COMMUNAUTÉ FRANÇAISE DE BELGIQUE

LIÈGE UNIVERSITÉ–GEMBLOUX AGRO-BIO TECH

FUNCTIONAL DIVERSITY AND MOWING REGIME OF FLOWER STRIPS AS TOOLS TO SUPPORT POLLINATORS AND TO SUPPRESS WEEDS

ROEL UYTTENBROECK

Promotor: Arnaud Monty
Co-Promotor: Frédéric Francis
Year: 2017

Original dissertation presented to obtain
the degree of Doctor in Agronomical
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SUMMARY

Intensification of agriculture during past decades is one of the causes of biodiversity declines. Ecological intensification has been proposed as a more sustainable alternative of intensive agriculture that should be able to fulfill worldwide demands of food, by optimizing ecosystem functions and services and reducing environmental impacts. One way to restore ecosystem functions and services in arable fields is creating flower strips in field margins. These flower strips enable wild plant communities to thrive and provide food and shelter to associated fauna. It is often suggested that increasing plant functional diversity could be a tool to optimize ecosystem functioning and ecosystem service delivery, and it could thus be a goal for the creation and management of flower strips. An example of ecosystem functioning studied in this manuscript, is the mutualistic interaction between plants and pollinators.

To convince European farmers to implement flower strips, they are included in the subsidized Agri-Environment Schemes. However, there exists no clear appraisal of the pros and cons of flower strips for farmers. By systematically reviewing the literature for pros and cons, we found that most studies concerned agronomical and ecological processes related to flower strips, but few or no studies were dedicated to the social and economic aspects. Furthermore, pollination appears to be an important pro, and weed infestation a possible con, depending on flower strip creation and management. We focused on these two examples in the further study. We investigated (1) whether the increase of plant functional diversity can be used as tool to optimize flower strips for pollinators, (2) whether forb competition and adapting timing and frequency of mowing can be used as tools to limit weeds in flower strips, and (3) whether flower strips perform equally in supporting pollinators as the natural habitat for which they are thought to be a surrogate.

To use functional diversity as a tool to optimize flower strips for pollinators, we first tested whether it is possible to create a flower strip with a desired functional diversity level. We sew experimental flower strips with increasing functional diversity, based on visual, morphological and phenological flower traits and surveyed the vegetation composition the first year after sowing. The sown gradient of functional diversity was present, but with lower absolute values due to unequal cover of sown species and due to the presence of spontaneous species. To test the effect on pollinator support, we monitored the plant-pollinator networks in the experimental strips during two years. In contrast to our expectations, pollinator species richness and evenness were not influenced by functional

diversity, and increasing functional diversity even resulted in lower flower visitation rates. To investigate the effect of forb competition and timing and frequency of mowing on weed infestation, we created experimental flower strips either with grass and forb species in the seed mixture, either with only grass species. Three different mowing regimes were applied: summer mowing, autumn mowing and mowing both in summer and autumn. The cover of important weed, *Cirsium arvense*, was limited by adding forbs to the seed mixture and by mowing in summer or in summer and autumn. At last, by surveying plant-pollinator networks in perennial flower strips and natural hay meadows in the same landscape context, we observed that both the plant and the pollinator communities differed between the flower strips and the meadows. Perennial flower strips can thus be considered as a complementary habitat in the landscape and not a hay meadow surrogate.

This study suggests that it is possible to manipulate the vegetation as well as infestation by certain weeds in flower strips by adapting the seed mixture and the mowing regime. However, to promote pollinators in flower strips, increasing plant functional diversity appears not to be the key, and the abundance of certain attractive plant species can be more important. Moreover our results suggest that pollinators perceived a lower redundancy of functional plant trait values when functional diversity was higher, as they had more separate feeding niches (less visited flower species in common). Our results also suggest that there could be a trade-off between the increase of functional trait diversity and the floral resource abundance per niche or functional trait combination.

With the results of the tested flower strip creation and management methods and their effect on pollinator support and weed infestation, farmers and administrations can try to create and manage flower strips with the desired balance between pros and cons, and researchers can try to refine these methods and test the effects on other pros and cons.

RÉSUMÉ

L’intensification de l’agriculture au cours des dernières décennies est une des causes de la perte de la biodiversité. L’intensification écologique a été proposée comme une alternative plus durable à l’agriculture intensive. Celle-ci devrait pouvoir répondre à la demande alimentaire mondiale en optimisant les fonctions écologiques et les services écosystémiques tout en réduisant les impacts environnementaux. Une façon de restaurer les fonctions écologiques et les services écosystémiques dans les champs agricoles est la mise en place de bandes fleuries en bordure de champs. Ces bandes fleuries permettent aux communautés de plantes de s’épanouir et de fournir des ressources alimentaires et un abri à la faune associée. Il est souvent suggéré que l’augmentation de la diversité fonctionnelle des plantes peut être un outil pour optimiser les fonctions écologiques et la fourniture des services écosystémiques. Ainsi, l’augmentation de la diversité fonctionnelle peut être un objectif lors de la création et de la gestion des bandes fleuries. Un exemple de fonction écologique étudié dans ce manuscrit est l’interaction mutualiste entre les plantes et les pollinisateurs.

Afin de convaincre les agriculteurs Européens de mettre en place des bandes fleuries, celles-ci sont incluses dans les Mesures Agro-Environnementales subsidiées. Cependant, une analyse des avantages et inconvénients des bandes fleuries n’est pas encore disponible. Dès lors, nous avons effectué une revue systématique de la littérature sur ces avantages et inconvénients. Nous avons appris que la majorité des études traitaient de processus agronomiques et écologiques, et peu d’études traitaient des aspects socio-économiques. Néanmoins, la pollinisation a paru être un avantage important, et l’infestation de mauvaises herbes un inconvénient possible, dépendant de la création et de la gestion des bandes fleuries. Dans la présente étude, on s’est focalisé sur ces deux exemples. On a étudié (1) si une augmentation de la diversité fonctionnelle des plantes peut être utilisée comme un outil pour optimiser les bandes fleuries pour les pollinisateurs, (2) si la compétition par des plantes herbacées non graminoïdes et l’adaptation du timing et de la fréquence de la fauche peuvent être des outils pour limiter les mauvaises herbes dans les bandes fleuries et (3) si la performance des bandes fleuries à soutenir les pollinisateurs est égale à celle de l’habitat naturel qu’elles sont supposées substituer

Afin d’utiliser la diversité fonctionnelle comme outil pour l’optimisation des bandes fleuries pour les pollinisateurs, nous avons d’abord testé s’il est possible de créer une bande fleurie avec un niveau de diversité fonctionnelle désiré. Nous avons semé des bandes fleuries expérimentales au niveau de diversité fontionnelle croissant et basé sur des traits visuels,

morphologiques et phénologiques des fleurs. La composition de la végétation était ensuite caractérisée un an après le semis. Le gradient semé de diversité fonctionnelle était présent, mais avec des valeurs absolues plus faibles, à cause d'un recouvrement inégale des espèces semées et d'une présence d'espèces spontanées. Afin de tester l'effet favorable sur les pollinisateurs, nous avons surveillé les réseaux plantes-pollinisateurs dans les bandes expérimentales pendant deux ans. Contrairement à nos hypothèses, la richesse et la régularité en espèces des pollinisateurs n'étaient pas influencées par la diversité fonctionnelle. Une augmentation de la diversité fonctionnelle menait même à des taux de visites des fleurs plus faibles. Afin de tester l'effet de la compétition par des plantes herbacées non graminoïdes et l'adaptation du timing et de la fréquence de la fauche sur l'infestation de mauvaises herbes, nous avons créé des bandes fleuries expérimentales avec soit des graminées et des plantes herbacées non graminoïdes dans le mélange, soit uniquement des graminées. Trois régimes de fauche différents ont été appliqués : une fauche en été, une fauche en automne ou une fauche en été et en automne. Le recouvrement de *Cirsium arvense,* une mauvaise herbe importante, était limité par l'ajout de plantes herbacées non graminoïdes au mélange et par la fauche en été ou en été et automne. En observant des réseaux plantes-pollinisateurs dans des bandes fleuries pérennes et dans des prairies de fauche, toutes deux dans le même contexte paysager, nous avons enfin constaté différentes communautés de plantes et de pollinisateurs. Par conséquence, les bandes fleuries pérennes peuvent être considérées comme un habitat complémentaire dans le paysage et non comme un substitut des prairies de fauche.

Cette étude suggère qu'il est possible de gérer la végétation aussi bien que l'infestation par certaines mauvaises herbes dans les bandes fleuries par l'adaptation du mélange de graines et le régime de fauche. Par contre, pour être favorable aux pollinisateurs, l'augmentation de la diversité fonctionnelle des plantes dans les bandes fleuries ne semble pas être la clé. L'abondance de certaines espèces de plante attractives pourrait être plus importante. Par ailleurs, nos résultats suggèrent que les pollinisateurs ont aperçu une redondance des traits fonctionnels de plantes plus faible lorsque la diversité fonctionnelle était plus élevée, comme elles avaient des niches alimentaires plus distinctes (moins d'espèces de fleur visitées en commun). Nos résultats suggèrent également qu'il peut y avoir un compromis à trouver entre l'augmentation en diversité fonctionnelle et l'abondance minimale en ressources florales par niche ou combinaison de traits fonctionnels.

Avec les résultats des méthodes testées de création et gestion des bandes fleuries et leur effet sur le soutien aux pollinisateurs et sur l’infestation par des mauvaises herbes, des agriculteurs et administrations peuvent essayer de créer et gérer des bandes fleuries avec l’équilibre souhaité entre les avantages et inconvénients. Quant aux chercheurs, ceux-ci peuvent essayer d’affiner ces méthodes et tester les effets sur des autres avantages et inconvénients.

SAMENVATTING

Intensivering van de landbouw tijdens de afgelopen decennia is één van de oorzaken van biodiversiteitsverlies. *Ecological intensification* wordt voorgesteld als meer duurzaam alternatief voor intensieve landbouw en moet de wereldwijde vraag naar voedsel beantwoorden door ecosysteemfuncties en ecosysteemdiensten te optimaliseren en door de milieu-impact te verkleinen. Een manier om ecosysteemfuncties en -diensten te herstellen in akkers, is het creëren van bloemenstroken in akkerranden. Deze bloemenstroken kunnen wilde plantgemeenschappen herbergen en voorzien voedsel en schuilplaatsen voor geassocieerde fauna. Er wordt vaak gesuggereerd dat het verhogen van de functionele plantdiversiteit een instrument kan zijn om ecosysteemfunctioneren en ecosysteemdiensten te optimaliseren, en dit zou bijgevolg een doelstelling kunnen zijn bij de aanleg en het onderhoud van bloemenstroken. Een voorbeeld van ecosysteemfunctioneren dat in dit onderzoek is bestudeerd, is de mutualistische interactie tussen planten en bestuivers.

Om Europese landbouwers te overtuigen tot het aanleggen van bloemenstroken, zijn deze opgenomen in de gesubsidieerde beheersovereenkomsten. Er bestaat echter geen duidelijk overzicht van de voor- en nadelen van bloemenstroken voor landbouwers. In een systematische literatuurstudie naar voor- en nadelen, vonden we dat de meeste studies gerelateerd waren tot de agronomische en ecologische processen, maar weinig studies belichtten de socio-economische aspecten. Daarnaast bleek bestuiving een belangrijk voordeel, en onkruiddruk een mogelijk nadeel, afhankelijk van de aanleg en het beheer van de bloemenstrook. We richtten ons op deze twee voorbeelden in het verdere onderzoek. We onderzochten (1) of de verhoging in functionele plantdiversiteit gebruikt kan worden als instrument om bloemenstroken te optimaliseren voor bestuivers, (2) of concurrentie door kruidachtige planten en het aanpassen van maaitijdstip en -frequentie instrumenten zijn om onkruiddruk in bloemenstroken te beperken, en (3) of bloemenstroken even goed presteren in het ondersteunen van bestuivers als de natuurlijke habitat waarvoor ze een surrogaat geacht worden te zijn.

Om functionele diversiteit als instrument te gebruiken om bloemenstroken te optimaliseren voor bestuivers, testten we eerst of het mogelijk is om een bloemenstrook met een gewenst niveau aan functionele diversiteit te creëren. We zaaiden experimentele bloemenstroken met toenemende functionele diversiteit, gebaseerd op visuele, morfologische en fenologische functionele kenmerken en volgden de vegetatiesamenstelling op gedurende het eerste jaar na inzaai. De gezaaide gradiënt in functionele diversiteit bleek aanwezig te zijn, maar met

lagere absolute waarden door ongelijke bedekking van gezaaide soorten en door de aanwezigheid van spontane soorten. Om het effect op de ondersteuning van bestuivers te testen, volgden we de plant-bestuiversnetwerken op in de experimentele bloemenstroken gedurende twee jaar. In tegenstelling tot onze verwachtingen, werden de soortenrijkdom en *evenness* van bestuivers niet beïnvloed door de functionele diversiteit, en resulteerde een toename in functionele diversiteit zelfs tot een lager aantal bloembezoeken. Om het effect van concurrentie door kruidachtige planten en van het maaitijdstip en de maaifrequentie te onderzoeken, creëerden we experimentele bloemenstroken met ofwel grassen en kruidachtigen in het zaadmengsel, ofwel enkel grassen. Drie verschillende maairegimes werden toegepast: een maaibeurt in de zomer, een maaibeurt in de herfst, of een maaibeurt in zowel zomer als herfst. De bedekking van *Cirsium arvense*, een belangrijk onkruid, werd beperkt door de toevoeging van kruidachtigen aan het zaadmengsel en door maaien in de zomer of in zowel de zomer als de herfst. Door plant-bestuiversnetwerken te bemonsteren in meerjarige bloemenstroken en natuurlijke hooilanden in dezelfde landschapscontext, konden we ten slotte vaststellen dat zowel de plant- als de bestuiversgemeenschappen verschilden tussen bloemenstroken en hooilanden. Meerjarige bloemenstroken kunnen bijgevolg beschouwd worden als een complementair habitat in het landschap, en niet als een surrogaat voor hooilanden.

Dit onderzoek suggereert dat het mogelijk is om zowel de vegetatie als de bedekking van bepaalde onkruiden te manipuleren in bloemenstroken door het aanpassen van het zaadmengsel en het maaibeheer. Om bestuivers te ondersteunen in bloemenstroken bleek het verhogen van de functionele plantendiversiteit echter niet de sleutel te zijn, en de abundantie van bepaalde aantrekkelijke plantensoorten leek van groter belang te zijn. Daarnaast suggereren de resultaten dat bestuivers een lagere *redundancy* aan functionele plantkermerken ervaarden wanneer de functionele diversiteit hoger was, aangezien ze meer van elkaar gescheiden voedingsniches hadden (minder bezochte bloemensoorten gemeenschappelijk). Onze resultaten doen ook vermoeden dat er een trade-off zou kunnen bestaan tussen een toename in functionele diversiteit en de abundantie van bloemaanbod per niche of combinatie van functionele kenmerken.

Met deze resultaten van de geteste aanleg- en beheermethodes van bloemenstroken en hun effect op ondersteuning van bestuivers en op onkruiddruk, kunnen landbouwers en administraties trachten bloemenstroken te creëren en te beheren met het gewenste evenwicht tussen voor- en nadelen, en kunnen onderzoekers deze methodes verder proberen te verfijnen en het effect op andere voor- en nadelen onderzoeken.

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CHAPTER 1

INTRODUCTION

1. INTRODUCTION

In the introduction chapter, some general concepts upon which this thesis is built are firstly introduced in the General introduction section. This section is followed by a review paper, putting flower strips in the socio-economical context of farmers by systematically screening the literature on existing knowledge. To end this introduction chapter, a last section describes the objectives and scientific approach of this study.

1.1. GENERAL INTRODUCTION

BIODIVERSITY IN AGROECOSYSTEMS

Agriculture in Western Europe and Northern America has known an intensification during last decades. This intensification mainly consists in scale increase, simplification of crop rotation, increased pesticide and fertilizer inputs, and creation of drainage and irrigation systems (Stoate et al., 2001). While intensive agriculture can be an efficient way to produce food, feed, fiber and fuel, the sustainability of this production system can be questioned. Sources of fossil fuel for energy input and minerals for fertilizer production are limiting, and the use of chemical inputs has caused important environmental damage (Cordell et al., 2009; Tilman et al., 2002).

Furthermore, non-crop habitats in agricultural landscapes decreased in area and got fragmented. Together with the abovementioned aspects of agricultural intensification, this has caused biodiversity loss (Kruess and Tscharntke, 1994; Stoate et al., 2001; Tscharntke et al., 2005). However, farmland biodiversity can deliver important ecosystem services. Ecosystem services are defined as the benefits people obtain from ecosystems. They include provisioning services, such as food production, regulating services, such as pollination and pest control, cultural services, such as recreation and supporting services, such as nutrient cycling (Millenium Ecosystem Assessment, 2005).

As a response to the increasing demand of food worldwide and the contradiction between agricultural intensification and ecosystem services by its adverse effects on biodiversity, the principle of ecological intensification was developed. Ecological intensification tries to optimize agricultural efficacy by using benefits obtained from ecological processes delivered by nature (Bommarco et al., 2013). In developed countries, this mainly results in a status quo of production, while the reliance on chemical and fuel inputs has to be maximally replaced by ecological processes. In developing countries this rather means an increase of the production by optimizing the ecological processes (Bommarco et al., 2013).

FLOWER STRIPS, THE SUBSIDIZED FIELD BORDERS TO INCREASE BIODIVERSITY

Measures for the ecological intensification strategy can be applied at different scales. Inside the field, the use of compost or manure, crop residue management and reduced tillage practices are typical examples to improve soil quality and increase soil biodiversity (Bommarco et al, 2013; Lemtiri et al., 2016; Kovács-Hostyánszki et al., 2017; but see Degrune et al., 2016). Furtermore, increasing plant diversity within the cropping zone by intercropping, or using semiochemicals, are within-field methods applied among others for pest management (e.g. Lopes et al., 2015; Xu et al., 2017). In field edges or borders between fields, hedgerows and buffer strips can be created to reduce soil erosion, water runoff and nutrient leaching and to serve as source habitat for 'functional agrobiodiversity' (see below) (Tscharntke et al, 2005; Wratten et al, 2012). At the landscape scale, semi-natural habitats can be provided and networks of ecological infrastructure can connect theses habitats with crop fields (Tscharntke et al., 2005; Bommarco et al., 2013; Kovács-Hostyánszki et al., 2017). These

FIGURE 1.1. PERENNIAL FLOWER STRIP WITH ADJACENT OILSEED RAPE CROP IN FAIMES, BELGIUM (MAY 2015)

measures are close to the concept of ‘agro-ecological practices’ (Hatt et al., 2016). As for field edges, an example of a measure, and the focus in this study, is the flower strip.

A flower strip is a part of a field, mostly the field edge, which is covered with herbaceous non-crop vegetation. This vegetation can develop spontaneously, or a seed mixture can be sown with the desired species. Seed mixtures can contain grass species, forb species or both. Flower strips can be annual or perennial (Haaland et al., 2011). In many European countries, flower strips are part of the subsidized agri-environment schemes of the Common Agricultural Policy. Farmers adopting such a scheme to reduce the environmental impacts of their agricultural practices get subsidized to reimburse the yield loss (e.g. by a reduction in cropping area in case of a flower strip) (European Commission, 2005; Haaland and Gyllin, 2011; Haaland et al., 2011). The type of strips, management and subsidies vary considerably between countries, depending on their policy regarding agri-environment schemes (Haaland et al., 2011). Annual or biennial strips are ploughed and reseeded or translocated every one or two years respectively. Perennial strips are either left without management, either managed by mowing to avoid succession. In the former case, the strip has to be ploughed after several years, because the vegetation becomes dominated by grasses and woody species (Haaland et al., 2011). In Wallonia (Belgium), perennial strips are usually managed by mowing with a part of the strip that is left unmown as refuge (Natagriwal asbl, 2017a).

Flower strips mainly aim to enhance farmland biodiversity by providing food and shelter for insects and other animals, and an area for wild plants to grow and reproduce (Haaland et al., 2011). On the one hand, they aim to contribute to biodiversity conservation, by increasing biodiversity or supporting endangered or emblematic species. For this conservation function, flower strips need to provide one or more of the resources of the species to be supported. The other resources can be provided by the semi-natural habitats the species in question rely on, or by the other ecological infrastructure present in the agricultural landscape. Bumblebees for instance, can use flower strips to provide them with food resources when flowers are present, while they may rely on flower resources in the surrounding landscape in early season (Scheper et al., 2015) and on nesting sites in semi-natural habitats (Kells and Goulson, 2003; Svensson et al., 2000). Scheper et al. (2013) showed that agri-environment schemes are most effective in an intermediate landscape between cleared (homogeneous intensive arable landscape, <1% cropped area) and complex (heterogeneous landscape with arable land and semi-natural habitat, >20% cropped area), which was already suggested by Tscharntke et al. (2005). In cleared landscape, the very limited source populations are not sufficient to colonize agri-environment schemes. Complex landscapes contain already a high biodiversity level everywhere, so agri-environment schemes do not have a significant effect. Furthermore, Kleijn et al. (2011) argue that the efficacy of agri-environment schemes depends on the 'ecological contrast' they deliver, compared to a situation without the scheme. Indeed, Scheper et al. (2015) showed that flower strips only have an effect on bees when these strips increase local flower richness. They argue to increase the number of flower species in flower strips seed mixtures and to use management strategies that maintain this flower species richness on the long term (Scheper et al., 2015).

The positive effect of flower strips compared to cropped area on insect abundance and diversity has been extensively shown (reviewed by Haaland et al., 2011). However, few studies verified if flower strips really serve as a surrogate habitat for insect communities or rather as new habitat with another associated insect community. Indeed, flower strips are, in contrast to other agri-environment schemes, considered as a rather new habitat in the agricultural landscape, making it difficult to define guidelines for their creation and management. In countries where grasses are added to the mixtures of perennial flower strips, and strips are managed by mowing, they can be compared to hay meadows (Haaland et al., 2011). Öckinger and Smith (2007) showed in a Swedish experiment that the original semi-natural habitat (grassland) functions as a source population for the species to colonize the surrogate habitat (uncultivated field margins). Similarly, Ekroos et al. (2013) found that abundance and diversity of bumblebees and butterflies, but not syprhid flies, was lower in linear habitat elements more distant from semi-natural grassland. However, Haaland and Bersier (2011) found in their study in Switzerland that the butterfly species community in perennial flower strips was not a subset of the butterfly community in extensive meadows. More research is needed to identify the role of agri-environment schemes in comparison to the semi-natural habitat for which they are thought to be a surrogate.

On the other hand, the aim of flower strips is to attract and support useful arthropods, also called 'functional agrobiodiversity' (Bianchi et al., 2013), like pollinators (Nicholls and Altieri, 2012) and natural enemies of crop pests (Landis et al., 2000). Flower strips have been shown to increase pollination services to crops by supporting pollinators (Barbir et al., 2015; Blaauw and Isaacs, 2014; Feltham et al., 2015), while some studies found no effect (e.g. Campbell et al., 2017). To attract these arthropods, recent studies propose to develop tailored flower strips to maximize the regulating services delivered by flower strips to the crop (e.g. Tschumi et al., 2014, 2016). For this kind of strips, a specific set of plant species is selected that is known to attract the specific set of functional arthropods for the crop in the adjacent field (Tschumi et al., 2014). This results however in annual or biennial flower strips that are included in a crop rotation and for which the longer term conservation value can be questioned. Perennial flower strips in contrary, could host a permanent community of plants and associated fauna that can deliver multiple and stable ecosystem services on a longer term. Tscharntke et al. (2005) argue to focus on a diversity of species and processes in land-use management to increase resilience of the system. Next to pollination and pest control services, flower strips are also expected to deliver other ecosystem services. They can limit soil erosion, nutrient leaching and surface water runoff, and improve nutrient cycling. Furthermore, flower strips can help suppressing weeds, and improve rural prosperity and landscape aesthetics (Wratten et al., 2012).

FUNCTIONAL DIVERSITY, THE KEY COMPONENT OF BIODIVERSITY?

Increasing biodiversity has been shown to be a strategy to optimize ecosystem functioning and ecosystem services (Díaz et al., 2005). Increasing plant diversity could thus be a goal for the creation and management of flower strips, as suggested by Scheper et al. (2015).

However, in the relationship between biodiversity and ecosystem functioning and ecosystem services, not species per se, but their functional traits have been suggested to play a key role (Díaz and Cabido, 2001). Functional traits are defined as "morphological, biochemical, physiological, structural, phenological, or behavioral characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the response of such organisms to the environment and/or their effects on ecosystem properties" (Díaz et al., 2013). Not the species, but their functional traits define their response to the environment and to other species and their effect on other organisms and on ecosystem processes. For illustration, the example of the study of Fontaine et al. (2006) is given here. They studied the interaction of pollinators and plants in a cage experiment. Two plant types were defined regarding corolla depth: open flowers and tubular flowers (see Figure 1.2). The corolla depth

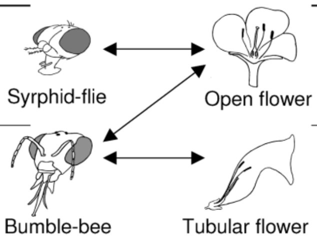
Pollinators species and groups	Mouthpart length (mm ± S.E.)	Theoretical pollination network	Plants species and groups	Accessibility	
				pollen	nectar
Sphaerophoria sp.	2.66 ± 0.35		*M. officinalis*	easy	easy
E. balteatus	2.3 ± 0.20		*E. cicutarium*	easy	easy
E. tenax	5.47 ± 0.29		*R. raphanistrum*	easy	difficult
B. terrestris	9.02 ± 0.19		*M. guttatus*	easy	difficult
B. hortorum	9.21 ± 1.02		*M. sativa*	difficult	difficult
B. lapidarius	8.10 ± 0.86		*L. corniculatus*	difficult	difficult

FIGURE 1.2. EXAMPLE OF A CAGE EXPERIMENT WITH POLLINATOR AND PLANT SPECIES GROUPED FOR THEIR FUNCTIONAL TRAITS 'MOUTHPART LENGTH' AND 'COROLLA DEPTH' (FONTAINE ET AL., 2006)

can be considered as a functional effect trait in this experiment (Díaz et al., 2013; Lavorel et al., 2013), as it defines whether floral rewards (pollen and nectar) are easily accessible or not for pollinators (Figure 1.2). Secondly, two pollinator types were defined regarding their mouthparts length: syrphid flies (Diptera: Syrphidae) with short mouthparts and bumblebees (Hymenoptera: Apidae) with long mouthparts. Mouthparts length can be considered as a functional response trait in this experiment, as it defines whether the pollinator can access floral rewards in a flower (Díaz et al., 2013; Lavorel et al., 2013). Syrphid flies with short mouthparts are not expected to pollinate tubular flowers, while bumblebees with long mouthparts are expected to pollinate both types of flowers (Figure 1.2). As these traits determine the access to floral rewards, the presence or absence of plant and pollinator species with the different levels for the traits can influence the reproductive success of plants (Fontaine et al., 2006). When applying this approach to flower strips, sowing strips containing plant species with different levels for the trait 'corolla depth' can attract a higher diversity of flower-visiting insects than sowing strips containing only one level (Campbell et al., 2012; Wratten et al., 2012). The number of levels of a functional trait is also called the 'functional group richness' and signifies the number of functional groups represented. It is an example of a metric of functional diversity (FD), which is the value and range of functional traits (Tilman, 2001). This FD is not to be confounded with functional agrobiodiversity (see above), i.e. biodiversity that provides ecosystem services for sustainable agricultural production (Bianchi et al., 2013). Functional group richness appears to be the most commonly used metric of FD in community ecology studies (Mason et al., 2005), as it is easy and quick to group species that are similar in their functional traits.

More precise indices of FD try to measure it on a continuous scale and are related to the ecological niches of the species present. Three groups of indices can be distinguished (Mason et al., 2005; Schleuter et al., 2010): Functional richness indices (the trait value range or niche range occupied by the species community), functional evenness indices (the degree of equal distribution of the trait values occupied in the trait value range), and functional divergence indices (the degree of niche differentiation, or the degree of clustering of species or abundances at the edges of trait values range). Depending on the index, one or several traits can be used to calculate the index (Schleuter et al., 2010). A FD metric that was used in this manuscript is the Rao quadratic entropy index (Botta-Dukát, 2005). This functional divergence metric is based on Simpson's species diversity index and calculates the variance of the functional dissimilarities between all species pairs, weighted for their abundance (Botta-Dukát, 2005; Schleuter et al., 2010). The following equation shows the calculation of this index (for S species, with d_{ij} the distance between species i and species j based on their functional traits, and p_i and p_j the relative abundances of species i and j):

$$FD_{Rao} = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j$$

The advantage of this metric is that it takes into account the relative abundance of different species and thus of their trait values, unlike functional richness metrics. Furthermore, it is not correlated with species richness and it is the only functional divergence metric that can both take into account multiple traits and categorical traits (Schleuter et al., 2010).

As functional traits may play a key role in the biodiversity-ecosystem functioning relationship, it is often suggested that biodiversity should be approached as FD, which is thought to be a better predictor than species diversity in this relationship (Díaz and Cabido, 2001). Therefore, increasing plant functional diversity instead of plant species diversity can be a tool to optimize ecosystem functioning and ecosystem service delivery in flower strips. However, few evidence exists on this relationship, especially in the context of flower strips.

ECOSYSTEM FUNCTIONING: THE CASE OF PLANT-POLLINATOR NETWORKS

An example of ecosystem functioning studied in this manuscript, is the mutualistic interaction between plants and pollinators. Wild pollinators are among the functional groups that suffered declines due to land use intensification (Biesmeijer et al., 2006; Potts et al., 2010; Winfree et al., 2009). In the IPBES "Assessment report on pollinators, pollination and food production", ecological intensification, strengthening existing diverse farming systems and investing in ecological infrastructure were identified as complementary methods to both maintain healthy pollinator communities and productive agriculture (IPBES, 2016). Pollinators visit plant flowers to obtain floral rewards like nectar and pollen. By visiting different flowers and transporting pollen between flowers, they contribute to the pollination of these plants. As such, animal pollinators play an important role in the pollination of wild plants and crops worldwide (Klein et al., 2007; Potts et al., 2010). For wild plants, 60 to 80% of the species depend on animal pollinators (Kremen et al., 2007). As for crops, Klein et al. (2007) calculated that the production of 70% of the most important crops worldwide is increased with animal pollination. In terms of production mass, only 36% of the produced crop mass is increased with animal pollination, as the crops with the highest production are wind-pollinated or passively self-pollinated. Moreover, while some animal-pollinated crops need pollination to produce fruits that are consumed, other crops are produced for the consumption of vegetative parts and pollination is only needed for reproduction or breeding (Klein et al., 2007). For Belgium, it was calculated that 11.1% of the crop production value in 2010, or 251.62 million €, was dependent on pollinators. 82% of this amount was attributed to fruits production, 18% to vegetables and less than 1% to oil crops and legumes (Jacquemin et al., 2017). Furthermore, as the crop pollination service is mainly delivered by a set of common pollinator species, this ecosystem service may not be a sufficient argument for the conservation of pollinator diversity including rare species (Kleijn et al., 2015).

Studying the complex network of interactions between plant species and pollinator species delivers interesting information on the structure, stability and intensity of this ecosystem functioning (Tylianakis et al., 2010). Some examples of interaction networks are given in Figure 1.3. These networks are constructed by observing which pollinator species visit which plant species (‘links’) and how frequently these visits occur (‘interactions’). A metric that is often calculated for plant-pollinator networks is ‘network connectance’ (Figure 1.3). This is the ratio between the number of realized links and the number of possible links of the network (Tylianakis et al., 2010). In Figure 1.3 for instance, the highly connected network has got 11 out of 25 possible links that are realized, while the lowly connected network only 6. A higher network connectance is associated with a higher rate of ecosystem processes and a higher ecosystem process stability (Thébault and Fontaine, 2010; Tylianakis et al., 2010). Another metric is network nestedness (Figure 1.3). In a nested network, species interacting with specialists are a proper subset of species interacting with generalists. As specialists have higher chance to go extinct, in a nested network their interaction partners are secured by also interacting with generalist species (Thébault and Fontaine, 2010; Tylianakis et al., 2010). In the highly nested network in Figure 1.3 for instance, if the specialist plant species D (it only interacts with pollinator species 1) goes extinct, pollinator species 1 is well secured from secondary extinction as it interacts with generalist plant species A and B.

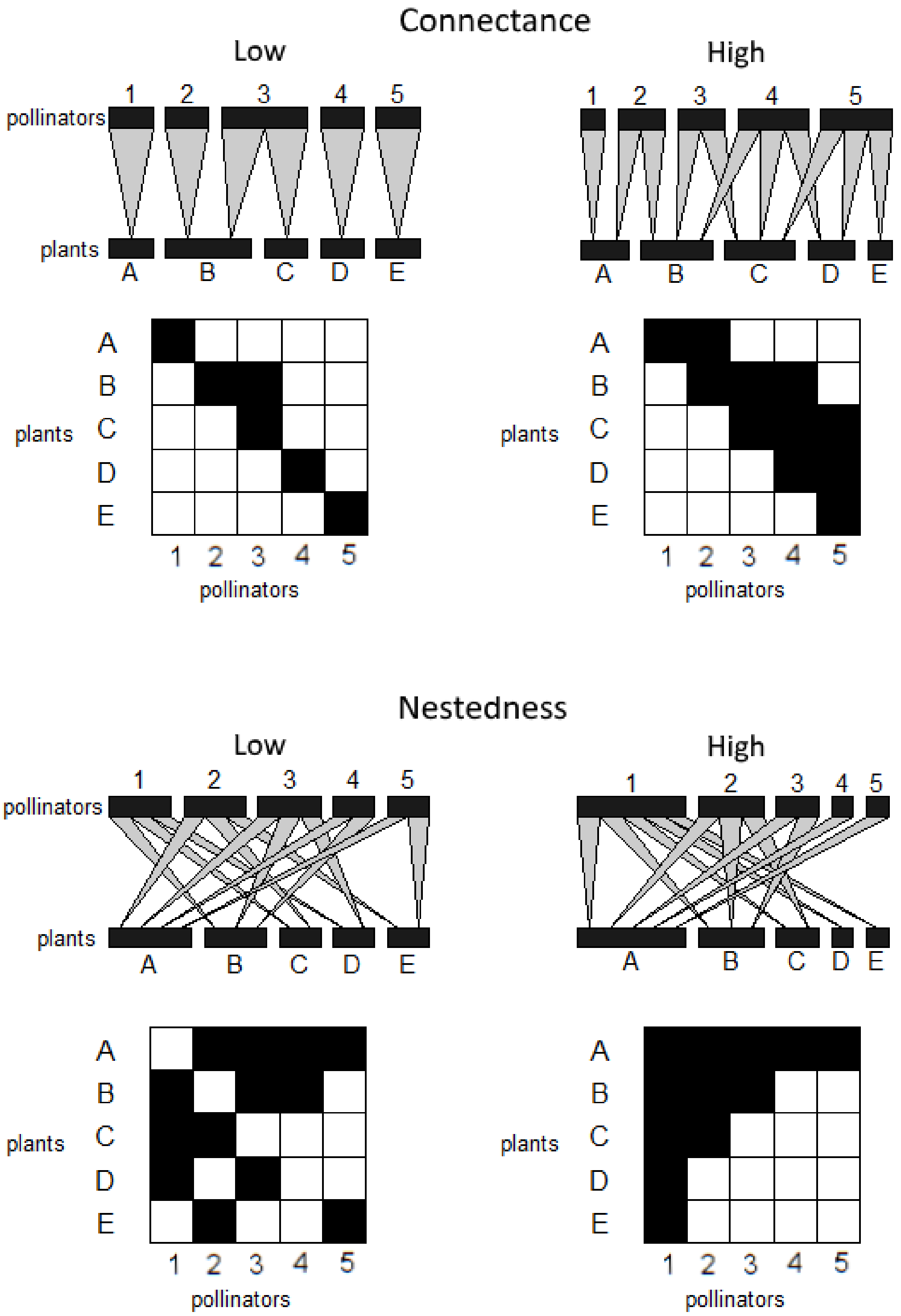


FIGURE 1.3. EXAMPLES OF NETWORKS DIFFERING IN CONNECTANCE AND NESTEDNESS

Example networks are plotted both as a bipartite graph (upper graphs) and as a matrix grid (lower graphs) for each metric.

Furthermore, interaction networks can also deliver information on which feeding niches pollinators take (which plant species are visited by which pollinator species and with which interaction frequency) and to detect effects of a change in plant FD on these feeding niches

(Junker et al., 2013). Indeed, changing the niches available by changing the plant FD can be expected to affect the composition of pollinator species that are able to find their required feeding niche and the complementarity or redundancy of these pollinator species in their feeding niche. When increasing plant species richness per se, each additional species can bring either complementary or redundant trait values to the trait value composition of the plant species community. Redundant species can play the role of 'insurance species' and take the functions of other species with the same functions in case of the loss of these species due to disturbance (Díaz and Cabido, 2001). While some argue that only few abundant key species deliver the important ecosystem services (Kleijn et al., 2015; Winfree et al., 2015), this insurance effect of redundant species might be important to take into account in the development of sustainable agri-environment schemes (Tscharntke et al., 2005).

1.2. PROS AND CONS OF FLOWER STRIPS FOR FARMERS. A REVIEW

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ABSTRACT

Description of the subject. To counteract environmental problems due to agricultural intensification, European farmers can apply agri-environmental schemes in their fields. Flower strips are one example of these schemes, with the aim of supporting biodiversity, leading to an increase in 'useful' species groups such as pollinators for crop pollination and natural enemies for pest control. However, to our knowledge, a complete appraisal of the pros and cons of flower strips, from a farmer's point of view, does not yet exist. It is proposed that better and more complete information could increase the adoption and implementation of such agri-environmental schemes.

Objectives. This study aims 1) to assess the pros and cons of flower strips, from a farmer's point of view, and 2) to highlight the knowledge gaps that exist in the scientific literature, for the different types of pros and cons.

Method. We listed the different components of the appraisal of pros and cons and conducted a systematic screening of the scientific literature on flower strips and these components.

Results. The largest part of the 31 selected studies was concerning agronomical and ecological processes, such as pollination and animal pest control. Most of them indicated positive effects of flower strips. For many components of the appraisal, mostly economic and social ones, few or no studies were found.

Conclusions. While a positive balance of pros and cons, from a farmer's point of view, came from our literature screening, large research gaps still remain and more research is required, especially in the economic and social components of the evaluation.

