

**The influence of crop management and adjacent agri-environmental
scheme type on natural pest control in differently structured
landscapes**

Der Effekt von Feldkultur und angrenzenden Agrarumweltmaßnahmen auf natürliche
Schädlingskontrolle in unterschiedlich strukturierten Landschaften



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"If the world is to contain a public space, it cannot be erected for one generation and planned for the living only; it must transcend the life-span of mortal men."

[Hannah Arendt, *The Human Condition*. Chapter II: The Public and the Private Realm, 1958]

Affidavit

I hereby confirm that my thesis entitled ‘The influence of crop management and adjacent agri-environmental scheme type on natural pest control in differently structured landscapes’ is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore, I confirm that this thesis has not yet been submitted as part of another examination process neither in identical nor in similar form.

Würzburg, 16.12.2020

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, die Dissertation ‚Der Effekt von Feldkultur und angrenzenden Agrarumweltmaßnahmen auf natürliche Schädlingskontrolle in unterschiedlich strukturierten Landschaften‘ eigenständig, d.h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat.

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Modern agricultural landscapes have been designed and optimized to reach maximal yields and to ease mechanized field management. Fields are large, strictly geometrical and habitats such as hedgerows, green margins, flowering fields or semi-natural habitats are scarce as a maximum of the area is used for crop production.

Summary

Chapters I & II: General Introduction & General Methods

Agriculture is confronted with a rampant loss of biodiversity potentially eroding ecosystem service potentials and adding up to other stressors like climate change or the consequences of land-use change and intensive management. To counter this ‘biodiversity crisis’, agri-environment schemes (AES) have been introduced as part of ecological intensification efforts. These AES combine special management regimes with the establishment of tailored habitats to create refuges for biodiversity in agricultural landscapes and thus ensure biodiversity mediated ecosystem services such as pest control. However, little is known about how well different AES habitats fulfil this purpose and whether they benefit ecosystem services in adjacent crop fields. Here I investigated how effective different AES habitats are for restoring biodiversity in different agricultural landscapes (Chapter V) and whether they benefit natural pest control in adjacent oilseed rape (Chapter VI) and winter cereal fields (Chapter VII). I recorded biodiversity and pest control potentials using a variety of different methods (Chapters II, V, VI & VII). Moreover, I validated the methodology I used to assess predator assemblages and predation rates (Chapters III & IV).

Chapter III: How to record ground dwelling predators?

Testing methodology is critical as it ensures scientific standards and trustworthy results. Pitfall traps are widely used to record ground dwelling predators, but little is known about how different trap types affect catches. I compared different types of pitfall traps that had been used in previous studies in respect to resulting carabid beetle assemblages. While barrier traps collected more species and deliver more complete species inventories, conventional simple pitfall traps provide reliable results with comparatively little handling effort. Placing several simple pitfall traps in the field can compensate the difference while still saving handling effort.

Chapter IV: How to record predation rates?

A plethora of methods has been proposed and used for recording predation rates, but these have rarely been validated before use. I assessed whether a novel approach to record predation, the use of sentinel prey cards with glued on aphids, delivers realistic results. I compared different sampling efforts and showed that obtained predation rates were similar and could be linked to predator (carabid beetle) densities and body-sizes (a proxy often used for food intake rates). Thus, the method delivers reliable and meaningful predation rates.

Chapter V: Do AES habitats benefit multi-taxa biodiversity?

The main goal of AES is the conservation of biodiversity in agricultural landscapes. I investigated how effectively AES habitats with different temporal continuity fulfil this goal in differently structured landscapes. The different AES habitats investigated had variable effects on local biodiversity. Temporal continuity of AES habitats was the most important predictor with older, more temporally continuous habitats harbouring higher overall biodiversity and different species assemblages in most taxonomic groups than younger AES habitats. Results however varied among taxonomic groups and natural enemies were equally supported by younger habitats. Semi-natural habitats in the surrounding landscape and AES habitat size were of minor importance for local biodiversity and had limited effects. This stresses that newly established AES habitats alone cannot restore farmland biodiversity. Both AES habitats as well as more continuous semi-natural habitats synergistically increase overall biodiversity in agricultural landscapes.

Chapter VI: The effects of AES habitats on predators in adjacent oilseed rape fields

Apart from biodiversity conservation, ensuring ecosystem service delivery in agricultural landscapes is a crucial goal of AES. I therefore investigated the effects of adjacent AES habitats on ground dwelling predator assemblages in oilseed rape fields. I found clear distance decay effects from the field edges into the field centres on both richness and densities of ground dwelling predators. Direct effects of adjacent AES habitats on assemblages in oilseed rape fields however

were limited and only visible in functional traits of carabid beetle assemblages. Adjacent AES habitats doubled the proportion of predatory carabid beetles indicating a beneficial role for pest control. My results show that pest control potentials are largest close to the field edges and beneficial effects are comparably short ranged.

Chapter VII: The effects of AES habitats on pest control in adjacent cereal fields

Whether distance functions and potential effects of AES habitats are universal across crops is unknown. Therefore, I assessed distance functions of predators, pests, predation rates and yields after crop rotation in winter cereals using the same study design as in the previous year. Resulting distance functions were not uniform and differed from those found in oilseed rape in the previous year, indicating that the interactions between certain adjacent habitats vary with habitat and crop types. Distance functions of cereal-leaf beetles (important cereal pests) and parasitoid wasps were moreover modulated by semi-natural habitat proportion in the surrounding landscapes. Field edges buffered assemblage changes in carabid beetle assemblages over crop rotation confirming their important function as refuges for natural enemies. My results emphasize the beneficial role of field edges for pest control potentials. These findings back the calls for smaller field sizes and more diverse, more heterogeneously structured agricultural landscapes.

Chapter VIII: General Discussion

Countering biodiversity loss and ensuring ecosystem service provision in agricultural landscapes is intricate and requires strategic planning and restructuring of these landscapes. I showed that agricultural landscapes could benefit maximally from (i) a mixture of AES habitats and semi-natural habitats to support high levels of overall biodiversity and from (ii) smaller continuously managed agricultural areas (i.e. smaller field sizes or the insertion of AES elements within large fields) to maximize natural pest control potentials in crop fields. I propose a mosaic of younger AES habitats and semi-natural habitats to support ecosystem service providers and increase edge density for ecosystem service spillover into adjacent crops. The optimal extent and density of this

network as well as the location in which AES and semi-natural habitats interact most beneficially with adjacent crops need further investigation. My results provide a further step towards more sustainable agricultural landscapes that simultaneously allow biodiversity to persist and maintain agricultural production under the framework of ecological intensification.

Zusammenfassung

Kapitel I & II: Allgemeine Einleitung & Allgemeine Methodik

Die Landwirtschaft sieht sich einem gravierenden Verlust an biologischer Vielfalt gegenüber, der möglicherweise Ökosystemdienstleistungen erodiert und zusätzlich zu anderen Stressoren wirkt, wie etwa dem globalen Klimawandel oder den Folgen veränderter Landnutzung und intensiven Managements. Um dieser ‚Biodiversitätskrise‘ entgegen zu wirken wurden im Rahmen der ökologischen Intensivierung Agrarumweltmaßnahmen (AES) eingeführt. Diese AES verbinden spezielle Managementregime mit der Schaffung designer Habitate, die als Refugien für Biodiversität in Agrarlandschaften dienen und dadurch Ökosystemdienstleistungen, die auf Biodiversität beruhen, wie natürliche Schädlingskontrolle, sicherstellen sollen. Wie gut verschiedene AES jedoch diese Ziele erfüllen und ob Ökosystemdienstleistungen in angrenzenden Feldern tatsächlich davon profitieren, ist weitgehend unbekannt. In meiner Doktorarbeit untersuche ich wie effektiv verschiedene AES Habitate darin sind, Biodiversität in unterschiedlichen Agrarlandschaften wieder her zu stellen (Kapitel V) und ob diese natürliche Schädlingskontrolle in angrenzenden Rapsfeldern (Kapitel VI) und Wintergetreidefeldern (Kapitel VII) von diesen Habitaten profitiert. Biodiversität und Potentiale natürlicher Schädlingskontrolle wurden mit diversen unterschiedlichen Methoden erfasst (Kapitel II, V, VI & VII). Zusätzlich habe ich Methoden, die ich zur Erfassung von Räubergesellschaften und Prädationsraten verwendet habe, validiert (Kapitel III & IV).

Kapitel III: Wie erfasst man bodenaktive Räuber?

Das Testen von Methoden ist essenziell, da es wissenschaftliche Standards und vertrauenswürdige Ergebnisse sicherstellt. Bodenfallen werden häufig verwendet, um bodenaktive Prädatoren zu erfassen, aber wie verschiedene Bodenfallentypen das Fangergebnis beeinflussen ist weitgehend unbekannt. Ich habe verschiedene, in früheren Studien verwendete, Bodenfallentypen hinsichtlich der resultierenden Laufkäfergesellschaften verglichen. Während Fallen mit Leitschienen die meisten Arten fingen und dadurch die vollständigsten Artenlisten ergaben, lieferten einfache

Bodenfallen verlässliche Ergebnisse bei vergleichsweise geringem Aufwand. Das Platzieren einiger einfacher Bodenfallen kann bei immer noch geringerem Aufwand die Unterschiede kompensieren.

Kapitel IV: Wie erfasst man Prädationsraten?

Eine Fülle verschiedener Methoden zur Erfassung von Prädationsraten wurde vorgeschlagen und verwendet, jedoch wurden diese meist nicht validiert, bevor sie verwendet wurden. Ich habe getestet ob eine neuartige Methode zur Erfassung von Prädationsraten, die Verwendung von Prädationskarten mit aufgeklebten Blattläusen, realistische Resultate liefert. Dazu wurden verschiedene Karten mit unterschiedlichem Aufwand getestet. Die resultierenden Prädationsraten waren vergleichbar und durch Räuber- (Laufkäfer-) Dichten sowie deren mittlere Körpergröße (ein oft genutzter Indikator für Nahrungsaufnahmeraten) erklärt werden konnten. Daher liefert diese Methode verlässliche und sinnvolle Prädationsraten.

Kapitel V: Profitiert multi-Taxa Biodiversität von AES?

Das Hauptziel von AES ist der Erhalt der Biodiversität in Agrarlandschaften. Ich habe untersucht, wie effektiv AES Habitate mit verschiedener zeitlicher Kontinuität dieses Ziel in unterschiedlich strukturierten Landschaften erfüllen. Die verschiedenen AES Habitate hatten variierende Effekte auf die lokale Biodiversität. Zeitliche Kontinuität der AES Habitate war der wichtigste Einfluss da ältere, kontinuierlichere Habitate eine höhere Gesamtbiodiversität und in den meisten taxonomischen Gruppen andere Artengemeinschaften beherbergten als jüngere AES Habitate. Die Ergebnisse variierten jedoch zwischen den taxonomischen Gruppen und natürliche Feinde von Agrarschädlingen wurden auch durch jüngere AES Habitate gleichwertig unterstützt. Halbnatürliche Habitate in der Landschaft sowie die Größe des AES Habitats waren von geringerer Bedeutung für die lokale Biodiversität und hatten lediglich begrenzte Effekte. Diese Ergebnisse betonen, dass neu angelegte AES Habitate allein die Biodiversität in der Agrarlandschaft nicht wiederherstellen können. AES Habitate wirken synergistisch zusammen

mit kontinuierlicheren halbnatürlichen Habitaten und sichern mit diesen ein Maximum an biologischer Vielfalt in Agrarlandschaften

Kapitel VI: Die Effekte von AES Habitaten auf Räuber in angrenzenden Rapsfeldern

Neben dem Erhalt der Artenvielfalt ist das Sicherstellen von Ökosystemdienstleistungen in Agrarlandschaften ein essenzielles Ziel von AES. Ich untersuchte daher die Effekte angrenzender AES Habitate auf bodenaktive Prädatoren in Rapsfeldern. Für die Artenvielfalt als auch für die Dichten von bodenaktiven Prädatoren zeigten sich klare Distanzfunktionen von den Feldrändern abnehmend zur Feldmitte. Direkte Effekte angrenzender AES auf die Räubergesellschaften in Rapsfeldern waren hingegen limitiert und nur auf der Ebene der funktionellen Merkmale von Laufkäfergesellschaften festzustellen. Angrenzende AES Habitate verdoppelten den Anteil räuberischer Laufkäfer in den Gesellschaften, was auf einen positiven Effekt auf natürliche Schädlingsbekämpfung schließen lässt. Meine Ergebnisse deuten darauf hin, dass Potentiale natürlicher Schädlingsbekämpfung nahe den Feldrändern am größten sind und nicht relativ weit ins Feld hinein reichen.

Kapitel VII: Die Effekte von AES Habitaten auf natürliche Schädlingskontrolle in angrenzenden Getreidefeldern

Es ist allerdings noch gänzlich unbekannt, ob Distanzfunktionen und potenzielle Effekte angrenzender AES Habitate universell auf andere Feldfrüchte übertragbar sind. Ich habe daher im gleichen Studiendesign wie im vorangegangenen Jahr Distanzfunktionen von natürlichen Feinden, Schädlingen, Prädationsraten und Erträgen nach dem Fruchtwechsel in Wintergetreide erfasst. Die gefundenen Distanzfunktionen waren verschieden und unterschieden sich von den im Vorjahr im Raps erfassten Distanzfunktionen, was darauf schließen lässt, dass die Interaktion zwischen verschiedenen Feldfrüchten und Nachbarhabitaten variieren. Distanzfunktionen von Getreidehähnchen (wichtigen Getreideschädlingen) und parasitoiden Wespen waren zusätzlich durch den Anteil halbnatürlicher Habitate in der Landschaft moduliert. Feldränder pufferten die

Veränderungen in Laufkäfergesellschaften über den Fruchtwechsel ab, was deren wichtige Funktion als Refugialhabitate für natürliche Schädlingsbekämpfer verdeutlicht. Meine Ergebnisse betonen die Rolle von Feldrändern für die natürliche Schädlingsbekämpfung. Die Ergebnisse stärken die Forderung nach kleineren Feldgrößen und diverseren, heterogener strukturierten Agrarlandschaften.

Kapitel VIII: Allgemeine Diskussion

Der Kampf gegen den Verlust der biologischen Vielfalt und das Sicherstellen von Ökosystemdienstleistungen in Agrarlandschaften ist komplex und erfordert ein strategisches Planen und eine Transformation dieser Landschaften. Ich habe gezeigt, dass Agrarlandschaften von (i) einer Mischung aus AES Habitaten und halbnatürlichen Habitaten, die zusammen eine große Artenvielfalt unterstützen, und von (ii) einer geringeren kontinuierlich bewirtschafteten Agrarfläche (d.h. kleineren Feldgrößen oder dem Einfügen von AES Habitaten in bestehende große Felder) um natürliche Schädlingskontrolle zu maximieren, profitieren würden. Ich schlage vor ein Mosaik aus jüngeren AES Habitaten und halbnatürlichen Habitaten zu schaffen, um Ökosystemdienstleistungen zu unterstützen und das Netzwerk an Feldrändern zu vergrößern wodurch Ökosystemdienstleistungen in angrenzenden Feldkulturen maximiert werden könnten. Um die optimale Ausdehnung und Dichte dieses Netzwerks wie auch die optimale Platzierung, in der AES und halbnatürliche Habitate die größtmöglichen Effekte auf angrenzende Feldkulturen haben, zu klären, bedarf es weiterer Forschung. Meine Ergebnisse liefern einen weiteren Schritt hin zu nachhaltigeren Agrarlandschaften die im Rahmen der ökologischen Intensivierung gleichzeitig sowohl ein Fortbestehen der Biodiversität als auch landwirtschaftliche Produktion erlauben.



Over the last decades, agricultural landscapes across Europe have experienced an unprecedented decline of biodiversity and insect abundances. This loss is not only threatening the conservation of species and genetic diversity, it also endangers agricultural production as many insect species are important ecosystem service providers.

Chapter I: General Introduction

I.1 The state of agricultural production

Agricultural production feeds the planet and is the basis of human civilization. Its importance is steadily increasing with rising world population as nutrition is a basic necessity with a doubling in demand expected by 2050 (Tilman *et al.* 2011). Intensification of agricultural production since the middle of the 20th century has led to an increase in suitable cropland as well as in yields (Foley *et al.* 2011). This ‘green revolution’ has drastically increased global per capita food supply and managed to feed the growing mass of consumers (Tilman *et al.* 2002; Foley *et al.* 2005; Godfray *et al.* 2010).

This ‘green revolution’ came, however, with a price tag. Progressing intensification and mechanisation as well as the simultaneous land-use change in agricultural landscapes were detrimental to the resources needed for agricultural production and to local and global climate (Foley *et al.* 2005; Foley *et al.* 2011). Widespread irrigation causes salinification of approximately 1.5 million hectares of cropland worldwide per year and depletes aquifers (Foley *et al.* 2005). Overuse of fertilizers has degraded freshwater quality in many regions and up to 40 percent of global cropland is currently threatened by soil erosion (Foley *et al.* 2005; Montgomery 2007). With the growing need for more farmland, many natural habitats have been converted to cropland (Foley *et al.* 2005; Foley *et al.* 2011). This land-use change and agricultural production itself are also responsible for up to 35 percent of global greenhouse gas emissions and therefore one of the main drivers of global climate change (Smith & Olesen 2010; Foley *et al.* 2011).

In the future, agricultural production will once again need to be revolutionized. Currently, roughly 38 percent of the earth’s terrestrial surface are used for agricultural production and the increasing demand leads to ever growing competition for land and water (Godfray *et al.* 2010; Foley *et al.* 2011). As in many highly productive agricultural regions an expansion of agricultural land is hardly possible due to population density and environmental consequences,

the pressure on agriculture to raise effectivity with the given resources is growing (Foley *et al.* 2011; Tilman *et al.* 2011). However, over the recent decades, yields of the major staple crops (wheat, rice, maize and soybeans) have stopped increasing, stagnated or even collapsed in many regions worldwide (Tilman *et al.* 2002; Ray *et al.* 2012). Additionally, ongoing climate change and its consequences pose a novel threat for agriculture: Climate change reduces overall yields of important staple crops like wheat and maize significantly (Lobell, Schlenker & Costa-Roberts 2011) and at the same time increases crop pest pressure (Deutsch *et al.* 2018). Thus, accumulating evidence indicates that modern, intensive agriculture has reached a plateau of productivity and simultaneously erodes its foundations.

Future agriculture thus needs to solve different problems at the same time: More consumers with rising demands need to be fed, agriculture must cope with depleted and deteriorated resources and it has to decrease its footprint on ecosystems (Godfray *et al.* 2010; Foley *et al.* 2011). To fulfil these expectations, future agricultural production will, however, have to preserve the resources it is based on and mitigate its effects on global climate change (Foley *et al.* 2011; Tilman *et al.* 2011). Only if agriculture becomes more sustainable, can it ensure food production for a growing population.

I.2 The rebirth of biodiversity in agricultural landscapes

One important factor in the challenge to make agricultural production sustainable is reviving, re-establishing and supporting biodiversity in agricultural landscapes. Biodiversity is a key aspect in ecological intensification, an ‘ecological revolution’ of agricultural practices. Ecological intensification aims at replacing current management practices with biodiversity driven ecosystem services and thus intensifying agriculture ecologically and sustainably (Foley *et al.* 2011; Bommarco, Kleijn & Potts 2013; Garibaldi *et al.* 2017; Kleijn *et al.* 2019).

This ecological approach aims at removing management pressure from agricultural ecosystems and thus allowing local biodiversity, soils and nutrient cycles to recover

(Bommarco, Kleijn & Potts 2013; Garibaldi *et al.* 2017). Natural pest control can partly replace agrochemical inputs, soil biodiversity and cover crops can replace radical soil management, mitigate soil erosion and maintain soil fertility without inorganic fertilizers and thereby protect aquifers from pollution (Garibaldi *et al.* 2017; Garibaldi *et al.* 2019).

Many of the essential ecosystem service agents involved in this approach are insects. Ecosystem services ensuring crop yields such as pollination or natural pest control have been shown to be directly driven by insect biodiversity (Dainese *et al.* 2019). However, insect biodiversity and biomass in agricultural landscapes are in decline and these declines have been related to past and current agricultural land-use (Seibold *et al.* 2019; van Klink *et al.* 2020). Species with low dispersal abilities are especially affected and may get lost in intensive agricultural landscapes, resulting in a simplified and impoverished subset of generalist agricultural biodiversity jeopardizing the stability of ecosystem service provision (Kleijn *et al.* 2006; Seibold *et al.* 2019). Therefore, agricultural management as well as the agricultural landscape need to change and become more biodiversity-friendly to ensure the future of food production.

I.3 Interactions between landscapes and ecosystem service potentials

Ecological intensification involves both a change in local management and a change in land-use (Bommarco, Kleijn & Potts 2013). Composition (i.e. the amounts of different habitat types within the landscape) as well as configuration (i.e. the spatial arrangement of habitat types) of agricultural landscapes are crucial factors affecting biodiversity in the landscapes (Fahrig *et al.* 2011). Especially landscape heterogeneity as a measure of configuration has been shown to be at least as important for biodiversity as local field management (Martin *et al.* 2019; Martin *et al.* 2020).

In order to exploit ecosystem service potentials, agricultural landscapes thus need to be tailored towards supporting the functional biodiversity that is needed to deliver these services.

Conserving biodiversity requires safe havens such as semi-natural habitats (SNH) for species to persist, forage, procreate, nest and hibernate within intensively managed agricultural landscapes (Tschardt *et al.* 2005). With natural habitats having been lost to and transformed by human land-use, semi-natural habitats that were created by extensive land-use centuries ago are now ironically the most natural habitat types in agricultural landscapes and widely considered to be biodiversity hotspots in Central Europe (WallisDeVries, Poschlod & Willems 2002; Poschlod, Bakker & Kahmen 2005).

While habitat area is positively correlated with both species richness as well as larger, more stable populations (Connor, Courtney & Yoder 2000; Turner & Tjørve 2005) it is still under debate whether fewer large habitats or a network of many smaller habitats with the same total area are better suited for biodiversity conservation (Rösch *et al.* 2015; Grass *et al.* 2019; Batáry *et al.* 2020). The latter option simultaneously increases landscape heterogeneity which is an essential factor securing farmland biodiversity (Benton, Vickery & Wilson 2003; Martin *et al.* 2020).

Both compositional and configurational aspects have been shown to benefit biodiversity and ecosystem services in agricultural landscapes. Specifically, edge-density, the diversity of planted crops and SNH cover have been shown to support farmland diversity (Martin *et al.* 2019; Sirami *et al.* 2019; Alignier *et al.* 2020). The transformation towards more sustainable agricultural landscapes likely needs a combination of both compositional and configurational changes, including spared habitats as shelters for biodiversity (Fahrig *et al.* 2011; Batáry *et al.* 2020).

Agricultural landscapes thus need to be remodelled in order to make ecological intensification work. Current simplified agricultural landscapes cannot, however, be changed easily due to regulations and the many stakeholders involved (Sirami *et al.* 2019). Ecological intensification therefore needs subsidized incentives to encourage farmers to reintroduce heterogeneity and diversity into agricultural landscapes.

I.4 Agri-environment schemes to counter biodiversity loss

To achieve landscapes and agricultural management practices that allow sustainable food production and ecological intensification, agri-environment schemes (AES) have been introduced under the common agricultural policy (CAP) of the European Union (Ekroos *et al.* 2014). Under AES, field management is restricted and special habitats are established as shelters for biodiversity and ecosystem service providers (Tschardt *et al.* 2005; Ekroos *et al.* 2014). Payments included in AES compensate farmers for lower yields and resulting financial disadvantages due to mandatory environmentally-friendly management practices and crop area used for AES habitats (Hodge, Hauck & Bonn 2015).

Under AES, tailored habitats are created to conserve biodiversity and foster ecosystem services in agricultural landscapes (Scheper *et al.* 2013). In many European countries, sown flowering fields are established as on field AES (Haaland, Naisbit & Bersier 2011). AES habitats are comparatively simple means to reduce disturbance levels at field scales and introduce complexity in agricultural landscapes. Previous studies occasionally showed benefits of AES for selected taxonomic groups but also found that these vary between the type of AES investigated and between taxonomic groups (Kleijn *et al.* 2006; Batáry *et al.* 2011; Batáry *et al.* 2015). However, beneficial effects of AES on the landscape scale are scarce (but see Sutter *et al.* (2018)) and direct beneficial effects of AES habitats on ecosystem services in adjacent crop fields have rarely been shown (but see Dainese *et al.* (2017a) or Tschumi *et al.* (2016a)).

Assessing the effects of AES habitats is difficult as a plethora of different habitats are created under AES across the European Union, differing in vegetation structure, size, age and connectivity (Ekroos *et al.* 2014; Batáry *et al.* 2015). However, these characteristics likely determine the effectivity of AES habitats. Species need time to find and colonize AES habitats and effects on biodiversity are often only visible after years (Haaland, Naisbit & Bersier 2011; Blaauw & Isaacs 2014). Larger habitats can maintain larger, more stable populations and are more advantageous for pest control (Blaauw & Isaacs 2012). Beneficial effects of AES habitats

are expected to be bigger in comparatively simple landscapes than in complex landscapes (Tscharntke *et al.* 2005; Scheper *et al.* 2013) and a low ecological contrast between AES habitats and the surrounding complex landscape may disguise beneficial effects (Marja *et al.* 2019). Few previous studies have, however, considered and addressed this dependence of AES habitat effectivity on habitat characteristics, which has led to very heterogenous results across studies.

Achieving both goals of biodiversity conservation and ecosystem service provision simultaneously with the same AES measure is intricate (Scheper *et al.* 2013). Unsurprisingly, the effectivity of AES is constantly under debate and their overall value for securing biodiversity and ecosystem service provision varies between the studied systems and many aspects remain unknown (Kleijn *et al.* 2011; Kleijn *et al.* 2019; Batáry *et al.* 2020). Recently, European AES and the CAP have been criticised for not being targeted enough and thus not fulfilling their ambitious goals (Pe'er *et al.* 2017; Pe'er *et al.* 2019). Thus, more data is needed on which AES habitats fulfil the goals and whether and how they affect ecosystem services in adjacent agricultural fields and agricultural landscapes. In this context, it is crucial to know in which landscapes AES habitats work best and how big they have to be. Only if these aspects are known, can the AES habitats best suited for ecological intensification be established.

1.5 Pest control ensures sustainable yields

Pests are one of the most important burden in modern agriculture significantly reducing potential yields (Savary *et al.* 2019). Pest control is thus one of the most important services determining the efficiency of crop production. While farmers aim at controlling crop pests actively via the application of chemical agents, a large part of the total pest control is actually provided clandestinely by natural enemies (Pimentel 2005). European agricultural landscapes currently have, however, comparably low natural pest control potentials (Rega *et al.* 2018).

Intensive agricultural management accompanied with agriculturally optimized landscapes often disrupt and deteriorate natural pest control services.

On the local scale, the application of insecticides can lead to long lasting reduction in natural enemy densities while pests recover rapidly due to their high reproduction rate (Krauss, Gallenberger & Steffan-Dewenter 2011). After crop harvest, natural enemies seek refuge in adjacent habitats (Schneider *et al.* 2016). Such semi-permanent or permanent habitats are important as they allow for hibernation and oviposition and provide shelter and alternative prey in times of need (Bianchi, Booij & Tschardt 2006; Holland *et al.* 2016). Occasionally, such habitats have been shown to directly support natural pest control, e.g. in the case of annual flower strips (Tschumi *et al.* 2016a; Tschumi *et al.* 2016b).

On the landscape scale, the composition and configuration of agricultural landscapes are important drivers for natural pest control with landscape simplification decreasing natural enemy richness and weakening natural pest control (Rusch *et al.* 2013; Karp *et al.* 2018; Haan, Zhang & Landis 2019). Edge-density and the proportion of semi-natural habitats support natural enemies in agricultural landscapes (Martin *et al.* 2019; Sirami *et al.* 2019). Landscape level crop diversity as well as diverse crop rotations benefit natural pest control (Rusch *et al.* 2013; Redlich, Martin & Steffan-Dewenter 2018).

Natural enemy richness is directly driving pest control services but apart from diversity and densities, functional traits and functional diversity within natural enemy assemblages are also important predictors for pest control services (Gagic *et al.* 2015; Greenop *et al.* 2018; Dainese *et al.* 2019). While recent synergy studies and meta-analyses have primarily focused on the drivers of natural pest control on the landscape level, many of the local drivers remain poorly understood.

I.6 Spillover and distance effects

Field edges differ from field centres in many ways: Pressures caused by mechanical management and fertilizer input are lower near the field edge (Van Vooren *et al.* 2018; Martin *et al.* 2020). At the same time, field edges are affected by adjacent habitats in both abiotic and biotic ways – edge effects can alter local microclimate and animal assemblages as animals spill over from the adjacent habitat (Murcia 1995; Tschardtke, Rand & Bianchi 2005; Schneider *et al.* 2016).

Although within-field distance and adjacent habitats are major factors changing species assemblages and therefore also ecosystem service potentials in crop fields, they are rarely studied. It is generally accepted that many beneficial arthropods spill over from undisturbed source habitats (such as perennial or permanent semi natural habitats but also field margins or farm roads) into adjacent agricultural fields and provide important ecosystem services there (Holland & Luff 2000; Tschardtke, Rand & Bianchi 2005). Occasionally, the distance to certain adjacent habitats such as margins or flower strips has been shown to be a predictor for natural enemy densities or pest control services (Hof & Bright 2010; Tschumi *et al.* 2016a; Woodcock *et al.* 2016; Fusser *et al.* 2018). Other studies have, however, found no such patterns or even the highest densities of natural enemies in field centres and not near the field edges (Anjum-Zubair *et al.* 2010; Birkhofer, Wolters & Diekötter 2014).

Spillover of natural enemies from suitable adjacent habitats and edge effects on natural enemy assemblages might provide the necessary pest control services to enable ecological intensification. However, as previous results have been inconclusive, essential factors in the understanding of distance functions of natural enemies in agricultural fields seem to be missing. Despite their crucial importance, the extent of spillover and edge effects on natural enemies, pest control and ultimately crop yields as well as the role of different crops, different adjacent habitat types or landscape context remain largely unknown.

I.7 Ensuring reliable results in ecosystem service assessments

Foundational research is one of the most important disciplines in science. The replication of scientific studies to confirm accepted theories and the control of scientific protocols and methodology based on the latest knowledge is essential and leads to reliable and valid results (Nakagawa & Parker 2015; Kelly 2019). Recently, many scientific fields, especially psychology and social sciences have discovered a so called ‘replication crisis’ as many study outcomes could not be replicated in later studies, mainly due to a lack of transparency and unsuitable methodology that biased results (Parker *et al.* 2016; Kelly 2019).

In ecological research, methods for data collection in the field are rarely evaluated as it is tedious, not exceptionally novel and potentially questions methods that are both widely used and accepted (Nakagawa & Parker 2015). However, a critical approach towards methodology should be one of the core principles of applied scientific research – only if methods are continuously checked for validity and improved where necessary, can predictions drawn from the data acquired using these methods be accurate.

In order to reliably quantify ecosystem services, the used methods need to be critically tested and improved if necessary. For quantifying pest control services, it is essential to know the local natural enemy populations as well as the service performed (i.e. the actual predation). Many important natural enemies in agriculture are ground dwelling arthropods that are typically assessed with passive pitfall traps first proposed over a century ago by Dahl (1896) and continuously refined since then (Kotze *et al.* 2011; Brown & Matthews 2016). Many different designs are available, and a considerable subset is used for different research questions, yet little is known about which design provides the best trade-off between efficiency and precision when assessing natural enemy assemblages. The predation service itself has only recently gained attention and many methods using different sentinel prey items for quantifying predation rates in the field have been proposed (Birkhofer *et al.* 2017). Although these methods are used, evidence that resulting predation rates can be linked to natural enemy assemblages is often lacking.

I.8 Study system and research questions

Assessing the value of different AES habitats for biodiversity conservation and natural pest control in adjacent fields

The main goals of AES are securing biodiversity and biodiversity mediated ecosystem services in agricultural landscapes (Ekroos *et al.* 2014). Within the scope of this thesis, I investigated the effects of three types of sown flowering fields established under AES along a gradient of temporal continuity on local biodiversity in comparison to semi-natural calcareous grasslands (Figure I.1).



Figure I.1 The four different AES types studied: (A) new sown flowering fields (aka ‘KULAP new’ in Chapter V); (B) refreshed flowering fields (aka ‘KULAP old’ in Chapter V); (C) continuous flowering fields (aka ‘set-aside greening’ in Chapter V) and (D) semi-natural calcareous grasslands.

AES habitats were not only selected within a gradient of temporal continuity but, in contrast to previous studies, also within independent gradients of habitat size and SNH in the surroundings (i.e. landscape context) to assess the factors determining local biodiversity. I investigated the potential of AES habitats for biodiversity conservation in agricultural landscapes across 12 different taxonomic groups collected with various traditional methods and identified by taxonomists as well as through DNA metabarcoding (explained in more detail in the material and methods sections of Chapter V, Figure I.2).

Apart from conserving biodiversity, the other main goal of AES habitats in agricultural landscapes is ensuring biodiversity mediated ecosystem services like pest control (Ekroos *et al.* 2014; Dainese *et al.* 2019). Therefore, I investigated whether AES habitats benefit predator assemblages and natural pest control in adjacent crop fields and how far potential effects reach into the fields. I assessed ground dwelling predator assemblages in adjacent oilseed rape fields up to 65 meters from the field edge and investigated the effects of the presence of AES habitats and of different adjacent AES types on the resulting distance functions (explained in more detail in the material and methods sections of Chapter VI, Figure I.2). Using the same design, I recorded ground dwelling predator assemblages, pest densities, predation rates as well as crop yields in winter cereals in the subsequent year following crop rotation. I assessed whether distance functions of natural pest control were affected by adjacent AES habitats and landscape level SNH proportion (explained in more detail in the material and methods sections of Chapter VII, Figure I.2).

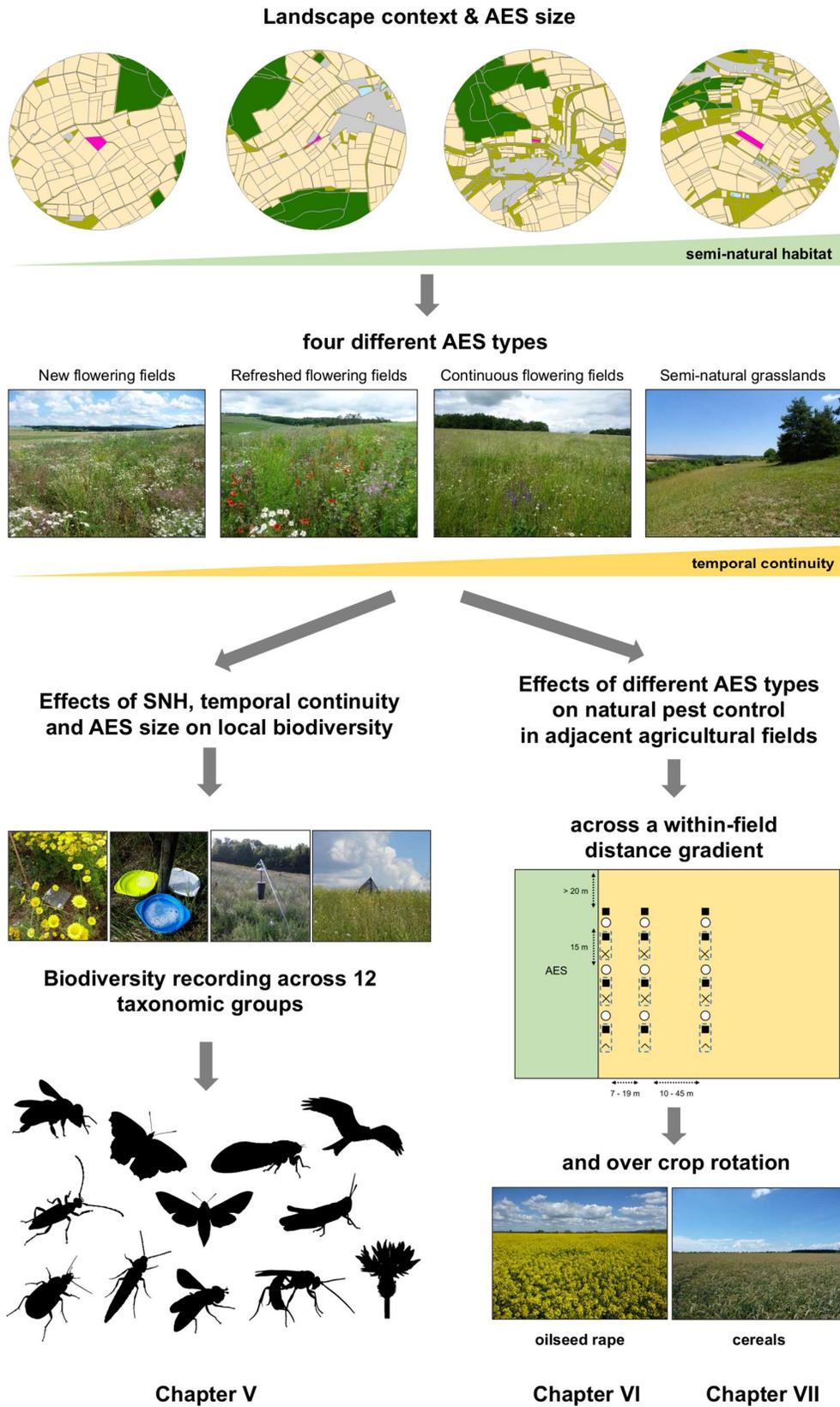


Figure I.2 (on previous page) Conceptual study design with main research questions. The study design was comprised of four different agri-environment scheme (AES) habitats along a gradient of temporal continuity (three types of flowering fields as well as semi-natural calcareous grasslands). The AES habitats were located within gradients of habitat size and semi-natural habitat (SNH) in the surrounding landscapes. Using different collection methods, I investigated the importance of habitat size, semi-natural habitat and temporal continuity on local biodiversity (Chapter V). Furthermore, I examined potential effects of AES habitats on adjacent agricultural fields. I recorded natural enemies, predation rates and yields across a distance gradient from the AES habitat into the fields and over crop rotation from oilseed rape (Chapter VI) to winter cereals (Chapter VII).

My study design comprised 31 sites in the agricultural landscape around Würzburg (Bavaria, Germany) including three types of flowering fields with increasing temporal continuity and semi-natural calcareous grasslands bordering crop fields as well as control fields without adjacent AES habitat (Figures I.3).

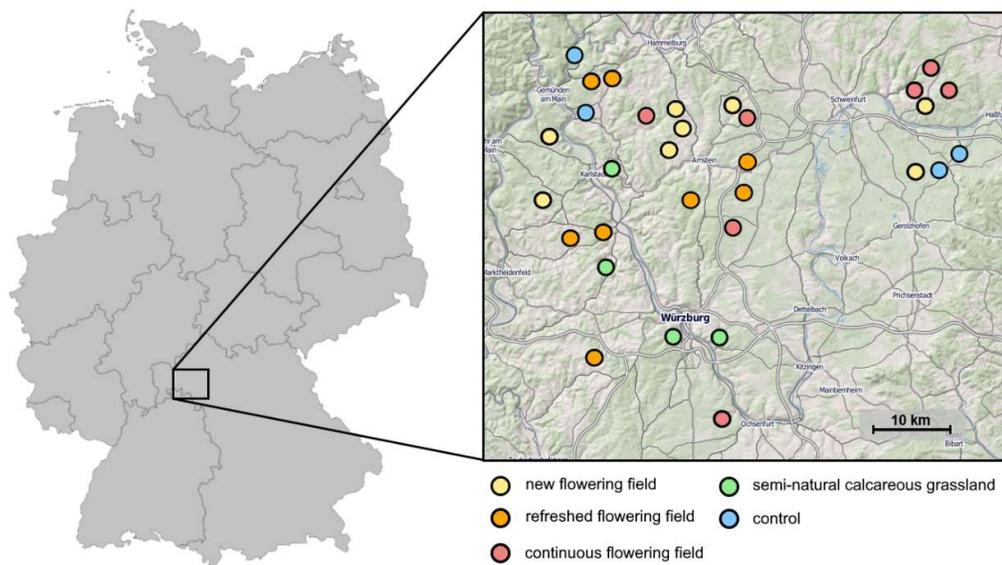


Figure I.3 Map showing the location of all 31 study sites within the study area around Würzburg / Germany. The five different types of habitats / habitat combinations studied were: new sown flowering fields (aka ‘KULAP new’ in Chapter VI; yellow); refreshed flowering fields (aka ‘KULAP old’ in Chapter VI; orange); continuous flowering fields (aka ‘set-aside greening’ in Chapter VI; red); semi-natural calcareous grasslands (green) and control fields without adjacent AES habitats (blue). Map modified after: © OpenStreetMap-contributors.

Validating methods for assessing natural pest control

I used a variety of observational and experimental methods for assessing pest control and natural enemy assemblages. Studies in applied ecological research rarely validate the methods used and accept methods used in previous studies as reliable. Here, I tested both established as well as novel methodology in order to assure that the methods used in the field were reliable and delivered meaningful results.

Many important natural enemies in agriculture are ground-dwelling such as carabid beetles, staphylinid beetles or spiders. These ground-dwelling natural enemies are usually recorded with pitfall traps. However, as many different designs of pitfall traps have been proposed, I tested which pitfall trap type is best suited for this assessment (Chapter III).

Recording of predation rates is commonly performed using sentinel-prey methods. I used sentinel-prey cards with glued on aphids and for the first time validated whether resulting predation rates can be linked to natural enemy assemblages and are therefore meaningful (Chapter IV).



Predation is one of the essential interactions between animals in ecosystems. Occasionally, predators also prey on other predators, a phenomenon called 'intraguild predation', seen here in the jumping spider *Asianellus festivus* (C. L. Koch, 1834) feeding on a fellow jumping spider of the genus *Salticus*.

Chapter II: General Methods

Within the scope of this thesis, I used a variety of different methods to gather and analyse data. I used pitfall traps to collect ground dwelling predators (carabid beetles, staphylinid beetles and spiders) and validated the reliability of this method (Chapters III, V, VI & VII). Insect diversity across different taxonomic groups on AES habitats was recorded with pan traps, light traps and transect walks (Chapter V). Additionally, flying insects were collected with malaise traps and subsequently assessed using next generation sequencing and DNA metabarcoding (Chapter V).

For the quantification of natural enemy densities, I recorded ground dwelling predators in fields adjacent to AES habitats with pitfall traps and flying parasitoid wasps with crossed window traps (flight interception traps; Chapters VI & VII). Pest densities were recorded with sweep netting along standardized transect walks (Chapters VI & VII). Predation rates were recorded with sentinel prey cards using glued on aphids, a method I also validated (Chapters IV & VII).

All samples and specimens collected in the field were processed in the lab and collected specimens were subsequently identified by specialized taxonomists. Statistical analyses were performed in R (R Development Core Team 2019) and consisted mainly of mixed effects modelling combined with likelihood ratio testing. Detailed information on the specific methods used, the statistical approaches and the packages used for specific analyses are given in the Materials and methods sections in each chapter.



Ground dwelling predators are among the most important natural enemies in agricultural systems. Usually, the term ‘ground dwelling predators’ refers to carabid beetles (such as this *Cylindera germanica* (Linnaeus, 1758), a representative of the tiger beetles (Cicindelinae), a subfamily of the ground beetles (Carabidae)), staphylinid beetles and spiders.

Chapter III: How to record ground dwelling predators?

As published in: Boetzi, F.A., Ries, E., Schneider, G., Krauss, J. (2018) It's a matter of design—how pitfall trap design affects trap samples and possible predictions. PeerJ 6: e5078.

Summary

Background. Pitfall traps are commonly used to assess ground dwelling arthropod communities. The effects of different pitfall trap designs on the trapping outcome are poorly investigated however they might affect conclusions drawn from pitfall trap data greatly.

Methods. We tested four pitfall trap types which have been used in previous studies for their effectiveness: a simple type, a faster exchangeable type with an extended plastic rim plate and two types with guidance barriers (V- and X shaped). 20 Traps were active for 10 weeks and emptied biweekly resulting in 100 trap samples.

Results. Pitfall traps with guidance barriers were up to five times more effective than simple pitfall traps and trap samples resulted in more similar assemblage approximations. Pitfall traps with extended plastic rim plates did not only perform poorly but also resulted in distinct carabid assemblages with less individuals of small species and a larger variation.

Discussion. Due to the obvious trait filtering and resulting altered assemblages, we suggest not to use pitfall traps with extended plastic rim plates. In comprehensive biodiversity inventories, a smaller number of pitfall traps with guidance barriers and a larger number of spatial replicates is of advantage, while due to comparability reasons, the use of simple pitfall traps will be recommended in most other cases.

Introduction

Proposed nearly a century ago, pitfall traps remain one of the most commonly applied sampling methods in ecological field studies and are widely used for the assessment of ground dwelling arthropod taxa which are of high importance in modern ecosystem functioning research (Brown & Matthews 2016). Although the limitations of pitfall traps in respect to trait filtering and reflecting diversity and abundances in a habitat appropriately have been intensively discussed, the method is still the best standardized and comparable approach to study ground dwelling arthropods and due to comparative low handling time allows for sufficient replication (Driscoll 2010; Kotze *et al.* 2011).

Different features of pitfall trap designs have undergone review and research over the last decades in order to improve and standardize trap designs: colour of traps (Buchholz *et al.* 2010), the presence and colour of rain covers (Buchholz & Hannig 2009; Csázár *et al.* 2018), sampling intervals (Schirmel *et al.* 2010), spatial distribution (Ward, New & Yen 2001), different preservatives (Schmidt *et al.* 2006; Skvarla, Larson & Dowling 2014) as well as pitfall trap diameters and the use of funnels (Lange, Gossner & Weisser 2011; Csázár *et al.* 2018). A recent meta-analysis by Brown and Matthews (2016) discussed many pitfall trap parameters (diameter, depth, colour, rain covers, preservatives and the use of funnels) and even proposed a standardized trap design. However, the authors did not consider additions to pitfall trap designs such as extended rim plates or guidance barriers although these have been used in previous studies.

