

Institut für Biochemie und Biologie
Biodiversitätsforschung und Spezielle Botanik

**Boon and bane – how semi-natural habitats shape
biodiversity-driven ecosystem (dis)services
in agricultural landscapes**

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von
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General introduction

Biodiversity provides ecosystem services

Ecosystems comprise different living organisms that are involved in complementary ecosystem processes through their resource use and interactions with the biotic and abiotic environment (Kumar, 2010). These ecosystem processes can ultimately generate ecosystem services — benefits that humans obtain from ecosystems for their well-being (Daily, 1997; Millennium Ecosystem Assessment, 2005). The functioning of an ecosystem under constant conditions may depend on a small number of living species — the necessary functional diversity (Díaz *et al.*, 2007; Srivastava *et al.*, 2009). However, in changing environments a larger number of species and therewith a higher biodiversity is essential to maintain the stability and resilience of an ecosystem and its functions (Naeem and Li, 1997; Yachi and Loreau, 1999; Loreau *et al.*, 2001). Importantly, the functional role of biodiversity can be manifold. It can act as a regulator of ecosystem processes that supports ecosystem services (e.g., soil-animal diversity determining dynamics of many soil nutrients), but biodiversity can also directly be an ecosystem service (e.g., pollinators) and a good itself (e.g., charisma and aesthetic appeal of large vertebrates; Mace, Norris and Fitter, 2012).

Ecosystem services are classified into provisioning (e.g., food, fuel and timber), regulating (e.g., water, climate and disease regulation), cultural (e.g. recreation, spiritual, aesthetic values) and supporting services (e.g., soil formation, nutrient cycles), and are harnessed from ecosystems depending on human demands (Millennium Ecosystem Assessment, 2005). While most provisioning ecosystem services are fostered and increasing world-wide, regulating and non-material services decrease (IPBES, 2018).

Ecosystem services in agricultural landscapes

Especially agricultural ecosystems (crop land and pastures), occupying globally 40% of land surface (Foley, 2005), have been optimized towards the provisioning service which has resulted in an undesired decline in most other ecosystem services in agricultural landscapes (Zhang *et al.*, 2007; Power, 2010). However, producing food and other goods depends upon a variety of supporting and regulating services (Fig. T1), whereof three services (nutrient cycling, pollination, and pest control) are regarded as highly influential being mediated through biodiversity (Power, 2010). (i) Earthworms and other soil-invertebrates, as well as microorganisms perform a range of soil-borne ecosystem functions associated to nutrient cycling and soil structuring (Hendrix *et al.*, 1990; Altieri, 1999) supporting crop plants' growth. (ii) Animal-pollinated crop plants rely on pollinators, such as insects, birds and bats, a service

that 35% of the global food crops depend on (Klein *et al.*, 2007). (iii) Natural pest control can be provided by generalist and specialist predators as well as parasitoids to suppress pest populations and contain their damage to crop plants (Naylor and Ehrlich, 1997). These biodiversity-mediated ecosystem services can be considered as services to the agricultural system (Zhang *et al.*, 2007).

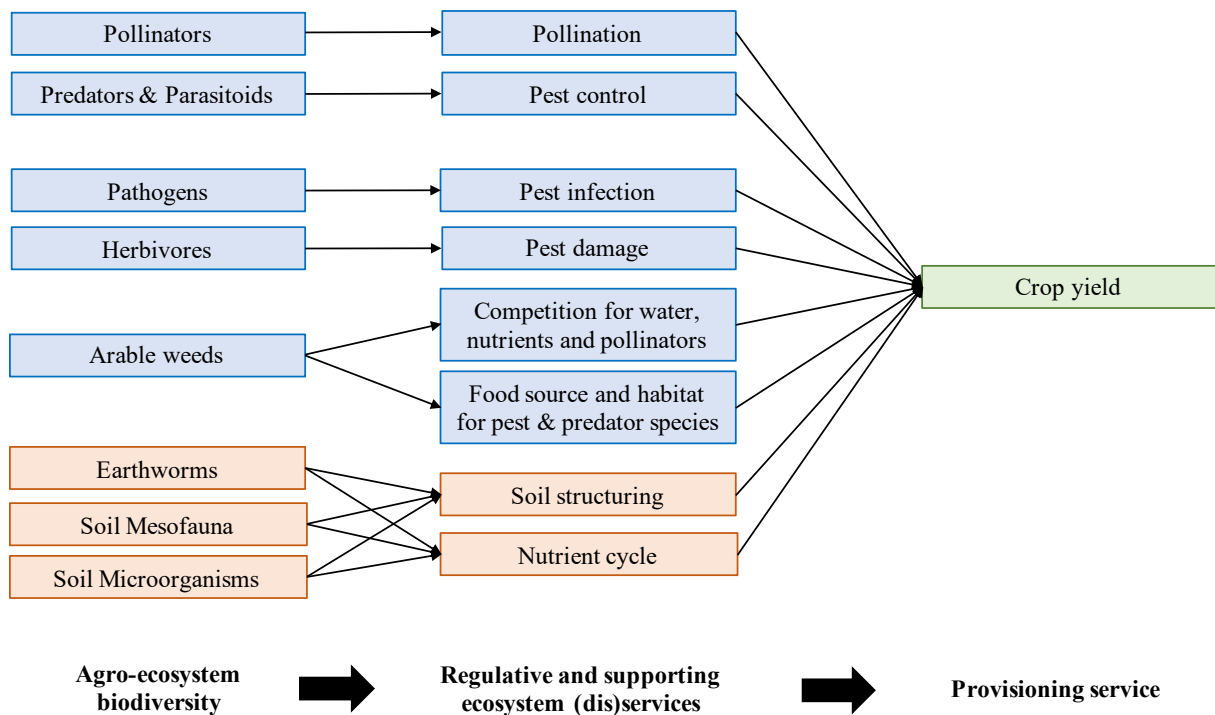


Figure T1: Biodiversity-driven supporting (orange) and regulating (blue) ecosystem (dis)services influencing crop production in agroecosystems adapted from Altieri (1999) and Zhang *et al.* (2007)

Besides ecosystem services, agriculture also receives ecosystem disservices that reduce productivity (Zhang *et al.*, 2007; Fig. T1): Fungal or viral pathogens infect crop plants and non-crop vegetation, i.e. arable weeds, compete with the crop plant for water, nutrients and pollinators. Also, animal crop pests, including herbivores, frugivores, and crop seed-eaters, can decrease crop yield, potentially resulting in complete crop losses (Zhang *et al.*, 2007). Without any mechanical or chemical regulation, arable weeds account for the highest crop losses (34%) induced by biotic crop antagonists while pathogens and herbivores make up 18% and 16%, respectively (Oerke, 2006). Crop protection measures, such as herbicides or manual removal, can lower these yield losses considerably for weeds whereas the protection from animal pests and pathogens rely on regular and intense chemical inputs (Oerke, 2006). Solely animal pests cause more than US\$30 billion crop damage in the United States each year (Pimentel *et al.*, 2005). Hence, the impact of disservices on agricultural ecosystems depends in large parts on how agricultural ecosystems are managed.

Agricultural intensification and its impacts on ecosystem service provision

In order to meet growing demands on provisioning services, agriculture has been intensified in the last decades (Matson, 1997; Tilman *et al.*, 2002). Agricultural landscapes have been transformed to vast monocultures that require large inputs of resources, such as fertilizers, pesticides and water, which generally are not environmentally or economically sustainable (Wright, 2009). This agricultural intensification has led to biodiversity losses (Kleijn *et al.*, 2009) and has strongly affected the delivery of regulating and supporting ecosystem services (Hooper *et al.*, 2005). Modern agricultural practices impose persistent negative effects on biodiversity (Geiger *et al.*, 2010) while naturally provided functions from agricultural species are replaced by chemical inputs (Bommarco, Kleijn and Potts, 2013). These chemical inputs pollute aquatic and terrestrial habitats entering into other ecosystems through leaching and volatilization (Tilman *et al.*, 2002), and harm non-targeted organisms (Isenring, 2010). The over-reliance on pesticides inevitably results in resistance evolution potentially leading into pest outbreaks (Zhang *et al.*, 2007) which may in turn further reduce the natural ability of the ecosystem to provide services. Hence, most organisms living in agricultural ecosystems are pushed back to the few remaining non-cropped semi-natural areas whose composition and functioning thus becomes important for the delivery of naturally provided ecosystem services (Holland *et al.*, 2016).

Semi-natural habitats as a source of ecosystem services

Historically, semi-natural habitats (SNHs), such as hedgerows or herbaceous strips at field borders, had the functions to fence livestock and mark ownerships (Baudry *et al.*, 2000; Marshall and Moonen, 2002). Nowadays, these mostly linear habitats represent important refugia for biodiversity. They provide breeding and nesting habitats, alternative food sources and shelter agricultural species from disturbances (Bianchi, Booij and Tschardtke, 2006; Billeter *et al.*, 2008; Birkhofer, Wolters and Diekötter, 2014). Moreover, they have the potential to support ecosystem services in agricultural landscapes (Dainese *et al.*, 2015; Van Vooren *et al.*, 2017). There is a growing body of evidence showing that SNHs have positive effects on pollination (e.g., Albrecht *et al.*, 2007; Lindgren, Lindborg and Cousins, 2018) and biological control (Holland *et al.*, 2016; Rusch, Chaplin-Kramer, *et al.*, 2016). Pest predators may spill over into agricultural fields (Fig. T2) to control pest populations (Martin *et al.*, 2015; Grab *et al.*, 2018), leading to less damage on crop plants and ultimately to higher crop yield (Liere *et al.*, 2015; González *et al.*, 2020). However, SNHs may equally act as source of detrimental organisms (e.g., pests and weeds) colonising fields from the edges (Fig. T2; Williams and

Ferguson, 2010; Blitzer *et al.*, 2012). Therefore, SNHs can — via modulating the biodiversity of ecosystem providers — indirectly affect crop yield.

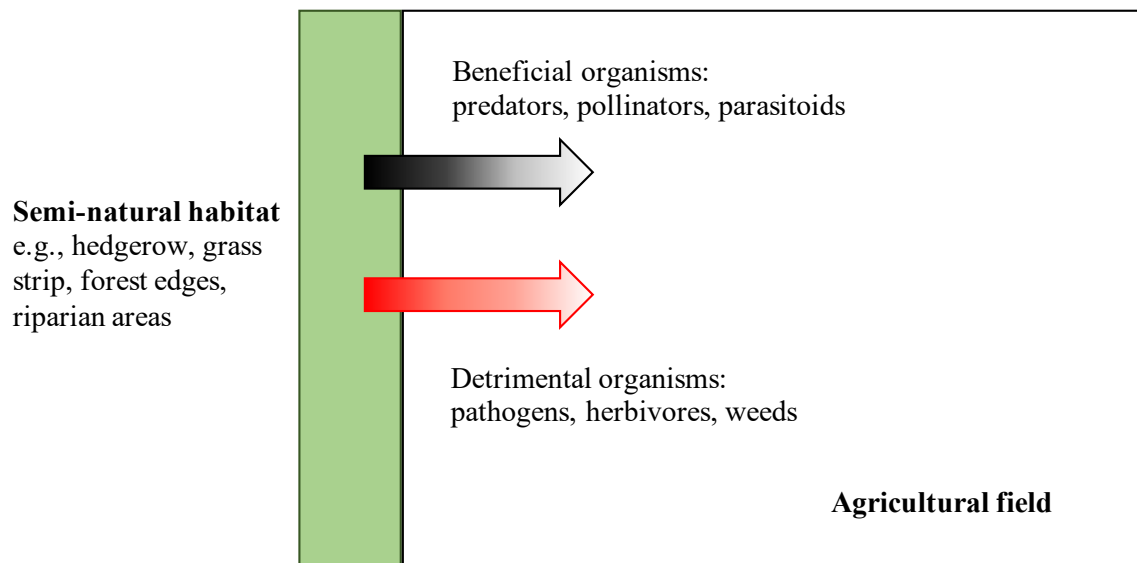


Figure T2: Illustration of the spill-over effect of SNH at the field borders into arable fields

Semi-natural habitats at the field scale

Woody and herbaceous linear habitats are the most thoroughly investigated SNHs in agricultural landscapes (Holland *et al.*, 2017), offering a great potential to provide resources and refugia for ecosystem service providers (Holland *et al.*, 2016). In a recent meta-analysis, particularly flower strips have been found to enhance pest control by 16% whereas hedgerows show increased but inconsistent pest control (Albrecht *et al.*, 2020). Tschumi *et al.* (2015, 2016) demonstrated that annual as well as perennial sown flower strips can cause a significant reduction in pest densities and pest-induced crop damage leading to increased crop yield mostly attributed to pest control. In contrast, wildflower strips may increase both, pests and predators, resulting in no effect on pest suppression, but having the potential to increase crop productivity solely by augmenting pollination services (Balzan, Bocci and Moonen, 2016). Also hedgerows provide a valuable habitat for biodiversity, including pollinators (Ponisio, M’Gonigle and Kremen, 2016) and pest predators (Amy *et al.*, 2015) which spill over into neighbouring fields performing beneficial services to the crop plants (Garratt *et al.*, 2017). Besides these indirect effects that modulate the presence of ecosystem service providers, hedgerows can also have direct effects on crop yield acting as windbreaks to ameliorate microclimate and shelter crop plants from soil erosion (Kowalchuk and Jong, 1995; Lenka *et al.*, 2012). However, trees and shrubs can also inhibit crop production through shade (e.g., Esterka, 2008) and competition for nutrients and water (e.g., Kowalchuk and Jong, 1995). Furthermore, hedgerows augment the aesthetic value of agricultural landscapes (Borin *et al.*, 2010), they maintain landscape

connectivity (Staley *et al.*, 2012) and therewith facilitate movement of organisms in the landscape (Morandin, Long and Kremen, 2014). However, their contrasting vegetation structure compared to arable fields might also present barriers to species adapted to open landscapes (Thomas, Holland and Brown, 2002). Van der Vooren *et al.* (2017) point out that the benefit of grass strips and hedgerows for regulating services can reduce crop production, but that this trade-off might be buffered with an appropriate design of both habitat types.

Semi-natural habitats at the landscape scale

The multifaceted roles of SNHs at the field scale may be complemented by mechanisms acting on the landscape scale. Agricultural landscapes with a higher share of SNHs have been shown to harbour higher abundances of pest predators (Chaplin-Kramer *et al.*, 2011; Veres *et al.*, 2013). Even though predators show mostly positive responses to landscape complexity, patterns of pest density in relation to SNHs at the landscape scale are rather inconsistent (Karp *et al.*, 2018). Several studies observed a reduction of animal pests and their damage rates with increasing landscape complexity (e.g., Chaplin-Kramer and Kremen, 2012), either due to an effective pest control mediated through SNHs (Rusch, Chaplin-Kramer, *et al.*, 2016), or a reduced amount of cropped habitat (Dominik *et al.*, 2018). However, pest densities and herbivory rates might also increase in complex landscapes due to harmful trophic cascades when predators from the fourth trophic level, such as birds, feed on specialist pest predators (Martin *et al.*, 2013) or simply when SNHs benefit the pests but fail to promote the predator species (Tscharntke *et al.*, 2016). Hence, a successful habitat management to improve naturally provided ecosystem services in agricultural systems requires a landscape perspective (Tscharntke *et al.*, 2012) additional to the field-scale perspective of adjacent habitats to arable field borders.

The knowledge gaps

Still, it remains largely unexplored how different SNHs and their distributions in the surrounding landscape contribute to a provision of ecosystem services and disservices within arable fields that ultimately affect agricultural yield. Few ecological studies have made the attempt to incorporate crop yield as a parameter of provisioning ecosystem services when studying the role of SNHs in ecosystem services delivery (Holland *et al.*, 2017). Studies that included yield in their analyses focused on the effect of SNHs on pollination services and revealed a subsequent increase in crop yield (Hoehn *et al.*, 2008; Holzschuh, Dudenhöffer and Tscharntke, 2012; Bartomeus *et al.*, 2014), while there are hardly any studies on the effect of SNHs on pest control that directly measured yield (but see Tschumi *et al.*, 2016). Moreover,

measuring yield changes with an expanded perspective on the presence of SNHs at the field scale embedded in an increasing habitat complexity at the landscape scale has been largely neglected. This, however, is crucial to conserve and enhance naturally provided ecosystem services in order to obtain ecological solutions to agricultural challenges within a highly economically shaped ecosystem.

The approach

In this thesis, I investigate regulating ecosystem services and disservices to agricultural production of winter wheat and how semi-natural habitats (SNHs) shape the provision of these services at the field and landscape scale in an intensive agricultural landscape (Fig. T3).

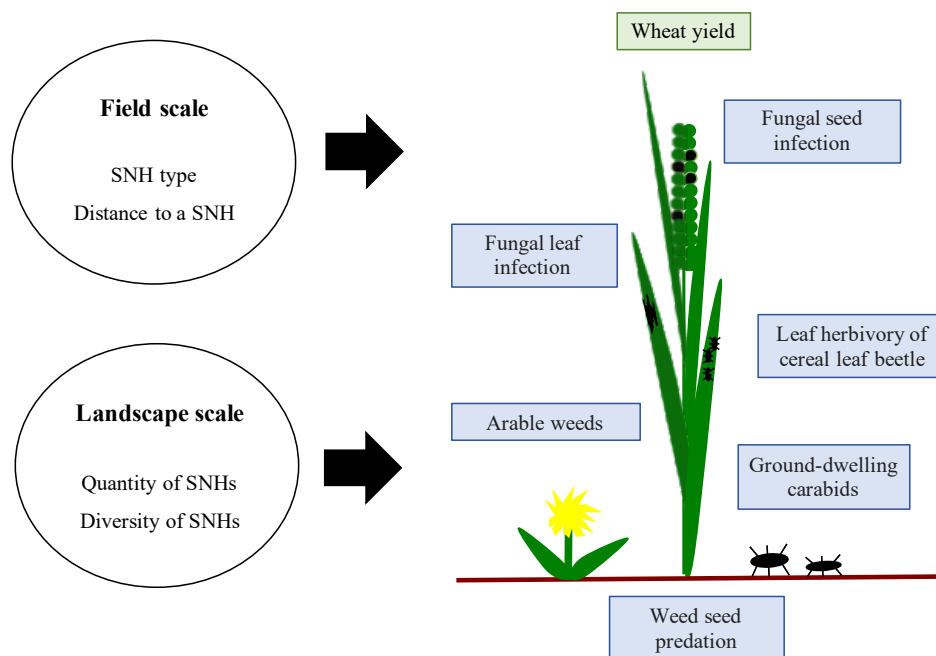


Figure T3: Overall approach of the thesis investigating the effect of SNHs at the field (SNH type and distance to a SNH) and at the landscape scale (quantity and diversity of SNHs) on regulating ecosystem services and disservices (blue = regulating services) to agricultural production of winter wheat (green = provisioning service).

I focused on winter wheat as model species because wheat is one of the three main crops worldwide besides maize and rice accounting for 57% of the world's cultivated nutrition plants (Ray *et al.*, 2012). In Germany, 54% of the cereal production areas are cultivated with wheat yielding on average 7.7 t ha⁻¹ (Macholdt and Honermeier, 2017) in 2016, the main year of my investigation. Based on the rapid ecosystem function assessment (REFA) proposed by Meyer *et al.* (2015), I measured detrimental and beneficial rates of organisms on winter wheat plants within conventionally managed fields with easy-to-use, low-tech, and cost-effective methods to obtain a range of regulating functions affecting seed biomass. I combined these rates with

diversity assessments of the involved taxa to investigate the critical role of biodiversity as a regulator of ecosystem processes (Mace, Norris and Fitter, 2012). An important aspect of my work is that I considered not only services but also disservices to crop production by recording pest rates (including pathogens and herbivores) on wheat plants. Pests are responsible for 29% of wheat yield losses on average — despite crop protection practices. Among those pests, pathogens account for 10% (Oerke, 2006), but remain poorly investigated in the context of SNHs (Holland *et al.*, 2017). Hence, my thesis enlarges the scope of disservices to crop production investigated with regard to SNHs in agricultural landscapes by considering an extended pest profile. In addition, I want to emphasize the role of arable weeds on winter wheat by introducing a highly contradictory aspect: Arable weeds are commonly considered as a disservice to crop production increasing the inter-species competition for light, nutrients and water (Gallandt and Weiner, 2015). However, arable weeds may equally act as a service due to increased plant diversity within the field, e.g., through bottom-up processes providing refugia and resources for pest predators (Balvanera *et al.*, 2014), or deceiving specialist herbivores from the crop plant (Letourneau *et al.*, 2011).

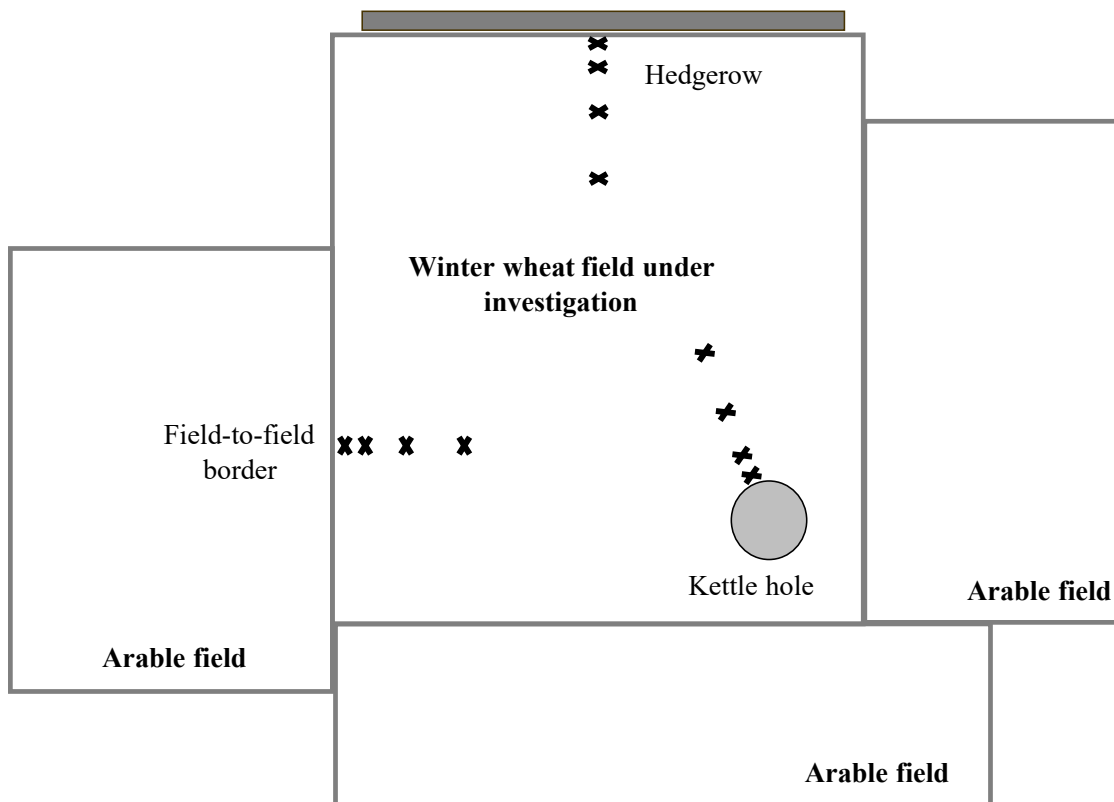


Figure T4: General study design illustrating the transects with several in-field distances starting either from a semi-natural habitat (hedgerow or kettle hole) or from a field-to-field border. Please note that this simplified sketch is not reflected in all studies, e.g., not all three transects are always within the same wheat field.

For all measured organisms and their functions, I tested the effect of SNHs at two different scales, at the field scale and the landscape scale. At the field-scale, I established transects from the field border into the field and assessed organisms and their ecosystem functions at several in-field distances from an adjacent SNH (Fig. T4). The SNH was either a hedgerow or a kettle hole, both of which are frequent habitats in agricultural landscapes in Northeast Germany (Appendix T1, Fig. AT1.1 and Fig. AT1.2). At the landscape scale, I focused on the effect of landscape complexity in terms of quantity and diversity of SNHs. Kettle holes are small water bodies of less than 1 ha that intersperse arable fields as glacial remnants of the last ice-age (Kalettka and Rudat, 2006). They can provide numerous ecosystem services such as regulation of water cycles, flood control, regulation of waste as well as habitat for many species (Vasic *et al.*, 2020). Besides harbouring a high species diversity of aquatic and terrestrial plant species (Pätzig *et al.*, 2012; Altenfelder, Raabe and Albrecht, 2014; Lozada-Gobilard *et al.*, 2019), they provide refugia and source of food and water for animals such as rodents, deer, bats, and wild pollinators (Fischer and Schröder, 2014; Flaherty *et al.*, 2018; Roeleke, Johannsen and Voigt, 2018; Vickruck *et al.*, 2019). However, the delivery of ecosystem services from kettle holes is threatened by agricultural intensity, e.g., chemical inputs that eutrophicate and pollute kettle holes while tillage and soil erosion increase sediment deposition within those habitats (Vasic *et al.*, 2020). This thesis presents one of the first studies addressing the spill-over of ecosystem service providers from kettle holes supporting or opposing agricultural production.

In summary, I investigated the contribution of SNHs on biodiversity-driven ecosystem services and disservices ultimately affecting crop production particularly emphasizing the role and interplay of habitat type, distance to the habitat and landscape complexity at various spatial scales. Specifically, my research aimed at answering the following questions:

- i. Does the delivery of ecosystem (dis)services depend on habitat type at field border?
- ii. How far into the field do ecosystem (dis)services emanating from SNHs last?
- iii. What role does landscape complexity play for the delivery of these (dis)services?
- iv. Can the investigated ecosystem (dis)services influence crop production?

Outline of the thesis

Study 1

In the first study, which is published in *Ecology and Evolution*, I investigated the direct effects of semi-natural habitats, such as forests, hedgerows, and kettle holes, as well as agricultural roads and field-to-field borders on winter wheat yield at a field scale. Here, we were solely interested in the range of the effect of a bordering structure on yield depending if and which type of habitat was present at the field border. The study highlights that yield losses are particularly severe at woody habitats mostly due to abiotic impacts, such as shading, while yield values increase rapidly to mid-field yield after less than 20 meters distance to a forest or a hedgerow. Intriguingly, yield losses were found to be negligibly small at kettle holes compared to field-to-field borders which might give a first glimpse of a weaker trade-off between ecosystem services at those SNHs within agricultural fields of North-eastern Germany.

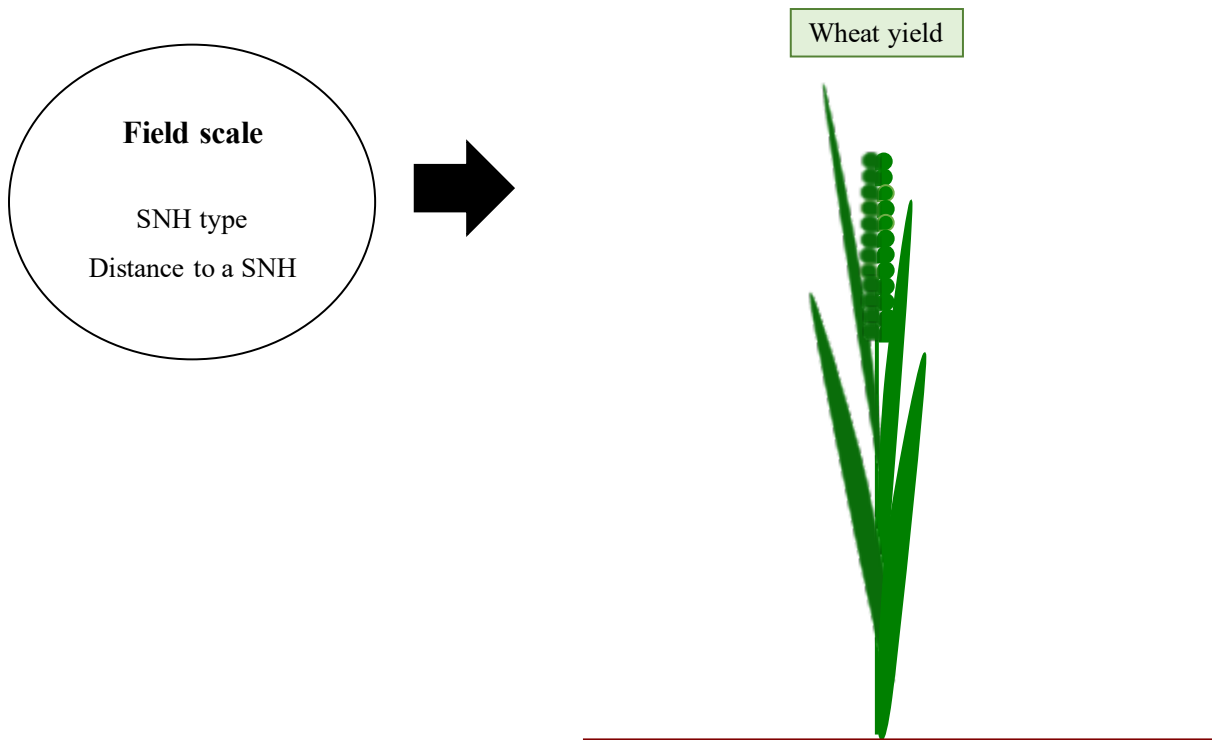
Study 2

In the second study, which is under review in *Ecology and Evolution*, I studied potential indirect effects of SNHs on wheat production via biodiversity-driven ecosystem disservices in order to reveal potential biotic drivers of yield losses at field borders. Therefore, I assessed fungal seed and leaf infection, herbivory by cereal leaf beetle larvae, and the cover of arable weeds and investigated local and landscape effects of SNHs on the selected wheat pests. I assumed that these pest groups would benefit from the presence of a SNH at the field border, but might be responding differently with an increasing percentage or diversity of SNHs in a radius of 1000 m. A particular highlight of this study is the experimental approach where I set up plots of a single wheat variety within conventionally managed winter wheat fields and assessed damage rates directly at the experimental plants. With this approach, I revealed that the only biotic culprit of yield losses emanating from adjacent SNH were arable weeds having their strongest impact on yield directly next to the field border. Although the other investigated pests were unrelated to yield losses, particularly fungal leaf infection and herbivory rates of cereal leaf beetle larvae responded positively to the presence of kettle holes while leaf pathogens were promoted by SNH quantity close to a kettle hole and cereal leaf beetle by SNH diversity on transects adjacent to kettle holes. Moreover, I found out that wheat yield itself was diminished by an increasing percentage of SNHs in the landscape which could not be associated to any of the investigated pests.

Study 3

In the third study, I focused on biodiversity-driven regulating ecosystem functions provided by arable weeds and ground-dwelling carabids as well as weed seed predation per se in agricultural landscapes and at which spatial scales they operate. Here, arable weeds are investigated with respect to their function as resource and habitat for beneficial species representing a bottom-up regulation of pest populations. Contrastingly, ground-dwelling carabids provide a top-down pest regulation by feeding on different pest populations, e.g., invertebrates and weed seeds. For all ecosystem functions and their providers, I studied the range of their spill-over from SNHs into wheat fields depending on the SNH type at field borders and determined if quantity or diversity of SNHs is more important by looking at three different landscape radii (250 m, 500 m and 1000 m). Most of the investigated ecosystem functions responded positively to the presence of kettle holes compared to hedgerows even though none of them showed drawbacks on transects without an adjacent SNH. While arable weeds (species richness and cover) and carabid species richness decreased with distance to the field border, weed seed predation increased. While weed seed predation was affected at smaller landscape radii, species richness of carabid and weeds responded to SNH at larger landscape radii whereas SNH quantity was more important for carabids and SNH diversity for weeds. These mixed responses of ecosystem function providers to SNH at the field and the landscape scale highlight that habitat management with the aim to provide ecosystem services will have to account for a variety of different spatial ranges and habitat preferences of species.

Study 1:
How much do we really lose? —
Yield losses in the proximity of natural landscape
elements in agricultural landscapes



Study 1: How much do we really lose? — Yield losses in the proximity of natural landscape elements in agricultural landscapes

with Nina Bacchi, Karin Pirhofer Walzl, Michael Glemnitz, Marina E. H. Müller, Jasmin Joshi and Christoph Scherber

Abstract

Natural landscape elements (NLEs) in agricultural landscapes contribute to biodiversity and ecosystem services, but are also regarded as an obstacle for large-scale agricultural production. However, the effects of NLEs on crop yield have rarely been measured. Here, we investigated how different bordering structures, such as agricultural roads, field-to-field borders, forests, hedgerows, and kettle holes influence agricultural yields. We hypothesized that (i) yield values at field borders differ from mid-field yields and that (ii) the extent of this change in yields depends on the bordering structure.

We measured winter wheat yields along transects with log-scaled distances from the border into the agricultural field within two intensively managed agricultural landscapes in Germany (2014 near Göttingen, and 2015 – 2017 in the Uckermark).

We observed a yield loss adjacent to every investigated bordering structure of 11% to 38% in comparison to mid-field yields. However, depending on the bordering structure, this yield loss disappeared at different distances. While the proximity of kettle holes did not affect yields more than neighbouring agricultural fields, woody landscape elements had strong effects on winter wheat yields. Notably, 95% of mid-field yields could already be reached at a distance of 11.3 meters from a kettle hole and at a distance of 17.8 meters from hedgerows as well as forest borders.

Our findings suggest that yield losses are especially relevant directly adjacent to woody landscape elements, but not adjacent to in-field water bodies. This highlights the potential to simultaneously counteract yield losses close to the field border and enhance biodiversity by combining different NLEs in agricultural landscapes such as creating strips of extensive grassland vegetation between woody landscape elements and agricultural fields. In conclusion, our results can be used to quantify eco-compensations to find optimal solutions for the delivery of provisioning and regulating ecosystem services in heterogeneous agricultural landscapes.

Introduction

During the last decades, agricultural management turned previously heterogeneous landscapes into machine-efficient monocultures leading to a degradation and local depletion of natural landscape elements (NLEs) (Vitousek *et al.*, 1997; Tilman *et al.*, 2001). However, NLEs represent valuable habitats and food resources for many animals, e.g., invertebrates and birds (Fuller and Gregory, 1995; Staley *et al.*, 2012; Amy *et al.*, 2015) delivering a range of ecosystem services such as biological pest control (Chaplin-Kramer *et al.*, 2011; Woodcock *et al.*, 2016) and pollination services (Hipólito, Boscolo and Viana, 2018; Lindgren, Lindborg and Cousins, 2018).

While the biodiversity value of NLEs has been frequently studied (e.g., Billeter *et al.*, 2008), effects of NLEs on crop production are less regularly considered, although the amount of NLEs often is a ‘conflict zone’ in the debate on biodiversity conservation vs. food production in agricultural landscapes (Phalan *et al.*, 2011).

Studies investigating yield, reported divergent effects depending on NLE type: Ghosh *et al.* (2012) showed that wheat production increased if field margins were sown with local grass species. Tschumi *et al.* (2015) found 10% higher yields close to flower strips, which they attributed to indirect benefits from pest control. In contrast, Sutter *et al.* (2018) demonstrated that ecological focus areas, such as wildflower strips, had no significant effect on oilseed-rape yield, even though pollination and pest control had been increased by around 10%. From studies of hedgerows, we know that negative effects on crop yields can occur within the first meters from the field border (Kort, 1988). This effect may be caused by abiotic factors, such as shading (Esterka, 2008), but also by biotic factors, such as competition for nutrients and water (Kowalchuk and Jong, 1995), or by pests and diseases (Thies and Tschardtke, 1999; Esterka, 2008). Kort (1988), however, also showed that with increasing distance to the hedgerow, crop yields may increase above mid-field yield values due to reduced evapotranspiration caused by wind shelter.

The relationship between distance to field border and yield was shown throughout different crop types (De Snoo, 1994; Sparkes *et al.*, 1998) and investigated in order to disentangle different factors such as weed abundance, pest incidence and soil compaction (Boatman and Sotherton, 1988; Wilcox *et al.*, 2000). Still, the effect of different structures at field borders has rarely been investigated in a comparative analysis. Many authors have focused on particular structures, i.e. woody or grassy landscape elements and did not incorporate other elements such as small water bodies. Moreover, most studies lacked a proper control (i.e. no field-field borders were included) to identify effects on yield arising solely from the bordering structure itself.

Here, we quantified the effects of a wide range of bordering structures, specifically agricultural roads, forest borders, hedgerows and in-field water bodies, on crop yields of winter wheat (*Triticum aestivum* L.) at increasing distances from the field border. As a control, we assessed yields at field-to-field borders. In contrast to other studies that investigated only the difference between yields at field borders and mid-field yields (Sklenicka and Salek, 2005; Esterka, 2008), we surveyed a range of sampling points along transects starting from the border into the wheat field to detect changes in crop yield at different distances. We wanted to know (i) how far into the field yields remain notably below mid-field yields and (ii) whether the yield increase depends on the bordering structure. We hypothesised that yield losses at field borders would be stronger at tall bordering structure, such as forests, due to stronger competition effects for light, nutrient and water.

Material and methods

Study area

Field sampling was performed at two sites in Germany differing in climatic and edaphic conditions — the experimental farm ‘Klostergut Deppoldshausen’ (Göttingen, Lower Saxony, Germany; 2014) and the research platform ‘AgroScapeLab Quillow’ (Agricultural Landscape Laboratory Quillow) of the Leibniz Centre for Agricultural Landscape Research (ZALF) (Uckermark, Brandenburg, Germany; 2015 – 2017).

The Deppoldshausen site (5 km²) has a mean annual temperature of 7.7°C, annual precipitation of 645 mm (Universität Göttingen, 2009) and calcareous soils with low water-holding capacity. On a total of 185 ha, 160 ha are used for agriculture (94% arable land and 6% permanent grassland), accompanied by 6 ha of woody habitats (forest patches and hedgerows), 5 ha of agricultural roads and ditches, as well as less than 1 ha of settlement. Half of the arable fields are managed organically; the other half is managed conventionally. On conventional fields (with 180 kg N ha⁻¹ annual fertilization), winter wheat (average yields of 6.9 t ha⁻¹; measured from 2002 to 2008) is grown in rotation with winter barley and oil-seed rape or depending on soil fertility with winter barley and sugar beet (Universität Göttingen, 2009).

The Quillow catchment area (250 km²) has a sub-continental climate with 8.7°C mean annual temperature and an annual precipitation of 475 mm (ZALF field station, Dedelow), and sandy to loamy Luvisols. The region was covered by ice during the Weichsel glaciations, so that sedimentary deposition by the glacier provided suitable conditions for an intensive agriculture with medium to high yield potentials (Domnick and Ebert, 1996). Today, local land use in the Uckermark is dominated by agriculture (62%), interspersed by forests (24%), water surfaces

(5%) and settlements (5%), as well as planted hedgerows and kettle holes (small water bodies as remnants of the last ice age). 84% of the agriculturally used area accounts for arable land and 16% for permanent grasslands. The main crops on arable fields are winter cereals, oil-seed rape and silage maize cultivated on an average field size of 19 ha. Winter wheat, as the most dominant crop, yields on average 7.4 t ha⁻¹ with 180 – 220 kg N ha⁻¹ annual fertilization (measured from 2011 to 2016; Amt für Statistik Berlin-Brandenburg, 2017, 2018) in a crop rotation most commonly after oil-seed rape.

Box 1.1: Definition of terms

<i>Bordering structure</i>	are all types of landscape elements bordering an agricultural field, such as an agricultural road, another agricultural neighbouring field, a forest, hedgerow or kettle hole.
<i>Natural landscape elements (=NLEs)</i>	are only semi-naturally occurring landscape elements such as forests, hedgerows and kettle holes. Thus, NLE is not equal to bordering structure or transect type.
<i>Transect type</i>	describes the different types of transects according to the bordering structure at the field border. There are five different transect types in this study, namely transects at agricultural roads, field-to-field borders, forests, hedgerows and kettle holes.
<i>Transect</i>	is our term for the linear arrangement of four distances from a field border into the field. In our design it is a repetitive unit occurring one to three times within a winter wheat field under investigation.

Study design

We established a total of 65 transects in 34 different winter wheat fields from the field border into the field over four different years at two different sites (N = 260). Yield samples were always taken at four distances along each transect, departing either from a natural landscape element (forest, hedgerow, or kettle hole), an agricultural road, or a field-to-field border between the winter wheat field under investigation and another cereal field (Box 1.1, Table 1.1). In the following, the most distantly measured sampling point from the field border (4th distance) shall represent typical yields measured within the field and is referred to as mid-field yield.

In 2014 (‘Klostergut Deppoldshausen’), we established eight transects on winter wheat fields, variety *Hermann*, four of them bordering woody landscape elements: two at forests (tree height: 9 m and 19 m) and two at hedgerows (tree height: 5 and 7.5 m). The remaining four transects were either situated at agricultural roads or at field-to-field borders (Appendix A1: Table A1.1). Samples were taken at logarithmic distances (1 m, 4 m, 16 m and 64 m); in one case, the furthest distance was shortened to 34 m because of small field size. At each sampling location (N = 32), we established three quadrats of 50 cm x 50 cm, where all heads of winter wheat plants (growth stage 87) were harvested by hand and threshed with a lab threshing machine. Seed biomass was

cleaned afterwards (Sample cleaner MLN, Pfeuffer, Kitzingen, Germany), dried at 65 °C for 48 h and weighed. For analyses, measurements were converted to grain yield in t ha⁻¹.

Table 1.1: Overview about study design for four years winter wheat harvest in ‘Klostergut Deppoldshausen’ (Lower Saxony, Germany, 2014) and in the ‘AgroScapeLab Quillow’ (Brandenburg, Germany, 2015-2017)

	2014 Deppoldshausen	2015 Quillow	2016 Quillow	2017 Quillow
Transects starting at field borders with NLE	Forest (2) Hedgerow (2)	Forest (12)	Hedgerow (7) Kettle hole (6)	Hedgerow (8) Kettle hole (9)
Transects starting at field borders without NLE	Agricultural road (2) Field-to-field (2)	-	Field-to-field (4)	Agricultural road (4) Field-to-field (7)
Distances	1 m, 4 m, 16 m, 64 m	3 m, 6 m, 30 m, 33 m	1 m, 5 m, 20 m, 50 m	1 m, 5 m, 20 m, 50 m
Sampling points	32	48	68	112

In 2015 (‘AgroScapeLab Quillow’), six winter wheat fields were chosen adjacent to forest patches (tree height: 18 m – 25 m). On each field, two transects were established ranging from the forest edge into the field. No transects at field-to-field borders were established in that year (Table A1.1). Samples were taken at four distances, two of which were close to the forest (3 m and 6 m) and two further away towards field centre (30 m and 33 m). At all sampling points (N = 48), winter wheat plants (growth stage 87 – 89) were harvested aboveground in 1 m x 1 m plots with a sickle, threshed and their seed biomass dried at 70°C for at least 48 h, weighed and converted to grain yield in t ha⁻¹.