Key words

Agroecosystems, ecosystem services, sustainable agriculture, agricultural practices, intensive farming, crop yield, compensation, farm income, attitudes, biological control

INTRODUCTION

Agricultural intensification during the last few decades has led to large biodiversity losses, due to habitat destruction and fragmentation, increased field size, simplified crop rotations and intensification of crop management (Kruess and Tscharntke, 1994; Stoate et al., 2001; Tscharntke et al., 2005). Simultaneously, the concept of Ecosystem Services (ES) arose, defined as the benefits that people obtain from ecosystems (Millenium Ecosystem Assessment, 2005). In the field of agriculture, ES are, among others, biomass production, pollination, pest control, soil conservation and fertility (Zhang et al., 2007). As biodiversity is known to play a key role in ES, biodiversity losses can cause disruption of ES delivered by the agricultural landscape (Tscharntke et al., 2005; Zhang et al., 2007). Increasing and restoring biodiversity in the agricultural landscape can, thus, be a strategy to support these ES. Therefore, European farmers are encouraged through European subsidies of the Common Agricultural Policy to implement agri-environmental schemes, such as planting hedgerows, grass buffer strips or flower strips (European Commission, 2005; Haaland et al., 2011). A flower strip is a part of a field that is preserved for herbaceous vegetation. The strip can be created by sowing a mixture of forb species, with or without grass species. The strip can also be created by spontaneous vegetation. Both annual and perennial strips exist. The type of strips, management and subsidies vary considerably between countries, depending on their policy (Haaland et al., 2011). The main goal of flower strips is to enhance farmland biodiversity by providing food and shelter for insects and other animals, and an area for wild plants to grow and reproduce (Haaland et al., 2011). Additionally, their focus is to attract and support functional arthropods like pollinators (Nicholls and Altieri, 2012) and natural enemies (Landis et al., 2000). These functional arthropods can be beneficial to the crop by delivering pollination and pest control services and can reduce inputs like pesticide use or renting bee hives (Haaland et al., 2011), making flower strips a valuable measure to play a role in ecological intensification (Bommarco et al., 2013). Apart from supporting and attracting functional arthropods, habitat enhancement, like the implementation of flower strips, can also provide other advantages, such as reduction of soil erosion or improvement of the landscape's aesthetic value (Fiedler et al., 2008; Wratten et al., 2012).

While some of these advantages have already been shown, agri-environmental schemes have been discussed over the years, as they are not always effective (Batáry et al., 2015). Reviews exist on sown flower strips (Haaland et al., 2011) or field margins (Marshall and Moonen, 2002), but they are restricted to the effect of sown flower strips on insect conservation (Haaland et al., 2011) and interactions of field margins with agriculture (Marshall and Moonen,

2002) and do not provide a complete appraisal of the advantages and disadvantages of flower strips. Some attempts have been made to evaluate the pros and cons of habitat enhancement, such as in Fiedler et al., (2008) and Wratten et al. (2012), but not yet for flower strips specifically. Bommarco et al. (2013) argue that existing knowledge gaps on several services and processes, as well as on their synergies and trade-offs, have implications for decision making in ecological intensification measures. Moreover, many studies about the farmers' attitude towards the adoption of agri-environmental schemes demonstrate the importance of providing information on the diverse aspects of their implementation (Burton and Paragahawewa, 2011; Mante and Gerowitt, 2007; Mathijs, 2003; Sattler and Nagel, 2010; Vanslembrouck et al., 2002). Apart from environmental concern, compensation rates and the effect on agronomic production, the farmers' acceptance of agri-environmental schemes is also driven by implementation time and effort, effectiveness, associated risks, additional transaction costs, their ease in communication and their relations with the subsidizing institution and its contact person (Falconer, 2000; Mante and Gerowitt, 2007; Mathijs, 2003; Sattler and Nagel, 2010). It was shown that farmers who are more informed and more convinced about the usefulness of agri-environmental schemes, are more likely to implement them in their farms (Vanslembrouck et al., 2002). Moreover, Burton and Paragahawewa (2011) argue that this information would increase the adoption of environmental practices in their farming culture and conventional 'good farming' practice. Therefore, it could be useful to gain comprehensive insight into the advantages and disadvantages of the implementation of flower strips for farmers (Fiedler et al., 2008; Wratten et al., 2012). In this context, we conducted a systematic literature screening aiming at 1) assessing the pros and cons from a farmer's point of view, and 2) highlighting the knowledge gaps in the literature for the different types of pros and cons.

LITERATURE SCREENING

To make an appraisal of the pros and cons of flower strips, a list was made of the possible different components of this appraisal, that is, aspects of the farming system that may be influenced by a flower strip. This list of components was iteratively composed and completed by a panel of experts. This panel was comprised of the authors of this manuscript, being researchers and professors with a MSc or PhD degree and having expertise in crop science, ecology, weed science, ecosystem service valuation, agroecology, food science, pollination and biological control. The components can be found in Table 1.1. They were divided into four categories: i) Agronomical and ecological processes: the effect on the crop of ecosystem processes in the flower strip; ii) Economic balance (costs): the different economic inputs that can be influenced by flower strips; iii) Economic balance (income): the different economic outputs that can be influenced by flower strips; iv) Social recognition: the different ways that a farmer's relationship with other stakeholders can be influenced by flower strips, and the farmer's perception of flower strips.

For each component, a search query was done in Scopus (Elsevier B.V., 2014) scientific literature database on 31 October 2014. For this, keywords were chosen to find literature addressing flower strips and the respective component. The query syntax required the papers to have title, abstract or keywords containing at least one of the search terms about flower strips and at least one of the search terms about the respective component. The search terms about flower strips were 'flower strip(s)', 'wildflower strip(s)', 'flowering border(s)', 'flower margin(s)', 'margin strip(s)', 'sown strip(s)', 'sown margin(s)', 'sown margin strip(s)', 'weed strip(s)', 'sown weed strip(s)', 'herb strip(s)', 'sown herb strip(s)', 'field margin(s) AND sowing', 'field boundary/boundaries AND sowing' and 'field border(s) AND sowing'. The search terms for the components are listed in Table 1.1. Search terms were chosen to find as many papers as possible that were clearly about flower strips and the respective component. For this, the list of search terms was again subject to validation by the panel of experts.

To retain only the papers that met the objectives of this review, the references obtained from the Scopus search query were listed, per component, and divided between the authors to select the references of interest based on a set of criteria (see below). If an abstract was not available, the reference was not considered. Review papers were not considered, as these are based on other studies. Double records, or studies published more than once, were only considered once.

To be selected, a paper had to meet four criteria. Firstly, the study had to be about flower strips, a part of a field that contained one or more forb (herbaceous flowering) species. This part could be at the margin or inside the field, the vegetation could be spontaneous or sown, the plant species could be native or not, and annual or perennial. Excluded were pure grass strips, hedgerows (strips of ligneous plants), crop associations and companion plants. Included were strips where a crop and annual forbs were mixed. The decision for this criterion was made based on the abstract, but if the detailed characteristics of the flower strip could not be derived from the abstract, they were verified in the body of the article. Secondly, the study had to be conducted in an agricultural context. This means that the part of the field, that is not flower strip, had to be cropland, pasture or orchard. It also means the study had to be conducted in the field, not in controlled conditions (lab, greenhouse, growth chamber, etc.). The decision was taken based on the abstract, but if the agricultural context was not clear from the abstract, it was verified in the body of the article. Thirdly, the study had to be about the respective component of the appraisal. For this, a clear question was formulated for each component to evaluate the abstracts. The questions are listed in Table 1.1. This criterion had to be clear from the abstract. As the presence of a healthy pollinator community and a healthy natural enemy community are considered to be beneficial for crop pollination and crop pest control, respectively (e.g. Albrecht et al., 2012; Chaplin-Kramer et al., 2011; Hoehn et al., 2008; Tscharntke et al., 2007; Tschumi et al., 2015; Winfree et al., 2015), they were also used in the third criterion for the components 'pollination' and 'animal pests'. For this third criterion, the selection procedure was cross-checked by providing the set of references, meeting each criterion, to another author to evaluate them again, with the third criterion. Fourthly, the study had to be conducted in the North Temperate Zone (between the Arctic Circle and the Tropic of Cancer). If this was not clear from the abstract, it could be verified in the body of the article.

TABLE 1.1. OVERVIEW OF THE COMPONENTS AND THEIR RESPECTIVE SEARCH TERMS, QUESTIONS AND EFFECT DEFINITIONS FOR THE SCOPUS QUERY

	Components	**Search terms**	**Question: Does the paper investigate…**	**Positive effect: Flower strips result in…**	**Neutral effect: No effect of flower strips is found on…**	**Negative effect: Flower strips result in…**
Agronomical and ecological processes	Pollination	pollination, pollinator(s)	whether flower strips have an impact on crop pollination or on a healthy pollinator community (abundance, diversity,…)?	better or more crop pollination or in a healthier pollinator community (abundance, diversity,…)	crop pollination or on the health of the pollinator community (abundance, diversity,…)	worse or less crop pollination or in a less healthy pollinator community (abundance, diversity,…)
	Animal pests	insects pests, animal pests, slugs, rodents, pest management, pest control, natural enemies, predators, predation, parasitism, parasitoids, herbivory, herbivores	whether flower strips have an impact on animal pests on crops or whether it affects the natural enemy community (abundance, diversity)?	fewer animal pests on crops or in a healthier natural enemy community (higher abundance, diversity)	animal pests on crops or on the natural enemy community (abundance, diversity)	more animal pests on crops or in a less healthy natural enemy community (lower abundance, diversity)
	Weeds	weed, weeds	whether flower strips have an impact on weeds (spreading) in the cropping area?	less weeds (spreading) in the cropping area	weeds (spreading) in the cropping area	more weeds (spreading) in the cropping area
	Diseases	diseases, fungi, pathogens, infection, virus, bacteria, plant pathology, phytopathology, immunology, epidemiology	whether flower strips have an impact on crop diseases?	less crop diseases	crop diseases	more crop diseases
Economic balance: costs	Labor	labor, human labor, labour, human labour	whether flower strips have an impact on the farmer's labor?	a decrease in farmer's labor	on the farmer's labor	an increase of farmer's labor
	Fuel use	fuel, energy	whether flower strips have an impact on the farmer's fuel use?	a decrease of the farmer's fuel use	the farmer's fuel use	an increase of the farmer's fuel use
	Fertilizer use	fertilizers, fertilizer, manure	whether flower strips have an impact on the fertilizer use in the crop field?	less fertilizer use in the crop field	on fertilizer use in the crop field	greater fertilizer use in the crop field
	Pesticide use	pesticides, crop protection, herbicide, insecticide, biocide, fungicide, molluscicide	whether flower strips have an impact on the pesticide use in the crop field?	less pesticide use in the crop field	on pesticide use in the crop field	greater pesticide use in the crop field
	Buying machinery	equipment, machine, mowing, cutting	whether flower strips have an impact on the equipment the farmer has to buy/rent/own?	a decrease in the equipment the farmer has to buy/rent/own	on the equipment the farmer has to buy/rent/own	an increase in the equipment the farmer has to buy/rent/own

TABLE 1.1 (CONTINUED). OVERVIEW OF THE COMPONENTS AND THEIR RESPECTIVE SEARCH TERMS, QUESTIONS AND EFFECT DEFINITIONS FOR THE SCOPUS QUERY

	Components	**Search terms**	**Question: Does the paper investigate…**	**Positive effect: Flower strips result in…**	**Neutral effect: No effect of flower strips is found on…**	**Negative effect: Flower strips result in…**
Economic balance: income	Reduction in crop surface area	crop surface, crop area, cultivated surface, cultivated area	whether flower strips have an impact on the surface on which cropping can be done?	a greater surface area on which cropping can be performed	the surface on which cropping can be performed	a reduced surface on which cropping can be performed
	Crop yield	Yield	whether flower strips have an impact on the crop yield?	a higher crop yield	the crop yield	lower crop yield
	Subsidies	subsidies, reward, refunding, politics, incentive, policy, compensation	whether flower strips have an impact on the farmer's subsidies?	more subsidies for the farmer	the farmer's subsidies	less subsidies for the farmer
	Hay yield	hay, forage, herbage, grazing, fibre, protein, biofuel, bioenergy, bioethanol	whether flower strips have an impact on the hay yield produced in the field (by the flower strip), or whether this hay is a profitable product?	more hay yield produced in the field (by the flower strip); or the produced hay to be a profitable product	the hay yield produced in the field (by the flower strip); or there is no net profitability of the hay as product	a lower hay yield produced in the field (by the flower strip); or the produced hay to be an unprofitable product
Social recognition	Bee hives	hive, Apis mellifera, honey bee, beekeeping, honey	whether flower strips have an impact on the number of bee hives that can be put in the field, or on the honey production?	more bee hives that can be put in the field or more honey production	the amount of bee hives that can be put in the field or on the honey production	less bee hives that can be put in the field or less honey production
	Wild game	wild game, hunting, hunters	whether flower strips have an impact on the wild game in the landscape?	more wild game in the landscape	the wild game in the landscape	less wild game in the landscape
	Farmer's perception	farmer perception, farmer acceptance	the farmer's perception/acceptance of flower strips?	a positive perception of flower strips by farmers	farmer's perception of flower strips	a negative perception of flower strips by farmers
	Public image	farmer, image, esteem	whether flower strips have an impact on the image society has of a farmer?	a better image of a farmer held by society	the image of a farmer held by society	a worse image of a farmer held by society
	Erosion control	erosion, runoff, soil loss	whether flower strips have an impact on the soil loss from the field?	a decrease of the soil loss from the field	the soil loss from the field	an increase of the soil loss from the field
	Water protection	leaching, water protection, water quality, ground water, surface water	whether flower strips have an impact on the water quality or water pollution?	an improvement of water quality or less water pollution	the water quality or water pollution	lower water quality or more water pollution
	Landscape aesthetics	Landscape, tourism, ecotourism, aesthetic, recreation	whether flower strips have an impact on the landscape aesthetics, tourism or recreation?	better landscape aesthetics, more tourism, or more recreation	the landscape aesthetics, tourism or recreation	worse landscape aesthetics, less tourism, or less recreation

Based on the number of selected papers per component, the knowledge gaps and research needs were highlighted. The selected papers were then screened for the type of effect they showed. We considered as an effect a relationship, found in a study, showing an influence of flower strips on the considered component: a ‘positive effect’ if the study showed that flower strips had a significant influence on the component that was beneficial for the farmer; a ‘negative effect’ if the study showed that flower strips had a significant influence on the component that was disadvantageous for the farmer; and a ‘neutral effect’ if the study contained a relationship for which no significant influence on the component could be shown (see Table 1.1 for a clear definition of the effects per component). A single paper could show positive, neutral, as well as negative effects, which, in that case, were all considered. If a paper showed an effect for which no statistical test was needed, it was also taken into consideration. The information on the effects was based on the abstract, but if the information could not be derived from the abstract, it was verified in the body of the article. The effects were summed, per component, to identify the predominant effect.

FLOWER STRIPS’ PROS AND CONS FOR FARMERS: A POSITIVE BALANCE SO FAR

The Scopus search retrieved 245 unique records, among which some appeared for several components, resulting in a total of 593 records. Only 34 records met the criteria for selection, of which 30 were unique papers. The selected papers addressed 6 of the 20 components (see Table 1.2): pollination, animal pests, weeds, subsidies, hay yield and wild game. Most selected papers addressed the animal pests component (18), followed by pollination (7) and weeds (6). Figure 1.4 shows a radar plot of the log-transformed (log [n+1]) number of selected papers, for each component. Most selected papers (31 out of 34) appeared in the ‘agronomical and ecological processes’ category, while the components of the other categories had only one selected paper, or none at all.

Figure 1.5 shows the percentage of positive, negative and neutral effects (from a farmer’s point of view) of the selected papers, for each component. In total, 80% of the papers reported positive effects, 24% reported negative effects and 29% reported neutral effects. This resulted in 27 positive effects reported, 10 negative effects and 8 neutral effects. As explained before, a single paper could contain a positive, a negative, as well as a neutral effect. There was not a single case among the components where the negative effects outweighed the positive effects. While this already suggests a positive balance of pros and cons, the lack of research for most of components makes it too early to draw any general conclusions.

Table 1.2. Results of the Scopus query, with for each component the number of papers in the query output, the number of papers that met the criteria for selection and the references of these papers

‘+’: the paper shows a positive effect; ‘-‘: the paper shows a negative effect; ‘0’: the paper shows a neutral effect

Components	**Number of papers output**	**Number of selected papers**	**References selected papers**
Pollination	23	7	Balzan et al., 2014^{+}; Carvell et al., 2011^{+}; Heard et al., 2007^{+}; Korpela et al., 2013^{+}; Potts et al., 2009^{+}; Pywell et al., 2011^{+}; Rundlöf et al., 2014^{+}
Animal pests	95	18	Anjum-Zubair et al., 2010$^{+,0}$; Balzan et al., 2014$^{+,-}$ Bigger and Chaney, 1998^{0}; Büchi, 2002^{0}; Denys and Tscharntke, 2002^{+}; Eyre et al., 2011^{0}; Fitzgerald and Solomon, 2004^{0}; Hausammann, 1996^{+}; Hickman and Wratten, 1996$^{+,0}$; Meek et al., 2002$^{+,0}$; Pascual-Villalobos et al., 2006^{-}; Pfiffner and Luka, 2000^{+}; Pfiffner et al., 2009$^{+,0}$; Pywell et al., 2011$^{+,-}$; Roy et al., 2008^{+}; Skirvin et al., 2011^{+}; Walton and Isaacs, 2011$^{+,-}$; Wyss, 1996$^{+,0}$
Weeds	71	6	Bokenstrand et al., 2004$^{+,0}$; De Cauwer et al., 2008$^{+,-}$; Denys and Tscharntke, 2002$^{+,-}$; Marshall, 2001^{+}; Moonen and Pywell et al., 2011^{-}; Smith et al., 1999^{0}
Diseases	15	0	
Labor	0	0	
Fuel use	7	0	
Fertilizer use	30	0	
Pesticide use	73	0	
Buying machinery	46	0	
Reduction crop surface area	41	0	
Crop yield	35	0	
Subsidies	58	1	Mante and Gerowitt, 2007^{+}
Hay yield	38	1	De Cauwer et al., 2006^{+}
Bee hives	8	0	
Wild game	13	1	Casas and Viñuela, 2010^{+}
Farmers perception	0	0	
Public image	24	0	
Erosion control	8	0	
Water protection	5	0	
Landscape aesthetics	3	0	

For the pollination component, all seven selected papers showed a positive effect, being an increase in either abundance or diversity of pollinators, or both. Haaland et al. (2011) and Marshall and Moonen (2002) already mentioned some work suggesting the beneficial effect of flower strips for pollinators in their reviews. Five out of these papers considered bumblebees as the taxonomic group to study pollination. No paper was found investigating the effect on crop pollination explicitly.

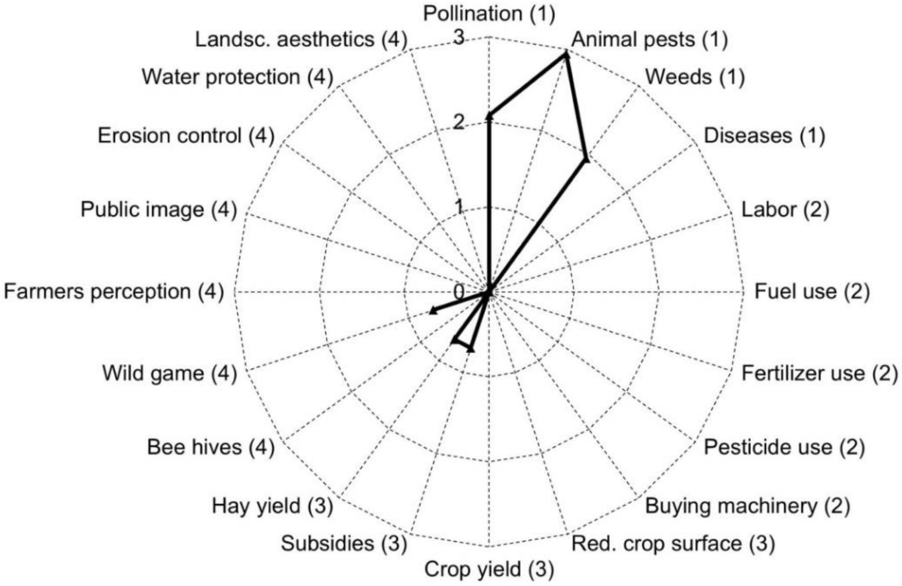

FIGURE 1.4. RADAR PLOT OF THE LOG-TRANSFORMED (LOG (N+1)) NUMBER OF PAPERS SELECTED FOR EACH COMPONENT

Numbers between brackets indicate the category to which the component belongs, with (1) being ‘Agronomical and ecological processes’, (2) ‘Economic balance: costs’, (3) ‘Economic balance: income’ and (4) ‘Social recognition’.

For the animal pests component, 13 papers showed a positive effect, 5 papers showed a negative effect, and 8 papers contained a neutral effect. Effects concerned either an increase or decrease in abundance or diversity of pests, either an increase or decrease in abundance or diversity of natural enemies, or both. The positive effects, consisting in the reduction of pests or the increase of natural enemies, have also been mentioned in the review of Marshall and Moonen (2002) while the reviewed papers in Haaland et al. (2011) also showed mixed effects (reviewed papers partly overlapping with the papers in the present review). While abundance was the most frequently used metric, four papers also studied diversity, or species richness, of pests or natural enemies. Some of the papers indicated that effects can be species dependent (Pfiffner et al., 2009; Roy et al., 2008). Also for this component, papers tended to report an effect on the abundance or the diversity of pest and natural enemy species, and not on crop damage, per se.

While increased abundance or diversity of pollinators and natural enemies have already been shown to increase crop pollination and decrease crop damage, respectively (Albrecht et al., 2012; Hoehn et al., 2008; Tscharntke et al., 2007; Tschumi et al., 2015; Winfree et al., 2015), this relationship is not found in all studies (Chaplin-Kramer et al., 2011). This suggests that more research is required to explore under what conditions this relationship is valid or not, and that studies on flower strips should focus on the direct effects on crop pollination and crop damage.

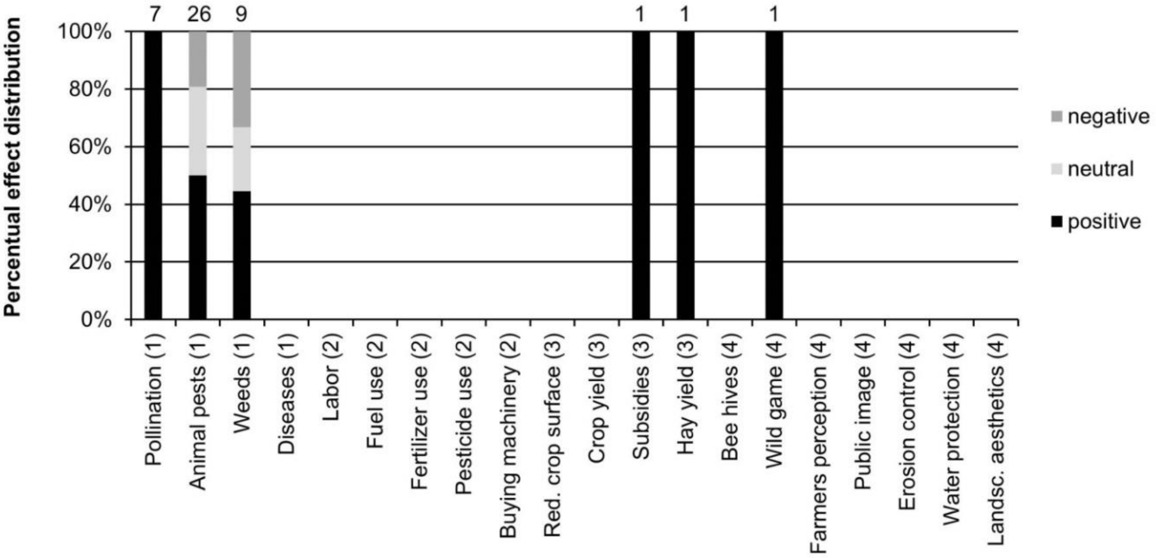

FIGURE 1.5. BAR CHART WITH THE PERCENTAGE DISTRIBUTION OF POSITIVE, NEGATIVE AND ZERO EFFECTS FOR EACH COMPONENT (SEE TABLE 1.2)

Numbers above the bars indicate the number of effects identified in the selected papers, for that component. Components without a bar had no selected papers. Numbers between brackets indicate the category to which the component belongs, with (1) being 'Agronomical and ecological processes', (2) 'Economic balance: costs', (3) 'Economic balance: income' and (4) 'Social recognition'.

For the weeds component, three papers showed a negative effect, four papers showed a positive effect, and two papers contained a neutral effect. There was a clear link to the type of flower strip vegetation: negative effects were reported for flower strips with spontaneous vegetation, in which noxious weeds could easily settle within the vegetation, while positive and neutral effects were reported for sown flower strips, in which the competitive sown species were able to suppress harmful weed species from settling in the strip. Marshall and Moonen (2002) also mention research pointing out that sowing grass, or grass and flower mixes, reduces the risk of weed spreading.

For the subsidies, the hay yield as well as the wild game component, only one paper was selected, each one showing a positive effect of flower strips. For the other components, either no papers were found or the papers did not meet the criteria. The small number of selected papers, therefore, makes it impossible to draw general conclusions. However, for certain components, the effects of flower strips might be obvious. For example, flower strips can produce hay, while crops mostly don't. Hay yield is, thus, expected not to be negatively affected by implementing flower strips instead of crops.

RESEARCH GAPS AND NEED FOR FURTHER RESEARCH

While a total of 593 records came out of the database query, only 34 met the criteria for inclusion. This shows that, from the considerable amount of research on flower strips, only a few studies explicitly considered the influence of flower strips in terms of the advantages or disadvantages for the farmer. For pollination, animal pests, and weeds, many papers had to be excluded as they reported on insects or weeds in the crop or flower strip, without a proper comparison to a no-strip control. This partly explains the low number of selected papers for these components, and suggests the need for well-designed field studies to demonstrate the effects of flower strips. Moreover, only one study was carried out over 10 years, while the other studies lasted only for four years or less. More long-term research could, therefore, produce interesting results, even if agri-environmental schemes like flower strips are often based on a short-term agreement (Service Public de la Wallonie, 2012) and their advantages for farmers should be present already in the short term. The selected papers on the pollination component were all more recent, with all selected papers published after 2006. For the other components, selected papers were equally spread over time starting from 1996.

Thirty-one papers reported on research conducted in Europe, while only three were conducted in the USA. This suggests that more research is done on flower strips in Europe, possibly as a result of the variable subsidizing policy in the EU and the USA for creating flower strips (Haaland et al., 2011; USDA, 2015). The majority of the selected studies (30) were conducted on flower strips adjacent to arable crops. Only three studies looked at flower strips in orchards, and only one examined flower strips in pastureland.

Haaland and Gyllin (2010) and Marshall and Moonen (2002) mentioned some other practical advantages of flower strips for farmers that we didn't consider. Flower strips can be used for turning tractors or other agronomic vehicles, for visual inspection for pests and weeds, for hedge or other boundary management without disturbing or damaging the crop, or for recreational pathways (Haaland and Gyllin, 2010; Marshall and Moonen, 2002). However, depending on the country, agri-environmental scheme regulations may prohibit one or more of these uses, e.g. tractor turning may cause disturbance of the vegetation and fauna in the strip (Service Public de la Wallonie, 2012).

The evaluation of pros and cons could also depend on the type of flower strip. A perennial strip with successively flowering plant species, providing continuous pollen and nectar resources, would be the preferred option to support pollinators (Wratten et al., 2012). For biological pest control, however, targeted annual strips with flower species adapted to the crop rotation, would be preferred (e.g. Tschumi et al., 2015), while for erosion control and water protection, simple grass strips would be sufficient. This suggests the need to analyze the trade-offs between the different pros and cons in the context of the particular farm.

Furthermore, the choice of seed mixture, and the management of flower strips, will determine the vegetation development during the years following establishment (De Cauwer et al., 2005; Chapters 2, 3, 4). This can consequently influence the evaluation of pros and cons. Seed mixture and management differ between countries and geographical regions. Management can include one or more cutting a year, with or without hay removal, or no cutting at all (Haaland et al., 2011). De Cauwer et al. (2006) already showed a difference in hay yield and herbage quality between sown and unsown flower strips, but more research on this and other components is needed.

The majority of the selected papers belonged to the category of 'agronomical and ecological processes', while there is a paucity of research in the 'economic balance: costs', the 'economic balance: income' and the 'social recognition' categories. This indicates that, along with more research in the agronomical and ecological processes, interactions with researchers from Economics and Social Sciences could be useful to provide a more complete evaluation of pros and cons, which is necessary for effective ecological intensification (Bommarco et al., 2013). This research can be compared with the findings about factors determining farmers' acceptance of agri-environmental schemes (Burton and Paragahawewa, 2011; Mante and Gerowitt, 2007; Mathijs, 2003; Sattler and Nagel, 2010; Vanslembrouck et al., 2002) to identify the aspects on which farmers need more information.

A better and more informed farmer is more likely to implement agri-environmental measures (Fiedler et al., 2008; Vanslembrouck et al., 2002; Wratten et al., 2012) and could adopt this practice in his farming culture (Burton and Paragahawewa, 2011). However, studies on farmers' trajectories from intensive agriculture to more sustainable agricultural systems demonstrate that information is only one of the factors determining if, how and how fast a farmer will make a transition to a more sustainable farming system (Chantre and Cardona, 2014; Lamine, 2011). The so-called 'lock-in' effect can even force farmers to keep their conventional agricultural practices, and should be taken into account when promoting measures like flower strips (Cowan and Gunby, 1996; Wilson and Tisdell, 2001).

CONCLUSIONS

We can conclude that so far, the balance of pros and cons of flower strips, from a farmers' point of view, tends to be positive. This was, however, mostly the case for agronomical and ecological processes, like pollination and animal pest control. Weed infestation was only less problematic for sown flower strips, while spontaneous ones tended to increase weed problems. For the other components of the appraisal, large research gaps are still present, especially in terms of the influence of flower strips on the farmer's economical balance and social recognition. We expect that more research on the different components of the appraisal of pros and cons, combined with better information for farmers, can lead to a higher uptake of flower strips in farming.

Acknowledgements

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1.3. OBJECTIVES AND SCIENTIFIC APPROACH

This PhD project was part of a multidisciplinary platform AgricultureIsLife (Monty et al., 2016) with as general objective to develop a sustainable agriculture for the future. Projects were launched around four axes: (1) performance of non-conventional agroecosystems, (2) optimizing the crop residue management in agroecosystems, (3) new tools to increase sustainability of agroecosystems, and (4) valorization of agroecosystem products (Gembloux Agro-Bio Tech - Université de Liège, 2014a). Different research disciplines and equipment were combined and an experimental farm was made available to the different projects, containing, among others, fields with agroforestry, cover cropping, residue management and flower strip experiments (Figure 1.6a). Multidisciplinary collaboration around the theme of flower strips, both for a project on natural enemies and pest control, and a project on food and non-food compounds from flower strips, has led to six publications as a co-author:

Hatt, S., Uyttenbroeck, R., Lopes, T.M., Paul, A., Danthine, S., Bodson, B., Piqueray, J., Monty, A., and Francis, F. (2015). Do Wildflower Strips Favor Insect Pest Populations at Field Margins? Agric. Agric. Sci. Procedia 6, 30–37.

Hatt, S., Uyttenbroeck, R., Bodson, B., Piqueray, J., Monty, A., and Francis, F. (2015). Des bandes fleuries pour la lutte biologique : état des lieux, limites et perspectives en Wallonie – Une synthèse bibliographique. Entomol. Faun. - Faun. Entomol. 68, 149–158.

Hatt, S., Uyttenbroeck, R., Lopes, T., Mouchon, P., Chen, J., Piqueray, J., Monty, A., and Francis, F. (2017). Do flower mixtures with high functional diversity enhance aphid predators in wildflower strips? EJE 114, 66–76.

Paul, A., Frederich, M., Uyttenbroeck, R., Hatt, S., Malik, P., Lebecque, S., Hamaidia, M., Miazek, K., Goffin, D., Willems, L., et al. (2016). Grasshoppers as a food source? A review. BASE 20, 337–352.

Paul, A., Frederich, M., Uyttenbroeck, R., Malik, P., Filocco, S., Richel, A., Heuskin, S., Alabi, T., Megido, R.C., Franck, T., et al. (2016). Nutritional composition and rearing potential of the meadow grasshopper (Chorthippus parallelus Zetterstedt). J. Asia-Pac. Entomol. 19, 1111–1116.

Paul, A., Frederich, M., Megido, R.C., Alabi, T., Malik, P., Uyttenbroeck, R., Francis, F., Blecker, C., Haubruge, E., Lognay, G., et al. (2017). Insect fatty acids: A comparison of lipids from three Orthopterans and Tenebrio molitor L. larvae. J. Asia-Pac. Entomol. 20, 337–340.

For the project that is the subject of this PhD manuscript, experimental wildflower strips were created in AgricultureIsLife Zone 1 (Figure 1.6b-d). Both the strips in the 'Wildflower strips within crop' field (WC field) and in the 'Wildflower strips with mowing regime' field (WM field) were sown with a set of seed mixtures to create a gradient of plant FD. The WC-field contained larger plots to study the effects on insect communities (Figure 1.6c and Figure

1.7). The WM-field contained smaller plots and received three different experimental mowing regimes to monitor weed communities (Figure 1.6d). Furthermore, real-existing flower strips and meadows under agri-environment scheme were selected for a part of this project in the 'Parc Naturel des Vallées de la Burdinale et de la Mehaigne' in the Hesbaye region between Huy, Andenne and Hannut (Parc Naturel de la Burdinale et de la Mehaigne, 2017).

From the introduction sections 1.1 and 1.2, pollination service appears as a typical pro of flower strips, and weed infestation disservice as a typical con. **The general objective of this PhD was test methods of flower strips creation and management to maximize pollinator support and minimize weed infestation.** To reach this objective, 4 research questions were defined based on the state of the art of scientific evidence described in sections 1.1 and 1.2.

Firstly, it was mentioned in the introduction that functional traits are suggested to play a key role in the biodiversity – ecosystem functioning relationship. Therefore, increasing plant functional diversity can be a tool to optimize perennial flower strips for pollinator support. To test this, we used the flower strips created in AgricultureIsLife Zone 1 in the WC field (Figure 1.6c and Figure 1.7). To use FD as a tool to optimize flower strips, a farmer should be able to create a desired level of FD by sowing a seed mixture. However, vegetation dynamics after sowing a mixture can influence the abundance of the sown plant species and spontaneous species can colonize the flower strip (e.g. De Cauwer et al., 2005; Leps̑ et al., 2007), which can influence the realized value of FD. This leads to the first research question:

- ➔ ***Q1: Can we create plant functional diversity in flower strips?***

This question will be addressed in **Chapter 2**. The vegetation composition of the flower strips was surveyed the first year after sowing and the effects of spontaneous species and abundance of sown species on realized FD were investigated. The further development of the realized FD in the second year after sowing will be shortly addressed in Chapter 3.

When it is possible to apply FD as a tool, it can be studied what is the effect on pollinator communities. This leads to the second research question:

- ➔ ***Q2: Is functional diversity the key to promote pollinators in flower strips?***

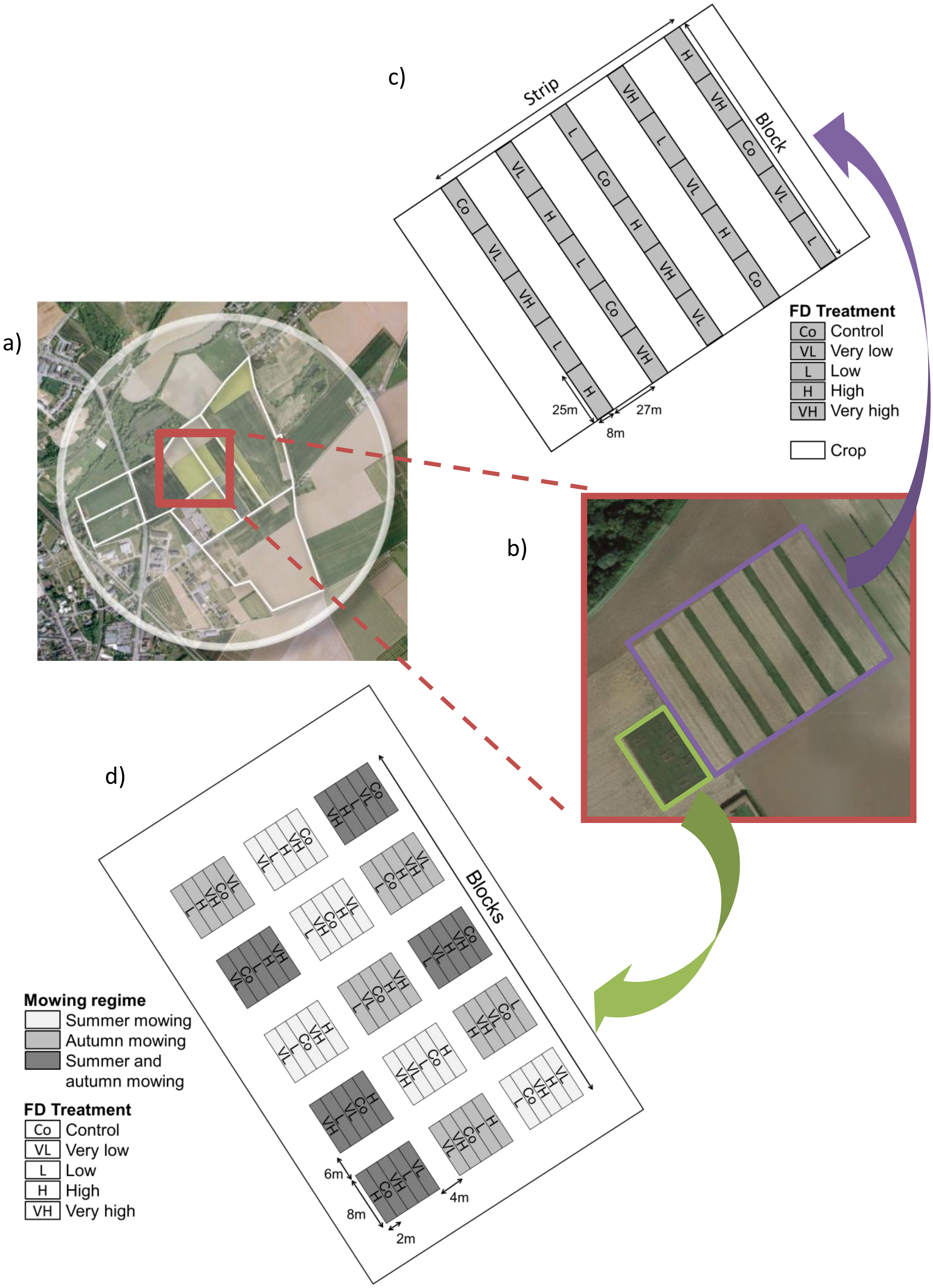

Figure 1.6. Plan of the experimental fields in Gembloux

a) shows the plan of the experimental farm with fields for flower strips, agroforestry, cover cropping, residue management and others (adapted from Gembloux Agro-Bio Tech - Université de Liège, 2014). b) shows AgricultureIsLife Zone 1 in which the experimental fields of this project were created (Google Inc., 2017). c) shows the 'Wildflower strips within crop' field. d) shows the 'Wildflower strips with mowing regime' field.