In a conventional simple pitfall trap as proposed by the pioneers Dahl (1896), Barber (1931) and Greenslade (1964) which is basically a container sunk in the soil, a large proportion of ground dwelling beetle species occurring in a habitat will not be detected with sufficient certainty as they are comparatively rare in assemblages (Driscoll 2010). To overcome this limitation without increasing the sampling effort and workload, guidance barrier pitfall traps have been introduced. The use of guidance barriers is meant to increase capture efficiency and the number of singletons which are particularly important in conservation studies where

complete biodiversity inventories are desired (Hansen & New 2005). However, only few studies investigated the actual effect of guidance barriers on pitfall trap catches and these studies suffered from low sample sizes and unbalanced sampling efforts with a different number of pitfall traps used in the studied pitfall trap designs (Winder *et al.* 2001; Hansen & New 2005). Moreover, guidance barrier pitfall traps are not commonly used in applied research (but see Hossain *et al.* (2002) and Schneider *et al.* (2016)). To our knowledge, the effects of barriers on assemblages or traits have so far not been investigated at all.

To reduce handling time in the field as well as the so called ‘digging in effects’ (Greenslade 1973; Digweed *et al.* 1995), pitfall traps with extended PVC rim plates screwed on top of a pitfall trap glass jar have been designed. With this design, hardly any digging or filling of gaps between the pitfall trap and the surrounding soil is needed in the process of exchanging pitfall trap containers and therefore handling time and the release of soil CO₂ are reduced. The latter is known to increase ground dwelling arthropod activity and could therefore affect pitfall trap catches and lead to an overestimation of activity densities (Joosse & Kapteijn 1968; Schirmel *et al.* 2010). Another advantage of this design is the enhanced standardization of the transition between the pitfall trap and surrounding soil. However, it is unknown how these traps perform in comparison with simple pitfall traps and whether the extended plastic rim plate affects resulting ground dwelling arthropod assemblages.

In this study, we investigate the effects of different pitfall trap designs on the catches of the three most commonly studied ground dwelling arthropod taxa (carabid beetles, staphylinid beetles and spiders) and possible effects on assemblage structure and trait filtering in carabid beetles.

Materials and methods

Study design

The study was performed on a semi-natural meadow with hedgerows near the Biocenter of the University of Würzburg in central Germany (49.779416° N, 9.973360° E). On this meadow five plots of each four pitfall traps were established. The five plots always consisted of four different pitfall trap designs:

- i. Conventional simple pitfall traps (Fig III.1 A)
- ii. Pitfall traps with a squared extended PVC rim plate screwed on top of the glass jar used as pitfall trap for avoidance of digging in effects and easier exchange (10 x 10 cm²; diameter 7 cm; Fig III.1 B)
- iii. V-shaped guidance barrier pitfall traps using two 75 cm long metal barriers (height: 7 cm, angle: 90°, proposed by Smith (1976); Fig III.1 C)
- iv. X-shaped guidance barrier pitfall traps using four 75 cm long metal barriers (height: 7 cm angle: 90°, proposed by Morrill, Lester and Wrona (1990); Fig III.1 D)

The minimum distance between plots was 45 m while the pitfall traps within a plot were placed in a row and separated from each other by 10 m to minimize possible detrimental effects of neighbouring pitfall traps on pitfall trap catches. All pitfall traps were located 2 m apart from an adjacent hedgerow to make trap samples comparable.

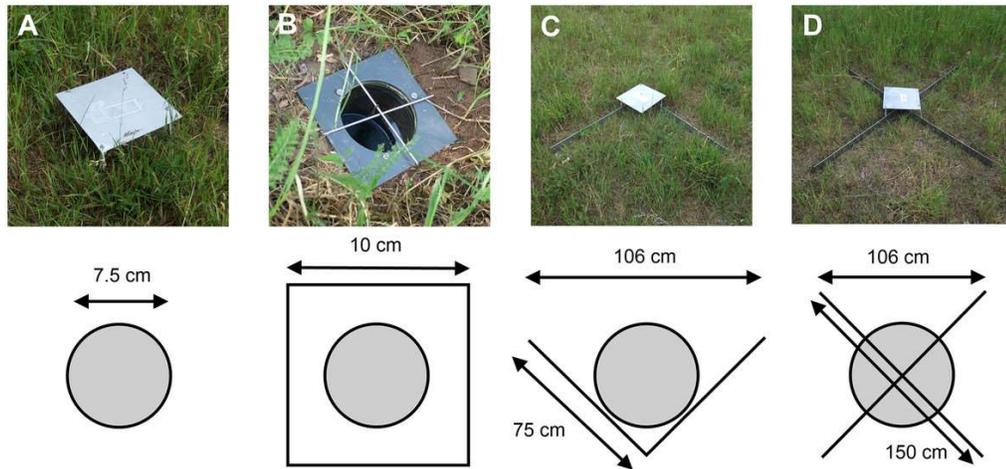


Figure III.1 Pitfall trap designs investigated. (A) Conventional pitfall trap, (B) pitfall trap with a squared extended PVC rim plate (shown without metal roof), (C) pitfall trap with V-shaped guidance barriers, (D) pitfall trap with X-shaped guidance barriers. Arrows indicate measurements of the corresponding parts.

Data collection

Pitfall traps were set up at the 13th March 2012 and emptied biweekly until the 22nd May 2012 which results in 100 trap samples (5 plots x 4 pitfall traps per plot x 5 sampling intervals). As pitfall trap containers, we used conventional glass honey jars (height: 9 cm, diameter: 7.5 cm, transparent) filled with 200 ml 3 parts water with 1 part ethylene glycol (automobile antifreeze, H. Kerndl GmbH) mixture with odourless detergent as trapping liquid and preservative in each pitfall trap design. Pitfall traps were covered by metal roofs (25 x 25 cm², approximately 10 cm above ground) to protect against flooding. To minimize small vertebrate bycatch, all traps except for the X-shaped guidance barrier type were additionally covered by a wire cross (length: 10 cm, width: 2 mm; Fig III.1B).

Pitfall trap samples were sorted for carabid beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Araneae). All individuals from these taxa were counted and all carabid beetles were identified to species level following Müller-Motzfeld (2006). Carabid body size was obtained from the online database ‘carabids.org’ (Homburg *et al.* 2014).

Statistical analyses

All statistical analyses were performed in R 3.3.1 for Windows (R Development Core Team 2016).

For all analyses the pitfall trap samples of the same plot and pitfall trap design were pooled over all five sampling intervals to account for phenological shifts in the assemblages and reduce the influence of outliers (Williams *et al.* 2010; Kotze *et al.* 2011).

We used linear mixed effects models (LMER; using ‘lmer’ from the package lme4 (Bates *et al.* 2015)) to analyse the effects of pitfall trap type on the response variables ‘carabid species richness’, ‘carabid beetle activity density’, ‘staphylinid beetle activity density’, ‘spider activity density’, the ‘proportion of small (< 6 mm) carabid beetles’, the ‘proportion of large (> 10 mm) carabid beetles’ and ‘carabid beetle community weighted mean body size’. Activity densities were square root transformed to account for heteroscedasticity. All LMERS contained ‘plot ID’ as a random effect to account for the nested design and were analysed using the command ‘anova’ (type II sums of squares, Kenward-Roger approximation of denominator degrees of freedom) from the package ‘lmerTest’ (Kuznetsova, Brockhoff & Christensen 2017) and subsequent Tukey-HSD posthoc tests (‘HSD.test’ command from the package agricolae (De Mendiburu 2016)). All models met the model assumptions for linear mixed effects models. All response variables were tested for spatial autocorrelation using the ‘Moran.I’ command from the package ape (Paradis, Claude & Strimmer 2004) but no spatial autocorrelation was detected.

Additionally, we compared the resulting carabid assemblages (transformed to proportion data) in a NMDS analysis based on Bray-Curtis dissimilarities using the ‘metaMDS’ command (package ‘vegan’ (Oksanen *et al.* 2019)). The NMDS fit was tested for significant differences between pitfall trap designs in a PERMANOVA (‘adonis’ command). To compare the capture efficiency of the different pitfall trap designs we calculated species accumulation curves using the ‘specaccum’ function (including 95% confidence intervals).

Results

On the five plots, a total of 655 carabid beetles from 42 species, as well as 626 staphylinid beetles and 4557 spiders were trapped over the course of the five sampling intervals (Tables III.1 & III.2).

Table III.1: Total activity densities and carabid species richness in the different pitfall trap designs over all plots and sampling intervals.

response variable	(i) simple type	(ii) extended PVC rim plate type	(iii) V-shaped barrier type	(iv) X-shaped barrier type
<i>Carabid beetles</i>				
<i>species richness</i>	17	17	29	35
<i>activity density</i>	55	39	208	353
<i>Staphylinid beetles</i>				
<i>activity density</i>	103	44	131	348
<i>Spiders</i>				
<i>activity density</i>	576	354	973	2654

Activity densities of all three investigated taxa were at least three times higher in the pitfall traps with X-shaped guidance barriers compared to simple pitfall traps and lowest in the pitfall traps with extended PVC rim plate (not significant in carabid beetles; Table III.1; Figure III.2). The pitfall traps with V-shaped guidance barriers caught more carabid beetles and spiders than the simple ones but less than the pitfall traps with X-shaped guidance barriers in all three taxa (carabid beetles: LMER: $F_{3,12} = 69.0$, $p < 0.001$; Figure III.2 A; staphylinid beetles: LMER: $F_{3,12} = 35.8$, $p < 0.001$; Figure III.2 B; spiders: LMER: $F_{3,12} = 99.7$, $p < 0.001$; Figure III.2 C).

Chapter III: How to record ground dwelling predators?

Table III.2: Carabid beetle species present in the different pitfall trap designs over all plots.

species	(i) simple type	(ii) extended PVC rim plate type	(iii) V-shaped barrier type	(iv) X-shaped barrier type
<i>Abax parallelepipedus</i>				1
<i>Amara aenea</i>	1	1	14	30
<i>Amara convexior</i>	3	2	4	17
<i>Amara equestris</i>		1		
<i>Amara eurynota</i>			1	1
<i>Amara familiaris</i>	1		3	3
<i>Amara lucida</i>			1	3
<i>Amara lunicollis</i>	1		1	2
<i>Amara ovata</i>		1	1	5
<i>Amara similata</i>			3	
<i>Anchomenus dorsalis</i>			1	4
<i>Badister bullatus</i>	1	1	1	1
<i>Badister lacertosus</i>				2
<i>Bembidion lampros</i>	2	1	5	13
<i>Bembidion properans</i>				2
<i>Brachinus crepitans</i>			1	6
<i>Calathus melanocephalus</i>	2		3	2
<i>Carabus coriaceus</i>	1	1		
<i>Harpalus affinis</i>		1		1
<i>Harpalus pumilus</i>	3	1	20	32
<i>Harpalus rubripes</i>	5	9	21	62
<i>Harpalus rufipes</i>	1	1	1	
<i>Harpalus subcylindricus</i>		2	2	18
<i>Harpalus tardus</i>	8	9	27	54
<i>Lebia cruxminor</i>	1			
<i>Masoreus wetterhalii</i>			2	
<i>Microlestes maurus</i>		1	2	1
<i>Notiophilus biguttatus</i>				1
<i>Notiophilus palustris</i>			2	2
<i>Ophonus laticollis</i>			1	
<i>Panagaeus bipustulatus</i>	1		2	3
<i>Paradromius linearis</i>			1	2
<i>Philorhizus notatus</i>			2	1
<i>Philorhizus sigma</i>				1
<i>Poecilus cupreus</i>	4	1	10	11
<i>Poecilus lepidus</i>		5	10	25
<i>Poecilus versicolor</i>				1
<i>Pterostichus strenuus</i>				5
<i>Syntomus foveatus</i>			7	2
<i>Syntomus truncatellus</i>	19	1	59	37
<i>Synuchus vivalis</i>				1
<i>Trechus quadristriatus</i>				1

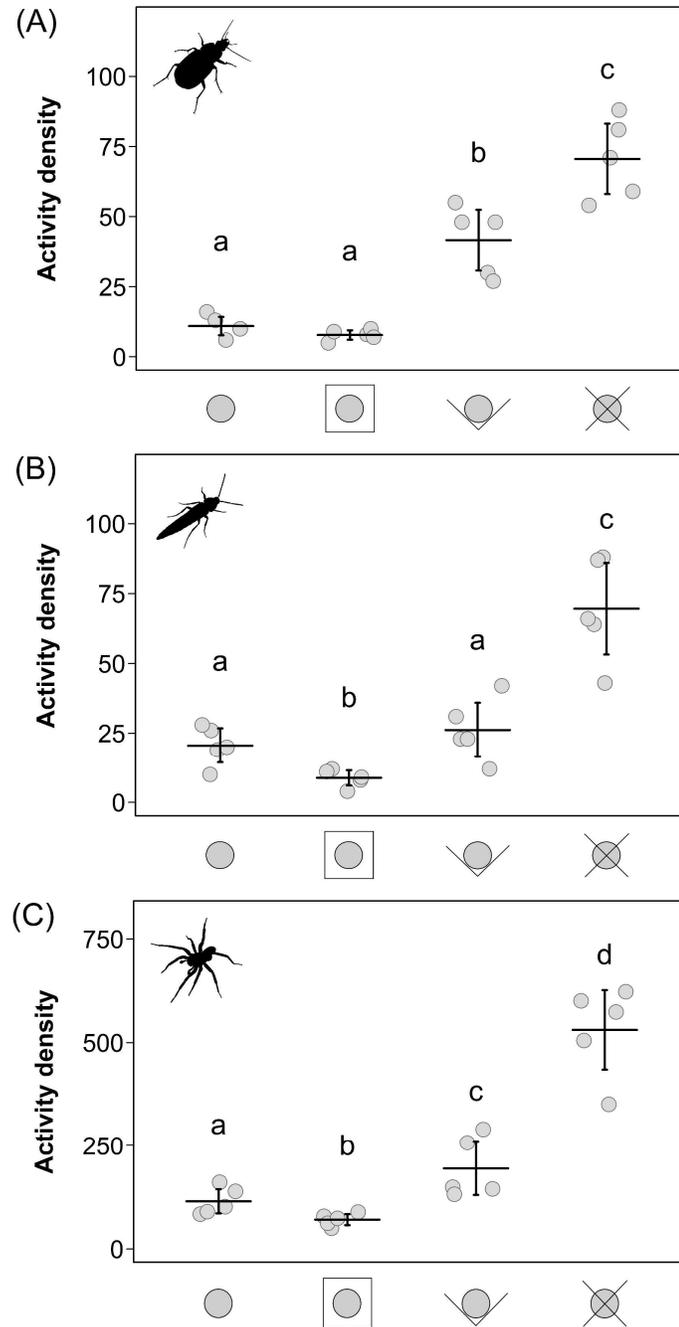


Figure III.2 Activity densities (mean \pm 95% CI) of carabid beetles (A), staphylinid beetles (B) and spiders (C) for the four different pitfall trap types. Different letters above indicate significant differences ($p < 0.05$). Pitfall trap designs from left to right: simple type; PVC rim type; V-shaped guidance barrier type; X-shaped guidance barrier type.

The carabid assemblages in the pitfall trap samples of the pitfall trap designs using guidance barriers had approximately twice as many species than the assemblages in the two remainder types (LMER: $F_{3,12}= 20.6$, $p < 0.001$; Figure III.3 A). The pitfall traps with extended PVC rim plate caught significantly less small species (< 6 mm; LMER: $F_{3,12}= 12.3$, $p < 0.001$) and more large species (> 10 mm; LMER: $F_{3,12}= 4.38$, $p = 0.027$) which resulted in a larger community weighted mean body size than in the other pitfall trap designs (LMER: $F_{3,12}= 69.0$, $p < 0.001$; Figure III.3 B).

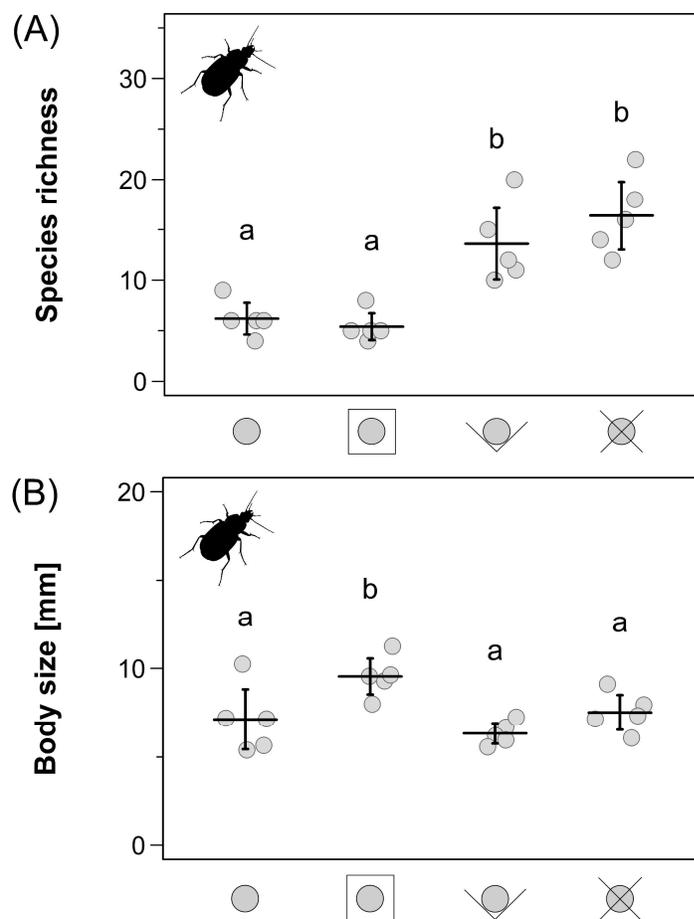


Figure III.3 Carabid beetle species richness (A) and community weighted mean body size within the carabid assemblages (B) for the four different pitfall trap types. Means \pm 95% CI. Different letters above indicate significant differences ($p < 0.05$). Pitfall trap designs from left to right: simple type; PVC rim type; V-shaped guidance barrier type; X-shaped guidance barrier type.

The NMDS ordination (stress 0.18) showed considerably less variation among the very similar carabid assemblages in the pitfall traps with guidance barriers while carabid assemblages in the pitfall trap designs without guidance barriers showed larger variation between plots. Pitfall trap design influenced the trapped assemblages significantly (PERMANOVA: 9999 permutations, $F_{3,19} = 2,68$, $p < 0.001$) as the pitfall traps with extended PVC rim plates had rather different assemblages compared to the other pitfall trap types (Figure III.4 A).

The species accumulation curves indicated that using one single pitfall trap with X-shaped guidance barriers is approximately as effective as using four to five simple pitfall traps (Figure III.4B).

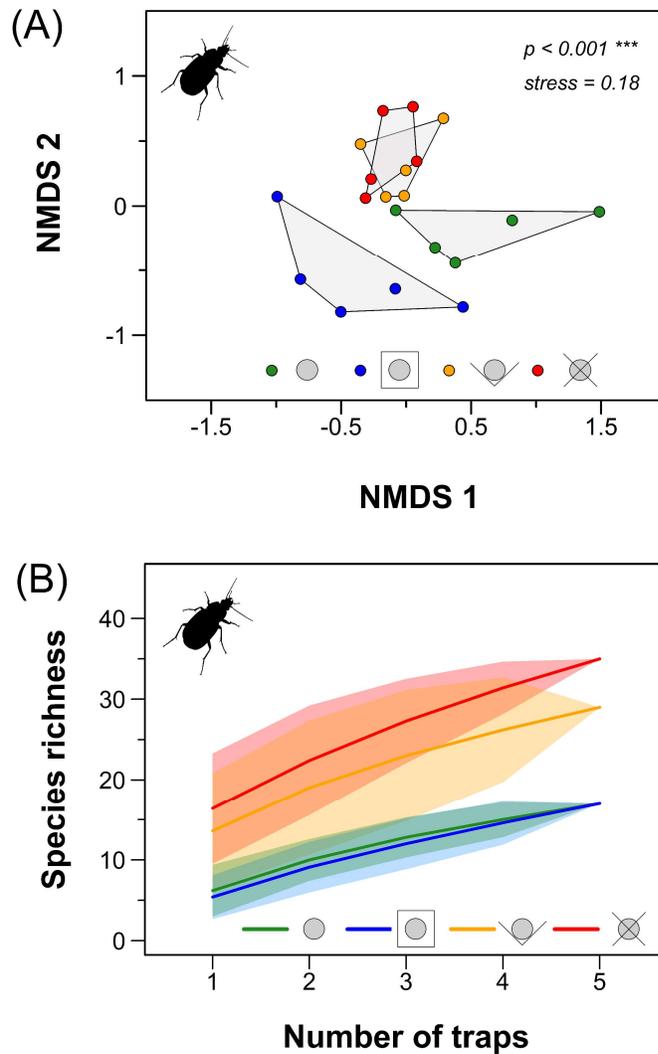


Figure III.4 Carabid beetle assemblage characteristics. (A) NMDS ordination of the carabid assemblages in the different pitfall trap types. (B) Species accumulation curves (\pm 95% CI) for the four different pitfall trap types. Colours: green: conventional pitfall trap; blue: pitfall trap with a squared PVC rim; orange: pitfall trap with a V-shaped guidance barrier; red: pitfall trap with a X-shaped guidance barrier. Pitfall trap designs from left to right: simple type (green); PVC rim type (blue); V-shaped guidance barrier type (orange); X-shaped guidance barrier type (red).

Discussion

We showed that the choice of pitfall trap design affects the final outcome of a study and results in different assemblage approximations even though we tested one habitat which has a finite carabid species pool and a unique assemblage structure. Pitfall trap design might therefore affect conclusions drawn from the study outcome and pitfall trap designs unsuitable for the hypotheses will result in poor results and poor management recommendations.

Pitfall traps with guidance barriers proved most effective in our study and showed coherent carabid beetle assemblage structures. These pitfall trap designs have been proposed several times in the past but have seen little use so far (Durkis & Reeves 1982; Winder *et al.* 2001; Hansen & New 2005). According to our results, the use of few pitfall traps with guidance barriers would be recommended over the use of many simple pitfall traps – especially when comprehensive biodiversity inventories are desired. One single pitfall trap with guidance barriers was approximately as effective as four to five simple pitfall traps in regards of species richness – therefore the use of pitfall traps with guidance barriers could spare handling time in the field and in the laboratory. The guidance barrier designs are (i) more time consuming in the construction with higher payloads in the field and (ii) at least in the X-shaped design traps need to be renewed in each sampling interval in order to exchange the trap container (a problem that could probably be overcome by revisiting the design of the guidance barriers). Nonetheless a reduced overall number of traps and overall reduced handling time subsequently saved in sample processing later on increases the efficiency. However, pitfall traps with guidance barriers need a more or less plain ground: For the study of uneven surfaces (for example rocky ground), simple pitfall traps will be more suitable and efficient. The increased visibility of guidance barrier traps could also result in a higher rate of vandalism which is a problem in pitfall trap studies but might be minimized by using transparent barriers as used by Durkis and Reeves (1982). Moreover, as for now not many studies used pitfall traps with guidance barriers, for means of comparability between studies it will be necessary to use simple pitfall traps in many fields of ecological research.

In contrast to Winder *et al.* (2001), we did not find barrier pitfall trap designs to catch more carabid beetles of a certain size as community weighted mean body size and percentages of small and large carabid beetles remained approximately the same as in the simple pitfall traps. The shape of the guidance barriers only affected total activity densities and not species richness or assemblage composition – therefore, the V-shaped guidance barrier pitfall traps which have a lower impact on ecosystems as their catchment area is only a quarter of those of the X-shaped guidance barrier pitfall traps can be used in biodiversity inventories. This design has also the advantage that the guidance barriers are not covering the pitfall trap container which makes the exchange or collection of pitfall trap samples much easier and faster.

Although simple pitfall traps caught less species and fewer individuals as the pitfall traps containing guidance barriers, the resulting carabid assemblages were over all rather similar to those from the pitfall traps with guidance barriers. The remaining differences could probably be compensated by using a higher number of simple pitfall traps in habitats and situations where the use of guidance barriers is not possible.

The use of extended PVC rim plates mainly aims at reducing set up time for pitfall traps and digging-in effects. Although this method is – apart from the use of funnels in combination with a two cup system as described in Brown and Matthews (2016) – probably the most efficient in terms of handling time in the field and quite good for standardizing the transition between surrounding soil and pitfall trap, it resulted in low catch rates and considerable alteration of the resulting carabid beetle assemblages in comparison to all other tested pitfall trap designs. Yet, as activity densities were not drastically different from those in the simple pitfall traps, we argue that the ‘digging in effect’ did not boost activity densities essentially in our study.

However, trait filtering against small sized carabid species was apparent when using extended PVC rim plates. This effect is completely contrary to the original idea of a more standardized transition between surrounding soil and pitfall trap which should help to catch more small carabid beetles as pitfall trap sampling bias due to the perception of edges is decreasing with increasing body size (Lang 2000; Engel *et al.* 2017). Carabid beetles most likely avoided the

relatively smooth PVC surface and as smaller species would have to cover longer distances in relation to their body size, this effect results in trait filtering. It might be reduced by covering the surface with sand (fixed with spray glue) or other more natural organic substrates. For the moment, due to the reduced and size-biased catches produced by this pitfall trap design, we suggest to refrain from its use.

Conclusions

Many studies on ground dwelling predators (carabid beetles, staphylinid beetles, spiders) use pitfall traps to draw conclusions on habitat conservation and ecosystem services including functional traits of species without being aware of the bias of certain pitfall trap designs. We show that pitfall trap design not only affects species richness and activity densities but also the trait composition of the resulting assemblages. For comprehensive biodiversity inventories, we therefore recommend to use a small number of highly effective pitfall traps with overall spared handling time, as the X or V shaped barrier trap designs in our study. However, for most ecological studies the use of simple pitfall trap designs is recommended, to increase comparability to other studies. We hereby recommend to use a nested design of several simple pitfall traps per plot followed by a pooling of the data as suggested by Kotze *et al.* (2011) in order to get a more conclusive picture of the local assemblages. We can currently not recommend the use of pitfall traps with an extended PVC rim plate, as especially small species tend not to cross such plates.

Acknowledgements

We are grateful to Sascha Buchholz and two anonymous reviewers for their helpful comments on the manuscript, to the nature conservation authorities of Lower Franconia for permits.



Natural pest control is an essential ecosystem service. Many insect predators prey on agricultural crop pests and regulate their densities naturally. The pest control services provided by these natural enemies can help replace artificial inputs in modern agriculture. Especially specialized predators, like this lacewing larva preying on aphids, are effective in controlling specific pest species.

Chapter IV: How to record predation rates?

As published in: Boetzl F.A., Konle A., Krauss J. (2019) Aphid cards – Useful model for assessing predation rates or bias prone nonsense? *Journal of Applied Entomology*, 144, 74-80.

Abstract

Predation on pest organisms is an essential ecosystem function supporting yields in modern agriculture. However, assessing predation rates is intricate and they can rarely be linked directly to predator densities or functions. We tested whether sentinel prey aphid cards are useful tools to assess predation rates in the field. Therefore, we looked at aphid cards of different sizes on the ground level as well as within the vegetation. Additionally, by trapping ground dwelling predators, we examined whether obtained predation rates could be linked to predator densities and traits. Predation rates recorded with aphid cards were independent of aphid card size. However, predation rates on the ground level were three times higher than within the vegetation. We found both predatory carabid activity densities as well as community weighted mean body size to be good predictors for predation rates. Predation rates obtained from aphid cards are stable over card type and related to predator assemblages. Aphid cards therefore are a useful, efficient method for rapidly assessing the ecosystem function predation. Their use might especially be recommended for assessments on the ground level and when time and resource limitations rule out more elaborate sentinel prey methods using exclosures with living prey animals.

Introduction

Pests remain a severe burden for modern agriculture and with climate change additionally pressuring crops, enhancing natural pest control is essential both to control pests and to limit pesticide use and their negative impact on the environment (Deutsch *et al.* 2018; Savary *et al.* 2019). While good standardized methods exist for measuring pest and predator densities, assessing the actual pest control function remains intricate and several studies used different techniques yielding contradicting results (see e.g. Greenop *et al.* (2019), Zaller *et al.* (2009) and Rusch *et al.* (2015)). Apart from very time and labour consuming exclusion experiments, sentinel or artificial prey experiments have been proposed and performed to assess predation rates but so far, no standardized methods and protocols exist (Birkhofer *et al.* 2017; Lövei & Ferrante 2017).

The use of sentinel prey cards with dead aphids ('aphid cards') for recording invertebrate predation via prey removal gained popularity over the last years (Winqvist *et al.* 2011; Ximenez-Embun, Zaviero & Grez 2014; Holland *et al.* 2017; Jeanneret *et al.* 2017). Apart from the use of artificial plasticine caterpillars, it is the suggested method for assessing predation rates in the Rapid Ecosystem Function Assessment (REFA) and is therefore on the way of becoming a standard method for recording predation rates (Meyer, Koch & Weisser 2015). Conveniently, aphids are actual agricultural pests, have a suitable size for most predators in agroecosystems and in contrast to plasticine caterpillars, they are more realistic. In previous studies carabid and staphylinid beetles as well as spiders were identified as aphid predators under field conditions (Symondson, Sunderland & Greenstone 2002; Thies *et al.* 2011).

In theory, two main factors drive predation on sentinel prey cards: (i) detection, as the cards must be found by predators, and (ii) consumption, as not all predators consume the same amount of prey or the same prey types. It could be assumed that detection is facilitated by placing a larger quantity of smaller cards (and therefore covering more area) instead of fewer, larger ones. For consumption, assumptions are more intricate: If detected, predation on larger

sentinel prey cards could be higher due to high consumption rates of certain predators (and because not all of the smaller cards were detected). However, larger sentinel prey cards are more efficient in manufacturing and handling. Larger cards are (i) faster assembled than a comparable amount of smaller ones, (ii) require less storage space and (iii) handling time during fieldwork is reduced due to the lower number of cards in total. However, it is currently unknown whether predation rates are biased by sentinel prey card size and if resulting predation rates are comparable.

Sentinel prey cards have been used both on the ground and within the vegetation – but rarely within the same study (but see Ximenez-Embun, Zaviezo and Grez (2014)). Therefore, little is known about whether and how much predation rates differ between the vegetation level and the ground level. As agricultural pests develop, disperse and forage on different vegetation levels and are therefore potentially also affected by different predator guilds (Dainese *et al.* 2017b), assessing predation rates on different levels could unravel important information about pest control. However, it remains unclear whether the same methods are suitable for assessing predation rates on ground and the vegetation level.

Recorded predation rates do not necessarily represent the pest control function as all methods for recording predation rates introduce some levels of artificiality into the system and might on the one hand exclude potential predators or on the other hand ease predation as prey items are gathered at one spot. Predation rates which are recorded with one type of sentinel prey allow to estimate potential pest control on the field level on the actual mix of different crop pests. Ideally, predation rates can be linked to predator assemblage characteristics such as density or body size. Densities of predators are the major driver of predation rates as with an increasing number of individuals, predation benefits from both additive but also synergistic effects due to species specific preferences and traits (Gagic *et al.* 2015). This relation is generally accepted in agroecological studies dealing with pest control services but has rarely been shown. Menalled, Lee and Landis (1999) and Greenop *et al.* (2019) showed that

predation rates depended on activity densities of ground beetles but Rusch *et al.* (2015) did not observe this dependence in an exclusion experiment.

Another trait of ground dwelling predator assemblages that is associated with predation rates is body size. Prey consumption is a function of body size with larger individuals consuming a higher prey biomass to keep their metabolic equilibrium (Reichle 1968). On the contrary, Rusch *et al.* (2015) found that predation rates decreased with increasing body size in ground dwelling predator assemblages indicating assemblages dominated by larger species to be less efficient in biocontrol. As species differ in many aspects apart from body-size and have a species-specific set of traits and prey preferences, prey consumption might not only be dependent on body-size.

In this study, we investigate the effects of card size and positioning of the sentinel prey card within the field on the resulting predation rates. We also examined whether observed predation rates could be linked to actual ground dwelling predator assemblage characteristics on the commonly used example of carabid beetles. Concluding, we give recommendations for the use of aphid cards for predation rate monitoring. We followed three main research questions:

- i. How does card size and positioning affect predation rates drawn from aphid cards?
- ii. Can the obtained predation rates be linked to activity densities of carabid beetles?
- iii. Does carabid beetle community weighted mean body size explain the obtained predation rates?

Materials and methods

Study design

We selected 10 plots within 5 large winter wheat fields (2 plots per field) around the agricultural estate 'Gut Gieshügel' (Germany, Bavaria, Gerbrunn) near the university campus of the University of Würzburg. All plots (including their subplots) had minimum distances of 75 m to the closest neighbouring plot (mean: 99.4 ± 4.9 m) and of 60 m to the closest field edge (mean: 78.5 ± 6 m). We conducted the experiment on one farm to homogenize landscape composition around the plots and therefore standardize the potential impact of landscape level effects on predation rates. All winter wheat fields were sown with the same cultivar and managed by the same farmer in the same way to avoid management bias. At each plot, 6 subplots containing different treatments (see below) were established circularly around a central pitfall trap with distances between subplots and to the central pitfall trap being approximately 5 m (Figure IV.1).

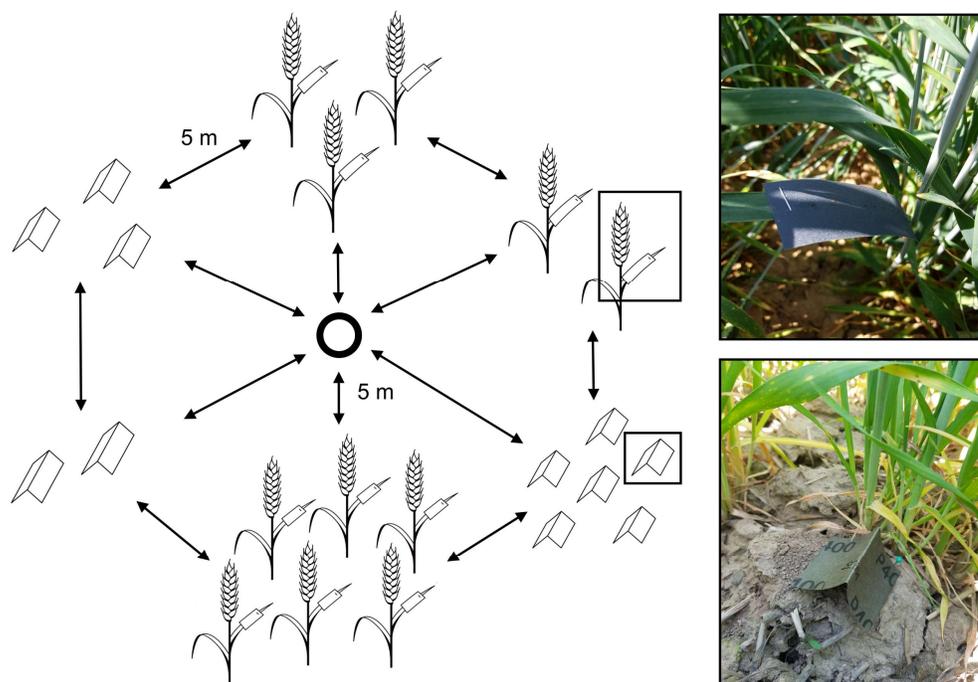


Figure IV.1 Schematic representation of predation rate assessment on each plot. Each plot had six subplots with one of the six combinations of the two positions (ground level and vegetation level) and the three card sizes (small, medium and large) on each subplot. Pictures show an aphid card (large) applied to a wheat plant and an aphid card (small) set up on the ground in the field. The central open circle represents the pitfall trap position, all arrows indicate distances of approximately 5 meters.

Data collection

To test for the effects of positioning and card size, we manufactured six different types of aphid cards. Cards which were placed on the ground level were folded up like a gable (with the aphids on one of the interior sides) and were therefore twice as broad as the cards which were placed within the vegetation. The sides containing the aphids were of same size in both designs. For both positionings, we made three different types of aphid cards containing different numbers of aphids: 3 (small), 6 (medium) and 9 (large). At each subplot, we randomly placed cards of one type with a total of 18 aphids per subplot with distances of 0.5 m between the cards on the same subplot (Table IV.1 & Figure IV.1).

Table IV.1: Different types of aphid cards used.

position	ground			vegetation		
	small	medium	large	small	medium	large
card size						
width [cm]	6	6	6	3	3	3
length [cm]	4	7	10	4	7	10
# aphids	3	6	9	3	6	9
# per subplot	6	3	2	6	3	2

Aphid cards were manufactured out of conventional sandpaper (grain-size 400). Adult aphids (Grain Aphid, *Sitobion avenae* (Fabricius, 1775)) were glued alive onto the cards using a brush and placed centrally on the cards (1.5 cm from the lateral edges of the cards and 1 cm from each other and the front / hind edges). As glue, we used the water soluble polysaccharide and food supplement astragalus (Tragant-powder 1 g in 100 ml H₂O) to avoid chemical evaporations from conventional glues which could attract or deter predators (Birkhofer *et al.* 2017). After gluing, the aphid cards were immediately frozen at -20°C and stored until use (not longer than 3 days).

In the field, aphid cards on the ground level were fixed with a pin punched through the side containing no aphids as described by Winqvist *et al.* (2011), the cards within the vegetation were stapled to a wheat leaf in approximately 70 cm height as described in Jeanneret *et al.* (2017) (Figure IV.1).

Sentinel prey cards were exposed over 3 sampling intervals from the end of May to the end of June 2018, which corresponded to the period of milk ripening in winter wheat in the region. In this period, wheat is very vulnerable for pests and therefore pest control is essential. After 24 hours of exposure in the field, sentinel prey cards were collected, and remaining aphids were counted.

Simultaneously, we recorded the ground dwelling predator potential on each plot using a conventional pitfall trap (height: 9 cm, diameter: 7.5 cm, transparent) filled with 200 ml

oversaturated saltwater (200 g NaCl per 11 H₂O). Pitfall traps were activated on the same day the sentinel prey cards were placed and were active for 7 days.

Carabid beetles (Carabidae) were sorted from the trap samples, counted and identified following Müller-Motzfeld (2006). Carabid beetle life history traits (diet and mean body size) were obtained from the online database ‘carabids.org’ (Homburg *et al.* 2014). Staphylinid beetles and spiders were also counted, however as initial analyses showed no relations to predation rates, results are not shown.

Statistical analyses

All statistical analyses were performed in R 3.5.2 for Windows (R Development Core Team 2019), using the packages ‘lme4’ (Bates *et al.* 2015), ‘lmerTest’ (Kuznetsova, Brockhoff & Christensen 2017) and ‘MuMIn’ (Barton 2018).

Instead of using crossed random intercepts for plot and interval, we pooled data over all three sampling intervals as otherwise, models were overparameterized. In a linear mixed effects model (‘lmer’) we calculated effects of aphid card ‘position’ and ‘card size’ (as well as their interaction) on predation rates (aphids gone / aphids total) using ‘plot ID’ as random intercept.

To assess whether predation rates could be linked to predator assemblage characteristics, we calculated predation rates on the ground level over all card sizes (as there were no significant differences between card sizes) and intervals. To assess whether predation rates could be linked to ground dwelling predator assemblage characteristics, we calculated separate linear mixed effects models (‘lmer’) relating the response predation rates to the two mainly found predictors in previous studies: ‘carabid beetle activity density’ and ‘carabid beetle community weighted mean body-size’ (again including ‘plot ID’ as random intercept). For these models, we excluded species which are known to be granivorous as they should not be involved in pest control (Supplementary Material Table IV.S1). Carabid beetle activity densities were square-root transformed to improve normality.

Model results were obtained using the command ‘anova’ (type II sums of squares, Kenward–Roger approximation of denominator degrees of freedom) from the package ‘lmerTest’. All models were checked carefully and met the required assumptions on residual and variance distributions. R^2 -values (marginal) were obtained from the ‘r.squaredGLMM’ function from the package ‘MuMIn’.

Results

In total, we used 3240 aphids on 660 sentinel prey cards (360 small, 180 medium and 120 large). Predation was found in 43 percent of all aphid cards (38.3 percent in small, 49.4 percent in medium and 45.8 percent in large) after 24 hours of exposure.

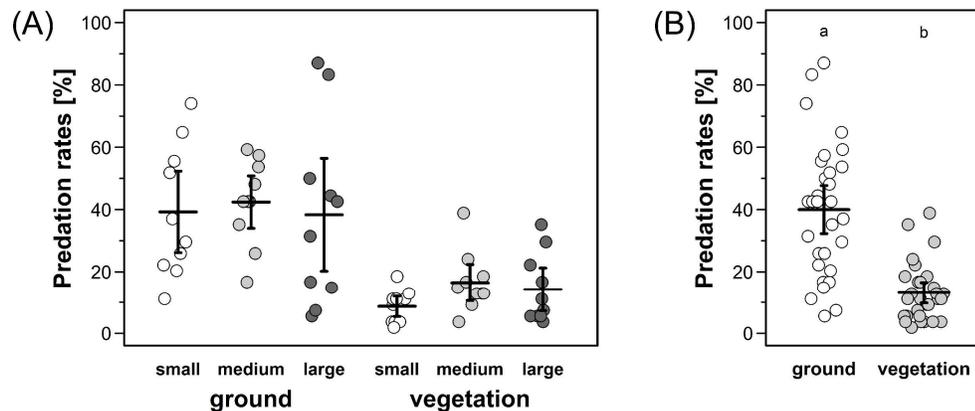
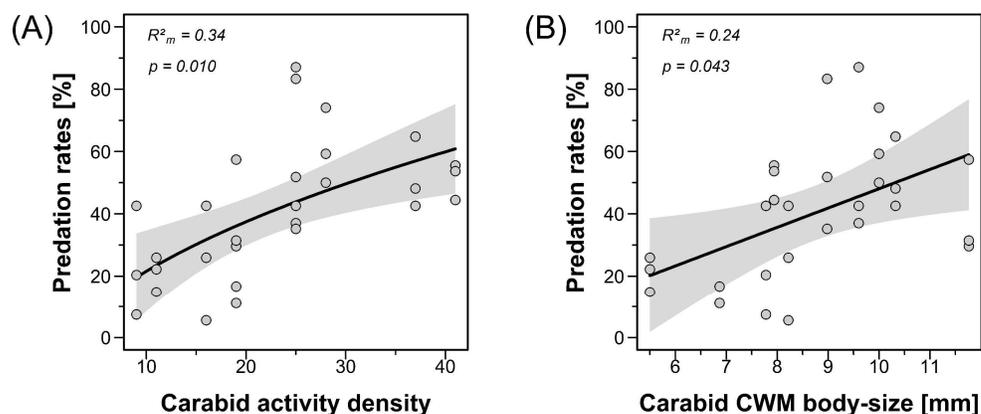


Figure IV.2 Predation rates (mean \pm 95% CI) obtained from aphid cards over (A) different positions and card sizes as well as (B) only between the two tested positions. Different letters above indicate significant differences ($p < 0.05$; for statistics see results section).

Predation rates did not vary significantly between aphid cards of different sizes (LMER: $F_{2,45} = 0.80$, $p = 0.454$; Figure IV.2 A). Positioning of the aphid cards however was an important predictor for predation rates with mean predation rates on the ground level ($40.0 \pm 3.9\%$) being three times higher than those within the vegetation ($13.1 \pm 1.7\%$; LMER: $F_{1,45} = 57.8$, $p < 0.001$; Figure IV.2 A & B). Predation rates on the ground were marginally positively correlated with those within the vegetation (LMER: $F_{1,25} = 4.01$, $p = 0.056$; Figure IV.S1). We

did not find a significant interaction effect between aphid card size and positioning of the aphid card (LMER: $F_{2,45} = 0.30$, $p = 0.744$).



Over the three intervals, we collected a total of 258 carabid beetles from 22 species (thereof

Figure IV.3 Predation rates in relation to (A) carabid beetle activity densities and (B) carabid beetle community weighted mean body size. Model predictions with 95% confidence interval. For statistics see results section.

230 individuals from 18 species were predatory or omnivorous; Supplementary Table IV.1). Predation rates were increasing with increasing predatory and omnivorous carabid beetle activity density (LMER: $F_{1,8} = 11.13$, $p = 0.010$; Figure IV.3 A). Moreover, also a larger community weighted mean body size of predatory and omnivorous carabid beetles resulted in higher predation rates (LMER: $F_{1,8} = 5.75$, $p = 0.043$; Figure IV.3 B).

Discussion

Predation rates obtained from aphid cards were independent of card size but differed between cards positioned on the ground and within the vegetation with mean predation on the ground level being three times higher than within the vegetation. Predation rates were positively related to activity density as well as community weighted mean body size of predatory carabid beetles.

In our study, predation rates obtained from aphid cards were independent from card size. This means, larger, more rapidly manufactured and more easily transported and therefore more efficient cards can be used instead of a large number of small cards. The use of large aphid cards results in a drastic reduction of labour and field work time and makes their use more convenient. This result also indicates that results obtained from aphid cards can potentially be compared between studies even if aphid cards used differed in card size (i.e. the total number of aphids used). As medium sized aphid cards featuring six aphids per card had the lowest number of 0 or 100 percent predation extremes, we would recommend their use as they seem to resemble the optimal compromise between handling time efficiency and reduction of outliers due to non-detection or maximum predation.

