FLOWERING HABITATS TO ENHANCE BIODIVERSITY AND PEST CONTROL SERVICES IN AGRICULTURAL LANDSCAPES

by

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Abstract

Meeting growing demands for agricultural products requires management solutions that enhance food production, whilst minimizing negative environmental impacts. Conventional agricultural intensification jeopardizes farmland biodiversity and associated ecosystem services through excessive anthropogenic inputs and landscape simplification. Agri-environment schemes (AES) are commonly implemented to mitigate the adverse effects of conventional intensification on biodiversity. However the moderate success of such schemes thus far would strongly benefit from more explicit goals regarding ecosystem service provisioning. Providing key resources to beneficial organisms may improve their abundance, fitness, diversity and the ecosystem services they provide. With targeted habitat management, AES may synergistically enhance biodiversity and agricultural production and thus contribute to ecological intensification.

We demonstrate that sown perennial wildflower strips, as implemented in current AES focusing on biodiversity conservation also benefit biological pest control in nearby crops (Chapter 2). Comparing winter wheat fields adjacent to wildflower strips with fields without wildflower strips we found strongly reduced cereal leaf beetle (*Oulema sp.)* density and plant damage near wildflower strips. In addition, winter wheat yield was 10 % higher when fields adjoined wildflower strips. This confirms previous assumptions that wildflower strips, known for positive effects on farmland biodiversity, can also enhance ecosystem services such as pest control and the positive correlation of yield with flower abundance and diversity suggests that floral resources are key.

Refining sown flower strips for enhanced service provision requires mechanistic understanding of how organisms benefit from floral resources. In climate chamber experiments investigating the impact of single and multiple flowering plant species on fitness components of three key arthropod natural enemies of aphids, we demonstrate that different natural enemies benefit differently from the offered resources (Chapter 3). Some flower species were hereby more valuable to natural enemies than others overall. Additionally, the mixture with all flowers generally performed better than monocultures, yet with no transgressive overyielding.

By explicitly tailoring flower strips to the requirements of key natural enemies of crop pests we aimed to maximise natural enemy mediated pest control in winter wheat (Chapter 4) and potato (Chapter 5) crops. Respecting the manifold requirements of diverse natural enemies but not pests, in terms of temporal and spatial provisioning of floral, extra floral and structural resources, we designed targeted annual flower strips that can be included in crop rotation to support key arthropods at the place and time they are needed. Indeed, field experiments revealed that cereal leaf beetle density and plant damage in winter wheat can be reduced by 40 % to 61 % and aphid densities in potatoes even by 77 %, if a targeted flower strip is sown into the field. These effects were not restricted to the vicinity of flower strips and, in contrast to fields without flower strip, often prevented action thresholds from being reached. This suggests that targeted flower strips could replace insecticides. All adult natural enemies were enhanced inside targeted flower strips when compared to control strips. Yet, spillover to the field was restricted to key natural enemies such as ground beetles (winter wheat), hoverflies (potato) and lacewings (winter wheat and potato), suggesting their dominant role in biological control. In potatoes, targeted flower strips also enhanced hoverfly species richness in strips and crop, highlighting their additional benefits for diversity.

The present results provide more insights into the mechanisms underlying conservation biological control and highlight the potential of tailored habitat management for ecological intensification.

Zusammenfassung

Die wachsende Nachfrage nach landwirtschaftlichen Produkten benötigt Bewirtschaftungslösungen, die die Lebensmittelproduktion unter minimaler Beeinträchtigung der Umwelt steigern. Durch den übermässigen Einsatz künstlicher Hilfsstoffe und die Landschaftsvereinfachung gefährdet die konventionelle landwirtschaftliche Intensivierung die Biodiversität und die damit verknüpften Ökosystemleistungen im landwirtschaftlichen Raum. Agrarumweltmassnahmen (AES) werden häufig eingesetzt, um die negativen Auswirkungen konventioneller Intensivierung auf die Biodiversität zu mildern. Ihr bisher nur moderater Erfolg könnte jedoch von expliziteren Zielen bezüglich Ökosystemleistungen profitieren. Das Bereitstellen von Schlüsselressourcen für Nützlinge dürfte deren Häufigkeit, Fitness und Diversität, sowie die durch sie bereitgestellten Ökosystemleistungen begünstigen. Durch gezieltes Lebensraummanagement könnten AES sowohl die Biodiversität als auch die landwirtschaftliche Produktion fördern und so zu einer ökologischen Intensivierung beitragen.

Wir zeigen, dass gesäte mehrjährige Wildblumenstreifen, wie sie gegenwärtig in AES mit Fokus auf Biodiversitätsförderung umgesetzt werden, auch die biologische Kontrolle in benachbarten Kulturen fördern (Kapitel 2). Der Vergleich von Winterweizenfeldern mit angrenzendem Wildblumenstreifen, mit Feldern ohne Wildblumenstreifen, zeigte stark reduzierte Getreidehähnchendichten (*Oulema sp.*) und Pflanzenschaden nahe Wildblumenstreifen, sowie ein um 10 % gesteigerter Ertrag. Dies bestätigt Annahmen, wonach, für ihre positiven Auswirkungen auf die Biodiversität bekannte Wildblumenstreifen, auch Ökosystemleistungen, wie biologische Schädlingskontrolle fördern können. Die positive Korrelation des Ertrags mit Blütenabundanz und –diversität weist auf Blütenressourcen als Schlüsselfaktor hin.

Um gesäte Blühstreifen für die verstärkte Bereitstellung von Ökosystemleistungen zu verbessern, benötigt es ein mechanistisches Verständnis davon, wie Organismen von Blütenressourcen profitieren. In Klimakabinenversuchen, die den Einfluss von einzelnen und mehreren blühenden Pflanzenarten auf Fitnesskomponenten von drei grundlegenden natürlichen Feind-Arthropoden von Blattläusen untersuchten, zeigen wir, dass natürliche Feinde unterschiedlich von den angebotenen Ressourcen profitieren (Kapitel 3). Einige Blühpflanzenarten waren dabei im Allgemeinen wertvoller für natürliche Feinde als andere. Die Mischung aller Blütenpflanzen war zudem generell besser als Monokulturen, jedoch nicht besser als die jeweils beste Art in der Mischung (kein „transgressive overyielding“).

Durch gezieltes Massschneidern von Blühstreifen auf die Bedürfnisse von wichtigen natürlichen Feinden von Kulturschädlingen, versuchten wir, die durch natürliche Feinde vermittelte biologische Schädlingskontrolle in Winterweizen (Kapitel 4) und Kartoffelkulturen (Kapitel 5) zu maximieren. Unter Berücksichtigung der vielseitigen Ansprüchen von diversen natürlichen Feinden - aber nicht Schädlingen - bezüglich zeitlicher und räumlicher Bereitstellung von floralen, extrafloralen und strukturellen Ressourcen, konzipierten wir einjährige Nützlingsblühstreifen, die durch Einbau in die Kulturfolge wichtige Arthropoden an Ort und Zeit unterstützen, an denen sie benötigt werden. Tatsächlich zeigten Feldexperimente, dass Getreidehähnchen und Pflanzenschaden in Winterweizen um 40 % bis 61 % gesenkt werden können und Blattläuse in Kartoffelkulturen sogar um 77 %, wenn ein Nützlingsblühstreifen ins Feld gesät wurde. Diese Effekte waren nicht auf die Nähe zum Blühstreifen beschränkt und verhinderten oft, dass im Vergleich zu Feldern ohne Blühstreifen die Schadschwelle erreicht wurde. Dies zeigt, dass Nützlingsblühstreifen Insektizide ersetzen könnten. Alle adulten natürlichen Feinde waren innerhalb der Nützlingsblühstreifen zahlreicher als innerhalb von Kontrollstreifen. Der Überlauf (spillover) von Nützlingen ins Feld war jedoch auf wichtige natürliche Feinde, wie Laufkäfer (Winterweizen), Schwebfliegen (Kartoffeln) und Florfliegen (Winterweizen und Kartoffeln) beschränkt, was deren dominante Rolle für die biologische Schädlingskontrolle nahelegt. In Kartoffeln erhöhten Nützlingsblühstreifen auch die Artenzahl Schwebfliegen in Streifen und Feld, was einen zusätzlichen Nutzen für die Diversität heraushebt.

Die vorliegenden Resultate liefern Einblicke in die Mechanismen, die der biologischen Schädlingskontrolle durch Nützlingsförderung (conservation biological control) unterliegen und heben das Potential von massgeschneidertem Lebensraum-Management für eine ökologische Intensivierung hervor.

CHAPTER 1

General introduction

Matthias Tschumi

Global food security, biodiversity and ecosystem services

Assuring food security for a growing population requires innovative management solutions that enhance food production, whilst minimizing negative impacts on the environment (Tilman *et al.* 2002; Godfray *et al.* 2010). Agricultural intensification has successfully increased food production during the last decades (Matson *et al.* 1997). Yet, this has come at the cost of adverse effects on the environment including severe losses in the diversity of farmland plants, arthropods and vertebrates (Robinson & Sutherland 2002; Kleijn *et al.* 2009; Guerrero *et al.* 2012). Among the underlying factors, the concomitant simplification of agricultural landscapes (i.e. decrease of landscape diversity, heterogeneity and connectivity) seems to be one of the major drivers for the observed loss in biodiversity (Guerrero *et al.* 2012; Tscharntke *et al.* 2012). Semi-natural habitats such as extensively managed meadows, hedgerows or flower strips offer resources complementary to intensive cropland, which are often indispensable for communities of farmland animals (Devictor & Jiguet 2007; Billeter *et al.* 2008; Smith *et al.* 2014; Birkhofer, Wolters & Diekötter 2014). Further, or even as a consequence of landscape simplification (Meehan *et al.* 2011), increased anthropogenic inputs impose persistent negative effects on biodiversity (Geiger *et al.* 2010; Hallmann *et al.* 2014; Stehle & Schulz 2015). Crop protection still predominantly relies on chemical pesticides, which often harm non-target organisms including humans (Thomas 1999) and an over-reliance on pesticides may provoke pests to develop genetic resistance to pesticides, which could even result in an increase in pest outbreaks on the long term (Zhang *et al.* 2007). This makes pest control costly. Yet effective alternatives to pesticides are often scarce.

Beyond the inherent value of biodiversity, which makes sacrificing biodiversity morally questionable (Millennium Ecosystem Assessment 2005), ecosystem functioning depends on biodiversity (Hector *et al.* 1999; Hooper *et al.* 2005; Cardinale *et al.* 2012). Species are complementary in their resource use and functional characteristics (Hooper *et al.* 2005). Although the role of biodiversity in ecosystem processes is generally non-linear and saturating and ecosystem functions can be sustained by a few abundant species (Schwartz *et al.* 2000), diversity likely increases the stability and resilience of ecosystem functions over time (Tilman 1996; Naeem & Li 1997; Yachi & Loreau 1999; Cardinale *et al.* 2012). A diverse community, in which species respond differently to environmental change, stabilizes ecosystem functioning and rare species may even support vulnerable functions that insure against future uncertainty (Hooper *et al.* 2005; Mouillot *et al.* 2013).

Human well-being depends on the goods and services that ecosystems provide (ecosystem services). Loosely defined as “the benefits that humans obtain from ecosystems”, ecosystem services are classified into four main categories: provisioning, supporting, cultural and regulating services (Costanza *et al.* 1997; Daily 1997; Millennium

Ecosystem Assessment 2005; Fig. 1). In order to produce food, fibre or fuel, agriculture has optimized ecosystems towards provisioning services (i.e. crop yield). Yet, complex interactions between services have led to an undesired decline in most supporting and regulating services (Zhang *et al.* 2007; Power 2010). Alterations and declines in farmland biodiversity may strongly affect service delivery (Hooper *et al.* 2005), while more species are needed to sustain multiple services simultaneously (i.e. the multi-functionality of ecosystems; Cardinale *et al.* 2012). Pest control and crop pollination are considered among the services most at risk (Tscharntke *et al.* 2005; Biesmeijer *et al.* 2006; Isaacs *et al.* 2009; Geiger *et al.* 2010; Meehan *et al.* 2011). Some biological functions are concomitantly replaced by anthropogenic inputs in modern agricultural systems (Bommarco, Kleijn & Potts 2013). Ironically, such management practices can however further reduce the service providing ability of ecosystems or even stimulate 'disservices'. This may feedback to decrease productivity and ultimately adversely impact human welfare. In contrast, thoughtful management can significantly reduce trade-offs between ecosystem services and can stimulate synergies. A comprehensive understanding of how multiple services interact is therefore pivotal (Zhang *et al.* 2007; Bennett, Peterson & Gordon 2009; Power 2010; Birkhofer *et al.* 2015).

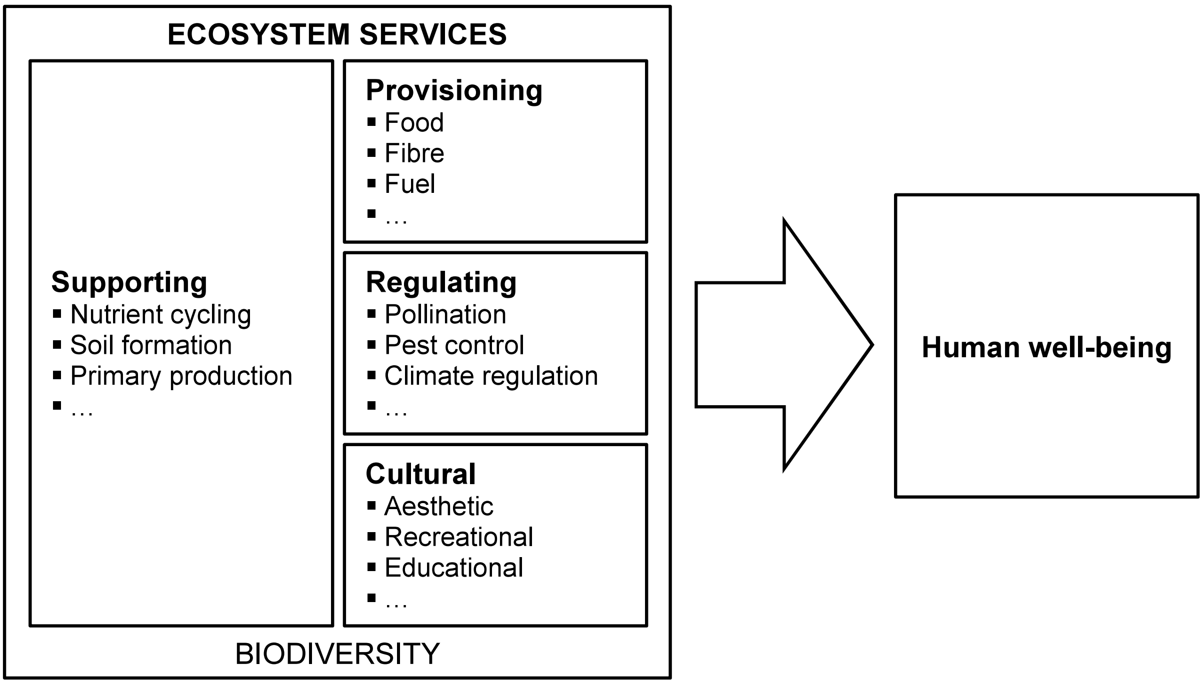

Fig. 1: Classification of ecosystem services into supporting, provisioning, regulating and cultural services that impact human well-being. Examples are focused on a farmland perspective (modified from Millennium Ecosystem Assessment 2005).

Habitat management and ecological intensification

In contrast to conventional agricultural intensification, ‘ecological intensification’ seeks for environment friendly management options that maximize production by replacing anthropogenic inputs with regulating and supporting ecosystem services (Bommarco, Kleijn & Potts 2013). By supporting service-providing organisms, adequate habitat management may have strong potential to increase yield at reduced levels of anthropogenic inputs. However, land-use opportunity costs for establishing semi-natural habitats and restrictions on management intensity may decrease yield locally, and the ability of mobile organisms to provide services on agricultural crops beyond the farm scale may create conditions for a Prisoner’s Dilemma-type problem and reduce land-owners’ willingness to adopt environmental friendly management (Lant, Ruhl & Kraft 2008; Cong *et al.* 2014; Ekroos *et al.* 2014). To counteract this trend, agri-environment schemes (AES) were implemented in many countries including the EU and Switzerland to support farmers through direct payments for compliance with environment friendly standards (Tilman *et al.* 2002; Aviron *et al.* 2009; Pe’er *et al.* 2014). AES often foresee payments for semi-natural habitats such as extensive meadows, hedges or flower strips (Kleijn *et al.* 2011). While AES are generally designed to support farmland biodiversity, many AES explicitly or implicitly entail the provisioning of ecosystem services such as animal-mediated pollination or pest control (Birkhofer *et al.* 2014). So far, the success of AES to deliver benefits for biodiversity and ecosystem services is controversial (Kleijn *et al.* 2006, 2011; Aviron *et al.* 2009; Pe’er *et al.* 2014), and it is argued that a clearer distinction between biodiversity and the delivery of ecosystem services is needed (Kleijn *et al.* 2011; Scheper *et al.* 2013; Ekroos *et al.* 2014). Yet, the adoption of improved evidence-based habitat management bears potential to contribute to both aims (Straub, Finke & Snyder 2008; Whittingham 2011; Rey Benayas & Bullock 2012). Including elements specifically tailored to species of conservation concern or service providers may improve effectivity of schemes and create “win-win” situations for both biodiversity and production. This may improve the reputation of AES and increase the likelihood of landowners adopting such schemes. Yet, little is known about the impact of habitat management on the actual provisioning of services and the implementation of ecosystem service management in crop production is still rare (Lundgren 2009; Whittingham 2011).

The successful management of ecosystem services requires a landscape perspective for at least two reasons. First, landscape characteristics affect services and moderate the effectiveness of habitat management measures (Tscharntke *et al.* 2012). The effects of habitat management are likely to be more pronounced in landscapes of intermediate complexity than in cleared or complex landscapes (Concepcion *et al.* 2012; Tscharntke *et al.* 2012). Cleared landscapes may lack the species pools required to support agri-environment measures, whereas the contrast created in complex landscapes may not be sufficient to significantly improve conditions (Kleijn *et al.* 2011; Tscharntke *et al.* 2012; Scheper *et al.* 2013). Yet this is not completely uncontroversial as other theories predict gains to be highest in areas where biodiversity is already high (Kleijn & Sutherland 2003; Kleijn *et al.* 2009; Whittingham 2011). Secondly, local management is likely to influence service delivery elsewhere (Power 2010). Service managers (e.g. land owners) are not always the beneficiaries of these services and many ecosystem services are public goods (Millennium Ecosystem Assessment 2005). Costs and benefits of habitat management need thus to be assessed at a landscape scale to be conclusive (Cong *et al.* 2014). Still, management decisions often focus on immediate and field- or farm- scale effects (Power 2010). Thus, demonstrating local short-term benefits from services such as pollination or pest control and developing cost-efficient solutions for the management of services may encourage stakeholder support. In summary, sustainable agricultural systems depend on multidisciplinary concepts and a thoughtful balance of local or short-term and landscape-wide or long-term costs and benefits.

The value of plant-provided resources and biological pest control

The biological control of insect pests is a highly valued service (Costanza *et al.* 1997; Losey & Vaughan 2006; Naranjo, Ellsworth & Frisvold 2015). Its performance often strongly depends on habitat quality (Veres *et al.* 2013). Crop yield losses as a result of insect pests are estimated to likely be no less than 10 % and are stable or increasing worldwide despite increasing insecticide use (Oerke 2006). Adequate habitat management can enhance natural enemy mediated pest control and thus offer a viable alternative to pesticides (‘conservation biological control’ - Barbosa 1998). Complex landscapes generally sustain larger and more diverse natural enemy populations (Andow 1991; Bianchi, Booij & Tscharntke 2006; Rusch *et al.* 2010), that are on average positively related to decreased pest pressure (Letourneau *et al.* 2009; Veres *et al.* 2013). Many generalist and specialist arthropod natural enemies depend on plant-provided resources during some of their life stages, among which ground beetles (Coleoptera: Carabidae; e.g. Diehl, Wolters & Birkhofer 2012), rove beetles (Coleoptera: Staphylinidae; e.g. Lys & Nentwig 1994), spiders (Araneae; e.g. Schmidt & Tscharntke 2005), ladybirds (Coleoptera: Coccinellidae; e.g. Obrycki *et al.* 2009), hoverflies (Diptera: Syrphidae; e.g. Haenke *et al.* 2014), lacewings (Neuroptera: Chrysopidae; e.g. Villenave *et al.* 2006), parasitic wasps (Hymenoptera; e.g. Wäckers 2004) and predatory true bugs (Hemiptera: Heteroptera; e.g. Perdikis, Fantinou & Lykouressis 2011) are likely of predominant importance. Woody and herbaceous vegetation provide shelter, overwintering sites and food sources such as floral and extra-floral nectar, pollen or alternative hosts and prey, that may enhance the abundance and fitness of natural enemies (Bianchi, Booij & Tscharntke 2006; Rusch *et al.* 2010). Yet, to enhance natural enemies but not pests, habitat management needs a refined selection of resources and well-adapted management (Lundgren 2009). Sown flower strips can effectively address these specific needs and are thus assumed to promote the delivery of pest control in nearby crops (Pfiffner & Wyss 2004). Their effectiveness, however, likely depends on the attractiveness, quantity, quality and accessibility of floral resources as well as the timing at which they are available (Wäckers & van Rijn 2012). In addition, the potentially distinct requirements of natural enemy guilds should be considered to promote functional diversity of communities that maximise complementarity and stability of pest control (Crowder & Jabbour 2014).

Semi-field and laboratory experiments on arthropod flower choice, consumption, accessibility, and the effects of individual resources on fitness deliver valuable information on the potential suitability of plant species to be included in seed mixtures for conservation biological control (e.g. Wäckers & van Rijn 2012 and citations therein). Different studies showed that for example floral resources from plant species of the family Apiaceae enhanced the longevity of hoverflies, lacewings and parasitoids and were often preferably chosen by hoverflies (reviewed in Wäckers & van Rijn 2012). Yet, since different natural enemies respond differently to floral resources, the selection of the 'right' flowering plants to optimize the species composition of flower strips requires that the performance and fitness consequences of plant species is directly assessed on multiple pest control providing taxa. Additionally, natural enemies may not react in the same way to floral resources in the field as under semi-field or laboratory conditions (Wäckers & van Rijn 2012) and enhanced natural enemy abundance in the field may not necessarily represent a reliable proxy for pest control (Thies, Roschewitz & Tscharntke 2005; Bianchi, Booij & Tscharntke 2006). If pests profit equally, or even more strongly from the offered resources (Heimpel & Jervis 2005; Wäckers, Romeis & van Rijn 2007) or if multitrophic interactions such as intraguild predation reduce the abundance or performance of actual service providers (Letourneau *et al.* 2009; Lundgren 2009; Cardinale *et al.* 2012; Martin *et al.* 2013), floral resources may inevitably enhance pests rather than reducing them. This requires that the actual delivery of services is assessed on pest density, plant damage or yield, to be conclusive about the success of conservation biological control. Yet, few studies have quantified the impact of flower strips on pest control and yield beyond natural enemy density or proxies such as parasitism.

Research questions

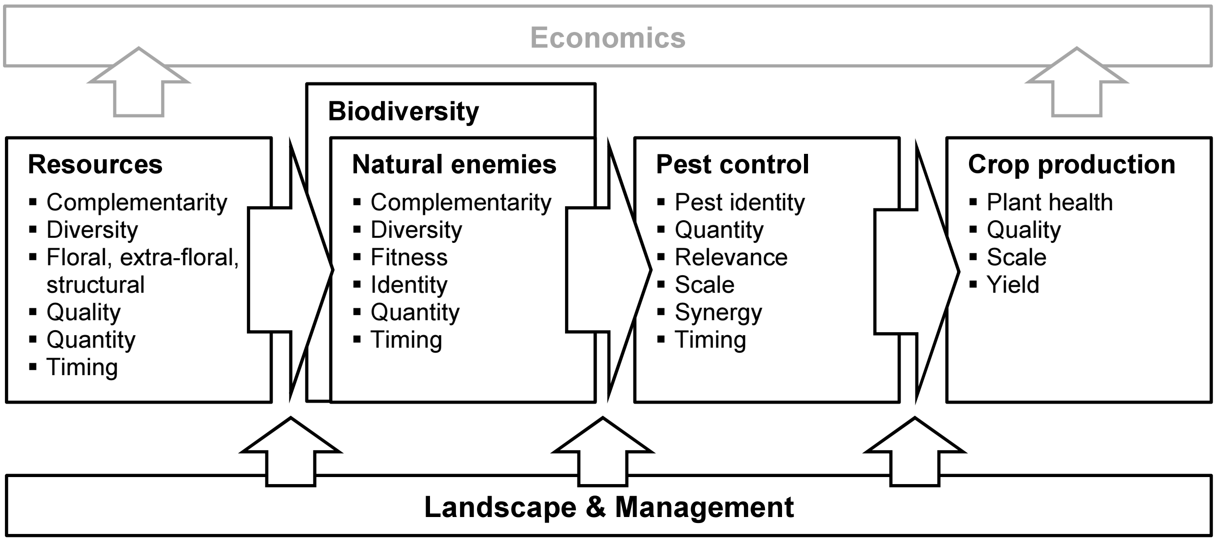

Fig. 2: Schematic illustration of the investigated agroecosystem. Plant-provided and other resources modified by habitat management affect general farmland biodiversity and specifically natural enemies of crop pests which provide pest control services in crops. The relationships may be influenced by landscape features and management of the particular farmland system and the balance of investments in habitat management and payoffs in terms of crop yield ultimately affect the economics of production. Bullet points illustrate properties that may be important drivers of the interactions but are exemplary here rather than conclusive.

The following main research questions were addressed to contribute to fill these knowledge gaps: (1) Do perennial, species-rich wildflower strips as currently implemented in agri-environment schemes benefit pest control in nearby fields? (2) What are the flower strip traits that drive the effectiveness of conservation biological control? (3) How do key aphid natural enemy species differ in their fitness response to single and mixtures of different plant species? (4) Can annual flower strips, specifically tailored to the requirements of key natural enemies of crop pests, enhance pest control at the field scale? (5) How are these effects moderated by landscape complexity? And (6) do measures tailored to the provisioning of pest control also benefit biodiversity?