This question will be addressed in **Chapter 3**. Plant-pollinator interaction networks were monitored during two years in the flower strips with different plant FD in the WC field (Figure 1.6c).

Concerning the weed infestation disservice of flower strips, in section 1.2 it was shown that sowing a seed mixture to create the flower strip can reduce weed infestation compared to spontaneous development of the vegetation. This suggests that competition by sown species can limit weed infestation. Furthermore, to maintain perennial flower strips, a mowing regime is often applied. Adapting timing and frequency of this mowing regime could influence abundance of noxious weed species (Smith et al., 2010). These two aspects lead to the third research question:

- ➔ ***Q3: Can adapting mowing regime and forb competition be used as tools to reduce weed infestation in perennial flower strips?***

This question will be addressed in **Chapter 4**. For this study, the 'Wildflower strips with mowing regime' field (Figure 1.6d) was used. This field was sown with the same mixtures as

FIGURE 1.7. PICTURE OF A WILDFLOWER STRIP IN THE 'WILDFLOWER STRIPS WITHIN CROP'-FIELD (JUNE 2015)

the 'Wildflower strips within crop' field. The control mixture with only grass species can be compared with the other mixtures containing grass and forb species to study the effect of forb competition on weed infestation. Three different mowing regimes that were applied in the field enable to study the effect of mowing regime.

Finally, literature showed that wildflower strips are a rather new habitat in the agricultural landscape, making it difficult to define optimal creation and management guidelines. Therefore the question arose whether flower strips are a surrogate of a type of semi-natural habitat in the surrounding landscape. The real-existing perennial flower strips in the 'Parc Naturel des Vallées de la Burdinale et de la Mehaigne' were used to address this question. They were compared with hay meadows with a 'high biological value grassland' agri-environment scheme (MC4; Natagriwal asbl, 2017) in the same Natural Park. This leads to the fourth research question:

➔ ***Q4: Are perennial flower strips a surrogate for hay meadows?***

This question will be addressed in **Chapter 5** by comparing five perennial flower strips with five hay meadows for their flower-visiting pollinator community.

To conclude, the specific objectives of the study are to investigate whether 1) increasing plant functional diversity can be used as tool to optimize flower strips for pollinators, 2) forb competition and adapting timing and frequency of mowing can be used as tools to limit weeds in flower strips, and 3) flower strips perform equally in supporting pollinators as the natural habitat for which they are thought to be a surrogate.

CHAPTER 2

CREATING PERENNIAL FLOWER STRIPS: THINK FUNCTIONAL!

2. CREATING PERENNIAL FLOWER STRIPS: THINK FUNCTIONAL!

Adapted from the conference paper published in Agriculture and Agricultural Science Procedia (2015), 6:95-101

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ABSTRACT

In last decades, farmland biodiversity came under large threat. To counteract farmland biodiversity loss and other environmental impacts of intensive agriculture, European farmers can apply Agri-environmental schemes. One of these is the creation of flower strips, a part of the cropping field where flowers are sown or naturally settled. Flower strips are known to increase biodiversity in the agricultural landscape, notably attracting specific insects groups, such as pollinators and natural enemies that can provide valuable pollination and biocontrol services to the crop. However, the plant species composition and management of the strips can have a large influence on the identity and amount of useful insects present in the strips, suggesting the need to develop tailored flower strips to maximize the services delivered. Functional diversity (FD) is sometimes proposed as a promising approach, focusing on plant functional traits rather than plant species itself. Yet, it is not certain that sowing a set of plant species results in the desired vegetation with the desired functional trait composition. Species from soil seed bank or dispersing from neighboring vegetation can settle in the strip, while sown species might not always be equally adapted to local conditions. To test this, we developed seed mixtures with four different levels of FD, based on flower traits, and sew them as flower strips in a conventional arable field. We monitored the vegetation to calculate the FD of the realized vegetation. While the absolute FD values of the realized vegetation were lower than the expected FD values, the realized vegetation showed the same FD gradient as expected from the sown mixtures, indicating that it is possible to manipulate FD in flower strips.

Key words

flower strips, vegetation monitoring, functional diversity, field experiment

INTRODUCTION

Agriculture has known a lot of changes in recent decades. An important direction of change is intensification. Farms increased in size, their management became more mechanized, field size increased and crop rotations were simplified. This intensification has led to habitat destruction and fragmentation and a reduction of landscape diversity and biodiversity (Kruess and Tscharntke, 1994; Stoate et al., 2001; Tscharntke et al., 2005). To counteract this loss of biodiversity and the consequent loss of ecosystem services, European authorities created the system of Agri-Environmental Schemes. Agri-Environmental Schemes were designed to convince farmers to reduce the environmental risks of modern agricultural practices and to preserve nature and cultivated landscapes (European Commission, 1998; European Commission, 2005). One example of Agri-Environmental Schemes is the creation of flower strips, a part of the cropping field where flowers are sown or naturally settled. Flower strips are known to increase biodiversity in the agricultural landscape, notably attracting specific insects groups, such as pollinators and natural enemies that can provide valuable pollination and biocontrol services to the crop (Haaland et al., 2011).

However, the plant composition and management of the strips can have a large influence on the identity and amount of useful insects present in the strips, suggesting the need to develop tailored flower strips to maximize the services delivered (Korpela et al., 2013; Tschumi et al., 2014). Functional diversity (FD) is sometimes proposed as a promising approach, focusing on plant functional traits rather than plant species itself (e.g. Campbell et al., 2012; Fontaine et al., 2006). Yet, it is not certain that sowing a set of plant species can result in the desired vegetation (De Cauwer et al., 2005; Lepŝ et al., 2007). Species from soil seed bank or dispersing from neighboring vegetation can settle in the strip, while sown species might not always be equally adapted to local conditions (Münzbergová and Herben, 2005). As a consequence, when sowing a wildflower strip with a certain plant species mixture, it is not sure that the established vegetation will have the desired functional trait composition or the desired FD level (Fukami et al., 2005). We tested in a replicated field experiment whether it is possible to create different levels of plant FD in sown flower strips.

Materials and methods

Experimental setup

To create a plant FD gradient, four plant species mixtures were prepared with equal species richness but contrasting diversity in functional traits. A list of 20 forb plant species was composed from perennial herbaceous species that were commonly found in grasslands, used in Agri-Environmental Schemes in Wallonia, Belgium and that were available from the market. Because the focus of the flower strip experiment was the provision of food sources to flower visiting pollinators and natural enemies, a set of seven floral functional traits was selected. These traits were (1) flower color, (2) flower class according to Müller (1881), (3) UV reflection in the peripheral part of the flower (5 classes), (4) presence of a UV pattern, (5) the month of the flowering start, (6) flowering duration in months and (7) the maximal height of the plant. For all 20 species, functional trait values for these traits were retrieved from TRY database (Kattge et al., 2011) for the former four traits and from Lambinon et al. (2008) for the latter three traits. Based on these traits, FD of every possible combination of seven plant species was calculated using Rao quadratic entropy index (Botta-Dukát, 2005) with equal importance of the traits and equal abundance of the plant species. The combinations with lowest and highest FD were selected, as well as the combinations with functional diversity closest to the 33rd and the 67th percentile of the range, resulting in four plant species mixtures with contrasting FD: very low (VL), low (L), high (H) and very high (VH) (Table 2.1). For these mixtures, in total 17 out of the 20 listed plant species were used.

Table 2.1. Species used in the four mixtures

VL: very low functional diversity (FD); L: low FD; H: high FD; VH: very high FD

Species	VL	L	H	VH
Achillea millefolium	x	x	x	x
Anthriscus sylvestris	x		x	x
Crepis biennis		x		
Galium verum	x	x		
Geranium pyrenaicum			x	
Heracleum sphondylium	x			
Hypochaeris radicata		x		
Knautia arvensis	x	x		
Leontodon hispidus		x	x	
Leucanthemum vulgare	x		x	
Lotus corniculatus				x
Lythrum salicaria		x		x
Malva moshata				x
Medicago lupulina				x
Origanum vulgare			x	
Prunella vulgaris			x	x
Trifolium pratense	x			

To create the plant species mixtures in the field, four seed mixtures were prepared, each containing equal seed mass (0.5 kg/ha) of the seven forb plant species. By sowing equal seed mass per species, we aim to create perfect evenness between the forb plant species, assuming that plant species with lower seed mass have seeds with higher mortality and thus need more seeds to establish the same abundance as plant species with higher seed mass. Furthermore, three grass species, *Festuca rubra* L., *Agrostis spp.* and *Poa pratensis* L. were added to the seed mixtures (11.5 kg/ha, 5 kg/ha and 5 kg/ha respectively). As the focus of the wildflower strips was to provide food sources for flower visitors, the floral traits of these grasses were not taken into account. Seeds were obtained from ECOSEM, Belgium. The seed mixtures were sown in an experimental field located in the experimental farm of Gembloux Agro-Bio Tech, 50°34'03''N; 4°42'27''E at 150 m elevation. The four mixtures and one control containing only the grass species were sown in a 5x5 Latin square design, consisting of five flower strips of 125x8 m with conventional cropping zones of 27 m between the strips and each of the five flower strips consisting of five 25x8 m plots. This results in five replicates of four FD treatments (VL, L, H and VH) and a control treatment. The control plots were not considered in this particular study because only sowing the grass species results in a lower total seed mass that was brought in the control plots while sowing, which could have influenced the vegetation dynamics. On 6 June 2013, the grass and forb species were sown superficially with a Wintersteiger plot seeder. Strips were mown yearly once in June and once in September with removal of hay.

Sampling

The vegetation development was monitored in 2014 in the 25 flower strip plots to evaluate the realized vegetation. For this, three permanent quadrats of 1x1 m were created in each plot. In June and September before mowing, the permanent quadrats were surveyed by estimating the proportion of horizontal cover of each forb plant species.

Statistical analysis

For each plot, the average cover of each forb plant species was calculated by summing up the cover in each of the three permanent quadrats in both survey periods, and dividing by six. For the not-sown plant species appearing in the permanent quadrats, the trait values of the seven functional traits were retrieved from the TRY database (Kattge et al., 2011) and from Lambinon et al. (2008). This results in a new species x trait matrix with all observed species and their trait values. With the average plant species cover as abundance and the floral traits for all plant species, the realized FD was calculated for each plot with the Rao quadratic entropy index to compare it with the expected FD of the treatment. As Rao's index is sensitive to the amount of species in the species x trait matrix, the expected FD of the four sown species mixtures was recalculated with the new species x trait matrix. The difference between the treatments for their mean realized FD was tested with Kruskal-Wallis rank sum tests and Nemenyi tests.

To investigate the effect of the not-sown species occurring in the vegetation, the realized FD based on only the sown species was calculated by giving the not-sown species zero abundance in the calculation. To investigate the effect of non-equal abundance of the sown species on the FD gradient, the FD based on only sown species and with presence/absence as abundance values of the sown plant species was calculated. For both of these realized FD measures, the difference between the treatments for their mean values was also tested with Kruskal-Wallis rank sum tests and Nemenyi tests.

The number of forb plant species present in each plot was calculated as the total amount of species in the three quadrats and the two sampling periods together. The difference between the means of species number per FD treatment was tested with a Kruskal-Wallis rank sum test and Nemenyi tests to verify whether a realized FD gradient was caused by a difference in species richness.

Data treatment was conducted in R (R Core Team, 2013).

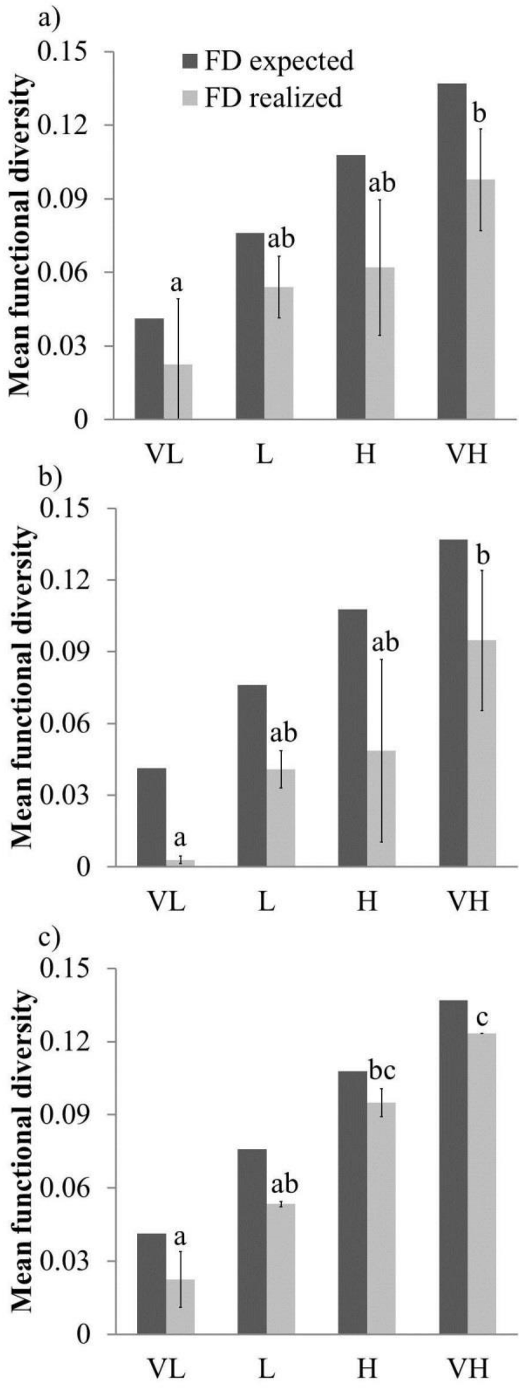

FIGURE 2.1. MEAN EXPECTED AND REALIZED FUNCTIONAL DIVERSITY (FD) PER TREATMENT

The realized FD is the mean value for each treatment based on a) the abundance of all plant species, b) the abundance of only sown species and c) the presence/absence of only sown species; VL: very low FD; L: low FD; H: high FD; VH: very high FD; error bars show standard error of the mean, letters above error bars show results of Nemenyi pairwise comparison of the means (P<0.05).

RESULTS AND DISCUSSIONS

In total, 35 plant species were found, of which 14 were sown species. The three sown species which did not appear in permanent quadrats, were *Anthriscus sylvestis* (L.) Hoffmann, *Lythrum salicaria* L. and *Trifolium pratense* L. It is possible that they needed more time to germinate or that the site conditions were not favorable enough for them to settle. The sown species *Heracleum sphondylium* L., appeared with only one individual and in a plot where it was not sown. Among the ten most abundant species were four not-sown species, namely *Cirsium arvense* (L.) Scop., *Sinapis alba* L., *Malva sylvestris* L. and *Rumex obtusifolius* L. *C. arvense*, *M. sylvestris* and *R. obtusifolius* have been reported as common weed species (Donald, 1994; Zaller, 2004; Zahedi & Ansari, 2011). This suggests that enough bare soil was available during the initial vegetation development for weeds to colonize the flower strips. *Sinapis alba* is commonly used as cover crop (Haramoto and Gallandt, 2004) and has been cultivated in the experimental field during the years preceding the experiment. This may have enabled this species to emerge from the soil seed bank.

Considering all the plant species found in the quadrats, the realized FD was significantly different over the treatments (*H*=12.04; *P*=0.007). Figure 2.1a shows the increasing realized FD with the treatments. This shows that it is possible to manipulate the FD level in flower strips. The realized FD was always lower than the expected FD.

Considering only the sown plant species found in the quadrats, the realized FD was significantly different over the treatments (*H*=14.63; *P*=0.002). Figure 2.1b shows the increasing realized FD with the treatments. Only for the VL treatment, the realized FD is lower when considering only sown plant species than when considering all plant species ('VL' in Figure 2.1b and Figure 2.1a), but the pairwise comparisons of the Nemenyi test did not show a different pattern. This suggests that additional plant species that colonized the plots mainly brought more diversity in traits to the plots with lowest FD treatment. Indeed, in the lower FD treatments, the chance may be higher that additional plants bring new traits to the vegetation.

The realized FD calculated with only presence/absence data of sown plant species was significantly different over the treatments (*H*=18.23; *P*<0.001). Figure 2.1c shows the increasing realized FD with the treatments. The trend was more pronounced then when the not-sown plants are included and with the relative abundance of the plant species (Figure 2.1a-b) and this was confirmed by the pairwise comparisons of the Nemenyi test. It suggests that the desired evenness of the sown species was not well established in the field. Some sown species had lower abundance than others or did not even emerge. The latter is clearly visible in Figure 2.2, where the mean realized number of sown species was always lower than the expected seven species. This might affect more the treatments with a higher FD value, as they have lower functional redundancy and losing a species consequently leads more likely to a loss of trait diversity.

No significant difference was found in the realized total number of forb plants species (*H*=4.91; *P*=0.178) over the treatments. However, there was a significant difference in the realized total number of sown ones (*H*=13.21; *P*=0.004), even if no clear trend was visible (Figure 2.2). It is possible that a little lower realized amount of sown plant species for the VL treatment has caused a lower realized FD value, but as mentioned before, the high functional redundancy can have reduced this effect. Because a vegetation with higher FD is expected to have more ecological niches filled (Mason et al., 2005), it may be possible that less additional species were able to colonize the plot with higher FD treatment, as observed by Lepŝ et al. (2007) and Van der Putten et al. (2000) for a higher species diversity. However, this was not observed in our experiment.

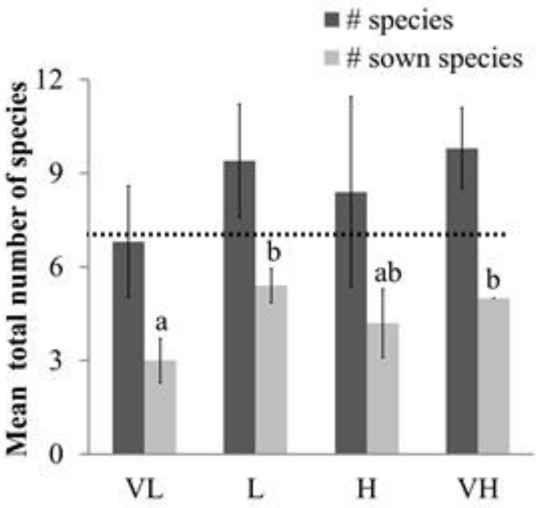

FIGURE 2.2. MEAN TOTAL REALIZED NUMBER OF FORB PLANT SPECIES AND SOWN FORB PLANT SPECIES FOR THE DIFFERENT TREATMENTS

VL: very low FD; L: low FD; H: high FD; VH: very high FD; error bars show standard error of the mean; letters above error bars show results of Nemenyi pairwise comparison of the means ($P < 0.05$) for the sown species number (for the total species number no significant difference was found between the treatments). The dotted line shows the level of seven species that were sown in each mixture.

While it was shown that it is possible to manipulate FD in flower strips by sowing a mixture, a continued monitoring of the vegetation will show if the FD gradient will remain during further vegetation development. Indeed, abundance of species can change during the years after sowing (De Cauwer et al., 2005; Lepŝ et al., 2007) and vegetation succession can lead to convergence of the functional trait composition (Fukami et al., 2005).

As manipulating FD seems to be a possible tool to develop tailored flower strips, further research could focus on how plant FD steers the diversity of flower visiting pollinators and natural enemies and the related and other ecosystem services delivered by flower strips.

CONCLUSIONS

A higher FD is not only leading to more biodiversity, it's also expected to deliver more ecosystem services. Manipulating FD can thus be an efficient way to maximize ecosystem service delivery, especially in Agri-Environmental Schemes. However, few studies investigated whether sowing a plant mixture results in a plant species composition with the desired FD. Here we have shown with an experimental study that it is possible to manipulate plant FD in flower strips by sowing a species mixture. The expected FD gradient was observed in the realized vegetation. However, the absolute FD values were lower than the expected FD values because sown species did not appear in even abundance, a part of them did not emerge and not-sown species appeared in the vegetation.

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CHAPTER 3

FUNCTIONAL DIVERSITY IS NOT THE KEY TO PROMOTE POLLINATORS IN WILDFLOWER STRIPS

3. FUNCTIONAL DIVERSITY IS NOT THE KEY TO PROMOTE POLLINATORS IN WILDFLOWER STRIPS

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ABSTRACT

Intensification of agriculture has been one of the major drivers for biodiversity loss in recent decades. Pollinators, which serve an important role in pollinating crops as well as wild plants, have shown a decline in species richness. Flower strips can be used to support pollinators in agro-ecosystems, however the question remains as to how their design can be optimized in order to best benefit pollinators. Increasing plant species diversity has been shown to be beneficial for pollinators, and it is often suggested that functional traits are driving this relationship. Therefore, increasing plant functional diversity could be a tool to support pollinator abundance and diversity. As experimental evidence on this relationship is scarce, we developed a field study with experimental sown flower strips with four functional diversity levels, based on multiple flower traits and with equal plant species richness. We monitored vegetation development, as well as the flower-visiting pollinator community and their interaction networks with flowers. We were able to create a functional diversity gradient while controlling for plant species richness and evenness. However, in contrast to our expectations, pollinator species richness and evenness were not influenced by functional diversity, and increasing functional diversity even resulted in lower flower visitation rates. Network stability metrics showed no effect or negative relationships with functional diversity. We conclude that increasing functional diversity was not the key for supporting pollinators in wildflower strips. Our results also suggest that, for a constant amount of flower resources, increasing plant functional diversity and thus decreasing redundancy of potential pollinator feeding niches, decreases the amount of flower resources present per feeding niche. As pollinator species tended to have less overlap in their feeding niches in flower strips with increased functional diversity, this may lead to a reduction of flower resources available for pollinator species with a more specialized feeding niche.

Key words

functional diversity, wildflower strips, plant-pollinator networks, niche overlap, agri-environment schemes, redundancy

INTRODUCTION

Intensification of agriculture has been one of the major drivers for biodiversity loss in recent decades (Stoate et al., 2001; Tilman et al., 2001). Among others, pollinators, which play a critical role in delivering pollination services to crops and wild plants (Klein et al., 2007; Potts et al., 2010), have seen declines in species richness and abundance (Biesmeijer et al., 2006; Potts et al., 2010; Winfree et al., 2009). The provision of food sources, shelter, and nesting sites in agro-ecosystems, by creating and managing ecological infrastructure, has been suggested as an important way to support pollinators (Klein et al., 2007; Nicholls and Altieri, 2012). One example is wildflower strips (Wratten et al., 2012), of which the main goal is to enhance biodiversity, while also attracting useful insects such as crop pollinators as well as natural enemies of crop pests (Haaland et al., 2011). Creating flower strips is in most cases beneficial for pollinators (section 1.2), however the question remains as to how to optimize their design to support pollinator abundance and diversity. Next to the intrinsic biodiversity conservation value, a higher abundance and diversity of pollinators can also enhance pollination services (e.g. Albrecht et al., 2007; Hoehn et al., 2008; Klein et al., 2003; Morandin and Winston, 2005).

Increasing the number of plant species in flower mixtures has been suggested to improve the effectiveness of flower strips for pollinator support (Scheper et al., 2015). Indeed, it has been reported that pollinator abundance and species richness are positively related to plant species richness (e.g. Ebeling et al., 2008; Hudewenz et al., 2012; Potts et al., 2003; however, see Grass et al., 2016). Also pollinator functional group richness (Hegland and Boeke, 2006) and pollinator functional diversity (based on pollinator feeding niche, i.e. the plant families they are reported to visit; Orford et al., 2016), were found to be positively related to plant species richness. Next to plant species richness, increasing flower abundance is often found to increase pollinator abundance and species richness (e.g. Hegland and Boeke, 2006; Ebeling et al., 2008). Increasing plant species richness offers more feeding niches to pollinators, which can allow more pollinator species to find floral resources (Blüthgen and Klein, 2011).

Whereas increasing plant species diversity is beneficial for pollinators, they perceive their host plants by their functional traits (Campbell et al., 2012; Fontaine et al., 2006; Junker et al., 2013). The shape of flower corolla for instance, determines the accessibility of floral nectar for flower visitors, while pollinators, depending on the length of their mouthparts, may prefer different corolla shapes (Fontaine et al., 2006). Flower functional traits can act as attractive features or as barriers for flower visitors. Traits related to flower phenology, morphology and visual cues have been reported to contribute more in defining the pollinator species feeding niche, compared to other traits, like flower nectar and pollen mass and display size (Junker et al., 2013). As these functional traits may be the underlying mechanism, increasing not plant species diversity per se, but increasing plant functional diversity (FD), i.e. the value and range of plant functional traits (Tilman et al., 2001), has been suggested as a tool to support pollinators and pollination services (Campbell et al., 2012; Fontaine et al., 2006; Junker et al., 2013). Increasing plant FD is expected to increase the number of feeding niches available for pollinators, and thus to support more pollinator species (Junker et al., 2013).

Experimental evidence for the relationship between plant FD and pollinator abundance and diversity, however, is scarce. Balzan et al. (2016, 2014) created a gradient of flower strips by increasing plant functional group richness. They found a positive effect of the presence of flower strips on the abundance of flower visitors, but in general no clear effect of a higher plant functional group richness. Campbell et al. (2012) created flower strips with one or two plant functional groups, based on corolla depth, and with similar total flower abundance. They found that flower strips with two plant functional groups attracted similar numbers of bumblebees (Hymenoptera: Apidae: *Bombus* sp.) and syrphid flies (Diptera: Syrphidae) as flower strips with one functional group, while the number of parasitoids (super-family Hymenoptera: Parasitica) was reduced in plots with two plant functional groups. The functional diversity gradient in these studies was however simplified to varying either a single trait (Campbell et al., 2012) or the number of functional groups (Balzan et al., 2016, 2014), and both studies did not control for plant species richness. To the best of our knowledge, an experiment with a plant FD gradient based on several functional traits and without increasing plant species richness, had not been conducted prior to this study.

When plant species richness is increased in a plant community, each additional species can add either complementary or redundant trait values to the functional trait spectrum of that plant community. This may result in a saturating increase of plant functional diversity and potential feeding niches, and thus a saturating increase of pollinator diversity, as simulated by Junker et al. (2013). When plant FD is increased with constant plant species richness, i.e. by replacing plant species by other plant species with more complementary trait values, the number of complementary feeding niches available for pollinators should also be higher. However, this may also imply that there is less overlap and thus less redundancy in these niches, as the same number of plant species has to provide more different functional trait values. Consequently, non-generalist pollinators are less likely to have several plant species providing their feeding niche in plant communities with high functional diversity. By consequence, they may visit fewer plant species, resulting in a less connected interaction web between plants and pollinators. Analyzing plant-pollinator interactions as a mutualistic network can deliver useful information on stability and structure of these interaction webs (Tylianakis et al., 2010). A change in network structure can decrease the resilience of the plant-pollinator interaction network and can be measured with network structure metrics such as connectance and nestedness (Devoto et al., 2012; Thébault and Fontaine, 2010; Tylianakis et al., 2010).

To use the plant FD approach in wildflower strips, these strips can be sown with a seed mix to create a desired level of FD. However, sowing a seed mix may not automatically result in the desired vegetation composition (De Cauwer et al., 2005; Lepŝ et al., 2007; Chapter 2). Other plant species can settle spontaneously from seeds in the soil seed bank or from dispersing seeds, while sown species may not always successfully settle (Münzbergová and Herben, 2005).

To test whether increasing FD is a key factor for supporting pollinators, we developed a field study with experimental flower strips establishing a FD gradient based on multiple flower traits and without increasing plant species richness. We monitored vegetation development, as well as the flower-visiting pollinator community and their interaction networks with flowers, aiming to explore the effect of increasing FD on (i) the community composition of the flower-visiting pollinator species, (ii) the species richness and evenness of pollinators, (iii) the visitation rate of pollinators, (iv) the structure of the plant-pollinator network, more specifically on network resilience metrics connectance and nestedness, and (v) the overlap in the feeding niches of the pollinators.

MATERIALS AND METHODS

Experimental setup

To test the use of FD in the establishment of wildflower strips for pollinators, we set up an experimental functional diversity gradient in wildflower strips in an arable field. The field setup is briefly described here. For a more detailed description, see Chapter 2.

The FD gradient was made by composing four mixtures of herbaceous species with contrasting levels of FD and equal species richness and evenness. From a list of 20 commercially available forb and legume species commonly found in grasslands and used in perennial flower strips (agri-environment scheme MC8c; Natagriwal asbl, 2017) in Wallonia, Belgium, we simulated all possible mixtures of seven species. To calculate the functional diversity of these mixtures, we selected seven functional traits related to flower morphology, flower visual cues and flower phenology, as these floral traits are expected to influence flower-visiting insect communities in wildflower strips and their interaction networks with plants (Hegland and Totland, 2005; Junker et al., 2013). The selected traits are (1) flower color (three classes: 'white', 'yellow' and 'violet/purple' with the last one containing red, pink, purple, violet, lilac and blue), (2) flower type according to Müller (1881) (categorical: 'Hymenoptere flowers', 'Bee flowers', 'Bumblebee flowers', 'Flowers with open nectar', 'Flowers with totally hidden nectar', 'Flower associations with totally hidden nectar'), (3) UV reflection in the periphery of the flower (categorical, 5 class means: 3.5%, 11.5%, 21.5%, 33.5%, 53%, 76%), (4) presence of a UV pattern (categorical: 'yes', 'no'), (5) the month of the initiation of flowering (numerical), (6) flowering duration in months (numerical) and (7) the maximal height of the plant. For these functional traits, trait values of the 20 selected species were retrieved from the TRY database (Kattge et al., 2011; trait 1-4) and from Lambinon et al. (2008; trait 5-7). With these trait values, FD of all simulated mixtures was calculated using Rao quadratic entropy index based on Gower distance (Botta-Dukát, 2005), with equal abundance of the seven plant species in a mixture. The mixtures with lowest and highest FD were selected, as well as the mixtures with functional diversity closest to the 33rd and 67th percentile of the FD range. This resulted in four plant species mixtures with contrasting FD: very low (VL), low (L), high (H) and very high (VH). For these mixtures, in total 17 out of the 20 listed plant species were used. Table 3.1 shows the four mixtures and the respective trait values of the plant species.

Table 3.1. Plant species used for the four mixtures and their trait values for the selected functional traits

Plant species mixtures follow a functional diversity gradient with very low (VL), low (L), high (H) and very high (VH) functional diversity. Flower type categories are Hymenoptere flowers (H), Bee flowers (Hb), Bumblebee flowers (Hh), Flowers with open nectar (A), Flowers with totally hidden nectar (B), Flower associations with totally hidden nectar (B’). The nomenclature of Lambinon et al. (2008) was used.

Species	**VL**	**L**	**H**	**VH**	**Flower color**	**Flower type**	**Flowering start**	**Flowering duration**	**Maximum height**	**UV periphery**	**UV pattern**
Achillea millefolium	x	x	x	x	white	B’	6	6	45	3.5	no
Anthriscus sylvestris	x		x	x	white	A	5	2	120	3.5	no
Crepis biennis		x			yellow	B’	6	3	120	33.5	yes
Galium verum	x	x			yellow	A	5	5	80	3.5	no
Geranium pyrenaicum			x		Violet/ purple	B	5	5	60	76	yes
Heracleum sphondylium	x				white	B’	6	3	150	3.5	no
Hypochaeris radicata		x			yellow	B’	6	4	60	33.5	yes
Knautia arvensis	x	x			Violet/ purple	B’	6	4	60	3.5	no
Leontodon hispidus		x	x		yellow	B’	6	5	40	53	yes
Leucanthemum vulgare	x		x		white	B’	5	4	60	3.5	no
Lotus corniculatus				x	yellow	Hb	5	5	30	3.5	no
Lythrum salicaria		x		x	Violet/ purple	B	6	4	150	76	yes
Malva moshata				x	Violet/ purple	B	7	3	80	53	yes
Medicago lupulina				x	yellow	H	4	7	50	3.5	no
Origanum vulgare			x		Violet/ purple	B	7	3	80	11.5	no
Prunella vulgaris			x	x	Violet/ purple	H	7	3	50	76	yes
Trifolium pratense	x				Violet/ purple	Hh	5	6	50	3.5	no

To establish the mixtures in the field as wildflower strips, 25 plots were put in an arable field of the AgricultureIsLife experimental farm of Gembloux Agro-Bio Tech (Monty et al., 2016), 50°34’03’’N; 4°42’27’’E at 150 m elevation (Figure 3.1) on a well-drained loamy soil (Service Public de la Wallonie et al., 2014). The surrounding landscape consists of a matrix of arable fields, with some semi-natural habitats and urban areas. Plots were organized as five 8m wide strips divided into five 25m long blocks, and separated by 27m wide conventional cropping areas (rapeseed (*Brassica napus* L.) in 2014, winter wheat (*Triticum aestivum* L.) in 2015, no insecticide treatment). The mixtures were sown with equal seed mass per plant species (0.5 kg/ha) with as aim to approximate a completely even community, assuming that plant species with lower seed mass have a lower competitive ability (Rees, 1995; Turnbull et al., 1999; but see Moles and Westoby, 2004). Three grass species, *Festuca rubra* L., *Agrostis* spp., and *Poa pratensis* L. were added to each mixture (11.5 kg/ha, 5 kg/ha and 5 kg/ha, respectively) and one control treatment mixture (Co) was applied with only these grass species. The resulting five mixture treatments were attributed to the 25 wildflower strip plots in a Latin square design with 'Strip' and 'Block' as blocking factors, aiming to control for soil heterogeneity and landscape effects. Mixtures were sown in June 2013 and were mown twice a year in 2014 (July and October) and 2015 (July and November) with hay removal. After sowing, the wildflower strips were not manipulated for prevention of colonization by spontaneous species, nor for differing germination and settling success of the sown species.

Vegetation sampling

After sowing the seed mixtures in the wildflower strip plots, the established vegetation was monitored to evaluate its realized functional diversity. To do so, three 1m^2 permanent quadrats (PQ) were placed in each plot (Figure 3.1). The PQs were marked with a metal nail in the soil, in order to find them after mowing with a metal detector. The vegetation in the PQs was surveyed twice a year during 2014 and 2015 before mowing, by recording the percentage of horizontal cover of all (sown and spontaneous) herbaceous plant species present. The horizontal cover of each plant species was averaged over the three PQs and over the two sampling occasions per year, in order to obtain an abundance value per plant species per plot for each year. The nomenclature of Lambinon et al. (2008) was used.

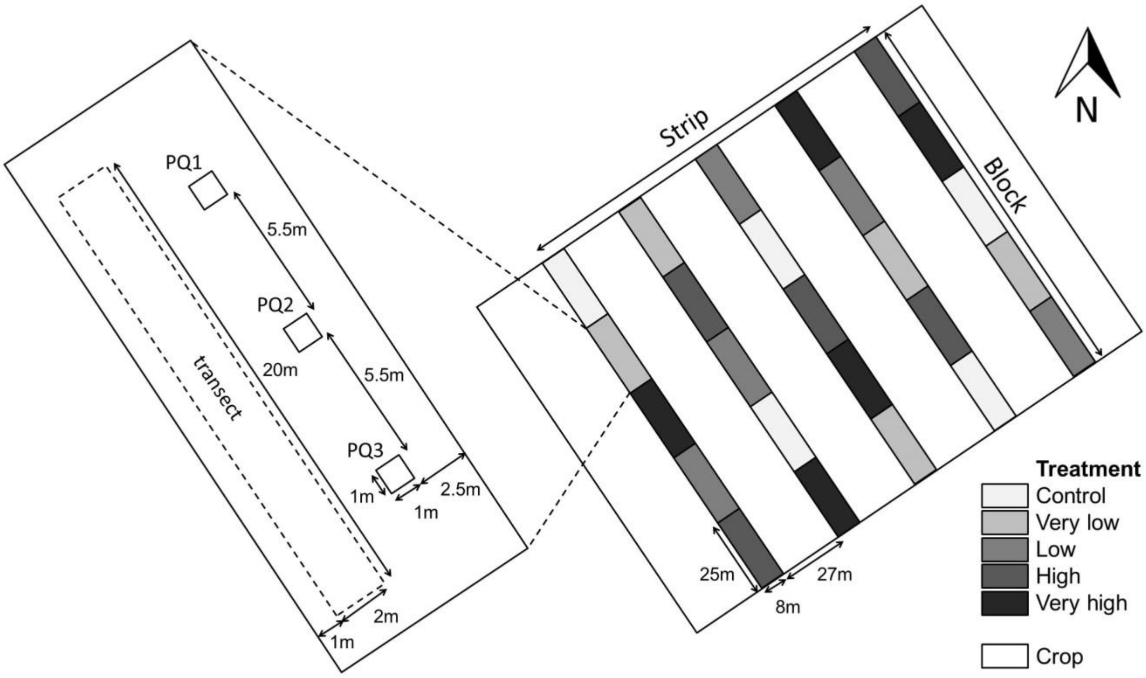

Figure 3.1. Experimental field setup, with Latin square design of sown mixture treatments and sampling setup per plot with permanent quadrats (PQ) for vegetation monitoring and a transect for plant-pollinator network sampling

Plant-pollinator networks

To sample the plant-pollinator interaction networks, a 20m*2m transect was placed in each plot (Figure 3.1). Within transects, three flower abundance quadrats of 0.5m*2m were put at fixed distances (5-5.5m, 10-10.5m and 15-15.5m, from northwest to southeast). Plant-pollinator networks were surveyed at least once a month when enough flowers were present, i.e. in April, May, June and September (twice) in 2014 and in May, June, August and September in 2015. Network surveys took place during weather conditions favorable for insect pollinator activity (days with no rain, forecasted daily maximum temperature >16°C for sunny days or >18°C for cloudy days, <4 Bft wind speed) and between 10 a.m. and 5 p.m. They consisted of listing the flowering species, sampling the plant-pollinator interactions and recording the flower abundance. During a first transect walk, all species with at least one open flower unit were listed. A flower unit was defined as a set of flower heads for which a pollinator would rather walk than fly between (e.g. Gibson et al., 2006; Woodcock et al., 2014). After this, the plant-pollinator interactions were surveyed twice, once in the morning, once in the afternoon. For all flowering plant species listed, the transects were walked separately, to facilitate efficient insect specimen collection. During the transect walks, every flower unit received an equal observation time, being ca. 2 seconds. Every flower visitor that visited a floral unit of the plant species, was recorded. When the flower visitor was unidentifiable in the field, it was collected for identification in the laboratory. We considered as flower visitor an insect making physical contact with a flower and looking for floral rewards. Thus, effective as well as non-effective pollinators were included, but insects sitting on flowers without looking for floral rewards (e.g. flies exposing to sunlight), were not. Bees (Hymenoptera: Apoidea: Apiformes), syrphid flies, dagger flies (Diptera: Empididae), butterflies and moths (Lepidoptera), digger wasps (Hymenoptera: Sphecinae), social wasps (Hymenoptera: Vespidae), and soldier flies (Diptera: Stratiomyidae) were identified to species level if possible. Beetles (Coleoptera) were identified to species or morphospecies level. Sawflies (Hymenoptera: Symphyta), bugs (Hemiptera), flies (Diptera) other than syrphids, dagger flies and soldier flies, and wasps (Hymenoptera: Apocrita) other than social wasps and digger wasps, were not identified and grouped to Symphyta, Hemiptera, Diptera and Apocrita, respectively. The flower abundance monitoring was conducted in the flower abundance quadrats. For every flowering plant species in the quadrats, the number of open flower units was counted in each plot.

