Effects of adjacent habitats and landscape composition on biodiversity in semi-natural grasslands and biological pest control in oilseed rape fields

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Zwei Seelen wohnen, ach! in meiner Brust

(Johann Wolfgang von Goethe, Faust I)

Table of Contents

Ehrenwörtliche Erklärung

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation mit dem Titel „Effects of adjacent habitats and landscape composition on biodiversity in semi-natural grasslands and biological pest control in oilseed rape fields" selbstständig, am Lehrstuhl für Tierökologie und Tropenbiologie (Zoologie III) der Julius-Maximilians-Universität Würzburg, unter der Anleitung und Betreuung durch Herrn PD Dr. Jochen Krauss und Herrn Prof. Dr. Ingolf Steffan-Dewenter angefertigt habe und dabei keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Ich erkläre außerdem, dass die vorliegende Dissertation weder in gleicher, noch in ähnlicher Form bereits in einem Prüfungsverfahren vorgelegen hat. Des Weiteren habe ich außer den mit dem Zulassungsantrag urkundlich vorgelegten Graden keine weiteren akademischen Grade erworben oder zu erwerben versucht.

Würzburg, 20.05.2015

Gudrun Schneider

Summary

1) Modern European agricultural landscapes form a patchy mosaic of highly fragmented natural and semi-natural habitat remnants embedded in a matrix of intensively managed agricultural land. In those landscapes many organism frequently cross habitat borders including the crop – non-crop boundary, hereby connecting the biotic interactions of multiple habitat types. Therefore biodiversity and ecosystem functions within habitats are expected to depend on adjacent habitat types and the surrounding landscape matrix. In this thesis the biodiversity of non-crop habitats, and ecosystem services and disservices in crop habitats were studied in the human-dominated agricultural landscape in the district Lower Franconia, Bavaria, Germany. First we examined the effect of adjacent habitat type on species composition, diversity and ecosystem functions in semi-natural calcareous grasslands, a biodiversity-rich habitat of high conservation value (chapter 2 and 3). Second we studied the effect of habitat composition in the landscape on herbivory, biological pest control and yield in oilseed rape fields (chapter 4).

2) We examined the effect of adjacent habitat type on the diversity of carabid beetles in 20 calcareous grasslands using pitfall traps. Half of the grasslands were adjacent to a coniferous forest and half to a cereal crop field. We found different species compositions of carabid beetles depending on adjacent habitat type. In addition calcareous grasslands adjacent to crop fields harboured a higher species richness and activity density but a lower evenness of carabid beetles than calcareous grasslands adjacent to forests. These differences can be explained by the spillover of carabid beetles from the adjacent habitats. After crop harvest carabid beetle activity density in crop fields decreased while in parallel the activity density in the calcareous grasslands adjacent to the crop fields increased, indicating an unidirectional carabid beetle spillover. Our results underline that type and management of adjacent habitats affect community composition and diversity in calcareous grasslands. Therefore nature conservation measures, which focused on the improvement of local habitat quality so far, additionally need to consider adjacent habitat type.

3) In addition to carabid beetle communities we also surveyed predation rates of ground-dwelling predators on the same calcareous grasslands in two study periods (June and

late August). As ground-dwelling predators of forests or crop fields can move into adjacent calcareous grasslands we expected different predation rates depending on adjacent habitat type. We exposed in total 32.000 lady bird eggs as prey items on the calcareous grasslands in distances of 5 and 20m from the habitat border. We found higher predation rates on calcareous grasslands adjacent to forests than on calcareous grasslands adjacent to crop fields, but only on cool days. On warm days a very high extent (often 100%) of the exposed prey items were consumed adjacent to both habitat types, which did not allow the detection of possible differences between the adjacent habitat types. Predation rates differed not between the two study periods or the two distances to the habitat edge. The higher predation rates adjacent to forests can be explained by the spillover of ground-dwelling predators from forests into calcareous grasslands. Our results show, that spillover into semi-natural habitats affects ecosystem functioning in addition to species composition and diversity.

4) In chapter 4 of this thesis we examined the effect of spatiotemporal changes in crop cover on pest - natural enemy interactions and crop yields. During two study years we surveyed the abundance of adult and larval pollen beetles, parasitism of pollen beetle larvae by a hymenopteran parasitoid and oilseed rape yields of 36 oilseed rape fields. The surrounding landscape of the fields (1 km radius) differed in the oilseed rape proportion and in the inter-annual change in the oilseed rape proportion since the previous year. We found a dilution effect, i.e. a decreasing abundance with increasing oilseed rape proportions, for pollen beetle larvae and parasitoids in both study years and for adult pollen beetles in one study year. Oilseed rape yields increased with increasing oilseed rape proportions. Inter-annual changes in oilseed rape proportions led to inter-annual crowding and dilution effects for pollen beetles, but had no effect on parasitism or yield. Our results indicate the potential to reduce pest loads and increase yields in intensively managed oilseed rape fields by a coordinated management of the spatiotemporal oilseed rape cover in the landscape.

5) In summary, we showed in this thesis that the biodiversity and functioning of crop and non-crop habitats within agricultural landscapes is affected by the spillover of organisms and thus by the habitat composition in the close surrounding and in the broader landscape context. Spillover affects also ecosystem services and disservices and therefore crop productivity. Thereby the spatial and temporal variation of specific crop types in the landscape can be of particular importance for crop yields. Thus a coordinated landscape wide management can help to optimize both biodiversity conservation and the delivery of

ecosystem services and thus crop yields. Future studies integrating landscape effects across several ecosystem functions, multiple taxonomic groups and different crop types are necessary to develop definite landscape management schemes.

Zusammenfassung

1) Heutige europäische Agrarlandschaften bestehen aus einem Mosaik stark fragmentierter natürlicher und halbnatürlicher Habitate, die in eine Matrix aus intensiv bewirtschafteten Agrarflächen eingebettet sind. In solchen Landschaften überqueren Organismen häufig Habitatgrenzen, einschließlich der Grenze zwischen Agrar- und Nichtagrarhabitaten. Dabei verknüpfen sie die biotischen Interaktionen der verschiedenen Habitate miteinander. Deshalb ist zu erwarten, dass die Diversität und die Ökosystemfunktionen in Habitaten auch von den Nachbarhabitaten und der umgebenden Landschaft beeinflusst werden. In der vorliegenden Arbeit untersuchten wir die Diversität halbnatürlicher Habitate sowie die Ökosystemdienstleistungen in Agrarhabitaten im Bezirk Unterfranken in Bayern, Deutschland. Zum einen untersuchten wir den Einfluss von zwei verschiedenen Nachbarhabitattypen auf die Artenzusammensetzung, die Diversität und die Ökosystemfunktionen in halbnatürlichen Kalkmagerrasen, einem sehr artenreichen Habitat mit hohem Naturschutzwert (Kapitel 2 und 3). Zum anderen untersuchten wir den Einfluss der Habitatzusammensetzung in der Landschaft auf die Herbivorie, die biologische Schädlingskontrolle und den Ertrag in Rapsfeldern (Kapitel 4).

2) Mit Hilfe von Barberfallen untersuchten wir den Einfluss von zwei benachbarten Habitattypen auf die Diversität von Laufkäfern in 20 Kalkmagerrasen. Die Hälfte der Kalkmagerrasen grenzte an einen Nadelwald, die andere Hälfte an einen Getreideacker. Wir fanden unterschiedliche Artenzusammensetzungen der Laufkäfer in Abhängigkeit vom Nachbarhabitat. Außerdem fanden wir auf den Kalkmagerrasen neben Getreideäckern einen höheren Artenreichtum und eine höhere Aktivitätsdichte sowie eine geringere Evenness der Laufkäfer als auf den Kalkmagerrasen neben Nadelwäldern. Diese Unterschiede können durch den spillover von Laufkäfern aus den zwei unterschiedlichen Nachbarhabitaten erklärt werden. Nach der Getreideernte sank die Aktivitätsdichte der Laufkäfer auf den Getreideäckern und stieg parallel in den benachbarten Kalkmagerrasen an. Das weist auf einen einseitig gerichteten Spillover der Laufkäfer vom Acker auf die Kalkmagerrasen nach der Getreideernte hin. Unsere Ergebnisse zeigen, dass sowohl der Habitattyp als auch das Management benachbarter Habitate die Artenzusammensetzung und die Diversität auf Kalkmagerrasen beeinflusst. Daher sollten Naturschutzmaßnahmen, welche sich bisher nur

auf die Verbesserung der lokalen Habitatqualität konzentrierten, zusätzlich den Habitattyp und das Management benachbarter Habitate berücksichtigen.

3) Neben der Zusammensetzung der Laufkäfergemeinschaften untersuchten wir auf den gleichen Kalkmagerrasen die Prädationsraten von auf dem Boden lebenden Prädatoren in zwei Untersuchungszeiträumen (Juni und Ende August). Da Prädatoren benachbarter Wälder oder Äcker auch in Kalkmagerrasen eindringen können, erwarteten wir unterschiedliche Prädationsraten in Abhängigkeit vom Nachbarhabitat. Wir brachten insgesamt 32.000 Marienkäfereier als Beute auf den Kalkmagerrasen aus. Die Eier wurden in Distanzen von 5 m und 20 m zur Habitatgrenze exponiert. Wir fanden höhere Prädationsraten auf den Kalkmagerrasen neben Wäldern als auf denen neben Äckern, allerdings nur an kühlen Tagen. An warmen Tagen wurden die exponierten Eier neben beiden Nachbarhabitaten zu sehr hohen Anteilen (oft zu 100%) konsumiert, was es nicht ermöglichte potentielle Unterschiede zwischen den beiden Nachbarhabitattypen zu ermitteln. Wir fanden keine Unterschiede in den Prädationsraten zwischen den beiden Untersuchungszeiträumen oder zwischen den zwei Distanzen zur Habitatgrenze. Die höheren Prädationsraten auf Kalkmagerrasen neben Wäldern an kühlen Tagen können durch den spillover von am Boden lebenden Prädatoren aus den Wäldern in die Kalkmagerrasen erklärt werden. Unsere Ergebnisse zeigen, dass Spillover in halbnatürliche Habitate neben der Zusammensetzung der Lebensgemeinschaft auch Ökosystemfunktionen beeinflussen kann.

4) In Kapitel 4 dieser Arbeit untersuchten wir den Einfluss von räumlichen und zeitlichen Änderungen in der Rapsanbaufläche auf die Interaktionen zwischen Schädlingen und natürlichen Gegenspielern sowie auf Erträge. Dazu untersuchten wir in zwei Jahren auf insgesamt 36 Rapsfeldern die Abundanz adulter und larvaler Rapsglanzkäfer, Parasitierungsraten von Rapsglanzkäferlarven durch eine Schlupfwespe und Rapserträge. Die Landschaften im 1km Radius um die Rapsfelder unterschieden sich im Rapsanteil und in der Änderung des Rapsanteils seit dem Vorjahr. Wir fanden Verdünnungseffekte, d.h. eine sinkende Abundanz mit zunehmendem Rapsanteil, für Rapsglanzkäferlarven und Parasitoide in beiden Untersuchungsjahren und für adulte Rapsglanzkäfer in einem Untersuchungsjahr. Rapserträge stiegen mit höheren Rapsanteilen in der Landschaft. Eine Vergrößerung des Rapsanteils seit dem Vorjahr führte zu einer Verdünnung der Rapsglanzkäferpopulationen auf der vergrößerten Rapsfläche und eine Verringerung des Rapsanteils zur Konzentration auf der verkleinerten Rapsfläche. Die zeitliche Änderung des Rapsanteils hatte aber keinen Einfluss

auf die Parasitierungsrate oder den Ertrag. Unsere Ergebnisse unterstreichen das Potential durch Management der räumlichen und zeitlichen Verteilung der Rapsanbaufläche Schädlingsdichten verringern und Rapserträge erhöhen zu können.

5) Zusammenfassend zeigt die vorliegende Arbeit, dass die Biodiversität und die Funktionen von Agrar- und Nichtagrarhabitaten in Agrarlandschaften durch den Spillover von Organismen und folglich durch die Habitatzusammensetzung in der unmittelbaren und weiteren Umgebung bestimmt werden. Spillover beeinflusst dabei auch Ökosystemdienstleistungen und daher die Produktivität in der Landwirtschaft. Die räumliche und zeitliche Variation der Anbaufläche einzelner Anbaufrüchte hat dabei eine besondere Bedeutung für landwirtschaftliche Erträge. Daher kann ein koordiniertes Landschaftsmanagement helfen, sowohl die Biodiversität in der Landschaft als auch die Produktivität von Agrarhabitaten zu optimieren. Um konkrete Landschaftsmanagementpläne entwickeln zu können, sind weitere Studien, die gleichzeitig mehrere Ökosystemfunktionen, verschiedene taxonomische Gruppen und unterschiedliche Anbaufrüchte untersuchen, nötig.

Chapter 1: General Introduction

Agricultural intensification in European landscapes

Natural European landscapes were used by man since the colonization of the European continent about 40,000 years ago (Mellars 2004). But only since the spread of cereal cultivation and human settlement in the Neolithic time (3000-1100 BC), humans started to transform landscapes at a large scale (Vos & Meekes 1999). In the 19th century highly fragmented, multi-functionally managed European landscapes integrating forest remnants, arable cultures and grazing systems had developed (Vos & Meekes 1999). During the 20th century agricultural intensification characterized by the development of machine-driven farming methods, increasing inputs of fertilizers and pesticides, and the cultivation of monocultures accompanied by a decreasing crop diversity led to further landscape changes: Field sizes increased, former perennial habitats were converted to arable land and landscapes became more homogeneous with a decreasing number of land use types and more compact farms (Tscharntke *et al.* 2005).

Even though land use intensification increased productivity, it is also a major driver for the global loss of biodiversity (including functional diversity) among varying taxa (Flynn *et al.* 2009; Newbold *et al.* 2015). As biodiversity affects ecosystem functions, an ongoing loss of biodiversity also threatens ecosystem services, i.e. those ecosystem functions that support human well-being (Chapin III *et al.* 2000; Hooper *et al.* 2005). Therefore, modern landscape management should aim to provide a balance of productivity and biodiversity conservation (Gabriel *et al.* 2013). Even though intensively used agricultural land offers important habitats for a huge diversity of species, many of them depend on additional semi-natural habitats (Duelli & Obrist 2003). Thus the development of sustainable land use strategies requires an deeper understanding of interacting effects of intensively managed and semi-natural habitat types on species composition and ecosystem services in the landscape (Matson 1997). This thesis focuses on one important process overarching different habitat types and shaping species communities: the movement of organisms across habitat borders.

Cross-habitat spillover

Cross-habitat spillover describes the flux of energy, resources and organisms across habitat borders (Tscharntke *et al.* 2012). In this thesis we focused on the spillover of organisms including passive diffusion, dispersal and the search for resources. Spillover can result from (i) differences in the primary production of adjacent habitats, (ii) complementary resources in adjacent habitats, and (iii) temporal resource changes (Rand, Tylianakis & Tscharntke 2006). In addition different requirements of species during different life cycle stages can cause spillover (Benton, Vickery & Wilson 2003). In patchy landscapes combining several crop and non-crop habitat types spillover takes place (i) among crop habitats (Macfadyen & Muller 2013), (ii) among non-crop habitats (possibly using corridors or other connecting landscape elements) (Hunter 2002), (iii) from non-crop to crop habitats (Tscharntke, Rand & Bianchi 2005), or (iv) from crop to non-crop habitats (Blitzer *et al.* 2012). In annual crop systems movements across the crop – non-crop border occur regularly in both directions as many arthropods cyclically migrate into crop fields during crop growth and move into semi-natural habitats after crop harvest or other disturbing management measures (Wissinger 1997). However, spillover from non-crop to crop habitats received much more attention in spillover research than spillover in the opposite direction (Blitzer *et al.* 2012).

Cross-habitat spillover influences community composition and population dynamics in the involved habitats (Tscharntke *et al.* 2012). Additionally, spillover can result in a functional spillover, when the function that an organism fulfilled in the habitat where it came from is then fulfilled in the habitat where it moved to (Blitzer *et al.* 2012). For example organisms moving into crop fields can provide ecosystem services like pollination or biological pest control (Bianchi, Booij & Tscharntke 2006; Garibaldi *et al.* 2011). But also disservices like herbivory or infection by pathogens can be transferred into crop fields (Power & Mitchell 2004; Thies, Roschewitz & Tscharntke 2005). Similarly, organisms moving from crop fields into semi-natural habitats can alter ecological functions there. For example generalist predators, which were subsidized by high resource amounts in crop habitats, may spillover in comparatively high numbers into surrounding non-crop habitats resulting in increased predation rates there (Holt & Hochberg 2001; Rand & Louda 2006). Thus, cross-habitat spillover can strongly affect biodiversity and ecosystem functions in crop and non-crop habitats. However, it is poorly understood how the habitat assemblage in the landscape influences spillover effects. A deeper knowledge on this topic is required as an ecologically

and economically reasonable landscape management needs to consider effects of the habitat assemblage in the landscape on biodiversity and ecosystem functions (Batary *et al.* 2010).

The project

Many biological processes such as the spillover of organisms are scale-dependent, determined by the activity range and dispersal abilities of the involved species (Wiens 1989; Schmidt *et al.* 2008). However, nature conservation and landscape management measures often do not match the scale of biological processes as they depend on the scale of political decision making (Cumming, Cumming & Redman 2006). The FP 7 EU-project SCALES ("Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal, and Ecological Scales", www.scales-project.net) aims to close this gap (Henle *et al.* 2010). For this purpose 31 working groups of 19 European countries and Australia and Taiwan are cooperating with the aim to improve the understanding of the scale-dependence of anthropogenic impacts on biodiversity and ecological processes and to transfer this knowledge into political decisions and management measurements. This PhD thesis is embedded within work package 2 ("Scaling biotic processes and biodiversity") of the scales project. This thesis aims to improve our understanding of how habitat assemblage affects biodiversity and ecosystem services at the local, landscape and temporal scale. Therefore we studied the effect of adjacent habitat type on the species community and ecosystem functions in semi-natural calcareous grasslands (chapter 2 and 3), and the effect of spatially and temporally varying oilseed rape proportions at a landscape scale on biological pest control and yield in oilseed rape fields (chapter 4).

