

**Arthropods in agricultural landscapes –  
Effects of land use on beetle and spider diversity**

by

Tamara Rischen (Al Najjar)

from Nastätten

Accepted Dissertation thesis for the partial fulfilment of the requirements  
for a Doctor of Natural Sciences

Fachbereich 3: Mathematik/Naturwissenschaften

Universität Koblenz-Landau

Date of the oral examination: 19 May 2022

---

# TABLE OF CONTENTS

<b>SUMMARY .....</b>	<b>2</b>
<b>ZUSAMMENFASSUNG .....</b>	<b>4</b>
<b>GENERAL INTRODUCTION .....</b>	<b>6</b>
Introduction .....	7
Study region .....	12
Selected land-use types .....	13
Chapter outline .....	16
<b>CHAPTER 1 Biodiversity in agricultural landscapes: Grassy field margins and semi-natural fragments both foster spider diversity and body size .....</b>	<b>18</b>
<b>CHAPTER 2 Biodiversity in agricultural landscapes: different non-crop habitats increase diversity of ground-dwelling beetles (Coleoptera) but support different communities.....</b>	<b>19</b>
<b>CHAPTER 3 Farmland biodiversity: wildflower-sown islands within arable fields and grassy field margins both promote spider diversity .....</b>	<b>20</b>
<b>CHAPTER 4 Responses of selected beetle families (Carabidae, Chrysomelidae, Curculionidae) to non-crop habitats in an agricultural landscape .....</b>	<b>21</b>
<b>CHAPTER 5 Configurational landscape heterogeneity: crop-fallow boundaries enhance the taxonomic diversity of carabid beetles and spiders .....</b>	<b>22</b>
<b>GENERAL DISCUSSION .....</b>	<b>23</b>
Land-use effects on beetle and spider communities (Q1) .....	24
Evaluation of non-crop habitats as conservation measures (Q2) .....	27
Body size as suitable bioindicator for land-use intensity (Q3) .....	28
Effects of configurational landscape heterogeneity (Q4/Q5).....	28
Conclusions .....	30
<b>REFERENCES.....</b>	<b>32</b>
<b>FUNDING .....</b>	<b>43</b>

---

## SUMMARY

---

Agricultural intensification is leading to a severe decline in farmland biodiversity worldwide. The resulting landscape simplification through the expansion of monocultures and removal of non-crop habitats has a major impact on arthropod communities in agricultural landscapes. While arable fields are often highly disturbed and ephemeral habitats that are unsuitable for many species, non-crop habitats in agroecosystems can provide important refugia. The creation of non-crop habitats through agri-environmental schemes (AES) in intensive agricultural landscapes, such as the ‘Maifeld’ region in western Germany, is intended to mitigate the negative effects of agricultural intensification, although the effectiveness of these measures for nature conservation is still controversial. Therefore, this work focuses on the taxonomic and functional diversity of beetles (Coleoptera) and spiders (Araneida), being important providers of ecosystem services, between wheat fields and different non-crop habitats, namely grassy field margins adjacent to wheat and oilseed rape fields, small- and large-scale set-aside areas sown with wildflowers, and permanent grassland fallows. Arthropods were collected between 2019 and 2020 using pitfall traps and suction sampling. Land-use type influenced beetle and spider diversity in the study area, with significantly higher values in grassland fallows than wheat fields. Surprisingly, species diversity differed little among all non-crop habitats, but all harboured distinct species assemblages. In particular, large long-term grassland fallows showed the largest within-group variation of beetle and spider assemblages and represented important habitats, especially for habitat specialists and threatened species, likely due to their variable soil moisture and complex habitat structure. In contrast, the homogeneous arthropod assemblages of wheat fields exhibited lower trait richness and were dominated by a few predatory species adapted to such disturbed, man-made habitats. Interestingly, all conservation measures complemented each other in that they contributed in different ways to supporting beetles and spiders in agricultural landscapes. Even small-scale non-crop habitats and existing habitat boundaries in an agricultural matrix appear to be valuable habitats for farmland arthropods by enhancing taxonomic diversity. Field

margins and small wildflower-sown patches can link isolated non-crop habitats and contribute to a heterogeneous agricultural landscape. Consequently, a combination of various small- and large-scale greening measures leads to increased compositional and configurational landscape heterogeneity, resulting in improved beetle and spider diversity. Considering the ongoing loss of farmland biodiversity worldwide, agri-environmental schemes should be promoted in the future, as they are particularly important for arthropod conservation in intensive agricultural landscapes such as the Maifeld region.

---

## ZUSAMMENFASSUNG

---

Die Intensivierung der Landwirtschaft führt weltweit zu einem fortschreitenden Verlust der biologischen Vielfalt in Agrarlandschaften. Die daraus resultierende Homogenität der Landschaft, die mit der Ausweitung von Monokulturflächen und dem Verlust naturnaher Lebensräume einhergeht, hat schwerwiegende Auswirkungen auf Arthropoden in Agrarlandschaften. Während Ackerflächen aufgrund intensiver und häufiger Störungen für viele Arten ungeeignete Habitate darstellen, können naturnahe Lebensräume in Agrarökosystemen als wichtige Rückzugsflächen fungieren. Die Erschaffung von naturnahen Lebensräumen durch Agrarumweltmaßnahmen in intensiven Agrarlandschaften, wie der Maifelder Agrarlandschaft in Westdeutschland, sollen den negativen Auswirkungen der landwirtschaftlichen Intensivierung entgegenwirken. Allerdings ist die Wirksamkeit dieser Maßnahmen für den Artenschutz noch umstritten. Aus diesem Grund wird in dieser Arbeit die Artenvielfalt der Käfer (Coleoptera) und Spinnen (Araneida) auf Weizenfeldern und verschiedenen naturnahen Lebensräumen (grasbewachsene Feldränder angrenzend an Weizen- und Rapsfelder; klein- und großflächige, mit Wildblumenmischungen eingesäte, Stilllegungsflächen; dauerhafte Grünlandbrachen) miteinander verglichen. Hierfür wurden die Arthropoden in den Jahren 2019 und 2020 mit Bodenfallen und Saugproben erfasst. Die vorliegenden Ergebnisse zeigen, dass die Landnutzung die Käfer- und Spinnendiversität im Untersuchungsgebiet beeinflusst, mit einer deutlich höheren Artenvielfalt auf den Grünlandbrachen als auf den Weizenfeldern. Überraschenderweise bestanden zwischen allen naturnahen Lebensräumen nur geringe Unterschiede, jedoch beherbergten sie unterschiedliche Artengemeinschaften. Hier unterschieden sich vor allem die Käfer- und Spinnengemeinschaften der großflächigen Grünlandbrachen deutlich von allen anderen untersuchten Landnutzungstypen. Insbesondere für Habitatspezialisten und gefährdete Arten stellten die Grünlandbrachen wichtige Lebensräume dar, wahrscheinlich aufgrund ihrer variablen Bodenfeuchtigkeit und komplexen Lebensraumstruktur. Im Gegensatz dazu wiesen Weizenfelder homogene Arthropodengemeinschaften mit einem geringeren Merkmalsreichtum auf und wurden von einigen wenigen räuberischen Arten dominiert,

die sich an derartig intensive Lebensräume angepasst haben. Die Ergebnisse deuten darauf hin, dass sich alle Schutzmaßnahmen ergänzen, indem sie auf unterschiedliche Weise zur Förderung der Käfer und Spinnen auf landwirtschaftlichen Flächen beitragen können. Selbst kleinflächige naturnahe Lebensräume und bestehende Habitatgrenzen in einer landwirtschaftlichen Matrix scheinen wertvolle Lebensräume für Arthropoden in Agrarökosystemen darzustellen, indem sie zur Erhöhung der taxonomischen Vielfalt beitragen. Feldränder und kleine, mit Wildblumen eingesäte Flächen, können isolierte naturnahe Lebensräume miteinander verbinden und zu einer heterogenen Agrarlandschaft beitragen. Folglich führt eine Kombination verschiedener klein- und großflächiger Begrünungsmaßnahmen zu einer erhöhten Landschaftsheterogenität, die sich wiederum positiv auf die Käfer- und Spinnenvielfalt auswirkt. In Anbetracht des weltweit anhaltenden Verlustes der Artenvielfalt in Agrarlandschaften, sollten Agrarumweltmaßnahmen in Zukunft gefördert werden, da sie für den Arthropodenschutz in intensiven Agrarlandschaften, wie im Maifeld, besonders bedeutsam sind.

---

# GENERAL INTRODUCTION

---



## **Introduction**

The ongoing global loss of biodiversity in agricultural landscapes in the last decades is mainly driven by agricultural intensification (Benton et al. 2003; Dudley and Alexander 2017). Due to local and regional management, agricultural landscapes were once characterised by a mosaic of farmland and semi-natural structures (Antrop 1997, 2005). Traditional agroecosystems provided vital goods for human survival and contained many different habitat types that harboured a variety of wildlife (Plieninger et al. 2006; Berglund et al. 2014). However, incessant human population growth and the resulting increase in demand for agricultural products have led to intensification and expansion of agricultural land (Tilman et al. 2011), replacing natural ecosystems by human-dominated mosaic landscapes (Tscharntke et al. 2012b). At the expense of semi-natural landscape features, arable fields have been enlarged to facilitate cultivation and increase the machine operational efficiency (Stoate et al. 2001). Furthermore, the use of synthetic fertilisers and pesticides has been increased to maximise crop production and thus crop yields (Tscharntke et al. 2012a). To meet global demand, landscape simplification occurred in many areas of the world through the establishment of large monoculture fields (Tscharntke et al. 2005b; Tryjanowski et al. 2011). Consequently, the proportion of semi-natural habitats valuable for a variety of agricultural taxa such as birds, bees, butterflies, beetles and spiders declined in agricultural landscapes (e.g. Meek et al. 2002; Woodcock et al. 2005; Carvell et al. 2007; Perkins et al. 2011).

### *Arthropods in agricultural landscapes*

Because arthropods make up a large proportion of animal biomass and link many trophic levels, they play a vital role in the functioning of ecosystems on which humans depend (Bowler et al. 2019; Seibold et al. 2019). For example, they contribute to biocontrol of weeds and agricultural pests as well as pollination (Tscharntke et al. 2005a; Michalko et al. 2019). In addition, many birds, bats or lizards depend on the presence of arthropods as they serve as important food (Roberts 1995; Vickery et al. 2001; Benton et al. 2002). Due to their high abundance and taxonomic as well as functional diversity in agricultural landscapes, they are particularly important for providing ecosystem services (Kromp 1999; Symondson et al. 2002). A decline of arthropod diversity on agricultural lands as a result of conventional agricultural intensification may therefore threaten the stability of

these habitats and numerous ecosystem services, potentially leading to global ecological and economic consequences (Wagner et al. 2021).

