



UNIVERSITY OF  
HOHENHEIM

***Suitability of conventional flowering fields  
and organic lentil mixed-crops to promote  
biodiversity on arable land***

**Dissertation**

**to obtain the doctoral degree of Agricultural Sciences (Dr. sc. agr.)**

**Faculty of Agricultural Sciences**

**University of Hohenheim**

Institute of Landscape and Plant Ecology; Institute of Ecology and Botany, Centre  
for Ecological Research, Hungarian Academy of Sciences (MTA)

submitted by

*Christoph Robert Gayer*

born in *Bad Saulgau, Germany*

*Nürtingen, April 2020*

**In der lebendigen Natur geschieht nichts,  
was nicht in Verbindung mit dem Ganzen steht.**

*Johann Wolfgang von Goethe*

**Der Mensch macht sich nicht selbst.  
Er ist Geist und Wille, aber er ist auch Natur.**

*Papst Benedikt XVI*

This thesis was accepted as doctoral dissertation in fulfilment of the requirements for the degree “Doktor der Agrarwissenschaften” (Dr. sc. agr.) by the Faculty of Agricultural Sciences at the University of Hohenheim on September 24, 2020.

Date of oral examination: November 12, 2020

**Examination committee**

1 <sup>st</sup> Supervisor and Reviewer:	Prof. Dr. Martin Dieterich
2 <sup>nd</sup> Supervisor and Reviewer:	P.D. Dr. Péter Batáry
Additional Examiner:	Prof. Dr. Ingo Graß
Head of Committee:	Prof. Dr. Uwe Ludewig

# TABLE OF CONTENTS

List of Figures .....	v
List of Tables .....	vii
Summary .....	x
Zusammenfassung .....	xii
List of publications included in this thesis.....	xiv
<b>1. Chapter: General Introduction .....</b>	<b>1</b>
1.1 Biodiversity loss through agricultural intensification .....	1
1.2 Biodiversity and ecosystem services .....	2
1.3 Promoting biodiversity on arable land .....	3
1.4 Flowering fields.....	6
1.5 Lentil mixed-crops.....	7
1.6 Edge and landscape effects .....	8
1.7 Research objectives .....	9
1.8 Thesis outline .....	10
1.9 References .....	12
<b>2. Chapter: Additive effects of flowering fields, organic farming and edge habitats promote diversity of plants, flower-visiting and ground-dwelling arthropods in arable fields .....</b>	<b>23</b>
2.1 Abstract .....	24
2.2 Introduction .....	25
2.3 Materials and methods.....	27
2.3.1 Study area and design .....	27
2.3.2 Farming practices .....	27
2.3.3 Sampling of organisms .....	28
2.3.4 Landscape analysis .....	30
2.3.5 Statistical analysis.....	30
2.4 Results .....	31
2.4.1 Crop-use type effects .....	31
2.4.2 Edge and landscape effects .....	36
2.5 Discussion .....	38
2.5.1 Crop-use type effects .....	38
2.5.2 Edge and landscape effects .....	39
2.5.3 Conclusions .....	40
2.6 Acknowledgements .....	40
2.7 References .....	41
2.8 Supplementary material .....	46
<b>3. Chapter: Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats .....</b>	<b>63</b>
3.1 Abstract .....	64
3.2 Introduction .....	65
3.3 Materials and methods.....	66

3.3.1	Study area and study design.....	66
3.3.2	Farming characteristics of study fields .....	68
3.3.3	Landscape analysis .....	70
3.3.4	Carabid and plant survey .....	70
3.3.5	Carabid trait analysis .....	71
3.3.6	Statistical analysis.....	71
3.4	Results .....	72
3.5	Discussion .....	74
3.5.1	Effects of crop-use type .....	75
3.5.2	Edge and landscape effects .....	76
3.5.3	Conclusions .....	77
3.6	Acknowledgements .....	77
3.7	References .....	78
3.8	Supplementary material .....	84
<b>4.</b>	<b>Chapter: Landscape-wide attraction of flowering fields and vicinity to organic winter cereals support bumblebee colonies in agricultural landscapes .....</b>	<b>93</b>
4.1	Abstract .....	94
4.2	Introduction .....	95
4.3	Materials and methods.....	96
4.3.1	Study area and design .....	96
4.3.2	Bumblebee experiment .....	97
4.3.3	Farming practice- and vegetation characteristics .....	99
4.3.4	Landscape analysis .....	100
4.3.5	Statistical analysis.....	101
4.4	Results .....	102
4.5	Discussion .....	105
4.6	Acknowledgements .....	108
4.7	References .....	108
4.8	Supplementary material .....	113
<b>5.</b>	<b>Chapter: General Discussion.....</b>	<b>117</b>
5.1	Overview of results.....	117
5.2	Biodiversity effects of annual flowering fields in conventional farming .....	118
5.3	Biodiversity effects of lentil mixed-crops in organic farming.....	120
5.4	Comparison with similar studies.....	121
5.5	Landscape perspective on the implementation of local agri-environmental measures .....	122
5.6	Methodical limitations of the study .....	125
5.7	Conclusions and Recommendations .....	127
5.8	References .....	129
<b>6.</b>	<b>Acknowledgments .....</b>	<b>135</b>
<b>7.</b>	<b>Author's Declaration .....</b>	<b>137</b>
<b>8.</b>	<b>Curriculum vitae .....</b>	<b>138</b>

# LIST OF FIGURES

**Fig. 2.1.** Effect of crop-use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil mixed-crop (LMC)) and transect position (edge, center) on wild plant cover (a) and abundance (number of individuals) of carabid beetles (b), spiders (c), butterflies (d) and wild bees (e). Bars are means  $\pm$  SE. .... 34

**Fig. 2.2.** Effect of crop-use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil mixed-crop (LMC)) and transect position (edge, center) on species richness (number of species) of wild plants (a), carabid beetles (b), spiders (c), butterflies (d) and wild bees (e). Bars are means  $\pm$  SE. .... 35

**Fig. 2.3.** Redundancy analysis ordination (RDA) plots of survey transects (triangles) for wild plants (a), carabid beetles (b), spiders (c), butterflies (d) and wild bees (e). Minimum convex polygons of the four crop-use types are shown. .... 37

**Fig. S2.1.** Cross-nested study design. The four crop-use types (winter wheat (WW), flowering field (FF), winter spelt (WS), lentil mixed-crop (LMC)) were spatially nested per study site (black circle) and nested by the two farmers managing the study fields (conventional farmer: dark-blue ellipse; organic farmer: light-blue ellipse) and the two crop-types (cereal crop: light-orange ellipse; flowering crop: dark-orange ellipse) within each site. .... 48

**Fig. S2.2.** Exemplary photo of a flowering field (left) and a lentil mixed-crop field (right). Indicated in red are the lentil plant (light green) intercropped with a supporting crop (oat, dark green). © Photos: C.Gayer (left), T.Weiss (right). .... 52

**Fig. S2.3.** Sampling design indicating position and distance of pitfall traps (black dots), plant survey plots (green rectangle), butterfly survey transects (blue arrows) and wild bees transects (yellow arrows with point count locations (circles)) within a study field. .... 52

**Fig. 3.1.** Effect of crop-use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil-mixed-crop (LMC)) and transect position (edge, center) on community weighted mean (CWM) of feeding type (a), body size (b) and flight ability (c). Bars are means  $\pm$  SE. .... 74

**Fig. S3.1.** Location of study fields (center transect) according to crop-use type and study year (unfilled symbols: 2016, symbols with black dot: 2017) in southwest Germany. All fields were located near the city of Münsingen in the administrative districts (solid lines) Alb-Donau-Kreis, Esslingen or Reutlingen within the Biosphere Reserve Swabian Alb (grey area). .... 84

<b>Fig. S3.2.</b> Cross-nested design of crop-use types and experimental set-up of pitfall traps. Five traps were placed at the edge and another five at the centre transect, in a distance of 10m between traps. Distance between edge and centre transect was 12m in 2016 and 15m in 2017. ....	91
<b>Fig. S3.3.</b> Exemplary photo of a lentil mixed-crop field. Indicated are the lentil plant (light green) intercropped with a supporting crop (oat, dark green). © Photo: T. Weiss. ....	91
<b>Fig. S3.4.</b> Effect of crop- use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil mixed-crop (LMC)) and transect position (edge, centre) on functional divergence (FDvar) of feeding type (a), body size (b) and flight ability (c). Bars are means $\pm$ SE. ....	92
<b>Fig. 4.1.</b> Mean ( $\pm$ SE) colony weight of <i>Bombus terrestris</i> colonies (n=37) over the course of five week exposure at study fields. ....	98
<b>Fig. 4.2.</b> Differences (mean $\pm$ SE) in (a) maximum weight gain, (b) foraging activity (number of individuals entering and leaving the colony), (c) body size of workers (inter-tegular width), (d) total amount of queen brood cells, and (e) pollen diversity (Shannon index) of pollen stores between <i>Bombus terrestris</i> colonies placed at arable fields of four crop-use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil-mixed-crop (LMC)). Further effects of percental flower cover in 500 m radius (arcsine transformed values) on pollen diversity (f) with a regression line based on a linear model. Different letters indicate significant differences between crop-use types at $P < 0.05$ . ....	105
<b>Fig. S4.1.</b> Bumblebee nest box locations according to the crop-use type at the Biosphere Reserve Swabian Alb within the federal state Baden-Württemberg (below left) in southwest Germany (below right). ....	114
<b>Fig. S4.2.</b> Exemplary photo of a nest box location with two colonies of <i>Bombus terrestris</i> placed on a wooden palette and sheltered by a styrodur roof (© Alina Biermann). ....	115
<b>Fig. S4.3.</b> Cross-nested study design. The four crop-use types (winter wheat (WW), flowering field (FF), winter spelt (WS), lentil mixed-crop (LMC)) were spatially nested per study site (black circle) and nested by the two farmers managing the study fields (conventional farmer: dark-blue ellipse; organic farmer: light-blue ellipse) and the two crop-types (cereal crop: light-orange ellipse; flowering crop: dark-orange ellipse) within each site. ....	115

# LIST OF TABLES

<b>Table 2.1.</b> Farming practice characteristics, achieved yield and subsidy amount of studied crop-use types sampled in 2016, 2017 and 2018 (mean $\pm$ SE; n=68). Results (F-value of ANOVA table) of linear mixed-effects models are given to test for significant differences between crop-use types. Bold values indicate significant effect at $P < 0.05$ . ....	29
<b>Table 2.2.</b> Effects of landscape (% of arable cover), crop-use type (winter wheat (WW) vs. flowering field (FF) vs. winter spelt (WS) vs. lentil-mixed-crop (LMC)) and transect position (edge (E) vs. center (C)) on abundance and species richness of five taxa. Results were calculated by multi-model averaging of linear mixed-effects models. Importance of predictor variables, parameter estimates with standard error (SE) and t/z-values. Only models with $< 2 \Delta \text{AICc}$ of the best model are shown. Landscape complexity or interaction terms were never retained among such best fit models. Bold values indicate significant effect at $P < 0.05$ . ....	32
<b>Table 2.3.</b> Results of an RDA to analyse the effects of landscape complexity (% of arable cover), crop-use type (winter wheat, flowering field, winter spelt, lentil-mixed-crop) and transect position (edge, center) on community composition of five taxa. Percentage of explained variation, $F$ - and $P$ -values (bold if $P < 0.05$ ) are given. ....	36
<b>Table S2.1.</b> Composition of the two types of seed mixture used for establishment of flowering fields. Percentile weighting per species in the seed mixture are given as well as their origin status (native/non-native) in the study area (Germany). ....	48
<b>Table S2.2.</b> Location and farming practice before sowing of crops for each study field. For lentil crop respective mixed crop species is given. ....	50
<b>Table S2.3.</b> Vegetation characteristics at the edge and centre transect of studied crop-use types sampled between 2016-2018 (mean $\pm$ SE). Results ( $F$ -values of ANOVA table) of linear mixed-effects models are given to test for significant differences between study years, crop-use types and transects. Bold values indicate significant effect at $P < 0.05$ . ....	53
<b>Table S2.4.</b> List of plant species (only if identified to species level) and the respective number of transects with the plant species present at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields. Grey marked species names are plants of the seed mixture sown for the establishment of flowering fields. For plants of the seed mixture numbers refer to the study years 2017 and 2018 (without 2016). ....	53