For the field studies of 2016 and 2017 (‘AgroScapeLab Quillow’), winter wheat fields were selected to be situated either adjacent to hedgerows or an in-field kettle hole. In both years, transects at field-to-field borders were established; in 2017 additionally at agricultural roads (Table 1.1). Every transect type was situated in a different winter wheat field. Distances along transects were selected at 1 m, 5 m, 20 m and 50 m. In 2016, seven transects started from a hedgerow (tree height: 4 m – 13 m) and six transects from a kettle hole, each on a different winter wheat field. On four of these 13 fields, a control transect was additionally set up at a field-to-field border (Table A1.1). In 2017, 28 transects were established in eleven winter wheat fields. Each field contained a transect either departing from an agricultural road or a field-to-field border and at least one transect departing from a NLE, either from a hedgerow (tree height: 4 m– 13 m) or a kettle hole. At six of eleven fields, it was possible to establish three different transect types within one field, so that we were able to harvest in total four transects at agricultural roads, seven transects at field-to-field borders, eight transects at hedgerows and

nine at kettle holes (Table A1.1). In 2016 and 2017, we harvested the total aboveground biomass of wheat plants at seed maturation (growth stage 87 – 89) in 1 m x 1 m plots at all sampling locations (2016: N = 68 and 2017: N = 112). After wheat plants were threshed and dried at 70°C for at least 48 h, seed biomass was weighed and converted to yield in t ha⁻¹.

Statistical analyses

Responses of yield to transect types and distances were analysed using two different kinds of analyses using R, version 3.3.1 (R Core Team, 2018): (1) with linear mixed-effects models to qualitatively distinguish yield losses between our measured categorical distances using the package *nlme* (Pinheiro *et al.*, 2018) and (2) with a non-linear mixed-effects model using the package *nlstools* (Baty *et al.*, 2015) and assuming different competition effects per transect type at field borders as well as yields that converge asymptotically to mid-field yields as the influence from the border vanishes.

For the full linear mixed-effects model, we fitted the terms ‘transect type’ (agricultural road, field-to-field border, forest, hedgerow and kettle hole), categorical ‘distance’ in spatial sequence along transects (1st, 2nd, 3rd, 4th) and their interaction term as fixed effects. Additionally, we inserted year as covariate and as random effects transects nested within fields (Tables 1.2 and 1.3). Significance levels were assessed obeying to the principle of marginality, using Wald Chi² tests (type II), testing each term after all others, but ignoring the term's higher-order relatives, using the *Anova* function (Fox and Weisberg, 2019) in the *car* package (Fox *et al.*, 2012). In addition, we ran four smaller models (Table 1.4), analysing only one transect type (forest, kettle hole, hedgerow or agricultural road) at a time, with categorical ‘distance’ in spatial sequence as fixed effect and transects nested within fields as random effect. Here, we used a more conservative significance level of $\alpha = 0.01$ to adjust for the number of models analysed. In all linear mixed-effects models, we set the 4th distance as reference level to compare the farthest distance from the field border (referred as mid-field yield) to those being closer to the bordering structure.

For the non-linear mixed-effects model, we implemented a self-starting function with varying yield values at field border (Y_c), a fixed rate (c) at which yields putatively increase as well as varying mid-field yields (Y_m) at which the curves converge asymptotically per transect type:

Equation 1.1

$$Y(x) \sim e^{-cx} * (Y_c - Y_m) + Y_m$$

Y_c and Y_m were modelled as functions of transect type with random effect of transects nested within fields to allow the function to vary at field border and at mid-field yields per transect type (Table 1.5). Unfortunately, the low number of sampling points did not allow us to vary all three parameters per transect type and we thus fixed the exponential decay rate at $c = 0.1 \text{ m}^{-1}$ after visual inspection.

With this function at hand we were able to quantify the distance at which 95% of mid-field yield per transect type were reached (Fig. 1.3 and Table 1.6):

Equation 1.2

$$0.95 Y_m = e^{-cx_{95\%}} * (Y_c - Y_m) + Y_m$$

$$x_{95\%} = -\ln\left(\frac{0.05}{1 - \frac{Y_c}{Y_m}}\right) c^{-1}$$

In addition, we calculated absolute yield loss (L) in kg per meter field border by subtracting each surface integral (A) from the total area under the asymptote until 95% of mid-field yield:

Equation 1.3

$$F(x) = \int_0^{x_{95\%}} e^{-cx} * (Y_c - Y_m) + Y_m$$

$$A = -\frac{1}{c} e^{-cx_{95\%}} * (Y_c - Y_m) + Y_m x_{95\%} + \frac{1}{c} * (Y_c - Y_m)$$

$$L [\text{kg m}^{-1}] = (Y_m x_{95\%} - A) / 10$$

With this, we could quantify relative yield loss over the area from the field border until the distance where yield reaches 95% of mid-field yield per meter field border.

Table 1.2: Type-II-analysis of variance table for linear mixed-effects model on crop yield as a function of year (2014, 2015, 2016, 2017), transect type (field-to-field, forest, hedgerow, kettle hole, agricultural road), categorical distance in chronological sequence along transects (1st, 2nd, 3rd, 4th) and their interaction term with the random effect term of transects nested within fields [$yield \sim year + transect\ type * distance, random = \sim 1 | field / transect$], reference level for ‘distance’ is the 4th distance of each year (2014 = 64 m, 2015 = 33 m, 2016/17 = 50 m) that represents mid-field yields; reference level for ‘transect type’ is field-to-field border; bold font: significant ($P < 0.05$), normal font: not significant ($P > 0.05$); N= 260, 65 transects in 34 fields.

	Df	Chisq	p-value
Year	3	3.75	0.290
Transect type	4	41.36	< 0.001
Distance	3	135.08	< 0.001
Transect type : Distance	12	36.82	< 0.001
Random term	1 field/transect		Std. Dev = 0.22

Table 1.3: Summary table of linear mixed-effects model on crop yield as a function of year (2014, 2015, 2016, 2017), transect type (field-to-field, forest, hedgerow, kettle hole, agricultural road), categorical distance in chronological sequence along transect (1st, 2nd, 3rd, 4th) and their interaction term with the random effect term of transects nested within fields [$yield \sim year + transect\ type * distance, random = \sim 1 | field / transect$], reference level for ‘distance’ is the 4th distance of each year (2014 = 64 m, 2015 = 33 m, 2016/17 = 50 m) that represents mid-field yields; reference level for ‘transect type’ is field-to-field border; bold font: significant ($P < 0.05$), normal font: not significant ($P > 0.05$); N = 260; 65 transects in 34 fields.

	Value	Std. Error	df	t-value	p-value
Intercept	7.56	0.75	180	10.09	< 0.001
2015 vs. 2014	+1.29	0.85	29	1.51	0.142
2016 vs. 2014	+0.68	0.75	29	0.90	0.374
2017 vs. 2014	+0.89	0.75	29	1.20	0.242
Forest vs. field-to-field	-0.51	1.09	29	-0.47	0.642
Hedgerow vs. field-to-field	-0.83	0.41	28	-2.03	0.052
Kettle hole vs. field-to-field	-0.24	0.42	28	-0.58	0.567
Agricultural road vs. field-to-field	+0.16	0.56	28	0.29	0.775
1 st distance vs. 4 th distance	-1.11	0.41	180	-2.72	0.007
2 nd distance vs. 4 th distance	-0.47	0.41	180	-1.14	0.254
3 rd distance vs. 4 th distance	-0.56	0.41	180	-1.38	0.170
1 st distance between forest vs. field-to-field	-1.37	0.57	180	-2.42	0.017
1 st distance between hedgerow vs. field-to-field	-1.76	0.54	180	-3.23	0.001
1 st distance between kettle hole vs. field-to-field	-0.29	0.56	180	-0.53	0.600
1 st distance between agricultural road vs. field-to-field	+0.14	0.73	180	0.19	0.853
2 nd distance between forest vs. field-to-field	-1.26	0.57	180	-2.21	0.028
2 nd distance between hedgerow vs. field-to-field	-0.74	0.54	180	-1.37	0.173
2 nd distance between kettle hole vs. field-to-field	-0.42	0.56	180	-0.75	0.453
2 nd distance between agricultural road vs. field-to-field	-0.08	0.73	180	-0.11	0.915
3 rd distance between forest vs. field-to-field	+0.36	0.57	180	0.64	0.523
3 rd distance between hedgerow vs. field-to-field	+0.63	0.54	180	1.16	0.246
3 rd distance between kettle hole vs. field-to-field	+0.37	0.56	180	0.65	0.513
3 rd distance between agricultural road vs. field-to-field	-0.12	0.73	180	-0.17	0.865

Table 1.4: Summary tables of linear mixed-effects models on crop yield as a function of categorical distance in chronological sequence along transect (1st, 2nd, 3rd, 4th) with the random effect term of transects nested within fields per transect type [$yield \sim distance, random = \sim 1|field / transect$], reference level for ‘distance’ is the 4th distance; bold font: significant ($P < 0.01$), normal font: not significant ($P > 0.01$).

	Value	Std. Error	df	t-value	p-value
<i>Forest (N = 56, 14 transects in 8 fields)</i>					
Intercept	8.03	0.47	39	17.25	< 0.001
1 st distance vs. 4 th distance	-2.49	0.35	39	-7.10	< 0.001
2 nd distance vs. 4 th distance	-1.73	0.35	39	-4.93	< 0.001
3 rd distance vs. 4 th distance	-0.20	0.35	39	-0.57	0.572
Random effects (Std. Dev)	1 field = 1.11		1 field/transect = 3.29 * 10 ⁻⁵		
<i>Hedgerow (N = 68, 17 transect in 17 fields)</i>					
Intercept	7.54	0.38	48	19.75	< 0.001
1 st distance vs. 4 th distance	-2.87	0.38	48	-7.53	< 0.001
2 nd distance vs. 4 th distance	-1.21	0.38	48	-3.18	0.003
3 rd distance vs. 4 th distance	+0.70	0.38	48	0.18	0.855
Random effects (Std. Dev)	1 field = 0.79		1 field/transect = 0.79		
<i>Kettle hole (N = 60, 15 transects in 15 fields)</i>					
Intercept	8.05	0.40	42	20.07	< 0.001
1 st distance vs. 4 th distance	-1.41	0.42	42	-3.38	0.002
2 nd distance vs. 4 th distance	-0.89	0.42	42	-2.14	0.038
3 rd distance vs. 4 th distance	-0.20	0.42	42	-0.47	0.638
Random effects (Std. Dev)	1 field = 0.75		1 field/transect = 0.75		
<i>Agricultural road (N = 24, 6 transects in 6 fields)</i>					
Intercept	7.96	0.39	15	20.26	< 0.001
1 st distance vs. 4 th distance	-0.98	0.36	15	-2.74	0.015
2 nd distance vs. 4 th distance	-0.55	0.36	15	-1.53	0.146
3 rd distance vs. 4 th distance	-0.69	0.36	15	-1.93	0.072
Random effects (Std. Dev)	1 field = 0.52		1 field/transect = 0.52		

Table 1.5: Summary table of non-linear mixed-effects model on crop yield as self-starting function with varying yield values at field border (Y_c), a fixed rate (c) at which yields increase as well as varying mid-field yields (Y_m) at which yields converge asymptotically per transect type (Equation 1.1). Y_c and Y_m were modelled as functions of transect type with random effect of transects nested within fields; reference level is field-to-field; bold font: significant ($P < 0.05$), normal font: not significant ($P > 0.05$); $N = 260$; 65 transects in 34 fields.

	Value	Std. Error	df	t-value	p-value
C	0.12	0.02	185	5.63	< 0.001
Y_c (Intercept)	7.15	0.46	185	15.46	< 0.001
Y_c (forest)	-2.49	0.74	185	-3.37	< 0.001
Y_c (hedgerow)	-2.73	0.57	185	-4.81	< 0.001
Y_c (kettle hole)	-0.71	0.57	185	-1.23	0.221
Y_c (agricultural road)	+0.28	0.78	185	+0.37	0.712
Y_m (Intercept)	8.08	0.27	185	29.69	< 0.001
Y_m (forest)	-0.01	0.46	185	-0.02	0.988
Y_m (hedgerow)	-0.38	0.28	185	-1.36	0.177
Y_m (kettle hole)	-0.09	0.27	185	-0.32	0.749
Y_m (agricultural road)	+0.24	0.38	185	+0.63	0.527
Random effect (b)	1 field = $1.34 * 10^{-7}$				
Random effect (Y_c)	1 field = 0.93			1 field/transect = 1.17	
Random effect (Y_m)	1 field = 0.89			1 field/transect = 0.19	

Results

We measured an average winter wheat yield of $6.42 \pm 1.14 \text{ t ha}^{-1}$ (mean \pm standard deviation) seed biomass in ‘Klostergut Deppoldshausen’ (2014), as well as $7.23 \pm 1.67 \text{ t ha}^{-1}$ (2015), $6.99 \pm 1.61 \text{ t ha}^{-1}$ (2016) and $7.49 \pm 1.77 \text{ t ha}^{-1}$ (2017) in the ‘AgroScapeLab Quillow’. Generally, winter wheat yields increased from the field border into the agricultural field ($\chi^2(3) = 135.1$, $P < 0.001$; Fig. 1.1; Table 1.2). Adjacent to the investigated bordering structures, we observed a yield reduction compared to yields measured farthest from it (1st to 4th distance) of $1.11 \pm 0.41 \text{ t ha}^{-1}$ (13%) at field-to-field borders ($t_{180} = -2.7$, $P < 0.01$; Table 1.3), $2.49 \pm 0.35 \text{ t ha}^{-1}$ (32%) at forest borders ($t_{39} = -7.1$, $P < 0.001$; Table 1.4), $2.87 \pm 0.38 \text{ t ha}^{-1}$ (38%) at hedgerows ($t_{48} = -7.5$, $P < 0.001$), $1.41 \pm 0.42 \text{ t ha}^{-1}$ (17%) at kettle holes ($t_{42} = -3.4$, $P < 0.01$), and $0.98 \pm 0.36 \text{ t ha}^{-1}$ (11%) at agricultural roads ($t_{15} = -2.7$, $P < 0.05$). This significant yield loss persisted adjacent to forest borders ($t_{39} = -4.9$, $P < 0.001$) and hedgerows ($t_{48} = -3.2$, $P < 0.01$) when comparing the 2nd and 4th distances from field border. At the 3rd sampling point, all yield

differences were negligible between investigated transect types (Fig. 1.1). Yield losses varied between transect types ($\chi^2(12) = 36.8, P < 0.001$; Fig. 1.1; Table 1.2), especially when comparing field-to-field borders with woody landscape structures: Forest borders affected yields negatively compared to a neighbouring agricultural field at the 1st and 2nd distance ($t_{180} [1^{st}] = -2.4, P < 0.05$; $t_{180} [2^{nd}] = -2.2, P < 0.05$; Table 1.3). Yields at hedgerows differed only within the 1st distance to yields measured at field-to-field borders ($t_{180} = -3.2, P < 0.01$). However, we found that yield losses adjacent to kettle holes were similar to those observed next to another agricultural field ($t_{180} = -0.5, P > 0.5$).

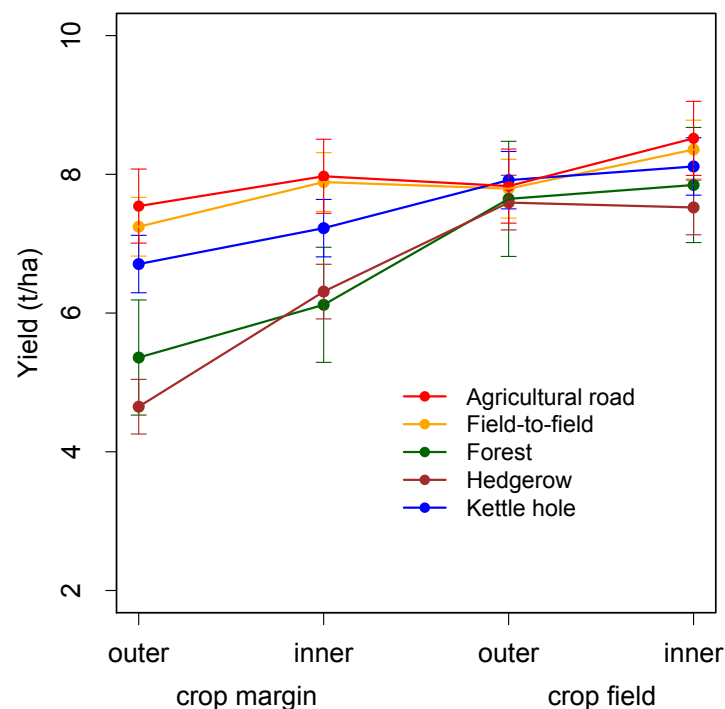


Figure 1.1: Winter wheat yield, measured as seed biomass [$t\ ha^{-1}$], along transects departing from the field border towards the field centre measured in four categorical distances in chronological sequence (1st = outer crop margin, 2nd = inner crop margin, 3rd = outer crop field, 4th = inner crop field) over four years of investigation (2014 = 1 m, 4 m, 16 m, 64 m; 2015 = 3 m, 6 m, 30 m, 33 m; 2016 and 2017 = 1 m, 5 m, 20 m, 50 m) adjacent to agricultural roads (N = 24; red), to field-to-field borders (N = 52; orange), to forest borders (N = 56; green) to hedgerows (N = 60; brown) and to kettle holes (N = 60; blue); for detailed attributions of transect types per year see Table A1.1. Values are depicted as fitted values with confidence intervals of 95% taken from the linear mixed-effects model with crop yield as a function of year, transect type, categorical distance and their interaction term with the random effect term of transects nested within fields. N = 260, 65 transects in 34 fields.

Fitting the yield increase from the field border into the field with a non-linear asymptotic function (Eq. 1.1) revealed a similar pattern (Fig. 1.2). At forest borders and hedgerows, winter wheat yields proximate to the bordering structure (Y_c) were significantly lower than at field-to-field borders (forest: $t_{185} = -3.4; P < 0.001$; hedgerow: $t_{185} = -4.8; P < 0.001$; Table 1.5). Adjacent to kettle holes however, no yield reduction could be observed compared to a

neighbouring agricultural field ($t_{185} = -1.2$; $P > 0.1$). The effect of a bordering structure vanished further into the field and transect type had no influence on mid-field yields (Y_m). To specify how far this yield reduction lasted into the field, and how this depended on transect type, we calculated the distance until 95% of mid-field yields are reached using the asymptotic function (Fig. 1.3). We found that agricultural roads reduced yields up to 6.3 m into the field (Table 1.6). Up to this distance the farmer loses 7.5% per meter agricultural road of the yield that could have been achieved without any field border. Field-to-field borders affected yields up to 6.9 m for 95% mid-field yields with a loss of 7.8% per meter field border. Woody landscape elements showed the most far-ranging effect of the investigated transect types with yield losses of 17.5% until 95% of mid-field yields. These yields were reached for both transect types after 17.8 m from forest borders or hedgerows. Per meter kettle hole, 10.6% of seed biomass was lost until 11.3 m, where the benchmark of 95% of mid-field yields is met (Fig. 1.3, Equations 1.2 and 1.3 and Table 1.6).

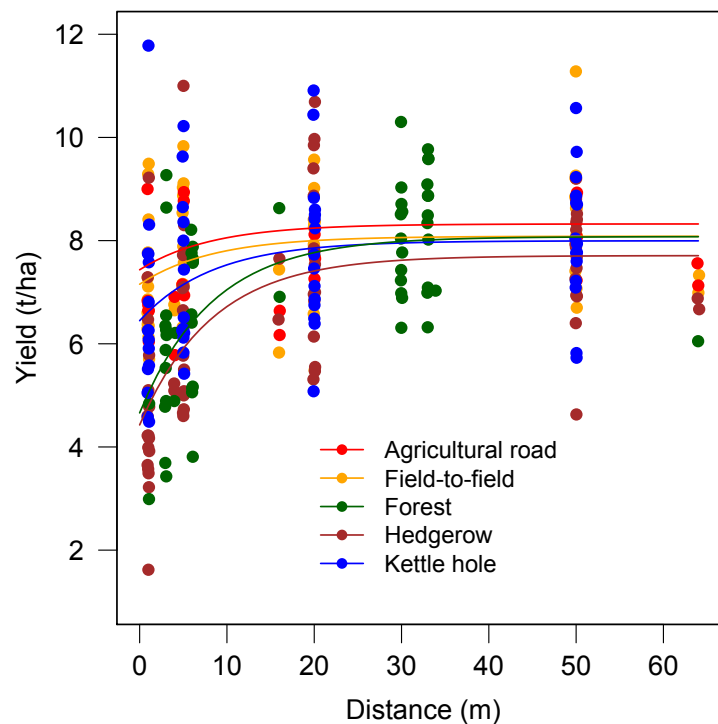


Figure 1.2: Winter wheat yield, measured as seed biomass [$t\ ha^{-1}$], along transects departing from the field border towards the field centre fitted in a non-linear mixed-effects model as a self-starting function with varying yield values at field border (Y_c), a fixed rate (c) at which yields increase as well as varying mid-field yields (Y_m) at which yields converge asymptotically per transect type (Equation 1.1). Y_c and Y_m were modelled as functions of transect type with random effect of transects nested within fields. Transect types were agricultural roads ($N = 24$; red), field-to-field borders ($N = 52$; orange), forest borders ($N = 56$; green) hedgerows ($N = 60$; brown) and kettle holes ($N = 60$; blue); for detailed attributions of transect types per year see Table A1.1. $N = 260$, 65 transects in 34 fields.

Table 1.6: Calculated values for the distance [m] ($x_{95\%}$) at which 95% of mid-field yields were reached (Equation 1.2) and absolute [kg m^{-1}] as well as relative [%] yield losses that occurred from the field border until $x_{95\%}$ compared to no field border (Equation 1.3). Yield loss is calculated as subtraction of the surface integral (A) bounded between 0 and $x_{95\%}$ of the total area of mid-field yields (Y_m) multiplied by the distance ($x_{95\%}$) at which 95% of mid-field yields are reached; all values are given per transect type.

	$x_{95\%}$ [m]	Losses [kg m^{-1}]	Losses [%]
Agricultural road	6.32	0.39	7.48
Field-to-field	6.93	0.44	7.80
Forest	17.79	2.51	17.47
Hedgerow	17.85	2.41	17.54
Kettle hole	11.28	0.96	10.60

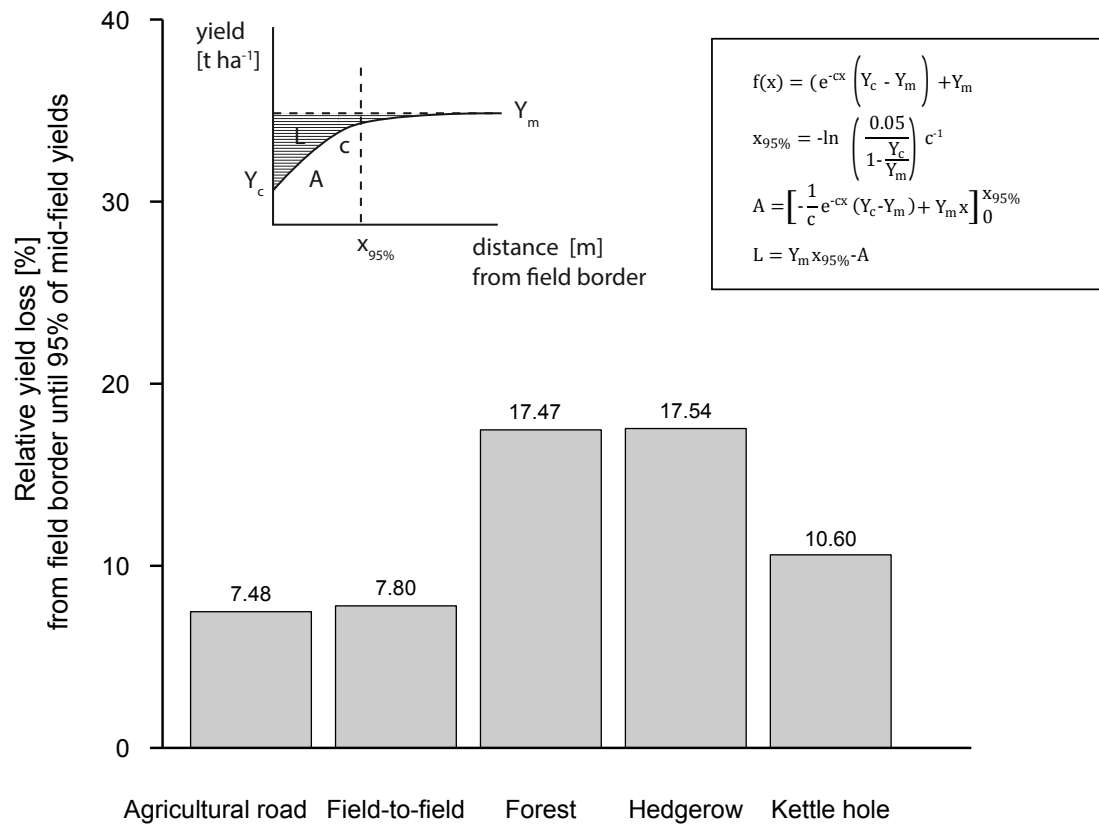


Figure 1.3: Relative yield loss [%] from the field border until 95% of mid-field yields are reached per transect type (agricultural road, field-to-field border, forest, hedgerow and kettle hole) with a simplified sketch of the relationship between distance [m] from field border and yield [t ha^{-1}] as a non-linear function with varying yield values at field border (Y_c), a fixed rate (c) at which yields increase as well as varying mid-field yields (Y_m) at which the yields converge asymptotically per transect type (Equation 1.1) where yield loss (L) is calculated as subtraction of the surface integral (A) bounded between 0 and $x_{95\%}$ of the total area of mid-field yields (Y_m) multiplied by the distance ($x_{95\%}$) at which 95% of mid-field yields are reached (Equation 1.2 and 1.3).

Discussion

We investigated the effect of different natural landscape structures (NLE: forests, hedgerows and kettle holes) on winter wheat yields comparing yields along transects from NLEs as well as from agricultural roads and field-to-field borders into agricultural fields across two German regions. At all transect types, yields next to the field border (one to three meters) were reduced compared to mid-field yields. However, depending on the bordering structure, yield differences vanished at varying distances: For woody landscape elements yield loss was still considerably high at the 2nd measured distance (four to six meters) and reached 95% of mid-field yields only after 17 meters. In contrast, yield reduction adjacent to kettle holes did not differ compared to field-to-field borders. Here, yields converged already within 11 meters to 95% of seed biomass values measured within the field.

Negative effects of natural landscape elements close to the border

A potential explanation for lower yields close to NLEs could simply be that farmers do not apply chemical inputs such as fertilisers, plant promoters and plant protection in full amounts close to field borders. Law restricts the application of fertilizers and pesticides at field borders in Germany. For plant protection issues, distance restrictions to any NLE neighbouring agricultural fields are set by EU regulation (No. 1107/2009) and detailed by the German plant protection law (Deutscher Bundestag, 2012). The restrictions vary regarding the active agents of the plant protection measure, the kind of neighbouring NLE and the amount of NLEs in the surrounding landscape (Bayerische Landesanstalt für Landwirtschaft, 2018). Still, most restrictions range between 5 and 20 m, agreeing with the distances of noticeable yield loss next to our investigated NLEs. Adjacent to water bodies, farmers are additionally restricted by regulations for fertilization to maintain a minimum spraying distance depending on fertiliser types, spreading technique and slope of the field border (BMEL, 2017). Therefore, the reduced nutrient and plant protection input may contribute to lower yields close to these landscape elements.

Another factor that potentially causes yield losses at field borders is soil compaction due to turning of machinery (Boatman and Sotherton, 1988; Wilcox *et al.*, 2000). This occurs mostly where tram tracks are perpendicular to field border and therewith to the bordering structure. As we did not control for this factor originally, some of our transects were aligned parallel to tram tracks and thus situated at field borders where machinery turns. However, a smaller share of our transects was situated at field borders with turning edges and these did not result into lower

yields compared to non-turning edges (Appendix A1: Fig. A1.1, Tables A1.2 and A1.3). Thus, we cannot conclusively show that turning edges had an influence on our results.

Previously, NLEs had been hypothesized to increase crop yield, for example because of overall enhanced biodiversity and bio-control (e.g., Tschumi *et al.*, 2015). While we did not assess predator abundance or bio-control efficiency in this study, it is likely that predator-prey interactions (e.g., with pest antagonists) were not an important mechanism to explain crop yields in the intensively managed winter wheat fields in our study that were treated with pesticides (Tscharncke *et al.*, 2016), albeit less intensively at field margins. Insect pest populations may even have benefitted from the presence of a NLE by using it as habitat or food resource when the annual crops were harvested (Blitzer *et al.*, 2012). Thus, reduced crop yields close to NLEs could be caused by a combination of reduced chemical inputs and increased pest pressure — but the exact mechanisms remain to be tested in future studies.

However, the most cited explanation for yield reduction close to NLEs is shading, especially adjacent to tall vegetation structures (Kort, 1988; Burgess *et al.*, 2004; Esterka, 2008). Lyles, Tatarko and Dickerson (1984) showed yield reductions within winter wheat fields up to a distance equivalent to twice the height of the trees, with an average decrease by 31% compared to mid-field yield. Shade may also preserve soil moisture next to the NLE, resulting in a higher risk of crop-pathogen infection (Müller *et al.*, 2016). Müller and colleagues reported that abundances of fungal wheat pathogens were correlated to higher soil moisture.

Different natural landscape elements — different effects

There is hardly any data available showing the impact of different NLE types on yield. In consistence with our second hypothesis, we have shown that the type of bordering structure influenced the relationship between yield and distance to the field border. For kettle holes, yield reduction was not as severe as for woodlands; already after 11.3 m 95% of mid-field yields were obtained. Hence, only 5.0 m and 4.4 m more than the observed distance from agricultural roads or field-to-field borders, respectively. Still, yields measured closest to kettle holes were affected negatively in both years of investigation (2016 and 2017), probably because of reduced chemical plant protection and fertilization close to water bodies. Nonetheless, seed biomass values adjacent to kettle holes were statistically indistinct from yields measured at field-to-field border. Especially in 2016, we observed a trend to higher yield at 20 m distance to the kettle hole compared to field-to-field borders suggesting that in years with low precipitation (2016: 422 mm; ZALF field station, Dedelow) these natural water islands can act as water supplier for the crop plant (Fig. A1.2). Thus, yield losses near kettle holes may be negligible and the value

of this NLE for biodiversity conservation and regulating services for the crop may not incur any economic losses for the farmer.

Yield reductions observed close to forest borders and hedgerows might be driven in large part by shading from trees (Burgess *et al.*, 2004) or by tree roots entering arable land belowground conferring competition for water and nutrients (Huber *et al.*, 2013). Regarding shading effects, as we did not explicitly choose our transects according to their exposure, we unfortunately could not clearly show in our analyses that yields at south oriented transects were at an advantage compared to those measured at north orientated transects (Fig. A1.3, Table A1.4). We observed only a trend at hedgerows that was not confirmed by forest borders. Among others, Sklenicka and Salek (Sklenicka and Salek, 2005) reported crop yield losses to become insignificant at a distance between twice to three times the height of the adjacent trees. In 2015, the investigated forest borders ranged between 18 m and 24 m tree height and most of our investigated hedgerows in the ‘AgroScapeLab Quillow’ in 2016 and 2017 were 4 m to 13 m tall. Still, significant yield losses could only be detected for the 1st and 2nd distance (four to six meters) at forest and hedgerows compared to the respective mid-field yields. At the 3rd distance (16 m to 30 m) yields were indistinct to yields measured at field-to-field borders as well as to mid-field yields. The non-linear function we applied to capture the increase of yields away from the field border revealed that already at a distance of 17.8 m from both woody landscape elements 95% of mid-field yields could be reached. These results indicate that in our study yield losses are not as severe as reported in former literature (Lyles, Tatarko and Dickerson, 1984; Kort, 1988; Sklenicka and Salek, 2005; Esterka, 2008).

In addition, we could observe trends to higher yields at 20 m distance from woody landscape elements compared to mid-field yields in 2014 and 2016 (Fig. A1.2). It is therefore likely that woodlands have also provided a positive (potentially sheltering) effect for the crop that had been outside the trees’ shading scope. There, not being light-limited, the crop could have benefitted from reduced evapotranspiration as woodlands are known to act as wind barriers and can lower wind speed to distances from twice to four times the height of the trees (Kowalchuk and Jong, 1995; Peter and Bozsik, 2009). These shelter effects can be particularly relevant in drought years or in future drier scenarios under climate change, where maintained soil moisture becomes highly valuable (Thaler *et al.*, 2012). Accordingly, in wet years, the shelter effect was shown to be less pronounced or even absent (Bruckhaus and Buchner, 1995; Kowalchuk and Jong, 1995). This pattern can also be observed in our data (Fig. A1.2), as this yield peak was more evident in the dry year of 2016 (422 mm of precipitation) compared to 2017 (755 mm of

precipitation, ZALF field station, Dedelow). We tried to capture the shelter effect in our data by fitting a bi-exponential function to our data:

Equation 1.4

$$yield \sim (e^{-cx} * (Y_c - Y_m) + Y_m) * (e^{-sx} * (Y_s - Y_m) + Y_m)$$

Unfortunately, we were unable to achieve convergence due to scarcity of data points given the larger number of free parameters. The intended function incorporates detrimental competition effects that decrease into the field at rate c and beneficial effects of shelter that decrease into the field as well at a somewhat lower rate s . In addition, yield values at field borders affected only by the shelter effect (Y_s), thus excluding competition, should be higher than mid-field yields (Y_m) in contrast to those affected from only the competition effect (Y_c) being lower than mid-field yields. We would like to encourage further investigations on yield losses at different bordering structures to design their studies based on these two effects.

Management recommendations

In order to profit from the beneficial effect of woody landscape elements (even though yields are lowered proximate to it), we propose cutting hedgerows on a regular basis. Such management regimes are already in place in Switzerland, where hedgerow height is limited by a compulsory rotational trimming management at least every 8 years (Federal Office of Agriculture FOAG Switzerland, 2018). Such standards could reduce disadvantages of shading and competition for nutrients and water for the proximate crop plants, while the advantages of e.g., reduced evapotranspiration and pest control would be kept.

Another measure could be to design more efficient field borders at woody landscape elements by combining different NLEs to strengthen advantages for biodiversity and the provision of regulating and supporting ecosystem services such as water regulation and pest control. In particular, an option could be to keep a broad fringe of extensive grassland vegetation at borders between a forest or hedgerow and an agricultural field as recommended by Berger *et al.* (2011) and implemented by Swiss agricultural directives. Pywell *et al.* (2015) already showed that the creation of grassy wildlife-friendly habitats at field borders not only increases pollinator abundance but also leads to increased yields proximate to it. Moreover, they demonstrated that removing 8% of the farmland at field borders for those habitats can balance overall yield losses and pay off already after five years of maintenance. The width of such habitats should cover the zone of severe yield losses depending on the bordering structure, but ensure that crop production benefits from the positive effect of e.g., woody landscape elements after release from competition. As herbaceous landscape elements do not result in significant yield losses

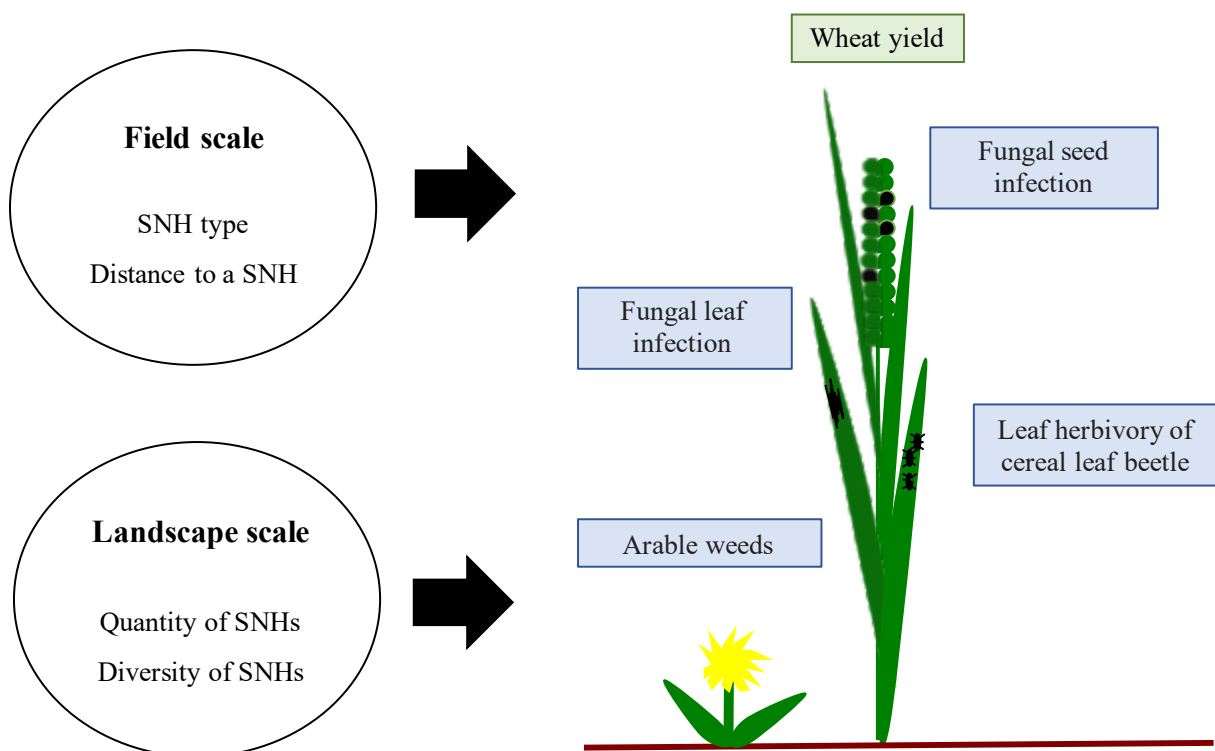
(Tschumi *et al.*, 2015; Sutter, Albrecht and Jeanneret, 2018), a herbaceous strip with a diverse mix of short-lived and perennial native plants as applied in Pywell *et al.* (2015) could be a perfect habitat to obtain multiple advantages: No severe yield loss at field borders, combined with further positive effects from different habitats — wind shelter and erosion control gained by the woody landscape element and high pollinators and pest predator abundances obtained by the herbaceous landscape element.

Conclusion

Natural landscape elements (NLEs) in agroecosystems are crucial, not only for biodiversity conservation but also for promoting regulating and supporting services such as water regulation and pest control. Our findings can add to the debate on economic gains and losses from specific NLEs as we quantified yield losses depending on the bordering structure. In particular, we showed that the effect of NLEs on crop yields vary between NLE types. They can be negligible (as for kettle holes), negative close to woody landscape elements and even slightly positive at more than twice the distance of tree height from hedgerows or forest borders. We therefore recommend aligning a second NLE with lower vegetation (e.g., an herbaceous strip) in-between the field border and a woody landscape element to maintain their longer-ranged positive effects and buffer their short-ranged negative effects by naturally provided ecosystem services that can benefit farmers at low economic costs. Future studies should focus on finding the optimal balance between the provisioning service for crop production and sustainable land management, where NLEs are an important part of agricultural landscapes.

Study 2:

Who is the culprit: Is pest infestation responsible for yield losses close to semi-natural habitats?



Study 2: Who is the culprit: Is pest infestation responsible for yield losses close to semi-natural habitats?

with Karin Pirhofer Walzl, Marina E. H. Müller, Christoph Scherber and Jasmin Joshi

Abstract

Semi-natural habitats (SNHs) are becoming increasingly scarce in modern agricultural landscapes. This may reduce natural ecosystem services such as pest control with its putatively positive effect on crop production. In agreement with other studies, we recently reported wheat yield reductions at field borders which were linked to the type of SNH and the distance to the border. In this experimental landscape-wide study, we disentangle the biotic drivers of these yield depressions and analyse fungal seed and fungal leaf pathogens, herbivory of cereal leaf beetles and weed cover as hypothesized mediator variables between SNHs and yield.

We established experimental winter wheat plots of a single variety within conventionally managed wheat fields at fixed distances either to a hedgerow or an in-field kettle hole. For each plot, we recorded the fungal infection rate on seeds, fungal infection and herbivory rates on leaves, and weed cover. Using structural equation modelling (SEM), we tested the effects of SNHs at a field scale (SNH type and distance to a SNH) and at a landscape scale (percentage and diversity of SNHs within a 1000m-radius) assuming that SNHs may influence yield either directly or indirectly by affecting pest infection rates.

Wheat plants of experimental plots confirmed the dependency of yield losses on SNH type and distance to a SNH while being unaffected by fungal infection rates of seeds and leaves as well as by herbivory rates. Only weed cover was negatively associated with yield values while decreasing strongly with distance to a SNH. None of the pest rates affected the relationship between SNHs in the landscape and yield.

Our findings highlight how intricate the relationship between SNHs and crop production is and that the benefits of SNHs in terms of biodiversity-mediated provision of ecosystem services for crop production is still far from foreseeable.

Introduction

Intensification of agriculture has led to a depletion of semi-natural habitats (SNHs) in agricultural landscapes and to associated losses of biodiversity (Sala *et al.*, 2000; Tilman *et al.*, 2002; Foley, 2005). However, SNHs have been shown to provide important biodiversity-mediated ecosystem services (Tschardtke *et al.*, 2005) such as pollination (Bianchi, Booij and Tschardtke, 2006; Garibaldi *et al.*, 2011) and pest control (Chaplin-Kramer *et al.*, 2011; Veres *et al.*, 2013). Especially landscape complexity in terms of amount and diversity of SNHs was reported to be of major importance for beneficial species (Tschardtke *et al.*, 2007; Chaplin-Kramer *et al.*, 2011; Rusch *et al.*, 2013), whereas pest populations often showed inconsistent responses to higher landscape complexity (Papaix *et al.*, 2011; Karp *et al.*, 2018). Several studies observed a decrease in pest densities with increasing landscape complexity (e.g., Chaplin-Kramer and Kremen, 2012) either due to an effective pest control mediated through SNHs (Rusch, Chaplin-Kramer, *et al.*, 2016) or a reduced amount of cropped habitat (Dominik *et al.*, 2018). However, SNHs can also act in favour of pest populations as they provide alternative food resources or refugia against agricultural disturbances (Tschardtke *et al.*, 2016). Thus, SNHs provide habitats not only for natural enemies or pollinators, but also for pests that subsequently may spill-over from SNHs into agricultural fields (Blitzer *et al.*, 2012). Perez-Alvarez, Nault and Poveda (2018) observed that even the presence of a single SNH type, here meadows, can produce mixed pest responses reducing one pest species, but augmenting another that spilled-over from the SNH into agricultural fields. Hence, understanding the role of SNHs on pest population dynamics and corresponding crop damage is a prerequisite for developing ecologically sustainable crop-protection strategies in order to reduce intensive use of agrochemical inputs (Skellern *et al.*, 2017).