Crop fields comprise man-made habitats that are unsuitable for many organisms due to periodic disturbances (Samu and Szinetár 2002; Butt and Sherawat 2012). The use of agrochemicals combined with the removal of structuring vegetation through regular harvesting and tillage results in a variety of local impacts on arthropods, including loss of habitats, reduced food supply, and changes in microclimate (Batáry et al. 2008). Management impacts can affect arthropod abundance in crop fields, either directly through higher mortality and emigration rates or indirectly through habitat disruption (Weibull and Östman 2003; Thorbek and Bilde 2004; Diekötter et al. 2010). Because most arthropods survive more readily in structurally and vegetatively rich perennial habitats than in uniform crop fields, there is an increasing need for less disturbed sites in agricultural landscapes (Sunderland and Samu 2000; Pluess et al. 2008).

#### *Non-crop habitats*

Non-crop habitats contribute to a heterogeneous environment and can be important biodiversity reservoirs by providing refugia for farmland species (Tschardt et al. 2005b; Kovács-Hostyánszki et al. 2011). For example, arthropods benefit from remnants of natural vegetation and long-term fallows in agroecosystems, but their proportion has steadily declined in recent decades due to agricultural intensification (Geiger et al. 2009; Holland et al. 2017). Today, however, modern agriculture aims to maintain the level of agricultural production while minimising the impact of agriculture on the environment (Foley et al. 2011). As a result, there is a growing public and policy awareness for promoting agricultural sustainability (Duelli and Obrist 2003; Clough et al. 2005). Various approaches, such as the conservation of non-crop habitats in agricultural landscapes, aim to reduce negative agricultural impacts on the environment and on biodiversity (Feng et al. 2021). To this end, agri-environment schemes (AES) have been created under the Common Agricultural Policy (CAP) of the European Union (EU) to help preserve permanent crops and promote ecologically beneficial elements through greening measures. For example, farmers receive subsidies for setting aside arable land or maintaining landscape elements such as hedgerows and field margins (Regulation No. 1307/2013). The creation of non-crop habitats in agricultural landscapes has an important

impact at the local scale, but also affects the landscape scale by increasing heterogeneity (Gallé et al. 2020). Some studies have already demonstrated the effectiveness of greening measures on arthropod diversity in agricultural landscapes (e.g. Schmidt-Entling and Döbeli 2009; Hof and Bright 2010; Palmu et al. 2014), but beneficial effects may differ between non-crop habitat types.

*Compositional and configurational landscape heterogeneity*

The spatial separation of habitat elements in agricultural mosaic landscapes forces many species to use multiple habitats during their life cycle (Kremen et al. 2007; Marrec et al. 2017). Population dynamics and community structures of farmland animals are therefore strongly related to landscape heterogeneity, which is composed of compositional (i.e. diversity of habitat types) and configurational heterogeneity (i.e. spatial arrangement and size of habitat patches; Fahrig et al. 2011; Sirami et al. 2019). Increasing compositional heterogeneity, particularly an increasing percentage of non-crop habitats, generally increases the availability of niches in agroecosystems that support arthropod diversity (Pluess et al. 2010; Miyashita et al. 2012; Duflot et al. 2017). Furthermore, an increasing configurational heterogeneity is associated with a greater edge density, which influence taxonomic and functional diversity (Holzschuh et al. 2010; Perovic et al. 2015). For example, field boundaries are susceptible to edge and spillover effects, which can often lead to higher arthropod diversity than in adjacent habitats (e.g. Magura 2002; Knapp and Řezáč 2015; Knapp et al. 2019). Landscape structure (i.e. landscape composition and configuration) thus plays a crucial role in cross-habitat movements. One reason for such movements is ‘landscape complementation’, in which organisms can make complementary use of spatially separated resources such as foraging, breeding, and hibernation sites (Dunning et al. 1992; Tschardt et al. 2012b). Several studies have already found increases in diversity of beetles (Coleoptera) and spiders (Araneida) with increasing spatial heterogeneity (e.g. Fahrig et al. 2015; Gallé et al. 2018b), supporting the importance of landscape structure for different arthropod taxa.

Among arthropods in agroecosystems, mainly beetles and spiders contribute to the provision of important ecosystem services due to their predatory behaviour (Collins et al. 2002; Michalko et al. 2019). They have been reported to be able to prey on a variety of insect pests, making them one of the most important biological control agents of winter

wheat (Clough et al. 2005; Diekötter et al. 2010). However, the occurrence of beneficial arthropods depends strongly on landscape structure and composition (e.g. Knapp and Řezáč 2015). Therefore arthropod communities can differ substantially between uniform croplands and adjacent non-crop habitats (e.g. Marasas et al. 2010; Feng et al. 2021). Communities in intensively managed habitats are remarkably homogeneous, whereas they are often more diverse in semi-natural habitats (e.g. Benton et al. 2003; Hendrickx et al. 2007). Even set-aside fields, which are usually only available for a few years (Van Buskirk and Willi 2004), and small field margins tend to have higher species richness than cultivated fields (Kovács-Hostyánszki et al. 2011; Frank et al. 2012). These non-crop habitats also connect isolated fragments of semi-natural habitats and contribute to landscape heterogeneity (Critchley et al. 2004; Morris et al. 2011). Although establishing non-crop habitats is an important part of conservation that positively impacts arthropod species (Pffigner and Luka 2000; Tscharrntke et al. 2002), the role of the type and size of these habitats is still controversial (Knapp and Řezáč 2015; Mestre et al. 2018; Ganser et al. 2019). Evidence suggests that the size and spatial configuration of non-crop habitats play an important role in maintaining viable populations in agricultural landscapes (Öberg et al. 2007; Knapp and Řezáč 2015; Šálek et al. 2018). More complex landscapes consisting of different smaller habitat types have higher edge densities that favour exchange opportunities (Martin et al. 2019). Cross-habitat spillover can influence ecosystem processes and community composition (Tscharrntke et al. 2012b), however, potential conservation implications of spillover and edge effects in agricultural landscapes are still debated (Ewers et al. 2007; Blitzer et al. 2012).

#### *Arthropod traits*

The way arthropod species respond to non-crop habitats may also depend on species-specific requirements. For example, management of conventional wheat fields requires a combination of different methods (e.g. harvesting, tillage and fertilisation) that may affect arthropod species differently (Batáry et al. 2008, 2012). Species which are negatively affected primarily include specialists that rely on additional habitat structures in non-crop habitats (Schmidt and Tscharrntke 2005; Duflot et al. 2015), while adaptable, generalist species increasingly occupy the vacated niches (Sánchez-Bayo and Wyckhuys 2019). Thus, croplands are often dominated by so-called ‘agrobionts’, predatory arthropod

species that have adapted to ephemeral habitats (Samu and Szinetár 2002; Anjum-Zubair et al. 2015). In addition, cropland communities often have lower trait diversity and are characterised by species with smaller body size and higher dispersal ability (Birkhofer et al. 2015). For example, small species have been reported to be least affected by conventional tillage (Hatten et al. 2007), so studies on the relationship between land-use intensity and body size suggest that increasing intensification leads to a reduction in body size of beetles and spiders (e.g. Birkhofer et al. 2015b, 2017; Schirmel et al. 2016). Accordingly, biodiversity loss on agricultural land is often accompanied by a loss of functional diversity or changes in the trait composition of communities (Ribera et al. 2001; Birkhofer et al. 2015).

#### *Aims and research questions*

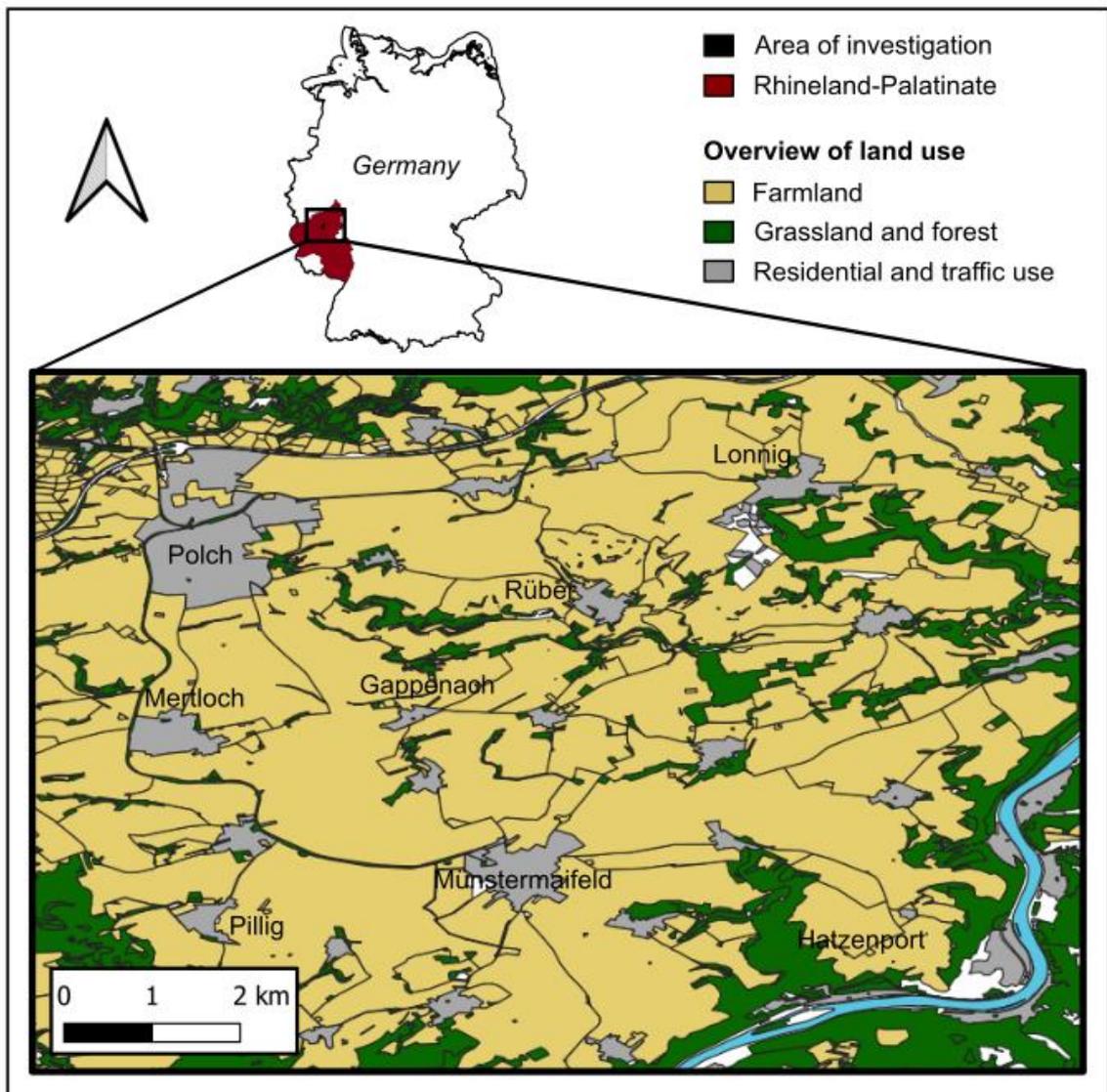
Beetles and spiders are among the most abundant and diverse invertebrate groups in agroecosystems and are easily sampled in high numbers, making them suitable model organisms for ecological studies in agricultural landscapes (Rainio and Niemela 2003; Prieto-Benítez and Méndez 2011; Michalko et al. 2019). Because of their sensitivity to changes in environmental conditions, they can act as bioindicators of human disturbance, as arthropod traits can provide information on the intensity of land use (Simons et al. 2016). Given the specific habitat requirements of many species, generalist predators (mainly spiders, carabids and rove beetles) are particularly valuable for the development of sustainable low-input agricultural systems (Lövei and Sunderland 1996; Ekschmitt et al. 1997; Nyffeler and Sunderland 2003). The intensive land use of the agricultural landscape called ‘Maifeld’ in western Germany poses a threat to local biodiversity. This landscape, which is dominated by arable land, contains only a small proportion of other habitat types such as meadows, fallows and field margins. Although agri-environmental schemes for biodiversity protection already exist, the effectiveness of these habitat types for nature conservation has not yet been clarified. This research aims to better understand the influence of land-use types within an agricultural landscape on species diversity and community composition of beetles and spiders. The goal is to determine which factors influence the taxonomic and functional diversity of the two arthropod taxa and to what extent. The findings will contribute to a better understanding of the benefits of various greening measures for the conservation of farmland arthropods.