In contrast to the difference in predation rates between the ground and the vegetation levels observed in our study, Ximenez-Embun, Zaviezo and Grez (2014) found similar predation rates on aphid cards placed on the ground level and 30 cm above ground within the vegetation. However, in the study of Ximenez-Embun, Zaviezo and Grez (2014), aphid cards were regularly replaced every 3 hours. Many ground dwelling predators are rather generalistic and complementary in the function they deliver (Roubinet *et al.* 2018). We suspect that predators that are not that generalistic (like many vegetation dwelling predators such as syrphid larvae, lacewings and their larvae and coccinellid beetles) rather reject the dead and continuously desiccating aphids. Not all ground dwelling predators however are climbing up into the vegetation. This, combined with the lower number of vegetation level predators that potentially accept the sentinel prey offered, explain the lower predation rates within the vegetation level. Aphid cards are therefore recommended when the aim is to investigate ground dwelling predator potential as many of the contemplable species are rather generalistic (e.g. many carabid beetles). In studies specifically aiming at aphid pest control (which typically takes place within the vegetation), we recommend using more 'realistic' sentinel prey methods such as inoculating plants with living aphids in exclusion experiments as performed by e.g. Martin *et al.* (2013), Rusch *et al.* (2013) or Karp *et al.* (2016). Such methods however

have the disadvantage that preparation and observation in the field is more time and labour consuming and they limit the amount of additional work that can be done simultaneously.

A demonstration of the ability of sentinel prey cards to reflect natural pest control is to link measured predation rates to predator assemblages or their pest control function. In our study, we could link the predation rates measured with aphid cards to two predictors investigated in previous studies: the activity densities and the community weighted mean body sizes of predatory carabid beetles (as a commonly used example for ground dwelling predators). This link however has not been found consistently in previous studies. While some found density effects on predation rates (Menalled, Lee & Landis 1999; Greenop *et al.* 2019) or pest control (Zaller *et al.* 2009), other studies did not find these activity density driven effects (Rusch *et al.* 2015). However, trait composition within assemblages might differ between studies and relations between activity densities and predation functions could be disguised by functional limitations of the species present in the assemblages.

Functional traits of animal ecosystem service providers have been shown to be better predictors for the ecosystem functions provided than richness or densities of these organisms (Gagic *et al.* 2015). Apart from diet, body size should be the main trait influencing pest control in predators as larger individuals generally need a higher food intake to maintain activity. Surprisingly, Rusch *et al.* (2015) found the exact opposite relation for ground dwelling carabid beetles and spiders combined (although not significant for carabid beetles alone). In contrast, we found predation rates increasing with mean predatory carabid beetle body size as it would be suspected.

In both analyses, we limited the data used to non-exclusively granivorous carabid beetles as we assumed that only species consuming animal prey would contribute to the predation function of the assemblage. Including all carabid beetle species might alter results depending on the distributions of species and traits in the specific assemblage compositions of different studies. Relationships for predatory species might be disguised by the presence of granivorous species and the resulting trait shifts in the assemblages. However, filtering of species affords

prior sophisticated knowledge about their life history traits which is not yet available for most regions in the world.

Aphid cards are a simple, cost effective way to measure predation rates. Other methods such as the use of living organisms in enclosure experiments are undoubtedly more elaborate but also much more time consuming, costly and labour intensive. With a magnitude of sentinel prey methods and organisms of different sizes falling into different predator feeding spectra (including e.g. aphids (Gardiner *et al.* 2009; Ximenez-Embun, Zaviezo & Grez 2014; Karp *et al.* 2016), corn earworm eggs (Meehan *et al.* 2012), fall armyworm larvae (Meehan *et al.* 2012), wax moth larvae (Meehan *et al.* 2012; Zirbel *et al.* 2017), cabbage moth larvae (Ferrante, Barone & Lövei 2017), ladybird eggs (Schneider, Krauss & Steffan-Dewenter 2013), onion fly pupae (Menalled, Lee & Landis 1999), earthworms (Tschumi *et al.* 2018), mealworms (Tschumi *et al.* 2018) as well as artificial plasticine caterpillars (Howe, Lövei & Nachman 2009; Howe, Nachman & Lövei 2015; Lemessa, Hambäck & Hylander 2015)) proposed, comparability between studies is questionable. While these differences in methods can be useful to answer specific questions in specific environments (Macfadyen, Davies & Zalucki 2015; Birkhofer *et al.* 2017), this generally highlights the need for a unified and standardized design to record predation rates under the REFA regime to allow comparability in large scale assessments. While plasticine caterpillars are handy and convenient to use, it remains unclear whether predation rates measured in this very artificial system designed for bird caused predation relate to actual pest control services (see e.g. Jeanneret *et al.* (2017) for comparison with other sentinel preys). How predation rates obtained from different methods and different sentinel prey types actually relate to each other is largely unknown and requires a deeper investigation. In cases where the aim is to study specific crop systems, living sentinel prey of the specific crop pests will undoubtedly always remain the best method for obtaining trustworthy pest control information. With more basic research being needed to unravel the relations between methods, aphid cards are however a good simple alternative to record predation rates of generalist ground dwelling predators in the field.

Conclusions

Aphid cards are very efficient in the sense of how much investment goes into their use: They are easily made from cheap and readily available materials, can be stored in the freezer and are easily transported and applied to the sites of interest, with handling time during fieldwork being minimized. In terms of REFA, they are a good method to assess predation rates quickly and over large spatial scales and designs and they resemble more realistic prey than plasticine caterpillars. However, these advantages come with drawbacks: The use of dead aphids might not relate directly to the pest control function provided by natural enemies against living aphid pests (but might still be more realistic than the use of artificial plasticine caterpillars). If resources and time are not limited, we would recommend using sentinel prey methods involving living prey items that ideally resemble the actual pest species in the crop of interest. But as we could show that predation rates obtained from aphid cards are stable and can be linked to ground dwelling predators – which are one of the most important predatory guilds in agroecosystems – our results suggest that their use can be recommended to get a quick pest control assessment within the REFA framework.

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Supplementary material IV

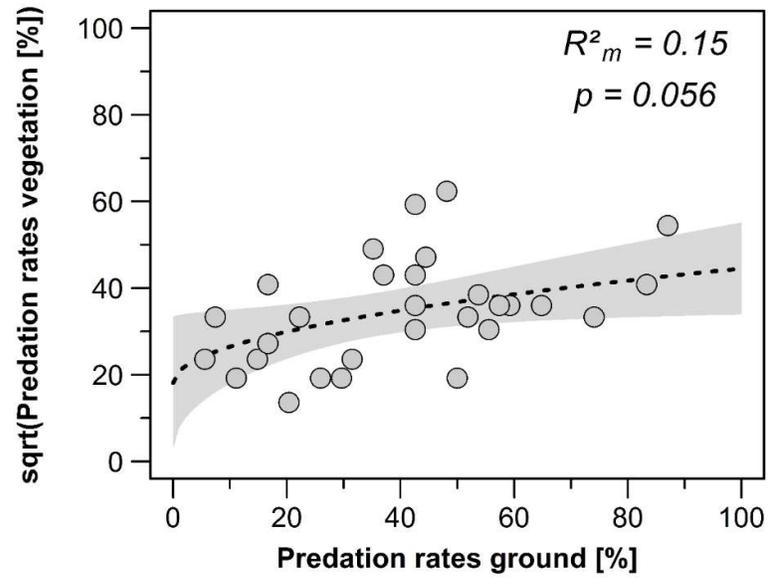


Figure IV.S1 Relationship between predation rates on the ground and predation rates within the vegetation measured at the same plots and aphid card types.

Chapter IV: How to record predation rates?

Table IV.S1: Species present over all plots as well as mean body-size [mm] and diet traits used in the analyses as well as total sums of species, activity densities and community weighted mean body sizes (rounded to 1 decimal) for all carabid beetles and all but granivorous carabid beetles ('Predator') over all plots.

species	1	2	3	4	5	6	7	8	9	10	body-size	diet
<i>Anchomenus dorsalis</i>	3	4	8	9	8	3	7	8	4	5	6.5	predatory
<i>Asaphidion flavipes</i>				1							3.5	predatory
<i>Badister bullatus</i>	1			1							5	predatory
<i>Badister sodalis</i>									2		3.5	predatory
<i>Bembidion lampros</i>	1		2	1	1	1		1		1	3	predatory
<i>Bembidion lunulatum</i>	7										3.5	predatory
<i>Bembidion obtusum</i>	4			1	1	1	2	2		1	2.5	predatory
<i>Bembidion quadrimaculatum</i>	2	1									2.5	predatory
<i>Carabus convexus</i>		1									17	predatory
<i>Carabus violaceus</i>								1			30	predatory
<i>Demetrias atricapillus</i>		1									5	predatory
<i>Harpalus affinis</i>	1	1	3	4	3	2	2	2	1	2	10	granivorous
<i>Harpalus atratus</i>									2		11.5	granivorous
<i>Harpalus rufipes</i>	1					2		1			13.5	granivorous
<i>Harpalus serripes</i>		1									10.5	granivorous
<i>Loricera pilicornis</i>	3	5	4	4			5		1		7	predatory
<i>Notiophilus aestuans</i>	1										4.5	predatory
<i>Notiophilus biguttatus</i>		2			1		1	1			4.5	predatory
<i>Poecilus cupreus</i>	12	2	4	2	2		2	2		1	11	omnivorous
<i>Pterostichus melanarius</i>	6	8	10	7	13	13	1	1	2		15	predatory
<i>Stomis pumicatus</i>					2						7	predatory
<i>Trechus quadristriatus</i>		1			4	1	1			2	3.5	predatory
Total species richness	12	11	6	8	9	7	8	9	6	7	-	-
Total activity densities	42	27	31	30	35	23	21	19	12	12	-	-
Total cwm body size	8.1	9.7	10	9.1	10.3	11.8	7.2	8.2	8.6	6.2	-	-
Predator species richness	10	9	5	7	8	5	7	7	4	6	-	-
Predator activity densities	40	25	28	26	32	19	19	16	9	10	-	-
Predator cwm body size	7.9	9.6	10	9.0	10.3	11.8	6.9	8.2	7.8	5.5	-	-



Cymindis axillaris (Fabricius, 1794), an endangered, weak dispersing carabid beetle species occurring only in calcareous grasslands. This species cannot be supported by sown flowering fields, which emphasizes the importance of semi-natural habitats for the conservation of biodiversity.

Chapter V: Do AES habitats benefit multi-taxa biodiversity?

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Abstract

Agri-environmental schemes (AES) aim to restore biodiversity and biodiversity-mediated ecosystem services in landscapes impoverished by modern agriculture. However, a systematic, empirical evaluation of different AES types across multiple taxa and functional groups is missing. Within one orthogonal design, we studied sown flowering AES types with different temporal continuity, size and landscape context and used calcareous grasslands as semi-natural reference habitat. We measured species richness of twelve taxonomic groups (vascular plants, cicadas, orthopterans, bees, butterflies, moths, hoverflies, flower visiting beetles, parasitoid wasps, carabid beetles, staphylinid beetles and birds) representing five trophic levels. A total of 54,955 specimens were identified using traditional taxonomic methods and bulk arthropod samples were identified through DNA metabarcoding, resulting in a total of 1077 and 2110 taxa, respectively. Species richness of most taxonomic groups as well as multidiversity and richness of pollinators increased with temporal continuity of AES types. Some groups responded to size and landscape context but multidiversity and richness of pollinators and natural enemies were not affected. AES flowering fields supported different species assemblages than calcareous grasslands, but assemblages became more similar to those in semi-natural grasslands with increasing temporal continuity. Our results indicate that AES flowering fields and semi-natural grasslands function synergistically. Flowering fields support

biodiversity even when they are relatively small and in landscapes with few remaining semi-natural habitats. We therefore recommend a network of smaller, temporally continuous AES flowering fields of different ages combined with permanent semi-natural grasslands to maximize benefits for biodiversity conservation and ecosystem service delivery in agricultural landscapes.

Significance statement

The loss of biodiversity challenges agriculture as crop yields depend on biodiversity-mediated ecosystem services. Targeted agri-environmental schemes (AES) like sown flowering fields provide limiting food resources and shelter for wild plants and animals. Therefore, AES have been implemented to restore biodiversity in agricultural landscapes and ensure ecosystem services provision. However, little is known about the comparative benefits of different AES for functional biodiversity and whether temporal continuity, covered area, or perennial source habitats in the surrounding landscape, limit the success of an AES. Here, we systematically evaluate within one study design how temporal continuity, size and semi-natural habitat cover in the surrounding landscape affect multi-taxa diversity in different AES types and assess their potential for biodiversity conservation in agricultural landscapes.

Introduction

Human societies are facing a worldwide loss of biodiversity with alarming declines of insect diversity in temperate agricultural landscapes (Steffen *et al.* 2015; Seibold *et al.* 2019). This loss of biodiversity is jeopardising agricultural production as important ecosystem services ensuring crop yields are directly driven by biodiversity (Dainese *et al.* 2019). Biodiversity, however, requires suitable habitats for species to persist, forage, nest, reproduce and hibernate (Haaland, Naisbit & Bersier 2011; Bartual *et al.* 2019). This challenge has been recognized and agri-environmental schemes (AES) have been introduced in the European Union and other regions to reverse biodiversity declines, to restore functional diversity and to harness the benefits of ecosystem services like pollination and pest control in agricultural landscapes (Ekroos *et al.* 2014; Pe'er *et al.* 2017; Batáry *et al.* 2020).

An important component of AES to fulfil these goals, is the establishing of habitats that provide limiting resources such as food and shelter for a broad range of organisms. Typically, farmers are financially compensated on a per area basis, but the effectiveness of schemes is often unclear. Thus compensations might not direct farmers' decisions among different AES to the ecologically most meaningful ones (Ekroos *et al.* 2014). A variety of different habitats are created as AES, ranging from hedgerows to sown flower strips or flowering fields with the latter being widely used due to their flexible applicability and public appreciation (Haaland, Naisbit & Bersier 2011). Recent assessments, however, found that overall, European AES are not fulfilling their goals (Pe'er *et al.* 2017; Pe'er *et al.* 2019). Particularly the value of AES for securing biodiversity is under debate (Kleijn *et al.* 2011; Kleijn *et al.* 2019). Beneficial effects previously reported focused on single taxonomic or trophic levels or ecosystem services and varied among study designs, taxa or services assessed (Scheper *et al.* 2013; Boetzl *et al.* 2019; Albrecht *et al.* 2020). Conclusive multi-taxa approaches assessing potential services and disservices in one design are missing (Batáry *et al.* 2020). Further, it is unclear how different properties of AES habitats (e.g. their temporal continuity or size) and varying landscape context affect biodiversity across multiple taxonomic groups.

Temporal continuity is an important factor affecting biodiversity. Higher temporal continuity increases heterogeneity within a habitat and creates niches for more species (Aavik *et al.* 2008; Fritz, Gustafsson & Larsson 2008). Temporal continuity also enables weak dispersers and higher trophic levels to colonize a habitat with the latter being dependent on established populations of lower trophic levels (Fritz, Gustafsson & Larsson 2008). In AES habitats, the influence and the effects of temporal continuity have so far been neglected. Newly established flowering fields were found to be more attractive to pollinators than older flowering fields but pollination services in adjacent fields peak two years after initial sowing (Krimmer *et al.* 2019; Albrecht *et al.* 2020). Older AES habitats could potentially also benefit rare and endangered species with specific habitat requirements, if species assemblages in AES habitats change towards those in permanent species-rich semi-natural grasslands with time or increased temporal continuity (Dengler *et al.* 2014).

Apart from temporal continuity, size might be an important predictor for the conservation value of AES habitats. Increasing habitat size leads to an increased species richness as it is accompanied with the establishment of larger, more stable populations and allows higher trophic levels to persist (Holt *et al.* 1999; Connor, Courtney & Yoder 2000; Turner & Tjørve 2005). It is unclear whether biodiversity in a landscape benefits more from few large habitats or a network of many small habitats (Rösch *et al.* 2015; Grass *et al.* 2019). Relationships between size and species richness might therefore be essential for the planning and strategic placement of AES habitats.

Source habitats for biodiversity are needed in agricultural landscapes to build up local populations in newly established AES habitats from regional species pools (Suding 2011). Semi-natural habitats embedded in agricultural landscapes have been shown to support farmland diversity (Martin *et al.* 2019; Sirami *et al.* 2019), and thus AES habitats in complex landscapes with high proportions of semi-natural habitats potentially host the highest diversity.

Here, we investigate the effects of AES differing in temporal continuity, size and surrounding landscape context over several years on multiple taxonomic groups within one study design.

Different types of flowering fields are commonly established by farmers as part of AES to provide additional flower resources. These fields are sown with seed mixtures adapted to local soil properties and taken from regional species pools. After a certain timespan often varying between 1-10 years, flowering fields are returned to crop production. The studied flowering fields differed in temporal continuity from (i) newly sown on arable land, over (ii) refreshed, i.e. flower fields re-sown after five years to (iii) continuous, 6 years old flowering fields. Species-rich calcareous grasslands were used as permanent control (Table V.1). Calcareous grasslands are semi-natural biodiversity hotspots in Europe and are preserved by low intensive mowing or grazing (WallisDeVries, Poschlod & Willems 2002). We investigated species richness in these four AES types across 12 taxonomic groups belonging to five trophic levels, including pollinators (bees, butterflies, moths, flower visiting beetles and hoverflies) and natural enemies (parasitoid wasps, carabid beetles, staphylinid beetles and birds) as providers of important ecosystem services (Dainese *et al.* 2019). Species were identified by classic taxonomic techniques (vascular plants, orthopterans, bees, butterflies, moths, flower visiting beetles, carabid beetles, staphylinid beetles and birds) and DNA metabarcoding (cicadas, hoverflies and parasitoid wasps). Repeated recordings of a subset of four taxonomic groups (plants, orthopterans, bees and carabid beetles) within two years were performed to clarify whether short term succession changed assemblages in newly established flowering fields towards those in semi-natural calcareous grasslands. Apart from analyses for each taxonomic group, we performed a multi-diversity analysis by calculating a diversity index across all taxa, pollinators and natural enemies (Allan *et al.* 2014). Our study aims to judge which types of AES fulfil the goal of restoring biodiversity and ecosystem services in agricultural landscapes best and should therefore be fostered. Such data is urgently needed to build the scientific basis for a successful transition of EU and global policies to biodiversity-friendly and sustainable crop production.

We expected that (1) benefits of temporal habitat continuity differ among taxonomic groups, pollinators and natural enemies, (2) temporal continuity and short-term succession alter species assemblages of sown flowering fields towards those in semi-natural grasslands, and

(3) multidiversity in sown flowering fields benefits most from the combination of temporal continuity, large habitat size and high proportion of semi-natural habitats in the landscape.

Methods

Study design

To assess the effectiveness of different agri-environment schemes (AES) for biodiversity conservation, we established a study design comprised of three different flowering field types as well as species rich and permanent calcareous grasslands as controls. The flowering fields differed in size and were located within separated landscapes covering a gradient of landscape-scale cover of semi-natural habitats (Figure V.1).

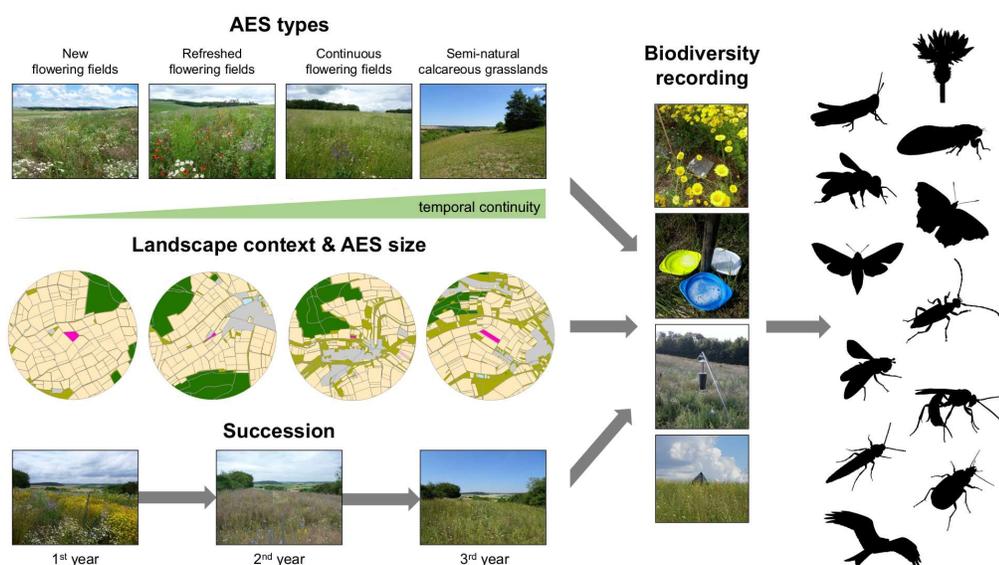


Figure V.1 Study design on the landscape and site level. Biodiversity across 12 different taxonomic levels (from top to bottom: vascular plants, orthopterans, cicadas, bees, butterflies, moths, flower visiting beetles, hoverflies, parasitoid wasps, carabid beetles, staphylinid beetles, birds) was recorded using a variety of classical methods (pan traps, pitfall traps, transect walks, light traps combined with taxonomic identification) as well as metabarcoding analyses (using samples collected with Malaise traps). The different types of flowering fields and calcareous grasslands were located along a gradient of temporal continuity (Table V.1). All agri-environment scheme (AES) types covered independent gradients of semi-natural habitat in the surrounding landscape and habitat size (purple: AES; yellow: arable land; light green: semi-natural habitat; dark green: forest; grey: urban). Repeated recordings in two years were performed for vascular plants, orthopterans, bees and carabid beetles to assess whether succession shifted assemblages in flowering fields towards those in semi-natural calcareous grasslands.

The study was conducted between 2016 and 2018 in 27 study sites within a 60 km radius around Würzburg (Bavaria / Germany; Supplementary Table V.S1). Diversity across 12 different taxonomic groups was recorded in four types of AES habitats (three types of flowering fields and semi-natural calcareous grassland habitats under AES management; in the following ‘AES types’). The four different AES types included (a) new flowering fields (N = 8), (b) refreshed flowering fields (N = 8), (c) continuous flowering fields (N = 7) and (d) semi-natural calcareous grasslands (N = 4). The studied AES types were characterized by differences in current and past management (Table V.1): temporal continuity increased from (a) to (d). Flowering fields (a) and (b) were subsidized under governmental AES and sown with a specific customized flower mixture adapted to local flora, soil and microclimatic limitations in fall of 2015 and subsequently remained unmanaged for five years. Both flowering fields (a) and (b) differed in site history: while (a) had been regular agricultural fields previously used for crop production, (b) had already been flowering fields for 5 years and were ploughed and then re-sown as flowering fields under the same program, which results in an extended seed bank already present in their soils. The continuous flowering fields (c) had also been flowering fields under the same AES for 5 years but were transformed without soil disturbance into ecological focus areas under the Common Agricultural Policy of the European Union (CAP) in 2013 - 2015. Plant communities on the continuous flowering fields were shaped by succession but vegetation was mulched once per year above ground to prevent the growth of shrubs. Calcareous grasslands (d) are protected semi-natural habitats that were created due to extensive human land-use and are nowadays often highly fragmented and considered as biodiversity hotspots in Europe (WallisDeVries, Poschlod & Willems 2002). While calcareous grasslands are not established under AES, their conservation involves management under AES, mostly mowing once a year or extensive grazing by sheep or goats to prevent succession. Calcareous grasslands are typically rich in different structures and contain e.g. open soil patches and shrubs (mostly juniper).

Table V.1: Differences in temporal continuity - resulting from habitat age and management - of the studied agri-environment scheme (AES) types in 2016 (first year of the study).

	habitat age	last soil disturbance	temporal continuity	previous land use	management	vegetation
(a) new sown flowering field	1 year	1 year	low	arable land	none	customary flower seed mixture; sown in the previous year
(b) refreshed sown flowering field	> 6 years	1 year	low - intermediate	sown flowering field (5 years)	none	customary flower seed mixture; sown in the previous year
(c) continuous sown flowering field	> 6 years	> 6 years	intermediate - high	sown flowering field (5 years)	Mulching above ground once per year after June	customary flower seed mixture sown > 6 years ago; strongly shaped by succession
(d) calcareous grassland	> 20 years	> 20 years	high	NA	Grazing or mowing once per year after June	semi-natural xerothermic grassland vegetation

The areas of the flowering fields ranged from 0.29 ha to 2.92 ha (Mean \pm SE: new flowering field: 1.32 ± 0.38 ha; refreshed flowering field: 1.05 ± 0.30 ha; continuous flowering field: 1.12 ± 0.25 ha). The minimum distance between study sites was 2.1 km. The amount of semi-natural habitat (forest edges, field margins, bank borders, roadside vegetation, small wood groves, hedgerows, orchard meadows and extensive pastures, calcareous grasslands and grassland taken out of agricultural production (Krimmer *et al.* 2019)) in a 1km radius around study sites ranged from 3.6 to 25.0 %. (Supplementary Table V.S1).

Data collection

On the 27 sites, we recorded biodiversity at different trophic levels over three years. In total, we recorded 12 different taxonomic groups using classical taxonomic methods as well as identifications based on sequenced data (metabarcoding). The taxa recorded included groups predominantly ranked to one of five different trophic and functional groups: (i) primary producers (vascular plants; recorded with Braun Blanquet Plots), (ii) herbivores (orthopterans (Orthoptera; recorded with variable transect walks), cicadas (Auchenorrhyncha; recorded with Malaise traps and identified by metabarcoding), (iii) pollinators with herbivorous larvae (bees (Apoidea; recorded with variable transect walks and pan traps), butterflies and moths

(Lepidoptera; recorded with variable transect walks and light traps), flower visiting beetles (several families; recorded with pan traps)), (iv) pollinators with predatory larvae (hoverflies (Syrphidae; recorded with Malaise traps and identified by metabarcoding)) and (v) predators (carabid beetles (Carabidae; recorded with pitfall traps), staphylinid beetles (Staphylinidae; recorded with pitfall traps), parasitoid wasps (several families; recorded with Malaise traps and identified by metabarcoding) and birds (Aves recorded with point counts)). Four of the taxa (vascular plants, orthopterans, bees and carabid beetles) were recorded in two of the three years using the same methodology. Detailed sampling protocols for all taxa are given in the supplementary material (Supplementary Information V.1).

Statistical analyses

All statistical analyses were performed in R 3.6.1 for Windows (R Development Core Team 2019). We calculated species richness for taxonomic groups identified by taxonomists and taxa richness for taxonomic groups identified by metabarcoding for all taxa on each site and year as response variables. On each site, all recordings over the course of the year and subplots were pooled for each taxonomic group. Additionally, an index of multidiversity was calculated following Allan *et al.* (2015): In a first step, we calculated the proportion of species for each site out of the total species pool across all sites recorded for each taxon. In a second step, we calculated the mean of these proportions across all taxa recorded for each site resulting in the multidiversity index. Apart from overall multidiversity, we also calculated multidiversity of potential pollinators (bees, butterflies, moths, flower visiting beetles and hoverflies, henceforth ‘pollinator diversity’) and natural enemies (parasitoid wasps, non-granivorous carabid beetles, staphylinid beetles and non-granivorous birds, henceforth ‘natural enemy diversity’).

In a first step, all response variables were tested against ‘AES type’ using linear models (LM) to detect possible differences between the four AES types (in separate models for each year a taxonomic group was recorded). In a second step, we tested for the flowering fields only

(excluding semi-natural calcareous grasslands) whether richness was dependent on semi-natural habitat proportion and flowering field size (response ~ ‘flowering field type’ * ‘semi-natural habitat proportion’ + ‘flowering field size’). In this step, we performed LMs for taxonomic groups recorded in only one year and linear mixed effects models (LMER; ‘lmer’ from the ‘lme4’ package (Bates *et al.* 2015)) for taxonomic groups recorded in two years, including ‘year’ as fixed effect to account for annual fluctuations and ‘site’ as random intercept to account for pseudoreplication in each site. Excluding the calcareous grasslands was necessary as (i) they were located in landscapes with high semi-natural habitat proportion. As a result, the factor ‘AES type’ was correlated with semi-natural habitat proportion (which was not the case if calcareous grasslands were excluded); (ii) we intended to test the effects of semi-natural habitat proportion on biodiversity in established AES habitats and not on permanent semi-natural habitats managed under AES that cannot be newly established (i.e. calcareous grasslands).

To assess the effects of different temporal continuity and short-term succession on species assemblages, we compared species assemblages using nonmetric multidimensional scaling (NMDS, ‘metaMDS’, 999 permutations). We tested for the effects of ‘AES type’ as a measure of temporal continuity and, in case of taxa that were recorded in two years, assemblage homogenization over time in the different AES types (species matrix ~ AES type (+ year)). Prior to ordinations and analyses, species matrices were standardized using the proportions of the species. In datasets obtained from metabarcoding (cicadas, hoverflies and parasitoid wasps), species observations were treated as presence / absence data and therefore, Jaccard dissimilarities were used in ordinations and statistical testing. For all other groups we tested for differences between obtained clusters in NMDS ordinations using a PERMANOVA (‘adonis’ from the ‘vegan’ package (Oksanen *et al.* 2019), 9999 permutations, Bray-Curtis distances).

All models were checked graphically and fulfilled model assumptions. All models were analysed using type 2 SS ANOVA tests (for LMs with ‘Anova’ from the ‘car’ package (Fox

& Weisberg 2019) and for LMERS with ‘anova’ from the ‘lmerTest’ package (Kuznetsova, Brockhoff & Christensen 2017) using ‘Kenward-Roger’ approximation of denominator degrees of freedom). Models comparing all four AES types were subsequently tested with Tukey posthoc tests (‘glht’ from the ‘multcomp’ package (Hothorn, Bretz & Westfall 2008)).

Results

Using different sampling approaches and classical taxonomic identification, we recorded a total of 331 vascular plant species as well as 746 animal species (5,466 orthopterans of 27 species, 2,441 bees of 143 species, 4,188 flower visiting beetles of 91 species, 3,020 butterflies of 56 species, 798 moths of 120 species, 27,558 carabid beetles of 111 species, 11,151 staphylinid beetles of 141 species and 666 birds of 57 species) with a total of 55,288 identified specimens. Molecular DNA metabarcoding yielded an additional 2,110 taxa from various, predominantly flying, insect orders of which we selected cicadas (54 taxa), hoverflies (66 taxa) and parasitoid wasps (322 taxa) for further analyses as these groups are important indicators (cicadas) or ecosystem service providers (hoverflies & parasitoid wasps). A total of 442 taxa from DNA metabarcoding were included in the analyses (Supplementary Figure V.S2 & Supplementary Table V.S2 & V.S3).

Effects of temporal continuity on multidiversity in agri-environmental schemes (AES)

Multi-taxa diversity (the percentage of species in each site of the total species pool (Allan *et al.* 2014)) increased on average by 39 percent with temporal continuity from new flowering fields to calcareous grasslands with the latter having a significantly higher multidiversity than all flowering field types (Figure V.2 A & D; Supplementary Table V.S4). Calcareous grasslands supported a higher pollinator diversity than flowering fields, while there were no differences among AES types with different temporal continuity in diversity of natural enemies (Figure V.2 B, C, E & F, Supplementary Table V.S4).

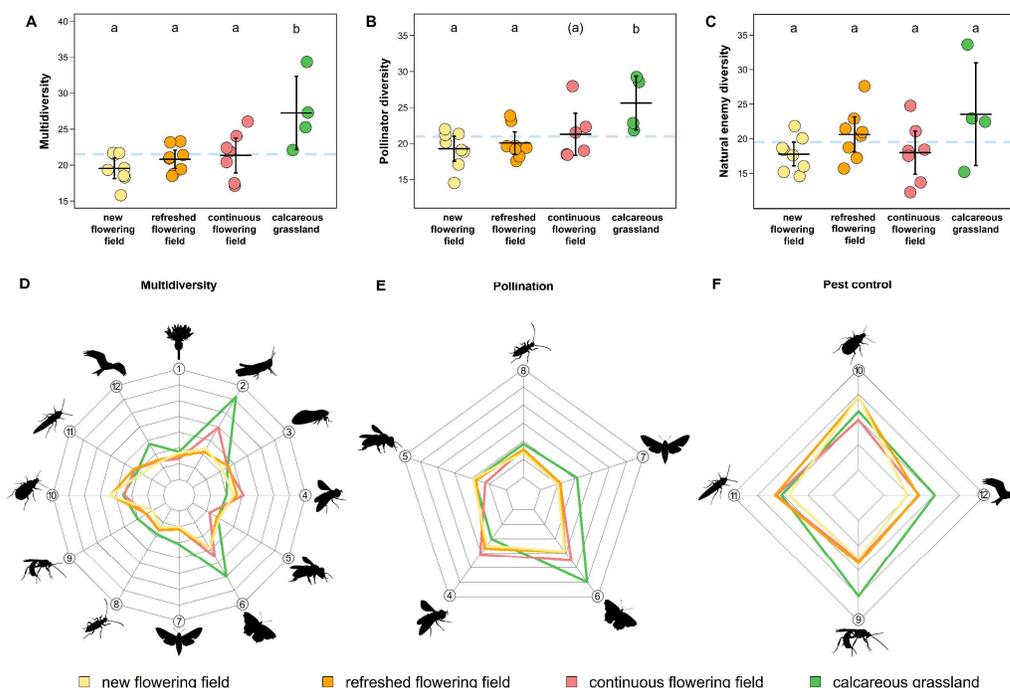


Figure V.2 (A) Overall multidiversity, (B) diversity of pollinators and (C) diversity of natural enemies in the different agri-environment scheme (AES) types along a gradient of temporal continuity (increasing from left to right; percentages of species in each site of the total species pool \pm 95 % confidence interval; blue dashed lines indicate means across all sites.). Proportion of species present in each AES type (mean) for (D) all taxa, (E) pollinators and (F) natural enemies. In radar charts, one interval equals 10 percent starting from the centre of the chart. Taxonomic groups were (1) vascular plants, (2) orthopterans, (3) cicadas, (4) hoverflies, (5) bees, (6) butterflies, (7) moths, (8) flower visiting beetles, (9) parasitoid wasps, (10) carabid beetles, (11) staphylinid beetles and (12) birds. Statistics see Table V.S4.

Different taxonomic groups showed variable responses to temporal continuity. Plants (in 2016) and carabid beetles (in 2017) were most species-rich in the new and refreshed flowering fields (Figure V.3 A & K, Supplementary Table V.S4). Orthoptera, butterflies and parasitoid wasps had the highest richness in calcareous grasslands and the lowest richness in new and refreshed flowering fields, with continuous flowering fields being intermediate (Figure V.3 B & E, Supplementary Table V.S4). Moths and birds were more species-rich in calcareous grasslands than in all types of flowering fields (Figure V.3 F & M, Supplementary Table V.S4). For cicadas, bees, flower visiting beetles, hoverflies and staphylinid beetles we found

no differences in richness between the AES types with different temporal continuity (Figure V.3 C, D, G, H, I & L, Supplementary Table V.S4).

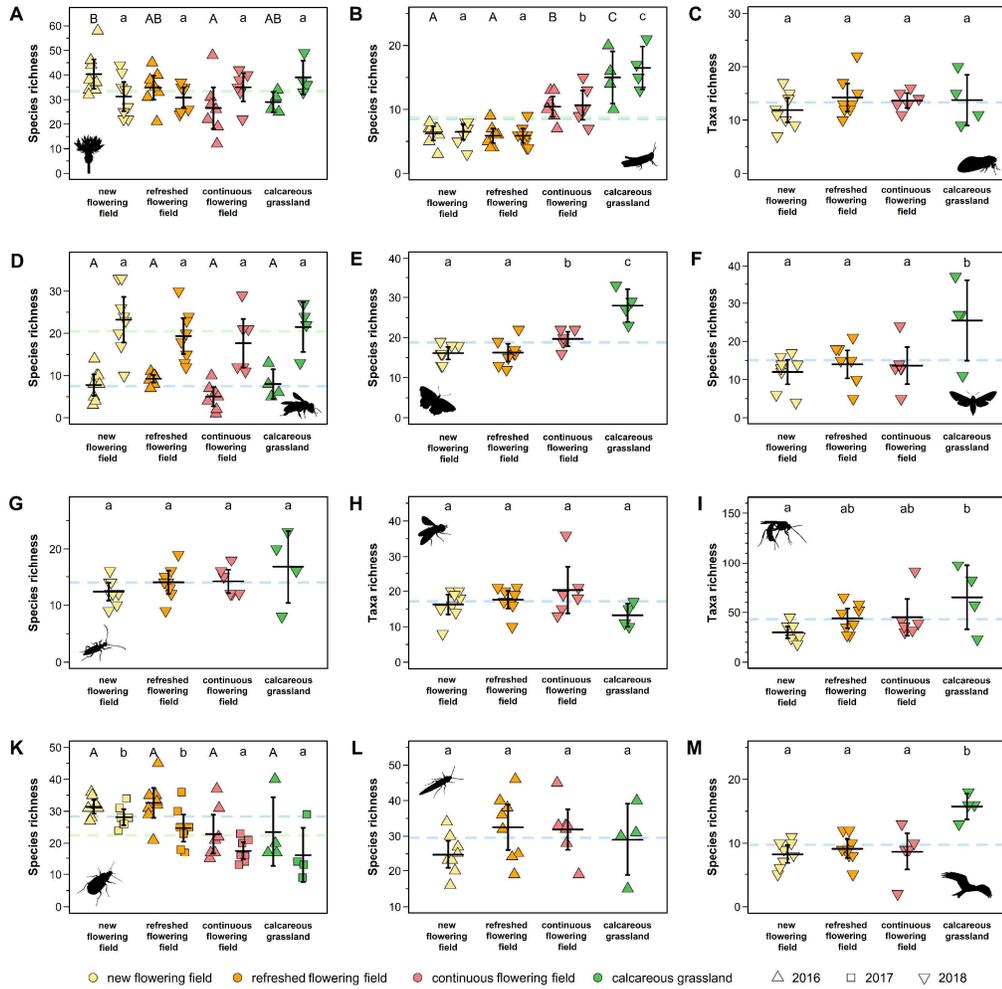


Figure V.3 Species richness of 12 taxonomic groups in the four studied agri-environment scheme (AES) types along a gradient of temporal continuity (increasing from left to right). Taxonomic groups were (A) vascular plants, (B) orthopterans, (C) cicadas, (D) bees, (E) butterflies, (F) moths, (G) flower visiting beetles, (H) hoverflies, (I) parasitoid wasps, (K) carabid beetles, (L) staphylinid beetles and (M) birds (A, B, D & K were recorded in two seasons, all other groups in one season). Means \pm 95 % confidence interval. Dashed lines indicate means across all sites (in groups with recordings in two years, blue lines indicate means of the first and green lines means of the second year). For statistics, see Table V.S4. Different letters indicate significant differences ($p < 0.05$).

Effects of temporal continuity and short-term succession on species assemblages

Ordinations showed that for all taxonomic groups except cicadas, moths and birds, AES with different temporal continuity shaped species assemblages. In plants, butterflies, parasitoid wasps, carabid beetles and staphylinid beetles a gradual increase in the similarity between assemblages along the gradient of temporal continuity was visible (Figure V.4 A, E, I, K, L & M, Supplementary Table V.S5). Orthopterans, bees and flower visiting beetles had similar assemblages in all flowering fields but different assemblages in calcareous grasslands (Figure V.4 B, C, D & G, Supplementary Table V.S5).

Short-term succession was measured between two years in four selected taxonomic groups (plants, orthopterans, bees and carabid beetles) with repeated recordings (using the same methodology in both years). Plant assemblages of flowering fields became more similar to those in calcareous grasslands in the second year of recording (Figure V.4 A, Supplementary Table V.S5). Bee assemblages did not differ among AES types but changed essentially between the repeated recordings in all AES types (Figure V.4 D, Supplementary Table V.S5). Assemblages of orthopterans and carabid beetles did not change in any of the AES types between repeated recordings while carabid richness was higher in the first than in the second year (Figure V.4 B & K, Supplementary Figure V.S3, Supplementary Tables V.S5 & V.S6).

Effects of flowering field size and landscape context on local diversity

Multidiversity as well as diversity of pollinators and natural enemies were not significantly affected by flowering field size and semi-natural habitat proportion in the surrounding landscape (Supplementary Table V.S6). However, increasing flowering field size decreased staphylinid beetle richness (Supplementary Table V.S6). An increasing proportion of semi-natural habitats in the landscape enhanced the richness of bees (Supplementary Table V.S6). All other taxonomic groups showed no significant relation to flowering field size or proportion of semi-natural habitats.

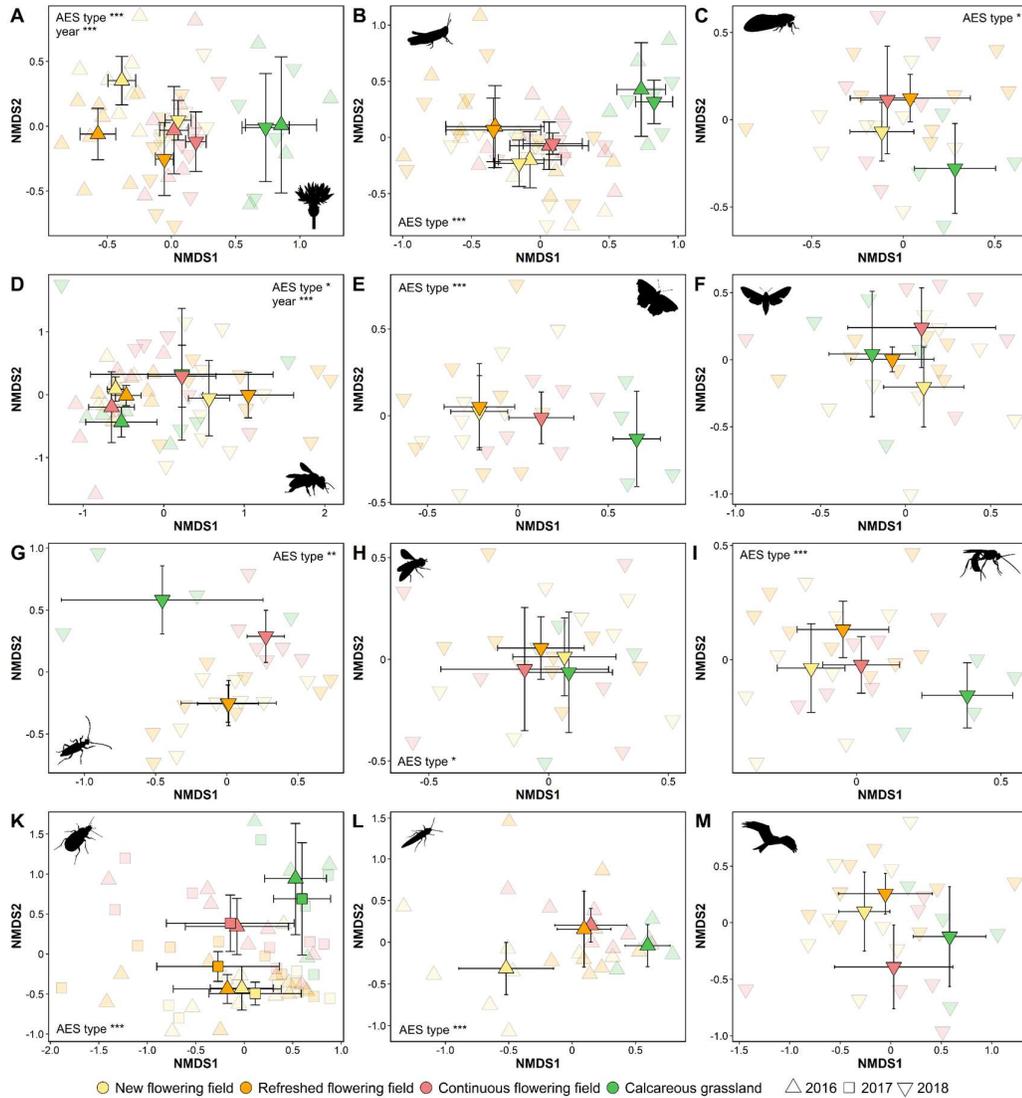


Figure V.4 Species assemblages of 12 taxonomic groups (NMDS ordination) in the four studied agri-environment scheme (AES) types; partly for two years (A, B, D & K). Taxonomic groups were (A) vascular plants, (B) orthopterans, (C) cicadas, (D) bees, (E) butterflies, (F) moths, (G) flower visiting beetles, (H) hoverflies, (I) parasitoid wasps, (K) carabid beetles, (L) staphylinid beetles and (M) birds. Centroids of the four AES types \pm 95 % confidence interval. NMDS and PERMANOVA used Bray-Curtis distances except for taxa recorded and identified by DNA metabarcoding on a presence absence level ((C), (H) & (I)) which used Jaccard distances. Significant factors in PERMANOVA tests indicated in the corners of the respective panels (* indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$). Statistics see Table V.S5.

Discussion

We show that flowering fields support biodiversity and ecosystem services in agricultural landscapes. However, they cannot replace species-rich semi-natural grasslands as they support different species assemblages and for most taxa lower diversity. The parallel or contrasting responses of different taxonomic groups, representing multiple trophic levels (plants, herbivores, predators), functional groups (pollination and pest control services), species traits (e.g. body size and mobility) and conservation status broaden the scientific basis for evidence-based designs of agri-environment schemes (AES), regional prioritisations and allocation of subsidies.

The importance of temporal continuity

We found temporal continuity of AES habitats to be important: multidiversity as well as pollinator diversity benefited from flowering fields with higher temporal continuity and permanent semi-natural grasslands while natural enemy multidiversity was unaffected by temporal continuity.