<b>Table S2.5.</b> List of carabid species and the respective number of individuals sampled at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields. ....	57
<b>Table S2.6.</b> List of spider species (only if identified to species level) and the respective number of individuals sampled at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields. ....	58
<b>Table S2.7.</b> List of butterfly species (only if identified to species level) and the respective number of individuals sampled at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields. ....	60
<b>Table S2.8.</b> List of wild bee species and the respective number of individuals sampled at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields. ....	61
<b>Table 3.1.</b> Farming practice characteristics, achieved yield and subsidy amount of studied crop-use types sampled in 2016 and 2017 (mean $\pm$ SE; n=48). Results (F-value of ANOVA table) of linear mixed-effects models are given to test for significant differences between crop-use types. Bold values indicate significant effect at $P < 0.05$ . ....	69
<b>Table 3.2.</b> Effects of landscape (% of arable cover), crop-use type (winter wheat (WW) vs. flowering field (FF) vs. winter spelt (WS) vs. lentil-mixed-crop (LMC)) and transect position (edge vs. center) on community weighted mean (CWM) and functional divergence (Fdvar) of carabid traits (body size, food-type, flight ability). Results were calculated by multi-model averaging of linear mixed-effects models. Importance of predictor variables, parameter estimates with standard error (SE) and t/z-values. Only models with $< 2 \Delta AICc$ of the best model are shown. Bold values indicate significant effect at $P < 0.05$ . ....	73
<b>Table S3.1.</b> Composition of the two types of seed mixture used for establishment of flowering fields. Percentile weighting per species in the seed mixture are given as well as their origin status (native/non-native) in the study area (Germany). ....	85
<b>Table S3.2.</b> Location (geographical coordinates) and farming practice before sowing of crops for each study site. For lentil crop respective mixed crop species is given. ....	86
<b>Table S3.3.</b> Vegetation characteristics at the edge and centre transect of studied crop-use types sampled in 2016 and 2017 (mean $\pm$ SE; n=48). Results ( $F$ -values of ANOVA table) of linear mixed-effects models are given to test for significant differences between study years, crop-use types and transects. Bold values indicate significant effect at $P < 0.05$ . ....	87



**Table S3.4.** List of sampled carabid species and their trait classification according to body size (geometric mean), feeding type and their flight ability according to wing morphology. Further number of individuals per carabid species recorded at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields. .... 88

**Table 4.1.** Effects of crop-use type (winter wheat (WW) vs. flowering field (FF) vs. winter spelt (WS) vs. lentil-mixed-crop (LMC)) and percental flower cover in 500m radius on maximum weight gain, foraging activity (entering+leaving individuals), body size of workers (inter-tegular width), the total amount of queen brood cells and pollen diversity (Shannon index) of pollen stores of *Bombus terrestris* colonies. Results were calculated by separate linear mixed-effects models for the two explanatory variables. Parameter estimates with standard error (SE) and t- values are given. Bold values indicate significant effect at  $P < 0.05$ ..... 102

**Table 4.2.** Most abundant pollen types ( $\geq 1$  % of the total amount of pollen grains) found in *Bombus terrestris* colonies placed at four different crop-use types (conventional winter wheat (WW; n=6), conventional flowering field (FF; n=6), organic winter spelt (WS; n=5), organic lentil mixed-crop (LMC; n=4)). Bold pollen types indicate plant species sown in the seed mixture for establishing flowering fields. Percental pollen amount (mean  $\pm$  SE) per crop-use type are given as well as results (F-value of ANOVA table) of linear mixed-effects models to test for significant differences between them. Bold F-values indicate significant effect at  $P < 0.05$ ..... 104

**Table S4.1.** Composition of the two types of seed mixture used for establishment of flowering fields. Percentile weighting per species in the seed mixture are given as well as their origin status (native/non-native) in the study area (Germany). .... 114

**Table S4.2.** Farming practice characteristics, achieved yield and subsidy payment of studied crop-use types in 2018 (mean  $\pm$  SE; n=23). Results (F-value of ANOVA table) of linear mixed-effects models are given to test for significant differences between crop-use types. Bold values indicate significant effect at  $P < 0.05$ ..... 116

**Table S4.3.** Vegetation characteristics of studied crop-use types (mean  $\pm$  SE). Results (F-values of ANOVA table) of linear mixed-effects models are given to test for significant differences. Bold values indicate significant effect at  $P < 0.05$ ..... 116

## SUMMARY

The rapid agricultural intensification during the last decades is among the main drivers of the dramatic and ongoing biodiversity loss on earth. The decline of species diversity and associated ecosystem services due to highly intensified farming practices and structural simplified agricultural landscapes includes the reduction of species richness and abundance of species. The loss of species and related shifts in species communities can also lead to altered functional traits within species communities. It can also include deteriorated population developments of single species known to be important ecosystem service suppliers for agricultural production. In Europe, billions of euros are spent each year to support farmers for applying environmentally friendly practices, but so far biodiversity continues to decline. This calls for the development of more effective biodiversity conservation measures on agricultural land. Within the framework of agri-environmental measures, agronomically non-productive measures exist such as the establishment of flowering fields, but there are also production integrated measures such as the organic farming of crops. Further, the growing of flowering lentil mixed-crops could be a valuable, but rarely studied option to further increase the biodiversity benefits of organic farming systems. Up to that, little is known about the relative effectiveness of non-productive flowering fields under conventional management and organically farmed mono- as well as lentil mixed-crops for the promotion of biodiversity on arable land.

Within the scope of this thesis, I studied biodiversity effects in response to the establishment of annual flowering fields under conventional management, organically managed winter spelt as well as organic lentil mixed-crops. These three crop-use types were compared to conventional winter wheat (control). Besides, I took into account biodiversity effects of the within-field position (field edge versus interior) as well as the surrounding landscape complexity in 500 m around each study field. To get a comprehensive overview about potential biodiversity effects and related ecosystem functions in response to the four crop-use types, I assessed the abundance, species richness and community composition of wild plants (primary producers), carabids and spiders (ground-dwelling predators) as well as butterflies and wild bees (flower-visiting arthropods). I further assessed the functional diversity of carabids as an important species group for biological pest control. To quantify functional diversity in comparison between the four crop-use types, I used the community weighted means and functional divergence of three ecological traits – body size, feeding type, and flight ability. These traits can affect mobility (body size, flight ability) as well as pest and weed seed predation (feeding type, body size) of carabids. Last, I measured the population development of colonies of *Bombus terrestris*, which is an important pollinator in European agricultural landscapes. I observed weight gain, foraging activity, worker body size, queen brood cell number and stored pollen types of colonies exposed at each study field in 2018.

I found clear taxon-specific effects of the total abundance and species richness in response to the studied crop-use types. No distinct differences were found for the community composition, which

was similar between crop-use types. Arable wild plants benefited most strongly from organic farming, in particular from lentil mixed-crops, but also from field edges. Ground-dwelling arthropods were also mainly promoted by field edges, whereas flower-visiting arthropods solely benefited from conventional flowering fields and organic lentil mixed-crops. Carabid functional diversity was higher at the field edge than the interior irrespectively of crop-use type. Feeding type diversity (carnivorous, omnivorous, herbivorous) of carabid assemblages did also profit from conventional flowering fields and organic winter spelt. Colonies of *Bombus terrestris* had higher foraging activity and larger body sizes, if exposed at organic winter spelt fields, whereas weight gain and queen brood cell numbers were unaffected by local crop-use type. Pollen stores within the colonies were dominated by *Phacelia* (*Phacelia tanacetifolia*) irrespectively of crop-use type. *Phacelia* was part of the sown seed-mixture in flowering fields, indicating a landscape-wide attraction of flowering fields as pollen source for *Bombus terrestris*. Over all studies i found only minor effects of the surrounding landscape, except the negative correlation between flower cover and pollen diversity of *Bombus terrestris* colonies.

In summary, this thesis revealed that the establishing of annual flowering fields can be an appropriate measure to enhance biodiversity in conventional farming systems. Organic lentil mixed-crops are appropriate to further increase biodiversity benefits of organic farming systems. Within the conducted studies, different crop-use types promoted specific species groups and thereby different components of biodiversity. Hence, the results of this thesis reveal, that there is no single best measure for the promotion of biodiversity on arable land. Instead, the additive effects of non-productive and productive measures as well as field edge habitats underline, that a mosaic of different types of measures hold the greatest potential to benefit overall biodiversity in agricultural landscapes. Therefore, future agri-environmental schemes should provide particular incentives for individual farmers to apply a diversity of different measures on their farmland and should foster the collaboration and spatially coordinated implementation of complementary biodiversity measures between multiple farmers at the landscape scale.

# ZUSAMMENFASSUNG

Die Intensivierung der Landwirtschaft im Laufe der letzten Jahrzehnte ist eine der Hauptursachen für den dramatischen und fortschreitenden Verlust der globalen Biodiversität. Der Biodiversitätsverlust auf Grund von hoch intensiven Bewirtschaftungsweisen und strukturell verarmten Agrarlandschaften kann sich im Rückgang von Arten und deren Häufigkeit zeigen. Der Rückgang von Arten und die daran gebundene Verschiebung von Artenspektren kann jedoch auch eine Verschiebung von funktionellen Eigenschaften innerhalb von Artengemeinschaften bedeuten. Ebenso können Populationen einzelnen Arten beeinträchtigt sein, welche jedoch wichtige Ökosystemdienstleister für die landwirtschaftliche Produktion sind. In der EU werden jährlich Milliarden von Euro dafür ausgegeben, Landwirte für die Umsetzung von umweltfreundlichen Bewirtschaftungsweisen zu unterstützen, bisher jedoch ohne den Biodiversitätsverlust aufhalten zu können. Dies verdeutlicht die Notwendigkeit stärker wirksamer Biodiversitätsschutzmaßnahmen für landwirtschaftlich genutzte Flächen zu entwickeln. Im Rahmen von Agrarumweltmaßnahmen werden im Ackerbau produktionsseparierte, landwirtschaftlich unproduktive Maßnahmen wie die Anlage von Blühflächen gefördert. Darüber hinaus gibt es aber auch produktionsintegrierte Ansätze, wie die Bewirtschaftung von Ackerkulturen nach den Kriterien des ökologischen Landbaus. Die Bedeutung des ökologischen Landbaus für die Biodiversität könnte durch den Anbau von Linsen-Mischkulturen weiter erhöht werden. Bisher mangelt es jedoch an wissenschaftlichen Vergleichsstudien bezüglich der Biodiversitätseffekte von einjährigen Blühflächen im Rahmen einer konventionellen Bewirtschaftung, im Vergleich zu einer ökologischen Bewirtschaftung von Mono-, wie auch Linsen-Mischkulturen.

In der vorliegenden Dissertation habe ich die Biodiversitätseffekte von einjährigen, konventionell bewirtschafteten Blühflächen, ökologisch bewirtschafteten Winterdinkelkulturen, sowie ökologisch bewirtschafteten Linsen-Mischkulturen untersucht. Diese drei Kulturen wurden mit konventionell bewirtschafteten Winterweizenkulturen verglichen (Kontrollgruppe). Daneben habe ich die Biodiversitätseffekte der Lage der Untersuchungsflächen im Ackerschlag (Feldrand versus Feldinnenbereich) und die Komplexität der umgebenden Landschaft in einem Radius von 500 m um jedes Untersuchungsfeld untersucht. Um einen umfassenden Überblick über mögliche Biodiversitätseffekte der Kulturen und damit verbundene Ökosystemfunktionen zu erhalten, wurden die Abundanz, der Artenreichtum und die Komposition der Artengemeinschaften der Artengruppen Ackerwildpflanzen (Primärproduzenten), Laufkäfer und Spinnen (epigäische Prädatoren) sowie Tagfalter und Wildbienen (blütenbesuchende Insekten) erfasst. Für die Gruppe der Laufkäfer als wichtige Träger der natürlichen Schädlingskontrolle, wurde darüber hinaus die funktionale Diversität betrachtet. Die funktionale Diversität im Vergleich der untersuchten Kulturen wurde durch die Berechnung von gewichteten Mittelwerten (community weighted means) und der funktionellen Divergenz von drei ökologischen Eigenschaften gemessen, nämlich der Körpergröße, des Ernährungstyps und der Flugfähigkeit. Diese Eigenschaften können die Mobilität (Körpergröße, Flugfähigkeit) sowie den Prädationsdruck von Laufkäfern auf Schadinsekten und Ackerunkrautsamen

(Ernährungstyp, Körpergröße) beeinflussen. Schließlich habe ich die Populationsentwicklung von Erdhummelvölkern (*Bombus terrestris*) untersucht, welches eine wichtige Bestäuberart in europäischen Agrarlandschaften ist. Dafür habe ich die Gewichtszunahme, die Futterflug-Aktivität, die Körpergröße der Arbeiterinnen, die Anzahl von Königinnenbrutzellen, sowie die gesammelten Pollentypen der an jedem Untersuchungsfeld ausgebrachten Erdhummelkolonien im Jahre 2018 analysiert.