In this context, the following main research questions were addressed:

- Q1.** How does land use affect beetle and spider communities in the studied agricultural landscape?
- Q2.** Which type of non-crop habitat is the most effective conservation measure to support farmland arthropods?
- Q3.** Does body size of both arthropod taxa represent a suitable indicator for land-use intensity?
- Q4.** Does the spatial arrangement of habitat patches (configurational landscape heterogeneity) have an impact on arthropod diversity in agroecosystems?
- Q5.** What role do habitat boundaries play in nature conservation?

### **Study region**

The study area called ‘Maifeld’ is an intensively used agricultural landscape located in western Germany in the federal state of Rhineland-Palatinate (50°14' N, 7°21' E; Fig. 1). The oceanic climate of the region near the Eifel mountain range is characterised by mild summers and cool winters, with an average annual precipitation of ~598 mm and an average annual temperature of ~10 °C (Agrarmeteorologie Rheinland-Pfalz 2020). Due to the fertile loess soils, cereals, rapeseed and root crops are grown at a large scale in the study region. With the intensification of arable farming, the proportion of grasslands or meadow orchards declined in the past. Today, non-crop habitats such as wet meadows (later grassland fallows) and field margins are limited to small remnant areas (MUEEF RLP 2021). 72 % of the area in the municipality of Maifeld (total area of 161.79 km<sup>2</sup>) was used for agriculture in 2020, which corresponds to 116.59 km<sup>2</sup>. Forests and grasslands jointly accounted for 13.5 %, while another 13.9 % was covered by residential and traffic areas (Statistisches Landesamt Rheinland-Pfalz 2020).



**Fig. 1** Location of the study area ‘Maifeld’ within the Rhineland-Palatinate in Germany. The map was generated using GGIS version 3.14 ([www.qgis.org](http://www.qgis.org)).

## Selected land-use types

Within the scope of this thesis, the following areas of different land-use types (hereafter: ‘habitat types’) were investigated:

### 1. WHEAT FIELDS (CHAPTER 1-5)

Arable fields sown with *Triticum aestivum* and conventionally managed with nitrogen fertilisers as well as herbicide and fungicide spraying.

**2. WHEAT MARGINS (CHAPTER 1-4)**

Grassy field margins bordering wheat fields and mown once or twice during the season (Fig. 2).

**3. OILSEED RAPE MARGINS (CHAPTER 1-2)**

Grassy field margins bordering oilseed rape fields and mown once or twice during the season (Fig. 2).



**Fig. 2** Examples of grassy field margins; a wheat margin (left) and an oilseed rape margin (right).

**4. SET-ASIDE FIELDS (CHAPTER 1-2)**

Young (1-2 years old) fallows sown with a mixture of wildflower seeds as ‘greening’ measure (Fig. 3).

**5. POWER POLE ISLANDS (CHAPTER 1-4)**

Two years old fallows located within wheat fields under poles of a power line (12 x 12 m), sown with a mixture of wildflower seeds as ‘greening’ measure (Fig. 3).



**Fig. 3** Examples of set-aside wildflower-sown areas; a set-aside field (left) and a power pole island (right; picture: © Daniel Ruppert).

## **6. GRASSLAND FALLOW (CHAPTER 1-5)**

Unmanaged, permanent grassland fallows with a diverse semi-natural vegetation cover, formerly used as meadows but abandoned decades ago (Fig. 4). Partially uncultivable due to high soil moisture.



**Fig. 4** Example of a permanent grassland fallow.

## Chapter outline

This thesis focuses on different non-crop habitats in agricultural landscapes and their role as potential habitats for beetles and spiders. Overall, the results of this dissertation are based on 45,304 beetles and 23,542 spiders collected between 2019 and 2020 in an intensive agricultural landscape in western Germany, using pitfall traps and suction samplings.

First, the effects of five different land use types, namely wheat fields, two types of grassy field margins (wheat and oilseed rape margins), set-aside fields, and grassland fallows, on the taxonomic and functional diversity of ground-dwelling beetles (**CHAPTER 1**) and spiders (**CHAPTER 2**) were investigated in 2019 using pitfall traps. The role of habitat type, size and shape in relation to the arthropod assemblages and their trait characteristics were examined in more detail. Because highly disturbed habitats, such as intensively used wheat fields, are typically inhabited by smaller species (Gray 1989; Blake et al. 1994; Simons et al. 2016), we also investigated the suitability of arthropod body size as indicators for human disturbance.

**CHAPTER 1:** Plath E, Rischen T, Mohr T, Fischer K (2021) Biodiversity in agricultural landscapes: Grassy field margins and semi-natural fragments both foster spider diversity and body size. *Agric Ecosyst Environ* 316:107457. <https://doi.org/10.1016/j.agee.2021.107457>.



**CHAPTER 2:** Rischen T, Frenzel T, Fischer K (2021) Biodiversity in agricultural landscapes: different non-crop habitats increase diversity of ground-dwelling beetles (Coleoptera) but support different communities. *Biodivers Conserv* 30:3965–3981. <https://doi.org/10.1007/s10531-021-02284-7>.



The following year, the effectiveness of creating small habitat islands within wheat fields ('power pole islands') for maintaining arthropod diversity was studied and compared to other non-crop habitats. In addition to pitfall traps, suction samples were also taken to record ground- and vegetation-dwelling species. We here compared taxonomic and functional diversity of spiders (**CHAPTER 3**) as well as the three beetle families Carabidae,

Chrysomelidae and Curculionidae (**CHAPTER 4**) on grassy field margins, power pole islands, grassland fallows and wheat fields.

**CHAPTER 3:** Rischen T, Geisbüsch K, Ruppert D, Fischer K (2021) Farmland biodiversity: wildflower-sown islands within arable fields and grassy field margins both promote spider diversity. *J Insect Conserv* 1-10. <https://doi.org/10.1007/s10841-021-00363-2>.

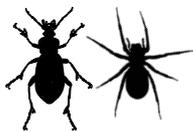


**CHAPTER 4:** Rischen T, Ehringhaus K, Heyer M, Fischer K (2022) Responses of selected beetle families (Carabidae, Chrysomelidae, Curculionidae) to non-crop habitats in an agricultural landscapes. *Biologia*. <https://doi.org/10.1007/s11756-022-01100-z>



In addition to compositional heterogeneity (e.g. the diversity of non-crop habitats), configurational heterogeneity (e.g. patch size and boundary length of habitats) also influences arthropod diversity in agricultural landscapes (Holzschuh et al. 2010; Tschamntke et al. 2012b; Perovic et al. 2015). Because boundaries are prone to edge and spillover effects (Ries et al. 2004; Roume et al. 2011), they may have higher diversity than adjacent habitats. Using pitfall traps, we therefore examined variation in taxonomic and functional carabid beetle and spider diversity across the habitat boundary between wheat fields and grassland fallows in **CHAPTER 5**.

**CHAPTER 5:** Rischen T, Kaffenberger M, Plath E, Wolff J, Fischer K (*in review*) Configurational landscape heterogeneity: crop-fallow boundaries enhance the taxonomic diversity of carabid beetles and spiders.





---

## CHAPTER 1

# Biodiversity in agricultural landscapes: Grassy field margins and semi-natural fragments both foster spider diversity and body size

---

**Paper 1**

Published article

Authors: Plath, E., Rischen, T., Mohr, T. & Fischer, K. (2021)

Agric Ecosyst Environ 316:107457. <https://doi.org/10.1016/j.agee.2021.107457>

### ABSTRACT

Agricultural intensification is one of the most important drivers of biodiversity loss. To preserve taxonomic diversity in agricultural landscapes, there is an increasing need for refuge areas within agroecosystems, but best practices for providing such sites are debated. Here, we compared the taxonomic diversity and trait composition of spiders, being important terrestrial predators, among cereal fields, grassy field margins, set aside fields sown with wildflowers, and semi-natural sites within an agricultural landscape in western Germany. Spider taxonomic diversity was similarly high in all non-crop habitats, indicating a surprisingly high value of field margins and set-aside fields. Cereal fields, in contrast, were dominated by a few, mainly euryecious species. Moreover, community mean body size was smallest on cereal fields but highest on semi-natural sites, suggesting that spider body size may serve as a valuable indicator of the level of anthropogenic disturbance. Spider communities differed partly among non-crop habitats, stressing the need for combining different conservation measures to maximise taxonomic biodiversity and trait composition. These should also include remnants of natural vegetation, which were especially important for large and red list species and therefore for reaching the aims of nature conservation.