The study region

This study was conducted in the agricultural landscape of Lower Franconia, Bavaria, Germany (Fig. 1). The study region is situated between about 49°32' and 50°14' North and 9°42' and 10°9' East. The main river within the study region is the river "Main". Lower Franconia is characterized by a temperate climate with a mean annual temperature of 9.6°C and a mean annual precipitation of 601 mm (weather station Würzburg, mean of the years 1981-2010) ('Deutscher Wetterdienst' 2013). The study region is mainly agrarian-oriented with about 62% agricultural land and 24% commercial forests. The main sedimentary rock within the study region is shell limestone ('Bayerisches Landesamt für Umwelt'), which facilitated the development of calcareous grasslands.
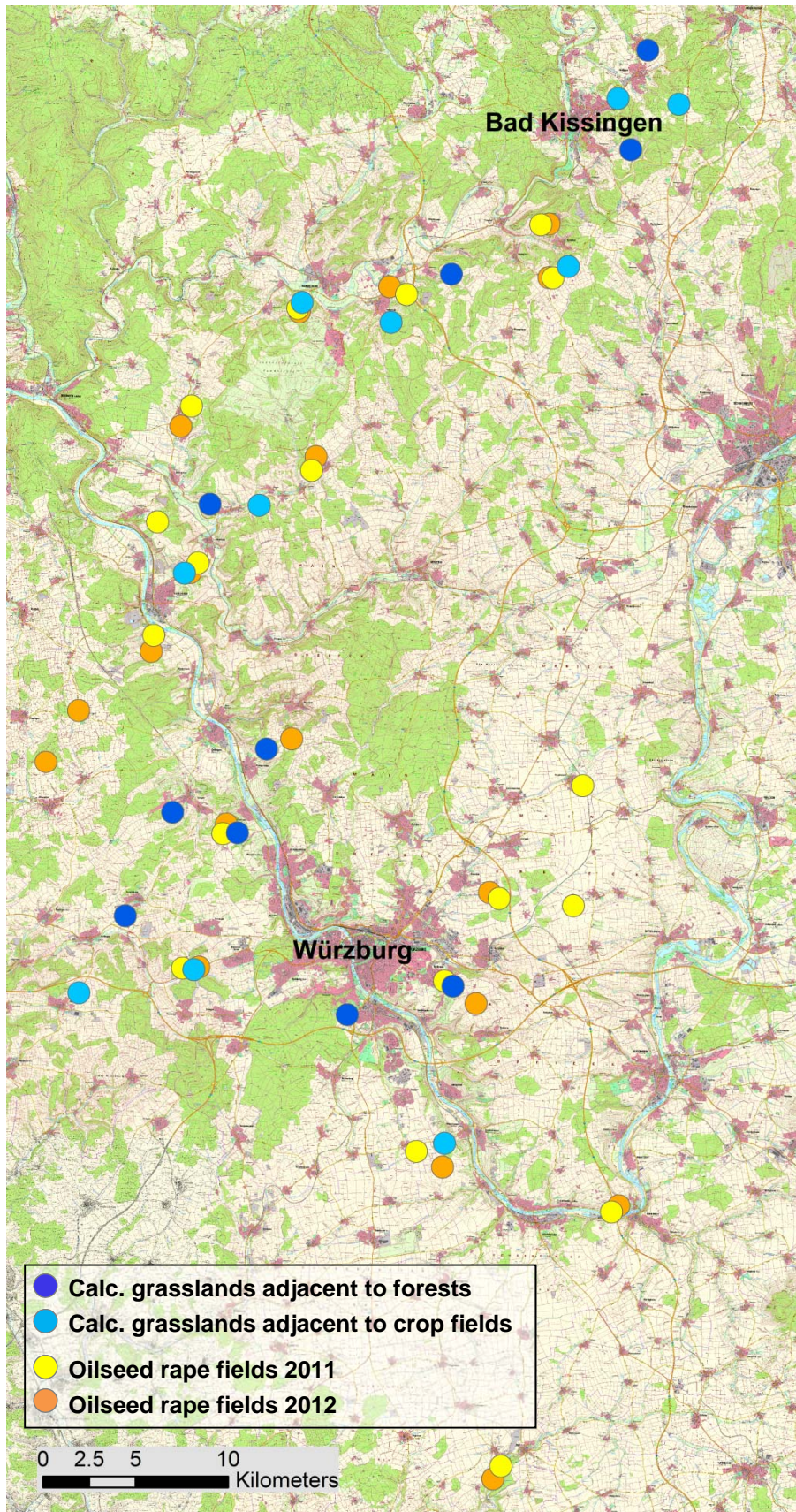
Fig. 1 Study sites in the study region Lower Franconia. Light and dark blue points indicate calcareous grasslands studied in chapter 2 and 3 of this thesis and yellow and orange points indicate oilseed rape fields studied in chapter 4 of this thesis.

Effect of adjacent habitat type on the species community and ecosystem functions in semi-natural calcareous grasslands

Chapter 2 and 3 of this thesis were conducted on 20 calcareous grasslands in the region Lower Franconia in Germany (Fig. 1). These dry, nutrient-poor grasslands mainly developed due to traditional management practices like extensive grazing or mowing (Poschlod & WallisDeVries 2002). The calcareous grasslands are typically very species rich and considered as biodiversity hotspots within agricultural landscapes (Niemelä & Baur 1998; van Swaay 2002; Cremene *et al.* 2005). In the last century the amount of calcareous grasslands in Europe drastically declined, because many of them were abandoned when the extensive management was no longer profitable (Poschlod & WallisDeVries 2002). Abandoned grasslands were either endangered by shrub encroachment, converted into arable fields or afforested (Poschlod, Bakker & Kahmen 2005; Schrautzer *et al.* 2009).

Today's remaining calcareous grasslands are often protected and the local habitat quality is preserved by the maintenance or resumption of traditional management practices. Nevertheless, during the last decades many calcareous grasslands suffered changes in the species community often characterized by a decline of calcareous grassland specialists (Newton *et al.* 2012). In general three main causes are associated with these changes: (i) fragmentation and the loss of habitat area (Polus *et al.* 2006; Krauss *et al.* 2010), (ii) eutrophication due to nutrient inputs from the surrounding landscape (Van Den Berg *et al.* 2011; Diekmann *et al.* 2014), and (iii) the loss of heterogeneity within the grasslands as well as in the surrounding landscape (Diacon-Bolli *et al.* 2012; Rösch *et al.* 2013). Even though the last two points highlight the importance of interactions with the surrounding habitat matrix, studies examining the impact of different adjacent habitat types on the species community in calcareous grasslands are missing. But a deeper understanding of interactions with adjacent habitats can help to protect biodiversity and ecosystem processes.

Because coniferous forests and crop fields are the most common adjacent habitats of calcareous grasslands in Europe (Poschlod & WallisDeVries 2002) we studied the influence of these two adjacent habitat types on carabid beetle communities in calcareous grasslands using pitfall traps (Fig 2). We chose carabid beetles as they are an important functional group of mostly polyphagous predators occurring in nearly all terrestrial habitats (Lovei & Sunderland 1996; Kotze *et al.* 2011). In chapter 2 we present how adjacent habitat type affects carabid beetle species composition and diversity in calcareous grasslands. In addition we show temporal variations in the carabid beetle spillover, with a particular strong spillover from adjacent crop fields into calcareous grasslands after crop harvest.

Beside the effects on carabid beetle communities we also examined the effect of adjacent habitat type on predation rates of ground-dwelling predators in the calcareous grasslands. Therefore we exposed ladybird eggs as prey items at the soil surface of the grasslands (Fig. 3) and determined the number of eggs that were left after 24h to estimate predation rates. In chapter 3 we show that also ecosystem functions such as predation rates are affected by adjacent habitat type.
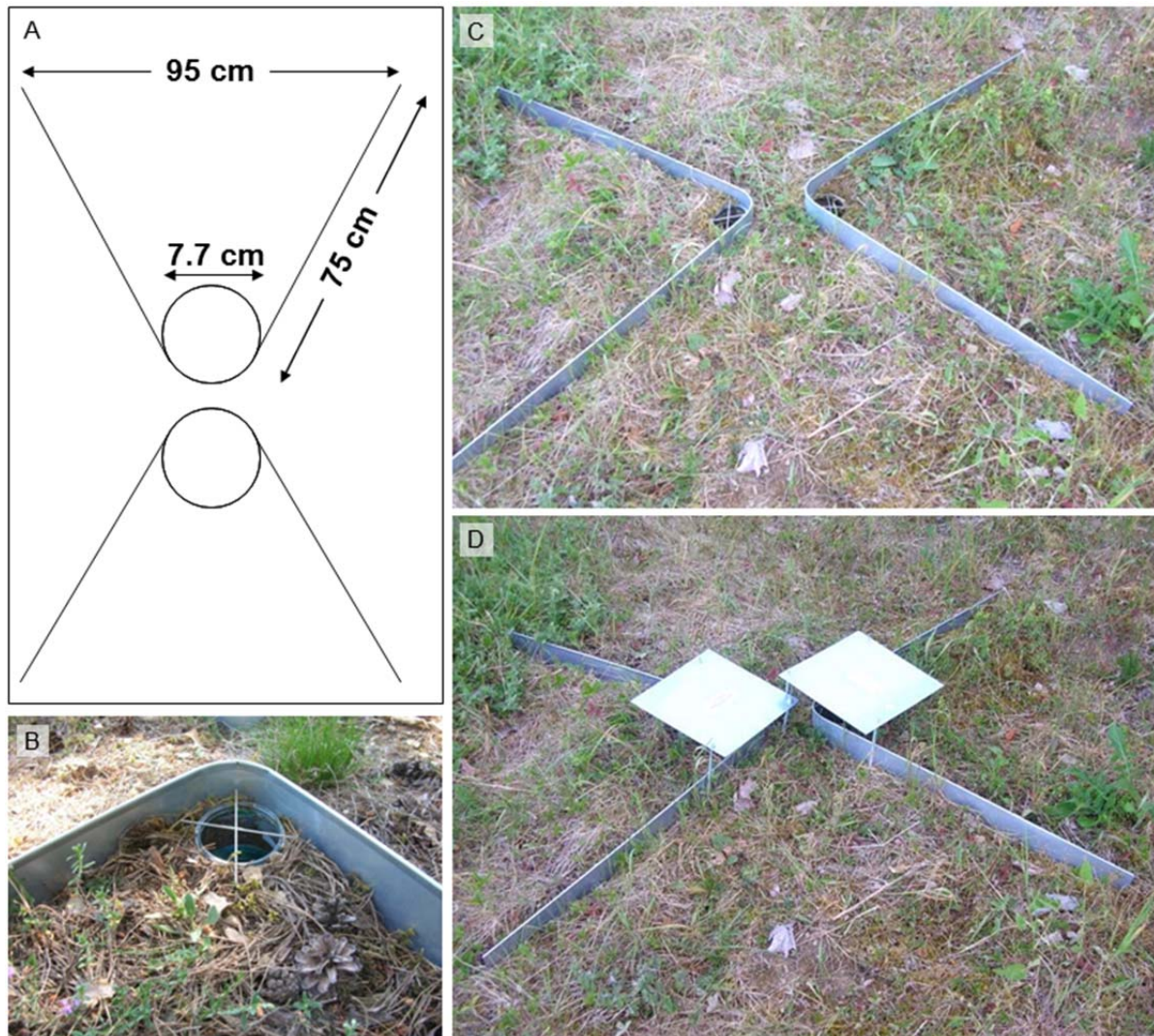

Fig 2 Pitfall traps. A) Schematic depiction of a pair of pitfall traps with metal barriers that lead ground-dwelling organisms into the trapping cup. B) Opening of a trapping cup. Two metal rods crossed the cup opening to prevent small vertebrates from falling into the trap. C) Pitfall traps were installed pairwise to distinguish movement directions. D) Finally, the cup openings were covered by small rooflets to prevent flooding.
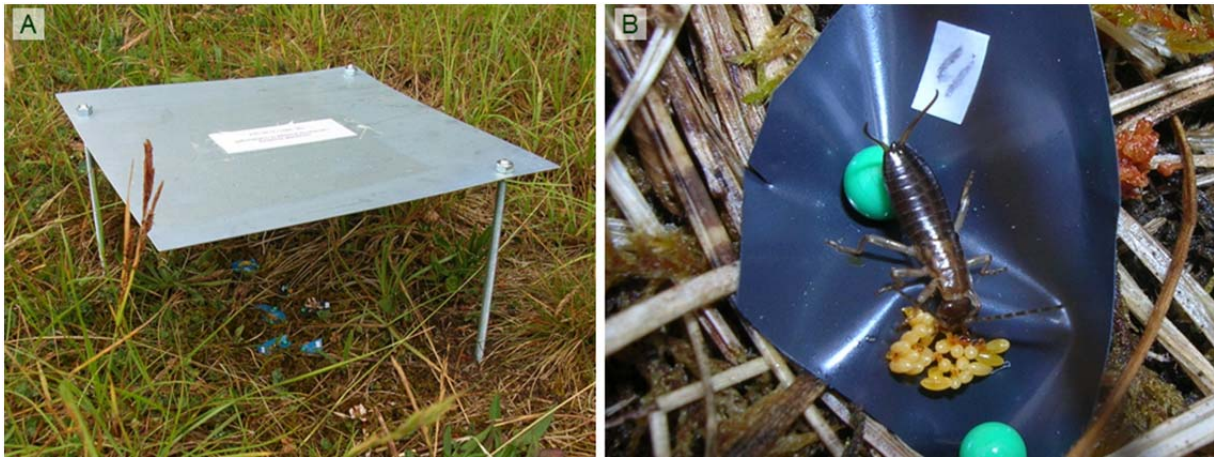
Fig. 3 A) Plastic sheets with ladybird eggs were exposed at the calcareous grasslands as prey items for 24h. The sheets were covered by a metal rooflet to protect them against rain. B) Species of the order Dermaptera feeding on the lady bird eggs.

Effects of spatial and temporal crop cover dynamics on biological pest control and yield in oilseed rape fields

In chapter 4 of this thesis we focused on biological pest control as an important ecosystem service in agricultural landscapes. This part of the thesis was conducted on 36 conventionally managed oilseed rape fields in the region Lower Franconia, Germany in two study years (Fig. 1). Oilseed rape is one of the most important non-food biofuel crops for biodiesel production in Europe (Knight 2010). But it is also used for human nutrition or as animal feed. The harvested area in Europe doubled within ten years to 9.3 million hectare in 2013 (FAO 2015). Within the European Union Germany and France are the major oilseed rape producers with a production of 11.8 million tonnes in 2014 (European Union 2014). But heavy yield losses of up to 80% in spring oilseed rape can occur due to sever attacks by pest insects (Hansen 2004). Therefore most oilseed rape fields were regularly treated with insecticides. However, negative effects of pesticide applications on non-target organisms including natural enemies or pollinators may be hazardous for biodiversity and can reduce the efficiency of ecosystem services (Brittain *et al.* 2010; Geiger *et al.* 2010). In addition the number of insecticide resistances rose during the last decades (Heckel 2012) resulting in an increasing demand on alternative pest control strategies. Biological pest control is one promising approach, but up to now it is poorly understood how the habitat assemblage in a landscape affects pest species, natural enemies and crop yields (Chaplin-Kramer *et al.* 2011). Two landscape factors are particularly expected to affect biological control efficiency: the amount of semi-natural habitats and the proportion of crops that are host to particular pest species. The amount of semi-natural habitats has often been shown to increase natural enemy

abundance and sometimes biological pest control (Rusch *et al.* 2010). The few studies investigating host crop proportion led to contradictory results, with either negative or positive effects on the pest species abundance (reviewed in Veres *et al.* 2013). In addition, the host crop proportion within a landscape changes between years as most annual crops are grown in crop rotations. Such inter-annual changes can additionally affect pest and natural enemy abundance (Zhao *et al.* 2013).

In chapter 4 we studied oilseed rape fields that differed in both the proportion of oilseed rape within a 1km landscape radius (Fig. 4) and in the inter-annual change of oilseed rape proportion. We present the effects on the abundance of pollen beetles (the most important oilseed rape pest within the study region (Thieme *et al.* 2008; Williams 2010)), parasitism by their natural enemy and oilseed rape yields.
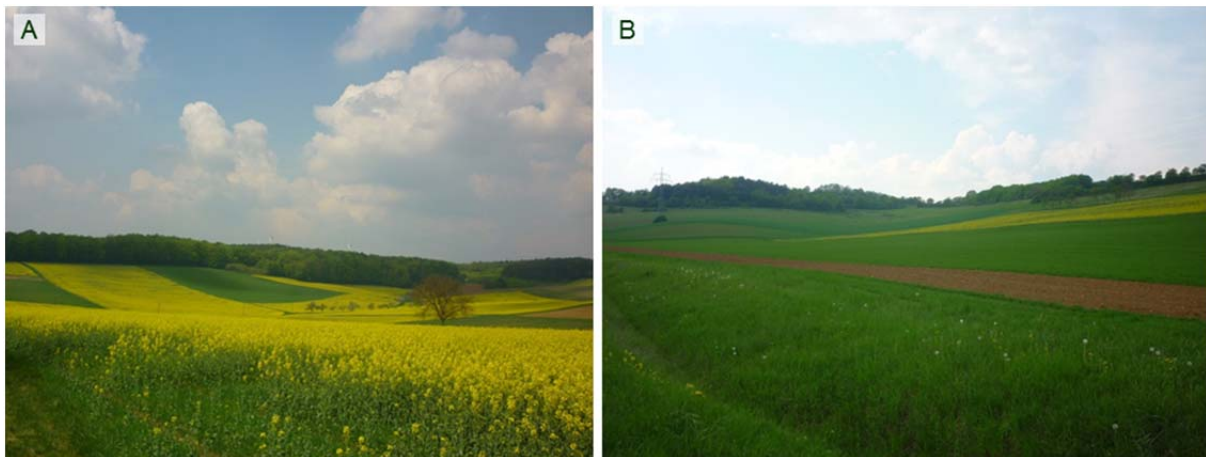

Fig. 4 Studied landscapes with A) a high oilseed rape proportion of 21% in the 1km landscape radius and B) a low oilseed rape proportion of 4% in the 1km landscape radius.

Chapter 2: Spillover from adjacent crop and forest habitats shapes carabid beetle communities in fragmented semi-natural grasslands

Abstract

Semi-natural grasslands in Europe are biodiversity hotspots and can be considered as important source habitats delivering ecosystem services to adjacent agricultural land by species spillover. However, this spillover might also occur in the opposite direction, affecting the diversity of semi-natural grasslands. This opposite spillover has got little attention in scientific literature even though species penetrating into the grasslands can affect the biodiversity and thus the conservation value of the habitat. In this study we examined spillover effects from two different adjacent habitat types on carabid beetle communities in 20 semi-natural calcareous grasslands. The grasslands were either adjacent to a cereal crop field or to a coniferous forest. We found distinct community compositions of carabid beetles in the calcareous grasslands depending on adjacent habitat type. In addition, species richness and activity density was higher, but the evenness lower in calcareous grasslands adjacent to crop fields compared with calcareous grasslands adjacent to coniferous forests. Further, we found a strong spillover of carabid beetles from crop fields to adjacent calcareous grasslands after crop harvest, which may result in transiently altered ecosystem functions. Our results highlight, that species composition, diversity and ecosystem processes within semi-natural habitats are affected by type and management of surrounding habitats. This needs to be considered by nature conservation measures, which aim to protect specialised species of semi-natural grasslands.

Keywords: crop harvest, edge effects, evenness, species richness, spillover movements

Introduction

Cross-habitat spillover, i.e. the movement of organisms across habitat borders (including foraging and dispersal) shapes ecosystem processes and community composition in landscapes with different habitat types (Tscharntke *et al.* 2012). The spillover from natural or semi-natural habitats into production areas got much attention in spillover research as it often provides ecosystem services. For example fish spillover from marine protection areas increase fishery yields in adjacent fishing grounds (Kerwath *et al.* 2013). Similarly, crop yields benefit from increased pollination and pest control with nearby semi-natural habitats (Tscharntke, Rand & Bianchi 2005; Kremen *et al.* 2007). But spillover also occurs in the opposite direction, i.e. from agricultural habitats into adjacent semi-natural or natural habitats (Rand, Tylianakis & Tscharntke 2006). Such effects of agricultural habitats on conservation areas needs to be considered to protect biodiversity and delivered ecosystem services (Balmford, Green & Phalan 2012). However, up to now, studies are missing, which examine the spillover from agricultural land into natural or semi-natural habitats (Blitzer *et al.* 2012).