Data analysis

Data analysis was performed in R 3.0.1 (R Core Team, 2013) and Microsoft Excel 2010 (Microsoft Corporation, 2010). Vegetation monitoring data, plant pollinator networks, as well as flower abundance data were always pooled per year, and analysis was performed separately for 2014 and 2015. Data were tested for normality and homoscedasticity, and transformed if necessary.

Functional diversity gradient

Data of vegetation sampling was used to evaluate the species richness, evenness and FD gradient of the wildflower strip plots after vegetation establishment. The abundance (horizontal cover) of the different plant species was pooled per plot and per year to calculate species richness and Shannon evenness. The realized FD was calculated for every wildflower strip plot after vegetation development. The same functional traits were used as those used for the FD calculation of the sown mixtures, and trait values for spontaneous species that colonized the wildflower strips were also retrieved from the TRY database (Kattge et al., 2011). A Rao quadratic entropy index based on Gower distance (Botta-Dukát, 2005) was calculated for the different wildflower strip plots for 2014 and 2015, based on the abundance of the different plant species per plot (function ‘dbFD’ from ‘FD’ package (Laliberté et al., 2014)).

As flower abundance (and thus, the abundance of flower traits) is often found as an important factor in pollination studies (e.g. Ebeling et al., 2011, 2008; Hegland and Boeke, 2006), and is a good proxy for nectar and pollen resources (Hicks et al., 2016), it was also taken into account as covariate in further analyses. It was calculated as the total flower abundance per plot by summing the flower abundance of the different species recorded in the flower abundance quadrats per plot per year. Flower abundance was log-transformed prior to analysis.

Species richness, Shannon evenness, realized FD and flower abundance were compared between the mixtures for 2014 and for 2015 with ANOVA, taking into account the ‘Strip’ and ‘Block’ factor of the Latin square design and with Tukey post-hoc tests (functions ‘aov’ from ‘stats’ package (R Core Team, 2013) and ‘glht’ from ‘multcomp’ package (Hothorn et al., 2008)).

Plant-pollinator interaction network

The composition of the flower-visiting insect community in the different plots was examined with Principal Coordinate Analysis, based on Bray-Curtis distance. The different wildflower strip plots were plotted against the two first ordination axes to explore whether different mixture treatments were visited by different insect communities (functions ‘cmdscale’, ‘ordiplot’ and ‘ordiellipse’ from ‘vegan’ package (Oksanen et al., 2015)). Likewise, it was explored whether there were spatial gradient effects by checking for grouping with the Block and Strip factors.

Plant-pollinator networks were calculated with the R package ‘bipartite’ (Dormann et al., 2009) by pooling interactions over different sampling events in a year to obtain a network per plot for each year. To study the role of the different plant and pollinator species in the plant-pollinator networks, graphical representations of the pooled networks per mixture treatment and per year were interpreted visually. Furthermore, we calculated six metrics for every plot. The first set of metrics related to pollinator support: (1) the species richness of interacting pollinators, (2) the Shannon evenness of interacting pollinators, and (3) the visitation rate (i.e. the total number of interactions per plot). A second set of metrics related to the structure and resilience of the plant-pollinator networks: (4) the connectance of the network (i.e. the number of plant-pollinator links, divided by the number of possible links), and (5) the nestedness of the network (i.e. the ‘weighted NODF’ in the ‘bipartite’ package; in more nested networks, the more specialist species interact only with proper subsets of those species interacting with the more generalists (Bascompte et al., 2003)). The last metric related to the feeding niche overlap between the pollinator species: (6) the 'mean number of shared plant partners' of the pollinator level (i.e. the mean number of plant species shared by any two pollinator species). These metrics were calculated per wildflower strip plot for each year and compared between the mixtures with ANOVA, taking into account the 'Strip' and 'Block' factors of the Latin square design and with Tukey post-hoc tests.

Because the established vegetation in the different plots may not have resulted in a clear FD gradient, the effect of realized FD on network metrics was directly modeled with linear mixed models, including Block and Strip as random effects and realized FD, the log-transformation of flower abundance and their interaction as fixed effects. The control treatment was omitted in this analysis. Models were selected with backward selection by comparing nested models with likelihood ratio test ($P<0.05$) starting from the full model with the interaction term.

Finally, to explore how the network metrics relate to the value and diversity of single traits, we calculated the Community Weighted Mean (CWM; Lavorel et al., 2008) and the FD (Rao quadratic entropy index based on Gower distance (Botta-Dukát, 2005)) for each single trait for the different wildflower strip plots for 2014 and 2015, based on the abundance (horizontal cover) of the different plant species per plot (function 'dbFD' from 'FD' package (Laliberté et al., 2014)). For categorical traits, CWM was calculated for the percentage of each trait level (e.g. weighted mean percentage of yellow flowers). Pearson correlations were calculated between CWM and single trait values on the one hand and network metrics on the other hand (function 'cor.test' from 'stats' package (R Core Team, 2013)). Also for this analysis, the control treatment was omitted. For flower color: green, and some flower type classes that were poorly represented in the plant community, CWMs were not calculated.

RESULTS

Creating a functional diversity gradient

During vegetation sampling in 2014, 35 forb species were found, among which were 14 sown species. One sown species (*Heracleum sphondylium*) was only found once in a control treatment plot. As for 2015, 24 forb species were found, among which were 14 sown species. Several spontaneous ruderal plant species disappeared while sown perennial species covered the soil. Sown species that were not found in the PQs were *Anthriscus sylvestris*, *Lythrum salicaria*. *Trifolium pratense* and *Origanum vulgare* were only found once in one plot. In 2014, the most abundant species were *Leucanthemum vulgare*, *Achillea millefolium*, *Hypochaeris radicata*, *Cirsium arvense* and *Sinapis alba*. The first three species were sown, while *C. arvense* is a common weed and *S. alba* was planted as a winter crop in the years prior to the experiment and has probably settled from the soil seed bank. In 2015, the most abundant species were *L. vulgare*, *A. millefolium*, *C. arvense*, *H. radicata* and *Galium verum*. These were all sown species, except for *C. arvense*. An overview of the abundance of all sown and spontaneous species for the different mixture treatments can be found in Supplementary Table 3.3.

Mixture treatments were not significantly different in plant species richness in 2014 (F=2.820, P=0.073). While there was a significant difference in 2015 (F=5.926, P=0.007), only the control plots had a significantly lower species richness than the L (t=4.426, P=0.006), H (t=3.272, P=0.043) and VH (t=3.657, P=0.022) plots. Shannon evenness was not significantly different between the mixtures in 2014 (F=2.996,P=0.063) and 2015 (F=3.325, P=0.051).

The realized FD was significantly different between the mixtures in 2014 (F=7.235, P=0.003) but with only a significant difference between the VL and the VH plots and between the VH and the control plots (Figure 3.2a). In 2015, the differences between the mixtures became stronger (F=14.197, P<0.001), but the L and H plots switched their position along the sown FD gradient (Figure 3.2a).

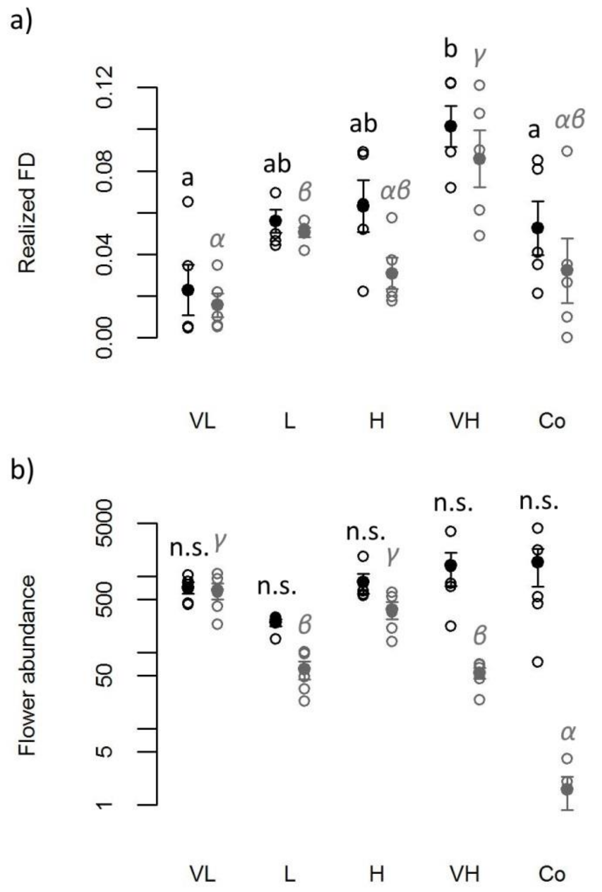

FIGURE 3.2. A) REALIZED FUNCTIONAL DIVERSITY (FD) AND B) FLOWER ABUNDANCE IN THE DIFFERENT MIXTURE TREATMENTS: VERY LOW FD (VL), LOW FD (L), HIGH FD (H), VERY HIGH FD (VH), AND THE CONTROL TREATMENT (CO)

The left black dots show the results for 2014 and the right grey dots for 2015. Solid dots denote the mean per mixture treatment, hollow dots denote the observed values, and error bars show the standard error of the mean. Letters (a, b and c for 2014, α, β and γ for 2015) above error bars show the significant differences of Tukey post-hoc multiple comparison tests of the group means (*P*<0.05) or 'n.s.' in case of no significant differences.

Flower abundance in 2014 was not significantly different between the mixtures. While *S. alba* was an abundant plant in all plots, subtracting the flower abundance of this species from the total flower abundance only resulted in the control treatment to be significantly different from the other mixtures. In 2015, flower abundance was significantly higher in the VL and H plots than in the other ones (Figure 3.2b).

Pollinator species composition

In total, 68 pollinator species were observed as flower visitors, of which there were 58 in 2014 and 40 in 2015. They performed 2,282 pollinator-plant interactions (1,399 in 2014, 883 in 2015) on 27 plant species (21 in 2014, 19 in 2015). Syrphid flies were the most frequent visitors, with 828 interactions, of which 592 were by *Eristalis tenax* L. With 25 species, syrphid flies were also the most diverse group. Non-identified Diptera sp. were responsible for 678 interactions, followed by 288 interactions by honeybees (Hymenoptera: Apidae: *Apis mellifera* L.). Other groups with more than 100 interactions were dagger flies, bumblebees and solitary bees (Hymenoptera: Apoidea: Apiformes). Eighteen species of solitary bees were found, with *Andrena flavipes* Panzer (Hymenoptera: Andrenidae) as the most abundant visitor.

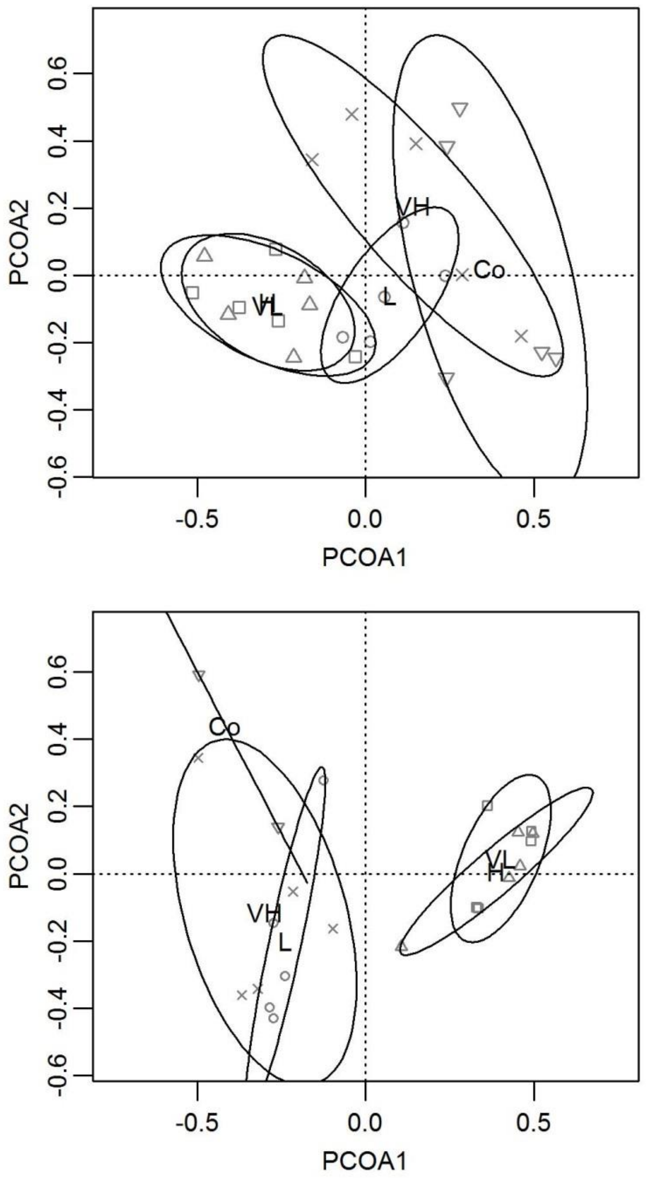

FIGURE 3.3. WILDFLOWER STRIP PLOTS PLOTTED AGAINST THE TWO FIRST ORDINATION AXES OF PRINCIPAL COORDINATE ANALYSIS BASED ON THE COMMUNITY COMPOSITION OF THEIR FLOWER-VISITING INSECT COMMUNITY A) IN 2014 AND B) IN 2015

Ellipses show the 80% confidence interval of the plots grouped by functional diversity (FD) mixture: VL for very low FD, L for low FD, H for high FD, VH for very high FD, and Co for the control mixture.

Ordination of the wildflower strip plots based on the composition of their flower-visiting insect community showed that not all flower mixtures were visited by the same insect species (Figure 3.3). Only the VL and H plots overlapped almost completely in their visiting insect community, both in 2014 and 2015. The graphical representations with Block or Strip as grouping factors did not show any difference between groups, indicating that there was no spatial effect on the visiting insect community composition.

Plant-pollinator networks

Leucanthemum vulgare was responsible for a large part of the interactions in the VL (62% to 97% in 2014 and 84% to 100% in 2015) and H (50% to 88% in 2014 and 71% to 98% in 2015) plots, where it was an abundantly flowering plant (VL: 25±8 and 42±32 flower units per m^2 and per survey in 2014 and 2015 respectively; H: 13±8 and 29±17 flower units per m^2 and per survey in 2014 and 2015 respectively). It was also present in the L and VH plots, where the species was not sown, but settled spontaneously and appeared with a lower flower abundance than in the VL and H mixtures (L: 1±1 and 1±3 flower units per m^2 and per survey in 2014 and 2015 respectively; VH: 1±2 and 2±2 flower units per m^2 and per survey in 2014 and 2015 respectively). Both *E. tenax* and Diptera sp. were the dominant visitors of *L.*

vulgare in the former ones in the VL an H plots (see the pooled networks per mixture in Supplementary material Figure 3.8 - Figure 3.17).

Pollinator species richness did not tend to increase or decrease along the sown FD gradient (Figure 3.4a). Species richness was significantly lower in the control plots than in the VL and H plots in 2014, but no difference was observed between the four mixtures. In 2015, species richness was also higher in the VL, L and H plots than in the control plots. Moreover, it was on average twice as high in the H plots as in the VH plots. Likewise, the evenness of pollinators did not tend to increase or decrease along the sown FD gradient (Figure 3.4b). In 2014, no significant difference was observed, while in 2015, the L and VH plots had a significantly higher evenness (on average 32% higher) than the VL and H ones. The visitation rate showed clearer differences across the mixtures (Figure 3.4c, visitation rate was log-transformed for 2015 to obtain normality and homoscedasticity of residuals). In 2014, there was no clear increase or decrease along the sown FD gradient, but the VL and H plots had a significantly higher visitation rate than the VH and the control plots (on average three times as high, non-transformed data). In 2015, where the L and H plots had switched their realized FD rank in the sown FD gradient (see above), a decrease along the FD gradient appeared, with the VL and H plots having a significantly higher visitation rate than the L and VH ones (on average five times as high, non-transformed data). The control plots had a significantly lower visitation rate than all the other treatments.

Network stability metrics did not show an increase or decrease along the sown FD gradient (Figure 3.4d-g). The networks in the control plots showed a higher connectance compared to the L and VH plots in 2014 (90% higher on average) and the L plots in 2015 (on average three times as high). As for nestedness, no significant differences were detected.

The mean number of shared plant partners between pollinators was not different across the mixtures in both years (Figure 3.4h).

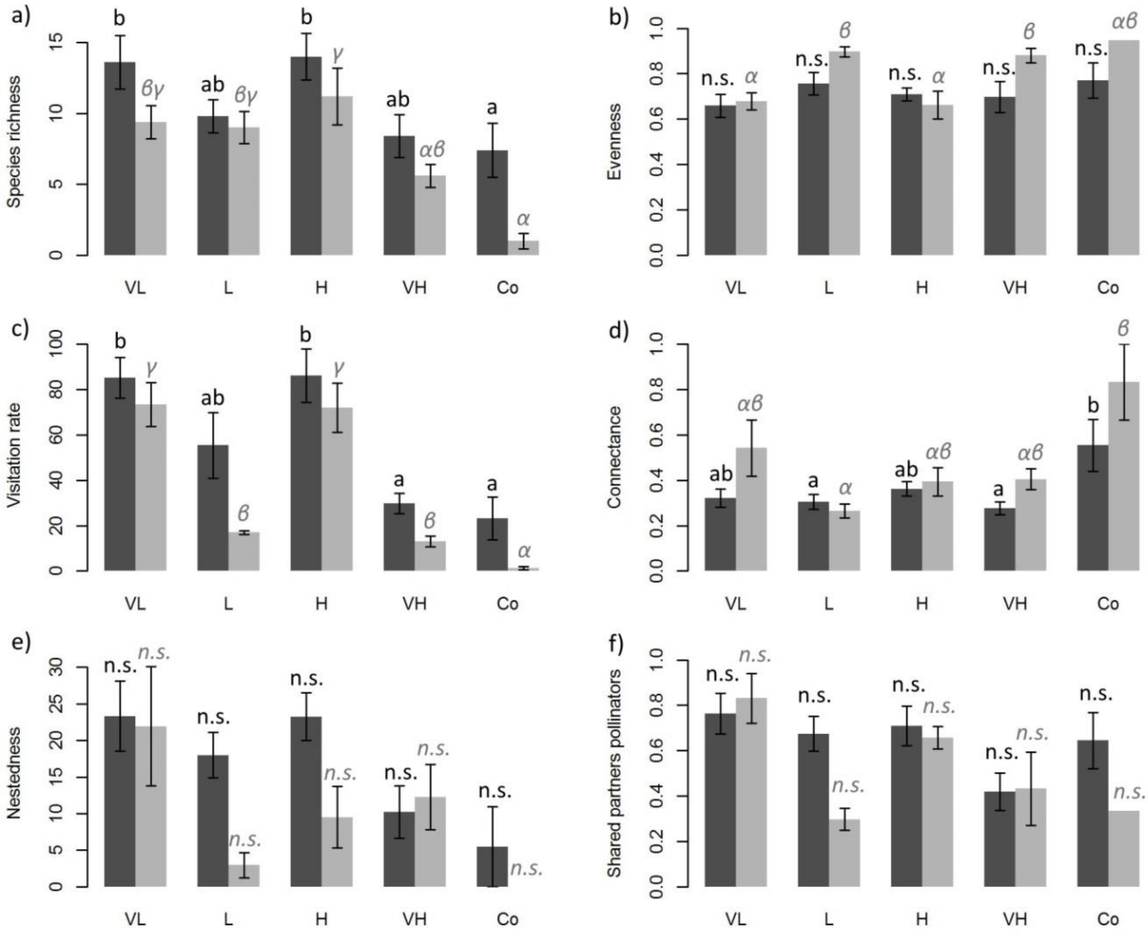

Figure 3.4. Bar plots of mean values of the plant-pollinator network metrics for the different functional diversity (FD) treatments: VL (very low FD), L (low FD), H (high FD), VH (very high FD) and Co (control mixture)

a) shows the species richness of pollinators, b) the evenness of pollinators, c) the visitation rate, d) the network connectance, e) the network nestedness, and f) the mean number of shared plant partners of the pollinators (see section 2.4.2 for calculation of these metrics). Dark grey bars show the results for 2014 and light grey bars for 2015. Error bars show standard error of the mean (not calculated for some metrics due to a lack of data in Co treatment networks). Letters (a, b and c for 2014, α, β and γ for 2015) above error bars show the significant differences of Tukey post-hoc multiple comparison tests of the group means (*P*<0.05) or 'n.s.' in case of no significant differences.

Effect of realized functional diversity and flower abundance on plant-pollinator networks

Fixed effects of the final mixed models are shown in Table 3.2. Different network metrics showed different responses to realized FD and flower abundance as well as between years. In 2014, only realized FD appeared in the final models, while in 2015, flower abundance was also a significant explanatory variable.

Species richness and evenness of pollinators were not influenced by realized FD in 2014. In 2015, both realized FD, flower abundance, and their interaction affected pollinator species richness (Table 3.2). For average flower abundance in the final model, species richness showed a slight decrease with realized FD (Figure 3.5a). In 2015, evenness was negatively related to flower abundance, independently of realized FD (Table 3.2, Figure 3.5b). The visitation rate was negatively related to realized FD both in 2014 and in 2015 (for average flower abundance, see Figure 3.5c,d). In 2015, flower abundance and the interaction with realized FD also affected the visitation rate (Table 3.2). In 2015, plots with a higher visitation rate all belong to the VL and H treatments, where *L. vulgare* had a high number of inflorescences. Adding the log-transformed abundance of *L. vulgare* flowers to the mixed models showed that *L. vulgare* flower abundance is a slightly better predictor than flower abundance (*ΔAICc* = 1.26 between a model with *L. vulgare* flower abundance and FD as fixed factors and a model with flower abundance and FD as fixed factors), but still with realized FD as a significant effect in the final model.

Network connectance was not significantly affected by realized FD in 2014, while in 2015, there was a significant effect of realized FD, flower abundance, and their interaction (Table 3.2). For average flower abundance in the final model, realized FD did not show a clear effect on connectance (Figure 3.5e). Network nestedness was negatively affected by realized FD in 2014 and in 2015 (for average flower abundance, see Figure 3.5f). In 2015, network nestedness was also affected by flower abundance and its interaction with realized FD (Table 3.2).

The mean number of shared plant partners of the pollinator level was negatively related to FD in 2014 and positively related to flower abundance in 2015 (Table 3.2, Figure 3.5h). A model with only FD as a fixed effect in 2015 was also significant (χ^2=4.134, P=0.042), with a negative parameter estimate.

Table 3.2. Intercept and fixed effects of the selected mixed models for the network metrics with Likelihood-ratio tests for the predictor variables in the final models

Table shows main affect functional diversity (FD) and flower abundance (FA) as well as their interaction (FD:FA).

Network metric	Year	predictor	Parameter estimate	standard error	χ^2	df χ^2	*P*-value
Species richness	2014	intercept	11.450	1.166			
	2015	intercept	21.325	5.908			
		FD	-364.329	117.950	9.354	1	0.002
		FA	-2.038	1.050	4.225	1	0.040
		FD:FA	69.642	25.067	7.874	1	0.005
Evenness	2014	intercept	0.706	0.030			
	2015	intercept	1.224	0.080			
		FA	-0.089	0.015	19.299	1	<0.001
Visitation rate (log(n+1) transformed for 2015)	2014	intercept	94.650	13.420			
		FD	-501.730	177.530	5.748	1	0.017
	2015	intercept	2.940	0.749			
		FD	-41.038	15.090	7.091	1	0.008
		FA	0.212	0.133	2.828	1	0.093
		FD:FA	6.650	3.224	4.284	1	0.038
Connectance	2014	intercept	0.316	0.021			
	2015	intercept	-0.568	0.329			
		FD	14.116	6.573	5.086	1	0.024
		FA	0.183	0.058	9.558	1	0.002
		FD:FA	-2.864	1.399	4.658	1	0.031
Nestedness	2014	intercept	27.528	3.785			
		FD	-145.325	50.802	6.948	1	0.031
	2015	intercept	-49.879	23.579			
		FD	959.869	473.344	4.603	1	0.032
		FA	12.141	4.369	7.891	1	0.005
		FD:FA	-207.309	102.073	4.616	1	0.032
Robustness pollinators	2014	intercept	0.585	0.015			
	2015	intercept	0.553	0.007			
Mean number of shared plant partners	2014	intercept	0.885	0.077			
		FD	-4.002	1.107	10.917	1	<0.001
	2015	intercept	-0.299	0.211			
		FA	0.171	0.041	13.495	1	<0.001

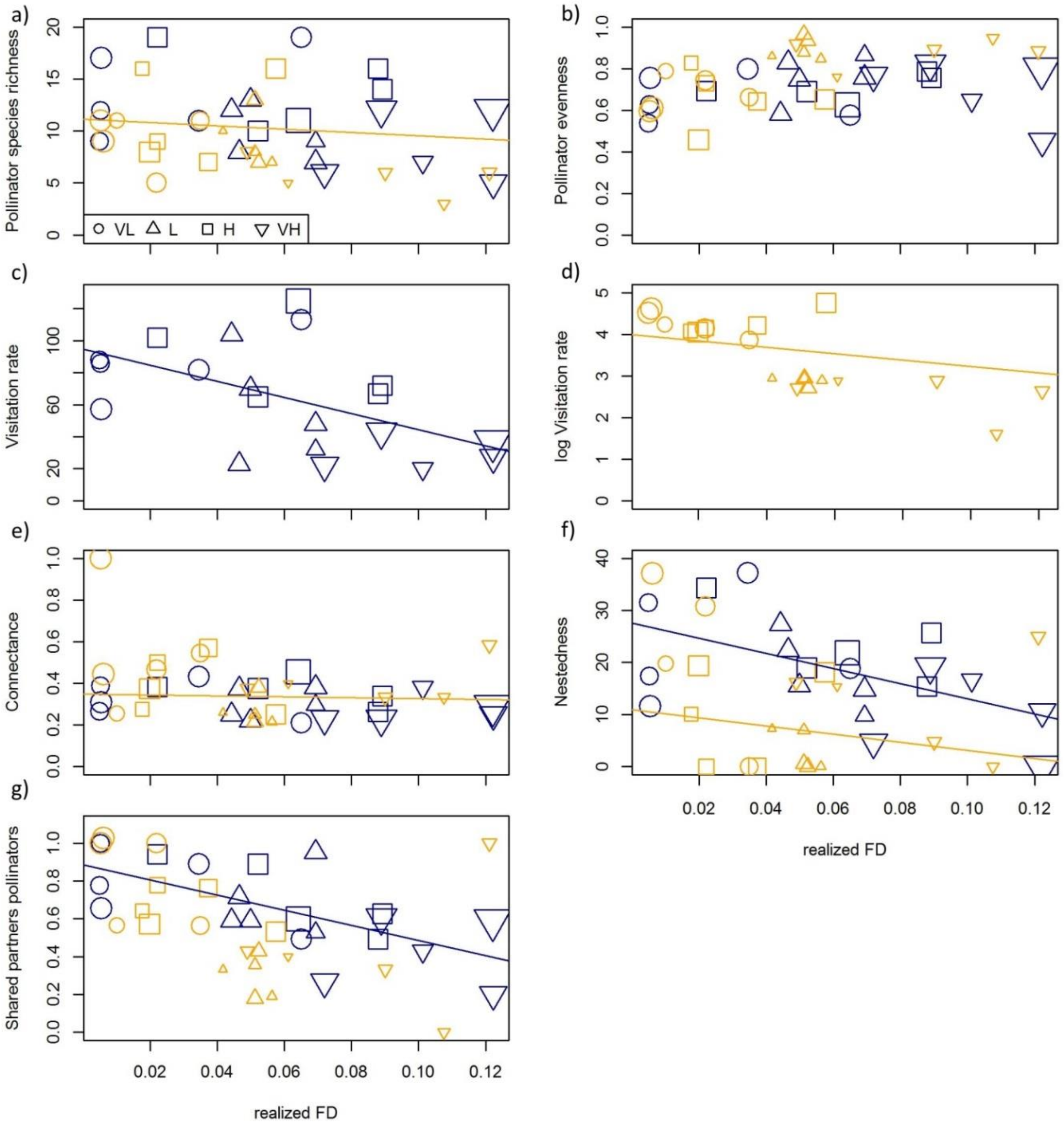

FIGURE 3.5. NETWORK METRIC VALUES IN FUNCTION OF REALIZED FUNCTIONAL DIVERSITY (FD) IN BLUE FOR 2014 AND IN RED FOR 2015

a) shows the species richness of pollinators, b) the evenness of pollinators, c) the visitation rate in 2014, d) the log-transformed visitation rate in 2015, e) the network connectance, f) the network nestedness, and g)the mean number of shared plant partners of the pollinators (see the Material and methods section for calculation of these metrics). Dot shapes show the mixtures: circles for very low FD, triangles for low FD, squares for high FD and inverted triangles for very high FD. Lines show the effect of realized FD, estimated by the final linear mixed models and for the mean log-transformed flower abundance if it was kept in the final model (see Table 3.2). Dot size is proportional to log-transformed flower abundance.

Effects of single traits value and diversity

Figure 3.6 shows the significant correlations between the CWM trait values and the network metrics and Figure 3.7 the significant correlations between the FD of single traits and the network metrics. Pollinator species richness is related to a higher percentage of white flowers in 2014, to a higher percentage of flower associations with totally hidden nectar in 2015 and to communities with an averagely earlier start of the flowering period in both years. Furthermore, it is negatively related to a higher FD of flower type, flowering start and flowering duration, only in 2015. Pollinator evenness was only related to the CWM of single traits and single trait FDs in 2015. Visitation rate was related to several single trait values, having a consistent positive relationship in 2014 and 2015 with the CWM percentage of white flowers and flower associations with totally hidden nectar, and a consistent negative relationship over both years with the CWM percentage of hymenoptere flowers and the CWM start of the flowering period. Furthermore, it was negatively related with several single trait FD values, having a relationship in both years with the FD of flowering duration.

Network connectance was only negatively related to the CWM flowering duration and the FD of UV pattern, both only in 2015. No other significant correlations were found. Network nestedness was related to several single trait CWMs, but only consistently negatively related in both years to the CWM percentage of white flowers. Furthermore it was negatively related to the FD of flower type and flowering duration in 2014 and to the FD of flower color and UV pattern in 2015.

The mean number of shared plant partners of the pollinator level was related to different single trait CWMs in both years. Furthermore, it was negatively related with the FD of all single traits in 2014, except for UV pattern, and only with the FD of flower color and UV pattern in 2015.

None of the network metrics were related to the CWM maximum plant height and the CWM percentage of flowers with open nectar. The significant correlation coefficients of the single trait FD values were always negative for the network metrics, except for pollinator evenness, where all the significant correlations were positive.

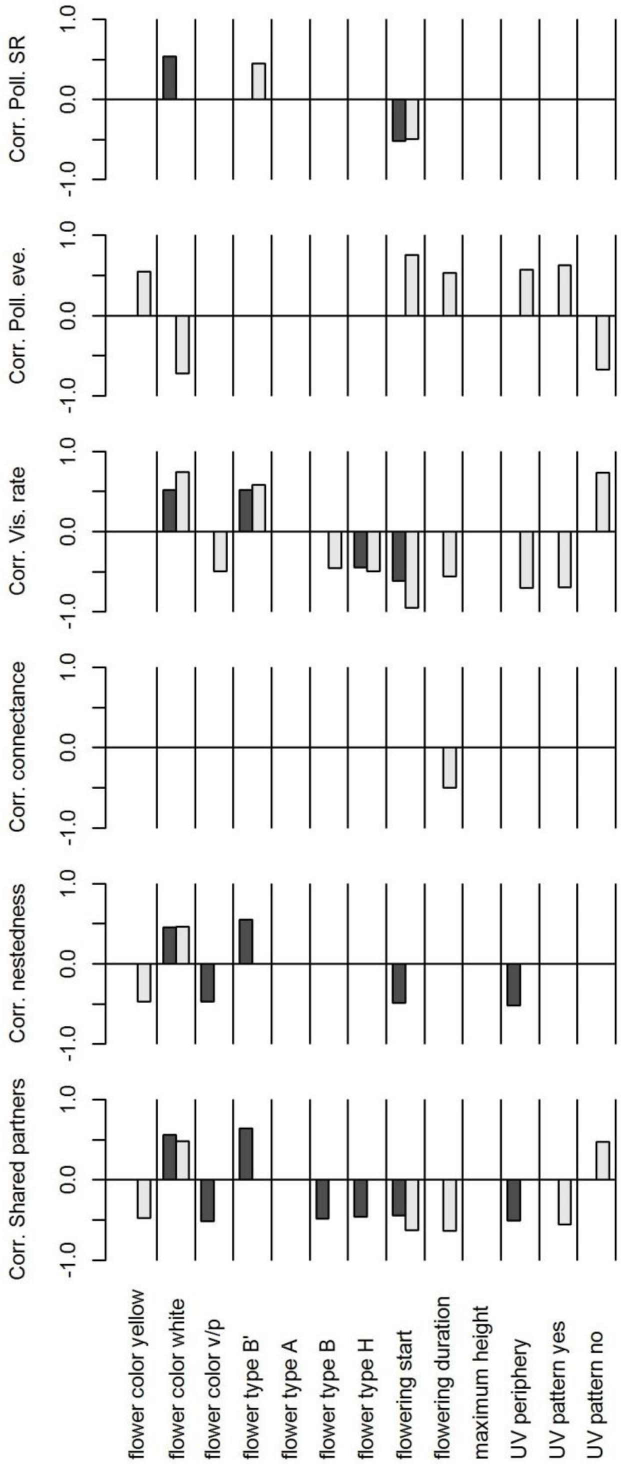

FIGURE 3.6. BARPLOT OF SIGNIFICANT (P<0.05) PEARSON CORRELATIONS BETWEEN THE COMMUNITY WEIGHTED MEANS OF SINGLE TRAITS AND THE NETWORK METRICS

Non-significant correlations are not shown. Dark grey bars denote the correlations for 2014, light grey bars for 2015. Flower color v/p stands for violet/purple. Flower type B' stands for flower associations with totally hidden nectar, B for flowers with totally hidden nectar, A for flowers with open nectar, and H for Hymenoptere flowers.

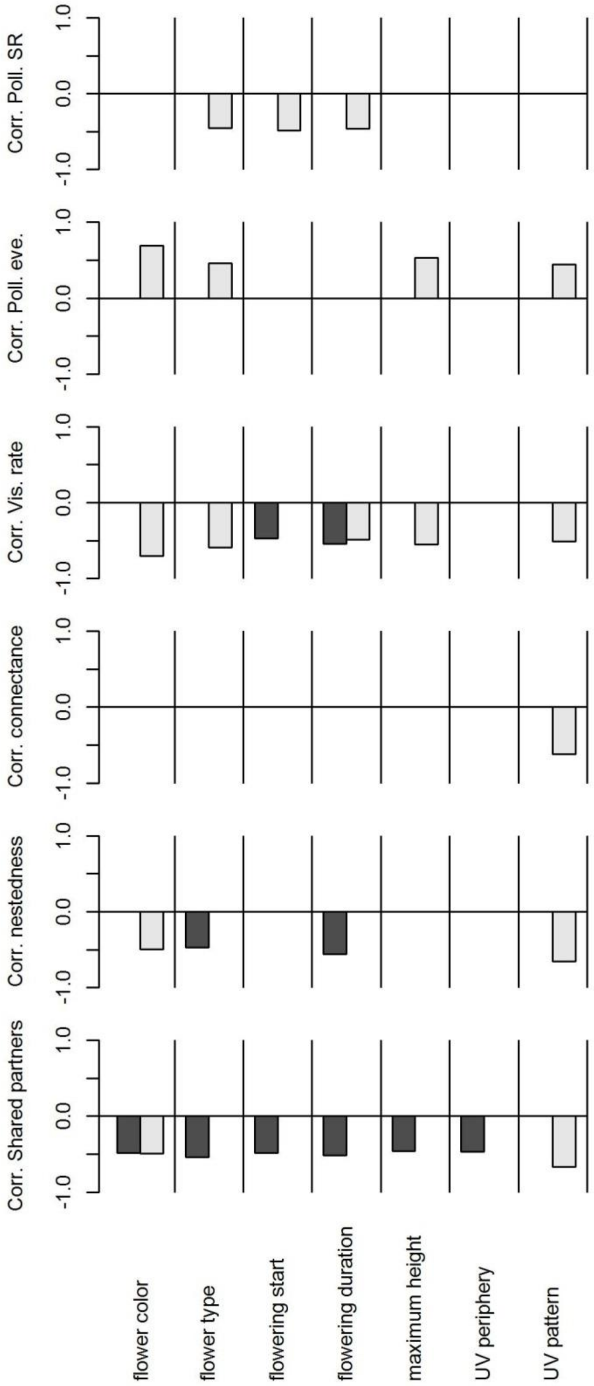

Figure 3.7. Barplot of significant ($P<0.05$) Pearson correlations between the functional trait diversity of single traits and the network metrics

Non-significant correlations are not shown. Dark grey bars denote the correlations for 2014, light grey bars for 2015.

DISCUSSION

Creating a functional diversity gradient

The goal of the field experiment was to create a plant FD gradient, while controlling for species richness and evenness, by sowing seven forb plant species per treatment with equal sown seed mass per species. With the analysis of the realized FD of the vegetation after sowing, we have shown that it was possible to establish a gradient in plant FD. While the two intermediate mixtures L and H switched their rank in the FD gradient in 2015, the extreme mixtures VL and VH showed clearly distinct realized FD in both years.

Despite spontaneous plant species settling in the strips, and not all sown species occurring, there were still no significant differences of plant species richness between the four mixtures. In the control plots, some spontaneous herbaceous species settled, and this treatment consequently had a species richness that was not significantly different from most of the mixtures. Also, species evenness was not significantly different among the mixtures, albeit close to significance (see Results section). However, evenness values ranged from 0.241 to 0.928, indicating that perfect evenness was not created and that other factors than seed mass may have influenced the abundance of the species. Indeed, in their review, Moles and Westoby (2004) showed that there is not a simple trade-off between seed mass and seed number for the reproduction strategy of plants. Seed density tests prior to the sowing of the experimental vegetation could provide information to determine the optimal seed mass ratios between species in future experiments.