Still, it has remained largely unexplored which particular types of SNHs and their distribution in the landscape contribute to an optimal provision of ecosystem services and potentially also to increasing crop yield. According to Holland *et al.* (2017), only few studies have made the attempt to evaluate the effect of SNHs on yield representing the most valued service for farmers in agricultural landscapes.

A global synthesis has recently revealed that landscape complexity can increase yield mediated through predator and pollinator richness (Dainese *et al.*, 2019). Further, Liere *et al.* (2015) found that with increasing habitat diversity cascading effects from high predator abundances led to lower pest densities, less plant damage and therewith slightly increased yield. However, if high landscape complexity favours species from higher trophic levels, trophic cascades may be indirectly beneficial to herbivores, again resulting in a yield decrease (Martin *et al.*, 2013).

These contrasting responses of pest populations and their consequences for crop yield have also been frequently studied at a field scale, where especially the effects of hedgerows and grass strips have been in focus (Holland *et al.*, 2016; Van Vooren *et al.*, 2017). Although hedgerows have been shown to enhance parasitism and pollination (Dainese *et al.*, 2017), the direct impacts of tall vegetation structures at field borders often leads to lower yield due to shading and competition for nutrients and water (Kort, 1988; Kowalchuk and Jong, 1995). This emphasizes a trade-off between crop production and regulating ecosystem services next to woody habitats (Van Vooren *et al.*, 2018). Grass strips generally have been reported to increase pest control, with lower pest densities having either no consequences (Albrecht *et al.*, 2020) or positive effects on yield (Tschumi *et al.*, 2015; Gurr *et al.*, 2016). In a recent study, we demonstrated that the effect of SNHs on yield varies between SNH types (Raatz *et al.*, 2019). In proximity to woody structures, such as forest borders and hedgerows, yield losses were high compared to field-to-field borders, whereas in the vicinity of kettle holes yield losses were negligible.

In the present study, we aim to shed light on the biotic culprits of yield losses close to SNHs by focusing on four different wheat-specific pests (Oerke, 2006) potentially associated with SNHs and entailing ecosystem disservices by reducing crop production. We chose fungal seed pathogens, fungal leaf pathogens, cereal leaf beetle larvae (*Oulema* spp., hereafter CLB) and arable weeds. The taxa studied represent the major pest groups of winter wheat in the temperate zone with pathogens accounting for 10% of global wheat yield losses, followed by animal pests and weeds (each 8%) in the presence of crop protection practices (Oerke, 2006). Adapted to the rapid ecosystem function assessment method (Meyer, Koch and Weisser, 2015), we measured fungal seed and leaf infection rates, herbivory rates, and weed cover to relate these pest groups to yield.

While the effect of SNHs for weeds is intensively studied (e.g., Fried *et al.*, 2009), less is known about the role of SNHs for fungal pathogens and CLB larvae (Holland *et al.*, 2017, but see Tschumi *et al.*, 2015). Therefore, we additionally assessed the effect of SNHs also on those wheat pests. To investigate if the response of pest rates to SNH type and the distance to a SNH is altered by increasing landscape complexity, we extended our scope to the landscape scale by accounting for the percentage and diversity of SNHs within a radius of 1000 m.

Our approach is based on experimental plots where a single wheat variety is sown at several in-field points in conventionally managed winter wheat fields. This allows to measure seed biomass and pest rates in a highly standardized way across different agricultural fields.

To find the culprit of yield losses associated with SNHs, we investigated direct and indirect effects of SNHs on yield and asked the following questions:

- a. Are the measured pest rates (fungal seed and leaf infection, herbivory of CLB, and weed cover) directly associated to yield losses close to SNHs?
- b. At what spatial scale are pest rates affected by SNHs? Field scale (distance to a SNH and SNH type) or landscape scale (percentage and diversity of SNHs)?
- c. Can fungal seed and leaf infection, herbivory of CLB, and weed cover mediate indirect effects of SNHs on yield?

Methods

Study area

We conducted our study from September 2015 to July 2016 at the ZALF research platform ‘AgroScapeLab Quillow’ (250 km², Uckermark, Brandenburg, Germany). This area is characterised by a sub-continental climate with 8.7°C mean annual temperature and a low mean annual precipitation of 475 mm year⁻¹ (ZALF field station, Dedelow). The landscape is dominated by agricultural fields and grasslands (62%) interspersed with forests (24%), water bodies (5%), and small settlements (5%). Frequent semi-natural habitats (SNHs) in the catchment are tall hedgerows along fields as well as kettle holes — small water bodies (<1 ha, Kalettka and Rudat, 2006) — within fields as remnants of the last ice age. More than one third of agricultural fields in the area are cultivated with winter wheat that yields on average 7.4 t ha⁻¹ (Amt für Statistik Berlin-Brandenburg, 2017, 2018).

We selected twelve winter wheat fields based on the biotope map of Brandenburg 2009 (Landesamt für Umwelt, Brandenburg, Germany) and the regional land-use data of the ‘AgroScapeLab Quillow’ from 2015 and 2016 in ArcGIS 10.4.1 (ESRI, Redlands, California, USA). Selected fields had to meet the following criteria to make them comparable: (i) winter wheat as the main crop in 2016, (ii) oil-seed rape as the winter wheat pre-crop in 2015 and (iii) a field size ranging from 20 – 75 ha. In each field, one transect was established from an adjacent SNH being either a hedgerow (N = 6) or a kettle hole (N = 6) into the winter wheat field with four distances at a modified logarithmic scale (1 m, 5 m, 20 m, and 50 m; see Raatz *et al.*, 2019 for details).

Experimental plots

At each wheat field (N = 12), we established one experimental plot at each of the four distances along the transect within a 1-m squared area (yielding N = 48) by sowing 300 seeds of the winter wheat variety ‘Julius’, a frequently used variety for the study area, with a manual sowing machine into a 1-m² plot composed of 6 rows (inter-row distance = 12 cm with 300 seeds / m²).

All experimental plots were managed identically as the crop wheat plants on the field by the farmer. Winter wheat in the study area is generally treated with three to four fertiliser applications per year (total: 180 – 220 kg N ha⁻¹). Pesticides are applied according to infestation rates, whereof generally in autumn a herbicide is dispersed against annual weeds and in spring up to three fungicide treatments against root diseases, *Septoria*, brown rust or *Fusarium*. In general, the only insecticide employed by farmers is against aphids depending on animal abundance.

Experimental plots were harvested aboveground at seed maturation (growth stage 87 – 89), threshed with a laboratory threshing machine and dried at 65°C for 48 hours to constant dry weight. Seed biomass was weighed and converted to grain yield in t ha⁻¹. To validate our experimental approach, we compared the yield of our sown wheat plants with the yield of winter wheat sown by the farmer (hereafter field wheat) harvested in the same design (for further details see dataset of 2016 in Raatz *et al.*, 2019).

Selected pest groups of wheat

To assess potential yield losses at increasing distances to hedgerows and kettle holes (SNH types), we measured rates of fungal pathogens (on seeds and leaves) as well as one animal pest (CLB larvae) of winter wheat directly on the plants of our experimental plots and arable weeds, as main competitors of crop plants for nutrients, light, and space, next to the experimental plants.

Ten wheat ears were collected per experimental plot prior to harvest at growth stage 83 – 85. Ten seeds of the wheat ears per plot were randomly selected, the outer husks were removed and the naked seeds were incubated on potato dextrose agar (PDA) for three days at 25°C in darkness followed by three days with a 12h / 12h black light (emission 310 – 360 nm) / darkness cycle. A total fungal infection rate was calculated by counting the fungal colonies (colony forming units, CFU) and extrapolated to number of CFUs per 100 seeds. Additionally, the phytopathogenic fungi of the genera *Alternaria* and *Fusarium* were taxonomically determined and counted as genus-specific CFUs per 100 seeds.

Fungal leaf pathogens (mainly brown and yellow rust, powdery mildew, and *Septoria* spp.) were visually inspected on three flag leaves per row (N = 18 leaves per plot). We only studied flag leaves as they contribute up to 60% to grain yield, whereas leaves below the flag only modestly contribute to grain yield (Thorne, 1966). Here as well, we recorded an unspecific

fungal infection rate (independently of fungal group) as the proportion of infected flag leaves to the total number of investigated flag leaves per experimental plot (N = 48).

Herbivory was recorded by visually detecting the characteristic feeding patterns of the CLB larvae on three flag leaves per row (N = 18 leaves per plot). CLB larvae skeletonize the leaves by feeding on all leaf tissue except the lower epidermis (Gallun, Everly and Yamazaki, 1967), which reduces the photosynthetic capacity of the plant resulting in a decline of the number of grains per spike and the thousand-grain weight. A damage threshold for wheat where feeding damage leads into measurable yield losses is often indicated at 10% loss of flag leaf area corresponding to about 10% yield loss (Hoffmann and Schmutterer, 1999; Kirch, 2006). Thus, we quantified herbivory rate as the proportion of leaves damaged greater than 10% to the total number of investigated leaves per experimental plot (N = 48) by making use of a scoring scale from 1 (no damage) to 9 (very severe damage) adapted from (Moll, Flath and Piepho, 2000) while all scoring levels above 4 were greater than 10% damage per leaf area (Appendix A2: Table A2.1). Within the herbivory dataset, we had two missing data points which we replaced by the median of all other herbivory rates.

We recorded total cover of weeds close to each experimental plot after Braun Blanquet (1951) in six 1-m² areas — three areas to the left and three areas to the right of the plot while being parallel to the field border. Single scores were converted to percentage values (Table A2.2) and averaged per experimental plot (N = 48).

Landscape complexity

We were interested if landscape complexity altered putative effects on yield of the four selected pests at the field scale. Therefore, we analysed the effect of percentage and diversity of SNHs within a 1000-m radius around each experimental plot on fungal seed and leaf infection, herbivory of CLB larvae, and weed cover. We identified water bodies (including kettle holes), ruderal areas, fens, grasslands, hedgerows, and forests to represent SNHs in our study area and calculated the percentage as well as the Shannon diversity index (SDI) of these six biotope classes with Fragstats 4.2 (McGarigal and Marks, 1995) using the eight-cell-neighbourhood rule in a grid of 1 m x 1 m within a 1000-m radius around each experimental plot (N = 48). Percentage of SNHs ranged from 4.7% – 27.4% and SDI of SNHs from 0.74 – 1.58. These compositional landscape metrics were not significantly correlated to each other ($r(46) = 0.27$, $P > 0.05$).

Statistical analyses

To unravel the culprit of yield losses due to SNHs, we analysed the effects of fungal seed and fungal leaf infection rates, herbivory rates, and weed cover on winter wheat yield in our experimental plots, as well as the local and landscape effects of SNHs on the selected pests performing several single generalised linear mixed-effects models in the packages *nlme* (Pinheiro *et al.*, 2018) and *lme4* (Bates *et al.*, 2015) in R version 4.0.3. (R Core Team, 2020). As a prerequisite and to verify our methodical approach, we first analysed the yields of our experimental plots and the field wheat of 2016 in a joint model (model 1; Table 2.1) by entering: $yield \sim yield\ type\ (experimental\ plots\ vs.\ agricultural\ field) * distance\ to\ a\ SNH * SNH\ type\ (hedgerow\ vs.\ kettle\ hole), random = 1|field$. From the field wheat dataset, we excluded one outlier that would have strongly affected the results (N = 47). As the visual inspection of residual plots with either yield type as response variable did not reveal any obvious deviations from homoscedasticity or normality, we performed a linear mixed-effects model. ‘Distance to a SNH’ was log-transformed for a better fit of the model. Random effects of field identity were included to account for field variability. Log-transformation of distance and field identity as random effect was maintained throughout all further models.

Table 2.1: Type-II-analysis of variance for the linear mixed-effects model (1) on winter wheat yield as a function of yield type (experimental plots vs. field wheat), distance to a SNH (1 m, 5 m, 20 m, 50 m), SNH type (hedgerow, kettle hole), and all their interaction terms with field as random effect [$yield \sim yield\ type * distance\ to\ a\ SNH * SNH\ type, random = 1|field$] (N= 95); bold font: significant ($P < 0.05$). The table is the result from a likelihood ratio Chi-square test with individual model terms taking up only 1 degree of freedom (df).

<i>Model 1 (LMM)</i>	Chisq	df	p-value
Yield type	48.69	1	< 0.001
Distance to a SNH	38.04	1	< 0.001
SNH type	2.30	1	0.130
Yield type x distance	4.56	1	0.033
Yield type x SNH type	0.01	1	0.922
Distance x SNH type	8.10	1	0.004
Yield type x distance x SNH type	0.02	1	0.883
Random effect (1 field)	SD = 0.62		

For direct effects of the selected pests on wheat yield of the experimental plots (N = 48), we performed a linear mixed-effects model (model 2a; Table 2.2): $yield \sim (distance\ to\ a\ SNH + SNH\ type) * (fungal\ seed\ infection + fungal\ leaf\ infection + herbivory + weed\ cover) + distance\ to\ a\ SNH\ x\ SNH\ type, random = 1|field$. As reported in Raatz *et al.* (2019), yield losses were only detectable within the two most proximate distances to a SNH along our transects. Hence, we repeated our analysis using only yield values of the experimental plots at 1-m and 5-m

distance to an adjacent SNH (N = 24) omitting the fixed effect ‘Distance to a SNH’ and all interaction terms from the model (model1b): $yield \sim SNH\ type + fungal\ seed\ infection + fungal\ leaf\ infection + herbivory + weed\ cover, random = 1|field$.

Table 2.2: Type-II-analysis of variance for linear mixed-effects models (2a and 2b) examining relationships between local factors of SNHs (distance to a SNH and SNH type) and fungal seed and fungal leaf infection, herbivory of CLB larvae and weed cover on winter wheat yield of experimental plots with field as random effect; model 2a including exp. plots at all four distances (1 m, 5 m, 20 m, 50 m): $[yield \sim (distance\ to\ a\ SNH + SNH\ type) * (fungal\ seed\ infection + fungal\ leaf\ infection + herbivory + weed\ cover) + distance\ to\ a\ SNH \times SNH\ type, random = 1|field]$ (N = 48); model 2b including only exp. plots at the two proximate distances (1 m and 5 m): $[yield \sim SNH\ type + fungal\ seed\ infection + fungal\ leaf\ infection + herbivory + weed\ cover, random = 1|field]$ (N = 24); bold font: significant ($P < 0.05$). The table is the result from a likelihood ratio Chi-square test with individual model terms taking up only 1 degree of freedom (df).

Model 2a and 2b (LMM)	with all distances			only with proximate distances		
	Chisq	df	p-value	Chisq	df	p-value
Distance to a SNH	3.93	1	0.048	-	-	-
SNH type	0.57	1	0.450	2.24	1	0.134
Distance x SNH type	1.47	1	0.226	-	-	-
Fungal seed infection	1.67	1	0.196	1.41	1	0.235
Fungal leaf infection	0.00	1	0.954	0.01	1	0.906
Herbivory of CLB	0.05	1	0.824	0.89	1	0.345
Weed cover	0.91	1	0.341	6.58	1	0.010
Distance x Seed infection	0.02	1	0.891	-	-	-
Distance x Leaf infection	0.17	1	0.683	-	-	-
Distance x Herbivory	0.75	1	0.385	-	-	-
Distance x Weed cover	0.11	1	0.739	-	-	-
SNH type x Seed infection	0.87	1	0.351	-	-	-
SNH type x Leaf infection	0.90	1	0.343	-	-	-
SNH type x Herbivory	0.89	1	0.346	-	-	-
SNH type x Weeds	0.42	1	0.518	-	-	-
Random effect (1 field)	SD = 0.93			SD = 0.29		

Furthermore, each selected pest group was analysed separately concerning local and landscape factors of SNHs on their rates. Here, we entered the following fixed effects in four single models (models 3a – 3d; Table 2.3): $pest \sim distance\ to\ a\ SNH * SNH\ type + Percentage\ of\ SNH * (distance\ to\ a\ SNH + SNH\ type) + Diversity\ of\ SNH * (distance\ to\ a\ SNH + SNH\ type), random = 1|field$. For fungal leaf infection rate and herbivory rate, we used binomial distributions in generalised linear mixed-effects models. For fungal seed infection rate and weed cover, we used linear mixed-effects models even though weed cover had to be log-transformed to obtain normality.

Table 2.3: Type-II-analysis of variance for (generalized) linear mixed-effects models (3a – 3d) examining relationships between local (distance to a SNH and SNH type) and landscape factors (percentage [%SNH] and Shannon diversity [SDI]) of SNHs on fungal seed and fungal leaf infection, herbivory of CLB larvae and weed cover with field as random effect; [*pest* ~ *distance to a SNH* * *SNH type* + *Percentage of SNH* * (*distance to a SNH* + *SNH type*) + *Diversity of SNH* * (*distance to a SNH* + *SNH type*), *random* = 1|*field*] (N = 48 for each pest group); weed cover is log-transformed; bold font: significant ($P < 0.05$). The table is the result from a likelihood ratio Chi-square test with individual model terms taking up only 1 degree of freedom (df).

<i>Model 3a (LMM)</i> <i>and 3b (GLMM)</i>	Fungal seed infection			Fungal leaf infection		
	Chisq	Df	p-value	Chisq	df	p-value
Distance to a SNH	0.00	1	0.995	2.99	1	0.084
SNH type	0.02	1	0.896	0.46	1	0.497
Percentage of SNHs [%SNH]	1.53	1	0.216	0.23	1	0.633
Diversity of SNHs [SDI]	0.73	1	0.394	0.02	1	0.882
Distance x SNH type	0.63	1	0.429	16.50	1	< 0.001
Distance x %SNH	0.15	1	0.702	15.85	1	< 0.001
SNH type x %SNH	3.04	1	0.081	0.31	1	0.579
Distance x SDI	0.38	1	0.537	0.02	1	0.895
SNH type x SDI	0.23	1	0.629	3.61	1	0.057
Random effect (1 field)	SD = 51.74			SD = 2.27		
<i>Model 3c (GLMM)</i> <i>and 3d (LMM)</i>	Herbivory of CLB			Weed cover		
	Chisq	Df	p-value	Chisq	df	p-value
Distance to a SNH	1.56	1	0.212	31.80	1	< 0.001
SNH type	5.42	1	0.020	0.05	1	0.827
Percentage of SNHs [%SNH]	0.02	1	0.876	5.04	1	0.025
Diversity of SNHs [SDI]	0.00	1	0.976	0.53	1	0.467
Distance x SNH type	0.62	1	0.431	0.98	1	0.323
Distance x %SNH	0.71	1	0.399	0.08	1	0.773
SNH type x %SNH	0.21	1	0.650	1.62	1	0.203
Distance x SDI	0.08	1	0.777	1.06	1	0.304
SNH type x SDI	5.58	1	0.018	1.92	1	0.166
Random effect (1 field)	SD = 0.59			SD = 0.65		

In a final step, we used a structural equation model (SEM) with the package *piecewiseSEM* (Lefcheck, 2016) to investigate direct effects of SNHs on yields of our experimental plots and indirect effects of SNHs mediated by fungal seed and fungal leaf infection rates, herbivory rates, and weed cover. For the metamodel, we specified a total of five linear mixed-effects models, where each endogenous variable (yield, fungal seed infection, fungal leaf infection, herbivory, and weed cover) was related to the four exogenous local and landscape factors of SNHs (distance to a SNH, SNH type, percentage of SNHs and diversity of SNHs), always including field identity as a random effect (Table 2.4). A direct path was added from each of the four pest groups to yield. Fungal leaf infection and herbivory were logit-transformed and weed cover log-transformed to achieve a normal distribution of residuals and a better model fit. Beyond that we interlinked the four pests to each other in order to capture a more realistic

picture: We hypothesized that higher weed cover benefits fungal infection and herbivory because arable weeds may serve as alternative sources for seed and leaf fungi within the field (e.g., Wisler and Norris, 2005) and as alternative host plants for CLB (e.g., Glogoza, 2002) to recolonise the wheat plant. Furthermore, we assumed that fungal leaf infection rates would be affected positively by herbivory rates because fungi may enter more easily if the plant tissue is destroyed (e.g., Munkvold, 2003).

Table 2.4: Summary table of linear mixed-effects models in final piecewise SEM ($C_{30} = 15.33$; $P = 0.988$) examining relationships between local (SNH type and distance to a SNH) and landscape factors (percentage and diversity within 1000 m radius around the plots) of SNHs and winter wheat yield of experimental plots, fungal seed and fungal leaf infection, herbivory of CLB larvae and weed cover; bold font: significant ($P < 0.05$), grey font: non-significant ($P > 0.1$); each variable $N = 48$.

Response	Predictor	Estimate	Std. Estimate	Std. Error	df	p-value
<i>Yield</i>	Distance to a SNH	0.189	0.207	0.126	31	0.143
	%SNH	-0.060	-0.398	0.031	31	0.060
	SDI	-1.553	-0.270	1.017	31	0.137
	Leaf infection	0.131	0.156	0.138	31	0.351
	Weed cover	-0.316	-0.293	0.180	31	0.089
		$R^2_{\text{marginal}} = 0.32$		$R^2_{\text{conditional}} = 0.51$		
<i>Seed infection</i>	Distance to a SNH	-4.679	-0.108	4.808	34	0.337
	Weed cover	-9.950	-0.194	7.246	34	0.179
		$R^2_{\text{marginal}} = 0.03$		$R^2_{\text{conditional}} = 0.70$		
<i>Leaf infection</i>	Distance to a SNH	-0.110	-0.101	0.103	32	0.298
	%SNH	0.059	0.326	0.050	32	0.247
	Herbivory of CLB	-0.425	-0.188	0.268	32	0.123
	Weed cover	-0.211	-0.164	0.163	32	0.203
		$R^2_{\text{marginal}} = 0.17$		$R^2_{\text{conditional}} = 0.82$		
<i>Herbivory</i>	Weed cover	-0.108	-0.189	0.067	35	0.114
	SNH type	-	-	-	1	0.083
	hedgerow	-2.583	-	0.234	11	-
	kettle hole	-2.008	-	0.234	10	-
		$R^2_{\text{marginal}} = 0.17$		$R^2_{\text{conditional}} = 0.64$		
<i>Weed cover</i>	Distance to a SNH	-0.439	-0.522	0.079	34	< 0.001
	%SNH	-0.048	-0.345	0.024	34	0.051
		$R^2_{\text{marginal}} = 0.38$		$R^2_{\text{conditional}} = 0.60$		

The SEM was simplified by successively removing paths with the highest p-values until further removals did not further decrease the overall model fit. Goodness-of-fit was assessed based on Shipley's test of directed separation that combines the p-values of all independent claims in Fisher's C (Shipley, 2009). At last, we manually calculated direct, indirect, and total effects of the remaining local and landscape factors of SNHs on yield mediated through the selected drivers based on Finney (1972).

Results

Winter wheat yields

Overall, winter wheat plants of experimental plots (that were sown approximately four weeks later than the agricultural crops) yielded on average less ($5.3 \pm 1.4 \text{ t ha}^{-1}$) than winter wheat plants sown by the farmer ($6.9 \pm 1.6 \text{ t ha}^{-1}$; $X^2(1) = 48.7$, $P < 0.001$; Table 2.1). Yields measured at experimental plots confirmed the findings of Raatz *et al.* (2019): i. Yields increased with distance to an adjacent SNH ($X^2(1) = 3.9$, $P < 0.05$; Table 2.2). Field yields increased more steeply from the field border towards field centre compared to yields of experimental plots ($X^2(1) = 4.6$, $P < 0.05$; Table 2.1). ii. Yield values were lower close to hedgerows compared to yields close to kettle holes and increased more steeply to mid-field yields with increasing distance to a hedgerow compared to a kettle hole, independently of yield type ($X^2(1) = 8.1$, $P < 0.01$; Fig. 2.1).

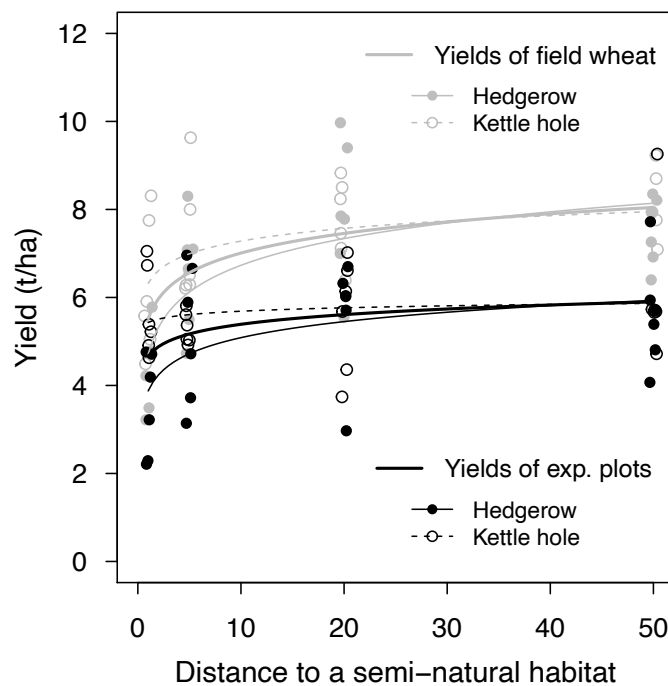


Figure 2.1: Effect of distance to a semi-natural habitat (SNH) per SNH type (hedgerow: solid line and kettle hole: dashed line) on winter wheat yield measured as seed biomass in t ha^{-1} of experimental plots ($N = 48$; black) and field wheat ($N = 47$; grey). Curves represent fitted values according to the linear mixed-effects model 1 (Table 2.1).

Analysing the impact of fungal infection rates, herbivory rate, and weed cover on yield of experimental plots, the first model including yield at all distances, revealed that none of the pests affected yield significantly, neither solely, nor depending on the distance to a SNH nor on the SNH type (Appendix A2: Fig. A2.1). However, when only analysing yield close to field borders (at 1m- and 5m-distances), arable weeds reduced wheat yield up to 49% ($X^2(1) = 7.9$, $P < 0.01$; Fig. 2.2).

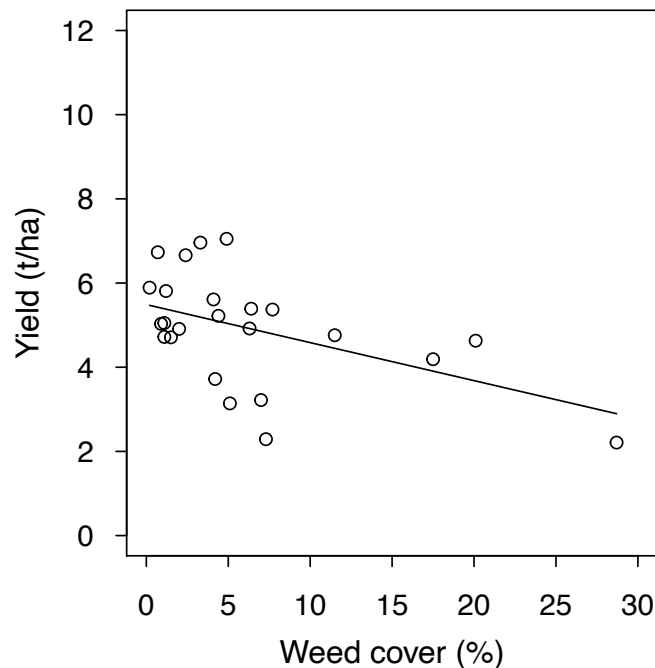


Figure 2.2: Weed cover (%) at each experimental plot correlated with winter wheat yield measured as seed biomass in $t\ ha^{-1}$ of the experimental plots at 1-m and 5-m distances to a SNH ($N = 24$). Curve represents fitted values according to a linear mixed-effects model 2b (Table 2.2).

Effects of SNHs on pests

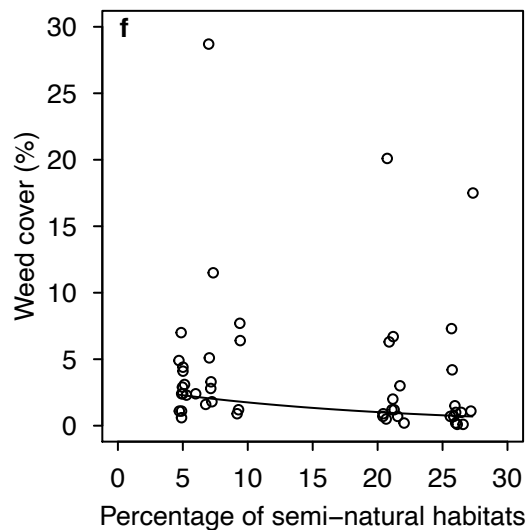
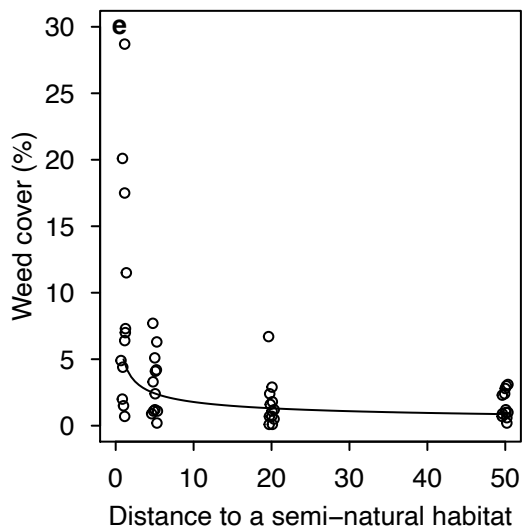
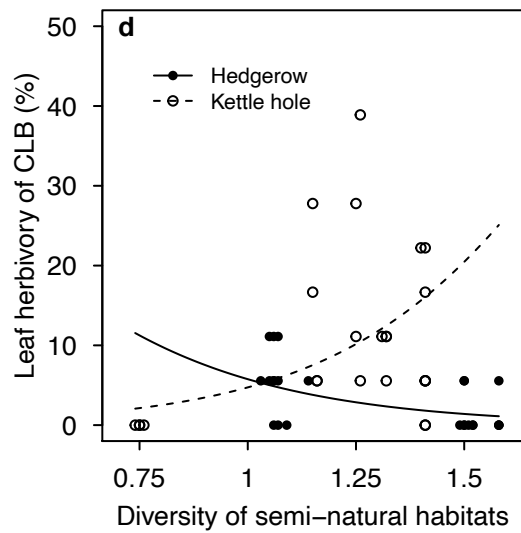
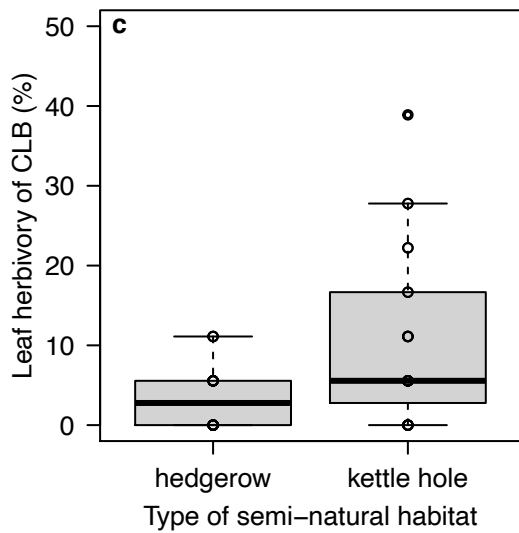
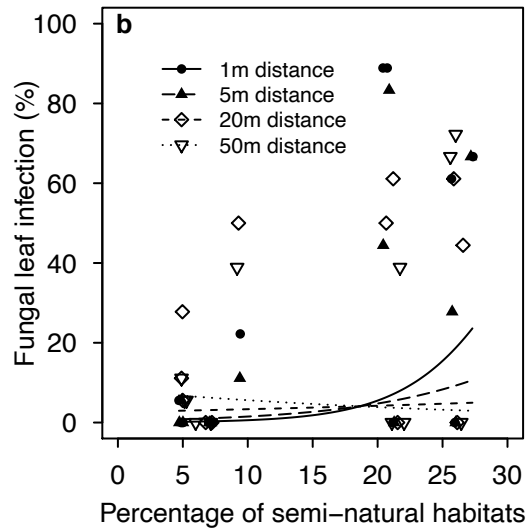
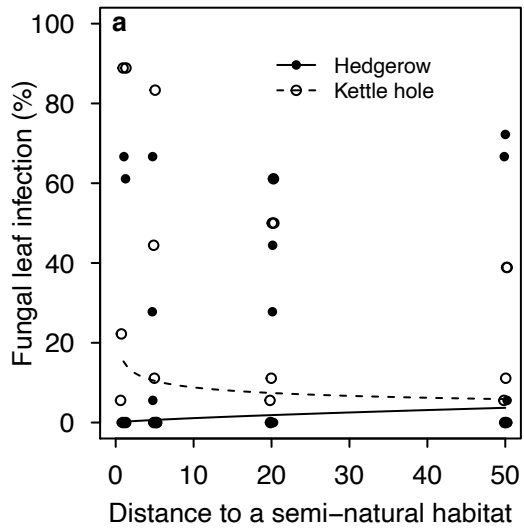
Fungal infection on wheat seeds of experimental plots ranged from 120 – 400 colony forming units (CFUs) per 100 wheat seeds with a median of 290 CFUs. Most colonies could be attributed to *Alternaria* species (mean: $46\% \pm 12\%$) whereas *Fusarium* species were little represented (mean: $2\% \pm 6\%$). Fungal infection rates on the sampled wheat seeds were neither affected by distance to a SNH ($X^2(1) = 0.0$, $P > 0.05$; Table 2.3), nor by SNH type ($X^2(1) = 0.0$, $P > 0.05$), by any metrics of landscape composition (%SNH: $X^2(1) = 1.5$, $P > 0.05$; SDI: $X^2(1) = 0.7$, $P > 0.05$), and nor by the interaction between field and landscape scale.

Fungal infection on winter wheat flag leaves ranged from 0% – 88.9% with a median of 5.6%. Close to kettle holes, infection rates decreased from field border to field centre by 62%, whereas close to hedgerows rates remained nearly unchanged ($X^2(1) = 16.5$, $P < 0.001$; Fig. 2.3a). With increasing percentage of SNHs at the landscape scale, fungal infection increased depending on

distance to a SNH ($X^2(1) = 15.9, P < 0.001$; Fig. 2.3b): At low percentages of SNHs, infection rates were similarly low at all distances whereas the more SNHs were present in a radius of 1000 m the more leaves were infected close to the SNH (22% infection rate at 27% SNH) compared to leaves of wheat plants further in the wheat field (5% infection rate at 27% SNH). Herbivory rates greater than 10% of the leaf surface caused by CLB larvae on flag leaves ranged from 0% – 38.9% with a median of 5.6%. More flag leaves were damaged at kettle holes (10.4%) compared to leaves at hedgerows (2.8%; $X^2(1) = 5.4, P < 0.05$; Fig. 2.3c) and with increasing diversity of SNHs in a 1000m-radius around experimental plots, the percentage of damaged leaves greater than 10% increased on plots at kettle holes whereas at hedgerows herbivory rates decreased ($X^2(1) = 5.6, P < 0.05$; Fig. 2.3d).

Percentage weed cover ranged from 0.1% – 28.7% with a median of 2.2%. Weed cover was affected by distance to a SNH ($X^2(1) = 31.8, P < 0.001$; Fig. 2.3e) and by percentage of SNHs at the landscape scale ($X^2(1) = 5.0, P < 0.05$; Fig. 2.3f) whereby both, increasing distance but also increasing percentage of SNHs, decreased weed cover by 83% and 69%, respectively.

Figure 2.3 (next page): Local (left) and landscape (right) factors of semi-natural habitats (SNHs) on a. and b. the percentage of fungal leaf infection, c. and d. the percentage of herbivory (> 10% per leaf) caused by CLB larvae, e. and f. weed cover (each pest group with $N = 48$). Percentage of SNHs and Shannon diversity of SNHs was calculated within a radius of 1000 m around each experimental plot. Curves represent fitted values according to generalized linear mixed-effects models (3b and 3c) with binomial distribution for fungal leaf infection rate and herbivory of CLB and according to linear mixed-effects model (3d) for weed cover (log-transformed). All drawn relationships are significant ($P < 0.05$). Points of subfigures a and e (with distance as explanatory variable) jitter by 0.5.



Indirect effects of SNHs on wheat yield

For the structural equation model (SEM; Fig. 2.4a), we investigated all single term relationships of SNHs at the field scale (distance to a SNH and SNH type) and at the landscape scale (percentage and diversity of SNHs in 1000-m radius around the plots) on wheat yield of experimental plots and the four selected pest rates as mediator between SNHs and wheat yield. The final SEM fitted the data well (best simplified model: $C_{30} = 15.33$; $P = 0.99$; Fig. 2.4b) and none of the independence claims remained significant, indicating that no important links were missing in the model. In the final model, wheat yield of experimental plots was no longer affected by distance to a SNH or SNH type (Table 2.4). Weed cover was the only variable having a direct, marginal negative effect on yield of experimental plots (standardized effect size: -0.29 ; $P < 0.1$). Weed cover also took a larger share of the indirect effect of distance to a SNH on wheat yield than any other pest group. However, the marginal negative impact of percentage of SNHs on yield could not be explained by the selected pests (Table 2.5). Fungal infection rates were unaffected by single term effects of SNHs, and herbivory rate was only marginally influenced by SNH type. Weed cover diminished significantly with increasing distance to a SNH but was also slightly reduced by the percentage of SNHs in the surrounding. Also, fungal seed and fungal leaf infection, herbivory by CLB larvae, and weed cover remained uncoupled from each other (Fig. 2.4b; Table 2.4).

Table 2.5: Relative strengths of the direct and indirect effects in the final piecewise SEM examining relationships between local (distance to a SNH) and landscape factors (percentage of SNHs) of SNHs, crop pests (fungal leaf infection and weed cover) and winter wheat yield (Fig. 2.4).

Response variable, predictor, and type of effect	Mediator variable	Standardized path coefficient
Winter wheat yield of exp. plots		
Distance to a SNH		
Direct	none	0.207
Indirect	Fungal leaf infection	-0.016
Indirect	Weed cover	0.153
Percentage of SNHs		
Direct	none	-0.398
Indirect	Fungal leaf infection	0.051
Indirect	Weed cover	0.101

Note: Fungal seed infection and herbivory of CLB larvae as mediator are not included because both are no longer predictors of yield in the final piecewise SEM (Table 2.4).

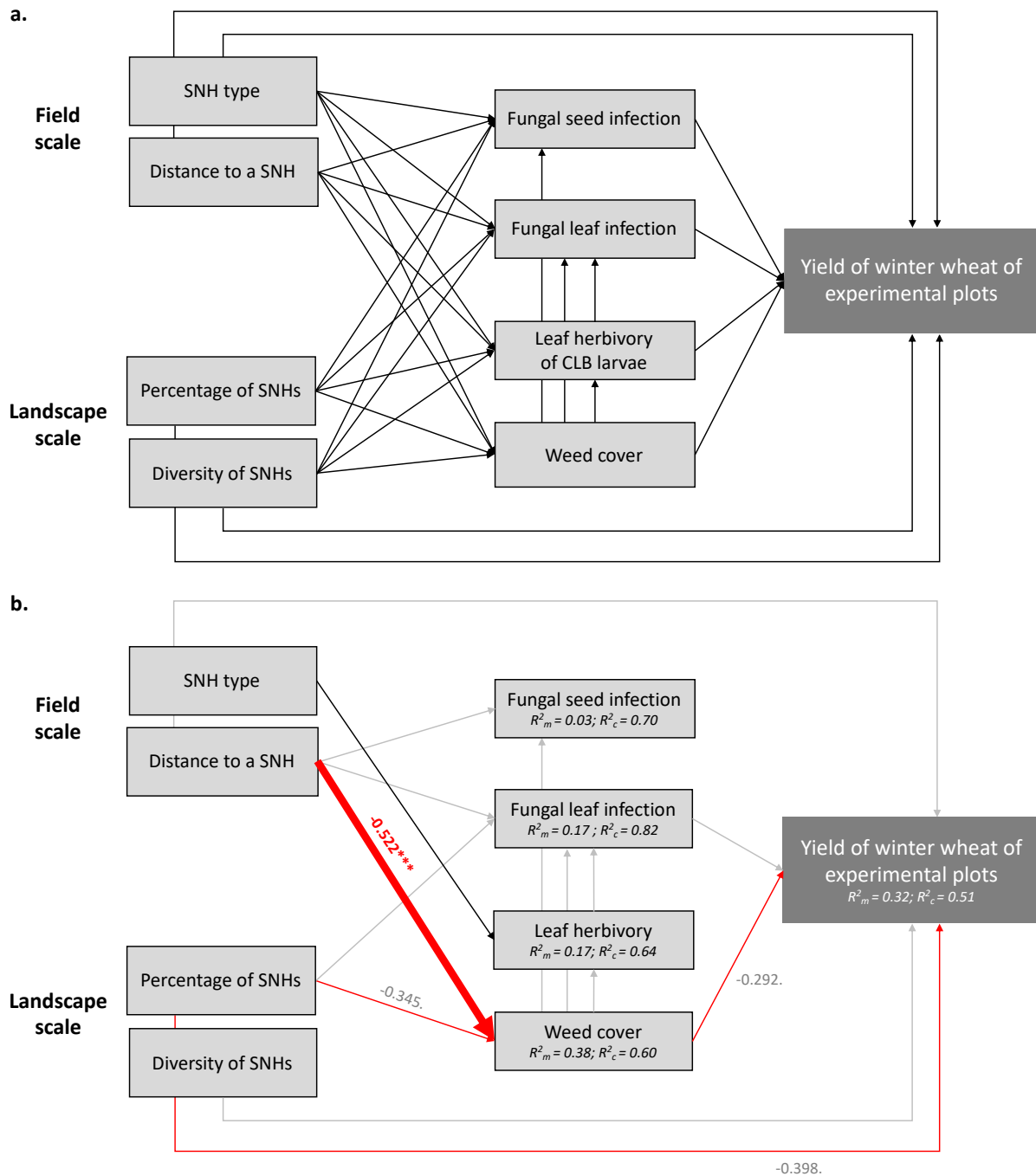


Figure 2.4: a. Metamodel and b. final SEM ($C_{30} = 15.33$; $P = 0.988$) analysing the relationship between semi-natural habitats at field scale (SNH type and distance to a SNH) and landscape scale (percentage and diversity of SNHs within 1000 m radius around the plots) and winter wheat yield of experimental plots, fungal seed infection, fungal leaf infection, herbivory of CLB larvae and weed cover. Black arrows indicate positive and red arrows negative relationships. Widths of arrows and adjacent values indicate standardized effect size of each predictor variable. Asterisks denote significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Grey standardized effect sizes represent relationships of only marginal significance ($P < 0.1$) and grey arrows are non-significant ($P > 0.1$); $N = 48$.