The investigated taxonomic groups reacted differently to temporal continuity. Carabid beetles as important natural enemies had the highest richness in newly established flowering fields. Orthopterans, butterflies, moths, parasitoid wasps and birds, however, benefitted from older, more temporally continuous habitats and richness peaked in calcareous grasslands. Many species of these taxonomic groups are endangered habitat specialists with habitat requirements that younger AES types fail to fulfil. AES with higher temporal continuity are more heterogeneous in structural aspects due the successional change than uniformly sown young flowering fields. Further, grasslands provide e.g. shrubs for birds or specific food plants for orthopterans or butterflies and moths which are not present in seed mixtures and potentially increase their suitability for these taxa (Haaland, Naisbit & Bersier 2011; Bartual *et al.* 2019).

Consequently, species assemblages of these groups in continuous flowering fields were more similar to those in calcareous grasslands than to those in young flowering fields. This trend was also visible in the assemblage structures of plants, carabid beetles and staphylinid beetles although no differences in richness were visible. Short-term succession overall did not change species assemblages of younger AES towards assemblage structures of AES with higher temporal continuity. We assume that the observed changes in plant and bee assemblages in all AES types were mainly driven by different weather conditions between the years. Both 2017 and 2018 were exceptionally warm years in the study region, which could have shifted assemblages in comparison to 2016.

As biodiversity directly drives pest control and pollination services (Dainese *et al.* 2019), maintaining biodiversity in agricultural landscapes is essential to ensure ecosystem services provision. We show that in this context, temporal continuity is an essential component. Implementing AES habitats over the span of several years is therefore important, but not a silver bullet for biodiversity conservation due to their eventual discontinuation. Flowering fields only support a subset of the total regional biodiversity - likely rather common species (Haaland, Naisbit & Bersier 2011). Semi-natural calcareous grasslands, however, support and conserve additional species and host the highest overall diversity. Habitats with increased temporal continuity allow slow colonisers to establish populations and are shaped by natural processes like succession and selection of better adapted species from the regional species pool and thus become gradually more similar to calcareous grasslands. Therefore, they can harbour both the species of the agricultural landscape as well as species with more specific habitat requirements, which makes habitats with higher temporal continuity especially important for conservation efforts (Kleijn *et al.* 2006).

While AES habitats with higher temporal continuity promote pollinator diversity, natural enemy diversity was equally high in newly established habitats. Together with calcareous grasslands, flowering fields also provide shelter to buffer disturbances occurring regularly in adjacent agricultural fields (e.g. soil management, application of pesticides, harvest) as they

remain comparatively undisturbed. Both flowering fields and calcareous grasslands together function synergistically and thus maximize benefits for biodiversity if provided simultaneously in a landscape.

Single large or several small?

The size of a habitat often determines the number of species it contains (Turner & Tjørve 2005). Especially in biodiversity conservation, the last decades were dominated by the debate whether single large or several small habitat patches in a landscape were to be preferred (Rösch *et al.* 2015; Grass *et al.* 2019). Within our gradient from 0.29 ha to 2.92 ha, flowering field size affected neither multi-taxa diversity nor the diversity of pollinators or natural enemies. The richness of most of the taxonomic groups was unaffected by flowering field size but staphylinid beetle richness decreased with flowering field size.

Our results indicate that overall, within the range investigated, the size of flowering fields is not limiting the biodiversity they can harbour (this might be different for very small fields below 0.29 ha). Within the studied range, a network of small flowering fields could be more beneficial for agricultural landscapes than single large fields, as beneficial effects within crops e.g. for pest control are limited by distance from AES habitats (Boetzl *et al.* 2019; Albrecht *et al.* 2020; Boetzl *et al.* 2020). With such a network, edge areas promoting beneficial spillover and edge-effects into adjacent crop fields in the landscape increase (Krimmer *et al.* 2019; Albrecht *et al.* 2020; Boetzl *et al.* 2020). This network would also increase overall landscape heterogeneity, which was shown to benefit ecosystem functioning and biodiversity (Martin *et al.* 2019; Martin *et al.* 2020). In such networks, AES could comprise habitats of different age with a certain proportion being renewed or replaced and re-established elsewhere every year. This would ensure that undisturbed habitats for overwintering are continuously available at reachable spatial distances in a landscape. In order to implement such landscape planning policies, further clarification is needed on how beneficial connectivity between AES habitats

is, how different types of AES interact with adjacent crop fields and how dense such a green network in agricultural landscapes should ideally be.

How effective are flowering fields in different agricultural landscapes?

After establishment, AES habitats need to be colonised by organisms from source habitats in the surroundings. While different types of semi-natural habitats serve as potential source habitats it is unclear how much and which types of source habitats are needed. AES were previously found to be especially effective in landscapes with few remaining semi-natural habitats (Tschardtke, Batáry & Dormann 2011; Li *et al.* 2020).

In our study, multidiversity in flowering fields was independent from the amount of semi-natural habitat in the landscape. While landscape level semi-natural habitat positively affected the richness of bees, most of the taxa investigated did not benefit from landscapes with high semi-natural habitat proportions. This indicates that relatively small amounts of semi-natural habitats as sources in a 1 km landscape were sufficient to proliferate biodiversity into newly established flowering fields. We, however, did not investigate agricultural landscapes with very small amounts of semi-natural habitat left and the effectiveness of flowering fields in such landscapes could be lower (the minimum semi-natural habitat cover was 3.6 %). In contrast to our results within flowering fields, multidiversity in agricultural fields is driven by semi-natural habitat cover in the surrounding landscape (Sirami *et al.* 2019). While agricultural fields constantly need recolonization after major disturbances (such as soil management or harvest), flowering fields can remain undisturbed for a longer period and are therefore less dependent on continuous influx from source habitats. After an initial colonization phase, they provide continuous shelter and are assumed to act as source habitats for adjacent agricultural fields. Our results indicate that in this phase, landscape level semi-natural habitat is less important, presumably because the subset of the regional species pool that can prosper in AES habitats already reached them. Semi-natural habitats, however, support many species, which were not present in flowering fields and therefore will not colonize and establish populations

there. This emphasizes (i) that AES habitats can restore diversity in rather simple landscapes with low proportion of semi-natural habitat and (ii) that semi-natural habitats cannot be replaced by temporary AES to secure biodiversity.

Conclusion

Using a unique dataset comprising 1519 taxa across 12 taxonomic groups on several trophic levels, we showed that temporal continuity is an important factor driving multidiversity in AES habitats. According to our results, flowering fields cannot replace permanent semi-natural grasslands as flowering fields only support a subset of biodiversity from the regional species pool. Semi-natural grasslands on the other hand provide habitat for species that do not occur on flowering fields and therefore are a valuable addition to these. A combination of both, flowering fields and semi-natural grasslands, is needed to maintain a high overall biodiversity in agricultural landscapes. Increasing heterogeneity in agricultural landscapes benefits biodiversity conservation and can be achieved through the strategic placement of AES (Martin *et al.* 2020). Our results indicate that the size of flowering fields and landscape level proportion of semi-natural habitats are of lesser importance for the multi-taxa diversity they harbour, whereas the diversity of bees, which often is of crucial interest in AES programs, benefits from semi-natural source habitats in the landscape. Overall, even small habitats in landscapes with low remaining semi-natural habitats can therefore be beneficial and support biodiversity as well as promote ecosystem service provision.

Many studies have pointed out that AES habitats should be tailored more precisely to the specific targets they aim at fulfilling (Batáry *et al.* 2011; Holland *et al.* 2016; Cole *et al.* 2020). For this, the specific local habitat structures supporting different ecosystem service agents (e.g. nesting structures and locations, habitat requirements, food resources) need to be identified. While younger flowering fields are richer in flowers and therefore raise attractiveness and acceptance for these structures in the general public and among farmers, the provision of pollination in adjacent croplands increases with flowering field age (Albrecht *et al.* 2020). Our

results show that more continuous flowering fields and semi-natural grasslands support higher pollinator diversities while natural enemies were equally diverse also in younger habitats. As pollinators operate on a wider spatial range within the landscape than the predominantly soil dwelling natural enemies, a network of few, more continuous AES habitats and semi-natural grasslands to support pollinator populations supplemented by a variety of more evenly distributed smaller and more frequently rotating flowering fields to foster local natural enemy populations in adjacent fields could be most effective (similar to the interconnected network of habitats proposed by Cole *et al.* (2020) for pollinators). With a combination of these measures, landscape complexity is simultaneously increased, which allows more species to persist, benefits functional biodiversity and ultimately enhances crop yields (Dainese *et al.* 2019; Martin *et al.* 2019). We conclude that agri-environmental schemes (AES) can be an important and successful component to restore biodiversity in agricultural landscapes that face a severe decline in insects and other taxa (Seibold *et al.* 2019). However, a more fundamental transformation of farmland management including large-scale restoration of permanent semi-natural grasslands are mandatory for long-term preservation of biodiversity and its multiple functions.

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Supplementary material V

Supplementary Information 1

Biodiversity of different taxonomic groups was sampled in three years from 2016 to 2018. In 2016, 27 sites were sampled, in 2017 one refreshed flowering field was not sampled while in 2018 one continuous flowering field was lost due to field changed management, bringing the total to 26 sites in both 2017 and 2018.

New and refreshed flowering fields were funded by the KULAP (“Kulturlandschaftsprogramm”), an agri-environment scheme (AES) of the Bavarian state. Continuous flowering fields were funded by a different AES and running under the designation ‘Ökologische Vorrangfläche’ (ecological focus area).

Plants

Plant diversity was recorded on 4 squared Braun Blanquet plots (Braun-Blanquet 1964) of 1 x 1 m² (small AES habitats < 1 ha) or 6 plots of 1 x 1 m² (large AES habitats > 1 ha). Half of the plots were located near the habitat edge (5 m to the edge), the other half in the habitat centre and all plots together formed a rectangle. The distance between the nearest plots was 5 to 10 m in small AES habitats and 20 to 25 m in large AES habitats.

We recorded vascular plants (except grass species) in two intervals from 20 May to 6 June 2016 and 14 July to 10 August 2016 to account for plant phenology. In 2018, vascular plants (except Poaceae) were recorded on the same plots in two intervals from 10 May to 9 June 2018 and from 30 July to 11 August 2018.

Malaise traps and metabarcoding

To record overall diversity of flying insects across several taxa, we placed a malaise trap (height front: 90 cm; height back: 170 cm; length: 155 cm; width front and back: 155 cm)

centrally in each of the AES habitats. The traps were active for two sampling intervals from 28 May to 08 June and from 16 July to 26 July 2018. In each sampling interval, each malaise trap was active for 7 days (168 hours). Insects were collected in a collection tube located at the highest point of the malaise traps in 99% pure ethanol. Samples ranged from 1.4 to 19.6 g (dry weight; mean: 8.43 ± 0.47 g). In the lab, samples were freeze dried, homogenized and sent to a commercial company for DNA extraction, metabarcoding (CO1) and analysing (AIM - Advanced Identification Methods GmbH, Leipzig, Germany).

DNA extraction for all samples was carried out in a 90:10 solution of animal lysis buffer (buffer ATL, Qiagen DNEasy Tissue Kit, Qiagen, Hilden, Germany) and Proteinase K. Lysis was performed overnight in a 56 °C oven. Samples were then allowed to cool to room temperature, 200 µL aliquots of the lysate were taken, and DNA was extracted from them using the DNEasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions.

From each sample, 5 µL of extracted genomic DNA was used, along with Plant MyTAQ (Bioline, Luckenwalde, Germany), and High Throughput Sequencing (HTS) adapted mini-barcode primers targeting a 313bp fragment of the CO1-5P barcoding region (Leray *et al.* 2013) were applied for multiplex PCR. Amplification success and fragment length were observed using gel electrophoresis. Amplified DNA was cleaned up and resuspended in 50 µL molecular water for each sample before proceeding. Illumina Nextera XT (Illumina Inc., San Diego, USA) indices were ligated to the samples in a second PCR reaction applying the same annealing temperature as for the first PCR reaction but with only 7 cycles, and ligation success confirmed by gel electrophoresis. DNA concentrations were measured using a Qubit fluorometer (Life Technologies, Carlsbad, USA), and samples were combined into 40 µL pools containing equimolar concentrations of 100 ng each. Pools were purified using MagSi-NGSprep Plus (Steinbrenner Laborsysteme GmbH) beads. A final elution volume of 20 µL was used. High-Throughput Sequencing (HTS) was performed on an Illumina MiSeq using v3 (2*300bp, 600 cycles, maximum of 25mio paired-end reads) chemistry.

FASTQ files were combined and sequence processing was performed with the VSEARCH v2.4.3 suite (Rognes *et al.* 2016) and cutadapt v1.14 (Martin 2011). Due to not all sequenced samples yielding reverse reads of sufficient quality to enable paired-end merging, only forward reads were utilized. Forward primers were removed with cutadapt. Quality filtering was with the fastq_filter program of VSEARCH, fastq_maxee 2, minimum length of 100 bp. Sequences were dereplicated with derep_fulllength, first at the sample level, and then concatenated into one '.fasta' file, which was then dereplicated. Chimeric sequences were filtered out from the large '.fasta' file using uchime_denovo. Remaining sequences were clustered into OTUs at 97% identity with cluster_size, and OTU table created with usearch_global. To reduce likely false positives, a cleaning step was employed which excluded read counts in the OTU table of less than 0.01% of the total. OTUs were blasted against a custom database downloaded from GENE BANK (a local copy of the NCBI nucleotide database downloaded from ftp://ftp.ncbi.nlm.nih.gov/blast/db/), including taxonomy and BIN information, by means of Geneious (v.10.2.5 – Biomatters, Auckland – New Zealand), and following methods described in Morinière *et al.* (2016). The resulting csv file which included the OTU ID, BOLD Process ID, BIN, Hit-%-ID value (percentage of overlap similarity (identical basepairs) of an OTU query sequence with its closest counterpart in the database), length of the top BLAST hit sequence, phylum, class, order, family, genus, and species information for each detected OTU was exported from Geneious and combined with the OTU table generated by the bioinformatic pipeline. The combined results table was then filtered by Hit-%-ID value and total read numbers per OTU. Entries with identifications below 97% and total read numbers below 0.01% of the summed reads per sample have not been removed from the analysis, as low hit-% matches are expected for the local fauna. Interactive Krona charts were produced from the taxonomic information using KronaTools v1.3 (Ondov, Bergman & Phillippy 2011).

After bioinformatical processing, the samples yielded a total of 4501 distinct sequences of insects (class Insecta) of which 4455 found matches in the BOLD library which could be grouped to 2110 taxa with an overlap in sequences above 97% (the rest was discarded; Supplementary Table V.S3). An overlap of above 97% (Hit-%-ID value) between an amplicon

and a reference sequence is generally used as a minimum criterion for reliable species identification within DNA barcoding and DNA metabarcoding sciences (see Leray and Knowlton (2015)).

Orthopterans

We recorded orthopteran assemblages on each study site during two separate surveys per site between mid-July and late August both in 2016 and in 2018. We conducted variable transect walks (not a priori fixed transects) to maximize species detection. Transect walks were performed between 10 am and 5 pm and only when weather conditions were favorable (temperature > 15 °C, cloud cover < 50 %, wind strength < 4 Beaufort scale). In the transect walks, orthopterans were recorded using acoustic and visual detection during five-minute intervals as well as sweep netting. In each survey, six independent transect walks were performed to cover the microhabitat variation within the study sites. In this way, all habitat structures present at the sites were surveyed. Species were identified in the field by song and morphological characteristics. Due to our sampling techniques, we excluded hardly detectable soil-dwelling species (such as *Myrmecophilus acervorum* and *Gryllotalpa gryllotalpa*) as well as arboricolous species that rarely occur in grasslands from the sampling data.

Cicadas

For assessing Cicada diversity, we used records obtained from the Malaise traps and subsequent DNA metabarcoding (as described above). We chose cicadas as they are an important group often used as indicators for habitat quality and trap samples contained enough taxa to perform meaningful analyses (2.6% of all taxa obtained from metabarcoding; Supplementary Table V.S3). We included all observations of Hemiptera in the families ‘Aphrophoridae’, ‘Cercopidae’, ‘Cicadellidae’, ‘Cixiidae’, ‘Delphacidae’ and ‘Issidae’ (all families of Auchenorrhyncha present in our dataset). All analyses were performed on the

presence – absence level due to the reasons stated below (paragraph '*Data processing for statistical Analyses*').

Bees

We recorded bees via sweep netting in three intervals (18 April to 04 May, 09 to 22 May and 06 July to 02 August) at each site in 2016. During each visit, two transect walks were performed for a total of 20 minutes on small sites (0.19 to 1 ha) and for 30 minutes on large sites (1 to 17.4 ha) in order to cover all habitat structures. Each transect covered 25 m per 5 minutes resulting in two 50 m transects in small sites and two 75 m transects in large sites. One transect was started 5 m inside the site on one of the edges and followed the edge, the other transect was placed centrally in each site. The sites were visited randomly in each round of visits to minimize the influence of daytime. Transect walks were performed from 10 am to 5 pm, if temperature was above 18°C and wind strength below 5.5 m/s (< 4 Beaufort scale). Bees were recorded up to a distance of 1 m from the transect to both sides. In 2018, bees were recorded using the same methodology on five visits per site (17 to 21 April, 05 to 09 May, 28 May to 04 June, 27 June to 02 July, 19 to 25 July 2018). The dates used to compare changes between years were aligned by oilseed rape phenology in the years.

Additionally, we recorded bees in 2018 using pan traps (0.5 l, 16 cm diameter, 4.5 cm depth; coloured white, yellow and blue with UV reflecting spray colour (Sparvar Leuchtfarbe, Spray-Colour GmbH)). At each site, one cluster of pan traps (one of each colour) was placed centrally at vegetation height. The traps were filled with water (approximately 450 ml) with a small amount of detergent. Pan traps were active for 48 hours twice from 06 to 09 May 2018 and from 17 to 20 June 2018.

Hoverflies

Hoverfly diversity was obtained from the Malaise traps with subsequent DNA metabarcoding (as described above). We selected hoverflies as they are an important pollinator group in agricultural landscapes and trap samples contained enough taxa to perform meaningful analyses (3.1% of all taxa obtained from metabarcoding; Supplementary Table V.S3). We included all observations of Diptera in the family ‘Syrphidae’. All analyses were performed on the presence – absence level due to the reasons stated below (paragraph ‘*Data processing for statistical Analyses*’).

Flower visiting beetles

Flower visiting beetles were collected using pan traps (0.5 l, 16 cm diameter, 4.5 cm depth). Pan traps were coloured white, yellow and blue with UV reflecting spray colour (Sparvar Leuchtfarbe, Spray-Colour GmbH; <https://www.spraycolor.de/>). At each site, one cluster of pan traps (one of each colour) was placed centrally at vegetation height. The traps were filled with water (approximately 450 ml) with a small amount of detergent. Pan traps were active for 48 hours twice from 06 to 09 May 2018 and from 17 to 20 June 2018.

As flower visiting beetles, we classified all members of families that are commonly observed visiting flowers, either feeding on pollen, nectar or on plant tissue (classified by taxonomical consultants). These families included ‘Apionidae’, ‘Buprestidae’, ‘Cantharidae’, ‘Cerambycidae’, ‘Chrysomelidae’, ‘Cleridae’, ‘Elateridae’, ‘Melyridae’, ‘Mordellidae’, ‘Nitidulidae’, ‘Oedemeridae’ and ‘Scarabaeidae’.

Butterflies

We recorded butterflies in five transect walks per site (17 to 21 April, 05 to 09 May, 28 May to 04 June, 27 June to 02 July, 19 to 25 July 2018). The sites were visited randomly in each

round of transects to minimize the influence of daytime. Transect walks were performed from 10 am to 5 pm, if temperature was above 18°C and wind strength below 5.5 m/s (< 4 Beaufort scale). To account for differences in sites, transect walks were performed for 20 minutes on small sites (0.19 to 1 ha) and for 30 minutes on large sites (1 to 17.4 ha) at a speed of approximately 0.3 m/s. Butterflies were recorded up to a distance of 2.5 m from the transect to both sides.

Moths

Moths were collected using an UV-Light trap that was placed centrally in each study site. The trap consisted of three crossed clear plastic windows (10.5 x 35 cm²), a central UV light tube (Narva LT 15W / 073 BLACKLIGHT blue T8, G13; <https://www.narva-bel.de/>) and a collection bag underneath. The light source was placed 1.5 m above ground using a metal tripod (arm length 2.5 m) to make collecting independent from trees or other high objects. Light trapping was performed in nights above 15°C when the sky was clear or slightly cloudy. The UV light tube was automatically activated at dusk and deactivated at dawn using a brightness sensor. We activated the light traps two times in each study site, once in a first sampling season from 04 to 21 June 2018 and from and once in a second sampling season from 06 to 23 August 2018. The moths were collected on the next day, frozen, mounted and identified.

Carabid and staphylinid beetles

Pitfall traps were used to record carabid and staphylinid beetles. In each study site, three pitfall traps were installed along a transect in the centre of the AES habitat 15 m apart from each other and from the edges. Pitfall traps were active over two years from 5/6 April to 23/24 August (20 weeks) and 11/12 April until 04/05 July 2017 (12 weeks) and emptied biweekly summing up to a total of 810 trap samples in 2016 and 468 trap samples in 2017 in (total:

1278). A total of 22 pitfall trap samples in 2016 (2.7 %) and 7 pitfall trap samples in 2017 (1.5 %) were lost to wild animals and vandalism (total: 29; 2.3 %).

As pitfall trap containers, conventional glass honey jars (height: 9 cm, diameter: 7.5 cm) filled with 200 ml 1:3 ethylene glycol (auto-mobile antifreeze, H. Kerndl GmbH)–water mixture with odourless detergent as preservative were used. Traps were covered by clear polycarbonate roofs (25 × 25 cm²; ~10 cm above the ground). Trap samples were sorted in the lab for carabid beetles (Carabidae) and staphylinid beetles (Staphylinidae). Carabid beetles from both years as well as staphylinid beetles from 2016 were subsequently identified to species level. In staphylinid beetles, the genera *Atheta*, *Oligota* and *Amischa* were not identified to species level and individuals from these genera were not used for further analyses. In all analyses combining carabid datasets from both years, we only used comparable time intervals (i.e. the trap samples from the first 12 weeks in 2016).

Parasitoid wasps

We used parasitoid Hymenoptera caught in the Malaise traps and identified to taxon level in the DNA metabarcoding (as described above). We selected parasitoid wasps as they are an important group providing natural pest control in agricultural landscapes and trap samples contained enough taxa to perform meaningful analyses (15.3% of all taxa obtained from metabarcoding; Supplementary Table V.S3). We used species records as presence – absence data due to the reasons stated below (paragraph ‘*Data processing for statistical Analyses*’). As ‘Parasitoid wasps’ we included all predatory Hymenoptera except Aculeata.

Birds

We used the point count method to assess avian diversity centrally in each of our sites in three intervals during breeding season (03 to 10 April, 29 April to 04 May, 25 to 30 May 2018). Bird counts were performed from sunrise onwards over the following six hours. With wind

strength above 5.5 m/s or rainy weather conditions, no counts were performed. In each visit, we counted all birds on foraging or mating flights in a surrounding of 100 m around the central point in our sites for 5 minutes. Birds were recorded acoustically and visually. Birds passing in higher altitudes (obviously migrating) were not counted.

Data processing for statistical Analyses

Richness data for nine taxa was obtained by classical methods (vascular plants, orthoptera, bees, butterflies, moths, flower visiting beetles, carabid beetles, staphylinid beetles, birds) while the remaining three taxa were obtained by metabarcoding (cicadas, hoverflies and parasitoid wasps). Both approaches were not mixed. Species richness data obtained from metabarcoding cannot simply be used for abundance estimations due to the biomass differences between specimens and potential differences in the effectivity of the used primers. Therefore, we treated data obtained from DNA-metabarcoding as presence-absence data and used Jaccard instead of Bray-Curtis distances in ordinations and PERMANOVA analyses.

To assess local bee diversity, we combined the observations made with sweep netting (111 species; 797 specimens) and pan traps (81 species; 807 specimens) in 2018, resulting in a total of 134 species (1604 specimens).

In all comparisons of taxa between years (plants, orthopterans, bees and carabid beetles), we synchronized datasets by excluding all sampling intervals that were not performed in both years in order to standardize sampling effort (especially in bee datasets where we only selected the 3 corresponding transect intervals performed in both years). In the comparisons using ‘flowering field size’ as explanatory variable, we excluded additional sampling intervals (bees, butterflies) or plots (plants) assessed only in large sites in order to avoid biased results due to the increased sampling effort in larger sites.

In the plant dataset, not all specimens could be identified to species level. As the morphospecies between both studied years could not be linked with certainty, we excluded all

observations not identified to species level (6.8 % overall; 8.1 % in 2016 and 5.8 % in 2018) in the analyses comparing the assemblages between both years in order not to overestimate potential assemblage changes.

Figure V.S1: Distribution of the study sites within the study region

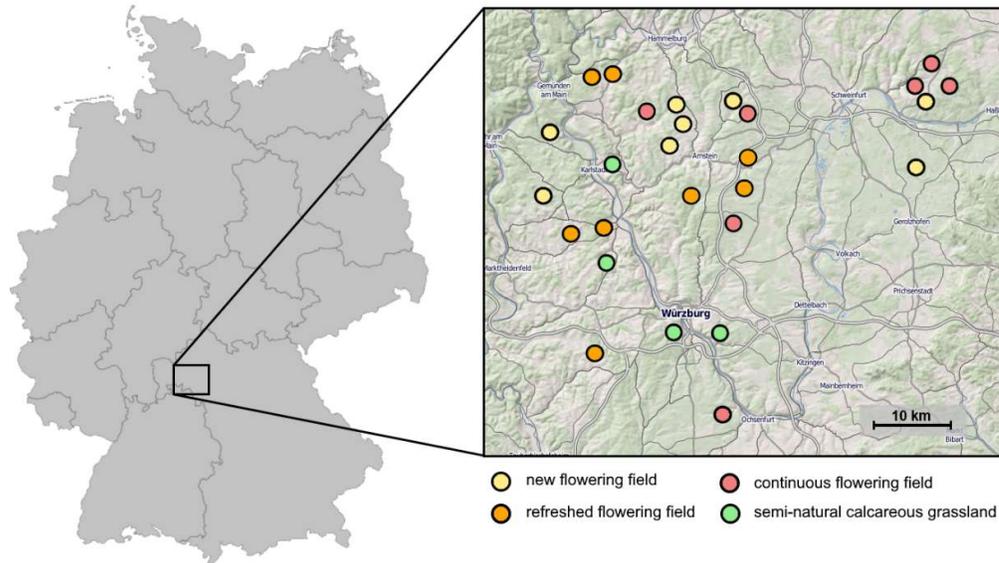


Figure V.S1: Map showing the location of all study sites within the study area with agri-environment scheme (AES) type. Map modified after: © OpenStreetMap-contributors.

Figure V.S2: Taxa metabarcoding

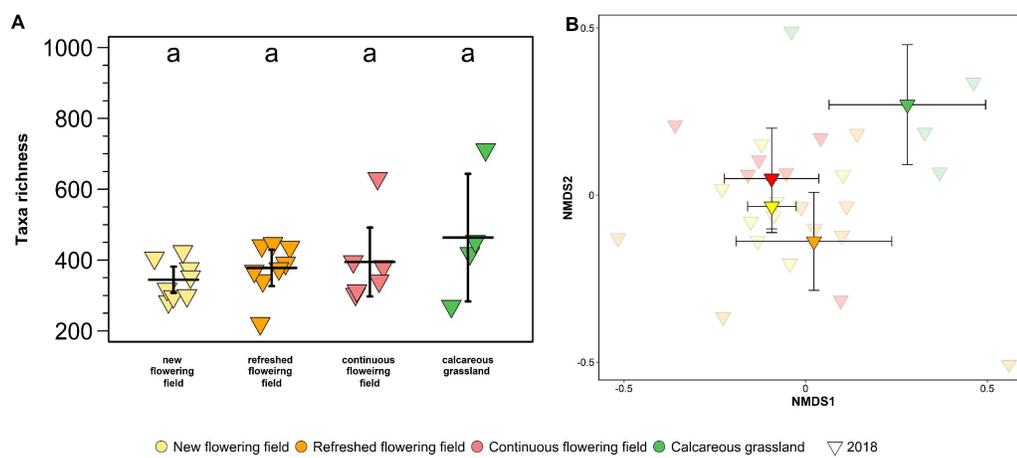


Figure V.S2: (A) Taxa richness obtained for insects from DNA metabarcoding across the four agri-environment scheme (AES) types. (B) NMDS ordination for the taxa assemblages (based on presence / absence data and Jaccard distances) obtained for insects from DNA metabarcoding across the four AES types

No significant differences were visible in taxa numbers between the AES types (linear model: $F_{3,22} = 1.22$, $p = 0.383$, $R^2 = 0.03$; see Supplementary Tables V.S2 & V.S3) and taxa numbers in the AES types were neither affected by flowering field size (linear model: $F_{1,15} = 0.13$, $p = 0.722$, $R^2 < 0.01$) nor by semi-natural habitat in the surrounding landscapes (linear model: $F_{1,15} = 0.05$, $p = 0.827$, $R^2 < 0.01$). However, the assemblage structure differed between flowering fields (all three types had overall similar assemblages) and calcareous grasslands (PERMANOVA: $F_{3,24} = 1.35$, $p < 0.001$, $R^2 = 0.16$, Jaccard distances).

Figure V.S3: Species richness difference between repeated recordings

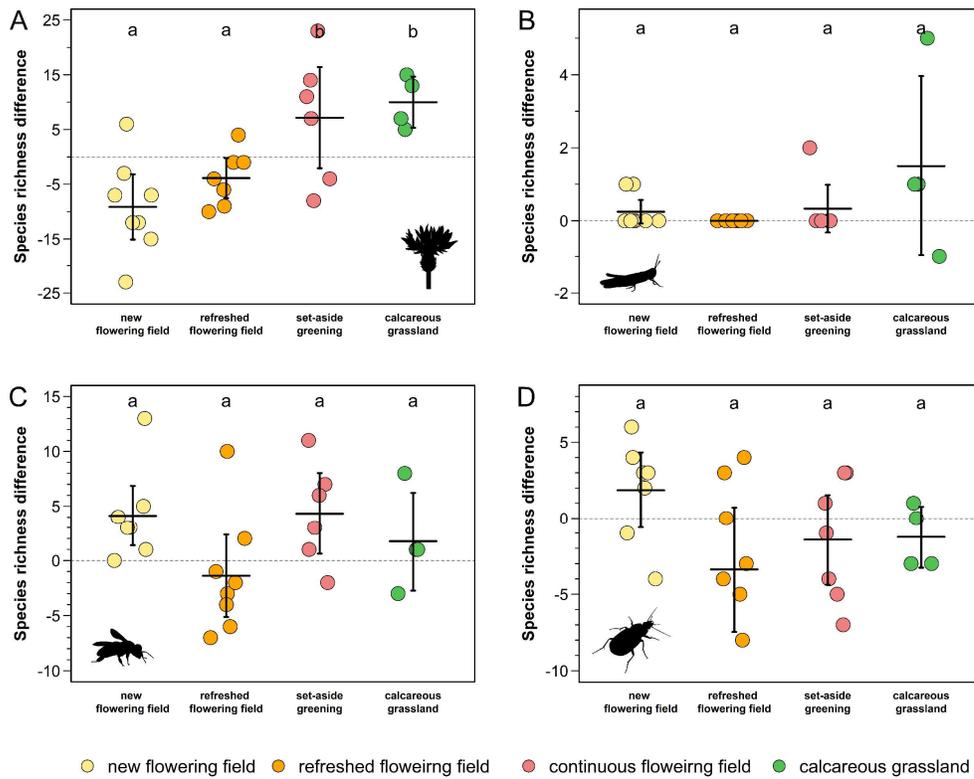


Figure V.S3: Differences in species richness between the second year of recording and the first year of recording across the four agri-environment scheme (AES) types for (A) vascular plants, (B) orthopterans, (C) bees and (D) carabid beetles. Positive values indicate higher richness in the second recording year. Means \pm 95 % confidence interval. Dashed line represents zero change.

Table V.S1: Study sites

Table V.S1: Location of the study sites with area of agri-environmental scheme (AES) and proportion of semi-natural habitat (SNH) in the surrounding.

Site ID	Nearest village	Administrative district	AES type	GPS (WGS 84)	Area AES [ha]	SNH
01_REU	Reuchelheim	Main-Spessart	new flowering field	49.994097N 9.913864E	1.5	17.6
02_BUE	Büchold	Main-Spessart	new flowering field	50.010878N 9.945164E	2.92	9.85
03_WS1	Waldsachsen	Schweinfurt	new flowering field	50.041283N 10.371989E	1.67	6.74
04_SHW	Schwebenried	Main-Spessart	new flowering field	50.03625N 10.013122E	3	4.61
05_WIE	Wiesenfeld	Main-Spessart	new flowering field	49.995194N 9.685569E	0.29	18.63
06_STE	Steinfeld	Main-Spessart	new flowering field	49.941772N 9.678022E	0.31	11.6
07_GAU	Gauschach	Bad Kissingen	new flowering field	50.03565N 9.927058E	0.53	6.1
08_DUR	Dürrfeld	Schweinfurt	new flowering field	49.969153N 10.352558E	0.32	3.64
09_ZEL	Zellingen	Main-Spessart	refreshed flowering field	49.895914N 9.796075E	2.01	20.98
10_BIL	Billingshausen	Main-Spessart	refreshed flowering field	49.877894N 9.720292E	2.07	10.27
11_RIE	Rieden	Würzburg	refreshed flowering field	49.934694N 10.031019E	1.77	6.49
12_OBA	Oberaltertheim	Würzburg	refreshed flowering field	49.735775N 9.777983E	2.07	4.4
13_MUL	Mühlhausen	Schweinfurt	refreshed flowering field	49.96405N 10.050228E	0.25	16.76
14_HOL	Höllrich	Main-Spessart	refreshed flowering field	50.070453N 9.794578E	0.19	9.8
15_WEY	Weyersfeld	Main-Spessart	refreshed flowering field	50.081411N 9.771431E	0.44	6.8
16_GRA	Gramschatz	Würzburg	refreshed flowering field	49.924433N 9.961481E	0.31	4.65
17_BUR	Bühler	Main-Spessart	continuous flowering field	50.022803N 9.863192E	1.49	13.85
18_ERB	Erbshausen	Würzburg	continuous flowering field	49.906492N 10.011397E	1.52	10.13
19_WS2	Waldsachsen	Schweinfurt	continuous flowering field	50.054467N 10.352353E	1.39	7.46
20_BUC	Buch	Haßberge	continuous flowering field	50.057131N 10.421064E	2.38	3.62
21_DAS	Darstadt	Würzburg	continuous flowering field	49.677386N 10.005922E	0.69	14.6
22_VAS	Vasbühl	Schweinfurt	continuous flowering field	50.033525N 10.054167E	0.73	7.55
23_ABF	Abersfeld	Schweinfurt	continuous flowering field	50.083306N 10.399783E	0.47	6.69
24_BLO	Würzburg	Würzburg	calcareous grassland	49.761483N 9.923436E	4.55	19.56
25_KAS	Karlstadt	Main-Spessart	calcareous grassland	49.974089N 9.792319E	0.81	26.56
26_LEI	Leinach	Würzburg	calcareous grassland	49.851717N 9.801561E	0.46	21.65
27_MAW	Gerbrunn	Würzburg	calcareous grassland	49.76735N 10.000133E	18.33	36.38

Table V.S2: Number of species / taxa and individuals collected for each taxonomic group (and for the total metabarcoding samples) and year in each agri-environment scheme (AES) type and total. Total numbers, minima and maxima as well as means with standard error are provided.

	Year	(i) New flowering fields				(ii) Refreshed flowering fields				(iii) Continuous flowering fields				(iv) Calcareous grasslands				Total	
		Species richness		N	Mean ±SE	Species richness		N	Mean ±SE	Species richness		N	Mean ±SE	Species richness		N	Mean ±SE	Species richness	N
		Total	Min/ Max			Total	Min/ Max			Total	Min/ Max			Total	Min/ Max				
Plants	2016	128	32/58	40.4±3.1	NA	111	21/45	34.9±2.5	NA	82	12/48	26.6±4.3	NA	86	25/34	29.0±2.1	NA	254	NA
	2018	91	22/44	31.3±3.0	NA	78	24/37	31.0±2.1	NA	55	22/42	35.0±2.9	NA	56	33/49	39.0±3.5	NA	170	NA
Orthopterans	2016	11	5/8	6.3±0.6	509	13	5/9	5.9±0.6	398	19	7/13	10.4±0.8	835	21	10/20	15.0±2.1	618	26	2360
	2018	12	3/8	6.5±0.6	663	13	4/9	5.9±0.6	490	19	7/15	10.7±1.2	1086	23	13/21	16.5±1.7	867	27	3106
Cicadas	2018	26	7/17	11.9±1.2	NA	42	10/22	14.3±1.3	NA	31	11/16	13.7±0.7	NA	30	9/20	13.8±2.4	NA	54	NA
Bees	2016	27	3/14	7.8±1.3	318	29	7/11	9.3±0.5	302	19	1/10	5.0±1.2	140	21	5/13	8.0±1.8	77	49	837
	2018	86	10/33	23.3±2.8	557	71	13/30	19.4±2.2	523	54	11/29	17.7±2.9	346	59	13/27	21.5±3.0	178	134	1604
Hoverflies	2018	39	8/20	16.3±1.4	NA	41	10/21	17.6±1.3	NA	48	13/36	20.3±3.3	NA	23	10/17	13.3±1.7	NA	66	NA
Flower visiting beetles	2018	37	9/16	12.4±0.8	1466	43	9/19	14.0±1.0	1251	37	12/18	14.2±1.0	1239	44	8/23	16.8±3.3	232	91	4188
Butterflies	2018	32	13/19	16.1±0.8	924	33	12/22	16.3±1.1	671	36	16/22	19.7±0.9	883	47	23/33	28.0±2.1	542	56	3020
Moths	2018	57	4/17	12.0±1.6	183	60	5/21	14.0±1.9	215	60	5/24	13.7±2.5	153	67	11/37	25.5±5.4	247	120	798
Carabid beetles	2016	68	27/36	31.4±1.1	5659	79	21/45	32.6±2.4	6402	57	15/37	22.8±3.1	1394	55	17/40	23.5±5.5	1027	100	14482
	2017	61	24/34	28.1±1.3	7788	69	17/36	24.8±2.2	3616	44	14/23	17.6±1.4	1108	42	9/29	16.3±4.4	674	90	13186
Staphylinid beetles	2016	68	16/34	24.8±2.0	1871	95	19/46	32.5±3.3	5083	81	19/45	31.9±2.9	2723	67	15/40	29.0±5.2	1474	141	11151
Parasitoid wasps	2018	122	18/45	29.9±3.0	NA	177	27/65	43.9±5.0	NA	145	30/91	45.0±9.4	NA	160	23/98	65.0 ± 16.3	NA	322	NA
Birds	2018	30	5/11	8.3±0.8	171	36	5/12	9.1±0.8	171	23	2/13	8.7±1.5	162	32	13/18	15.8±1.0	162	57	666
Metabarcoding total	2018	1031	283/424	344.6± 18.8	NA	1284	221/447	377.9± 26.1	NA	1088	304/631	394.7± 49.5	NA	1063	270/712	463.5± 91.9	NA	2110	NA

Table V.S3: Number of insect taxa obtained from DNA metabarcoding of malaise trap samples by order and family. All 2110 taxa included matched sequences deposited in the BOLD library in at least 97 percent of the bases.

Order	Family	Number of taxa	Percentage of total
Blattodea			2
			0.09 %
Coleoptera	Ectobiidae	2	
			190
			9.00 %
	Anthribidae	1	
	Attelabidae	1	
	Brentidae	2	
	Buprestidae	3	
	Cantharidae	12	
	Carabidae	10	
	Cerambycidae	17	
	Chrysomelidae	29	
	Coccinellidae	7	
	Corylophidae	1	
	Cryptophagidae	1	
	Curculionidae	13	
	Elateridae	11	
	Erotylidae	2	
	Eucnemidae	1	
	Geotrupidae	1	
	Kateretidae	1	
	Lampyridae	1	
	Latridiidae	4	
	Leiodidae	2	
	Melandryidae	2	
	Melyridae	6	
	Monotomidae	1	
	Mordellidae	13	
	Nitidulidae	3	
	Oedemeridae	6	
	Phalacridae	1	
	Ptinidae	1	
	Scarabaeidae	2	
	Scirtidae	2	
	Scraptiidae	4	
	Silphidae	1	
	Staphylinidae	25	
	Tenebrionidae	2	
	Throscidae	1	
Dermaptera			2
			0.09 %
Diptera	Forficulidae	2	
			895
			42.42 %
	Acroceridae	1	
	Agromyzidae	69	
	Anisopodidae	3	
	Anthomyiidae	34	
	Anthomyzidae	1	
	Asilidae	7	
	Asteiidae	1	
	Bombyliidae	1	
	Calliphoridae	17	
	Cecidomyiidae	94	
	Ceratopogonidae	14	
	Chamaemyiidae	2	
	Chironomidae	33	
	Chloropidae	34	
	Clusiidae	1	
	Conopidae	5	
	Culicidae	9	
	Diadocidiidae	1	
	Ditomyiidae	1	
	Dolichopodidae	25	
	Drosophilidae	8	
	Empididae	14	
	Ephydriidae	5	
	Fanniidae	19	
	Heleomyzidae	7	
	Hybotidae	27	
	Keroplastidae	3	
	Lauxaniidae	8	
	Limoniidae	1	
	Lonchaeidae	4	
	Lonchopteridae	1	
	Milichiidae	3	
	Muscidae	48	
	Mycetophilidae	10	
	Opomyzidae	3	
	Phoridae	98	
	Pipunculidae	19	

	Platystomatidae	1		
	Polleniidae	1		
	Psilidae	2		
	Psychodidae	9		
	Ptychopteridae	1		
	Rhagionidae	3		
	Rhinophoridae	4		
	Sarcophagidae	27		
	Scathophagidae	3		
	Sciaridae	31		
	Sepsidae	3		
	Simuliidae	5		
	Sphaeroceridae	14		
	Stratiomyidae	7		
	Syrphidae	66		
	Tabanidae	2		
	Tachinidae	68		
	Tephritidae	7		
	Therevidae	1		
	Tipulidae	5		
	Trichoceridae	1		
	Ulidiidae	2		
	Xylomyidae	1		
Ephemeroptera			2	0.09 %
Hemiptera	Baetidae	2		
			138	6.54 %
	Aleyrodidae	2		
	Alydidae	1		
	Aphalaridae	1		
	Aphididae	21		
	Aphrophoridae	3		
	Cercopidae	1		
	Cicadellidae	45		
	Cixiidae	2		
	Coreidae	2		
	Delphacidae	2		
	Dictyopharidae	1		
	Issidae	1		
	Miridae	37		
	Nabidae	3		
	Pentatomidae	5		
	Plataspidae	1		
	Pyrrhocoridae	1		
	Reduviidae	1		
	Rhopalidae	3		
	Rhyparochromidae	3		
	Triozidae	2		
Hymenoptera			479	22.70 %
	Andrenidae	12		
	Apidae	16		
	Argidae	2		
	Bembicidae	2		
	Bethylidae	2		
	Braconidae	64		
	Cephidae	3		
	Ceraphronidae	1		
	Chalcididae	1		
	Chrysididae	3		
	Cimbicidae	1		
	Colletidae	5		
	Crabronidae	4		
	Cynipidae	1		
	Diapriidae	1		
	Dryinidae	1		
	Eulophidae	6		
	Eurytomidae	2		
	Figitidae	6		
	Formicidae	19		
	Halictidae	19		
	Ichneumonidae	211		
	Megachilidae	11		
	Megaspilidae	1		
	Melittidae	1		
	Mymaridae	1		
	Pemphredonidae	1		
	Pompilidae	11		
	Proctotrupidae	1		
	Pteromalidae	8		
	Sphecidae	1		
	Tenthredinidae	51		
	Torymidae	1		
	Vespidae	9		
Lepidoptera			357	16.92 %
	Adelidae	2		
	Alucitidae	1		
	Argyresthiidae	3		
	Blastobasidae	1		

	Bucculatricidae	4		
	Choreutidae	1		
	Coleophoridae	7		
	Crambidae	21		
	Depressariidae	1		
	Drepanidae	3		
	Elachistidae	4		
	Epermeniidae	1		
	Erebidae	17		
	Gelechiidae	27		
	Geometridae	42		
	Glyphipterigidae	1		
	Gracillariidae	9		
	Hepialidae	3		
	Hesperiidae	7		
	Lasiocampidae	1		
	Lycaenidae	9		
	Lyonetiidae	1		
	Lypusidae	1		
	Momphidae	2		
	Nepticulidae	4		
	Noctuidae	55		
	Nolidae	1		
	Notodontidae	1		
	Nymphalidae	19		
	Oecophoridae	4		
	Papilionidae	1		
	Pieridae	5		
	Plutellidae	1		
	Prodoxidae	1		
	Psychidae	3		
	Pterophoridae	8		
	Pyalidae	5		
	Scythrididae	3		
	Sesiidae	2		
	Sphingidae	3		
	Tineidae	2		
	Tischeriidae	1		
	Tortricidae	63		
	Yponomeutidae	4		
	Ypsolophidae	1		
	Zygaenidae	1		
Mecoptera			3	0.14 %
	Panorpidae	3		
Neuroptera			11	0.52 %
	Chrysopidae	5		
	Coniopterygidae	4		
	Hemerobiidae	2		
Odonata			1	0.05 %
	Coenagrionidae	1		
Orthoptera			19	0.90 %
	Acrididae	6		
	Gryllidae	1		
	Tettigoniidae	12		
Plecoptera			2	0.09 %
	Nemouridae	1		
	Taeniopterygidae	1		
Psocodea			3	0.14 %
	Caeciliusidae	1		
	Stenopsocidae	2		
Raphidioptera			3	0.14 %
	Raphidiidae	3		
Trichoptera			3	0.14 %
	Philopotamidae	1		
	Polycentropodidae	1		
	Sericostomatidae	1		

Table V.S4: Species / taxa richness as well as multidiversity of all taxonomic groups and of pollinators and natural enemies in all agri-environment scheme (AES) types. (*) indicates $p < 0.1$, * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$.