The effect of spillover in semi-natural habitats is expected to depend on the surrounding habitat types, as different habitat characteristics lead to different movement rates across habitat borders: (i) The availability of food resource (both diversity and amount) determines foraging movements in the landscape (Brotons *et al.* 2005; Jha & Kremen 2013). (ii) The habitat structure determined by vegetation height and vegetation density can also affect spillover. Movement rates are often higher across habitat borders with a low boundary contrast, like the border between two open habitats, than across habitat borders with a high boundary contrast, like the border between an open habitat and a closed forest (Eycott *et al.* 2012). (iii) Differences in the primary production of two habitat types affect the magnitude of spillover. Species of highly productive agricultural habitats have often high population growth rates during crop growth, resulting in high abundances and thus strong spillover (Rand, Tylianakis & Tscharntke 2006). This may lead to the dominance of agriculturally subsidized species in adjacent habitats. However, up to now little is known about how specific habitat assemblages affect community composition and diversity in semi-natural habitats, even though species richness, species identity and evenness of communities also affects ecosystem functioning (Cardinale *et al.* 2006; Hillebrand, Bennett & Cadotte 2008).

In addition to habitat assemblage, also temporal variations affect spillover. The availability of resources like food, shelter, and nesting sites changes over the year, resulting in a seasonally changing habitat quality (Boyce 1979; Holt 2008). Thereby, the effect of

seasonality on species richness and diversity differs depending on habitat type (Tylianakis, Klein & Tscharntke 2005). Additionally, natural or anthropogenic disturbances can result in suddenly altered resource availabilities. One regularly occurring disturbance in agricultural habitats is crop harvest. When resources in crop fields decline or become unavailable after harvest, surviving individuals are expected to actively emigrate in adjacent semi-natural or natural systems (Wissinger 1997; Rand, Tylianakis & Tscharntke 2006). Therefore, regularly disturbed habitats may have a stronger impact on adjacent semi-natural habitats than less disturbed habitats like forests.

In this study we compared carabid beetle communities in semi-natural calcareous grasslands with either cereal crop fields or coniferous forests as adjacent habitat. This allowed us to compare the effects of a highly disturbed and a more stable adjacent habitat type on carabid beetle diversity and community composition in a semi-natural habitat with high conservation value (WallisDeVries, Poschlod & Willems 2002). We studied carabid beetles as an important functional group of predominantly generalist predators in crop and non-crop habitats (Lovei & Sunderland 1996; Tscharntke, Rand & Bianchi 2005). As carabid beetles have relatively low dispersal capacities, adjacent habitats should have a higher impact on community composition than landscape composition at larger spatial scales (Pearce & Venier 2006; Gardiner *et al.* 2010).

Hypotheses:

(1) Species composition, species richness and activity density of carabid beetles in calcareous grasslands differs depending on adjacent habitat type as the abundance and diversity of carabids that spill over into calcareous grasslands depends on the habitat type where the carabids come from.

(2) Evenness of carabid beetle communities is lower in grasslands adjacent to crops than adjacent to forests as species from highly productive crop fields can spillover in very high abundances resulting in the dominance of agriculturally subsidized species on the adjacent grassland.

(3) Crop harvest leads to a transient increase of carabid beetle spillover into adjacent semi-natural habitats due to the declining resource availability on crop fields after harvest.

Material and methods

Study sites

The study was conducted in 2011 on 20 calcareous grasslands, ten cereal crop fields and ten forest habitats (i.e. 40 sites in total) in northern Bavaria, Germany. Ten of the grasslands were adjacent to the ten conventionally managed cereal crop fields and ten grasslands were adjacent to the ten coniferous forests. We selected the calcareous grasslands using the following criteria: (i) mapped as calcareous grassland by the Bavarian State Office for Environment ("Bayerisches Landesamt für Umwelt") to achieve comparability of habitat quality, (ii) a clear border (< 2 m) either to a cereal crop field or to a coniferous forest instead of a gradual transition zone, and (iii) permission of the nature conservation authorities. The minimum distance between the grasslands was 2 km. The area of the grasslands adjacent to crop fields and those adjacent to coniferous forests were not significantly different (Wilcoxon rank sum test: $W = 36$, $n_1 = n_2 = 10$, $P = 0.32$). All studied grasslands were either extensively managed or unmanaged (Schneider, Krauss & Steffan-Dewenter 2013).

Data collection

At each of the 40 study sites we installed four pitfall traps, adding up to 160 traps. The trapping cups had an 8 cm wide opening, were filled with a 1:3 ethylene glycol (automobile antifreeze, H. Kerndl GmbH)-water-mixture with detergent as trapping liquid (Schmidt *et al.* 2006) and were protected against rain by a metal rooflet (25 cm x 25 cm and 15 cm high). Crossed metal rods over the cup opening prevented small vertebrates from falling into the trap. The traps were equipped with 7 cm high, angled, metal barriers to direct ground-dwelling arthropods into the trapping cup. The four traps per study site were placed in two pairs at a distance of 5 m from the habitat border. Each pair contained one trap opening towards the habitat border, and one trap opening towards the habitat centre (Fig. 1). We chose this design to measure differences in movement directions of carabid beetles. But as we found no consistent differences in the activity density, species richness or composition between the two directions, we pooled the data of the paired pitfall traps for further analyses.

All pitfall traps were set up at the beginning of May 2011 and were removed at the beginning of October 2011. The traps were emptied in two week intervals (11 collection intervals × 40 sites × 4 traps, i.e. 1760 samples in total). The total sampling period in our study was 22 weeks, which allows us to cover the main activity period of carabid beetles. About 1.4% of the samples (25 out of 1760) were lost during field work due to vandalism and

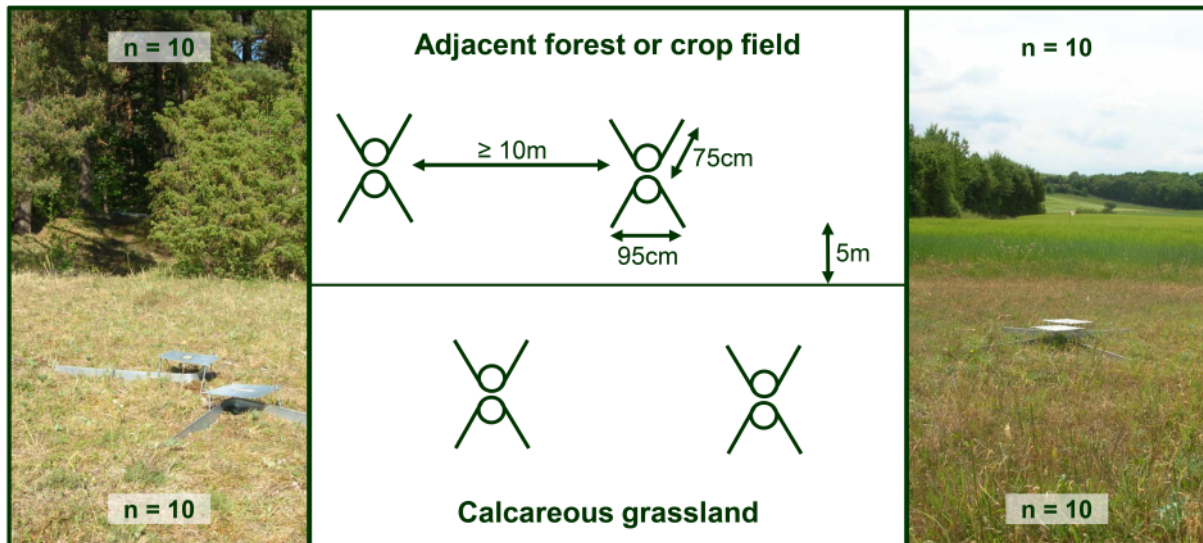farming activities. All carabid beetles were determined to species level according to Müller-Motzfeld 2004.

Fig. 1 Sampling design. Circles represent trapping cups and lines at the circles metal barriers which lead ground-dwelling arthropods into the pitfall traps. Photos show pairs of pitfall traps in a calcareous grassland adjacent to a coniferous forest (left) or adjacent to a cereal crop field (right).

Statistical analyses

Statistical analyses were performed using the R package vegan (Oksanen *et al.* 2013) in the software R 3.0.2 (R Core Team 2013). All models were simplified using a stepwise backward selection procedure based on likelihood ratio tests (Zuur *et al.* 2009).

Species saturation

For the estimation of the asymptotic species richness we summed the data of all pitfall traps per site over the whole sampling period. The abundance-based asymptotic species richness estimator ACE (Gotelli & Colwell 2011) was computed for each site to verify that our sampling effort of eleven samples per site was sufficient. We calculated species saturation per site as the percentage of the observed species richness from the estimated species richness. Species saturation was similar between the four habitat types (mean ± SE of crop fields: 74 ± 4%, calcareous grasslands adjacent to crop fields: 71 ± 3%, calcareous grasslands adjacent to forests: 65 ± 6%, forests: 53 ± 5%). Estimated species richness and observed species richness correlated over all study sites (r = 0.72, $P < 0.001$).

Dissimilarity and diversity of carabid beetle communities

For dissimilarity and diversity measures we summed the data of all pitfall traps per site over the whole sampling period. We used non-metric multidimensional scaling (NMDS) based on Bray-Curtis Dissimilarities to analyse compositional differences of carabid beetle communities between the four habitat types. Calculation of Bray-Curtis dissimilarities was based on proportion data to standardize differences in total carabid beetle abundance. Multi-response Permutation Procedure (MRPP) also based on Bray-Curtis-Dissimilarities was used to test for differences between the communities of the four habitat types (McCune & Grace 2002). To reveal differences between calcareous grasslands adjacent to crop fields and calcareous grasslands adjacent to coniferous forests, we tested whether community dissimilarities within the two grassland types are smaller than community dissimilarities between the two grassland types. Therefore a Bray-Curtis dissimilarity matrix with all combinations of the 20 calcareous grasslands was computed. In addition we used a binary distance matrix (Gower's distances) assigning a distance of 1 to the pairs of calcareous grasslands with different adjacent habitats and a distance of 0 to the pairs of calcareous grasslands with equal adjacent habitats. We tested the correlation between the dissimilarity and the distance matrix using a Mantel Test with 999 permutations. Additionally, activity density, species richness, and Pielou's evenness (Pielou 1966) were compared between the 10 crop fields and the 10 coniferous forests, as well as between the 10 calcareous grasslands adjacent to crop fields and the 10 calcareous grasslands adjacent to coniferous forests using Welch's two sample t-tests. To achieve the assumption of normality activity density was log transformed.

Effects of crop harvest

Each of the eleven sampling intervals was considered separately to detect temporal dynamics. Thereby all pitfall traps per site were summed. We calculated the difference of the relative activity density (act) of carabid beetles between calcareous grasslands (cg) and the adjacent habitat (ah) for each sampling interval with the equation:

$\Delta = (act_{ah} - act_{cg} / act_{cg + ah} \times 100)$.

A positive Δ indicates higher activity densities of carabid beetles in the adjacent habitat, whereas a negative Δ indicates higher activity densities in the calcareous grassland. If $\Delta = 0$ activity densities of carabid beetles are equal in both adjoining habitats. We compared the mean Δ of the three sampling intervals before crop harvest with the mean Δ of the three sampling intervals after crop harvest using a paired t-test. In further paired t-tests we

compared activity densities between crop fields and adjacent calcareous grasslands in the sampling interval before crop harvest and the sampling interval after crop harvest to look at short term effects. To achieve the assumption of normality, activity density was square root transformed.

Results

In total, 28,846 carabid beetles of 119 species were trapped and identified. We found 15,936 individuals of 94 species in ten cereal crop fields, 3324 individuals of 61 species in ten forest sites and 9586 of 99 species in 20 calcareous grasslands (8327 beetles of 87 species in grasslands adjacent to crop and 1259 beetles of 74 species in grassland adjacent to forest).

Community similarity

The composition of carabid beetle communities differed significantly between crop fields, coniferous forests, calcareous grasslands adjacent to crop fields and calcareous grasslands adjacent to coniferous forests (Fig. 2). Carabid beetle communities in calcareous grasslands with the same adjacent habitat (either both adjacent to forests or both adjacent to crop fields) were more similar than carabid beetle communities in calcareous grasslands with different adjacent habitats (Mantel-test: r = 0.35, *P* = 0.001).

Activity density, species richness and evenness

The activity density, species richness and evenness of carabid beetle communities differed between crop and forest sites and were affected by the adjacent habitat type in grasslands. We found about 5 times higher activity densities (t = 6.0, n = 10, *P* < 0.001) and twice as many species (t = 9.7, n = 10, *P* < 0.001) of carabid beetles in crop fields compared to coniferous forests (Fig. 3a and c). We also found about 7 times higher activity densities (t = 4.7, n = 10, *P* < 0.001) and 57% more species (t = 3.8, n = 10, *P* < 0.01) of carabid beetles in calcareous grasslands adjacent to crop fields compared to calcareous grasslands adjacent to coniferous forests (Fig. 3b and d). However, Pielou's evenness of carabid beetle communities differed not significantly between crop fields and coniferous forests (t = 0.1, n = 10, *P* = 0.93) (Fig. 3e), but was significantly lower in calcareous grasslands adjacent to crop fields compared to those adjacent to coniferous forests (t = 3.3, n = 10, *P* < 0.01) (Fig. 3f).
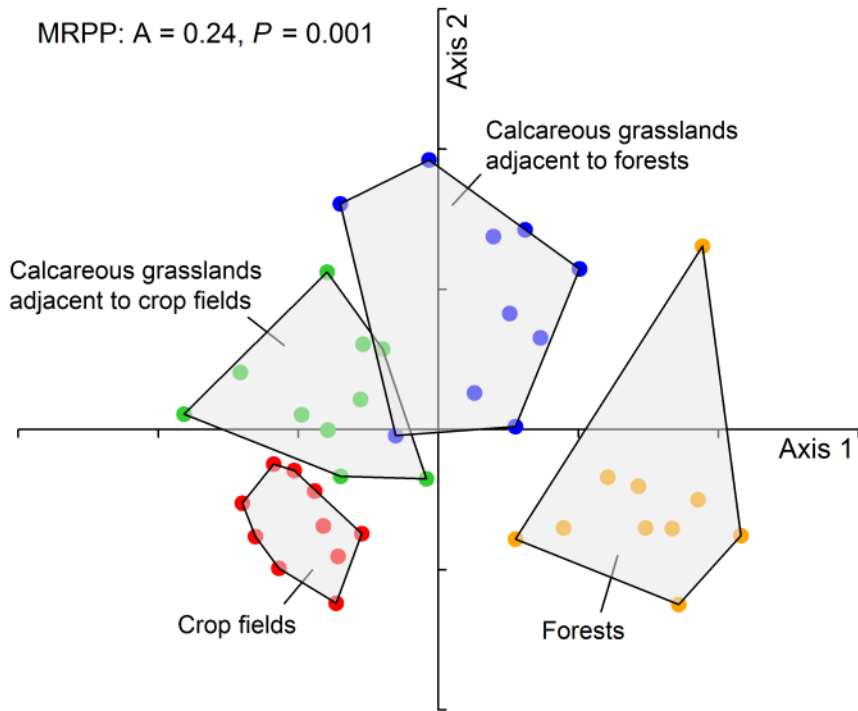
Fig. 2 Non-Metric multidimensional Scaling (NMDS) ordination of carabid beetle communities in 40 sampling plots (10 cereal crop fields, 10 calcareous grasslands adjacent to cereal crop fields, 10 coniferous forests and 10 calcareous grasslands adjacent to coniferous forests) (Stress: 0.19). Colours represent the four habitat types. Polygons indicate clustering of communities based on habitat type. Results of the MRPP based on 999 permutations show significant differences between the four habitat types.
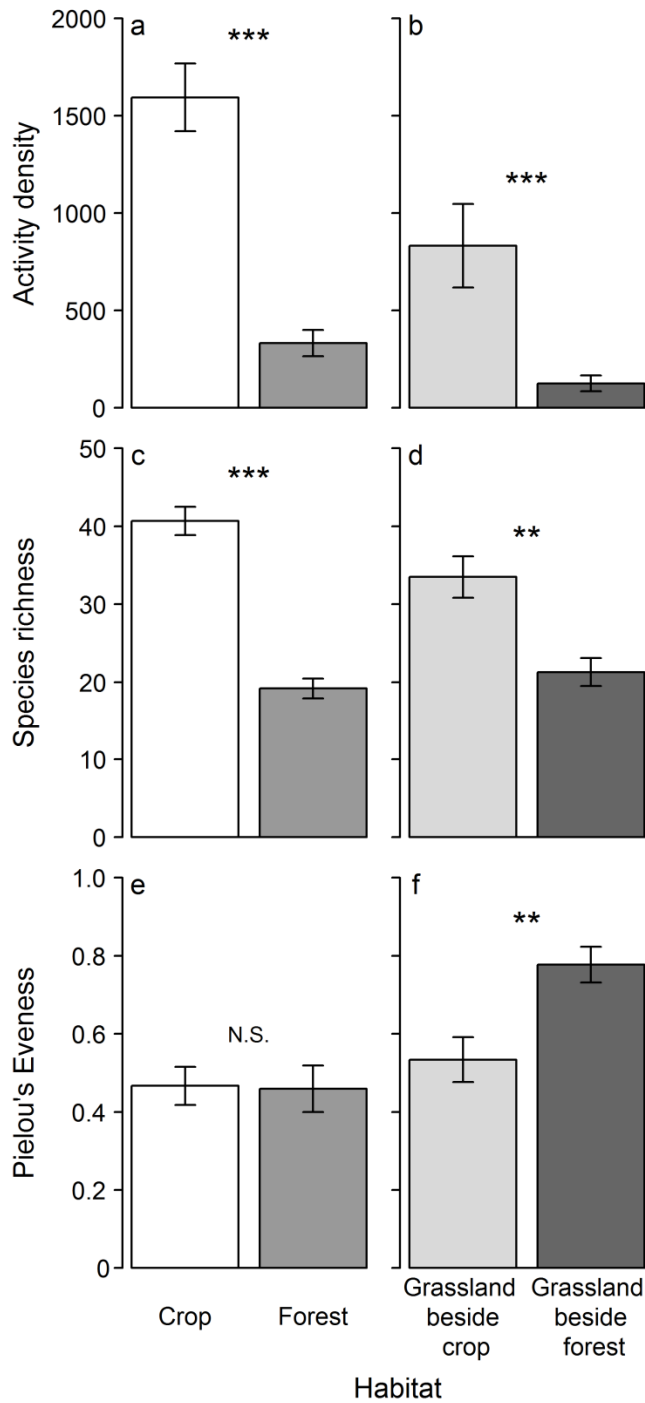
Fig. 3 Activity density, species richness and evenness of carabid beetles (mean ± SE) in crop fields and coniferous forests (a, c, e) and in calcareous grasslands adjacent to crop fields and calcareous grasslands adjacent to coniferous forests (b, d, f) (n = 10 per habitat). *** $P < 0.001$, ** $P < 0.01$, N.S. = not significant.

Effect of crop harvest

Until the beginning of harvest season in August, carabid beetles had a higher activity density in crop fields than in adjacent calcareous grasslands, whereas after crop harvest the activity densities were similar (Fig. S1). This is confirmed by a significant decline of Δ after crop harvest (t = 3.9, n = 9, *P* < 0.01, Fig. 4a). Similar results were obtained when considering the activity density for one sampling interval before and after harvest: In the sampling interval before harvest a two times higher activity density of carabid beetles was found in crop fields than in adjacent calcareous grasslands (t = 4.14, n = 10, *P* < 0.01, Fig. 5). After harvest a lower activity density was found in crop fields than in grasslands (Fig. 5), however the difference was not significant due to large variability among study sites (t = -0.57, n = 9, *P* = 0.58).