Increasing functional diversity affects interaction networks, but does not promote pollinator richness and flower visitation rate

Ordinations showed that the visiting insect community reacted to the different flower mixtures that were provided, despite the fact that they were in the same field. This is consistent with Hegland and Boeke (2006), who also observed that the presence and visitation frequency of flower visitors was affected by small-scale differences in density and diversity of flower resources. Network graphs and network metrics confirmed that the differences in plant composition on this field scale affected the visitation pattern. Moreover, no effect of the Block and Strip factors of the Latin square design were observed in the ordinations, indicating that there was no spatial gradient in the visiting insect community e.g. due to neighboring source populations. The most important flower visitors in our study appeared to be syrphid flies and other dipterans, while honey bees, solitary bees and bumblebees were less frequent visitors. Flower visitors other than bees and syrphid flies, called the ‘non-prominent’ flower visitors by Grass et al. (2016), were responsible for 39.9% of the flower visits, compared to 53.1% by such visitors in their work (Grass et al., 2016).

Surprisingly, FD did not have a clear influence on pollinator species richness and evenness. To our knowledge, no other studies experimentally tested the effect of plant FD on pollinator diversity, whereas more comparable studies are required to verify our conclusions. However, a comparison can be made to some studies on plant species diversity and pollinator diversity. As in our study, Orford et al. (2016) did not observe an effect of increasing sward diversity by adding legume and forb species, on pollinator species richness. Similarly, Grass et al. (2016) did not find an effect of plant species richness on pollinator species richness in a field study in wildflower plantings in an agricultural landscape. However, most other studies showed a positive relationship between plant species richness and pollinator species richness (Ebeling et al., 2008; Holzschuh et al., 2007; Hudewenz et al., 2012; Potts et al., 2003; Steffan-Dewenter and Tscharntke, 2001), and a weakly positive effect on pollinator functional group richness (Hegland and Boeke, 2006). The FD of some single traits and some single trait CWMs were however related to pollinator species richness and evenness. This suggests that pollinator species richness and evenness may be influenced by certain traits or trait combinations rather than the FD of several traits together. However, our experimental design was aiming to create a gradient of FD based on multiple functional traits. Therefore certain traits values or diversity levels may have been underrepresented, making it difficult to draw conclusions on the relative importance of different traits for the effect of their value and diversity on pollinator support. This could be the subject of further research, as well as testing the effects of other traits, like flower pollen and nectar volume.

As for flower visitation rate, it even decreased with increasing FD. This was the case in both years, and is supported by several negative correlations of single trait FD’s with visitation rate. This is in contrast to Balzan et al. (2014), who found an increase of wild bee abundance with FD, while for other flower visitors, they did not find an effect of FD. However, they found a positive effect of flower strips, compared to a no-strip control, on diversity and abundance of flower visitors and other arthropod groups (Balzan et al., 2016, 2014). This is in accordance with our experiment in 2015, where the control treatment provided fewer flower resources and plant species, resulting in significantly lower visitation rate. Studies relating plant species richness to pollinator abundance found a positive effect (Ebeling et al., 2008; Hudewenz et al., 2012) or no effect (Grass et al., 2016; Potts et al., 2003; Steffan-Dewenter and Tscharntke, 2001) of plant species richness. Some of them also show that the abundance of flowers is an important, or even the main factor affecting pollinator abundance or activity (e.g. Ebeling et al., 2008; Steffan-Dewenter and Tscharntke, 2001), which was the case in our experiment in 2015. Realized FD interacted with flower abundance in the mixed model for visitation rate, and the final model for pollinator evenness even had only flower abundance as a significant predictor. Balzan et al. (2016, 2014) observed in their experiment that Apiaceae species, present in all three tested mixtures, attracted a large number of flower visitors, possibly causing the similar effects on flower visitor abundance along their FD gradient. Ebeling et al. (2008) also observed that the presence of attractive plant species resulted in a higher flower visitation rate, while it did not affect the pollinator species richness. According to Hegland and Totland (2005), plant species with large inflorescences or flowering in dense patches attract more flower visitors. *L. vulgare* could be considered as such a species in our study, as it appeared as a key species in the networks of the plots where it was abundantly flowering (see Supplementary material Figure 3.8 - Figure 3.17). This was confirmed by the positive relationship between the CWM percentage of white (the main flower color of *L. vulgare*) flowers and visitation rate. Hence, the dense flower patches of this species could have caused concentration of some flower visitor species to certain plots, resulting in a dilution in other plots. Indeed, flower visitors tend to forage optimally by visiting flowers of the same species in dense patches, only changing to other species or less dense patches when rewards diminish. Moreover, they are more likely to switch between flowers of different plant species when these flowers are functionally more similar (Chittka et al., 1997). Therefore, plots with lower plant FD, having more overlap of potential feeding niches, may be more likely to deliver enough resources to the flower visitor species preferring these niches and easily switching between similar flower species. Conversely, plots with a higher FD, where plant species have less overlap in the potential feeding niches for flower visitors, may not have been able to deliver sufficient resources per niche. The significant interaction effects between realized FD and flower abundance on pollinator species richness and visitation rate are supporting this hypothesis of lack of resources in higher FD plots. For high flower abundance, the effect of realized FD on pollinator species richness was positive, and on visitation rate slightly positive. This indicates that, when flower resources are abundant enough, pollinators are able to find enough floral rewards in the separate feeding niches delivered by the plant species in the higher FD plots.

Interestingly, of the network resilience metrics, only nestedness showed a clear decrease with plant FD. The absence of effect on network connectance is also reflected in the nearly absence of significant correlations with single trait FD and CWM. However, connectance does not take into account the relative frequency of interactions of links between plants and pollinators, which may have caused a low sensitivity to network change with increasing plant FD. This metric has also been discussed for its dependency on sample size (e.g. Blüthgen et al., 2006). The decrease in mean number of shared partners showed however that pollinator species in networks in plant communities with higher FD shared less plant partners, and thus had more separate feeding niches. This suggests that pollinators perceived a lower redundancy in plant functional traits when plant FD is increased. All functional traits seem to have contributed to this relationship. Their single trait FD was negatively related to the mean number of shared partners at least in one of both years, and even in both years for flower color FD (Figure 3.7). Studies relating the pollinator functional niches to plant species richness showed an increased complementarity of feeding niches (Orford et al., 2016) and an increased complementarity and decreased overlap of the spatio-temporal niches of flower visitation (Venjakob et al., 2016). The decrease in feeding niche overlap with increasing realized FD in our study could also have caused the decrease in nestedness, as nested networks require a core group of generalists densely interacting with each other, to which the more specialist species are linked (Bascompte et al., 2003). This may be more likely to happen in networks where generalist pollinators are able to share more plant species offering similar feeding niches.

Conclusion

It is often suggested that the effect of increasing plant species diversity on ecosystem processes, like plant-pollinator interactions, is caused by the increase of the underlying functional trait diversity. With this experiment, we have shown that increasing plant FD per se, without increasing plant species richness, is not the key for supporting pollinators in flower strips. Our results showed that an increase in plant FD caused a decrease in redundancy of potential pollinator feeding niches, which resulted in pollinator species having less overlap in their feeding niche. Our results also suggested that on a certain surface of flower resources, there can be a trade-off between increasing FD and having sufficiently abundant flower resources per feeding niche. We therefore suggest that flower strip creation should not only focus on maximizing functional complementarity, but also provide enough resources per feeding niche by using functionally redundant species with sufficient abundance.

Acknowledgements

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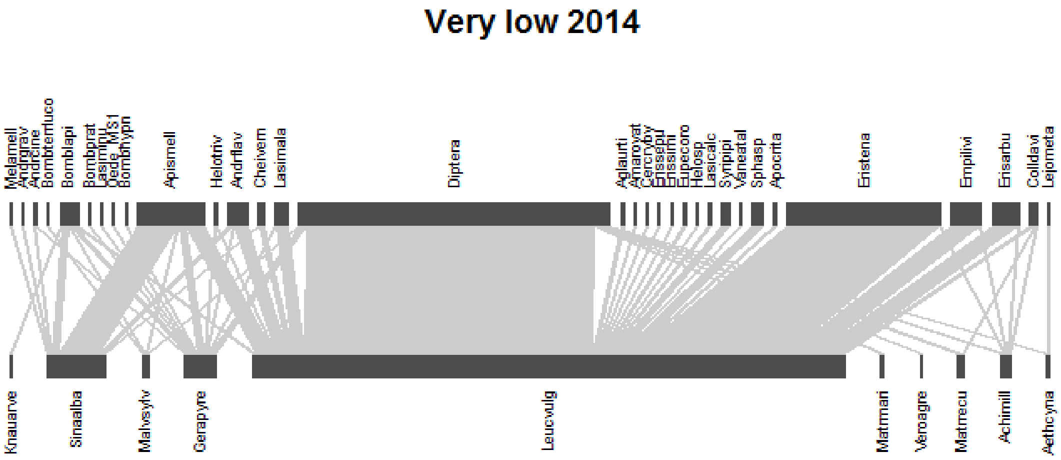

FIGURE 3.8. POOLED PLANT-POLLINATOR NETWORK FOR THE VERY LOW FUNCTIONAL DIVERSITY MIXTURE IN 2014, WITH PLANT TAXA AT THE BOTTOM AND POLLINATOR TAXA AT THE TOP.

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

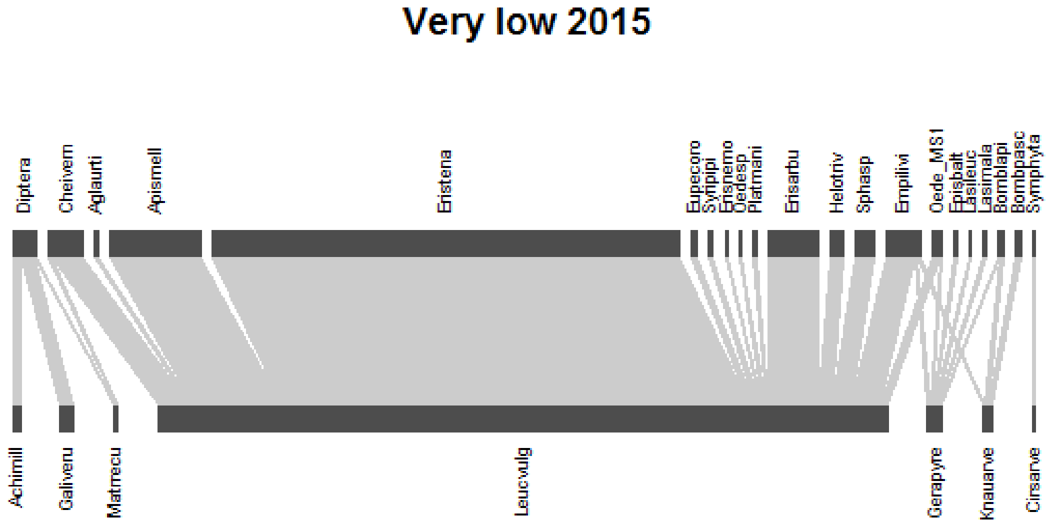

FIGURE 3.9. POOLED PLANT-POLLINATOR NETWORK FOR THE VERY LOW FUNCTIONAL DIVERSITY MIXTURE IN 2015, WITH PLANT TAXA AT THE BOTTOM AND POLLINATOR TAXA AT THE TOP

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

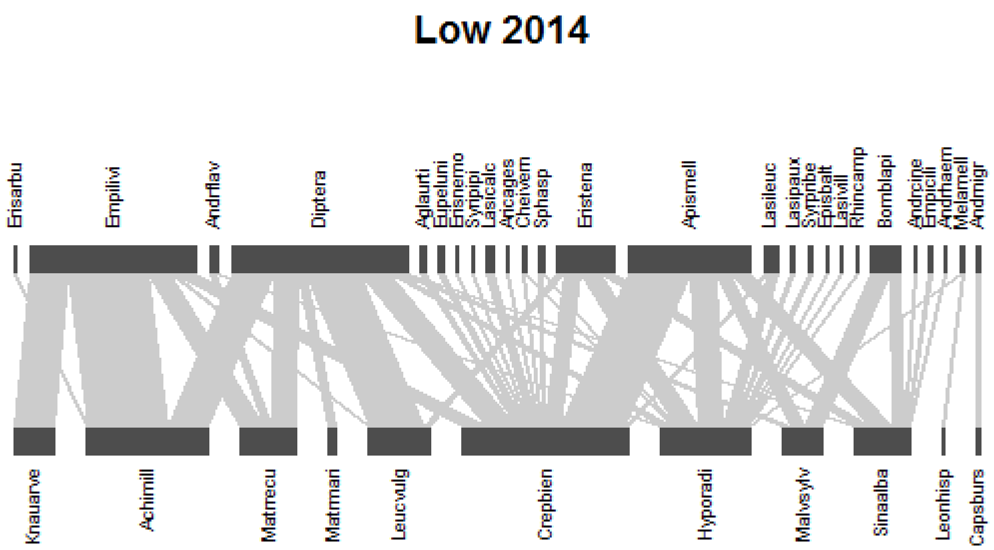

FIGURE 3.10. POOLED PLANT-POLLINATOR NETWORK FOR THE LOW FUNCTIONAL DIVERSITY MIXTURE IN 2014, WITH PLANT TAXA AT THE BOTTOM AND POLLINATOR TAXA AT THE TOP

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

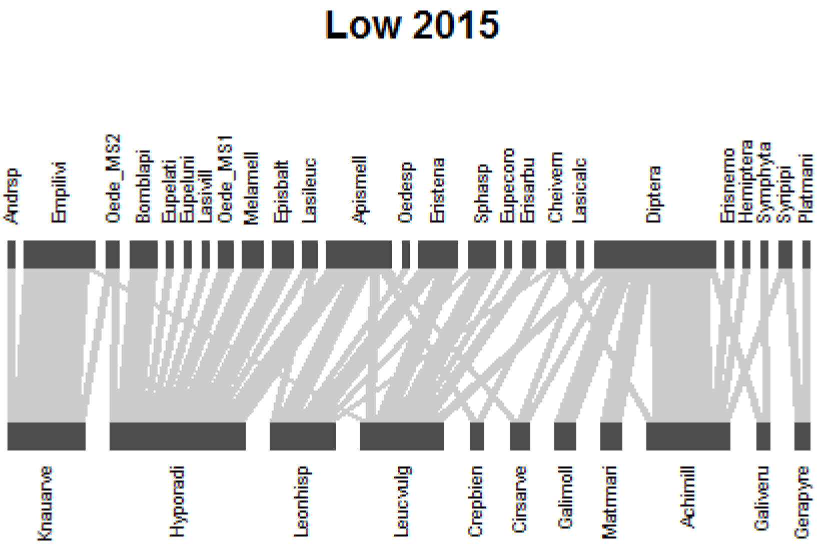

FIGURE 3.11. POOLED PLANT-POLLINATOR NETWORK FOR THE LOW FUNCTIONAL DIVERSITY MIXTURE IN 2015, WITH PLANT TAXA AT THE BOTTOM AND POLLINATOR TAXA AT THE TOP

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

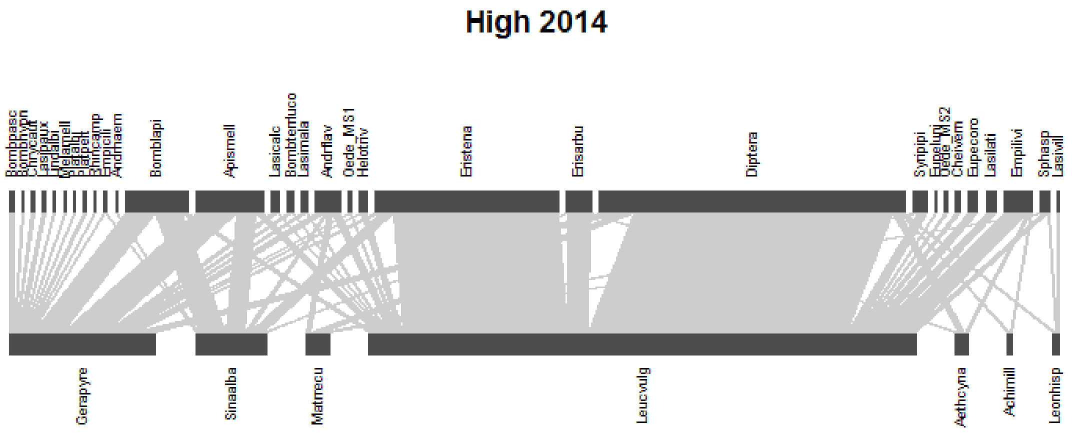

FIGURE 3.12. POOLED PLANT-POLLINATOR NETWORK FOR THE HIGH FUNCTIONAL DIVERSITY MIXTURE IN 2014, WITH PLANT TAXA AT THE BOTTOM AND POLLINATOR TAXA AT THE TOP

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

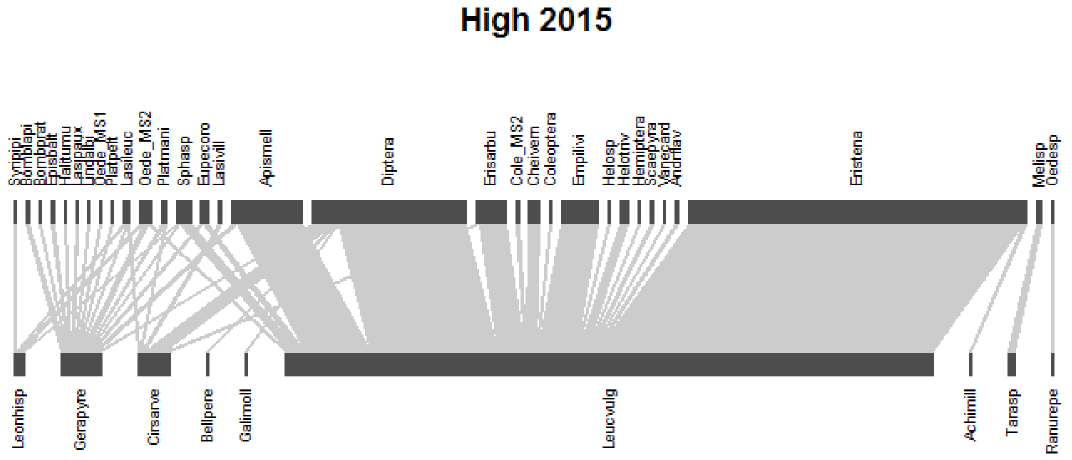

FIGURE 3.13. POOLED PLANT-POLLINATOR NETWORK FOR THE HIGH FUNCTIONAL DIVERSITY MIXTURE IN 2015, WITH PLANT TAXA AT THE BOTTOM AND POLLINATOR TAXA AT THE TOP

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

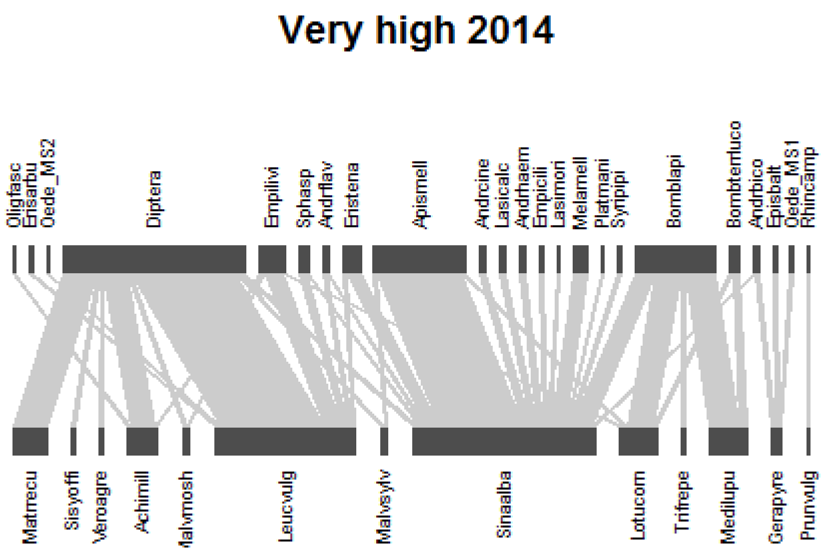

Figure 3.14. Pooled plant-pollinator network for the very high functional diversity mixture in 2014, with plant taxa at the bottom and pollinator taxa at the top

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

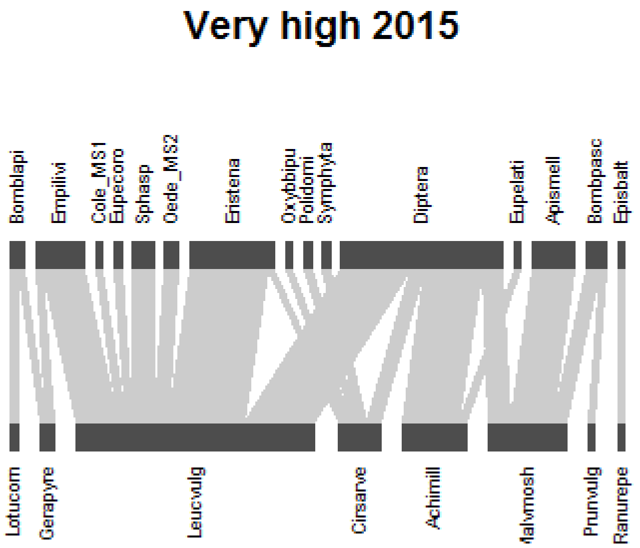

Figure 3.15. Pooled plant-pollinator network for the very high functional diversity mixture in 2015, with plant taxa at the bottom and pollinator taxa at the top

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

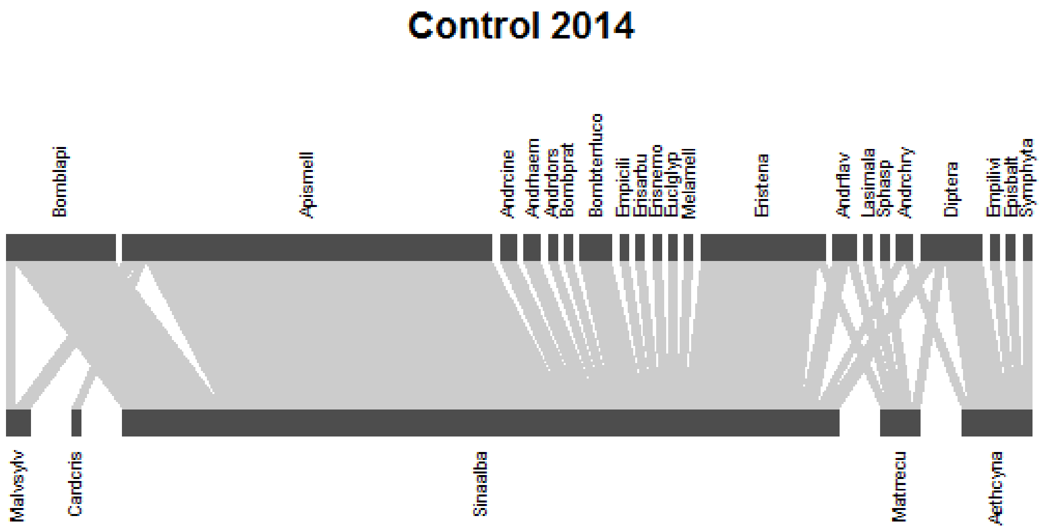

FIGURE 3.16. POOLED PLANT-POLLINATOR NETWORK FOR THE CONTROL MIXTURE IN 2014, WITH PLANT TAXA AT THE BOTTOM AND POLLINATOR TAXA AT THE TOP

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

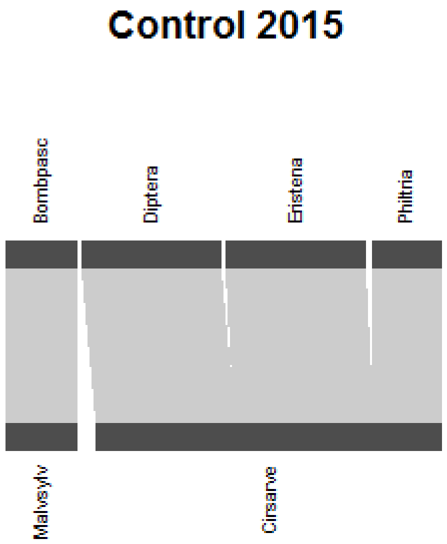

FIGURE 3.17. POOLED PLANT-POLLINATOR NETWORK FOR THE CONTROL MIXTURE IN 2015, WITH PLANT TAXA AT THE BOTTOM AND POLLINATOR TAXA AT THE TOP

For the plant and pollinator taxa corresponding to the taxon codes, see Supplementary Table 3.4 and Table 3.5.

Table 3.3. Mean ± SEM per mixture of the cover of the different plant species found in the permanent quadrats

	2014					2015				
	VL	**L**	**H**	**VH**	**Co**	**VL**	**L**	**H**	**VH**	**Co**
Sown species										
Achillea millefolium	5.60±2.01	6.63±2.39	5.43±2.64	3.90±1.16	0.23±0.15	10.57±2.00	13.60±2.51	11.97±3.78	16.40±4.43	0.67±0.33
Crepis biennis	0.03±0.03	2.73±0.71	0.00±0.00	0.07±0.07	0.03±0.03	0.00±0.00	1.20±0.50	0.03±0.03	0.00±0.00	0.00±0.00
Galium verum	1.13±0.32	1.13±0.35	0.37±0.33	0.03±0.03	0.03±0.03	2.47±0.62	2.67±0.92	0.97±0.93	0.03±0.03	0.13±0.06
Geranium pyrenaicum	0.17±0.17	0.10±0.10	1.70±0.81	0.00±0.00	0.00±0.00	0.03±0.03	0.13±0.13	1.43±0.78	0.00±0.00	0.03±0.03
Heracleum sphondylium	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.33±0.33	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.70±0.70
Hypochaeris radicata	0.00±0.00	11.37±3.62	0.07±0.07	0.00±0.00	0.10±0.10	0.10±0.10	8.07±2.80	0.13±0.13	0.00±0.00	0.13±0.13
Knautia arvensis	0.03±0.03	0.10±0.04	0.03±0.03	0.00±0.00	0.00±0.00	0.03±0.03	0.17±0.09	0.13±0.13	0.00±0.00	0.00±0.00
Leontodon hispidus	0.03±0.03	1.10±0.40	0.13±0.10	0.00±0.00	0.00±0.00	0.23±0.23	2.60±1.03	0.70±0.37	0.00±0.00	0.00±0.00
Leucanthemum vulgare	41.67±4.63	1.30±0.80	17.33±6.11	0.70±0.42	0.10±0.10	52.27±6.1	1.93±1.12	28.80±5.73	1.40±1.23	0.37±0.37
Lotus corniculatus	0.03±0.03	0.00±0.00	0.00±0.00	4.03±3.24	0.00±0.00	0.03±0.03	0.03±0.03	0.00±0.00	0.83±0.75	0.00±0.00
Malva moschata	0.03±0.03	0.03±0.03	0.20±0.16	3.67±1.49	0.00±0.00	0.00±0.00	0.07±0.07	0.10±0.07	2.87±1.01	0.07±0.07
Medicago lupulia	0.00±0.00	0.00±0.00	0.00±0.00	1.10±0.50	0.00±0.00	0.17±0.17	0.07±0.07	0.07±0.07	1.03±0.62	0.00±0.00
Origanum vulgare	0.00±0.00	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Prunella vulgaris	0.10±0.10	0.00±0.00	1.23±0.85	0.93±0.27	0.00±0.00	0.50±0.34	0.00±0.00	0.60±0.34	1.60±0.31	0.23±0.23
Trifolium pratense	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

TABLE 3.3 (CONTINUED). MEAN ± SEM PER MIXTURE OF THE COVER OF THE DIFFERENT PLANT SPECIES FOUND IN THE PERMANENT QUADRATS

	2014					**2015**				
	VL	**L**	**H**	**VH**	**Co**	**VL**	**L**	**H**	**VH**	**Co**
Spontaneous species										
Aethusa cynapium	0.03±0.03	0.10±0.07	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Anchusa arvensis	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Artemisia vulgaris	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Capsella bursa-pastoris	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Cichorium intybus	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Cirsium arvense	0.50±0.36	0.80±0.41	0.93±0.61	0.57±0.26	3.20±1.71	0.77±0.42	3.10±2.07	4.20±3.46	1.57±0.15	6.70±2.45
Conyza canadensis	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Erodium cicutarium	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Geranium molle	0.03±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Malva sylvestris	1.43±1.43	2.27±2.14	0.13±0.13	0.00±0.00	0.03±0.03	0.00±0.00	0.03±0.03	0.03±0.03	0.00±0.00	0.00±0.00
Matricaria recutita	0.10±0.10	0.00±0.00	0.03±0.03	0.43±0.28	0.17±0.09	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Mercurialis annua	0.07±0.04	0.00±0.00	0.00±0.00	0.10±0.10	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Plantago major	0.10±0.07	0.10±0.07	0.10±0.07	0.03±0.03	0.07±0.04	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.03±0.03
Ranunculus repens	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03
Rumex crispus	0.00±0.00	0.00±0.00	0.03±0.03	0.10±0.10	0.03±0.03	0.07±0.07	0.00±0.00	0.00±0.00	0.13±0.13	0.20±0.20
Rumex obtusifolius	1.57±1.37	0.33±0.29	0.07±0.04	1.17±0.84	0.40±0.40	0.87±0.57	0.33±0.29	0.30±0.23	2.13±1.36	0.23±0.16
Silene latifolia	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00
Silene vulgaris	0.00±0.00	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Sinapis alba	0.00±0.00	0.00±0.00	1.40±1.40	0.50±0.50	2.70±1.70	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Sisymbrium officinale	0.00±0.00	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Trifolium hybridum	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00
Trifolium repens	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00	0.17±0.07	0.00±0.00
Urtica dioica	0.00±0.00	0.10±0.10	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00
Verbascum thapsus	0.00±0.00	0.00±0.00	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

TABLE 3.4. TAXON CODES OF PLANT TAXA

Taxon code	**Plant taxon**
Achimill	*Achillea millefolium*
Aethcyna	*Aethusa cynapium*
Bellpere	*Bellis perennis*
Capsburs	*Capsella bursa-pastoris*
Cardcris	*Carduus crispus*
Cirsarve	*Cirsium arvense*
Crepbien	*Crepis biennis*
Galimoll	*Galium mollugo*
Galiveru	*Galium verum*
Gerapyre	*Geranium pyrenaicum*
Hyporadi	*Hypochaeris radicata*
Knauarve	*Knautia arvensis*
Leonhisp	*Leontodon hispidus*
Leucvulg	*Leucanthemum vulgare*
Lotucorn	*Lotus corniculatus*
Malvmosh	*Malva moschata*
Malvsylv	*Malva sylvestris*
Matrmari	*Matricaria maritima*
Matrrecu	*Matricaria recutita*
Medilupu	*Medicago lupulina*
Prunvulg	*Prunella vulgaris*
Ranurepe	*Ranunculus repens*
Sinaalba	*Sinapis alba*
Sisyoffi	*Sisymbrium officinale*
Tarasp	*Taraxacum* sp.
Trifrepe	*Trifolium repens*
Veroagre	*Veronica agrestis*

TABLE 3.5. TAXON CODES OF POLLINATOR TAXA

Taxon code	Pollinator taxon	Order
Aglaurti	*Aglais urticae*	Lepidoptera
Amarovat	*Amara ovata*	Coleoptera
Andrbico	*Andrena bicolor*	Hymenoptera
Andrchry	*Andrena chrysosceles*	Hymenoptera
Andrcine	*Andrena cineraria*	Hymenoptera
Andrdors	*Andrena dorsata*	Hymenoptera
Andrflav	*Andrena flavipes*	Hymenoptera
Andrgrav	*Andrena gravida*	Hymenoptera
Andrhaem	*Andrena haemorrhoa*	Hymenoptera
Andrnigr	*Andrena nigroaenea*	Hymenoptera
Andrsp	*Andrena* sp.	Hymenoptera
Apismell	*Apis mellifera*	Hymenoptera
Apocrita	Apocrita	Hymenoptera
Aricages	*Aricia agestis*	Lepidoptera
Bombhypn	*Bombus hypnorum*	Hymenoptera
Bomblapi	*Bombus lapidarius*	Hymenoptera
Bombpasc	*Bombus pascuorum*	Hymenoptera
Bombprat	*Bombus pratorum*	Hymenoptera
Bombterrluco	*Bombus terrestris/lucorum*	Hymenoptera
Cercryby	*Cerceris rybyensis*	Hymenoptera
Cheivern	*Cheilosia vernalis*	Diptera
Chrycaut	*Chrysogaster cemiteriorum*	Diptera
Cole_MS1	Coleoptera morphospecies 1	Coleoptera
Cole_MS2	Coleoptera morphospecies 2	Coleoptera
Coleoptera	Coleoptera	Coleoptera
Colldavi	*Colletes daviesanus*	Hymenoptera
Diptera	Diptera	Diptera
Empicili	*Empis ciliata*	Diptera
Empilivi	*Empis livida*	Diptera
Episbalt	*Episyrphus balteatus*	Diptera
Erisarbu	*Eristalis arbustorum*	Diptera
Erisnemo	*Eristalis nemorum*	Diptera
Erissepu	*Eristalinus sepulchralis*	Diptera
Erissimi	*Eristalis similis*	Diptera
Eristena	*Eristalis tenax*	Diptera
Euclglyp	*Euclidia glyphica*	Lepidoptera
Eupecoro	*Eupeodes corollae*	Diptera
Eupelati	*Eupeodes latifasciatus*	Diptera
Eupeluni	*Eupeodes luniger*	Diptera
Halitumu	*Halictus tumulorum*	Hymenoptera
Helosp	*Helophilus* sp.	Diptera
Helotriv	*Helophilus trivittatus*	Diptera
Hemiptera	Hemiptera	Hemiptera

TABLE 3.5 (CONTINUED). TAXON CODES OF POLLINATOR TAXA

Taxon code	Pollinator taxon	Order
Lasicalc	*Lasioglossum calceatum*	Hymenoptera
Lasilati	*Lasioglossum laticeps*	Hymenoptera
Lasileuc	*Lasioglossum leucozonium*	Hymenoptera
Lasimala	*Lasioglossum malachurum*	Hymenoptera
Lasiminu	*Lasioglossum minutissimum*	Hymenoptera
Lasimori	*Lasioglossum morio*	Hymenoptera
Lasipaux	*Lasioglossum pauxillum*	Hymenoptera
Lasivill	*Lasioglossum villosulum*	Hymenoptera
Lejometa	*Lejogaster metallina*	Diptera
Lindalbi	*Lindenius albilabris*	Hymenoptera
Melamell	*Melanostoma mellinum*	Diptera
Melisp	*Meligethes* sp.	Coleoptera
Oede_MS1	*Oedemera* morphospecies 1	Coleoptera
Oede_MS2	*Oedemera* morphospecies 2	Coleoptera
Oedesp	*Oedemera* sp.	Coleoptera
Oligfasc	*Oligia fasciuncula*	Lepidoptera
Oxybbipu	*Oxybelus bipunctatus*	Hymenoptera
Philtria	*Philanthus triangulatum*	Hymenoptera
Platalbi	*Platycheirus albimanus*	Diptera
Platmani	*Platycheirus manicatus*	Diptera
Platpelt	*Platycheirus peltatus*	Diptera
Polidomi	*Polistes dominula*	Hymenoptera
Rhincamp	*Rhingia campestris*	Diptera
Scaepyra	*Scaeva pyrasti*	Diptera
Sphasp	*Sphaerophoria* sp.	Diptera
Symphyta	Symphyta	Hymenoptera
Syripipi	*Syritta pipiens*	Diptera
Syrpribe	*Syrphus ribesii*	Diptera
Vaneatal	*Vanessa alatanta*	Lepidoptera
Vanecard	*Vanessa cardui*	Lepidoptera

CHAPTER 4

SUMMER MOWING AND INCREASING FORB COMPETITION AS TOOLS TO MANAGE CIRSIUM ARVENSE IN FIELD MARGIN STRIPS

4. SUMMER MOWING AND INCREASING FORB COMPETITION AS TOOLS TO MANAGE *CIRSIUM ARVENSE* IN FIELD MARGIN STRIPS

Research paper in revision for Weed Research

ROEL UYTTENBROECK, JULIEN PIQUERAY, SÉVERIN HATT, GRÉGORY MAHY, ARNAUD MONTY

ABSTRACT

Infestation by noxious weeds is a potentially important disservice of field margin strips and can reduce farmers' acceptance of this agri-environment measure. The strip seed mixture composition and management can be expected to influence infestation by noxious weeds. To test this, we created experimental strips by sowing four different seed mixtures with grass and forb species and one grass-only mixture. Three different mowing regimes were applied: summer mowing, autumn mowing and mowing both in summer and autumn. Cover of non-sown weeds was monitored during three years and the number of flower heads produced by *Cirsium arvense* was counted in the third year. Summer mowing and mowing twice a year resulted in a lower *C. arvense* cover from the third year on, and it prevented the species from producing mature flowers. Adding forb species to the seed mixture resulted in lower cover of *C. arvense* from the second year on in two forb mixtures and a higher sown forb cover was related to a lower *C. arvense* cover. Other weed species were not affected, but their abundance remained relatively low. Our results suggest that it is possible to limit infestation by *C. arvense* by adding forbs to the seed mixture to reduce the number of available recruitment gaps and by adapting the timing of mowing to reduce its nutrient stock, and to increase the cover of other forb species.

Key words

competition, flowering, germination, management, perennial weed, phenology, seed production, sustainable agriculture

INTRODUCTION

In response to biodiversity losses due to agricultural intensification (Stoate et al., 2001), European farmers have been encouraged through financial incentives to adopt agri-environment schemes (European Commission, 2005). Perennial field margin strips are an example of such schemes, and consist of sown or spontaneously developed grassland-like vegetation in the margin of arable fields. Their principal aim is to enhance biodiversity in the agroecosystem by creating an area for wild plants to grow and reproduce, providing food and shelter for animals. Depending on the policy of EU countries, the management prescriptions, type of strips and subsidies vary (Haaland et al., 2011). Different seed mixtures can be used for sown field margin strips and can contain grasses, forb species or both (Marshall and Moonen, 2002; Haaland et al., 2011).

While field margin strips have been shown to be beneficial in several cases for pollination and pest control services to crops, they can deliver disservices as well (Zhang et al., 2007), and for many of these different services and disservices, studies are scarce (Uyttenbroeck et al., 2016). An often appearing fear of farmers is the disservice of weeds, possibly settling in the strips and spreading to neighbouring arable fields (e.g. van der Meulen et al., 1996). Indeed, weeds can spread from the strip to the crops by rhizomes or seeds (De Cauwer et al., 2008), possibly reducing crop yield or increasing management costs. While problems are expected to be less when weed pressure before sowing is low (Bokenstrand et al., 2004), many studies report important abundance of noxious weeds in field margin strips (De Cauwer et al., 2008; Westbury et al., 2008; Smith et al., 2010). One of the noxious weed species reported, was *Cirsium arvense* (L.) Scop. (De Cauwer et al., 2008; Westbury et al., 2008; Smith et al., 2010). This species is known for its ability to colonize arable field with adventitious shoots and roots up to several meters per year (Tiley, 2010). Weed presence in strips can also discourage farmers who already adopted an agri-environment scheme to extend their contracts.