Discussion

In this study, arable weeds could be identified as the only putative culprit (albeit only on a 10% significance level) out of the four selected pests causing yield losses close to semi-natural habitats (SNHs). Weeds had a significant negative effect on yield only when we confined our analysis to the two proximate distances to a SNH (yield at 1-m and 5-m distance). Our structural equation model (SEM) confirmed that wheat yield tended to be affected only by weed cover representing the most important mediator between distance to a SNH and yield of the investigated pests in this study. In addition, the SEM revealed a marginal negative influence of percentage of SNHs in the landscape on wheat yield of the experimental plots.

Weed cover as culprit for yield losses at SNHs

Weed plants are competitors for light, nutrients, and water to the crop plant and most weed species are adapted to the agricultural habitat (Gallandt and Weiner, 2015). However, in this agricultural management system, weed plants cannot establish permanently within the fields due to intensive and regular use of herbicides and tillage (Geiger *et al.*, 2010; Isenring, 2010). Therefore, SNHs may represent refugia and source habitats for weeds and enable a constant recolonization of arable fields (Baudry *et al.*, 2000; Lozada-Gobilard *et al.*, 2019). Distance restrictions of pesticide applications to SNHs set by EU regulation (No. 1107/2009) and detailed by the German plant protection law (Deutscher Bundestag, 2012) prohibit to apply herbicides in direct proximity to a SNH. Hence, the result that weed cover was only marginally affecting yield along the whole transect, but significantly at the most proximate distances to a SNH, can be explained by the interplay of SNHs as source habitat for weeds and regulations to pesticide applications: While weed cover was still elevated close to the SNH, herbicides may be the cause of rapid decrease towards the field centres. This pattern is exactly opposite to the effect of distance on yield: With increasing distance to a SNH, yields rapidly recovered to mid-field yield. Consequently, weed cover seemed to be the most promising biotic candidate of the investigated pests to explain parts of yield losses at the field scale, especially as the indirect effect of distance to a SNH is foremost taken up by weed cover compared to other pests. Considering, however, the larger direct effect of distance to a SNH on yield than the effect mediated through weeds, wheat yield close to SNHs might rather be restricted by abiotic conditions, such as shading by the SNH itself as elaborated in Raatz *et al.* (2019).

The potential of fungal infection and herbivory of CLB due to an adjacent SNH

Remarkably, yield was unaffected by fungal seed and fungal leaf infection rate as well as herbivory rate of CLB larvae. Thus, we have to assume that the unspecific fungal rates as well as the herbivory of the selected animal pests were not the causes of yield reduction close to a SNH. Yet, fungal leaf infection and herbivory of CLB were affected in different ways by the type and distance to a SNH whereas fungal seed infection remained unaffected of SNHs.

The latter result is rather unexpected because several studies have shown that seed-inhabiting fungi can be associated with a variety of non-crop plants. Especially for phytopathogenic fungi of the genus *Fusarium*, Fulcher *et al.* (2019, 2020) and Suproniene *et al.* (2019) observed a remarkable influence of weed patches to an increased incidence of *Fusarium graminearum*, the causal agent of Fusarium head blight, on wheat plants. The authors found a high *Fusarium* abundance on several non-crop grasses providing a permanent habitat for the fungi, especially in the overwintering periods. We also expected these relationships between the grass verges of our investigated kettle holes and hedgerows and therewith hypothesized an increased fungal seed infection rate in the proximity of the SNHs. However, our study did not confirm this pattern for the year of investigation. One explanation could be that the incidence of *Fusarium* on non-crop grasses and the dispersal to the wheat plants is strongly affected by annual and regional environmental conditions, mainly by precipitation, humidity and weed density (Fulcher *et al.*, 2020). We assume that the relatively dry year 2016 influenced the abundance of the total fungal infection rates (here: median 5.6%) as well as the fungal population structures on wheat plants. The high proportion of *Alternaria* fungi in the total fungal seed infection rates indicates this influence of low air humidity: this genus develops and spreads very homogeneously in wheat fields under warm and dry environmental conditions (Schiro *et al.*, 2018, 2019). At the same time, *Alternaria* fungi can act as a competitor to *Fusarium* fungi in the same habitat and suppresses its growth (Müller *et al.*, 2015), which we might see in this study: 46% of the seed-inhabiting fungi were *Alternaria* fungi, but only 2% of them were identified as *Fusarium* fungi. A wetter year may completely change this population structure and favour *Fusarium* fungi instead (Müller *et al.*, 2016). A multi-year investigation and a comprehensive analysis of the fungal community is thus needed to better understand the underestimated relationships between fungal seed pests on grassy weeds and their impact on crop production and yield losses.

Although fungal leaf pathogens had no significant effect on yield, they might have been promoted by an adjacent SNH as those harbour alternative host plants. We could show that infection rates were elevated at wheat plants close to kettle holes compared to those in field

interior. However, we could not confirm this trend at hedgerows. As humidity is of particular importance for fungal infections (Savary *et al.*, 2015; Figueroa, Hammond-Kosack and Solomon, 2018), the grass verge around kettle holes might have provided a more suitable habitat than the vegetation in hedgerows and therewith fungal populations could spill-over from kettle holes more effectively.

Herbivory rates of cereal leaf beetles (CLB) had also no effect on wheat yield. This might be due to the fact that herbivory was predominantly affected by SNH type, which in turn had no effect on yields of experimental plots. Herbivory was on average three times higher on plots adjacent to kettle holes compared to those at hedgerows. This stands in contrast to the fact, that woody habitats account for more than a third of the explained variance of adult densities of CLBs in agricultural landscapes (Sawyer and Haynes, 1986), as sexually immature adults of CLBs overwinter predominantly in woody habitats under bark or leaf litter from which they spill-over in spring to colonise cereal fields (Buntin *et al.*, 2004). Nonetheless, Honek (1991) showed that the females of CLB preferably select plants with a higher water content to deposit their eggs. Thus, higher herbivory rates of CLB larvae at wheat plants close to kettle holes could be due to a higher water content of the leaves and therewith a preferred site for hatched CLB larvae.

Inconsistent responses of pests to landscape complexity

Fungal leaf infection rates in proximity of a SNH were enhanced with increasing percentage of SNHs at a landscape scale. Hence, fungal leaf pathogens might have profited by a higher share of alternative host plants within SNHs in the surroundings. This stands in contrast to Papaix *et al.* (2014) who demonstrated that a complex landscape of susceptible and resistant host plants to fungal plant pathogens was found to be more efficient in impeding the distribution of the pathogen.

In contrast, damage rates of the selected animal pest, CLB, were not affected by the percentage of SNHs, but rather by the interplay of SNH type and diversity of SNHs in the landscape: Herbivory increased at kettle holes whereas it decreased at hedgerows with increasing diversity of SNHs within a 1000-m radius. Natural enemies, such as ladybirds, lacewings, parasitic wasps, and hoverflies, are known to respond positively to landscape complexity (Chaplin-Kramer *et al.*, 2011; Veres *et al.*, 2013) and are more likely to perform pest control in SNH-rich surroundings (Martin *et al.*, 2015; Grab *et al.*, 2018). However, natural enemies of CLBs might have been more abundant at hedgerows compared to kettle holes embedded in agricultural fields because woody habitats and other perennial field boundaries represent

important habitats for many insect species (e.g., Holland and Fahrig, 2000; Morandin, Long and Kremen, 2014). In contrast, we have kettle holes, where zoophagous animals are more likely to be restricted to water surfaces and do not colonise arable fields in such extent (but see Raitif, Plantegenest and Roussel, 2019). Hence, in our study area, at kettle holes, landscape complexity might have attracted pest population and therewith herbivory rates of CLB larvae, whereas at hedgerows, landscape complexity might have increased predator populations of CLBs and feeding rates decreased.

These inconsistent responses of landscape complexity depending on SNHs at the field scale on pest groups emphasise that managing pest populations of one crop species might require different landscape properties and should be taken into consideration when designing agriculture landscapes supporting naturally provided ecosystem services.

Negative effects of landscape complexity on yield

We observed a minor reduction of wheat yield in the intensively managed fields with an increasing share of SNHs in the landscape. In terms of landscape structure, a higher share of SNHs was closely linked to a higher edge density (ED) (% SNH and ED in 1000m: $r(46) = 0.86, P < 0.001$) and smaller fields (% SNH and field size: $r(46) = -0.44, P < 0.01$).

A higher share of field borders — that restrict the use of pesticides and fertilizers in the studied agricultural system — added to an overall negative effect of SNHs in the landscape.

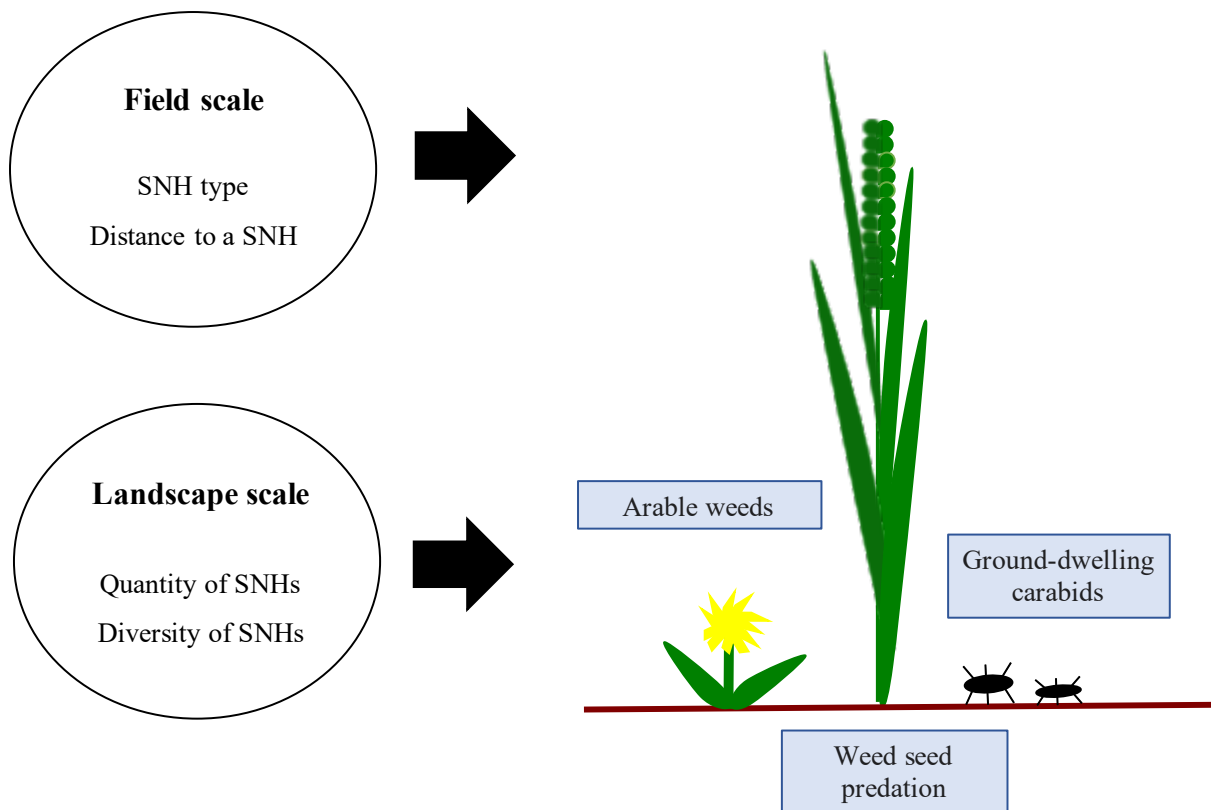
Deng *et al.* (2017) postulated that the positive ecological effect of landscape complexity on crop production is ruled out by the strength of the negative effect of reducing cultivated land, so that at the end the net effect of landscape complexity on crop production is slightly negative. Perhaps in our study area, due to intensive agricultural management positive ecological effects of SNHs might not have come to play.

Conclusion

In our intensively managed study area, arable weeds tended to be the only putative biotic culprit of the ones selected for yield depression adjacent to a semi-natural habitat (SNH). However, their negative effect on wheat yield was only measurable in the proximity of the SNH where pesticide application is prohibited due to distance regulations. Hence, in our study system potential spill-over effects of the investigated pest groups might have been impeded by farming practices. Unfortunately, information about pest management were not available and we have to point out that yield depends most likely on multiple factors including, e.g., nutrient availability. Further studies should incorporate a wider set of yield drivers, including biotic and abiotic drivers as well as farming practices.

Our study presents a further step towards understanding the role of SNHs on crop production and it emphasizes that in intensively managed systems spill-over from adjacent SNHs — may it be pest or predator populations — can be overshadowed by crop management. Hence, targeting a more environmentally sustainable agriculture, we need the combined effort of providing suitable habitat conditions (type of habitat as well as habitat composition and configuration at the landscape scale) for pest control in conjunction with adapted farming strategies.

Study 3: Biodiversity-driven ecosystem functions along the edges — quantifying the effects of field borders in agricultural landscapes



Study 3: Biodiversity-driven ecosystem functions along the edges — quantifying the effects of field borders in agricultural landscapes

with Michael Glemnitz, Karin Pirhofer Walzl, Christoph Scherber and Jasmin Joshi

Abstract

Context Field edges have been considered as hot-spots for biodiversity and naturally provided ecosystem services. However, the spatial ranges at which these services spill-over into arable fields may vary.

Objectives In this study, we investigated the impact of field edges on ecosystem functions, among others pest regulation and niche diversity, to understand their interactions with the surrounding landscape, the neighbouring habitat type and their spatial ranges within the agricultural field.

Methods We quantified arable weeds, ground-dwelling carabids and weed seed predation on several in-field distances from the field border and assessed the relative importance of habitat quantity and diversity at three landscape scales (250 m, 500 m and 1000 m).

Results Weed species richness and seed predation were affected by surrounding habitat diversity, while carabids and weed cover were influenced by habitat quantity. Field-to-field borders showed no generic reductions for any of the investigated functions compared to field borders with semi-natural habitats. Carabid species richness was promoted by kettle holes whereas hedgerows marginally impeded seed predation. Edge effects on function performance were partly opposite and had various spatial ranges: Weeds decreased rapidly in species richness and cover in contrast to seed predation that increased with distance to a semi-natural habitat.

Conclusions We revealed that different parameters of semi-natural habitats are important for particular ecosystem functions. Our findings emphasize the need to take both, quantity and quality of semi-natural habitats in agricultural landscapes, into account and to focus on functional traits and mobility of ecosystem service providers.

Introduction

The intensification of land use leading to a homogenization of landscapes is one of the main drivers for the ongoing biodiversity declines (Chaplin-Kramer *et al.*, 2011; Tschardtke *et al.*, 2012). Already Benton *et al.* (2003) synthesized that the homogenization in agricultural landscapes as such is a complex phenomenon with multiple dimensions: Less semi-natural habitats, reduced number of crops, larger fields, more unified plant protection in space and time (Gámez-Virués *et al.*, 2015; Landis, 2017). Scientific and public discussion about thresholds for field sizes and the importance of field edges has a long history and unsolved controversy. From the ecological point of view, field edges inhabit higher species diversity, provide habitat connection or corridors and serve as refugial habitats or reproduction hot spots for many arable species re-colonizing arable fields regularly (Fahrig *et al.*, 2015; Šálek *et al.*, 2018). Accordingly, reducing field sizes and the provision of more non-cropped habitats is proclaimed as a tool to reverse biodiversity losses in agricultural landscapes (Šálek *et al.*, 2018). In contradiction to this are findings that larger fields are better for habitat specialist species of the open range, e.g., dry habitat specialist among insects or birds that avoid tree structures (Caballero-López *et al.*, 2012). There is a growing body of evidence, that the trait diversity of wildlife species in the field edges will result in a higher biocontrol potential in landscapes with smaller agricultural fields (Gallé *et al.*, 2018). Studies especially report about the effects of field edges on the dispersal of single species (e.g., aphids, Bousem Baillod *et al.*, 2017; mice, Fischer, Thies and Tschardtke, 2011).

The efficiency of field edges for biodiversity and related ecosystem services may vary in regard to the surrounding landscapes (Bretagnolle and Gaba, 2015; Duflot *et al.*, 2015; Landis, 2017). Gallé *et al.* (2018) reported different edge effects for the occurrence of carabids and spiders between small-scale and large-scale landscapes, which differed mainly in regard to field sizes and the amount of surrounding semi-natural habitats. Gámez-Virués *et al.* (2015) found that landscape complexity filters species traits and thus impacts ecosystem services.

Moreover, observed spill-over effects of neighbouring habitats in regard to ecosystem functions may vary strongly between different configurations of field edges. Differences have been reported comparing the effects of grassy strips or hedgerows surrounding arable fields (Van Vooren *et al.*, 2018). Different neighbouring semi-natural habitat types are represented by different kind of specializations. An increasing share of woodlots and hedgerows may decrease more mobile carabid species that are adapted to arable fields and favour open landscapes in contrast to forest species with lower dispersal power that may benefit from those woody habitats (Aviron *et al.*, 2005). Especially regarding ecosystems functions the impact of adjacent and

surrounding semi-natural habitats on regulating functions is quite variable, impacted by additional parameters needing further research (Holland *et al.*, 2016).

Many studies focus on species compositions and quantify their potential ecological functionality by analysing species functional traits. These studies address e.g., the pest regulation potential (Fusser *et al.*, 2017; Gallé *et al.*, 2018). We measured empirically three different ecosystem functions directly in the field by applying the methods from the Rapid Ecosystem Function Assessment (REFA) toolbox (Meyer, Koch and Weisser, 2015). While weed seed predation presents a regulating service in itself contributing to pest control, species richness and abundances of ground-dwelling carabids and arable weeds are related to various ecosystem services.

Arable weeds can indirectly contribute to soil protection and fertility, shelter and resource for beneficial species, as well as regulating pests through bottom-up processes (Letourneau *et al.*, 2011; Balvanera *et al.*, 2014). Even though plant species may spread directly from the semi-natural habitat into the field (Marshall, 1989), the extent to which adjacent habitats are favourable to the weed flora and act as potential sources of colonizers in arable fields remains unclear (Munoz *et al.*, 2020).

Most of the carabid species feed either in the larval or in the adult stage predatorily and eradicate huge amounts of insects (Kromp, 1999) or other animals, e.g., slugs (Bohan *et al.*, 2000), that can harm crops, and have therefore, a high potential to control pests. Labruyere *et al.* (2016) found that management intensity affects carabid community composition at the plot scale, whilst specific neighbouring habitats, especially grassland (Massaloux *et al.*, 2020), may have positive effects at the farm and landscape scale. Spill-over effects for carabids between boundary habitats and arable fields vary by species, in positive or negative terms (Jowett *et al.*, 2019). Still, landscape elements such as hedgerows and field margins are presumed to provide refugial, breeding and hibernation habitats (Thomas, Holland and Brown, 2002).

Seed predation has been shown to be directly related to the abundance of potential seed predators (Menalled *et al.*, 2007; Trichard *et al.*, 2013), which is indirectly affected by high cover of arable weeds (Meiss *et al.*, 2010). Thus, we expect less weed seed predation in the field interior where abundances of arable weeds should be low (Gabriel *et al.*, 2006). Seed predation rate is also mainly influenced by seed species traits (Fischer, Thies and Tschardt, 2011). Hence, we selected weed species based on their different seed sizes (small: *Capsella bursa-pastoris* and *Viola arvensis*, large: *Galium aparine*) with the assumption that small seeds are eaten by small and large granivorous animals and large seeds only by large granivorous animals (Honek *et al.*, 2007). With an increasing share of SNHs in the landscape, the selection

for certain seeds should decrease again, as the diversity of seed predators might increase (Fischer, Thies and Tschardtke, 2011).

Hypotheses

1. The spatial scale at which semi-natural habitats (SNHs) affect ecosystem functions differs among the ecosystem functions considered.
2. Ecosystem functions vary depending on type of adjacent habitat, and benefit from SNHs such as hedgerows and kettle holes at field borders compared to field-to-field borders without any neighbouring SNH.
3. Ecosystem functions are generally reduced with increasing distance to a SNH, however have different spatial ranges into the field as organisms providing the ecosystem functions have different mobilities.

Methods

Our study was conducted at the landscape laboratory ‘AgroScapeLab Quillow’ (Brandenburg State, Germany) which is located in the northeast of the German lowlands. The area is 290 km² large with an altitude that ranges between 0 m - 100 m above sea level. The soil conditions and landscape structures are typical of the northern part of central continental Europe. The landscape is of glacial origin, and is characterised by the following soil types which show a high spatial heterogeneity: luvisols, arenosols, phaeozem, retisols, histosols and planosols (Wilfried Hierold, personal communication). The catchment area has a subcontinental climate with 8.7°C mean annual temperature and an annual precipitation of 475 mm (ZALF field station, Dedelow). The landscape is dominated by arable fields and grasslands (62%) being interspersed with forests (24%), water bodies (5%) and small settlements (5%). Frequent semi-natural habitats (SNHs) in the catchment are hedgerows and kettle holes — small water bodies (<1 ha) within fields as remnants of the last ice age.

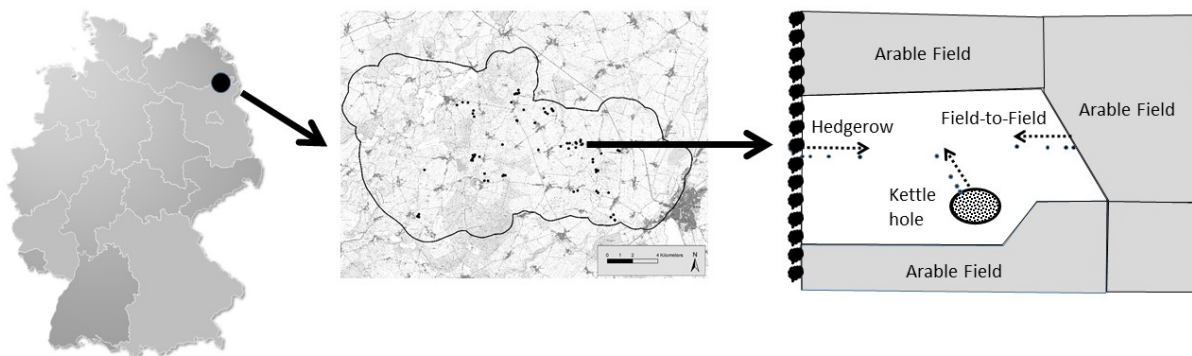


Figure 3.1: Spatially nested maps showing the location of the study area ‘AgroScapeLab Quillow’ (Brandenburg State, Germany) up to a schematic design of the three transect types within one wheat field under investigation

Main crops are winter cereals, oilseed rape, and silage maize cultivated on an average field size of 19 ha. More than one third of agricultural fields are cultivated with winter wheat that yields on average 7.4 t ha⁻¹ (Amt für Statistik Berlin-Brandenburg, 2017, 2018). In the catchment, winter wheat is generally treated with 180 – 220 kg N ha⁻¹ per year. Pesticides are applied according to infestation rates and animal abundances.

A total of 52 transects were established in 26 different winter wheat fields over four years (2016 – 2019; Fig. 3.1). Transects were set at three different types of field borders, two with a neighbouring SNH (hedgerow or kettle hole) and one without any neighbouring SNH (field-to-field border) with four distances (1 m, 5 m, 20 m and 50 m), departing from the field border into the field. Whenever possible, the three different transect types have been investigated nested within the same wheat field to keep management impacts as similar as possible (Table 3.1).

Table 3.1: Study design in winter wheat fields in the ‘AgroScapeLab Quillow’ (Brandenburg, Germany, 2016-2019) on three types of transects (field-to-field, hedgerows, kettle hole) with on average four distance (1 m, 5 m, 20 m, 50 m) starting from the field border into the field under investigation. Farthest distance (50 m) was not investigated on field-to-field transects in 2016. Additional intermediate distances at 10 m and 15 m were only recorded in 2017 and 2018 for arable weeds and ground-dwelling carabids.

	2016	2017	2018	2019
Fields	8	4	4	10
Transect types	Field-to-field (4) Hedgerow (4) Kettle hole (4)	Field-to-field (4) Hedgerow (4) Kettle hole (4)	Field-to-field (4) Hedgerow (4) Kettle hole (4)	Field-to-field (6) Kettle hole (10)
Distances	1 m, 5 m, 20 m, (50 m)	1 m, 5 m, (10 m), (15 m), 20 m, 50 m	1 m, 5 m, (10 m), (15 m), 20 m, 50 m	1 m, 5 m, 20 m, 50 m
Sample points	44	48 (72)	48 (72)	64

Ecosystem functions considered

Different organisms and their functions contributing to regulating ecosystem services in agricultural landscapes, namely arable weeds, ground-dwelling carabids and weed seed predation have been investigated (Table 3.2) following the basic idea of rapid ecosystem assessment methods (REFA; Meyer, Koch and Weisser, 2015). We selected some typical and easy to measure biodiversity components for arable fields, which also have high indicatory power and scientific background.

Table 3.2: Investigated species numbers (arable weeds and ground-dwelling carabids) and abundances (weed cover and activity-density of carabid) as well as a functional rate (weed seed predation) and their contributions to ecosystem functions in agricultural landscapes.

Biodiversity parameter	Related ecosystem function
Number of weed species	Biodiversity, niche diversity
Weed cover	Soil protection, promotion of phytophagous species, shelter for other species, resource for other species, disservice to crop yield
Number of carabid species	Biodiversity, niche diversity, pest regulation
Activity density of carabids	Pest regulation, resource for other species
Weed seed predation	Pest regulation

The three regulating functions have been measured following a consistent design, corresponding to each other, but not always all together in single years (Table 3.3). All ecosystem functions have been analysed on the same fields, at the same transects and the four distances. Additionally, weeds and carabids were also monitored in 2017 and 2018 at intermediate distances of 10 m and 15 m along the transects (Fig. 3.2).

Table 3.3: Sample sizes of ecosystem functions along transects in winter wheat fields over four years (2016 – 2019); vegetation surveys were conducted with 6 spatial repetitions of 1m² plots and seed predation with 3 spatial repetitions of all three weed species per distance.

	2016	2017	2018	2019	N
Vegetation surveys	6x 44 plots	6x 72 plots	6x 72 plots	6x 64 plots	252
Carabids	44 traps	72 traps	66 traps	-	182
Seed predation	3x 132 cards	3x 144 cards	-	3x 192 cards	468

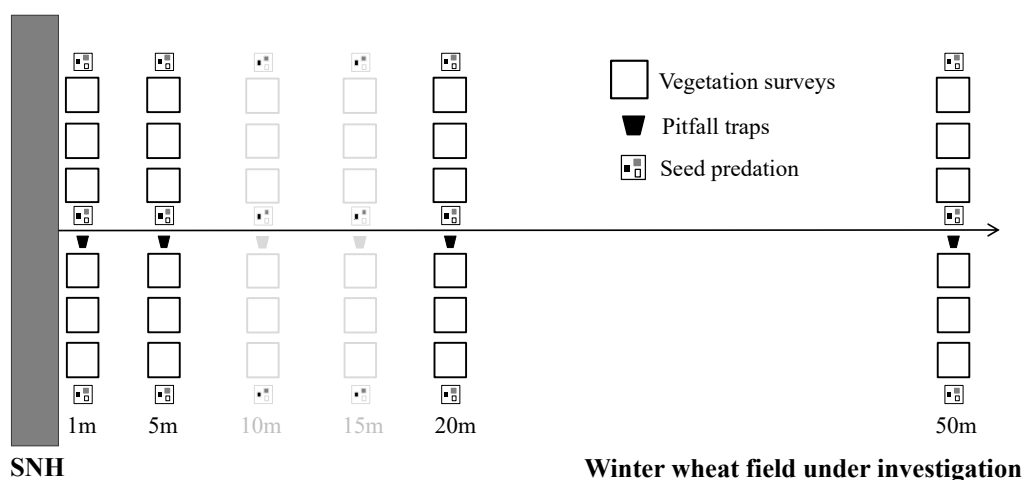


Figure 3.2: Sampling scheme for a single transect depicting the arrangement of vegetation surveys, pitfall traps and seed predation cages at each distance (1 m, 5 m, 20 m, 50 m) starting from the field border into the field under investigation. Intermediate distances at 10 m and 15 m were sampled only in 2017 and 2018 for weeds and carabids.

In addition, landscape composition was assessed using available biotope maps (map of Brandenburg 2009 (MLUL, 2014), and the regional land-use data of the ‘AgroScapeLab Quillow’ from 2016 to 2019) within ArcGIS 10.4.1 (ESRI, Redlands, California, USA) at three different radii (250 m, 500 m and 1000 m) around the midpoint of each transect by calculating the percentage of SNHs (%SNH) as habitat quantity, and the number of SNH types (#SNH) as habitat diversity (Appendix A3: Table A3.1). In our analyses, the SNH types were represented by six biotope classes: water bodies, ruderal areas, fens, grasslands, hedgerows, and forests.

Vegetation surveys

Arable weeds were recorded in May in six replicated 1 m² plots per distance parallel to the field border at four distances in 2016 and 2019 (1 m, 5 m, 20 m and 50 m) and six distances in 2017 and 2018 (1 m, 5 m, 10 m, 15 m, 20 m and 50 m; Fig. 3.2). Weeds were determined to species level and their cover was estimated by applying the scoring scale of Braun-Blanquet (1951). Single scores were converted to percentages (Table A3.2) and averaged per distance to the field borders.

Carabid sampling

Carabids were sampled from the end of May until the beginning of June using pitfall traps (diameter 75 mm, depth 115 mm) half filled with a 3% formaldehyde solution and a drop of detergent. Along all transects, the traps were installed at four distances in 2016 (1 m, 5 m, 20 m and 50 m) and six distances in 2017 and 2018 (1 m, 5 m, 10 m, 15 m, 20 m and 50 m; Fig. 3.2) for two weeks. The trapped animals were conserved in 70% ethanol and identified to species level using the nomenclature of Müller-Motzfeld (2004) and Köhler and Klausnitzer (1998). The counted animals, however, are rather a measure of the species activity during the study period and the density of the ground-dwelling organisms in the agricultural landscape, so that we will refer to those abundances as ‘activity-density’ (Brown and Matthews, 2016). For both, species number and activity-density, we omitted one transect of 2018 departing from a kettle hole from the dataset having conspicuously high numbers of carabids due to the extremely high occurrence of a single species.

Weed seed predation

The investigation on weed seed predation followed the methodological descriptions of Westerman *et al.* (2003). With our study design we aimed at considering different plant families and seed sizes. Thus, we used seeds with different sizes corresponding to three different plant

species: *Capsella bursa-pastoris* (L.) MED. (2,5 mm), *Galium aparine* L. (4 mm) and *Viola arvensis* MURRAY (2 mm). These species were selected based on their high frequency on arable fields in the study area, being investigated already in other recent studies and reproducing exclusively generatively.

Seeds of *Capsella*, *Galium* and *Viola* were exposed in three spatial repetitions at four distances (1 m, 5 m, 20 m and 50 m) along the transects for 2 weeks in June 2016, 2017 and 2019 (Fig. 3.2). Following Westerman *et al.* (2003), we displayed three coarse-grained, high-quality sandpaper cards (50 mm x 57 mm) per sample point each containing seeds of one plant species. On each card 20 seeds were glued with spray adhesive and additionally sprinkled with beach sand to prevent seed predators themselves from sticking to the cards. To exclude vertebrates from seed predation, we positioned cages of 200 x 200 x 100 mm and with a mesh size of 12 mm on top of a set of three cards and anchored it to the ground using tent pegs. In addition, to provide rain shelter, all cages were covered with a 0.4 mm transparent PVC-sheet. Seed predation was quantified as the proportion of removed seeds to the total number of seeds disposed on the cards. Due to cage damages and missing seed cards, we had nine missing data points which we replaced by the median of all other seed predation values. Then, seed predation rates of the three spatial replica per distance along the transect were averaged for each plant species.

Statistical analyses

We used R, version 4.0.3 (R Core Team, 2020) performing mixed-effects models. In all models, we used the predictor variables ‘transect type’ (field-to-field, hedgerow and kettle hole), ‘distance’ (1 m, 5 m, (10 m), (15 m), 20 m and 50 m), ‘landscape composition’ (%SNH or #SNH) and their two-fold interaction terms. ‘Distance’ was log-transformed for a better fit of the model. We included ‘year’ as covariate in all models except of the model for weed cover and applied transect identity nested in field identity as random effect term to account for field variability in all models.

Because most of the response variables were not normally distributed, we used generalised linear mixed-effects models (package: *glmmTMB*, Brooks *et al.*, 2017) using the following distributions for the single response variables: ‘compois’ with log-link for number of weed species and activity-density of carabids, ‘gamma’ with log-link for weed cover, and ‘betabinomial’ with logit-link for seed predation rates. Only species numbers of carabids was normally distributed and was analysed with a linear mixed-effects model (package: *nlme*, Pinheiro *et al.*, 2018). Outliers in the datasets of weeds and carabids were interpreted in

compliance with Meyers *et al.* (2013) and handled according to the inter-quartiles-distance method after Tukey (1977). Additionally, we scaled weed cover yearly between 0 and 1 by the division of the year's maximum value, since the values of 2019 had a much wider range than the three previous years and added 0.0001 to avoid zeros for a model fit with gamma distribution. Wald chi-squared tests were performed to test for the significance of predictor variables using the *Anova* function (Fox and Weisberg, 2019) in the *car* package (Fox *et al.*, 2012).

In order to identify the model-relevant radii of the selected landscape composition metrics on the observed ecosystem functions, we compared AIC values between models with either %SNH or #SNH at three different radii (250 m, 500 m, 1000 m) for each response variable (Table A3.3 – A3.5). Since mobile organisms may benefit more from structurally simple than of cleared or complex landscapes (Tscharntke *et al.*, 2012), we assumed a hump-shaped relationship between landscape composition and carabids. Thus, we implemented a hump-shaped curve by using a polynomial of second order for the best radii of both landscape metrics on the species number and activity-density of carabids (Table A3.4).

Results

Influence of the surrounding landscape: Determination of the model-relevant radii

As first analytical step, we tested the impact of landscape composition at different radii around the investigated transect on the accuracy (measured with AIC-values) of the statistical models. According to our hypothesis, we found that semi-natural habitats (SNHs) influenced ecosystem functions at different radii (Table 3.4). The best model predicting the effect of SNHs on weed species richness was found by including SNHs at the largest chosen scale (1000 m radius) whereas the model for weed cover showed their best fit with the inclusion of SNHs at the smallest scale (250 m radius). Best model fits for species number and activity-density of carabids were both obtained with SNHs in a radius of 1000 m around transects. Weed seed predation was mostly affected by landscape composition at smaller scales (250 m radius) while diversity of SNHs seemed more important than quantity.

The quantity of SNHs in the surrounding of the sampling plots (%SNH) improved the explanatory power of the statistical model for weed cover, species richness and activity-density of carabids, while the SNH gradient length (expressed by the number of different SNH types) resulted in highest model power for weed species richness and weed seed predation. The SNH parameters with the lowest AIC values at the particular radii have been selected and included in the final statistical models for the single target variables.

Table 3.4: AIC-values comparing radii (250 m, 500 m, 1000 m) of landscape metrics (percentage of SNHs and number of SNH types) within single (generalized) linear mixed-effects models of local and landscape factors of SNHs on weeds (species numbers and cover), carabids (species numbers and activity-density) and seed predation rates. Landscape metrics within carabid models are analysed as polynomial of second order for hump-shaped relationship. Bold values represent lowest AIC-value for each response variable.

	Percentage of SNHs (%)			Number of SNH types (#)		
	250 m	500 m	1000 m	250 m	500 m	1000 m
Number of weed species	1062.4	1065.6	1060.7	1066.1	1060.6	1059.8
Weed cover	-360.4	-358.2	-356.7	-355.3	-359.0	-355.1
Number of carabid species	934.3	933.6	930.5	940.8	NA*	934.9
Carabid activity-density	1776.6	1772.5	1761.2	1784.1	NA*	1762.9
Seed predation	2537.8	2548.3	2538.3	2537.1	2539.6	2538.9

* Model did not converge

Arable weeds

Overall, we found 77 different weed species, whereof 46 species were recorded on transects starting from field-to-field borders without any adjacent SNH, 39 species on transects at hedgerows and 64 species on transects at kettle holes. Weed cover ranged from 0% to 100% with a median of 3.1% (1st quartile: 0.5% and 3rd quartile: 10.7%; Table A3.6).

Besides of strong annual variability, the statistical models for weed species richness and cover showed a common basic structure (Table 3.5). Both weed parameters were mostly impacted by distance to the field border and an interaction between transect type and distance, indicating a different behaviour along different transect types. Weed species richness was additionally significantly influenced by the gradient of SNH in the 1000 m environment. The main effect of transect types on weed species number missed narrowly the 5% significance threshold.

Table 3.5: Type-II-analysis of variance tables for GLMMs on arable weeds as a function of year (2016 – 2019), transect type (field-to-field border, hedgerow and kettle hole), distance (1 m – 50 m), landscape composition and their pairwise interaction terms; transect ID nested within field ID as random effect; Number of species were analysed with number of SNH types (#SNH) within 1000 m and cover with percentage of SNHs (%SNH) within 250 m around each transect as landscape composition metrics. Bold font: significant ($P < 0.05$), normal font: non-significant ($P > 0.05$); each N = 252, 52 transects in 26 fields.

	Number of weed species (GLMM with #SNH at 1000 m)			Weed cover (GLMM with %SNH at 250 m)		
	Chisq	Df	p-value	Chisq	Df	p-value
Year	29.25	3	< 0.001	-	-	-
Transect type	4.84	2	0.089	3.93	2	0.140
Distance	45.97	1	< 0.001	33.11	1	< 0.001
Landscape	4.58	1	0.032	0.66	1	0.417
Type x distance	6.02	2	0.049	7.47	2	0.024
Type x landscape	3.76	2	0.152	2.83	2	0.243
Distance x landscape	0.13	1	0.716	2.15	1	0.143
(1 field/transect)	SD = 3.4*10 ⁻⁵			SD = 4.6*10 ⁻⁵		
(1 field)	SD = 0.42			SD = 0.75		

* Year was not included as covariable in the model for weed cover as data points were already scaled by the division of the year's maximum value

Number of weed species decreased significantly from field border into the field centre ($X^2(1) = 46.0, P < 0.001$; Fig. 3.3a) which was less steep along transects at kettle holes compared to those at hedgerows or field-to-field borders ($X^2(2) = 6.0, P < 0.05$). At a landscape scale, a higher number of SNH types within a radius of 1000 m affected weed species richness positively ($X^2(1) = 4.6, P < 0.05$; Fig. 3.3b).

Showing the same local pattern as species richness, weed cover diminished rapidly with increasing distance to field border ($X^2(1) = 33.1, P < 0.001$; Fig. 3.3c). This decrease was similarly steep along transects starting from hedgerows and field-to-field borders, whereas along transects at kettle holes weed cover dropped less strongly ($X^2(2) = 7.5, P < 0.05$). Landscape composition had no significant effect on weed cover (Fig. 3.3d), neither in the best model ($X^2(1) = 0.7, P > 0.05$), nor with number of SNH types nor with any other of the tested radii for both landscape metrics (Table A3.3).

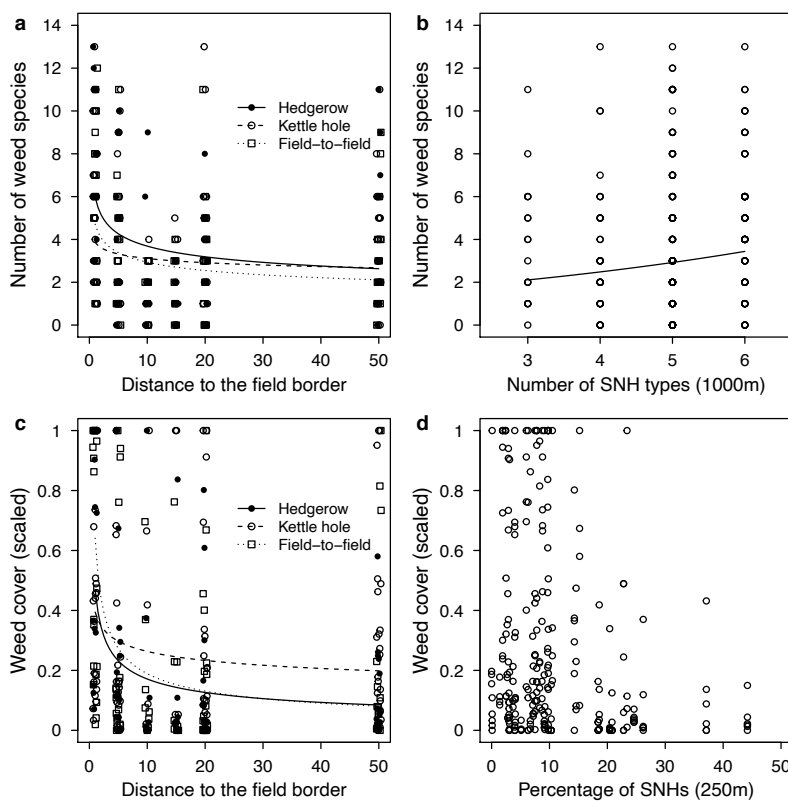


Figure 3.3: Effect of a. Distance to the field border per transect type (hedgerow: solid line; kettle hole: dashed line; field-to-field border: dotted line), b. Number of SNH types in a radius of 1000 m on number of weed species, c. Distance to the field border per transect type and d. Percentage of SNHs in a radius of 250 m on weed cover (scaled by year) along/around transects in winter wheat fields from 2016 – 2019. Curves represent fitted values according to the GLMMs with lowest AIC for weed species (#SNH at 1000 m) and for weed cover (%SNH at 250 m) with distance being log-transformed; each subfigure N = 252.

Ground-dwelling carabids

In total, we caught 14,877 carabids belonging to 94 carabid species across all three years of investigation (2016 – 2018; Table A3.6). 4,878 carabids (33%) of 62 species were trapped on transects starting from field-to-field borders, 4,045 carabids (27%) of 72 species on transects at hedgerows and 5,954 carabids (40%) of 76 carabid species were trapped on transects at kettle holes. The most frequent species were *Bembidion lampros* (16.5%), *Poecilus cupreus* (16.3%) and *Anchomenus dorsalis* (14.9%).