**Keywords:** agricultural intensification • Araneae • farmland • landscape heterogeneity • nature conservation • non-crop habitats



---

## CHAPTER 2

# **Biodiversity in agricultural landscapes: different non-crop habitats increase diversity of ground-dwelling beetles (Coleoptera) but support different communities**

---

**Paper 2**

Published article

Authors: Rischen, T., Mohr, T. & Fischer, K. (2021)  
Biodivers Conserv 30:3965–3981. <https://doi.org/10.1007/s10531-021-02284-7>

### **ABSTRACT**

Agricultural intensification poses a major threat to the conservation of biodiversity and associated ecosystem services. Since non-crop habitats are regarded as important refuges for farmland biodiversity, various greening measures have been proposed to halt biodiversity loss. However, the effectiveness of these measures for biodiversity conservation is still under debate. Therefore, we here compared ground-dwelling beetle (Coleoptera) assemblages of different non-crop habitats (field margins, set-aside fields sown with wildflowers, and permanent grassland fallows) and wheat fields within an intensively used agricultural landscape in western Germany. Taxonomic diversity of Carabidae, Staphylinidae and other coleopteran families and their conservation value were higher in all non-crop habitats than on wheat fields. Surprisingly, though, different types of non-crop habitats did not differ in species richness or the number of threatened species. Thus, field margins and sown wild-flower fields were as effective in promoting beetle diversity as grassland fallows. However, different non-crop habitats supported different species assemblages, and several species, in particular especially large ones, were restricted to grassland fallows. These results suggest that different greening measures are effective in promoting the biodiversity of beetles, and that permanent grassland fallows are essential for nature conservation. The fact that habitat types harboured different assemblages stresses the need to combine a variety of greening measures to yield the highest benefit for biodiversity.

**Keywords:** Agricultural intensification • Carabidae • Non-crop habitats • Staphylinidae • Synergistic effects



---

## CHAPTER 3

# Farmland biodiversity: wildflower-sown islands within arable fields and grassy field margins both promote spider diversity

---

**Paper 3**

Published article

Authors: Rischen, T., Geisbüsch, K., Ruppert, D. & Fischer, K. (2021)  
J Insect Conserv. <https://doi.org/10.1007/s10841-021-00363-2>

### ABSTRACT

Agricultural intensification and the concomitant landscape homogenisation is leading to a worldwide decline in farmland biodiversity. Non-crop habitats in agroecosystems may counteract the loss of arthropods such as spiders and thus contribute to sustainable agriculture. However, the effectiveness of field margins and set-aside wildflower-sown patches in maintaining spider diversity is not well understood. Here, we investigated the effects of three different non-crop habitats, namely field margins, set-aside wildflower-sown patches under power poles ('power pole islands'), and grassland fallows on spider diversity as compared to wheat fields in an agricultural landscape in western Germany. Using pitfall trapping and suction sampling, we show that species richness and overall conservation value were higher in non-crop habitats than in wheat fields. Interestingly, field margins and power pole islands differed from long-term grassland fallows only in conservation value, which was significantly higher in grassland fallows. Species assemblages differed considerably between grassland fallows, field margins and power pole islands, and wheat fields, documenting the added value of using different conservation strategies.

### *Implications for insect conservation*

Small-scale non-crop habitats adjacent to wheat fields were surprisingly effective in promoting spider diversity in an agricultural landscape, with field margins and power pole islands being equally effective. To maximise overall diversity in agricultural landscapes, we propose a combination of larger long-term fallows and smaller non-crop habitats such as field margins or set-aside wildflower-sown patches.

**Keywords:** Agriculture • Biodiversity conservation • Body size • Non-crop habitat • Pitfall trapping • Suction sampling



---

# CHAPTER 4

## Responses of selected beetle families (Carabidae, Chrysomelidae, Curculionidae) to non-crop habitats in an agricultural landscape

---

### Paper 4

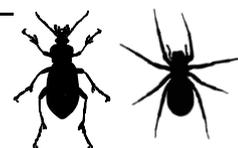
Published article

Authors: Rischen, T., Ehringhausen, K., Heyer, M. & Fischer, K. (2022)  
Biologia. <https://doi.org/10.1007/s11756-022-01100-z>

#### ABSTRACT

Agricultural intensification has caused a simplification of agricultural landscapes, accompanied by increasing field sizes and a reduction of non-crop habitats. To mitigate negative impacts of intensification, it is necessary to understand to what extent different non-crop habitats contribute to the maintenance of biodiversity in agroecosystems. Here, we compared the taxonomic diversity of three beetle families among four habitat types - wheat fields, grassy field margins, wildflower-sown areas under power poles, and permanent grassland fallows, in an agricultural landscape in western Germany. Carabidae were caught by pitfall trapping, Chrysomelidae and Curculionidae by suction sampling. We found surprisingly little variation among habitat types, though the rarefied species number tended to be higher in grassland fallows and field margins than under power poles and in wheat fields. Nevertheless, species assemblages differed substantially among habitat types. In Carabidae, grassland fallows were dominated by hygrophilous species with poor dispersal ability as opposed to all other habitat types being dominated by open landscape species with high dispersal ability. In Chrysomelidae and Curculionidae, power pole islands differed from the other habitat types with predominantly open landscape species, whereas wheat fields and grassland fallows were clearly dominated by eurytopic species. Our results thus highlight the need for a combination of different conservation measures for enhancing the functional diversity of beetle assemblages.

**Keywords:** Agriculture • biodiversity conservation • dispersal ability • non-crop habitat • pitfall trapping • suction sampling



---

## CHAPTER 5

# Configurational landscape heterogeneity: crop-fallow boundaries enhance the taxonomic diversity of carabid beetles and spiders

---

**Paper 5**

Submitted article

Authors: Rischen, T., Kaffenberger, M., Plath, E., Wolff, J. & Fischer, K. (*in review*)

### ABSTRACT

Arthropod biodiversity in agricultural landscapes is favoured by high levels of compositional and configurational heterogeneity. In terms of composition, the high value of non-crop habitats is firmly established. In contrast, the causes underlying positive effects of configurational heterogeneity, i.e. patch size and boundary length, are less well understood. We here test the hypothesis that boundaries comprise valuable habitats in its own right by enhancing the taxonomic diversity of carabid beetles and spiders. We used pitfall traps placed along transects running from the interior of wheat fields across the habitat boundary to the interior of grassland fallows. Taxonomic diversity was highest around the boundaries due to (1) spillover effects but also (2) species showing a distinct preference for edge habitat. For carabids, habitat boundaries harboured distinct species assemblages. Grassland fallows had, especially in spiders, positive effects on the taxonomic diversity of crop fields close to the boundary, while no negative effects of crop fields on adjacent fallows could be found. Overall, taxonomic diversity was higher in grassland fallows than in crop fields, though differences were surprisingly small. The high taxonomic diversity found for boundaries suggest that these may comprise valuable habitats in its own rights, which in turn may causally underpin positive effects of configurational heterogeneity on arthropod diversity in agroecosystems. Thus, increasing configurational heterogeneity, e.g. by promoting small-scale farming, seems an important tool for preserving farmland biodiversity.

**Keywords:** agroecosystems • biodiversity conservation • compositional landscape heterogeneity • edge effects • non-crop habitat

---

# GENERAL DISCUSSION

---



© Christian Geisbüsch

Land-use type affected the taxonomic and functional diversity of beetles and spiders in the intensively used agricultural landscape studied here. Long-term grassland fallows with their complex habitat structures and variation in soil moisture were particularly effective in maintaining both arthropod taxa. Here, beetle and spider diversity was significantly higher in grassland fallows than wheat fields, which is in line with other agroecological studies (e.g. Hanson et al. 2016; Birkhofer et al. 2018). Surprisingly, all non-crop habitat, namely grassy field margins, set-aside wildflower-sown patches and grassland fallows, were statistically indistinguishable. Furthermore, species assemblages differed substantially among land-use types, with the largest within-group variation on grassland fallows, while wheat fields were remarkable homogeneous. Arthropod communities in wheat fields exhibited lower trait richness and were dominated by a low number of species adapted to such ephemeral habitats, whereas grassland fallows provided suitable habitats for habitat specialists and threatened species in agroecosystems, as reflected in higher conservation values. Overall, all types of non-crop habitats studied here support beetle and spider diversity in the agricultural landscape in different ways and complement each other. The surprisingly high taxonomic diversity found for habitat boundaries also suggest that these may comprise valuable habitats in its own rights for supporting arthropods in agricultural landscapes.

In the following sections, the main research questions posed at the beginning (**Q1-5**) are addressed and discussed in detail.

### **Land-use effects on beetle and spider communities (Q1)**

Beetle and spider communities had as expected the lowest taxonomic and functional diversity in wheat fields, i.e. the most disturbed land-use type. The lower the land-use intensity the higher the arthropod diversity, with consistently highest values in grassland fallows. However, the diversity of grassland fallows did not differ statistically from grassy field margins and set-aside wildflower-sown habitats. Nevertheless, long-term grassland fallows in agricultural landscapes are important habitats for arthropods, serving as sources and consequently often have higher diversity (Hendrickx et al. 2007; Birkhofer et al. 2018; Feng et al. 2021). Although all non-crop habitats were preferentially colonised by beetles and spiders compared to wheat fields, different land-use types appear to shape

arthropod community structures. Consequently, there were strong differences in the assemblages among habitat types, with rather homogeneous assemblages found among wheat fields, while those of grassland fallows showed the largest within-group variation. Accordingly, all types of non-crop habitats had positive impacts on farmland arthropods, which can be explained by the reduced land-use intensity, allowing species to move into these habitats during field disturbances (Schneider et al. 2016).