Furthermore, farmers are often legally obligated to treat against certain weed species. In Belgium, this is the case for *C. arvense, Cirsium vulgare* (Savi) Ten., *Cirsium palustre* (L.) Scop. and *Carduus crispus* L. (Agentschap Natuur & Bos, 2017), in the United Kingdom for *C. arvense, C. vulgare, Rumex obtusifolius* L., *Rumex crispus* L., and *Senecio jacobaea* L. (The National Archive, 2017), and in France for *C. arvense* (Secrétariat général du gouvernement, 2017). Therefore, there is a need to reduce the possible weed infestation in field margin strips, especially in perennial strips where soil tillage is often prohibited after vegetation establishment.

While in some countries, or in some agri-evironmental schemes, perennial sown field margin strips are not managed after sowing, annual mowing is often applied in other cases to keep a diverse meadow-like vegetation (Haaland et al., 2011; Tarmi et al., 2011). It can reduce annual ruderal weeds (Westbury et al., 2008), as competitive perennial species resist better to mowing and will dominate under this management (e.g. Maron and Jefferies, 2001). As a consequence however, competitive perennial weeds may also persist in mown strips. Timing and frequency of mowing could be adapted to the phenology of noxious species to reduce weed infestation (Smith et al., 2010), however studies are scarce. Especially for perennial anemochorous weeds, adapting the timing of mowing could be an efficient method to reduce both their abundance and the risk of seed dispersal. According to De Cauwer et al. (2008), seed rain from anemochorous weeds in field margin strips to adjacent crops comes from annual species during the first years after establishment, though decreases strongly afterwards, while perennial anemochorous species could create a risk on the long term.

Another strategy to decrease weed infestation of field margin strips is sowing a seed mixture to cover the soil at establishment phase. Indeed, sown strips tend to host a smaller amount of weeds than spontaneous strips (Uyttenbroeck et al., 2016), as sown species compete with species from the soil seed bank to settle. Forb species are generally added to grass mixtures to more quickly obtain diverse flower strips with a high associated biodiversity (Critchley et al., 2006; Haaland et al., 2011). Yet, it is not clear how the seed mixture composition can influence weed abundance in the years after sowing. Studies showed that simple sown grass strips reduce arable weed pressure in field margins compared to a cropped field edge (Marshall, 2009; Cordeau et al., 2012). However, it can be expected that annual and perennial weeds have lower chance to establish in sown strips with forbs in the seed mixture, where recruitment gaps are taken by these forbs (Westbury et al., 2008).

We performed an experimental field study to test the effect of (1) the mowing regime and (2) adding forbs to the seed mixture on the weed infestation of field margin strips. We hypothesized that (1) timing and frequency of mowing affect infestation and seed production by perennial weeds, (2) adding forb species to the seed mixture can limit infestation by perennial weeds, and (3) higher cover of sown forb species results in lower cover of perennial weeds.

MATERIALS AND METHODS

Experimental field

The experiment was conducted in an arable field of the AgricultureIsLife Experimental Farm (Monty et al., 2016) of Gembloux Agro-Bio Tech (Belgium, 50°34'01"N 4°42'22"E) at 155 m elevation. To test the effect of adding forb species to the seed mixture of a field margin strip, four seed mixtures containing grass and forb species were compared to a control mixture containing only grass species. The seed mixtures were developed in another study and were based on functional traits related to flower visitors (see Uyttenbroeck et al., 2015). Four mixtures (F1-F4, Table 4.1) contained seven forb species (3.5 kg/ha) and three grass species (21.5 kg/ha). The control mixture (Co) contained only the three grass species (21.5 kg/ha). Seeds were obtained from Ecosem, Belgium (Ecosem sprl., 2017a).

TABLE 4.1. SPECIES COMPOSITION OF THE SEED MIXTURES WITH THE SOWING DENSITY USED PER SPECIES

Species	F1	F2	F3	F4	Co	Sowing density (kg/ha)
Achillea millefolium L.	x	x	x	x		0.5
Anthriscus sylvestris L. Hoffmann	x		x	x		0.5
Crepis biennis L.		x				0.5
Galium verum L.	x	x				0.5
Geranium pyrenaicum Burm. f.			x			0.5
Heracleum sphondylium L.	x					0.5
Hypochaeris radicata L.		x				0.5
Knautia arvensis (L.) Coulter	x	x				0.5
Leontodon hispidus L.		x	x			0.5
Leucanthemum vulgare Lam.	x		x			0.5
Lotus corniculatus L.				x		0.5
Lythrum salicaria L.		x		x		0.5
Malva moschata L.				x		0.5
Medicago lupulina L.				x		0.5
Origanum vulgare L.			x			0.5
Prunella vulgaris L.			x	x		0.5
Trifolium pratense L.	x					0.5
Festuca rubra L.	x	x	x	x	x	11.5
Agrostis spp.	x	x	x	x	x	5
Poa pratensis L.	x	x	x	x	x	5

The seed mixtures were sown in 75 2x8m strips in a split-plot design with seed mixture as subplot treatment and mowing regime as whole plot treatment (Supplementary Figure 4.5).

The whole plots were organized in five blocks. The seed mixtures were sown in June 2013 with a Wintersteiger® plot seeder.

To evaluate the effect of mowing date and frequency, three mowing regimes were tested: summer mowing ('S', end of June to beginning of July), autumn mowing ('A', end of September to beginning of October) and both summer and autumn mowing ('SA'). Vegetation was cut with a flail cutter in September 2013. Mowing treatment was applied from 2014 on with a Wintersteiger® plot forage harvester. The cut material was harvested and weighed after mowing. Whole plots were separated by grass-only vegetation that was mown twice a year, simultaneously with the SA mowing treatment.

Weeds and sown forbs monitoring

In the centre of each subplot, a permanent quadrat of 1x1m was used to monitor the vegetation development after sowing from 2014 to 2016. All quadrats were visited twice a year before mowing (in June and September) resulting in six surveys over three years. In each quadrat, all sown and spontaneous forb species were listed and their percentage of horizontal cover was estimated. *Cirsium arvense* was abundant in our experiment, and is known to produce anemochorous seeds that can spread to neighbouring fields (Heimann and Cussans, 1996). Therefore, its number of open flower heads was counted in each quadrat from May to September 2016 with two to four weeks interval, and pooled per quadrat. The produced biomass was sampled in June and September 2016 in the subplots that were mown only. The fresh biomass was harvested and weighed, and a subsample was weighed, oven-dried at 70°C for seven days and weighed again to obtain the ratio of dry to fresh biomass. Total dry biomass per subplot was calculated as the product of the total fresh biomass and the dry to fresh biomass ratio. The dry biomass values of June and September were summed for the subplots that were mown twice a year.

Data analysis

Data analysis was performed in R (R Core Team, 2013). The forb species were split up into sown and spontaneous species. One abundant annual (*Sinapis alba* L.) and three abundant perennial weed species (*C. arvense*, *R. obtusifolius* and *R. crispus*) were selected for analysis, as they were the most abundant spontaneous forbs in the experiment. *R. obtusifolius* and *R. crispus* were pooled to *Rumex spp*. The other spontaneous species were grouped into 'other weeds', but were not analysed further because of their very low cover. Response variables were ln(n+1)-transformed prior to analysis, except for sown forb cover (square root transformed) and total dry biomass (not transformed), to improve normality and homoscedasticity.

The effect of seed mixture, mowing regime and their interaction with time (categorical variable with the six different weed surveys times) on *C. arvense*, *Rumex spp*. and *S. alba* cover was tested with linear mixed-effects models ('lmer' function from the 'lme4' R package, Bates et al. (2014)) with seed mixture, mowing regime, time and their first and second order interactions as fixed effects and with block, whole plot and subplot as nested random effects. When a significant interaction occurred with time, the effect of seed mixture, mowing regime and their interaction was tested for each survey separately with linear mixed-effects models (block and whole plot as nested random effects). Furthermore, when time interacted with mowing regime, the time effect was tested for the mowing regimes separately with linear mixed-effects models (whole plot and subplot as nested random effects). As weed species can respond differently to different forb mixtures, both the sown forb cover and biomass produced in the forb mixtures were compared to explain these differences. The effect of seed mixture (F1-F4) and mowing regime on sown forb cover was tested with a linear mixed-effects model with mowing regime, seed mixture, time and their first and second order interactions as fixed effects and with block, whole plot and subplot as nested random effects. When a significant interaction occurred with time, the effect of seed mixture (F1-F4), mowing regime and their interaction was tested for each survey separately. The effect of seed mixture (F1-F4), mowing regime and their interaction on the total dry biomass in 2016 was tested with a linear mixed-effects model with mowing regime, seed mixture and their interaction as fixed effects and with block and whole plot as nested random effects. The direct relationship between the sown forb cover and the weed species cover was explored for each survey in the F1-F4 subplots with a linear mixed-effects model with block and whole plot as nested random effects. The direct relationship between the total dry biomass and the weed species cover was explored in the F1-F4 subplots with a linear mixed-effects model with block and whole plot as nested random effects. To obtain the independent response of the *C. arvense* number of flower heads to the treatments, the residuals of the linear regression ($R^2=0.389$, $P<0.001$) between the ln(n+1)-transformed cover of *C. arvense* in June 2016 and the number of flower heads were computed. These residuals were used as response variable in a linear mixed-effects model with seed mixture, mowing regime and their interaction as fixed effects and block and whole plot as nested random effects.

Significance (*P*<0.05) of fixed effects and their interactions was tested using *F*-tests with Kenward-Roger degree of freedom estimation (function 'Anova' of 'car' R package, Fox and Weisberg (2011)). For models with significant factors, post-hoc comparisons (function 'glht' of 'multcomp' R package, Hothorn et al. (2008)) were performed after removing non-significant interactions from the model. For seed mixture, the values of the four forb mixtures (F1-F4) were compared with the value of the control mixture (Co) for the weed species cover responses, and all pairwise comparisons between the forb mixtures were made for the sown forb cover and the total dry biomass response. For mowing regime and time, all pairwise comparisons were made.

RESULTS

Cirsium arvense was the most abundant spontaneous forb species over the whole experiment, with a mean cover of 3.1%. It was the third most abundant forb species after the sown species *Leucanthemum vulgare* Lam. and *Achillea millefolium* L. Second and third most abundant spontaneous species were *Rumex spp.* (1.0%) and *S. alba* (0.9%). All other spontaneous species had a mean cover lower than 0.2% over the whole experiment. While *S. alba* was only present during the first year after sowing, *C. arvense* and *Rumex spp.* maintained their presence (Figure 4.1). An overview of the cover of sown and spontaneous species in 2016 in the different seed mixtures is given in Supplementary Table 4.3.

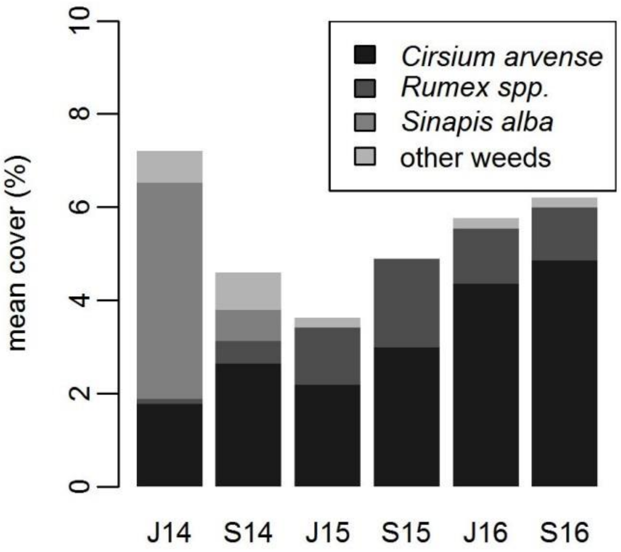

FIGURE 4.1. STACKED BAR GRAPH OF THE MEAN COVER OVER ALL QUADRATS OF *CIRSIUM ARVENSE*, RUMEX SP. SINAPIS ALBA AND THE OTHER WEEDS FROM JUNE 2014 (J14) TO SEPTEMBER 2016 (S16)

Only *C. arvense* cover showed a significant effect of seed mixture and mowing regime, both interacting with time (Table 4.2). As for *Rumex spp.* and *S. alba* cover, only time had a significant effect (Table 4.2). Separate analyses for the different surveys showed a significant effect of mowing regime on *C. arvense* cover in September 2016 (Supplementary Table 4.4). Post-hoc comparisons showed that S and SA subplots had a significantly lower cover than A subplots (Figure 4.2a, back-transformed means of 2.7%, 2.2% and 6.4% respectively). Separate analysis for the different mowing regimes showed a significant effect of time in S subplots and in A subplots, while SA subplots were not significantly affected (Supplementary Table 4.5). Post-hoc comparisons showed an increased *C. arvense* cover for S subplots starting from September 2015, compared to their cover in June 2014 (Figure 4.2a). For A subplots, the differences of *C. arvense* cover between surveys showed a stronger increase over time.

TABLE 4.2. RESULTS OF F-TESTS ON THE FIXED EFFECTS OF THE FULL MODELS

For each response variable, the first line shows the *F*-values and the second line the *P*-values. All response variables were ln(n+1)-transformed prior to analysis, except for sown forb cover (square root transformed) and total dry biomass (not transformed). The values for *C. arvense* number of flower heads response variable are the residuals of the linear regression between the ln(n+1)-transformed cover of *C. arvense* in June 2016 and the number of flower heads.

		mowing	mixture	mowing: mixture	time	mowing: time	mixture: time	mowing: mixture: time
Cirsium arvense cover	*F*	0.84	**4.06**	**2.19**	**20.41**	**5.11**	**1.83**	0.89
	P	*0.468*	***0.006***	***0.045***	***<0.001***	***<0.001***	***0.018***	*0.661*
Rumex spp. cover	*F*	1.57	0.55	0.79	**2.83**	1.08	0.71	0.78
	P	*0.227*	*0.701*	*0.616*	***0.016***	*0.375*	*0.816*	*0.831*
Sinapis alba cover	*F*	0.04	0.72	0.24	**19.83**	0.12	1.01	0.31
	P	*0.961*	*0.582*	*0.981*	***<0.001***	*1.000*	*0.449*	*1.000*
Sown forb cover	*F*	**9.73**	**3.92**	0.78	**21.81**	**3.89**	**4.39**	**1.75**
	P	***0.007***	***0.016***	*0.594*	***<0.001***	***<0.001***	***<0.001***	***0.012***
Total dry biomass	*F*	**4.58**	1.18	1.86	-	-	-	-
	P	***0.007***	*0.356*	*0.116*				
Cirsium arvense number of flower heads	*F*	**16.80**	1.32	1.37	-	-	-	-
	P	***0.001***	*0.274*	*0.236*				

Separate analyses for the different surveys showed a significant effect of seed mixture on *C. arvense* cover in June 2015, June 2016 and September 2016 (Supplementary Table 4.4). Post-hoc comparisons showed that its cover was significantly higher in the Co mixture than in the F1 and F2 forb mixtures in these surveys (Figure 4.3a, back-transformed means of 2.4%, 2.0% and 5.8% for F1, F2 and Co mixtures respectively in September 2016). When comparing the average of the four forb mixtures together to the Co mixture, the forb mixtures had a significantly lower cover of *C. arvense* in these surveys (z=2.71, P=0.025 for June 2015; z=2.83, P=0.017 for June 2016; z=3.45, P=0.002 for September 2016). No significant interaction between seed mixture and mowing regime was found for the separate surveys.

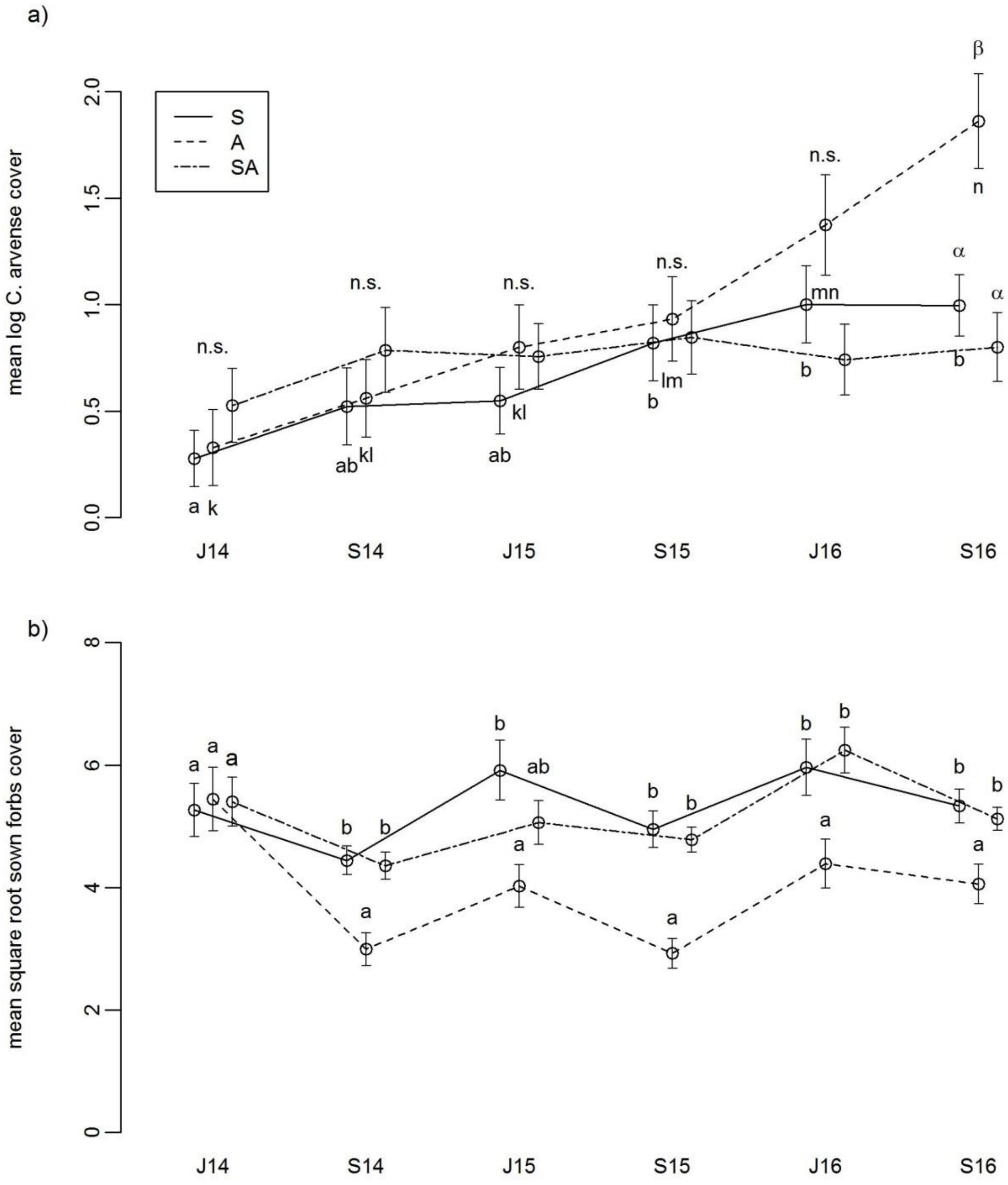

Figure 4.2. Evolution of (a) the mean ln(n+1)-transformed cover of *Cirsium arvense* and (b) the mean square root transformed sown forb cover per mowing regime.

The horizontal axes show the different surveys from June 2014 (J14) to September 2016 (S16). The mowing treatments are mowing in summer (S), mowing in autumn (A) and mowing both in summer and autumn (SA). Error bars show the standard error of the mean. In (a), Greek letters above error bars denote post-hoc differences (*P*<0.05) between different mowing regimes for each survey with a significant effect of mowing regime, or 'n.s.' in case of no significant difference. Latin letters below error bars denote post-hoc differences (*P*<0.05) between different surveys for the S (a-b) and the A (k-m) mowing treatment. For the SA mowing regime, time had no significant effect. In (b) Latin letters above error bars denote post-hoc differences (*P*<0.05) between different mowing regimes for each survey with a significant effect of mowing regime. In (b) the Control mixture was not included in the analysis.

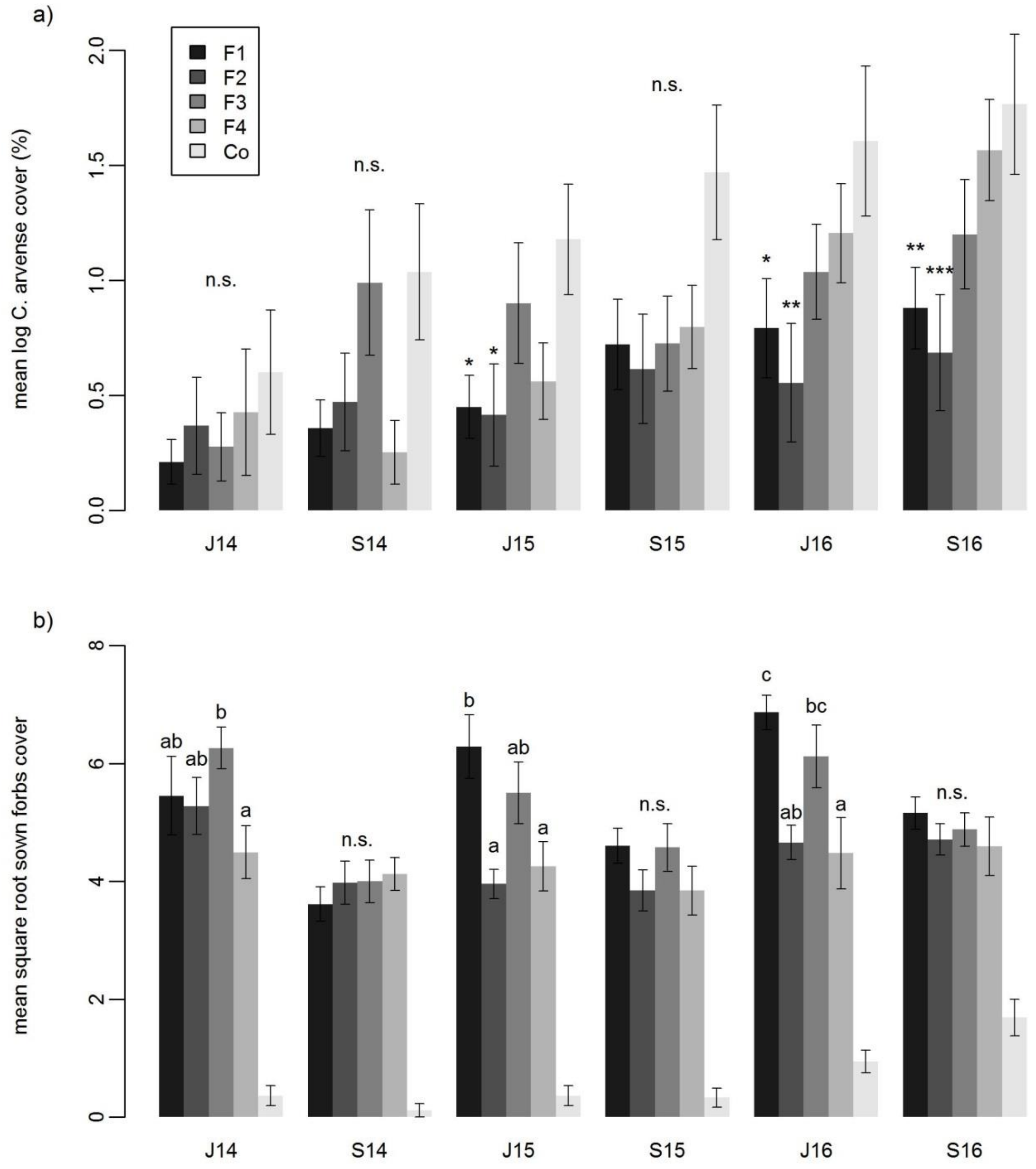

FIGURE 4.3. MEAN PER SEED MIXTURE OF (A) THE LN(N+1)-TRANSFORMED COVER OF *CIRSIUM ARVENSE* AND (B) THE SQUARE ROOT TRANSFORMED SOWN FORB COVER

The horizontal axes show the different surveys from June 2014 (J14) to September 2016 (S16). Error bars show the standard error of the mean. In (a), stars above error bars denote post-hoc differences (*: $0.01<P<0.05$; **: $0.001<P<0.01$; ***: $P<0.001$) between the forb mixtures (F1-F4) and control mixture (Co) for surveys with a significant effect of seed mixture, or 'n.s.' in case of no significant effect of seed mixture. In (b) letters above error bars denote post-hoc differences ($P<0.05$) between the different forb mixtures for each survey with a significant effect of seed mixture, or 'n.s.' in case of no significant difference. The value for the Co mixture is given for information in (b) but was not included in the analysis.

Sown forb cover was significantly affected by seed mixture and mowing regime and these effects interacted with time (Table 4.2). Separate analyses for the different surveys showed a significant effect of seed mixture in June of all three years, and a significant effect of mowing regime in all surveys, except in June 2014 (Supplementary Table 4.6). Post-hoc comparisons showed that the seed mixtures with higher sown forb cover did not correspond with the seed mixtures with lower *C. arvense* cover (Figure 4.3a-b). However, A subplots had a lower sown forb cover than S and SA subplots starting from June 2014, which corresponded with higher values of *C. arvense* cover (Figure 4.2a-b). Total dry biomass in 2016 was significantly affected by seed mixture (Table 4.2). Post-hoc comparisons showed no significant differences between the forb mixtures.

Cirsium arvense cover significantly decreased with increasing sown forb cover in June (*F*=8.23, *P*=0.006) and September (*F*=8.86, *P*=0.004) 2016, but not in 2014 and 2015. Figure 4.4a shows this relationship for September 2016. *Cirsium arvense* cover significantly increased both for June (*F*=8.72, *P*=0.005) and for September (*F*=8.33, *P*=0.005; Figure 4.4b) 2016 with total biomass in 2016.

Mowing regime had a significant effect on the number of *C. arvense* flower heads response, independent of the effect of its cover (Table 4.2). Autumn mowing was associated with significantly more flower heads than summer and summer and autumn mowing (*z*=5.25, *P*<0.001 and *z*=4.76, *P*<0.001 respectively). Seed mixture and the interaction between seed mixture and mowing regime had no significant effect.

DISCUSSION

Cirsium arvense appeared as the most abundant spontaneous species in our experimental strips. Mowing in summer or both in summer and autumn performed better in limiting its cover than mowing in autumn only, and enabled to reduce its flower head production, hence its ability to produce seeds. For mowing both in summer and autumn, no increase of *C. arvense* cover over time was detected. Furthermore, sowing forb species along with grass species enabled to reduce its abundance from the second year of vegetation establishment, although not for all forb mixtures. As it is a noxious weed species reported to persist in perennial field margin strips (e.g. Smith et al., 2010), these results are promising for future strip management. Other spontaneous species disappeared from the strip vegetation or were kept to relatively low levels, irrespective of mowing regime or seed mixture. *S. alba*, an annual former cover crop that may have germinated from seeds present in the seed bank, was abundantly present in the first year after sowing, but was unable to establish in the

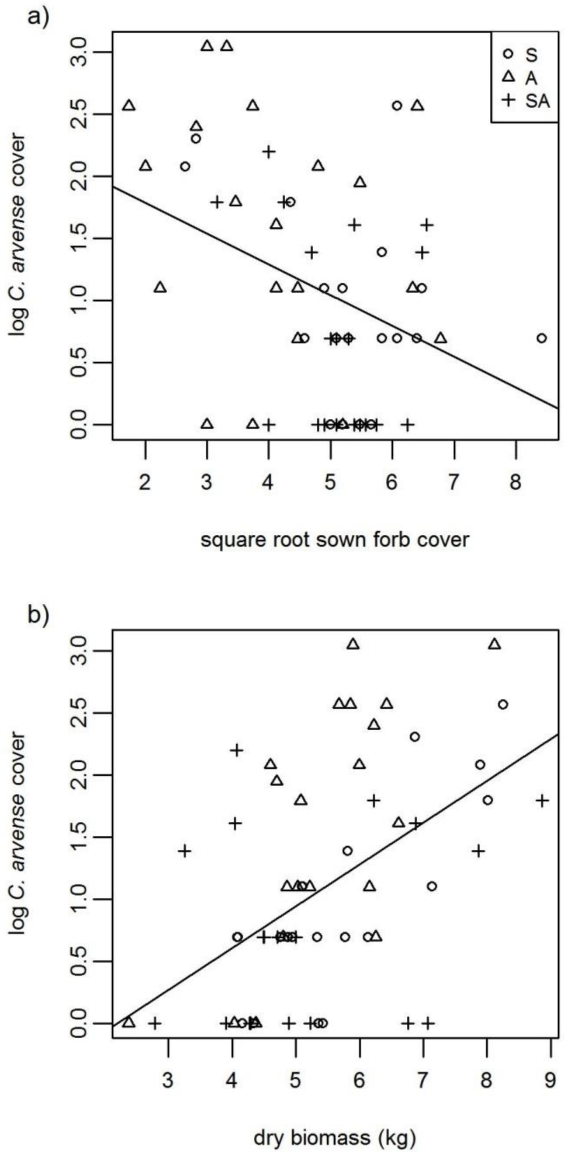

FIGURE 4.4. PLOT OF THE LN(N+1)-TRANSFORMED COVER OF *CIRSIUM ARVENSE* IN SEPTEMBER 2016 IN FUNCTION OF (A) THE SQUARE ROOT TRANSFORMED SOWN FORB SPECIES COVER IN SEPTEMBER 2016 AND (B) THE TOTAL DRY BIOMASS IN 2016

The point shape indicates the different mowing regimes: summer mowing (S), autumn mowing (A) and mowing both in summer and autumn (SA). The regression lines show the model fit of the mixed-effects models.

second year, probably due to the lack of soil disturbance. This is consistent with Smith et al. (2010), who found a quick decrease of annuals in sown strips, irrespective of mowing regime. While *R. obtusifolius* and *R. crispus* are rhizomatous species like *C. arvense*, they were not influenced by mowing regime at the time scale of the experiment. Similarly, Westbury et al. (2008) did not observe an increase of *R. obtusifolius* in field margin strips, neither did they observe an effect of sward management.

For perennial weeds, like *C. arvense*, timing and frequency of mowing were expected to influence the level of infestation. For this species, summer mowing appeared to keep infestation to a low level in a later vegetation development stage. While mowing in June can initially stimulate this species to develop new shoots from the rhizomes, continued mowing in following years can indeed reduce its performance (Kluth et al., 2003). Likewise, Smith et al. (2010) reported a decreased abundance of *C. arvense* in mown compared to unmown field margin strips and in strips mown twice compared to strips mown once. They found no effect of timing, but they compared mowing twice in spring and summer with mowing twice in spring and autumn. Westbury et al. (2008) found no different response of *C. arvense* cover to different management options of field margin strips (mowing in spring, sward scarification and selective graminicide) but observed a significant increase over time. The timing of the summer cut in our experiment (end of June, beginning of July) may have been appropriate to reduce the energy stock of *C. arvense* rhizomes by exporting their aboveground parts when they were nearly in their reproductive stage (Bicksler and Masiunas, 2009; Tiley, 2010). Moreover, summer mowing and mowing twice a year resulted in higher forb cover, already from the first year after sowing. This suggests that applying the right mowing regime may also affect *C. arvense* cover indirectly by increasing the competition by other forb species, which was confirmed by the negative relationship between sown forb cover and *C. arvense* cover in the later vegetation development stage.

Furthermore, summer mowing turned out to be an efficient strategy to prevent *C. arvense* from flowering and thus from producing seeds, as it coincided with the start of its reproductive stage. This species can flower from June to September in the region of Western Europe (Lambinon et al., 2008). While some plant species in meadow vegetation can react by producing compensatory flower shoots after mowing (e.g. Jantunen et al., 2007), this was only observed during the first year of repeated mowing regime for *C. arvense* by Kluth et al. (2003). A low number of flower heads may not only reduce the propagule pressure in the neighbouring crop field, it may also reduce the potential of new seeds to settle in the field margin strip itself. However, this may not have been the cause of the lower *C. arvense* cover in summer mown subplots in our experiment. Indeed, the small scale of the experiment and longer distance dispersal of *C. arvense* seeds may have enabled plants from autumn mown subplots to spread seeds to the other subplots.

Sowing forbs along with grass species was expected to reduce the niches available for weeds to settle in the strips. This effect was observed for *C. arvense* from the second year after sowing. Westbury et al. (2008) also found that grass-only mixtures had a higher abundance of some spontaneous species, like *Galium aparine* L., than mixtures with grass and forbs, although other species, like *C. arvense* were not affected by the mixture composition. Likewise, some studies comparing species poor (more niches available) with species rich (less niches available) swards sown in former arable fields reported a reduced weed infestation in species rich swards (Van der Putten et al., 2000; Lepŝ et al., 2007), while other studies found no difference (Pywell et al., 2002; Critchley et al., 2006). The significantly lower *C. arvense* cover in only two forb mixtures compared with the grass-only mixture in our experiment suggests that some forb species might be more competitive to perennial weeds than others. In the strips with the F2 mixture for instance, where *C. arvense* cover was the lowest among the seed mixtures in 2016, the sown rosette plant *Hypochaeris radicata* L. had a large cover

(Supplementary Figure 4.3). Tiley (2010) reviewed several studies indicating that *C. arvense* growth is reduced by competition and shade of neighbouring plants, but some species have larger effects than others. The cover of these forb species appears to play a role, as suggested by the negative relationship between sown forb cover and *C. arvense* cover in our study, although sown forb cover did not explain the different response of *C. arvense* cover to forb mixtures. Likewise, the dry biomass production did not explain this difference. It even increased with *C. arvense* cover, which could be due to the biomass of *C. arvense* plants themselves. Future studies could try to determine which forb species are better competitors to perennial weeds in field margin strips.

While these results suggest that summer mowing could be a tool to reduce *C. arvense* infestation, management choices should also take into consideration the effect of mowing timing and frequency on other services and disservices of field margin strips. For example, rotational mowing, by letting a part of the strip as refuge for arthropods and mowing it later, could increase the weeds disservice from a part of the strip, but increase the biodiversity conservation value and associated services, as was found for hay meadows (Buri et al., 2014; Lebeau et al., 2015). Also, the importance of some weeds species, like *C. arvense*, to pollinators and natural enemies of pests (Tiley, 2010), by providing pollen, nectar and alternative hosts (Landis et al., 2000), may question whether they should be completely eradicated in field margin strips. Further research could try to identify management options that maximize services and minimize disservices.

Acknowledgements

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SUPPLEMENTARY MATERIAL

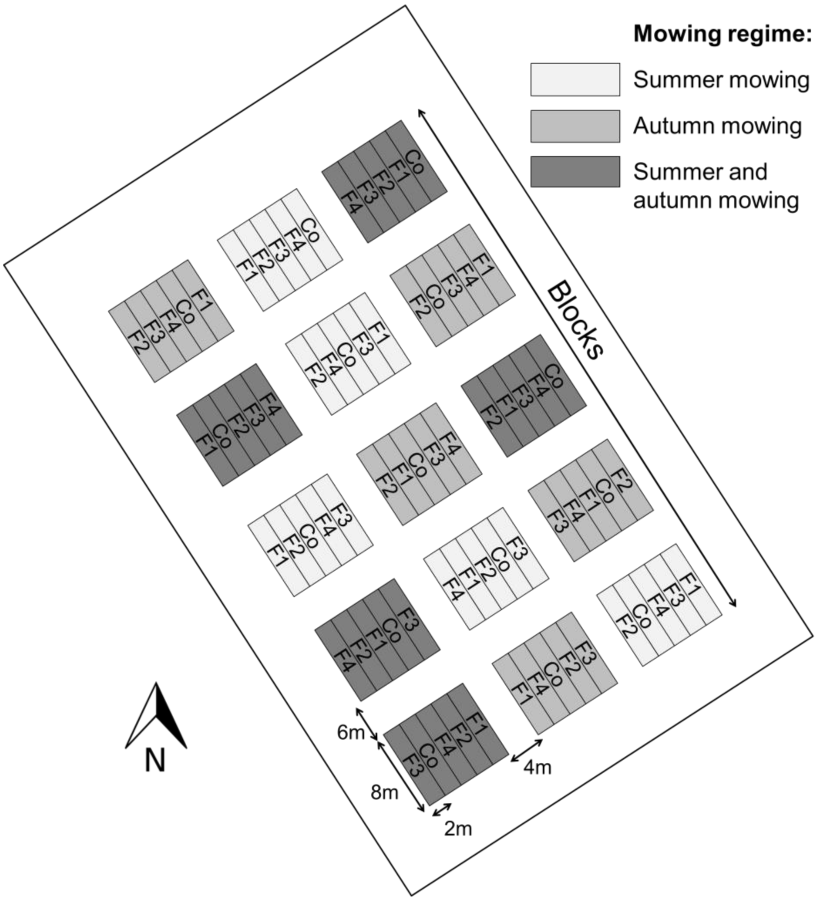

FIGURE 4.5. PLAN OF THE EXPERIMENTAL FIELD

Five blocks were divided in three whole plots with each five subplots. Whole plot mowing treatments are indicated in colors. Subplot mixture treatments are indicated on the plan in the subplots with F1-F4 being the mixtures containing grass and forb species and Co being the control mixture with only grass species.