The statistical model output for carabid species richness and activity-density showed accordance only regarding the effect of year and the influence of the quantity of SNHs at a large scale (1000 m) following a hump-shaped curve (Table 3.6). Carabid species richness was also highly influenced by the transect type and showed a significant variation along the distances to the field border. Activity-density of carabid beetles showed a significant different behaviour at the different transect types interacting either with distance or the amount of SNH in the surrounding landscape.

Number of carabid species were elevated on transects adjacent to kettle holes compared to those starting at hedgerows and field-to-field borders ($X^2(2) = 11.7$, $P < 0.01$, Fig. 3.4a) and decreased with increasing distance to the field border independent of transect type ($X^2(1) = 4.8$, $P < 0.05$). With increasing percentage of SNHs in the surrounding, carabid species richness decreased ($X^2(2) = 16.7$, $P < 0.001$; Fig. 3.4b), whereas the number of SNH types considering a hump-shaped relationship peaked at four SNH types in 1000 m around the transects ($X^2(2) = 10.7$, $P < 0.01$; Fig. 3.4c; Table A3.4).

Table 3.6: Type-II-analysis of variance tables for (G)LMMs on carabids as a function of year (2016 – 2018), transect type (field-to-field border, hedgerow and kettle hole), distance (1 m – 50 m), landscape composition and their pairwise interaction terms with transect ID nested within field ID as random effect; Number of species as well as activity-density were analysed with percentage of SNHs (%SNH) within 1000 m around each transect as landscape composition metrics. Landscape metrics are analysed as polynomial of second order for hump-shaped relationship. Bold font: significant ($P < 0.05$), normal font: non-significant ($P > 0.05$); each N = 182, 35 transects in 16 fields.

	Number of carabid species (LMM with %SNH at 1000 m)			Activity-density of carabids (GLMM with %SNH at 1000 m)		
	Chisq	Df	p-value	Chisq	Df	p-value
Year	41.16	2	< 0.001	18.23	2	< 0.001
Transect type	11.70	2	0.003	4.82	2	0.090
Distance	4.79	1	0.029	0.48	1	0.490
Landscape	16.69	2	< 0.001	30.06	2	< 0.001
Type x distance	1.86	2	0.395	19.38	2	< 0.001
Type x landscape	0.89	4	0.926	10.00	4	0.040
Distance x landscape	0.13	2	0.938	3.26	2	0.196
(1 field/transect)	SD = 1.36			SD = 0.13		
(1 field)	SD = 2.0*10 ⁻⁴			SD = 0.15		

The overall activity-density of carabids was neither affected by transect type ($X^2(2) = 4.8$, $P > 0.05$) nor by distance ($X^2(1) = 0.5$, $P > 0.05$). However, depending on transect type activity-density varied with increasing distance to the field border ($X^2(2) = 19.4$, $P < 0.001$, Fig. 3.4d): At hedgerow they increased, at field-to-field borders they decreased whereas at kettle holes they remained rather constant. Especially at the farthest distance from the field border (50 m) activity-density of carabids were higher where a SNH (hedgerows, kettle holes) was present at field borders compared to activity-density within fields without any SNH at field borders.

Percentage of SNHs decreased activity densities depending on transect type ($X^2(4) = 10.0$, $P < 0.05$; Fig. 3.4e). Here, the relationship between increasing landscape complexity and carabids followed a hump-shaped curve at hedgerows with highest activity-density at approximately 10% of SNHs in the surrounding, whereas the relationship decreased linearly at kettle holes. An intermediate number of SNH types had a positive effect on activity-density depending on distance to the field border whereby the farthest distance (50 m) revealed the steepest hump-shaped relationship ($X^2(2) = 10.5$, $P < 0.01$; Fig. 3.4f; Table A3.4).

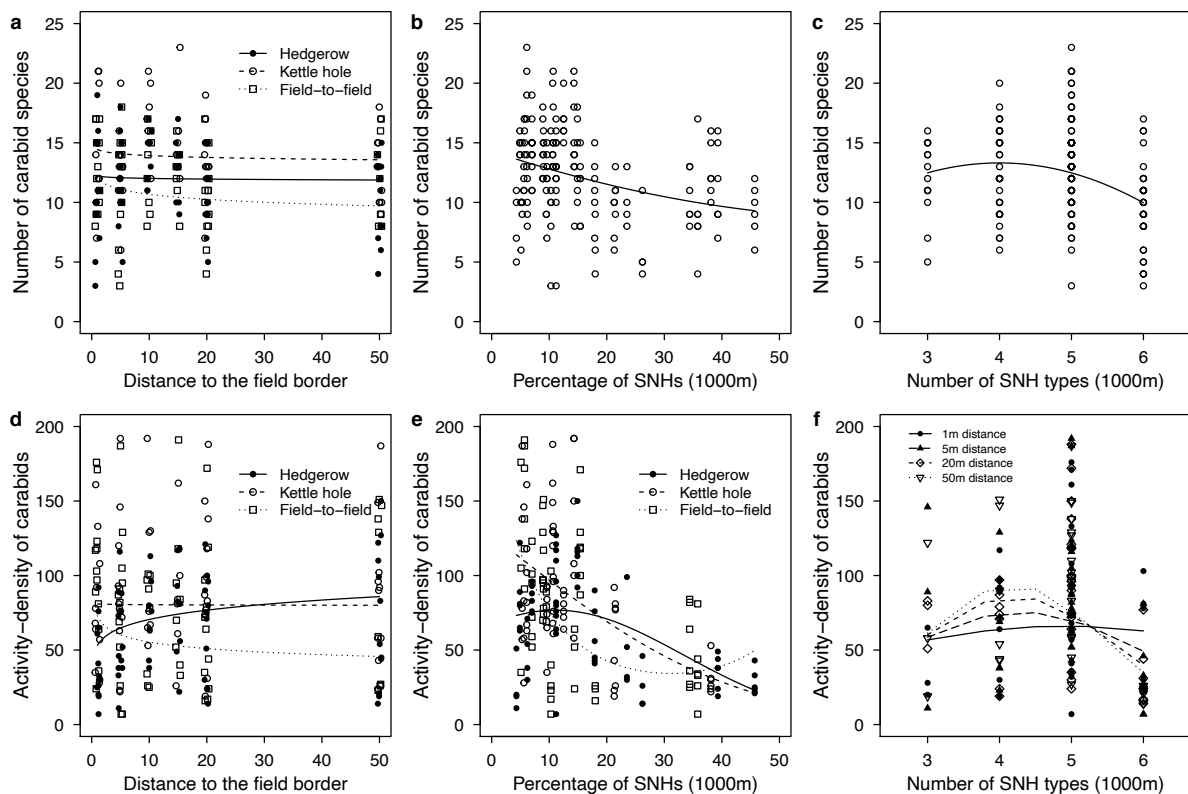


Figure 3.4: Effect of distance to the field border per transect type (hedgerow: solid line; kettle hole: dashed line; field-to-field border: dotted line), percentage of SNHs, number of SNH types in a radius of 1000 m on number of carabid species (a – c) and activity-density of carabids (d – f) along / around transects in winter wheat fields of 2016 – 2018. Curves represent fitted values according to the LMM for carabid species and the GLMM for activity-density with lowest AIC (both: %SNH at 1000 m) with distance being log-transformed and landscape metrics as polynomial of second order for hump-shaped relationship; each subfigure N = 182.

Weed seed predation

The analysis on weed seed predation showed the high complexity of the whole function in general as indicated by significant effects of several factor interactions. First of all, the model results showed a very strong dependency of the weed species of the seeds displayed ($X^2(2) = 61.3$, $P < 0.001$; Table 3.7), which was the factor with the highest Chi^2 value. Thereby, seeds of *Viola arvensis* were eaten the most (1.Q.: 30%, median: 75%, 3.Q.: 100%), followed by seeds of *Capsella bursa-pastoris* (1.Q.: 23%, median: 61%, 3.Q.: 88%), and those of *Galium aparine* (1.Q.: 10%, median: 30%, 3.Q.: 71%; Table A3.7). Moreover, seed predation of the different kinds of seeds varied significantly between the transect types and depending on the SNH gradient in the surrounding landscape whereas they responded similar to distance in general and distance depending on transect type.

Besides a strong yearly variation, distance to the field border affected the overall seed predation significantly being distinctively pronounced depending on the presence of a SNH at field border or not. The main effect of the transect types, however, failed narrowly at the 5% significance threshold.

Table 3.7: Type-II-analysis of variance table for the GLMM on seed predation as a function of year (2016, 2017, 2019), weed species of displayed seeds (*Capsella bursa-pastoris*, *Galium aparine*, *Viola arvensis*), transect type (field-to-field border, hedgerow and kettle hole), distance (1 m – 50 m), landscape composition and their interaction terms with transect ID nested within field ID as random effect; Predation rates were analysed with number of SNH types (#SNH) within 250 m around each transect. Bold font: significant ($P < 0.05$), normal font: non-significant ($P > 0.05$); each N = 468, 40 transects in 22 fields.

	Weed seed predation (GLMM with #SNH at 250 m)		
	Chisq	Df	p-value
Year	15.77	2	< 0.001
Weed species (spec)	61.25	2	< 0.001
Transect type	5.34	2	0.069
Distance	6.85	1	0.009
Landscape	1.90	1	0.168
Type x distance	12.50	2	0.002
Type x landscape	2.50	2	0.287
Distance x landscape	0.01	1	0.912
spec x type	9.63	4	0.047
spec x distance	1.32	2	0.517
spec x landscape	6.77	2	0.034
spec x type x distance	3.30	4	0.508
spec x type x landscape	6.18	4	0.186
spec x distance x landscape	1.67	2	0.434
(1 field/transect)		SD = 0.24	
(1 field)		SD = 0.41	

Weed seed predation was less on transects close to hedgerows than on transects close to kettle holes or at field-to-field borders ($X^2(2) = 5.3, P < 0.1$), and the proportion of seeds eaten increased with distance to the field border ($X^2(1) = 6.9, P < 0.01$). This increasing trend was evident both at hedgerows and kettle holes, at field-to-field borders it was decreasing ($X^2(2) = 12.5, P < 0.01$; Fig. 3.5a). In terms of landscape composition at a 250 m-radius around transects, neither percentage of SNHs nor number of SNH types showed an impact on the overall seed predation (%SNH: $X^2(1) = 0.3, P > 0.05$; Table A3.5; #SNH: $X^2(1) = 1.9, P > 0.05$; Table 3.7). However, depending on weed species of displayed seeds landscape metrics had different effects (%SNH: $X^2(2) = 8.3, P < 0.05$; Fig. 3.5b; #SNH: $X^2(2) = 6.8, P < 0.05$; Fig. 3.5c): Predation rates of *Capsella* decreased with increasing landscape composition, whereas seed predation of *Galium* increased in landscapes with a higher quantity and diversity of SNH. Predation rates of *Viola* were not affected by percentage of SNHs while with increasing number of SNH types seed predation of *Viola* diminished.

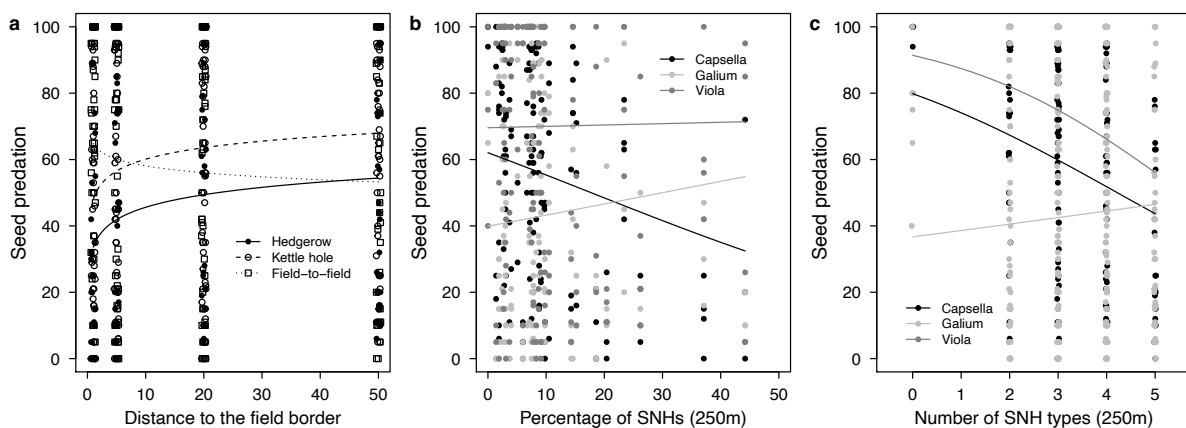


Figure 3.5: Effect of a. Distance to the field border per transect type (hedgerow: solid line; kettle hole: dashed line; field-to-field border: dotted line), b. Percentage of SNHs, c. Number of SNH types per weed species displayed (*Capsella bursa-pastoris*, *Galium aparine*, *Viola arvensis*) on seed predation in a radius of 250 m along / around transects in winter wheat fields in 2016, 2017 and 2019. Curves represent fitted values according to a GLMM for seed predation (#SNH at 250 m) with lowest AIC and distance being log-transformed; each subfigure N = 468.

Discussion

Synthesis of results

Biodiversity-driven ecosystem functions within winter wheat fields were analysed regarding the impact of three main factors: i. The composition of the surrounding landscape (quantity and diversity of SNHs), ii. the specific type of SNH directly adjacent to the agricultural field and iii. the distance to the field border. We found different factor combinations being relevant for each of the investigated ecosystem function (Table 3.8).

Table 3.8: Synthesis of results of semi-natural habitats (SNHs) at a local and landscape scale on the measured ecosystem functions (arable weeds, ground-dwelling carabids and weed seed predation). Landscape metrics are percentage of SNHs (%SNH) and number of SNH types (#SNH). Transect types are abbreviated (FtF: field-to-field, HR: hedgerow, KH: kettle hole). The straight line (-) indicates that this factor was non-significant for the considered ecosystem function.

	Number of weed species	Weed cover	Number of carabid species	Activity-density of carabids	Weed seed predation
relevant landscape metric	#SNH	%SNH	%SNH	%SNH	#SNH
relevant spatial scale	1000 m	250 m	1000 m	1000 m	250 m
Transect type	-	-	KH > FtF, HR	-	FtF, KH > HR
Distance	Rapidly decreasing	Rapidly decreasing	decreasing	-	increasing
depending on transect type	KH: less steep	KH: less steep	-	HR: increasing KH: constant FtF: decreasing	HR: increasing KH: increasing FtF: decreasing
Landscape complexity	increasing	-	decreasing	decreasing	-
Interrelationships between local and landscape effects of SNHs	-	-	-	%SNH x type #SNH x distance	-

Surrounding landscape

The impact of semi-natural habitats (SNHs) in the surrounding landscape on the investigated ecosystem functions was tested with two different landscape composition parameters: i. The number of different SNH types describing the habitat diversity or gradient lengths of habitat conditions in the surrounding landscape and ii. the quantity of SNHs in the surrounding landscape describing the probability or strengths of lateral impacts.

Our results revealed that both landscape parameters can provide high variance explanations depending on the observed ecosystem function. The number of weed species and weed seed predation were stronger affected by the number of different SNH types, while ground-dwelling carabids (species number and activity-density) and weed cover were rather influenced by the amount of SNHs in the surrounding landscapes. With an increasing number of SNH types it is

expected that the number of ecological niches increases (Steinmann *et al.*, 2011) while an increasing percentage of SNH may also stand for an increase in area of a single or a few different habitat types. Hence, while species richness of weeds as well as weed seed predation were affected by SNH diversity emphasising their response to more niches for weed plants (e.g., Gaba *et al.*, 2010) and seed predators (Menalled *et al.*, 2000; Trichard *et al.*, 2013), carabids might have responded to the increase in area of specific habitats. This is in line with findings from Purtauf *et al.* (2005) who found strong associations of spring-breeding carabids with landscape complexity, whereby one habitat type (grasslands) had particular strong effects. In their study, surrounding grassland appeared to act as an overwintering site and a source habitat for farmland carabids (Purtauf *et al.*, 2005).

The measured ecosystem functions were affected most strongly by landscape composition at different spatial scales. According to Aviron *et al.* (2005), identifying the appropriate spatial scales for the studied species is crucial for biodiversity conservation as it will necessarily determine the appropriate scales for establishing management schemes. We found that number of weed species, number of carabid species and activity-density of carabids were most strongly affected by the large spatial scale (1000 m) and weed cover, weed seed predation by the small spatial scale (250 m). For weed species richness, this contradicts results suggesting that landscape variables affect weeds at very small scales (200 m, Gaba *et al.*, 2010). For carabid species assemblages, Aviron *et al.* (2005) revealed a higher variance explanation by considering woody habitats at a 500 m-radius in comparison to a 50 m-radius. They also demonstrate that more mobile carabid species do not respond to landscape complexity measured at scales until 500 m. Evans *et al.* (2016) stated that the effect of landscape complexity on taxonomic richness of carabids becomes most obvious at even larger scales of 1000 m and 6000 m. This is in agreement with our finding that carabid species richness and activity-density responded best to landscape composition at larger scale (1000 m) which suggests that carabid species in our study area mostly belonged to mobile species. A recent study and to our knowledge the only one comparing the effect of different spatial scales on seed predation demonstrated stronger effects of hedge length at 1000 m radius compared to 250 m for predation rates of *Viola* seeds (Badenhausser *et al.*, 2020). The spatial scale associated to seed predation is most likely related to the spatial ranges of their main seed predators. While Badenhausser *et al.* (2020) associated their predation rates to carabid beetles and spiders operating at larger scale (1000 m) the predation rates in our study were best predicted by at a small scale (250 m) suggesting that the seeds in our study area were predated by less mobile species.

Concerning the impacts of landscape complexity on the investigated ecosystem functions, weed cover was not significantly impacted by SNHs in the surrounding landscape emphasising that the impacts of SNHs are taking place predominantly at a local scale (Marshall, 1989). Nevertheless, we found weed species richness being promoted by a higher number of SNH types in a radius of 1000 m around transects. Winqvist *et al.* (2011) observed positive effects for weed species richness and cover with decreasing percentage of arable fields, being consistent with results of Gabriel *et al.* (2006). They justified a higher plant richness in more complex landscapes with a greater species pool within habitat-rich landscapes resulting into the shorter distances for colonisation from non-crop habitats.

In contrast, carabids were rather negatively affected by landscape complexity following a hump-shaped curve. This adds to the suggestion that most carabids of our study areas preferred open landscapes relying on the presence of a few SNHs. Several studies revealed that carabid abundance was elevated in landscapes with a high percentage of arable fields and/or permanent grasslands (Dainese *et al.*, 2017; Petit *et al.*, 2017) and that carabid species richness decreases with increasing percentage of SNH (Jonason *et al.*, 2013; Rusch, Binet, *et al.*, 2016). However, others found positive effects (Trichard *et al.*, 2013; Fusser *et al.*, 2017) or only positive effects within organically managed fields (Purtauf *et al.*, 2005; Fusser *et al.*, 2018) on carabid species richness with increasing percentage of SNHs.

In our study, species richness and activity-density of carabids followed a hump-shaped curve with maxima in simple landscapes. Hence, after a first increase, values decreased along the increasing gradient of landscape complexity. This emphasizes that carabids benefit from a minimum endowment of SNHs, probably due to a higher attachment to specific habitats. Especially for activity-density of carabids, the hump-shaped relationship was found dependent on the field scale: Carabids benefitted from simple landscapes (approx. 10% SNHs) compared to cleared landscapes (< 5% SNHs) and complex landscapes (> 25% SNHs) at hedgerows, only, whereas at kettle holes they decreased linearly. Further, activity-density peaked in field interiors (50 m-distance) at intermediate number of SNH types (4 SNHs) whereas at field border activity-density remained constant with increasing habitat diversity. This is in agreement with the intermediate landscape complexity hypothesis (Tscharntke *et al.*, 2012), stating that landscape-moderated effectiveness is highest when only few habitats occur.

While the averaged weed seed predation was unaffected by landscape complexity, we found a higher number of SNH types in the surrounding landscape impacting predation of smaller seeds negatively (*Capsella* and *Viola*) and predation of larger seeds positively (*Galium*) probably due to a shift in seed predators with increasing SNH diversity. Some studies on weed seed predation

found no effects of the surrounding landscape (Diekötter *et al.*, 2010; Rusch, Binet, *et al.*, 2016; Tschumi *et al.*, 2018; Fischer *et al.*, 2021), whereas other studies showed that weed seed predation were positively related to landscape complexity (Menalled *et al.*, 2000; Trichard *et al.*, 2013). In agreement with our results, Jonason *et al.* (2013) demonstrated that landscape simplification promotes seed predation of *Capsella* and *Viola* attributing it to carabids as main predators inhabiting predominantly arable fields. In contrast to our results, Fischer *et al.* (2011) found a different pattern for seed predation of *Galium* seeds. Another explanation for divergent predation rates of *Capsella*, *Viola* and *Galium* with increasing SNH diversity may derive from the fact that species richness of granivorous carabids is greater with increasing landscape complexity (Trichard *et al.*, 2013) and that seed size is positively correlated with carabid body mass (Honek *et al.*, 2007). If we assume that more diverse carabid assemblages are more likely to include a greater range of body sizes (Gayer *et al.*, 2019) preying on a greater range of seeds, we can expect similar predation rates for different seed sizes in complex landscapes whereas predation rates should become dissimilar in simple landscapes. This was found very conclusively in our results, because predation rates converged with increasing diversity of SNHs in the landscape.

Type of semi-natural habitat (SNH)

Contrary to our expectations, none of the investigated ecosystem functions showed lower performance on transects without a neighbouring SNH (at field-to-field borders) compared to those with SNH at field border. However, species number of carabids were particularly promoted by adjacent kettle holes whereas hedgerows marginally impeded weed seed predation. This stands in contrast to the findings of Aviron *et al.* (2005) who found that particularly woody landscape elements including hedgerows influence species assemblage of carabids, especially due to the addition of forest specialists. Nonetheless, hedgerows and kettle holes are scarcely investigated in comparison until now. French *et al.* (2001) found that grassland and riparian edges share the most carabid species. Fusser *et al.* (2017) observed higher species richness in herbaceous compared to woody habitats. One possible explanation for the positive effects of adjacent kettle holes in contrast to hedgerows on carabids might be the contrasting spatio-temporal soil moisture patterns in their surroundings. Here, the SNH types (hedgerows and kettle holes) seem to strongly shape the habitat quality for wildlife organisms in their close surrounding. The role of soil moisture for the activity and reproduction of soil fauna and arthropods is well described (Holland *et al.*, 2007) and can be expected as having major impacts on related ecosystem functions. Moreover, we found lower seed

predation on transects at hedgerows compared to transects adjacent to kettle holes and field-to-field borders. This might also be due to different species assemblage of predator species. As we excluded vertebrates with wired cages, chances are high that granivorous carabids predated on the displayed seeds (e.g., Honek, Martinkova and Jarosik, 2003; Menalled *et al.*, 2007; Saska *et al.*, 2008). However, other species might have been important for seed removal in our study area being associated with higher moisture at kettle holes, such as slugs (Kollmann and Bassin, 2001; Honek *et al.*, 2009; Türke *et al.*, 2013) or earthworms (Eisenhauer *et al.*, 2009, 2010) as well as smaller species such as ants (Jacob *et al.*, 2006; Evans and Gleeson, 2016) or isopods (Saska *et al.*, 2008).

Distance to the field border

Distance was a significant factor in all analyses except for carabid beetle activity-density, indicating the existence of edge effects in general. With increasing distance to the field border, ecosystem functions responded in various ways:

(i) Arable weeds decreased rapidly in species number and cover already at short distances. Marshall (1989) found only 30% of the species occurring in the field edges also being present in the field centre. Many of the species were found only within 2 m – 5 m inside the field border. Moreover, some arable weeds appeared to originate in the margin. Accordingly, Fried *et al.* (2009) regard field edges as important refugia for weed conservation. Although weeds were clearly mostly affected by distance to a neighbouring SNH (Marshall, 1989), species numbers and cover decreased less rapidly along transects at kettle holes compared to transects at hedgerows. The results of Munoz *et al.* (2020) indicate that a significant proportion of arable weeds are mainly associated to permanent herbaceous habitats, which are common around the kettle holes.

(ii) Number of carabid species diminished as well with increasing distance to the field border independent of transect type; whereas activity-density of carabids seemed generally unaffected by distance. However, if a hedgerow or a kettle hole was present at the field border activity-density of carabids were higher in field interiors (50 m-distance) compared to field interiors without an adjacent SNH. These findings are in line with results of Fusser *et al.* (2018) and Boetzl *et al.* (2019) who also showed that carabid richness declines from field border to interior. A study of Gayer *et al.* (2019) related this pattern to a higher feeding type distribution among carabids at the edges resulting in higher species richness. They also stated that towards field centre, upon a distance of 12 m – 15 m from the border, habitat conditions remain adequately good for larger, mobile, carnivorous carabids, who might show large abundances there due to

a sufficient availability of their food resources. The latter could explain the pattern of increased species richness in field interior when a SNH is present at field border.

(iii) Weed seed predation increased with distance to a SNH whereas with distance to a field border without a SNH they decreased. This finding is contrary to most results from seed predation experiments, who found no differences in weed seed removal between the field edge and field interior (Marino, Gross and Landis, 1997; Westerman, Hofman, *et al.*, 2003; Alignier *et al.*, 2008; Fischer, Thies and Tschardtke, 2011). Especially as the lower availability of food resources at the field interior is often regarded as limiting factor, also for weed seed predation (Fischer, Thies and Tschardtke, 2011). Studies reporting on seed predation by ants (Jacob *et al.*, 2006) and birds (Navntoft *et al.*, 2009) even showed higher predation rates adjacent to SNHs mostly due to the fact that granivorous animals are attracted by large food supplies (Fischer, Thies and Tschardtke, 2011). However, few studies demonstrated in agreement with our findings that predation increases from the field border into the field (Saska *et al.*, 2008; McHugh *et al.*, 2020). A greater food supply at the edges could have diluted seed predation of displayed seeds (Saska *et al.*, 2008) and vice versa increased predation on displayed seeds, since no other source of food is available. Granivorous animals can be omnipresent at field edges equally as in field interior when food supplies are low which they compensate by larger home ranges (Breitbach *et al.*, 2010), increasing foraging time (MacArthur and Pianka, 1966) and a higher exploitation of food patches by the prevalence of dietary generalist (Duffy *et al.*, 2007).

Conclusion

In recent years, the importance of studying not only biodiversity per se, but also associated ecosystem functions and the resulting ecosystem services has been emphasized (Letourneau and Bothwell, 2008). Empirical studies on the impact of landscape composition and the presence of SNHs at the field scale on the provision of ecosystem services are still scarce and show contrasting results (Winqvist *et al.*, 2011). Here, we fill a knowledge gap by quantifying multiple spatial scales in an agricultural landscape as well as spill-over ranges of ecosystem functions from field borders at the field scale:

- (i) We could show that surrounding landscape matters differently for most analysed ecosystem functions: carabids favour a lower number of specific habitats at larger scales (probably grasslands) while weed species richness and seed predation are related to the amount of specific habitat qualities. Both findings stress the need for an evaluation framework taking into account both quantity and quality aspects of SNHs. It also emphasizes that valuable information of habitat complexity at a landscape scale might get lost if SNHs are grouped together into a single land cover category (Dufлот *et al.*, 2015).
- (ii) We found evidence that the type of adjacent SNH is mainly impacting habitat qualities at the edges and might in this way increase or decrease the quantity of ecosystem functions. Especially kettle holes seemed to play an important role for ecosystem services in our study area as their presence led to higher performance of ecosystem functions emphasizing that riparian areas should be part of further investigations about habitat management in agricultural landscapes.
- (iii) We found edge effects being relevant for all analysed ecosystem functions except for carabid activity-density, however, with partly opposite trends depending on main process drivers. These results highlight the need to focus on biodiversity functional traits to better understand the underlying processes (Duffy *et al.*, 2007; Trichard *et al.*, 2013; Munoz *et al.*, 2020).

The different spatial ranges, at which these organisms and functions operate, highlight that habitat management with the aim to provide natural ecosystem services emanating from SNHs will have to account for the ecology and demography of the single ecosystem service providers.

General Discussion

In the previous chapters, I presented three case studies on the effect of semi-natural habitats on ecosystem services investigating (i) a provisioning service, i.e. winter wheat yield (Study 1), (ii) several regulating disservices to the crop plant, i.e. damage rates of several pest groups (Study 2), and (iii) potential regulating services, i.e. species richness and abundances of ecosystem service providers and a predation rate (Study 3). Within each of these studies, I examined these (dis)services close to two frequent habitat types, hedgerows and kettle holes, in agricultural landscapes in Northeast Germany and assessed the range of the edge effect at the field scale. In the studies 2 and 3, I extended my scope to the landscape scale, and investigated how the quantity and diversity of semi-natural habitats at the landscape scale can shape the measured regulating ecosystem services and disservices. Within the following, I will synthesise how far semi-natural habitats shaped the delivery of ecosystem (dis)services depending on habitat type, the distance to a neighbouring habitat and their amount or diversity on a landscape scale. Then, I will relate these findings to crop production and finally highlight the implications of my studies.

Provision of regulating (dis)services differs with SNH type and distance to the field border

Semi-natural habitats (SNHs) interspersing agricultural landscapes provide refugia for many plant and animal species (Bianchi, Booij and Tschardtke, 2006; Billeter *et al.*, 2008) during winter, agricultural disturbance or for reproduction. Especially hedgerows have been shown to harbour a high species richness of beneficial species for agricultural production, such as pollinators and pest predators (Garratt *et al.*, 2017). Despite beneficial species, pest populations may equally benefit from SNHs at the field borders for the same reasons (Blitzer *et al.*, 2012). However, it has been recognized that a wider range of pest predator species depend on SNHs during their life cycle compared to pest species (Keller and Häni, 2000). The preference of habitat types may depend on the species, its resource use and life cycle. In the second and third study, I found consistently higher rates of ecosystem services and disservices as well as higher species richness at kettle holes compared to hedgerows (Fig. T5): Herbivory rates of cereal leaf beetle (CLB) larvae were three times higher (pairwise comparison with Mann-Whitney *U* test: $W = 166.5$, $P < 0.01$; $N = 48$; Study 2) on transects adjacent to kettle holes compared to those adjacent to hedgerows. Similarly, weed seed predation ($W = 6958.5$, $P < 0.001$; $N = 312$; Study 3 et seq.), carabid species richness (t-test: $t = -3.55$, $P < 0.001$; $N = 122$) and activity-density of carabids ($W = 1292.5$, $P < 0.01$; $N = 122$) were elevated by 53%, 20%, and 39%, respectively, adjacent to kettle holes compared to hedgerows.

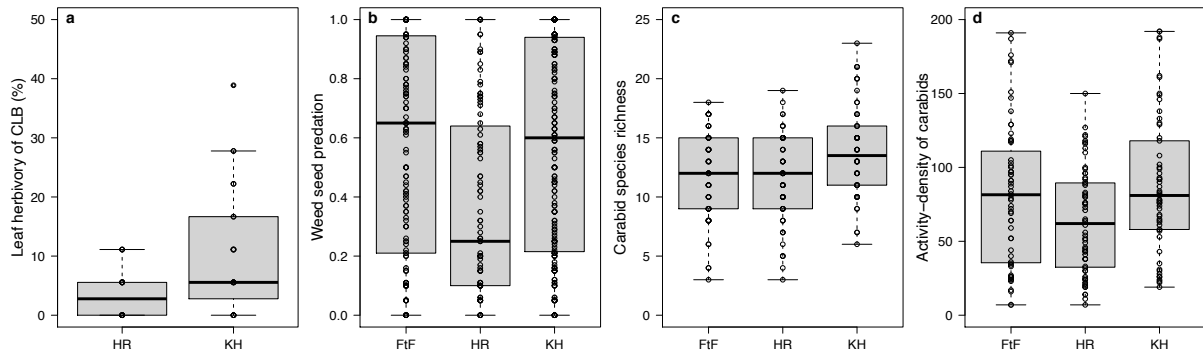


Figure T5: Presence and type of semi-natural habitat (FfF: field-to-field border: no SNH, HR: hedgerow, KH: kettle hole) on a. leaf herbivory of CLB larvae (N = 48), b. weed seed predation (N = 468), c. carabid species richness (N = 182), d. activity-density of carabids (N = 182); figure presents a compilation of results of Study 2 (a) and Study 3 (b – d).

For beetles, such as CLBs and carabids, a water-bearing habitat may be attractive because of the improved micro-climate due to higher moisture emanating from this habitat (Vasic *et al.*, 2020). CLB adults and carabid species have been shown to be influenced by moisture in plants (Honek, 1991) and soil (Holland *et al.*, 2007) for oviposition. The distinct discrepancy between habitat types for damage rates of CLB larvae may further be explained by another characteristic of kettle holes in our study area. Kettle holes are mostly situated within fields, thus rather isolated from other SNHs (Lozada-Gobilard *et al.*, 2019; Schöpke *et al.*, 2019). Hence, pest predators of CLB larvae might have been less abundant at these in-field habitats than within linear and more connected habitats at field borders, such as hedgerows. Particularly along grass strips predation rates of CLB larvae have been demonstrated to reduce damage rates by up to 61% (Tschumi *et al.*, 2015).

Comparing field borders without adjacent SNH to field borders with SNH shows that the performance of ecosystem functions indeed rather depends on the SNH type than on the actual presence of a SNH (Fig. T5): Weed seed predation and activity-density of carabids were equally high at field-to-field borders and kettle holes, and species richness of carabids was indistinct between field-to-field borders and hedgerows. In the case of weed seed predation, the presence of a hedgerow even impeded predation rates compared to field borders without SNH. Here, higher seed predation at field-to-field borders might originate from a higher attractiveness of the displayed seeds due to a generally lower food availability. This would suggest that at field borders with SNH the predation rates should have been lower than at field borders without SNH. However, a higher species richness of carabids at kettle holes (Fig. 3.4a) and a larger number of additional seed predators such as slugs, isopods and earthworms being associated with more moist habitats, may explain an effectively equally high weed seed predation at kettle holes as at field-to-field borders.

The range at which ecosystem services and disservices emanating from SNHs can be provided may depend on the mobility of the species and their resistance to agricultural changes. While less mobile species occur only in proximate distances to the field border, more mobile species can be omnipresent and perform ecosystem functions throughout the agricultural field (Aviron *et al.*, 2005). These principles may hold for pest as well as predator species providing ecosystem services and disservices. In Study 2 and 3, I showed that fungal leaf infection, weed cover, as well as species richness of arable weeds and ground-dwelling carabids decreased with increasing distance to the field border (Fig. T6). This does not only highlight the reliance of species on SNHs in agricultural landscapes, but also the importance of field borders as biodiversity hot-spots in agricultural landscapes.

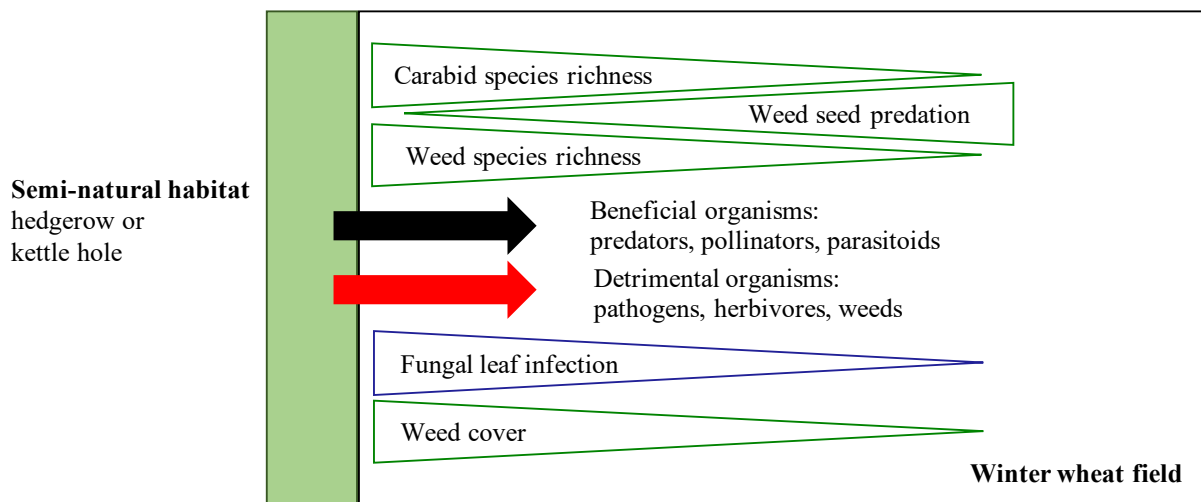


Figure T6: Distance effects of measured beneficial and detrimental organisms and ecosystem functions from the field border (with either a hedgerow or a kettle hole) into the winter wheat field. Green fringe refers to a distance effect independent of SNH type and blue fringe to a distance effect dependent on SNH type.

Particularly for arable weeds field borders might represent sources from which they re-colonize the field. Their rapid decline in cover and species richness within the arable field might be due to regular herbicide applications by the farmer but also due to a limited dispersal range of a few meters when reproduction is primarily vegetative. Declines in carabid species richness can be associated with a wider feeding type distribution at field borders, while towards the field interior food availability and conditions may remain good only for certain species, e.g., omnivorous or predatory carabids (Gayer *et al.*, 2019). The finding that species richness in general decreases with distance to the field border is in accordance with the ‘landscape-heterogeneity filtering species traits’ hypothesis (Gámez-Virués *et al.*, 2015) that states that species are filtered out by changes in conditions. Nonetheless herbivory rates of CLB larvae and carabid activity-density were unaffected by distance to an adjacent SNH, emphasizing that pest and predator species

can be mobile enough to colonize entire wheat fields. Especially carabids are known to be well adapted to arable fields (Dainese *et al.*, 2017; Petit *et al.*, 2017) and to enlarge their home ranges when food resources are low resulting in higher activity-density and mobility (Petit, Boursault and Bohan, 2014). The only investigated ecosystem service increasing with increasing distance — especially when an SNH was present at field borders — was weed seed predation. A higher food availability at field borders can dilute the predation on experimental seeds and cause lower seed predation measurements at field borders comparable to a reduction of relative mortality in larger populations of prey (Saska *et al.*, 2008).

Summarizing the effects of SNHs at the field scale, I could show that the provision of regulating ecosystem services and disservices can be influenced by habitat type. Especially kettle holes played a particular role as habitat for beneficial and detrimental organisms in the study area and should be investigated further to understand their contribution to other ecosystem services. The spatial range of ecosystem service provision emanating into the field varied depending on species mobility, i.e. arable weeds diminished rapidly while carabids and CLB were less affected by the distance to a SNH.

Landscape complexity can modulate responses of regulating (dis)services

Landscape complexity in terms of quantity and diversity of SNHs can enhance species richness and therewith contribute to a stronger provision of regulating services, such as pest control (e.g., Dainese *et al.*, 2019). Especially in moderately simple landscapes with intermediate percentage of SNHs (1 – 20%) pest control seemed most effective (Tscharntke *et al.*, 2012; Jonsson *et al.*, 2015). Higher abundances and diversity of pest predators, however, do not necessarily provide enhanced pest control, since pest densities may also respond positively to landscape complexity (Thies, Roschewitz and Tscharntke, 2005), although their response to landscape complexity were found to be inconsistent (Karp *et al.*, 2018).

Half of the studied pest groups in Study 2 showed increased damage rates when landscape complexity increased emphasising that pest populations can be positively associated to SNHs within the landscape in our study area. While fungal leaf pathogens might have profited from a higher share of alternative non-crop hosts (Wisler and Norris, 2005), the benefit of landscape complexity for CLB larvae was dependent on SNH type at the field scale: While damage rates increased close to kettle holes, they decreased at hedgerows with increasing habitat diversity. This interplay between landscape and field scale stresses that pest populations may especially profit from an SNH when pest control emanating from the adjacent habitat, i.e. from a kettle hole, is too weak due to the small size and isolation degree of the habitat even if landscape complexity increases in the surrounding. While the elaborated damage rates of fungal pathogens

and CLB larvae were positively associated with landscape complexity, species richness of arable weeds and carabids showed contrasting patterns: Number of weed species increased with diversity of SNHs which is in agreement with several studies (Roschewitz *et al.*, 2005; Gabriel *et al.*, 2006; Gaba *et al.*, 2010). In contrast, carabids seemed rather negatively affected by a higher share of SNHs, i.e. their species richness was lower in habitat-rich landscapes compared to habitat-poor landscapes. However, this decrease in species richness and activity-density with increasing landscape complexity followed a hump-shaped curve with highest values in simple landscapes (either with 10% SNHs or four SNH types in the surrounding). One explanation can be that carabids profit from a minimum endowment of SNHs, probably due to a higher attachment to specific habitats, e.g., grasslands (Purtauf *et al.*, 2005; Petit *et al.*, 2017) while being well adapted to open landscapes. Hence, a further increase in landscape complexity creates no further benefit and could even impede carabids physically or by an increasing mortality due to top-predators, such as birds (Martin *et al.*, 2013).

Even though the effect of SNH diversity on weed seed predation in Study 3 depended on weed species displayed (i.e. small sized seeds decreased, whereas larger sized seeds increased) predation rates converged in complex landscapes. This was probably due to a greater species pool of seed predators with a higher richness of habitats feeding on a wider range of preys including small and large sizes of weed seeds. This finding points out that even if landscape complexity in our study area might not always enhance pest control, it can stabilize the provision of this ecosystem service.

Concluding, I found that landscape complexity matters for most of the investigated regulating ecosystem (dis)services, although in different ways modulating the effects of habitat type and distance to it at the field scale. My results add to the general idea that ecosystem (dis)service providers, may they be pests or pest predators, respond inconsistently to landscape complexity (Karp *et al.*, 2018). Concerning spatial scales, my findings are in line with Bommarco, Kleijn and Potts (2013) who emphasized that weed control is rather affected by the field scale whereas animal pest control can be governed by quantity and configuration of SNHs in the surrounding landscape. However, it seems to be crucial to account for habitat preferences of species and investigate those on the field and the landscape scale (Boetzi *et al.*, 2020). Hence, it might be advisable for future studies to consider separate habitat types at the landscape scale because ecological responses of certain taxa might get lost if SNHs are grouped together into a single cover category (Dufnot *et al.*, 2015; Bartual *et al.*, 2019).