Because of their dryness and periodic disturbances (e.g. due to agrochemical use or tillage), arable fields represent unsuitable areas for many organisms and therefore have a detrimental effect on farmland diversity (Thorbeck and Bilde 2004; Batáry et al. 2008, 2012). More frequently disturbed land-use types such as wheat fields are often characterised by species with higher dispersal ability and smaller body size as well as communities with lower trait diversity (Birkhofer et al. 2015). This pattern is also reflected in the wheat field communities found here, which were dominated by xerophilous and euryoecious species characteristic for croplands. Despite the low arthropod diversity, wheat fields were dominated by ground-dwelling predators that thrive in arable fields. For example, common carabid species typical of arable fields, such as *Anchomenus dorsalis*, *Poecilus cupreus* and *Pterostichus melanarius*, were found with high numbers of individuals in wheat fields. Among spiders, so-called ‘agrobionts’, such as *Agyreta rurestris*, *Oedothorax apicatus* and *Tenuiphantes tenuis* dominated the wheat fields in high densities, as also shown in other studies (Topping and Sunderland 1998; Gallé et al. 2018a). In particular, many spider species of the Linyphiidae thrive in agricultural landscapes (Pluess et al. 2008), as they readily recolonise fields after agricultural disturbances through aerial dispersal (Pfiffner and Luka 2003; Öberg et al. 2007). Predatory arthropods, including carabids, staphylinids and spiders, generally contribute to pest control by e.g. reducing aphid densities in arable fields (Sunderland and Samu 2000; Collins et al. 2002). To increase the sustainability of agroecosystems, more and more cropping systems are being promoted that rely on ecosystem services such as biological control (see Rusch et al. 2010). However, the development of such beneficial arthropod populations additionally relies on adjacent non-crop habitats as important sources from which natural enemies can spillover into fields (Tschardt et al. 2007; Schmidt-Entling and Döbeli 2009; Schneider et al. 2016).

In the present study, many species of Carabidae, Staphylinidae and spiders in particular showed a preference for field margins adjacent to wheat fields and oilseed rape fields, which may be related to resource complementation (Dunning et al. 1992). Field margins in agricultural landscapes play an important role for many ground beetle species, for example, as they use several different habitat types for food resources or overwintering during their life span (Coombes and Sothertons 1986; Dufлот et al. 2017). In addition, frequent movement of ground-dwelling arthropods between wheat fields and adjacent habitats may result in higher activity densities in field margins (Birkhofer et al. 2018). Because crop type shapes the species community within fields, species composition differed between field margins adjacent to wheat and oilseed rape fields. The slightly higher proportion of carabids and spiders in oilseed rape margins compared to wheat margins is likely due to the higher availability of prey species attracted to flowering rapeseed (Haddad et al. 2009). This effect also appears to be reflected in set-aside wildflower-sown areas, in that these areas have been colonised by many predatory beetle and spider species that are also common in wheat fields. Establishment of additional plant species by sowing seed mixtures attracts primarily phytophagous beetle families such as Chrysomelidae and Curculionidae (Frank et al. 2012). Thus, the occurrence of many phytophagous species in set-aside fields and power pole islands was related to the presence of their food plants. Overall, all non-crop habitats support an arthropod community with higher trait richness than wheat fields, which was most pronounced in grassland fallows. The latter proved to be an essential habitat type for hygrophilous species and also supported larger species and species with lower dispersal ability. In particular, specialists were able to use grassland fallows as refuges because they had different environmental conditions than the surrounding area. Nonetheless, all non-crop habitats provided suitable habitats for a variety of threatened beetle and spider species, as reflected in the higher conservation values compared to wheat fields. The lack of significant differences in the number of individuals among habitat types in this thesis may be related to the higher densities of agrobionts in wheat fields. The use of pitfall traps also records activity density rather than abundance (Sunderland and Topping 1995). For example, arthropod activity is strongly influenced by temperature, so activity density may be increased in habitats with sparse vegetation, such as wheat fields (see Saska et al.

2013). Denser vegetation in non-crop habitats may also limit movement on the ground surface, resulting in lower activity densities (c.f Lemke and Poehling 2002).

### **Evaluation of non-crop habitats as conservation measures (Q2)**

Interestingly, all non-crop habitats did not differ significantly in species diversity and richness of beetles and spiders. The linear grassy field margins and recently set-aside areas were similarly effective for ground-dwelling predatory arthropod taxa as long-term grassland fallows. However, small-scale non-crop habitats (field margins and power pole islands) showed lower values than grassland fallows in some cases, which may be related to the loss of diversity due to the proximity of wheat fields (Rand et al. 2006). In addition, a recent study showed that newly created non-crop habitats (such as wildflower-sown areas studied) exhibited a similar carabid diversity than crop fields (Hussain et al. 2021), with the lifespan of such areas being an important factor (see e.g. Ganser et al. 2019). Nevertheless, arthropod species appear to migrate to adjacent non-crop habitats when within-field conditions are unfavourable (e.g. due to harvest events and crop rotation; Burel et al. 2013). Even the small-scale power pole islands within wheat fields harboured surprisingly high arthropod diversity and provided suitable habitats, especially for phytophagous species. Such habitats can connect isolated fragments of non-crop habitats and create a more heterogeneous agricultural landscape (Critchley et al. 2004; Kovács-Hostyánszki et al. 2011; Morris et al. 2011)

Long-term grassland fallows occur sporadically in the agricultural landscape of Maifeld and are surrounded by cropland. Due to the long history of intensive agriculture in the study area, there may have been an impoverishment of the local species pool, which may explain the lack of significant differences among all studied non-crop habitats. For example, Sirami et al. (2019) point out the importance of landscape-level effects on biodiversity decline in agricultural landscapes, as strong effects lead to homogenisation of habitat types within a landscape. Nevertheless, long-term grassland fallows showed the largest variation in species composition compared to all other habitat types. Therefore, the results of the present work highlight the particular importance of long-term grassland fallows as essential habitats for the survival of threatened species and specialists in agroecosystems that may otherwise become extinct.

### **Body size as suitable bioindicator for land-use intensity (Q3)**

When carabids and staphylinids were excluded, the remaining beetle families showed a decrease in community mean body size with increasing land-use intensity, with highest values in grassland fallows. The above-mentioned higher activity densities of large predatory carabids such as *P. melanarius* in wheat fields and grassy field margins due to the availability of prey species may be one reason why carabids are less suitable indicators of land-use intensity (Collins et al. 2002). For spiders, community mean body size decreased with increasing human disturbance, with significantly lower values in wheat fields and the highest in grassland fallows. The strong influence of land-use intensification on spider community body size has been also observed in previous studies (Rusch et al. 2014, 2015; Schirmel et al. 2016; Birkhofer et al. 2017). Therefore, highly dynamic habitats tend to be inhabited by smaller species compared to more stable habitats, often due to their better dispersal ability (Simons et al. 2016). For example, large spider species cannot disperse by ballooning, whereas small species can recolonise disturbed habitats more quickly due to aeronautical dispersal (Samu et al. 1999; Entling et al. 2011). Consequently, spider body size may be a valuable bioindicator of land-use intensity in agriculture landscapes. However, body size may also be influenced by various mechanisms such as dispersal, competition or resource use (Entling et al. 2010; Gallé et al. 2018a). Other studies already suggest that the observed size pattern may also occur in other environments (e.g. Bonte et al. 2002; Schmidt et al. 2004; Schirmel et al. 2012; Birkhofer et al. 2015b), so further investigations are needed.

### **Effects of configurational landscape heterogeneity (Q4/Q5)**

Landscape heterogeneity, consisting of composition and configuration of matrix habitats (Fahrig et al. 2011), influences the arthropod diversity in agricultural landscapes (Purtauf et al. 2005; Duflot et al. 2014). In terms of compositional heterogeneity (number and proportion of different habitat types), the present work highlights the importance of non-crop habitats in agroecosystems. Thus, an increasing proportion of non-crop habitats leads to an increase in farmland biodiversity, which may also be attributed to resource complementarity (Tschardt et al. 2012b; Duflot et al. 2017). However, variation in configurational heterogeneity, i.e., patch size and boundary length, can also influence

ecological processes (e.g. Schweiger et al. 2005) and thus arthropod communities. Habitat size did not affect taxonomic and functional diversity of carabids and spiders here, as even small non-crop habitats such as linear field margins and power pole islands favoured biodiversity. Especially in fragmented agriculture landscapes, many arthropod species use edge habitats for migration (Roume et al. 2011; Blitzer et al. 2012; Nardi et al. 2019). Smaller non-crop habitats can therefore serve as stepping stones that improve connectivity in highly fragmented landscapes (Schirmel et al. 2016) and contribute to the conservation of farmland biodiversity (Bianchi et al. 2006; Hendrickx et al. 2007). Nonetheless, edge effects can also shape species communities in field margins and power pole islands due to their small patch size and proximity to wheat fields (Samu and Szinetár 2002; Blitzer et al. 2012). Since spillover effects are amplified at patch edges, they are more likely in smaller areas due to their high edge-interior ratio (Madeira et al. 2016). Therefore, the higher diversity observed in these habitats is related to the presence of additional species, such as agrobionts, from the surrounding area.

Considering the boundaries between wheat fields and grassland fallows, edge effects led to partial mixing of communities of both adjacent habitat types, resulting in a particularly high arthropod diversity at the boundaries. Because habitat boundaries are susceptible to edge and spillover effects caused by local variation in abiotic and biotic parameters (Ries et al. 2004), the high taxonomic diversity at crop-fallow boundaries can be explained mainly by spillover effects. Boundary assemblages were therefore composed of species preferring wheat fields, grassland fallows or the boundary itself (see also Benton et al. 2003). For carabids in particular, habitat boundaries harboured different species communities compared to adjacent habitat types. Duflot et al. (2017) describe boundaries as essential habitats for farmland beetles, and their positive influence is enhanced with increasing boundary length and dissimilarity between both habitat types. Therefore, the different site conditions of wheat fields and grassland fallows may have enhanced the edge effect on arthropod diversity here. Indeed, the more different the habitat type adjacent to wheat fields, the stronger the spillover effect (Madeira et al. 2016). Nonetheless, the results suggest that habitat boundaries are valuable habitats in their own right, which in turn may underlie the positive effects of configurational heterogeneity on arthropod diversity in agricultural landscapes. The demonstrated positive effect of

grassland fallows on wheat field diversity near the boundaries further supports the importance of nearby non-crop habitats for cropland communities (Michalko et al. 2019), and the positive effects of configurational heterogeneity on biodiversity.