Contrary to crop fields, carabid beetle activity densities in forests did not drop compared to adjacent calcareous grasslands after the beginning of the harvest season (t = 0.9, n = 10, *P* = 0.42). Only at the end of September until October activity densities were equal between coniferous forests and adjacent calcareous grasslands (Fig. 4b, Fig. S2).
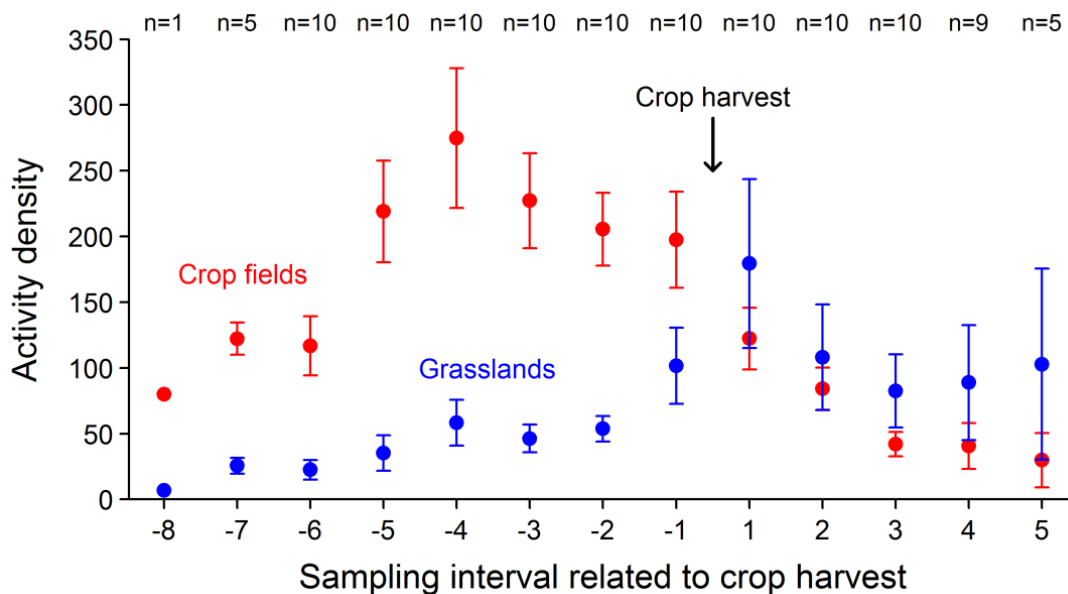
Fig. S1 Activity density of carabid beetles (mean ± SE) in crop fields (n = 10) and in adjacent calcareous grasslands (n = 10) related to the date of crop harvest. -8 to -1 indicate the eight sampling intervals before crop harvest and 1 to 5 indicate the five sampling intervals after crop harvest. As the crop fields were harvested at different dates, data for the 7th and 8th sampling interval before harvest and the 4th and 5th sampling interval after harvest were not available for all ten field sites. The sample size for all sampling intervals is given on top of the graphic.
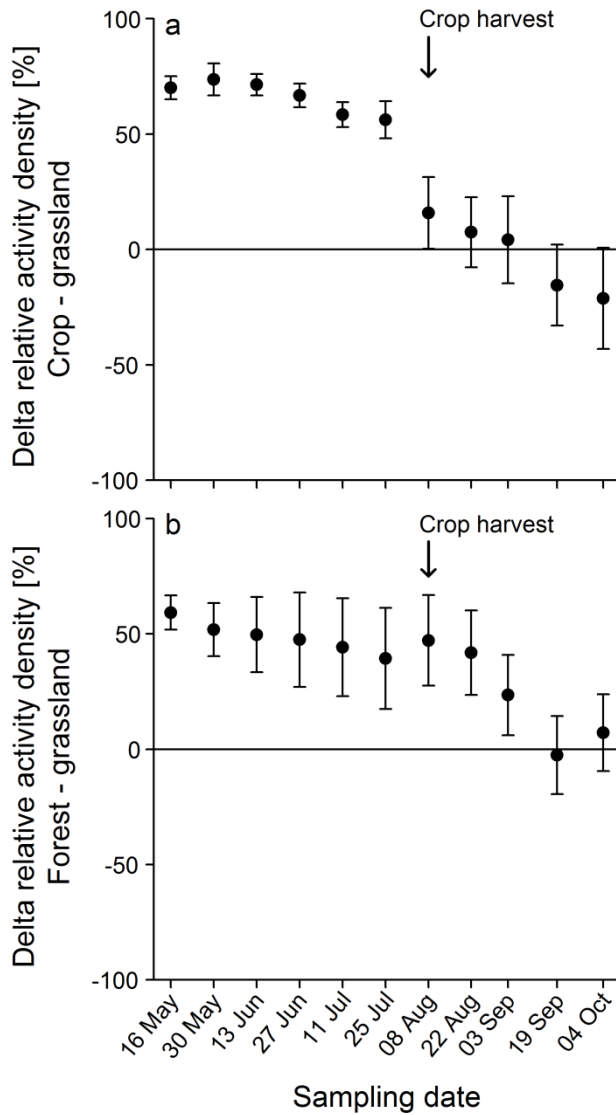
Fig. 4 Effect of crop harvest on carabid beetle activity density. The figure shows the difference in the realtive activity density of carabid beetles between calcareous grasslands and adjacent crop fields (a) or between calcareous grasslands and adjacent forests (b). The arrows highlight the beginning of crop harvest season. A positive delta shows a higher activity density in the crop fields or forests; a negative delta shows a higher activity density in the calcareous grasslands. Points with bars show mean and standard error.
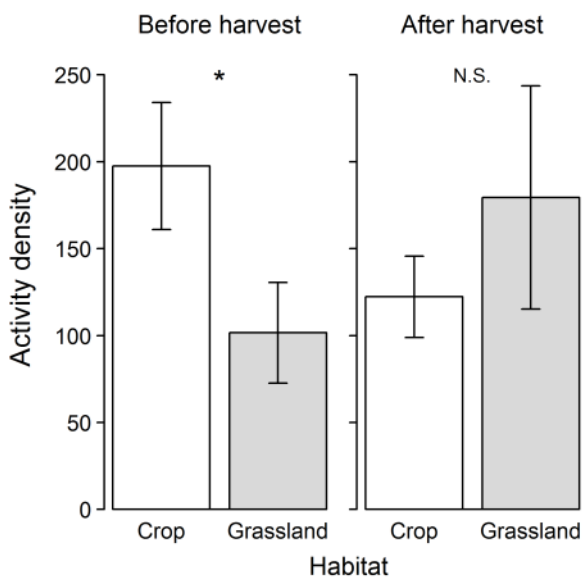
Fig. 5 Activity density of carabid beetles (mean ± SE) in cereal crop fields and adjacent calcareous grasslands before and after crop harvest, * $P < 0.05$, N.S. not significant.
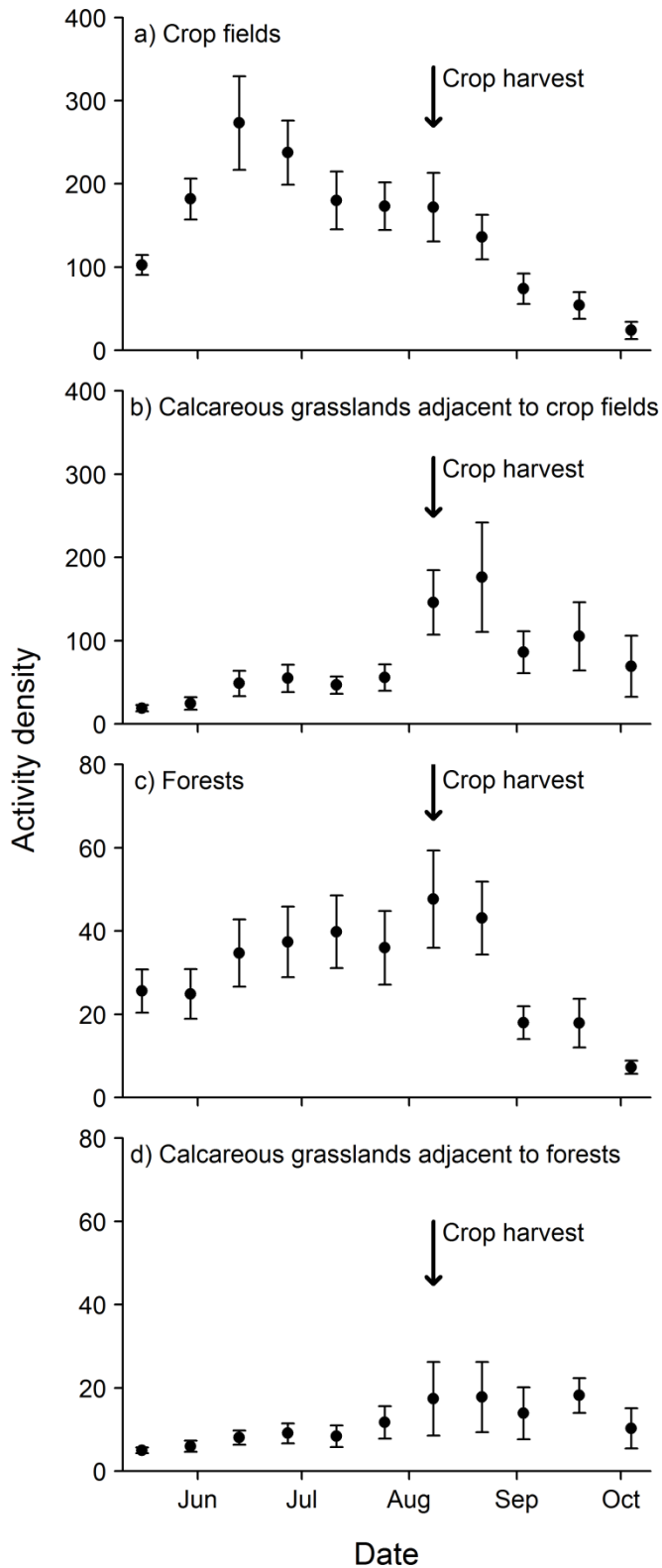
Fig. S2 Activity density of carabid beetles (mean ± SE) depending on the sampling interval in the four habitat types cereal crop field (a), calcareous grassland adjacent to cereal crop field (b), coniferous forest (c), and calcareous grassland adjacent to coniferous forest (d) (n = 10 per habitat type). Arrows highlight the beginning of crop harvest season.

Discussion

In this study, we analysed the role of adjacent habitat type and management for carabid beetle communities in fragmented semi-natural grasslands of high conservation value. Our results demonstrate that the diversity and community composition in grassland habitats is driven by the adjacent habitats. Our results further highlight the importance of crop harvesting in adjacent fields for semi-natural grassland communities.

The role of adjacent habitat for beetle communities in grasslands

In accordance with our first hypothesis we found a different species composition, species richness and activity density of carabid beetles in calcareous grasslands depending on adjacent habitat type. Different habitat or edge associated species of forests and crop fields penetrate into adjacent calcareous grasslands influencing the species composition (Lacasella *et al.* 2015). Species richness and activity density of carabid beetles was higher in calcareous grasslands adjacent to crops than adjacent to forests. Thus spillover transferred the higher species richness and activity density of crop fields compared to forests into adjacent grasslands (Brudvig *et al.* 2009). As fertilized crop fields have a higher primary production than coniferous forests (Field *et al.* 1998) they harbour larger populations resulting in a stronger spillover due to passive diffusion or density-dependent dispersal (Rand, Tylianakis & Tscharntke 2006). Additionally, the habitat structure of crop fields is more similar to calcareous grasslands than the habitat structure of forests, which further facilitates spillover between the two open habitats (Ries & Debinski 2001; Ries *et al.* 2004). In addition to the spillover of organisms, also microclimatic differences in the more shaded grasslands adjacent to coniferous forests and the more sunny grasslands adjacent to cereal crop fields can contribute to higher activity densities adjacent to crop fields. In accordance with our second hypothesis we found a lower evenness of carabid beetles in grasslands adjacent to crops than adjacent to forests. In our study the lowered evenness in calcareous grasslands adjacent to crop fields can be explained by the high dominance of the species *Anchomenus dorsalis*. This zoophag species, which is mainly associated with open habitats, may profit from the high abundance of aphids and other insect prey in cereal crop fields and then spill over into adjacent semi-natural habitats.

We cannot exclude, that the observed differences depending on adjacent habitat type were only edge effects and do not affect species communities in the habitat centre. However, it is likely that the community composition measured at a distance of 5 m from the habitat

edge represents the habitat centre adequately, because the studied calcareous grasslands are relatively small (median 1.78 ha, range 0.39 - 13.3 ha). Additional data from seven of the studied calcareous grasslands measured carabid beetle communities at distances of 1, 5 and 20 m from the habitat edge (where a distance of 20 m represents the habitat centre at many study sites). These data showed that the community composition at 5 m from the edge was as similar to the community composition at 1 m from the edge as to the community composition at 20 m from the edge (Fabian Bötzl, unpublished data).

Effects of crop harvest on spillover

In accordance with our third hypothesis we found a strong impact of crop harvest on the activity density of carabid beetles. After harvest, the activity density decreased in crop fields and increased in calcareous grasslands adjacent to crop fields, indicating a strong spillover from crop fields into adjacent semi-natural grasslands. This result supports the few other studies that show that crop harvest results in spillover into adjacent semi-natural habitats (Hossain *et al.* 2002; Opatovsky & Lubin 2012; Bong *et al.* 2013). However, the strong increase of activity density in calcareous grasslands adjacent to crop fields after crop harvest is mainly caused by the common species *Anchomenus dorsalis*. Other species may suffer a comparatively higher mortality during crop harvest.

The higher activity density after crop harvest in calcareous grasslands adjacent to crop fields declined within 2 – 4 weeks. This can be the result of density-dependent dispersal or higher mortality rates due to resource competition or predation (Stiling 1988; Hossain *et al.* 2002). However, as we found a simultaneous decline of activity density in the other habitat types, too, seasonal changes can also explain the decreasing activity density (e.g. Castro et al. 2014). Importantly, the transient spillover of generalist predators like *Anchomenus dorsalis* after crop harvest can result in higher predation on adult or larval stages of rare and endangered species in calcareous grasslands or a stronger competitive pressure on specialist grassland predators (Holt & Hochberg 2001; Tscharntke, Rand & Bianchi 2005; Rand & Louda 2006).

Conclusion

The observed patterns of varying diversity and species assemblages in dependence on adjacent habitat type can lead to varying ecosystem functions. For example, a previous study, conducted on the same calcareous grasslands, showed that predation rates of ground-dwelling predators differed depending on adjacent habitat type (Schneider, Krauss & Steffan-Dewenter

2013). But also other ecosystem functions like herbivory, parasitism, pollination or infection by pathogens may be affected by spillover (Blitzer *et al.* 2012). Therefore conservation schemes for fragmented semi-natural habitats like European calcareous grasslands need to consider adjacent habitat types and their management. In other taxonomic groups also the landscape context at larger spatial scales may affect species assemblage and diversity (Schmidt *et al.* 2008; Jauker *et al.* 2009; Flick, Feagan & Fahrig 2012). The spatial scale at which species are affected depends on the activity range of the species, which is mainly determined by foraging distances, the resource distribution in the landscape and dispersal abilities (Kremen *et al.* 2007). For example, ballooning spiders or flying insects often react to larger spatial scales than carabid beetles, which mainly disperse by walking (Martin *et al.* in prep.; Gardiner *et al.* 2010).

In conclusion, community composition and species diversity depends not only on the habitat type studied, but is also driven by surrounding habitats. This is of special importance for nature conservation measures, which aim to protect endangered species in semi-natural or natural habitats but currently are only targeted to improve local habitat quality.

Chapter 3: Predation rates on semi-natural grasslands depend on adjacent habitat type

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Abstract

Spillover in ecological systems, that is the dispersal or foraging of organisms across habitat borders, can affect ecosystem functioning and food web interactions of local communities. While spillover of organisms from perennial habitats into agricultural fields received some attention in the context of ecosystem service provisioning, the spillover into semi-natural habitats has rarely been addressed, although spillover of generalist predators or competition for pollinators can have consequences for nature conservation. We studied predation rates of ground-dwelling predators on 20 calcareous grasslands, with either coniferous forest or a crop field as adjacent habitat. As prey items we exposed 32,000 ladybird eggs on the grasslands. Within two study periods (June to September) predation rates were higher at warm compared to cool days, but did not depend on the study period itself or the distance from the edge where prey items were placed. In each study period we found higher predation rates when coniferous forest was the adjacent habitat, however, only on cool days. On warm days, prey items were consumed to very high extents (often 100%), which did not allow the detection of possible differences between adjacent habitat types. The higher predation rates on grasslands adjacent to forests can be explained by predator spillover from forests to grasslands. We conclude that semi-natural habitats provide not only ecosystem services in adjacent human dominated habitats, but are also exposed to antagonistic spillover effects. Such antagonistic spillover should be considered in conservation strategies for semi-natural habitats.

Keywords: edge effects, ground-dwelling predators, ecosystem services, nature conservation, habitat fragmentation, land-use change, landscape ecology, functional spillover

Introduction

Biotic interactions in communities are influenced by the spillover of organisms from or to the surrounding landscape (Knight *et al.* 2005; McCoy, Barfield & Holt 2009). For example predator or prey species which cross habitat borders can influence food web interactions of communities. It is therefore necessary to detect not only the number of species and individuals that spill over between adjacent habitats, but also to address the functional responses in the habitats (Polis, Anderson & Holt 1997; Rand, Tylianakis & Tscharntke 2006). Functional spillover is the movement of organisms across habitat borders resulting in changed ecosystem functions, e.g. predation or pollination (Blitzer *et al.* 2012). The functional spillover of predators into agricultural fields has been studied, particularly with regard to biological pest control. Complex landscapes with many semi-natural habitats had a better pest control on agricultural fields due to higher densities of natural enemies compared to fields in simple and intensively used landscapes (Bianchi *et al.* 2005; Bianchi, Booij & Tscharntke 2006). However most of the existing studies disregarded the functional consequences of spillover effects in the opposite direction i.e. from human-dominated to semi-natural habitats (Tscharntke, Rand & Bianchi 2005; Blitzer *et al.* 2012). One study demonstrated that mass flowering crops adjacent to semi-natural grasslands compete for pollinators, thereby leading to insufficient pollination of a rare grassland species (Holzschuh *et al.* 2011), but studies on antagonistic food web interactions are missing. Shifts in food web interactions of semi-natural habitats caused by spillover of organisms such as predators can be important for nature conservation, particularly in habitats that host threatened prey species. Small populations of rare prey animals can be seriously threatened by high predation pressures leading to possible local extinctions (Wagner *et al.* 2005; Kramer & Drake 2010).

Functional spillover in ecological systems can be driven by differences in the primary production of habitats. In theory, high productive habitats can support large prey populations and thus high predator abundances. Predators occurring in high densities spill over into adjacent low productive habitats (Rand, Tylianakis & Tscharntke 2006; Brudvig *et al.* 2009). Apart from the primary production, adjacent habitat type affects the functional spillover due to different species pools (French *et al.* 2001; Diacon-Bolli *et al.* 2012). Spillover effects between habitats should be strongest at the edges of neighbouring habitats. Although edge effects can extend over distances larger than 250 m (Ewers & Didham 2008), differences in the magnitude of an edge effect can be detectable below 20 m (Hajek *et al.* 2007; Roume *et al.* 2011). An accumulation of generalist predators near habitat edges has been shown (Ries &

Fagan 2003; Wimp *et al.* 2011) and can be explained by the proximity of alternative resources in adjacent habitats (Rand, Tylianakis & Tscharntke 2006). Therefore predation rates are expected to be highest in close proximity to the edges of habitats (Andren & Angelstam 1988; Thomson & Hoffmann 2013).