Chapter outline

CHAPTER 2: PERENNIAL, SPECIES-RICH WILDFLOWER STRIPS ENHANCE PEST CONTROL AND YIELD

Perennial, species-rich wildflower strips are implemented in Swiss and European agri-environment schemes with the main aim of general farmland biodiversity conservation. While the effects of perennial, species-rich wildflower strips on biodiversity have been repeatedly investigated, studies quantifying their impact on pest control are largely lacking. To address this knowledge gap, we compared ten winter wheat fields adjacent to perennial, species-rich wildflower strips with ten fields without flower strip in terms of cereal leaf beetle *Oulema sp.* (CLB) density, plant damage and yield. Additionally we investigated flower strip traits which correlate with yield. The findings of chapter 2 highlight the potential of wildflower strips to enhance biological pest control and suggest that flower diversity and abundance are decisive.

CHAPTER 3: FITNESS EFFECTS OF SINGLE AND MULTIPLE FLOWER SPECIES TO DIFFERENT NATURAL ENEMIES OF APHIDS

To optimize the composition of flower strips for pest control, it is essential to know which plant species are associated with the highest fitness gains for key natural enemies of crop pests. In chapter 3 we thus experimentally examined the influence of single and multiple flowering plant species treatments on fitness components of three key natural enemy species of aphids under climate chamber conditions. The results of this chapter provide information on the suitability of individual flowering plant species for conservation biological control - yet the pronounced differences between natural enemy species and the generally high performance of flower mixtures particularly highlight the value of diverse plant species mixtures. Diverse flower mixtures are likely to support diverse natural enemy communities and enhance the chances for effective biological control more effectively than single-species flower strips.

CHAPTER 4: HIGH EFFECTIVENESS OF TAILORED FLOWER STRIPS IN REDUCING PESTS AND CROP PLANT DAMAGE

Chapter 4 examines the performance of annual flower strips specifically targeted at the promotion of natural pest control in winter wheat. Flower strips were experimentally sown along 10 winter wheat fields across a gradient of landscape complexity and compared to 15 fields with wheat control strips in terms of natural enemy abundance, cereal leaf beetle (CLB) density and plant damage. Chapter 4 demonstrates the high effectiveness of tailored annual flower strips in promoting pest control, reducing CLB pest levels below the economic threshold. This may even make tailored flower strips economically self-sustaining. The effects on natural enemies, pests and plant damage were largely independent of landscape complexity.

CHAPTER 5: TAILORED FLOWER STRIPS PROMOTE NATURAL ENEMY BIODIVERSITY AND PEST CONTROL IN POTATO CROPS

Analogous to chapter 4, we tested the performance of tailored flower strips on pest control - but focussing on aphids in potato crops. We compared 9 potato fields with sown tailored flower strips to 9 fields with potato control strips in term of aphid density and their key natural enemies (hoverflies, lacewings and ladybirds). The results of this chapter underline the effectiveness of tailored annual flower strips for pest control and demonstrate that they are at least as suitable for controlling aphids in potatoes as for controlling CLB in winter wheat. In addition, positive effects on hoverfly species richness suggest complementary benefits of tailored flower strips for functional biodiversity that may maximise complementarity and stability of pest control services and provide additional benefits to agro-ecosystems in terms of biodiversity conservation and pollination.

CHAPTER 2

Perennial, species-rich wildflower strips enhance pest control and crop yield

Matthias Tschumi, Matthias Albrecht, Cédric Bärtschi, Jana Collatz, Martin H. Entling, Katja Jacot

Abstract

The effectiveness of agri-environment schemes (AES) such as wildflower strips in promoting farmland biodiversity has been relatively well studied. Their effects on biodiversity-mediated ecosystem services, such as natural pest control, in contrast, remain poorly evaluated and their consequences on crop yield largely unexplored. We assessed the effect of sown, species-rich, perennial wildflower strips, promoted through the Swiss AES, on pest control services and their consequences for crop yield in nearby winter wheat. We found strong reductions in cereal leaf beetle *Oulema sp.* (CLB) density (eggs: 44%, larvae: 66%) and crop damage (40%) caused by CLB in winter wheat close to wildflower strips (N = 10) compared with control fields without wildflower strip (N = 10). Moreover, average crop yield was increased by 10% in winter wheat next to wildflower strips. Among the tested flower strip properties, traits related to flower density and diversity were the best predictors of crop yield. Our study demonstrates that diverse wildflower strips with known positive benefits for farmland biodiversity can also promote biological pest control and crop yield. This creates a win-win situation for crop production and biodiversity conservation, through which such AES may contribute to ecological intensification.

Keywords: Agri-environment schemes (AES); conservation biological control (CBC); ecological intensification; ecosystem services (ES); flower strip traits; functional biodiversity; habitat management; natural enemies; *Oulema melanopus* L.; plant damage; semi-natural habitat; sown field margin

1. Introduction

The optimization of agricultural systems for provisioning services such as food, fiber or biofuel production has imposed increasing pressure on regulating ecosystem services and farmland biodiversity (Cardinale *et al.* 2012). The performance of agri-environment schemes (AES) in promoting biodiversity has been found to be mixed (Kleijn *et al.* 2006), although some schemes perform moderately well in counteracting declines of farmland biodiversity (Albrecht *et al.* 2007; Birrer *et al.* 2007; Aviron *et al.* 2009). Yet, land-use opportunity costs and restrictions on management intensity through AES may reduce crop yield, thereby jeopardizing the reputation of biodiversity measures among land managers and society, as long as the provision of food is regarded as the predominant task - even of multifunctional agriculture (Burton, Kuczera & Schwarz 2008; Ekroos *et al.* 2014; Home *et al.* 2014). Additionally, negative consequences on biodiversity may be exported if yield reductions increase the pressure to convert land of high ecological value to intensive farmland elsewhere (Tilman *et al.* 2011; Tuck *et al.* 2014).

This argument, however, largely ignores the fact that positive effects of AES on functional biodiversity may promote important organism-provided regulating ecosystem services, such as crop pollination and natural pest control, which may indeed enhance crop production (Holland *et al.* 2012; Korpela *et al.* 2013). Such regulating services could contribute to closing the yield gap at minimal environmental costs (Ekström & Ekbom 2011; Bommarco, Kleijn & Potts 2013).

Sown flower strips can effectively enhance natural enemies of crop pests (Landis, Wratten & Gurr 2000; Isaacs *et al.* 2009; Haaland, Naisbit & Bersier 2011; Ramsden *et al.* 2014). Alongside pollen and nectar, which serve as an additional adult food source for many carnivorous arthropods (Wäckers & van Rijn 2012), perennial flower strips offer structural resources and undisturbed habitats that support the long-term persistence of natural enemy populations (Pfiffner & Wyss 2004). Perennial, species-rich wildflower strips designed for biodiversity conservation may thus concurrently support organism-provided ecosystem services (Schmidt-Entling & Döbeli 2009; Ekroos *et al.* 2014). Yet, positive effects of wildflower strips on crop yield through enhancing pest control have rarely been demonstrated and we lack an understanding of the flower strip traits that drive their effectiveness in supporting pest control (Whittingham 2011). Demonstrating benefits of agri-environmental measures for pest control and crop yield can improve the reputation of AES and increase the likelihood of land-owners to take responsibility for the services affected by their actions (Cardinale *et al.* 2012).

Cereal leaf beetles (hereafter CLB) *Oulema* sp. are major cereal crop pests in Europe, Asia and parts of North-America and cause significant economic damage to cereal crops at densities above 0.4 larvae or 0.5 eggs per tiller (Ihrig *et al.* 2001; Buntin *et al.* 2004;

Olfert & Weiss 2006; Evans *et al.* 2013). CLB are generally controlled by pesticides (Reisig *et al.* 2012). Yet, pesticides can be costly and potentially harmful to biodiversity and to provided ecosystem services (Geiger *et al.* 2010; Chaplin-Kramer *et al.* 2011). Alternative control strategies for CLB remain, however, largely unexplored. This may hamper the adoption of alternative wheat management, such as low-input or organic farming.

The main objectives of the present study are (i) to quantify the effectiveness of species-rich, perennial wildflower strips designed for biodiversity conservation in providing pest control services; (ii) to examine their consequences on crop damage and yield; and (iii) to assess the importance of different flower strip traits for their effects on crop yield.

2. Methods

2.1. STUDY DESIGN

Field experiments were conducted between April and July 2014. Twenty winter wheat fields (hereafter focal fields) were selected in the central Swiss plateau (cantons Zurich and Aargau) within an area representative of the typical agricultural landscape of the Swiss lowlands, characterized by a small-scaled mosaic of arable crops, grasslands and forest fragments. Focal fields (average size: 1.31 ha ± 0.14 ha) were selected in pairs, with similar agricultural management and landscape composition. In each pair, one field was selected next to a perennial wildflower strip (age ≥ 2 years), whereas the other field was adjacent to a crop field (i.e. winter wheat, maize, sunflower or grassland; hereafter control crop). All winter wheat fields were managed without the application of insecticides, to avoid potential pesticide-mediated bias on CLB or their arthropod antagonists.

The investigated perennial sown wildflower strips (hereafter wildflower strips) are part of the Swiss agri-environment scheme aimed at promoting biodiversity and ecosystem services, which compensates farmers for any costs associated with the establishment of these strips (Bundesrat 2015). The seed mixtures consist of 24 to 41 plant species (indigenous forbs, legumes and grasses). Farmers can choose from different mixtures with varying compositions of plant species adapted to the prevailing site conditions (Supplementary material Table S1; Pfiffner & Wyss 2004; Jacot *et al.* 2007). According to the restrictions of cross-compliance, no fertilizers and no pesticides (except targeted herbicide application to individual problematic plants) were applied in the wildflower strips and cutting followed a defined protocol (Junge *et al.* 2009; Eggenschwiler *et al.* 2013).

2.2. CEREAL LEAF BEETLE DENSITY AND CROP DAMAGE

Cereal leaf beetles (CLB) *Oulema sp.* are major cereal crop pests in Europe, Asia and parts of North America, with increasing importance in warming climates (Ihrig *et al.* 2001; Olfert & Weiss 2006; Evans *et al.* 2013). CLB larvae skeletonize the leaves of cereal plants, thereby reducing their photosynthetic activity during plant growth and grain assimilation with negative consequences for tillering, kernel weight or seed number, depending on the time and location of plant damage (Haynes & Gage 1981; Buntin *et al.* 2004; Reay-Jones 2010). Increased water loss due to CLB-induced injuries and increased risk of secondary infection through microbes or viruses can further amplify the negative consequences on yield (Haynes & Gage 1981). Natural enemies of CLB comprise specialized parasitic wasps and generalist predators such as ground beetles, rove beetles, ladybirds, predatory bugs and lacewing larvae (Schärer 1994; Meindl *et al.* 2001; Malschi, Tritean & Serbanescu 2010; Evans *et al.* 2013). Of the two species of CLB (*Oulema melanopus* L. and *Oulema gallaeciana* Heyden) which occur on winter wheat in the study area, *O. melanopus* is dominant (97% of adults sampled in this study). The larvae and eggs of the two CLB species are not easily distinguished from one another in the field and were thus analyzed together. The two species have similar pest status' (Schärer 1994).

CLB density and crop damage were assessed at two distances (near = 5 m and far = 10 m) from wildflower strips or control crops in each focal field. In three plots at both distances, the number of CLB eggs and larvae was recorded for 25 wheat tillers (wheat shoot including stem, leaves and ear). In each plot the number of eggs and larvae were sampled twice during the peak of their appearance (eggs: late April and mid-May; larvae: mid-May and late May; Schärer 1994; Ihrig *et al.* 2001). Likewise, CLB adults of the second generation were sampled twice using standardized sweep netting (60 sweeps at each distance in each focal field, 40 cm sweep net diameter) at the time they emerge from pupae (late June and early July in the study region). This second generation of adult CLB should, in contrast to the first generation of beetles colonizing fields, directly reflect the cumulative impact of biological control on eggs, larvae and pupae. Crop damage was assessed at the end of CLB larval activity (late June) as the percent of the flag leaf damaged by CLB larvae of the same winter wheat tillers on which CLB egg and larval density was assessed. Furthermore, wheat density (number of wheat tillers per m^2) and average wheat height was assessed in 1 m^2 plots at each location where CLB were sampled, as wheat density and height varied due to field conditions.

2.3. CROP YIELD ASSESSMENT

To assess crop yield we harvested all wheat plants in two 1 m^2 plots, at both distances at which CLB density and crop damage were assessed at the same period when farmers harvested winter wheat fields in the region (mid-July). After air-drying for 6 days at 34° C, wheat samples were processed with a small-sample threshing machine (Saatmeister by Kurt Pelz Maschinenbau, Germany), seeds where weighed and seed number was assessed using a seed counter (Contador by Pfeuffer GmbH, Germany). Seed weight per m^2 (hereafter agronomic wheat yield), thousand seed weight (TSW), average seed number per tiller and average ear weight were calculated.

2.4. VEGETATION TRAITS OF WILDFLOWER STRIPS

Vegetation traits of wildflower strips were assessed twice (in early May and early June) to identify the supply of temporally changing structural and floral resources to arthropods. We visually recorded the percentage cover of broadleaved plants and grasses, and the number of flowers or inflorescences of each flowering forb and legume species identified according to Lauber, Wagner & Gygax (2012) in the central 30 m of all wildflower strips (Supplementary material Table S2; Table S3). Flower density was calculated by dividing total flower number by the corresponding sampling area (Supplementary material Table S2).

2.5. STATISTICAL ANALYSES

The effects of wildflower strips (focal fields with sown wildflower strip vs. focal fields without wildflower strip) on CLB density (response variables: total number of CLB eggs, larvae and adults pooled across sampling plots of each distance) in adjacent winter wheat fields were tested using generalized linear mixed-effects models (GLMMs). Due to significant overdispersion in all CLB density counts (poisson error distribution), GLMMs with negative binomial error distributions (log-link function) were fitted using the Automatic Differentiation Model Builder (glmmADMB) package (Skaug *et al.* 2013) in R. To evaluate the effects of wildflower strips on crop damage (arcsine-square root-transformed, pooled across sampling plots of each distance) and yield (response variables: agronomic wheat yield [g/m^2], TSW [g], average seed number per tiller and average ear weight [g] pooled across sampling plots of each distance), we used linear mixed-effects models. All full models contained the fixed effects: wildflower strip (factor: wildflower strip vs. control crop), distance (factor: near vs. far) and their interaction and the continuous covariate wheat density (except for the model with the response variable average ear weight, as wheat density was used to calculate average ear weight), and the random blocking factors pair identity and field identity nested in pair identity (and sampling round as an additional crossed random factor in the models for CLB density). Wheat density was standardized to obtain a predictor with a mean of zero and standard deviation of one for all evaluations, thus avoiding numerical precision problems. Colinearity among covariates was assessed using pairwise scatterplots, correlation coefficients and variance inflation factors (VIF) and wheat height was excluded from the set of candidate models as it was positively correlated with wheat density (correlation coefficient > |0.5|; Zuur *et al.* 2009). Model selection based on likelihood ratio tests following recommendations by Zuur *et al.* (2009) and minimum adequate models were used for statistical inference. Using Moran's I autocorrelation index (Paradis, Claude & Strimmer 2004) no spatial autocorrelation in the residuals of the models was detected.

The impact of flower strip traits (averaged across sampling rounds; Supplementary material Table S2) on agronomic wheat yield ([g/m^2], pooled across sampling plots of each distance) was assessed for fields with wildflower strips only. For each response and explanatory variable we fitted separated linear mixed-effects models with field identity as random effect. For all models assumptions were checked according to the graphical validation procedures recommended by Zuur *et al.* (2009). All statistical analyses were carried out using R 3.1.2 statistical software (R Core Team 2014).

3. Results

3.1. IMPACT OF WILDFLOWER STRIPS ON CLB DENSITY AND CROP DAMAGE

We found significant interactive effects of wildflower strip presence with edge distance on CLB eggs, CLB larvae and crop damage caused by CLB (Table 1, Fig. 1a, b and d). CLB eggs, larvae and crop damage were lower in winter wheat fields adjacent to wildflower strips compared with winter wheat fields adjacent to control crops, but only at the near (5 m) and not at the far (10 m) distance from the field border (Fig. 1a, b and d). Despite similar patterns of average values, there was no statistically significant main effect of wildflower strip presence or its interaction with within-field distance on adult CLB density (Table 1, Fig. 1c).

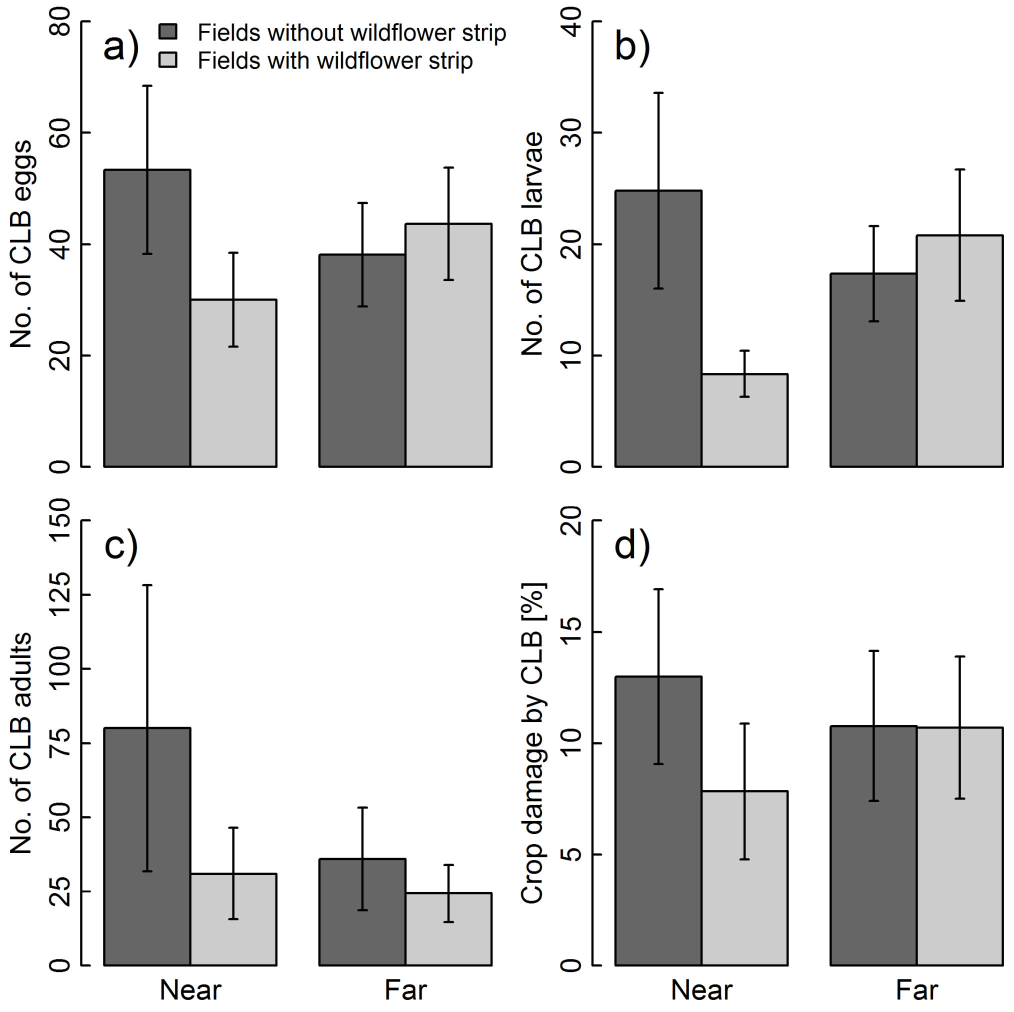

Fig. 1: Effects of wildflower strips on pest densities and crop damage. Mean (± 1 SE) **a)** number of cereal leaf beetle (CLB) eggs, **b)** number of CLB larvae, **c)** number of adult CLB of the second generation and **d)** percentage crop damage caused by CLB on 75 winter wheat tillers in fields adjacent to wildflower strips (light grey; n = 10) and fields adjacent to control crops (dark grey; n = 10). Near: 5 m distance to wildflower strip or control crop, respectively, Far: 10 m distance.

Table 1: Effects of wildflower strip (factor with two levels: wildflower strip or control crop), distance from wildflower strip or control crop (factor with two levels: near = 5 m and far = 10 m) and their interaction on cereal leaf beetle (CLB) density, crop damage (arcsine-square root-transformed) and crop yield. Degrees of freedom (df), Chi-square values (χ^2) and *P*-values from likelihood-ratio tests of the model selection procedure (see Material and Methods section) are shown. Significant *P*-values (< 0.05) of explanatory variables are in bold lettering.

	df	χ^2	$P(\geq\chi^2)$
Pest density			
CLB eggs			
Treatment	1	0.10	0.757
Distance	1	0.25	0.620
Treatment x Distance	1	7.82	**0.005**
CLB larvae			
Treatment	1	0.20	0.655
Distance	1	2.91	0.088
Treatment x Distance	1	8.01	**0.005**
CLB adults			
Treatment	1	0.06	0.813
Distance	1	0.05	0.806
Treatment x Distance	1	0.23	0.629
Crop damage			
Crop damage by CLB			
Treatment	1	0.33	0.502
Distance	1	1.56	0.482
Treatment x Distance	1	7.50	**0.003**
Crop yield			
Agronomic wheat yield [g/m^2]			
Treatment	1	4.34	**0.037**
Distance	1	0.02	0.899
Treatment x Distance	1	0.46	0.498
Thousand seed weight			
Treatment	1	1.74	0.187
Distance	1	0.01	0.908
Treatment x Distance	1	0.62	0.430
Number of seeds per tiller			
Treatment	1	2.45	0.117
Distance	1	0.54	0.461
Treatment x Distance	1	0.83	0.362
Ear weight			
Treatment	1	5.69	**0.017**
Distance	1	0.51	0.475
Treatment x Distance	1	0.30	0.587

3.2. IMPACT OF WILDFLOWER STRIPS ON CROP YIELD

Agronomic wheat yield [g/m^2] strongly increased with wheat density. In addition, it was significantly enhanced by neighboring wildflower strips (Table 1; Fig. 2) irrespective of within-field distance (Table 1). After accounting for wheat density, the yield increase averaged 10% (77 g per m^2) in the presence of wildflower strips (Fig. 2). Increases in the average thousand seed weight (TSW) and seed number per tiller in fields with a wildflower strip, compared to fields without a wildflower strip, were not statistically significant (Table 1, Fig 3a, b). However, average ear weight was significantly increased by 0.15 g (9%) in winter wheat fields adjacent to wildflower strips compared with winter wheat fields adjacent to control crops (Table 1, Fig 3b).

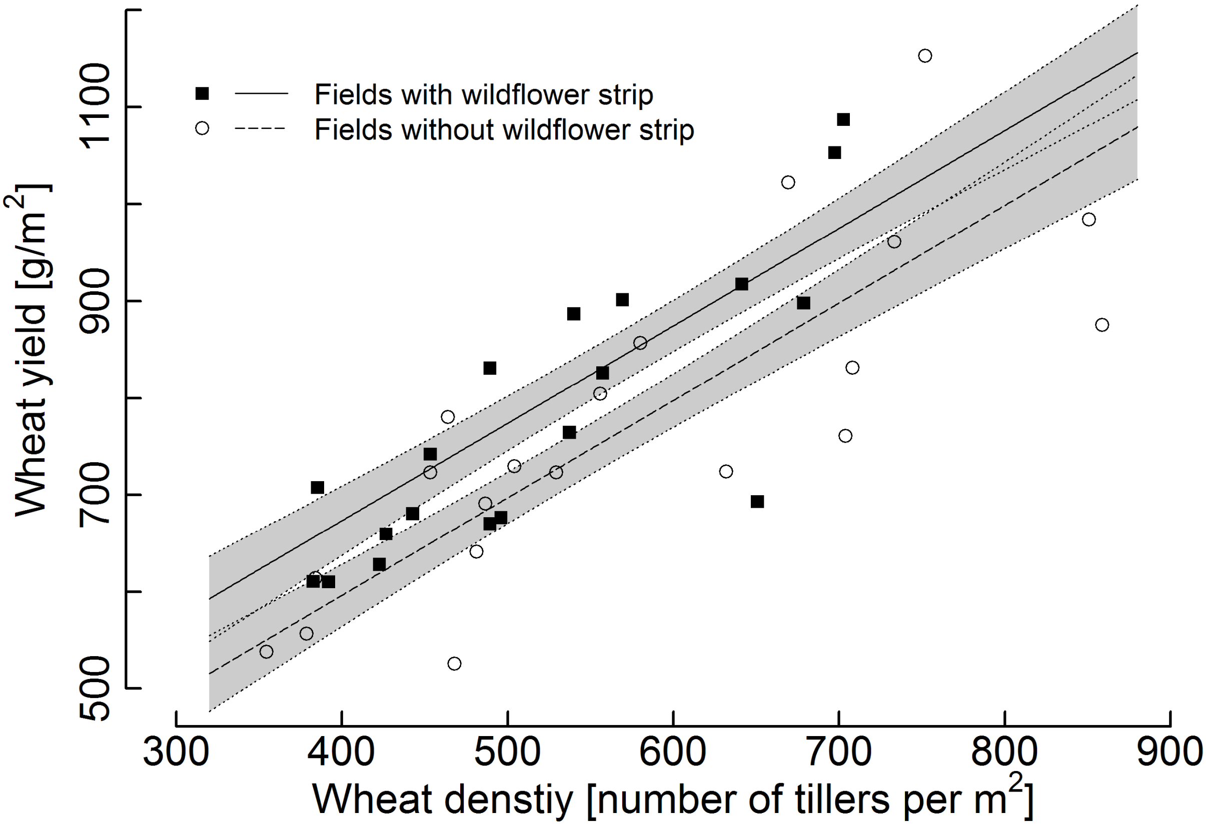

Fig. 2: Effects of wildflower strips and wheat density on agronomic wheat yield (seed weight per m^2). Wheat yield assessed from winter wheat fields adjacent to wildflower strips (filled squares; pooled across sampling plots of each distance from n = 10 fields) and winter wheat fields adjacent to control crops (empty points; pooled across sampling plots of each distance from n = 10 fields) in response to wheat density. Lines represent model-predicted yield and grey areas represent standard error intervals for fields adjacent to wildflower strips (solid line) and for fields adjacent to control crops (dashed line) based on the minimum adequate model containing flower strip treatment and wheat density as fixed effects.