Bezüglich der Abundanz und des Artenreichtums konnte ich Artengruppen-spezifische Unterschiede zwischen den untersuchten Kulturen feststellen. Keine klaren Unterschiede ergaben sich bei der Zusammensetzung der Artengemeinschaften zwischen den untersuchten Kulturen. Ackerwildkräuter profitierten am stärksten von einer ökologischen Bewirtschaftung, insbesondere von Linsen-Mischkulturen, aber auch der Lage am Feldrand. Bodenbewohnende Arthropoden wurden ebenfalls hauptsächlich am Feldrand gefördert. Blütenbesuchende Arthropoden profitieren von konventionellen Blühflächen und ökologischen Linsen-Mischkulturen. Die funktionelle Diversität von Laufkäfern war am Feldrand höher als im Feldinnenraum unabhängig von der jeweiligen Kultur. Die Diversität an unterschiedlichen Ernährungstypen (karnivor, omnivor, herbivor) innerhalb der Laufkäfergemeinschaften wurde zudem durch konventionelle Blühflächen und ökologische Winterdinkelkulturen gefördert. Am ökologischen Winterdinkel exponierte Erdhummelkolonien zeigten eine höhere Futterflug Aktivität und hatten größere Arbeiterinnen als an anderen Kulturen exponierte Völker. Die Gewichtszunahme und die Anzahl der Königinnenbrutzellen wurde dagegen nicht vom lokalen Kulturtyp bestimmt. Unabhängig vom Standort der Exposition wurden die Pollenspeicher der Kolonien vom Pollen der *Phacelia* (*Phacelia tanacetifolia*) dominiert. *Phacelia* war Teil der ausgesäten Saatmischung auf Blühflächen, was auf eine landschaftsweite Anziehungswirkung von Blühflächen auf Erdhummeln hinweist. Über alle Studien hinweg habe ich nur sehr geringe Effekte der umgebenden Landschaft festgestellt, mit Ausnahme der negativen Korrelation des Blühbedeckungsgrades mit der Pollendiversität bei Kolonien von *Bombus terrestris*.

Die Doktorarbeit zeigt, dass die Anlage konventioneller Blühflächen eine geeignete Maßnahme sein kann, um die Biodiversität in der konventionellen Landwirtschaft zu steigern. Ökologische Linsen-Mischkulturen sind geeignet die Biodiversitätswirkungen des ökologischen Landbaus weiter zu stärken. Unterschiedliche Kulturen fördern in den vorliegenden Untersuchungen jeweils spezifische Artengruppen und damit unterschiedliche Biodiversitätskomponenten. Die Ergebnisse der vorgelegten Forschungsarbeiten zeigen somit auch, dass es nicht die eine Optimalkultur zur Förderung der Biodiversität im Ackerbau gibt. Die additiven Effekte von nicht-produktiven und produktiven Maßnahmen, wie auch Feldrand-Habitaten verdeutlichen, dass ein Mosaik aus unterschiedlichen Maßnahmentypen das größte Potential hat, um die Gesamtbiodiversität in Agrarlandschaften zu fördern. Zukünftige Agrarumweltprogramme sollten daher stärkere Anreize schaffen, dass Landwirte eine Diversität von unterschiedlichen Maßnahmen auf ihren Flächen umsetzen, und sollten auf Landschaftsebene die koordinierte und kooperative Umsetzung komplementärer Biodiversitätsmaßnahmen zwischen unterschiedlichen Landwirten fördern.

# LIST OF PUBLICATIONS INCLUDED IN THIS THESIS

In accordance with the regulations for cumulative dissertations at the Faculty of Agricultural Sciences, three scientific articles have been included as separate chapters within this thesis, which were either published or submitted to peer-reviewed international journals:

## **Chapter 2:**

Gayer, C., Berger, J., Dieterich, M., Gallé, R., Reidl, K., Witty, R., Woodcock, B.A. & Batáry, P. (2020) Additive effects of flowering fields, organic farming and edge habitats promote diversity of plants, flower-visiting and ground-dwelling arthropods in arable fields. Submitted to *Journal of Applied Ecology*.

## **Chapter 3:**

Gayer, C., Lövei, G. L., Magura, T., Dieterich, M., & Batáry, P. (2019) Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats. Published in *Agriculture, Ecosystems and Environment*, 284, 106579, doi.org/10.1016/j.agee.2019.106579.

## **Chapter 4:**

Gayer, C., Biermann, A., Dieterich, M., Reidl, R. & Batáry, P. (2020) Landscape-wide attraction of flowering fields and vicinity to organic winter cereals support bumblebee colonies in agricultural landscapes. Submitted to *Insect Conservation and Diversity*.

# 1. CHAPTER

## General Introduction

### 1.1 Biodiversity loss through agricultural intensification

Agricultural land is the largest land use type on earth covering about 40% of the world's land surface (Foley *et al.*, 2005; Dudley & Alexander, 2017). About 78% of the human appropriation of the global net primary production is used for agriculture, with 50% used for crop production (Haberl *et al.*, 2007). The rapid intensification of agricultural land use practices due to the mechanisation and industrialisation of agriculture during the last century led to an enormous increase in agricultural productivity, but was also identified as a main driver of the global decline in terrestrial biodiversity (Stoate *et al.*, 2009; Foley *et al.*, 2011; Beckmann *et al.*, 2019; Sánchez-Bayo & Wyckhuys, 2019). It is estimated by 2050 that the human population will grow up to 9.7 billion people (UN DESA, 2019) and that the demand for agricultural commodities will further increase up to 70% - 100% (Tilman *et al.*, 2011; Zabel *et al.*, 2019). These developments might further extend the high pressure towards highly intensive agricultural land use practices, with accelerating effects on the ongoing biodiversity loss. Hence, sustainable agriculture has to meet the challenge of reconciling increasing food demands with the conservation of biodiversity and associated ecosystem services.

In Central Europe, agricultural used land harbours the majority of biodiversity including many species of conservation concern, due to the land use history of low-intensity farming practices, which were applied for millennia (Tscharntke *et al.*, 2005; Batáry *et al.*, 2015; Sutcliffe *et al.*, 2015). The preservation of low-intensive agricultural land use types is therefore a main focus of nature conservation in Central Europe (Batáry *et al.*, 2015). Nevertheless, recently the dominant type of European agricultural land use consists of conventional farmed crop- and grasslands with highly intensive farming practices. These include high input of mineral and organic fertilizers, chemical pesticides, dense mono-crop stands of high-yielding crop varieties, or drainages and high mowing frequencies of grasslands (Dierschke & Briemle, 2002; Tilman *et al.*, 2002; Kovács-Hostyánszki *et al.*, 2017). Such farming practices can have detrimental effects on biodiversity, which was shown *inter alia* for wild plants and arthropods in response to the application of herbicides and insecticides (Geiger *et al.*, 2010), ploughing (Holland & Reynolds, 2003) or mowing (Gossner *et al.*, 2016). Highly intensive farming practices can harm individuals and species by direct effects (e.g. by direct killings through ploughing or application of pesticide). But they can also indirectly impair habitat conditions for species by reducing the availability of food resources, leading to less favourable microclimate conditions or altering plant communities and vegetation structures (Haddad *et al.*, 2000; Seibold *et al.*, 2019). On a landscape scale, agricultural intensification led to less diverse crop numbers (Khoury *et al.*, 2014) and structural simplified landscapes with a low amount of non-crop habitat elements (Tscharntke *et al.*, 2005). Simplified

agricultural landscapes are dominated by intensively farmed arable crops and grasslands and overall offer a poor quantity and quality of food, shelter, reproduction and over-wintering habitats on the landscape scale.

Recently, the decline of biodiversity over the last decades has been documented for many taxa and different parameters. For instance, in Germany strong declines have been shown for the biomass of flying insects (Hallmann *et al.*, 2017), species richness and diversity of carabids (Homburg *et al.*, 2019), butterfly abundance and species richness (Habel *et al.*, 2019a; Habel *et al.*, 2019b), as well as the biomass, abundance and species richness of coleoptera and hemiptera taxa (Seibold *et al.*, 2019). All of these studies point to the negative effects of agricultural intensification as a major reason to explain their findings. These reports even attracted media and public attention in Germany and worldwide, and fostered discussions in society and policy how to strengthen insect conservation (Mupepele *et al.*, 2019). In Germany, it even led to political action programs of the government targeting biodiversity- and insect conservation, such as the program “*Aktionsprogramm Insektenschutz*” (BMU, 2019) or the draft law “*Gesetzesentwurf Rettet die Biene*” in Baden-Württemberg (Landesregierung Baden-Württemberg, 2019). The existence of such programs depict the exceptionally high public interest in biodiversity conservation issues in recent times. However, the strength and spatial expanse of the observed decline of species, numbers of individuals and the total insect biomass underline, that nature conservation efforts need to take into account the agricultural sector and the development of biodiversity friendly farming practices. Such measures hold the potential to promote biodiversity over larger spatial scales than reached by the comparatively small size covered by protected areas.

## 1.2 Biodiversity and ecosystem services

Agricultural intensification not only threatens biodiversity, but can have detrimental effects on ecological functions in agroecosystems by reducing the number of species and individuals or altering species community composition (Tscharnkte *et al.*, 2005). Agricultural intensification can also negatively affect ecosystem processes beneficial to humanity, so-called ecosystem services (Emmerson *et al.*, 2016). Ecosystem services include the provision of ecological functions, which are essential for the sustainability of crop production and food security such as biological pest control and crop pollination (Landis, 2017). It is estimated that about one third of the global crop yield loss is caused by pest species such as weeds and insect pests. However, an increased application of pesticides during the last decades did not result in decreased crop losses (Oerke, 2006). This might be related to decreased biological pest control caused by negative effects of agricultural intensification on natural enemy populations, which can act as antagonist against pest populations (Bianchi *et al.*, 2006). Further, more than 70% of the leading global food crops depend on animal pollination (Klein *et al.*, 2007), but crop pollination and yield is threatened due to detrimental effects of agricultural intensification on animal pollinators (Ricketts *et al.*, 2008; Potts *et al.*, 2010).



It is generally assumed that the delivery of ecosystem services through species can be driven by the overall abundance, the diversity of the species community as well as by the spatial distribution of species and individuals (Jowett *et al.*, 2019). Overall abundance can drive the magnitude of specific ecosystem services and can be a better predictor for ecosystem service supply than diversity metrics such as species richness. For example, crop pollination was shown to depend more strongly on the abundance of common species than species richness, because rare species contribute little to this ecosystem function (Kleijn *et al.*, 2015, Winfree *et al.*, 2015). Weed seed removal by carabids can be dominated by the activity-density of few common- or even just one species (Rusch *et al.*, 2016). Nevertheless, more diverse species communities can also benefit the provision of ecosystem services through different mechanisms such as resource partitioning (i.e. more species will use greater range of resource types), facilitation (i.e. presence of one species enhances the functional contribution of another species), sampling effects (higher probability of including species that has greater contribution to ecosystem services) and higher adaptability towards environmental changes (Flombaum *et al.*, 2014, Wood *et al.*, 2015).

