumers' food label preferences: an exploratory study of sustainability labels in France, Quebec, Spain and the US. International Journal of Consumer Studies 37, 605–616. doi:10.1111/ijcs.12041

Zhang, L., Spiertz, J.H.J., Zhang, S., Li, B., van der Werf, W., 2008. Nitrogen economy in relay intercropping systems of wheat and cotton. Plant and Soil 303, 55–68. doi:10.1007/s11104-007-9442-y

Zhang, L., van der Werf, W., Zhang, S., Li, B., Spiertz, J.H.J., 2007. Growth, yield and quality of wheat and cotton in relay strip intercropping systems. Field Crops Research 103, 178–188. doi:10.1016/j.fcr.2007.06.002

Zhang, S.H., 1990. Improvement of integrated control of cotton diseases and insect pests at seedling stage. China Cottons 3, 42–43.

Zhang, W., Ricketts, T.H., Kremen, C., Carney, K., Swinton, S.M., 2007. Ecosystem services and dis-services to agriculture. Ecological Economics 64, 253–260. doi:10.1016/j.ecolecon.2007.02.024

Zhao, J.Z., Yang, Q.H., Xie, Y.Q., 1987. Effect of intercropping of wheat with cotton on cotton pest. China Cottons.

Zhao, Z.-H., Reddy, G.V.P., Hui, C., Li, B.-L., 2016. Approaches and mechanisms for ecologically based pest management across multiple scales. Agriculture, Ecosystems & Environment 230, 199–209. doi:10.1016/j.agee.2016.06.010

Zhou, H.B., Chen, J.L., Cheng, D.F., Liu, Y., Sun, J.R., 2009a. Effects of wheat-pea intercropping on the population dynamics of Sitobion avenae (Homoptera: Aphididae) and its main natural enemies. Acta Ecologica Sinica 52, 775–782.

Zhou, H.B., Chen, J.L., Liu, Y., Francis, F., Haubruge, É., Bragard, C., Sun, J.R., Cheng, D.F., 2013a. Influence of garlic intercropping or active emitted volatiles in releasers on aphid and related beneficial in wheat fields in China. Journal of Integrative Agriculture 12, 467–473. doi:doi:10.1016/S2095-3119(13)60247-6

Zhou, H.B., Chen, L., Chen, J.L., Cheng, D.F., Liu, Y., Sun, J.R., 2009b. Effect of intercropping between wheat and pea on spatial distribution of Sitobion avenae based on GIS. Scientia Agricultura Sinica 42, 3904–3913. doi:10.3864/j.issn.0578-1752.2009.11.018

Zhou, H.B., Chen, L., Chen, J.L., Francis, F., Haubruge, E., Liu, Y., Bragard, C., Cheng, D.F., 2013b. Adaptation of wheat-pea intercropping pattern in China to reduce Sitobion avenae (Hemiptera: Aphididae) occurrence by promoting natural enemies. Agroecology and Sustainable Food Systems 37, 1001–1016. doi:10.1080/21683565.2013.763887

Zhu, J., Park, K.-C., 2005. Methyl salicylate, a soybean aphid-induced plant volatile attractive to predator Coccinella septempunctata. Journal of Chemical Ecology 31, 1733–1746. doi:10.1007/s10886-005-5923-8

Appendix - Publications and communications

1. Publications included in the thesis

Hatt S., Uyttenbroeck R., Lopes T., Chen J., Piqueray J., Monty A., Francis F. (2017). Effect of flower traits and hosts on the abundance of parasitoids in perennial multiple species wildflower strips sown within oilseed rape (*Brassica napus* L.) crops. *Arthropod-Plant Interactions* (Accepted).

Hatt S., Uyttenbroeck R., Lopes T., Mouchon P., Chen J., Piqueray J., Monty A., Francis F. (2017). Do flower mixtures with high functional diversity enhance aphid predators in wildflower strips? *European Journal of Entomology*, 114, 66-76.

Hatt S., Lopes, T. Boeraeve F., Chen J., Francis F. (2017). Pest regulation and support of natural enemies in agriculture: Experimental evidence of within field wildflower strips. *Ecological Engineering*, 98, 240-245.