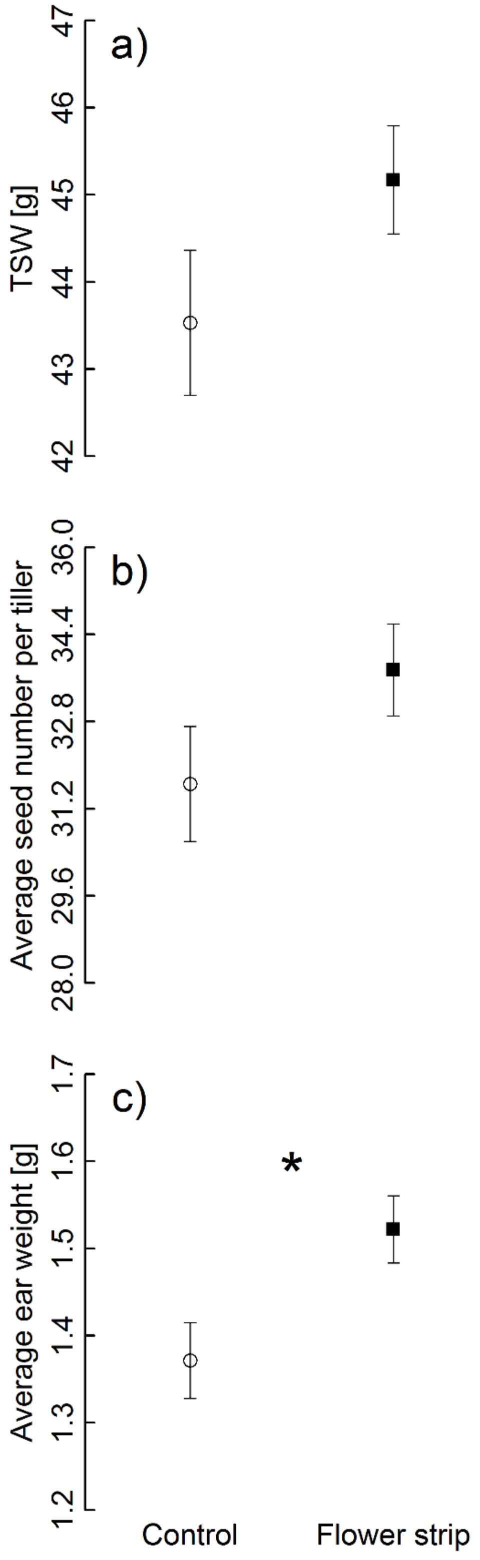

Fig. 3: Effects of wildflower strips on mean (± 1 SE) **a)** thousand seed weight (TSW), **b)** seed number per tiller and **c)** ear weight in winter wheat fields adjacent to control crops (open circles) and winter wheat fields adjacent to wildflower strips (filled squares). The asterisk indicates a significant effect ($P \leq 0.05$).

3.3. FLOWER STRIP TRAITS

Agronomic wheat yield increased with flower density and cover of broadleaved plants in the adjacent wildflower strip, and tended to also increase with the number of flowering species present in the wildflower strip (Table 2).

Table 2: Effects of vegetation traits of wildflower strips (averaged among sampling rounds) on crop yield in adjacent winter wheat fields. Degrees of freedom (df), Chi-square values (χ^2) and *P*-values from likelihood-ratio tests of the model selection procedure (see Material and Methods section) are shown. Significant *P*-values (< 0.05) of explanatory variables are in bold lettering.

	df	χ^2	$P(\geq\chi^2)$	Estimate
Agronomic wheat yield [g/m^2]				
Broadleaved cover (%)	1	5.11	**0.024**	+
Flowering species richness	1	3.22	0.073	+
Flower density (#/m^2)	1	5.23	**0.022**	+

4. Discussion

We demonstrate that perennial, species-rich wildflower strips, primarily implemented for biodiversity conservation through the Swiss AES, can reduce cereal leaf beetle numbers and improve winter wheat yield in adjacent fields. Wildflower strips with a high density and diversity of floral resources were generally more effective in delivering yield benefits than flower strips with fewer flowers. This study thus provides a strong argument in favor of perennial, plant species and flower rich AES, highlighting multiple benefits for crop production; through yield gains in addition to known benefits for biodiversity conservation.

The 44% reduction in CLB egg numbers close to wildflower strips, from 0.71 (± 0.20) per tiller in control fields to 0.40 (± 0.11) in fields with an adjacent wildflower strip, brings egg numbers under the action threshold for pesticide application of 0.5 eggs per tiller suggested by Ihrig *et al.* (2001). This indicates that wildflower strips can prevent action thresholds being reached and thus could reduce insecticide application in conventional winter wheat production. The high effectiveness of the tested wildflower strip in reducing pest levels and enhancing crop yield could also facilitate the adoption of a low-input or organic production scheme. Refraining from insecticide treatments near wildflower strips in addition buffers unintended drift both into wildflower strips and nearby habitats and thus avoids non-target effects of insecticides on biodiversity and disservices such as water contamination (Hahn, Lenhardt & Brühl 2014; Stehle & Schulz 2015). Average CLB larvae densities were even reduced by 66% and average crop damage by 40% close to wildflower strips, corroborating the high effectiveness of the tested wildflower strips in providing CLB control services. Average larvae levels were, however, consistently below the economic threshold (suggested by Ihrig *et al.* 2001; Buntin *et al.* 2004) of 0.4 larvae per tiller (control: 0.33 ± 0.12; wildflower strip: 0.11 ± 0.03). Still, three of the control fields had larvae averages exceeding this threshold, whereas none of the wildflower strip fields did. Wildflower strips may thus not only decrease pest and crop damage on average, but also prevent pest outbreaks and contribute to less unpredictable variation in pest densities.

A key finding of our study is that crop yield was significantly increased in wheat fields adjacent to wildflower strips, and this effect was consistent across the two assessed within-field distances. Previous studies investigating the impact of CLB on winter wheat yield identified either reduced kernel weight (defoliation at growth stages), or reduced seed number per tiller (defoliation during flag leaf emergence) to impair yield depending on the timing of defoliation (Buntin *et al.* 2004). The observed infection of winter wheat by CLB during growth and flag leaf emergence, resulting in trends of decreased grain filling (TSW) and decreased seed set respectively, may thus in combination explain the net yield decrease observed in fields without adjacent wildflower strips. An early and continuing intervention of natural enemies during the whole crop growing season, as encouraged by the perennial wildflower strips tested here, could have played an important role in preventing the establishment and spread of CLBs, other insect pests and pest-induced yield losses in adjacent wheat fields.

Crop yield is determined by complex interactions of abiotic and biotic factors (Frederick & Bauer 1999). Although our findings demonstrate consistent patterns of increased CLB control, reduced crop damage through CLB and enhanced crop yield in wheat fields adjacent to wildflower strips, it is important to note that they do not allow inferring causality between CLB control and crop yield. For example, it is conceivable that wildflower strips similarly promoted control of other pests, which may have contributed to the observed yield increase in adjacent wheat crops. Species-rich perennial wildflower strips are valuable habitats for a large range of natural enemies and potential pest-control service providers of a series of insect pests, including arthropods, birds and insect pathogenic fungi (Schmidt-Entling & Döbeli 2009; Schneider *et al.* 2012; Zollinger *et al.* 2013). Aphids for example are effectively controlled by hoverflies, which are highly mobile and are effectively supported by floral resources offered through flower strips (Haenke *et al.* 2009; Wäckers & van Rijn 2012; Jönsson *et al.* 2015). Consequently, positive effects on yield may be likely at greater distances from wildflower strips. Future research should therefore include scales beyond the distances sampled in this study to help infer the implications for spatial management of wildflower strips.

Our analysis of flower strip traits underpins the correlative evidence for flower strip-mediated increases in natural pest control to account for the observed increase in crop yield. Several other studies have reported a positive effect of flower abundance and diversity on natural enemy abundance in flower strips (Haenke *et al.* 2009; Ramsden *et al.* 2014; Blaauw & Isaacs 2014b). Our study is however among the first which show that such increases in flower density and flower diversity can ultimately increase crop yield. Diverse resources are expected to support a higher diversity of pest antagonist communities, which may, for example through complementarity mechanisms, result in a higher and more stable provisioning of pest control services (Tilman 1996; Naeem & Li 1997; Hegland & Boeke 2006; Jha & Kremen 2013).

5. Conclusions

The positive effects of perennial, species-rich wildflower strips on natural pest control and crop yield found in this study highlights the value of such AES for crop production. The observed 10% yield increase implies that a notable amount of farmland could be devoted to diverse perennial wildflower strips without compromising crop yield. However, further research is needed to corroborate these results in other crops and agro-ecosystems. Our findings provide a strong argument for policy to promote and for farmers to adopt such schemes, as they are promising in reconciling the objectives of biodiversity conservation and ecological intensification in crop production.

7. Supplementary material

Table S1: Seed mixtures to establish perennial, species-rich wildflower strips. Farmers can choose from four different mixtures containing varying compositions of annual, biennial or perennial plant species (forbs, legumes and grasses) adapted to the prevailing site conditions.

Plant species	Mixture 1	Mixture 2	Mixture 3	Mixture 4
Annual				
Agrostemma githago L.	X	X		
Anchusa arvensis (L.) M.B.		X		
Buglossoides arvensis (L.) JOHNSTON		X		
Camelina sativa (L.) CRANTZ		X		
Centaurea cyanus L.	X	X	X	X
Consolida regalis GRAY		X		
Fagopyrum esculentum MOENCH	X	X		
Legousia speculum-veneris (L.) CHAIX	X	X		
Misopates orontium (L.) RAFIN.		X		
Nigella arvensis L.		X		
Papaver dubium L. S.L.		X		
Papaver rhoeas L.	X	X	X	
Silene noctiflora L.		X		
Stachys annua (L.) L.		X		
Vaccaria hispanica (MILL.) RAUSCHERT		X		
Valerianella rimosa BAST.		X		
Biennial				
Alliaria petiolata (M.B.) CAVARA ET GRANDE				X
Cichorium intybus L.	X	X	X	
Daucus carota L.	X	X	X	
Dipsacus fullonum L.	X	X		
Echium vulgare L.	X	X	X	
Malva sylvestris L.	X	X	X	
Melilotus albus MED.	X	X	X	
Pastinaca sativa L. S.L.	X	X	X	
Reseda lutea L.		X	X	
Silene alba (RAFN.) GODR.	X	X	X	
Silene dioica (L.) CLAIRV.			X	X
Tragopogon orientalis L. S.L.		X		
Verbascum densiflorum BERTOL.	X	X	X	
Verbascum lychnitis L.	X	X		
Perennial				
Achillea millefolium AGG.	X	X	X	
Agrostis gigantean ROTH				X
Anthemis tinctoria L.	X	X		
Arrhenatherum elatius (L.) PRESL			X	
Artemisia vulgaris L.			X	
Bromus erectus HUDSON S.L.			X	
Campanula trachelium L.			X	X
Carex flacca SCHREB.				X
Centaurea jacea L. S.L.	X	X	X	X
Cirsium oleraceum (L.) SCOP.				X
Clinopodium vulgare L.			X	X
Eupatorium cannabinum L.				X
Festuca pratensis HUDSON S.L.			X	X
Festuca rubra rubra L. AGG.			X	X
Filipendula ulmaria (L.) MAXIM.				X
Galium mollugo AGG.			X	
Galium verum L. S.L.			X	X
Geum rivale L.				X
Hypericum hirsutum L.				X
Hypericum perforatum L.	X	X	X	
Knautia arvensis (L.) COULTER			X	

(continued)

(continued)

Knautia dipsacifolia Kreutzer				X
Lathyrus pratensis L.				X
Leucanthemum vulgare agg.	X	X	X	X
Lolium perenne L.			X	X
Lotus corniculatus agg.			X	
Lotus pedunculatus Cav.				X
Lycopus europaeus L. s.l.				X
Lysimachia vulgaris L.				X
Lythrum salicaria L.				X
Malva moschata L.	X	X	X	
Mentha longifolia (L.) Huds.				X
Onobrychis viciifolia Scop.	X	X		
Ononis spinosa L. s.l.			X	
Origanum vulgare L.	X	X	X	
Poa pratensis agg.			X	X
Picris hieracioides L.			X	
Pulcaria dysenterica (L.) Bernh.				X
Salvia pratensis L.			X	
Saponaria officinalis L.			X	X
Scrophularia nodosa L.			X	X
Silene flos-cuculi (L.) Clairv.				X
Solidago virgaurea L. s.l.			X	X
Stachys officinalis (L.) Trevisan			X	X
Tanacetum vulgare L.	X	X	X	
Thalictrum aquilegiifolium L.				X
Valeriana officinalis agg.				X
Verbascum nigrum L.			X	
Vicia cracca L. s.l.				X
Vicia sepium L.			X	X

Table S2: Descriptive statistics of flower strip traits. Basic statistical parameters of flower strip traits which were considered as predictors for the pest density, crop damage and crop yield models. Flower density was calculated for each field from the number of flowers and inflorescences and the corresponding flower strip sampling area. Shown are arithmetic means (Mean), standard errors (SE), minima (Min) and maxima (Max) from round-averaged data.

Flower strip property	Unit	Mean	SE	Min	Max
Flower strip sampling area	m^2	561.0	247.5	150.0	2700.0
Broadleaved cover	%	51.8	7.4	3.5	82.0
Grass cover	%	29.5	8.2	3.0	86.5
Flowering species richness	#	4.4	0.8	1.0	8.5
Flower abundance	#	20280.2	11008.3	3.0	105160.0
Flower density	$\#/m^2$	31.9	13.5	0.0	116.8

Table S3: Descriptive statistics of flowering forb and legume species recorded in flower strips. Shown are arithmetic means (Mean), standard errors (SE), minima (Min) and maxima (Max) of round-averaged numbers of flowers (Flo) and inflorescences (Inf) of each forb and legume species flowering in wildflower strips.

Flowering plant species	Unit	Mean	SE	Min	Max
Ajuga reptans L.	Flo	225.0	213.5	0.0	2250.0
Anthemis tinctoria L.	Inf	25.0	23.7	0.0	250.0
Brassica napus L.	Flo	1000.8	949.4	0.0	10007.5
Cardamine hirsuta L.	Flo	540.0	512.3	0.0	5400.0
Centaurea cyanus L.	Inf	1800.3	1707.6	0.0	18000.0
Centaurea jacea L. s.l.	Inf	103.5	70.3	0.0	750.0
Chrysanthemum leucanthemum Lam	Inf	3512.5	2818.6	0.0	30000.0
Echium vulgare L.	Flo	1.5	1.4	0.0	15.0
Fragaria vesca L.	Flo	39.0	35.4	0.0	375.0
Galium aparine L.	Flo	135.0	128.1	0.0	1350.0
Galium mollugo agg.	Flo	9425.0	830.1	0.0	90000.0
Galium verum L. s.l.	Flo	875.0	830.1	0.0	8750.0
Geranium dissectum L.	Flo	41.3	33.1	0.0	350.0
Geranium molle L.	Flo	244.0	212.1	0.0	2250.0
Geranium robertianum L.	Flo	0.6	0.6	0.0	6.0
Geum urbanum L.	Flo	51.2	28.1	0.0	250.0
Glechoma hederacea L.	Flo	170.0	114.7	0.0	1200.0
Knautia arvensis (L.) Coulter	Inf	0.1	0.1	0.0	0.5
Leucanthemum vulgare agg.	Inf	1000.0	948.7	0.0	10000.0
Linaria vulgaris Mill	Flo	125.0	118.6	0.0	1250.0
Lotus comiculatus agg.	Flo	135.0	128.1	0.0	1350.0
Malva sylvestris L.	Flo	28.6	26.5	0.0	280.0
Matricaria chamomilla L.	Inf	5.0	5.0	0.0	50.0
Myosotis arvensis L. Hill	Flo	3.8	2.9	0.0	30.0
Papaver rhoeas L.	Flo	0.3	0.2	0.0	2.0
Picris hieracioides L.	Inf	0.3	0.3	0.0	3.0
Ranunculus repens L.	Flo	252.6	239.0	0.0	2520.0
Rhinanthus alectorolophus (Scop.) Pollich	Flo	30.0	28.5	0.0	300.0
Salvia pratensis L.	Flo	0.2	0.1	0.0	1.5
Salvia verticillata L.	Flo	2.5	2.4	0.0	25.0
Silene alba (Rafn.) Godr.	Flo	72.8	56.2	0.0	600.0
Sonchus asper (L.) Hill	Inf	0.1	0.1	0.0	1.0
Taraxacum officinale Weber s.l. agg	Inf	6.6	3.6	0.0	35.0
Trifolium repens L.	Inf	10.0	9.5	0.0	100.0
Urtica dioica L.	Inf	195.0	117.1	0.0	1200.0
Veronica chamaedrys L.	Flo	159.3	120.4	0.0	1270.0
Veronica persica Poiret	Flo	7.5	7.1	0.0	75.0
Vicia sepium L.	Flo	41.3	39.1	0.0	412.5

CHAPTER 3

Fitness effects of single and multiple flower species to different natural enemies of aphids

Matthias Albrecht, Jolanda Steiner, Matthias Tschumi, Martin H. Entling, Katja Jacot

Abstract

The provision of floral resources to beneficial insects can enhance biological pest control and pollination services in agro-ecosystems. To optimize the effectiveness of tailored flower strips aimed at promoting aphid control, it is essential to know which plant species are associated with the highest fitness gains for key natural enemies of aphids. Here, we experimentally examined the influence of single and multiple food plant species treatments on three key natural enemy species of aphids, *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae), *Aphidius ervi* Haliday (Hymenoptera: Braconidae) and *Episyrphus balteatus* De Geer (Diptera: Syrphidae). The following plant species – all proposed as food plants for tailored flower strips -, were tested as monoculture and mixture treatments: *Centaurea cyanus* L., *Coriandrum sativum* L., *Fagopyrum esculentum* Moench and *Phacelia tanacetifolia* Benth., and compared to water and sucrose controls. Natural enemies were caged pairwise in acetate containers arranged in climate chambers, provided with a bunch of freshly cut inflorescences or controls, guaranteeing water and resources *ad libitum*. Food plant species enhancing longevity differed between the natural enemy species, in agreement with niche-ecological predictions, and also between males and females of the same species. Females of all natural enemy species lived longer, and *C. carnea* females produced on average more eggs in mixtures than in monocultures, but differences among mixtures and the best-performing monoculture treatments were not significant. Performance and fitness results could only partially be explained by flower resource use observations. These findings highlight the importance of directly assessing performance and fitness consequences of different plant species on multiple pest control provider taxa to optimize the species composition of flower strips. We conclude that diverse plant species mixtures better support diverse natural enemy communities and thus the chances for effective biological control than single-species flower strips.

Keywords: Accessibility; agri-environment schemes (AES); conservation biological control; ecosystem services (ES); extra-floral nectar; functional biodiversity; parasitoids; pollen; predators; sown flower strips

1. Introduction

Arthropod-mediated ecosystem services, such as natural pest control, are at risk from agricultural intensification (Gurr, Wratten & Luna 2003). Many generalist and specialist natural enemies of crop pests depend on plant-provided resources that have often become rare in intensely cultivated landscapes (Landis, Wratten & Gurr 2000). Sown flower strips can mitigate this risk by providing rich floral, extra-floral and structural resources (Haaland, Naisbit & Bersier 2011; Korpela *et al.* 2013). Yet their effectiveness likely depends on the selection of plant species that benefit natural enemies but not pests (Wäckers & van Rijn 2012).

To optimize the effectiveness of tailored flower strips aimed at promoting aphid control, it is crucial to know which plant species is associated with the highest fitness gain for key natural enemies. Moreover, most pest groups are controlled by a multitude of natural enemy groups and a higher biodiversity of natural enemies is generally associated with more effective pest control (Cardinale *et al.* 2003). Thus it is important to simultaneously assess the fitness consequences of different food plant species on multiple natural enemy species. Different enemies of aphids may respond differently to floral food resources because of resource-exploitation differences such as differences in resource accessibility, different preferences of nectar and pollen composition or differences in required nutrient content (Lundgren 2009; Wäckers & van Rijn 2012; Lu *et al.* 2014). Experimental studies testing these hypotheses are largely lacking.

Positive effects of diverse plant mixtures may be expected due to positive sampling and/or resource complementarity mechanisms. A positive sampling effect occurs, if a plant species with specific trait values in the mixture dominates the mixture (Tilman, Lehman & Thomson 1997). A positive complementary effect occurs, if the variation of plant traits enhances collective performance of the mixture (Huston 1997; Loreau 2000; Loreau & Hector 2001). To our knowledge, these mechanisms have hitherto not been examined for the plant resource use of multiple natural enemy species assemblages.

In this study, we experimentally investigated the fitness consequences of four annual plant species - and a mixture of these species combined - on key aphid enemies of three different insect orders: the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae), the hoverfly *Episyrphus balteatus* De Geer (Diptera: Syrphidae) and the lacewing *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae). Moreover, we performed resource use observations and determined resource accessibility of natural enemies species to better understand the potential drivers of these fitness consequences.

Specifically, we addressed the following questions: (1) How do key aphid enemy species differ in their fitness response to different plant species? (2) Do multiple-species plant mixtures enhance fitness of key aphid enemies more than individual species (monocultures)? (3) Which mechanisms contribute to these effects?

2. Material and Methods

2.1. PLANTS

The following annual plant species were used for the experiment: *Centaurea cyanus* L. (Asteraceae), *Coriandrum sativum* L. (Apiaceae), *Fagopyrum esculentum* Moench var. Lileja (Polygonaceae) and *Phacelia tanacetifolia* Bentham var. Julia (Hydrophyllaceae). These species were selected because they have shown promise as food plants in biological control programs targeting at the promotion of parasitoids, hoverflies or lacewings (Patt, Hamilton & Lashomb 1997; Landis, Wratten & Gurr 2000; Laubertie, Wratten & Hemptinne 2012; Wäckers & van Rijn 2012). The species provide floral nectar and pollen, and *C. cyanus* additionally extra-floral nectar (EFN) by sepal nectaries (Keeler 1979). All four flowering plant species were grown from seeds (purchased from UFA Samen, Winterthur, Switzerland) in an insect-proof greenhouse at Agroscope in Zürich, Switzerland. A new set of seeds of each species was sown every second week from 16 April to 16 November 2013 into pots (2 l) filled with common gardening soil (Ökohum Staudenerde, Obi-Ter, Märwil, Switzerland; approximately 90 pots of each species at each sowing date) to ensure that flowers and extra-floral resources were available during the entire course of the experiment. Plants were watered as required. For all experiments, flower shoots were cut and placed in water no longer than 2 h before usage.

2.2. INSECTS

Aphidius ervi is a solitary endoparasitoid that attacks several species of aphids of economic importance (Pennacchio *et al.* 1994). It is native to Europe where it is widely distributed and has been introduced to other continents as biological control agent against aphids (Snyder & Ives 2003). *Episyrphus balteatus* and *Chrysoperla carnea* are both generalist predators widely distributed in European agricultural landscapes (Hagen *et al.* 1999). Their preference for feeding on aphids makes them effective for aphid control (Wäckers & van Rijn 2012). Pupae of *E. balteatus* and *A. ervi* mummies were provided by Welte Nützlinge (Insel Reichenau, Germany). *Chrysoperla carnea* (strain 88) were home-reared at Agroscope on *Ephestia kuehniella* Zeller eggs as food for the larvae. Mummies, larvae and pupae were maintained at controlled conditions (22 °C ± 2 °C and 16:8 h (L:D) photoperiod) until emergence of adults. Only starved < 24 h old adult insects were used for the experiments.

2.3. EXPERIMENTAL DESIGN

The experiment was performed in two climate chambers between June 25 and November 19, 2013. A fully randomised factorial design with the following seven treatments was used to address our research questions: each of the resource treatments *P. tanacetifolia*, *F. esculentum*, *C. sativum*, *C. cyanus*, plant mixture (resources of all four species present), water (negative control) and sucrose (2 M; positive control) were offered to a pair (male and female) of each of three natural enemy species: *A. ervi*, *E. balteatus* and *C. carnea*. Each experimental unit consisted of a cylindrical acetate container (height: 15.5 cm, diameter: 10.5 cm; volume: 1.3 l) covered with a fine meshed polyamide (*A. ervi* and *E. balteatus*) or cotton (*C. carnea*) gauze (hereafter "cage"), enclosing a water-filled plastic tube (height: 6.3 cm, diameter: 3 cm, volume: 50 ml) containing either a bunch of freshly cut inflorescences (plant species treatments), or a glass vial (volume: 2.5 ml) filled with cotton that was soaked with either water (water control) or freshly defrosted sucrose (2 M; Sigma-Aldrich, Steinheim, Germany). To prevent insects from drowning while still guaranteeing *ad libitum* access to water, plant bunches as well as vials filled with water or sucrose were wrapped with water soaked cotton wool. Plant resource treatments (both single-species and mixture treatments) consisted of a total of 25-30 fully open flowers. To achieve approximately constant number of flowers across plant resource treatments, four freshly cut inflorescences per plant species were used for the *C. cyanus*, *C. sativum* and *P. tanacetifolia* treatments, and eight inflorescences of the *F. esculentum* treatment. The plant mixture treatment (hereafter "mixture") consisted of one inflorescence of each of the plant species of *P. tanacetifolia*, *C. sativum* and *C. cyanus* and two inflorescences of *F. esculentum*. Using excised inflorescences rather than entire potted plants is an adequate and robust technique for the comparative assessment of the performance and fitness consequences of floral and extra-floral resources provided by plant species on insects (Wade & Wratten 2007). Plant species, sucrose and water treatments were replaced every 3 days to guarantee fresh and fully exploitable resources *ad libitum*. A total of 20 cages of each treatment for each of the two species *A. ervi* and *E. balteatus*, and 14 cages of each treatment for *C. carnea* were randomly assigned to two identical, gradually tempered climate chambers with identical conditions (18:21 ± 3 °C (night:day), 60 ± 10 % RH, photoperiod 16:8 h (L:D)) and two experimental rounds. Thus, a total of 378 cages and 756 insects (378 females and 378 males, 252 individuals per species) were used for the experiment. The spatial position of cages within climate chambers was randomized every day.

2.4. FITNESS OF NATURAL ENEMIES

All cages were checked daily between 08:00 and 10:00 a.m. for dead insects and longevity determined for each individual of all three natural enemy species. For *C. carnea*, total fecundity (total number of eggs laid during the entire life-time of a female) and pre-oviposition period (number of days from emergence to the first oviposition) was determined. Reproduction parameters for *A. ervi* and *E. balteatus* were not assessed due to their dependency on the presence of aphids (which were not included in the experiment to avoid bias of the resource treatment effects): the endoparasitoid *A. ervi* obviously relies on the presence of aphids for reproduction, but also oviposition of *E. balteatus* is stimulated by cues from its aphid prey, with oviposition rate depending on aphid densities (Scholz & Poehling 2000).