Beside abundance and diversity metrics, an increasing number of studies point to the importance of functional identity of species as well as the distribution and diversity of functional traits within species communities (e.g. Wood *et al.* 2015; Gagic *et al.*, 2015). Gagic *et al.*, (2015) found that trait-based indices are better predictors of ecosystem functioning than species richness or abundance. They also state that a functional trait approach supports a more mechanistical understanding how changes of species communities translate into the provision of ecosystem services. For instance, Greenop *et al.*, (2018) report that predator functional diversity positively affected biological pest control and Woodcock *et al.*, (2019) found that pollinator functional diversity enhanced crop pollination and yield. For carabids, it became evident that their potential for weed seed control is driven by their feeding type, because weed seed predation is related to omnivorous and granivorous but not carnivorous carabids (Trichard *et al.*, 2013). Diekötter *et al.*, (2016) also found higher weed seed predation per capita with increased body size of a granivorous carabid species. Different traits such as feeding type and body size can also interactively effect weed seed control. This was shown by González *et al.*, (2020) who found that pest predation was mainly driven by medium and large carnivorous carabids, whereas weed seed predation was increased by medium sized herbivorous carabids. Hence, for a comprehensive assessment of biodiversity effects and associated ecosystem services, a holistic approach is needed taking into account the abundance and species richness responses of functionally different taxa as well as the functional diversity of species communities which are important suppliers of ecosystem services.

### **1.3 Promoting biodiversity on arable land**

The major objective of cultivating arable land is the production of high yielding crops, which is mostly related to frequent disturbance regimes (i.e. crop rotation and regular ploughing) and high amount of external inputs such as fertilizers and pesticides. For these reasons arable land was traditionally

considered as less important habitat for most taxa (Tschardtke *et al.*, 2012b). However, a plethora of studies revealed that arable land can still be important resource habitats for many taxa occurring with high numbers of species and individuals. This was inter alia shown for ground-dwelling arthropods (Holland, 2002; Perner & Malt, 2003), which can use arable fields to reproduce and search for prey, arable weeds (Albrecht, 2003) or wild bees foraging on flowering crops (Westphal *et al.*, 2009). For instance, one hectare (ha) of a conventional managed cereal field still harbors several 100,000 individuals and several 100 of predator species (e.g. beetles, spiders, flies) (Tischler, 1980), which can reduce pest species such as cereal aphids (Tschardtke *et al.*, 2012a). The type and intensity of farming practices on arable habitats is therefore an important factor for biodiversity conservation and the provision of ecosystem services in agricultural landscapes.

In the EU the majority of measures to halt the loss of biodiversity and mitigate harmful effects on ecosystem functions are subsidized within the framework of agri-environmental schemes (AES). AES are part of the European agricultural fund for rural development, which is known as the “second pillar” of the common agricultural policy (CAP). AES were initiated by the European Union (EU) in 1992 to financially compensate individual farmers for environmental friendly practices applied mostly at the field scale (Henle *et al.*, 2008; Caro *et al.*, 2016). Between 2014 - 2020 the EU spent 100 billion € within the rural development fund, of which about 25 billion € were spent for AES excluding the national co-financing (European Commission, 2019). About 16,1 % of the total European agricultural land (about 28 million ha) is under management contracts supporting biodiversity emphasizing the widespread implementation of measures under the AES regime in Europe (European Commission, 2019). In addition, most EU member states spend equal or exceeding amount of money for AES than for all other nature conservation measures (Batáry *et al.*, 2015). But despite large expenditures for the promotion of biodiversity, several studies revealed that many types of AES are ineffective for the promotion of biodiversity (especially horizontal schemes not targeted on the promotion of specific species or habitats) and altogether cannot stop general biodiversity decline in Europe (Kleijn & Sutherland, 2003; Kleijn *et al.*, 2011). Studies also criticize that many AES measures may promote the abundance of common generalist species, but do not present effective tools to mitigate loss of specialist, rare and endangered species (Scheper *et al.*, 2013; Batáry *et al.*, 2015). Hence, increasing the effectiveness of current AES is of great importance for the conservation of biodiversity on farmland, but also for an efficient spending of tax money.

Further, organic farming is supported on more than 25 million ha by AES regimes within the EU (European Commission, 2019). Organic farming is principally a global concept and can also be a pure certification scheme which is not necessarily supported as specific measure under the national AES regime for all countries in the EU. Nevertheless, almost all EU countries have AES types that subsidise organic farming and it is considered as most widespread agri-environmental measure in Europe (Tuck *et al.*, 2014; Batáry *et al.*, 2015). Based on its principles organic farming is not specifically targeted on the promotion of biodiversity, as its objective is the holistic improvement of the overall agri-environment

(all biotic and abiotic components). To achieve that, organic farming regulations target less intensive and less external input dependent farming practices such as the ban of mineral fertilizers and chemical pesticides as well as the principle of circularity within the organic farming system (IFOAM, 2005). Even though most organic farming practices do not specifically target biodiversity, a plethora of empirical studies already confirmed an overall positive effect of organic farming on biodiversity compared to conventional farming systems (reviewed in Bengtsson *et al.*, 2005 and Tuck *et al.*, 2014).

Besides, strategies how to promote biodiversity on arable land include debates whether a “land sparing” (spatial segregation of biodiversity conservation and agricultural production) or a “land sharing” (integration of conservation and production on the same land) concept would be more appropriate (Fischer *et al.*, 2014). Because plenty of species require un- or sparsely disturbed natural or semi-natural habitats, the establishment of non-crop habitats in the context of a land sparing approach might be more suitable to reconcile agricultural production and biodiversity conservation (Phalan *et al.*, 2011). In contrast, some species groups like arable weeds or farmland birds breeding in open agricultural landscapes with minimum amount of vertical structures are adapted to regular farming practices and cannot be conserved in unfarmed habitats. Hence, environmental sensitive farming practices of land sharing systems can also be effective tools to promote biodiversity as well as pollination and pest control as shown for the example of organic farming (Tuck *et al.*, 2014; Senapathi *et al.*, 2015; Grass *et al.*, 2019). Segregating areas for biodiversity is often classified as “non-productive measure” such as the establishment of flowering strips and -fields, hedges or grassy field margins, whereas integrative approaches like less intensive farming practices are classified as “productive measure” as farmers can still gain crop yield on such land (Batáry *et al.*, 2015). Non-productive measures might be more effective to promote biodiversity than productive ones (Batáry *et al.*, 2015). This might be due to the fact that non-productive measures can be better targeted towards specific species groups, their specific habitat requirements as well as their limited resources which are essential to sustain viable populations (e.g. pollen and nectar resources for bees). Additionally, non-productive measures can potentially create a larger ecological contrast to conventional farming than productive ones. Ecological contrast was shown to be more important for the effectiveness of agri-environmental measures than local farming intensity or landscape structure (Marja *et al.*, 2019). Nevertheless, Grass *et al.*, (2019) emphasizes the complementarity of land sparing and land sharing approaches regarding natural or semi-natural land versus agricultural land. They argue that non-productive (sparing) measures might be more effective for the conservation of species which are sensitive to agricultural production, whereas productive (sharing) measures could be more effective to promote species which are essential to the provision of ecosystem services in agricultural landscapes. They conclude that both approaches need to be combined within a landscape matrix to optimize landscape-wide connectivity between natural or semi-natural habitats and productive agricultural land. However, further studies are still needed to reveal, if the same conclusions apply to productive and temporarily non-productive measures on arable land.

## 1.4 Flowering fields

During the funding period 2014-2020 the member states were more flexible with regard to the design of their AES regimes (Pe'er *et al.*, 2014). In this context the establishment of sown flowering fields, which are also termed under synonyms such as wildflower areas, wildflower mixtures or flower-rich fields, became a popular measure supported under the AES regime in countries such as Austria, Germany, Sweden, Switzerland or the UK (Haaland *et al.*, 2011). The establishment and management of flowering fields can greatly differ between regions regarding their size (often flowering strips instead of whole fields are supported), the sown seed-mixture (number of species, native or non-native species), time period (annual, perennial) or farming intensity. But establishing flowering fields usually includes the conversion of farmed arable land into fallow land by sowing a standardised seed-mixture of flowering crop- or wild plants in order to create a mass-flowering habitat with no or restricted permission to farming practices.

Flowering fields primarily support pollinators and predators contributing to biological pest control (Haaland *et al.*, 2011), but are generally intended to promote biodiversity in agricultural landscapes as well as the scenic landscape quality for the people. Farmers and the public often have positive attitudes towards flowering fields (Junge *et al.*, 2009) and prefer this measure compared with other types of agri-environmental measures (Marshall & Moonen, 2002; Haaland *et al.*, 2011). Beside the high aesthetic value, this might be due to the comparatively high spatial and temporal flexibility for farmers and the possibility for more effective weed control. Weed suppression in flowering fields is promoted by the sown flowering species and regular ploughing before sowing, which is especially relevant for annually established flowering fields. Farmers' preference towards this measure was also depicted in the regional AES regime of the German federal state Baden-Württemberg called *FAKT* (Förderprogramm für Agrarumwelt-, Klimaschutz und Tierwohl) (MLR, 2016). Within two years after introducing the measure (annual flowering field) in 2015, 5,511 conventional farmers already established the measure on a total area of 13,745 ha (1,7 % of the total arable land) (personal request at the agricultural ministry Baden-Württemberg (MLR) 2017).

So far, studies evaluating biodiversity and ecosystem function effects mostly considered flowering strips tailored to crop fields, while far less is known about effects of converting whole fields into flowering fields (but see Frank *et al.*, 2012; Mader *et al.*, 2017; Baulechner *et al.*, 2019). For flowering strips a plethora of studies showed positive effects on the abundance and diversity of a range of arthropod taxa as well as birds or small mammals, although some studies also found neutral or negative effects (reviewed in Haaland *et al.*, 2011; Dietzel *et al.*, 2019). Flowering strips were also shown to promote ecosystem services, in particularly pollination service to crops (Blaauw & Isaacs, 2014), biological pest control and crop yield in adjacent crop fields (Tschumi *et al.*, 2016). Further, the majority of studies measured effects by comparing it with conventional farmed mono-crops, but there is still a lack of understanding regarding the biodiversity effects of flowering fields compared to organically farmed crops which are also known to enhance biodiversity on arable land (Bengtsson *et al.*,

2005; Tuck *et al.*, 2014). Because productive measures still gain crop yield for the implementing farmer, they might be more cost-efficient than non-productive ones assuming similar biodiversity effects for both measure types. A detailed understanding of the relative effects of those measures (non-productive flowering fields versus productive organic crops) on biodiversity therefore contributes to the improvement of future AES types.

### 1.5 Lentil mixed-crops

Lentils (*Lens culinaris* Medic.) are among the oldest crop plants in Central Europe (Ali *et al.*, 2009) and up until present times it is a traditional and popular food there (Horneburg, 2006). Due to the introduction of mineral fertilizers and stronger yield increases in other crop types, the production of lentils in Central Europe became economically unattractive for farmers, which resulted in an almost total absence of lentil cropping until the mid of the 20<sup>th</sup> century for this region (Gruber *et al.*, 2012). Currently consumed lentils in Central Europe are mainly produced in Southern Europe and North America (Wang *et al.*, 2012). As a protein-rich legume plant, lentils can increase the crop diversity and provide nitrogen input into soil by fixation, which is an important argument especially for organic farming systems (Wang *et al.*, 2012). In Central Europe, but also in some other regions, lentils were traditionally intercropped with a supporting crop (mainly cereals) to stabilize the lentil crop and to reduce weed pressure. Mixed cropping of lentils is still the common type of growing lentils in Central Europeans organic farming systems, as it benefits yield, weed control and crop lodging resistance compared to lentil mono-crops (Wang *et al.*, 2012). In recent years a renaissance of lentil cropping started in Germany and some other countries like Switzerland, especially in organic farming systems, even though it still covers a marginal area compared with commonly grown crops such as cereal, maize or oilseed rape (Gruber *et al.*, 2012). In Baden-Württemberg, lentils were grown on 560 ha by just 0.12 % of all farmers (MLR, 2018). However, the Biosphere Reserve Swabian Alb in Baden-Württemberg has become a regional hotspot of lentil cropping due to a farmer cooperation with about 80 participating farmers, who promoted the cultivation of organic lentil mixed-crops and did successfully initiate a regional marketing of lentils during the last 15 years.