Finally, the size and spatial configuration of landscape features are important predictors of local arthropod diversity in agricultural landscapes, which in turn determine the level of edge density and therefore the configurational landscape heterogeneity (Holzschuh et al. 2010; Perovic et al. 2015). Increased heterogeneity of the agricultural matrix through small-scale structures may favour habitat boundaries and contribute to increased farmland biodiversity (Aviron et al. 2005; Hendrickx et al. 2007).

## **Conclusions**

In intensive agricultural landscapes, long-term grassland fallows represent important conservation areas for arthropods (Geiger et al. 2009; Holland et al. 2017), evidenced by a high taxonomic and functional diversity of spiders and beetles in such habitat types in the region Maifeld. Together with other non-crop habitats, such as linear field margins or set-aside wildflower-sown areas, they can counteract the negative effects of agricultural intensification (Benton et al. 2003; Kovács-Hostyánszki et al. 2011). Hence, the establishment of non-crop habitats through agri-environmental schemes is important for a large number of taxa (Hendrickx et al. 2007; Billeter et al. 2008), e.g. due to lower local disturbances. All conservation measures investigated here promote beetle and spider diversity in different ways and complement each other, which indicates the positive effects of compositional landscape heterogeneity (Perovic et al. 2015). However, since arthropods use different habitat types in a complementary manner during their life span and are susceptible to edge effects (Blitzer et al. 2012; Duflot et al. 2017), configurational heterogeneity also appears to be important. The present results indicate that small-scale non-crop habitats influence arthropod communities in the agricultural matrix due to their higher edge-interior ratios, and boundaries are important habitats in their own right. The fact that threatened species and specialists were mainly found in long-term grassland fallows suggests that habitat age and vegetation structure are critical factors affecting arthropod communities. Apart from the high conservation value of grassland fallows, all non-crop habitats were equally effective in promoting arthropods, possibly reflecting the

long history of intensive agriculture in the study area, which may have generally impoverished biodiversity (Sirami et al. 2019). Maintaining existing grassland fallows, creating additional non-crop habitats, and increasing habitat boundaries in agricultural landscapes are essential for improving local beetle and spider diversity. Although small-scale linear or rectangular non-crop habitats make up a relatively small proportion of the overall landscape, they can contribute to the connection of different habitat types and resource complementarity for farmland species (Critchley et al. 2004; Duflot et al. 2017). Consequently, a combination of various small- and large-scale greening measures combined with reduced field sizes would increase the compositional and configurational landscape heterogeneity of the region Maifeld and counteract the loss of farmland biodiversity.

---

## REFERENCES

---

- Agrarmeteorologie Rheinland-Pfalz (2020) Langjährige Mittelwerte der Wetterstation Münstermaifeld. <https://www.am.rlp.de>. Accessed 10 Sep 2020
- Anjum-Zubair M, Entling MH, Bruckner A, et al (2015) Differentiation of spring carabid beetle assemblages between semi-natural habitats and adjoining winter wheat. *Agric For Entomol* 17:355–365. <https://doi.org/10.1111/afe.12115>
- Antrop M (2005) Why landscapes of the past are important for the future. *Landsc Urban Plan* 70:21–34. <https://doi.org/10.1016/j.landurbplan.2003.10.002>
- Antrop M (1997) The concept of traditional landscapes as a base for landscape evaluation and planning. The example of Flanders Region. *Landsc Urban Plan* 38:105–117. [https://doi.org/10.1016/S0169-2046\(97\)00027-3](https://doi.org/10.1016/S0169-2046(97)00027-3)
- Aviron S, Burel F, Baudry J, Schermann N (2005) Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agric Ecosyst Environ* 108:205–217. <https://doi.org/10.1016/j.agee.2005.02.004>
- Batáry P, Holzschuh A, Orci KM, et al (2012) Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agric Ecosyst Environ* 146:130–136. <https://doi.org/10.1016/j.agee.2011.10.018>
- Batáry P, Kovács A, Báldi A (2008) Management effects on carabid beetles and spiders in Central Hungarian grasslands and cereal fields. *Community Ecol* 9:247–254. <https://doi.org/10.1556/ComEc.9.2008.2.14>
- Benton TG, Bryant DM, Cole L, Crick HQP (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *J Appl Ecol* 39:673–687. <https://doi.org/https://doi.org/10.1046/j.1365-2664.2002.00745.x>
- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol Evol* 18:182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)
- Berglund BE, Kitagawa J, Lagerås P, et al (2014) Traditional farming landscapes for sustainable living in Scandinavia and Japan: Global revival through the Satoyama initiative. *Ambio* 43:559–578. <https://doi.org/10.1007/s13280-014-0499-6>
- Bianchi FJJA, Booij CJH, Tschamtker T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc R Soc B* 273:1715–1727. <https://doi.org/10.1098/rspb.2006.3530>

- Billetter R, Liira J, Bailey D, et al (2008) Indicators for biodiversity in agricultural landscapes: A pan-European study. *J Appl Ecol* 45:141–150. <https://doi.org/10.1111/j.1365-2664.2007.01393.x>
- Birkhofer K, Fevrier V, Heinrich A, et al (2018) The contribution of CAP greening measures to conservation biological control at two spatial scales. *Agric Ecosyst Environ* 255:84–94. <https://doi.org/10.1016/j.agee.2017.12.026>
- Birkhofer K, Gossner MM, Diekötter T, et al (2017) Land-use type and intensity differentially filter traits in above- and below-ground arthropod communities. *J Anim Ecol* 86:511–520. <https://doi.org/10.1111/1365-2656.12641>
- Birkhofer K, Smith HG, Weisser WW, et al (2015) Land-use effects on the functional distinctness of arthropod communities. *Ecography (Cop)* 38:001–012. <https://doi.org/10.1111/ecog.01141>
- Blake S, Foster GN, Eyre MD, Luff ML (1994) Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia (Jena)* 38:502–512
- Blitzer EJ., Dormann CF, Holzschuh A, et al (2012) Spillover of functionally important organisms between managed and natural habitats. *Agric Ecosyst Environ* 146:34–43. <https://doi.org/10.1016/j.agee.2011.09.005>
- Bonte D, Baert L, Maelfait J-P (2002) Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *J Arachnol* 30:331–343. [https://doi.org/https://doi.org/10.1636/0161-8202\(2002\)030\[0331:SASASI\]2.0.CO;2](https://doi.org/https://doi.org/10.1636/0161-8202(2002)030[0331:SASASI]2.0.CO;2)
- Bowler DE, Heldbjerg H, Fox AD, et al (2019) Long-term declines of European insectivorous bird populations and potential causes. *Conserv Biol* 33:1120–1130. <https://doi.org/10.1111/cobi.13307>
- Burel F, Aviron S, Baudry J, et al (2013) The structure and dynamics of agricultural landscapes as divers of biodiversity. In: Fu B, Jones KB (eds) *Landscape Ecology for Sustainable Environment and Culture*. Springer-Verlag, pp 285–308
- Butt A, Sherawat SM (2012) Effect of different agricultural practices on spiders and their prey populations in small wheat fields. *Acta Agric Scand* 62:374–382. <https://doi.org/10.1080/09064710.2011.624544>
- Carvell C, Meek WR, Pywell RF (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J Appl Ecol* 44:29–40. <https://doi.org/10.1111/j.1365-2664.2006.01249.x>
- Clough Y, Kruess A, Kleijn D, Tscharrntke T (2005) Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *J Biogeogr* 32:2007–2014. <https://doi.org/10.1111/j.1365-2699.2005.01367.x>
- Collins KL, Boatman ND, Wilcox A, et al (2002) Influence of beetle banks on cereal

- aphid predation in winter wheat. *Agric Ecosyst Environ* 93:337–350.  
[https://doi.org/https://doi.org/10.1016/S0167-8809\(01\)00340-1](https://doi.org/https://doi.org/10.1016/S0167-8809(01)00340-1)
- Coombes DS, Sothertons NW (1986) The dispersal and distribution of polyphagous predatory Coleoptera in cereals. *Ann Appl Biol* 108:461–474.  
<https://doi.org/10.1111/j.1744-7348.1986.tb01985.x>
- Critchley CNR, Allen DS, Fowbert JA, et al (2004) Habitat establishment on arable land: assessment of an agri-environment scheme in England, UK. *Biol Conserv* 119:429–442. <https://doi.org/10.1016/j.biocon.2004.01.004>
- Diekötter T, Wamser S, Wolters V, Birkhofer K (2010) Landscape and management effects on structure and function of soil arthropod communities in winter wheat. *Agric Ecosyst Environ* 137:108–112. <https://doi.org/10.1016/j.agee.2010.01.008>
- Dudley N, Alexander S (2017) Agriculture and biodiversity: a review. *Biodiversity* 18:45–49. <https://doi.org/10.1080/14888386.2017.1351892>
- Duelli P, Obrist MK (2003) Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat islands. *Basic Appl Ecol* 4:129–138.  
<https://doi.org/10.1078/1439-1791-00140>
- Duflot R, Aviron S, Ernoult A, et al (2015) Reconsidering the role of ‘semi-natural habitat’ in agricultural landscape biodiversity: a case study. *Ecol Res* 30:75–83.  
<https://doi.org/10.1007/s11284-014-1211-9>
- Duflot R, Ernoult A, Aviron S, et al (2017) Relative effects of landscape composition and configuration on multi-habitat gamma diversity in agricultural landscapes. *Agric Ecosyst Environ* 241:62–69. <https://doi.org/10.1016/j.agee.2017.02.035>
- Duflot R, Georges R, Ernoult A, et al (2014) Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica* 56:19–26.  
<https://doi.org/10.1016/j.actao.2014.01.004>
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175
- Ekschmitt K, Wolters V, Weber M (1997) Spiders, carabids, and staphylinids: the ecological potential of predatory macroarthropods. In: Benckiser G (ed) *Fauna in Soil Ecosystems*. Marcel Dekker, New York, pp 307–362
- Entling MH, Stämpfli K, Ovaskainen O (2011) Increased propensity for aerial dispersal in disturbed habitats due to intraspecific variation and species turnover. *Oikos* 120:1099–1109. <https://doi.org/10.1111/j.1600-0706.2010.19186.x>
- Entling W, Schmidt-Entling MH, Bacher S, et al (2010) Body size–climate relationships of European spiders. *J Biogeogr* 37:477–485. <https://doi.org/https://doi.org/10.1111/j.1365-2699.2009.02216.x>
- Ewers RM, Thorpe S, Didham RK (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. 88:96–106.