Response	year	Df	F	p	adj. R ²
Vascular plants	2016	3, 23	3.65	0.027 *	0.23
	2018	3, 21	1.42	0.265	0.05
Orthopterans	2016	3, 23	19.2	< 0.001 ***	0.68
	2018	3, 22	23.1	< 0.001 ***	0.73
Cicadas	2018	3, 22	0.70	0.562	0
Bees	2016	3, 23	2.69	0.070 (*)	0.16
	2018	3, 22	0.85	0.480	0
Butterflies	2018	3, 22	18.1	< 0.001 ***	0.67
Moths	2018	3, 22	4.45	0.014 *	0.29
Flower visiting beetles	2018	3, 22	1.48	0.248	0.05
Hoverflies	2018	3, 22	1.66	0.204	0.07
Parasitoid wasps	2018	3, 22	3.15	0.045 *	0.21
	2016	3, 23	3.49	0.032 *	0.22
Carabid beetles	2017	3, 22	6.66	0.002 **	0.4
	2016	3, 23	1.5	0.241	0.05
Staphylinid beetles	2016	3, 23	1.5	0.241	0.05
Birds	2018	3, 22	8.62	< 0.001 ***	0.48
Multidiversity		3, 23	6.44	0.003 **	0.39
Multidiversity of pollinators		3, 22	4.51	0.013 *	0.30
Multidiversity of natural enemies		3, 23	2.11	0.127	0.11

Table V.S5: PERMANOVA analyses of species assemblages in relation to agri-environment scheme (AES) type (representing different levels of temporal continuity) and in taxa recorded over two years (vascular plants, orthopterans, bees and carabids) in relation to year. * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$.

Response	Df	F	p	R²	distance used
Vascular plants					
AES type	3, 47	3.68	< 0.001 ***	0.18	Bray-Curtis
Year	1, 47	5.19	< 0.001 ***	0.08	
Orthopterans					
AES type	3, 48	7.83	< 0.001 ***	0.32	Bray-Curtis
Year	1, 48	1.29	0.266	0.02	
Cicadas					
AES type	3, 22	1.05	0.382	0.13	Jaccard
Bees					
AES type	3, 48	1.47	0.043 *	0.07	Bray-Curtis
Year	1, 48	11.12	< 0.001 ***	0.18	
Butterflies					
AES type	3, 22	2.69	< 0.001 ***	0.27	Bray-Curtis
Moths					
AES type	3, 22	1.14	0.223	0.13	Bray-Curtis
Hoverflies					
AES type	3, 22	1.41	0.028 *	0.16	Jaccard
Flower visiting beetles					
AES type	3, 22	3.15	< 0.001 ***	0.30	Bray-Curtis
Parasitoid wasps					
AES type	3, 22	1.40	< 0.001 ***	0.16	Jaccard
Carabid beetles					
AES type	3, 48	3.79	< 0.001 ***	0.19	Bray-Curtis
Year	1, 48	1.02	0.413	0.02	
Staphylinid beetles					
AES type	3, 23	2.37	< 0.001 ***	0.24	Bray-Curtis
Birds					
AES type	3, 22	1.33	0.118	0.15	Bray-Curtis

Table V.S6: Species / taxa richness as well as multidiversity and multidiversity of pollinators and natural enemies in the three flowering field types in relation to flowering field type (representing different levels of temporal continuity), semi-natural habitat (SNH) proportion in the surrounding landscape and flowering field size (as well as an interaction between flowering field type and SNH). Taxa recorded over two years (vascular plants, orthopterans, bees and carabids) were analysed with linear mixed effects models (R^2_m shown), all other with linear models (adjusted R^2 shown). (*) indicates $p < 0.1$, * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$. '+' (positive) and '-' (negative) indicate direction of relation in significant SNH or size effects.

Response / Factors	df	F	p	Relation	adj. R^2 / R^2_m
Vascular plants					
Flowering field type	2, 15	0.64	0.543		
SNH proportion	1, 15	0.47	0.504		
Flowering field size	1, 15	2.01	0.176		0.18
Year	1, 21	1.72	0.203		
Flowering field type : SNH proportion	2, 15	0.29	0.750		
Cicadas					
Flowering field type	2, 15	1.20	0.328		
SNH proportion	1, 15	2.57	0.129		0
Flowering field size	1, 15	0.17	0.683		
Flowering field type : SNH proportion	2, 15	0.24	0.793		
Orthopterans					
Flowering field type	2, 16	0.43	0.661		
SNH proportion	1, 16	0.16	0.696		
Flowering field size	1, 16	0.73	0.407		0.51
Year	1, 21	2.91	0.103		
Flowering field type : SNH proportion	2, 16	0.31	0.736		
Bees					
Flowering field type	2, 15	1.37	0.282		
SNH proportion	1, 15	8.36	0.011 *	+	
Flowering field size	1, 15	0.06	0.812		0.70
Year	2, 21	92.46	< 0.001 ***		
Flowering field type : SNH proportion	2, 15	1.12	0.351		
Butterflies					
Flowering field type	2, 15	3.14	0.073 (*)		
SNH proportion	1, 15	1.75	0.206		0.30
Flowering field size	1, 15	2.62	0.126		
Flowering field type : SNH proportion	2, 15	1.61	0.233		
Moths					
Flowering field type	2, 15	0.28	0.757		
SNH proportion	1, 15	1.05	0.321		0
Flowering field size	1, 15	0.01	0.957		
Flowering field type : SNH proportion	2, 15	0.05	0.954		
Flower visiting beetles					
Flowering field type	2, 15	1.19	0.331		
SNH proportion	1, 15	0.15	0.706		0.23
Flowering field size	1, 15	0.89	0.359		
Flowering field type : SNH proportion	2, 15	2.87	0.088 (*)		
Hoverflies					
Flowering field type	2, 15	0.63	0.544		
SNH proportion	1, 15	2.59	0.129		0.11
Flowering field size	1, 15	1.69	0.213		
Flowering field type : SNH proportion	2, 15	1.08	0.364		
Parasitoid wasps					
Flowering field type	2, 15	1.79	0.201		
SNH proportion	1, 15	0.01	0.961		0
Flowering field size	1, 15	0.01	0.943		
Flowering field type : SNH proportion	2, 15	0.25	0.779		
Carabid beetles					
Flowering field type	2, 16	3.22	0.067 (*)		
SNH proportion	1, 16	0.18	0.674		0.51
Flowering field size	1, 16	1.26	0.278		
Year	1, 21	26.20	< 0.001 ***		
Flowering field type : SNH	2, 16	1.26	0.311		
Staphylinid beetles					
Flowering field type	2, 16	2.44	0.119		0.23
SNH proportion	1, 16	0.55	0.468		

Chapter V: Do AES habitats benefit multi-taxa biodiversity?

Flowering field size	1, 16	4.69	0.046 *	-
Flowering field type : SNH proportion	2, 16	1.06	0.368	
Birds				
Flowering field type	2, 15	0.18	0.837	
SNH proportion	1, 15	1.53	0.236	0
Flowering field size	1, 15	0.03	0.869	
Flowering field type : SNH proportion	2, 15	0.43	0.658	
Multidiversity				
Flowering field type	2, 16	0.97	0.400	
SNH proportion	1, 16	0.05	0.826	0
Flowering field size	1, 16	0.28	0.601	
Flowering field type : SNH proportion	2, 16	0.59	0.565	
Multidiversity of pollinators				
Flowering field type	2, 15	0.85	0.448	
SNH proportion	1, 15	0.12	0.738	0
Flowering field size	1, 15	0.13	0.725	
Flowering field type : SNH proportion	2, 15	1.25	0.316	
Multidiversity of natural enemies				
Flowering field type	2, 16	1.60	0.232	
SNH proportion	1, 16	0.02	0.888	0.05
Flowering field size	1, 16	2.39	0.142	
Flowering field type : SNH proportion	2, 16	0.78	0.474	



Not all carabid beetles are predators – some species, genera and even whole subfamilies live on an exclusively granivorous diet. This *Amara similata* (Gyllenhal, 1810) is feeding on the seeds of the meadow foxtail (*Alopecurus pratensis* Linnaeus 1758) during the phase of milk ripening. Granivorous carabid beetles are often regarded as important weed control agents but might also prey on cereal or oilseed rape seeds and therefore be regarded as pests.

Chapter VI: The effects of AES habitats on predators in adjacent oilseed rape fields

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Abstract

1. Rising demands for agricultural products and high environmental costs of intensive agriculture reinforce the need for ecological replacements in agricultural management. In Europe, agri-environmental schemes (AES) are implemented to enhance species richness and provision of ecosystem services, but the effectiveness of different AES types and the spatial extent of possible beneficial effects are little understood. In this study we assessed the effects of different AES types on diversity, species traits and distance-decay functions of ground-dwelling predators in adjacent crop fields.

2. On 31 study sites with winter oilseed rape (OSR) adjacent to four types of AES differing in management intensity and habitat age we recorded ground-dwelling predators (carabid beetles, staphylinid beetles and spiders) during OSR growth from April to July. Effects of the AES on species richness, activity densities and different traits of these taxa were examined with transects of pitfall traps running along a continuous distance gradient from the AES across the habitat border into the OSR fields.

3. Ground-dwelling predator communities benefitted similarly from the different AES types. In adjacent OSR, activity densities, carabid species richness and the proportion of predatory carabid beetles declined from the field edge while mean body size increased. Adjacent AES increased the

proportion of predatory species and simultaneously decreased the proportion of granivorous or frugivorous species in adjacent OSR fields.

4. *Synthesis and applications.* Our results indicate a beneficial effect of adjacent agri-environmental schemes (AES) on ground-dwelling predators in oilseed rape (OSR), mostly irrespective of AES type and therefore management intensity and habitat age. The short-ranged distance decay effects on natural enemies in OSR underpin that a strategic spatial placement of AES in agricultural landscapes is required to maximise biological pest control. This could help replace anthropogenic input in modern agriculture and secure adequate yields.

Introduction

Driven by incessant human population growth and increasing food demands, modern agriculture has reached a crossroads: While the level of agricultural production needs to be maintained, the footprint of agriculture on the environment has to be minimized in order to increase resilience and maintain stability of agricultural systems (Foley *et al.* 2011). Ecological intensification in which anthropogenic input is replaced by biodiversity mediated ecosystem services is a promising approach to overcome this impasse (Bommarco, Kleijn & Potts 2013).

A commonly used method of ecological intensification is the establishment of semi-natural and low managed habitat patches (agri-environmental schemes (AES)) in the agricultural matrix to reduce pressure on biodiversity by providing places of refuge and increasing biodiversity mediated ecosystem functioning and agricultural productivity (Bommarco, Kleijn & Potts 2013; Ekroos *et al.* 2014). Recent ecological intensification policies in Central Europe focus on different AES (e.g. flowering fields, flower strips, hedgerows) and the conservation of existing semi-natural habitats (e.g. grasslands) in order to promote ecosystem functions (e.g. pest control) in adjacent arable fields but differ in implementation between (federal) states (Ekroos *et al.* 2014). However, although AES are highly subsidized, the extent of their potential beneficial effects on adjacent arable land is mainly based on expectations. In particular, direct comparisons of different AES types, quantitative distance decay functions of predator diversity in adjacent crop fields and species trait-related variation in the effectiveness of different AES are currently lacking.

From AES, natural enemies disperse into adjacent agricultural fields increasing biodiversity near the edge and transporting their functions into the adjacent ecosystem (Ries & Sisk 2004; Blitzer *et al.* 2012; Schneider *et al.* 2016). These spillover effects are bidirectional and directed from source habitats with high primary productivity to sink habitats with lower productivity and can be asymmetric due to productivity driven abundance differences (Tscharntke, Rand & Bianchi 2005; Rand, Tylianakis & Tscharntke 2006; Boetzl, Schneider & Krauss 2016). Although of high economic importance, only few studies have addressed the effects of spillover in agricultural landscapes and the extent and change of these effects with distance is widely unknown.

The promotion and conservation of biodiversity in agricultural landscapes is essential, as even highly intensified modern agriculture to some extent remains dependent on species-mediated services for obtaining sufficient yields (Tscharntke *et al.* 2012). Concerning pest control, diversity of predators is crucial as they differ in traits, consumption rates and pest preferences and predator diversity is believed to insure against environmental fluctuations and to increase pest control stability (Yachi & Loreau 1999; Williams *et al.* 2010; Rusch *et al.* 2015). Carabid beetles are among the most effective biocontrol agents - in enclosure experiments carabid beetles reduced emerging pollen beetles (*Meligethes aeneus*) and stem weevils (*Ceutorhynchus sp.*), two of the most important oilseed rape (OSR) pests, by up to 50 – 90 percent (Zaller *et al.* 2009; Dainese *et al.* 2017b). Apart from diet, body size is an important predictor for pest consumption as large species consume higher amounts of larger pests (Williams *et al.* 2010; Rusch *et al.* 2015). However, most large predatory species have limited dispersal abilities and thus low managed and perennial habitats are needed for the conservation of these natural enemies (Woodcock *et al.* 2012; Hanson *et al.* 2016). Increasing management intensity not only decreases biodiversity but harms beneficial taxa that serve as biocontrol agents (Gonthier *et al.* 2014). Apart from predator diversity, predator activity density is generally directly linked to pest abundance and pest control services (Kromp 1999; Haschek *et al.* 2012). With decreasing management intensity and increasing habitat age, AES should sustain larger populations as well as a higher diversity of dispersal limited predatory species and may act as source habitats for spillover of beneficial natural enemies.

With non-crop habitats holding a substantial proportion of the biodiversity in agricultural landscapes, spillover from non-crop habitats to crop fields and vice versa could be essential for biocontrol (Bianchi, Booij & Tschamntke 2006). However, little is known about how different taxa react to different types of AES and about the extent of spillover effects into adjacent intensive agricultural fields. In this study, we investigated the effects of different types of AES on the main ground-dwelling predator taxa carabid beetles, staphylinid beetles and spiders along a continuous distance gradient from the AES across the field edge into adjacent OSR fields. OSR is a major cash-crop in Central European agriculture and seriously affected by different agricultural pests (Bourke *et al.* 2014) yet biocontrol by parasitoids was weak in the study region in a previous study (Schneider *et al.* 2015). However, as many OSR pests are vulnerable to predation on the ground at certain phases in their life cycle, promoting ground-dwelling predator communities by adjacent AES could benefit OSR yields (Williams *et al.* 2010; Dainese *et al.* 2017b). Based on this framework, we tested the following main predictions:

- (i) Spillover from AES results in a decline of species richness and activity densities of ground-dwelling predators in adjacent OSR fields with increasing distance to the AES.
- (ii) Adjacent AES shape carabid beetle assemblages in OSR fields in respect of assemblage and trait composition due to spillover.
- (iii) AES which support old and relatively undisturbed habitats have stronger beneficial effects on ground-dwelling predators and further extending distance decay functions than annual and high-disturbed AES.
- (iv) AES which support old and relatively undisturbed habitats favour dispersal limited, large and predatory species regarded as beneficial for pest control in adjacent OSR fields.

Materials and methods

Study design

A total of 31 conventional winter OSR fields in the administrative districts Würzburg, Bad Kissingen, Main-Spessart, Schweinfurt and Haßberge (Germany, Bavaria, Lower Franconia, study region size ~ 2600 km²) were selected as study sites. On 27 of the study sites, one of four types of AES was adjacent to the OSR field (eight “KULAP new”, eight “KULAP old”, seven set-aside greenings, and four calcareous grasslands). The four remaining OSR fields were used as controls and were adjacent to crop fields. The minimum distance between two study sites was 2.1 km (Figure VI.1 A & Supporting Information Table VI.S1).

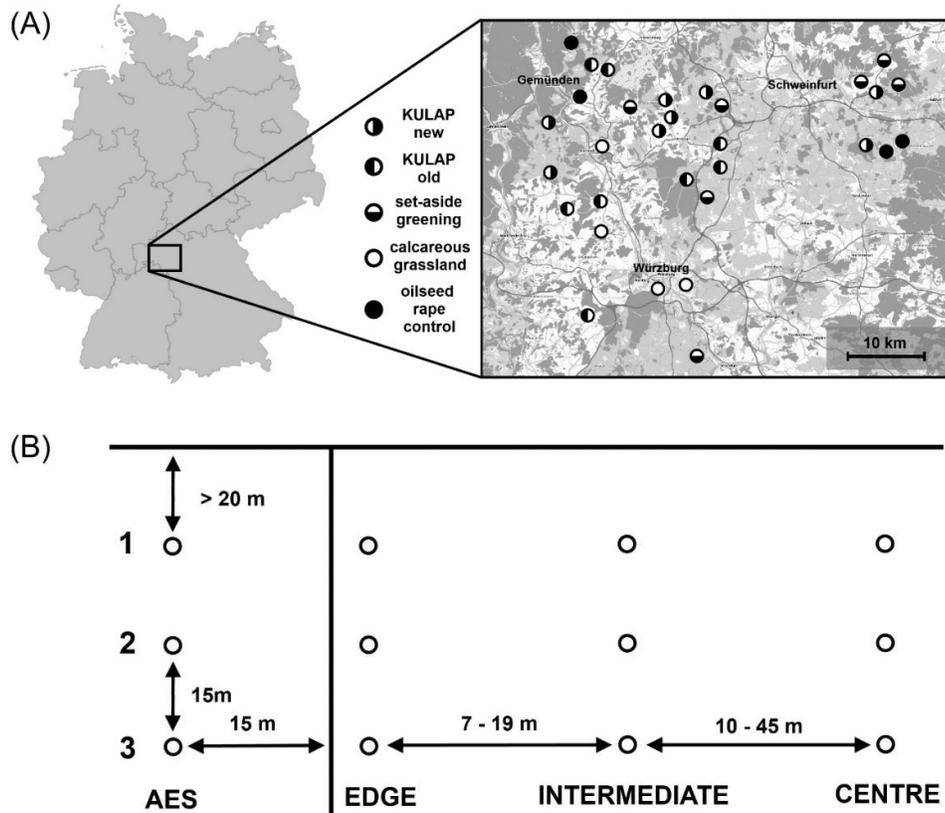


Figure VI.1 (A) Map showing the location of all study sites within the study area and AES type. Map modified after: © OpenStreetMap-contributors. (B) Sampling design on the study site level. Circles represent pitfall traps. Numbers on the left indicate transects, names on the bottom indicate used distance classes with distances. Right: oilseed rape field; left: agri-environmental scheme; solid lines: field edges.

The four different types of AES, (i) KULAP new, (ii) KULAP old, (iii) set-aside greenings and (iv) calcareous grasslands were characterized by different management and habitat age (Table VI.1): Management intensity decreased from (i) to (iv) while habitat age without severe disturbance increased simultaneously. While KULAP flowering fields are AES funded by the governmental “Kulturlandschaftsprogramm” (KULAP), set-aside greenings are ecological focus areas within the EU common agricultural policy (CAP). Calcareous grasslands are highly fragmented protected semi-natural habitats considered as biodiversity hotspots (van Swaay 2002).

Table VI.1: Differences in habitat age and management among the four different studied AES types.

	(i) KULAP new	(ii) KULAP old	(iii) set-aside greening	(iv) calcareous grassland
Habitat age	1 year	> 6 years	> 6 years	> 20 years
Years since last soil disturbance (ploughing)	1 year	1 year	> 6 years	> 20 years
Previous land use	Arable land	KULAP flowering field (5 years)	KULAP flowering field (5 years)	-
Management	none	none	Mulching above ground once a year after June	Grazing or mowing once a year after June
Vegetation	customary flower seed mixture; sown in the previous year	customary flower seed mixture; sown in the previous year	customary flower seed mixture sown > 6 years ago; strongly shaped by succession	semi-natural xerothermic grassland vegetation

Flower mixtures of KULAP fields are designed to benefit pollinators yet the tailoredness of vegetation composition is altered with succession and decreases from (i) to (iv). In the majority of the study sites, the AES was either directly adjacent to the OSR field (8 sites, 30 %) or separated through a narrow grassy field margin (12 sites, 44%). At the remaining 7 study sites, the AES were separated from the OSR fields by non-tarred dirt farm vehicle tracks.

The areas of the AES patches extended from 0.29 ha to 18.33 ha (Mean \pm SE: KULAP new: 1.32 \pm 0.38 ha; KULAP old: 1.05 \pm 0.30 ha; set-aside greening: 1.12 \pm 0.25 ha; calcareous grassland: 6.04 \pm 3.64 ha) while those of the adjacent OSR fields and the OSR controls ranged from 0.31 ha to 11.91 ha (Mean \pm SE: 3.18 \pm 0.43 ha; 1 ha = 0.01 km²; Supporting Information Table VI.S1).

We selected study sites along a gradient of semi-natural habitat (SNH) within a radius of 1km around the study site replicated in each study site type (in total ranging from 3.6 to 32.5 %).

Data collection

At each site, 3 transects of pitfall traps were set up between 30th March and 04th April and traps were activated on 05th/ 06th April 2016. In each transect, one trap was placed in the AES approximately at a distance of 15 m from the OSR field (at most sites approximately the centre of the AES) and three traps were placed inside the adjacent OSR field at three different distances (resulting in 360 pitfall traps over all sites). All transects were located 5 - 10 m (depending on field size) from the other transects and at least 20 m from other field edges to prevent lateral spillover effects. Transects were placed along perpendicular tractor tracks in order to maintain accessibility later in the season wherever possible (17 sites, 55 %). Otherwise, parallel tractor tracks were used (14 sites, 45 %) but transect distances were always kept. The pitfall traps in the OSR fields were placed always 1 m away from the tractor tracks. To generate a continuous distance gradient, trap distances in the OSR fields varied among sites. We applied four sets of distances replicated within study site types with three distance classes each: (I) 1 m + 8 m + 30 m, (II) 1 m + 10 m + 40 m, (III) 1m + 15 m + 55 m and (IV) 1 m + 20 m + 65 m (Figure VI.1 B, Supporting Information Table VI.S1).

As pitfall traps, we used conventional glass honey jars (height: 9 cm, diameter: 7.5 cm) filled with 200 ml 1:3 ethylene glycol (automobile antifreeze, H. Kerndl GmbH)-water-mixture with odourless detergent as preservative. Trap roofs (25 x 25 cm²; ~10 cm above the ground) were fabricated out of clear polycarbonate in order to avoid changes in light regimes.

Trapping started on 05th / 06th April and ended with the beginning of the crop harvest on 28th / 29th June. All 360 pitfall traps were emptied biweekly resulting in a total of 2160 pitfall trap samples. Due to field management and wild animals, we lost approximately 2.7 % (59 traps) of

all pitfall trap samples without significant bias towards study sites or trap positions and therefore regarded as negligible.

The trap samples were subsequently sorted for carabid beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Araneae & Opiliones). All individuals from these taxa were counted and preserved in 70% ethanol. All carabid beetles were identified to species level following Müller-Motzfeld (2006). Species traits (diet, wing shape and body size) were obtained from the online database ‘carabids.org’ (Homburg *et al.* 2014). Species lacking aerial dispersal ability (wingless or short winged) were considered as ‘wingless’. Moreover, species were divided into three body size classes: ‘small’ (< 6 mm), intermediate (6 – < 10 mm) and ‘large’ (≥ 10 mm) according to Winqvist *et al.* (2014).

Statistical analyses

All statistical analyses were performed in R 3.3.1 for Windows (R Development Core Team 2019).

For all analyses using carabid beetle species richness or assemblage composition, we pooled the pitfall trap samples in the same distance class within the three transects at each study site for each sampling interval and then pooled trap samples over all six sampling intervals to account for phenological shifts in the assemblages, reduce the influence of outliers and account for natural within-field differences due to microclimatic conditions (Williams *et al.* 2010; Kotze *et al.* 2011). For the analysis of activity densities, we calculated the individuals per trap over the whole sampling period. We first calculated the means of the corresponding pitfall trap samples in the three transects for each sampling interval and then the sum of these means over the whole sampling period in order to account for both occasional trap losses and phenological changes in activity densities throughout the season. The resulting value is henceforth referred to as activity density for better comprehensibility.

To investigate spillover of carabid beetles, we calculated the Bray-Curtis similarity between the carabid beetle assemblages in the AES and the carabid assemblages in the different distances to the field edge within the adjacent OSR fields using ‘vegdist’ from the vegan package (Oksanen *et al.* 2019). A higher Bray-Curtis similarity value indicates that carabid beetle assemblages are similar in species identity and proportions of single species.

To analyse the effects of adjacent AES type (including OSR control for the fields without adjacent AES) and position within the transect (distance to the AES) as well as their interaction within the OSR fields on the response variables carabid species richness, Bray-Curtis similarity, carabid beetle activity density, staphylinid beetle activity density and spider activity density we calculated linear mixed effects models (LMER) using ‘lmer’ from the package lme4 (Bates *et al.* 2015). The same analyses were conducted for the proportions of different carabid beetle traits (predatory species, wingless species and large species) and the community weighted mean body size of carabid beetles. As all response variables fit linear relations, no non-linear relations were tested. In all LMERs, study site ID was included as a random effect. Additionally, we compared all response variables among the four AES types with linear models (LM) using ‘lm’ only using trap samples from the AES. All LMs and LMERs were analysed using the command ‘anova’ (type II sums of squares, Kenward-Roger approximation of denominator degrees of freedom) from the package ‘lmerTest’ (Kuznetsova, Brockhoff & Christensen 2017) and subsequent Tukey-HSD posthoc tests (‘HSD.test’ command from the package agricolae (De Mendiburu 2016)). All models were checked for random distribution of residuals and homogeneity of variance and all models shown met the model assumptions. Activity densities as well as the proportions of wingless and omnivorous species were square root transformed to account for heteroscedasticity. All response variables were tested for spatial autocorrelation using the ‘Moran.I’ command from the package ape (Paradis, Claude & Strimmer 2004) but no spatial autocorrelation was detected. In additional LMERs, the effect of the different habitat border types (‘direct’, ‘grassy margin’ and ‘dirt farm vehicle tracks’) on all response variables was tested and as different distance sets were used, we also computed LMERs including ‘distance’ as random slope. Moreover, we tested all response variables for effects of the proportion of SNH in the surrounding of the study sites but

did not find any significant relations (results not shown). For visualization, all models were simplified using likelihood ratio tests and keeping only significant factors with $p < 0.05$. In the figures, we show the model predictions for the best fit calculated by using the 'predict' function with standard errors.

Results

During the six sampling intervals, a total of 62,552 carabid beetles from 119 species were caught on all sites (Supporting Information Table VI.S2, VI.S3 & VI.S4). Thereof, 47.7 % (29818 from 74 species) were predatory, 10.4 % (6488 from 6 species) were omnivorous and 42.0 % (26246 from 39 species) granivorous or frugivorous. Additionally, we trapped 52,778 staphylinid beetles and 48,805 spiders. Activity densities of all three taxa peaked towards the end of the sampling time in late June and therefore shortly prior to OSR harvest (Supporting Information Figure VI.S1).

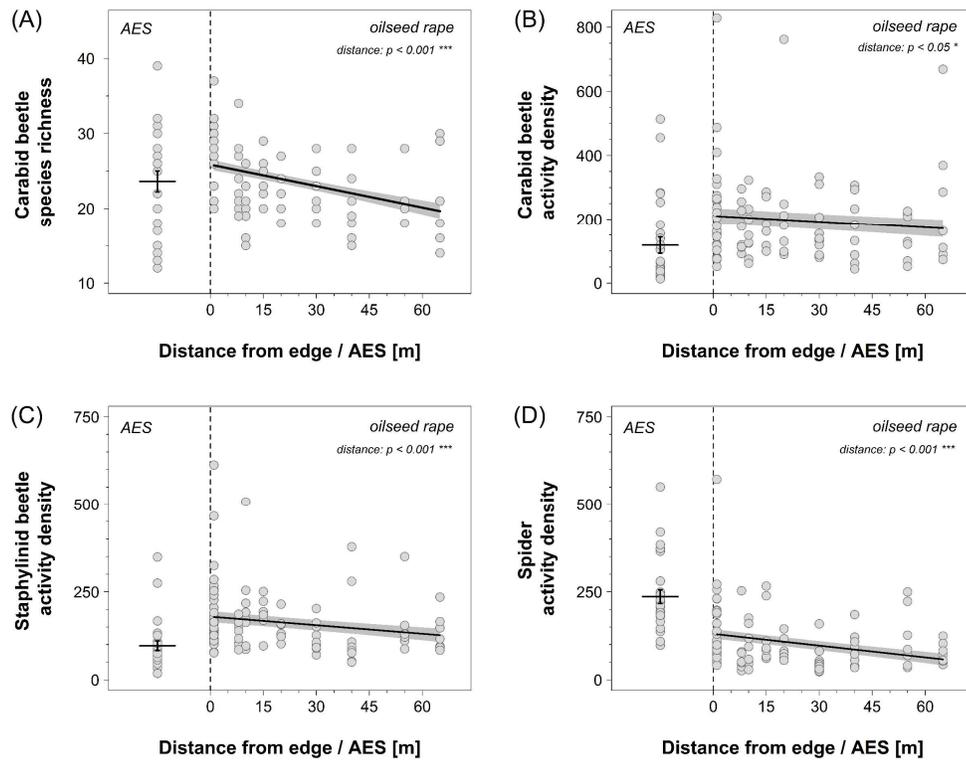


Figure VI.2 Carabid beetle species richness (A) and accumulated per trap activity densities of carabid beetles (B), staphylinid beetles (C) and spiders (D) in different distances to the field edge in oilseed rape fields and adjacent agri-environmental schemes (AES). AES: Mean \pm SE over all AES types; OSR: Solid line represents the best model fit including all significant factors with standard error; dashed line represents the field edge.

Table VI.2: Results obtained from linear mixed effects models (lmer) including a random intercept for 'study site ID' on ground-dwelling predator assemblage characteristics. d.f. = degrees of freedom (numerator, denominator); F & p-values obtained by type II sums of squares ANOVA with Kenward-Roger approximation; bold printing indicates significant p-values < 0.5.

Model	d.f.	F	p-value
carabid beetle species richness			
AES type	4,47	0.38	0.82
distance	1,61	24.7	< 0.001 ***
AES type * distance	4,61	0.7	0.593
carabid beetle activity density			
AES type	4,30	1.09	0.381
distance	1,58	4.21	0.045 *
AES type * distance	4,58	1.46	0.225
staphylinid beetle activity density			
AES type	4,35	0.71	0.589
distance	1,59	12.4	< 0.001 ***
AES type * distance	4,59	0.54	0.709
spider activity density			
AES type	4,31	0.7	0.618
distance	1,58	33.3	< 0.001 ***
AES type * distance	4,58	2.53	0.05 (*)
Bray-Curtis similarity			
AES type	3,29	5.85	0.003 **
distance	1,51	7.23	0.009 **
AES type * distance	3,51	0.24	0.868

Distance-decay functions of ground-dwelling predator richness and activity densities in OSR fields

We found clear distance decay effects on ground-dwelling predators in the OSR fields: Carabid beetle species richness declined from the edge towards the centre by 16 percent (Figure VI.2 A, Table VI.2) and the accumulated per trap activity densities of all three taxa decreased from the field edge towards the field centre (Figure VI.2 B - D, Table VI.2). This effect on activity densities was most pronounced in spiders (slope: -1.15, decrease \approx 56%) and weaker in staphylinid beetles (slope: -0.94, decrease \approx 33%) and carabid beetles (slope: -0.64, decrease \approx 20%). In spider activity density, there was also a trend towards an interaction of distance and adjacent AES type

caused by constant low activity densities in the OSR controls without any considerable decline with distance.

Distance-decay functions of carabid beetle traits in OSR fields

The percentage of predatory species in the carabid beetle assemblages of the OSR fields declined from the field edges to the field centres by 30% and was with approximately 52% near the edge in OSR fields adjacent to an AES nearly twice as high as in the OSR controls with approximately 28% near the edge (Figure VI.3 A, Table VI.3). The percentage of omnivorous species simultaneously more than doubled from 7.2 to 16.4 % from the field edges to the field centres (Figure VI.3 C, Table VI.3). We found no trend in the percentage of granivorous or frugivorous species with increasing distance from the field edge, however, the percentage of granivorous or frugivorous species in the OSR controls was nearly twice as high as in the OSR fields adjacent to an AES (Figure VI.3 E, Table VI.3). Community weighted mean body size of carabid beetles increased from the field edges towards the centres by roughly 0.5 mm (Figure VI.3 B, Table VI.3). Similarly the proportion of large species increased in all OSR fields adjacent to an AES from the field edge to the field centre by on average 6% but decreased in the OSR controls by 10 % while the proportion of small species decreased in all OSR fields from the field edge towards the centre by 28% (Figure VI.3 D & F, Table VI.3). We found no effects on intermediate sized species or wing shape within the carabid beetle assemblages in respect of distance to the field edge or adjacent habitat type (Table VI.3).

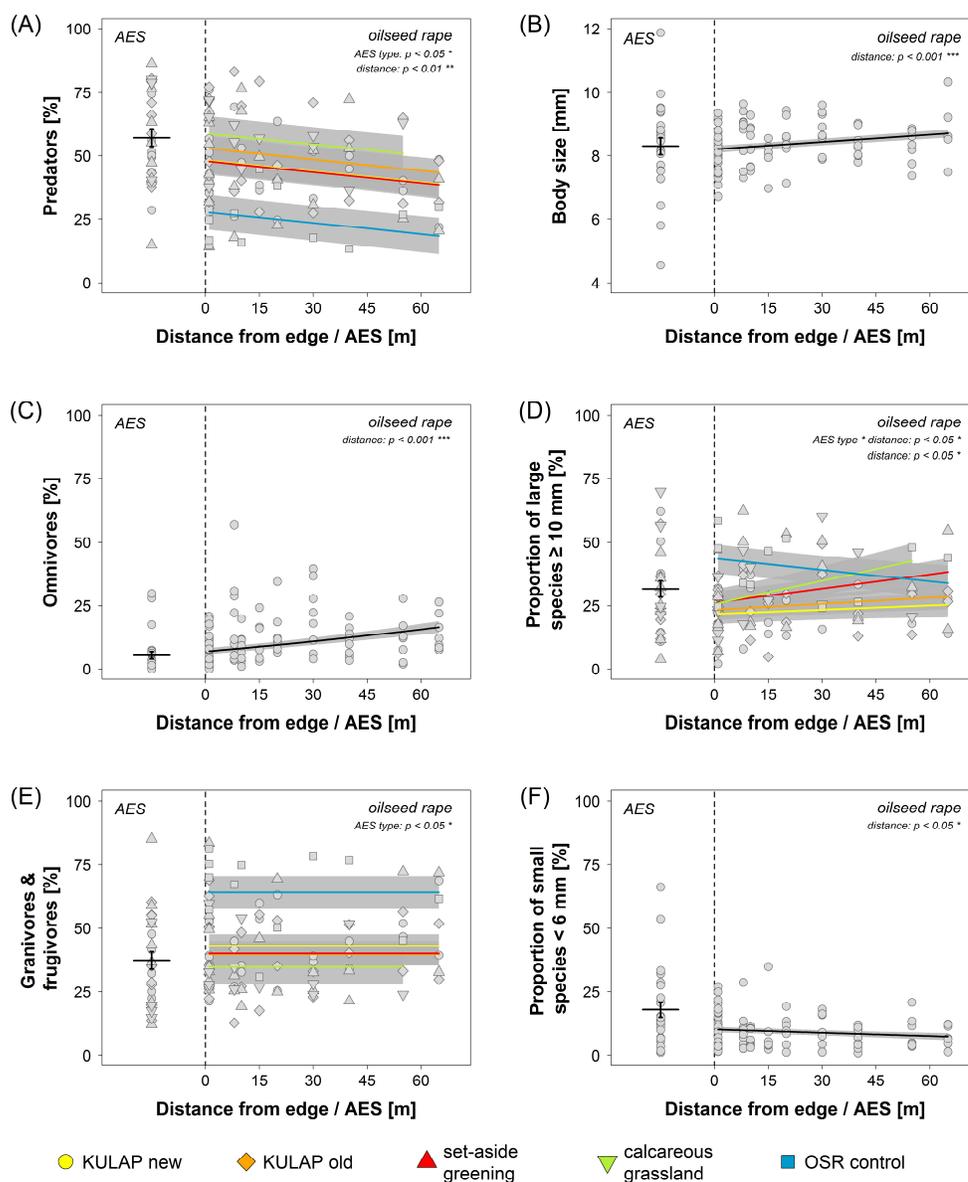


Figure VI.3 Proportions of the three different dietary trait groups predators (A), omnivores (C) and granivores or frugivores (E) as well as community weighted mean body size (B) and the proportions of large (D) and small species (F) within carabid beetle assemblages in different distances to the field edge in oilseed rape fields and adjacent agri-environmental schemes (AES). AES: Mean \pm SE over all AES types; OSR: Solid line represents the best model fit including all significant factors with standard error; dashed line represents the field edge. Colours and symbols in (A), (D) and (E) explained below. Predictions for KULAP new in (A) and KULAP old in (E) are partly hidden behind the predictions for set-aside greenings.

Table VI.3: Results obtained from linear mixed effects models (lmer) including a random intercept for ‘study site ID’ on carabid beetle species traits. d.f. = degrees of freedom (numerator, denominator); F & p-values obtained by type II sums of squares ANOVA with Kenward-Roger approximation; bold printing indicates significant p-values < 0.5.

Model	d.f.	F	p-value
proportion of predatory species			
AES type	4,31	2.8	0.042 *
distance	1,58	11	0.002 **
AES type * distance	4,58	0.34	0.848
proportion of omnivorous species			
AES type	4,35	0.88	0.488
distance	1,59	21.7	< 0.001 ***
AES type * distance	4,59	1.7	0.162
proportion of granivorous or frugivorous species			
AES type	4,34	2.72	0.046 *
distance	1,59	0.21	0.652
AES type * distance	4,58	0.52	0.721
proportion of wingless species			
AES type	4,43	0.21	0.933
distance	1,60	0.13	0.724
AES type * distance	4,60	1	0.416
proportion of winged species			
AES type	4,31	1.25	0.311
distance	1,58	0.02	0.881
AES type * distance	4,58	0.58	0.679
community weighted mean body size			
AES type	4,32	1.71	0.172
distance	1,58	20.2	< 0.001 ***
AES type * distance	4,58	1.35	0.263
proportion of small species < 6 mm			
AES type	4,35	1.2	0.33
distance	1,59	4.24	0.044 *
AES type * distance	4,59	0.22	0.927
proportion of intermediate sized species (6 – 10 mm)			
AES type	4,32	1.2	0.33
distance	1,58	0.89	0.35
AES type * distance	4,58	1.77	0.146
proportion of large species ≥ 10 mm			
AES type	4,32	2.22	0.089 (*)
distance	1,58	5.65	0.021 *
AES type * distance	4,58	2.74	0.037 *

We did not detect detrimental effects of different habitat border types on any of the response variables – on the contrary, OSR fields with grassy margins or dirt farm vehicle tracks between AES and OSR field even had a higher proportion of predatory species than sites with direct adjacency (and therefore lower proportion of granivorous or frugivorous species; Supporting Information Table VI.S5), while in all models all other observed effects remained the same. We did not obtain essentially different results from models containing an additional random slope on ‘distance’ compared to the models only containing random intercepts for ‘study site’ (Supporting Information Table VI.S6).

Effects of different AES on species richness, activity densities, traits and assemblage similarity

Between the assemblages in the different AES types, we found only small differences: Carabid beetle species richness was highest in the young KULAP flowering fields and roughly one third lower in set-aside greenings and calcareous grasslands but did not significantly differ from old KULAP flowering fields (LM: $F_{3,23} = 4.67$, $p = 0.011$). Activity densities of carabid beetles tended to be higher in young KULAP flowering fields (LM: $F_{3,23} = 2.86$, $p = 0.059$) and staphylinid beetles were most abundant in old KULAP flowering fields (LM: $F_{3,23} = 3.91$, $p = 0.022$) while in spiders no significant differences were found (LM: $F_{3,23} = 1.61$, $p = 0.215$). None of the examined carabid beetle traits differed between AES types – specifically we did not find any significant differences in the proportions of predatory (LM: $F_{3,23} = 1.01$, $p = 0.406$), large (LM: $F_{3,23} = 1.07$, $p = 0.379$) or wingless (LM: $F_{3,23} = 2.00$, $p = 0.142$) species or in community weighted mean body size (LM: $F_{3,23} = 0.68$, $p = 0.575$).

Bray-Curtis similarities between carabid beetle assemblages in the OSR fields and the adjacent AES peaked at the field edges with 0.15 – 0.38 depending on the adjacent AES type. Carabid beetle assemblage similarity subsequently decreased towards the field centres. The similarity between carabid beetle assemblages in KULAP flowering fields and adjacent OSR fields was generally higher than the similarity between carabid beetle assemblages in set-aside greenings or calcareous grasslands and adjacent OSR fields (Figure VI.4, Table VI.2).

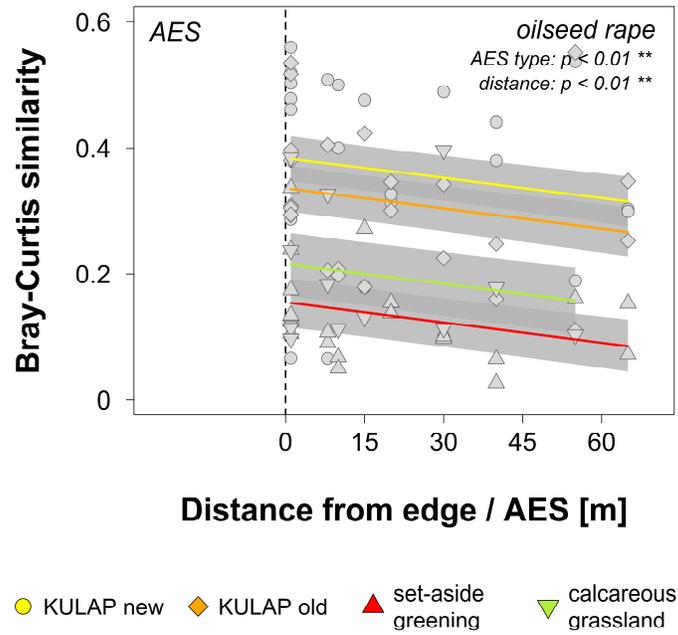


Figure VI.4 Bray-Curtis similarity between the carabid beetle assemblages in different distances within the oilseed rape fields and carabid assemblages in the adjacent agri-environmental scheme (AES). Solid line represents the best model fit including all significant factors with standard error; dashed line represents the field edge. Colours and symbols explained below.

Discussion

In this study, we investigated the effects of different types of AES on biocontrol agents in adjacent OSR fields. We found beneficial edge effects on ground-dwelling predator activity densities, species richness of carabid beetles and the proportion of predatory carabid species with a distance decay into the OSR fields. In contrast, carabid beetle body size increased with increasing distance to the field edge. The presence of an adjacent AES approximately doubled the proportion of predatory carabid beetles while it decreased the proportion of granivorous or frugivorous carabid species in OSR fields. These effects were driven by spillover as similarity between carabid beetle assemblages in the AES and carabid beetle assemblages in the OSR fields decreased with increasing distance to the field edge. Our results are important for the assessment of different AES and the implementation of management concepts for agricultural landscapes that aim for enhanced predator richness and activity densities in adjacent crop fields.

Carabid beetle species richness decreased from the OSR field edges towards the centres. Although OSR is regarded as beneficial to many species of carabid beetles and OSR fields generally have a comparably high species richness, the AES supported different carabid beetle assemblages due to altered environmental conditions in comparison to the OSR fields (Williams *et al.* 2010; Eyre, Luff & Leifert 2013; Marrec *et al.* 2015). As a result of overlapping different assemblages in AES and adjacent OSR, species richness peaked near the field edge – a pattern driven by spillover and described as ‘reciprocal positive edge response’ by Rand, Tylianakis and Tschamtkke (2006). In accordance with our results, it has been shown that the amount of edges and adjacent grasslands or flowering strips increase carabid species richness in arable fields (Purtauf *et al.* 2005; Batáry *et al.* 2012). We showed that this effect is characterized by a distance decay which potentially affects biocontrol as species richness is essential to buffer fluctuations in pest control (Yachi & Loreau 1999; Williams *et al.* 2010).

Activity densities of all three taxa strongly declined from field edges towards the centres of the OSR fields. Perennial semi-natural habitats as well as newly implemented AES are important for many predatory taxa as they allow breeding, overwintering and provide shelter and season-long

food resources as they remain relatively undisturbed (Tschamtkke, Rand & Bianchi 2005). Therefore, AES and other semi-natural habitats may sustain predator banks in agricultural landscapes. In accordance with our results, it was shown that adjacent grasslands positively affect carabid beetles and spiders and even annual flower strips increase activity densities of natural enemies and subsequently reduce pest densities and plant damage and increase yields in adjacent winter wheat fields (Batáry *et al.* 2012; Tschumi *et al.* 2015; Tschumi *et al.* 2016a). Activity densities of ground-dwelling predators have been found to be directly linked to pest control services (Kromp 1999; Dainese *et al.* 2017b). As these edge effects on predator activity densities were short ranged, we expect the potential for adjacent AES to enhance biocontrol in OSR to be largest near the field edge. Importantly, we characterize for the first time quantitative distance-decay functions which provide the basis for spatial landscape models that could predict the biocontrol potential of AES depending on spatial arrangement, type and adjacent crop.