TABLE 4.3. MEAN AND STANDARD ERROR OF THE COVER OF SOWN AND SPONTANEOUS FORB SPECIES IN JUNE AND SEPTEMBER 2016 FOR THE FOUR FORB MIXTURES (F1-F4) AND THE CONTROL MIXTURE (CO)

	F1		F2		F3		F4		Co	
	June	September	June	September	June	September	June	September	June	September
Sown forb species										
Achillea millefolium L.	6.1±2.0	4.6±0.9	4.1±1.1	5.1±1.2	9.8±2.3	7.9±1.3	8.3±4.2	6.6±2.0	0.1±0.1	0.2±0.1
Anthriscus sylvestris L. Hoffmann	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Crepis biennis L.	0.3±0.3	1.4±0.4	1.3±0.4	2.6±0.5	0.0±0.0	0.4±0.2	0.3±0.2	0.9±0.3	0.5±0.2	2.3±0.8
Galium verum L.	2.9±0.5	3.0±0.4	2.6±0.3	3.3±0.7	0.0±0.0	0.0±0.0	0.1±0.1	0.3±0.3	0.1±0.1	0.1±0.1
Geranium pyrenaicum Burm. f.	0.1±0.1	0.2±0.1	0.1±0.1	0.1±0.1	0.9±0.2	0.7±0.2	0.1±0.1	0.3±0.1	0.1±0.1	0.4±0.2
Heracleum sphondylium L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Hypochaeris radicata L.	0.2±0.1	0.1±0.1	12.0±2.3	9.1±1.7	0.1±0.1	0.1±0.1	0.0±0.0	0.1±0.1	0.1±0.1	0.4±0.2
Knautia arvensis (L.) Coulter	1.1±0.2	2.4±1.3	1.0±0.3	1.1±0.4	0.1±0.1	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Leontodon hispidus L.	0.1±0.1	0.0±0.0	1.6±0.3	1.7±0.4	0.9±0.3	0.9±0.3	0.0±0.0	0.0±0.0	0.1±0.1	0.1±0.1
Leucanthemum vulgare Lam.	36.0±2.9	15.7±2.1	0.1±0.1	0.1±0.1	26.5±4.4	12.9±2.3	1.7±1.3	2.1±1.7	0.3±0.2	0.7±0.4
Lotus corniculatus L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.4±0.4	0.1±0.1	5.2±2.1	8.5±3.2	0.1±0.1	0.1±0.1
Lythrum salicaria L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Malva moschata L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.1±0.1	4.9±1.7	1.9±0.7	0.0±0.0	0.0±0.0
Medicago lupulina L.	0.0±0.0	0.0±0.0	0.3±0.3	0.3±0.2	1.2±1.2	0.4±0.4	2.7±1.6	2.6±1.7	0.1±0.1	0.0±0.0
Origanum vulgare L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.3±0.2	0.5±0.4	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Prunella vulgaris L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.9±0.3	0.8±0.3	2.0±1.2	1.3±0.5	0.0±0.0	0.0±0.0
Trifolium pratense L.	1.5±1.3	0.2±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0

Table 4.3 (continued). Mean and standard error of the cover of sown and spontaneous forb species in June and September 2016 for the four forb mixtures (F1-F4) and the control mixture (Co)

	F1		F2		F3		F4		Co	
	June	September	June	September	June	September	June	September	June	September
Spontaneous forb species										
Centaurea jacea L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Cerastium fontanum Baumg.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0
Cirsium arvense (L.) Scop.	2.5±1.3	2.1±0.8	2.5±1.7	2.7±1.5	3.0±1.2	3.7±1.0	3.6±1.1	5.5±1.4	10.2±4.3	10.2±3.5
Cirsium vulgare (Savi) Ten.	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Galium mollugo L.	0.0±0.0	0.1±0.1	0.1±0.1	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Geranium molle L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0
Rumex spp.	3.3±3.3	2.7±2.7	1.5±1.2	2.2±1.7	0.0±0.0	0.0±0.0	0.5±0.4	0.3±0.2	0.5±0.3	0.5±0.3
Silene vulgaris (Moench) Garcke	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Sonchus asper (L.) Hill	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0	0.0±0.0	0.1±0.1	0.3±0.1	0.0±0.0	0.1±0.1	0.1±0.1
Taraxacum sp.	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0
Trifolium repens L.	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0	0.1±0.1	0.0±0.0	0.0±0.0

TABLE 4.4. RESULTS OF THE F-TESTS ON THE FIXED EFFECTS OF THE MODELS FITTED FOR EACH SURVEY WITH *CIRSIUM ARVENSE* COVER AS RESPONSE VARIABLE

For each survey, the first line shows the *F*-values and the second line the *P*-values. The *C. arvense* cover was ln(n+1)-transformed. The *F*- and *P*-values of the interaction between the mowing regime and the seed mixture are from the full model, the *F*- and *P*-values of the main effects are from the reduced model with only main effects.

		mowing	mixture	mowing: mixture
June 2014	*F*	0.58	0.52	1.14
	P	*0.580*	*0.722*	*0.356*
September 2014	*F*	0.59	2.53	1.46
	P	*0.576*	*0.050*	*0.197*
June 2015	*F*	0.41	**2.78**	1.88
	P	*0.675*	***0.035***	*0.086*
September 2015	*F*	0.08	2.47	1.64
	P	*0.919*	*0.055*	*0.140*
June 2016	*F*	2.66	**3.22**	1.74
	P	*0.130*	***0.019***	*0.113*
September 2016	*F*	**8.12**	**7.54**	2.07
	P	***0.012***	***<0.001***	*0.058*

TABLE 4.5. RESULTS OF THE F-TESTS ON THE FIXED EFFECTS OF THE MODELS FITTED FOR EACH MOWING REGIME WITH *CIRSIUM ARVENSE* COVER AS RESPONSE VARIABLE

For each mowing regime, the first line shows the *F*-values and the second line the *P*-values. The *C. arvense* cover was ln(n+1)-transformed. The *F*- and *P*-values of the interaction between the seed mixture and time are from the full model, the *F*- and *P*-values of the main effects are from the reduced model with only main effects.

		mixture	time	mixture: time
Summer mowing	*F*	0.53	**5.66**	1.65
	P	*0.719*	***<0.001***	*0.056*
Autumn mowing	*F*	**5.40**	**17.71**	0.95
	P	***0.006***	***<0.001***	*0.528*
Summer and Autumn mowing	*F*	2.78	1.41	1.03
	P	*0.063*	*0.223*	*0.435*

TABLE 4.6. RESULTS OF THE F-TESTS ON THE FIXED EFFECTS OF THE MODELS FITTED FOR EACH SURVEY WITH SOWN FORB COVER AS RESPONSE VARIABLE

For each survey, the first line shows the F-values and the second line the P-values. The sown forb cover was square root transformed. The *F*- and *P*-values of the interaction between the mowing regime and the seed mixture are from the full model, the *F*- and *P*-values of the main effects are from the reduced model with only main effects if the interaction is not significant.

		mowing	mixture	mowing: mixture
June 2014	*F*	0.06	**2.88**	**3.05**
	P	*0.938*	***0.049***	***0.016***
September 2014	*F*	**11.17**	0.62	1.61
	P	***0.005***	*0.607*	*0.173*
June 2015	*F*	**7.32**	**7.26**	0.57
	P	***0.016***	***<0.001***	*0.752*
September 2015	*F*	**24.23**	2.67	0.49
	P	***<0.001***	*0.060*	*0.813*
June 2016	*F*	**8.16**	**8.15**	0.50
	P	***0.012***	***<0.001***	*0.805*
September 2016	*F*	**6.25**	0.60	0.85
	P	***0.023***	*0.620*	*0.542*

CHAPTER 5

ARE PERENNIAL FLOWER STRIPS A SURROGATE FOR HAY MEADOWS?

5. ARE PERENNIAL FLOWER STRIPS A SURROGATE FOR HAY MEADOWS?

Paper in preparation

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ABSTRACT

Wildflower strips are created to promote insect diversity in agricultural landscapes. While several agri-environment schemes have a reference habitat on which creation and management guidelines can be based, flower strips are considered as a new habitat in the agricultural landscape. While perennial flower strips are sometimes considered as a hay meadow surrogate, it is not clear whether they host the same insect species community. We tested this by comparing five wildflower strips and five hay meadows in the same agricultural landscape. We surveyed plant-pollinator interactions in both habitat types during one year and recorded flower abundance of flowering plant species. Both the flower visiting pollinator community and the flowering plant community differed in their composition between wildflower strips and hay meadows. Flower visitation rate was significantly higher in wildflower strips, while no difference was found for pollinator diversity, plant diversity and flower abundance. We concluded that wildflower strips are not a surrogate of hay meadows for pollinators. We suggest that, if conservation of local hay meadow specialist insect species is a goal of the wildflower strip, seed mixture composition should be adapted to the local meadow plant species for sowing the strips.

Keywords

source populations, agri-environment schemes, mutualistic interaction networks, field margins, biodiversity

INTRODUCTION

To reverse the trend of biodiversity decline in agricultural landscapes, agri-environment schemes, like wildflower strips, can be adopted by farmers (European Commission, 2005). Wildflower strips are mostly created with the aim to promote insect diversity by providing them with food and shelter (Haaland et al., 2011). They have been shown to increase insect abundance and diversity compared to cropped area (Haaland et al., 2011). However, the effect of agri-environment schemes depends on the landscape context (Kleijn et al., 2011; Scheper et al., 2013; Tscharntke et al., 2005). In complex landscapes, the added value of an agri-environment scheme is low and will not considerably increase the biodiversity level (Scheper et al., 2013). Solitary bees, for instance, were only affected by flower strips when they increase the local flower species richness and when the floral resources on the landscape scale were low (Scheper et al., 2015). In very simple landscapes, efficacy of agri-environment schemes is low due to a lack of source populations to colonize the schemes (Tscharntke et al., 2005). In a moderately complex landscape, semi-natural habitats can act as source for insect populations in agri-environment schemes, while these schemes locally improve biodiversity (Scheper et al., 2013; Tscharntke et al., 2005).

Creation and management guidelines for several types of agri-environment schemes can be built on clear targets or knowledge of similar habitats or landscape elements. For an extensive hay meadow scheme, for instance, clear regulations for mowing date and frequency, and manure input, can be derived from similar habitats under nature conservation. Maintenance of hedgerows on the other hand can be based on historical hedgerow management in complex landscapes (European Commission, 2005; Haaland et al., 2011). As semi-natural habitats in the landscape serve as population source for agri-environment schemes (Scheper et al., 2013; Tscharntke et al., 2005), those habitats similar to the habitat created in the scheme may be the main source habitat (Öckinger and Smith, 2007). However, in contrast to other agri-environment schemes, wildflower strips are a rather new habitat in the agricultural landscape (Haaland et al., 2011). Therefore, it is not clear by which habitat type their creation and management can be inspired. As wildflower strips can simultaneously serve to promote pollination services, species diversity and conservation of habitat specialists (Korpela et al., 2013), adapting their design and management to similar semi-naturel habitats could increase their ability to promote species diversity, habitat specialists and ecosystem services. Perennial flower strips have a permanent vegetation and can host local insect populations that may be less dependent on continuous population sources (Korpela et al., 2013). In some regions, like Wallonia (Belgium) or the UK, perennial wildflower strips are created by sowing seed mixtures containing grassland species (Ecosem, 2017b; Emorsgate Seeds, 2017; Chapter 2) and are managed by mowing, resulting in a meadow-like vegetation (Haaland et al., 2011). While perennial flower strips are often smaller in size than hay meadows, with their meadow-like vegetation with grasses and herbaceous species and their management by mowing, they can be expected to support an insect community similar to the one in hay meadows. However, field studies comparing the insect community of these habitats are scarce. In their study in Switzerland, Haaland and Bersier (2011) found that the butterfly species community in perennial flower strips was not a subset of the butterfly community in extensive meadows. Furthermore, the interactions between insects and their food ressources, e.g. plant-pollinator interaction networks, can deliver information about the ecosystem functioning of wildflower strips and hay meadows and are important to include in conservation planning and monitoring (Tylianakis et al., 2010). However, research comparing plant-pollinator networks in wildflower strips and in their potential surrogate habitat is lacking.

Therefore, we compared five perennial wildflower strips with five hay meadows in the same agricultural landscape for their flowering plant community and their flower-visiting insect community. We hypothesized that both habitats have a similar pollinator and plant community and flower visitation rate.

MATERIALS AND METHODS

Study site

The experiment was conducted in the intensive agricultural landscape of the Natural Park "Parc Naturel de la Burdinale et de la Mehaigne" in the northern part of Wallonia, Belgium (Parc Naturel de la Burdinale et de la Mehaigne, 2017). In this Natural Park, agri-environment schemes are adopted by farmers. We selected five perennial wildflower strips (WFS) under the MC8c scheme (Natagriwal asbl, 2017a) and five hay meadows (HM) under the MC4 scheme (Natagriwal asbl, 2017b; Piqueray et al., 2016). WFSs and HMs were managed by mowing once or twice a year starting from summer.

Plant-pollinator interaction surveys

To survey plant-pollinator networks, a 20x2m transect was put in each WFS and each HM. Because one WFS consisted of two parts and one HM had a heterogeneous vegetation, the transect in these two cases was split in two parts of 10m to cover the heterogeneity. When a WFS or HM was mown with refuge strip, the transect was translocated to the refuge strip. The transects were visited in total four times in May, June, July and September 2015 with at least 3 weeks interval and during time and weather conditions favorable for insect activity (between 10 a.m. and 17 a.m., days with no rain, maximum daily temperature >16°C for sunny days or >18°C for cloudy days, maximum 4 Bft wind speed). During a transect visit, all species with at least one open flower unit were listed. A flower unit was defined as a set of flower heads for which a pollinator would rather walk than fly between (e.g. Gibson et al., 2006; Woodcock et al., 2014). After this, the plant-pollinator interactions were surveyed twice, once in the morning, once in the afternoon, by walking the transect for each flowering plant species separately. This facilitated efficient insect specimen collection per plant species. During the transect walks, every flower unit received an equal observation time, being ca. 2 seconds. Each flower visitor making physical contact with a flower unit of the plant species and looking for floral rewards, was recorded. Unidentified individuals were collected for identification in the laboratory. Bees (Hymenoptera: Apoidea: Apiformes), syrphid flies, dagger flies (Diptera: Empididae), butterflies and moths (Lepidoptera), digger wasps (Hymenoptera: Sphecinae), and soldier flies (Diptera: Stratiomyidae) were identified to species level if possible. The genus *Spaerophoria* (Diptera: Syrphidae) was not identified to species level. *Bombus terrestris* (Hymenoptera: Apidae) and *Bombus lucorum* (Hymenoptera: Apidae) were grouped to the complex *Bombus terrestris/lucorum*. *Cheilosia carbonaria* (Diptera: Syrphidae) and *Cheilosia cynocephali* (Diptera: Syrphidae) were grouped to *Cheilosia carbonaria/cynocephali*. Beetles (Coleoptera) were identified to species or morphospecies level. Sawflies (Hymenoptera: Symphyta), bugs (Hemiptera), flies (Diptera) other than syrphids, dagger flies and soldier flies, and wasps (Hymenoptera: Apocrita) other than digger wasps, were not identified and grouped to Symphyta, Hemiptera, Diptera and Apocrita, respectively.

During each survey, the flower abundance was monitored in three flower abundance quadrats of 0.5m*2m within the transects at fixed distances (5-5.5m, 10-10.5m and 15-15.5m, four quadrats for transects split in two at 3-3.5m, 7-7.5m, 13-13.5m and 17-17.5m). For each flowering plant species in the quadrats, the number of open flower units was counted.

Data analysis

Plant-pollinator interactions of the four surveys were pooled to one network per transect, resulting in five WFS and five HM networks. Flower abundances of the three or four quadrats per transect were averaged per transect and subsequently averaged over the four surveys to obtain an average flower abundance per m^2 for each species in each WFS and HM.

Analyses were performed in R (R Core Team, 2013). Based on the flower visitor species assemblages and their visitation rates (number of interactions), the WFSs and HMs were ordinated with Principal Coordinate Analysis based on Bray-Curtis distance to compare the species composition of both habitat types (functions 'cmdscale', 'ordiplot' and 'ordiellipse' of 'vegan' package (Oksanen et al., 2015)). The same was done to compare the plant species composition based on the recorded flower abundance. Indicator Species Analysis (Dufrêne and Legendre, 1997) was performed on plant and pollinator community in order to obtain indicator species for both habitats (function 'indval' from 'labdsv' package (Roberts, 2013).

The number of visits of each pollinator species (ln(n+1) transformed), the pollinator species richness and Shannon evenness and the visitation rate were compared over both habitat types with Student t-tests (function 't.test' from 'stats'-package (R Core Team, 2013)). Also the flower species richness and flower abundance (ln(n+1) transformed), obtained from the flower abundance monitoring, and the species richness of visited flowers in the networks were compered between both habitats using Student t-tests. Mean values are given with standard error of the mean.

RESULTS

In total, 54 pollinator taxa were found involved in 602 visits of 24 flower species. Flower abundance monitoring resulted in 25 flowering plant species. Figure 5.1 and Figure 5.2 show the plant-pollinator networks in the HM and WFS transects respectively. Two HM transects contained no flowering plants anymore in July and September, as did two WFS transects in September. Very few plant pollinator interactions were observed in these two HM transects (one and four interactions in total in HM1 and HM2 respectively). Table 5.1 and Table 5.2 show the occurrence of respectively pollinator and flowering plant species in the HM and WFS transects. The habitats had 18 out of 54 pollinator taxa (33%) and five out of 25 plant taxa (20%) in common (three out of 24 (13%) visited plant taxa). However, only three out of 116 observed unique interaction pairs (3%; *Centaurea jacea* with *Bombus lapidarius*, *C. jacea* with Hemiptera, and *Cirsium arvense* with Diptera) were found in both habitat types.

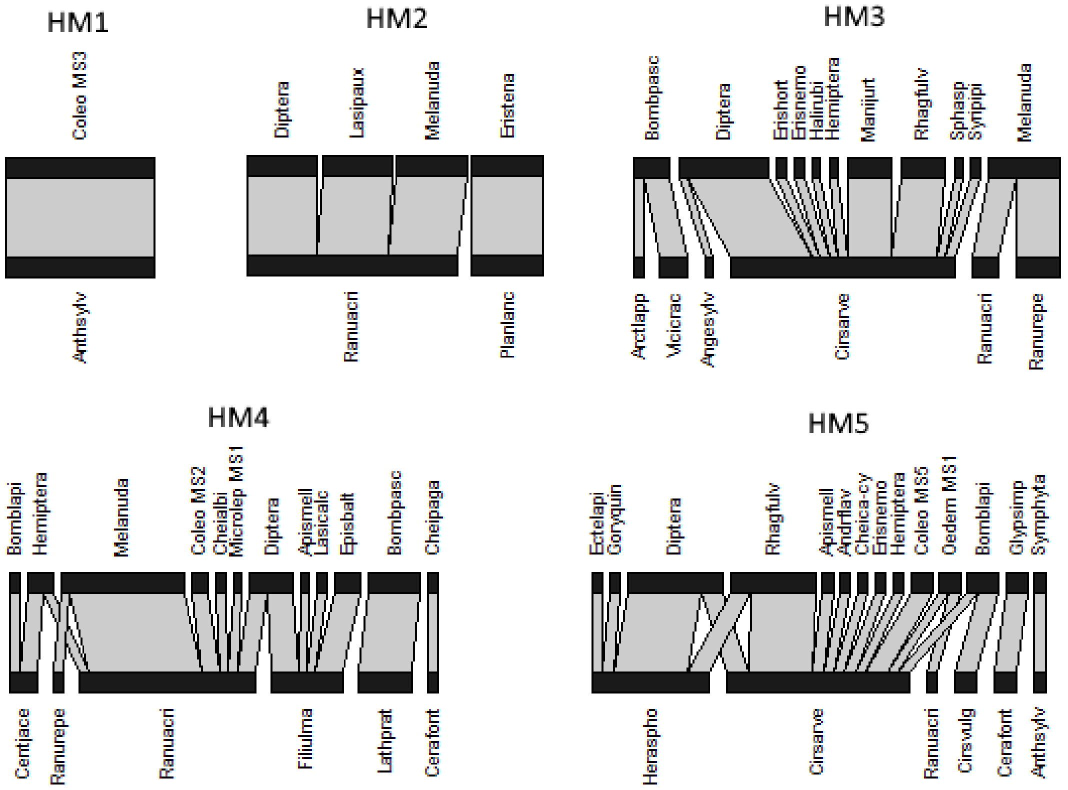

FIGURE 5.1. PLANT-POLLINATOR NETWORKS IN THE HAY MEADOWS

The top of each network graph shows the pollinator species and the bottom the plant species. The width of the parallelograms linking the species is proportional to the number of interactions of the link within the network. Full species names can be found in Table 5.1 and Table 5.2.

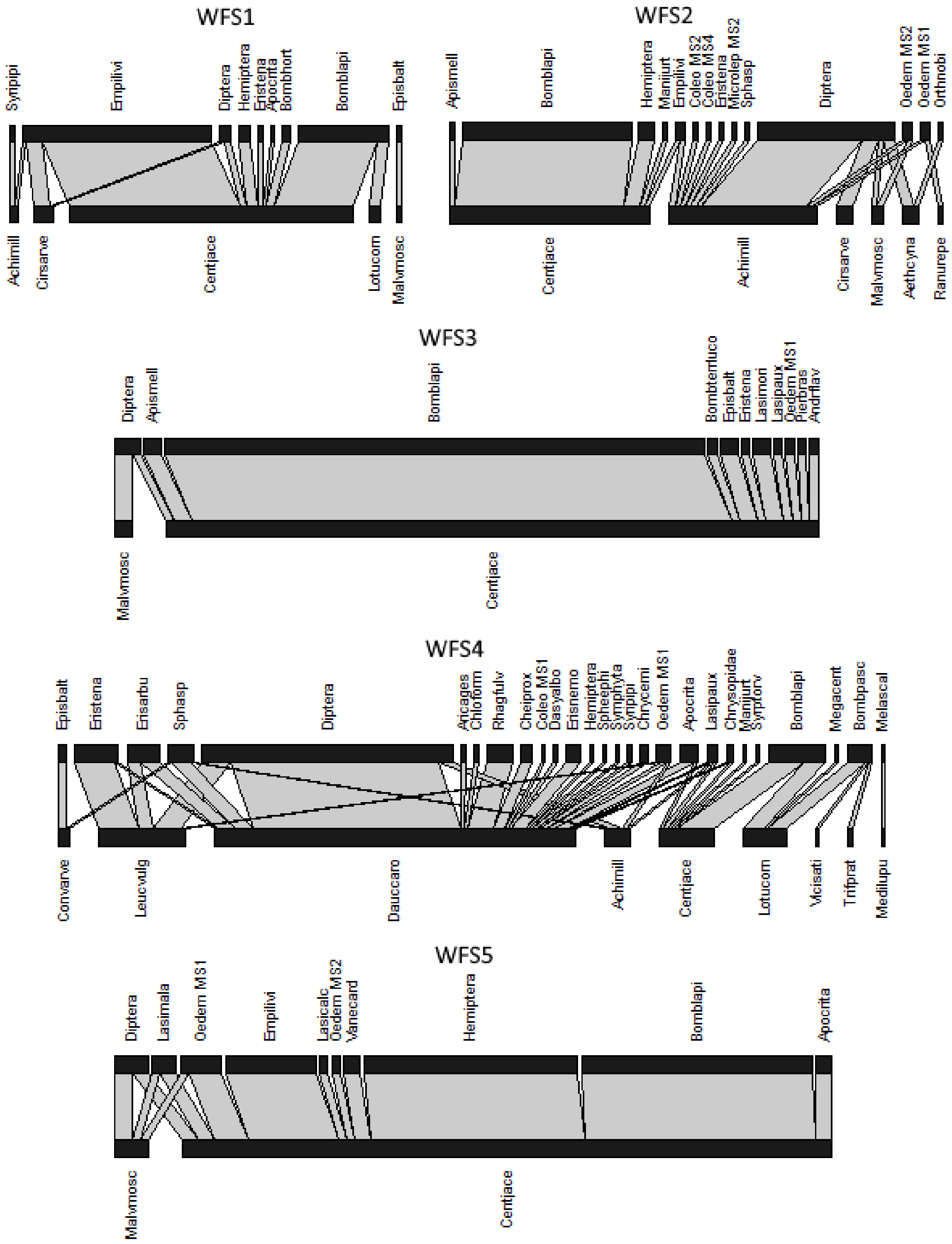

FIGURE 5.2. PLANT-POLLINATOR NETWORKS IN THE WILDFLOWER STRIPS

The top of each network graph shows the pollinator species and the bottom the plant species. The width of the parallelograms linking the species is proportional to the number of interactions of the link within the network. Full species names can be found in Table 5.1 and Table 5.2.

TABLE 5.1. POLLINATOR SPECIES OCCURRENCE IN THE TWO HABITATS

Species are grouped according to their occurrence in the hay meadows (HM) and wildflower strips (WFS). The columns 'HM' and 'WFS' show the mean (± standard error) number of visits for each species in the HM and WFS networks.

	Species	**Order**	**HM**	**WFS**
Species occurring in both habitats	*Andrena flavipes*	Hymenoptera	0.2±0.4	0.2±0.4
	Apis mellifera	Hymenoptera	0.4±0.5	0.6±0.9
	Bombus lapidarius	Hymenoptera	0.8±1.3	32.4±17.6
	Bombus pascuorum	Hymenoptera	2.0±2.8	1.4±3.1
	Coleoptera morphospecies 2	Coleoptera	0.4±0.9	0.2±0.4
	Diptera	Diptera	5.0±4.5	21.2±29
	Episyrphus balteatus	Diptera	0.6±1.3	1.0±1.0
	Eristalis nemorum	Diptera	0.4±0.5	0.8±1.8
	Eristalis tenax	Diptera	0.2±0.4	3.0±5.0
	Hemiptera	Hemiptera	1.0±1.2	6.6±10.9
	Lasioglossum calceatum	Hymenoptera	0.2±0.4	0.2±0.4
	Lasioglossum pauxillum	Hymenoptera	0.2±0.4	0.8±1.3
	Maniola jurtina	Lepidoptera	1.0±2.2	0.4±0.5
	Oedemera morphospecies 1	Coleoptera	0.4±0.9	2.4±2.1
	Rhagonycha fulva	Coleoptera	2.6±3.7	1.4±3.1
	Sphaerophoria sp.	Diptera	0.2±0.4	1.6±3.0
	Symphyta	Hymenoptera	0.2±0.4	0.2±0.4
	Syritta pipiens	Diptera	0.2±0.4	0.4±0.5
Species occurring in HM only	*Cheilosia albitarsis*	Diptera	0.2±0.4	-
	Cheilosia carbonaria/cynocephala	Diptera	0.2±0.4	-
	Cheilosia pagana	Diptera	0.2±0.4	-
	Coleoptera morphospecies 3	Coleoptera	0.2±0.4	-
	Coleoptera morphospecies 5	Coleoptera	0.4±0.9	-
	Ectemnius lapidarius	Hymenoptera	0.2±0.4	-
	Eristalis horticola	Diptera	0.2±0.4	-
	Glyphipterix simpliciella	Lepidoptera	0.4±0.9	-
	Gorytes quinquecinctus	Hymenoptera	0.2±0.4	-
	Halictus rubicundus	Hymenoptera	0.2±0.4	-
	Melanogaster nuda	Diptera	4.6±6.2	-
	Microlepidoptera morphospecies 1	Lepidoptera	0.2±0.4	-

TABLE 5.1 (CONTINUED). POLLINATOR SPECIES OCCURRENCE IN THE TWO HABITATS

	Species	**Order**	**HM**	**WFS**
Species occurring in WFS only	Apocrita	Hymenoptera	-	1.6±2.1
	Aricia agestis	Lepidoptera	-	0.2±0.4
	Bombus hortorum	Hymenoptera	-	0.4±0.9
	Bombus terrestris/lucorum	Hymenoptera	-	0.2±0.4
	Cheilosia proxima	Diptera	-	0.6±1.3
	Chloromyia formosa	Diptera	-	0.2±0.4
	Chrysogaster cemiteriorum	Diptera	-	0.4±0.9
	Chrysopidae	Chrysopidae	-	0.4±0.9
	Coleoptera morphospecies 1	Coleoptera	-	0.2±0.4
	Coleoptera morphospecies 4	Coleoptera	-	0.2±0.4
	Dasysyrphus albostriatus	Diptera	-	0.2±0.4
	Empis livida	Diptera	-	12.6±21.4
	Eristalis arbustorum	Diptera	-	1.8±4.0
	Lasioglossum malachurum	Hymenoptera	-	0.6±1.3
	Lasioglossum morio	Hymenoptera	-	0.4±0.9
	Megachile cenctuncularis	Hymenoptera	-	0.2±0.4
	Melanostoma scalare	Diptera	-	0.2±0.4
	Microlepidoptera morphospecies 2	Lepidoptera	-	0.2±0.4
	Oedemera morphospecies 2	Coleoptera	-	0.6±0.9
	Orthonevra nobilis	Diptera	-	0.2±0.4
	Pieris brassicae	Lepidoptera	-	0.2±0.4
	Sphecodes ephippius	Hymenoptera	-	0.2±0.4
	Syrphus torvus	Diptera	-	0.2±0.4
	Vanessa cardui	Lepidoptera	-	0.4±0.9

Figure 5.3 shows the ordinations of the flowering plant and flower-visiting pollinator communities. First and second ordination axes explained 27.3% and 16.2% of the variation of the flowering plant community composition and 27.9% and 21.8% of the variation of the pollinator community composition. The ordination based on the flowering plant community composition showed that WFSs had a distinct place from HMs along the first ordination axis (Figure 5.3a). The ordination based on the pollinator community composition shows an even more explicit distinction between both habitats (Figure 5.3b). Furthermore, the flower plant composition shows a larger variability among WFS transects than among HM transects along the second ordination axis (Figure 5.3a). The opposite is true for the pollinator species composition, which is more variable among HM than the WFS transects (Figure 5.3b). Species scores on the ordination plots show that several species are associated to specific transects, both for flowering plants and for pollinators. However, only one plant species (*Centaurea*

jacea) and one pollinator species (*Bombus lapidarius*) were obtained as significant indicator species for habitat type from the Indicator Species Analysis. They were both indicator species for the WFS habitat (*B. lapidarius*: *IV*=0.976, *P*=0.010; *C. jacea*: *IV*=0.996, *P*=0.008).

Similarly, only for the log-transformed number of flower visits of *Bombus lapidarius* (Linnaeus 1758; Hymenoptera: Apidae), a significant difference was found between WFSs and HMs (mean log-transformed number of visits in WFSs: 3.41±0.21, and in HMs: 0.42±0.28; *t*=8.55, *P*<0.001). The same goes for plant species, where only the log-transformed flower abundance of *Centaurea jacea* L. was significantly different between WFSs and HMs (mean log-transformed abundance in WFSs: 2.88±0.54, and in HM: 0.08±0.08; *t*=5.10, *P*<0.001).

TABLE 5.2. POLLINATOR SPECIES OCCURRENCE IN THE TWO HABITATS

Species are grouped according to their occurrence in the hay meadows (HM) and wildflower strips (WFS). The columns 'HM' and 'WFS' show the mean (± standard error) number of visits for each species in the HM and WFS networks.

	Species	**Family**	**HM**	**WFS**
Species occurring in both habitats	*Centaurea jacea*	Asteraceae	0.1±0.2	27.8±25.6
	Cerastium fontanum	Caryophyllaceae	2.3±2.6	0.2±0.4
	Medicago lupulina	Fabaceae	0.2±0.4	31.3±68.2
	Plantago lanceolata	Plantaginaceae	5.1±11.5	0.3±0.7
	Vicia sativa	Fabaceae	10.1±9.0	1.3±1.7
Species occurring in HM only	*Angelica sylvestris*	Apiaceae	0.1±0.1	-
	Anthriscus sylvestris	Apiaceae	2.6±4.3	-
	Cerastium glomeratum	Caryophyllaceae	7.7±17.3	-
	Cirsium arvense	Asteraceae	1.1±1.6	-
	Filipendula ulmaria	Rosaceae	1.3±2.8	-
	Galeopsis tetrahit	Lamiaceae	0.1±0.2	-
	Geranium dissectum	Geraniaceae	1.3±1.6	-
	Lathyrus pratensis	Fabaceae	9.5±20.4	-
	Ranunculus acris	Ranunculaceae	7.1±13.1	-
	Ranunculus repens	Ranunculaceae	0.5±0.8	-
	Stellaria graminea	Caryophyllaceae	0.3±0.7	-
Species occurring in WFS only	*Achillea millefolium*	Asteraceae	-	11.0±22.3
	Crepis capillaris	Asteraceae	-	0.1±0.1
	Daucus carota	Apiaceae	-	2.6±5.8
	Leucanthemum vulgare	Asteraceae	-	40.2±89.9
	Lotus corniculatus	Fabaceae	-	76.2±124.4
	Malva moschata	Malvaceae	-	2.4±3.5
	Senecio jacobaea	Asteraceae	-	0.1±0.1
	Silene latifolia	Caryophyllaceae	-	0.6±1.0
	Trifolium pratense	Fabaceae	-	0.3±0.7

Flower visitation rate was significantly higher in WFSs than in HMs (Table 5.3). No difference was found for pollinator species richness and evenness or for flower abundance, flower species richness and visited flower species richness.

DISCUSSION

WFSs and HMs were compared for their pollinator and flowering plant community composition. This comparison showed that WFSs were not a surrogate habitat of HMs. The WFSs attracted a different pollinator community than HMs. This is consistent with the conclusions of Haaland and Bersier (2011) on butterfly communities in WFSs and HMs. While the plant species composition of WFS seed mixtures is based on species occurring in grasslands, our results showed also a difference in species composition of flowering plants between WFSs and HMs. This could be an explanation of the difference in pollinator community composition. Both different plant and pollinator communities confirm that WFSs may be considered as a new habitat rather than a restored habitat, even if their creation and management may be inspired from HMs (Haaland et al., 2011). Furthermore, while the plant-pollinator networks in both habitat types had 33% of their pollinator species and 13% of their plant species in common, this was only true for 3% of the unique interaction pairs. This suggests that common pollinator species had a different diet in both habitat types, while common plant species had a different pollinator guild. Also, the plant community composition was found to be more variable among WFSs than among HMs, while the community composition of flower visitors varied more among HMs and was more similar among WFSs. A possible explanation is that the same species pool of generalist pollinators present in the agricultural landscape colonized WFSs, while HMs contain another set of, more specialist, pollinator species, that varies among HM’s due to other differences in environmental conditions that don’t play for the generalist species.

While WFSs and HMs were not significantly different in their flower abundance and diversity, the visitation rate by pollinators was found to be lower in HMs. This suggests that either the different plant community composition, either other landscape or environmental factors have influenced the visitation rate. WFSs may have contained more attractive plant species, like *C. jacea*, which was more abundant in WFSs and almost not found in HMs. This plant species was already found to

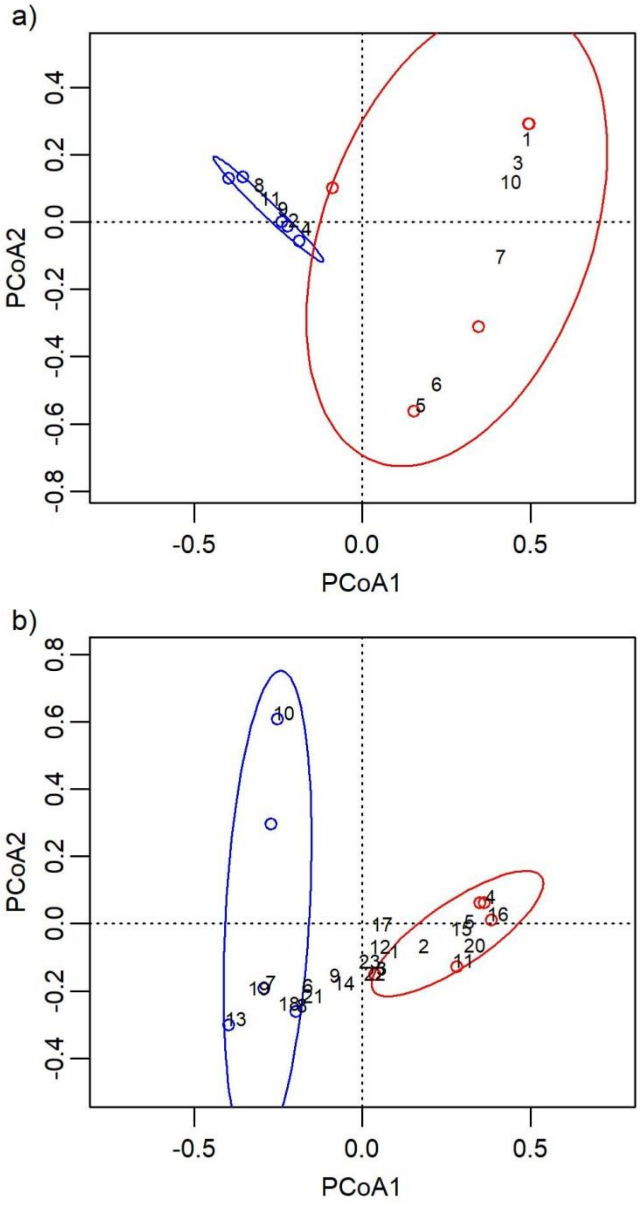

FIGURE 5.3. PRINCIPAL COORDINATE ANALYSIS ORDINATIONS OF THE FIVE WILDFLOWER STRIPS (RED CIRCLES) AND THE FIVE HAY MEADOWS (BLUE CIRCLES)

a) shows the ordination based on the flowering plant species composition and their flower abundance and b) the ordination based on the flower visiting pollinator community composition. Ellipses show the 80% confidence interval of the locations grouped by habitat. Species scores are represented with numbers. For (a): 1:, *Achillea millefolium*, 2: *Angelica sylvestris*, *Anthriscus sylvestris*, *Cerastium glomeratum*, *Filipendula ulmaria*, *Galeopsis tetrahit*, *Geranium dissectum*, *Lathyrus pratensis*, *Ranunculus repens*, *Stellaria graminea*, 3: *Centaurea jacea*, 4: *Cerastium fontanum*, *Cirsium arvense*, 5: *Crepis capillaris*, *Daucus carota*, *Leucanthemum vulgare*, *Medicago lupulina*, *Senecio jacobaea*, *Trifolium pretense*, 6: *Lotus corniculatus*, 7: *Malva moschata*, 8: *Plantago lanceolata*, 9: *Ranunculus acris*, 10: *Silene latifolia*, 11: *Vicia sativa*. For (b): 1: *Andrena flavipes*, *Apis mellifera*, *Eristalis tenax*, 2: Apocrita, *Oedemera* MS (morphospecies) 1, 3: *Aricia agestis*, *Cheilosia proxima*, *Chloromyia formosa*, *Chrysogaster cemiteriorum*, Chrysopidae, Coleoptera MS 1, *Dasysyrphus albostriatus*, Diptera, *Eristalis arbustorum*, *Megachile cenctuncularis*, *Melanostoma scalare*, *Sphecodes ephippius*, *Syrphus torvus*, 4: *Bombus hortorum*, *Bombus terrestris/lucorum*, *Empis livida*, *Lasioglossum morio*, *Pieris brassicae*, 5: *Bombus lapidarius*, 6: *Bombus pascuorum*, 7: *Cheilosia albitarsis*, *Cheilosia pagana*, Microlepidoptera MS 1, 8: *Cheilosia carbonaria/ cynocephali*, Coleoptera MS 5, *Ectemnius lapidarius*, *Glyphipterix simpliciella*, *Gorytes quinquecinctus*, 9: Coleoptera MS 2, 10: Coleoptera MS 3, 11: Coleoptera MS 4, Microlepidoptera MS 2, *Orthonevra nobilis*, 12: *Episyrphus balteatus*, *Lasioglossum calceatum*, 13: *Eristalis horticola*, *Halictus rubicundus*, 14: *Eristalis nemorum*, Symphyta, 15: Hemiptera, 16: *Lasioglossum malachurum*, *Vanessa cardui*, 17: *Lasioglossum pauxillum*, 18: *Maniola jurtina*, 19: *Melanogaster nuda*, 20: *Oedemera* MS 2, 21: *Rhagonycha fulva*, 22: *Sphaerophoria sp.*, 23: *Syritta pipiens*.

be abundant in WFSs (Korpela et al., 2013) and to be a key species in plant-pollinator networks (Hegland and Totland, 2005; Korpela et al., 2013) and also took a key position in the networks in WFSs in our study. Attractive key plant species have been observed to attract large numbers of pollinators in WFSs (Balzan et al., 2014, 2016; Chapter 4) and grasslands (Ebeling et al., 2008) and thus to take a key position in plant-pollinator networks (Chapter 4). Furthermore, the bumblebee *B. lapidarius*, and bumblebees in general, have been shown to have a flower preference for, among others, *C. jacea* (Fründ et al., 2010; Haaland and Gyllin, 2010), which may have caused its larger number of visits in WFSs. Also, the potential presence of mass-flowering crops close to the WFSs might be an explanation. Indeed, mass-flowering crops, like oilseed rape, are known to increase bumblebee abundance and colony size in agricultural landscapes (Westphal et al., 2003, 2009). However, the visitation rate excluding the visits of *B. lapidarius* was still significantly higher in WFSs than in HMs. Another explanation would be a concentration effect of pollinators to WFSs. Indeed, in structurally simple landscapes with few patches providing flower resources, WFSs can attract a larger abundance and diversity of pollinators (Carvell et al., 2011; Haenke et al., 2009).