- [https://doi.org/https://doi.org/10.1890/0012-9658\(2007\)88\[96:SIBEEA\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2007)88[96:SIBEEA]2.0.CO;2)
- Fahrig L, Baudry J, Brotons L, et al (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol Lett* 14:101–112.  
<https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- Fahrig L, Girard J, Duro D, et al (2015) Farmlands with smaller crop fields have higher within-field biodiversity. *Agric Ecosyst Environ* 200:219–234.  
<https://doi.org/10.1016/j.agee.2014.11.018>
- Feng L, Arvidsson F, Smith HG, Birkhofer K (2021) Fallows and permanent grasslands conserve the species composition and functional diversity of carabid beetles and linyphiid spiders in agricultural landscapes. *Insect Conserv Divers*.  
<https://doi.org/10.1111/icad.12520>
- Foley JA, Ramankutty N, Brauman KA, et al (2011) Solutions for a cultivated planet. *Nature* 478:337–342. <https://doi.org/10.1038/nature10452>
- Frank T, Aeschbacher S, Zaller JG (2012) Habitat age affects beetle diversity in wildflower areas. *Agric Ecosyst Environ* 152:21–26.  
<https://doi.org/10.1016/j.agee.2012.01.027>
- Gallé R, Császár P, Makra T, et al (2018a) Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites. *Landsc Ecol* 33:1435–1446. <https://doi.org/10.1007/s10980-018-0677-1>
- Gallé R, Geppert C, Földesi R, et al (2020) Arthropod functional traits shaped by landscape-scale field size, local agri-environment schemes and edge effects. *Basic Appl Ecol* 48:1–10. <https://doi.org/10.1016/j.baae.2020.09.006>
- Gallé R, Happe A-K, Baillod AB, et al (2018b) Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *J Appl Ecol* 56:63–72. <https://doi.org/10.1111/1365-2664.13257>
- Ganser D, Knop E, Albrecht M (2019) Sown wildflower strips as overwintering habitat for arthropods: Effective measure or ecological trap? *Agric Ecosyst Environ* 275:123–131. <https://doi.org/10.1016/j.agee.2019.02.010>
- Geiger F, Wäckers FL, Bianchi FJJA (2009) Hibernation of predatory arthropods in semi-natural habitats. *BioControl* 54:529–535. <https://doi.org/10.1007/s10526-008-9206-5>
- Gray JS (1989) Effects of environmental stress on species rich assemblages. *Biol J Linn Soc* 37:19–32. <https://doi.org/https://doi.org/10.1111/j.1095-8312.1989.tb02003.x>
- Haddad NM, Crutsinger GM, Gross K, et al (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecol Lett* 12:1029–1039.  
<https://doi.org/https://doi.org/10.1111/j.1461-0248.2009.01356.x>
- Hanson HI, Palmu E, Birkhofer K, et al (2016) Agricultural land use determines the trait composition of ground beetle communities. *PLoS One* 11:1–13.

- <https://doi.org/10.1371/journal.pone.0146329>
- Hatten TD, Bosque-Pérez NA, Labonte JR, et al (2007) Effects of tillage on the activity density and biological diversity of carabid beetles in spring and winter crops. *Environ Entomol* 36:356–368. [https://doi.org/10.1603/0046-225X\(2007\)36\[356:EOTOTA\]2.0.CO;2](https://doi.org/10.1603/0046-225X(2007)36[356:EOTOTA]2.0.CO;2)
- Hendrickx F, Maelfait J, Van Wingerden W, et al (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J Appl Ecol* 44:340–351. <https://doi.org/10.1111/j.1365-2664.2006.01270.x>
- Hof AR, Bright PW (2010) The impact of grassy field margins on macro-invertebrate abundance in adjacent arable fields. *Agric Ecosyst Environ* 139:280–283. <https://doi.org/10.1016/j.agee.2010.08.014>
- Holland JM, Douma JC, Crowley L, et al (2017) Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agron Sustain Dev* 37:31. <https://doi.org/10.1007/s13593-017-0434-x>
- Holzschuh A, Steffan-dewenter I, Tschamntke T (2010) How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *J Anim Ecol* 79:491–500. <https://doi.org/10.1111/j.1365-2656.2009.01642.x>
- Hussain RI, Brandl M, Maas B, et al (2021) Re-established grasslands on farmland promote pollinators more than predators. *Agric Ecosyst Environ* 319:107543. <https://doi.org/10.1016/j.agee.2021.107543>
- Knapp M, Řezáč M (2015) Even the smallest son-crop habitat islands could be beneficial: distribution of carabid beetles and spiders in agricultural landscape. *PLoS One* 1–20. <https://doi.org/https://doi.org/10.1371/journal.pone.0123052>
- Knapp M, Seidl M, Knappová J, et al (2019) Temporal changes in the spatial distribution of carabid beetles around arable field-woodlot boundaries. *Sci Rep* 9:8967. <https://doi.org/10.1038/s41598-019-45378-7>
- Kovács-Hostyánszki A, Korösi Á, Orci KM, et al (2011) Set-aside promotes insect and plant diversity in a Central European country. *Agric Ecosyst Environ* 141:296–301. <https://doi.org/10.1016/j.agee.2011.03.004>
- Kremen C, Williams NM, Aizen MA, et al (2007) Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecol Lett* 10:299–314. <https://doi.org/10.1111/j.1461-0248.2007.01018.x>
- Kromp B (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agric Ecosyst Environ* 74:187–228. <https://doi.org/10.1016/b978-0-444-50019-9.50014-5>

- Lemke A, Poehling HM (2002) Sown weed strips in cereal fields: overwintering site and “source” habitat for *Oedothorax apicatus* (Blackwall) and *Erigone atra* (Blackwall) (Araneae: Erigonidae). *Agric Ecosyst Environ* 90:67–80. [https://doi.org/10.1016/S0167-8809\(01\)00173-6](https://doi.org/10.1016/S0167-8809(01)00173-6)
- Lövei GL, Sunderland KD (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annu Rev Entomol* 41:231–256. <https://doi.org/10.1146/annurev.ento.41.1.231>
- Madeira F, Tschardt T, Elek Z, et al (2016) Spillover of arthropods from cropland to protected calcareous grassland – the neighbouring habitat matters. *Agric Ecosyst Environ* 235:127–133. <https://doi.org/10.1016/j.agee.2016.10.012>
- Magura T (2002) Carabids and forest edge: Spatial pattern and edge effect. *For Ecol Manage* 157:23–37. [https://doi.org/10.1016/S0378-1127\(00\)00654-X](https://doi.org/10.1016/S0378-1127(00)00654-X)
- Marasas ME, Sarandón SJ, Cicchino A (2010) Semi-natural habitats and field margins in a typical agroecosystem of the Argentinean Pampas as a reservoir of carabid beetles. *J Sustain Agric* 34:153–168. <https://doi.org/10.1080/10440040903482563>
- Marrec R, Caro G, Miguet P, et al (2017) Spatiotemporal dynamics of the agricultural landscape mosaic drives distribution and abundance of dominant carabid beetles. *Landsc Ecol* 32:2383–2398. <https://doi.org/10.1007/s10980-017-0576-x>
- Martin EA, Dainese M, Clough Y, et al (2019) The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecol Lett* 22:1083–1094. <https://doi.org/10.1111/ele.13265>
- Meek B, Loxton D, Sparks T, et al (2002) The effect of arable field margin composition on invertebrate biodiversity. *Biol Conserv* 106:259–271. [https://doi.org/10.1016/S0006-3207\(01\)00252-X](https://doi.org/10.1016/S0006-3207(01)00252-X)
- Mestre J, Schirmel J, Hetz J, et al (2018) Both woody and herbaceous semi-natural habitats are essential for spider overwintering in European farmland. *Agric Ecosyst Environ* 267:141–146. <https://doi.org/10.1016/j.agee.2018.08.018>
- Michalko R, Pekár S, Dul’a M, Entling MH (2019) Global patterns in the biocontrol efficacy of spiders: A meta-analysis. *Glob Ecol Biogeogr* 28:1366–1378. <https://doi.org/10.1111/geb.12927>
- Miyashita T, Chishiki Y, Takagi SR (2012) Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape. *Popul Ecol* 54:573–581. <https://doi.org/10.1007/s10144-012-0329-2>
- Morris AJ, Hegarty J, Báldi A, Robijns T (2011) Setting aside farmland in Europe: The wider context. *Agric Ecosyst Environ* 143:1–2. <https://doi.org/10.1016/j.agee.2011.07.013>
- MUEEF RLP (2021) Großlandschaften und Landschaftsräume. In: Minist. für Umwelt,

- Energie, Ernährung und Forsten Rheinland-Pfalz.  
<https://naturschutz.rlp.de/index.php?q=node/97>. Accessed 21 Feb 2022
- Nardi D, Lami F, Pantini P, Marini L (2019) Using species-habitat networks to inform agricultural landscape management for spiders. *Biol Conserv* 239:.  
<https://doi.org/10.1016/j.biocon.2019.108275>
- Nyffeler M, Sunderland KD (2003) Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. *Agric Ecosyst Environ* 95:579–612. [https://doi.org/10.1016/S0167-8809\(02\)00181-0](https://doi.org/10.1016/S0167-8809(02)00181-0)
- Öberg S, Ekbom B, Bommarco R (2007) Influence of habitat type and surrounding landscape on spider diversity in Swedish agroecosystems. *Agric Ecosyst Environ* 122:211–219. <https://doi.org/10.1016/j.agee.2006.12.034>
- Palmu E, Ekroos J, Hanson HI, et al (2014) Landscape-scale crop diversity interacts with local management to determine ground beetle diversity. *Basic Appl Ecol* 15:241–249. <https://doi.org/10.1016/j.baae.2014.03.001>
- Perkins AJ, Maggs HE, Watson A, Wilson JD (2011) Adaptive management and targeting of agri-environment schemes does benefit biodiversity: a case study of the corn bunting *Emberiza calandra*. *J Appl Ecol* 48:514–522.  
<https://doi.org/10.1111/j.1365-2664.2011.01958.x>
- Perovic D, Gámez-Virués S, Börschig C, et al (2015) Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *J Appl Ecol* 52:505–513. <https://doi.org/10.1111/1365-2664.12394>
- Pfiffner L, Luka H (2000) Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agric Ecosyst Environ* 78:215–222.  
[https://doi.org/10.1016/S0167-8809\(99\)00130-9](https://doi.org/10.1016/S0167-8809(99)00130-9)
- Pfiffner L, Luka H (2003) Effects of low-input farming systems on carabids and epigeal spiders - a paired farm approach. *Basic Appl Ecol* 4:117–127.  
<https://doi.org/10.1078/1439-1791-00121>
- Plieninger T, Höchtl F, Spek T (2006) Traditional land-use and nature conservation in European rural landscapes. *Environ Sci Policy* 9:317–321.  
<https://doi.org/10.1016/j.envsci.2006.03.001>
- Pluess T, Opatovsky I, Gavish-Regev E, et al (2008) Spiders in wheat fields and semi-desert in the Negev (Israel). *J Arachnol* 36:368–373. <https://doi.org/10.1636/CT07-116.1>
- Pluess T, Opatovsky I, Gavish-Regev E, et al (2010) Non-crop habitats in the landscape enhance spider diversity in wheat fields of a desert agroecosystem. *Agric Ecosyst Environ* 137:68–74. <https://doi.org/10.1016/j.agee.2009.12.020>
- Prieto-Benítez S, Méndez M (2011) Effects of land management on the abundance and