The magnitude of the distance decay of activity densities was taxon dependent: It was most prominent in spiders and less strong in staphylinid beetles and carabid beetles. In spiders, other factors such as vegetation structure could be confounded and might interfere with habitat management as many spiders use higher vegetation levels and only move to the ground occasionally. This emphasizes the need of multi-taxa approaches as different taxonomic groups although carrying similar ecosystem functions may react differently to changes in management intensity and habitat heterogeneity (Batáry *et al.* 2012; Cameron & Leather 2012).

Age and management intensity of AES did not affect ground-dwelling predator communities as much as we expected and all AES types were mostly equally beneficial for maintaining ground-dwelling predators in agricultural landscapes. Ground-dwelling predators had rather similar activity densities among all AES types and we found no differences in the distribution of carabid beetle traits. However, carabid beetle assemblage composition was directly affected by AES type: Set aside greenings and semi-natural calcareous grasslands hosted carabid beetle assemblages less similar to those in the adjacent OSR fields and more diverse than those in the younger KULAP flowering fields. The more intensive management in KULAP flowering fields probably created

similar conditions as found in crop fields which ultimately resulted in a more similar assemblage composition. Carabid beetle richness was previously shown to be positively related to disturbance and early succession stages due to an increased habitat heterogeneity allowing both generalist and specialist species to persist (Dahms *et al.* 2010; Barber *et al.* 2017). However, similarity between the carabid beetle assemblages of the OSR fields and adjacent AES was rather low even near the field edges indicating considerable differences in assemblage composition. Moreover, a spillover-driven distance decay from the AES towards the OSR fields in assemblage composition similarity was evident. AES therefore benefit ground-dwelling predators mostly irrespective of habitat age and management intensity.

Frequent disturbances shift carabid beetle assemblages to more generalist, omnivore and mobile species, while specialized, predominantly predatory and dispersal limited species which are important biocontrol agents depend on low disturbance levels and consistent conditions as provided in AES habitats (Gobbi & Fontaneto 2008; Cardarelli & Bogliani 2014; Barber *et al.* 2017). The presence of an AES roughly doubled the proportion of predatory species in adjacent OSR fields irrespective of AES type. However, this effect has to be interpreted with care due to the lower sample size of OSR controls in our study design. The proportion of predatory species decreased with distance to the field edge indicating a beneficial role of AES for pest control in adjacent crops. Similarly, Sutter *et al.* (2018) showed that activity densities of predatory ground beetles increase with the proportion of ecological focus areas in the landscape, yet, in contrast to our results this effect was not dependent on direct adjacency and a distance gradient was not measured. The proportion of predatory species was also elevated if the AES was separated from the OSR field by a grassy margin or dirt farm vehicle tracks, indicating an additional effect of these perennial undisturbed structures for predator banks. A considerable percentage of the carabid beetles found were granivorous or frugivorous, which is regarded as beneficial for within field weed control by an increasing number of studies (Bohan *et al.* 2011; Labruyere *et al.* 2016) but may also affect OSR yields negatively as some species are known to feed on OSR seeds (Williams *et al.* 2010). Adjacent AES roughly cut the percentage of granivorous or frugivorous carabid beetles by half. Only small percentages of the carabid assemblages in both AES and OSR

fields consisted of dispersal limited species as management regimes in the AES could still be too intensive for these often large and predatory species. Carabid body size and the proportion of large species decreased near the habitat edge while the proportion of small species increased. Larger, more mobile species seemed to disperse further into the oilseed rape fields from adjacent AES than smaller species while in the OSR controls their percentage was decreasing towards the field centres. In accordance to our findings, Barber *et al.* (2017) showed that young grassland remnants were mainly beneficial to small species. While carabid beetle body size is an important predictor for pest control services as it directly relates to pest consumption rates (Rusch *et al.* 2015), the distribution of body sizes within an assemblage ensures biocontrol due to size-dependent prey preferences and resulting complementarity among predators (Williams *et al.* 2010). Habitats that offer both, a relatively high percentage of effective, large predators and a good distribution of body-sizes of predators to cover a wide range of pest species are likely to be ideal.

Conclusions

We showed that AES enhance ground-dwelling predator communities and beneficial traits in adjacent oilseed rape fields independent of SNH proportion in the surrounding landscape. In the context of increasing demands for agricultural products and simultaneously increasing depletion of natural resources, AES as part of ecological intensification policies could therefore help replace anthropogenic inputs in modern agroecosystems. As the beneficial effects on biocontrol agents underlie a strong distance decay and are relatively short ranged, small field sizes or AES strips inside fields to create a dense non-crop - crop interface in the landscape as suggested by Rusch *et al.* (2013) and Ekroos *et al.* (2014) would be recommended. This would also ensure the provision of sufficient amounts of source habitat for effective predator spillover and help maintain biodiversity in agricultural landscapes (Ekroos *et al.* 2014; Tschamntke *et al.* 2016). Additionally, as perennial predators use arable fields only temporarily as these fields undergo intensive management after harvest, one major benefit of adjacent AES is the provision of refuge and

overwintering sites for ground-dwelling predators after harvest and thereby also predator banks for a rapid reinvasion of adjacent arable lands in the next season (Tscharntke, Rand & Bianchi 2005; Williams *et al.* 2010). Our results underpin that the implementation of management concepts for agricultural landscapes need to take into account the spatial arrangement of AES. Landscape models that use quantitative distance-decay function to predict biological pest control potential in crop fields could support decision making of farmers. Governmental subsidies adapted to such spatial cost-benefit analyses could further improve the implementation of effective AES policies. In this way, a strategic placement of multiannual AES in agricultural landscapes has the potential to contribute to ecological intensification via enhancing and ensuring natural pest control.

Acknowledgements

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Supplementary material VI

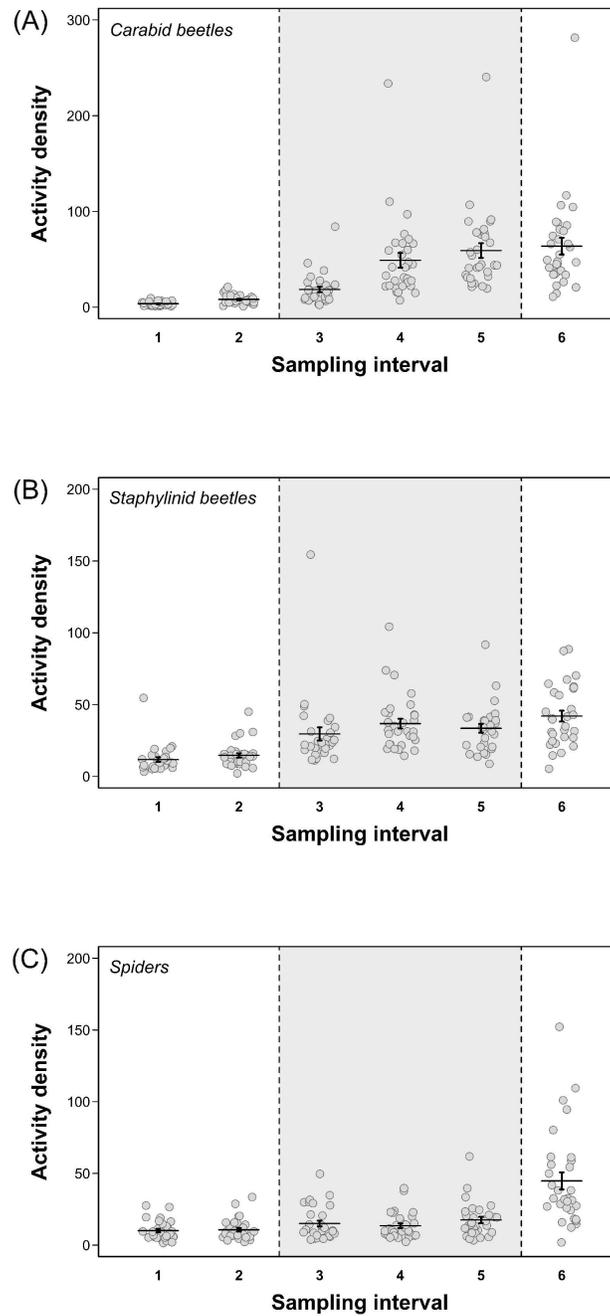


Figure VI.S1 Overall per trap and per site activity densities of carabid beetles (A), staphylinid beetles (B) and spiders (C) for the six sampling intervals with mean and standard error. Grey background between the dashed lines represents roughly oilseed rape flowering in the study

Chapter VI: The effects of AES habitats on predators in adjacent oilseed rape fields

Table VI.S1: Location of the study sites with type of the adjacent agri-environmental scheme (AES type), its size and the distance set used in the adjacent oilseed rape field.

Site ID	Nearest village	Administrative district	AES type	GPS (WGS 84)	Area AES [ha]	Distance set used
01_REU	Reuchelheim	Main-Spessart	KULAP new	49.994097N 9.913864E	1.5	II
02_BUE	Büchold	Main-Spessart	KULAP new	50.010878N 9.945164E	2.92	IV
03_WS1	Waldsachsen	Schweinfurt	KULAP new	50.041283N 10.371989E	1.67	III
04_SHW	Schwebenried	Main-Spessart	KULAP new	50.03625N 10.013122E	3	I
05_WIE	Wiesenfeld	Main-Spessart	KULAP new	49.995194N 9.685569E	0.29	I
06_STE	Steinfeld	Main-Spessart	KULAP new	49.941772N 9.678022E	0.31	III
07_GAU	Gauschach	Bad Kissingen	KULAP new	50.03565N 9.927058E	0.53	II
08_DUR	Dürrfeld	Schweinfurt	KULAP new	49.969153N 10.352558E	0.32	IV
09_ZEL	Zellingen	Main-Spessart	KULAP old	49.895914N 9.796075E	2.01	I
10_BIL	Billingshausen	Main-Spessart	KULAP old	49.877894N 9.720292E	2.07	III
11_RIE	Rieden	Würzburg	KULAP old	49.934694N 10.031019E	1.77	II
12_OBA	Oberaltertheim	Würzburg	KULAP old	49.735775N 9.777983E	2.07	IV
13_MUL	Mühlhausen	Schweinfurt	KULAP old	49.96405N 10.050228E	0.25	III
14_HOL	Höllrich	Main-Spessart	KULAP old	50.070453N 9.794578E	0.19	II
15_WEY	Weyersfeld	Main-Spessart	KULAP old	50.081411N 9.771431E	0.44	IV
16_GRA	Gramschatz	Würzburg	KULAP old	49.924433N 9.961481E	0.31	I
17_BUR	Bühler	Main-Spessart	set-aside greening	50.022803N 9.863192E	1.49	II
18_ERB	Erbshausen	Würzburg	set-aside greening	49.906492N 10.011397E	1.52	III
19_WS2	Waldsachsen	Schweinfurt	set-aside greening	50.054467N 10.352353E	1.39	IV
20_BUC	Buch	Haßberge	set-aside greening	50.057131N 10.421064E	2.38	I
21_DAS	Darstadt	Würzburg	set-aside greening	49.677386N 10.005922E	0.69	I
22_VAS	Vasbühl	Schweinfurt	set-aside greening	50.033525N 10.054167E	0.73	II
23_ABF	Abersfeld	Schweinfurt	set-aside greening	50.083306N 10.399783E	0.47	IV
24_BLO	Würzburg	Würzburg	calcareous grassland	49.761483N 9.923436E	4.55	III
25_KAS	Karlstadt	Main-Spessart	calcareous grassland	49.974089N 9.792319E	0.81	IV
26_LEI	Leinach	Würzburg	calcareous grassland	49.851717N 9.801561E	0.46	II
27_MAW	Gerbrunn	Würzburg	calcareous grassland	49.76735N 10.000133E	18.33	IV
28_ADE	Adelsberg	Main-Spessart	oilseed rape control	50.032794N 9.743556E	-	IV
29_SHF	Schonderfeld	Main-Spessart	oilseed rape control	50.102178N 9.726753E	-	I
30_DAM	Dampfach	Haßberge	oilseed rape control	49.984758N 10.440328E	-	III
31_DON	Donnersdorf	Schweinfurt	oilseed rape control	49.963361N 10.407189E	-	II

Distance sets: We applied four sets of distances with three distance classes each: (I) 1 m + 8 m + 30 m, (II) 1 m + 10 m + 40 m, (III) 1m + 15 m + 55 m and (IV) 1 m + 20 m + 65 m .At the eight sites with OSR fields adjacent to the same type of AES, each set of distances was applied twice. In the OSR control fields, each set of distances was applied once. In the OSR fields adjacent to calcareous grasslands, each set of distances was applied once but the distance set (II) was applied twice replacing the distance set (IV) due to the small size of the adjacent OSR field. In the OSR fields adjacent to set-aside greenings, the distance set (III) was only applied once as one site had to be excluded from the study because of a change in crops.

Table VI.S2: Carabid species richness and number of individuals in the different habitats over the full sampling period.

Type	adjacent to	N	Individuals	species
KULAP new	-	8	3841	59
KULAP old	-	8	4498	72
set-aside greening	-	7	979	49
calcareous grassland	-	4	379	42
AES total	-	27	9697	89
oilseed rape field	KULAP new	8	10079	67
oilseed rape field	KULAP old	8	16154	81
oilseed rape field	set-aside greening	7	10023	67
oilseed rape field	calcareous grassland	4	8565	57
oilseed rape field	- (control)	4	8034	68
oilseed rape total	-	31	52855	104
Total	-	31	62552	119

Table VI.S3: List of species and their presence in the different habitat types.

Species	oilseed rape field	KULAP new	KULAP old	set-aside greening	calcareous grassland
<i>Abax parallelepipedus</i>	9	1	3	3	3
<i>Abax parallelus</i>	5				
<i>Acupalpus interstitialis</i>	3		2		
<i>Acupalpus meridianus</i>	61	4	32		
<i>Agonum micans</i>	2				
<i>Agonum muelleri</i>	13				
<i>Agonum sexpunctatum</i>	1				
<i>Amara aenea</i>	232	86	57	19	3
<i>Amara apricaria</i>	1				
<i>Amara aulica</i>	10	8	31	5	
<i>Amara bifrons</i>		5	2		
<i>Amara communis</i>	1		2	1	
<i>Amara consularis</i>	35	9	38		
<i>Amara convexior</i>	6	1	15	27	3
<i>Amara eurynota</i>	7	1	14		
<i>Amara familiaris</i>	87	9	29	4	2
<i>Amara littorea</i>	26		4		2
<i>Amara lucida</i>				1	1
<i>Amara lunicollis</i>	4			5	1
<i>Amara montivaga</i>	12	9	2		2
<i>Amara ovata</i>	14320	170	139	22	3
<i>Amara plebeja</i>	3			1	
<i>Amara sabulosa</i>			2		
<i>Amara similata</i>	1695	122	28	4	
<i>Amara strenua</i>				2	
<i>Anchomenus dorsalis</i>	12191	307	91	3	2
<i>Anisodactylus binotatus</i>	161	14	24	5	
<i>Asaphidion flavipes</i>	33				
<i>Badister bullatus</i>	90	13	7	30	2
<i>Badister lacertosus</i>	4			8	
<i>Badister sodalis</i>	51	1	3	3	2
<i>Bembidion guttula</i>	2				
<i>Bembidion lampros</i>	509	71	90		2
<i>Bembidion lunulatum</i>	173	4			
<i>Bembidion mannerheimii</i>			1		
<i>Bembidion obtusum</i>	1088	66	59	56	
<i>Bembidion properans</i>	6	7	7		
<i>Bembidion quadrimaculatum</i>	4	1	1		
<i>Bembidion tetracolum</i>	1				
<i>Brachinus crepitans</i>	3586	1270	2187	252	102
<i>Brachinus explodens</i>	564	75	23	8	10
<i>Bradycellus harpalinus</i>			2		
<i>Calathus ambiguus</i>	6				
<i>Calathus cinctus</i>	25				
<i>Calathus erratus</i>	2				
<i>Calathus fuscipes</i>	154	8	2		4
<i>Calosoma inquisitor</i>	3				
<i>Carabus auratus</i>	1				
<i>Carabus cancellatus</i>					1
<i>Carabus convexus</i>	1				
<i>Carabus coriaceus</i>				2	
<i>Carabus granulatus</i>			1		
<i>Carabus nemoralis</i>	2				
<i>Carabus ulrichii</i>	1	1			
<i>Carabus violaceus</i>	2				
<i>Cicindela campestris</i>		5	1		
<i>Clivina fossor</i>	133	2	14	8	
<i>Demetrias atricapillus</i>	7				

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<i>Diachromus germanus</i>	1		1		
<i>Harpalus affinis</i>	3746	226	560	103	2
<i>Harpalus atratus</i>	45	1	1		2
<i>Harpalus dimidiatus</i>	390	108	168	53	25
<i>Harpalus distinguendus</i>	921	302	188	1	
<i>Harpalus honestus</i>	2				
<i>Harpalus laevipes</i>	1				
<i>Harpalus latus</i>	16	5	10	6	2
<i>Harpalus luteicornis</i>	102	8	37	120	
<i>Harpalus pumilus</i>			1		
<i>Harpalus rubripes</i>	40	11	4	1	16
<i>Harpalus rufipes</i>	509	93	74	3	5
<i>Harpalus serripes</i>	6		1		
<i>Harpalus signaticornis</i>	351	9	152		
<i>Harpalus subcylindricus</i>	5		1	16	13
<i>Harpalus tardus</i>	33	2			1
<i>Leistus ferrugineus</i>	16	3	3		
<i>Leistus rufomarginatus</i>	1				
<i>Leistus spinibarbis</i>	7				
<i>Limodromus assimilis</i>	35		2		
<i>Loricera pilicornis</i>	93	4			
<i>Microlestes maurus</i>	115	21	12	41	26
<i>Microlestes minutulus</i>	58	17	14	19	11
<i>Molops elatus</i>	2				18
<i>Molops piceus</i>	6				
<i>Nebria brevicollis</i>	187	7	9	1	
<i>Nebria salina</i>	1952	5	18		45
<i>Notiophilus aestuans</i>	73	5	2		
<i>Notiophilus biguttatus</i>	684	25	21		1
<i>Notiophilus germyni</i>	21	3	3		1
<i>Notiophilus palustris</i>	21	1	3	5	1
<i>Ophonus ardosiacus</i>	13	38	51	9	1
<i>Ophonus azureus</i>	44	49	33	6	
<i>Ophonus laticollis</i>	1				
<i>Ophonus rupicola</i>			1		
<i>Panagaeus bipustulatus</i>	7			4	10
<i>Panagaeus cruxmajor</i>	2				
<i>Paradromius linearis</i>			2	1	1
<i>Pedius longicollis</i>	7	4		2	
<i>Philorhizus notatus</i>	1				
<i>Poecilus cupreus</i>	5862	449	41	6	3
<i>Poecilus lepidus</i>	1				
<i>Poecilus versicolor</i>	10	23	5	2	
<i>Polistichus connexus</i>	5	1		12	1
<i>Pterostichus anthracinus</i>	3				
<i>Pterostichus macer</i>	32	20	19	28	7
<i>Pterostichus madidus</i>					5
<i>Pterostichus melanarius</i>	1447	105	53	17	3
<i>Pterostichus melas</i>	6		19		
<i>Pterostichus niger</i>			2		
<i>Pterostichus nigrita</i>	2				
<i>Pterostichus oblongopunctatus</i>	11				
<i>Pterostichus ovoideus</i>	11			8	
<i>Pterostichus strenuus</i>	24		17	1	
<i>Pterostichus vernalis</i>	105	3	1	8	
<i>Stomis pumicatus</i>	14		5		
<i>Syntomus truncatellus</i>	8	1	1	36	6
<i>Tachys bistriatus</i>	16	2	3		
<i>Trechoblemus micros</i>	19		1		
<i>Trechus quadristriatus</i>	430	20	46	1	28
<i>Zabrus tenebrioides</i>	2				

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Table VI.S4: Species list including species traits (diet, dispersal ability, mean body size and body size group) according to carabids.org (Homburg *et al.* 2014). Body size group: small < 6mm, intermediate 6 - < 10 mm, large ≥ 10 mm.

Species	diet	dispersal ability	mean body size [mm]	body size group
<i>Abax parallelepipedus</i>	predatory	wingless	19	large
<i>Abax parallelus</i>	predatory	wingless	15.5	large
<i>Acupalpus interstitialis</i>	omnivorous	winged	2.5	small
<i>Acupalpus meridianus</i>	omnivorous	winged	3.5	small
<i>Agonum micans</i>	predatory	winged	6	intermediate
<i>Agonum muelleri</i>	predatory	winged	7.5	intermediate
<i>Agonum sexpunctatum</i>	predatory	winged	7.5	intermediate
<i>Amara aenea</i>	granivorous / frugivorous	winged	7	intermediate
<i>Amara apricaria</i>	granivorous / frugivorous	winged	7.5	intermediate
<i>Amara aulica</i>	granivorous / frugivorous	winged	12.5	large
<i>Amara bifrons</i>	granivorous / frugivorous	winged	6	intermediate
<i>Amara communis</i>	granivorous / frugivorous	winged	6	intermediate
<i>Amara consularis</i>	granivorous / frugivorous	winged	8	intermediate
<i>Amara convexior</i>	granivorous / frugivorous	winged	8	intermediate
<i>Amara eurynota</i>	granivorous / frugivorous	winged	11	large
<i>Amara familiaris</i>	granivorous / frugivorous	winged	7	intermediate
<i>Amara littorea</i>	granivorous / frugivorous	winged	7.5	intermediate
<i>Amara lucida</i>	granivorous / frugivorous	winged	5	small
<i>Amara lunicollis</i>	granivorous / frugivorous	winged	7.5	intermediate
<i>Amara montivaga</i>	granivorous / frugivorous	winged	8	intermediate
<i>Amara ovata</i>	granivorous / frugivorous	winged	8.5	intermediate
<i>Amara plebeja</i>	granivorous / frugivorous	winged	7	intermediate
<i>Amara sabulosa</i>	granivorous / frugivorous	winged	5.5	small
<i>Amara similata</i>	granivorous / frugivorous	winged	8.5	intermediate
<i>Amara strenua</i>	granivorous / frugivorous	winged	9	intermediate
<i>Anchomenus dorsalis</i>	predatory	winged	6.5	intermediate
<i>Anisodactylus binotatus</i>	granivorous / frugivorous	winged	10.5	large
<i>Asaphidion flavipes</i>	predatory	winged	3.5	small
<i>Badister bullatus</i>	predatory	winged	5	small
<i>Badister lacertosus</i>	predatory	winged	6.5	intermediate
<i>Badister sodalis</i>	predatory	dimorphic	3.5	small
<i>Bembidion guttula</i>	predatory	dimorphic	2.5	small
<i>Bembidion lampros</i>	predatory	dimorphic	3	small
<i>Bembidion lunulatum</i>	predatory	winged	3.5	small
<i>Bembidion mannerheimii</i>	predatory	dimorphic	2.5	small
<i>Bembidion obtusum</i>	predatory	dimorphic	2.5	small
<i>Bembidion properans</i>	predatory	dimorphic	3.5	small
<i>Bembidion quadrimaculatum</i>	predatory	winged	2.5	small
<i>Bembidion tetracolum</i>	predatory	dimorphic	5	small
<i>Brachinus crepitans</i>	predatory	winged	8	intermediate
<i>Brachinus explodens</i>	predatory	winged	5.5	small
<i>Bradycellus harpalinus</i>	omnivorous	winged	4	small
<i>Calathus ambiguus</i>	predatory	winged	10	large
<i>Calathus cinctus</i>	predatory	dimorphic	7.5	intermediate
<i>Calathus erratus</i>	predatory	dimorphic	10	large
<i>Calathus fuscipes</i>	predatory	dimorphic	12	large
<i>Calosoma inquisitor</i>	predatory	winged	21.5	large
<i>Carabus auratus</i>	predatory	wingless	23.5	large
<i>Carabus cancellatus</i>	predatory	wingless	26	large
<i>Carabus convexus</i>	predatory	wingless	17	large
<i>Carabus coriaceus</i>	predatory	wingless	37	large
<i>Carabus granulatus</i>	predatory	dimorphic	21.5	large
<i>Carabus nemoralis</i>	predatory	wingless	23	large
<i>Carabus ulrichii</i>	predatory	wingless	24.5	large
<i>Carabus violaceus</i>	predatory	wingless	30	large
<i>Cicindela campestris</i>	predatory	winged	12	large
<i>Clivina fossor</i>	predatory	dimorphic	6	intermediate

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<i>Demetrias atricapillus</i>	predatory	winged	5	small
<i>Diachromus germanus</i>	granivorous / frugivorous	winged	8.5	intermediate
<i>Harpalus affinis</i>	granivorous / frugivorous	winged	10	large
<i>Harpalus atratus</i>	granivorous / frugivorous	dimorphic	11.5	large
<i>Harpalus dimidiatus</i>	granivorous / frugivorous	winged	12.5	large
<i>Harpalus distinguendus</i>	granivorous / frugivorous	winged	9	intermediate
<i>Harpalus honestus</i>	granivorous / frugivorous	dimorphic	8.5	intermediate
<i>Harpalus laevipes</i>	granivorous / frugivorous	winged	10.5	large
<i>Harpalus latus</i>	granivorous / frugivorous	winged	9.5	intermediate
<i>Harpalus luteicornis</i>	granivorous / frugivorous	winged	6.5	intermediate
<i>Harpalus pumilus</i>	granivorous / frugivorous	dimorphic	5	small
<i>Harpalus rubripes</i>	granivorous / frugivorous	winged	10	large
<i>Harpalus rufipes</i>	granivorous / frugivorous	winged	13.5	large
<i>Harpalus serripes</i>	granivorous / frugivorous	winged	10.5	large
<i>Harpalus signaticornis</i>	granivorous / frugivorous	winged	6.5	intermediate
<i>Harpalus subcylindricus</i>	granivorous / frugivorous	winged	6.5	intermediate
<i>Harpalus tardus</i>	predatory	winged	9	intermediate
<i>Leistus ferrugineus</i>	predatory	winged	6.5	intermediate
<i>Leistus rufomarginatus</i>	predatory	dimorphic	8	intermediate
<i>Leistus spinibarbis</i>	predatory	winged	8.5	intermediate
<i>Limodromus assimilis</i>	predatory	winged	11.5	large
<i>Loricera pilicornis</i>	predatory	winged	7	intermediate
<i>Microlestes maurus</i>	predatory	dimorphic	2	small
<i>Microlestes minutulus</i>	predatory	winged	2.5	small
<i>Molops elatus</i>	predatory	wingless	15	large
<i>Molops piceus</i>	predatory	wingless	11.5	large
<i>Nebria brevicollis</i>	predatory	winged	11.5	large
<i>Nebria salina</i>	predatory	winged	11	large
<i>Notiophilus aestuans</i>	predatory	dimorphic	4.5	small
<i>Notiophilus biguttatus</i>	predatory	dimorphic	4.5	small
<i>Notiophilus germinyi</i>	predatory	dimorphic	5	small
<i>Notiophilus palustris</i>	predatory	dimorphic	5	small
<i>Ophonus ardosiacus</i>	granivorous / frugivorous	winged	12	large
<i>Ophonus azureus</i>	granivorous / frugivorous	dimorphic	7.5	intermediate
<i>Ophonus laticollis</i>	granivorous / frugivorous	winged	9.5	intermediate
<i>Ophonus rupicola</i>	granivorous / frugivorous	winged	8	intermediate
<i>Panagaeus bipustulatus</i>	omnivorous	winged	7	intermediate
<i>Panagaeus cruxmajor</i>	omnivorous	winged	8	intermediate
<i>Paradromius linearis</i>	predatory	dimorphic	4.5	small
<i>Pedius longicollis</i>	predatory	dimorphic	6	intermediate
<i>Philorhizus notatus</i>	predatory	dimorphic	2.5	small
<i>Poecilus cupreus</i>	omnivorous	winged	11	large
<i>Poecilus lepidus</i>	predatory	dimorphic	12	large
<i>Poecilus versicolor</i>	predatory	winged	10	large
<i>Polistichus connexus</i>	predatory	winged	8	intermediate
<i>Pterostichus anthracinus</i>	predatory	dimorphic	10.5	large
<i>Pterostichus macer</i>	predatory	winged	13	large
<i>Pterostichus madidus</i>	predatory	dimorphic	16.5	large
<i>Pterostichus melanarius</i>	predatory	dimorphic	15	large
<i>Pterostichus melas</i>	predatory	wingless	16	large
<i>Pterostichus niger</i>	predatory	dimorphic	18.5	large
<i>Pterostichus nigrita</i>	predatory	dimorphic	10	large
<i>Pterostichus oblongopunctatus</i>	predatory	dimorphic	10.5	large
<i>Pterostichus ovoideus</i>	predatory	dimorphic	7	intermediate
<i>Pterostichus strenuus</i>	predatory	dimorphic	6	intermediate
<i>Pterostichus vernalis</i>	predatory	dimorphic	6.5	intermediate
<i>Stomis pumicatus</i>	predatory	dimorphic	7	intermediate
<i>Syntomus truncatellus</i>	predatory	dimorphic	2.5	small
<i>Tachys bistriatus</i>	predatory	winged	1.5	small
<i>Trechoblemus micros</i>	predatory	winged	4.5	small
<i>Trechus quadristriatus</i>	predatory	dimorphic	3.5	small
<i>Zabrus tenebrioides</i>	granivorous / frugivorous	winged	15	large

Table VI.S5: Results obtained from linear mixed effects models (lmer) including a random intercept for 'study site ID' on ground-dwelling predator assemblage characteristics and different carabid species traits. d.f. = degrees of freedom (numerator, denominator); F & p-values obtained by type II SS ANOVA analyses (Kenward-Roger approximation); bold printing indicates significant p-values < 0.5.

Model	d.f.	F	p-value
carabid beetle species richness			
habitat border type	2,24	0.9	0.42
AES type	4,42	0.396	0.811
distance	1,61	24.8	< 0.001 ***
AES type * distance	4,61	0.75	0.56
carabid beetle activity density			
habitat border type	2,24	0.3	0.741
AES type	4,27	1.02	0.412
distance	1,58	4.19	0.045 *
AES type * distance	4,58	1.47	0.224
staphylinid beetle activity density			
habitat border type	3,23	1.67	0.2
AES type	4,31	0.97	0.438
distance	1,59	12	0.001 **
AES type * distance	4,59	0.55	0.699
spider activity density			
habitat border type	3,23	0.35	0.787
AES type	4,27	0.42	0.79
distance	1,58	33.8	< 0.001 ***
AES type * distance	4,58	2.53	0.05 (*)
Bray-Curtis similarity			
habitat border type	2,21	1.85	0.182
AES type	3,27	3.73	0.023 *
distance	1,51	7.49	0.009 **
AES type * distance	3,51	0.29	0.835
proportion of predatory species			
habitat border type	2,24	4.87	0.017 *
AES type	4,30	4.84	0.004 **
distance	1,58	10.8	0.002 **
AES type * distance	4,58	0.34	0.848
proportion of omnivorous species			
habitat border type	2,24	0.42	0.662
AES type	4,32	0.76	0.561
distance	1,59	21.9	< 0.001 ***
AES type * distance	4,58	1.69	0.166
proportion of granivorous or frugivorous species			
habitat border type	2,24	6.36	0.006 **
AES type	4,34	5.27	0.002 **
distance	1,59	0.18	0.673
AES type * distance	4,59	0.45	0.77
proportion of wingless species			
habitat border type	2,24	1.37	0.273
AES type	4,40	0.24	0.915
distance	1,60	0.16	0.692
AES type * distance	4,60	1.06	0.383
proportion of winged species			
habitat border type	2,24	0.83	0.449
AES type	4,28	1.17	0.346
distance	1,58	0.02	0.893
AES type * distance	4,58	0.56	0.696
community weighted mean body size			
habitat border type	2,24	2.62	0.093 (*)
AES type	4,30	2.17	0.096 (*)
distance	1,58	20	< 0.001 ***
AES type * distance	4,58	1.35	0.264
proportion of small species < 6 mm			
habitat border type	2,24	< 0.01	0.996
AES type	4,31	1.11	0.368
distance	1,59	4.2	0.045 *
AES type * distance	4,58	0.21	0.929
proportion of intermediate sized species (6 – 10 mm)			
habitat border type	2,24	0.38	0.688
AES type	4,29	1.04	0.406
distance	1,58	0.91	0.344
AES type * distance	4,58	1.78	0.145
proportion of large species ≥ 10 mm			
habitat border type	2,24	0.6	0.56
AES type	4,29	1.96	0.127
distance	1,58	5.69	0.02 *
AES type * distance	4,58	2.76	0.036 *

Table VI.S6: Results obtained from linear mixed effects models (lmer) including a random intercept for ‘study site ID’ as well as a random slope on ‘distance’ on ground-dwelling predator assemblage characteristics and different carabid species traits. d.f. = degrees of freedom (numerator, denominator); F & p-values obtained by type II SS ANOVA analyses (Kenward-Roger approximation); bold printing indicates significant p-values < 0.5.

Model	d.f.	F	p-value
carabid beetle species richness			
AES type	4,30	0.42	0.796
distance	1,19	23.1	< 0.001 ***
AES type * distance	4,21	0.64	0.637
carabid beetle activity density			
AES type	4,29	1.07	0.391
distance	1,19	3.93	0.062 (*)
AES type * distance	4,20	1.41	0.267
staphylinid beetle activity density			
AES type	4,29	0.55	0.698
distance	1,26	10.3	0.003 **
AES type * distance	4,28	0.38	0.824
spider activity density			
AES type	4,29	0.62	0.653
distance	1,19	30.4	< 0.001 ***
AES type * distance	4,20	2.34	0.089 (*)
Bray-Curtis similarity			
AES type	3,28	6.54	0.002 **
distance	1,19	6.86	0.017 *
AES type * distance	3,21	0.3	0.826
proportion of predatory species			
AES type	4,28	2.36	0.077 (*)
distance	1,22	10.7	0.004 **
AES type * distance	4,24	0.39	0.815
proportion of omnivorous species			
AES type	4,32	0.94	0.451
distance	1,20	20.9	< 0.001 ***
AES type * distance	4,22	1.64	0.201
proportion of granivorous or frugivorous species			
AES type	4,31	2.6	0.055 (*)
distance	1,20	0.14	0.71
AES type * distance	4,22	0.42	0.792
proportion of wingless species			
AES type	4,28	0.18	0.947
distance	1,21	0.23	0.635
AES type * distance	4,23	0.78	0.547
proportion of winged species			
AES type	4,31	1.35	0.275
distance	1,20	0.01	0.911
AES type * distance	4,22	0.49	0.745
community weighted mean body size			
AES type	4,31	1.82	0.15
distance	1,20	19.4	< 0.001 ***
AES type * distance	4,21	1.24	0.324
proportion of small species < 6 mm			
AES type	4,30	1.04	0.401
distance	1,19	4	0.06 (*)
AES type * distance	4,21	0.23	0.92
proportion of intermediate sized species (6 – 10 mm)			
AES type	4,31	1.37	0.268
distance	1,21	0.96	0.339
AES type * distance	4,23	1.89	0.147
proportion of large species ≥ 10 mm			
AES type	4,33	2.84	0.04 *
distance	1,27	5.69	0.024 *
AES type * distance	4,29	3.02	0.034 *



Carabid beetles (Carabidae) such as this *Poecilus cupreus* are not only beautiful encounters; they are also important natural enemies regulating pest densities in agricultural fields.

Chapter VII: The effects of AES habitats on pest control in adjacent cereal fields

As published in: Boetzl, F.A., Schuele, M., Krauss, J. & Steffan-Dewenter, I. (2020) Pest control potential of adjacent agri-environment schemes varies with crop type and is shaped by landscape context and within-field position. *Journal of Applied Ecology*, 56, 10-20.

Abstract

1. Increasing natural pest control in agricultural fields is an important aim of ecological intensification. Combined effects of landscape context and local placement of agri-environmental schemes on natural pest control and within field distance functions of natural pest control agents have rarely been addressed but might affect the distribution of biocontrol providers. Importantly, it is currently unknown whether ecosystem services provided by adjacent agri-environmental schemes (AES) are consistent for different crop types during crop rotation.
2. In this study, we assessed whether crop rotation from oilseed rape to cereals altered within-field distance functions of ground dwelling predators from adjacent agri-environmental fields along a gradient in landscape context. Additionally we recorded crop pests, predation rates, parasitoids as well as crop yields on a total of 30 study sites.
3. Distance functions varied between trophic levels: Carabid richness decreased while densities of carabid beetles, staphylinid beetles as well as crop yields increased towards the field centres. Distance functions of parasitoids and pests were modulated by the amount of semi-natural habitat in the surrounding landscape, while the effects of adjacent AES were limited.

4. Distance decay functions found for ground dwelling predators in oilseed rape in the previous year were not always present in cereals. Increasing distance to the field edge also increased effects of crop rotation on carabid beetle assemblages, indicating a source habitat function of field edges.
5. *Synthesis and applications.* Distance functions of natural pest control are not universal and the effects of agri-environmental schemes (AES) in different adjacent crops during crop rotation vary and depend on ecological contrasts. A network of semi-natural habitats and spatially optimised AES habitats can benefit pest control in agricultural landscapes, but constraints as a result of crop type need to be addressed by annually targeted, spatially shifting agri-environment schemes for different crops.

Introduction

Increasing natural pest control in agricultural fields is one of the main goals of ecological intensification. As many different biotic factors influence crop yields, ecological intensification aims at understanding and fostering these biotic relations and at replacing external fertiliser and pesticide input by biodiversity mediated functions to make modern agriculture more sustainable (Bommarco, Kleijn & Potts 2013; Garibaldi *et al.* 2019).

A widely implemented approach to increase ecosystem services in agricultural landscapes is the creation of agri-environmental scheme habitats (AES) as safe-havens for biodiversity and ecosystem service providers (Tscharntke *et al.* 2005; Ekroos *et al.* 2014). The benefits of AES in increasing species richness and abundance of plants and animals in croplands has been shown (Batáry *et al.* 2011). However, effectiveness varies between the types of AES implemented (Batáry *et al.* 2015) and it is largely unknown whether and how effectively AES support ecosystem services in adjacent crops (but see Dainese *et al.* (2017a)). In Central Europe, many habitats currently created under AES (e.g. temporary flower strips or fields) are tailored to support pollinators and potential off target effects on other ecosystem services like pest control are poorly understood and rarely investigated (but see Tschumi *et al.* (2016a)).

Recent comprehensive synthesis studies unveiled landscape level drivers of natural pest control in agricultural landscapes. Both landscape composition and configuration were shown to be important drivers with landscape simplification decreasing natural enemy richness and thereby weakening natural pest control (Karp *et al.* 2018; Dainese *et al.* 2019; Haan, Zhang & Landis 2019). Edge density as a measure of landscape complexity, proportion of semi-natural habitat as a measure of landscape composition as well as crop diversity in agricultural landscapes benefit natural enemies, pest control and ultimately increase yields (Redlich, Martin & Steffan-Dewenter 2018; Martin *et al.* 2019). However, translating these findings into practical management for ecological intensification is complex as most landscape characteristics cannot easily be restructured. While AES habitats are an accessible means by which policy makers can enhance diversity in agricultural landscapes, the types of landscapes types with the greatest benefits remain unclear (as suggested by Tschardtke, Batáry and Dormann (2011)).

Apart from landscape level drivers, the distribution of pest control agents could also be modulated by local crop rotation and within-field distance decay functions (Fusser *et al.* 2018; Boetzi *et al.* 2019). Crop rotation is a widely used method to counter weeds, diseases and pests by disrupting continuous host availability to maintain soil fertility. Previous studies on natural pest control and crop rotations focused on the landscape level aspect of crop rotations and not on changes within the same fields or interactions with adjacent habitats (e.g. Rusch *et al.* (2013) and Rusch *et al.* (2014)). Apart from crop type, crop rotation however changes specific management regimes (soil management, fertilization and agrochemical input) potentially affecting spillover and within field distribution of natural enemies and ecosystem services provided by adjacent AES habitats. The direct effects of crop rotation on local ecosystem service providers are however rarely assessed.

Field edges differ from field centres as they undergo less intensive management and are more affected by spillover from adjacent habitats (Tschardtke, Rand & Bianchi 2005; Boetzi *et al.* 2019). Yet, the extent of these effects on pest control and yields as well as the role of adjacent habitats remains unclear. To address this question, distance gradients have received more attention in recent years but few studies have actually addressed more than two within-field

distances (e.g. Birkhofer, Wolters and Diekötter (2014), Woodcock *et al.* (2016) and Van Vooren *et al.* (2018)) which limits the value of datasets as no predictions of distance functions are possible. Moreover, most existing datasets only contain single trophic levels and represent snapshots as they do not cover longer time periods. In a large field study conducted in winter oilseed rape with adjacent AES habitats tailored to support pollinators, distance decay functions of ground dwelling predators (Boetzl *et al.* 2019) and pollinators (Krimmer *et al.* 2019) were reported. Distance decay functions of pollinators were buffered by increasing amount of semi-natural habitats (SNH) in the surrounding landscape (Krimmer *et al.* 2019). In total however, data on distance functions especially across different trophic levels is still very limited and if distance functions are affected by different adjacent habitats, landscape context or crop type remains poorly understood. Further, no studies have so far addressed how crop rotation and the consequent replacement of crop types adjacent to AES habitats affects their provision of pest control services.

In this study, we investigated whether different trophic levels (agricultural pests, ground dwelling predators and flying parasitoids), predation rates and crop yields depend on distance from the field edge, SNH in the surrounding landscape and / or adjacent AES habitat presence and type within one large scale field study throughout the growing period. We assessed (i) how different pest control agents, pests and crop yields are affected by distance, landscape context (proportion of SNH) and adjacent AES habitats, (ii) whether distance decay functions persist during crop rotation in a different crop (from oilseed rape to cereals) as well as (iii) if crop rotation shifted carabid beetle assemblages in the same sites between years and how this depended on distance, proportion of SNH and adjacent AES habitat type.

Materials and methods

Study design

The study design comprised 30 study sites with 5 different treatments consistent of 4 different adjacent agri-environmental scheme habitats (new flowering fields, refreshed flowering fields, continuous flowering fields (CAP greenings) established on regular agricultural fields and permanent semi-natural calcareous grasslands) and controls with an adjacent arable field. In each field, all measurements were taken along a continuous distance gradient with three distances per field from the field edge (at the side of the adjacent AES habitat) into the field centres (1 - 65m). Distances varied with field size (Supplementary Information VII.1 & Supplementary Table VII.1).

For this study, we used the same study design and study sites as in Boetzl *et al.* (2019) and Krimmer *et al.* (2019). Following the typical crop rotation, winter cereals followed the previous field culture (oilseed rape; Supplementary Table VII.1). All studied winter cereal fields were managed conventionally, have undergone very similar management regimes in the study region and were therefore considered comparable.

To assess landscape level effects, non-overlapping landscapes with a radius of 1km around all study sites formed a gradient of semi-natural habitat (SNH) within each treatment ranging in total from 3.6 to 31.6 %. SNH included only permanent habitats (forest edges, field margins, bank borders, roadside vegetation, small wood groves, hedgerows, orchard meadows and extensive pastures as well as semi-natural calcareous grasslands and grassland taken out of agricultural production; see Krimmer *et al.* (2019) for more information).

Data collection

Along the distance transects, different variables were recorded over the vegetation period from early April until crop harvest in early July 2017 (Figure VII.1): (i) Pest densities using sweep netting; (ii) Parasitoid densities using crossed window traps; (iii) ground dwelling predators

(carabid beetles, staphylinid beetles and spiders) using pitfall traps; (iv) predation rates on the ground using aphid sentinel prey cards (Boetzl, Konle & Krauss 2019) and (v) crop yields. The factors (i), (ii) and (iv) were recorded during the sensitive period of milk ripening where cereals are both very attractive to pests and very sensitive to pest pressure. Detailed descriptions of all methods and sampling schemes are provided in the Supplementary Material (Supplementary

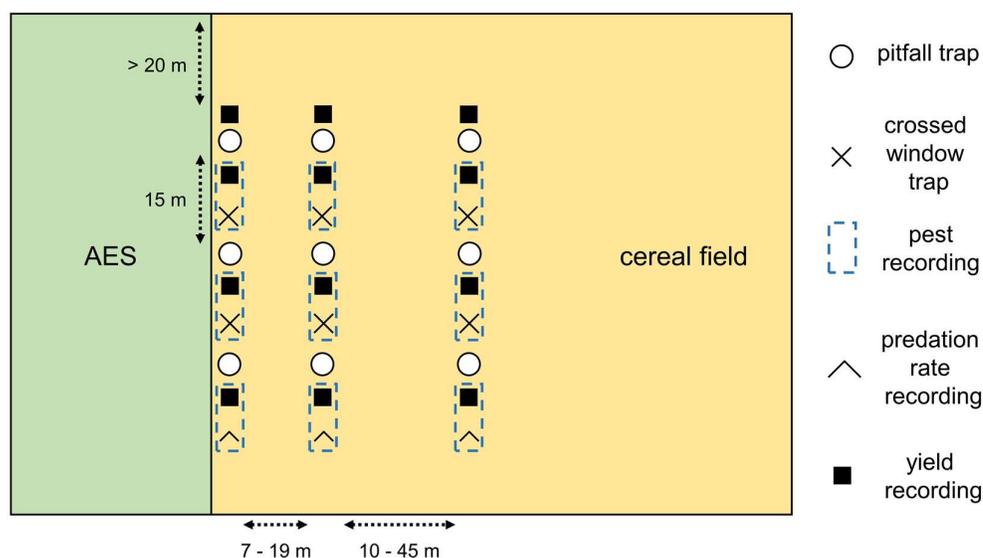


Figure VII.1 Schematic representation of the study design with symbols representing methods used and distances between within field positions and between pitfall trap transects (circle: pitfall trap for ground dwelling predator recording; cross: crossed window trap for parasitoid recording; dashed square: sweep netting for pest density assessment; angle: predation rate recording using aphid sentinel prey cards; square: yield harvest).

material VII).