In addition to spatial patterns also temporal patterns can cause variations in the functional spillover of predators. Such temporal patterns can arise from biotic factors like ontogenetic shifts in predation (Werner & Gilliam 1984) or by seasonal variations in abiotic factors such as temperature (Polis *et al.* 1996). Higher temperature lead to a higher activity of arthropods resulting in a higher probability of finding prey items (Kruse, Toft & Sunderland 2008). In addition, higher temperature causes higher metabolic rates and thus higher food requirements (Brown *et al.* 2004). The primary production of adjacent habitats can also vary over time which might affect the functional spillover (Rand et al., 2006; Blitzer et al., 2012). The primary production of agricultural fields can vary throughout the vegetation period, leading for example to emigration of predators after crop harvest (Rand, Tylianakis & Tscharntke 2006). Therefore agriculturally subsidized predators are expected to affect prey populations in semi-natural habitats adjacent to crop fields, especially after crop harvest.

In this study we investigated the predation rate of ground-dwelling predators in 20 calcareous grasslands. Calcareous grasslands are semi-natural habitats with a high biodiversity and conservation relevance in Europe (van Swaay 2002; Diacon-Bolli *et al.* 2012). During the last century, large parts of European calcareous grasslands had been converted into agricultural land or were afforested after abandonment so that the remaining areas are strongly fragmented (WallisDeVries, Poschlod & Willems 2002; Krauss *et al.* 2010). Today the remnants of the calcareous grasslands most often border agricultural fields or forests (Poschlod & WallisDeVries 2002). Our aim was to quantify spillover effects on predation rates, an important ecosystem function in calcareous grasslands, in dependence on the type of adjacent habitat and season.

Our predictions are:

1) Predation rates in semi-natural habitats depend on adjacent human dominated habitat types and are higher near predator-rich habitats e.g. coniferous forests compared to crop fields.

2) Predation rates are higher near the edge of semi-natural habitats compared to more central positions in the habitat.

3) Predation rates depend on the study period (June or August/September). Predation rates adjacent to crop fields differ more strongly between these two periods compared to forests due to predator spillover after crop harvest.

4) Predation rates are higher when the day temperature allows higher activity of ground-dwelling arthropods and vary therefore between days with different temperatures. Since daily temperature variations are especially pronounced in open habitats we expected a more pronounced temperature effect in crop fields than in forests.

Material and methods

Study sites

We selected 20 calcareous grasslands in the surroundings of the city of Würzburg, Bavaria, Germany. Half of the grasslands were adjacent to a coniferous forest and half of them to a conventionally managed cereal crop field. Cereals in the region are rarely sprayed with insecticides, but regularly with herbicides and fungicides (Krauss, Gallenberger & Steffan-Dewenter 2011). The total area of each of the grasslands ranged between 0.4 and 13 ha, but with no significant size difference between those adjacent to the coniferous forests and those adjacent to the crop fields (Wilcoxon rank sum test: $W=36$, $N_1=N_2=10$, $p=0.32$). The calcareous grasslands were selected using the following criteria: (i) mapped as calcareous grassland with flora typical for this habitat type, either extensively managed or unmanaged to achieve comparability of habitat quality, (ii) with a minimum size of 0.4 ha to avoid area effects on small grasslands with high perimeter-to-area ratios (iii) with a clear border (<2 m) either to a coniferous forest or to a crop field instead of a gradual transition, (iv) spatial independent distribution of grasslands adjacent to forests and grasslands adjacent to crop fields, (v) permission of the nature conservation authorities.

Data collection

The predation rate of ground-dwelling predators was tested using sentinel prey. This method requires immobile stages of arthropods like eggs or pupae as prey items (Luck, Shepard & Kenmore 1988). We used the eggs of seven-spot ladybird beetles (*Coccinella septempunctata*), as high quantities of eggs could easily be obtained from a commercial biotech supplier (Katz Biotech AG, Baruth). We exposed the eggs at the soil surface of the calcareous grasslands to measure the predation of ground-dwelling predators like carabids which prey on arthropod eggs (Lovei & Sunderland 1996). The eggs were laid on small plastic sheets (< 10 cm²) by captive breeding ladybird beetles. We stored the egg sheets at

4 °C until exposition, to avoid early hatching. At all grasslands the plastic sheets with eggs were pinned to the soil surface.

A total of 32,000 eggs were used for the study. On each of the 20 grasslands we placed two times 800 eggs in four separate clusters of 200 eggs. Each egg cluster comprised several egg batches since ladybird beetles lay 30-50 eggs per clutch (Dixon & Guo 1993). Of the four egg-clusters per field, two were placed 5 m from the edge of the grassland adjacent either to the coniferous forest or to the crop field (= edge position). The other two clusters were placed at a distance of 20 m from the edge (= central position; Fig. 1). The distances of 5 and 20 m from the habitat edge were chosen because carabids showed edge effects within 4.9 ± 2.3 m (mean $\pm$ SD) in woodlots and within 14.4 ± 12.3 m (mean $\pm$ SD) in open habitats (Roume *et al.* 2011). Each cluster with eggs was protected against rain by a metal rooflet (25 cm x 25 cm and 10 cm high). After 24 hours of exposition on the grasslands we counted the remaining eggs to calculate predation rates.
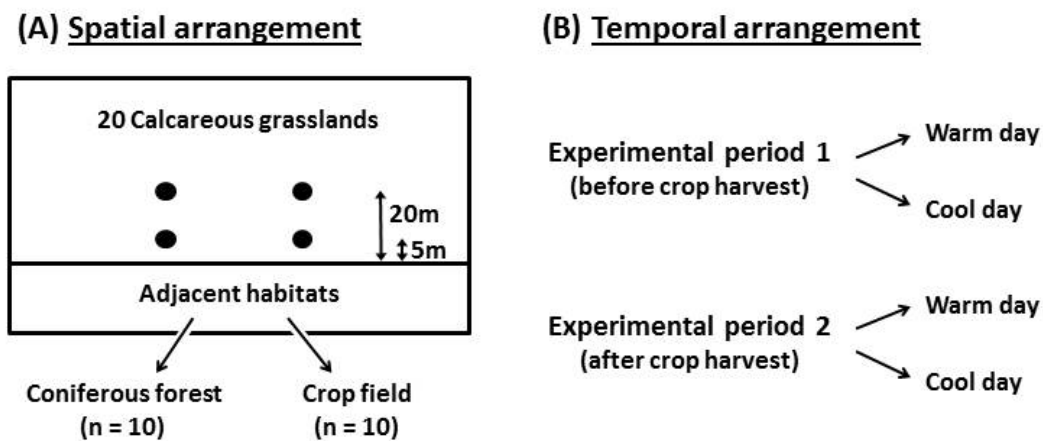

Fig. 1 Experimental design: (A) arrangement of the egg clusters (black dots) on the calcareous grasslands (study sites), (B) temporal arrangement of the two experimental periods.

The experiment was conducted two times at two different experimental periods: (i) in mid-June during growth of the crops on the adjacent fields and (ii) after harvest in late August/ early September (Fig. 1). Within each experimental period we conducted the survey on two days within a week surveying half of the 20 grasslands per day. On each of the two days, five of ten surveyed grasslands were adjacent to a forest and five were adjacent to a crop field. During the 24-h experiment a few larvae hatched in some of the clusters. As ladybird larvae tend to be cannibalistic we excluded the egg batches containing hatched larvae from further analyses, so that in some cases less than 200 exposed eggs were considered in the analysis (~7% of all 32000 eggs).

Temperature data during the experiments were obtained from the nearest local weather stations (Würzburg and Bad Kissingen). The first experimental period in June had lower air temperatures than the second period in August. But there were also temperature differences within the experimental periods. During the first experimental period the maximum temperature of the first survey day was 2-3 °C warmer compared to the second survey; in the second experimental period the first survey was even 2-5 °C warmer compared to the second survey (see Table S1). We tested the influence of temperature by comparing the warm and cool days within each experimental period.

Table S1 Maximal temperatures measured at the national local weather stations in Würzburg and Bad Kissingen at the experimental days (WetterOnline Meteorologische Dienstleistungen GmbH 2012, www.wetteronline.de).

Exp. period	Experimental day	Würzburg	Bad Kissingen	Classification
1	18.06.2011	18.3°C	18.6°C	warm
1	25.06.2011	16.5°C	15.5°C	cool
2	25.08.2011	29.7°C	26.2°C	warm
2	01.09.2011	24.4°C	24.0°C	cool

Statistical Analyses

The predation rates were analysed using generalized linear mixed-effects models fitted by Laplace approximation in R 2.15.2 (R Core Team 2013). The predation rate was included as a two-vector response variable (eggs predated and eggs left) and a binomial error structure was used because we had proportion data. The explanatory variables were (1) adjacent habitat type with the two factor levels "coniferous forest" and "cereal crop field", (2) location in the grassland with the two factor levels "edge" or "centre", (3) experimental period with the two factor levels "one" (mid-June) and "two" (end of August/beginning of September) and (4) temperature with the two factor levels "cool" and "warm". Additionally, the two-way interaction between neighbouring habitat type and experimental period was included in the model to test for an influence of crop harvest. The interaction between neighbouring habitat type and temperature was included to test whether the temperature effect was stronger in open habitats. To account for our nested design, the locations in the grassland were nested in site and included as a nested random factor. The model was corrected for overdispersion (estimated scale parameter: 7.5) by including also an individual level random factor. We present the full models, but due to the balanced design of our experiments a model

simplification removing non-significant explanatory variables (P > 0.05) using stepwise backward selection based on likelihood ratio tests achieved almost the same statistical values. As the first surveys within each experimental period were essentially warmer than the second surveys and as these seasonal warm to cool day differences were highly significant and could have masked additional effects, we also analysed the data separately for warm and cool days. Study site area was not considered to play an important role in predation rates as we chose only calcareous grasslands > 0.4 ha. However we also tested the effect of study site area (log-transformed) on mean predation rates and found no significant relationship (simple regression: $F_{1,18} = 0.18$, P = 0.68).

Results

Day temperature within the experimental periods was a highly significant predictor for predation rates on calcareous grasslands (P < 0.001, Table 1). We found predation rates to be significantly higher on the warmer days (mean ± SD, 69.0% ± 33.7%) compared to the cooler days within the experimental periods (34.8% ± 30.8%) (Fig. 2). Predation rates of 100% were found more often on warm days (36.3% of the exposed egg clusters) compared to cool days (8.8% of the exposed egg clusters). The influence of adjacent habitat depending on temperature within the experimental periods is indicated by a marginally significant interaction term between adjacent habitat and temperature (P = 0.06, Table 1), while experimental period, the position of the egg clutches (edge or centre of the grassland) and the interaction between adjacent habitat and experimental period had no significant effect (Table 1).

Additionally, we calculated separate models for warm and cool days to confirm the marginal significant interaction between temperature and adjacent habitat. The model which considered only cool days showed that neighbouring habitat type is a highly significant predictor, while experimental period, the position of the egg clutches and the interaction between habitat and experimental period had no significant effect on the predation rate (Table 2). On the cool days, predation rate was significantly higher on the grasslands adjacent to coniferous forests (mean ± SD, 46.8% ± 33.2%) than on grasslands adjacent to crop fields (22.7% ± 23.1%); Fig. 3). In models with data from the warm days only, we found no significant effect of the explanatory variables on predation rates (Table 2, Fig. 3).

Table 1 Results of the generalized linear mixed-effects model for predation rates on calcareous grasslands in dependence on adjacent habitat, location in the grassland, experimental period, temperature, the interaction between adjacent habitat and experimental period and the interaction between adjacent habitat and temperature. Generalized linear mixed effects model, the full model is shown, significant p-values are shown in bold.

Fixed effects	χ^2	d.f.	P-value
Adjacent habitat (AH)	3.12	1	0.08
Location in the grassland	0.03	1	0.85
Experimental period (EP)	1.64	1	0.20
Temperature (T)	27.05	1	**<0.001**
AH x EP	2.92	1	0.09
AH x T	3.53	1	0.06

Table 2 Results of the generalized linear mixed-effects models for predation rates on calcareous grasslands separately for the two temperature categories "cool" and "warm" in dependence on adjacent habitat, location in the grassland, experimental period and the interaction between adjacent habitat and experimental period. Generalized linear mixed effects models, the full models are shown, significant p-values are shown in bold.

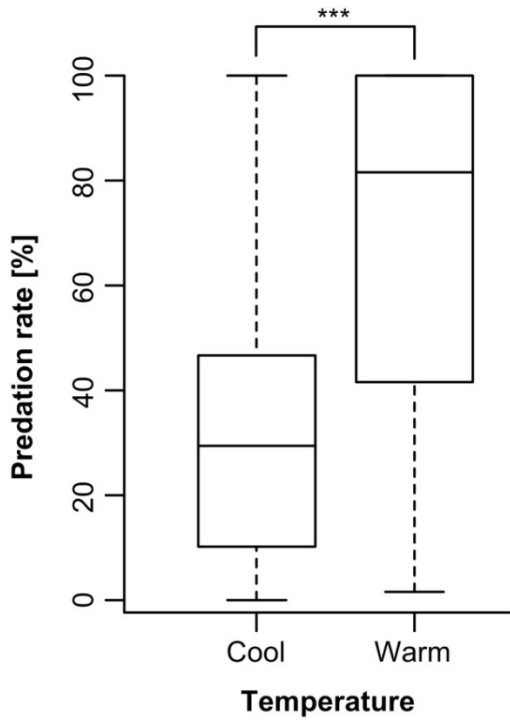| Response	Fixed effects	χ^2	d.f.	P-value
Predation rate on cool days	Adjacent habitat (AH)	10.94	1	**<0.001**
	Location in the grassland	0.58	1	0.45
	Experimental period (EP)	0.12	1	0.73
	AH x EP	2.68	1	0.10
Predation rate on warm days	Adjacent habitat (AH)	0.00	1	0.95
	Location in the grassland	0.14	1	0.71
	Experimental period (EP)	1.84	1	0.18
	AH x EP	0.47	1	0.49

Fig. 2 Effect of temperature on the predation rate. Boxplots show median, lower and upper quartile, minimum and maximum. *** p<0.001 (Statistics see Table 1).
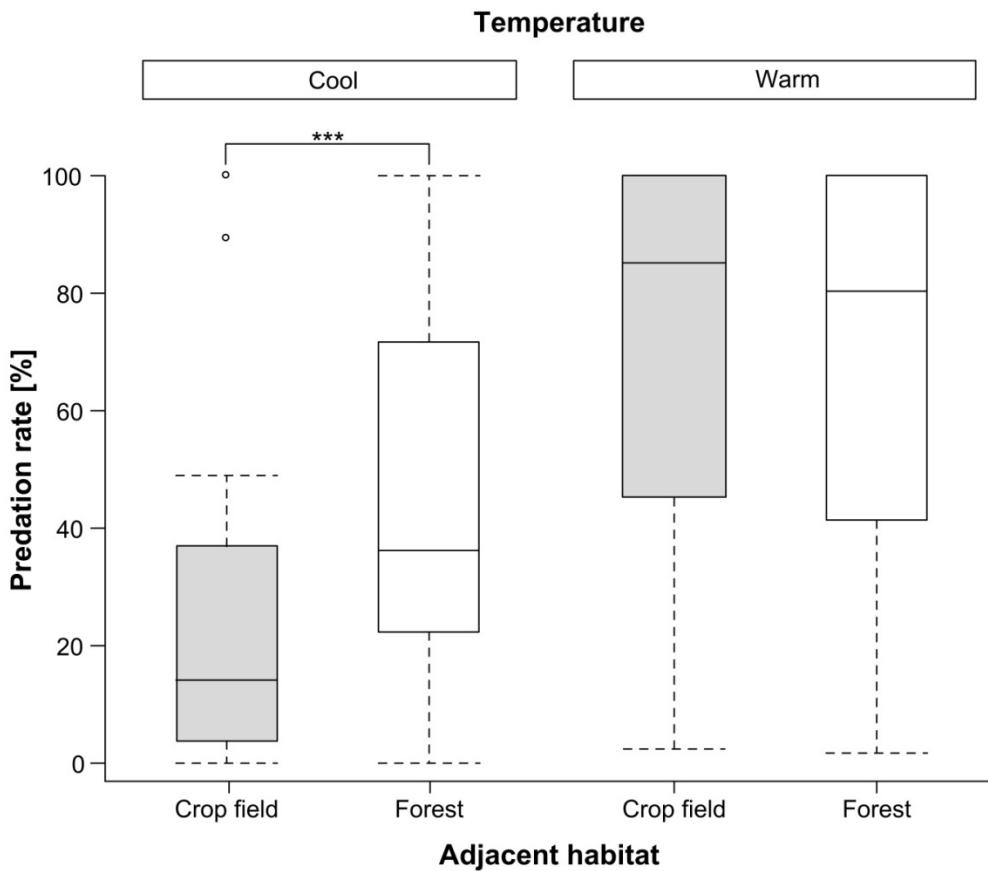

Fig. 3 Effect of adjacent habitat on predation rates. Boxplots show median, interquartile range, minimum, maximum and outliers. Predation rates differ depending on adjacent habitats only on cool days. *** p<0.001 (Statistics see Table 2).

Discussion

Temperature and the interaction between temperature and adjacent habitat type influenced predation rates. On the cooler days within the two experimental periods we found higher predation rates on calcareous grasslands adjacent to coniferous forests compared to calcareous grasslands adjacent to crop fields. Higher predation rates adjacent to forests can indicate a functional spillover of predators causing differences in predation pressures depending on adjacent habitat type in a semi-natural habitat. The predation pressure of ground-dwelling predators could affect all insects with at least one ground-dwelling life cycle stage, including endangered species on calcareous grasslands like the red-winged grasshopper (*Oedipoda germanica*) or the field cricket (*Gryllus campestris*) (Wagner *et al.* 2005; Hochkirch *et al.* 2007).

Higher predation rates on calcareous grasslands adjacent to coniferous forests compared to crop fields can be explained by predators immigrating from the forests or by predators emigrating to the crop fields. As forests have a higher primary production compared to calcareous grasslands (Lieth 1973) the patterns found by us are in accordance with the theory that organisms spill over from habitats with high primary production to habitats with low primary production (Rand, Tylianakis & Tscharntke 2006). Differences in primary production between calcareous grasslands and crop fields are less strong. In addition, predator populations in crop fields are often reduced by cultivation techniques (Thorbek & Bilde 2004) and pesticide usage (Thomas & Jepson 1997). Therefore forests probably host more ground-dwelling predators which can move into adjacent habitats leading to a higher predator density. Crop fields and forests further have distinct species communities (Bedford & Usher 1994; Magura 2002). Hence spillover movements may lead to different predator identities in semi-natural grasslands adjacent to forests and crop fields. Since forests host large species (Lovei & Sunderland 1996) with high food intakes (Reichle 1968) and large foraging distances (Peters 1986) predation rates may be higher adjacent to forests compared to crop fields. Beside spillover movements there are also alternative explanations, which could explain differences in predation rates. The arthropod assemblages on semi-natural grasslands depend on the plant species composition (Schaffers *et al.* 2008), which may differ due to different microclimatic conditions adjacent to forests and crop fields. In addition, differences in microclimate may lead to different predator activities. Earlier studies showed that arthropod species richness also depends on habitat area (Bolger *et al.* 2000), but in our experimental design we selected study sites of similar area and found no effect of area on predation rates.