- richness of spiders (Araneae): A meta-analysis. *Biol Conserv* 144:683–691. <https://doi.org/10.1016/j.biocon.2010.11.024>
- Purtauf T, Roschewitz I, Dauber J, et al (2005) Landscape context of organic and conventional farms: Influences on carabid beetle diversity. *Agric Ecosyst Environ* 108:165–174. <https://doi.org/10.1016/j.agee.2005.01.005>
- Rainio J, Niemela J (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers Conserv* 12:487–506. <https://doi.org/https://doi.org/10.1023/A:1022412617568>
- Rand TA, Tylianakis JM, Tscharntke T (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol Lett* 9:603–614. <https://doi.org/10.1111/j.1461-0248.2006.00911.x>
- Ribera I, Dolédec S, Downie IS, Foster GN (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology* 82:1112–1129. [https://doi.org/10.1890/0012-9658\(2001\)082\[1112:EOLDAS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1112:EOLDAS]2.0.CO;2)
- Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu Rev Ecol Evol Syst* 35:491–522. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130148>
- Roberts MJ (1995) *Spiders of Britain and northern Europe*. Collins field guide. Harper Collins Publishers, London
- Roume A, Deconchat M, Raison L, et al (2011) Edge effects on ground beetles at the woodlot-field interface are short-range and asymmetrical. *Agric For Entomol* 13:395–403. <https://doi.org/10.1111/j.1461-9563.2011.00534.x>
- Rusch A, Birkhofer K, Bommarco R, et al (2015) Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic Appl Ecol* 16:250–259. <https://doi.org/https://doi.org/10.1016/j.baae.2015.02.003>
- Rusch A, Birkhofer K, Bommarco R, et al (2014) Management intensity at field and landscape levels affects the structure of generalist predator communities. *Oecologia* 175:971–983. <https://doi.org/10.1007/s00442-014-2949-z>
- Rusch A, Valantin-Morison M, Sarthou J-P, Roger-Estrade J (2010) Biological control of insect pests in agroecosystems: effects of crop management, farming systems, and seminatural habitats at the landscape scale: a review. Elsevier Ltd
- Šálek M, Hula V, Kipson M, et al (2018) Bringing diversity back to agriculture: Smaller fields and non-crop elements enhance biodiversity in intensively managed arable farmlands. *Ecol Indic* 90:65–73. <https://doi.org/10.1016/j.ecolind.2018.03.001>
- Samu F, Sunderland KD, Szinetár C (1999) Scale-Dependent Dispersal and Distribution Patterns of Spiders in Agricultural Systems : A Review. *J Arachnol* 27:325–332
- Samu F, Szinetár C (2002) On the nature of agrobiont spiders. *J Arachnol* 30:389–402. <https://doi.org/https://doi.org/10.1636/0161->

- 8202(2002)030[0389:OTNOAS]2.0.CO;2
- Sánchez-Bayo F, Wyckhuys KAG (2019) Worldwide decline of the entomofauna: A review of its drivers. *Biol Conserv* 232:8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>
- Saska P, van der Werf W, Hemerik L, et al (2013) Temperature effects on pitfall catches of epigeal arthropods: A model and method for bias correction. *J Appl Ecol* 50:181–189. <https://doi.org/10.1111/1365-2664.12023>
- Schirmel J, Blindow I, Buchholz S (2012) Life-history trait and functional diversity patterns of ground beetles and spiders along a coastal heathland successional gradient. *Basic Appl Ecol* 13:606–614. <https://doi.org/https://doi.org/10.1016/j.baae.2012.08.015>
- Schirmel J, Thiele J, Entling MH, Buchholz S (2016) Trait composition and functional diversity of spiders and carabids in linear landscape elements. *Agric Ecosyst Environ* 235:318–328. <https://doi.org/10.1016/j.agee.2016.10.028>
- Schmidt-Entling MH, Döbeli J (2009) Sown wildflower areas to enhance spiders in arable fields. *Agric , Ecosyst Environ* 133:19–22. <https://doi.org/10.1016/j.agee.2009.04.015>
- Schmidt MH, Lefebvre G, Poulin B, Tscharrntke T (2004) Reed cutting affects arthropod communities, potentially reducing food for passerine birds. *Biol Conserv* 121:157–166. <https://doi.org/https://doi.org/10.1016/j.biocon.2004.03.032>
- Schmidt MH, Tscharrntke T (2005) The role of perennial habitats for Central European farmland spiders. *Agric Ecosyst Environ* 105:235–242. <https://doi.org/10.1016/j.agee.2004.03.009>
- Schneider G, Krauss J, Boetzel FA, et al (2016) Spillover from adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural grasslands. *Oecologia* 182:1141–1150. <https://doi.org/10.1007/s00442-016-3710-6>
- Schweiger O, Maelfait JP, Van Wingerden W, et al (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *J Appl Ecol* 42:1129–1139. <https://doi.org/10.1111/j.1365-2664.2005.01085.x>
- Seibold S, Gossner MM, Simons NK, et al (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574:671–674. <https://doi.org/10.1038/s41586-019-1684-3>
- Simons NK, Weisser WW, Gossner MM (2016) Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. *Ecology* 97:754–764. <https://doi.org/10.1890/15-0616>
- Sirami C, Gross N, Baillod AB, et al (2019) Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc Natl Acad Sci U S A*

- 116:16442–16447. <https://doi.org/10.1073/pnas.1906419116>
- Statistisches Landesamt Rheinland-Pfalz (2020) Verbandsgemeinde Maifeld - Flächennutzung. <http://www.infothek.statistik.rlp.de>. Accessed 10 Mar 2022
- Stoate C, Boatman ND, Borralho RJ, et al (2001) Ecological impacts of arable intensification in Europe. *J Environ Manage* 63:337–365. <https://doi.org/10.1006/jema.2001.0473>
- Sunderland KD, Samu F (2000) Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomol Exp Appl* 95:1–13. <https://doi.org/10.1046/j.1570-7458.2000.00635.x>
- Sunderland KD, Topping CJ (1995) Estimating population densities of spiders in cereals. In: Toft S, Riedel W (eds) *Arthropod natural enemies in arable land. I. Density, spatial heterogeneity and dispersal*. Aarhus University Press, Aarhus, pp 13–20
- Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Annu Rev Entomol* 47:561–594. <https://doi.org/https://doi.org/10.1146/annurev.ento.47.091201.145240>
- Thorbeck P, Bilde T (2004) Reduced numbers of generalist arthropod predators after crop management. *J Appl Ecol* 41:526–538. <https://doi.org/https://doi.org/10.1111/j.0021-8901.2004.00913.x>
- Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. *Proc Natl Acad Sci U S A* 108:20260–20264. <https://doi.org/10.1073/pnas.1116437108>
- Topping CJ, Sunderland KD (1998) Population dynamics and dispersal of *Lepthyphantes tenuis* in an ephemeral habitat. *Entomol Exp Appl* 87:29–41. <https://doi.org/10.1046/j.1570-7458.1998.00301.x>
- Tryjanowski P, Hartel T, Bldi A, et al (2011) Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. *Acta Ornithol* 46:1–12. <https://doi.org/10.3161/000164511X589857>
- Tscharntke T, Bommarco R, Clough Y, et al (2007) Conservation biological control and enemy diversity on a landscape scale. *Biol Control* 45:238–253
- Tscharntke T, Clough Y, Wanger TC, et al (2012a) Global food security, biodiversity conservation and the future of agricultural intensification. *Biol Conserv* 151:53–59. <https://doi.org/https://doi.org/10.1016/j.biocon.2012.01.068>
- Tscharntke T, Klein AM, Kruess A, et al (2005a) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecol Lett* 8:857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>
- Tscharntke T, Rand TA, Bianchi FJJA (2005b) The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. *Ann Zool Fennici*

---

42:421–432

- Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Contribution of small habitats to conservation of insect communities of grassland-cropland landscapes. *Ecol Appl* 12:354. <https://doi.org/10.2307/3060947>
- Tscharntke T, Tylianakis JM, Rand TA, et al (2012b) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol Rev* 87:661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Van Buskirk J, Willi Y (2004) Enhancement of farmland biodiversity within set-aside land. *Conserv Biol* 987–994. <https://doi.org/10.1111/j.1523-1739.2004.00359.x>
- Vickery JA, Tallowin JR, Feber RE, et al (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *J Appl Ecol* 38:647–664. <https://doi.org/10.1046/j.1365-2664.2001.00626.x>
- Wagner DL, Grames EM, Forister ML, et al (2021) Insect decline in the Anthropocene: Death by a thousand cuts. *Proc Natl Acad Sci U S A* 118:1–10. <https://doi.org/10.1073/pnas.2023989118>
- Weibull A-C, Östman Ö (2003) Species composition in agroecosystems: The effect of landscape, habitat, and farm management. *Basic Appl Ecol* 4:349–361. <https://doi.org/10.1078/1439-1791-00173>
- Woodcock BA, Westbury DB, Potts SG, et al (2005) Establishing field margins to promote beetle conservation in arable farms. *Agric Ecosyst Environ* 107:255–266. <https://doi.org/10.1016/j.agee.2004.10.029>

---

# FUNDING

---

This study was financially supported by the Ministry for Environment, Energy, Nutrition and Forest Rheinland-Pfalz through the ‘Aktion Grün’.