The low flower density in some of the HMs, especially in summer and autumn, suggests that the vegetation composition is still not optimal for pollinator conservation. This can be due to a history of intensive management. For such grasslands, it could be opted to apply a more frequent mowing regime during several years to improve vegetation composition towards a more diverse and flower rich one before switching to a management with only one or two cuts. We also suggest shifting the location of the refuge strip each year, to prevent vegetation succession.

TABLE 5.3. MEAN ± STANDARD ERROR OF THE DIFFERENT POLLINATOR AND PLANT COMMUNITY RESPONSES IN WILDFLOWER STRIPS AND HAY MEADOWS AND RESULTS OF THE STUDENT-T TEST TO COMPARE BOTH HABITATS

Response variable	**Mean WFS**	**Mean HM**	***t***	***P***
Pollinator species richness	11.4±2.9	6.8±2.0	1.32	0.224
Pollinator evenness	0.39±0.06	0.38±0.10	0.03	0.973
Visitation rate	**67.2±7.9**	**17.0±6.3**	**4.98**	**0.001**
Ln(Flower abundance+1)	4.42±0.73	3.72±0.30	0.92	0.385
Flower species richness	5.4±1.7	5.8±1.2	-0.19	0.855
Visited flower species richness	4.8±1.3	4.2±1.1	0.35	0.737

As our study showed that perennial WFSs are not a HM surrogate habitat for pollinators, further research is needed to test if this is true for other functional groups as well. Also, a landscape-scale comparison of pollinator species composition in several agricultural and semi-natural habitats could identify other habitats that host a similar insect community as perennial flower strips. Furthermore, the similar levels of pollinator species diversity in both habitats, and the higher level of visitation rate in WFSs, indicate the potential of WFSs to both promote pollinator diversity and pollination services, as shown by Korpela et al. (2013). As these two goals of WFSs can be combined with the conservation of local habitat specialists (Korpela et al., 2013), it could be tested whether protection of local HM pollinator species can be targeted in perennial WFSs by adapting the plant species composition of the WFSs to the local species composition of the HMs instead of using a uniform seed mixture for the whole agri-environment scheme administrative region.

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CHAPTER 6

GENERAL DISCUSSION

6. GENERAL DISCUSSION

In the previous chapters of this PhD thesis, we reported on the different studies that we conducted to test methods for flower strip creation and management to maximize pollinator support and minimize weed infestation, the general objective of this PhD project. In this chapter, some key findings of these studies are discussed in the context of existing knowledge in the literature. Furthermore, some research perspectives and implications for flower strips creation and management and for policy are derived from the results, as well as the general conclusions of this PhD thesis.

SEED MIXTURES: WHAT YOU SEED IS WHAT YOU GET?

In nature conservation, habitat restauration is usually counting on natural regeneration of species from the soil seed bank or recolonization from neighboring habitat patches (Bakker et al., 1996). Only in certain cases, e.g., when species disappeared from the seed bank and from the surrounding landscape, or for the creation of novel or analogous ecosystems, seeds from desired species are sown (Hölzel et al., 2012). In flower strip creation, the use of flower mixtures is more common (Haaland et al., 2011).

Our literature review (section 1.2) showed that, to create a flower strip, sowing a seed mixture is in general a better way to prevent colonization by noxious weeds than spontaneous regeneration. While in nature conservation areas, the soil seed bank can contain a lot of desired species (Bakker et al., 1996), the soils of arable fields under years of intensive management may contain mostly fast colonizing species favored by soil disturbance (e.g. Hutchings and Booth, 1996). Some of these species are considered as harmful by farmers and should be treated by law obligation in certain countries (e.g. Agentschap Natuur & Bos, 2017; Secrétariat général du gouvernement, 2017; The National Archive, 2017). Therefore, the desired species are often directly sown in the strip (section 1.2). In the case of perennial strips, the species composition of the seed mixtures is sometimes inspired by hay meadows (Haaland et al., 2011). As for annual and biennial strips, sown species may be arable flora typical for unsprayed cropping area, or other annuals, sometimes not indigenous (e.g. Tschumi et al., 2015).

Seed mixtures can contain grasses, forbs, or both (Haaland et al., 2011). When sowing only grasses to create a perennial flower strip, flower species are expected to colonize the strip spontaneously. While sowing grasses can already reduce weed pressure (Cordeau et al., 2012; Marshall, 2009), the additional effect of adding forbs to the seed mixture remained unexplored. We showed that adding forbs to the mixture could reduce the cover of *Cirsium arvense* (L.) Scop., a common noxious weed species, and that higher cover of forbs resulted in lower cover of this weed species (Chapter 4). Most of the other spontaneous ruderal plant species, while being abundant in the experimental flower strips during the first year after sowing (Chapters 2, 3 and 4), tended to disappear or to persist at relatively low levels (Chapters 3 and 4). Indeed, due to the lack of soil disturbance and the mowing regime, perennial competitive species are promoted (e.g. Maron and Jefferies, 2001; Westbury et al., 2008).

Furthermore, to optimize the forb species composition for pollinator support, different seed mixtures were tested in experimental flower strips (Chapters 2 and 3). Four mixtures with increasing level of plant functional diversity were composed, and their establishment monitored after sowing. From the experiments we could conclude that it was possible to create contrasting levels of functional diversity in the field (Chapter 2). The lowest and highest levels of functional diversity were significantly different in the first two years (Chapters 2 and 3). However, the intermediate levels did not differ from the extreme levels in the first year after sowing (Chapter 2) and only from the highest level in the second year after sowing (Chapter 3). This shows the variability of realized functional diversity, compared to the desired level sown. Different factors can influence the vegetation composition of a flower strip after sowing and were identified in our study. Sown species may germinate or not, or may appear in higher or lower abundance than desired, changing the functional trait composition. Spontaneous species may settle and bring additional or redundant trait values (Chapter 2; De Cauwer et al., 2005; Lepŝ et al., 2007; Münzbergová and Herben, 2005).

Complementary to the large flower strips in the WC-field (see section 1.3 and Figure 1.6) that were studied in Chapters 2 and 3, the WM-field (section 1.3, Figure 1.6 and Chapter 4 for the detailed field setup) provided the opportunity to follow the vegetation development of the sown mixtures during three years after sowing. As not all sown species germinated or appeared in uneven abundance (Chapters 2), it is interesting to know for all sown species how they perform on a longer term than the first year after sowing. Figure 6.1 shows the development over three years after sowing for the different sown forb species in each mixture. *Anthriscus sylvestris*, *Heracleum sphondylium*, and *Lythrum salicaria* did not appear at all in the vegetation surveys, as it was also the case in the WC-field (Chapter 2). In total, the cover of sown forb species was on average above 20% in all four mixtures (Figure 6.1), while their seed mass in the seed mixtures was only 14% of the total seed mass (3.5 kg/ha forb species, and 21.5 kg/ha grasses; see Chapter 2). None of the sown species found in the vegetation surveys completely disappeared during the three first years after sowing. *Leucanthemum vulgare* was the dominant species in the two mixtures where it was sown, and had strong seasonal effects, with more cover in June than in September. *Hypochaeris radicata* maintained its relativey high cover (on average always above 5%). Also *Achillea millefolium* and *Lotus corniculatus* had a stable cover of, on average, 3% or more. *Galium verum* had a stable, but relatively low cover over the years. As individuals of this species tended to be small, it did not establish a high cover per individual. *Malva moschata* was relatively abundant until June 2015 (cover on average more than 6%), and was lower in the three surveys thereafter. *Medicago lupulina* was present in the first year, had very low cover in the second year and was present again in the third year. *Geranium pyrenaicum* and *Crepis biennis* were only abundant in the first year, while in the following years they had a low to very low cover. *Knautia arvensis* and *Trifolium pratense* showed only from the second to the third year a relatively low cover, while they were not present or had a very low cover in the first year. *Leontodon hispidus*, *Prunella vulgaris* and *Origanum vulgare* had a low to very low cover during all three years (on average 2% or lower). While further sowing trials in other pedoclimatic conditions are needed to make sound conclusions, these results can already suggest some adaptations to the relative sowing densities of the forb species. For *L. vulgare*, it can be suggested to decrease the sowing density, when the aim is to decrease its dominance. For species with low cover, like *G. verum*, *K. arvensis*, *T. pratense*, *L. hispidus*, *P. vulgaris*, and *O. vulgare*, it can be suggested to increase sowing density. Creating seed mixtures with unequal seed mass per forb species, unlike our experimental mixtures (Chapters 2, 3 and 4) is in line with seed mixtures provided by suppliers for agri-environment schemes (e.g. Emorsgate Seeds, 2017). For species that started with a relatively high cover and that decreased over time (*M. moschata, M. lupulina, G. pyrenaicum, C. biennis*), it can be questioned whether the mowing regime is well-adapted, or whether they are poor competitors in later stages of vegetation development. Also factors like seeding date, seeding depth and machinery used, can have influenced germination success of different species, and thus their relative abundance in the established vegetation. As farmers creating flower strips may have different seeding machinery, seeding trials with different seeding conditions as well as sharing practical experiences among farmers may help to finetune these factors.

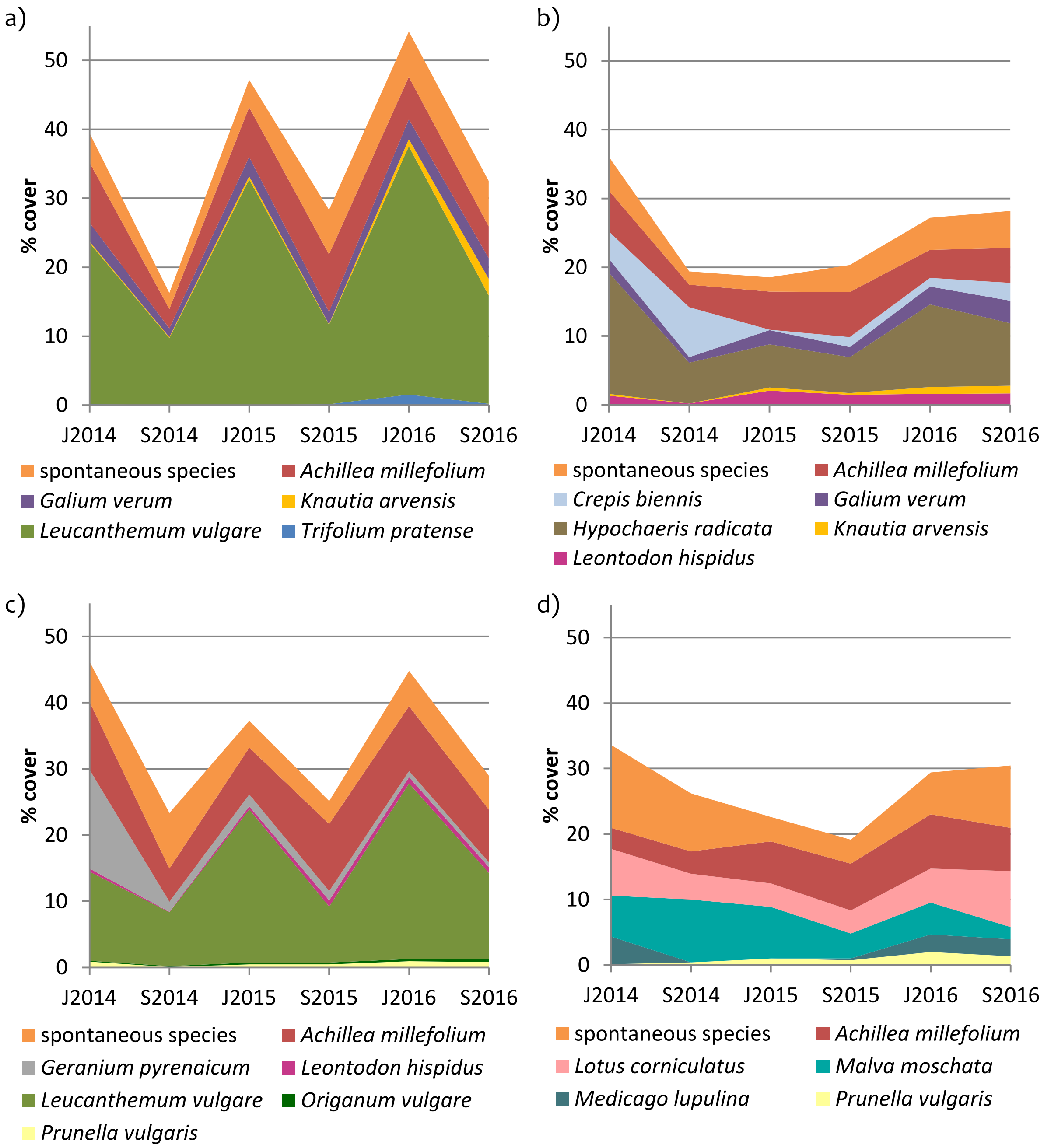

FIGURE 6.1. STACKED AREA CHART OF THE COVER OF SOWN FORB SPECIES IN THE WM FIELD OVER THREE YEARS

The four charts show the mean percentage cover per functional diversity (FD) mixture of the sown forb species in the mixture from June 2014 (J2014) to September 2016 (S2016): (a) the very low FD mixture, (b) the low FD mixture, (c) the high FD mixture, and (d) the very high FD mixture. For information, the cover of spontaneous forb species is shown, including also forb species from other mixtures. Species that are lacking in the charts (*Anthriscus sylvestris*, *Heracleum sphondylium*, *Lythrum salicaria*) did not appear in the vegetation surveys.

Furthermore, bare soil cover could give an idea whether the sowing has resulted in a successful and quick covering of the soil. For the vegetation surveys in the WM-field, the bare soil cover was 0.15±0.54% and 3.9±6.6% respectively in June and September 2014 and was on average less than 2% in the following years (1.4±1.5, 1.4±2.2, 1.8±1.4 and 1.6±1.1 in respectively in June and September 2015 and June and September 2016). These values indicate that already from the first year after sowing, the soil was well covered with vegetation. Sowing densities (25 kg/ha of seeds; 14% forb seeds) are in line with the sowing densities suggested by seed suppliers for perennial flower strips, e.g. 22 kg/ha with 9% forb seeds in the UK (Emorsgate Seeds, 2017) and 30 kg/ha with 15% flowers in Wallonia, Belgium (Ecosem sprl., 2017b).

MOWING FOR SERVICES AND DISSERVICES

Perennial flower strips are either not managed, and ploughed after several years when vegetation succession went too far, either they are managed by mowing (Haaland et al., 2011). Annual mowing with hay removal results in a meadow-like vegetation (Pywell et al., 2002), even if the plant and pollinator species composition might be different from meadows (see above and Chapter 2). Mowing of meadows, formerly aiming to harvest feed for animal husbandry, nowadays also serves for nature conservation purposes (Bakker et al., 2002). By mowing, a more diverse vegetation is created, and nutrients are partly exported by hay removal (e.g. Maron and Jefferies, 2001).

In Chapter 4, we studied whether mowing could be used as a tool to address the weed infestation disservice of flower strips. We observed in our study that adapting timing and frequency of the mowing regime could be used to limit *C. arvense* cover in perennial flower strips. Summer mowing and mowing twice a year resulted in a lower cover from the third year on, and it prevented the species from producing mature flowers. Moreover, these mowing regimes increased the forb cover over time, which can indirectly reduce *C. arvense* cover by increasing competition by forbs (see above and Chapter 4).

The use of the same mixtures in the WM experimental field as in the WC experimental field (see section 1.3) enabled us to test the influence of mowing regime on the realized functional diversity in the four mixtures (data not shown). Mowing regime did not significantly influence realized functional diversity (mixed model with mixture treatment, mowing treatment and time as fixed effects, like in Chapter 5), suggesting that it is possible to use the benefits of certain mowing regimes in flower strips (e.g. limiting weeds, Chapter 4) without disturbing the creation of a desired functional diversity level (Chapter 2). However, mowing can still influence the benefits obtained from a certain functional diversity level (e.g. pollinator support, approach of Chapter 3) by removing the flower resources. Indeed, after mowing, flowering plants take some time to develop new flowers, or stop flowering, while other plant species only start flowering after mowing (e.g. Jantunen et al., 2007). The higher forb cover under summer mowing and mowing in summer and autumn (Chapter 4) indicates already a higher potential of flower resources under these mowing regimes. The monitoring of flower abundance and richness in the WM-field (data not shown, method like C. *arvense* flower abundance monitoring in Chapter 4) enabled us to study the development of flower resources under different mowing regimes over a flowering season. Figure 6.2 shows the development of flower richness and abundance in 2016. Summer mown strips and strips mown in summer and autumn had higher flower richness than autumn mown plots in late June before mowing, while no difference in flower abundance was found. After mowing, summer mown and summer and autumn mown strips showed a second flowering peak in late August, where summer mown strips had more flowers and summer mown and summer and autumn mown strips had more flowering species than autumn mown strips. The autumn mown strips had a higher abundance and richness of flowers the weeks after summer mowing. As summer mowing and mowing twice a year turned out to be the better options to limit the weed disservice, rotational mowing with an autumn mown refuge could be an option to benefit pollinators by bridging the period with fewer flower resources. Rotational mowing has been proven to benefit insects in hay meadows (Buri et al., 2014; Lebeau et al., 2015) and is mandatory in Wallonia (Belgium) for wildflower strips and hay meadows of high biological value (MC8c and MC4 schemes; Natagriwal asbl, 2017a, 2017b).

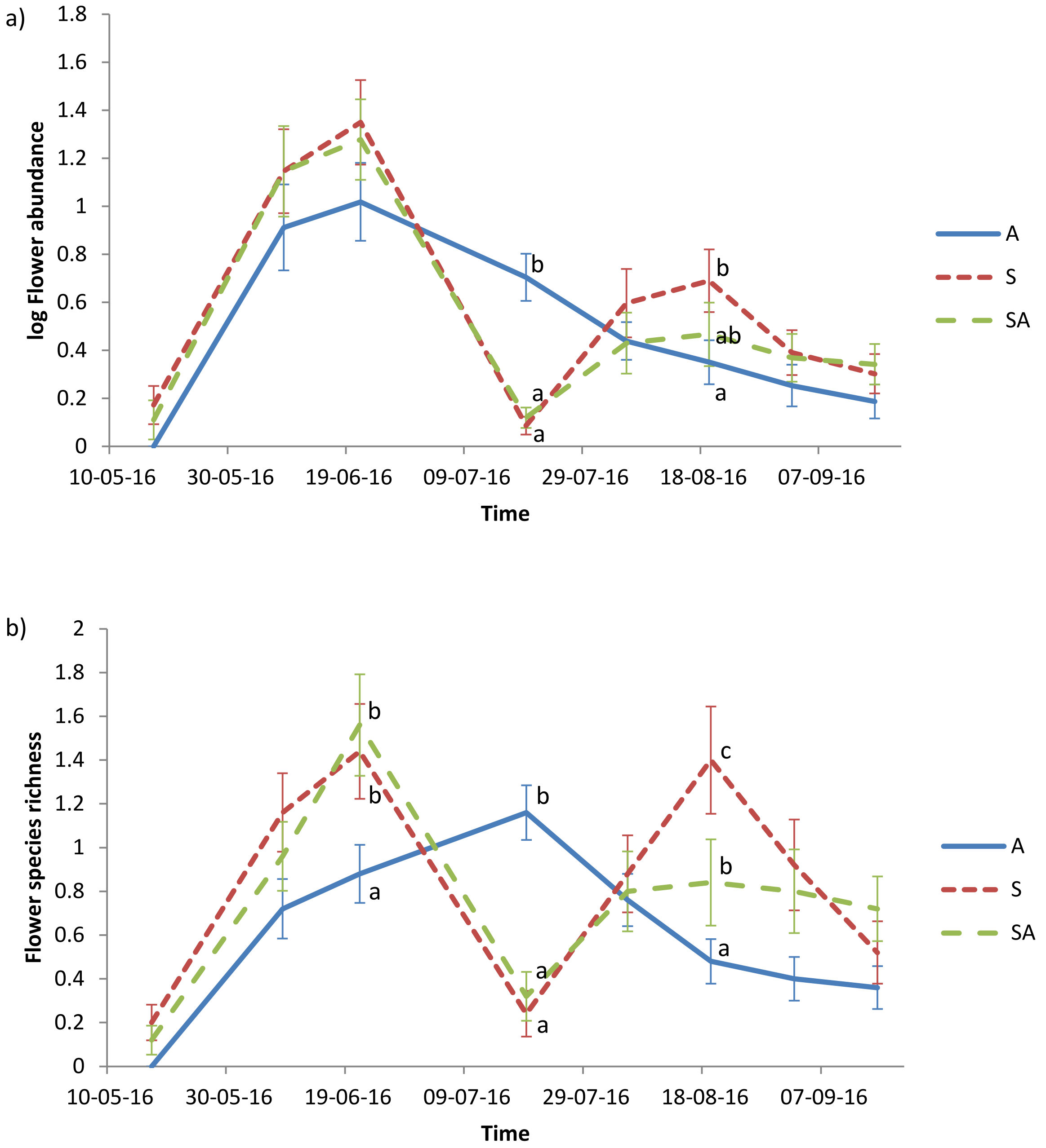

Figure 6.2. Development of (a) log-transformed flower abundance and (b) flower richness during the year 2016 in the WM field (Section 1.3)

Line styles show the mowing regime treatment: autumn mowing (A), summer mowing (S) and mowing both in summer and autumn (SA). Letters show significant post-hoc differences between the mowing regimes for surveys where mowing regime or its interaction with seed mixture was significant in the mixed model. In case of significant interaction, the post-hoc differences were tested for average seed mixture effect, in case of no significant interaction, the interaction effect was first removed from the model. Strips were mown on 29 June and 21 September.

IS FUNCTIONAL DIVERSITY THE KEY OR NOT?

While opinion papers and theoretical studies are proposing functional diversity as key to promote ecosystem functioning and ecosystem services, experimental evidence is rather scarce (Díaz and Cabido, 2001; Hooper et al., 2005). In our study, we created a plant functional diversity gradient (Chapters 2 and 3) to test whether increasing functional diversity can be a tool to promote pollinators in flower strips (Chapter 3). No effect was observed on pollinator species richness and evenness, and increased functional diversity even resulted in a lower visitation rate. We concluded that increasing functional diversity based on several traits, without increasing total flower abundance, was not the key to promote pollinators. It is expected that certain plant species or traits played a more important role than functional plant diversity for the structure of plant-pollinator networks (see further).

Functional traits and functional diversity can be used to make abstraction of the species identity and to treat organisms by their responses to and effects on the environment and other organisms (Díaz et al., 2013). However, studies on functional traits and functional diversity often still start from the species identity and attribute one fixed value per trait to each species. While it is way more time-consuming, real measurements of traits on individuals can provide more insight in intra-species variability of traits (Bolnick et al., 2011). Future research on functional diversity should also try to compare the effect of ‘potential’ versus ‘realized’ functional trait values. For instance, in our experiments, we used horizontal cover as a measure of abundance of plant species and thus the abundance of their functional trait values. However, pollinators can only perceive the floral plant traits when these plants produce flowers, thus future work can try to address the realization of these traits to make a closer link between plant effect traits and pollinator response traits (Lavorel et al., 2013). Furthermore, functional diversity can be described by three independent components: functional richness, functional evenness and functional divergence (Mason et al., 2005; Scheuter et al., 2010; section 1.1). As we only focused on functional divergence in this study (Chapters 2 and 3), by using Rao’s Quadratic Entropy index, future research can try to test the effect of functional richness and functional evenness and try to reveal the relative impact of the three components of functional diversity on plant-pollinator networks and other ecosystem functions.

While functional diversity was not found to be the key to promote pollinators in our study, similar studies in other regions and landscape contexts are needed. The region of Gembloux contains a large proportion of intensive arable fields with few semi-natural habitats or ecological infrastructure. This can result in a poor regional species pool to colonize the experimental flower strips, possibly resulting in a pollinator community mainly consisting of generalists. Pollinator responses to a functional diversity gradient in landscapes with higher structural complexity and more diverse species pools may be different. However, even if the experiment was conducted in a structurally simple landscape region, the experimental field was close to the small nature reserve 'L'Escaille' and a cemetery, which may host a diverse pool of pollinator species. Also the responses of the pollinator feeding niche to the functional diversity suggest that not all species were generalist in their flower choice (Chapter 3).

WILDFLOWER STRIP, THE ORPHAN HABITAT?

To find and evaluate methods to improve wildflower strips, it is useful to know whether a reference habitat exists. The characteristics and management of this reference habitat could serve as a source of inspiration for creation and management of flower strips. While flower strips, unlike many other agri-environment schemes, are in general considered as a new habitat, perennial flower strip creation and management are sometimes inspired by hay meadows (Haaland et al., 2011)

We concluded in Chapter 5, based on the plant-pollinator networks in perennial flower strips and hay meadows, that perennial flower strips were not a surrogate of hay meadows in the studied landscape. Both the flower visitor and flowering plant communities had different composition in the two habitats. Pollinator species richness, flowering plant species richness and flower abundance were not different, but wildflower strips had a higher visitation rate in the plant-pollinator networks than hay meadows.

Similarly, (Haaland and Bersier, 2011) observed different butterfly communities in wildflower strips and extensive meadows. These results give rise to two questions: (1) when perennial flower strips are not a surrogate for hay meadows, is there another habitat that has a similar pollinator community, and (2), do perennial flower strips have to be a hay meadow surrogate, or can they act as a 'new' habitat in the agricultural landscape?

To address the first question, a landscape-scale comparison of pollinator species composition in several agricultural and semi-natural habitats could try to identify which habitats have a similar pollinator community composition as perennial flower strips. This might help to understand the role of these strips compared to other habitats in supporting local habitat specialist pollinator species, diverse pollinator communities, abundant generalist pollinator guilds to provide crop pollination services, or a combination (Ekroos et al., 2014; Kleijn et al., 2015; Korpela et al., 2013). Comparing these habitats for other functional groups, like crop pest natural enemies, could reveal whether they have the same spatial distribution in the landscape as pollinators.

The second question suggests two possible options. For the first option (perennial flower strips have to serve as a hay meadow surrogate), it should be investigated for which reasons perennial flower strips don't have pollinator communities similar to the ones in meadows in certain studies (Chapter 5, Haaland and Bersier, 2011). A potential main reason found in Chapter 5, was the fact that the flowering plant community was different in both habitats. In this case, either the flower strip seed mixture is not containing the local hay meadow species and should be adapted, either the pedoclimatic conditions in both habitats are too different to obtain a similar vegetation. Adapting the seed mixture to local plant communities could be an interesting option to increase the plant and associated pollinator diversity not only at the local (α-diversity) but also at the regional level (β-diversity). This may prevent a homogenization at the regional scale of pollinator communities, which could be expected by using the same seed mixture for all strips at regional scale (Burkle and Alarcón, 2011; Carstensen et al., 2014; Simanonok and Burkle, 2014). For the second option (perennial flower strips don't have to serve as a hay meadow surrogate), perennial flower strips can be considered as a new complementary habitat, increasing landscape and between-field heterogeneity (Benton et al., 2003) and supporting its own species community with the ability to deliver ecosystem services complementary to those delivered by hay meadows.

FLOWER STRIPS AND THE LITERATURE

In section 1.2, we presented the results of a systematic literature review about the pros and cons of flower strips for farmers. Systematically reviewing scientific literature offers an interesting approach to draw general conclusions on topics that have been the subject of many studies, or to reveal research gaps. The latter was the case for our review. While research gaps may exist in scientific literature, this does not implicitly mean that the knowledge does not exist. Firstly, by fixing a search procedure and selection criteria, to proceed systematically, a part of the existing scientific literature is lost. We fixed, for instance, very strict criteria regarding the comparison of flower strip pros or cons to a control situation without a flower strip. Several studies indicating or suggesting a pro or con of flower strips without comparing it to a no-strip control had to be omitted. Also the use of several scientific literature data bases could have yielded more studies. Secondly, a bias towards positive or expected results exists in scientific literature, because negative results are less likely to get published (Dickersin, 1990). Thirdly, for certain questions, a strictly scientific study is less appropriate to find an answer, and reporting results in peer-reviewed literature less relevant. These results may be found in the 'grey literature', for which the inclusion in systematic review is discussed (Conn et al., 2003).

RESEARCH PERSPECTIVES AND IMPLICATIONS FOR MANAGEMENT

Identity effects in mixtures

In Chapter 4, four forb mixtures were compared to a grass-only mixture for their ability to limit noxious weeds. While forb mixtures were in general better to limit *C. arvense* than the grass-only mixture, only two mixtures had a significantly lower *C. arvense* cover than the grass-only mixture. This suggests that some mixtures contained species that were better than others in limiting this weed species. Similarly, in Chapter 3, certain mixtures differed from others in number of pollinator species, pollinator evenness, visitation rate, and other networks metrics. Furthermore, certain traits were correlated with these network metrics. While the functional diversity approach is promising, these results suggest that certain plant species had key combinations of trait values that make them play an important role in ecosystem functioning (also called the 'sampling effect'; Tscharntke et al., 2005), be it competing with weeds or promoting pollinators. Further studies creating a functional diversity gradient should try to vary not only the functional diversity level, but also the mixture species composition over similar levels of functional diversity, to take into account possible species identity effects. Furthermore, key species that structure plant-pollinator networks or that play a key role in competition with weeds, should be identified and included in seed mixtures.

Functional complementarity and redundancy

The results of the experiment in Chapter 4 showed that increasing functional diversity created flower trait values being more different, which was perceived by pollinators, as they had less overlap in their feeding niches (less visited flower species in common). As also the flower visitation rate decreased with increasing functional diversity, this suggests that pollinators might not be able to find sufficient resources per feeding niche when niche overlap is low (due to high functional diversity) and if a restricted number of flowers are available (due to the restricted surface on which the flower resources are provided). This points to a possible trade-off between functional diversity and resource abundance. Increasing functional diversity is focusing on increasing complementary trait values, i.e. filling new parts of the niche space. In a restricted area and species richness level (we kept species richness constant in our experiment, Chapters 2 and 3), this means that species with more redundant functional niches have to be replaced by species with more complementary niches. Some authors already pointed to the importance of redundancy in traits or niches for ecosystem stability (Díaz and Cabido, 2001; Montoya et al., 2012; Tscharntke et al., 2005). Our study suggests that a minimum level of functional redundancy could also be needed to insure that all parts of the functional niche space that are occupied, are represented by a minimal number of individuals.

Thistle management

While our study in Chapter 4 identified methods to treat against *C. arvense*, discussions are raising in some countries as to whether the legal obligation to treat against thistles is still necessary (e.g. Decleer and Leten, 1997). While *C. arvense* is considered as a noxious weed species for agriculture (Tiley, 2010), several studies showed the importance of thistles as nectar resource for pollinators (Carvell et al., 2007; Haaland and Gyllin, 2010; Tiley, 2010; Vray et al., 2017) and natural enemies of crop pests (Tiley, 2010) by providing nectar, pollen and alternative hosts (Landis et al., 2000). As summer mowing is expected to maintain *C. arvense* to a low level, while autumn mowing can lead to an increase in cover (Chapter 5), it should be tested whether the use of summer mowing with an alternating refuge strip, mown in autumn, can keep this thistle species to an acceptable level for farmers, while a part of the plants are allowed to flower in the refuge strip, delivering the important resources for insects.

Tailored strips or multifunctional strips?

Flower strips initially had the intention to support biodiversity, while certain components of this diversity, ‘useful species’ or ‘functional agro-biodiversity’, can deliver regulating and supporting ecosystem services to enhance crop production (Bianchi et al., 2013; Haaland et al., 2011). This fits well in the ecosystem service framework, which states that ecosystems, by their ecological processes and functioning, can provide humans with services (Millenium Ecosystem Assessment, 2005). Recent studies tried to put the focus on the service provision in developing flower strips, resulting in the so-called ‘tailored wildflower strips’ (e.g. Tschumi et al., 2015, 2016). These strips are developed by listing the ‘useful species’ needed to deliver e.g. pest control services to a certain crop that will be sown, and listing the plant species that should be sown to attract these ‘useful species’. This approach reduces a wildflower strip to sowing only the tailored list of species for the time they need to attract the ‘useful’ species, which mostly results in annual or biennial strips that are removed when the crop is harvested. The strips can be included in the crop rotation and reseeded following the requirements of the new crop.

While these tailored strips are expected to enhance service provision and thus the acceptance by farmers (Tschumi et al., 2016), some critics are possible on this tailored strip approach. Firstly, as these strips are not permanent or perennial, they rely on colonization by the desired species from surrounding habitats, as it is not likely that desired species can complete their entire life cycle within the strip rotation time (Haaland and Bersier, 2011). This implies that surrounding habitats have to harbor stable populations of these desired species that are attracted to the crop by tailored strips when they are needed. An alternative could be to increase the density of these habitats, so that crops can directly benefit from the stable populations present.

Secondly, tailored flower strips are focusing on the continuous delivery of high amounts of floral and extra-floral resources only at the time the crop needs the ‘useful’ species to be present (e.g. Tschumi et al., 2016). Many species using these resources also need other resources (shelter, nesting sites etc.) or resources at other periods. Bumblebees, for instance, are dependent on nectar and pollen resources from spring to autumn (Rundlöf et al., 2014; Scheper et al., 2015). Solitary bees on the other hand, may need non-ploughed soil, or hollow stems for nesting (Peeters et al., 2012). Pest predators may need alternative preys or hosts when pests are not present in the crop (Landis et al., 2000). Perennial strip are more likely to provide more of these resources and to provide them at longer term (Bianchi et al., 2013; Haaland and Bersier, 2011).

Thirdly, the focus on desired species only, goes beyond the fact that redundant species have their function in the ecosystem (Díaz and Cabido, 2001; Montoya et al., 2012; Tscharntke et al., 2005). Tscharntke et al. (2005) argue that only a diversity of redundant ‘insurance’ species in agricultural landscapes can result in a resilient ecosystem.

Contrary to annual tailored strips, perennial strips, like the ones studied in our experiments (Chapters 2-5), can be expected to harbor stable populations of ‘useful’, ‘useless’ and redundant species that have longer time to develop to densities which can be supported by the resources present. This way they can serve for biodiversity support as well as for the provision of multiple ecosystem services at longer term. More research on services and disservices, biodiversity support and the function of ‘useless’ and redundant species could support these hypotheses. However, some opportunistic species may benefit from the dynamic environment of annual strips, like typical arable flora (Marshall and Moonen, 2002). The creation of such annual strips could be a complementary scheme to perennial strips.

Flower strips as a part of (agro)ecological intensification?

To answer the global food demands, the global biodiversity crisis and the environmental impact of agricultural intensification, several concepts have been developed. Some examples are organic farming (Maeder et al., 2002; Rigby and Cáceres, 2001), land sparing vs. land sharing (Phalan et al., 2011; Tscharntke et al., 2012), ecosystem services (Costanza et al., 1997; Millenium Ecosystem Assessment, 2005), agroecology (Altieri, 1999; Hatt et al., 2016),and (agro)ecological intensification (Bommarco et al. 2013; Tscharntke et al., 2012). In some of these concepts flower strips are not of intrinsic importance, but can deliver an added value. In organic farming, for instance, natural enemies supported by flower strips, can control pests to replace pesticide use (Wyss et al., 2005). Conversely, the recent discovery of neonicotinoid residues in plant of flower strips, and the negative effect on honey bee fitness (Mogren and Lundgren, 2016), also suggest the importance of pesticide reduction that has to go along with implementing flower strips. Indeed, pesticides can affect both pests and 'useful insects' and can for instance reduce the effectiveness of biological control (Landis et al, 2000). In other concepts, like agroecology or (agro)ecological intensification, flower strips can be considered as an intrinsic part of the concept, together with several other implementations of ecological infrastructure (hedgerows, trees, semi-natural habitats), measures of crop diversification (mixed cropping, agroforestry, crop rotations, crop varieties), measures for soil quality improvement (reduced tillage, cover cropping, residue management), etc. A smart implementation of several of these measures at the landscape level is needed to establish stable populations of useful and redundant species, and to combine the positive effects of different measures (Bommarco et al., 2013). Next to the production, modifications to the distribution chain, the consumption patterns and the waste management are needed (Godfray et al., 2010).

CONCLUSIONS

Flower strips aim to support biodiversity in agricultural landscapes and can deliver several ecosystem services and disservices. One important service, pollination, and one important disservice, weed infestation, were addressed in this study.

For the creation of flower strips, seed mixtures are often used. We tested whether the vegetation composition can be steered by adapting the seed mixture to (1) promote pollinators and (2) limit infestation by weeds. While we were able to create contrasting functional diversity levels by adapting the seed mixture, an increased plant functional diversity did not have clear beneficial effects on the pollinator community. Key plant species or key plant functional traits could be more important than functional diversity based on several traits. However, our results suggest that pollinators perceived a lower redundancy of functional plant trait values when functional diversity was higher, as they had more separate feeding niches (less visited flower species in common), when functional diversity was higher. Our results also suggested that there could be a trade-off between the increase of functional trait diversity and the resource abundance per niche or trait combination in the functional trait spectrum.

By comparing seed mixtures with and without forb species, we were able to test the effect of forb competition in flower strips on weed infestation. While most weed species disappeared or were kept to relatively low levels regardless of the mixture, *C. arvense* was kept to low levels due to forb competition. By testing the effect of mowing regime on weed infestation, we revealed that *C. arvense* cover was limited by yearly summer mowing and mowing both in summer and autumn. Moreover, these mowing regimes increased forb cover, which could have an indirect negative effect on *C. arvense*. Considering the resource value of *C. arvense* for pollinators, it could be tested if summer mowing or mowing twice a year, with an alternating refuge strip, could be a good compromise between limiting *C. arvense* infestation and leaving some *C. arvense* plants to produce flowers for pollinators.

Perennial flower strip creation and management can be inspired by hay meadows, a semi-natural grassland habitat with similar vegetation management. We concluded from a comparison of plant-pollinator networks in perennial flower strips and hay meadows that both habitats have different plant and pollinator communities. We suggested that either perennial flower strip creation and management could be adapted to obtain species communities similar to hay meadows, either perennial flower strips could be considered as a new complementary habitat with other species communities.

Our results contribute to the growing body of research on flower strips and sustainable agriculture in general. With the results of the tested flower strip creation and management methods and their effect on services and disservices, farmers and administrations can try to create and manage flower strips with the desired balance between services and disservices, and researchers can try to refine methods and test the effects on other services and disservices.

CHAPTER 7

REFERENCES

7. REFERENCES

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