The difference in predation rates between calcareous grasslands adjacent to forests and calcareous grasslands adjacent to crop fields was only significant for cooler days within the experimental periods, while we found no difference for the warm days. The marginally significant interaction effect between adjacent habitat type and temperature may be due to the low number of exposed eggs (n = 200 per cluster). As a result, clusters may have been fully depleted on warm days, when predator activity is higher (Kruse, Toft & Sunderland 2008). A detection of differences in predation rates at higher temperatures would probably need more prey items. This question should be addressed in future studies.

We found no difference in the predation rates measured 5 and 20 m from the habitat edge. This is in contrast to previous studies which showed strong edge effects (Magura 2002; Ries & Fagan 2003; Wimp *et al.* 2011). One possible explanation is that an edge effect may have extended further into the surveyed grasslands, without a detectable decrease between 5 and 20 meters. Such far reaching edge effects up to 1 km had been shown for beetle communities in forest habitats (Ewers & Didham 2008). In accordance with our predictions, predation rates were higher on warm days within the experimental periods which can be explained by increased feeding rates (Vucic-Pestic *et al.* 2011) and a higher activity of predators at higher temperatures (Kruse, Toft & Sunderland 2008; Vucic-Pestic *et al.* 2011). However, we found no difference between predation rates in the two experimental periods (June vs. August/September), which indicates the existence of additional constraints affecting predation rates. For example, species composition and population densities of arthropod predator communities change over the year leading to varying proportions of differently sized predators (Juen, Steinberger & Traugott 2003) with different feeding rates (Reichle 1968). Also within species, feeding rates vary during the year which was shown for seed consumption rates of carabid beetles (Honek, Saska & Martinkova 2006). We detected no significant effect of crop harvest on predation rate. Maybe only few individuals spill over into the grasslands due to harvest so that they do not affect predation rates significantly. Similarly, no significant difference in the abundance of spiders on wheat fields and adjacent semi-natural habitats before and after crop harvest have been found, but the overall spider abundance decreased in the wheat fields and increased in the adjacent semi-natural habitats after harvest, indicating a spillover from the fields into semi-natural habitats after harvest (Opatovsky & Lubin 2012).

In conclusion, our results suggest that spillover of predators depends on the adjacent habitat type. Thus the conversion and management of habitats adjacent to conservation-relevant areas can affect ecosystem functions of such areas. Policy makers and conservation

authorities should be aware of functional spillover in both directions. Functional spillover can be beneficial for agricultural and human dominated habitats if semi-natural or natural habitats provide free ecosystem services, but functional spillover can also be detrimental for these habitats if adjacent habitats interfere in the food web interactions or ecosystem functioning of conservation areas.

Chapter 4: Biological pest control and yields depend on spatial and temporal crop cover dynamics

Abstract

1. Modern agricultural landscapes are dynamic systems with inter-annually changing proportions of different crop types. However, the effects of spatiotemporal changes in crop area on crop yields and crop–herbivore–antagonist interactions have been rarely considered, in contrast to documented beneficial effects of semi-natural habitats on biological pest control at local and landscape scales. In this study, we examined how the proportion of oilseed rape fields in a landscape and the annual increase or decrease of oilseed rape cover due to crop rotation affect oilseed rape herbivores, their natural enemies and crop yield.

2. During two study years we examined the abundance of adult and larval pollen beetles, parasitism of pollen beetle larvae by a parasitic ichneumonid, and crop yields (seed weight per plant) in the edge and centre of 36 oilseed rape fields. The fields differed in the proportion of oilseed rape in the surrounding landscape at 1-km radius and in the inter-annual change in the proportion of oilseed rape from the previous year to the respective study year.

3. Adult pollen beetle abundance decreased in one study year and larval pollen beetle abundance and parasitism rates decreased in both study years with spatially increasing oilseed rape proportion in the landscape, indicating dilution effects on both trophic levels. Crop yield was positively affected by spatially increasing proportions of oilseed rape. An inter-annual increase in the proportion of oilseed rape led to the dilution of pest species, but had no significant effect on yield or parasitism rate.

4. *Synthesis and applications.* The negative effects of pollen beetles on yields despite regular insecticide applications underpin the need for improved techniques for controlling this pest. Our results emphasize the potential to enhance crop yields by the management of spatiotemporal crop cover dynamics within landscapes. We recommend that future management schemes should coordinate the spatial aggregation and annual dynamics of

oilseed rape cover in a landscape as a potential way to reduce pest impacts in intensively managed oilseed rape fields.

Keywords: agri-environmental schemes, dilution effects, ecosystem services, inter-annual population dynamics, oilseed rape, parasitism, pollen beetles, resource concentration hypothesis

Introduction

Animal pests are a severe threat to global crop production, leading to an estimated average yield loss of about 20% without crop protection (Oerke 2006). However, the protection of crops using pesticides can cause ecological and economic risks (Pimentel 2005). For example, increasing use of insecticides in the last decades led to numerous insecticide resistances (Heckel 2012) and long-term harmful effects of insecticide applications on natural antagonists can cause low efficiency or even enhanced pest densities (Krauss, Gallenberger & Steffan-Dewenter 2011). Biological control agents can offer a means of sustainable pest control, but the interacting effects of local and landscape factors on pest and natural enemy abundance and crop yields are still poorly understood (Chaplin-Kramer *et al.* 2011; Martin *et al.* 2013).

Two landscape factors affecting natural enemies and pest species are semi-natural habitats and host crop area. Semi-natural habitats have been shown to often benefit natural enemies and increase biological pest control (reviewed in Veres *et al.* 2013). Host crop area can affect pest species in two ways. (1) The resource concentration hypothesis states that large patches of host plants are more easily detectable by pest insects and increase the probability that specialized insects remain in the patch (Root 1973). When applied to the landscape scale, this hypothesis predicts that landscapes with high proportions of host crop should be more attractive to pest species, resulting in higher pest abundance. (2) Contrary to the resource concentration hypothesis, crowding effects result in high pest abundance in landscapes with low proportions of host crop area, because all individuals crowd on the few available host crop patches. In parallel, dilution effects lead to low pest abundance in landscapes with high proportions of host crop areas because all occurring individuals spread out over the host crop area. Such dilution effects have been shown for pollinators (Holzschuh *et al.* 2011; Haenke *et al.* 2014). The few studies investigating the influence of host crop area on biological pest

control and pest abundance have delivered contradictory results. These studies reported either concentration or dilution of pest species with increasing host crop area (Veres *et al.* 2013). Even within the same crop–herbivore system contradictory results reporting either positive, neutral or negative effects of host crop area on pest insect abundance were found (Rusch *et al.* 2010). Some studies indicate that on a landscape scale dilution effects can be more important than resource concentration effects (Otway, Hector & Lawton 2005; Veddeler, Klein & Tscharntke 2006). To improve the understanding of the relationship between pest abundance and host crop area, more case studies including additional factors like the within-field distribution of pests are needed.

At the local scale most pest species are unevenly distributed within crop fields due to behavioural preferences (Ferguson *et al.* 2003). Pests overwintering outside of crop fields can be more abundant at the field edge, because they colonize fields from the edge (Williams & Ferguson 2010; but see: Kaasik *et al.* 2013). However, there is evidence that species distribute more evenly in the field later in the season (Williams & Ferguson 2010; Kaasik *et al.* 2013). Measuring several within-field positions can help to disentangle local and landscape scale effects on pest and natural enemy abundance.

Apart from effects of oilseed rape proportion at the landscape scale and within-field position at the local scale, changes across time can also affect pest abundance and biological pest control (Thies, Steffan-Dewenter & Tscharntke 2008). Proportions of different crops within a landscape regularly change between years because farmers often rotate crops to reduce pest outbreaks and enhance soil quality (Brust & King 1994; Karlen *et al.* 2006). Inter-annually decreasing crop proportions in a landscape can lead to crowding effects with increased population density, if hibernated individuals concentrate in the remaining fields (Grez *et al.* 2004). In contrast, inter-annually increasing crop proportions in a landscape can lead to dilution effects, if individuals spread over a larger crop area, resulting in a decreased population density. For example, inter-annual changes in wheat proportions led to crowding and dilution effects of aphids, parasitoids and specialized predators (Zhao *et al.* 2013). Hence, crowding and dilution effects at both spatial and temporal scales can affect ecosystem functioning (Tscharntke *et al.* 2012) and therefore crop yields. However, there is a paucity of studies investigating crop yields depending on crowding and dilution effects operating at different spatial and temporal scales.

In this study we analysed how pollen beetles *Brassicogethes* spp. (synonym *Meligethes* spp.) and their main parasitoid *Tersilochus heterocerus* Thomson affect the yield of oilseed rape *Brassica napus* L. at different spatial and temporal scales. Pollen beetles are

among the major insect pests of oilseed rape in Europe (Williams 2010), causing yield losses of up to 80% in spring oilseed rape (Hansen 2004). Hymenopteran parasitoids like *Tersilochus heterocerus* can reduce pollen beetle populations significantly when parasitism exceeds 30–40% (Hokkanen 2008). We surveyed pollen beetle abundance, parasitism rate by *Tersilochus heterocerus* and oilseed rape yields and related these to: (i) within-field position on the local scale, (ii) oilseed rape proportion on the landscape scale and (iii) the inter-annual change of oilseed rape on the temporal scale. Additionally, the effectiveness of biological control of pollen beetles by *Tersilochus heterocerus* was analysed by relating parasitism rates from the first study year to the population growth rate of pollen beetles. Based on this framework we tested the following main predictions:

1) Local scale: Pest abundance is higher at field edges compared to field centres, as fields are colonized from the edge. Parasitoids are expected to show the same distribution pattern as they also colonize fields from the edge. Therefore, the pest–parasitoid ratio should be similar at the field edge and field centre, leading to similar parasitism rates.

2) Landscape scale: An increasing proportion of host crop area in the landscape reduces pest and parasitoid abundance in the crop due to dilution effects on the landscape scale. Parasitism rates are not affected by the proportion of host crop area, as the pest–parasitoid ratio remains constant.

3) Temporal scale: An inter-annual increase in crop area leads to a dilution of pests and parasitoids in the following year while an inter-annual decrease in crop area leads to a crowding of pests and parasitoids in the following year. Parasitism rates are not affected by the inter-annual change in host crop area, as the pest–parasitoid ratio remains constant.

4) Pollen beetle abundance decreases with increasing parasitism rates in the previous year.

5) As increasing pollen beetle abundance should decrease the yield, we assume that oilseed rape proportion and inter-annual changes in oilseed rape proportion indirectly affect crop yields.

Material and methods

Study sites

This study was conducted in landscapes dominated by agriculture (with on average 69% agricultural land, 20% forest, 3% hedges and shrubs) in the surrounding of the city of Würzburg, Bavaria, Germany in 2011 and 2012. In both years we selected 18 conventionally managed winter oilseed rape fields (with different oilseed rape cultivars) with a mean field size of 1.8 ha ± 1.1 SD in 2011 and 2.0 ha ± 1.1 SD in 2012. The fields were surrounded by non-overlapping landscape sectors with a 1-km radius, since it has been shown that pollen beetles and parasitism respond to landscape variables at this scale (Zaller *et al.* 2008b; Thies & Tscharntke 2010). Fifteen of the eighteen landscape sectors in 2011 overlapped with the landscape sectors in 2012. We determined the proportion of oilseed rape (OSR) within the landscape sectors for the study year (2011 or 2012) and the previous year (2010 or 2011) using data from the "Bayerische Landesanstalt für Landwirtschaft (LfL)" (Freising, Germany) in the software ArcMap (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental System Research Institute, USA). We calculated the inter-annual change of OSR proportions (ΔOSR) as follows: $\Delta\text{OSR} = (\text{OSR}_{\text{study year}} - \text{OSR}_{\text{previous year}}) / \text{OSR}_{\text{previous year}}$. In the study years, the OSR proportion in the 1-km radius surrounding selected fields covered a range from 0.5% to 21.0% and ΔOSR varied from -74% to +521%. OSR proportion and inter-annual change of oilseed rape proportion (ΔOSR) were not correlated for all study sites ($r = 0.26$, $N = 36$, $P = 0.1$). In addition, we calculated the proportion of semi-natural habitats within the 1-km radius including calcareous grasslands, flowering strips, orchard meadows, one-year fallows, gardens outside settlements, hedges, and forest edges. Semi-natural habitat (ranging from 0.5% to 28.5%) correlated only weakly with OSR proportion ($r = -0.33$, $N = 36$, $P = 0.05$) and ΔOSR ($r = -0.35$, $N = 36$, $P = 0.04$).

Study organisms

In Germany the rape pollen beetle *Brassicogethes aeneus* F. (synonym: *Meligethes aeneus* F.) is the most dominant pollen beetle species, accounting for 80–100% of pollen beetle populations (Thieme *et al.* 2008). Pollen beetles overwinter in the upper soil layers of semi-natural habitats (Rusch *et al.* 2012). In spring, when temperatures exceed 15°C the majority of pollen beetles leave their overwintering sites (Ferguson *et al.* 2015) and start foraging on a wide variety of plant species before they search for cruciferous plants as mating and oviposition sites (Williams 2010). Therefore, oilseed rape fields are a highly suitable

habitat. Adults can cause much damage to the rape plants by destroying small buds (mostly < 2 mm) to feed on the pollen inside (Ferguson *et al.* 2015). After copulation, females lay their eggs in buds of 2–3 mm in size (Ekbom & Borg 1996; Ferguson *et al.* 2015). After a few days, larvae hatch. The first larval instar lives within buds and the second larval instar in open flowers, both feeding on pollen. After 2 weeks the last larval instar drops to the ground to pupate in the soil. During summer, adults of the new generation emerge and feed on several plants in the surrounding area before seeking overwintering habitats (Williams 2010).

The univoltine ichneumonid *Tersilochus heterocerus* is one of the most important parasitoids specialized on pollen beetles in the study region (Ulber *et al.* 2010). Presumably adult *T. heterocerus* like other hymenopteran parasitoids feed on nectar of various plant species, which may explain the reported facilitation by semi-natural habitats in the landscape (Scheid, Thies & Tscharntke 2011; Rusch *et al.* 2012). *T. heterocerus* lays its eggs preferentially in second instar pollen beetle larvae in open flowers. The parasitoid first instar larvae hatch before the pollen beetle larvae are ready to enter the soil (Nilsson 2003). After the pollen beetle larvae drop to the ground, *T. heterocerus* completes its development and kills the prepupal stage of its host. Then the adults diapause in their cocoons in the soil until emergence during the following spring (Ulber *et al.* 2010).

Data collection

In each of the 36 study fields, we surveyed two edge-parallel transects: one at a distance of 1 m from the field edge (referred to as edge), and one at a distance of 20 m from the field edge (referred to as centre). During rape flowering (BBCH growth stage 63–64, see Federal Biological Research Centre for Agriculture and Forestry 2001 for details on the universal BBCH code for growth stages), adult pollen beetles were counted on the main raceme of 25 randomly chosen rape plants at intervals of about 1 m in each transect. In addition, five flowering plants per transect (BBCH growth stage 64–65) were collected and frozen until further analysis. In the lab, pollen beetle larvae per frozen plant were counted. Parasitism by *Tersilochus heterocerus* was quantified by dissecting all pollen beetle larvae under a binocular and counting the black eggs of *T. heterocerus*.

For yield determination five additional plants per transect were collected during ripeness (BBCH growth stage 87–89) and frozen until further analysis in the lab. We recorded: (i) ripe pods / plant, (ii) seeds / pod, calculated as the mean of 20 randomly chosen pods, or less if too many ripe pods had already opened and (iii) dry weight of 200 randomly chosen seeds dried at 60°C for 24 h. These measures were used to calculate the seed weight

per plant as follows: first we calculated the mean seed weight per pod as the product of the mean individual seed weight and the mean number of seeds per pod. Then we calculated the seed weight per plant as the product of the mean seed weight per pod and the mean number of pods per plant. We calculated the dry weights for 34 of the 36 study fields as seed samples of two fields were lost. Additionally, we received yield data for our study fields (dt ha^{-1}) from 33 of the 36 farmers.

Statistical analyses

We analysed the effects of year, within-field position, oilseed rape proportion, semi-natural habitats and inter-annual change of oilseed rape proportion on: (i) the abundance of adult pollen beetles, (ii) the abundance of pollen beetle larvae, and (iii) the parasitism rate by *T. heterocerus* in three generalized linear mixed-effects models (see Table 1 for a detailed list of explanatory variables). To account for our nested design, transect position was nested in landscape and included as a nested random effect. We also included plant ID as individual-level random effect to account for over-dispersion (Elston *et al.* 2001; Pirk *et al.* 2013). Since adult and larval pollen beetle abundance are count data, we used a Poisson error distribution (Crawley 2007). Parasitism rate was included as a two-vector response variable and a binomial error structure was used (Crawley 2007).

In addition, for the 15 landscapes that overlapped in 2011 and 2012, we analysed the influence of parasitism rates in 2011 on the population growth rate of pollen beetles from 2011 to 2012. Population growth rate was calculated as ln (abundance of adult pollen beetles 2012 / abundance of adult pollen beetles 2011). We used a linear model with population growth rate of adult pollen beetles as response and parasitism rate in 2011 as explanatory variable.

Further, we correlated the calculated seed weight per plant either from the field edge or from the field centre with the yield data from farmers using a Pearson's product-moment correlation. As we found a better correlation for seed weights of plants from the field centre (centre: $r = 0.68$, $N = 31$, $P < 0.01$ (Fig. 1), edge: $r = 0.59$, $N = 31$, $P < 0.01$), we used seed weights from the field centre as a proxy for yield in our analyses (see Appendix S1 in Supporting Information). Then we analysed the effects of year, pollen beetles, oilseed rape proportion, semi-natural habitats and inter-annual change of oilseed rape proportion on the seed weight of plants from the field centre, in two linear mixed-effects models with square root-transformed seed weights as response variable (see Table 2 for a detailed list of explanatory variables). Landscape was included as random effect in both models. Abundance

of adult pollen beetles in the field centre and of pollen beetle larvae in the field centre were not correlated (r = 0.1, N = 34, *P* = 0.6).

All models were simplified using a stepwise backward selection procedure based on likelihood ratio tests (Crawley 2007). Statistical analyses were performed using the R package lme4 (Bates *et al.* 2013) in the software R 3.0.2 (R Core Team 2013).
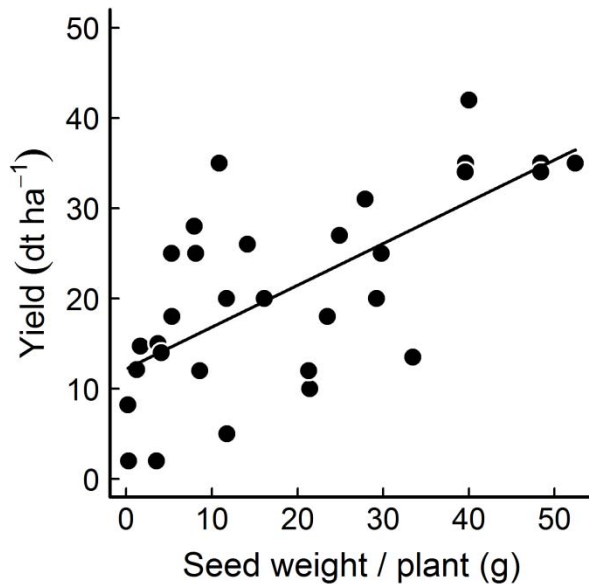

Fig. 1. Correlation between yields supplied from the farmers and mean seed weight per plant of the field centre.