2.5. RESSOURCE USE OF NATURAL ENEMIES

Floral and extra-floral resource use by the different natural enemy species was recorded daily for each mixture treatment cage. For each individual insect we recorded i) on which plant species it consumed resources and ii) which type of resource it consumed on *C. cyanus* (floral vs. extra-floral). Accessibility of resources was predicted by measurements of the mouthpart structures of the insects used in the experiment and compared to published data on the floral architecture of the study plant species (Baggen, Gurr & Meats 1999; Winkler 2005). For insect species without elongated mouthpart structures, such as *C. carnea* and *A. ervi*, head width is considered as the limiting factor in exploiting nectar from deep and narrow flower corollas (Winkler 2005). For *E. balteatus*, the limiting factor in exploiting nectar is the proboscis length (Gilbert 1981). We measured the head width (the extreme lateral margins of the eyes), and for *E. balteatus* the proboscis length, of 28 newly emerged individuals (14 males and 14 females) of each of the three natural enemy species, using a M165C Leica binocular and LAS V3.8 computer software (Leica, Heerbrugg, Switzerland).

2.6. STATISTICAL ANALYSIS

Linear mixed effect models were fitted to test the effect of treatment (fixed factor with the levels "*C. cyanus*", "*C. sativum*", "*F. esculentum*", "*P. tanacetifolia*", "mixture", "sucrose control" and "water control") on the longevity of natural enemies (log-transformed), with experimental round, climate chamber and cage as random factors. To test whether treatment effects differed among natural enemy species and sexes, the factors natural enemy species, sex and the two-way interactions among these two factors and treatment were included as fixed effects in the model. As treatment effects significantly varied across natural enemy species (significant treatment x natural enemy species interaction), separate analyses were performed for each natural enemy species. Model selection followed the recommendations of Zuur *et al.* (2009). Statistical inference for explanatory variables was based on likelihood ratio tests, and Tukey's HSD post-hoc tests were used to test for significant differences among treatment levels. The same model was fitted to test treatment effects on total fecundity (sqrt-transformed) and pre-oviposition period (log-transformed) of *C. carnea* females (without cage as random factor since only one female per cage was used as experimental unit).

To explore how natural enemy species differed in their frequency of using resources of the four plant species (floral resources and extra-floral nectar pooled in *C. cyanus*), standardized resource use frequencies of the plant mixture treatment were analysed. A two-step analysis was performed to account for the zero-inflation of the data (Zuur, Hilbe & Ieno 2013): first, a binomial generalized linear mixed model with a logit-link function was fitted to the binary version of the data set (0 = no resource used during any of the daily observations, 1 = resource used) using the glmer function of the lme4 package in R (Bates *et al.* 2014). Second, a linear mixed effect model was applied on the dataset considering only the resource use frequencies > 0. Both models consisted of the two fixed factors plant species and natural enemy species, the interaction among them, and the random factors experimental round and climate chamber. To further explore whether the natural enemy species exhibited different preferences for either floral resources (floral nectar and/or pollen) or extra-floral nectar in *C. cyanus*, the same approach was used as described above to account for the zero-inflation of the data. Models consisted of the two fixed factors resource type (floral vs. extra-floral) and natural enemy species, the interaction among them, and the random factors experimental round and climate chamber. For this analysis, observations of both, the single-species treatment of *C. cyanus* and the mixture treatment containing *C. cyanus*, were considered. No overdispersion was detected for any of the binomial models.

Linear model assumptions of normality and homoscedasticity of residuals were visually checked based on normal Q-Q plots and by plotting residuals against expected values. All analyses were performed with the statistical software R version 3.0.1 (R Core Team 2014).

3. Results

3.1. LONGEVITY OF NATURAL ENEMIES

Natural enemy species responded differently to treatments in terms of longevity (treatment x natural enemy species interaction: χ^2 = 141.12, df = 12, P < 0.001). Longevity of *A. ervi* differed between treatments (χ^2 = 75.24, df = 6, P < 0.001): Individuals of *A. ervi* lived longest in the sucrose treatment, and survived longer when feeding on the mixture treatment or the *C. cyanus*, *C. sativum*, *F. esculentum* single-species treatments than individuals feeding on *P. tanacetifolia* or water (Fig. 1a). No statistical difference in longevity was detected between the sexes of *A. ervi* across treatments (χ^2 = 1.67, df = 1, P = 0.196). Males and females of *C. carnea* and *E. balteatus*, however, responded differently to treatments (treatment x sex interaction: *C. carnea*: χ^2 = 47.39, df = 6, P < 0.001; *E. balteatus*: χ^2 = 23.17, df = 6, P < 0.001). While males of *C. carnea* lived longest when feeding on *F. esculentum* and the mixture, female longevity was highest in the mixture treatment (Fig. 1b). Males of *E. balteatus* lived longest in the mixture and sucrose treatment whereas females lived longest when feeding on *F. esculentum*, mixture and sucrose (Fig. 1c). Although, on average, females of *A. ervi* and *C. carnea* lived longest in the mixture treatment (Fig. 1a,b), longevity of neither females nor males of the studied natural enemy species was significantly higher in the mixture compared to the best-performing monoculture treatment (Fig. 1). Yet, females longevity in mixtures was higher than average longevity in monocultures in all three natural enemy species (Fig. 2; *A. ervi*: χ^2 = 9.50, df = 1, P = 0.002; *E. balteatus*: χ^2 = 7.37, df = 1, P = 0.007; *C. carnea*: χ^2 = 8.77, df = 1, P = 0.003), while male longevity was increased compared to average monoculture in *C. carnea* (Fig. 2; χ^2 = 7.39, df = 1, P = 0.007), but not in the other two species (*A. ervi*: χ^2 = 0.79, df = 1, P = 0.375; *E. balteatus*: χ^2 = 0.02, df = 1, P = 0.885).

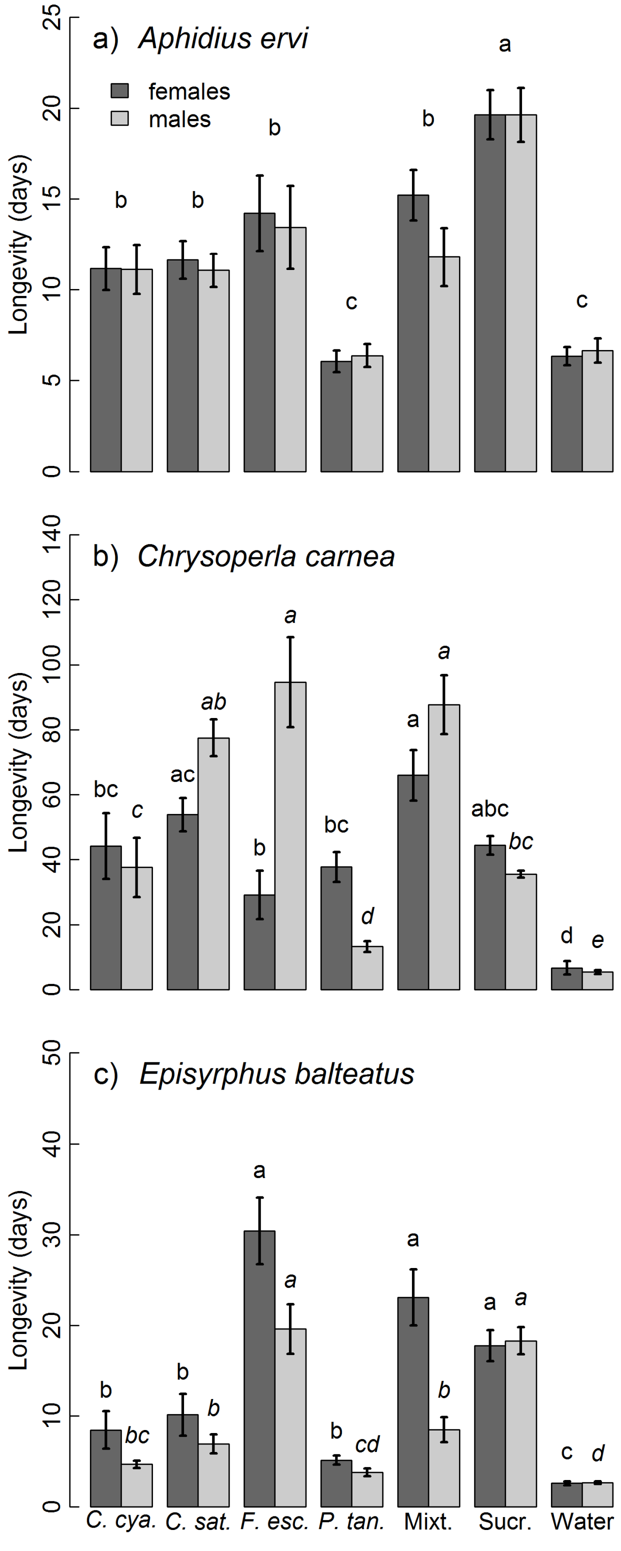

Fig. 1: Mean (± 1 SE) longevity of **a)** *Aphidius ervi* (Hymenoptera: Braconidae), **b)** *Chrysoperla carnea* (Neuroptera: Chrysopidae) and **c)** *Episyrphus balteatus* (Diptera: Syrphidae) feeding on different resource treatments: floral resources (nectar and pollen; and extra-floral nectar in *Centaurea cyanus*) of *C. cyanus* ("*C. cya.*"), *Coriandrum sativum* ("*C. sat.*"), *Fagopyrum esculentum* ("*F. esc.*"), and *Phacelia tanacetifolia* ("*P. tan.*") as single-species treatments, mixture of all four flowering species ("Mixt."), sucrose (2 M; positive control; "Sucr.") and water (negative control). The number of flowers was approximately constant across plant treatments (single-species and the mixture treatments). In *A. ervi* females and males did not respond significantly different across treatments and therefore the results of analyses with the pooled data of both sexes are shown. In *C. carnea* and *E. balteatus* females and males responded differently to treatments and sexes were analysed separately. Different letters indicate significant treatment differences based on Tukey's HSD post-hoc tests ($P < 0.05$).

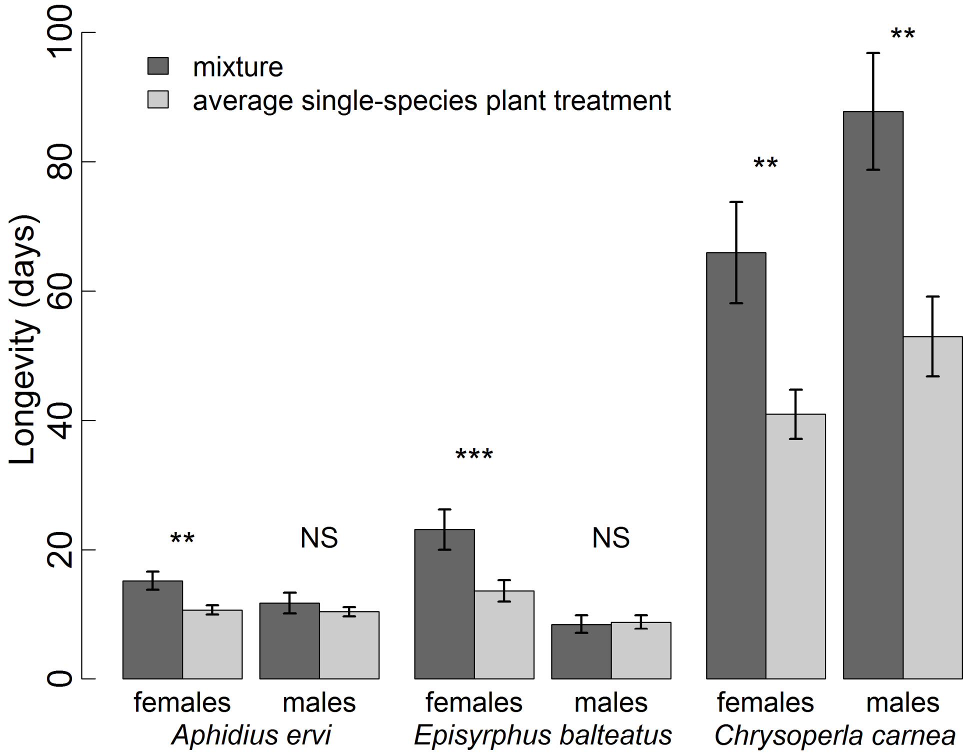

Fig. 2: Longevity of female and male *Aphidius ervi*, *Episyrphus balteatus* and *Chrysoperla carnea* under the average single-species resource plant treatment (mean of single-plant treatments of *Centaurea cyanus*, *Coriandrum sativum*, *Fagopyrum esculentum* and *Phacelia tanacetifolia* pooled together) and the mixture treatment consisting of all four plant species at approximately constant number of flowers across treatments. NS = not significant ($p \geq 0.05$), **$p < 0.01$, ***$p < 0.001$.

3.2. FECUNDITY OF *C. CARNEA*

In the two control treatments, water and sucrose, no eggs were laid by *C. carnea*. Therefore, the water and sucrose treatments were not included in the following analyses. Total fecundity of *C. carnea* females differed significantly between plant treatments (χ^2 = 60.24, df = 4, $P <$ 0.001): it was higher in the flower mixture and the *C. sativum* treatment compared to the *C. cyanus*, *F. esculentum* and P. *tanacetifolia* treatments (Fig. 3a). Moreover, pre-oviposition and oviposition period of *C. carnea* females differed between treatments (pre-oviposition period: χ^2 = 53.66, df = 4, P < 0.001; oviposition period: χ^2 = 12.79, df = 4, P = 0.012). Pre-oviposition period was longer for *C. carnea* females feeding on *P. tanacetifolia* than for females feeding on other plant species or the mixture (Fig. 3b).

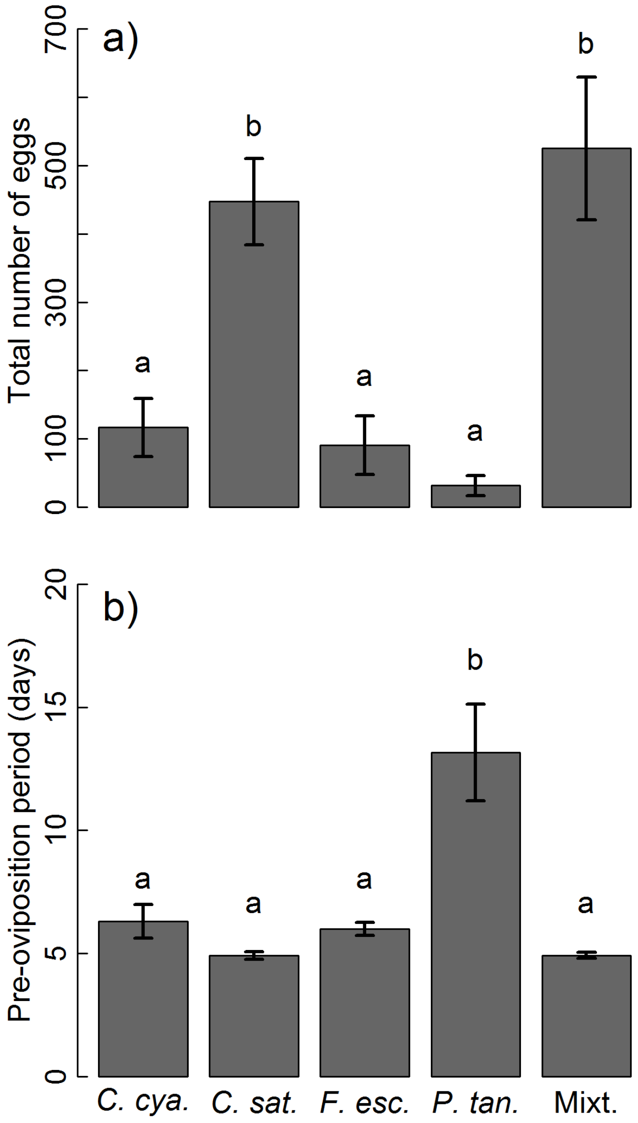

Fig. 3: a) Mean (± 1 SE) total fecundity and **b)** mean (± 1 SE) pre-oviposition period of *C. carnea* females under four single-species plant treatments (*Centaurea cyanus*: "*C. cya.*", *Coriandrum sativum*: "*C. sat.*", *Fagopyrum esculentum*: "*F. esc.*" and *Phacelia tanacetifolia*: "*P. tan.*") and the mixture ("Mixt.") treatment consisting of all four flowering plant species at approximately constant number of flowers across treatments. Different letters indicate significant treatment differences based on Tukey's HSD post-hoc tests ($P < 0.05$).

3.3. OBSERVATIONS OF PLANT RESOURCE USE BY NATURAL ENEMIES

The three natural enemy species differed in their use of resources provided by the different plant species, both in terms of the probability to use a resource (plant species x natural enemy species interaction of the binomial model: $\chi^2 = 21.94$, df = 6, $P < 0.001$) and the frequency of observed resource use events if they were observed to use resources of all plant species (plant species x natural enemy species interaction of the linear model considering only observed resource use events: $\chi^2 = 17.71$, df = 6, $P = 0.007$; Fig. 4). Moreover, although the probability of being observed to use at least once floral or extra-floral resources in *C. cyanus* did not differ between the natural enemy species (resource type x natural enemy species interaction of the binomial model: $\chi^2 = 1.34$, df = 2, $P = 0.512$), the relative frequency by which the species either used floral resources or extra-floral nectar if they were observed to use both resource types differed significantly (plant species x natural enemy species interaction of the linear model considering only observed resource use events: $\chi^2 = 11.52$, df = 2, $P = 0.003$).

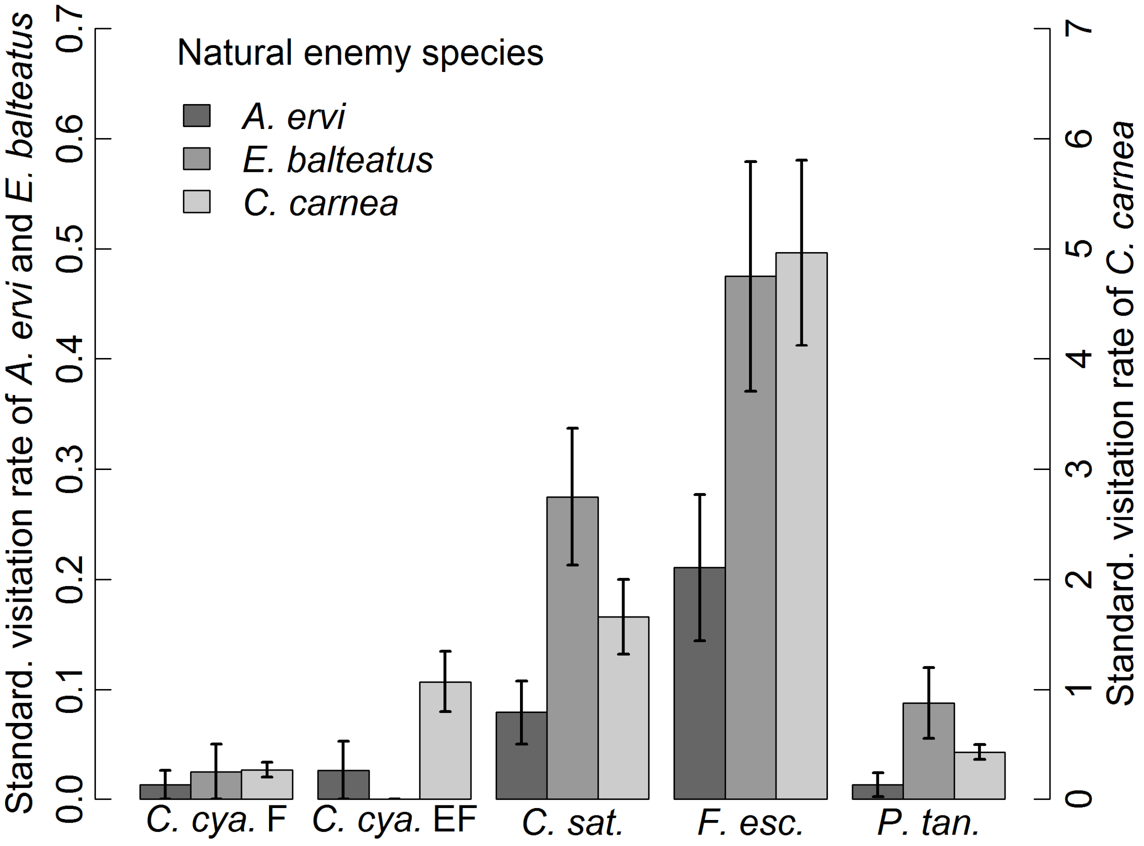

Fig. 4: Plant resource use (pollen and nectar) of *Aphidius ervi*, *E. balteatus* (y-axis on the left) and *C. carnea* (y-axis on the right), when offered *Centaurea cyanus* ("*C. cya.*"), *Coriandrum sativum* ("*C. sat.*"), *Fagopyrum esculentum* ("*F. esc.*") and *Phacelia tanacetifolia* ("*P. tan.*") in the mixture treatment. Floral (F) and extra-floral (EF) nectar consumption by natural enemies is shown for *C. cyanus*.

3.4. FLORAL RESOURCE ACCESSIBILITY

The comparison of measured head and mouthpart parameters of the natural enemies species with those of flower morphology of the studied plants indicates that all three natural enemies are able to access floral nectar of *F. esculentum* and *C. sativum*, but floral nectaries of *P. tanacetifolia* are only accessible for *A. ervi* and *C. carnea*, but not *E. balteatus* (Table 1). According to our analysis, none of the three natural enemy species are able to access floral nectar of *C. cyanus*, in contrast to the accessible extra-floral nectar offered by this plant species. The pollen of each tested plant species is well exposed and accessible for all three studied natural enemy species (Table 1).

Table 1: Head and mouthpart measures of *A. ervi*, *E. balteatus* and *C. carnea* (measured for 14 males and 14 females of each natural enemy species) compared with flower morphology of *C. sativum*, *C. cyanus*, *F. esculentum* and *P. tanacetifolia* (from Baggen, Gurr & Meats 1999[1] and Winkler 2005[2]) to predict floral resource accessibility. EFN = extra-floral nectar.

Natural enemy species	Head width / Proboscis length (mm)	Plant species	Corolla depth (mm)	Corolla aperture (mm)	Resource	Predicted access
A. ervi	0.49 ± 0.03	*F. esculentum*	0.54 ± 0.01[1]	6.59 ± 0.23[1]	floral nectar	yes
					pollen	yes
C. carnea	1.37 ± 0.04				floral nectar	yes
					pollen	yes
E. balteatus	1.14 ± 0.15				floral nectar	yes
					pollen	yes
A. ervi	0.49 ± 0.03	*C. sativum*	0.00 ± 0.00[1]	0.58 ± 0.02[1]	floral nectar	yes
					pollen	yes
C. carnea	1.37 ± 0.04				floral nectar	yes
					pollen	yes
E. balteatus	1.14 ± 0.15				floral nectar	yes
					pollen	yes
A. ervi	0.49 ± 0.03	*P. tanacetifolia*	(1) 7.07 ± 0.15[1] (2) 1.70 ± 0.05[1,a]	(1) 5.05 ± 0.18[1] (2) 0.15 ± 0.01[1,b]	floral nectar	(1) yes (2) no
					pollen	yes
C. carnea	1.37 ± 0.04				floral nectar	(1) yes (2) no
					pollen	yes
E. balteatus	1.14 ± 0.15				floral nectar	(1) no (2) no
					pollen	yes
A. ervi	0.49 ± 0.03	*C. cyanus*	(1) 7.59 ± 0.15[2,c] (2) 2.57 ± 0.07[2,d]	0.28± 0.02[2]	floral nectar	(1) no (2) no
					pollen	yes
					EFN	yes
C. carnea	1.37 ± 0.04				floral nectar	(1) no (2) no
					pollen	yes
					EFN	yes
E. balteatus	1.14 ± 0.15				floral nectar	(1) no (2) no
					pollen	yes
					EFN	yes

[a] Depth from stamen appendages to nectaries; [b] Size of gaps in stamen appendages; [c] Measurement from the deepest cleft of the corolla to the corolla base; [d] Measurement from the deepest cleft of the corolla to the point that the stamens inserted.

4. Discussion

This study is among the first simultaneously comparing the effects of different food plants in monoculture and as mixture on fitness parameters of multiple key natural enemy species of aphids. We found that different food plant species can vary strongly in their influence on the longevity of different natural enemy species, as well as males and females within the same species. In agreement with positive sampling effect predictions (Tilman, Lehman & Thomson 1997), plant mixture increased female longevity of all natural enemy species and total fecundity of *C. carnea* compared to the average performance of the monocultures, but not compared to the best-performing plant species in monoculture.

Our finding of increased longevity of *A. ervi* feeding on *F. esculentum* and *C. sativum* is in line with single-enemy studies (Araj *et al.* 2006; Wade & Wratten 2007) and the feeding on EFN of *C. cyanus* has been demonstrated to increase the longevity of other Braconidae species before (Jamont, Crépellière & Jaloux 2013). Morphological analyses suggest that, in contrast to *F. esculentum, C. sativum* and EFN of *C. cyanus,* floral nectar of *C. cyanus* is not accessible for *A. ervi*, indicating that EFN (and maybe pollen) are the floral resources of *C. cyanus* increasing longevity of *A. ervi*. Likewise, the gaps between the stamens and petals of *P. tanacetifolia* are probably too small to allow *A. ervi* accessing floral nectar, explaining the short longevity in these treatments. Surprisingly, *P. tanacetifolia* has been suggested to benefit *A. ervi* before (Araj *et al.* 2006). It is conceivable that morphological or chemical differences in cultivars (Araj *et al.* 2006 used the cultivar "Balo") may have contributed to these contrasting results. Our study provides evidence that *A. ervi* feeds predominantly on relatively open nectar sources as found in flowers of *F. esculentum*, *C. sativum* and EFN of *C. cyanus*, which is also supported by resource use observations. Sugar feeding is indispensable to parasitoid survival for males and females and can also increase female's daily fecundity (Azzouz *et al.* 2004; Wyckhuys *et al.* 2008; Wäckers & van Rijn 2012).

Lacewings require pollen in addition to sugar for maximal survival and reproduction (Li, Meissle & Romeis 2010; Wäckers & van Rijn 2012). This explains why lacewings performed markedly better on certain floral resources compared to sucrose. *F. esculentum,* flower mixture and *C. sativum* most strongly enhanced longevity of male *C. carnea,* whereas female longevity was enhanced the most when provided with flower mixture or *C. sativum*. Our results suggest that floral nectar of *P. tanacetifolia* is inaccessible for *C. carnea* and that increased longevity compared to the water control is probably based on pollen consumption. These results were also supported by the observations of resource use, but unfortunately, we could not discriminate between the sexes. Interestingly, longevity of *C. carnea* males increased more strongly than that of females when provided with *F. esculentum*. Reproductive activities of *C. carnea* females could explain the trend towards higher longevity of males compared to females, as high rates of egg production can lead to a decrease in survival (Partridge, Green & Fowler 1987). This is also supported by similar longevity of *C. carnea* males and females when feeding on sucrose, where females laid no eggs. Adult lacewings are unable to produce eggs without feeding on a protein-rich food source (Li, Meissle & Romeis 2008, 2010; Wäckers & van Rijn 2012). Mixtures of all four experimental plant species and *C. sativum* in monoculture supported female fecundity almost as well as artificial diet, specifically designed to promote *C. carnea's* fitness (Hagen & Tassan 1970). While low fecundity of *C. carnea* exclusively feeding on *P. tanacetifolia* is likely due to the low survival rate, low fecundity of *C. carnea* provided with *F. esculentum* is surprising, as floral resources of F. esculentum are well accessible. Possibly, the pollen of *F. esculentum* is not suitable for *C. carnea* females. This fact deserves further study, also because *F. esculentum* strongly promoted longevity of *C. carnea* males.