Bridging the gap between regulating ecosystem services and yield

The provisioning ecosystem service in terms of crop yield has been poorly studied with regard to the effect of SNHs at the field and landscape scale (Holland *et al.*, 2017). Most studies tackling yield changes as a consequence of the provision of regulating services or disservices could not reveal significant effects of the investigated services on yield (Martin *et al.*, 2016; Albrecht *et al.*, 2020). Studies on herbaceous strips are an exception, as an increase in pest control has been demonstrated to go along with yield increases (Tschumi *et al.*, 2015, 2016; Gurr *et al.*, 2016). However, an increase in regulating services from grassy strips does not always coincide with production improvement (Sutter, Albrecht and Jeanneret, 2018; Albrecht *et al.*, 2020). Particularly hedgerows can cause yield reductions at field borders as trees and shrubs may compete with crop plants for water and nutrients (Kowalchuk and Jong, 1995) and shade crops due to their tall vegetation structure (Kort, 1988; Esterka, 2008).

In Study 1, I could show that yield losses are greater on transects adjacent to hedgerows compared to those at kettle holes. With increasing distance to the field border yield increased to 95% of mid-field yields after 11 m adjacent to kettle holes and 18 m adjacent to hedgerows. In a recent study, wheat yield adjacent to flowering fields reached 95% of mid-field yield at 27 m distance to the field border (Boetzl *et al.*, 2020) emphasizing that the presence of other habitat types (besides the investigated habitats in Study 1) may also reduce yield close to field borders.

In Study 2, I tested if selected wheat pests were able to drive yield losses close to field borders. Here, I revealed that weed cover presents the only culprit to yield reduction in the study system being most pronounced proximate to the SNH. This is in line with Oerke *et al.* (2006) who showed that arable weeds can account for 34% of wheat yield reduction when no chemical inputs or mechanical removal takes place. The finding that this reduction predominantly occurs in the first meters close to a field border could represent an effect of management. Weeds can be regulated with herbicides that are restricted by law close to SNHs. This is in line with Study 3, where I showed that weed cover as well as weed species richness was elevated at field borders.

Knowing that weeds can represent a threat to wheat production emanating from SNHs, I conducted a post-analysis using data from Study 1 and Study 3 to test if natural weed control can influence yield at field borders identifying which part species richness of weeds and carabids might play for yield outcome. To do so, I constructed a structural equation model (SEM) relating arable weeds, ground-dwelling carabids and weed seed predation of two years of investigation (2016 and 2017 within Study 3) to wheat yield harvested on agricultural fields

within the same design and same years of Study 1). This allows to investigate the direct and indirect effects of SNHs at the field border on wheat yield mediated through weed seed predation being affected by density and species number of weeds and carabids (for details about hypotheses and statistical analysis see Appendix AT2: Fig. AT2.1; Table AT2.1 and AT2.2). First and foremost, the model confirms several relationships that I have discussed in the previous chapters (Fig. T7): While wheat yield increased, arable weeds (cover and species richness) decreased significantly with distance to the field border. Carabid species richness decreased as well with increasing distance although only marginally significantly. Further, weed cover reduced yield confirming the main finding of Study 2. Moreover, the model depicts a strongly positive effect of weed species richness on weed cover indicating that a greater species pool at the field border can add to a higher propagule pressure colonizing arable fields.

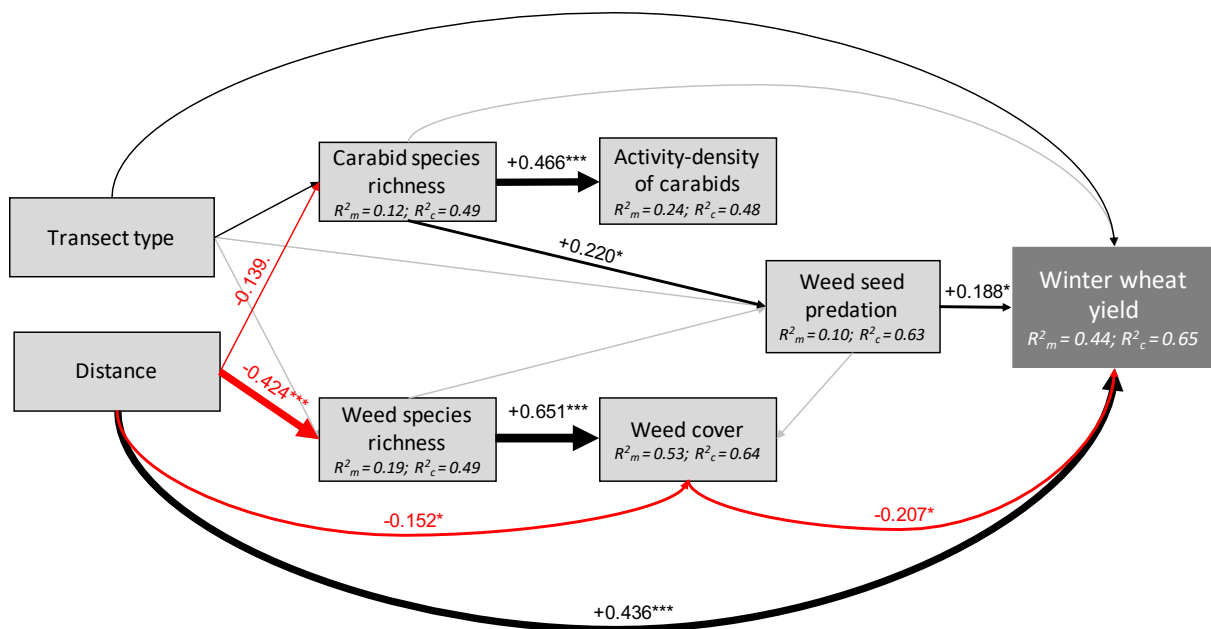


Figure T7: Final SEM ($C_{22} = 12.61$, $P = 0.943$) analyzing relationships between semi-natural habitats at field border (transect type and distance) and carabid species richness, activity-density of carabids, weed species richness, weed cover, weed seed predation, and winter wheat yield of 2016 and 2017 in the AgroScapeLab Quillow. Transect type refers to three types of transects: field-to-field borders, hedgerows and kettle holes. Distance refers to four in-field distances: 1 m, 5 m, 20 m and 50 m. Black arrows indicate positive and red arrows negative relationships. Widths of arrows and adjacent values indicate standardized effect size of each predictor variable. Asterisks denote significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; $P < 0.1$. Grey arrows are non-significant ($P > 0.1$); $N = 92$. Appendix AT2: Fig. AT2.1; Table AT2.2.

A new insight is that weed seed predation was positively associated to wheat yield (Fig. T7). This emphasises that seed predation, i.e. weed control, may enhance crop production. Seeds of the selected weed species in Study 3 were predated on average by $43\% \pm 24\%$. Already predation rates of 25% – 50% have the potential to substantially reduce weed populations

(Westerman *et al.*, 2005). Thus, seed predators in the study area may have the potential to suppress weed populations releasing wheat plants from competition, even though no relation between weed cover and seed predation remained in the final model.

In Study 3, I have shown that seed predation increased with distance to the field border if a SNH was present. However, within the field interior the predation rates were higher if transects were set at field borders with a kettle hole compared to those without a SNH (Fig. 3.5a). Hence, an increased weed control in the field interior might only be possible because of a greater pool of seed predators emanating from this habitat. Carabids are often associated with weed seed predation (Honek, Martinkova and Jarosik, 2003), being either strictly granivorous (Trichard *et al.*, 2013) or omnivorous (Menalled *et al.*, 2007). Indeed, in my post-analysis weed seed predation was positively associated with carabid species richness. This is in agreement with Gaines and Gratton (2010) who attributed a more diverse carabid community to a better performance of service delivery. A recent study showed that in particular intermediate levels of carabid species richness are related to high seed predation rates (Schumacher, Dieterich and Gerhards, 2020). They attributed this pattern to the fact that within even more diverse communities of carabids intraguild predation on granivorous species can diminish seed predation (Charalabidis *et al.*, 2017). Omnivorous carabid species have been shown to eat weed species and benefit from herbaceous filter strips at the field border (Menalled, Lee and Landis, 2001). Hence, in my post-analysis, an increase in carabid species richness may have resulted in higher seed predation because of an addition of granivorous and omnivorous species and less by the addition of predatory carabids. However, further investigations on the effect of SNHs on functional groups and species composition of carabids and their weed control are needed to understand these relationships. The findings from my studies collated in the post-analysis emphasize that natural ecosystem services and disservices emanate from SNHs and can influence crop yield. Furthermore, it stresses that besides identifying and measuring species richness and abundances of organisms the assessment of their ecosystem functions is indispensable to relate the actual delivery of services to crop production.

Implications for a sustainable agriculture

Understanding the role of SNHs for crop production via biodiversity-driven ecosystem services may allow to reduce chemical inputs without decreasing crop production. The general idea of sustainable agriculture is to regenerate the kind of biodiversity that can best sustain agroecosystems by providing natural ecosystem services such as pest control, pollination, nutrient cycling, and water and soil conservation (Nicholls and Altieri, 2004). However, the challenge lays in designing, implementing, and managing habitats in interaction with landscape

complexity to promote the provision of these services (Duru *et al.*, 2015). A recent meta-analysis pointed out that it is possible to manage agroecosystems to support ecosystem services without compromising on crop production (Tamburini *et al.*, 2020). So far, the following management strategies were identified to increase the delivery of regulating and supporting services in favour of a sustainable agriculture (Nicholls and Altieri, 2004; Duru *et al.*, 2015; Gaba *et al.*, 2015):

- (i) increasing plant diversity within fields,
 - a. spatially including intercropping and crop mixtures
 - b. temporally including legume-based crop rotations and cover crops
- (ii) minimizing mechanical and chemical disturbance through reduced chemical inputs and less tillage
- (iii) enhancing landscape complexity by establishing different semi-natural habitats at field borders and maintaining a mosaic of agricultural fields being interspersed with non-crop areas of natural vegetation

This thesis adds to the latter strategy and encompasses the effects of SNHs at the field scale as well as their amount and diversity at the landscape scale. With my research I demonstrated that spatial parameters of SNHs affect yield (Study 1), pest infestation (Study 2) and species richness of ecosystem service providers as well as weed control (Study 3).

The first of my studies showed that hedge height proved to be a crucial factor because the tall vegetation can shade crop plants which may overrule the benefits of hedgerows, i.e. ameliorate micro-climate, reduce evapotranspiration and protect soils from erosion. However, the delivery of expected ecosystem services emanating from SNHs might depend on the right combination of biotic and abiotic components (Mace, Norris and Fitter, 2012). For example, the effectiveness of flower strips is likely to depend on the attractiveness, quantity, quality and accessibility of floral resources, as well as the timing at which they are available (Wäckers and van Rijn, 2012). Hedgerows serve many species as overwintering habitats and corridor within agricultural landscapes (Dainese *et al.*, 2017; Montgomery, Caruso and Reid, 2020), but may benefit predator and pest species equally depending on e.g., hedge length.

The arrangement of SNHs, e.g., to keep a broad fringe of extensive grassland vegetation in-between a hedgerow and an agricultural field as recommended by Berger *et al.* (2011) may help to achieve a delivery of multiple ecosystem services. Although SNHs may be implemented for a specific function, e.g., conservation of a bird species, their design and management may impede their ability to support other ecosystem services, e.g., insect-induced pest control (Olson

and Wäckers, 2007). Thus, it is crucial to mind the provision of multiple services or combine SNHs in order to strengthen their simultaneous provision.

Further, the location of a SNH with regard to the focal field might play a role. In the course of my three studies I could demonstrate that kettle holes entail less yield losses (Study 1), higher species richness (Study 3), but also higher damage rates of pest species compared to hedgerows (Study 2). This pattern may foremost be explained by the different abiotic properties these habitats entail. However, differences in habitat preferences of species might also originate from the different locations: While hedgerows are situated at field borders and may influence an agricultural field from a single side, kettle holes are situated within fields. There, potential ecosystem services and disservices can spill-over in all directions not being restricted to field borders. Still, Haddaway *et al.* (2018) point out that only few studies considered in-field habitats, presumably because this is the most difficult habitat type for farmers to implement — particularly as it represents an obstacle during the management and reduces the effective field size (Kalettka and Rudat, 2006). Nonetheless, in-field habitats may act as stepping stones for beneficial species if they are implemented in a sufficient number and distance to each other to sustain the population and their delivery of ecosystem services.

However, semi-natural habitats may also fail to enhance ecosystem services (Tscharntke *et al.*, 2016), e.g., if habitats are a greater source for pest than predator populations or if the amount of SNHs is too scarce for predator populations to persist — as it might have been the case for the elevated damage rates of CLB larvae at kettle holes (Study 2). Especially the finding that their damage rates increased at kettle holes with increasing landscape complexity indicates that close to this isolated habitat a potential release from predators might have been complemented to the favourable micro-climate. Despite CLB larvae, carabids also favoured kettle holes over hedgerows (Study 3) emphasising that species living in agricultural landscapes have habitat preferences. For example, Sarthou *et al.* (2014) demonstrated that the overwintering refugia of natural enemy communities differ markedly between SNH types whereby highest abundances and species richness of carabids were found in managed grass strips. As Tscharntke *et al.* (2016) further state, it is important to remember that if the SNH type and its quantity can sustain such a predator population, individuals will still have to spill-over into the neighbouring agricultural field exerting a feeding pressure on the pest population. This feeding pressure must be effective enough to decimate the pest population and ultimately increase yield. This chain of events depicts not only the low chance that the presence of an ecosystem service provider may lead to an increase of crop production, but also how species-dependent the right habitat management can be. This implies that the spatial structuring of agricultural landscapes will strongly influence

the magnitude of the ecological services provided by organisms (Tscharntke *et al.*, 2005). Further, it shows that it is not only important to distinguish between SNH types at the field scale, but also to differentiate between SNH types at the landscape scale (Duflot *et al.*, 2015; Bartual *et al.*, 2019).

Limitations and suggestions for future research

Despite all the data that was channelled in this thesis, the findings discussed above can only depict a puzzle piece of the contribution of ecosystem service providers to crop production in the light of SNHs — especially as crop production is influenced by multiple factors including abiotic drivers such as chemical inputs, water availability, soil type and environmental conditions. Further, the ecosystem services and disservices investigated in this thesis represent only a selection of biotic drivers. Thus, the impact of SNHs might be different for crop seed predators such as rodents (e.g., Fischer *et al.*, 2018) or other crop-specific pests such as aphids (Holland and Thomas, 1997; Thies, Roschewitz and Tscharntke, 2005; Martin *et al.*, 2015). Also, specialist predators might be more vulnerable to landscape simplification than carabids (e.g., Thies, Steffan-Dewenter and Tscharntke, 2003). Therefore, the results of my thesis could serve as a basis for future studies to broaden the investigation of SNH effects at the field scale and their relationship with landscape complexity.

A drawback of my studies is the use of taxonomic diversity instead of functional diversity. Initially, I decided for species richness because biodiversity per se can act as a regulator of ecosystem process supporting ecosystem services (Mace, Norris and Fitter, 2012) while maintaining the stability of an ecosystem (Yachi and Loreau, 1999) — both representing key ideas of a sustainable agriculture. In contrast, functional diversity indicates the ability of organisms to perform ecosystem services and can directly be related to effect traits (Duru *et al.*, 2015). Hence, future research on the interplay between SNHs, organisms and their ecosystem functions supporting or opposing crop production might incorporate functional diversity for clearer insights about the actual habitat preferences of these ecosystem service providers.

Even though within my thesis I investigated services and disservices to crop production the focus was restricted on regulating ecosystem services only, while in the last decade research aims to include multiple ecosystem services in order to understand their trade-offs (Zhang *et al.*, 2007; Bennett, Peterson and Gordon, 2009; Power, 2010; Birkhofer *et al.*, 2015). In a meta-analysis, Garibaldi *et al.* (2018) emphasized that regulating and supporting ecosystem services provided by biodiversity (pest regulation, pollination, and nutrient cycling) most often show complementary effects on crop production while the actual provisioning service per se is rarely

quantified. Hence, future research will have to do the splits of investigating these trade-offs while evaluating habitat requirements of single species providing these ecosystem services.

Conclusion

In this thesis, I advanced the knowledge on the importance of two semi-natural habitats, namely hedgerows and kettle holes, on the spill-over of biodiversity-driven ecosystem services and disservices in agricultural landscapes. My findings emphasize that organisms can provide ecosystem services and disservices to agricultural production. However, the provision depends on habitat type and varies in spatial range within agricultural fields while landscape complexity can modulate this performance depending on the mobility of the organism.

Summary

Semi-natural habitats (SNHs) in agricultural landscapes represent important refugia for biodiversity including organisms providing ecosystem services. Their spill-over into agricultural fields may lead to the provision of regulating ecosystem services such as biological pest control ultimately affecting agricultural yield. Still, it remains largely unexplored, how different habitat types and their distributions in the surrounding landscape shape this provision of ecosystem services within arable fields. Hence, in this thesis I investigated the effect of SNHs on biodiversity-driven ecosystem services and disservices affecting wheat production with an emphasis on the role and interplay of habitat type, distance to the habitat and landscape complexity.

I established transects from the field border into the wheat field, starting either from a field-to-field border, a hedgerow, or a kettle hole, and assessed beneficial and detrimental organisms and their ecosystem functions as well as wheat yield at several in-field distances. Using this study design, I conducted three studies where I aimed to relate the impacts of SNHs at the field and at the landscape scale on ecosystem service providers to crop production.

In the first study, I observed yield losses close to SNHs for all transect types. Woody habitats, such as hedgerows, reduced yields stronger than kettle holes, most likely due to shading from the tall vegetation structure. In order to find the biotic drivers of these yield losses close to SNHs, I measured pest infestation by selected wheat pests as potential ecosystem disservices to crop production in the second study. Besides relating their damage rates to wheat yield of experimental plots, I studied the effect of SNHs on these pest rates at the field and at the landscape scale. Only weed cover could be associated to yield losses, having their strongest impact on wheat yield close to the SNH. While fungal seed infection rates did not respond to SNHs, fungal leaf infection and herbivory rates of cereal leaf beetle larvae were positively influenced by kettle holes. The latter even increased at kettle holes with increasing landscape complexity suggesting a release of natural enemies at isolated habitats within the field interior.

In the third study, I found that also ecosystem service providers benefit from the presence of kettle holes. The distance to a SNH decreased species richness of ecosystem service providers, whereby the spatial range depended on species mobility, i.e. arable weeds diminished rapidly while carabids were less affected by the distance to a SNH. Contrarily, weed seed predation increased with distance suggesting that a higher food availability at field borders might have

diluted the predation on experimental seeds. Intriguingly, responses to landscape complexity were rather mixed: While weed species richness was generally elevated with increasing landscape complexity, carabids followed a hump-shaped curve with highest species numbers and activity-density in simple landscapes. The latter might give a hint that carabids profit from a minimum endowment of SNHs, while a further increase impedes their mobility. Weed seed predation was affected differently by landscape complexity depending on weed species displayed. However, in habitat-rich landscapes seed predation of the different weed species converged to similar rates, emphasising that landscape complexity can stabilize the provision of ecosystem services. Lastly, I could relate a higher weed seed predation to an increase in wheat yield even though seed predation did not diminish weed cover. The exact mechanisms of the provision of weed control to crop production remain to be investigated in future studies.

In conclusion, I found habitat-specific responses of ecosystem (dis)service providers and their functions emphasizing the need to evaluate the effect of different habitat types on the provision of ecosystem services not only at the field scale, but also at the landscape scale. My findings confirm that besides identifying species richness of ecosystem (dis)service providers the assessment of their functions is indispensable to relate the actual delivery of ecosystem (dis)services to crop production.

Zusammenfassung

Naturnahe Habitats, wie zum Beispiel Hecken und Sölle, stellen wichtige Refugien für die Biodiversität in Agrarlandschaften dar, weil aus diesen Habitats Organismen in die Agrarflächen einwandern und dort regulierende Ökosystemdienstleistungen, wie zum Beispiel biologische Schädlingsbekämpfung, erbringen können. Weitgehend unerforscht ist bisher, in welcher Art und Weise die verschiedenen Habitattypen und ihre Verteilung in der umgebenden Landschaft die Bereitstellung dieser Ökosystemdienstleistungen, die letztlich auch einen Einfluss auf die landwirtschaftlichen Erträge haben können, beeinflussen.

Daher habe ich den Einfluss von naturnahen Habitattypen auf biodiversitätsbedingte Ökosystemdienstleistungen und ihre Auswirkung auf die Weizenproduktion untersucht. Der Schwerpunkt meiner Arbeit lag auf dem Einfluss und dem Zusammenspiel von Habitattyp, Entfernung zum naturnahen Habitat und der umgebenden Landschaftsvielfalt. Auf intensiv bewirtschafteten Weizenfeldern habe ich entlang von Transekten von der Feldgrenze in das Feld hinein Nützlinge und Schädlinge, Ökosystemfunktionen sowie den Weizenertrag ermittelt.

In der ersten Studie habe ich am Feldrand für alle Habitattypen einen Ertragsverlust im Vergleich zur Feldmitte beobachtet, wobei Hecken die stärkste Ertragsreduktion aufwiesen. Dieses Resultat führe ich auf die Beschattung durch die hohe Vegetationsstruktur zurück. Um Ertragsverluste besser zu verstehen, habe ich in der zweiten Studie den Schädlingsbefall durch ausgewählte Weizenschädlinge sowie den direkten Einfluss der naturnahen Habitats auf die Schädlingsraten auf der Feld- und Landschaftsskala untersucht. Nur die Unkrautbedeckung konnte mit dem Ertragsverlust in Verbindung gebracht werden, wobei sie einen stärkeren Einfluss auf die Ernteerträge in der Nähe der naturnahen Habitats hatte. Darüber hinaus konnte ich zeigen, dass die Befallsraten von Blattpathogenen und die Fraßraten der Larven des Getreidehähnchens an Söllen erhöht waren. Letzteres stieg sogar an Söllen mit zunehmender Landschaftsvielfalt an, was auf den Wegfall natürlicher Feinde an isolierten Habitats im Feldinneren, wie Söllen, schließen lässt.

In meiner dritten Studie fand ich heraus, dass auch Ökosystemdienstleister, wie Laufkäfer sowie die Samenprädation von Unkräutern, von Söllen profitieren. Die Entfernung zu einem naturnahen Habitat verringerte den Artenreichtum der Ökosystemdienstleister, im Gegensatz zur Samenprädation, welche zur Feldmitte zunahm. Dies deutet darauf hin, dass eine höhere Nahrungsverfügbarkeit an Feldrändern die Prädation von Versuchssamen abgeschwächt haben

könnte. Während mit zunehmender Landschaftsvielfalt die Artenanzahl an Unkräutern anstieg, war bei den Laufkäfern die höchste Artenzahl und Aktivitätsdichte in Landschaften mit geringer Vielfalt zu beobachten. Das lässt den Schluss zu, dass eine Minimalausstattung an naturnahen Habitaten für Laufkäfer vorteilhaft ist, während ein zu großer Anteil an naturnahen Habitaten ihre Mobilität behindern könnte. Die ausgelegten Samen wurden in habitatarmen Landschaften unterschiedlich stark gefressen, wohingegen sie sich in habitatreichen Landschaften anglichen. Dieses Resultat unterstreicht, dass Landschaftsvielfalt die Bereitstellung von Ökosystemdienstleistungen stabilisieren kann.

Abschließend konnte ich zeigen, dass mit ansteigender Samenprädation von Unkräutern ein Anstieg des Weizenertrages einherging, wenn auch die Unkrautbedeckung nicht verringert wurde. Die genauen Mechanismen der Bereitstellung von natürlicher Unkrautbekämpfung für die Pflanzenproduktion sollten in zukünftigen Studien weiter untersucht werden.

Zusammenfassend lässt sich sagen, dass die untersuchten Ökosystemdienstleister und ihre Schädlings- sowie Prädationsraten Habitatpräferenzen aufwiesen. Diese Tatsache unterstreicht die Notwendigkeit, die Auswirkungen verschiedener Habitattypen auf die Bereitstellung von Ökosystemdienstleistungen nicht nur auf der Feldskala, sondern auch auf der Landschaftsskala zu bewerten. Meine Ergebnisse bestätigen, dass neben der Aufnahme des Artenreichtums von Ökosystemdienstleistern die Bewertung ihrer Funktionen unerlässlich ist, um die tatsächliche Bereitstellung von Ökosystemdienstleistungen mit dem landwirtschaftlichen Ertrag in Beziehung zu setzen.

References

- Albrecht, M. *et al.* (2007) 'The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland', *Journal of Applied Ecology*, 44(4), pp. 813–822.
- Albrecht, M. *et al.* (2020) 'Global synthesis of the effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield', *Ecology Letters*, 23(10), pp. 1488–1498.
- Alignier, A. *et al.* (2008) 'Variation of post-dispersal weed seed predation according to weed species, space and time', *Journal of Plant Diseases and Protection, Supplement*, (21), pp. 221–226.
- Altenfelder, S., Raabe, U. and Albrecht, H. (2014) 'Effects of water regime and agricultural land use on diversity and species composition of vascular plants inhabiting temporary ponds in northeastern Germany', *Tuexenia*, 34(1), pp. 145–162.
- Altieri, M. A. (1999) 'The ecological role of biodiversity in agroecosystems', *Agriculture, Ecosystems and Environment*, 74(1–3), pp. 19–31.
- Amt für Statistik Berlin-Brandenburg (2017) *Statistischer Bericht, Bodennutzung der landwirtschaftlichen Betriebe im Land Brandenburg 2017*. Potsdam.
- Amt für Statistik Berlin-Brandenburg (2018) *Statistischer Bericht, Ernteberichterstattung über Feldfrüchte und Grünland im Land Brandenburg 2017*. Potsdam.
- Amy, S. R. *et al.* (2015) 'Hedgerow rejuvenation management affects invertebrate communities through changes to habitat structure', *Basic and Applied Ecology*, 16(5), pp. 443–451.
- Aviron, S. *et al.* (2005) 'Carabid assemblages in agricultural landscapes: Impacts of habitat features, landscape context at different spatial scales and farming intensity', *Agriculture, Ecosystems and Environment*, 108(3), pp. 205–217.
- Badenhausser, I. *et al.* (2020) 'Increasing amount and quality of green infrastructures at different scales promotes biological control in agricultural landscapes', *Agriculture, Ecosystems and Environment*, 290(March 2019), p. 106735.
- Balvanera, P. *et al.* (2006) 'Quantifying the evidence for biodiversity effects on ecosystem functioning and services', *Ecology Letters*, 9(10), pp. 1146–1156.
- Balvanera, P. *et al.* (2014) 'Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps', *BioScience*. Oxford University Press, pp. 49–57.
- Balzan, M. V., Bocci, G. and Moonen, A. C. (2016) 'Utilisation of plant functional diversity in wildflower strips for the delivery of multiple agroecosystem services', *Entomologia Experimentalis et Applicata*, 158(3), pp. 304–319.
- Bartomeus, I. *et al.* (2014) 'Contribution of insect pollinators to crop yield and quality varies with agricultural intensification', *PeerJ*, 2014(1), pp. 1–20.
- Bartual, A. M. *et al.* (2019) 'The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes', *Agriculture, Ecosystems and Environment*, 279, pp. 43–52.
- Bates, D. *et al.* (2015) 'Fitting Linear Mixed-Effects Models Using lme4', *Journal of Statistical Software*, 67(1), pp. 1–48.
- Baty, F. *et al.* (2015) 'A Toolbox for Nonlinear Regression in R : The Package nlstools',

- Journal of Statistical Software*, 66(5), pp. 1–21.
- Baudry, J. *et al.* (2000) ‘A holistic landscape ecological study of the interactions between farming activities and ecological patterns in Brittany, France’, *Landscape and Urban Planning*, 50(1–3), pp. 119–128.
- Bayerische Landesanstalt für Landwirtschaft (2018) *LfL Pflanzenschutz: Abstandsauflagen beim Einsatz von Pflanzenschutzmitteln*.
- Bennett, E. M., Peterson, G. D. and Gordon, L. J. (2009) ‘Understanding relationships among multiple ecosystem services’, *Ecology Letters*, 12(12), pp. 1394–1404.
- Benton, T. G., Vickery, J. A. and Wilson, J. D. (2003) ‘Farmland biodiversity: Is habitat heterogeneity the key?’, *Trends in Ecology and Evolution*, 18(4), pp. 182–188.
- Berger, G. *et al.* (2011) *Naturschutzbrachen im Ackerbau - Anlage und optimierte Bewirtschaftung kleinflächiger Lebensräume für die biologische Vielfalt - Praxishandbuch*. Rangsdorf: Natur & Text.
- Bianchi, F. J. J. A., Booij, C. J. H. and Tschardt, T. (2006) ‘Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control’, *Proceedings of the Royal Society B: Biological Sciences*, 273(1595), pp. 1715–1727.
- Billetter, R. *et al.* (2008) ‘Indicators for biodiversity in agricultural landscapes: a pan-European study’, *Journal of Applied Ecology*, 45, pp. 141–150.
- Birkhofer, K. *et al.* (2015) ‘Ecosystem services-current challenges and opportunities for ecological research’, *Frontiers in Ecology and Evolution*, 2, pp. 1–12.
- Birkhofer, K., Wolters, V. and Diekötter, T. (2014) ‘Grassy margins along organically managed cereal fields foster trait diversity and taxonomic distinctness of arthropod communities’, *Insect Conservation and Diversity*, 7(3), pp. 274–287.
- Blitzer, E. J. *et al.* (2012) ‘Spillover of functionally important organisms between managed and natural habitats’, *Agriculture, Ecosystems & Environment*, 146(1), pp. 34–43.
- BMEL (2017) *Verordnung zur Neuordnung der guten fachlichen Praxis beim Düngen. Bundesgesetzblatt Jahrgang 2017 Teil I Nr. 32*. Bonn.
- Boatman, N. D. and Sotherton, N. W. (1988) ‘The agronomic consequences and costs of managing field margins for game and wildlife conservation’, *Aspects of Applied Biology*, 17(1), pp. 47–56.
- Boetzel, F. A. *et al.* (2019) ‘Agri-environmental schemes promote ground-dwelling predators in adjacent oilseed rape fields: Diversity, species traits and distance-decay functions’, *Journal of Applied Ecology*, 56(1), pp. 10–20.
- Boetzel, F. A. *et al.* (2020) ‘Pest control potential of adjacent agri-environment schemes varies with crop type and is shaped by landscape context and within-field position’, *Journal of Applied Ecology*, 57(8), pp. 1482–1493.
- Bohan, D. A. *et al.* (2000) ‘Spatial dynamics of predation by carabid beetles on slugs’, *Journal of Animal Ecology*, 69, pp. 367–379.
- Bommarco, R., Kleijn, D. and Potts, S. G. (2013) ‘Ecological intensification: Harnessing ecosystem services for food security’, *Trends in Ecology and Evolution*, 28(4), pp. 230–238.
- Borin, M. *et al.* (2010) ‘Multiple functions of buffer strips in farming areas’, *European Journal of Agronomy*, 32(1), pp. 103–111.
- Bosem Baillod, A. *et al.* (2017) ‘Landscape-scale interactions of spatial and temporal

- cropland heterogeneity drive biological control of cereal aphids', *Journal of Applied Ecology*, 54(6), pp. 1804–1813.
- Braun-Blanquet, J. (1951) *Pflanzensoziologie: Grundzüge der Vegetationskunde*. 2nd edn. Wien: Springer-Verlag.
- Breitbach, N. *et al.* (2010) 'Bird diversity and seed dispersal along a human land-use gradient: High seed removal in structurally simple farmland', *Oecologia*, 162(4), pp. 965–976.
- Bretagnolle, V. and Gaba, S. (2015) 'Weeds for bees? A review', *Agronomy for Sustainable Development*, 35(3), pp. 891–909.
- Brooks, M. E. *et al.* (2017) 'glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling', *The R Journal*, 9(2), pp. 378–400.
- Brown, G. R. and Matthews, I. M. (2016) 'A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity', *Ecology and Evolution*, 6(12), pp. 3953–3964.
- Bruckhaus, A. and Buchner, W. (1995) 'Hecken in der Agrarlandschaft: Auswirkungen auf Feldfruchtertrag und ökologische Kenngrößen', *Berichte über Landwirtschaft*, 17(3), pp. 435–465.
- Buntin, G. D. *et al.* (2004) 'Damage loss assessment and control of the cereal leaf beetle (Coleoptera: Chrysomelidae) in winter wheat', *J Econ Entomol*, 97(2), pp. 374–382.
- Burgess, P. J. *et al.* (2004) 'Poplar (*Populus* spp) growth and crop yields in a silvoarable experiment at three lowland sites in England', *Agroforestry Systems*, 63, pp. 157–169.
- Caballero-López, B. *et al.* (2012) 'Aphids and their natural enemies are differently affected by habitat features at local and landscape scales', *Biological Control*, 63(2), pp. 222–229.
- Chaplin-Kramer, R. *et al.* (2011) 'A meta-analysis of crop pest and natural enemy response to landscape complexity', *Ecology Letters*, 14(9), pp. 922–932.
- Chaplin-Kramer, R. and Kremen, C. (2012) 'Pest control experiments show benefits of complexity at landscape and local scales', *Ecological Applications*, 22(7), pp. 1936–1948.
- Charalabidis, A. *et al.* (2017) 'Risk of predation makes foragers less choosy about their food', *PLoS ONE*, 12(11), pp. 1–18.
- Daily, G. C. (1997) 'Introduction: what are ecosystem services.', in Daily, G. C. (ed.) *Nature's services: Societal dependence on natural ecosystems*. 1st edn. Washington D.C.: Island Press, pp. 1–19.
- Dainese, M. *et al.* (2015) 'Testing scale-dependent effects of semi-natural habitats on farmland biodiversity', *Ecological Applications*, 25(6), pp. 1681–1690.
- Dainese, M. *et al.* (2017) 'High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields', *Journal of Applied Ecology*, 54(2), pp. 380–388.
- Dainese, M. *et al.* (2019) 'A global synthesis reveals biodiversity-mediated benefits for crop production', *Science Advances*, 5(10), p. eaax0121.
- Deng, X., Gibson, J. and Wang, P. (2017) 'Relationship between landscape diversity and crop production: a case study in the Hebei Province of China based on multi-source data integration', *Journal of Cleaner Production*, 142, pp. 985–992.
- Deutscher Bundestag (2012) *Gesetz zum Schutz der Kulturpflanzen (Pflanzenschutzgesetz)*.
- Díaz, S. *et al.* (2007) 'Functional Diversity – at the Crossroads between Ecosystem Functioning and Environmental Filters', in Canadell, J., Pataki, D., and Pitelka, L. (eds)

- Terrestrial Ecosystems in a Changing World*. Berlin Heidelberg: Springer, pp. 81–91.
- Diekötter, T. *et al.* (2010) ‘Landscape and management effects on structure and function of soil arthropod communities in winter wheat’, *Agriculture, Ecosystems and Environment*, 137(1–2), pp. 108–112.
- Dominik, C. *et al.* (2018) ‘Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems’, *Journal of Applied Ecology*, 55(5), pp. 2461–2472.
- Domnick, H. and Ebert, W. (1996) ‘Die Märkische Eiszeitstraße - ein touristisches Projekt im Nordosten Brandenburgs’, *Brandenburgische Geowissenschaftliche Beiträge*, 3(1), pp. 137–147.
- Duffy, J. E. *et al.* (2007) ‘The functional role of biodiversity in ecosystems: Incorporating trophic complexity’, *Ecology Letters*, 10(6), pp. 522–538.
- Duflot, R. *et al.* (2015) ‘Reconsidering the role of “semi-natural habitat” in agricultural landscape biodiversity: a case study’, *Ecological Research*, 30, pp. 75–83.
- Duru, M. *et al.* (2015) ‘How to implement biodiversity-based agriculture to enhance ecosystem services: a review’, *Agronomy for Sustainable Development*, 35(4), pp. 1259–1281.
- Eisenhauer, N. *et al.* (2009) ‘Direct and indirect effects of endogeic earthworms on plant seeds’, *Pedobiologia*, 52(3), pp. 151–162.
- Eisenhauer, N. *et al.* (2010) ‘Earthworms as seedling predators: Importance of seeds and seedlings for earthworm nutrition’, *Soil Biology and Biochemistry*, 42(8), pp. 1245–1252.
- Esterka, J. (2008) ‘The influence of woody edges on wheat yield’, *Journal of Landscape Studies*, 1, pp. 19–26.
- Evans, T. A. and Gleeson, P. V. (2016) ‘Direct measurement of ant predation of weed seeds in wheat cropping’, *Journal of Applied Ecology*, 53(4), pp. 1177–1185.
- Evans, T. R. *et al.* (2016) ‘The impact of landscape complexity on invertebrate diversity in edges and fields in an agricultural area’, *Insects*, 7(1), pp. 1–16.
- Fahrig, L. *et al.* (2015) ‘Farmlands with smaller crop fields have higher within-field biodiversity’, *Agriculture, Ecosystems and Environment*, 200.
- Federal Office of Agriculture FOAG Switzerland (2018) *Legal conditions for direct payments for biodiversity enhancements in agriculture*.
- Figuroa, M., Hammond-Kosack, K. E. and Solomon, P. S. (2018) ‘A review of wheat diseases—a field perspective’, *Molecular Plant Pathology*, 19(6), pp. 1523–1536.
- Finney, J. M. (1972) ‘Indirect effects in path analysis’, *Sociological Methods & Research*, 1(2), pp. 175–186.
- Fischer, C. *et al.* (2018) ‘Ecosystem services and disservices provided by small rodents in arable fields: Effects of local and landscape management’, *Journal of Applied Ecology*, 55(2), pp. 548–558.
- Fischer, C. *et al.* (2021) ‘Large carabids enhance weed seed removal in organic fields and in large-scale, but not small-scale agriculture’, *Landscape Ecology*, 36(2), pp. 427–438.
- Fischer, C. and Schröder, B. (2014) ‘Predicting spatial and temporal habitat use of rodents in a highly intensive agricultural area’, *Agriculture, Ecosystems and Environment*, 189, pp. 145–153.
- Fischer, C., Thies, C. and Tschardtke, T. (2011) ‘Mixed effects of landscape complexity and

- farming practice on weed seed removal', *Perspectives in Plant Ecology, Evolution and Systematics*, 13(4), pp. 297–303.
- Flaherty, K. L. *et al.* (2018) 'Timing of white-tailed deer browsing affects wetland plant communities', *Plant Ecology*, 219(3), pp. 313–324.
- Foley, J. A. (2005) 'Global Consequences of Land Use', *Science*, 309(5734), pp. 570–574.
- Fox, J. *et al.* (2012) 'Package "car" - An R Companion to Applied Regression'. Thousand Oaks, CA: Vienna: R Foundation for Statistical Computing.
- Fox, J. and Weisberg, S. (2019) *An R Companion to Applied Regression*. 3rd edn. Sage Publications.
- French, B. W. *et al.* (2001) 'Effects of Riparian and Grassland Habitats on Ground Beetle (Coleoptera: Carabidae) Assemblages in Adjacent Wheat Fields', *Environmental Entomology*, 30(2), pp. 225–234.
- Fried, G. *et al.* (2009) 'Arable weed decline in Northern France: Crop edges as refugia for weed conservation?', *Biological Conservation*, 142(1), pp. 238–243.
- Fulcher, M. R. *et al.* (2019) 'Variable interactions between non-cereal grasses and *Fusarium graminearum*', *Canadian Journal of Plant Pathology*, 41(3), pp. 450–456.
- Fulcher, M. R. *et al.* (2020) 'The incidence of *Fusarium graminearum* in wild grasses is associated with rainfall and cumulative host density in New York', *Plant Disease*, 104(10), pp. 2681–2687.
- Fuller, R. and Gregory, R. (1995) 'Population declines and range contractions among lowland farmland birds in Britain', *Conservation Biology*, 9(6), pp. 1425–1441.
- Fusser, M. S. *et al.* (2017) 'Effects of field margin type and landscape composition on predatory carabids and slugs in wheat fields', *Agriculture, Ecosystems and Environment*, 247, pp. 182–188.
- Fusser, M. S. *et al.* (2018) 'Interactive effects of local and landscape factors on farmland carabids', *Agricultural and Forest Entomology*, 20(4), pp. 549–557.
- Gaba, S. *et al.* (2010) 'Weed species richness in winter wheat increases with landscape heterogeneity', *Agriculture, Ecosystems and Environment*, 138(3–4), pp. 318–323.
- Gaba, S. *et al.* (2015) 'Multiple cropping systems as drivers for providing multiple ecosystem services: from concepts to design', *Agronomy for Sustainable Development*, 35(2), pp. 607–623.
- Gabriel, D. *et al.* (2006) 'Beta diversity at different spatial scales: Plant communities in organic and conventional agriculture', *Ecological Applications*, 16(5), pp. 2011–2021.
- Gaines, H. R. and Gratton, C. (2010) 'Seed predation increases with ground beetle diversity in a Wisconsin (USA) potato agroecosystem', *Agriculture, Ecosystems and Environment*, 137(3–4), pp. 329–336.
- Gallandt, E. R. and Weiner, J. (2015) 'Crop-Weed Competition', in *Encyclopedia of Life Sciences*. John Wiley & Sons Ltd., pp. 1–9.
- Gallé, R. *et al.* (2018) 'Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids', *Journal of Applied Ecology*, 56(1), pp. 63–72.
- Gallun, R. L., Everly, R. T. and Yamazaki, W. T. (1967) 'Yield and Milling Quality of Monon Wheat Damaged by Feeding of Cereal Leaf Beetle', *Journal of Economic Entomology*, 60(2), pp. 356–359.
- Gámez-Virués, S. *et al.* (2015) 'Landscape simplification filters species traits and drives

- biotic homogenization', *Nature Communications*, 6(1), pp. 1–8.
- Garibaldi, L. A. *et al.* (2011) 'Stability of pollination services decreases with isolation from natural areas despite honey bee visits.', *Ecology Letters*, 14(10), pp. 1062–72.
- Garibaldi, L. A. *et al.* (2018) 'Complementarity and synergisms among ecosystem services supporting crop yield', *Global Food Security*, pp. 38–47.
- Garratt, M. P. D. *et al.* (2017) 'The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context', *Agriculture, Ecosystems and Environment*, 247, pp. 363–370.
- Gayer, C. *et al.* (2019) 'Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats', *Agriculture, Ecosystems and Environment*, 284, p. 106579.
- Geiger, F. *et al.* (2010) 'Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland', *Basic and Applied Ecology*, 11(2), pp. 97–105.
- Ghosh, B. N. *et al.* (2012) 'Effects of grass vegetation strips on soil conservation and crop yield under rainfed conditions in the Indian sub-Himalayas', *Soil Use and Management*, 28(4), pp. 635–646.
- Glogoza, P. (2002) *North Dakota Small Grain Insects: Cereal Leaf Beetle*, North Dakota State University.
- González, E. *et al.* (2020) 'Forest cover and proximity decrease herbivory and increase crop yield via enhanced natural enemies in soybean fields', *Journal of Applied Ecology*, 57(11), pp. 2296–2306.
- Grab, H. *et al.* (2018) 'Landscape simplification reduces classical biological control and crop yield', *Ecological Applications*, 28(2), pp. 348–355.
- Gurr, G. M. *et al.* (2016) 'Multi-country evidence that crop diversification promotes ecological intensification of agriculture', *Nature Plants*, 2(3), pp. 22–25.
- Haddaway, N. R. *et al.* (2018) 'The multifunctional roles of vegetated strips around and within agricultural fields', *Environmental Evidence*, 7(1), pp. 1–43.
- Hendrix, P. F. *et al.* (1990) 'Soil biota as components of sustainable agroecosystems', in Edwards, C. A. *et al.* (eds) *Sustainable agricultural systems*. 1st edn. CRC Press, pp. 637–654.
- Hipólito, J., Boscolo, D. and Viana, B. F. (2018) 'Landscape and crop management strategies to conserve pollination services and increase yields in tropical coffee farms', *Agriculture, Ecosystems & Environment*, 256, pp. 218–225.
- Hoehn, P. *et al.* (2008) 'Functional group diversity of bee pollinators increases crop yield', *Proceedings of the Royal Society B: Biological Sciences*, 275(1648), pp. 2283–2291.
- Hoffmann, G. M. and Schmutterer, H. (1999) *Parasitäre Krankheiten und Schädlinge an landwirtschaftlichen Nutzpflanzen*. 2nd edn. Ulmer Verlag.
- Holland, J. and Fahrig, L. (2000) 'Effect of woody borders on insect density and diversity in crop fields: A landscape-scale analysis', *Agriculture, Ecosystems and Environment*, 78(2), pp. 115–122.
- Holland, J. M. *et al.* (2007) 'Spatio-temporal distribution and emergence of beetles in arable fields in relation to soil moisture', *Bulletin of Entomological Research*, 97(1), pp. 89–100.
- Holland, J. M. *et al.* (2016) 'Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies', *Pest management*

- science*, pp. 1638–1651.
- Holland, J. M. *et al.* (2017) ‘Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review’, *Agronomy for Sustainable Development*, 37(4).
- Holland, J. M. and Thomas, S. R. (1997) ‘Quantifying the impact of polyphagous invertebrate predators in controlling cereal aphids and in preventing wheat yield and quality reductions’, *Annals of Applied Biology*, 131(3), pp. 375–397.
- Holzschuh, A., Dudenhöffer, J. H. and Tschardt, T. (2012) ‘Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry’, *Biological Conservation*, 153, pp. 101–107.
- Honek, A. (1991) ‘Einfluß der Pflanzenbestandsdichte auf die Abundanz von Getreidehähnchen (*Oulema* spp.) in Winterweizen (Coleoptera, Chrysomelidae)’, *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz*, 98, pp. 174–178.
- Honek, A. *et al.* (2007) ‘Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera)’, *Basic and Applied Ecology*, 8(4), pp. 343–353.
- Honek, A. *et al.* (2009) ‘Role of post-dispersal seed and seedling predation in establishment of dandelion (*Taraxacum* agg.) plants’, *Agriculture, Ecosystems and Environment*, 134(1–2), pp. 126–135.
- Honek, A., Martinkova, Z. and Jarosik, V. (2003) ‘Ground beetles (Carabidae) as seed predators’, *European Journal of Entomology*, 100, pp. 531–544.
- Hooper, D. U. *et al.* (2005) ‘Effects of biodiversity on ecosystem functioning: a consensus of current knowledge’, *Ecological Monographs*, 75(1), pp. 3–35.
- Huber, J. *et al.* (2013) ‘Einfluss von Agroforstsystemen auf den Humus- und Nährstoffhaushalt, die C-Sequestrierung und Bodenfunktionen’, in Wagener, F., Heck, P., and Böhmer, J. (eds) *Nachwachsende Rohstoffe als Option für den Naturschutz... Naturschutz durch Landbau? Schlussbericht zu ELKE III. Umwelt-Campus Birkenfeld*, pp. 162–179.
- IPBES (2018) *Summary for policymakers of the regional assessment report on biodiversity and ecosystem services for Europe and Central Asia of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Edited by M. Fischer *et al.* Bonn, Germany: IPBES secretariat.
- Isenring, R. (2010) *Pesticides and the loss of biodiversity: How intensive pesticides use affects wildlife populations and species diversity*, PAN Europe. London.
- Jacob, H. S. *et al.* (2006) ‘Variation in postdispersal weed seed predation in a crop field’, *Weed Science*, 54(1), pp. 148–155.
- Jonason, D. *et al.* (2013) ‘Landscape simplification promotes weed seed predation by carabid beetles (Coleoptera: Carabidae)’, *Landscape Ecology*, 28(3), pp. 487–494.
- Jonsson, M. *et al.* (2015) ‘Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity’, *Journal of Applied Ecology*, 52(5), pp. 1274–1282.
- Jowett, K. *et al.* (2019) ‘Species matter when considering landscape effects on carabid distributions’, *Agriculture, Ecosystems and Environment*, 285, p. 106631.
- Kaletka, T. and Rudat, C. (2006) ‘Hydrogeomorphic types of glacially created kettle holes in North-East Germany’, *Limnologica*, 36(1), pp. 54–64.
- Karp, D. S. *et al.* (2018) ‘Crop pests and predators exhibit inconsistent responses to surrounding landscape composition’, *PNAS*, 115(33), pp. E7863–E7870.