Lopes T.*, Hatt, S.*, Xu, Q., Chen, J., Liu, Y., Francis, F. (2016). Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control. *Pest Management Science*, 72, 2193-2202. [*Equally contributed authors]

Hatt S.*, Artru S.*, Brédart D., Lassois L., Francis F., Haubruge E., Garré S., Stassart P. M., Dufrêne M., Monty A., Boeraeve F. (2016). Towards sustainable food systems: the concept of agroecology and how it questions current research practices. A review. *Biotechnology, Agronomy, Society and Environment*, 20(S1), 215-224. [*Equally contributed authors]

Hatt S., Uyttenbroeck R., Bodson B., Piqueray J., Monty A., Francis F. (2015). Des bandes fleuries pour la lutte biologique : état des lieux, limites et perspectives en Wallonie – Une synthèse bibliographique. *Entomologie Faunistique*, 68, 159-168.

Hatt S., Xu Q., Francis F., Chen J. Does wheat – oilseed rape intercropping combined with the slow release of ladybeetle sex pheromone allow reducing aphids and increasing their natural enemies in China? *Submitted to Journal of Asia-Pacific Entomology.*

Hatt S., Boeraeve F., Artru S., Dufrêne M., Francis F. From biological control of insect pests to the provision of multiple ecosystem services: Spatial diversification of crop and non-crop habitats in an agroecological perspective. *Submitted to Biological Conservation.*

2. Publications not included in the thesis

Brédart D.*, Hatt S.*, Méhu M., Francis F., Stassart P. M. (2017). Quelle coordination entre conservation de la nature et agriculture ? Pistes pour une prise en compte renforcée des compétences des agriculteurs dans l'action agro-environnementale. *Mille Lieux* (Accepted). [*Equally contributed authors]

Xu Q., Hatt S., Lopes T., Zhang Y., Bodson B., Chen J., Francis F. (2017). A push-pull strategy to control aphids combines intercropping with semiochemical releases. *Journal of Pest Science* (in press). DOI:10.1007/s10340-017-0888-2

Guo J., Hatt S., He K., Chen J., Francis F., Wang Z. (2017). Nine facultative endosymbionts in aphids. A review. *Journal of Asia-Pacific Entomology*, 20(3), 794-801.

Uyttenbroeck R., Hatt S., Paul A., Boeraeve F., Piqueray J., Francis F., Danthine S., Frederich M., Dufrêne M., Bodson B., Monty A. (2016). Pros and cons of flower strips for farmers. A review. *Biotechnology, Agronomy, Society and Environment*, 20(S1), 225-235.

Paul A., Frederich M., Uyttenbroeck R., Hatt S., Malik P., Lebecque S., Hamaïdia M., Miazek K., Goffin D., Willems L., Deleu M., Fauconnier M.-L., Richel A., De Pauw E., Blecker C., Monty A., Francis F., Haubruge E., Danthine S. (2016). Grasshoppers as a food source? A review. *Biotechnology, Agronomy, Society and Environment*, 20(S1), 337-352.

Lopes T., Libert P.-N., Starý P., Japoshvili G., Hatt S., Francis F. (2016). Checklist of Aphidiinae (Hymenoptera: Braconidae) and Aphelinus (Hymenoptera: Aphelinidae) species from Belgium with respectively four and three new records. *Zootaxa*, 4092(4), 548-560.

Lopes T., Hatt S., Starý P., Francis, F. (2016). Inventaire et mise en collection d'espèces de pucerons et de parasitoïdes collectés en grandes cultures, et premier enregistrement de Metopolophium frisicum (Hille Ris Lambers 1947) et Acyrthosiphon primulae (Theobald 1913) (Hemiptera: Aphididae) en Belgique. *Entomologie Faunistique*, 69, 49-55.

Hatt S., Uyttenbroeck R., Lopes T., Paul A., Danthine S., Bodson B., Piqueray J., Monty A., Francis F. (2015). Do wildflower strips favor insect pest populations at field margins? *Agriculture and Agricultural Science Procedia*, 6, 30-37.

Uyttenbroeck R., Hatt S., Piqueray J., Paul A., Bodson B., Francis F., Monty A. (2015). Creating perennial flower strips: think functional! *Agriculture and Agricultural Science Procedia*, 6, 95-101.

Paul A., Frederich M., Uyttenbroeck R., Filocco S., Hatt S., Malik P., Monty A., Francis F., Blecker C., Danthine S. (2015). Proximate analysis of seeds from some field border flowering strips. Scientific Bulletin. *Series F. Biotechnologies*, 19, 354-359.