Likewise, in the longevity of *E. balteatus*, significant differences between treatments in males and females were found. Common trends towards higher longevity of females compared to males confirms previous findings (Geusen-Pfister 1987; Pinheiro *et al.* 2013). Of the tested plant treatments, *F. esculentum*, and in particular the mixture extended female longevity the most, while male longevity was promoted most when exclusively feeding on *F. esculentum*. Nectar is an important energy source for hoverflies such as *E. balteatus*, whilst pollen is needed by both the males and the females for sexual maturation (Haslett 1989; van Rijn 2006). It is, however, suggested that males demand more nectar (energy) but less pollen than females, while females need to balance pollen and nectar intake (Gilbert 1981; Haslett 1989; Sutherland, Sullivan & Poppy 1999). Floral nectar of *P. tanacetifolia* and *C. cyanus* is likely not accessible for *E. balteatus*, probably explaining the relatively short longevities of this species when these plants were provided in monoculture. For *E. balteatus*, probably only flowers with nectar available at a depth of less than 2 mm are suitable (van Rijn & Wäckers 2010). Despite well accessible EFN of *C. cyanus*, we observed almost never EFN resource use by *E. balteatus*.

Two not mutually exclusive mechanisms have contributed to the increased fitness parameters of all three natural enemy species in plant mixtures compared to single plant species (pooled together): i) positive sampling effect, ii) complementarity in resource use. The positive sampling effect can be explained by particularly beneficial plant species in the mixture, which may have primarily accounted for the enhanced performance of the three natural enemy groups. Yet, complementary effects seem also to play a role, as average fitness values of mixture treatments were often higher than those of the best performing monoculture (e.g. fecundity of *C. carnea*, longevity of *A. ervi* females and *C. carnea* females) although statistically only significant for *C. carnea* fecundity. Despite realised with relatively few species, our experiment indicate strong differences and a tendency towards positive diversity effects. Moreover, we extrapolate that a higher number of enemy species would show still more diverse resource preferences. As higher biodiversity of natural enemies is generally associated with more effective pest control (Cardinale *et al.* 2003), this supports the idea of flower mixtures to promote aphid biocontrol.

Nevertheless, it would be ideal to assess additional fitness parameters (fecundity, development) to draw conclusions about natural enemy's benefit, as increased longevity not necessarily correspond with increased fecundity (Laubertie, Wratten & Hemptinne 2012). Additionally, the often highly significant differences in responses of females and males found in our study indicate that performance and fitness studies, as well as observations of flower visitation by natural enemies should differentiate between sexes. According to our results, predictions concerning suitability of flowering plants based on visitation rates are only convincing if the sexes can be differentiated.

5. Conclusions

Our results highlight the importance of considering multiple natural enemy taxa when assessing the suitability of food plant species for flower strips aimed at promoting natural enemy communities and associated biocontrol services. Confirming niche-ecological predictions there was no single plant species providing the greatest benefits (increased longevity) for all three natural enemy taxa, but rather the best-performing plant species differed between the enemy species and between males and females within species. Overall, mixtures increased average female longevity of all three natural enemy species more than monocultures. We therefore recommend that tailored flower strips aimed at promoting diverse natural enemy communities and maximizing pest control should comprise diverse mixtures providing different floral and extra-floral resources rather than consisting of only few or even single food plant species.

CHAPTER 4

High effectiveness of tailored flower strips in reducing pests and crop plant damage

Matthias Tschumi, Matthias Albrecht, Martin H. Entling, Katja Jacot

Abstract

Providing key resources to animals may enhance both their biodiversity and the ecosystem services they provide. We examined the performance of annual flower strips targeted at the promotion of natural pest control in winter wheat. Flower strips were experimentally sown along 10 winter wheat fields across a gradient of landscape complexity (i.e. proportion non-crop area within 750 m around focal fields) and compared with 15 fields with wheat control strips. We found strong reductions in cereal leaf beetle (CLB) density (larvae: 40%; adults of the second generation: 53%) and plant damage caused by CLB (61%) in fields with flower strips compared with control fields. Natural enemies of CLB were strongly increased in flower strips and in part also in adjacent wheat fields. Flower strip effects on natural enemies, pests and crop damage were largely independent of landscape complexity (8% to 75% non-crop area). Our study demonstrates a high effectiveness of annual flower strips in promoting pest control, reducing CLB pest levels below the economic threshold. Hence, the studied flower strip offers a viable alternative to insecticides. This highlights the high potential of tailored agri-environment schemes to contribute to ecological intensification and may encourage more farmers to adopt such schemes.

Keywords: Conservation biological control; ecosystem functioning; habitat management; landscape context; *Oulema melanopus* L.; wildflower strip

1. Introduction

Meeting growing demands for agricultural products, while minimizing negative environmental impacts, is among the biggest challenges to mankind (Godfray *et al.* 2010). Productivity increase per unit area achieved by conventional agricultural intensification has come at the cost of adverse effects on the environment, including losses of farmland biodiversity and associated ecosystem services, which may even have negative feedbacks on sustainable crop production (Matson *et al.* 1997; Kleijn *et al.* 2009). Plant protection measures are still predominantly based on chemical pesticides which, however, are costly in terms of monetary investment and their impact on biodiversity and environment (Geiger *et al.* 2010; Chaplin-Kramer *et al.* 2011). The often concomitant simplification of agricultural landscapes further tends to disrupt ecosystem services (Caballero-Lopez *et al.* 2012), with biological pest control considered as being one of the services most at risk (Chaplin-Kramer *et al.* 2011).

Ecological intensification, in contrast, seeks environmentally friendly alternatives to anthropogenic chemical inputs by harnessing ecosystem services (Bommarco, Kleijn & Potts 2013). Effective promotion of natural enemy mediated pest control through adequate habitat management, for example, may have a strong potential to increase yields at reduced levels of pesticide inputs (Letourneau *et al.* 2009). Besides promoting farmland biodiversity, a key goal of many agri-environment schemes (AES) is to foster ecosystem services, such as biological pest control or animal provided pollination (Haaland, Naisbit & Bersier 2011; Ekroos *et al.* 2014). Whereas biodiversity effects of AES have been repeatedly studied in the last decade (Kleijn *et al.* 2006; Batary *et al.* 2011; Kampmann *et al.* 2012), effects of AES on ecosystem services such as natural pest control or pollination remained much less studied and the consequences of pest control on crop damage or yield were rarely quantified (Whittingham 2011). Sown wildflower strips tailored to the needs of functionally important arthropod groups such as crop pollinators or pests' natural enemies may effectively promote the delivery of ecosystem services in nearby crops (Haaland, Naisbit & Bersier 2011; Korpela *et al.* 2013).

Many service-providing arthropods depend on plant-provided resources (e.g. nectar, pollen and shelter) at least during some life stages. These resources have become rare in intensified agricultural landscapes, but may be effectively substituted by sown flower strips (Haenke *et al.* 2009; Winkler *et al.* 2010; Wäckers & van Rijn 2012; Korpela *et al.* 2013). Maximizing ecosystem services through habitat management needs a refined selection of floral resources and a well-adapted management to ensure that the right resources are provided at the place and time they are needed. Annual flower strips within crop rotations can meet this objective and offer a flexible tool for practitioners to manage ecosystem services at the field scale. However, such transient habitat elements rely on the colonisation by service providers from less disturbed perennial semi-natural habitats. Therefore, their effectiveness in providing pest control services is expected to be contingent on the amount of perennial habitats in the agricultural landscape (i.e. landscape complexity; Batary *et al.* 2011; Tscharntke *et al.* 2012; Scheper *et al.* 2013). Recent studies underline the role of floral resources for natural enemy performance at the plot and field scale (Lundgren 2009; Caballero-Lopez *et al.* 2012; Wäckers & van Rijn 2012; Diehl *et al.* 2013). In addition, landscape complexity can be an important driver of natural enemy and pest assemblages at large spatial scales (Chaplin-Kramer *et al.* 2011). Yet, there is a lack of studies simultaneously addressing the effects of targeted floral resources on natural enemies, pest suppression and the consequences on crops at various levels of landscape complexity (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer *et al.* 2011 but see e.g. Woltz, Isaacs & Landis 2012).

Cereal leaf beetles (hereafter CLB), *Oulema* sp., are among the major cereal pests in Europe, Asia and North America, and cause economic damage at densities above 0.4 larvae per tiller (wheat shoot including stem, leaves and ear; Ihrig *et al.* 2001; Buntin *et al.* 2004). To date, CLB control largely relies on insecticide use. Alternative control strategies are highly desired. To our knowledge, this is one of the first replicated studies exploring the potential of tailored agri-environmental measures to control CLB.

Here, we examined the effectiveness of experimentally established annual flower strips specifically designed to promote natural control of cereal pests along a gradient of landscape complexity. By focusing on CLB control by its natural enemies, we addressed the following questions: (i) Do flower strips promote natural enemies of CLB? (ii) Do they reduce CLB densities in adjacent winter wheat? (iii) To what extent does this translate into lower plant damage? (iv) How does landscape complexity interact with flower strip effectiveness?

2. Materials and methods

2.1. STUDY DESIGN

Field experiments were conducted between April and July 2012. Thirty winter wheat fields (hereafter focal fields) were selected along a gradient of landscape complexity in the central Swiss plateau (cantons Zurich and Aargau). The region represents the typical agricultural landscape of the Swiss plateau consisting of a relatively small-scaled mosaic of arable crops (predominantly cereals, maize, sugar-beets, oilseed rape and potatoes), grasslands and forests (Supplementary material Table S1). Field size was 2.03 ha (± 0.18 ha) on average and the minimum distance between focal fields was 900 m (mean ± SE: 7918 m ± 232 m). All focal fields were managed without fungicides, insecticides or growth regulators (Swiss IP extenso; Bundesrat 2015). Along the full length of a randomly selected border of 15 focal fields, a standardized 3 m-wide flower strip was sown in April 2012. In the other 15 focal fields, a 3 m-wide winter wheat strip along the full length of a randomly chosen border served as a control strip.

The seed mixture of the flower strips consisted of the following annual plant species: *Anethum graveolens* L. (Apiaceae), *Anthemis arvensis* L. (Asteraceae), *Anthriscus cerefolium* (L.) Hoffm. (Apiaceae), *Centaurea cyanus* L. (Asteraceae), *Coriandrum sativum* L. (Apiaceae), *Fagopyrum esculentum* Moench (Polygonaceae) and *Papaver rhoeas* L. (Papaveraceae) (see supplementary material Table S2 for quantities of seeds sown per area). These species were selected based on a review of existing evidence for positive effects of floral and extra-floral (*C. cyanus*) resources offered by these species on the performance, fitness or population dynamics of key natural enemies of major wheat pests, such as CLB and aphids, i.e. ladybirds (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae), parasitic wasps (Hymenoptera), predatory bugs (Hemiptera: Heteroptera) and hoverflies (Diptera: Syrphidae) (Heimpel & Jervis 2005; Bianchi & Wäckers 2008; Fiedler, Landis & Wratten 2008; Isaacs *et al.* 2009; Haaland, Naisbit & Bersier 2011; Géneau *et al.* 2012; Wäckers & van Rijn 2012). A further criterion for the selection of the plant species was that the provision of floral and extra-floral resources, as well as shelter, matches the time at which crop pests are most effectively controlled by their natural enemies (April-July in the study area) along with agronomic (agronomical unproblematic species) and esthetical considerations (Junge *et al.* 2009). No pesticide treatments (except targeted herbicide application to individual plants), mowing or fertilization were conducted in the flower strips. Five flower strips had to be abandoned because they were overgrown by spontaneous weedy vegetation and/or the sown plant species failed to establish properly.

2.2. ASSESSMENT OF CEREAL LEAF BEETLE DENSITY AND PLANT DAMAGE

Cereal leaf beetles (CLB) *Oulema* sp. are major cereal crop pests in Europe, Asia and North America (Ihrig *et al.* 2001; Evans *et al.* 2013). Overwintering predominantly in woody habitats, CLB adults disperse into cereal crops in spring, where the larvae cause damage by removing the photosynthetic tissue of cereal plants (Buntin *et al.* 2004). The economic threshold has been estimated at 0.4 larvae per tiller (Buntin *et al.* 2004). Natural enemies comprise generalist predators such as ground beetles, rove beetles, ladybirds, predatory bugs and lacewing larvae, and specialized parasitic hymenoptera (Schärer 1994; Meindl *et al.* 2001; Malschi, Tritean & Serbanescu 2010; Evans *et al.* 2013), but quantitative knowledge on the relative importance of different CLB natural enemies is largely lacking. In the study region, two CLB species, O. *melanopus* L. and *O. gallaeciana* Heyden occur in wheat crops. However, *O. melanopus* is by far more abundant than *O. gallaeciana*. As larvae of the two CLB species cannot be easily discriminated in the field, we did not analyse them separately. The two CLB species have a similar pest status (Schärer 1994).

CLB density and plant damage were assessed at two distances (near vs. far) from the flower strips or wheat control strips following a stratified random approach. First, a 'near' sector ranging from 0.5 m to 10.4 m from the strip border and a 'far' sector between 10.5 m and 20.4 m from the strip border were defined. In a second step, we randomly selected a distance within the 'near' sector and then defined the 'far' distance as the near distance plus 10 m. This design allows the modelling of a 'near' and a 'far' distance category as well as distance as a continuous variable. All CLB larvae of 25 wheat tillers from two randomly selected plots at each distance and focal field were recorded twice during the peak of larval appearance (Schärer 1994; Ihrig *et al.* 2001; End of May / mid-June; BBCH 40 to 70; Supplementary material Table S3). Adult CLB were sampled using standardized sweep netting (60 sweeps at each distance and focal field, 40 cm sweep net diameter). We assessed the second generation of beetles that develop from larvae at the beginning of July (BBCH 77 to 87; Supplementary material Table S3), which should, in contrast to the first generation of adult beetles colonizing fields, directly reflect the overall impacts of natural enemies on eggs, larvae and pupae. Plant damage caused by CLB was assessed as percentage leaf damage of the same 2 x 25 wheat tillers per distance used for the sampling of CLB larvae in mid-June (Supplementary material Table S3) within six categories (1: <1%; 2: 1 - 5%; 3: 5 - 10%; 4: 10 - 25%; 5: 25 - 50%; 6: >50%; Schärer 1994).

2.3. SAMPLING OF NATURAL ENEMIES

Natural enemies were sampled at the same distances as CLB and plant damage, and additionally in flower and control strips. Predatory bugs, ladybirds (adults and larvae) and lacewings (adults and larvae) were sampled using standardized sweep netting (sweep net diameter: 40 cm; 60 sweeps); ground beetles were sampled with pitfall traps (two pitfalls per distance; 10 cm funnel diameter; 70% Ethanol). Sweep net sampling was carried out during two rounds in Mid-June and at the beginning of July (Supplementary material Table S3). Pitfall sampling was carried out during three sampling rounds of one week from May 5th to July 5th (Supplementary material Table S3). All captured individuals were identified to species or, if not possible (e.g. Heteroptera nymphs), genus level. Hymenopteran parasitoids could not be analysed in this study.

2.4. LANDSCAPE COMPLEXITY

To examine effects of landscape complexity and potential interactions with flower strip on natural enemies, CLB and wheat plant damage, percentage of non-crop area was calculated in a radius of 750 m around focal fields (Supplementary material Table S1). This scale is considered adequate to study responses of specialist pests and natural enemies to the landscape context (e.g. Chaplin-Kramer *et al.* 2011). Information on land use classes was derived from official digital land-use maps (vector25 and TLM3D, swisstopo, Wabern) and verified using aerial photographs (SWISSIMAGE, swisstopo, Wabern). Where necessary, additional information about agricultural land use in the study year was acquired from local administration agencies (Office of Landscape, Agriculture and Environment of the canton of Zurich; Agrofutura AG, canton of Aargau). The calculation of non-crop area was performed with ArcMap 10.1 GIS software (ESRI 2014).

2.5. STATISTICAL ANALYSES

Generalized linear mixed-effects models (GLMMs) were fitted to test the effect of flower strip on natural enemies (response variables: ground beetles, predatory bugs, adult ladybirds, ladybird larvae, adult lacewings and lacewing larvae; total number of individuals pooled from all sampling rounds) and CLB density (response variables total CLB larvae per 50 wheat tillers and total number of CLB adults) within adjacent winter wheat fields. GLMMs with Poisson error distribution (log-link function) were used to analyse natural enemies, except for the number of ground beetles: these data were better fitted by a Gaussian error distribution with identity-link function. To account for overdispersion in the CLB density data, GLMMs with negative binomial error distributions (log-link function) were fitted using the Automatic Differentiation Model Builder (glmmADMB) package (Skaug *et al.* 2013) in R. A linear mixed-effects model (LME) was used to model plant damage. Mean leaf damage was calculated for each distance per field using mean percentage values from categories attributed to each plot. Percentages were arcsine-square root-transformed to achieve normally distributed residuals and avoid heteroscedasticity. All full models contained the fixed effects flower strip (factor: focal field with flower strip vs. focal field with wheat control strip), distance (continuous explanatory variable) and their interaction, as well as the covariates wheat variety, wheat density (number of wheat tillers per m^2) and focal field area, and field identity as random blocking factor. The model for CLB larvae additionally included the crossed random factor sampling round. Collinearity among covariates was assessed using pairwise scatterplots, correlation coefficients and variance inflation factors (VIF). Wheat height, which was positively correlated with wheat density (correlation coefficient > |0.5|; Zuur *et al.* 2009) was excluded from the set of candidate models.

To additionally analyse natural enemies in the flower strips themselves compared with wheat control strips, negative binomial GLMs (log-link function) using the glm.nb function of the MASS package (Venables & Ripley 2002) with the explanatory variable flower strip and the covariate field area were fitted for each natural enemy group separately. Landscape complexity and its interaction with flower strip was included in the models described above in order to test the hypothesis that flower strip effects are contingent on landscape complexity. Moran's I similarity spline correlograms (Bjornstad & Falck 2001) indicated no spatial autocorrelation in the residuals of the models.

All numerical explanatory variables were standardized prior to the analyses (to get a predictor with mean of zero and standard deviation of one) to avoid numerical precision problems. Model selection based on likelihood ratio tests followed recommendations by Zuur *et al.* (2009) and minimum adequate models were used for statistical inference. Model assumptions were checked according to the graphical validation procedures recommended by Zuur *et al.* (2009). All statistical analyses were done using R 3.1.0 software (R Core Team 2014).

3. Results

3.1. IMPACT OF FLOWER STRIPS ON CLB DENSITY AND PLANT DAMAGE

The number of cereal leaf beetle (CLB) larvae was reduced by 40% in winter wheat fields with flower strips (hereafter flower strip fields) compared with winter wheat fields with winter wheat strips (hereafter control fields) (Table 1, Fig. 1a). CLB larvae increased with distance from flower strips (Table 1), but in a similar way as from wheat control strips (Fig. 1a). Consequently, significantly less adult CLB (-53%) re-emerged in flower strip fields than in control fields. Moreover, wheat plant damage caused by CLB was reduced by 61% in flower strip fields compared with control fields (Table 1, Fig. 1c). The decrease in wheat plant damage in flower strip fields compared to control fields tended to be higher towards the field centres, with highest plant damage in the interior of control fields (Table 1, Fig. 1c).

3.2. IMPACT OF FLOWER STRIPS ON NATURAL ENEMIES

Numbers of adults of all studied natural enemy groups increased strongly in flower strips compared with wheat control strips (Table 1, Fig. 2a-c,e), while the number of larvae of ladybirds and lacewings did not significantly differ (Table 1, Fig. 2d,f). In adjacent winter wheat, the number of predatory bugs tended to be higher in flower strip fields than control fields (Table 1, Fig. 2b). Moreover, the number of ground beetles was significantly higher - and that of adult lacewings tended to be higher - in flower strip fields, but only near flower strips (significant flower strip × distance interaction: Table 1, Fig. 2a,c). No significant flower strip effects were found for the numbers of other natural enemy groups (Table 1, Fig. 2d-f).

3.3. INTERACTIONS WITH LANDSCAPE COMPLEXITY

Landscape complexity calculated as percentage non-crop area within 750 m radius around focal fields (mean = 47.0 ± 3.3, range = 8.0 - 74.7) did not significantly influence the numbers of CLB larvae (χ^2 = 0.27, df = 1, *P* = 0.603), CLB adults (χ^2 = 0.00, df = 1, *P* = 1.000), or wheat plant damage (χ^2 = 0.56, df = 1, *P* = 0.453). Moreover, there was no significant interactive effect of flower strip and landscape complexity on the number of CLB larvae (χ^2 =

3.41, df = 1, $P = 0.065$), CLB adults ($\chi^2 = 0.06$, df = 1, $P = 0.813$) or wheat plant damage ($\chi^2 = 0.13$, df = 1, $P = 0.721$).

Similarly, no significant effect of landscape complexity or the interaction of flower strip × landscape complexity was found for any of the natural enemy groups, except for a significant flower strip × landscape complexity interaction for ladybird larvae within winter wheat fields ($\chi^2 = 4.99$, df = 1, $P = 0.025$; Supplementary material Table S4). Ladybird larvae in winter wheat fields adjoining flower strips tended to increase with landscape complexity ($z = 1.82$, $P = 0.069$), whereas the slope in winter wheat fields adjoining control strips was non-significant ($z = -1.52$, $P = 0.127$).

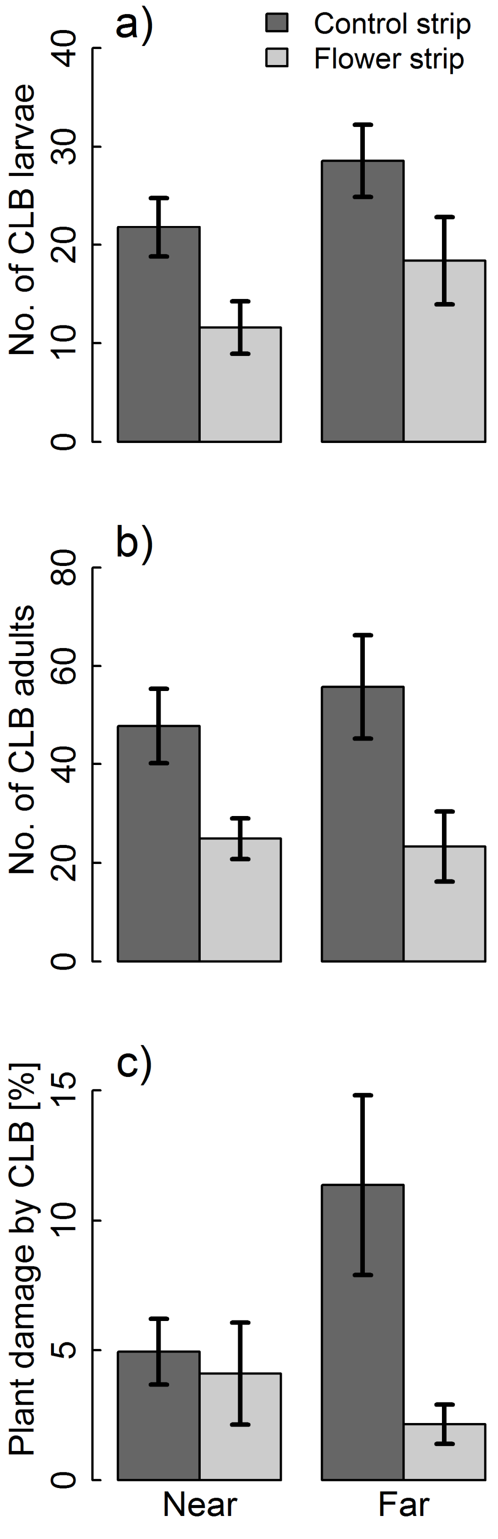

Fig. 1: Effects of flower strips on pest density and wheat plant damage. Mean (± 1 SE) **a)** number of cereal leaf beetle (CLB) larvae, **b)** number of adult cereal leaf beetles (second generation) and **c)** percentage leaf damage caused by cereal leaf beetles in winter wheat fields with wheat control strips (dark grey; n = 15) and winter wheat fields with flower strips (light grey; n = 10). Near: mean = 4.75 m, range = 0.6 m - 10.3 m; Far: mean = 14.75 m, range = 10.6 m - 20.3 m (see methods section). Statistical test summaries are given in Table 1.