- Keller, S. and Häni, F. (2000) 'Ansprüche von Nützlingen und Schädlingen an den Lebensraum', in Nentwig, W. (ed.) *Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder*. Bern: Verlag Agrarökologie, pp. 199–217.
- Kirch, G. (2006) *Auftreten und Bekämpfung phytophager Insekten an Getreide und Raps in Schleswig-Holstein*. Justus-Liebig-Universität Gießen.
- Kleijn, D. *et al.* (2009) 'On the relationship between farmland biodiversity and land-use intensity in Europe', *Proceedings of the Royal Society B: Biological Sciences*, 276(1658), pp. 903–909.
- Klein, A. M. *et al.* (2007) 'Importance of pollinators in changing landscapes for world crops', *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), pp. 303–313.
- Köhler, F. and Klausnitzer, B. (1998) 'Entomofauna Germanica: Verzeichnis der Käfer Deutschlands', *Entomologische Nachrichten und Berichte*, Beiheft 4.
- Kollmann, J. and Bassin, S. (2001) 'Effects of management on seed predation in wildflower strips in northern Switzerland', *Agriculture, Ecosystems and Environment*, 83(3), pp. 285–296.
- Kort, J. (1988) 'Benefits of Windbreaks to Field and Forage Crops', *Agriculture, Ecosystems & Environment*, 22/23, pp. 165–190.
- Kowalchuk, T. E. and Jong, E. de (1995) 'Shelterbelts and their effect on crop yield', *Canadian Journal of Soil Science*, 75(4), pp. 543–550.
- Kromp, B. (1999) 'Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement.', *Agriculture, Ecosystems & Environment*, 74, pp. 187–228.
- Kumar, P. (ed.) (2010) *The Economics of Ecosystems and Biodiversity (TEEB): Ecological and Economic Foundations*. London and Washington: UNEP/Earthprint.
- Labruyere, S. *et al.* (2016) 'Local, neighbor and landscape effects on the abundance of weed seed-eating carabids in arable fields: A nationwide analysis', *Basic and Applied Ecology*, 17(3), pp. 230–239.
- Landis, D. A. (2017) 'Designing agricultural landscapes for biodiversity-based ecosystem services', *Basic and Applied Ecology*, pp. 1–12.
- Lefcheck, J. S. (2016) 'piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics', *Methods in Ecology and Evolution*, 7(5), pp. 573–579.
- Lenka, N. K. *et al.* (2012) 'Soil carbon sequestration and erosion control potential of hedgerows and grass filter strips in sloping agricultural lands of eastern India', *Agriculture, Ecosystems and Environment*, 158, pp. 31–40.
- Letourneau, D. K. *et al.* (2011) 'Does plant diversity benefit agroecosystems? A synthetic review', *Ecological Applications*, 21(1), pp. 9–21.
- Letourneau, D. K. and Bothwell, S. G. (2008) 'Comparison of organic and conventional farms: Challenging ecologists to make biodiversity functional', *Frontiers in Ecology and the Environment*, 6(8), pp. 430–438.
- Liere, H. *et al.* (2015) 'Trophic cascades in agricultural landscapes: Indirect effects of landscape composition on crop yield', *Ecological Applications*, 25(3), pp. 652–661.
- Lindgren, J., Lindborg, R. and Cousins, S. A. O. (2018) 'Local conditions in small habitats and surrounding landscape are important for pollination services, biological pest control

- and seed predation', *Agriculture, Ecosystems and Environment*, 251, pp. 107–113.
- Loreau, M. *et al.* (2001) 'Biodiversity and ecosystem functioning: current knowledge and future challenges.', *Science*, 294, pp. 804–808.
- Lozada-Gobilard, S. *et al.* (2019) 'Environmental filtering predicts plant-community trait distribution and diversity: Kettle holes as models of meta-community systems', *Ecology and Evolution*, 9(4), pp. 1898–1910.
- Lyles, L., Tatarko, J. and Dickerson, J. D. (1984) 'Windbreak Effects on Soil Water and Wheat Yield', *Transactions of the ASAE*, 27(1), pp. 069–072.
- MacArthur, R. H. and Pianka, E. R. (1966) 'On Optimal Use of a Patchy Environment', *The American Naturalist*, 100(916), pp. 603–609.
- Mace, G. M., Norris, K. and Fitter, A. H. (2012) 'Biodiversity and ecosystem services: A multilayered relationship', *Trends in Ecology and Evolution*, 27(1), pp. 19–25.
- Macholdt, J. and Honermeier, B. (2017) 'Yield Stability in Winter Wheat Production: A Survey on German Farmers' and Advisors' Views', *Agronomy*, 7(3), p. 45.
- Marino, P. C., Gross, K. L. and Landis, D. A. (1997) 'Weed seed loss due to predation in Michigan maize fields', *Agriculture, Ecosystems and Environment*, 66(3), pp. 189–196.
- Marshall, E. J. . and Moonen, A. . (2002) 'Field margins in northern Europe: their functions and interactions with agriculture', *Agriculture, Ecosystems & Environment*, 89(1–2), pp. 5–21.
- Marshall, E. J. P. (1989) 'Distribution Patterns of Plants Associated with Arable Field Edges', *Journal of Applied Ecology*, 26(1), pp. 247–257.
- Martin, E. A. *et al.* (2013) 'Natural enemy interactions constrain pest control in complex agricultural landscapes', *Proceedings of the National Academy of Sciences*, 110(14), pp. 5534–5539.
- Martin, E. A. *et al.* (2015) 'Pest control of aphids depends on landscape complexity and natural enemy interactions', *PeerJ*, 3, p. e1095.
- Martin, E. A. *et al.* (2016) 'Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields', *Ecological Applications*, 26(2), pp. 448–462.
- Massaloux, D. *et al.* (2020) 'Complementarity of grasslands and cereal fields ensures carabid regional diversity in French farmlands', *Biodiversity and Conservation*, 29(9–10), pp. 2861–2882.
- Matson, P. A. (1997) 'Agricultural Intensification and Ecosystem Properties', *Science*, 277, pp. 504–509.
- McGarigal, K. and Marks, B. J. (1995) *FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351, United States Department of Agriculture, Pacific Northwest Research Station.*
- McHugh, N. M. *et al.* (2020) 'The contribution of semi-natural habitats to biological control is dependent on sentinel prey type', *Journal of Applied Ecology*, 57(5), pp. 914–925.
- Meiss, H. *et al.* (2010) 'Weed seed predation increases with vegetation cover in perennial forage crops', *Agriculture, Ecosystems and Environment*, 138(1–2), pp. 10–16.
- Menalled, F. D. *et al.* (2000) 'Post-dispersal weed seed predation in Michigan crop fields as a function of agricultural landscape structure', *Agriculture, Ecosystems and Environment*, 77(3), pp. 193–202.
- Menalled, F. D. *et al.* (2007) 'Impact of agricultural management on carabid communities and

- weed seed predation', *Agriculture, Ecosystems & Environment*, 118, pp. 49–54.
- Menalled, F. D., Lee, J. C. and Landis, D. A. (2001) 'Herbaceous filter strips in agroecosystems: Implications for ground beetle (Coleoptera: Carabidae) conservation and invertebrate weed seed predation', *Great Lakes Entomologist*, 34(1), pp. 77–91.
- Meyer, S. T., Koch, C. and Weisser, W. W. (2015) 'Towards a standardized Rapid Ecosystem Function Assessment (REFA)', *Trends in Ecology & Evolution*, 30(7), pp. 390–397.
- Meyers, L. S., Gamst, G. C. and Guarino, A. J. (2013) *Performing data analysis using IBM SPSS*. Hoboken, New Jersey: John Wiley & Sons.
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis*. Washington D.C.: Island Press.
- MLUL (2014) *Flächendeckende Biotop- und Landnutzungskartierung (BTLN) im Land Brandenburg - CIR-Biotoptypen 2009*. Potsdam.
- Moll, E., Flath, K. and Piepho, D. (2000) *Methodische Anleitung zur Bewertung der partiellen Resistenz von Getreidesortimenten und die SAS-Applikation RESI, Testing of Crop Cultivars for Resistance to Noxious Organisms at the Federal Biological Research Centre*. Berlin, Prarey.
- Montgomery, I., Caruso, T. and Reid, N. (2020) 'Hedgerows as Ecosystems: Service Delivery, Management, and Restoration', *Annual Review of Ecology, Evolution, and Systematics*, 51(1), pp. 81–102.
- Morandin, L. A., Long, R. F. and Kremen, C. (2014) 'Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape', *Agriculture, Ecosystems and Environment*, 189, pp. 164–170.
- Müller-Motzfeld, G. (2004) *Käfer Mitteleuropas, Bd. 2: Adephaga I: Carabidae [The beetles of Central Europe]*. Springer Spektrum.
- Müller, M. E. H. *et al.* (2015) 'Mycotoxins as antagonistic or supporting agents in the interaction between phytopathogenic *Fusarium* and *Alternaria* fungi', *World Mycotoxin Journal*, 8(3), pp. 311–321.
- Müller, M. E. H. *et al.* (2016) 'Crop biomass and humidity related factors reflect the spatial distribution of phytopathogenic *Fusarium* fungi and their mycotoxins in heterogeneous fields and landscapes', *Precision Agriculture*, 17(6), pp. 698–720.
- Munkvold, G. P. (2003) 'Epidemiology of *Fusarium* diseases and their mycotoxins in maize ears', *European Journal of Plant Pathology*, 109, pp. 705–713.
- Munoz, F. *et al.* (2020) 'Ecological specialization and rarity of arable weeds: Insights from a comprehensible survey in France', *Plants*, 9(7), pp. 1–16.
- Naem, S. and Li, S. (1997) 'Biodiversity enhances ecosystem reliability', *Nature*, 390, pp. 507–510.
- Navntoft, S. *et al.* (2009) 'Weed seed predation in organic and conventional fields', *Biological Control*, 49(1), pp. 11–16.
- Naylor, R. and Ehrlich, P. R. (1997) 'Natural pest control services and agriculture', in Daily, G. C. (ed.) *Nature's Services: societal dependence on natural ecosystems*. 1st edn. Washington D.C.: Island Press, pp. 151–174.
- Nicholls, C. I. and Altieri, M. A. (2004) 'Designing Species-Rich, Pest-Suppressive Agroecosystems through Habitat Management', *Agroecosystems analysis*, (43), pp. 49–61.
- Oerke, E. C. (2006) 'Crop losses to pests', *Journal of Agricultural Science*, 144(1), pp. 31–43.

- Olson, D. M. and Wäckers, F. L. (2007) 'Management of field margins to maximize multiple ecological services', *Journal of Applied Ecology*, 44(1), pp. 13–21.
- Papaïx, J. *et al.* (2011) 'Influence of cultivated landscape composition on variety resistance: An assessment based on wheat leaf rust epidemics', *New Phytologist*, 191, pp. 1095–1107.
- Papaïx, J. *et al.* (2014) 'Can epidemic control be achieved by altering landscape connectivity in agricultural systems?', *Ecological Modelling*, 284, pp. 35–47.
- Pätzig, M. *et al.* (2012) 'What governs macrophyte species richness in kettle hole types? A case study from Northeast Germany', *Limnologia*, 42(4), pp. 340–354.
- Perez-Alvarez, R., Nault, B. A. and Poveda, K. (2018) 'Contrasting effects of landscape composition on crop yield mediated by specialist herbivores', *Ecological Applications*, 28(3), pp. 842–853.
- Peter, S. and Bozsik, A. (2009) 'Research connection between winter wheat productivity and the distance of hedges', *Analele Universității din Oradea*, XIV, pp. 272–278.
- Petit, S. *et al.* (2017) 'Interactions between conservation agricultural practice and landscape composition promote weed seed predation by invertebrates', *Agriculture, Ecosystems and Environment*, 240, pp. 45–53.
- Petit, S., Boursault, A. and Bohan, D. A. (2014) 'Weed seed choice by carabid beetles (Coleoptera: Carabidae): Linking field measurements with laboratory diet assessments', *European Journal of Entomology*, 111(5), pp. 615–620.
- Phalan, B. *et al.* (2011) 'Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared', *Science*, 333, pp. 1289–1291.
- Pimentel, D. *et al.* (2005) 'Environmental, Energetic, and Economic Comparisons of Organic and Conventional Farming Systems', *BioScience*, 55(7), pp. 573–582.
- Pinheiro, J. *et al.* (2018) 'nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137', *R software*.
- Ponisio, L. C., M'Gonigle, L. K. and Kremen, C. (2016) 'On-farm habitat restoration counters biotic homogenization in intensively managed agriculture', *Global Change Biology*, 22(2), pp. 704–715.
- Power, A. G. (2010) 'Ecosystem services and agriculture: Tradeoffs and synergies', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1554), pp. 2959–2971.
- Purtauf, T. *et al.* (2005) 'Landscape context of organic and conventional farms: Influences on carabid beetle diversity', *Agriculture, Ecosystems and Environment*, 108(2), pp. 165–174.
- Pywell, R. F. *et al.* (2015) 'Wildlife-friendly farming increases crop yield: Evidence for ecological intensification', *Proceedings of the Royal Society B: Biological Sciences*, 282, pp. 1–8.
- R Core Team (2018) 'A language and environment for statistical computing'. Vienna, Austria: R Foundation for Statistical Computing.
- R Core Team (2020) 'R: A language and environment for statistical computing'. Vienna, Austria: R Foundation for Statistical Computing.
- Raatz, L. *et al.* (2019) 'How much do we really lose?—Yield losses in the proximity of natural landscape elements in agricultural landscapes', *Ecology and Evolution*, 9(13), pp. 7838–7848.

- Raitif, J., Plantegenest, M. and Roussel, J.-M. (2019) 'From stream to land: Ecosystem services provided by stream insects to agriculture', *Agriculture, Ecosystems & Environment*, 270–271, pp. 32–40.
- Ray, D. K. *et al.* (2012) 'Recent patterns of crop yield growth and stagnation', *Nature Communications*, 3, pp. 1293–1297.
- Roeleke, M., Johannsen, L. and Voigt, C. C. (2018) 'How bats escape the competitive exclusion principle-seasonal shift from intraspecific to interspecific competition drives space use in a bat ensemble', *Frontiers in Ecology and Evolution*, 6, pp. 1–11.
- De Rosario-Martinez, H., Fox, J. and R Core Team (2015) 'Package "phia" - Post-Hoc Interaction Analysis'.
- Roschewitz, I. *et al.* (2005) 'The effects of landscape complexity on arable weed species diversity in organic and conventional farming', *Journal of Applied Ecology*, 42(5), pp. 873–882.
- Rusch, A. *et al.* (2013) 'Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale', *Journal of Applied Ecology*, 50(2), pp. 345–354.
- Rusch, A., Chaplin-Kramer, R., *et al.* (2016) 'Agricultural landscape simplification reduces natural pest control: A quantitative synthesis', *Agriculture, Ecosystems and Environment*, 221, pp. 198–204.
- Rusch, A., Binet, D., *et al.* (2016) 'Local and landscape effects of agricultural intensification on Carabid community structure and weed seed predation in a perennial cropping system', *Landscape Ecology*, 31(9), pp. 2163–2174.
- Sala, O. E. *et al.* (2000) 'Global Biodiversity Scenarios for the Year 2100', *Science*, 287, pp. 1770–1774.
- Šálek, M. *et al.* (2018) 'Bringing diversity back to agriculture: Smaller fields and non-crop elements enhance biodiversity in intensively managed arable farmlands', *Ecological Indicators*, 90, pp. 65–73.
- Sarthou, J. P. *et al.* (2014) 'Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats', *Agriculture, Ecosystems and Environment*, 194, pp. 17–28.
- Saska, P. *et al.* (2008) 'Spatial and temporal patterns of carabid activity-density in cereals do not explain levels of predation on weed seeds', *Bulletin of Entomological Research*, 98(2), pp. 169–181.
- Saska, P. *et al.* (2014) 'Weeds determine the composition of carabid assemblage in maize at a fine scale', *Scientia Agriculturae Bohemica*, 2014(2), pp. 85–92.
- Savary, S. *et al.* (2015) 'Modelling and mapping potential epidemics of wheat diseases—examples on leaf rust and Septoria tritici blotch using EPIWHEAT', *European Journal of Plant Pathology*, 142(4), pp. 771–790.
- Sawyer, A. J. and Haynes, D. L. (1986) 'Cereal leaf beetle spatial dynamics: simulations with a random diffusion model', *Ecological Modelling*, 33, pp. 89–99.
- Schiro, G. *et al.* (2018) 'Alternaria and fusarium fungi: Differences in distribution and spore deposition in a topographically heterogeneous wheat field', *Journal of Fungi*, 4(2).
- Schiro, G. *et al.* (2019) 'The distribution of mycotoxins in a heterogeneous wheat field in relation to microclimate, fungal and bacterial abundance', *Journal of Applied Microbiology*, 126(1), pp. 177–190.

- Schöpke, B. *et al.* (2019) ‘Do dispersal traits of wetland plant species explain tolerance against isolation effects in naturally fragmented habitats?’, *Plant Ecology*, 220(9), pp. 801–815.
- Schumacher, M., Dieterich, M. and Gerhards, R. (2020) ‘Effects of weed biodiversity on the ecosystem service of weed seed predation along a farming intensity gradient’, *Global Ecology and Conservation*, 24, p. e01316.
- Shipley, B. (2009) ‘Confirmatory path analysis in a generalized multilevel context’, *Ecology*, 90(2), pp. 363–368.
- Skellern, M. P. *et al.* (2017) ‘Meteorological and landscape influences on pollen beetle immigration into oilseed rape crops’, *Agriculture, Ecosystems and Environment*, 241, pp. 150–159.
- Sklenicka, P. and Salek, M. (2005) ‘Effects of forest edges on the yield of silage maize (*Zea mays* L.)’, *Bodenkultur -Wien and München-*, 56(1/4), pp. 161–168.
- De Snoo, G. R. (1994) ‘Cost-benefits of unsprayed crop edges in winter wheat, sugar beet and potatoes’, in Boatman, N. D. (ed.) *Field Margins: Integrating Agriculture and Conservation*. Farnham: British Crop Protection Council Monograph, pp. 197–202.
- Sparkes, D. L. *et al.* (1998) ‘The effect of field margins on the yield of sugar beet and cereal crops’, *Annals of Applied Biology*, 132, pp. 129–142.
- Srivastava, D. S. *et al.* (2009) ‘Diversity has stronger top-down than bottom-up effects on decomposition’, *Ecology*, 90(4), pp. 1073–1083.
- Staley, J. T. *et al.* (2012) ‘Long-term effects of hedgerow management policies on resource provision for wildlife’, *Biological Conservation*, 145(1), pp. 24–29.
- Steinmann, K. *et al.* (2011) ‘Niches and noise - Disentangling habitat diversity and area effect on species diversity’, *Ecological Complexity*, 8(4), pp. 313–319.
- Suproniene, S. *et al.* (2019) ‘Weed species within cereal crop rotations can serve as alternative hosts for *Fusarium graminearum* causing *Fusarium* head blight of wheat’, *Fungal Ecology*, 37, pp. 30–37.
- Sutter, L., Albrecht, M. and Jeanneret, P. (2018) ‘Landscape greening and local creation of wildflower strips and hedgerows promote multiple ecosystem services’, *Journal of Applied Ecology*, 55(2), pp. 612–620.
- Tamburini, G. *et al.* (2020) ‘Agricultural diversification promotes biodiversity and multiple ecosystem services without compromising yield’, *Science Advances*, 6(45), p. eaba1715.
- Thaler, S. *et al.* (2012) ‘Impacts of climate change and alternative adaptation options on winter wheat yield and water productivity in a dry climate in Central Europe’, *Journal of Agricultural Science*, 150(5), pp. 537–555.
- Thies, C., Roschewitz, I. and Tschardtke, T. (2005) ‘The landscape context of cereal aphid-parasitoid interactions’, *Proceedings of the Royal Society B: Biological Sciences*, 272(1559), pp. 203–210.
- Thies, C., Steffan-Dewenter, I. and Tschardtke, T. (2003) ‘Effects of landscape context on herbivory and parasitism at different spatial scales’, *Oikos*, 101(1), pp. 18–25.
- Thies, C. and Tschardtke, T. (1999) ‘Landscape Structure and Biological Control in Agroecosystems’, *Science*, 285(5429), pp. 893–895.
- Thomas, C. F. G., Holland, J. M. and Brown, N. J. (2002) ‘The spatial distribution of carabid beetles in agricultural landscapes’, *The agroecology of carabid beetles*, pp. 305–344.

- Thorne, G. N. (1966) 'Physiological aspects of grain yield in cereals', in Milthorpe, F. L. and Ivins, J. D. (eds) *The Growth of Cereal and Grasses*. London: Butterworths Scientific Publications, pp. 88–105.
- Tilman, D. (1999) 'The Ecological Consequences of Changes in Biodiversity : A Search for General Principles', *Ecology*, 80(5), pp. 1455–1474.
- Tilman, D. *et al.* (2001) 'Forecasting agriculturally driven global environmental change.', *Science (New York, N.Y.)*, 292(5515), pp. 281–284.
- Tilman, D. *et al.* (2002) 'Agricultural sustainability and intensive production practices', *Nature*, 418(8), pp. 671–677.
- Tilman, D., Lehman, C. L. and Bristow, C. E. (1998) 'Diversity-stability relationships: Statistical inevitability or ecological consequence?', *American Naturalist*, 151(3), pp. 277–282.
- Trichard, A. *et al.* (2013) 'The relative effects of local management and landscape context on weed seed predation and carabid functional groups', *Basic and Applied Ecology*, 14(3), pp. 235–245.
- Tscharntke, T. *et al.* (2005) 'Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management', *Ecology Letters*, pp. 857–874.
- Tscharntke, T. *et al.* (2007) 'Conservation biological control and enemy diversity on a landscape scale', *Biological Control*, 43(3), pp. 294–309.
- Tscharntke, T. *et al.* (2012) 'Landscape moderation of biodiversity patterns and processes - eight hypotheses', *Biological Reviews*, 87(3), pp. 661–685.
- Tscharntke, T. *et al.* (2016) 'When natural habitat fails to enhance biological pest control – Five hypotheses', *Biological Conservation*, pp. 449–458.
- Tschumi, M. *et al.* (2015) 'High effectiveness of tailored flower strips in reducing pests and crop plant damage', *Proceedings of the Royal Society B: Biological Sciences*, 282(1814), p. 20151369.
- Tschumi, M. *et al.* (2016) 'Perennial, species-rich wild flower strips enhance pest control and crop yield', *Agriculture, Ecosystems and Environment*, 220, pp. 97–103.
- Tschumi, M. *et al.* (2018) 'Predation-mediated ecosystem services and disservices in agricultural landscapes', *Ecological Applications*, 28(8), pp. 2109–2118.
- Tukey, J. W. (1977) *Exploratory data analysis*. 2nd edn.
- Türke, M. *et al.* (2013) 'Weeds and endangered herbs have unforeseen dispersal helpers in the agri-environment: Gastropods and earthworms', *Renewable Agriculture and Food Systems*, 28(4), pp. 380–383.
- Universität Göttingen (2009) *Versuchsgut Reinhof, Klostergut Deppoldshausen*.
- Vasic, F. *et al.* (2020) 'Ecosystem services of kettle holes in agricultural landscapes', *Agronomy*, p. 1326.
- Veres, A. *et al.* (2013) 'Does landscape composition affect pest abundance and their control by natural enemies? A review', *Agriculture, Ecosystems and Environment*, 166, pp. 110–117.
- Vickruck, J. L. *et al.* (2019) 'Pothole wetlands provide reservoir habitat for native bees in prairie croplands', *Biological Conservation*, 232(August 2018), pp. 43–50.
- Vitousek, P. M. *et al.* (1997) 'Human Domination of Earth's Ecosystems', *Science*, 277(5325), pp. 494–499.
- Van Vooren, L. *et al.* (2017) 'Ecosystem service delivery of agri-environment measures: A

- synthesis for hedgerows and grass strips on arable land', *Agriculture, Ecosystems & Environment*, 244, pp. 32–51.
- Van Vooren, L. *et al.* (2018) 'Monitoring the Impact of Hedgerows and Grass Strips on the Performance of Multiple Ecosystem Service Indicators', *Environmental Management*, 62(2), pp. 241–259.
- Wäckers, F. L. and van Rijn, P. C. J. (2012) 'Pick and Mix: Selecting Flowering Plants to Meet the Requirements of Target Biological Control Insects', in Gurr, G. M. *et al.* (eds) *Biodiversity and Insect Pests: Key Issues for Sustainable Management*. 1st edn. John Wiley & Sons, Ltd., pp. 139–165.
- Westerman, P. R., Wes, J. S., *et al.* (2003) 'Annual losses of weed seeds due to predation in organic cereal fields', *Journal of Applied Ecology*, 40(5), pp. 824–836.
- Westerman, P. R., Hofman, A., *et al.* (2003) 'Relative importance of vertebrates and invertebrates in epigeic weed seed predation in organic cereal fields', *Agriculture, Ecosystems and Environment*, 95(2–3), pp. 417–425.
- Westerman, P. R. *et al.* (2005) 'Are many little hammers effective? Velvetleaf (*Abutilon theophrasti*) population dynamics in two- and four-year crop rotation systems', *Weed Science*, 53(3), pp. 382–392.
- Wilcox, A. *et al.* (2000) 'Factors affecting the yield of winter cereals in crop margins', *Journal of Agricultural Science*, 135(4), pp. 335–346.
- Williams, I. H. and Ferguson, A. W. (2010) 'Spatio-temporal distributions of pests and their parasitoids on the oilseed rape crop', in *Biocontrol-Based Integrated Management of Oilseed Rape Pests*. Dordrecht: Springer, pp. 245–271.
- Winqvist, C. *et al.* (2011) 'Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe', *Journal of Applied Ecology*, 48(3), pp. 570–579.
- Wisler, G. C. and Norris, R. F. (2005) 'Interactions between weeds and cultivated plants as related to management of plant pathogens', *Weed Science*, 53(6), pp. 914–917.
- Woodcock, B. A. *et al.* (2016) 'Spill-over of pest control and pollination services into arable crops', *Agriculture, Ecosystems & Environment*, 231, pp. 15–23.
- Wright, J. (2009) *Sustainable agriculture and food security in an era of oil scarcity: lessons from Cuba*. London: Earthscan.
- Yachi, S. and Loreau, M. (1999) 'Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis', *Proceedings of the National Academy of Sciences*, 96(4), pp. 1463–1468.
- Zhang, W. *et al.* (2007) 'Ecosystem services and dis-services to agriculture', *Ecological Economics*, 64(2), pp. 253–260.

Appendices

Appendix AT1: General Introduction

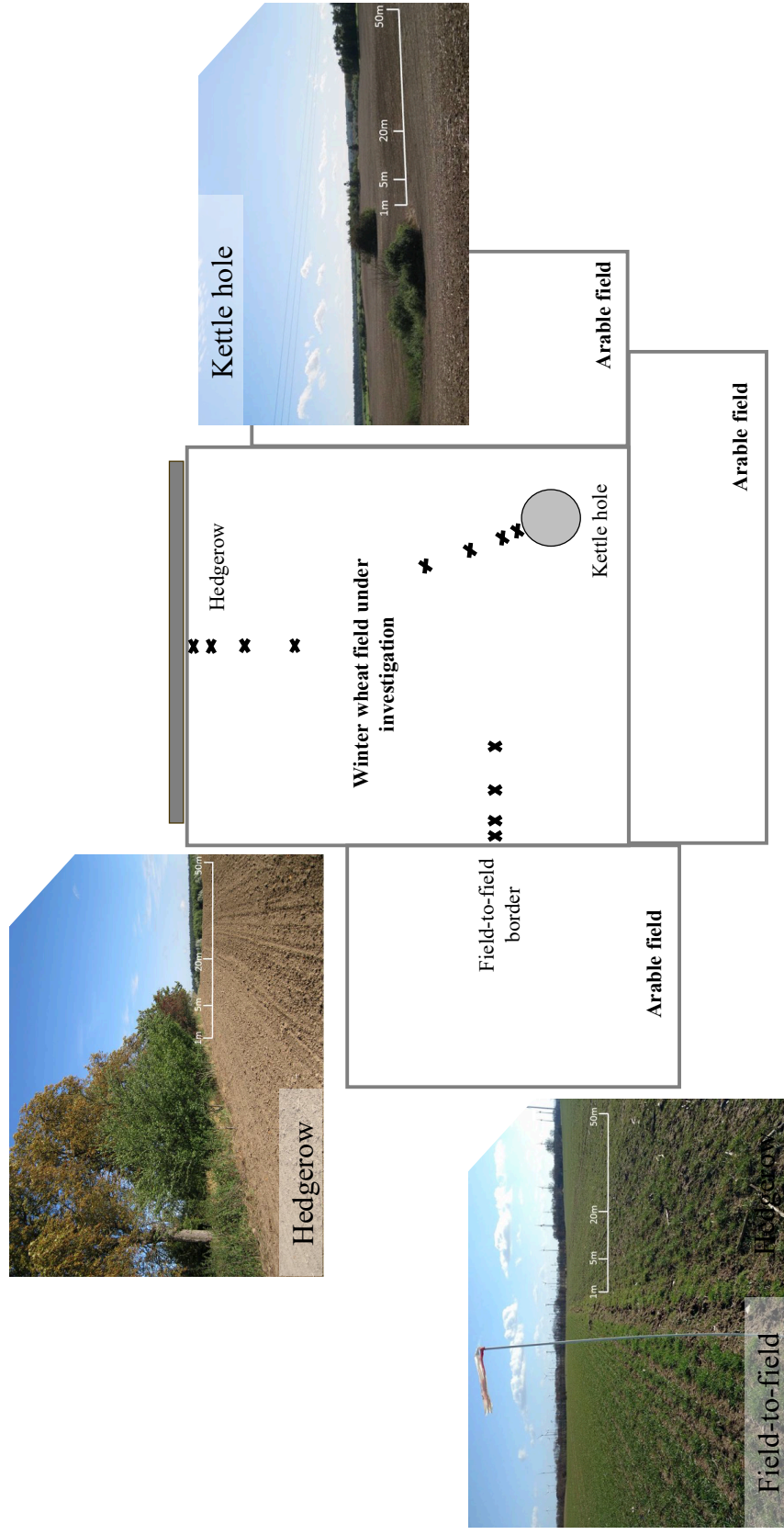


Figure AT1.1: General study design illustrating the transects with several in-field distances starting either from a semi-natural habitat (hedgerow or kettle hole) or from a field-to-field border. This is a duplicate of Fig. T4 additionally showing pictures of the semi-natural habitats (hedgerow and kettle hole) as well as an exemplary field-to-field border.

Appendix A1: Study 1

How much do we really lose? — Yield losses in the proximity of natural landscape elements in agricultural landscapes

with Nina Bacchi, Karin Pirhofer Walzl, Michael Glemnitz, Marina E. H. Müller,

Jasmin Joshi and Christoph Scherber

Table A1.1: Detailed characteristics of fields and transects in four years winter wheat harvest in ‘Deppoldshausen’ (Lower Saxony, Germany, 2014) and in the ‘AgroScapeLab Quillow’ (Brandenburg, Germany, 2015-2017) regarding transect type (agricultural road, field-to-field border, forest, hedgerow and kettle hole), turning edge (‘Yes’ or ‘No’) and transect exposition (NW, N, NE, E, SE, S, SW, W).

Year	Field	Transect type	Turning edge	Transect exposition
2014	1	Agricultural road	No	NW
		Field-to-field	Yes	NE
		Field-to-field	Yes	NE
		Hedgerow	No	NW
	2	Agricultural road	Yes	SE
		Hedgerow	No	NE
	3	Forest	No	SW
	4	Forest	No	SE
2015	1	Forest	No	E
		Forest	Yes	NE
	2	Forest	No	SE
		Forest	No	E
	3	Forest	Yes	W
		Forest	Yes	SW
	4	Forest	Yes	NE
		Forest	No	SE
	5	Forest	Yes	E
		Forest	Yes	NE
	6	Forest	No	E
		Forest	Yes	S
2016	1	Hedgerow	No	SE
	2	Field-to-field	No	SE
		Kettle hole	No	SE
	3	Kettle hole	No	W
	4	Hedgerow	No	NW
	5	Hedgerow	No	NW
	6	Field-to-field	No	NW
		Hedgerow	No	SE
	7	Field-to-field	No	E
Hedgerow		No	W	
8	Kettle hole	No	E	
9	Hedgerow	No	NW	

	10	Kettle hole	No	SE
	11	Field-to-field	No	E
		Kettle hole	No	E
	12	Kettle hole	No	SE
	13	Hedgerow	No	E
2017	1	Agricultural road	Yes	N
		Hedgerow	No	E
		Kettle hole	No	W
	2	Field-to-field	No	NW
		Hedgerow	No	NW
	3	Field-to-field	No	NW
		Hedgerow	No	E
		Kettle hole	Yes	NE
	4	Field-to-field	No	SE
		Kettle hole	No	NW
	5	Agricultural road	No	W
		Kettle hole	No	E
	6	Field-to-field	No	S
		Kettle hole	No	NE
	7	Agricultural road	No	E
		Hedgerow	No	W
	8	Field-to-field	Yes	E
		Hedgerow	Yes	W
		Kettle hole	No	N
	9	Field-to-field	No	E
		Hedgerow	Yes	S
		Kettle hole	No	W
	10	Agricultural road	No	SE
		Hedgerow	No	NW
		Kettle hole	No	SE
	11	Field-to-field	Yes	E
		Hedgerow	No	NW
		Kettle hole	Yes	E

Table A1.2: Type-II-analysis of variance table for linear mixed-effects model on crop yield as a function of year, turning edge and transect type [$yield \sim year + turning\ edge + transect\ type + turning\ edge \times transect\ type$, $random = \sim 1 | field / transect$], bold font: significant ($P < 0.05$), normal font: not significant ($P > 0.05$). Results show that turning edges had only a marginal effect on our yield data.

	df	Chisq	p-value
Year	3	2.3	0.5112
Turning edge	1	2.8	0.093
Transect type	4	29.4	< 0.001
Turning edge x transect type	4	5.8	0.218

Table A1.3: Post-hoc test with *phia* package (De Rosario-Martinez, Fox and R Core Team, 2015) of the interaction term turning edge differences per transect type in the linear mixed-effects model of Table A1.2. Bold font: significant ($P < 0.05$), normal font: not significant ($P > 0.05$). Results show that the marginal overall effect of turning edges was dominated by the hedgerow data. At hedgerows, yields were higher at field borders with turning edges compared to those without turning edges (Fig. A1.1). Thus, we cannot conclude that yields measured at field borders with turning edges lowered yields compared to those without turning edges.

	Value	df	Chisq	p-value
Field-to-field	-0.58	1	0.575	1.000
Forest	0.06	1	0.006	1.000
Hedgerow	-2.53	1	7.842	0.026
Kettle hole	-0.41	1	0.208	1.000
Agricultural road	0.06	1	0.004	1.000

Table A1.4: Type-II-analysis of variance tables for linear mixed-effect model on crop yield as a function of year, orientation to the sun, transect type and distance [$yield \sim year + sun + transect\ type + Distance + transect\ type \times sun, transect\ type \times distance, random = \sim 1 | field / transect$], bold font: significant ($P < 0.05$), normal font: not significant ($P > 0.05$).

	df	Chisq	p-value
Year	3	2.3	0.505
Orientation to the sun	1	0.1	0.760
Transect type	4	7.4	0.115
Distance	3	95.4	< 0.001
Transect type x sun	4	3.6	0.468
Transect type x distance	12	26.5	0.009

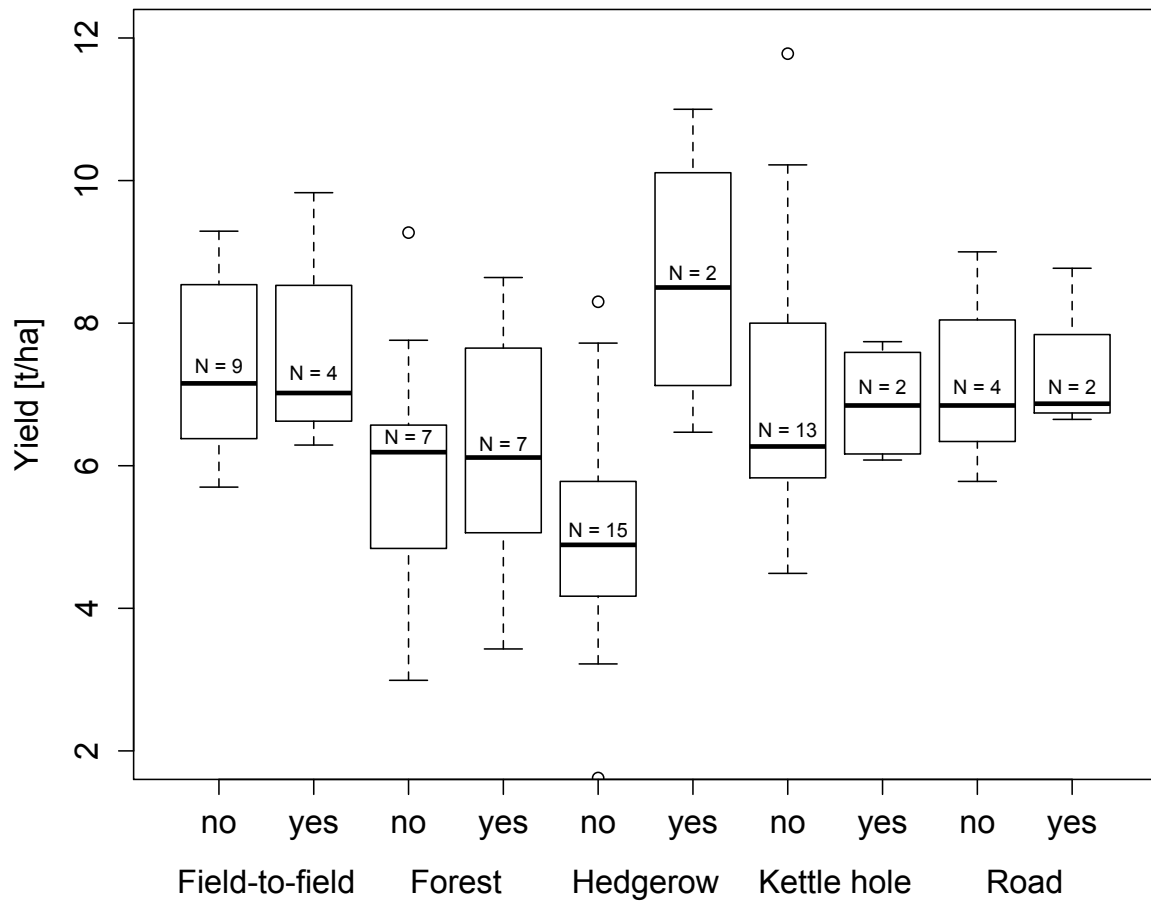


Figure A1.1: Boxplots of winter wheat yield [$t\ ha^{-1}$] at field borders (1st and 2nd distance) per transect type (field-to-field, forest, hedgerow, kettle hole and agricultural road) divided in either transects without turning edge (no) or with turning edge (yes) according to visual inspections of satellite images; N is given as number of transects, each with two sampling points, one at the 1st and the other at the 2nd distance.