Statistical analyses

All statistical analyses were performed in R 3.6.1 for Windows (R Development Core Team 2019), using the packages ‘lme4’ (Bates *et al.* 2015), ‘lmerTest’ (Kuznetsova, Brockhoff & Christensen 2017), ‘multcomp’ (Hothorn, Bretz & Westfall 2008), ‘vegan’ (Oksanen *et al.* 2019) and ‘ggeffects’ (Lüdtke 2018).

For all responses obtained from passive traps (pitfall & window traps), we calculated per day activity densities throughout the sampling period (to account for occasional trap losses, 1.6 % for both trap types combined). Species richness was the accumulated number of species at the end of the sampling period. For pest densities and predation rates, measured values were first averaged between replicates per plot (sampling distance per site) and then summed over the sampling period to obtain an accumulated pest pressure and predation value.

As calcareous grasslands are naturally located within landscapes that have a high proportion of SNH, they had significantly higher SNH percentages than all other AES types (linear model: $F_{4,25} = 4.96$, $p = 0.004$). We therefore excluded the fields bordering calcareous grasslands in all models investigating distance functions and SNH (models including these sites are shown in Supplementary Table VII.S3).

For all responses, we tested models including the fixed effects ‘distance’, ‘SNH’ and ‘AES habitat type’ as well as the interactions ‘AES habitat type : distance’ and ‘SNH : distance’ while ‘study site ID’ was used as random intercept. To select the best model for different hypothetical distance functions, distance was included in different ways: (i) linear, (ii) quadratic (for hump-shaped patterns) or logarithmic (for asymptotic patterns). For these comparisons, ‘distance’ and ‘SNH’ were rescaled in order to allow comparability among models. We compared the resulting models using the likelihood ratio approach and if models were significantly different, the best model was selected based on AIC (otherwise, the simple linear distance model was kept). Activity densities of carabid beetles, spiders and densities of cereal leaf beetle (CLB) larvae were square root transformed to improve normality. If significant differences between adjacent AES habitats types were detected, we performed Tukey-HSD post-hoc tests (function ‘glht’).

Changes between carabid beetle assemblages over crop-rotation were investigated based on Bray-Curtis similarities between the assemblages in the same distance and site in both years. Moreover, we assessed if crop rotation did change species assemblages using a PERMANOVA (‘adonis’, Bray-Curtis dissimilarities, 999 permutations) on a species-abundance table containing the pooled data of all within field distances per site (species proportions). Additionally, we calculated Bray-

Curtis similarities between carabid assemblages caught in both years in the same within field distances. Similarities were compared in a linear mixed effects model using 'study site ID' as random intercept (following the same procedures described above).

For the figures, we predicted the best model with 95 percent confidence intervals over the gradients of distance or SNH we investigated. If significant distance: SNH interactions were present, we predicted distance functions for the SNH levels 5, 10, 15, and 20 percent.

Results

Throughout the vegetation period, we caught 128 826 carabid beetles (~2.5 times the amount of the previous year in oilseed rape) from 119 species (one species less than in the previous year; Supplementary Table VII.2), 84 979 staphylinid beetles (~1.9 times the amount of the previous year), 86 682 spiders (~3.1 times the amount of the previous year) and 5 056 parasitoid wasps in the studied fields. For the analyses, we only used non-granivorous carabid beetles to predict pest control potential which were 117 391 individuals (~3.2 times the amount of the previous year) from 79 species (one species less than in the previous year; Supplementary Table VII.2). In pest recordings, we observed a total of 1 815 cereal leaf beetle larvae (CLB; *Oulema sp.*) on all transects. We used a total of 2 160 aphids of which 1 255 (58.1%) were consumed during predation rate assessments. Ultimately, we harvested a total of 45 282 ears containing 1 274 688 grains with a total weight of approximately 45.3 kg.

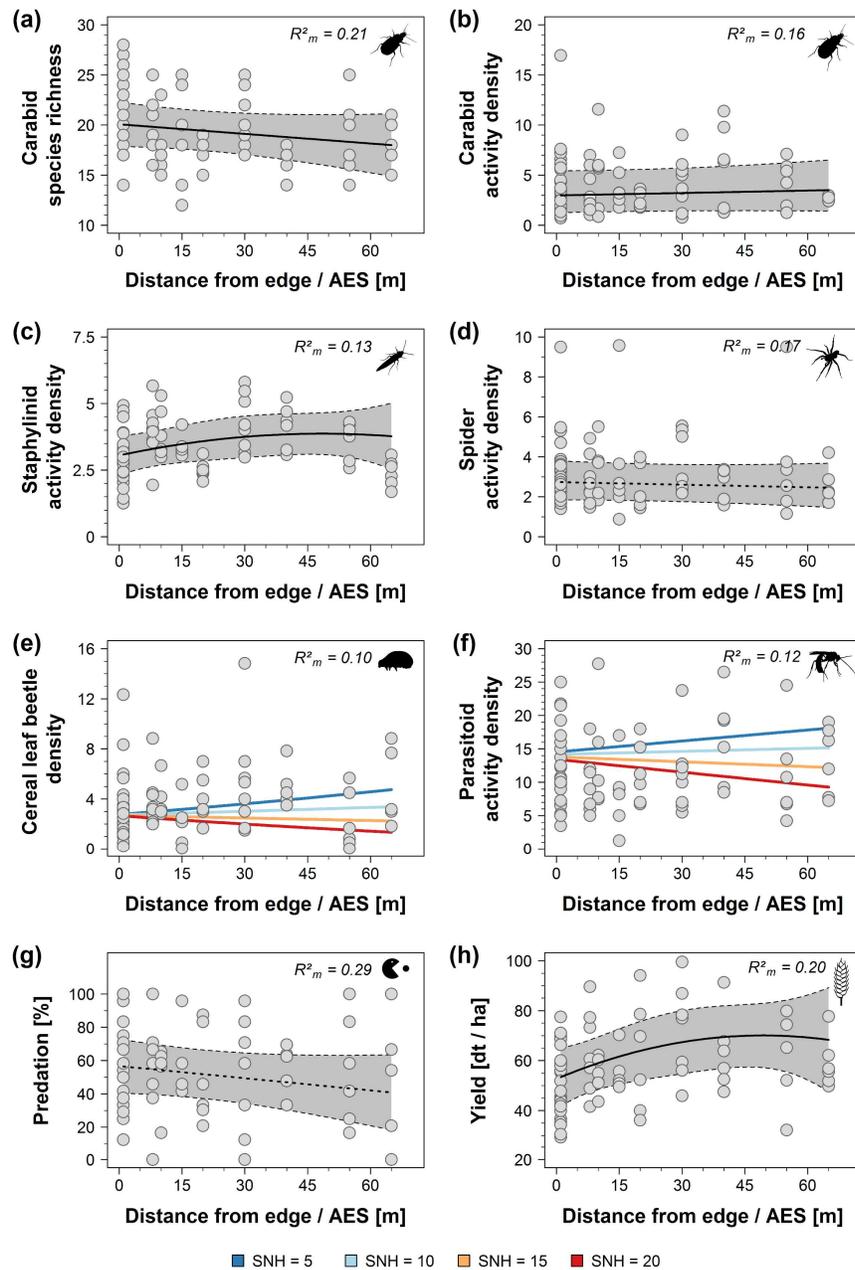


Figure VII.2: Distance functions of the different responses investigated: (a) Carabid beetle species richness (excluding exclusively granivorous species), (b) carabid beetle activity density (excluding exclusively granivorous species), (c) staphylinid beetle activity density and (d) spider activity density, (e) cereal leaf beetle and (f) parasitoid activity density, (g) predation rates and (h) crop yields. Model predictions (obtained from the full model), partly with 95% confidence intervals (a, b, c, d, g & h). Colours represent predictions for five different SNH levels (5, 10, 15 and 20 %) wherever the interaction between distance and SNH was significant. Solid lines indicate significant distance functions, dotted lines non-significant distance functions, R^2_m is the marginal R^2 value of the model (Statistics see text and Table VII.1).

Effects of within field distance and SNH

Carabid species richness was driven by a distance decay from the field edges towards the field centres declining by 10 percent within 65 meters (Table VII.1; Figure VII.2 a). Carabid activity density however was increasing towards the field centres by 17 percent (Table VII.1; Figure VII.2 b). The densities of cereal leaf beetles and parasitoids were moderated by both SNH proportion and distance to the field edge; they increase towards the field centres in landscapes with low SNH (at 5 percent SNH: 30 percent in cereal leaf beetles and 24 percent in parasitoids) and decrease in landscapes with comparably high SNH (at 20 percent SNH: 29 percent in cereal leaf beetles and 30 percent in parasitoids); Table VII.1; Figure VII.2 e & f). The same trend was found for carabid beetle activity densities, however not significant (Table VII.1; Supplementary Figure VII.1). The activity density of staphylinid beetles followed a hump-shaped pattern increasing by 22 percent from the edge to the peak at 45 m near the field centres (Table VII.1; Figure VII.2 c). There was no significant distance function found for spider activity density or predation rates (Table VII.1; Figure VII.2 d & g). Crop yields increased by 31 percent from the field edges towards the centres, reaching 95 percent of the maximum yield after 27 m and peaking at 49 m (Table VII.1; Figure VII.2 h). Carabid beetle activity densities tended to decrease by 81 percent with increasing SNH while spider activity densities were decreasing by 40 percent from landscapes with low SNH to landscapes with high SNH (Table VII.1; Figure VII.3 a & b). On the contrary, predation rates tended to increase by 75 percent from landscapes with low SNH towards landscapes with high SNH (Table VII.1; Figure VII.3 b).

Effects of adjacent AES

We did not find effects of adjacent AES habitat type or controls without adjacent AES habitat on densities of ground dwelling predators, parasitoids, cereal leaf beetles or yields (Table VII.1). However, predation rates were highest in fields adjacent to refreshed flowering fields and did not differ significantly in fields bordering the other AES habitat types (Table VII.1, Supplementary Figure VII.S2).

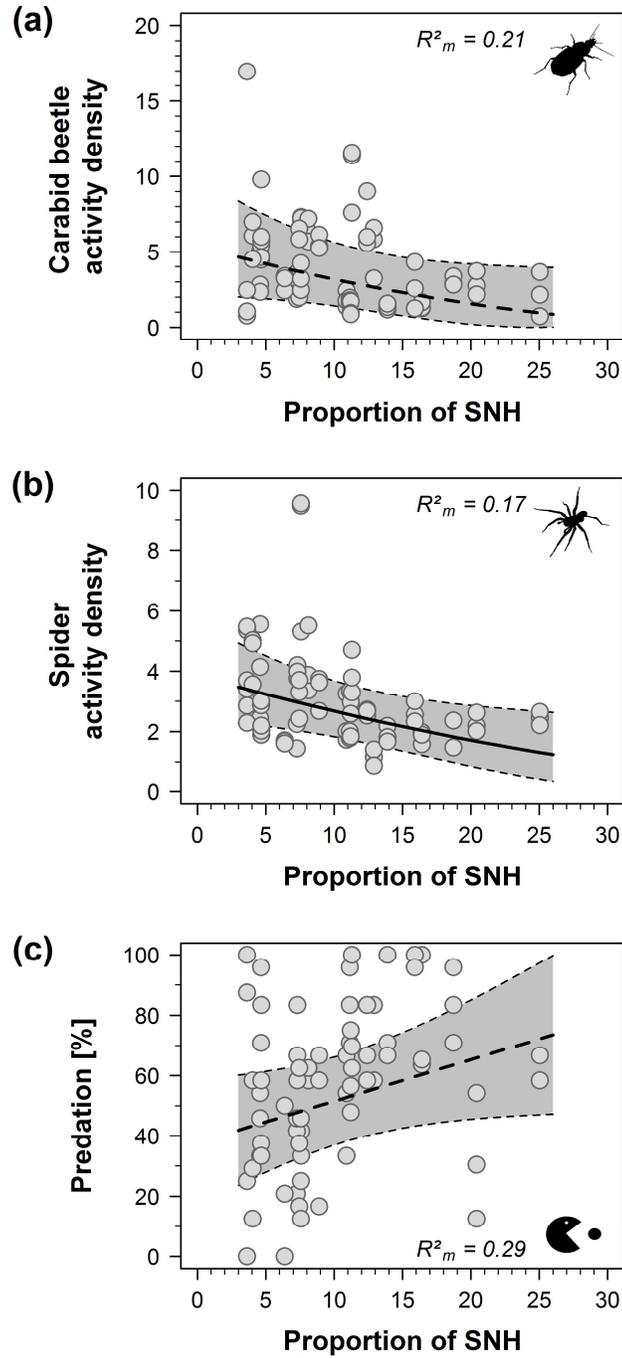


Figure VII.3: Carabid beetle activity density (a), spider activity density (b) and predation rates (c) in relation to landscape level SNH. Model predictions with 95% confidence intervals. Dotted lines indicate non-significant relations, R^2_m is the marginal R^2 value of the model (Statistics see text and Table VII.1).

Similarity between carabid assemblages in both years

Carabid beetle assemblages within the crop fields changed with crop rotation between the years (PERMANOVA crop field centres, $F_{1,59} = 5.02$, $p = 0.001$) while carabid assemblages in adjacent AES habitats did not change significantly (PERMANOVA, $F_{1,52} = 0.89$, $p = 0.669$; Supplementary Figure VII.S3). We therefore expect that the observed changes were driven by the change in crop type and not by annual variation. Although total species richness decreased by one species from 120 to 119 species (0.9%), 12 species were exclusively found in 2016 and 11 species were exclusively found in 2017 bringing the total species number over both years to 130. Assemblages recorded in 2017 (winter cereals) were most similar to the ones recorded in 2016 (winter oilseed rape) near the field edges and similarity decreased towards the field centres by 15 percent (Table VII.1; Figure VII.4).

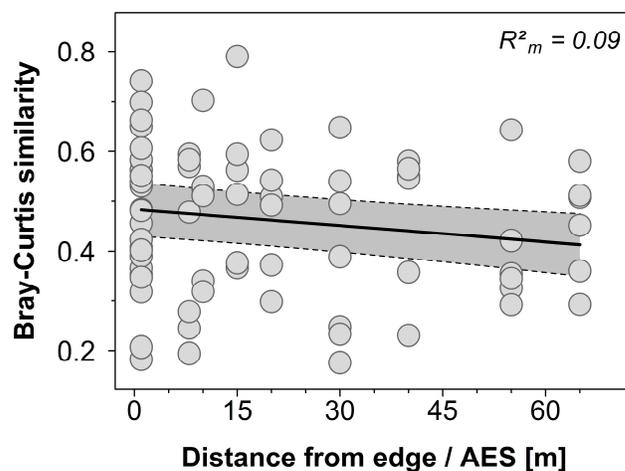


Figure VII.4: Bray-Curtis similarity of carabid beetle assemblages in the same within field distances at the same sites between oilseed rape (2016) and winter cereals (2017). Model prediction with 95% confidence interval, R^2_m is the marginal R^2 value of the model (Statistics see text and Table VII.1).

Table VII.1: Results obtained from linear mixed effects models (lmer) including a random intercept for “study site ID” on different responses. df = degrees of freedom (numerator, denominator); F and p-values obtained by type II sums of squares ANOVA with Kenward–Roger approximation; bold printing indicates significant $p < 0.5$; R^2_m = marginal R^2 ; R^2_c = conditional R^2 .

Response / Factors	distance as	df	F	p	R^2_m	R^2_c
Carabid species richness						
AES habitat type		3,22	1.71	0.195		
distance ¹		1,49	9.02	0.004 **		
SNH	linear	1,24	0.88	0.358	0.21	0.60
distance ¹ : AES habitat type		3,49	0.60	0.616		
distance ¹ : SNH		1,49	0.69	0.410		
Carabid activity density						
AES habitat type		3, 21	0.38	0.771		
distance ¹		1, 47	4.24	0.045 *		
SNH	linear	1, 22	3.89	0.061 (*)	0.16	0.88
distance ¹ : AES habitat type		3, 47	0.48	0.695		
distance ¹ : SNH		1, 48	3.28	0.077 (*)		
Staphylinid activity density						
AES habitat type		3, 22	0.14	0.932		
distance ¹		1, 45	0.52	0.473		
distance ²		1, 44	11.60	0.001 **		
SNH	quadratic	1, 25	0.33	0.573	0.13	0.61
distance ¹ : AES habitat type		3, 45	0.48	0.700		
distance ² : AES habitat type		3, 44	0.97	0.414		
distance ¹ : SNH		1, 47	0.57	0.456		
distance ² : SNH		1, 45	0.02	0.897		
Spider activity density						
AES habitat type		3, 21	0.51	0.679		
distance ¹		1, 48	0.59	0.448		
SNH	linear	1, 22	5.53	0.028 *	0.17	0.81
distance ¹ : AES habitat type		3, 48	0.26	0.855		
distance ¹ : SNH		1, 48	0.36	0.551		
Parasitoid activity density						
AES habitat type		3, 21	0.82	0.495		
distance ¹		1, 48	1.13	0.294		
SNH	linear	1, 22	1.85	0.188	0.10	0.83
distance ¹ : AES habitat type		3, 48	0.45	0.718		
distance ¹ : SNH		1, 48	5.86	0.019 *		
Cereal leaf beetle density						
AES habitat type		3, 22	0.62	0.609		
distance ¹		1, 48	4.74	0.034 *		
SNH	linear	1, 23	1.46	0.239	0.12	0.74
distance ¹ : AES habitat type		3, 48	0.31	0.820		
distance ¹ : SNH		1, 48	4.34	0.043 *		
Predation rates						
AES habitat type		3, 22	3.40	0.036 *		
distance ¹		1, 49	2.52	0.119		
SNH	linear	1, 24	3.85	0.061 (*)	0.29	0.65
distance ¹ : AES habitat type		4, 49	1.59	0.203		
distance ¹ : SNH		1, 49	0.55	0.461		
Yield [dt / ha]						
AES habitat type		3, 21	0.53	0.668		
distance ¹		1, 41	4.61	0.038 *		
distance ²		1, 40	8.23	0.007 **		
SNH	quadratic	1, 25	0.81	0.376	0.20	0.59
distance ¹ : AES habitat type		3, 42	0.16	0.925		
distance ² : AES habitat type		3, 41	0.57	0.641		
distance ¹ : SNH		1, 43	0.09	0.760		
distance ² : SNH		1, 42	0.41	0.527		
Similarity of carabid assemblages between years						
distance ¹	linear	1, 50	7.45	0.009 **	0.09	0.77

Discussion

Our results have broad implications for the spatiotemporal management of AES habitats at local and landscape scales as strong differences their effectiveness among different crop types and depending on landscape context were found. Apart from a clear distance decay of carabid species richness, distance functions of the densities of natural pest control agents and pests were not as clear as expected. Carabid beetle densities increased towards the field centres while staphylinid beetle densities and crop yields showed a hump-shaped distance function peaking near the field centres. Increasing SNH in the surrounding landscapes decreased densities of spiders irrespective of within field distance. Moreover, SNH modulated distance functions of pest and parasitoid densities. However, adjacent AES did not have clear effects on pest control agents, pests or crop yields in the responses investigated. The distance functions found for ground dwelling predators partly contradict the universal distance decay functions found in the previous year which indicates that distance functions changed with crop rotation.

Distance functions of natural pest control and yields

Carabid beetle species richness was driven by a clear distance decay which seems to be a general pattern as it was previously found for oilseed rape (Boetzl *et al.* 2019), pumpkin (Fusser *et al.* 2018) and winter cereals (Clough *et al.* 2007; Anjum-Zubair *et al.* 2010). Species preferring adjacent habitats regularly disperse into the edges of arable fields and add to the species pool already present in the fields, a process called spillover (Tschardtke, Rand & Bianchi 2005). This effect is typically decreasing with increasing distance to the field edge as these species are filtered out by changes in conditions within the field or limited mobility.

Contrary to the distance decay found for activity densities of ground dwelling predators in winter oilseed rape, we did not detect such uniform functions in winter cereals. While both carabid and staphylinid beetle densities increased towards the field centres, there was no clear distance function for spider densities. Distance effects on ground dwelling predators in winter cereals were

contradicting in previous studies. Several studies found increased activity densities of carabid beetles in field centres compared to field edges and concluded that this pattern might arise from productivity driven pest accumulations in the field centres (Anjum-Zubair *et al.* 2010; Birkhofer, Wolters & Diekötter 2014). However other studies have found either no relationship between within field position and carabid densities (Batáry *et al.* 2012) or a decrease from the field edges towards field centres (Pollier *et al.* 2019). Carabid densities and carabid species richness followed reverse trends within fields, indicating that fewer species coping well with agricultural management reached high densities in field centres.

Crop yields per unit area are expected to decrease towards field edges as management intensity and inputs are lower near the edge due to mechanical limitations and legal regulations. In contrast to Raatz *et al.* (2019), edge effects on yields reached 10 m farther into the field and crop yields reached 95 percent of the maximum only after 27 m. This suggests that distance functions of crop yields are not necessarily consistent across studies. We expect that crop yields are affected by habitat context, management but also by the magnitude of local ecosystem services or pest spillover, a factor not assessed by Raatz *et al.* (2019). Our results indicate that especially in small fields, edge effects reduce yields significantly.

SNH effects on pest control and distance functions

Decreased pest densities in the field centres together with predation rates marginally increasing with increasing landscape SNH proportion indicate that complex landscapes favour natural pest control which is in line with previous studies (Karp *et al.* 2016; Rusch *et al.* 2016; Martin *et al.* 2019). SNH also modulated densities of the natural enemies carabid beetles (marginally), parasitoid wasps (which are attracted to their hosts) and spiders likely driven by prey availability. As natural enemies were most abundant in landscapes with low SNH and high densities of pests, predators potentially disperse if local pest densities are too low. However, predation rates tended to increase with increasing SNH. An explanation for this contradiction could be the independent measuring of predation rates and natural enemy densities in our design. We used aphid cards to

record predation rates during the essential period of milk ripening while predators were accumulated over the whole growing period. Both measures therefore cover different timeframes and relations might be disguised. With this method, it is also impossible to control which predators are responsible for prey removal although we recorded the most important ground dwelling predators. A positive relation between natural pest control and the proportion of semi-natural habitats in a landscape has previously been reported (Karp *et al.* 2016; Rega *et al.* 2018; Sutter *et al.* 2018). Whether this relation is visible however depends on the type of sentinel prey used which might explain why it was only marginally significant in our study (McHugh *et al.* 2020).

The densities of cereal leaf beetles and parasitoids were modulated by landscape SNH, decreasing towards the field centres in landscapes with high SNH and increasing in landscapes with low SNH. We assume lower parasitoid densities arose from reduced host densities in complex landscapes. Landscape mediated effects on pests and parasitoids were most pronounced in the field centres and decreased towards the field edges. Field edges underlie a magnitude of different stressors influencing insect populations (e.g. gradients of management intensity, spillover and colonization effects) whereas conditions in field centres are much more controlled and stable. While our results for field centres are in line with the findings of Grab *et al.* (2018), the distance patterns found for cereal leaf beetles and parasitoids differ from previously reported patterns (Pollier *et al.* 2019). Previous studies generally neglected possible interactions of distance and landscape complexity, often only assessing densities in field centres (e.g. Grab *et al.* (2018)). Our study design allowed us to investigate effects of distance and SNH on predator densities independently. We assume that different patterns for distance functions previously reported in the literature could have arisen from modulation by landscape level SNH.

Our results suggest that distance functions, apart from depending on crop type, often interact with landscape characteristics such as SNH. In studies not addressing or standardizing landscape parameters, distance functions might be biased. However, little is known which landscape level parameters influence distance functions across different trophic levels. Different taxa are affected by different aspects of landscapes they utilise (e.g. parasitoids need floral nectar sources in

contrast to ground dwelling predators (Tscharnke, Rand & Bianchi 2005)) and the definitions of SNH in the literature vary with geographic location and individual preferences of authors. Therefore, more research is needed to clarify how distance functions respond to the surrounding landscape and how they can be managed to better exploit ecosystem service potentials.

Effects of adjacent AES habitats

AES are widely implemented to benefit biodiversity mediated ecosystem services in agricultural landscapes. In particular, the AES habitats investigated in this study are established to foster and ensure pollinator populations. AES habitats however have occasionally been shown to benefit pest control (Fusser *et al.* 2018; Mestre *et al.* 2018; Pollier *et al.* 2019). Beneficial effects of adjacent AES habitats varied between years. In oilseed rape, AES habitats benefitted ground dwelling predator assemblages at the trait level (body-size and diet; Boetzl *et al.* (2019)). Effects of AES habitats on adjacent crops however are potentially disguised or buffered by ecological contrast between AES habitats and the adjacent crops (Marja *et al.* 2019). In our study, this contrast is larger in oilseed rape than in cereal cultures. One important factor that might have influenced the activity patterns of ground dwelling predators is microclimate and shading. While oilseed rape has a closed canopy already early in the season retaining a dark, cool and moist microclimate at the ground, cereals remain largely open resulting in light and dry conditions. In contrast to Marja *et al.* (2019), we assume that a small contrast between AES habitat and crop is beneficial for ground dwelling predators as species supported by the AES habitats cannot persist in adjacent crop habitats if the contrast is too large. We assume the relatively low contrast between AES habitats and cereal fields facilitated ground dwelling predator spillover into the fields while the high contrast between AES habitats and oilseed rape fields filtered out ground dwelling predators resulting in distance decay functions.

Predation rates were higher in fields adjacent to refreshed flowering fields than in all other fields, although predator communities or densities did not differ. Predation rates however cannot simply be linked to predator densities recorded in our study due to the method of recording used (see

above). Ultimately, elevated predation rates could also be driven by other co-factors such as density-dependent aggregation of pests and predators.

Contrary to our results, Tschumi *et al.* (2016a) observed clear negative effects of adjacent AES habitats (flower strips) on densities of cereal leaf beetle (CLB) larvae and consequently positive effects on crop yields in winter wheat. CLB larvae densities measured in Tschumi *et al.* (2016a) were up to five times higher than densities measured in this study which potentially disguises effects. Our data show that relations might not be general and that effects of AES habitats are potentially blurred by other factors. However, we studied the effects of AES habitats during the growing season. We assume AES habitats benefit pest control essentially by providing undisturbed habitats for overwintering and by providing pest control agents for recolonization of the fields after disturbances (i.e. soil management or harvest; see Schneider *et al.* (2016)).

Crop rotation affects pest control services and species assemblages

Edges are important predictors for many ecosystem service agents on the landscape level as high edge-density increases landscape complexity and thereby the diversity of micro-habitats that allow species to persist, procreate and flourish also after crop harvest (Tschardtke *et al.* 2005; Martin *et al.* 2019). Distance decay functions of ecosystem service agents originating from edges would be expected. However, in winter cereals distance functions were not uniform and partly depended on landscape context (while they had been independent from landscape level SNH in oilseed rape in the previous year). Apparently, distance decay functions are not universal and potentially affected by a multitude of different factors. As many of these are still unknown predicting distance functions for pest control potentials remains difficult. More research is needed to identify effects of different crop rotations and how these depend on management and ecological contrast between crops.

Carabid species assemblages differed clearly between the study years as the field crop and the associated management changed. This difference was most pronounced in the field centres and

decreased towards the field edges. This illustrates the importance of field edges to stabilize and secure predator assemblages as they buffer crop and management driven assemblage shifts and allow different species to persist in a landscape over crop rotation. Together with increased species richness of carabid beetles towards field edges, this indicates that carabid assemblages in field centres are a subset of the local species pool of arable lands filtered by crop type and associated management. Simplifying landscapes by increasing field sizes for higher efficiency in modern agriculture might therefore be harmful in the long term as species affected by crop rotation driven assemblage shifts cannot find refuge in adjacent permanent habitats or field margins. Sirami *et al.* (2019) showed that decreasing field sizes (and therefore increasing landscape complexity as well as margin to field ratio) benefits biodiversity across multiple levels. Increasing field sizes might eventually eliminate dispersal limited, perennial species from the local species pools by reducing the amount and availability of suitable source and refuge habitats. As natural pest control is closely linked to predator diversity (Dainese *et al.* 2019), simple landscapes with large field sizes and low complexity might ultimately erode natural pest control potentials.

Conclusions

Under the current regime of conventional high input agriculture, farmers regulate pests by agrochemicals and cereal crop yields by fertilizer input. At the same time, natural pest regulation is not fully exploited or even hampered by pesticide applications (Krauss, Gallenberger & Steffan-Dewenter 2011). As this system is both cost intensive and potentially harmful to biodiversity mediated ecosystem functioning, replacements for inputs will be needed in the future. Understanding the distance functions underlying the distribution of beneficial ecosystem service providers as well as their interactions with landscape composition will be essential for the planning of agricultural landscapes under ecological intensification policies. Distance functions however are not universal - depending on the measured variable, distance functions are affected by crop type, landscape context or habitat configurations. This explains contradicting results obtained from previous studies and emphasizes the need for a deeper, holistic understanding of these functions and their drivers. Our results show that natural pest control is working in small as well as large fields. Field edges or margin habitats however are important to secure predator diversity in agricultural landscapes throughout management changes. We therefore recommend a network of margin structures (such as AES habitats) in agricultural landscapes to foster natural pest control as suggested by Martin *et al.* (2019). Also, semi-natural habitats in agricultural landscapes are beneficial and need to be conserved. Policymakers are advised to stop and preferably reverse simplification of agricultural landscapes. Effects of AES habitats on natural pest control in adjacent fields are not universal and affected by ecological contrast between the habitats and the adjacent crops as found by Marja *et al.* (2019) for pollinators. This relationship between AES habitats and adjacent crop fields could be exploited in the future to maximise benefits. AES habitats could be improved to provide refuges and resources to a variety of ecosystem service providers at the same time (e.g. open soil patches for ground nesting bees and wasps, flower resources for pollinators and parasitoids) to achieve both supporting pollination services as well as enhancing natural pest control. To better target ecosystem services, AES habitats need to be tailored more specifically towards a function they should fulfil in interaction with the adjacent crop (e.g. AES habitats could be used to pull pests from the crop or to provide

reservoirs of predators that can persist in the adjacent crop). Only if the effects of adjacent habitats, edge proximity and the distribution of ecosystem service agents within a field and across agricultural landscapes are understood, pest control potentials can be predicted precisely and utilised to the potential maximum. Within the framework of ecological intensification, these functions will be needed to reach an optimum between field size and ecosystem service potential to maximize yields in a sustainable way.

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Supplementary material VII

Data collection

Along the distance transects, different factors concerning natural pest control on various trophic levels were recorded on each study site using different methods throughout the vegetation period from 04. April until 14. July 2017. One field used in 2016 (07_GAU) was excluded to achieve comparability as it was sown with a summer crop (summer barley, sowing date end of April).

Pest recordings

Milk ripening in winter cereals in the study region usually takes place in June with the concrete duration and timing of this period being determined by local climate and weather. As pest pressure during this period will directly affect yields, cereals are considered most vulnerable during this period.

Therefore, pest densities (as well as predation rates) were recorded on three dates during this period (31 May / 01 June, 13 / 14 June & 27 / 28 June). Pest densities were recorded via sweep netting on the three transects parallel to the field edges at each of the three different distances to the field edges. Sweep netting protocol followed Krauss, Gallenberger and Steffan-Dewenter (2011) with 10 sweep net (gauze net with 40 cm diameter) swings per transect resulting in 30 swings per distance (Figure VII.1). After each transect, we counted densities of different pests and ladybirds. However, in general very few pests were found and in major cereal pests such as aphids, too few individuals were counted for proper analyses. We therefore only used CLB larvae (*Oulema sp.*) which were recorded in sufficient densities for the analyses and expected the effects of the other pests to be neglectable due to their low densities.

Predation rates

Predation rates were also assessed three times per field during the period of milk ripening (31 May to 03 June; 13 to 16 June; 27 to 30 June) using aphid cards on the soil level (Boetzl, Konle & Krauss 2019). We used one transect with one aphid card (10 cm x 6 cm folded in the middle along the longer side) containing 8 aphids (*Sitobion avenae*) per distance to the field edge (3 cards per site). The cards were made out of coarse sandpaper (grain 400) and set up like a roof with the aphids glued in a row to one of the insides in order to prevent the aphids from washing off during rainfall. The aphids were fixed to the card using water soluble spray glue (Cléopâtre Aéro Colle). All cards were placed in the freezer immediately after manufacturing and stored no longer than two days at -20°C. Aphid cards were exposed for 24 hours, subsequently recollected and immediately checked for predation.

Ground dwelling predators

Pitfall traps were used to record ground dwelling predators. In each study site, three transects of pitfall traps were installed perpendicular to the field edge with each transect containing three traps in the different distances to the field edge and one trap in the adjacent AES habitat (12 traps per site / 9 in the control fields without adjacent AES habitat). Pitfall traps were active from 11/12 April until 04/05 July 2017 and emptied biweekly summing up to a total of 1620 pitfall traps in the cereal fields and 468 in the adjacent AES habitats (total: 2088). We lost a total of 18 pitfall trap samples due to wild animals and vandalism (1.1 %).

As pitfall trap containers, conventional glass honey jars (height: 9 cm, diameter: 7.5 cm) filled with 200 ml 1:3 ethylene glycol (auto-mobile antifreeze, H. Kerndl GmbH)–water mixture with odourless detergent as preservative were used. Traps were covered by clear polycarbonate roofs (25 × 25 cm²; ~10 cm above the ground). Trap samples were sorted in the lab for carabid beetles (Carabidae), staphylinid beetles (Staphylinidae) and spiders (Araneae) and carabid beetles were subsequently identified to species level following Müller-Motzfeld (2006).

Parasitoids

We used crossed window traps to record parasitoid densities in two intervals during the milk ripening period (08 to 12 June and 22 to 26 June). The traps were installed 10 cm above the cereal ears and were made out of clear polycarbonate (area of the two crossed parts: 15 cm high x 11 cm wide = 165 cm²) covered by a clear, squared polycarbonate roof (20 cm x 20 cm = 400 cm²). In total, 180 window traps (6 per site in 2 transects and 3 distances to the field edge) were active in each of the two sampling intervals (resulting in 360 trap samples). Window traps were active for 72 hours and insects were captured in oversaturated saltwater (300 g NaCl per 1000 ml H₂O) with a few drops of odourless detergent. Due to vandalism, weather and field management, we lost a total of 14 window trap samples (3.8 %). Trap samples were sorted in the lab and parasitoid wasps were counted.

Yields

Yields were recorded using 4 transects from the field edges to the field centres with three plots of 25 cm² (50 cm x 50 cm) at the distances used for all recordings in the fields (resulting in a total of 1m² per each of the three distances in each field). We harvested the plots during cereal crop harvesting period 06 – 14 July whenever the weather at that time allowed us to. For 3 out of 30 fields (10 %), we unfortunately had no data as these fields were harvested before we arrived at these plots due to the short harvesting windows in the study year.

All stems carrying ears were counted, the grains were threshed by a professional agricultural company and subsequently dried in a drying chamber (40°C) until no additional weight loss was detected. Grains were then weighed, counted and total yields calculated as decitonnes (dt) per hectare (ha = 10000 m²).

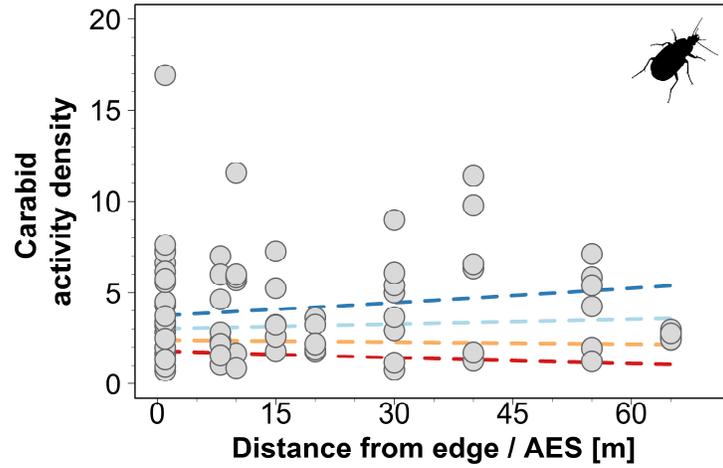


Figure VII.S1: Distance functions of carabid beetle activity density (excluding exclusively granivorous species). Colours represent predictions for four different SNH levels (from top to bottom 5, 10, 15 and 20 %). Dotted indicate lines non-significant distance functions (Statistics see text and Table VII.1).

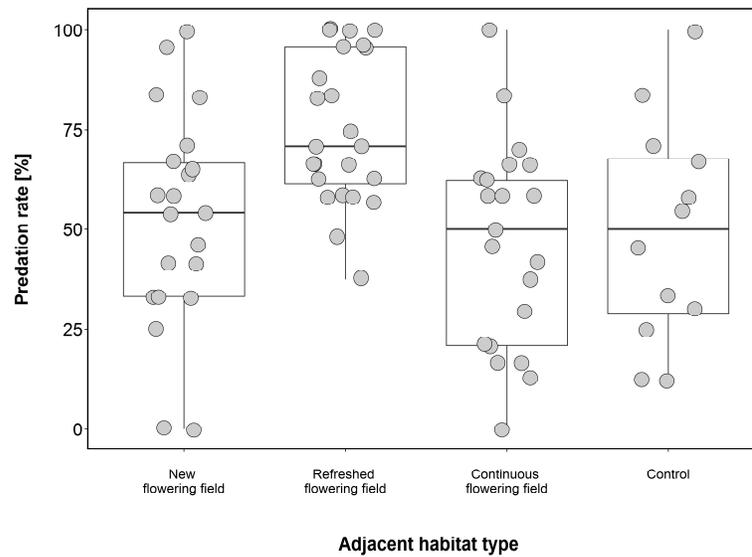


Figure VII.S2: Predation rates across the different study site types (excluding sites with calcareous grasslands). Statistics see text.

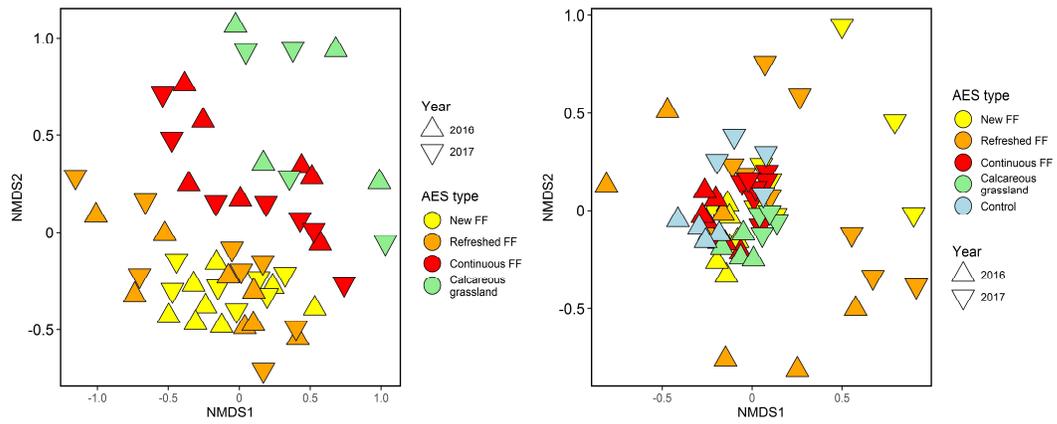


Figure VII.S3: NMDS ordinations for the carabid beetle assemblages between the two studied years. Left: AES habitats; Right: Crop field centres.

Table VII.S1: Location of the study sites with type of the adjacent agri-environmental scheme (AES habitat type), proportion of semi-natural habitat (SNH) in the surrounding landscape, AES habitat size as well as field size and the distances to the AES habitats used within the fields.

Site ID	Nearest village	AES habitat type	GPS (WGS 84)	crop	SNH [%]	Area AES [ha]	Area field [ha]	Within field Distances
01_REU	Reuchelheim	new flowering field	49.994097N 9.913864E	wheat	16.43	1.50	3.22	1 m, 10 m, 40 m
02_BUE	Büchold	new flowering field	50.010878N 9.945164E	wheat	10.90	2.92	4.80	1 m, 20 m, 65 m
03_WS1	Waldsachsen	new flowering field	50.041283N 10.371989E	wheat	7.59	1.67	2.30	1 m, 15 m, 55 m
04_SHW	Schwebenried	new flowering field	50.03625N 10.013122E	wheat	4.60	3.00	4.00	1 m, 8 m, 30 m
05_WIE	Wiesenfeld	new flowering field	49.995194N 9.685569E	wheat	18.73	0.29	0.31	1 m, 8 m, 30 m
06_STE	Steinfeld	new flowering field	49.941772N 9.678022E	triticale	12.92	0.31	1.50	1 m, 15 m, 55 m
08_DUR	Dürrfeld	new flowering field	49.969153N 10.352558E	barley	6.91	0.53	3.13	1 m, 10 m, 40 m
09_ZEL	Zellingen	refreshed flowering field	49.895914N 9.796075E	durum	3.63	0.32	2.66	1 m, 8 m, 30 m
10_BIL	Billingshausen	refreshed flowering field	49.877894N 9.720292E	barley	25.04	2.01	3.49	1 m, 8 m, 30 m
11_RIE	Rieden	refreshed flowering field	49.934694N 10.031019E	wheat	11.15	2.07	3.57	1 m, 15 m, 55 m
12_OBA	Oberaltertheim	refreshed flowering field	49.735775N 9.777983E	wheat	8.12	1.77	0.65	1 m, 10 m, 40 m
13_MUL	Mühlhausen	refreshed flowering field	49.96405N 10.050228E	rye	3.64	2.07	3.64	1 m, 20 m, 65 m
14_HOL	Höllrich	refreshed flowering field	50.070453N 9.794578E	spelt	15.92	0.25	1.00	1 m, 15 m, 55 m
15_WEY	Weyersfeld	refreshed flowering field	50.081411N 9.771431E	wheat	11.21	0.19	0.90	1 m, 10 m, 40 m
16_GRA	Gramschatz	refreshed flowering field	49.924433N 9.961481E	durum	7.32	0.44	1.21	1 m, 20 m, 65 m
17_BUR	Bühler	continuous flowering field	50.022803N 9.863192E	wheat	4.66	0.31	1.47	1 m, 8 m, 30 m
18_ERB	Erbshausen	continuous flowering field	49.906492N 10.011397E	wheat	11.30	1.49	4.30	1 m, 10 m, 40 m
19_WS2	Waldsachsen	continuous flowering field	50.054467N 10.352353E	wheat	8.90	1.52	4.12	1 m, 15 m, 55 m
20_BUC	Buch	continuous flowering field	50.057131N 10.421064E	wheat	7.29	1.59	2.60	1 m, 20 m, 65 m
21_DAS	Darstadt	continuous flowering field	49.677386N 10.005922E	wheat	4.04	2.43	5.45	1 m, 8 m, 30 m
22_VAS	Vasbühl	continuous flowering field	50.033525N 10.054167E	wheat	12.41	0.69	1.07	1 m, 8 m, 30 m
23_ABF	Abersfeld	continuous flowering field	50.083306N 10.399783E	wheat	7.46	0.73	2.09	1 m, 10 m, 40 m
24_BLO	Würzburg	calcareous grassland	49.761483N 9.923436E	wheat	6.39	0.47	6.40	1 m, 20 m, 65 m
25_KAS	Karlstadt	calcareous grassland	49.974089N 9.792319E	triticale	16.99	2.64	5.96	1 m, 15 m, 55 m
26_LEI	Leinach	calcareous grassland	49.851717N 9.801561E	barley	25.33	1.46	1.95	1 m, 8 m, 30 m
27_MAW	Gerbrunn	calcareous grassland	49.76735N 10.000133E	rye	21.14	0.41	2.38	1 m, 10 m, 40 m
28_ADE	Adelsberg	control	50.032794N 9.743556E	wheat	31.62	-	12.17	1 m, 8 m, 30 m
29_SHF	Schonderfeld	control	50.102178N 9.726753E	wheat	20.43	-	4.70	1 m, 10 m, 40 m
30_DAM	Dampfach	control	49.984758N 10.440328E	wheat	13.90	-	1.05	1 m, 20 m, 65 m
31_DON	Donnersdorf	control	49.963361N 10.407189E	wheat	7.57	-	1.33	1 m, 15 m, 55 m

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Table VII.S2: Species list for the different types of investigated cereals fields (ordered by adjacent AES habitat types; FF = flowering field) including the species' diet trait according to www.carabids.org (Homburg *et al.* 2014).