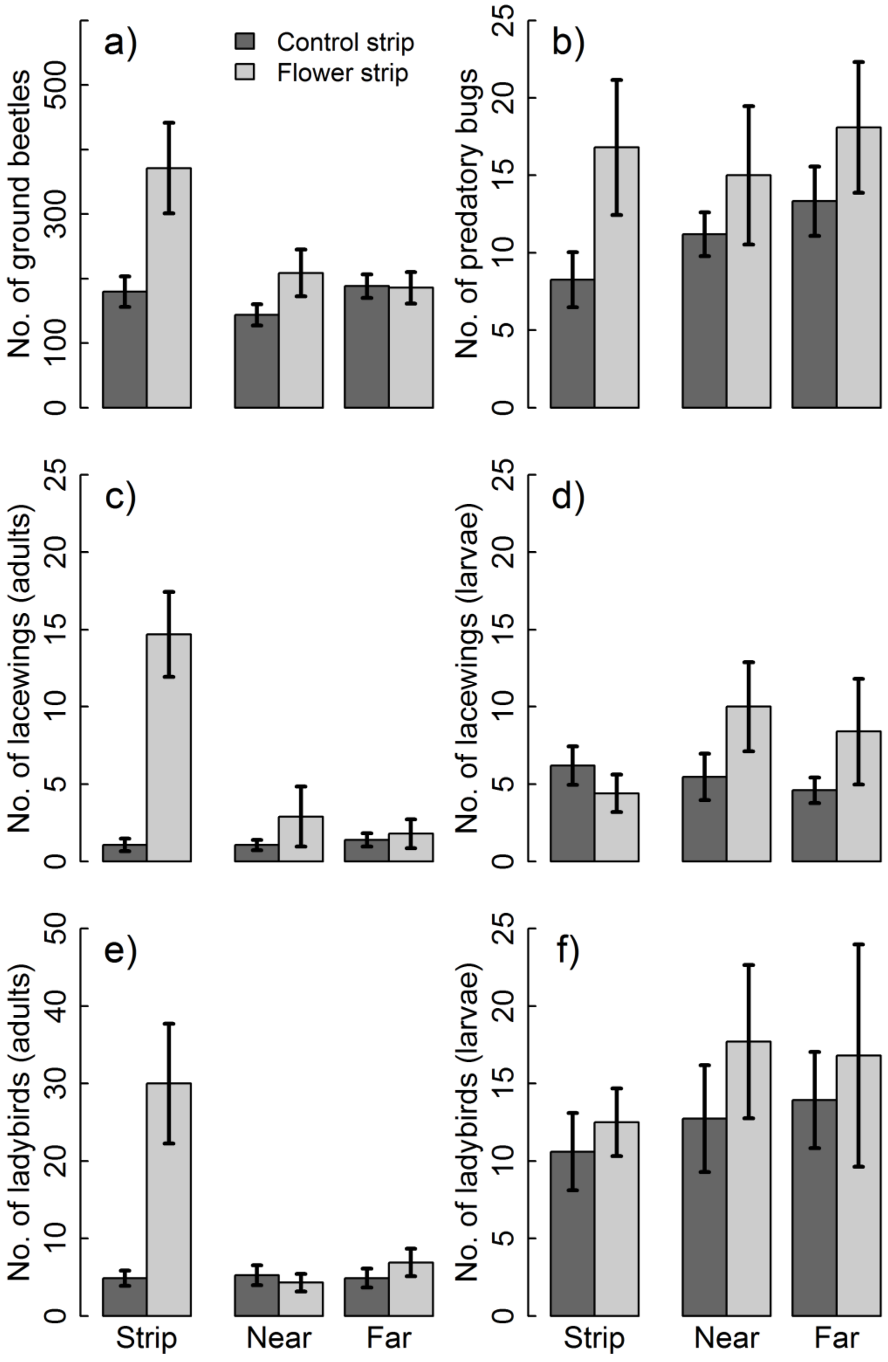

Fig. 2: Effects of flower strips on natural enemy density. Mean (± 1 SE) individual number of **a)** ground beetles (adults), **b)** predatory bugs (adults and nymphs), **c)** adult lacewings, **d)** lacewing larvae, **e)** adult ladybirds and **f)** ladybird larvae in winter wheat fields with wheat control strips (dark grey; n = 15) and winter wheat fields with flower strips (light grey; n = 10). Strip: centre of flower or wheat control strip; Near: mean = 4.75 m, range = 0.6 m - 10.3 m; Far: mean = 14.75 m, range = 10.6 m - 20.3 m (see methods section). Statistical test summaries are given in Table 1.

Table 1: Summary of main fixed effects treatment (factor with two levels: flower strip or wheat control strip), distance from flower or control strip (continuous variable) and their interaction on wheat plant damage (arcsine-square root-transformed), cereal leaf beetle (CLB) density and the density of different natural enemy groups in adjacent winter wheat fields and within the strips themselves (only natural enemies). Degrees of freedom (df), Chi-square values (χ^2) and *P*-values from likelihood-ratio tests of the model selection procedure (see Methods section) are shown. *P*-values of explanatory variables that were included in the final model are in bold lettering.

	Within winter wheat			Within strip		
	df	χ^2	*P*	df	χ^2	*P*
Pest density						
CLB larvae						
Treatment	1	4.93	**0.026**			
Distance	1	8.20	**0.004**			
Treatment x Distance	1	0.51	0.474			
CLB adults						
Treatment	1	4.51	**0.034**			
Distance	1	0.06	0.830			
Treatment x Distance	1	1.61	0.205			
Plant damage						
Wheat plant damage by CLB						
Treatment	1	4.39	**0.036**			
Distance	1	1.13	0.288			
Treatment x Distance	1	2.74	0.098			
Natural enemy abundance						
Ground beetles (adults)						
Treatment	1	0.60	0.437	1	10.60	**0.001**
Distance	1	0.51	0.478			
Treatment x Distance	1	9.48	**0.002**			
Predatory bugs (adults and nymphs)						
Treatment	1	2.86	**0.091**	1	4.42	**0.036**
Distance	1	0.38	0.540			
Treatment x Distance	1	0.00	0.989			
Lacewings (adults)						
Treatment	1	0.14	0.714	1	50.58	**<0.0001**
Distance	1	0.05	0.818			
Treatment x Distance	1	3.26	**0.071**			
Lacewings (larvae)						
Treatment	1	0.97	0.324	1	0.99	0.319
Distance	1	0.11	0.744			
Treatment x Distance	1	0.01	0.909			
Ladybirds (adults)						
Treatment	1	0.04	0.839	1	37.53	**<0.0001**
Distance	1	0.44	0.507			
Treatment x Distance	1	2.24	0.134			
Ladybirds (larvae)						
Treatment	1	0.10	0.748	1	0.25	0.619
Distance	1	11.99	**0.001**			
Treatment x Distance	1	0.00	0.964			

4. Discussion

This study demonstrates high effectiveness of annual flower strips in reducing CLB density and crop plant damage in adjacent winter wheat. Amongst the studied natural enemies of CLB, ground beetles, predatory bugs and lacewings showed the strongest positive responses to flower strips, suggesting a prominent role of these predator groups in CLB control. To our knowledge, this is one of the first replicated studies demonstrating high effectiveness of flower strips in reducing crop damage beyond reductions in pest densities, highlighting the potential of tailored flower strips for conservation biological control.

The observed reductions in pest levels (CLB larvae: 40%, second generation CLB adults: 53%) and the crop plant damage (61%) in the presence of flower strips are remarkably strong. Cereal leaf beetle larvae were reduced from an average of 0.50 (± 0.05) individuals per tiller to 0.30 (± 0.05) individuals, and thus below the economic threshold of 0.4 larvae per tiller (Buntin *et al.* 2004). Further, these high levels of pest control in wheat crops were not restricted to the immediate vicinity of the flower strips, but reached up to 20 m into the fields. This contrasts with earlier studies in which effects of field margins were restricted to their immediate vicinity (e.g. Tylianakis, Didham & Wratten 2004; Flückiger & Schmidt 2006; Skirvin *et al.* 2011). So far, studies investigating the effect of flower strips on pest control have mainly focused on parasitoid-host systems and parasitism (Heimpel & Jervis 2005; Winkler *et al.* 2010; Géneau *et al.* 2012; Balmer *et al.* 2013). Parasitism usually increased in the presence of flower strips. However, high parasitism does not necessarily translate into reductions of pest densities or crop damage (Heimpel & Jervis 2005). Indeed, only few studies found decreased pest levels or reduced crop damage in adjacent crops (Wyss 1995; Heimpel & Jervis 2005; Winkler *et al.* 2010). Conservation biocontrol measures are far from universally successful. No effects, or even increasing levels of crop pests and/or damage close to flower strips, have been reported for other study systems (Baggen & Gurr 1998; Winkler *et al.* 2010). These can arise, for example, if pests benefit similarly or even more strongly from the offered resources than their enemies (Heimpel & Jervis 2005; Wäckers, Romeis & van Rijn 2007) or from increased top down control of pest's natural enemies through (hyper-)parasitoids and predators (Prasad & Snyder 2006; Lundgren 2009). The first mechanism should not have compromised the effectiveness of flower strips in our study system because CLB are not expected to benefit from floral resources offered by herbaceous plant species (Schärer 1994). This may partly explain the strong reductions in pest and crop damage.

At least two other factors may have contributed to the high effectiveness of the tested flower strips in reducing CLB densities and plant damage. (i) The careful selection of plant species offering a large amount of floral, extra floral and structural resources that proved to benefit natural enemies (Fiedler, Landis & Wratten 2008; Griffiths *et al.* 2008; Wäckers & van

Rijn 2012) and (ii) the rather high diversity of flowering plants comprising the flower strips, characterised by a staggered provision of floral, extra-floral (*Centaurea cyanus*) and other resources (e.g. shelter and alternative prey) were found to be complementary in terms of attractiveness and accessibility for different natural enemy groups (M. Tschumi, unpublished data). Thus, species-rich flower strips may attract and benefit a higher diversity of natural enemies than species-poor or single-species strips (Pontin *et al.* 2006), which may be associated with enhanced pest control (Cardinale *et al.* 2006).

Highly increased numbers of all observed natural enemies (except larvae) inside flower strips compared with wheat control strips confirm that the offered floral and other resources were attractive for a broad range of natural enemies. This may also apply to other natural enemies taxa beyond the predators assessed here that may have contributed to biological control (e.g. parasitic wasps, rove beetles or birds). Floral resource provisioning was dominated by *F. esculentum, C. sativum* and *C. cyanus* at the time of CLB control (May & June), indicating that these species were particularly relevant in the studied system. Yet, due to bad weather conditions in early spring the seed mixture was sown slightly later in the season than in years with better weather during this time of the year. As a consequence, the onset of flowering was somewhat later than in typical years. However, in our study year the reduced abundance of CLB larvae started to appear before full flowering of the strips. Thus, in addition to floral resources, natural enemies are likely to have benefitted from other resources offered by flower strips, such as alternative prey, shelter and structural resources (Diehl, Wolters & Birkhofer 2012; Wäckers & van Rijn 2012).

Contrary to the strong effects of bordering flower strips, landscape complexity did not appear to affect CLB densities or crop damage, neither directly nor by modulating impacts of flower strips. This contrasts studies that have found highest effectiveness of habitat management in landscapes with intermediate complexity (Tscharntke *et al.* 2012). The lack of effects of landscape complexity may be explained by the relatively small-scaled landscape structure and the resulting moderate to high landscape complexity of Swiss agricultural landscapes compared with other countries. In many European regions, arable landscapes comprise only 0% to 40% of non-crop habitats (Concepcion *et al.* 2012). By contrast, the landscapes studied here embraced proportions of non-crop habitat between 8.0% and 74.7% (average 47.0% ± 3.3%), as is typical for the Swiss plateau (Concepcion *et al.* 2012). Only one of our landscapes fell below the 20% threshold that has been suggested for structurally poor landscapes impoverished in natural pest enemies (Tscharntke *et al.* 2012). This suggests that species pools of natural enemies were large enough and perennial semi-natural habitats offering complementary resources - such as adequate overwintering sites - sufficiently connected to annual flower strips to support their high performance in providing pest control services at the local (field) scale (Griffiths *et al.* 2008). In cleared landscapes with low proportions of permanent semi-natural habitats, however, annual flower strips may be less effective. An alternative reason for the low importance of landscape complexity in our study is that the scale of 750 m radius may not be appropriate. Yet, analyses at the smaller scale of 250 m radius did not yield any significant effects on leaf beetles or crop damage either (results not shown). Nevertheless, we cannot exclude possible effects of landscape complexity at larger scales.

Economic viability of tailored flower strips depends on associated costs and on their benefits in terms of increased crop yield and/or insecticide savings (Supplementary material B). The observed CLB reductions may enhance wheat yield (or mitigate yield damage) by 2.5% to 10% (Buntin *et al.* 2004; M. Tschumi, unpublished data). Assuming a moderate to high yield increase in winter wheat (i.e. ≥ 3.7%) or the substitution of insecticides, flower strips can become economically self-sustaining or even profitable, even if they are established on potential wheat cropping area (Supplementary material B). Concurrent benefits of tailored flower strips for aphid control, as observed for potato crops (M. Tschumi, unpublished data), may further benefit yield.

Tailored flower strips can be particularly valuable for and facilitate the adoption of low-input or organic management, because they provide one of few effective alternatives to insecticides. In Switzerland and the EU, the creation of ecological focus areas by farmers, including flower strips, is supported by direct payments (Aviron *et al.* 2009; Pe'er *et al.* 2014). If tailored flower strips are included, these agri-environment schemes compensate land opportunity and management costs, and benefits through enhanced pest control services could be an additional incentive for farmers to adopt these schemes.

5. Conclusions

We conclude that tailored flower strips are an effective tool for conservation biological control of cereal leaf beetles in winter wheat at intermediate to high levels of landscape complexity. By reducing cereal leaf beetle larvae below the suggested economic threshold, tailored flower strips can contribute to a reduction in insecticide use in conventional winter wheat production, and thus to effective ecological intensification. In organic wheat production, tailored flower strips provide an effective tool to mitigate CLB caused crop damage. The direct link between flower strips, pest control and crop damage reduction should encourage farmers to adopt such pest control measures, which may also benefit farmland biodiversity. We propose that existing AES should be complemented to include flower strips tailored at the provisioning of ecosystem services to sustainably assist agricultural food production.

7. Supplementary material A

Table S1: Descriptive statistics of land cover (in %) within landscape sectors of 750 m radius around focal fields. Shown are arithmetic means (Mean), standard errors (SE), minima (Min) and maxima (Max). Intensively cultivated grassland is included into crop area.

Landscape category	Mean	SE	Min	Max
Crop area	53.0	3.3	25.3	92.0
Extensively cultivated hay meadows	4.3	0.4	1.6	7.5
Extensively cultivated pastures	0.4	0.1	0.0	1.5
Perennial wildflower strips	0.4	0.1	0.0	2.0
Forest	20.3	3.4	0.0	57.6
Fruit plantations	1.9	0.3	0.0	5.1
Gravel	0.9	0.5	0.0	12.3
Hedgerows	0.5	0.1	0.0	2.6
Other, undefined areas	3.8	0.6	0.1	11.9
Sealed area	4.7	0.1	3.6	6.7
Settlements	8.5	1.9	0.0	42.8
Single trees	0.1	0.1	0.0	2.2
Vineyards	0.1	0.1	0.0	1.4
Water	1.2	0.4	0.0	7.3

Table S2: Composition of seed mixture used for flower strips.

Plant species	Seed quantity [kg/ha]
Anethum graveolens L.	0.13
Anthemis arvensis L.	0.43
Anthriscus cerefolium (L.) HOFFM.	0.23
Centaurea cyanus L.	1.33
Coriandrum sativum L.	0.73
Fagopyrum esculentum MOENCH	15.000
Papaver rhoeas L.	0.13

Table S3: Timeline illustrating the chronological order of the sampling (dark shaded boxes). Samples with identical letters were aggregated for the statistical analysis.

Month	**Mai**					**June**				**July**			
Week **Activity**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
CLB larvae counts				▨			▨						
CLB plant damage assessment							▨						
CLB adult sweeps										▨			
Enemy pitfall trapping					A	A			A				
Enemy sweeps							B			B			

Table S4: Summary of landscape effects (landscape complexity calculated as percentage non-crop area of 750 m radius landscape sectors around focal fields) and their interactions with treatment (tailored flower strip present or not) on different natural enemy groups of cereal leaf beetles in adjacent winter wheat fields and within the strips themselves. Degrees of freedom (df), Chi-square values (χ^2) and *P*-values from likelihood-ratio tests of the model selection procedure (see Methods section) are shown. *P*-values of explanatory variables that were included in the final model are in bold lettering.

	Within winter wheat			Within strip		
	df	χ^2	*P*	df	χ^2	*P*
Ground beetles (adults)						
Landscape	1	1.27	0.260	1	2.37	0.123
Treatment x Landscape	1	0.10	0.747	1	0.92	0.338
Predatory bugs (adults and nymphs)						
Landscape	1	3.81	0.051	1	1.59	0.207
Treatment x Landscape	1	0.30	0.582	1	3.47	0.062
Lacewings (adults)						
Landscape	1	2.06	0.151	1	1.84	0.175
Treatment x Landscape	1	1.62	0.204	1	0.23	0.632
Lacewings (larvae)						
Landscape	1	2.95	0.086	1	2.85	0.091
Treatment x Landscape	1	2.07	0.150	1	1.03	0.309
Ladybirds (adults)						
Landscape	1	0.18	0.667	1	0.17	0.679
Treatment x Landscape	1	0.15	0.701	1	0.86	0.352
Ladybirds (larvae)						
Landscape	1	0.14	0.706	1	0.01	0.937
Treatment x Landscape	1	4.99	**0.025**	1	0.60	0.438

8. Supplementary material B

8.1. Materials and methods

SIMPLE COST-BENEFIT ANALYSES OF TAILORED FLOWER STRIPS UNDER DIFFERENT SCENARIOS

For an economic evaluation of tailored flower strips we analysed simple cost-benefit scenarios (Supplementary material Table S5). We compared 6 scenarios under conventional (2 scenarios) and organic (4 scenarios) winter wheat production, with combinations of flower strip treatments (no flower strip vs. sown 3 m-wide flower strip) and insecticide input (yes vs. no; only for conventional scenarios) for a 1 ha field with the dimensions of 200 m * 50 m. For winter wheat and flower strips we used Swiss average costs and benefits under conventional or organic management, respectively (Boessinger *et al.* 2012; Supplementary material Table S6). For conventional production we assumed that either insecticide treatment or a tailored flower strip is used to reduce CLB density below the economic threshold (assuming equal effectiveness). For organic management we used scenarios under which flower strips increase winter wheat yield (or mitigate yield loss, respectively) by 2.5%; 5% or 10%, based on published and own unpublished empirical data on the negative relationship between CLB numbers (numbers of larvae per tiller) and winter wheat yield (2.5%: Buntin *et al.* (2004); 10%: M. Tschumi, unpublished data; 5%: intermediate scenario).

Table S5: Cost-benefit analysis scenarios. Combinations of different flower strip treatments (No: field without flower strip; Yes: 3 m-wide tailored flower strip sown into the field) and insecticide input (Yes vs. No) were evaluated under standard conventional and organic management for a 1 ha (200 m * 50 m) winter wheat field. Organic management includes scenarios under which flower strips increase winter wheat yield (or mitigate yield loss, respectively) by 2.5%; 5% or 10% (see Material and methods of supplementary material).

Scenario No.	Management regime	Flower strip	Insecticide input	Yield increase [%]
1	Conventional	No	Yes	0
2	Conventional	Yes	No	0
3	Organic	No	No	0
4	Organic	Yes	No	2.5
5	Organic	Yes	No	5
6	Organic	Yes	No	10

Table S6: Average costs and benefits for flower strip establishment and management, and winter wheat production (per ha) under conventional or organic management, respectively (in CHF) in Switzerland. If not indicated in footnotes, data derive from Boessinger *et al.* (2012).

	Flower strip (Conventional)			**Flower strip (Organic)**			**Winter wheat (Conventional)**			**Winter wheat (Organic)**		
	Quantity (Q)	Price pQ [CHF]	Price [CHF]	Quantity (Q)	Price pQ [CHF]	Price [CHF]	Quantity (Q)	Price pQ [CHF]	Price [CHF]	Quantity (Q)	Price pQ [CHF]	Price [CHF]
Costs												
Seeds	11.0 kg	45.45	500	11.0 kg	45.45	500	180.0 kg	1.29	232.20	200.0 kg	1.93	386.00
Fertilizer			0.00			0.00			407.00			40.00
Herbicides			0.00			0.00	1.0 bin	86.40	86.40			0.00
fungicides			0.00			0.00	2.0 bin	77.50	155.00			0.00
Insecticides*			0.00			0.00			85.00			0.00
Growth regulator			0.00			0.00	1.0 bin	48.10	48.10			0.00
Hail insurance			0.00			0.00	2.3 %	3630.50	83.50	2.3 %	4452.00	102.40
Yield cleaning			0.00			0.00	71.1 kg	2.85	202.64	43.7 kg	4.35	190.10
Yield drying			0.00			0.00	71.1 kg	1.10	78.21	43.7 kg	1.10	48.07
Various fees			0.00			0.00			64.31			5.15
Threshing			0.00			0.00			436.00			436.00
Machine costs*			358.00			371.00			472.50			699.00
Labour†	19.0 h	28.00	532.00	20.0 h	28.00	560.00	40.5 h	28.00	1134.00	53.0 h	28.00	1484.00
Total Costs			1390.00			1431.00			2350.85			1906.71
Benefit												
Product			0.00			0.00	68.5 dt	53.00	3630.50	42.0 dt	106.00	4452.00
Total Benefit			0.00			0.00			3630.50			4452.00

*Mouron *et al.* (2013)

†Basic costs from Boessinger *et al.* (2012) including extra costs for insecticide applications (conventional wheat production) following Mouron *et al.* (2013)

8.2. Results

SIMPLE COST-BENEFIT ANALYSES OF TAILORED FLOWER STRIPS UNDER DIFFERENT SCENARIOS

Costs for flower strips are low, as generally no management is needed after sowing (low machine and labour costs). Thus, a 3 m * 200 m tailored flower strip is less expensive than an average insecticide treatment of 1 ha winter wheat (Supplementary material Table S7). A 3 m * 200 m tailored flower strip is therefore economically viable to replace insecticides under conventional management assuming comparable pest control effectiveness of pesticides and tailored flower strips (Supplementary material Table S7; scenarios no. 1-2). Under organic management, tailored flower strips are profitable if yield increase is ≥ 3.7% (Supplementary material Table S7; scenarios No. 3-6).

Table S7: Cost-benefit analysis for different tailored flower strip scenarios (see Table S5). Total payoff of different scenarios is calculated from costs and benefits of a 1 ha winter wheat field (200 m * 50 m).

	Conventional		Organic			
Scenario	1	2	3	4	5	6
WINTER WHEAT						
Length [m]	*200.00*	*200.00*	*200.00*	*200.00*	*200.00*	*200.00*
Width [m]	*50.00*	*47.00*	*50.00*	*47.00*	*47.00*	*47.00*
Size [ha]	*1.00*	*0.94*	*1.00*	*0.94*	*0.94*	*0.94*
Costs						
Seeds	232.20	218.27	386.00	362.84	362.84	362.84
Fertilizer	407.00	382.58	40.00	37.60	37.60	37.60
Herbicides	86.40	81.22	0.00	0.00	0.00	0.00
Fungicides	155.00	145.70	0.00	0.00	0.00	0.00
Insecticides	85.00	0.00	0.00	0.00	0.00	0.00
Growth regulator	48.10	45.21	0.00	0.00	0.00	0.00
Hail insurance	83.50	78.49	102.40	96.25	96.25	96.25
Yield cleaning	202.64	190.48	190.10	183.16	187.62	196.56
Yield drying	78.21	73.52	48.07	46.32	47.45	49.70
Various fees	64.31	60.45	5.15	4.84	4.84	4.84
Threshing	436.00	409.84	436.00	409.84	409.84	409.84
Machine costs	472.50	419.24	699.00	657.06	657.06	657.06
Labour	1134.00	1052.80	1484.00	1394.96	1394.96	1394.96
Total costs wheat	3484.85	3157.79	3390.71	3192.86	3198.46	3209.65
Benefits						
Product	3630.50	3412.67	4452.00	4184.88	4184.88	4184.88
Yield increase*	0.00	0.00	0.00	104.62	209.24	418.49
Total benefits wheat	3630.50	3412.67	4452.00	4289.50	4394.12	4603.37
FLOWER STRIP						
Length [m]	*0.00*	*200.00*	*0.00*	*200.00*	*200.00*	*200.00*
Width [m]	*0.00*	*3.00*	*0.00*	*3.00*	*3.00*	*3.00*
Size [ha]	*0.00*	*0.06*	*0.00*	*0.06*	*0.06*	*0.06*
Costs						
Seeds	0.00	30.00	0.00	30.00	30.00	30.00
Machine costs	0.00	21.48	0.00	22.26	22.26	22.26
Labour	0.00	31.92	0.00	33.60	33.60	33.60
Total costs flower strip	0.00	83.40	0.00	85.86	85.86	85.86
Benefits						
Total benefits flower strip	0.00	0.00	0.00	0.00	0.00	0.00
Net benefits (total benefits minus total costs)	**145.65**	**171.48**	**1061.29**	**1010.78**	**1109.80**	**1307.85**

*Yield increase due to flower strip mediated increase in natural CLB control (according to the scenarios described in supplementary material Table S5)

CHAPTER 5

Tailored flower strips promote natural enemy biodiversity and pest control in potato crops

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Abstract

Sown flower strips are increasingly implemented within agri-environment schemes (AES) to increase functional biodiversity and ecosystem services such as pollination or natural pest control, but their effectiveness in achieving these goals remains poorly studied. We tested the performance of experimentally sown annual flower strips targeted at promoting natural enemies of aphids and their pest control services in adjacent potato crops compared to control fields in a total of nine field pairs (18 fields). Flower strips consisted of 11 plant species providing abundant floral and extra-floral resources. The abundance of key natural enemies of aphids (hoverflies, lacewings and ladybirds) and hoverfly species richness was greatly enhanced in flower strips compared to potato control strips. This resulted in an average increase in the number of eggs deposited by hoverflies and lacewings of 112 % and 55 %, respectively, and a reduction in the number of aphids of 77 % in adjacent potato crops. We conclude that tailored flower strips can be an effective agri-environmental measure to enhance natural enemies and aphid control in nearby crops. Indeed, tailored flower strips may help to reduce insecticide input in potato production as aphid action thresholds were, contrary to control fields, often not reached in fields containing flower strips. Promoting natural enemy abundance and functional diversity, as observed for hoverflies, may maximise the complementarity and stability of pest control services thus providing additional benefits to agro-ecosystems in terms of biodiversity conservation and pollination functions. This may encourage farmers to adopt agri-environment schemes and ultimately benefit both biodiversity and agricultural production.

Keywords: Agri-environment schemes (AES); conservation biological control; ecological intensification; ecosystem functioning; ecosystem services (ES); functional biodiversity; habitat management; predators; sown field margin; Syrphidae

1. Introduction

Environmentally-friendly solutions are increasingly required to ecologically enhance food production for a growing human population (Godfray *et al.* 2010). Conventional intensification can severely jeopardise biodiversity and its associated ecosystem services (Millennium Ecosystem Assessment 2005). Agri-environment schemes (AES) have the potential to contribute to ecological intensification (Bommarco, Kleijn & Potts 2013). Yet, payoffs are variable (Kleijn *et al.* 2006) and AES are often reluctantly implemented by farmers, as yield losses due to land-use opportunity costs and/or decreased management intensity are often more obvious than the potential benefits of AES.

To improve their effectiveness, there have been repeated calls for more explicit goals of schemes regarding biodiversity conservation and the provisioning of ecosystem services (Kleijn *et al.* 2011; Scheper *et al.* 2013; Ekroos *et al.* 2014). Most AES are designed as "biodiversity conservation schemes" and studies evaluating their performance have accordingly focussed largely on biodiversity promotion and conservation so far (Whittingham 2011; Ekroos *et al.* 2014). Although fostering functional aspects of biodiversity is often an implicit objective of AES (Kleijn *et al.* 2011; Ekroos *et al.* 2014), few schemes are explicitly targeted at augmenting biodiversity mediated services, such as crop pollination or natural pest control, and quantitative knowledge on the effectiveness in service provision by such AES is scant (Whittingham 2011; Ekroos *et al.* 2014). Schemes tailored to the needs of beneficial functional guilds may enhance services and thus convince farmers of the benefits of AES. As such elements can also benefit biodiversity (Pywell *et al.* 2012; Wratten *et al.* 2012), they may synergistically contribute to both aims.