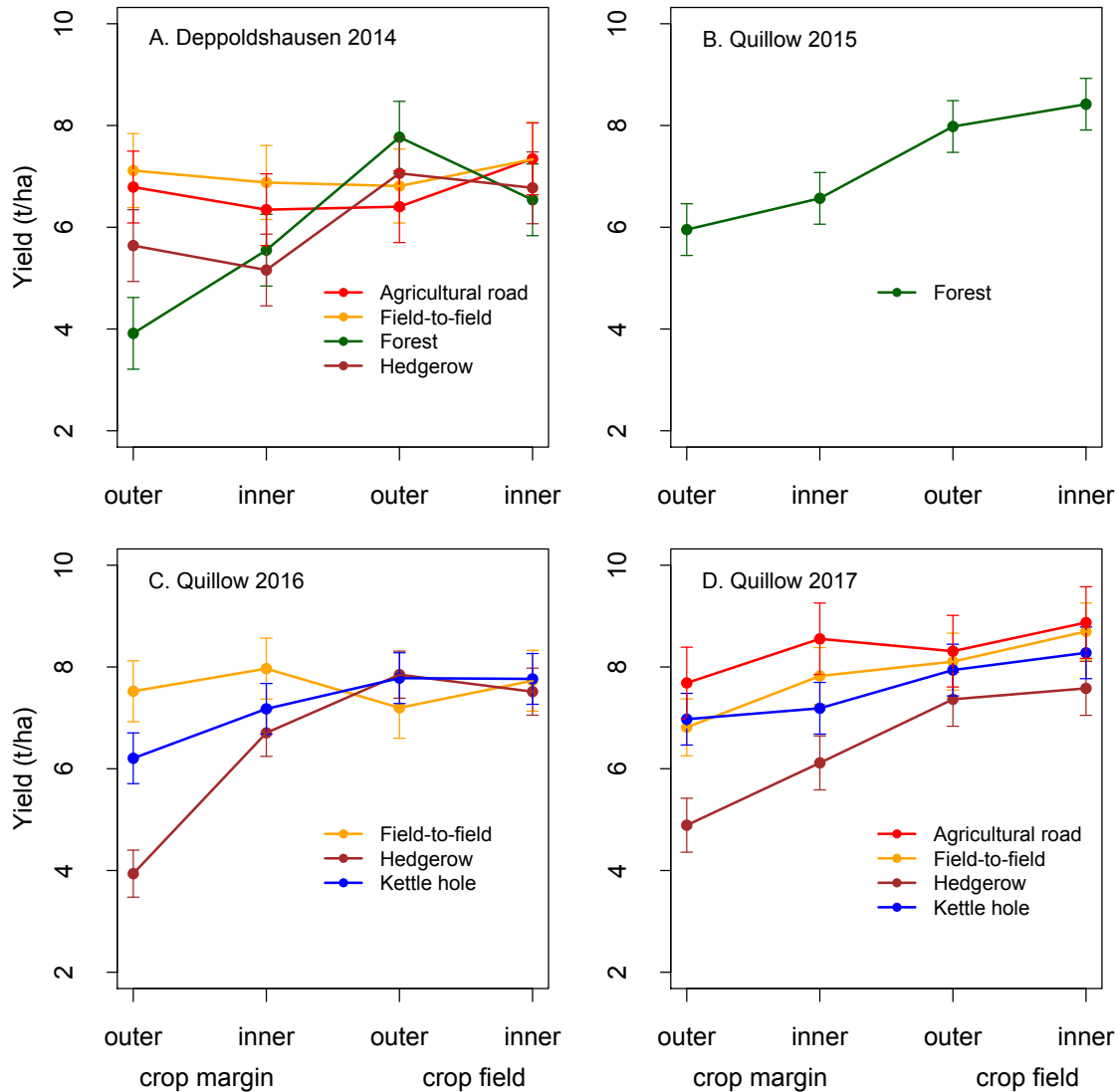


Figure A1.2: Winter wheat yield, measured as seed biomass [t ha^{-1}], along transects departing from the field border towards the field centre measured in four categorical distances in spatial sequence (1st = outer crop margin, 2nd = inner crop margin, 3rd = outer crop field, 4th = inner crop field) per year:

- 'Klostergut Deppoldshausen' (2014) adjacent to agricultural roads (N = 8; red), to field-to-field borders (N = 8; orange), to forest borders (N = 8; green) and to hedgerows (N = 8; brown) whereby categorical distances in spatial sequence are 1 m, 4 m, 16 m, and 64 m.
- 'AgroScapeLab Quillow' (2015) adjacent to forest borders (N = 48; green) whereby categorical distances in spatial sequence are 3 m, 6 m, 30 m, and 33 m.
- 'AgroScapeLab Quillow' (2016) adjacent to field-to-field borders (N = 16; orange), to hedgerows (N = 28; brown) and to kettle holes (N = 24; blue) whereby categorical distances in spatial sequence are 1 m, 5 m, 20 m, and 50 m.
- 'AgroScapeLab Quillow' (2017) adjacent to agricultural roads (N = 16; red), field-to-field borders (N = 28; orange), to hedgerows (N = 32; brown) and to kettle holes (N = 36; blue) whereby categorical distances in spatial sequence are 1 m, 5 m, 20 m, and 50 m.

Values are depicted as fitted values with confidence intervals of 95% taken from linear mixed-effects models with crop yield as a function of transect type, categorical distance and their interaction term with the random effect term of transects nested within fields.

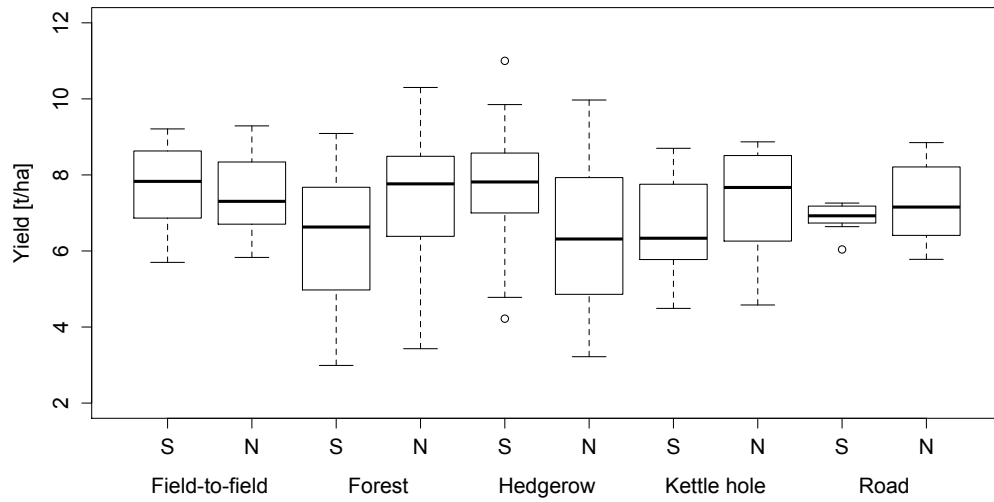


Figure A1.3: Boxplots of winter wheat yield [t ha^{-1}] per transect type (field-to-field, forest, hedgerow, kettle hole and agricultural road) divided in either transects north (N, NW, N, NE) or south (S, SE, S, SW) orientated from the field border into the field. N is given as number of transects, each with four sampling points.

Appendix A2: Study 2

Who is the culprit:

Is pest infestation responsible for yield losses close to semi-natural habitats?

with Karin Pirhofer Walzl, Marina E. H. Müller, Christoph Scherber and Jasmin Joshi

Table A2.1: Scoring scale from 1 (no damage) to 9 (very severe damage) adapted from (Moll, Flath and Piepho, 2000) of damaged flag leaves by cereal leaf beetle (CLB) larvae and their associated ranges of damage in percent

Scoring	Percentage values
1	0%
2	> 0% - 2%
3	> 2% - 5%
4	> 5% - 9%
5	> 9% - 14%
6	> 14% - 20%
7	> 20% - 35%
8	> 35% - 60%
9	> 60% - 100%

Table A2.2: Conversion of weed cover recorded with Braun-Blanquet (1951) to percentage values.

Braun-Blanquet scoring	Percentage values
1 1 small individual	0.1%
2 2 - 5 small individuals	1%
3 6 - 50 small individuals	2.5%
4 > 50 small individuals	5%
5 5% - 15% coverage	10%
6 15% - 25% coverage	20%
7 25% - 50% coverage	37.5%
8 50% - 75% coverage	62.5%
9 75% - 100% coverage	87.5%

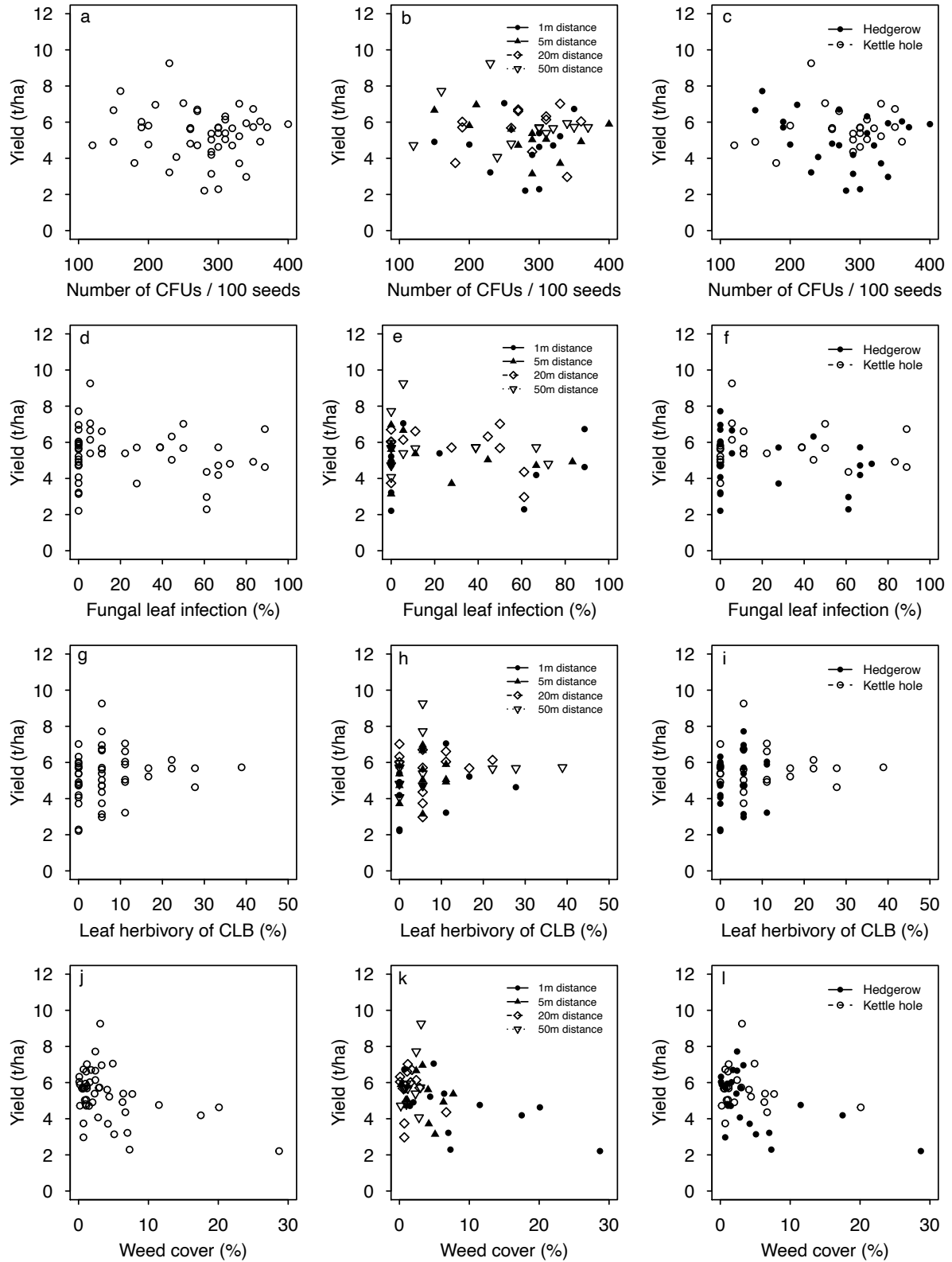


Figure A2.1: Effects of a – c number of fungal colony forming units (CFUs) per 100 wheat seeds, d – f the percentage of fungal leaf infection, g – i the percentage of herbivory (> 10% per leaf) caused by CLB larvae and j – l weed cover on winter wheat yield measured as seed biomass in $t\ ha^{-1}$ of the experimental plots ($N = 48$). The three subfigures per pest group present the single term effect on yield, their effect depending on distance to the SNH and their effect depending on SNH type. Curves represent fitted values according to a linear mixed-effects model 2a. All relationships were non-significant ($P > 0.05$).

Appendix A3: Study 3

Biodiversity-driven ecosystem functions along the edges — quantifying the effects of field borders in agricultural landscapes

with Michael Glemnitz, Karin Pirhofer Walzl, Christoph Scherber and Jasmin Joshi

Table A3.1: Dimensions of landscape metrics (percentage of SNHs and number of SNH types) per spatial scale (250 m, 500 m, 1000 m) around each transects (N = 52) in winter wheat fields (N = 26).

	Percentage of SNHs (%)			Number of SNH types (#)		
	250 m	500 m	1000 m	250 m	500 m	1000 m
Range	0.0 – 44.2	1.9 – 48.2	2.5 – 57.3	0 – 5	3 – 6	3 – 6
1 st quartile	4.0	5.3	9.0	3	4	5
2 nd quartile (median)	8.3	7.9	14.3	3	5	5
3 rd quartile	14.6	16.7	21.5	4	5	6

Table A3.2: Conversion of weeds coverage recorded with Braun-Blanquet (1951) to percentage values.

Braun-Blanquet scoring		Percentage values (%)
1	1 small individual	0.1%
2	2 - 5 small individuals	1%
3	6 - 50 small individuals	2.5%
4	> 50 small individuals	5%
5	5% - 15% cover	10%
6	15% - 25% cover	20%
7	25% - 50% cover	37.5%
8	50% - 75% cover	62.5%
9	75% - 100% cover	87.5%

Table A3.3: Type-II-analysis of variance tables for GLMMs on arable weeds (number of species and cover) as a function of year (2016 – 2019), transect type (field-to-field border, hedgerow and kettle hole), distance (1 m – 50 m), landscape composition and their pairwise interaction terms; transect ID nested within field ID as random effect. Landscape composition was investigated as either percentage SNHs (%) or number of SNH types within three different spatial scales (250 m, 500 m, 1000 m) around each transect. Bold font: significant ($P < 0.05$), normal font: non-significant ($P > 0.05$); each model with $N = 252$, 52 transects in 26 fields.

	Percentage of semi-natural habitats (%)						Number of semi-natural habitat types (#)											
	250 m		500 m		1000 m		250 m		500 m		1000 m							
	Chisq	Df	p-value	Chisq	Df	p-value	Chisq	Df	p-value	Chisq	Df	p-value	Chisq	Df	p-value			
Number of weed species																		
year	27.59	3	< 0.001	28.53	3	< 0.001	29.53	3	< 0.001	28.96	3	< 0.001	31.70	3	< 0.001	29.25	3	< 0.001
Transect type	4.34	2	0.114	2.70	2	0.259	2.69	2	0.260	2.63	2	0.269	2.54	2	0.281	4.84	2	0.089
Distance	45.75	1	< 0.001	44.81	1	< 0.001	45.85	1	< 0.001	44.92	1	< 0.001	45.68	1	< 0.001	45.97	1	< 0.001
Landscape	1.61	1	0.204	0.32	1	0.571	0.50	1	0.481	0.96	1	0.328	0.64	1	0.423	4.58	1	0.032
Type x distance	5.52	2	0.063	5.77	2	0.056	6.00	2	0.050	5.83	2	0.054	5.09	2	0.078	6.02	2	0.049
Type x landscape	3.21	2	0.201	2.13	2	0.344	3.98	2	0.137	0.44	2	0.801	3.07	2	0.216	3.76	2	0.152
Distance x landscape	0.94	1	0.331	0.22	1	0.638	3.59	1	0.058	0.80	1	0.372	3.57	1	0.059	0.13	1	0.716
Weed cover																		
Transect type	3.93	2	0.140	5.07	2	0.079	5.36	2	0.069	5.13	2	0.077	4.70	2	0.095	4.87	2	0.088
Distance	33.11	1	< 0.001	35.88	1	< 0.001	34.25	1	< 0.001	35.17	1	< 0.001	35.12	1	< 0.001	34.34	1	< 0.001
Landscape	0.66	1	0.417	0.01	1	0.908	0.19	1	0.666	0.23	1	0.632	0.50	1	0.480	0.03	1	0.865
Type x distance	7.47	2	0.024	8.42	2	0.015	7.04	2	0.030	7.49	2	0.024	6.34	2	0.042	7.14	2	0.028
Type x landscape	2.83	2	0.243	3.22	2	0.200	1.66	2	0.437	0.15	2	0.929	2.81	2	0.245	0.17	2	0.919
Distance x landscape	2.15	1	0.143	0.37	1	0.543	0.03	1	0.858	0.05	1	0.826	1.00	1	0.317	0.06	1	0.800

* Year was not included as covariable in the model for weed cover as data points were already scaled by the division of the year's maximum value

Table A3.4: Type-II-analysis of variance tables for (G)LMMs on carabids (number of species and activity-density) as a function of year (2016 – 2018), transect type (field-to-field border, hedgerow and kettle hole), distance (1 m – 50 m), landscape composition and their pairwise interaction terms; transect ID nested within field ID as random effect. Landscape composition was investigated as either percentage SNHs (%) or number of SNH types within three different spatial scales (250 m, 500 m, 1000 m) around each transect. Both metrics were analysed as polynomial of second order for hump-shaped relationship. Bold font: significant ($P < 0.05$), normal font: non-significant ($P > 0.05$); each model with $N = 182$, 35 transects in 16 fields.

	Percentage of semi-natural habitats (%)						Number of semi-natural habitat types (#)								
	250 m		500 m		1000 m		250 m		500 m*		1000 m				
	Chisq	Df	p-value	Chisq	Df	p-value	Chisq	Df	p-value	Chisq	Df	p-value	Chisq	Df	p-value
Number of carabid species															
year	21.36	2	< 0.001	39.58	2	< 0.001	41.16	2	< 0.001	14.93	2	< 0.001	28.30	2	< 0.001
transect type	12.83	2	0.002	12.89	2	0.002	11.70	2	0.003	9.98	2	0.007	10.89	2	0.004
distance	4.78	1	0.029	4.80	1	0.028	4.79	1	0.029	4.70	1	0.030	4.77	1	0.029
Landscape	5.15	2	0.076	11.57	2	0.003	16.69	2	< 0.001	0.76	2	0.683	10.74	2	0.005
type x distance	1.77	2	0.413	1.72	2	0.423	1.86	2	0.395	1.26	2	0.533	1.81	2	0.404
type x landscape	7.95	4	0.093	2.06	4	0.724	0.89	4	0.926	5.30	4	0.258	1.63	4	0.803
distance x landscape	0.07	2	0.965	0.46	2	0.795	0.13	2	0.938	0.25	2	0.882	0.35	2	0.840
Carabid activity density															
year	5.33	2	0.070	9.52	2	0.009	18.23	2	< 0.001	3.76	2	0.153	5.14	2	0.077
transect type	4.67	2	0.097	3.26	2	0.196	4.82	2	0.090	5.08	2	0.079	6.40	2	0.041
distance to NLE	0.51	1	0.473	0.49	1	0.484	0.48	1	0.490	0.51	1	0.473	0.46	1	0.496
Landscape	2.38	2	0.304	9.12	2	0.010	30.06	2	< 0.001	0.08	2	0.963	11.77	2	0.003
type x distance	13.06	2	0.001	19.36	2	< 0.001	19.38	2	< 0.001	15.87	2	< 0.001	19.39	2	< 0.001
type x landscape	7.44	4	0.114	4.86	4	0.302	10.00	4	0.040	1.34	4	0.855	1.83	4	0.767
distance x landscape	1.39	2	0.499	3.08	2	0.214	3.26	2	0.196	0.84	2	0.657	10.48	2	0.005

* Model did not converge

Table A3.5: Type-II-analysis of variance tables for GLMMs on weed seed predation as a function of year (2016, 2017, 2019), weed species of displayed seeds (*Capsella bursa-pastoris*, *Galium aparine*, *Viola arvensis*), transect type (field-to-field border, hedgerow and kettle hole), distance (1 m – 50 m), landscape composition and their interaction terms; transect ID nested within field ID as random effect; Landscape composition was investigated as either percentage SNHs (%) or number of SNH types within three different spatial scales (250 m, 500 m, 1000 m) around each transect. Bold font: significant ($P < 0.05$), normal font: non-significant ($P > 0.05$); each model $N = 468$, 40 transects in 22 fields.

	Percentage of semi-natural habitats (%)						Number of semi-natural habitat types (#)											
	250 m		500 m		1000 m		250 m		500 m		1000 m							
	Chisq	Df	p-value	Chisq	Df	p-value	Chisq	Df	p-value	Chisq	Df	p-value						
Seed predation																		
Year	12.50	2	0.002	15.87	2	< 0.001	19.29	2	< 0.001	15.77	2	< 0.001	20.24	2	< 0.001	23.09	2	< 0.001
Weed species (spec)	63.36	2	< 0.001	62.05	2	< 0.001	60.85	2	< 0.001	61.25	2	< 0.001	59.48	2	< 0.001	60.01	2	< 0.001
Transect type	6.05	2	0.049	5.18	2	0.075	5.65	2	0.059	5.34	2	0.069	6.52	2	0.038	10.15	2	0.006
Distance	6.49	1	0.011	6.26	1	0.012	6.34	1	0.012	6.85	1	0.009	6.24	1	0.012	6.15	1	0.013
Landscape	0.33	1	0.563	0.59	1	0.444	0.57	1	0.451	1.90	1	0.168	0.67	1	0.415	3.58	1	0.058
Type x distance	12.34	2	0.002	11.96	2	0.003	13.62	2	0.001	12.50	2	0.002	12.95	2	0.002	13.56	2	0.001
Type x landscape	1.65	2	0.439	0.87	2	0.646	1.35	2	0.510	2.50	2	0.287	1.97	2	0.373	4.41	2	0.110
Distance x landscape	0.04	1	0.840	0.36	1	0.549	0.01	1	0.916	0.01	1	0.912	0.18	1	0.671	0.00	1	0.993
spec x type	9.94	4	0.041	9.29	4	0.054	8.65	4	0.070	9.63	4	0.047	8.80	4	0.066	6.72	4	0.151
spec x distance	1.33	2	0.515	1.52	2	0.467	1.63	2	0.442	1.32	2	0.517	1.78	2	0.411	1.49	2	0.475
spec x landscape	8.32	2	0.016	2.56	2	0.278	5.61	2	0.061	6.77	2	0.034	4.34	2	0.114	0.44	2	0.804
spec x type x distance	3.16	4	0.531	2.99	4	0.559	2.43	4	0.657	3.30	4	0.508	3.29	4	0.510	2.41	4	0.661
spec x type x land.	4.61	4	0.330	1.43	4	0.840	2.50	4	0.644	6.18	4	0.186	6.46	4	0.167	5.02	4	0.286
spec x dist. x land.	1.70	2	0.428	1.85	2	0.397	7.87	2	0.020	1.67	2	0.434	2.52	2	0.284	4.84	2	0.089

Table A3.6: Number of weed species and weed cover recorded in the vegetation surveys and averaged over 6x replica of 1 m² plots per distance (N = 252) as well as number of carabid species and activity-density of carabids (N = 182) trapped in pitfall traps at each sample point along the transects per year (2016 – 2019), transect type (field-to-field border, hedgerow, kettle hole) and distances (1 m, 5 m, 10 m, 15 m, 20 m, 50 m). Weed cover is given in percent for 1st, 2nd (median) and 3rd quartiles.

	Number of weed species	Weed cover (range, median)			Number of carabid species	Activity-density of carabids
		1.Q	2.Q	3.Q		
Per year						
2016	35	0.9%	2.1%	4.4%	36	2580
2017	40	0.2%	2.4%	9.2%	70	4949
2018	23	0%	1.2%	7.4%	71	7348
2019	49	4.9%	10.6%	29.1%	-	-
Per transect type						
Field-to-field	46	0.6%	3.1%	13.6%	62	4878
Hedgerow [†]	39	0.5%	1.5%	6.1%	72	4045
Kettle hole	64	0.7%	5.5%	13.5%	76	5954
Per distance						
1 m	60	3.4%	10.2%	24.2%	66	2617
5 m	50	1.0%	3.3%	7.6%	64	2780
10 m*	20	0.1%	1.1%	7.2%	64	2013
15 m*	16	0.1%	0.5%	2.6%	53	2053
20 m	38	0.2%	1.7%	6.5%	57	2824
50 m	40	0.7%	3.2%	10.5%	52	2590

[†] only sampled from 2016 – 2018

* only sampled in 2017 and 2018

Table A3.7: Weed seed predation of *Capsella bursa-pastoris*, *Galium aparine* and *Viola arvensis* displayed on seed cards and averaged over the three spatial repetitions per distance (N = 468) at each sample point along the transects per year (2016, 2017, 2019), transect type (field-to-field border, hedgerow, kettle hole) and distances (1 m, 5 m, 20 m, 50 m). 1st, 2nd (median) and 3rd quartiles are given in percent.

	Total			<i>Capsella bursa-pastoris</i>			<i>Galium aparine</i>			<i>Viola arvensis</i>		
	1.Q	2.Q	3.Q	1.Q	2.Q	3.Q	1.Q	2.Q	3.Q	1.Q	2.Q	3.Q
Per year												
2016	25%	62%	91%	44%	68%	93%	15%	39%	76%	39%	71%	100%
2017	10%	21%	48%	5%	16%	29%	9%	15%	37%	11%	31%	69%
2019	39%	78%	100%	56%	76%	93%	14%	40%	86%	72%	100%	100%
Per transect type												
Field-to-field	21%	65%	94%	24%	62%	85%	10%	46%	85%	39%	93%	100%
Hedgerow	10%	25%	64%	11%	39%	71%	10%	15%	47%	16%	29%	60%
Kettle hole	22%	60%	94%	28%	64%	93%	11%	27%	71%	47%	84%	100%
Per distance												
1 m	20%	53%	89%	25%	59%	82%	10%	27%	66%	32%	69%	100%
5 m	11%	45%	89%	21%	55%	93%	6%	13%	46%	21%	75%	100%
20 m	21%	57%	90%	26%	62%	85%	10%	39%	81%	28%	81%	100%
50 m	24%	62%	94%	19%	68%	90%	20%	44%	83%	37%	78%	100%
Total	19%	55%	90%	23%	61%	88%	10%	30%	71%	30%	75%	100%

Appendix AT2: General Discussion

Yield data measured as seed biomass (t ha^{-1}) from wheat grown on agricultural fields was extracted from Study 1 and investigated ecosystem service providers and their functions, including arable weeds, ground-dwelling carabids, and weed seed predation, from Study 3. Both datasets were reduced to 24 transects of two years of investigation ($N = 92$) in the study area of the AgroScapeLab Quillow to ensure common spatial and temporal ground of the pooled data (Table AT2.1). Three types of transects starting either from a field-to-field border, a hedgerow or a kettle hole were incorporated into the analysis. All transects had four in-field sampling points (1 m, 5 m, 20 m and 50 m to the field border) with the exception of transects at field-to-field borders in 2016, i.e. samples were only taken at three distances to the field border (1 m, 5 m and 20 m).

Table AT2.1: Overview about study design and sample sizes for the sub-dataset of two years winter wheat harvest and assessment of ecosystem functions in the ‘AgroScapeLab Quillow’ (Brandenburg, Germany, 2016-2017); vegetation surveys were conducted with 6 spatial repetitions of 1m^2 plots and seed predation with 3 spatial repetitions of all three weed species per distance. Yield was harvested in 1m^2 plots at all distances. For detailed descriptions of sampling protocols see Study 1 and Study 3.

	2016	2017
Fields	8	4
	Field-to-field (4)	Field-to-field (4)
Transects types	Hedgerow (4)	Hedgerow (4)
	Kettle hole (4)	Kettle hole (4)
Distances	1 m, 5 m, 20 m, (50 m)	1 m, 5 m, 20 m, 50 m
Vegetation surveys	6x 44 plots	6x 48 plots
Carabids	44 traps	48 traps
Seed predation	3x 132 cards	3x 144 cards
Harvest	44 plots	48 plots

Statistical analysis

I used R, version 4.0.3 (R Core Team, 2020) performing mixed-effects models (package: *nlme*, version 3.1.150 Pinheiro *et al.*, 2018) within a structural equation model (SEM) (package *piecewiseSEM*, version 2.1.2, Lefcheck, 2016). As performed in Study 3, outliers in the sub-datasets of yield, weeds and carabids were interpreted in compliance with Meyers *et al.* (2013) and handled according to the inter-quartiles-distance method after Tukey (1977). Additionally, I scaled weed cover yearly between 0 and 1 by the division of the year’s maximum value. Weed seed predation and weed cover were logit-transformed to achieve a normal distribution of residuals and a better model fit.

For the metamodel, I specified a total of six linear mixed-effects models, where each endogenous variable (wheat yield, weed seed predation, species richness and activity-density of ground-dwelling carabids, species richness of arable weeds, and weed cover) was related to the two exogenous factors of SNHs (transect type and distance). ‘Distance’ was numeric and log-transformed. Random effects of all models included transect type nested in field identity to account for different number of transects per field as well as for field variability.

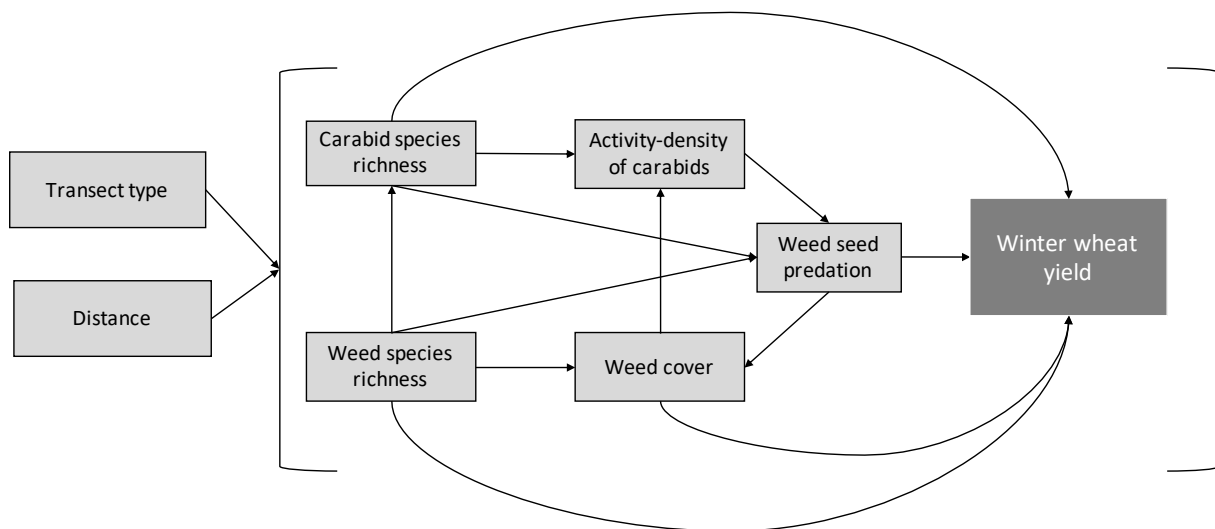


Figure AT2.1: Metamodel of SEM (Fig. T7) analyzing relationships between semi-natural habitats at field border (transect type and distance) and carabid species richness, activity-density of carabids, weed species richness, weed cover, weed seed predation, and winter wheat yield of 2016 and 2017 in the AgroScapeLab Quillow. Transect type refers to three types of transects: field-to-field borders, hedgerows and kettle holes. Distance refers to four in-field distances: 1 m, 5 m, 20 m and 50 m.

A direct path was drawn from weed seed predation and weed cover to wheat yield to test for the beneficial and detrimental effects of weed control, and weed competition, respectively. As weed control may directly reduce weed populations (Westerman *et al.*, 2005), I assumed that weed seed predation would impede weed cover. Further, I linked species richness of arable weeds and carabids to yield because a higher biodiversity might enhance crop production providing multiple ecosystem functions, e.g., pest regulation, habitat and resources for other beneficial species (e.g., Letourneau and Bothwell, 2008; Balvanera *et al.*, 2014). Beyond that I interlinked weed seed predation, carabids and weeds to each other in order to capture a more realistic picture: I hypothesized that higher weed species richness would increase weed cover as well as an increase of the number of carabid species would result into higher activity-density as a higher niche differentiation increases community biomass (Tilman, Lehman and Bristow, 1998; Tilman, 1999). In addition, weed species richness may influence weed seed predation directly (Balvanera *et al.*, 2006) and carabid species richness (Saska *et al.*, 2014; Schumacher, Dieterich and Gerhards, 2020) while carabid diversity was often shown to enhance weed seed predation (Gaines and Gratton, 2010; Trichard *et al.*, 2013; Schumacher, Dieterich and

Gerhards, 2020). Simultaneously, I assumed that a higher activity-density of carabids may increase weed seed predation and in turn might be influenced by weed cover (Saska *et al.*, 2008, 2014).

Table AT2.2: Summary table of linear mixed-effects models in final piecewise SEM ($C_{22} = 12.61$; $P = 0.943$) analysing relationships between semi-natural habitats at the field border (transect type and distance) and carabid species richness, activity-density of carabids, weed species richness, weed cover, weed seed predation, and winter wheat yield of 2016 and 2017 in the AgroScapeLab Quillow. Transect type refers to three types of transects: field-to-field borders, hedgerows and kettle holes. Distance refers to four in-field distances: 1 m, 5 m, 20 m and 50 m. Distance was log-transformed. Weed cover and weed seed predation were logit-transformed; bold font: significant ($P < 0.05$), grey font: non-significant ($P > 0.1$); each variable $N = 92$.

Response	Predictor	Estimate	Std. Estimate	Std. Error	df	p-value
<i>Yield</i>	Distance	0.483	0.436	0.085	64	< 0.001
	Seed predation	0.235	0.188	0.112	64	0.040
	Weed cover	-0.144	-0.207	0.062	64	0.023
	Carabid species richness	0.030	0.073	0.037	64	0.416
	Transect type	-	-	-	2	< 0.001
	<i>field-to-field</i>	7.991	-	0.336	11	
	<i>hedgerow</i>	6.477	-	0.324	10	
<i>kettle hole</i>	7.400	-	0.322	10		
		$R^2_{\text{marginal}} = 0.44$		$R^2_{\text{conditional}} = 0.65$		
<i>Seed predation</i>	Carabid species richness	0.073	0.220	0.034	66	0.035
	Weed species richness	-0.053	-0.131	0.037	66	0.156
	Transect type	-	-	-	2	0.152
	<i>field-to-field</i>	0.315	-	0.379	11	
	<i>hedgerow</i>	-0.335	-	0.381	10	
	<i>kettle hole</i>	0.023	-	0.376	10	
		$R^2_{\text{marginal}} = 0.10$		$R^2_{\text{conditional}} = 0.63$		
<i>Weed cover</i>	Distance	-0.242	-0.152	0.114	65	0.037
	Seed predation	0.109	0.061	0.139	65	0.436
	Weed species richness	0.478	0.651	0.060	65	< 0.001
		$R^2_{\text{marginal}} = 0.53$		$R^2_{\text{conditional}} = 0.64$		
<i>Activity-density (carabids)</i>	Carabid species richness	4.895	0.466	0.906	67	< 0.001
			$R^2_{\text{marginal}} = 0.24$		$R^2_{\text{conditional}} = 0.48$	
<i>Species richness (carabids)</i>	Distance	-0.374	-0.139	0.207	67	0.076
	Transect type	-	-	-	2	0.026
	<i>field-to-field</i>	9.880	-	1.006	11	
	<i>hedgerow</i>	9.290	-	0.976	10	
	<i>kettle hole</i>	12.290	-	0.976	10	
		$R^2_{\text{marginal}} = 0.12$		$R^2_{\text{conditional}} = 0.49$		
<i>Species richness (weeds)</i>	Distance	-0.918	-0.424	0.169	67	< 0.001
	Transect type	-	-	-	2	0.269
	<i>field-to-field</i>	4.287	-	0.746	11	
	<i>hedgerow</i>	3.920	-	0.722	10	
	<i>kettle hole</i>	5.138	-	0.722	10	
		$R^2_{\text{marginal}} = 0.19$		$R^2_{\text{conditional}} = 0.49$		

The SEM was simplified by successively removing paths with the highest p-values until further removals did not further decrease the overall model fit. Goodness-of-fit was assessed based on Shipley's test of directed separation that combines the p-values of all independent claims in Fisher's C (Shipley, 2009).

References of Appendices

- Balvanera, P. *et al.* (2006) 'Quantifying the evidence for biodiversity effects on ecosystem functioning and services', *Ecology Letters*, 9(10), pp. 1146–1156.
- Balvanera, P. *et al.* (2014) 'Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps', *BioScience*. Oxford University Press, pp. 49–57.
- Braun-Blanquet, J. (1951) *Pflanzensoziologie: Grundzüge der Vegetationskunde*. 2nd edn. Wien: Springer-Verlag.
- Gaines, H. R. and Gratton, C. (2010) 'Seed predation increases with ground beetle diversity in a Wisconsin (USA) potato agroecosystem', *Agriculture, Ecosystems and Environment*. Elsevier B.V., 137(3–4), pp. 329–336.
- Lefcheck, J. S. (2016) 'piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics', *Methods in Ecology and Evolution*, 7(5), pp. 573–579.
- Letourneau, D. K. and Bothwell, S. G. (2008) 'Comparison of organic and conventional farms: Challenging ecologists to make biodiversity functional', *Frontiers in Ecology and the Environment*, 6(8), pp. 430–438.
- Meyers, L. S., Gamst, G. C. and Guarino, A. J. (2013) *Performing data analysis using IBM SPSS*. Hoboken, New Jersey: John Wiley & Sons.
- Moll, E., Flath, K. and Piepho, D. (2000) *Methodische Anleitung zur Bewertung der partiellen Resistenz von Getreidesortimenten und die SAS-Applikation RESI, Testing of Crop Cultivars for Resistance to Noxious Organisms at the Federal Biological Research Centre*. Berlin, Prarey.
- Pinheiro, J. *et al.* (2018) 'Nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137', *R software*.
- R Core Team (2020) 'R: A language and environment for statistical computing'. Vienna, Austria: R Foundation for Statistical Computing.
- De Rosario-Martinez, H., Fox, J. and R Core Team (2015) 'Package "phia" - Post-Hoc Interaction Analysis'.
- Saska, P. *et al.* (2008) 'Spatial and temporal patterns of carabid activity-density in cereals do not explain levels of predation on weed seeds', *Bulletin of Entomological Research*, 98(2), pp. 169–181.
- Saska, P. *et al.* (2014) 'Weeds determine the composition of carabid assemblage in maize at a fine scale', *Scientia Agriculturae Bohemica*, 2014(2), pp. 85–92.
- Schumacher, M., Dieterich, M. and Gerhards, R. (2020) 'Effects of weed biodiversity on the ecosystem service of weed seed predation along a farming intensity gradient', *Global Ecology and Conservation*. Elsevier Ltd, 24, p. e01316.
- Shipley, B. (2009) 'Confirmatory path analysis in a generalized multilevel context', *Ecology*,

- 90(2), pp. 363–368.
- Tilman, D. (1999) ‘The Ecological Consequences of Changes in Biodiversity : A Search for General Principles’, *Ecology*, 80(5), pp. 1455–1474.
- Tilman, D., Lehman, C. L. and Bristow, C. E. (1998) ‘Diversity-stability relationships: Statistical inevitability or ecological consequence?’, *American Naturalist*, 151(3), pp. 277–282.
- Trichard, A. *et al.* (2013) ‘The relative effects of local management and landscape context on weed seed predation and carabid functional groups’, *Basic and Applied Ecology*, 14(3), pp. 235–245.
- Tukey, J. W. (1977) *Exploratory data analysis*. 2nd edn.
- Westerman, P. R. *et al.* (2005) ‘Are many little hammers effective? Velvetleaf (*Abutilon theophrasti*) population dynamics in two- and four-year crop rotation systems’, *Weed Science*, 53(3), pp. 382–392.

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Eidesstattliche Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation ‚Boon and bane — how semi-natural habitats shape biodiversity-driven ecosystem (dis)services in agricultural landscapes‘ von mir eigenständig und ohne unerlaubte Hilfe verfasst wurde und ich keine anderen als die zitierten Quellen und Hilfsmittel verwendet habe. Weiterhin erkläre ich, dass diese Arbeit noch keiner anderen Hochschule im In- oder Ausland zur Prüfung vorgelegt wurde.

Potsdam, 12.04.2021

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