Lentil mixed-crops grow slowly during the initial phase of their development, which is why the establishment and growth of arable weeds can be enhanced compared to other crops (Pekrun *et al.*, 2013; Wang *et al.*, 2012). The increased wild plant cover as well as increased vegetation heterogeneity might benefit biodiversity more strongly than mono-crops even in organic farming systems. Besides, the lentil plant, a flowering legume, potentially increases the flower resource supply on arable land especially if intercropped with a flowering supporting crops like camelina (*Camelina sativa* L.) or buckwheat (*Fagopyrum esculentum* Moench). Despite its high potential to promote biodiversity, to my knowledge there are currently no studies (except few grey literature), which comprehensively investigated biodiversity effects of lentil mixed-crops in Central Europe. As lentil mixed-crops in

Central Europe are mainly grown in organic farming systems, the question remains if they could enhance biodiversity compared to commonly grown mono-crops of organic farming.

## 1.6 Edge and landscape effects

Europe's agricultural landscapes mainly consist of a mosaic between arable fields, intensively used grasslands, semi-natural habitats (e.g. hedges, heathland), human infrastructure and occasional remnants of natural habitats (Marshall & Moonen, 2002). Many species use multiple habitats during their life cycle and switch regularly between different habitat patches within the agricultural landscape. Arable fields are commonly adjacent to linear, unploughed semi-natural habitats such as grassy field margins or hedges (Schirmel *et al.*, 2016). Such habitats can provide undisturbed shelter, overwintering and reproduction habitats, dispersal corridors, alternative food resources as well as different and higher amount of ecological niches compared to arable fields (Bianchi *et al.*, 2006; Schirmel *et al.*, 2016). Previous studies revealed regular random or deliberate dispersal of species such as ground-dwelling arthropods from semi-natural habitats into neighbouring crop fields (Bianchi *et al.*, 2006; Rusch *et al.*, 2010). But these so called "spill-over effects" were also shown vice versa (Madeira *et al.*, 2016), as crop fields provide highly productive habitats during the growing season (Tscharntke *et al.*, 2005). Spill-over effects from neighbouring habitats can superimpose effects of local farming practices on species richness or species abundance (Gabriel *et al.*, 2010). Due to the vicinity to neighbouring habitats and related spill-over effects as well as altered habitat conditions (e.g. different microclimate, vegetation structure, management intensity), species richness is often higher at the edge than the interior of arable fields (e.g. Batáry *et al.*, 2017).

Beside edge effects, biodiversity effects of local farming practices on arable fields can also be altered or superimposed by the surrounding landscape complexity. Ecological theory suggests that the effectiveness of local AES, such as organic farming or the establishment of flowering fields, is highest in landscapes with intermediated complexity (hump-shaped relationship between landscape complexity and local management on biodiversity) (Tscharntke *et al.*, 2005). In simplified landscapes there might be no remaining source populations left which could profit from the local improvement of habitat conditions, whereas in complex landscapes local differences of habitat conditions might be superimposed by spill-over effects from the surrounding landscape. This theory was confirmed by some empiric studies like Concepción *et al.*, (2012) (but not all e.g. Winquist *et al.*, 2011), who found highest species richness of birds, plants, spiders and bees at an intermediate level of landscape complexity. The response to landscape effects can also differ between taxa with larger responses for large and mobile species, whereas smaller and less mobile species might be more strongly affected by local habitat conditions (Concepción *et al.*, 2012). Studies investigating landscape effects often differentiate between the compositional landscape heterogeneity (number and proportions of different cover types) and the configurational landscape heterogeneity (spatial arrangement of cover types) (Fahrig *et al.*, 2011). Some studies report positive effects of increased landscape composition (Kennedy *et al.*, 2013), others found

that biodiversity within arable fields was enhanced by increased configurational heterogeneity (i.e. small-scale agricultural landscapes) (Fahrig *et al.*, 2015; Batáry *et al.*, 2017), and still others found different responses to both factors (Plecas *et al.*, 2014; Slancarova *et al.*, 2014).

However, in general it can be concluded that species assemblages of arable fields are not only shaped by local farming practices, but also by spill-over effects from and into neighbouring habitats as well as the compositional- and configurational complexity of the surrounding landscape matrix. For example, Labruyere *et al.*, (2016) could show that carabid abundance in arable fields was affected by local crop type, but also by the neighbouring habitat type and the cover of grassland and oilseed rape in the surrounding landscape. Farmland birds occurring on arable fields were also shown to be affected by the threefold interaction between landscape, farming practice and within-field position (edge versus interior) (Gayer *et al.*, 2019). Studies comparing biodiversity effects of local measures should therefore take into account edge- as well as landscape effects.

## 1.7 Research objectives

This thesis aimed at studying the effects of establishing conventional managed annual flowering fields compared to organically managed fields cultivated with mono-crops (organic winter spelt) as well as flowering mixed-crops (organic lentil mixed-crop) for the promotion of biodiversity on arable land. These three crop-use types were compared to the effects of conventional winter wheat which served as control. As local effects of these four crop-use types can be also affected or even superimposed by edge- and landscape effects, the thesis also compared differences between the edge and interior within each study field as well as effects of the surrounding landscape complexity in 500 m radius around each study field.

To get a comprehensive overview about potential biodiversity and related ecosystem function effects, I took into account different components and indicators of biodiversity. To this end, I assessed abundance and species richness of five functionally different taxa, which were wild plants (primary producers), carabids and spiders (ground-dwelling predators), and butterflies and wild bees (flower-visiting arthropods). Beside taxonomical diversity responses I studied the functional diversity of carabids as an important species group for biological pest control. Last, I assessed the population development of *Bombus terrestris*, which is an important pollinator in European agricultural landscapes. Measuring effects on the population level helps to evaluate long-term conservation and pollination service benefits.

Specifically, I wanted to answer the following research questions:

- (1) Do conventional flowering fields promote biodiversity in conventional farming systems and do these effects exceed effects of organically farmed mono- and mixed-crops?

- (2) Do lentil mixed-crops additionally promote biodiversity in organic farming systems?
- (3) Does the within field position (edge vs. interior) affect biodiversity on arable land and if so, are these effects more pronounced than local crop-use type effects?
- (4) Does the complexity of the surrounding landscape affect biodiversity on arable land and if so, are these effects more pronounced than local crop-use effects?

## 1.8 Thesis outline

This dissertation is a cumulative thesis, consisting of three different research articles in chapter 2 - 4 after a general introduction in the first chapter and followed by a general discussion in the last chapter. Each of these three articles represent a primary research paper published or submitted to peer-reviewed international journals. Within the scope of this thesis all data were sampled in the Biosphere Reserve Swabian Alb in southwest Germany between 2016 – 2018.

Chapter 2 addresses taxonomical diversity throughout different species groups by assessing the abundance, species richness and community composition of five taxa differing in their ecological functionality, -demands and mobility, that were wild plants, ground-dwelling carabids and spiders, butterflies and wild bees. Thereby, i aimed to reveal if there are similar, different or complementary effects of the four crop-use types on different taxa, which were sampled at the field edge and interior. Study sites were distributed over a gradient of landscape complexity measured by the amount of arable land in 500 m radius around each study field. I also conducted personal interviews with all farmers in order to characterize crop-use specific farming practices. I discuss the relevance of our findings for the application of future agri-environmental measures.

Chapter 3 focuses more specifically on the functional diversity within species assemblages in response to the effects of crop-use type, within field position and landscape complexity. I chose carabids as study organism, because they frequently occur on arable land, can vary markedly in several traits between different species and are known to be important ecosystem service suppliers for weed- and pest control in arable fields. I therefore used data from the carabids sampling in 2016 – 2017 and characterised functional diversity by using the community weighted mean and functional divergence of carabid assemblages regarding three ecological traits, that was body size, feeding type and flight ability.

Chapter 4 considers the population development of a common and generalist pollinator species in agricultural landscapes – *Bombus terrestris*. For that, I experimentally exposed *B. terrestris* colonies at the four crop-use types, which differed in their flower resource supply. I also analysed possible effects



of different flower cover in the surrounding landscape. I used commercially bred colonies, as it allows a high degree of standardization between study sites which is hardly possible if assessing wild-living populations. I studied colony development by measuring maximum weight gain, foraging activity, worker body size and the number of queen brood cells. I additionally analysed pollen stores to reveal possible differences in the collected pollen diversity between crop-use types as well as between landscapes differing in their flower cover supply.

## 1.9 References

- Albrecht, H. (2003) Suitability of arable weeds as indicator organisms to evaluate species conservation effects of management in agricultural ecosystems. *Agriculture, Ecosystems & Environment*, 98 (1), 201–211. Doi: 10.1016/S0167-8809(03)00081-1.
- Ali, M., Singh, K.K., Pramanik, S.C. & Ali, M.O. (2009) Cropping systems and production agronomy. *The lentil: botany, production and uses* (ed. by Erskine, W., Mühlbauer, F.J., Sarker, A. & Sharma, B.), pp. 213–228. *CABI Publishing*. Wallingsford, UK.
- Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29 (4), 1006–1016. Doi: 10.1111/cobi.12536.
- Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C.F., Mußhoff, O., Császár, P., Fusaro, S., Gayer, C., Happe, A.-K., Kurucz, K., Molnár, D., Rösch, V., Wietzke, A. & Tscharnkte, T. (2017) The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. *Nature Ecology & Evolution*, 1 (9), 1279–1284. Doi: 10.1038/s41559-017-0272-x.
- Baulechner, D., Diekötter, T., Wolters, V. & Jauker, F. (2019) Converting arable land into flowering fields changes functional and phylogenetic community structure in ground beetles. *Biological Conservation*, 231, 51–58. Doi: 10.1016/j.biocon.2019.01.005.
- Beckmann, M., Gerstner, K., Akin-Fajiye, M., Ceaşu, S., Kambach, S., Kinlock, N.L., Phillips, H.R.P., Verhagen, W., Gurevitch, J., Klotz, S., Newbold, T., Verburg, P.H., Winter, M. & Seppelt, R. (2019) Conventional land-use intensification reduces species richness and increases production: A global meta-analysis. *Global change biology*, 25 (6), 1941–1956. Doi: 10.1111/gcb.14606.
- Bengtsson, J., Ahnström, J. & Weibull, A.-C. (2005) The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology*, 42 (2), 261–269. Doi: 10.1111/j.1365-2664.2005.01005.x.
- Bianchi, F.J.J.A., Booij, C.J.H. & Tscharnkte, 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), 1715–1727. Doi: 10.1098/rspb.2006.3530.
- Blaauw, B.R. & Isaacs, R. (2014) Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, 51 (4), 890–898. Doi: 10.1111/1365-2664.12257.
- BMU (Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit) (2019) Aktionsprogramm Insektenschutz der Bundesregierung. Gemeinsam wirksam gegen das Insektensterben. <[www.bmu.de/fileadmin/Daten\\_BMU/Pool/Broschueren/aktionsprogramm\\_insektenschutz\\_kabine\\_ttversion\\_bf.pdf](http://www.bmu.de/fileadmin/Daten_BMU/Pool/Broschueren/aktionsprogramm_insektenschutz_kabine_ttversion_bf.pdf)> 7 November 2019.
- Caro, G., Marrec, R., Gauffre, B., Roncoroni, M., Augiron, S. & Bretagnolle, V. (2016) Multi-scale effects of agri-environment schemes on carabid beetles in intensive farmland. *Agriculture, Ecosystems & Environment*, 229, 48–56. Doi: 10.1016/j.agee.2016.05.009.

- Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tschardtke, T. & Verhulst, J. (2012) Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, 49 (3), 695–705. Doi: 10.1111/j.1365-2664.2012.02131.x.
- Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem functioning. *Trends in Ecology & Evolution*, 16, 646–655. Doi: 10.1016/S0169-5347(01)02283-2.
- Diekötter, T., Wamser, S., Dörner, T., Wolters, V., & Birkhofer, K. (2016) Organic farming affects the potential of a granivorous carabid beetle to control arable weeds at local and landscape scales. *Agricultural and Forest Entomology*, 18 (2), 167–173. Doi: 10.1111/afe.12150.
- Dierschke, H. & Briemle, G. (2002) Kulturgrasland. Eugen Ulmer, Stuttgart, Germany.
- Dietzel, S., Sauter M., Moosner, C., Fischer, C. & Kollmann, J. (2019) Blühstreifen und Blühflächen in der landwirtschaftlichen Praxis – eine naturschutzfachliche Evaluation. *ANLiegen Natur*, 41 (1), online preview, 14 p., Laufen, Germany.
- Dudley, N. & Alexander, S. (2017) Agriculture and biodiversity: a review. *Biodiversity*, 18 (2-3), 45–49. Doi: 10.1080/14888386.2017.1351892.
- Emmerson, M., Morales, M. B., Oñate, J. J., Batary, P., Berendse, F., Liira, J., Aavik, T., Guerrero, I., Bommarco, R., Eggers, S., Pärt, T., Tschardtke, T., Weisser, W., Clement, L. & Bengtsson, J. (2016) How agricultural intensification affects biodiversity and ecosystem services. *Advances in Ecological Research*, 55, 43–97. Doi: 10.1016/bs.aecr.2016.08.005.
- European Commission (2019) European Commission EU Rural Development Policy 2014 -2020. <<https://cohesiondata.ec.europa.eu/funds/eafrd#top>> 21 December 2019.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.-L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14 (2), 101–112. Doi: 10.1111/j.1461-0248.2010.01559.x.
- Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K.F., Mitchell, S. & Tischendorf, L. (2015) Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment*, 200, 219–234. Doi: 10.1016/j.agee.2014.11.018.
- Fischer, J., Abson, D.J., van Butsic, Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G. & Wehrden, H.v. (2014) Land sparing versus land sharing: Moving forward. *Conservation Letters*, 7 (3), 149–157. Doi: 10.1111/conl.12084.
- Flombaum, P., Sala, O. E., & Rastetter, E. B. (2014) Interactions among resource partitioning, sampling effect, and facilitation on the biodiversity effect: a modeling approach. *Oecologia*, 174 (2), 559–566. Doi: 10.1007/s00442-013-2775-8.
- Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, 309 (5734), 570–574. Doi: 10.1126/science.1111772.

- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D. & Zaks, D.P.M. (2011) Solutions for a cultivated planet. *Nature*, 478 (7369), 337–342. Doi: 10.1038/nature10452.
- Frank, T., Aeschbacher, S. & Zaller, J.G. (2012) Habitat age affects beetle diversity in wildflower areas. *Agriculture, Ecosystems & Environment*, 152, 21–26. Doi: 10.1016/j.agee.2012.01.027.
- Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E. & Benton, T.G. (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, 13 (7), 858–869. Doi: 10.1111/j.1461-0248.2010.01481.x.
- Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tschardtke, T., Weisser, W. & Bommarco, R. (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, 282 (1801), 20142620. Doi: 10.1098/rspb.2014.2620.
- Gayer, C., Kurucz, K., Fischer, C., Tschardtke, T. & Batáry, P. (2019) Agricultural intensification at local and landscape scales impairs farmland birds, but not skylarks (*Alauda arvensis*). *Agriculture, Ecosystems & Environment*, 277, 21–24. Doi: 10.1016/j.agee.2019.03.006.
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tschardtke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W. & Inchausti, P. (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, 11 (2), 97–105. Doi: 10.1016/j.baae.2009.12.001.
- González, E., Seidl, M., Kadlec, T., Ferrante, M. & Knapp, M. (2020) Distribution of ecosystem services within oilseed rape fields: Effects of field defects on pest and weed seed predation rates. *Agriculture, Ecosystems & Environment*, 295, 106894. Doi: 10.1016/j.agee.2020.106894.
- Gossner, M.M., Lewinsohn, T.M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S.C., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., Diekötter, T., Jorge, L.R., Jung, K., Keyel, A.C., Klein, A.-M., Klemmer, S., Krauss, J., Lange, M., Müller, J., Overmann, J., Pašalić, E., Penone, C., Perović, D.J., Purschke, O., Schall, P., Socher, S.A., Sonnemann, I., Tschapka, M., Tschardtke, T., Türke, M., Venter, P.C., Weiner, C.N., Werner, M., Wolters, V., Wurst, S., Westphal, C., Fischer, M., Weisser, W.W. & Allan, E. (2016) Land-use intensification causes multitrophic homogenization of grassland communities. *Nature*, 540 (7632), 266–269. Doi: 10.1038/nature20575.
- Greenop, A., Woodcock, B. A., Wilby, A., Cook, S. M., & Pywell, R. F. (2018) Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. *Ecology*, 99(8), 1771–1782. Doi: 10.1002/ecy.2378.

- Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., Udy, K., Westphal, C., Wurz, A. & Tschardtke, T. (2019) Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature*, 1 (2), 262–272. Doi: 10.1002/pan3.21.
- Gruber, S., Wahl E., Zikeli, S. & Claupein, W. (2012) Perspektiven und Grenzen der Unkrautregulierung bei Linsen (*Lens culinaris*) im Ökologischen Landbau. *Journal für Kulturpflanzen*, 64 (10), 365–377.
- Haaland, C., Naisbit, R.E. & Bersier, L.-F. (2011) Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, 4 (1), 60–80. Doi: 10.1111/j.1752-4598.2010.00098.x.
- Habel, J.C., Trusch, R., Schmitt, T., Ochse, M. & Ulrich, W. (2019a) Long-term large-scale decline in relative abundances of butterfly and burnet moth species across south-western Germany. *Scientific Reports*, 9 (1), 1–9. Doi: 10.1038/s41598-019-51424-1.
- Habel, J.C., Ulrich, W., Biburger, N., Seibold, S. & Schmitt, T. (2019b) Agricultural intensification drives butterfly decline. *Insect Conservation and Diversity*, 12 (4), 289–295. Doi: 10.1111/icad.12343.
- Haberl, H., Erb, K.H., Krausmann, F., Gaube, V., Bondeau, A., Plutzer, C., Gingrich, S., Lucht, W. & Fischer-Kowalski, M. (2007) Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, 104 (31), 12942–12947. Doi: 10.1073/pnas.0704243104.
- Haddad, N.M., Haarstad, J. & Tilman, D. (2000) The effects of long-term nitrogen loading on grassland insect communities. *Oecologia*, 124 (1), 73–84. Doi: 10.1007/s004420050026.
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. & de Kroon, H. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PloS one*, 12 (10), e0185809. Doi: 10.1371/journal.pone.0185809.
- Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F.A., Niemelä, J., Rebane, M., Wascher, D., Watt, A. & Young, J. (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—A review. *Agriculture, Ecosystems & Environment*, 124 (1), 60–71. Doi: 10.1016/j.agee.2007.09.005.
- Holland, J.M. (2002) *The Agroecology of Carabids*. Intercept Limited, Andover, UK.
- Holland, J.M. & Reynolds, C.J.M. (2003) The impact of soil cultivation on arthropod (Coleoptera and Araneae) emergence on arable land. *Pedobiologia*, 47 (2), 181–191. Doi: 10.1078/0031-4056-00181.
- Homburg, K., Drees, C., Boutaud, E., Nolte, D., Schuett, W., Zumstein, P., Ruschkowski, E. & Assmann, T. (2019) Where have all the beetles gone? Long-term study reveals carabid species decline in a nature reserve in Northern Germany. *Insect Conservation and Diversity*, 5, 93. Doi: 10.1111/icad.12348.

- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75 (1), 3–35. Doi: 10.1890/04-0922.
- Horneburg, B. (2006) Outcrossing in lentil (*Lens culinaris*) depends on cultivar, location and year, and varies within cultivars. *Plant Breeding*, 125 (6), 638–640. Doi: 10.1111/j.1439-0523.2006.01290.x.
- IFOAM, (2005) Principles of organic agriculture, IFOAM International Federation of Organic Agriculture Movements, Bonn, Germany, 4 p.  
<[https://www.ifoam.bio/sites/default/files/poa\\_english\\_web.pdf](https://www.ifoam.bio/sites/default/files/poa_english_web.pdf)> 1 March 2020.
- Jowett, K., Milne, A. E., Metcalfe, H., Hassall, K. L., Potts, S. G., Senapathi, D., & Storkey, J. (2019) Species matter when considering landscape effects on carabid distributions. *Agriculture, Ecosystems & Environment*, 285, 106631. Doi: 10.1016/j.agee.2019.106631.
- Junge, X., Jacot, K.A., Bosshard, A. & Lindemann-Matthies, P. (2009) Swiss people's attitudes towards field margins for biodiversity conservation. *Journal for Nature Conservation*, 17 (3), 150–159. Doi: 10.1016/j.jnc.2008.12.004.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalho, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S. & Kremen, C. (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16 (5), 584–599. Doi: 10.1111/ele.12082.
- Khoury, C.K., Bjorkman, A.D., Dempewolf, H., Ramirez-Villegas, J., Guarino, L., Jarvis, A., Rieseberg, L.H. & Struik, P.C. (2014) Increasing homogeneity in global food supplies and the implications for food security. *Proceedings of the National Academy of Sciences*, 111 (11), 4001–4006. Doi: 10.1073/pnas.1313490111.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G. & Tscharntke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution*, 26 (9), 474–481. Doi: 10.1016/j.tree.2011.05.009.
- Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, 40 (6), 947–969. Doi: 10.1111/j.1365-2664.2003.00868.x.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalho, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Adamson, N.L., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E.,

- Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tschamtkke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Ward, K.L., Westphal, C. & Potts, S.G. (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, 6, 7414. Doi: 10.1038/ncomms8414.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tschamtkke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings. Biological sciences*, 274 (1608), 303–313. Doi: 10.1098/rspb.2006.3721.
- Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A.J., Settele, J., Kremen, C. & Dicks, L.V. (2017) Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters*, 20 (5), 673–689. Doi: 10.1111/ele.12762.
- Labruyere, S., Bohan, D.A., Biju-Duval, L., Ricci, B. & Petit, S. (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), 230–239. Doi: 10.1016/j.baae.2015.10.008.
- Landesregierung Baden-Württemberg (2019) Eckpunkte zum Schutz der Insekten in Baden-Württemberg als Weiterentwicklung des Gesetzesentwurfes „Rettet die Bienen“. [https://www.baden-wuerttemberg.de/fileadmin/redaktion/mlr/intern/dateien/PDFs/Landwirtschaft/2019\\_10\\_15\\_gemeinsames-eckpunktepapier-mlr-um.pdf](https://www.baden-wuerttemberg.de/fileadmin/redaktion/mlr/intern/dateien/PDFs/Landwirtschaft/2019_10_15_gemeinsames-eckpunktepapier-mlr-um.pdf) 14 December 2019.
- Landis, D.A. (2017) Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, 18, 1–12. Doi: 10.1016/j.baae.2016.07.005.
- Madeira, F., Tschamtkke, T., Elek, Z., Kormann, U.G., Pons, X., Rösch, V., Samu, F., Scherber, C. & Batáry, P. (2016) Spillover of arthropods from cropland to protected calcareous grassland – the neighbouring habitat matters. *Agriculture, Ecosystems & Environment*, 235, 127–133. Doi: 10.1016/j.agee.2016.10.012.
- Mader, V., Diehl, E., Fiedler, D., Thorn, S., Wolters, V. & Birkhofer, K. (2017) Trade-offs in arthropod conservation between productive and non-productive agri-environmental schemes along a landscape complexity gradient. *Insect Conservation and Diversity*, 10 (3), 236–247. Doi: 10.1111/icad.12220.
- Marja, R., Kleijn, D., Tschamtkke, T., Klein, A.-M., Frank, T. & Batáry, P. (2019) Effectiveness of agri-environmental management on pollinators is moderated more by ecological contrast than by landscape structure or land-use intensity. *Ecology Letters*, 22 (9), 1493–1500. Doi: 10.1111/ele.13339.
- Marshall, E.J.P. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment*, 89 (1), 5–21. Doi: 10.1016/S0167-8809(01)00315-2.