Biological pest control is a highly valued ecosystem service (Costanza *et al.* 1997; Losey & Vaughan 2006), indispensable for sustainable food production (Thomas 1999). Effective natural enemy communities often depend on plant-provided resources (e.g. pollen, nectar and shelter), which have become rare in intensified agricultural landscapes (Landis, Wratten & Gurr 2000; Wäckers & van Rijn 2012). By promoting natural enemies, tailored habitat management can potentially increase yield at reduced levels of pesticide inputs (Letourneau *et al.* 2009). Hereby, attractiveness, quantity, quality and accessibility of resources, as well as the timing at which they are available, are key to the success of such measures (Wäckers & van Rijn 2012). In addition, the potentially distinct requirements of natural enemy guilds should be considered to promote functional diversity of communities, which maximises the complementarity and stability of pest control (Crowder & Jabbour 2014). Sown flower strips can effectively address these specific needs of many natural enemies (Haaland, Naisbit & Bersier 2011; Korpela *et al.* 2013). Annual flower strips, in particular, can be included in crop rotations to flexibly offer resources to natural enemies in the time and place they are needed (Tschumi *et al.* 2014). Yet, their effectiveness is likely dependent on the availability of undisturbed perennial habitats in the agricultural landscape, as annual elements require spillover of arthropods from semi-natural habitats offering for example suitable overwintering sites (e.g. Landis, Wratten & Gurr 2000; Bianchi, Booij & Tscharntke 2006; Haenke *et al.* 2014).

Aphids are common targets for biological control since they can damage numerous major crops (Östman, Ekbom & Bengtsson 2003; Brewer & Elliott 2004). The impact of transmitted plant viruses often surmounts the damage through sap-sucking alone, most notable in potato cultures (Dedryver, Le Ralec & Fabre 2010). Aphids can be efficiently controlled by enemies such as hoverflies, ladybirds, lacewings and parasitic wasps that depend on floral, extra-floral or structural resources offered in flower strips (Östman, Ekbom & Bengtsson 2003; Schmidt *et al.* 2003; Lundgren 2009; Wäckers & van Rijn 2012; Diehl *et al.* 2013). Yet, there is a surprising lack of studies examining the potential of tailored annual flower strips to enhance aphid control in adjacent crops.

This study thus aims to assess the performance of annual flower strips tailored at enhancing pest control in nearby potato crops. Specifically, we addressed the following questions: (i) Do tailored flower strips enhance the diversity and abundance of natural enemies? (ii) Does this result in increased aphid control in adjacent potato crops?

2. Materials and methods

2.1. STUDY DESIGN

Twenty potato fields (hereafter focal fields) were selected in the central Swiss plateau (cantons Zurich and Aargau). The study region represents the typical agricultural landscape of the Swiss lowlands, which is characterized by a small-scale mosaic of crop fields (average field size of focal fields: 1.71 ha ± 0.17 ha), meadows and forest fragments. Focal fields were selected in pairs with similar landscape compositions. The minimum distance between focal fields was 450 m (mean ± SE: 13386 m ± 602 m). In one of each pair of focal fields, a 3 m-wide tailored flower strip was sown along the full length of a randomly selected side, at the time potatoes were planted (end of April/beginning of May 2013). In the other field, a 3 m-wide potato strip along the full length of the field served as control strip. Due to poor development of the sown flowering plants in one flower strip, the corresponding pair had to be omitted, resulting in a total of nine focal field pairs (18 fields) studied.

The seed mixture of the annual flower strip was targeted to provide continuous high amounts of floral and extra-floral resources that are attractive and accessible to key natural enemies of aphids during the period when aphid control by natural enemies is required (mid-May to beginning of August in the study region). Plant species were selected based on an extensive literature survey of studies indicating positive effects of flowering species on the abundance and performance of key natural enemies of aphids such as hoverflies (Diptera:

Syrphidae), ladybirds (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae) and parasitic wasps (Hymenoptera) (e.g. Patt, Hamilton & Lashomb 1997; Landis, Wratten & Gurr 2000; Lundgren 2009; Laubertie, Wratten & Hemptinne 2012; Wäckers & van Rijn 2012) and own experimental and field studies (Tschumi *et al.* 2014; MT, unpublished data). The following plant species were selected: *Anethum graveolens* L. (Apiaceae), *Anthemis arvensis* L. (Asteraceae), *Anthriscus cerefolium* Hoffm. (Apiaceae), *Bellis perennis* L. (Asteraceae), *Calendula arvensis* L. (Asteraceae), *Camelina sativa* (L.) Crantz (Brassicaceae), *Centaurea cyanus* L. (Asteraceae), *Coriandrum sativum* L. (Apiaceae), *Fagopyrum esculentum* Moench (Polygonaceae), *Papaver rhoeas* L. (Papaveraceae) and *Sinapis arvensis* L. (Brassicaceae) (see supplementary material Table S1 for quantities of seeds sown per area). These species are either indigenous wildflowers or regionally cultivated herbs known to be agronomically unproblematic and of esthetical value (Junge *et al.* 2009). After sowing flower strips were left unmanaged (e.g. no pesticide or fertilizer applications).

2.2. SAMPLING OF APHIDS AND THEIR NATURAL ENEMIES

Aphids (all species present on potato leaves) were counted twice at the end of June and July 2013, respectively, on 100 randomly selected potato compound leaves (where one compound leaf corresponds to ca. 7 single leaves on average; MT, unpublished data). Leaves were collected at two distances from flower strips or potato control strips, respectively: 1 m (hereafter “near”) and 10 m (hereafter “far”). On the same leaves the eggs and larvae of hoverflies, ladybirds and lacewings, as well as aphid mummies were counted to determine parasitism rate (percentage mummies of the total number of aphids). Adult hoverflies, ladybirds and lacewings were passively collected using cornet traps, an adapted version of the Malaise trap, which have been shown to effectively capture flying natural enemies of aphids (Sarthou 2009; Eggenschwiler *et al.* 2012). One cornet trap was placed inside each flower- and potato control strip and at a distance of 10 m from the strips in the potato crops, during three sampling periods of two weeks (end of June, mid-July and beginning of August, see supplementary material Table S2). All captured hoverflies were determined to species level. Each hoverfly species was classified as aphidophagous or non-aphidophagous based on the trophic guild of the larvae, according to Röder (1990) (Supplementary material Table S3). As ladybirds were dominated by a few abundant species (mostly *Propylea quatuordecimpunctata* L. and *Coccinella septempunctata* L.) and lacewings consisted almost exclusively of *Chrysoperla carnea* Stephens, we did not evaluate species richness for these groups.

2.3. STATISTICAL ANALYSIS

To test the effect of flower strips on aphid density (response variable: aphid number; total number of individuals pooled across sampling rounds) and eggs of natural enemies (response variables: hoverfly eggs, lacewing eggs; total number of eggs pooled across sampling rounds) within potato fields, generalized linear mixed-effects models (GLMMs) with negative binomial error distributions (log-link function) were fitted using the Automatic Differentiation Model Builder (glmmADMB) package (Skaug *et al.* 2013) in R. Full models contained the fixed factors treatment (factor: focal field with flower strip vs. focal field with potato control strip), distance (factor: near vs. far) and their interaction, as well as the covariate field size, and the random blocking factors pair and field nested in pair.

To model the impact of flower strips on adult enemy abundance (response variables: adult hoverflies with aphidophagous larvae, adult ladybirds, adult lacewings; total number of individuals pooled across sampling rounds) and species richness of hoverflies (total number of species pooled across sampling rounds), GLMMs with Poisson error distributions (log-link function) were fitted. Separate models were used for natural enemies inside strips and inside potato crops, respectively. To account for overdispersion in hoverfly and ladybird abundance, GLMMs with negative binomial error distributions (log-link function) were fitted using glmmADMB. Full models contained the predictor treatment (factor: focal field with flower strip vs. focal field with potato control strip) and the continuous covariate field size and pair as random blocking factor. Numbers of ladybird eggs (1), numbers of natural enemy larvae (hoverflies: 80; ladybirds: 14; lacewings: 12) and percentage of parasitized aphids (<0.4 %) were too low for robust data evaluation.

Field size was standardized for all evaluations to avoid numerical estimation problems. Model selection based on likelihood ratio tests followed recommendations by Zuur *et al.* (2009) and minimum adequate models were used for statistical inference. Model assumptions were checked according to the graphical validation procedures recommended by Zuur *et al.* (2009). Moran's I autocorrelation index (Paradis, Claude & Strimmer 2004) indicated no spatial autocorrelation in the residuals of the models. All statistical analyses were done using R 3.1.2 software (R Core Team 2014).

3. Results

3.1. FLOWER ESTABLISHMENT

Total flower cover of all sown species was assessed at the end of June and in mid-July in all flower strips. In June flower strips were dominated by *Fagopyrum esculentum* (32.5 % ± 10.8 % of the total flower cover), *Camelina sativa* (25.8 % ± 12.3 %), *Calendula arvensis* (13.4 % ± 5.3 %) and *Sinapis arvensis* (11.5 % ± 3.6 %) flowers, whereas in July *Fagopyrum esculentum* (37.7 % ± 10.3 %), *Centaurea cyanus* (19.5 % ± 5.7 %), *Coriandrum sativum*

(11.0 % ± 5.9 %) and *Anthemis arvensis* (9.9 % ± 3.1 %) were the most abundant flowering species.

3.2. IMPACT OF FLOWER STRIPS ON APHID DENSITY

Aphid density was significantly reduced by 77 % on average, in fields adjacent to flower strips (hereafter “flower strip fields”) compared with fields adjacent to potato control strips (hereafter “control fields”) (Table 1, Fig. 1). This significant effect was consistent across distances (Table 1) and also held true when an extreme value, caused by a severe aphid outbreak in one control field, was excluded from the analysis ($\chi^2 = 4.00$, df = 1, $P = 0.045$; 63 % reduction of aphid density).

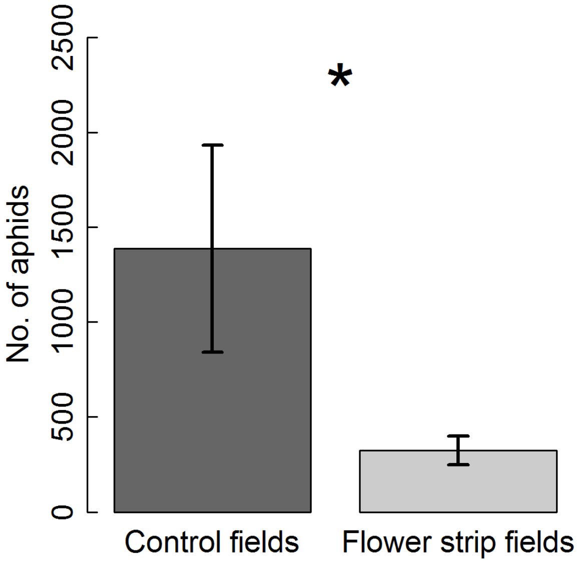

Fig. 1: Effects of flower strips on aphid density. Mean (± 1 SE) number of aphids on 200 potato compound leaves (100 compound leaves per sampling round where one compound leaf corresponds to ca. 7 single leaves on average, see methods section) of control fields (dark grey; n = 9) and fields adjacent to flower strips (light grey; n = 9) for pooled distances (1 m and 10 m). The asterisk indicates a significant effect ($P \leq 0.05$).

3.3. IMPACT OF FLOWER STRIPS ON NATURAL ENEMY ABUNDANCE AND SPECIES RICHNESS

Hoverfly egg numbers were significantly increased (Table 1, Fig. 2a) and egg numbers of lacewings tended to be higher (Table 1, Fig. 2b) in flower strip fields compared to control fields, with no significant difference regarding distance to strips (Table 1). Adult abundance of all three investigated natural enemy groups (hoverflies with aphidophagous larvae, ladybirds and lacewings) and species richness of hoverflies were strongly enhanced in flower strips compared with potato control strips (Table 1, Fig. 3). In potato crops adjacent to flower strips the number of adult lacewings and hoverfly species richness was increased compared with potatoes adjacent to control fields, but there was no difference in hoverfly or ladybird abundance (Table 1, Fig. 3). We recorded a total of 64 hoverfly species of which 43 are aphidophagous (75.4 % of all individuals) and 21 non-aphidophagous (24.6 % of all individuals) (Supplementary material Table S3). Flower strips attracted disproportionately more aphidophagous individuals (79.6 % of all individuals) than control strips (65.4 % of all individuals). Dominant aphidophagous hoverflies were individuals of the genus *Sphaerophoria* (40.7 % of all individuals), *Mellanostoma mellinum* L. (14.0 %), *Eupeodes corolla* Fabricius (12.0 %) and *Episyrphus balteatus* De Geer (3.9 %).

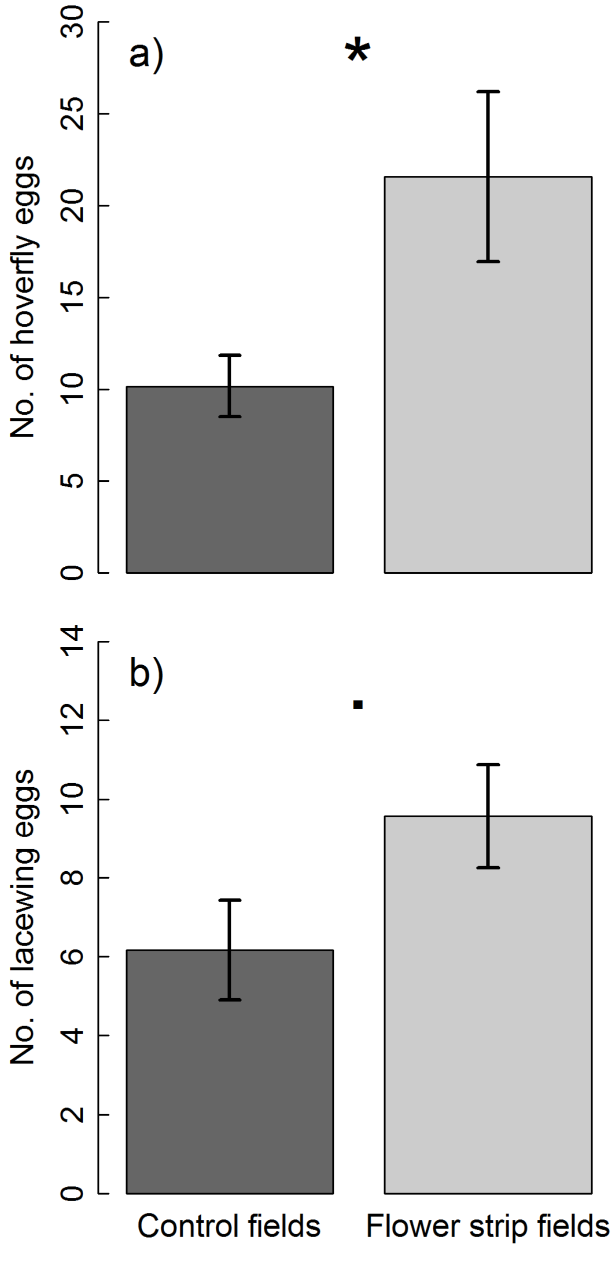

Fig. 2: Effects of flower strips on natural enemy eggs. Mean (± 1 SE) number of **a)** hoverfly eggs and **b)** lacewing eggs on 200 potato compound leaves (100 compound leaves per sampling round, where one compound leaf corresponds to ca. 7 single leaves on average, see methods section) from control fields (dark grey; n = 9) and fields adjacent to flower strips (light grey; n = 9) for pooled distances (1 m and 10 m). Symbols indicate flower strip effects (▪: 0.1 ≥ P ≥ 0.05; *: P ≤ 0.05).

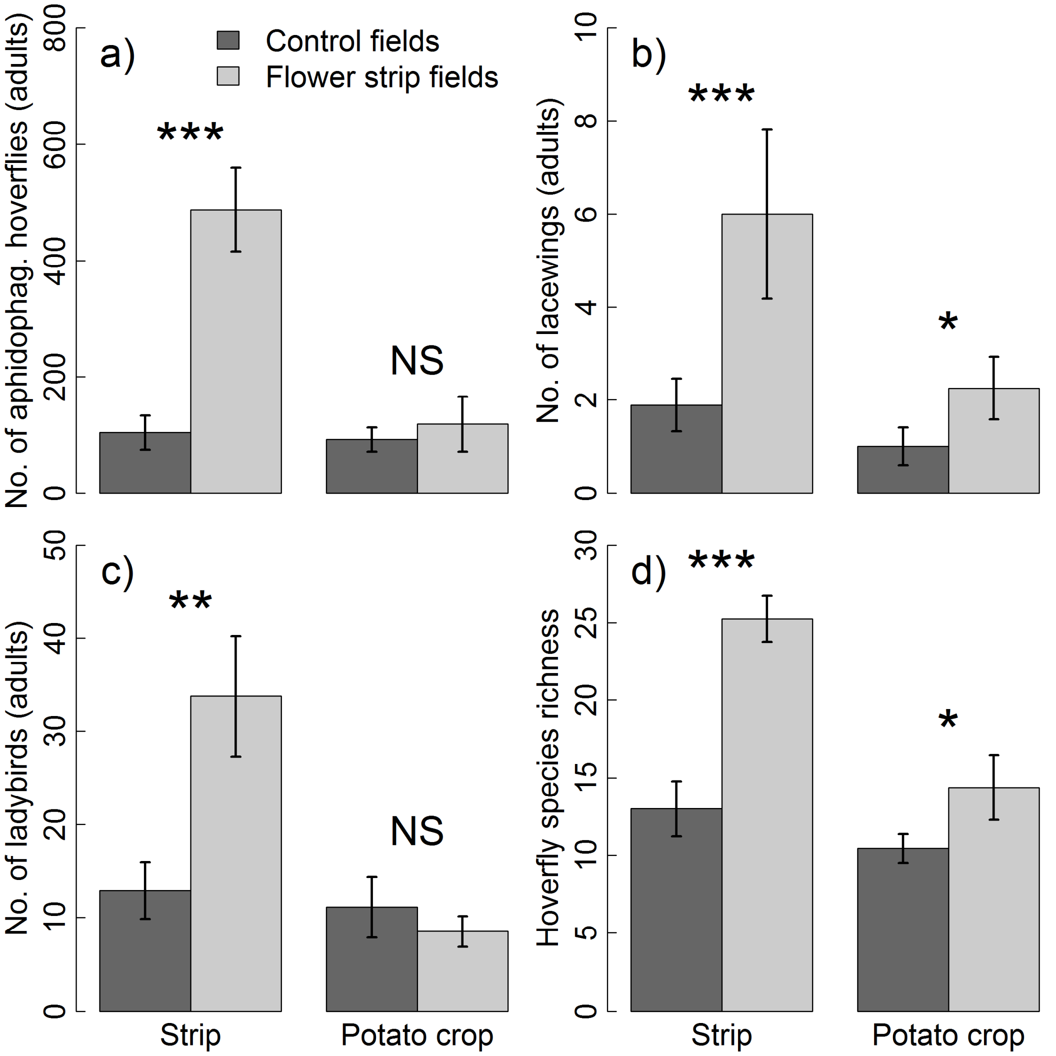

Fig. 3: Effects of flower strips on adult natural enemies. Mean (± 1 SE) individual number of **a)** adult hoverflies with aphidophagous larvae, **b)** adult lacewings, **c)** adult ladybirds and mean (± 1 SE) species number of **d)** adult hoverflies collected using cornet traps in control fields (dark grey; n = 9) and fields adjacent to flower strips (light grey; n = 9). Strip: inside flower or potato control strip, respectively; crop (10 m distance from strip inside potato crops. Asterisks indicate significant effects (*: P ≤ 0.05; **: P ≤ 0.01; ***: P ≤ 0.001). NS: no significant effect (P ≥ 0.05).

Table 1: Summary of main fixed effects treatment (factor with two levels: flower strip or potato control strip), distance from strip (flower or control strip, respectively; factor with two levels: near and far) and the interaction of treatment and distance on aphid density, natural enemy abundance and hoverfly species richness in adjacent potato crops and within the strips themselves (only adult individuals included). Degrees of freedom (df), Chi-square values (χ^2) and P-values from likelihood-ratio tests of the model selection procedure (see Methods section) are shown. P-values of explanatory variables, that were included in the final model, are in bold lettering.

	Within potato crop			Within strip		
	df	χ^2	P	df	χ^2	P
Aphid density						
Aphid number						
Treatment	1	4.04	**0.044**			
Distance	1	0.18	0.670			
Treatment x Distance	1	0.37	0.544			
Natural enemy abundance						
Hoverflies (eggs)						
Treatment	1	4.48	**0.034**			
Distance	1	0.14	0.710			
Treatment x Distance	1	0.46	0.499			
Lacewings (eggs)						
Treatment	1	3.19	**0.074**			
Distance	1	2.03	0.154			
Treatment x Distance	1	0.34	0.557			
Aphidophagous hoverflies (adults)						
Treatment	1	0.23	0.630	1	16.23	**<0.001**
Ladybirds (adults)						
Treatment	1	0.33	0.566	1	8.40	**0.004**
Lacewings (adults)						
Treatment	1	4.21	**0.040**	1	18.15	**<0.001**
Species richness						
Hoverfly species richness						
Treatment	1	4.09	**0.043**	1	32.05	**<0.001**

4. Discussion

The tested tailored flower strips were highly effective in attracting natural enemies of aphids and suppressing aphid densities in adjacent potato crops. Our findings suggest that hoverflies and lacewings, in particular, spilled over from flower strips into the potato crops, where higher numbers of eggs were deposited on aphid infested potato plants. Moreover, flower strips strongly promoted hoverfly diversity. These findings highlight the potential of tailored flower strips to promote pest control services and natural enemy biodiversity.

The flower strips reduced aphid densities from 56 per 100 leaves in control fields to only 11 per 100 leaves in flower strip fields and thus below action thresholds of 20-50 aphids per 100 leaves recommended for potato (Cancelado & Radcliffe 1979; Flanders, Radcliffe & Ragsdale 1991; Mowry 2001; van Toor *et al.* 2009). The degree of aphid reduction by tailored flower strips can thus reduce the need for insecticide applications in potato.

Successful conservation biological control largely depends on the selection of flowering plants that offer resources, which are attractive and accessible to natural enemies but not insect pests (Wäckers & van Rijn 2012). If pests profit equally or more from the offered resources, habitat management may enhance insect pests, rather than reducing them (Heimpel & Jervis 2005; Wäckers, Romeis & van Rijn 2007). Additionally, the timing at which resources are offered is decisive, as for example early control by natural enemies most efficiently curtails pest population build-up (Kindlmann & Dixon 2010). The careful selection of plant species offering a large amount of diverse floral and extra-floral (*Centaurea cyanus*) resources known to benefit natural enemies (Patt, Hamilton & Lashomb 1997; Lundgren 2009; Laubertie, Wratten & Hemptinne 2012; Wäckers & van Rijn 2012) and the combination of plant species with a staggered flowering time, including fast growing species offering readily accessible floral resources at the time aphids colonize potato fields (e.g. *Fagopyrum esculentum* or *Camelina sativa*), may explain the high effectiveness of the tested flower strips. Diverse resources and comprehensive temporal provision supported a high diversity of natural enemies likely to complement each other for pest control in adjacent crops (Schmidt *et al.* 2003; Wäckers & van Rijn 2012). Field observations confirm differential flower use by hoverflies, as e.g. *Sphaerophoria sp.* preferred *Anethum graveolens*, *Anthemis arvensis* and *Coriandrum sativum*, whereas *Episyrphus balteatus* preferred *Sinapis arvensis*, *Fagopyrum esculentum* and *Centaurea cyanus* (MT, unpublished data). In addition to plant-provided food resources, the studied flower strips should also benefit natural enemies by providing structural resources (i.e. shelter). Yet, annual flower strips require landscapes that also provide permanent, undisturbed habitats serving for example as overwintering sites to effectively promote pest control in nearby crops (Landis, Wratten & Gurr 2000; Bianchi, Booij & Tscharntke 2006; Haenke *et al.* 2014; Ramsden *et al.* 2014).

Increased numbers of adult natural enemies inside flower strips compared with potato controls (hoverflies: 390 %; ladybirds: 260 %; lacewings: 320 %) confirms the attractiveness of the offered resources, with particular benefit for aphidophagous species in the case of hoverflies. Furthermore, our findings show that natural enemies also spilled over into adjacent potato crops, which was particularly well reflected by increased numbers of hoverfly and lacewing eggs. The low parasitism rate (<0.4 %) indicates that predators were generally more relevant than parasitic hymenopterans (see Holland *et al.* 2012 and Alignier *et al.* 2014 for similar results). Hoverflies, lacewings and ladybirds are all highly efficient in locating aphid colonies and their high mobility allows them to localize aphid colonies early and lay eggs over large areas (Bond 1980; Evans 2003; Almohamad, Verheggen & Haubruge 2009).

The increase in hoverfly species richness in flower strips and adjacent potato crops indicates the complementary benefits of flower strips for pest control and biodiversity. Tailored flower strips may thus contribute to both ecosystem service provision and biodiversity conservation (Ekroos *et al.* 2014). Since hoverflies also provide pollination services to certain crops (e.g. oilseed rape; Bommarco, Marini & Vaissière 2012; Haenke *et al.* 2014), and flower strips also provide resources to other pollinators, such as bees (Haaland, Naisbit & Bersier 2011; Blaauw & Isaacs 2014a), the studied flower strips may indeed promote multiple ecosystem services. Diversity of service providers may seem less relevant for service provision than abundance, as pest control or pollination is often performed by a few abundant species (93.6 % of all aphidophagous individuals belonged to the four most abundant taxa). Yet, natural enemy diversity may enhance functional complementarity, insurance effects and resilience that may stabilize pest control services and effectively prevent pest outbreaks on a long term perspective (Yachi & Loreau 1999; Wilby & Thomas 2002).

5. Conclusions and management implications

We conclude that tailored flower strips enhance biological control of aphids in nearby potato crops and provide complementary benefits for biodiversity. The high pest reduction levels observed in combination with increased natural enemy diversity suggest that tailored flower strips established in target crops can inhibit pest outbreaks and reduce insecticide use. We expect that farmers will be more likely to adopt agri-environment schemes if benefits are demonstrated for both biodiversity conservation and ecosystem services. Tailored flower strips should thus complement existing schemes to synergistically enhance crop production and biodiversity.