Results

Local field scale

The abundance of adult and larval pollen beetles was strongly influenced by within-field position (Table 1). We found more than twice as many adult pollen beetles at the edge of rape fields compared with the centre (Fig. 2a). In contrast, pollen beetle larvae were 50% more abundant in the field centre compared with the field edge (Fig. 2b). Parasitism rates were not significantly affected by within-field position (Fig. 2c). Instead, the parasitism rate increased with increasing abundance of pollen beetle larvae (Table 1, y = -3.4 + 0.005 * x in 2011 and y = -2.8 + 0.005 * x in 2012). The population growth rate of adult pollen beetles was not significantly affected by parasitism rate in the previous year (d.f. = 1,13; F = 0.53; *P* = 0.48). In 2012, adult pollen beetles were seven times more abundant and parasitism rates were two times higher than in 2011.

Table 1 Generalized linear mixed effects models (Type III Wald chisquare tests). Final models after removing non-significant explanatory variables. Variables are year (2011, 2012), position (field edge, field centre), OSR proportion (proportion of oilseed rape in the landscape), ΔOSR (inter-annual change in oilseed rape in the landscape).

| Response	fixed effects	χ^2	d.f.	*P* value
Abundance of adult pollen beetle	year	1226.56	1	**< 0.001**
	position	29.27	1	**< 0.001**
	OSR proportion			NS
	semi-natural habitats			NS
	ΔOSR	251.94	1	**< 0.001**
	OSR proportion : year			NS
	ΔOSR : year			NS
	OSR proportion : position			NS
	ΔOSR : position	4.35	1	**0.04**
Abundance of pollen beetle larvae	year	4.03	1	**0.04**
	position	21.00	1	**< 0.001**
	OSR proportion	0.02	1	NS
	semi-natural habitats			NS
	ΔOSR	47.64	1	**< 0.001**
	OSR proportion : year			NS
	ΔOSR : year			NS
	OSR proportion : position	5.36	1	**0.02**
	ΔOSR : position			NS
Parasitism rate by *T. heterocerus*	year	6.94	1	**< 0.001**
	position			NS
	OSR proportion	12.15	1	**< 0.01**
	semi-natural habitats	6.73		**< 0.01**
	ΔOSR			NS
	host larvae per plant	4.22	1	**0.04**
	OSR proportion : year			NS
	ΔOSR : year			NS
	OSR proportion : position			NS
	ΔOSR : position			NS
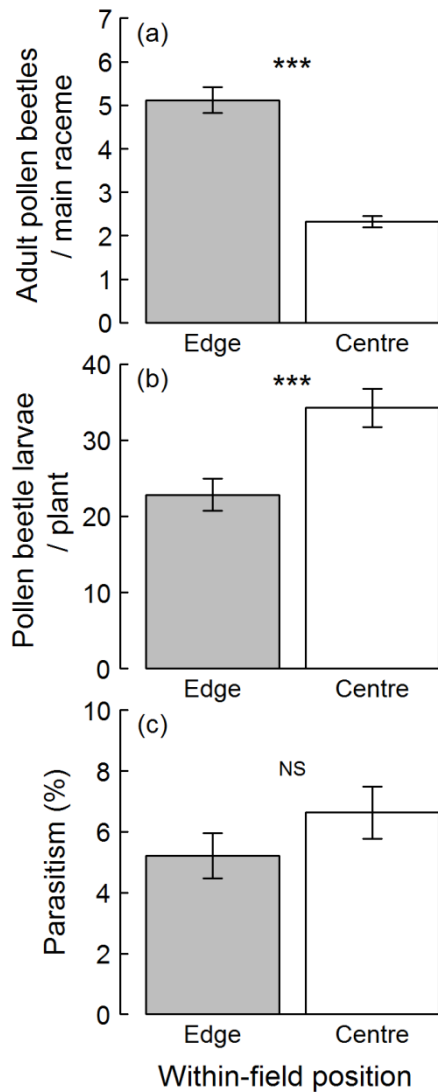
Fig. 2 Effect of within-field position (edge, centre) on the abundance of adult pollen beetles (a), pollen beetle larvae (b) and parasitism rate by *Tersilochus heterocerus* (c). Barplots show means and standard errors. *** $P < 0.001$, NS = not significant.

Landscape scale

An increasing proportion of oilseed rape in the landscape (OSR proportion) reduced the abundance of pollen beetle larvae in the field centre, but did not significantly affect pollen beetle larvae at the field edge (Fig. 3c, see also Table 1). Parasitism rate decreased with increasing oilseed rape proportion (Table 1, Fig. 3e). The effect of oilseed rape proportion on adult pollen beetle abundance was not significant across both study years (Table 1, Fig. 3a). However, as there was a tendency of OSR proportion to affect adult pollen beetle abundance we additionally looked at both study years separately. Indeed, adult pollen beetle abundance significantly decreased with an increasing proportion of oilseed rape in the landscape in 2012 ($\chi^2 = 7.92$, d.f. = 1, $P < 0.01$, Fig. S1) and marginally in 2011 ($\chi^2 = 3.16$, d.f. = 1, $P = 0.08$, Fig. S1). Neither adult pollen beetles nor pollen beetle larvae were significantly affected by the proportion of semi-natural habitats. Parasitism rate decreased with increasing proportions of semi-natural habitats (Table 1).
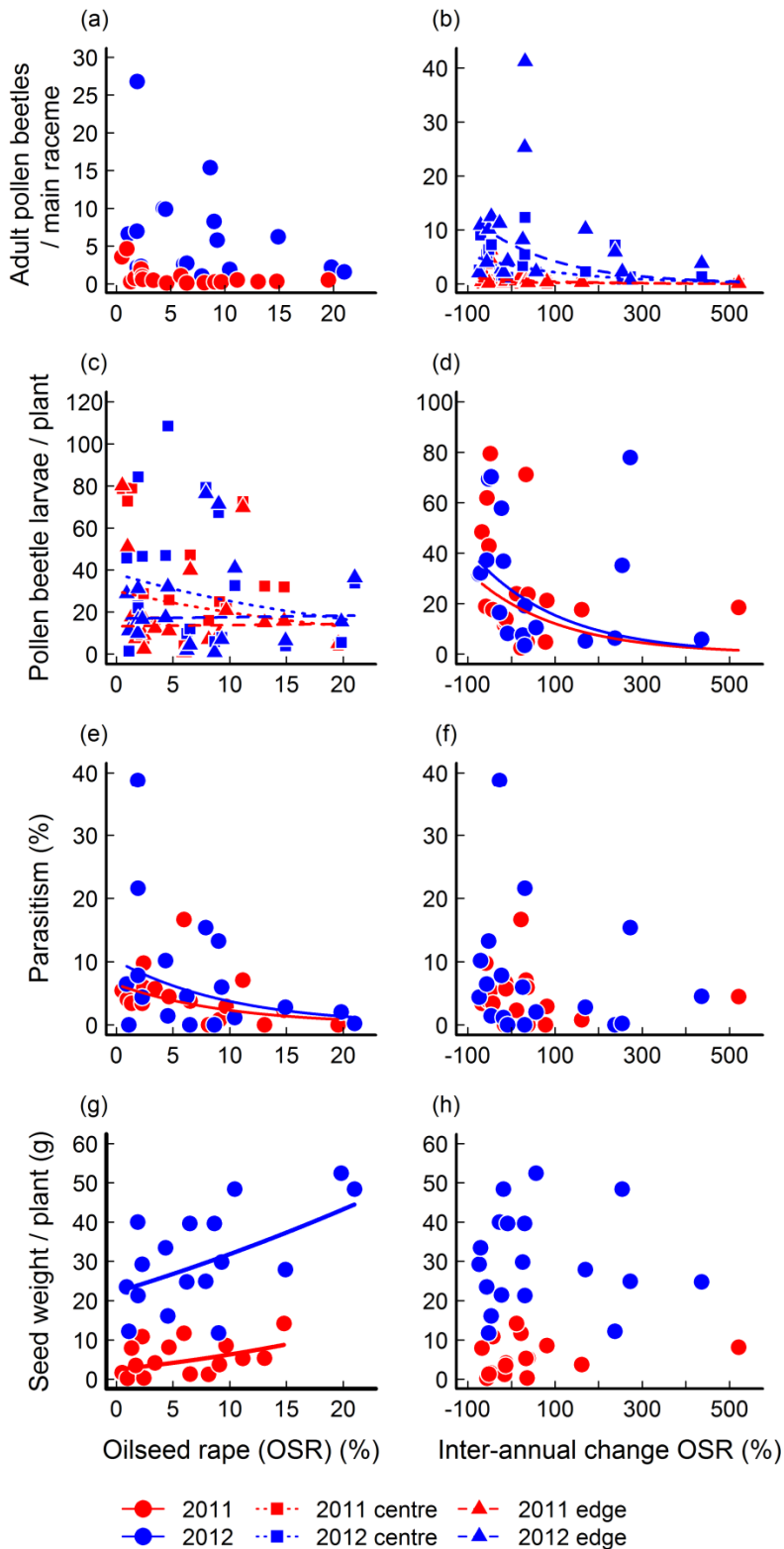
Fig. 3 Effects of oilseed rape (OSR) proportion and inter-annual change in oilseed rape (Δ OSR) on adult (a, b) and larval pollen beetle abundance (c, d), parasitism rate by *Tersilochus heterocerus* (e, f) and oilseed rape yields (g, h). Points represent means of the whole rape fields, whereas triangles and rectangles represent means of the field edge (triangles) and means of the field centre (rectangles). Lines were drawn when explanatory variables had a significant effect. Separate lines for edge and centre were drawn when the interaction with position was significant. See Tables 1 and 2 for statistical details.
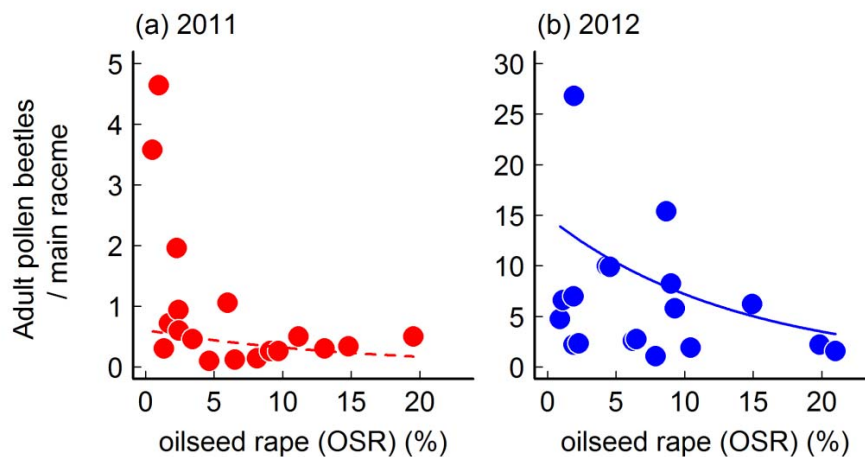
Fig. S1 Effect of oilseed rape (OSR) proportion on adult pollen beetle abundance in both study years. Solid line indicates significant effect, dashed line non-significant trend.

Temporal scale

The abundance of adult and larval pollen beetles increased in landscapes with an inter-annual reduction of oilseed rape and decreased in landscapes with an inter-annual expansion of oilseed rape, giving evidence for inter-annual crowding and dilution effects (Table 1, Fig. 3b and 3d). The significant interaction term of inter-annual change (Δ OSR) and position in the field for adult pollen beetles indicates that the effect was stronger at the field edge than in the centre. Parasitism rate was not significantly affected by the inter-annual change of oilseed rape (Δ OSR) (Table 1, Fig 3f).

Effects on crop yield

Yields of the oilseed rape fields were 35% lower in 2011 (16.2 ± 2.5 dt ha^{-1}) than in 2012 (mean ± SE, 24.8 ± 2.8 dt ha^{-1}). Yield decreased with decreasing proportion of oilseed rape in the landscape in both study years, but was not significantly affected by semi-natural habitats or the inter-annual change in oilseed rape proportions (Table 2, Fig. 3g and 3h). Our model predicts a yield reduction by 69% in 2011 and by 38% in 2012 when the oilseed rape proportion of a landscape decreases from 15% to 1% (Fig. 3g). The positive effect of oilseed rape cover on yield can be explained by indirect effects, i.e. the dilution of pollen beetles with increasing oilseed rape proportion in a landscape. In both years abundance of adult pollen beetles affected the yield negatively, while the abundance of pollen beetle larvae showed no significant effect (Table 2, Fig. 4a and 4b). According to our statistical model, in 2011 an increase of pollen beetle densities from one to four beetles per raceme reduced yields from 4.5 g to 2.7 g seed per plant (-41%) while highest beetle densities in 2012 (up to 12 beetles per raceme) lead to a yield reduction from 35.2 g to 16.4 g per plant (-53%) (Fig. 4a).

Table 2 General linear mixed effects models (Type III Wald chisquare tests) analysing the effects of herbivores (first model) and landscape parameters (second model) on seed weight. Final models after removing non-significant explanatory variables. Variables are year (2011, 2012); OSR proportion (proportion of oilseed rape in the landscape), ΔOSR (inter-annual change in oilseed rape in the landscape). (N=34).

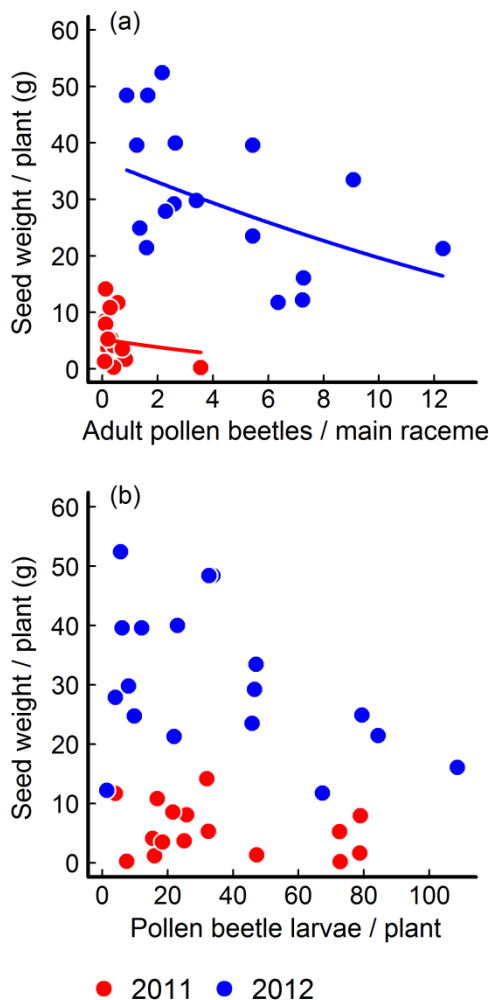| Response	fixed effects	χ^2	d.f.	*P* value
seed weight	year	115.01	1	**<0.001**
	adult pollen beetle abundance	6.60	1	**0.01**
	pollen beetle larvae abundance			NS
	adult pollen beetle abundance : year			NS
	pollen beetle larvae abundance : year			NS
seed weight	year	104.47	1	**< 0.001**
	OSR proportion	8.72	1	**< 0.01**
	semi-natural habitats			NS
	ΔOSR			NS
	OSR proportion : year			NS
	ΔOSR : year			NS

Fig. 4 Effect of adult pollen beetles (a) and pollen beetle larvae (b) on the seed weight of oilseed rape plants in the field centre. Lines were drawn when explanatory variables had a significant effect. See Table 2 for statistical details.

Discussion

This study shows that pest abundance declines with increasing host crop area on spatial and temporal scales depending on the within-field position. Moreover, we found evidence that reduced pest insect densities enhance crop yields. Our results indicate that the management of spatiotemporal crop cover dynamics within landscapes has the potential to be an important means of increasing crop yields.

Local and landscape scale

As hypothesized, adult pollen beetles were more abundant at the field edge compared to the field centre since they colonize fields from the edge (Williams & Ferguson 2010). In contrast pollen beetle larvae were more abundant in the field centre compared to the field edge, perhaps because ovipositing females avoid volatiles emitted by female conspecifics and dispersed further into the field to reduce intraspecific competition (Ruther & Thiemann 1997; Cook *et al.* 2006). Additionally, elevated predation rates may diminish the abundance of pollen beetle larvae at field edges (Büchs 2003).

Whilst pollen beetle larvae in the field centre decreased with increasing oilseed rape proportion, larval densities at the field edge were not affected by oilseed rape proportion. This may be related to the saturation of suitable oviposition sites at field edges, independently of oilseed rape proportions. Therefore crowding and dilution effects of pollen beetle larvae were more pronounced in the field centre. Further, higher predation pressure on beetle larvae in field edges might blur landscape-scale effects. Adult pollen beetles also showed a decrease with increasing oilseed rape proportion in one study year and a marginally significant trend to decrease with increasing oilseed rape proportion in the other study year. Thus, our pollen beetle data indicate dilution effects with increasing oilseed rape proportions on a landscape scale and do not support the resource concentration hypothesis. Such results are not unique to this system, other pests like the Andean potato weevil *Premnotrypes* spp. in potato fields and the plant bug *Lygus hesperus* in cotton fields occurred in lower densities with increasing host crop area (Carrière *et al.* 2006; Parsa, Ccanto & Rosenheim 2011). However, in other pest–crop systems the relationship between pest density and host crop area has seen to be positive, hump-shaped or constant, depending on the dispersal ability, reproduction rate and overwintering strategy of the pests and their natural enemies (Segoli & Rosenheim 2012). We would like to emphasize that managing the proportion of a single crop at a landscape scale is one novel option to reduce pest damage, but pests in other crops might show opposite effects,

because top–down control is more efficient and their natural enemies are more dependent on natural habitat. Therefore, we do not argue for large-scale monocultures but for advanced crop-specific landscape management schemes to optimize biological pest control and minimize the growth of pest populations without pesticide applications.

Although not the focus of our study, we additionally tested for effects of semi-natural habitats on pollen beetle abundance and parasitism rates. We found no positive effect of semi-natural habitats on pest control. However, earlier studies indicate that the proportion of non-crop area enhances pest control (Thies & Tscharntke 1999; Thies, Steffan-Dewenter & Tscharntke 2003). This discrepancy might be explained by: (i) different study designs (for example we maximized the landscape gradient in oilseed rape area instead of semi-natural area), (ii) changes in land use (e.g. a sharp decline of 'set-aside' fields during the last ten years (Lukasch, Frank & Schulze 2011)), and (iii) a negative correlation between oilseed rape and non-crop or semi-natural habitat cover (e.g. Scheid, Thies & Tscharntke 2011). Importantly, by taking into account the temporal dynamics of oilseed rape fields, pests and antagonists in managed fields, our study suggests a more important role of crop area and dynamics for pest control. Nonetheless, further studies on the role of different habitat types, spatiotemporal dispersal dynamics, and multitrophic interactions in differently structured landscapes are required to fully understand the population dynamics in host–antagonist systems (Martin *et al.* 2013).