- MLR (Ministerium für Ländlichen Raum und Verbraucherschutz Baden-Württemberg) (2016) Verwaltungsvorschrift des Ministeriums für Ländlichen Raum und Verbraucherschutz zum Förderprogramm für Agrarumwelt, Klimaschutz und Tierwohl. Verwaltungsvorschrift vom 27.01.2016 (Az.: 25-8872.53).
- MLR (Ministerium für Ländlichen Raum und Verbraucherschutz Baden-Württemberg) (2018) Gemeinsamer Antrag 2012 – 2018. Retrieved from < <https://ltz.landwirtschaft-bw.de/pb/,Lde/Startseite/Kulturpflanzen/Linse> > 5 March 2020.
- Mupepele, A.-C., Böhning-Gäse, K., Lakner, S., Plieninger, T., Schoof, N. & Klein, A.M. (2019) Insect conservation in agricultural landscapes. An outlook for policy-relevant research. *GAIA* (28), 342–347.
- Oerke, E.-C. (2006) Crop losses to pests. *The Journal of Agricultural Science*, 144 (1), 31–43. Doi: 10.1017/S0021859605005708.
- Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbé, A., Wulf, F. & Scott, A.V. (2014) EU agricultural reform fails on biodiversity. *Science*, 344 (6188), 1090–1092. Doi: 10.1126/science.1253425.
- Pekrun, C., Lenz, R., Reidl, K., Koch, A., Pflaum, S., Röhl, M., Zimmermann, C. (2013) Untersuchung zur Artenvielfalt auf Linsenäckern, Endbericht 2013. Studie im Auftrag der Stiftung Naturschutzfonds. < <https://kulturpflanzen-alb.de/files/kulturpflanzen-alb/forschungsarbeiten/dateien/ArtenvielfaltLinsenacker2013.pdf> > 29 February 2020.
- Perner, J. & Malt, S. (2003) Assessment of changing agricultural land use: response of vegetation, ground-dwelling spiders and beetles to the conversion of arable land into grassland. *Agriculture, Ecosystems & Environment*, 98 (1), 169–181. Doi: 10.1016/S0167-8809(03)00079-3.
- Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011) Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science*, 333 (6047), 1289–1291. Doi: 10.1126/science.1208742.
- Plecas, M., Gagic, V., Jankovic, M., Petrovic-Obradovic, O., Kavallieratos, N.G., Tomanovic, Z., Thies, C., Tschardtke, T. & Cetkovic, A. (2014) Landscape composition and configuration influence cereal aphid–parasitoid–hyperparasitoid interactions and biological control differentially across years. *Agriculture, Ecosystems & Environment*, 183, 1–10. Doi: 10.1016/j.agee.2013.10.016.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neuman, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25 (6), 345–353. Doi: 10.1016/j.tree.2010.01.007.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A. & Viana, B.F. (2008) Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, 11 (5), 499–515. Doi: 10.1111/j.1461-0248.2008.01157.x.



- 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. *Advances in Agronomy*, 219–259, Doi: 10.1016/B978-0-12-385040-9.00006-2.
- Rusch, A., Binet, D., Delbac, L. & Thiéry, D. (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), 2163–2174. Doi: 10.1007/s10980-016-0390-x.
- Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8–27. Doi: 10.1016/j.biocon.2019.01.020.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. & Kleijn, D. (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. *Ecology Letters*, 16 (7), 912–920. Doi: 10.1111/ele.12128.
- Schirmel, J., Thiele, J., Entling, M.H. & Buchholz, S. (2016) Trait composition and functional diversity of spiders and carabids in linear landscape elements. *Agriculture, Ecosystems & Environment*, 235, 318–328. Doi: 10.1016/j.agee.2016.10.028.
- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Naus, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S. & Weisser, W.W. (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, 574 (7780), 671–674. Doi: 10.1038/s41586-019-1684-3.
- Senapathi, D., Biesmeijer, J.C., Breeze, T.D., Kleijn, D., Potts, S.G. & Carvalheiro, L.G. (2015) Pollinator conservation—the difference between managing for pollination services and preserving pollinator diversity. *Current Opinion in Insect Science*, 12, 93–101. Doi: 10.1016/j.cois.2015.11.002.
- Slancarova, J., Benes, J., Kristynek, M., Kepka, P. & Konvicka, M. (2014) Does the surrounding landscape heterogeneity affect the butterflies of insular grassland reserves? A contrast between composition and configuration. *Journal of Insect Conservation*, 18 (1), 1–12. Doi: 10.1007/s10841-013-9607-3.
- Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzog, I., van Doorn, A., Snoo, G.R. de, Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21<sup>st</sup> century agricultural change in Europe—a review. *Journal of environmental management*, 91 (1), 22–46. Doi: 10.1016/j.jenvman.2009.07.005.
- Sutcliffe, L.M.E., Batáry, P., Kormann, U., Báldi, A., Dicks, L.V., Herzog, I., Kleijn, D., Tryjanowski, P., Apostolova, I., Arlettaz, R., Aunins, A., Aviron, S., Baležentienė, L., Fischer, C., Halada, L., Hartel, T., Helm, A., Hristov, I., Jelaska, S.D., Kaligarič, M., Kamp, J., Klimek, S., Koorberg, P., Kostiuková, J., Kovács-Hostyánszki, A., Kuemmerle, T., Leuschner, C., Lindborg, R., Loos, J., Maccherini, S., Marja, R., Máthé, O., Paulini, I., Proença, V., Rey-Benayas, J., Sans, F.X., Seifert,

- C., Stalenga, J., Timaeus, J., Török, P., van Swaay, C., Viik, E. & Tschardtke, T. (2015) Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity and Distributions*, 21 (6), 722–730. Doi: 10.1111/ddi.12288.
- Tilman, D., Balzer, C., Hill, J. & Befort, B.L. (2011) Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, 108 (50), 20260–20264. Doi: 10.1073/pnas.1116437108.
- Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. & Polasky, S. (2002) Agricultural sustainability and intensive production practices. *Nature*, 418 (6898), 671–677. Doi: 10.1038/nature01014.
- Tischler, W. (1980) *Biologie der Kulturlandschaft*. Gustav Fischer, Stuttgart, Germany.
- Trichard, A., Alignier, A., Biju-Duval, L. & Petit, S. (2013) The relative effects of local management and landscape context on weed seed predation and carabid functional groups. *Basic and Applied Ecology*, 14 (3), 235–245. Doi: 10.1016/j.baae.2013.02.002.
- Tschardtke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J. & Whitbread, A. (2012a) Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 151 (1), 53–59. Doi: 10.1016/j.biocon.2012.01.068.
- Tschardtke, T., Klein, A.M., Kruss, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8 (8), 857–874. Doi: 10.1111/j.1461-0248.2005.00782.x.
- Tschardtke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W. H. & Westphal, C. (2012b) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87 (3), 661–685. Doi: 10.1111/j.1469-185X.2011.00216.x.
- Tschumi, M., Albrecht, M., Bärtschi, C., Collatz, J., Entling, M.H. & Jacot, K. (2016) Perennial, species-rich wildflower strips enhance pest control and crop yield. *Agriculture, Ecosystems & Environment*, 220, 97–103. Doi: 10.1016/j.agee.2016.01.001.
- Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A. & Bengtsson, J. (2014) Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. *Journal of Applied Ecology*, 51 (3), 746–755. Doi: 10.1111/1365-2664.12219.
- UN DESA (United Nations, Department of Economic and Social Affairs, Population Division) (2019) World population prospects 2019: Ten key findings. <[https://population.un.org/wpp/Publications/Files/WPP2019\\_10KeyFindings.pdf](https://population.un.org/wpp/Publications/Files/WPP2019_10KeyFindings.pdf)> 29 February 2020.
- Wang, L., Gruber, S. & Claupein, W. (2012) Optimizing lentil-based mixed cropping with different companion crops and plant densities in terms of crop yield and weed control. *Organic Agriculture*, 2 (2), 79–87. Doi: 10.1007/s13165-012-0028-5.

- Westphal, C., Steffan-Dewenter, I. & Tschardtke, T. (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, 46 (1), 187–193. Doi: 10.1111/j.1365-2664.2008.01580.x.
- Winfrey, R., Fox, J.W., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, 18 (7), 626–635. Doi: 10.1111/ele.12424.
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Pärt, T., Thies, C., Tschardtke, T., Weisser, W.W. & Bommarco, R. (2011) Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology*, 48 (3), 570–579. Doi: 10.1111/j.1365-2664.2010.01950.x.
- Wood, S. A., Karp, D. S., de Clerck, F., Kremen, C., Naeem, S., & Palm, C. A. (2015) Functional traits in agriculture: agrobiodiversity and ecosystem services. *Trends in Ecology & Evolution*, 30 (9), 531–539. Doi: 10.1016/j.tree.2015.06.013.
- Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J., Lindström, S.A.M., Stanley, D., Ouvrard, P., Edwards, M.E., Jauker, F., McCracken, M.E., Zou, Y., Potts, S.G., Rundlöf, M., Noriega, J.A., Greenop, A., Smith, H.G., Bommarco, R., van der Werf, W., Stout, J.C., Steffan-Dewenter, I., Morandin, L., Bullock, J.M. & Pywell, R.F. (2019) Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nature communications*, 10 (1), 1–10. Doi: 10.1038/s41467-019-09393-6.
- Zabel, F., Delzeit, R., Schneider, J.M., Seppelt, R., Mauser, W. & Václavík, T. (2019) Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nature communications*, 10 (1), 2844. Doi: 10.1038/s41467-019-10775-z.



## 2. CHAPTER

### **Additive effects of flowering fields, organic farming and edge habitats promote diversity of plants, flower-visiting and ground-dwelling arthropods in arable fields**

A version of chapter 2 was submitted to *Journal of Applied Ecology*:

Gayer, C., Berger, J., Dieterich, M., Gallé, R., Reidl, K., Witty, R., Woodcock, B.A. & Batáry, P. (2020) Additive effects of flowering fields, organic farming and edge habitats promote diversity of plants, flower-visiting and ground-dwelling arthropods in arable fields. Submitted to *Journal of Applied Ecology*.



© Photos: C. Gayer: top (all, except T. Weiß: second left), bottom-central; Jutta Wieland: bottom-right, bottom-left

## **Additive effects of flowering fields, organic farming and edge habitats promote diversity of plants, flower-visiting and ground-dwelling arthropods in arable fields**

Christoph Gayer<sup>1</sup>, Jochen Berger<sup>2</sup>, Martin Dieterich<sup>2</sup>, Róbert Gallé<sup>3</sup>, Konrad Reidl<sup>1</sup>, Rosa Witty<sup>4</sup>, Ben A. Woodcock<sup>5</sup> & Péter Batáry<sup>3</sup>

<sup>1</sup>Institute of Landscape and Environment (ILU), University of Applied Science Nürtingen-Geislingen, 72622 Nürtingen, Germany;

<sup>2</sup>Landscape Ecology and Vegetation Science, University of Hohenheim, 70599 Stuttgart, Germany;

<sup>3</sup>MTA Centre for Ecological Research, Institute of Ecology and Botany, “Lendület” Landscape and Conservation Ecology Research Group, Vácrátót, Hungary;

<sup>4</sup> Department of Botany, University of Innsbruck, 6020 Innsbruck, Austria;

<sup>5</sup>NERC Centre for Ecology & Hydrology, Crowmarsh Gifford, Wallingford OX10 8BB, UK.

### **2.1 Abstract**

Increased farming intensity has led to a massive decline across multiple farmland taxa. In Europe, measures introduced to counteract these losses include those considered agronomically productive, such as organic farming, as well as those that support no direct production of crops, such as non-crop flowering fields in conventional farming systems. To assess impacts on farmland biodiversity relative to a control crop of conventionally managed winter wheat, we compared non-productive flowering fields managed under conventional farming to both an organically managed cereal mono-crop (organic winter spelt) and a flowering mixed-crop (organic lentil mixed-crop). These four crop-use types were studied on 68 study fields (17 sites) over a three years period to assess their impact on the abundance, species richness and community composition of wild plants, carabids, spiders, butterflies and wild bees. Species richness of wild plants was highest under organic farming and at field edges when compared to the interior. In the case of carabids and spiders, species richness was highest at the field edges, but there was no difference between the four crop-use types. In contrast, the abundance and species richness of butterflies and wild bees responded only to flowering crop-use types, showing no edge effects.

Landscape complexity surrounding the fields also affected community composition of all taxa, with the exception of spiders, but had only minor effects on overall abundance and species richness. Across a range of different taxa additive effects on biodiversity in response to the implementation of non-productive flowering fields, productive mono- and mixed-crop organic systems as well as field edge habitats emphasizes that a mosaic of different farming practices is likely to benefit regional species pool. Agricultural policy should foster coordination between both organic and non-organic farmers with the goal of establishing landscape scale complementarity between both productive and non-productive

agri-environmental measures. However, the effective implementation of these will likely require scaled incentives to reflect differences in direct economic gain provided by different measures in terms of crop production.

**Keywords:** Agri-environment schemes, butterfly, carabid beetle, edge effect, farmland biodiversity, landscape complexity, spider, wild bee.