3. Oral communications in international and national conferences (as presenting author only)

Hatt S., Uyttenbroeck R., Lopes T., Boeraeve F., Piqueray J., Dufrêne M., Monty A., Francis F. (2015). Wildflowers sown at field margins have positive and negative effects on pests and parasitoids. Paper presented at *Royal Entomological Society - Annual National Science Meeting & International Symposium - Ento '15 "Insects & Ecosystem Services"*, Dublin, Ireland.

Hatt S., Uyttenbroeck R., Lopes T., Paul A., Danthine S., Bodson B., Piqueray J., Monty A., Francis F. (2015). Do wildflower strips favor insect pest populations at field margins? Paper presented at *International Conference "Agriculture for Life, Life for Agriculture"*, Bucharest, Romania.

Artru S.*, Hatt S.*, Boeraeve F., Garré S., Francis F., Lassois L. (2015). Nature-based agricultural practices for healthier food and environment - The example of agroforestry and wildflower strips. Paper presented at *Nature-Based Solutions to Societal Challenges*, Ghent, Belgium. [*Equally contributed authors]

Hatt S.*, Artru S.*, Boeraeve F.*, Brédart D.*, Lassois L., Garré S., Dufrêne M., Dendoncker N., Stassart P. M., Francis F. (2014). Incorporate agroecology within research: The on-going story of four young researchers. Paper presented at *3rd Belgian Agroecology Meeting: Broadening Scopes on Food, Squeezing Urban Hinterlands*, Brussels, Belgium. [*Equally contributed authors]

Hatt S., Uyttenbroeck R., Bodson B., Monty A., Francis F. (2014). Wildflower strips: a help for crop protection? Paper presented at *ENVITAM PhD Student Day 2014*, Louvain-La-Neuve, Belgium.

4. Posters and abstracts in international and national conferences (as presenting author only)

Hatt S., Lopes T., Francis F. (2016). Association froment - fleurs: une double protection contre les pucerons (Hemiptera: Aphididae). Poster presented at *12ème Journée Entomologique de Gembloux*, Gembloux, Belgium.

Hatt S., Lopes T., Xu Q., Liu Y., Francis F., Chen J. (2016). Effect of wheat-based intercropping systems on pests and natural enemies: a review with a special focus on China. Abstract presented at *Meeting of the Entomological Society of Beijing*, Beijing, China.

Hatt S.*, Artru S.*, Boeraeve F.*, Brédart D.*, Winandy S.*, Sindic M., Lassois L., Garré S., Dufrêne M., Dendoncker N., Stassart P. M., Francis, F. (2015). Agroecology: Unity into diversity. Poster presented at *2ème Congrès Interdisciplinaire du Développement Durable* -

Comment accélérer la transition ? Louvain La Neuve - Brussels, Belgium. [*Equally contributed authors]

Hatt S., Uyttenbroeck R., Bodson B., Piqueray J., Monty A., Francis F. (2015). Wildflower strips for crop protection: What do we know? What should we know? Poster presented at *National Symposium on Applied Biological Sciences 2015*, Louvain-La-Neuve, Belgium.

Hatt S., Uyttenbroeck R., Bodson B., Monty A., Francis F. (2014). Wildflower strips: a help for crop protection? Poster presented at *ENVITAM PhD Student Day 2014*, Louvain-La-Neuve, Belgium.

Hatt S.*, Artru S.*, Boeraeve F.*, Brédart D.*, Bodson B., Dufrêne M., Francis F., Lassois L., Monty A., Stassart P. M., Haubruge, E. (2014). Three aspects, One concept: Agroecology. Agroecological practices and human interactions for a new approach for science. An example at the Univeristy of Liege. Poster presented at *National Symposium on Applied Biological Sciences 2014*, Gembloux, Belgium. [*Equally contributed authors]

Hatt S., Uyttenbroeck R., Garré S., Bodson B., Monty A., Francis F. (2013). Wildflower strips as a tool for conservation biological control and pollination service: Impact of functional diversity and mowing regime. Poster presented at *Functional agrobiodiversity in North-West Europe: What does the future hold?* Brussels, Belgium.

5. Science popularization activities

Hatt S. (2015). Les insectes dans l’agriculture. Conférence dans les écoles, Woluwe Saint Pierre, Belgium.

Hatt S.*, Brédart D.* (2014). Agricultures de demain? Produire avec la nature. La Nuit des Chercheurs, Liège, Belgium. [*Equally contributed authors]