Temporal scale

Adult and larval pollen beetles showed crowding with inter-annual oilseed rape reduction and dilution with inter-annual oilseed rape expansion. Parasitism rate by *Tersilochus heterocerus* was not significantly influenced by inter-annual changes in oilseed rape proportion. Other authors also found no inter-annual dilution for *T. heterocerus* parasitism, but for other hymenopteran parasitoids (Thies, Steffan-Dewenter & Tscharntke 2008). Possibly, other hymenopteran parasitoids have lower dispersal abilities than *T. heterocerus* and react therefore stronger to inter-annual landscape changes. This could lead to decreasing parasitism rates with inter-annual host crop expansions, resulting in a lower biological control efficiency (Thies, Steffan-Dewenter & Tscharntke 2008).

Biological pest control

Parasitism rates decreased with a spatially increasing oilseed rape proportion. Parasitism rates are presumably diminished in landscapes with high oilseed rape proportions

(and low beetle larvae densities) due to spatial dilution of parasitoids and positive density-dependent parasitism (Gladbach *et al.* 2010). In our study, parasitism rates were below 30% (except for one field), which is considered the threshold for effective biological control of pollen beetles (Hokkanen 2008). This may at least partially explain why increasing oilseed rape proportion in parallel decrease pollen beetle abundance and parasitism rates.

The low parasitism rates in our study may have been caused by low pollen beetle abundance in 2011 and a time delayed recovery of the univoltine parasitoid relative to pollen beetle populations. In addition, *Tersilochus heterocerus* overwinters in the soil of oilseed rape fields, thus a low abundance of parasitoids can be caused by upturning soil cultivation techniques like ploughing (Nilsson 2010). Further, most oilseed rape fields were regularly treated with insecticides during flowering. Insecticides often negatively affect hymenopteran parasitoids either lethally or sub-lethally, resulting in lower parasitism rates (Ulber, Klukowski & Williams 2010). Thus, more efficient biological control could be achieved by no-till management, reduced insecticide applications, and the provision of additional floral resources for pest antagonists (Wäckers 2004; Scheid, Thies & Tscharntke 2011).

Effects on crop yield

We found a strong annual variation in crop yields between 2011 and 2012 which was related to different weather and growth conditions. In 2011 freezing temperatures in late spring and drought until June led to much lower yields in the first than in the second study year (Federal Ministry of Food, Agriculture and Consumer Protection 2011). Nonetheless, landscape composition and herbivores affected yields in both years, emphasizing the importance of these factors.

This study demonstrates a strong effect of adult pollen beetles on oilseed rape yields, leading to yield reductions of up to 53%. Other studies have shown that increasing pollen beetle abundance led to an increasing amount of podless stalks (Zaller *et al.* 2008a), but since plants are able to compensate damage caused by herbivory, seed weight per plant is a much better proxy for oilseed rape yield than the number of flowers developing into fruits (Diepenbrock 2000). Importantly, we could also show that seed weight per plant in our samples was closely correlated with yield calculations of farmers at the field level.

In parallel, decreasing oilseed rape proportions led to yield losses of up to 69%, probably caused by increasing pest abundance. However, parasitism rate also increased with decreasing oilseed rape proportion. Therefore in landscapes with a parasitoid abundance above the threshold for effective biological control, decreasing oilseed rape proportion may

have a positive effect on oilseed rape yields due to increased biological control (Thies, Steffan-Dewenter & Tscharntke 2003; Chaplin-Kramer *et al.* 2011). We found no effect of inter-annual changes in oilseed rape on yield as primarily the abundance of adult pollen beetles at the field edge were affected by inter-annual changes, but the field centre contributed most to the yield (82.0 ± 5.6% (mean ± SD) considering a 5-m wide edge zone).

Conclusions and management implications

The dilution effects observed in this study can operate across a wide range of conditions. Therefore the spatial aggregation of oilseed rape fields and presumably also other annual crops can help to reduce damage by pest insects. Further, shifting the position of aggregated fields yearly between different landscape sectors could prevent pest populations from building up over several years. For example, indigenous agriculture in the Andes traditionally developed a system of spatially concentrated potato fields in yearly changing landscape sectors, resulting in a lower abundance of the Andean potato weevils (Parsa, Ccanto & Rosenheim 2011). Similar strategies can potentially be useful in modern integrated pest management. A possible landscape-scale management scheme could comprise an annual increase of crop area up to a maximum, a year with low crop cover where a balanced crowding of pests and antagonists maintains high yields and again a cycle of increasing crop cover. Therefore it would be necessary to coordinate spatiotemporal cropping patterns among farmers in landscapes consisting of many small farms. However, the advantage of lower pest abundances due to increased host crop area can be counteracted by the disadvantage of lowered biological pest control. Therefore, additional agri-environmental schemes and changes in local field management are necessary to improve the potential for biological pest control. Specialized parasitoids of pollen beetles could benefit from low-impact tillage of harvested oilseed rape fields to conserve hibernating parasitoid pupae (Nilsson 2010) and from additional floral resources before or after oilseed rape flowering.

Pest species affect oilseed rape yields interactively with pollinators and abiotic factors like soil quality, which can explain further variability in oilseed rape yields (Bartomeus, Gagic & Bommarco 2014). Similar to pollen beetles also wild bees show dilution effects with increasing oilseed rape proportions at a landscape scale (Holzschuh *et al.* 2011; Riedinger *et al.* 2014). Therefore, strong dilution effects may reduce effective pollination of the crop leading to reduced yields despite low pest abundance. In parallel, pollinators may benefit from high oilseed rape proportions on a long term due to enhanced population growth rates (Riedinger *et al.* 2014). Thus, future local and landscape-scale management schemes need to

integrate across multiple ecosystem services (Bommarco, Kleijn & Potts 2013). In conclusion, pest management schemes that optimize landscape scale annual rotation of crops and improve the local conditions for biological pest control could significantly reduce the dependency of modern agriculture on pesticide applications while maintaining high yields.

Supporting Information to Chapter 4

Appendix S1. Comparison of seed weights from the field edge and the field centre.

The mean seed weight per plant was significantly lower at the field edge (mean ± se, 12.4 ± 2.6) compared to the field centre (mean ± se, 18.6 ± 2.7) (paired t-test with square-root transformed seed weights: t = -5.38, df = 33, $P < 0.001$).

The correlation of seed weights per plant with yield data from farmers was slightly less strong for plants from the field edge (r = 0.59, N = 31, $P < 0.01$, Fig. A1) (2011: r = 0.53, N = 15, $P = 0.04$; 2012: r = 0.60, N = 16, $P = 0.01$) compared to plants from the field centre (r = 0.68, N = 31, $P < 0.01$, Fig. 1) (2011: r = 0.72, N = 15, $P < 0.01$; 2012: r = 0.80, N = 16, $P < 0.01$).
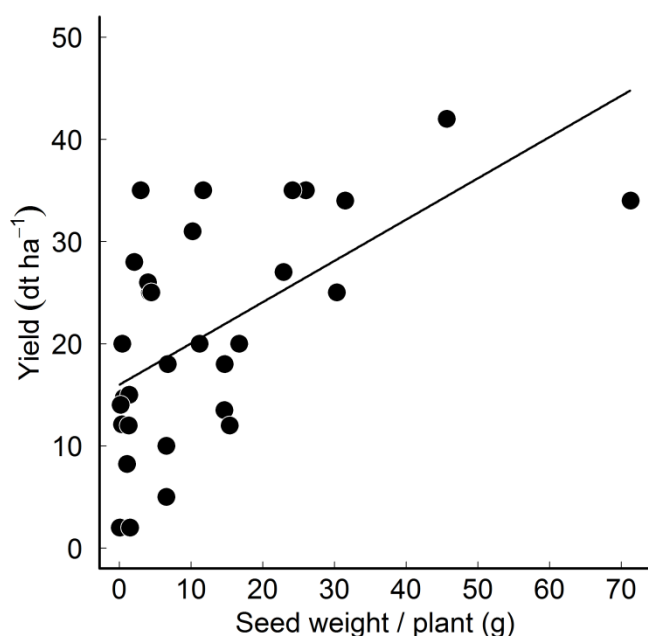

Fig. A1 Correlation between yields supplied from farmers and mean seed weight per plant of the field edge.

Chapter 5: General Discussion

Effects of habitat assemblage on the species community and ecosystem functions in semi-natural grasslands

Biodiversity-rich semi-natural habitats, like calcareous grasslands, are of high conservation value in agricultural landscapes. However, nature conservation measures aiming at local habitat quality failed to prevent a decline of habitat specialists within calcareous grasslands during the last decades (Newton *et al.* 2012; Diekmann *et al.* 2014). In this thesis we showed that interactions with the surrounding habitat matrix are of high importance for the community composition of calcareous grasslands. We found differences in the species composition, species number, evenness, and activity density of carabid beetles in calcareous grasslands depending on adjacent habitat type. Our results can be explained by the spillover of organisms from adjacent crop fields or forests into the grasslands. Thereby the higher activity density and species richness in crop fields compared to forests resulted in a comparatively higher activity density and species richness in grasslands adjacent to crop fields. This supports the view, that the spillover of both populations and biodiversity is greater around habitats that harbour large populations and a high species richness (Brudvig *et al.* 2009). Additionally to spillover also abiotic interactions with adjacent habitats can partially explain the observed patterns. For example the flux of nutrients from adjacent fertilized crop fields may alter species communities as the characteristic species of calcareous grasslands are adapted to nutrient poor soil conditions (Van Den Berg *et al.* 2011). Further, adjacent habitats can alter the microclimate. Grasslands adjacent to forests are more shaded, which results in a lower insect activity compared to warmer, more sunny grasslands (Honek 2013).

Importantly we show, that not only community composition but also ecosystem functions in calcareous grasslands were altered depending on adjacent habitat type. Cross habitat spillover is a major factor influencing trophic interactions as it connects food webs across habitat borders (Polis, Anderson & Holt 1997). We found higher predation rates adjacent to forests than adjacent to crop fields, at least when temperatures were comparatively low. Such a pattern can be explained by the spillover of generalist predators resulting in elevated predation rates adjacent to predator-rich habitats. The effect of predation spillover is expected to be especially strong when the source habitat of the predators has a higher primary production than the sink habitat, the movement rate of predators is substantial and the mortality of the predators in the habitat where it arrived is low (Holt & Hochberg 2001).

Interestingly, we found lower predation rates, but seven times higher carabid beetle activity densities in calcareous grasslands adjacent to crop fields compared to calcareous grasslands adjacent to forests. This contradiction could partly be explained by the in average larger body size of carabid beetles living in the less disturbed forests (Lovei & Sunderland 1996). Therefore forest species probably have a higher food intake (Reichle 1968) and larger foraging distances (Peters 1986) which may at least partially outweigh the lower activity density. But more importantly, carabid beetles are probably not the only predators on the exposed lady bird eggs. Our study design does not allow the identification of the ground-dwelling species groups that caused the differences in the predation rates. We rather measured a net effect of all species that forage on the ground. Therefore other taxonomic groups like ants, spiders or earwigs may play an important role as their predation activity is often higher compared to carabid beetles (Frank *et al.* 2007).

In addition, we show that crop harvest results in a transiently increased spillover from crop fields into adjacent semi-natural habitats. Crop harvest causes a sudden decline in habitat quality for those individuals that were not directly killed during harvest: resource availability decreases and the habitat offers less microhabitats and shelter making organisms more vulnerable to enemies (Thorbek & Bilde 2004). This may force surviving individuals to leave the crop fields and move into adjacent habitats of higher quality. Our results support other studies showing that semi-natural habitats can offer an important refuge habitat after crop harvest (Hossain *et al.* 2002; Opatovsky & Lubin 2012). However, we also show that the mass movement of agriculturally subsidized species into semi-natural habitats after crop harvest led to a transiently increased activity density. This could lead to transiently altered trophic interactions and increased competition for species in the calcareous grasslands. However, we found no difference in predation rates before and after crop harvest. Possibly, the main predators of our exposed prey items have small population sizes in crop fields and show therefore no increased spillover after crop harvest.

Our results highlight that nature conservation measures targeting semi-natural habitats which are embedded in an agricultural matrix need to consider the surrounding landscape context, as spillover effects into semi-natural habitats alter community composition and ecosystem processes. Thereby the impact of adjacent habitats has to be assessed over the whole year to take account of seasonal changes and to develop targeted management measures. The operating scale of spillover effects depends on the activity range of the species,

which is mainly determined by dispersal ability, foraging movements, and the distribution of resources in the landscape (Kremen *et al.* 2007). As carabid beetles have a relatively small activity range (Pearce & Venier 2006; Gardiner *et al.* 2010) we focused in our study on the effect of habitats that directly border calcareous grasslands. However, it is plausible that other taxonomic groups with larger activity ranges, e.g. flying insects or birds, are also affected by habitats in a larger distance (Hines & Hendrix 2005; Cunningham & Johnson 2006). Therefore biodiversity conservation in semi-natural grasslands requires in addition to the local improvement of habitat quality the consideration of interactions with the surrounding landscape at multiple landscape scales.

Effects of spatial and temporal crop cover dynamics on biological pest control and crop yields

Additionally to the biodiversity of semi-natural grasslands we also examined the effect of habitat assemblage in the landscape on biological pest control and crop yields in oilseed rape fields. In chapter 4 we showed that oilseed rape yields increase with increasing proportions of oilseed rape in the surrounding landscape. This was related to a parallel decrease in the abundance of the main pest insect (pollen beetles) with increasing oilseed rape proportions ('dilution effect'). Dilution effects can occur when a species has a high preference for a specific host plant, so that the major part of the population spreads over the available host plant patches (Tscharntke *et al.* 2012; Riedinger *et al.* 2014). As pollen beetles depend on cruciferous plants for oviposition, oilseed rape fields are an attractive habitat for reproduction. Thus high oilseed rape proportions result in comparatively low pollen beetle densities (dilution) and low oilseed rape proportions in comparatively high pollen beetle densities (concentration). Similar effects were found for the parasitoid *Tersilochus heterocerus*, which is a natural enemy of pollen beetles. This means that increasing oilseed rape proportion dilutes both, the ecosystem disservice of herbivory by pest insects, but also the ecosystem service of biological pest control by its natural enemy. Similarly, other functional groups providing additional ecosystem services or disservices might be affected by oilseed rape proportion at a landscape scale. For example, another study (conducted on 32 oilseed rape fields of which 30 were the same as in this thesis) found dilution effects also for pollinators, indicating reduced pollination with increasing oilseed rape proportions (Riedinger *et al.* 2014). Importantly, we show that the net effect of an increasing oilseed rape proportion on oilseed rape yield was positive in our study, indicating that the positive effect due to reduced pest abundances was more important for oilseed rape yields in the studied landscapes than the

negative effects due to reduced natural enemy and pollinator abundances. Further studies are required to proof whether this result can be transferred to other landscapes that differ for example in the biological control efficiency, which was very low or non-existent in the studied landscapes.

In addition we examined the temporal spillover of pollen beetles and their natural enemies from one year into the next year. We found inter-annual crowding and dilution effects for pollen beetles, meaning that an inter-annual increase of oilseed rape proportions in the landscape led to low pollen beetle abundances in the second year as relatively small populations from the first year spread over a comparatively large area in the second year (inter-annual dilution). In parallel inter-annual decreasing oilseed rape proportions in the landscape led to higher pollen beetle abundances in the second year as relatively large populations from the first year crowd on the comparatively small area in the second year (inter-annual crowding). Parasitism by *T. heterocerus* was not affected by inter-annual changes in oilseed rape proportion. Other authors also found no inter-annual crowding and dilution effects on parasitism by *T. heterocerus*, but for total parasitism including other parasitic ichneumonids (Thies, Steffan-Dewenter & Tscharntke 2008). This indicates that similar to dilution effects on the landscape scale also temporal crowding and dilution effects influence several functional groups. Thereby different species within the same functional group can respond differently to inter-annual crop changes (Zhao *et al.* 2013) making general predictions concerning crop yields difficult. In the studied landscapes we found no net effect of inter-annual changes in oilseed rape proportion on oilseed rape yield.

Our results indicate that a landscape wide management of the amount of one crop type at appropriate spatial and temporal scales can reduce pest infestation and increase crop yields. Regarding the increasing amount of insecticide resistances among varying pest species (Heckel 2012), the reduction of pest infestation by the management of specific crop proportions may be a good alternative to insecticide applications. Even though we found lower pollen beetle abundances in landscapes with high oilseed rape proportions, constant high oilseed rape proportions will probably not result in lowered pest densities on a long term, as pollen beetle populations will rapidly build-up if they are not limited by other resources. Therefore a reasonable landscape management should alternate high oilseed rape proportions which dilute pollen beetle abundances, with years with low proportions of oilseed rape in the landscape. In the years with low oilseed rape proportions pollen beetle populations may break down due to resource limitation and an increased density-dependent predation or parasitation

by natural enemies. If necessary, additionally biological control agents or insecticides can be applied in years with low oilseed rape proportions. One possible landscape management may be to shift high oilseed rape proportions between different landscape sectors, similarly to traditional potato cultivation in the Andes (Parsa, Ccanto & Rosenheim 2011). Another possible management scheme could comprise a gradual increase of oilseed rape proportions over several years up to a maximum, then a year with no or very low oilseed rape proportions, and again a cycle of increasing oilseed rape proportions. Further studies are necessary to compare the efficiency of these and similar landscape management strategies.

In addition, further studies are needed to examine the effect of specific crop proportions on other crop types. In other pest-crop-systems an increasing crop proportion in the landscape may result in increasing, hump-shaped or constant pest abundances, depending on the life cycles of pests and enemies (Segoli & Rosenheim 2012). Therefore an increasing proportion of a single crop in the landscape may be useful to increase oilseed rape yields, but other landscape management schemes are probably necessary for other crop types. Thereby the different functional groups which are affected by changing crop proportions have to be considered. Also trophic interactions within the same functional groups could alter the strength of the fulfilled ecosystem service (Martin *et al.* 2013). In the end the net effect of all ecosystem services and disservices must be optimized to increase crop yields. Therefore studies integrating across multiple ecosystem services are needed (Bommarco, Kleijn & Potts 2013). In addition, other habitat types like semi-natural habitats which are often used by both, pest and enemy species as well as local factors like field management have to be considered to optimize ecosystem services and crop yields. Altogether, there is a high potential that a coordinated landscape wide management of spatiotemporal crop cover dynamics results in economic and ecological advantages, as it can facilitate increased yields by reduced pesticide applications.

Synthesis

In summary, this thesis highlights that species communities and ecosystem processes of crop and non-crop habitats are affected by biotic interactions with the surrounding habitat matrix at different spatial and temporal scales. Therefore it is impossible to protect biodiversity or to optimize ecosystem services and yields without considering the contiguous and broader landscape context. Skilled and coordinated landscape management may help to improve both, nature conservation measures and ecosystem services and thus crop yields. In addition also local factors like the habitat management of both, semi-natural and crop habitats

affect species diversity and crop yields (Gonthier *et al.* 2014). For example the habitat quality of semi-natural grasslands can be maintained by extensive grazing or mowing (Kahmen, Poschlod & Schreiber 2002). Low impact soil management and reduced pesticide application on crop fields can help to promote the population build-up of pest antagonists (Ulber, Klukowski & Williams 2010; Nilsson 2010). Therefore, nature conservation measures and agricultural management needs to consider both the local and the landscape scale to preserve biodiversity and ecosystem services (Gonthier *et al.* 2014). Further studies are needed that simultaneously examine the effects of the same landscape parameters on crop and non-crop habitats to develop a landscape management that reaches a balance of high productivity and biodiversity conservation.

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Author contributions

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GS, JK and ISD designed the experiment, GS conducted the field work, analysed data and wrote the first draft of the manuscript, all authors interpreted the results and edited the manuscript.

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