7. Supplementary material

Table S1: Composition of the seed mixture used to establish flower strips in 10 focal fields in the Central Swiss Plateau.

Plant species	Seed quantity [kg/ha]
Anethum graveolens L.	0.13
Anthemis arvensis L.	0.43
Anthriscus cerefolium L.	0.23
Bellis perennis L.*	0.05
Calendula arvensis L.*	0.45
Camelina sativa (L.) Cranz*	0.10
Centaurea cyanus L.*	1.33
Coriandrum sativum L.	0.73
Fagopyrum esculentum Moench	15.00
Papaver rhoeas L.*	0.13
Sinapis arvensis L.*	0.20

*Swiss ecotypes

Table S2: Sampling periods and corresponding weeks at which cornet trap samples were collected.

Period Number	Sampling Period	Sampling Weeks
1	End of June	19.06.2013 – 26.06.2013
		26.06.2013 – 03.07.2013
2	Mid July	10.07.2013 – 17.07.2013
		17.07.2013 – 24.07.2013
3	Beginning of August	31.07.2013 – 07.08.2013
		07.08.2013 – 14.08.2013

Table S3: List of hoverfly species collected from flower strips (FSt), potato control strips (CSt), potato crop adjacent to flower strips (FFi) and potato crop adjacent to potato control strips (CFi). Species were classified as aphidophagous or non-aphidophagous based on the trophic guild of the larval stage according to Röder (1990).

Hoverfly species	FSt	CSt	FCr	CCr
Aphidophagous				
Chrysotoxum bicinctum L.			X	
Chrysotoxum cautum Harris	X	X		
Chrysotoxum elegans Loew	X			
Chrysotoxum fasciolatum De Geer		X		
Chrysotoxum intermedium Meigen	X			
Chrysotoxum verralli Collin	X			
Dasysyrphus albostriatus Fallen	X			
Epistrophe flava Doczkal & Schmid				X
Episyrphus balteatus De Geer	X	X	X	X
Eupeodes corollae Fabricius	X	X	X	X
Eupeodes lapponicus Zetterstedt	X	X	X	X
Eupeodes latifasciatus Macquart	X	X	X	X
Eupeodes luniger Meigen	X	X	X	
Eupeodes nielseni Dusek & Laska	X		X	
Eupeodes nitens Zetterstedt				X
Melanostoma mellinum L.	X	X	X	X
Melanostoma scalare Fabricius	X	X	X	X
Meliscaeva auricollis Meigen	X	X	X	X
Paragus finitimus Goeldlin de Tiefenau	X			
Paragus haemorrhous Meigen	X	X		
Paragus quadrifasciatus Meigen			X	
Pipiza lugubris Fabricius	X			
Pipiza noctiluca L.	X		X	
Pipizella viduata L.	X	X	X	X
Platycheirus albimanus Fabricius	X	X	X	X
Platycheirus angustatus Zetterstedt	X			
Platycheirus clypeatus Meigen	X	X	X	X
Platycheirus europaeus Goeldlin de Tiefenau, Maibach & Speight	X	X	X	X

(continued)

(continued)

Platycheirus occultus Goeldlin de Tiefenau, Maibach & Speight	X	X		
Pyrophaena rosarum Fabricius	X			
Scaeva pyrastri L.	X	X	X	X
Scaeva selenitica Meigen	X	X		X
Sphaerophoria interrupta Fabricius	X	X		
Sphaerophoria rueppellii Wiedemann	X		X	
Sphaerophoria scripta L.	X	X	X	X
Sphaerophoria taeniata Meigen	X	X	X	X
Syrphus ribesii L.	X	X	X	
Syrphus torvus Osten Sacken				X
Syrphus vitripennis Meigen	X	X	X	X
Trichopsomyia flavitarsis Meigen	X			
Trichopsomyia lucida Meigen			X	
Xanthandrus comtus Harris			X	
Xanthogramma pedissequum Harris	X			
Non-aphidophagous				
Chalcosyrphus nemorum Fabricius	X			
Cheilosia spec.	X	X	X	
Eristalinus aeneus Scopoli		X		
Eristalis arbustorum L.	X		X	X
Eristalis interrupta Poda	X		X	
Eristalis tenax L.	X	X	X	X
Eumerus ornatus Meigen	X			
Eumerus sogdianus Stackelberg	X	X	X	
Eumerus strigatus Fallen	X	X	X	X
Eumerus tricolor Fabricius	X		X	
Eumerus tuberculatus Rondani	X	X	X	X
Helophilus parallelus Harris	X	X	X	
Helophilus pendulus L.	X		X	
Lejogaster metallina Fabricius	X			
Merodon avidus Rossi	X			X
Myathropa florea L.	X		X	
Orthonevra nobilis Fallen	X			
Rhingia campestris Meigen	X			
Syritta pipiens L.	X	X	X	
Xylota coeruleiventris Zetterstedt	X			
Xylota segnis L.	X		X	X
Species richness (Total 64 species)	55	31	37	25

CHAPTER 6

Synthesis and outlook

Matthias Tschumi

Optimal resources for natural enemies of crop pests

Field and climate chamber experiments emphasize the value of plant-provided and particularly floral resources for the natural enemies of crop pests. Flower strips increased natural enemy numbers compared to control strips, and floral resources enhanced fitness components of different key antagonists of aphids in cages with floral supplements compared to treatments with water control. Hereby, some plants seemed generally more valuable to natural enemies than others, informing about the potential suitability for their use in flower strips. For example *Fagopyrum esculentum* enhanced the longevity of *Aphidius ervi*, *Episyrphus balteatus* and the longevity at least of *Chrysoperla carnea* males, whereas *Phacelia tanacetifolia* did not affect the longevity of any of the investigated natural enemies to a comparable extent. Increased abundances of all investigated adult natural enemies (ground beetles, predatory bugs, lacewings, ladybirds and hoverflies) in tailored flower strips compared to control strips, confirmed that the flowering plants included in mixtures were indeed valuable for the targeted enemies. In fact, *Phacelia tanacetifolia* was not included in any of the flower mixtures implemented in our field experiments.

The value of floral resources for service-providing arthropods is well documented in scientific literature (Landis, Wratten & Gurr 2000; Lundgren 2009; Haaland, Naisbit & Bersier 2011; Wäckers & van Rijn 2012; Ramsden *et al.* 2014). Pollinators and natural enemies of crop pests usually require floral resources during at least some of their life stages (Haaland, Naisbit & Bersier 2011). As floral resources are often scarce in crops, they may be substituted for by flower strips (Haaland, Naisbit & Bersier 2011; Wäckers & van Rijn 2012). Apart from pollen and nectar, other plant-provided resources such as shelter, a moderated microclimate, attraction of alternative hosts or the provisioning of overwintering sites may benefit natural enemies (Pfiffner & Wyss 2004; Jonsson *et al.* 2010). Ground beetles, for instance, likely depend more on structural resources than on pollen or nectar (Diehl, Wolters & Birkhofer 2012). Moreover structural components may, at least to some extent, replace floral resources in supporting natural enemies to curtail pest population build-up early in the year (Kindlmann & Dixon 2010). The strong effects of flower strips on natural enemies and pest control may thus be a combined outcome of rich floral and structural resources offered in flower strips (Pfiffner & Wyss 2004).

Above the beneficial effects of individual plants on natural enemies, the present results underline the value of diverse plant-provided resources for functional diversity. Confirming ecological niche predictions (e.g. Hutchinson 1959; Schoener 1989) no single plant species provided the greatest benefit for all three natural enemies in climate chambers, but rather the best-performing plant species differed amongst natural enemy species. Furthermore, flower mixtures generally performed better than average monocultures. In the field, hoverfly species showed different preferences for flowering plants of annual flower strips in flower visitation observations. In combination, these findings indicate a tendency towards positive diversity effects. Moreover, we assume that more species of natural enemies lead to still more diverse resource preferences. We thus conclude that diverse plant species mixtures support diverse natural enemy communities more effectively than single-species flower strips.

Further optimization of flower mixtures would benefit from more studies assessing the benefits natural enemies gain from floral resources. Amongst numerous studies investigating the benefits of floral resources on natural enemy performance (e.g. Patt, Hamilton & Lashomb 1997; Wäckers 2004; Pineda & Marcos-Garcia 2008; Laubertie, Wratten & Hemptinne 2012; Pinheiro *et al.* 2013; Lu *et al.* 2014), there is a distinct lack of experiments directly assessing performance and fitness consequences of different plant species on multiple pest control providing taxa. Beyond the climate chamber experiment described here, further comprehensive experiments evaluating more plant and natural enemy species in a combined approach - including additional fitness parameters such as fecundity or development - could help predict the global benefits of flower strips for enemy communities and pest control.

Maximizing flower strip effectiveness for biological control

The observed effects of flower strips on pest density and plant damage are remarkably strong. Among the few studies that have previously assessed pest density response to flower strips, effects were frequently inconsistent or weak (e.g. Baggen & Gurr 1998; Pfiffner *et al.* 2009; Winkler *et al.* 2010; Balzan & Moonen 2014) and studies with strong effects often comprised of either few or only a single study site (e.g. Wyss 1995; Hausammann 1996; van Rijn *et al.* 2008; Jacometti, Jorgensen & Wratten 2010; Skirvin *et al.* 2011). Beyond that, many studies focused on natural enemy abundance or parasitism rate (Thies & Tscharntke 1999; Tylianakis, Didham & Wratten 2004; Winkler *et al.* 2010; Haaland, Naisbit & Bersier 2011; Géneau *et al.* 2012; Balmer *et al.* 2013; Ramsden *et al.* 2014), which are, however, not necessarily reliable predictors for pest control (Heimpel & Jervis 2005; Bianchi, Booij & Tscharntke 2006).

Effective pest control confirms that the flower strips used here generally contained the 'right' floral species that support natural enemies but not pests (sensu Wäckers & van Rijn 2012). While this is relatively easily accomplished for cereal leaf beetles, which feed exclusively on grasses (Haynes & Gage 1981; Schärer 1994), aphids infesting potatoes may use a large range of host plants of diverse families (van Emden *et al.* 1969; Van Emden & Harrington 2007). Although flower selection for tailored flower strips included reviewing literature for undesirable side-effects of floral resources on pests, the potential benefits of flowering species for aphids still remain to some extent speculative. This is equally true for multitrophic interactions, which can seriously impair pest control (e.g. via intraguild predation) and are often hard to predict (Finke & Denno 2005; Prasad & Snyder 2006; Mooney *et al.* 2010; Martin *et al.* 2013). These were obviously not strong enough to affect natural enemy performance here either. We encourage further studies that investigate these aspects in detail to enhance the predictability of non-target effects of flower strips on pests and intraguild predation.

Annual flower strips may provide more abundant floral resources and suffer less from unpredictable shifts in plant composition than perennial flower strips (Pfiffner & Wyss 2004). In fact, comparably few spontaneous plants grew in targeted flower strips (MT, unpublished data). This likely helps constrain undesired side-effects of tailored flower strips and may be an additional explanation of their high effectiveness, which was not limited to the flower strip vicinity (in contrast to perennial flower strips – see also Flückiger & Schmidt 2006; Skirvin *et al.* 2011; Balzan & Moonen 2014). Annual sown flower strips are relatively easy to implement and are flexible to provide resources at the place and time they are required. The inclusion of fast growing and early flowering species such as *Fagopyrum esculentum*, *Sinapis arvensis* or *Camelina sativa* assures that natural enemies are supported at or before pest population build-up. On the downside, annual flower strips likely need support from perennial elements that offer for example overwintering sites. Arguably, perennial flower strips may thus rely less on landscape composition and provide more reliable conditions for natural enemies (Landis, Wratten & Gurr 2000). For effective habitat management, a combination of annual and perennial elements is thus recommendable.

Species richness of flower strips may also be pivotal for effective biological control. Diverse resources supported a high diversity of natural enemies, likely to complement each other for pest control in adjacent crops (Cardinale *et al.* 2003; Schmidt *et al.* 2003; Wäckers & van Rijn 2012). Beyond the investigated insects, flower strips may also support other antagonists of crop pests such as spiders (Schmidt-Entling & Döbeli 2009), rove beetles (Lys & Nentwig 1994) parasitoid wasps (Pfiffner *et al.* 2009; Balmer *et al.* 2013) or even entomopathogenic fungi (Schneider *et al.* 2012). In addition to functional complementarity, natural enemy diversity may enhance insurance effects and resilience that may stabilize pest control services and effectively prevent pest outbreaks on a long-term scale (Yachi & Loreau 1999; Wilby & Thomas 2002). Diverse flower strips may thus not only enhance the diversity of natural enemies but also their impact on pest control.

Flower strips for sustainable agriculture

Reductions of pests below economic thresholds suggest that sown flower strips can be an alternative to insecticides. Moreover, plant damage and yield benefits mediated by flower strips confirm their potential to increase agricultural production at reduced levels of anthropogenic input. Simple cost-benefit calculations suggest, that, under the assumption that flower strips are similarly or more effective than insecticides or notably increase yield, targeted flower strips may also be economically self-sustaining.

Such calculations still exclude the concurrent effects of flower strips on multiple pests and multiple ecosystem services. As tailored flower strips may for instance support the control of cereal aphids in winter wheat comparably to aphids in potato crops, the net benefit of flower strips in winter wheat may be even higher than predicted from calculations based solely on cereal leaf beetles (Östman, Ekbom & Bengtsson 2003; Dedryver, Le Ralec & Fabre 2010). This may also hold true for other crops, as control of cabbage moths for example (Pfiffner *et al.* 2009; Géneau *et al.* 2012; Balmer *et al.* 2013) or control of rape pollen beetles *Meligethes aeneus* Fabricius (Coleoptera: Nitidulidae; Büchi 2002; Scheid, Thies & Tscharntke 2011) was suggested to improve with flower strips as well. Furthermore, flower strips can enhance pollinator abundance and pollination services (Ekroos, Piha & Tiainen 2008; Haaland, Naisbit & Bersier 2011; Wratten *et al.* 2012; Blaauw & Isaacs 2014a) and provide cultural ecosystem services such as landscape aesthetics or educational value (Isaacs *et al.* 2009; Junge *et al.* 2009; Wratten *et al.* 2012).

Together with the known value of sown flower strips for farmland biodiversity (Aviron *et al.* 2009; Haenke *et al.* 2009; Haaland, Naisbit & Bersier 2011; Zollinger *et al.* 2013; Jönsson *et al.* 2015), the present results propose that sown flower strips can effectively meet the two main targets of AES: biodiversity conservation and improved ecosystem services (Kleijn *et al.* 2011; Ekroos *et al.* 2014) and thus ameliorate their controversial success. Farmers may be more likely to adopt AES if benefits are demonstrated for both biodiversity conservation and plant protection as it allows the combination of ecological measures with economic benefits. Complementing AES with elements tailored for the provisioning of ecosystem services may thus ultimately assist agricultural food production and biodiversity conservation at the same time.

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Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R* (eds M. Gail, K. Krickeberg, J.M. Samet, A. Tsiatis, and W. Wong). Springer Science+Business Media LLC, New York.

Appendix

A: Status and author contributions of publications

B: Author affiliations

C: Curriculum vitae

D: Declaration according to §8 of the Promotionsordnung des Fachbereichs 7: Natur- und Umweltwissenschaften der Universität Koblenz-Landau, Campus Landau vom 14.06.2013

Appendix A: Status and author contributions of publications

Chapter 2

Tschumi M, Albrecht M, Bärtschi C, Collatz J, Entling MH, Jacot K (under review) Perennial, species-rich wildflower strips enhance pest control and crop yield. *Agriculture, Ecosystems & Environment*

> MT, MA, CB, JC, MHE and KJ designed the study. MT, CB and KJ collected data. MT and CB processed samples and analysed the data. MT wrote the manuscript. MA, MHE and KJ provided statistical advice and MA, CB, JC, MHE and KJ provided editorial advice.

Chapter 3

Albrecht M, Steiner J, Tschumi M, Entling MH and Jacot K (in prep) Fitness effects of single and multiple flower species to different natural enemies of aphids.

> MA, JS, MT, MHE and KJ designed the study. MA, JS, MT and KJ collected data. MA, JS and MT analysed the data. MA, JS and MT wrote the manuscript. MHE and KJ provided statistical advice and editorial advice.

Chapter 4

Tschumi M, Albrecht M, Entling MH, Jacot K (in press) High effectiveness of tailored flower strips in reducing pests and crop plant damage. *Proceedings of the Royal Society B: Biological Sciences*, **282**: 20151369

> MT, MA, MHE and KJ designed the study. MT, MA and KJ collected data. MT processed samples, analysed the data and wrote the manuscript. MA, MHE and KJ provided statistical and editorial advice.

Chapter 5

Tschumi M, Albrecht M, Collatz J, Dubsky V, Entling MH, Najar-Rodriguez AJ, Jacot K (invitation to resubmit) Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. *Journal of Applied Ecology*

> MT, MA, JC, VD, MHE, AJNR and KJ designed the study. MT, MA, VD and KJ collected data. MT and VD processed samples and analysed the data. MT wrote the manuscript. MA, MHE and KJ provided statistical advice and MA, JC, VD, MHE, AJNR and KJ provided editorial advice.

Appendix B: Author affiliations

In alphabetical order:

Matthias Albrecht[1]
Cédric Bärtschi[1,3]
Jana Collatz[1,3]
Viktor Dubsky[1,3]
Martin H. Entling[2],
Katja Jacot[1]
Adriana J. Najar-Rodriguez[3]
Jolanda Steiner[1,4]
Matthias Tschumi[1,2]

[1] Agroscope, Institute for Sustainability Sciences, Reckenholzstrasse 191, CH-8046 Zürich, Switzerland
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[4] University of Zurich, Institute of Plant Biology, Zollikerstrasse 107, CH-8008 Zürich, Switzerland

Appendix C: Curriculum vitae

Name: Matthias Tschumi
Work address: Reckenholzstrasse 191
CH-8046 Zürich, Switzerland
Telephone work: +41 58 468 72 08
E-mail: matthias.tschumi@agroscope.admin.ch
Date of birth: 6th March 1986
Place of birth: Bern, Switzerland
Nationality: Swiss

Education

12/2011 – 09/2015	Ph.D. in natural sciences: Agroscope, Zürich, Switzerland and University of Koblenz-Landau, Landau (Pfalz), Germany; *Specialisation*: Agroecology
06/2010	Degree: M.Sc. in Ecology and Evolution, *Final assessment*: 6 (excellent; summa cum laude)
09/2008 – 03/2010	Graduate studies in Ecology and Evolution: University of Bern, Bern, Switzerland; *Specialisation*: Animal Ecology and Conservation
11/2008	Degree: B.Sc. in Biology, *Final assessment*: 5.5 (very good; insigni cum laude)
09/2005 – 07/2008	Undergraduate studies in Biology: University of Bern, Bern, Switzerland; *Specialisation*: Zoology
06/2004	Degree: Matura examination
08/2000 – 06/2004	High school Bern-Neufeld, Bern, Switzerland; *Specialisation*: Biology and Chemistry

Related professional experience

01/2011 - 12/2011	Swiss Federal Institute for Agriculture (FOAG): Internship, Research and Extension Unit
12/2010	University of Bern: Junior research assistant at the University of Bern, Division of Conservation Biology
05/2010 - 06/2010	Swiss Ornithological Institute: Internship

Publications

In progress

Tschumi M, Albrecht M, Collatz J, Dubsky V, Entling MH, Najar-Rodriguez AJ, Jacot K (invitation to resubmit to *Journal of Applied Ecology*) Tailored flower strips promote natural enemy biodiversity and pest control in potato crops.

Tschumi M, Albrecht M, Bärtschi C, Collatz J, Entling MH, Jacot K (under review at *Agriculture, Ecosystems & Environment*) Perennial, species-rich wildflower strips enhance pest control and crop yield.

Albrecht M, Steiner J, **Tschumi M**, Entling MH, Jacot K (in prep) Fitness effects of single and multiple flower species to different natural enemies of aphids.

Published (peer-reviewed)

Tschumi M, Albrecht M, Entling MH, Jacot K (in press) High effectiveness of tailored flower strips in reducing pests and crop plant damage. *Proceedings of the Royal Society B: Biological Sciences*, **282**: 20151369

Tschumi M, Schaub M, Arlettaz R (2014) Territory occupancy and parental quality as proxies for spatial prioritization of conservation areas. *PloS ONE* 9(5)

Published (non peer-reviewed)

Benz, R, Jucker, P, Albrecht, M, Charrière, J-D, Herzog, F, Jacot, K, **Tschumi, M**, Luka, H, Pfiffner, L, Ramseier, H, Knauer, K, Steinmann, P, Tschumi, E & Silvestri, G (2015) Blühstreifen für Bestäuber und andere Nützlinge / Bandes fleuries pour les pollinisateurs et les autres organismes utiles. Agridea, Lausanne. (In German and French)

Tschumi M, Albrecht M, Entling MH, Jactot K (2014) Targeted flower strips effectively promote natural enemies of aphids. *IOBC/WPRS Bulletin*, 100, 131-135

Lötscher M & **Tschumi M** (2012) Research master plan for the agri-food sector 2013-2016 / Forschungskonzept Land- und Ernährungswirtschaft 2013-2016. Bundesamt für Landwirtschaft (BLW), Bern. URL: http://www.blw.admin.ch/themen/00008/ (In German and French with English executive summary)

Tschumi M (2011) Die Wahl geeigneter Brutreviere beim Wiedehopf *Upupa epops. Der Ornithologische Beobachter* / Band 108 / Heft 1 / März 2011: 71-72 (In German)

Buess A, Gantner U, Lötscher M, Stöckli A, **Tschumi M** (2011) The agricultural knowledge system in Switzerland. *Agrarforschung Schweiz* 2 (11-12): 484-489 (In German and French)

Conference presentations

Tschumi M, Albrecht M, Bärtschi C, Dubsky V, Entling MH, Steiner J, Jacot K (2015) Flower strips enhance pest control in crops. Invited talk at animal ecology colloquium, May 26th 2015, Giessen University, Giessen, Germany

Tschumi M, Albrecht M, Entling MH, Dubsky V, Jacot K (2015) Weniger Schädlinge und Pflanzenschaden dank Nützlingsblühstreifen. Journée phytosanitaire Grandes Cultures, February 2nd 2015, Morat, Switzerland

Tschumi M, Albrecht M, Entling MH, Dubsky V, Jacot K (2015) Nützlingsblühstreifen – Biologische Schädlingskontrolle gezielt fördern. 2. Agroscope-Nachhaltigkeitstagung

"Funktionelle Biodiversität in der Landwirtschaft", January 22nd 2015, Zürich, Switzerland

Tschumi M, Albrecht M, Entling MH, Dubsky V, Jacot K (2014) Targeted flower strips promote natural pest control services in potato and winter wheat. 10th Annual Symposium of the PhD-Program in Sustainable Agriculture, November 6th 2014, Zürich, Switzerland*

Tschumi M, Albrecht M, Entling MH, Dubsky V, Jacot K (2014) High effectiveness of tailored flower strips in promoting pest control services. Colloquium in Biology, November 4th 2014, Landau, Germany

Tschumi M, Albrecht M, Entling MH, Dubsky V, Jacot K (2014) Targeted flower strips promote natural pest control services in potato and winter wheat. GfÖ 2014, September 8th-12th 2014, Hildesheim, Germany

Tschumi M, Albrecht M, Entling MH, Dubsky V, Jacot K (2014) Responses of crop pests and their natural enemies to modified flowering habitats at the plot scale and habitat features at the landscape scale. Workshop "Community responses to organic farming", June 16th-18th 2014, Lund, Sweden

Tschumi M, Albrecht M, Entling MH, Dubsky V, Jacot K (2014) Targeted flower strips promote natural enemies and pest control services. IOBC/WPRS Meeting, May 21st-25th 2014, Poznań, Poland

Tschumi M, Schaub M, Arlettaz R (2012) Breeding territory occupancy and reproductive success *vs* habitat and parental quality: proxies for spatial prioritization in a bird conservation program. Biology 2012, February 8th-10th 2012, Fribourg, Switzerland

*Presentation award: 1st place

Posters

Tschumi M, Entling MH, Albrecht M, Jacot K (2014) High effectiveness of flower strips designed for biological control. Postdoc Funding and Career Management, November 20th 2014, University of Zürich, Switzerland

Tschumi M, Entling MH, Albrecht M, Jacot K (2013) Targeted use of flower strips reduces cereal crop pests. 9th Annual Symposium of the PhD-Program in Sustainable Agriculture, November 21st 2013, Zürich, Switzerland

Tschumi M, Jacot K, Eggenschwiler L, Entling MH (2012) Blumenstreifen fördern Nützlinge. OpenART12, June 8th & 10th 2012, Zürich, Switzerland

Tschumi M, Eggenschwiler L, Jacot K, Entling MH (2012) Weniger Schädlinge dank ökologischen Ausgleichsflächen? Fachtagung 20 Jahre Integrierte Produktion im Ackerbau, March 16th 2012, Zürich, Switzerland

Teaching & Mentoring

2014	Joint supervision of one B.Sc. student (ETH Zürich)
2013	Joint supervision of two M.Sc. students (each one ETH Zürich and University of Zürich, respectively)
2008 - 2010	Private lessons in biology, chemistry and mathematics to high school students

Reviewing experience

Biological Conservation
Basic and Applied Ecology

Appendix D: Declaration according to §8 of the Promotionsordnung des Fachbereichs 7: Natur- und Umweltwissenschaften der Universität Koblenz-Landau, Campus Landau vom 14.06.2013

Erklärung des Doktoranden darüber,

dass er die eingereichte Dissertation selbstständig verfasst hat und alle von ihm für die Arbeit benutzten Hilfsmittel und Quellen in der Arbeit angegeben sowie die Anteile etwaig beteiligter Mitarbeiterinnen oder Mitarbeiter sowie anderer Autorinnen oder Autoren klar gekennzeichnet sind;

dass er nicht die entgeltliche Hilfe von Vermittlungs- oder Beratungsdiensten (Promotionsberater oder andere Personen) in Anspruch genommen hat;

dass er die Dissertation nicht in gleicher oder ähnlicher Form als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung im In- oder Ausland eingereicht hat;

ob er die gleiche oder eine andere Abhandlung in einem anderen Fachbereich oder einer anderen wissenschaftlichen Hochschule als Dissertation eingereicht hat, ggf. mit welchem Erfolg; - *nicht zutreffend*

dass ihm bewusst ist, dass ein Verstoß gegen einen der vorgenannten Punkte den Entzug des Doktortitels bedeuten und ggf. auch weitere rechtliche Konsequenzen haben kann;

Zürich, 01.10.2015

Matthias Tschumi