Species	New FF	Refreshed FF	Continuous FF	Calcareous grassland	control	diet
<i>Abax parallelepipedus</i>	1		1	1		predatory
<i>Abax parallelus</i>		1	1			predatory
<i>Acupalpus interstitialis</i>	5	7		1		omnivorous
<i>Acupalpus meridianus</i>	32	34	70	7	41	omnivorous
<i>Agonum muelleri</i>	18	20			125	predatory
<i>Amara aenea</i>	160	49	19	5	20	granivorous / frugivorous
<i>Amara apricaria</i>		1	2		5	granivorous / frugivorous
<i>Amara aulica</i>	36	113	10	2		granivorous / frugivorous
<i>Amara bifrons</i>	66	5				granivorous / frugivorous
<i>Amara communis</i>	1	1				granivorous / frugivorous
<i>Amara consularis</i>	3	160	6	22		granivorous / frugivorous
<i>Amara convexior</i>	19	45	58	9	1	granivorous / frugivorous
<i>Amara eurynota</i>	3					granivorous / frugivorous
<i>Amara familiaris</i>	8	4	5	2	1	granivorous / frugivorous
<i>Amara fulva</i>					1	granivorous / frugivorous
<i>Amara littorea</i>	2	2		1	2	granivorous / frugivorous
<i>Amara lucida</i>				2		granivorous / frugivorous
<i>Amara lunicollis</i>	5	2	3	1	8	granivorous / frugivorous
<i>Amara montivaga</i>	51	3		1		granivorous / frugivorous
<i>Amara ovata</i>	221	264	330	104	120	granivorous / frugivorous
<i>Amara plebeja</i>	68	5	11		7	granivorous / frugivorous
<i>Amara sabulosa</i>	4	4				granivorous / frugivorous
<i>Amara similata</i>	6	4	11		3	granivorous / frugivorous
<i>Anchomenus dorsalis</i>	7998	10310	12527	9242	1593	predatory
<i>Anisodactylus binotatus</i>	38	32	6		4	granivorous / frugivorous
<i>Asaphidion flavipes</i>	5	5	2	1	19	predatory
<i>Badister bullatus</i>	90	95	130	59	18	predatory
<i>Badister lacertosus</i>		1	6			predatory
<i>Badister sodalis</i>	78	168	76	123	3	predatory
<i>Bembidion deletum</i>	1					predatory
<i>Bembidion guttula</i>	7	3	82		2	predatory
<i>Bembidion lampros</i>	1168	594	794	178	411	predatory
<i>Bembidion lunulatum</i>	175	13	512	6	234	predatory
<i>Bembidion obtusum</i>	1282	1123	2009	460	561	predatory
<i>Bembidion properans</i>					16	predatory
<i>Bembidion quadrimaculatum</i>	5	1	7		5	predatory
<i>Bembidion tetracolum</i>					1	predatory
<i>Brachinus crepitans</i>	5420	15776	1274	941	156	predatory
<i>Brachinus explodens</i>	135	262	202	42	15	predatory
<i>Bradycellus harpalinus</i>	1	3				omnivorous
<i>Calathus ambiguus</i>	11				47	predatory
<i>Calathus cinctus</i>				1	132	predatory
<i>Calathus erratus</i>				3		predatory
<i>Calathus fuscipes</i>	28	11	29	39	3899	predatory
<i>Calathus melanocephalus</i>					12	predatory

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<i>Carabus auratus</i>	1	1				predatory
<i>Carabus convexus</i>				4		predatory
<i>Carabus coriaceus</i>			6	1		predatory
<i>Carabus granulatus</i>	2	1				predatory
<i>Carabus nemoralis</i>	2	2	2	4		predatory
<i>Carabus ulrichii</i>			1		5	predatory
<i>Carabus violaceus</i>	39		1	1		predatory
<i>Chlaenius vestitus</i>			1			predatory
<i>Clivina fossor</i>	107	15	69		23	predatory
<i>Demetrias atricapillus</i>	32	32	38	7	35	predatory
<i>Diachromus germanus</i>	4	2				granivorous / frugivorous
<i>Elaphrus uliginosus</i>			1			predatory
<i>Epaphius secalis</i>		20	1			predatory
<i>Harpalus affinis</i>	1111	1232	557	392	906	granivorous / frugivorous
<i>Harpalus atratus</i>	1	1	3	11		granivorous / frugivorous
<i>Harpalus dimidiatus</i>	120	150	33	109	21	granivorous / frugivorous
<i>Harpalus distinguendus</i>	320	314	35	14	7	granivorous / frugivorous
<i>Harpalus honestus</i>				1		granivorous / frugivorous
<i>Harpalus laevipes</i>					1	granivorous / frugivorous
<i>Harpalus latus</i>	11	17	8	1	2	granivorous / frugivorous
<i>Harpalus luteicornis</i>	43	90	107	16	17	granivorous / frugivorous
<i>Harpalus rubripes</i>	106	33	11	88	4	granivorous / frugivorous
<i>Harpalus rufipes</i>	821	1083	227	268	175	granivorous / frugivorous
<i>Harpalus serripes</i>		4	2	45	2	granivorous / frugivorous
<i>Harpalus signaticornis</i>	10	38	16	20	21	granivorous / frugivorous
<i>Harpalus subcylindricus</i>		1	9	5		granivorous / frugivorous
<i>Harpalus tardus</i>	4		1	6	9	predatory
<i>Lebia cruxminor</i>			2			predatory
<i>Leistus ferrugineus</i>	7	46	5	3	1	predatory
<i>Leistus spinibarbis</i>			1			predatory
<i>Limodromus assimilis</i>	29	16	13	4	8	predatory
<i>Loricera pilicornis</i>	100	183	124	17	144	predatory
<i>Microlestes maurus</i>	40	82	126	57	11	predatory
<i>Microlestes minutulus</i>	24	31	56	19	9	predatory
<i>Molops elatus</i>				11		predatory
<i>Molops piceus</i>		2	2			predatory
<i>Nebria brevicollis</i>	24	177	13	12	20	predatory
<i>Nebria salina</i>	62	134	44	130	181	predatory
<i>Notiophilus aestuans</i>	50	40	48	40	12	predatory
<i>Notiophilus biguttatus</i>	317	418	399	171	63	predatory
<i>Notiophilus germinyi</i>	23	13	3	3	1	predatory
<i>Notiophilus palustris</i>	40	37	35	2	5	predatory
<i>Ophonus ardosiacus</i>	285	71	10	4		granivorous / frugivorous
<i>Ophonus azureus</i>	103	59	35	15	1	granivorous / frugivorous
<i>Ophonus laticollis</i>		2				granivorous / frugivorous
<i>Ophonus puncticollis</i>		1		2		granivorous / frugivorous
<i>Ophonus rufibarbis</i>	3			1		granivorous / frugivorous
<i>Ophonus rupicola</i>	13	9	1	1		granivorous / frugivorous
<i>Panagaeus bipustulatus</i>	2	3	2	7	1	omnivorous
<i>Panagaeus cruxmajor</i>		3				omnivorous

Chapter VII: The effects of AES habitats on pest control in adjacent cereal fields

<i>Paradromius linearis</i>		1				predatory
<i>Pedius longicollis</i>	6	1	11	1	42	predatory
<i>Philorhizus melanocephalus</i>			1			predatory
<i>Philorhizus notatus</i>		1				predatory
<i>Poecilus cupreus</i>	1933	3248	3284	1773	1259	omnivorous
<i>Poecilus lepidus</i>				1	2	predatory
<i>Poecilus versicolor</i>	37	1	2	1	10	predatory
<i>Polistichus connexus</i>	5		10			predatory
<i>Pterostichus anthracinus</i>					1	predatory
<i>Pterostichus macer</i>	70	51	40	14		predatory
<i>Pterostichus melanarius</i>	1372	1535	1878	559	713	predatory
<i>Pterostichus melas</i>		31		1		predatory
<i>Pterostichus niger</i>		1				predatory
<i>Pterostichus oblongopunctatus</i>		1		1		predatory
<i>Pterostichus ovoideus</i>	6	11	9	1		predatory
<i>Pterostichus strenuus</i>	5	15	11		9	predatory
<i>Pterostichus vernalis</i>	28	43	139		19	predatory
<i>Stenolophus teutonius</i>		1				omnivorous
<i>Stomis pumicatus</i>	23	28	3	3	7	predatory
<i>Syntomus truncatellus</i>	2	1	38	9	3	predatory
<i>Synuchus vivalis</i>	3	5	2			granivorous / frugivorous
<i>Tachys bistriatus</i>	1	3	5		1	predatory
<i>Trechoblemus micros</i>	1	3				predatory
<i>Trechus quadristriatus</i>	3223	2312	6030	1081	1234	predatory
<i>Zabrus tenebrioides</i>					1	granivorous / frugivorous

Table VII.S3: Results obtained from linear mixed effects models (lmer) including a random intercept for “study site ID” on different responses over all study sites (including calcareous grasslands). df = degrees of freedom (numerator, denominator); F and p-values obtained by type II sums of squares ANOVA with Kenward–Roger approximation; bold printing indicates significant $p < 0.5$; R^2_m = marginal R^2 ; R^2_c = conditional R^2 .

Response / Factors	distance as	df	F	p	R^2_m	R^2_c
Carabid species richness						
AES habitat type		4, 25	1.29	0.299		
distance ¹		1, 56	11.02	0.002 **		
SNH	linear	1, 27	0.59	0.447	0.20	0.63
distance ¹ : AES habitat type		4, 56	0.87	0.487		
distance ¹ : SNH		1, 56	0.50	0.481		
Carabid activity density						
AES habitat type		4, 24	0.87	0.494		
distance ¹		1, 55	5.93	0.018 *		
SNH	linear	1, 25	3.39	0.078 (*)	0.14	0.86
distance ¹ : AES habitat type		4, 55	1.80	0.143		
distance ¹ : SNH		1, 55	5.32	0.025 *		
Staphylinid activity density						
AES habitat type		4, 26	0.23	0.918		
distance ¹		1, 53	< 0.01	0.964		
distance ²		1, 52	12.05	0.001 **		
SNH	quadratic	1, 32	0.65	0.425	0.14	0.55
distance ¹ : AES habitat type		4, 53	0.79	0.538		
distance ² : AES habitat type		4, 51	0.93	0.453		
distance ¹ : SNH		1, 55	0.53	0.472		
distance ² : SNH		1, 53	0.01	0.932		
Spider activity density						
AES habitat type		4, 25	0.69	0.609		
distance ¹		1, 55	0.58	0.451		
SNH	linear	1, 26	7.43	0.011 *	0.19	0.77
distance ¹ : AES habitat type		4, 55	0.44	0.781		
distance ¹ : SNH		1, 55	1.74	0.193		
Parasitoid activity density						
AES habitat type		4, 25	0.73	0.580		
distance ¹		1, 55	0.54	0.466		
SNH	linear	1, 25	2.42	0.132	0.16	0.83
distance ¹ : AES habitat type		4, 55	0.49	0.741		
distance ¹ : SNH		1, 55	5.80	0.019 *		
Cereal leaf beetle density						
AES habitat type		4, 25	0.57	0.689		
distance ¹		1, 55	4.43	0.040 *		
SNH	linear	1, 26	2.83	0.105	0.21	0.77
distance ¹ : AES habitat type		4, 55	0.74	0.567		
distance ¹ : SNH		1, 55	4.39	0.041 *		
Predation rates						
AES habitat type		4, 26	2.75	0.049 *		
distance ¹		1, 56	1.90	0.173		
SNH	linear	1, 28	3.37	0.077 (*)	0.26	0.62
distance ¹ : AES habitat type		4, 56	1.24	0.304		
distance ¹ : SNH		1, 57	0.05	0.831		
Yield [dt / ha]						
AES habitat type		4, 28	2.46	0.069 (*)		
distance ¹		1, 47	3.20	0.080 (*)		
distance ²		1, 45	10.1	0.003 **		
SNH	quadratic	1, 30	1.00	0.325	0.28	0.61
distance ¹ : AES habitat type		4, 46	1.27	0.296		
distance ² : AES habitat type		4, 45	1.42	0.242		
distance ¹ : SNH		1, 49	0.09	0.771		
distance ² : SNH		1, 47	0.16	0.691		



Flower rich agri-environment scheme habitats not only provide food sources for pollinators in rather simple agricultural landscapes, they also provide shelter for many species of natural enemies to persist in agricultural landscapes.

Chapter VIII: General Discussion

Pest control and pollination are essential ecosystem services securing agricultural production, however in times of global declines in biodiversity and insect biomasses, ecosystem service provisioning in agricultural landscapes is at stake. These dramatic declines add to the self-caused pressures challenging modern agricultural production such as soil degradation and over fertilization. Together, they threaten the future of agricultural production. To increase sustainability, agriculture needs to become more biodiversity friendly. This will only be possible through an ecological transition of current management. Although this transition has started, it is still in its fledgling stage with many of the concrete steps taken being of unknown efficiency. Among other measures, agri-environmental schemes (AES) are established in agricultural landscapes to add heterogeneity and support biodiversity, but their actual effects are largely unknown.

Here, I investigated on the example of real-life AES whether and how the goals of biodiversity conservation and ecosystem service provision can be achieved simultaneously. To obtain reliable results, I validated methods to assess biodiversity and ecosystem services. Standard pitfall traps proved to be a reliable and good method to investigate ground dwelling predator assemblages even though other trap types caught more species as these trap types are harder to handle and not universally applicable (Chapter III). I showed that sentinel prey cards using aphids recorded predation rates, delivered consistent results across different card types when sampling effort was standardized and that recorded predation rates could be linked to predator assemblages (Chapter IV). In my field studies, I showed that the main factor determining biodiversity in currently established AES habitats is their temporal continuity (Chapter V). The size of the AES habitats and landscape context are of lesser importance for overall biodiversity, but patterns differ among taxonomic groups (Chapter V). The effects on pest control and natural enemies in adjacent crop fields varied with crop type. In adjacent oilseed rape, AES habitats increased the proportion of predatory ground beetles and ground dwelling predators showed clear distance decay from the

field edges towards the field centres (Chapter VI). These functions were not always present in winter cereals but increasing distance to the field edge also increased effects of crop rotation on carabid beetle assemblages, indicating that field edges act as refuge and source habitats for beneficial carabid beetles (Chapter VII).

My findings highlight that AES habitats can and do reach their goals for some taxonomic groups, in some landscapes and in some adjacent crops. Beneficial effects are, however, not universal. Based on my results, current AES can be optimized but the effects of different combinations of adjacent habitats and crops need further investigation. Only if the interactions between specific habitat combinations and their effects on distance functions of natural enemies, pest control and yields are understood, can the placing of AES habitats in agricultural landscapes be planned optimally to maximize benefits. Maximizing pest control potentials and making agricultural landscapes biodiversity friendly will be crucial for both ecological intensification and a sustainable future for our food production.

VIII.1 Methods for assessing pest control potentials – why critical approaches are needed

Critical assessments of conventionally used methodology under the light of the latest scientific standards as well as replication of experiments to confirm supposedly known facts are highly important but often lacking (Nakagawa & Parker 2015; Parker *et al.* 2016; Kelly 2019).

Since its first use by (Dahl 1896), the general design of pitfall traps has undergone little changes. Various studies have investigated variations in different aspects of pitfall trap design (e.g. the colour of traps (Buchholz *et al.* 2010; Brown & Matthews 2016), the presence and colour of rain covers (Buchholz & Hannig 2009; Brown & Matthews 2016; Császár *et al.* 2018), the effects of sampling interval length (Schirmel *et al.* 2010), spatial distribution of traps (Ward, New & Yen 2001), different preservatives (Schmidt *et al.* 2006; Skvarla, Larson & Dowling 2014) as well as pitfall trap diameters and the use of funnels (Lange, Gossner & Weisser 2011; Brown & Matthews 2016; Császár *et al.* 2018)). These studies assessed the effects of variations in design on species richness and total catches. However, no study so far has looked deeper into resulting assemblages and how these are determined by different pitfall trap designs. These changes together with changes in functional aspects of natural enemy assemblages could, however, significantly bias predictions drawn from trap catches.

We compared four different commonly used pitfall trap types (standard pitfall traps, traps with plastic rims and with V- and X-shapes guidance barriers; Chapter III). While guidance barriers resulted in higher catches, species richness and more homogenous assemblages, traps with plastic rim caught less staphylinid beetles and spiders and significantly shifted carabid species assemblages compared to the other trap types and caught on average larger species (Chapter III). Ordinary simple pitfall traps caught similar assemblages than guidance barrier traps, but more traps were needed to reach a comparable species richness (Chapter III). We therefore recommend using guidance barrier traps where possible and wherever complete species inventories are needed but in all other cases, simple pitfall traps should be used. In order not to under-sample assemblages, traps should not be used individually but in several transects, as advised by Kotze *et al.* (2011). In the studies presented in Chapters V, VI and VII, we therefore used simple pitfall

traps in three transects that were subsequently pooled to obtain a more realistic assessment of the species assemblages.

Compared to pitfall traps, methods for assessing predation are relatively new. Quantifying ecosystem services has only recently attracted more attention in the context of global biodiversity loss and ecological intensification approaches (Birkhofer *et al.* 2017). Since the late 20th century, different approaches have been proposed to quantify pest control artificially in the field with sentinel and artificial prey methods being the simplest and most widely used methods. A magnitude of different sentinel prey types has been proposed and used (including e.g. aphids (Gardiner *et al.* 2009; Ximenez-Embun, Zaviezo & Grez 2014; Karp *et al.* 2016), corn earworm eggs (Meehan *et al.* 2012), fall armyworm larvae (Meehan *et al.* 2012), wax moth larvae (Meehan *et al.* 2012; Zirbel *et al.* 2017), cabbage moth larvae (Ferrante, Barone & Lövei 2017), ladybird eggs (Schneider, Krauss & Steffan-Dewenter 2013), onion fly pupae (Menalled, Lee & Landis 1999), earthworms (Tschumi *et al.* 2018), mealworms (Tschumi *et al.* 2018) as well as artificial plasticine caterpillars (Howe, Lövei & Nachman 2009; Howe, Nachman & Lövei 2015; Lemessa, Hambäck & Hylander 2015)) but measured predation rates could rarely be linked to predator assemblages and results were often contradicting (see e.g. Greenop *et al.* (2019), Zaller *et al.* (2009) and Rusch *et al.* (2015)).

This highlights the need for a standardized method that is both easy and universally applicable as well as delivering predation rates that can be linked to predator assemblages (i.e. the actual ecosystem service delivered). Sentinel prey cards using aphids are such a method. These aphid cards have gained popularity over the last few years (see e.g. Winqvist *et al.* (2011), Ximenez-Embun, Zaviezo and Grez (2014) or Holland *et al.* (2017)) and are included in the proposed methods for Rapid Ecosystem Function Assessment (REFA) (Meyer, Koch & Weisser 2015). Here, we tested this method critically and showed that obtained predation rates are independent from card size and are positively related to (non-granivorous) carabid beetle activity densities as well as body sizes (an important assumed predictor as large predators also need to consume more prey; Chapter IV). Aphid cards are a simple, cost effective way to record predation rates and

deliver meaningful results. These results also verify the method used in the field trials for quantifying predation rates along a distance transect in Chapter VII.

Future critical approaches should both verify existing methods as well as try to relate predation rates obtained by using different methods to each other and to the assumed underlying mechanistic drivers in natural enemy assemblages (i.e. densities, proportions of specialized predators, body-size etc.). While a unified method (or set of methods) to record natural enemy assemblages and quantify pest control would be ideal, researchers will likely not synchronize their methods on a larger scale. In many cases, more specific approaches might be more meaningful (i.e. if a specific crop pest is studied and predation on this specific crop pest is of interest) and diversity in methods also opens new frontiers and triggers new ideas on how to improve methodology.

We however showed that the choice in methods can affect resulting patterns - for example the choice in pitfall trap can bias resulting predator assemblages. As different guilds of natural enemies and predatory species vary significantly in mobility, target prey types, level of prey specialisation, food intake rates and activity windows, the selection of prey item, placing of sentinel prey items and the time when predator assemblages and predation are recorded could significantly affect resulting predictions (Birkhofer *et al.* 2017). In order to compare studies that do not use unified methodologies, such biases need to be critically investigated, quantified and heeded.

VIII.2 Giving biodiversity a future in agricultural landscapes

In the recent past, staggering declines in abundances and diversity of insects have been uncovered and have alerted policymakers (Hallmann *et al.* 2017; Seibold *et al.* 2019; van Klink *et al.* 2020). As insects are among the most important ecosystem service agents, they are a crucial backbone in the efforts to make agricultural production sustainable under ecological intensification (Bommarco, Kleijn & Potts 2013; Dainese *et al.* 2019). To stop biodiversity loss and restore ecosystem service potentials in agricultural landscapes, agri-environment schemes (AES) have

been introduced and specifically tailored habitats are established in agricultural landscapes (Scheper *et al.* 2013; Ekroos *et al.* 2014). These AES have two main goals, (i) conserving and supporting biodiversity and (ii) maintaining and enhancing ecosystem services, achieving both goals simultaneously is, however, intricate (Scheper *et al.* 2013; Ekroos *et al.* 2014). The effectiveness of AES habitats is constantly under debate (Kleijn *et al.* 2011; Kleijn *et al.* 2019; Batáry *et al.* 2020). Of special interest is the question how large AES and semi-natural habitats should ideally be and whether they work equally well in different types of landscapes (Tscharntke *et al.* 2005; Tscharntke, Batáry & Dormann 2011; Ekroos *et al.* 2014; Grass *et al.* 2019).

Here I compared the effects of four different examples of AES habitats (along independent gradients of habitat size and landscape semi-natural habitat (SNH) proportion) and semi-natural habitats along a gradient of temporal continuity (Chapter V). I investigated effects on species richness (conservation) as well as on ecosystem service agents across 12 taxonomic groups and 1519 taxa (Chapter V). I found temporal continuity of AES habitats to be the most important factor affecting local biodiversity (Chapter V). Multi-taxa diversity as well as diversity of pollinators and single taxonomic groups benefitted from more temporal continuous habitats (Chapter V). Within the gradients investigated, AES habitat size did not limit local biodiversity and landscape SNH proportion only positively affected bee richness (Chapter V). In contrast to previous studies, multi-diversity in AES habitats was not dependent on landscape SNH proportion (as shown for multi-diversity in crop fields by Sirami *et al.* (2019)) which indicates that AES habitats also work in landscapes with low remaining SNH as source habitats for biodiversity (Chapter V). Especially in such comparably simple landscapes with low remaining SNH, the effects of AES were previously predicted to be largest by Tscharntke, Batáry and Dormann (2011).

A previous assessment found that AES mainly support common generalist species of the agricultural landscape and not the conservation of rare and endangered species (Kleijn *et al.* 2006). While I cannot confirm this statement on the basis of my results, AES habitats did host different species assemblages compared to semi-natural habitats for most taxa investigated with

assemblages shifted along the axis of temporal continuity (Chapter V). This indicates that they are at least not equivalent to semi-natural habitats and cannot replace semi-natural habitats. Both habitat types work complementary to each other. This emphasizes that in order to provide refuge for a maximum of regional biodiversity, both habitat types are needed in agricultural landscapes.

While pollinators benefitted from AES habitats with higher temporal continuity, natural enemies were equally diverse in younger AES habitats with carabid beetles as an important group even reaching peak richness in these habitats (Chapter V). This indicates that AES habitats of different ages and temporal continuities may have additive effects on both overall ecosystem service potentials and overall biodiversity within a landscape. Some previous studies have called for AES habitats to be tailored more specifically towards the goals they are meant to fulfil (Batáry *et al.* 2011; Holland *et al.* 2016; Cole *et al.* 2020). Based on my results, different taxonomic and trophic groups reacted differently to the factors and habitat types investigated, which shows that a unified perfect solution is hardly feasible (Chapter V). In order to support a maximum of biodiversity and ecosystem service potentials simultaneously within agricultural landscapes, a mosaic of different habitat types increasing landscape heterogeneity might be more effective than a unified compromise solution.

VIII.3 Mind the context – distance functions of pest control depend on crop type and habitat configuration

While local management (e.g. fertilization, crop cultures, organic vs. conventional or land-use intensity) and landscape level factors (e.g. semi-natural habitat cover or landscape complexity) have been investigated to a larger extent, the effects of within-field distance have comparatively rarely been assessed. Therefore, distance functions of natural pest control in different landscapes and in relation to different crop cultures, management or adjacent habitats are mostly unknown. Field edges differ significantly from field interiors as they directly border adjacent habitats and are therefore affected by biotic and abiotic interactions with these (Tschardtke *et al.* 2005). Field edges undergo lower management intensity and are the corridors for species spillover and

invasions and thus provide a greater range of ecological niches (Batáry *et al.* 2012). Positive effects of field edges on natural enemies and pest control would therefore be expected.

I assessed natural enemy assemblages in crop fields bordering AES habitats in two consecutive years (with oilseed rape as crop in the first and winter cereals as crop in the second year. In winter cereals, I additionally recorded pest control and crop yields. In both years and both crops, carabid beetle richness decreased from the field edges towards the field centres (Chapters VI & VII). This distance decay in carabid species richness was previously also occasionally reported for pumpkin (Fusser *et al.* 2018) and winter cereals (Clough *et al.* 2007; Anjum-Zubair *et al.* 2010; Batáry *et al.* 2012) and could be a general pattern. If different habitat types (or crops) that support different species assemblages border each other, individuals from both habitats will regularly cross the border and spill over into the adjacent habitat increasing the species richness near the edge (Tscharntke, Rand & Bianchi 2005). This so called ‘reciprocal positive edge response’ decreases with increasing distance to the field edge as unfavourable conditions and limited mobility filter out species originating from the adjacent habitat or preferring edge areas (Rand, Tylianakis & Tscharntke 2006).

In this context, field edges seem to be important habitats allowing species to persist over crop rotations. Although carabid assemblages had the highest species richness near the field edge in both years, assemblages of both years were also most similar to each other near the field edge (Chapter VII). This indicates that field edges buffer crop management driven assemblage shifts and allow species to persist throughout crop rotations. Beneficial effects of edge density within agricultural landscapes have previously been shown with natural enemy densities peaking in landscapes with the highest edge density simultaneously increasing natural pest control (Martin *et al.* 2019). To increase edge density, field sizes need to be reduced as more habitat patches directly result in more edge areas. In smaller fields, the edge-interior ratio is increased which, according to my results, will likely increase mean carabid richness per field (Chapters VI & VII). Smaller field sizes have previously also been shown to increase overall biodiversity in agricultural landscapes (Sirami *et al.* 2019).

Activity densities of carabid beetles, staphylinid beetles as well as spiders in oilseed rape decreased with increasing distance to the field edge (Chapter VI). In winter cereals however, carabid and staphylinid activity densities increased towards the field centres while spiders showed no trend in activity densities (Chapter VII). Distance functions for these groups are thus not universal – they likely depend on crop type and / or management regimes. While distance effects on ground dwelling predators in oilseed rape had not been assessed previously, distance functions obtained for winter cereals in previous studies were contradictory. Several studies found increased activity densities of carabid beetles in field centres compared to field edges (Anjum-Zubair *et al.* 2010; Birkhofer, Wolters & Diekötter 2014) while others found either no relationship (Batáry *et al.* 2012) or a decrease from the field edges towards field centres (Pollier *et al.* 2019). These discrepancies could arise from different field management, prey availability, effects of adjacent habitats or could even be modulated by landscape context (as I showed for cereal leaf beetle larvae and parasitoids (Chapter VII)) and need further investigation as currently the underlying mechanisms driving distance functions are not yet fully understood.

Distance functions of cereal leaf beetle larvae as well as parasitoid wasps in winter cereals were modulated by landscape SNH proportion, with increased densities of both groups in the field centres in low SNH landscapes and decreased densities in the field centres in high SNH landscapes (Chapter VII). Such effects have previously not been shown and could possibly explain contradictory results in previous studies where landscape parameters were neither assessed nor standardized.

Despite positive effects on natural enemies, reduced management intensity near field edges lead to decreased crop yields (Raatz *et al.* 2019). In winter cereals, crop yields were affected by detrimental edge effects up to 27 m into the field (95 % of the maximum yield; Chapter VII) mainly due to a lower density of crop plants per area near the edge. These effects have to be considered as a reduction in field sizes might result in reduced crop yields due to the increase in edge area (Clough, Kirchweger & Kantelhardt 2020). A recent synthesis found, however, that increasing edge-density in agricultural landscapes (i.e. an increase in patches or a decrease in

individual field sizes) did not reduce yields (Martin *et al.* 2019). Yet, additional AES or semi-natural habitats also directly reduce crop area and it remains questionable if the resulting benefit in ecosystem services will replace losses in yield totals. To counter the problems of current intensive land-management and in order to make agriculture sustainable, we might however not be able to completely avoid such yield losses and will have to find a balance between sustainability and economic performance.

Direct effects of adjacent AES habitats on natural pest control or natural enemies have occasionally been shown (Fusser *et al.* 2018; Mestre *et al.* 2018; Pollier *et al.* 2019). In my studies, such effects were only visible on the level of functional traits in ground dwelling predator assemblages in oilseed rape. The presence of AES habitats roughly doubled the proportion of individuals of predatory carabid beetle species in adjacent oilseed rape fields compared to controls without adjacent AES habitats (Chapter VI). This proportion also showed a distance decay which emphasizes the positive effect of AES habitats for predatory species in oilseed rape (Chapter VI). Exclusively granivorous species made up 42.5 percent of all carabid beetle individuals in oilseed rape while they made up only 8.7 percent of all carabid beetle individuals caught in winter cereals in the following year. Whereas these granivorous carabid species are more and more frequently regarded as beneficial weed control agents (see e.g. Bohan *et al.* (2011) or Labruyere *et al.* (2016)) many of these species belong to the genus *Amara* and are known to occasionally feed on cruciferous seeds, thus could potentially also provide a disservice in oilseed rape (Müller-Motzfeld 2006; Williams *et al.* 2010). The increase in individuals of predatory species by adjacent AES habitats in oilseed rape could therefore be more beneficial to pest control as it seems at a first glance. Adjacent AES habitats also decreased the proportion of large species near the field edge in oilseed rape (Chapter VI). While body-size is generally linked to food intake (Rusch *et al.* 2015), species of different body-sizes usually prey on different food items and thus a more diverse size distribution equals a more diverse spectrum of consumed prey (Williams *et al.* 2010). In contrast to my results, Tschumi *et al.* (2016a) showed that flower strips decreased cereal leaf beetle (CLB) larvae densities near the field edge in adjacent cereal fields and that the presence of

flower strips increased crop yields. In 2017, I found overall significantly less CLB larvae than Tschumi *et al.* (2016a) in their study which might indicate higher overall pest control in my study region and might have disguised beneficial effects of adjacent AES habitats for additional pest control. Recent studies on pollinators have shown that beneficial effects of AES habitats can also be disguised or buffered by ecological contrast between the AES habitats and the adjacent crops which might also have resulted in the limited effects of these habitats on natural enemies, as observed in my studies (Batáry *et al.* 2015; Marja *et al.* 2019).

Although adjacent AES habitats had limited direct effects on distance functions of natural enemies, their real importance is likely not visible in my data. AES habitats, as all other permanent habitat structures in agricultural landscapes provide food sources throughout the season and undisturbed places of refuge for overwintering and in times of intensive field management and thus allow natural enemy populations to persist (Tschardtke, Rand & Bianchi 2005; Schneider *et al.* 2016). AES habitats are important steppingstones providing shelter to many beneficial species in times of need and acting as source habitats for ecosystem service agents in adjacent agricultural fields after major disturbances.

Distance functions of natural enemies and pest control likely depend on crop type, habitat context and at least partly also aspects of landscape composition and configuration. As the distance functions of natural pest control shown here are rather short ranged, the logical recommendation would be to reduce crop field sizes to exploit higher densities and species richness of natural enemies in edge areas (at least in some crops). However, as distance functions are poorly studied and many of the possible interactions with other local and landscape level factors have not been tested so far, knowledge about the drivers of distance functions in different groups is extremely limited. More conclusive research is needed to unveil underlying mechanisms to allow concrete predictions of pest control potentials. If these mechanisms are understood, agricultural landscapes could be optimized in order to exploit a maximum of natural pest control potentials. My results provide an important step in this direction as they show both real world distance functions of natural pest control as well as possible interactions that need further investigation.

VIII.4 Synthesis - designing landscapes for ecological intensification

Beneficial effects of both landscape composition and configuration on pest control and natural enemies have previously been shown. For landscape composition, crop diversity was shown to increase predation and reduce pest populations (Bosem Baillod *et al.* 2017; Redlich, Martin & Steffan-Dewenter 2018). Green infrastructure of low management intensity such as grasslands or greenings in the surrounding landscape has been shown to enhance carabid diversity and densities (Purtauf *et al.* 2005; Sutter *et al.* 2018). Grassy margins specifically decrease aphid populations in adjacent fields (Bosem Baillod *et al.* 2017) and flower strips decrease pest densities near the field edge and increase overall crop yields (Tschumi *et al.* 2016a; Albrecht *et al.* 2020). The cover of semi-natural habitats (SNH) in agricultural landscapes positively affects overall agricultural diversity (Sirami *et al.* 2019) as well as natural pest control (Karp *et al.* 2016; Rega *et al.* 2018; Sutter *et al.* 2018).

However, recent large scale synthesis analyses have found complex and partly contradictory patterns between natural pest control and SNH across studies indicating that true relations are more complex and also depend on other factors, such as the distribution of SNH within landscapes indicating that landscape configuration might play a major role in natural pest control (Karp *et al.* 2018; Martin *et al.* 2019). In this context, landscape complexity, edge-density and smaller field sizes (which are all linked to each other) were shown to decrease aphid populations (Bosem Baillod *et al.* 2017), increase overall species richness (Sirami *et al.* 2019; Martin *et al.* 2020), natural enemy populations and natural pest control (Rusch *et al.* 2016; Martin *et al.* 2019). Several studies have therefore called for more diverse, more heterogenous agricultural landscapes with smaller field sizes (increased edge-density) and embedded semi-natural habitats to ensure and exploit natural pest control potentials (Bosem Baillod *et al.* 2017; Martin *et al.* 2019; Sirami *et al.* 2019).

For pollinators, previous studies have found positive effects of SNH (Steffan-Dewenter *et al.* 2002), which also modulated distance functions in mass flowering crop fields (Krimmer *et al.* 2019). Pollinator densities as well as pollination services in crops declined with distance to

adjacent AES habitats (Krimmer *et al.* 2019; Albrecht *et al.* 2020). Effects of AES habitats on pollinators in adjacent crops are, however, most pronounced if the ecological contrast between both habitats is high which emphasizes the importance of strategic placement of AES habitats in agricultural landscapes and indicates that simple landscapes benefit the most (Tschardtke, Batáry & Dormann 2011; Marja *et al.* 2019). Cole *et al.* (2020) therefore proposed a network of interconnected and complementary AES habitats to support pollinators in agricultural landscapes.

In my field experiments, ecosystem service providers responded differently to the surrounding landscape and the provided AES habitats. Natural enemies were equally diverse in all landscapes and AES types. Their distance functions were unaffected by landscape level semi-natural habitat proportion (SNH) in oilseed rape and SNH was subsequently dismissed early in the analysis (Chapter VI), but in winter cereals, spider densities were negatively related to SNH, predation rates tended to increase with SNH and SNH modulated distance functions of CLB larvae and parasitoids, decreasing their densities in field centres in high SNH landscapes and increasing densities in field centres in low SNH landscapes (Chapter VII). Pollinators benefitted from landscapes with higher SNH and AES habitats with higher temporal continuity (Chapters V, VI & VII). Younger, flower rich AES habitats likely provide food sources for many pollinators but for nesting of many species, more permanent habitats are needed.

My results show that some beneficial effects of field edges and AES habitats on natural enemies underlie a strong distance decay in some crops and are relatively short ranged (Chapters VI & VII), thus edge structures and AES habitats need to be closely embedded in the crop matrix. Field edges or margin habitats are important to secure predator diversity in agricultural landscapes throughout management changes (Chapter VII). These results indicate that smaller field sizes (higher edge-interior ratio) and AES habitats embedded between fields (a dense non-crop - crop interface) as suggested by Rusch *et al.* (2013) and Ekroos *et al.* (2014) would be recommended to boost natural pest control.

Based on my results, agricultural landscapes need to provide permanent semi-natural habitats to secure pollinator populations (Chapter V). Younger AES habitats however also provide important

refugial habitats for natural enemies (Chapters VI & VII) and can easily be established on current cropland. A side effect in the establishment of AES habitats is that they are a comparably simple means to increase landscape heterogeneity and complexity and in this, they can be planned and placed with high flexibility. I thus propose agricultural landscapes that combine few permanent semi-natural habitats for highly mobile pollinators and a network of smaller semi-permanent and fluctuating AES habitats for less mobile natural enemies similar to and compatible with the network proposed for pollinator conservation by Cole *et al.* (2020) (Figure VIII.1). This network would ensure the provision of sufficient amounts of source habitat for ecosystem service providers as well as many edges for predator spillover (Ekroos *et al.* 2014; Tschamtkke *et al.* 2016).

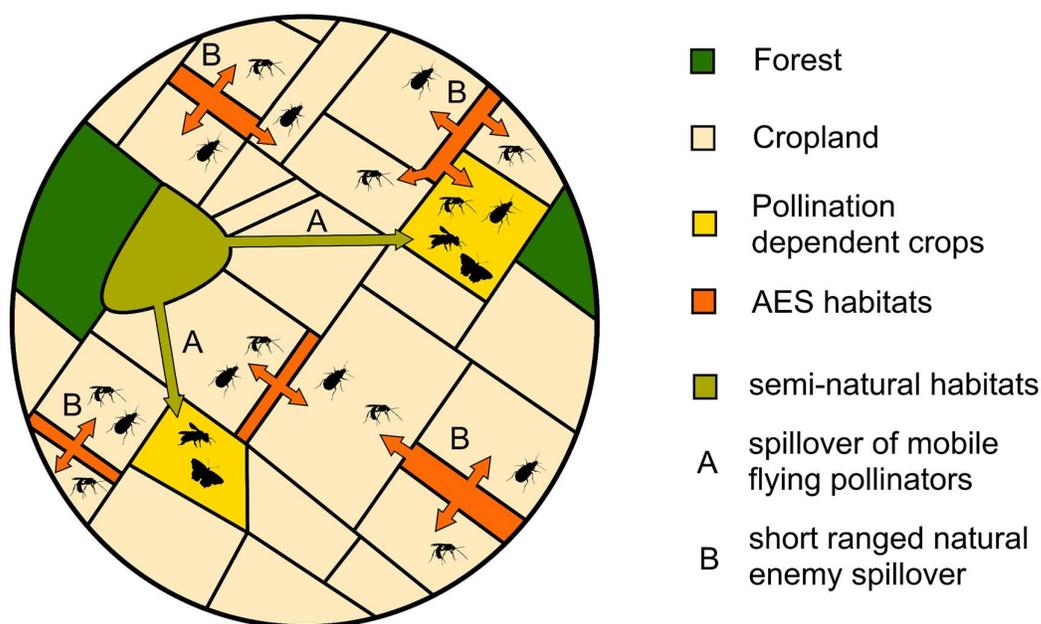


Figure VIII.1 Idealized scheme of an agricultural landscape for ecological intensification. A network of AES habitats (orange) ensures natural pest control in adjacent fields (B) while semi-natural habitats (light green) allow diverse pollinator communities to persist and provide pollination to pollinator dependent crops (A).

As diversity in AES habitats was independent from AES size (within the tested gradient; Chapter IV), this network of AES habitats could aim at maximizing edge areas via a wide distribution of comparably smaller habitat patches throughout the landscape increasing sites for natural enemy spillover.

At the same time, these AES habitats should be comprised of habitat patches in different stages of their lifespan. All perennial AES habitats currently established in Germany are limited to a certain lifespan and subsequently ploughed (Figure VIII.2). If these lifespans are synchronized, no refuge habitats will be available at certain points in time which should be prevented. A desynchronized network of AES habitats of different ages and ideally with different temporal continuity would allow a maximum of natural enemy diversity to persist in agricultural landscapes (Chapter V).



Figure VIII.2 The same continuous flowering field / set-aside greening in May 2017 (left) and May 2018 (right). Flowering fields funded under this program can be ploughed any time and taken out of the program. While new and refreshed flowering fields funded under the Bavarian KULAP are fixed for 5 years, they will subsequently most likely be turned into crop fields again. This emphasizes the need for coordinated planning to retain sufficient amounts of refuge habitats in agricultural landscapes at any point in time.

In this context, several questions will be essential:

(i) How much area in total should this network cover? More data is needed on how many semi-natural habitats, areas under extensive land use or how much agricultural land under conservation management would be ideal in landscapes. In this context, the debate whether biodiversity benefits more from single large or several small habitats is important – compared to few large habitats, several small habitats would simultaneously increase both landscape heterogeneity and edge areas for effective spillover (Grass *et al.* 2019). AES habitats likely have the largest benefits in simple landscapes and little to no benefits for complex and diverse landscapes (Tschardtke, Batáry & Dormann 2011; Marja *et al.* 2019). It will be essential to identify the optimal ratio of AES habitats in a landscape.

(ii) How dense should such a network be? How connected do AES habitats need to be to secure biodiversity, provide steppingstones and corridors for weak dispersing species and ecosystem service spillover into adjacent croplands?

(iii) Where should AES habitats in agricultural landscapes be placed? In order to determine where AES habitats should be established, more knowledge into specific AES habitat / crop interactions is needed. AES habitats should ideally be placed at locations where they can yield a maximum benefit for ecosystem services in adjacent crops throughout their lifespan. Yet, as these effects apparently depend on crop type and ecological contrast (Marja *et al.* 2019) predictions are not simple as most possible habitat crop combinations have not been studied so far.

The ultimate goal is to create a framework for strategic placement of AES habitats in the optimal amount and configuration in agricultural landscapes that maximizes overall ecosystem service delivery while at the same time providing widespread suitable refuge habitats for biodiversity and balancing negative effects on total crop yields due to the area lost for crop production. This goal will not be easy to reach as more knowledge about concrete interactions is needed and stakeholders need to be integrated and compensated for such efforts to succeed.

VIII.5 Conclusion

Modern agriculture has reached an essential tipping point. While intensification of agricultural production in the 20th century was able to feed the ever-growing world population, it simultaneously took the bread out of future generations' mouths as it deteriorated many essential foundations of agricultural production. The agriculture of the future thus needs to change and become more sustainable via combining achievements from the past era of conventional intensification with natural resources while at the same time considering natural limits and capacities. In this ecological conversion of agriculture, ecological intensification (i.e. the replacement of conventional inputs by biodiversity-mediated ecosystem services) is one promising way towards more sustainable agricultural production.

Here I investigated the potentials of agri-environmental scheme habitats for the conservation of biodiversity in agricultural landscapes and the provision of natural pest control in adjacent crop fields while at the same time also validating the used methodology. Multi-taxa biodiversity benefits most from a network of different agri-environmental schemes and semi-natural habitats in a landscape. Agri-environmental schemes and semi-natural habitats can help conserve biodiversity and can foster ecosystem service proliferation in adjacent fields if they are placed strategically in agricultural landscapes. As many beneficial effects of these habitats on adjacent crop cultures are rather short ranged, my results back the calls for more heterogenous and complex landscapes with smaller field sizes to maximize ecosystem service potentials. Planning landscapes for the optimal use of ecosystem services and for biodiversity conservation requires further evidence and testing. My results are small steps towards a better understanding of the interactions that drive biodiversity and natural pest control in agricultural landscapes and thus ultimately lead towards a more sustainable agricultural production and help design the agricultural landscapes of the future.



Agricultural landscapes used to be heterogenous and diverse – they were a mosaic of small fields, woodlots, pastures, grasslands, hedgerows and many other habitats. Our results indicate that such landscapes provide high ecosystem service potentials and habitats with high biodiversity and conservation value.

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List of Publications

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- Boetzl FA**^{1,2,3,4}, Schuele M, Krauss J, Steffan-Dewenter I (2020) Pest control potential of adjacent agri-environment schemes varies with crop type and is shaped by landscape context and within-field position. *Journal of Applied Ecology* **57**, 1482-1493. doi: 10.1111/1365-2664.13653
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1: designed the experiment; 2: conducted fieldwork; 3: analyzed data; 4: wrote the first draft of the manuscript

Schneider G, Krauss J, **Boetzl FA**³, Fritze M-A, Steffan-Dewenter I (2016) Spillover from adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural grasslands. *Oecologia* **182**, 1141-1150. doi: 10.1007/s00442-016-3710-6

Boetzl FA^{1,2,3,4}, Schneider G, Krauss J (2016) Asymmetric carabid beetle spillover between calcareous grasslands and coniferous forests. *Journal of Insect Conservation* **20**, 49-57. doi: 10.1007/s10841-015-9838-6

Publications (national)

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Hoffmann H & **Boetzl FA**^{1,2} (2018) Erstnachweis von *Astrapaeus ulmi* (Rossi, 1790) in Bayern (Coleoptera: Staphylinidae). *Entomologische Zeitschrift* **128**, 227-229.

Boetzl FA^{1,2,3,4} (2018) *Agonum* (*Olisares*) *viridicupreum* (GOEZE, 1777) - in Ostbayern übersehen? *Nachrichtenblatt der Bayerischen Entomologen* **67**, 100-102.

Reviewer activities

'Agricultural and Forest Entomology'; *'Agriculture, Ecosystems and Environment'*; *'Basic and Applied Ecology'*; *'Ecosphere'*; *'Ecosystems'*; *'Entomologia Experimentalis et Applicata'*; *'Entomological Science'*; *'European Journal of Forest Research'*; *'Environmental Entomology'*; *'Forest Ecology and Management'*; *'Journal of Applied Ecology'*; *'Landscape Ecology'*; *'Methods in Ecology and Evolution'*; *'Oecologia'*; *'PeerJ'*.

1: designed the experiment; 2: conducted fieldwork; 3: analyzed data; 4: wrote the first draft of the manuscript

Curriculum Vitae

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S1	FAB	EK	ISD	JK	
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Study Design	FAB	JK			
Methods Development	FAB				
Data Collection	AK				
Data Analysis and Interpretation	FAB	JK			
Manuscript Writing	FAB	JK	AK		
Writing of	FAB	JK	AK		
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Study Design	FAB	ISD	JK		
Methods Development	FAB	ISD	JK		
Data Collection	FAB	MS			
Data Analysis and Interpretation	FAB	ISD			
Manuscript Writing	FAB	ISD	JK	MS	
Writing of	FAB	ISD	JK	MS	
Introduction	FAB	ISD	JK	MS	
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Study Design	ISD	JK	FAB	EK	AH
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Data Collection	FAB	EK	SK	MP, JH, JJ	
Data Analysis and Interpretation	FAB	EM	ISD	HH	
Manuscript Writing	FAB	ISD	JK, AH,	SK, HH,	MP, JH, JJ
	FAB	ISD	EM	EK	MP, JH, JJ
	FAB	ISD	JK, AH,	SK, HH,	MP, JH, JJ
			EM	EK	
	FAB	ISD	JK, AH,	SK, HH,	MP, JH, JJ
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