## 2.2 Introduction

Globally and in Europe, increased farming intensity has led to massive declines across multiple taxa in terms of their biomass, abundance and species richness (Stoate *et al.*, 2009; Sánchez-Bayo & Wyckhuys, 2019). To counteract this loss, the European Union (EU) established agri-environmental schemes (AES) to financially compensate farmers for environment-friendly practices. Although AES are the highest biodiversity conservation related expenditure in the EU, broad debates about their cost efficiency have been launched (Kleijn *et al.*, 2011) as farmland biodiversity continues to decline (Pe'er *et al.*, 2014; Batáry, Dicks, Kleijn & Sutherland, 2015). It remains a key policy challenge to improve farming practices and in that context future AES towards higher biodiversity. While redesigning the AES concept remains problematic, it is likely that relatively minor changes in current implementation policy that foster increased quality and complementarity at landscape scales could potentially provide huge benefits for farmland biodiversity.

To enhance biodiversity on arable land, non-productive measures exist, such as annual flowering fields (fallow arable land planted with flowering forbs), which remove whole fields from crop production. In contrast there are also productive approaches, combining continued crop use and biodiversity upgrades on the same area, e.g. organically farmed arable crops. Flowering fields are commonly applied in a number of European countries as part of their AES programs (e.g. England, Germany, Switzerland) (Haaland *et al.*, 2011; Dietzel *et al.*, 2019). Annual establishment of flowering field is often preferred by farmers, as it allows better weed and pest control and greater flexibility for farm management. Several studies have reported positive effects on flower-visiting- and other arthropod groups (Haaland *et al.*, 2011; Dietzel *et al.*, 2019). In contrast, organic farming can also benefit biodiversity through reduced farming intensity (Bengtsson *et al.*, 2005; Tuck *et al.*, 2014). To date, direct comparisons of biodiversity effects between non-productive flowering fields and production integrated measures, such as organically farmed crops, are rare (but see Mader *et al.*, 2017). However, both measures are commonly applied in Europe.

Furthermore, there might be differences between different taxonomic and functional species groups in response to the implementation of annual flowering fields (Haaland *et al.*, 2011; Dietzel *et al.*, 2019) or organic farmed crops (Batáry *et al.*, 2012; Tuck *et al.*, 2014). Annual flowering fields create mass-flowering habitats, which are likely to be beneficial for highly mobile flower-visiting arthropods (e.g. bees) able to exploit this resource rapidly. In contrast, less mobile species, such as ground-dwelling

carabids and spiders, may take significantly longer to colonise, while also being less able to utilise such resources at landscape scales as is the case with bees that are able to forage over many kilometers. In contrast, organic farming in the EU includes a permanent conversion to less intensive farming practices (The EU Council, 2007; The EU Commission, 2008), such as permanent ban of chemical pesticides and mineral fertilizers and reduced crop plant density (Batáry *et al.*, 2017). Long term applications of less intensive farming practices might affect less mobile taxa more strongly than short term conversion of conventional crops into flowering fields. For instance, long term effects of organic farming were seen to promote carabid species diversity (Schröter & Irmeler, 2013; Irmeler, 2018) and spider abundance (Birkhofer *et al.*, 2008).

In addition, the impact of landscape complexity on biodiversity responses superimposed over these field scale farming practices, may be expected to affect large and mobile taxa more strongly than small and less mobile species groups (Concepción *et al.*, 2012; Tschamtker *et al.*, 2012). Indeed, such differences in mobility may also impact arthropod diversity at the scale of individual fields, with field edges having more diverse invertebrate populations than the interior in response to reduced management (Batáry *et al.*, 2012), immigration from neighbouring habitats (Woodcock *et al.*, 2016) and increased habitat heterogeneity (Bianchi *et al.*, 2006). Without simultaneous assessments of the responses of different taxa and functional groups to flowering fields and organic crops, it is not possible to assess if these have different effects on arable field biodiversity.

In this study we compared the effects of an AES that establishes flowers at a field scale under conventional management (annual flowering field) to both an organically managed cereal mono-crop (organic winter spelt) as well as a flowering mixed-crop (organic lentil mixed-crop) for the promotion of biodiversity on arable land. These were compared to a control crop of conventionally managed winter wheat. For these four crop-use types we measured biodiversity responses by the abundance, species richness and community composition of five functionally different taxa, which were wild plants (primary producers), carabids and spiders (ground-dwelling predators), and butterflies and wild bees (flower-visiting arthropods). We hypothesized that (1) flower-visiting arthropods would be the most abundant and species rich in conventional flowering fields, whereas plants and ground-dwelling arthropods benefit more strongly from organically managed mono- and mixed-crops. (2) In organic farming systems, flowering lentil mixed-crops would promote both the abundance and species richness of flower-visiting arthropods to a greater extent than mono-crops due to the increased flower resources. (3) Field edges would support higher abundance and species richness for all taxa, and (4) species richness of all taxa would be positively related to increased landscape complexity independent of crop-use type.



## 2.3 Materials and methods

### 2.3.1 Study area and design

Study sites were located in the UNESCO Biosphere Reserve Swabian Alb in southwest Germany. Terrain elevation of the Swabian Alb ranges between 460-860 m a.s.l. with a mean annual temperature of 6-7° C and a mean annual precipitation of 700-1000 mm (Fischer *et al.*, 2010). Soils are shallow, stony and poor luvisols or cambisols on a bedrock of White Jurassic limestone (soil type according to IUSS Working Group WRB, 2015).

We selected arable fields farmed under four crop-use types: 1) conventional winter wheat (*Triticum aestivum* L.) representing a control; 2) conventional flowering field (sown seed mixture of 15-18 species including *Centaurea cyanus*, *Helianthus annuus*, and *Phacelia tanacetifolia*; Table S2.1); 3) organic winter spelt (*Triticum aestivum* subsp. *spelta* L.) representing an organic cereal control; 4) and organic lentil (*Lens culinaris* Medic.) intercropped with a supporting crop (cereal or camelina (*Camelina sativa* L.)). In total we studied 68 arable fields distributed over 17 study sites in three years (4 crop-use types  $\times$  6 sites (5 sites in 2018)  $\times$  3 years). The mean field size was  $2.3 \pm 0.2$  hectares (ha) (mean  $\pm$  SEM) with similar field sizes between crop-use types (winter wheat:  $2.5 \pm 0.4$  ha; flowering field:  $2.4 \pm 0.4$  ha; winter spelt:  $2.1 \pm 0.2$  ha; lentil mixed-crop:  $2.1 \pm 0.4$  ha) and varied between study sites from  $1.4 \pm 0.3$  ha to  $3.9 \pm 1.1$  ha. The minimum distance between study fields of the same study site was much smaller ( $0.7 \pm 0.1$  km) than the minimum distance between study fields of different study sites ( $4.6 \pm 0.7$  km), which is in accordance with the spatially nested study design.

To standardize landscape context, soil and climate conditions, we blocked the four crop-use types in close spatial proximity. Further nesting within the blocks also existed as the individual farmers managing the study fields were not the same farmer for the two conventional- (winter wheat, flowering field) and both organic crop-use types (winter spelt, lentil mixed-crop) (except one site in 2018 with 3 farmers). In addition, each farmer managed one flowering- (flowering field, lentil mixed-crop) and one cereal- (winter wheat, winter spelt) crop type. Hence, crop-use types were nested within the random effects farmer also nested within site, while farmer and crop type were also crossed establishing a cross-nested study design (see Fig. S2.1).

### 2.3.2 Farming practices

The four crop-use types differed in management (conventional vs. organic farming), crop-type (cereal vs. flowering plant) and sowing time (autumn vs. spring sown crop) (Table 2.1, Table S2.2). Details about flowering fields and lentil mixed-crops can be found in the supporting information (Appendix A2.1) and are also described in Gayer *et al.*, (2019). Cereal crops (winter wheat and winter spelt) were sown in the previous autumn, whereas flowering crops (flowering field, lentil mixed-crop) were spring sown. Only winter wheat was treated with herbicides, fungicides, insecticides or mineral fertilizers.

Mechanical weed control was only substantially applied in organic winter spelt. Organically managed crop-use types had a more diverse crop rotation and more perennial crops in rotation (mainly clover-mixtures) (Table 2.1, Table S2). Tillage practice consisted of conversion ploughing, but in some cases minimum tillage practices were applied (32% of all study fields). This latter management was more frequently in winter spelt (53%). Further details about farming practices and vegetation characteristics see Appendix A2.1 and Table S2.3. To assess field specific management, we carried out personal interviews with farmers using a standardized questionnaire (n=35) (details about the questionnaire see Appendix A2.1).

### 2.3.3 *Sampling of organisms*

All taxa were sampled at two distances per study field (edge and interior; sampling design see Fig. S2.3). We sampled wild plants and ground beetles (Carabidae) over a three year period from 2016-2018 (n=17 per crop-use type) and spiders (Araneae), butterflies (diurnal Lepidoptera) and wild bees (Hymenoptera, Apidae, Apiformes) during two years (2017-2018, n=11).

We surveyed plants in five plots ( $5 \times 1$  m in size and 5 m distance between them) per transect (= 10 plots per study field; Fig. S2.3). For each plot we estimated cover per wild plant species according to the extended Braun-Blanquet scale (Reichelt & Willmanns, 1973). In 2016, we surveyed each plot once between 25 June and 4 August, while in 2017 and 2018 we surveyed each plot three times (in mid-June, early July, late July).

We sampled carabids and ground active spiders using pitfall traps with a diameter of 7.2 cm and filled with 30% ethylene glycol as trapping fluid. We placed five traps along each transect in a distance of 10 m between traps ( $2 \times 5$  traps per study field, Appendix A2.2., Fig. S2.3). Traps were opened for ten consecutive days and kept closed for the following ten days. We conducted three sampling rounds between 15 June and 3 August 2016, two sampling rounds between 15 June and 16 July 2017 and two sampling rounds between 17 June and 19 July 2018, which amounts to a total number of 70 trapping days.

We surveyed butterflies by walking four transect lines ( $75 \times 4$  m per transect). Two transects were located along field borders and two along the diagonal in the field interior (see Appendix Fig. S3). Each transect was walked at a uniform speed within a standardized duration of 5 min between 09:00 a.m. and 05:00 p.m. on sunny days with limited cloud cover (temperatures  $>15^{\circ}$  C). Wind speed during counts was  $<20$  Km h<sup>-1</sup>. In 2017 we conducted five survey rounds (late May, early June, mid-June, late June, early July) and in 2018 three survey rounds (mid-June, mid-July, late July).

We surveyed bees along two transects of 50 m per study field. Timing of sampling and weather conditions were the same as for the butterflies. One transect was designated along the field border, the other 15-20 m parallel to it in the interior of the study field (Fig. S2.3). We conducted five point count stops of 5 min along each transect with 10 m distance between point count locations. Per point count we surveyed all bees in a radius of 2 m. In 2017 we conducted three survey rounds (late May, mid-June,

mid-July) and in 2018 four survey rounds (mid-June, early July, mid-July, late July). Wild bees and butterflies were sampled on different sampling transects, but close to the pitfall trap transects (within 50 m distance except three cases with less than 100 m distance). Hence, for landscape analysis (see next section) a common set of landscape complexity data (surrounding landscapes) was used for all species groups. For further details about the species survey see Appendix A2.2.

**Table 2.1.** Farming practice characteristics, achieved yield and subsidy amount of studied crop-use types sampled in 2016, 2017 and 2018 (mean  $\pm$  SE; n=68). Results (F-value of ANOVA table) of linear mixed-effects models are given to test for significant differences between crop-use types. Bold values indicate significant effect at  $P < 0.05$ .

		Sowing date (calendar week)	Crops in rotation (number)	Fertilizer <sup>b</sup> (kg N ha <sup>-1</sup> )	Pesticide application (number)	Mechanical weeding <sup>c</sup> (number)	Yield (dt ha <sup>-1</sup> )	Subsidy by AES <sup>d</sup> (€ ha <sup>-1</sup> )
Conventional	Winter Wheat (n=17)	40.3 $\pm$ 0.3 (early October)	3.9 $\pm$ 0.2	184.8 $\pm$ 10.6	2.1 $\pm$ 0.3	0.1 $\pm$ 0.1	70.3 $\pm$ 2.7	none
	Flowering Field (n=17)	18.2 $\pm$ 0.2 (early May)	3.9 $\pm$ 0.2	1.4 $\pm$ 1.4	none	none	none	710
Organic	Winter Spelt (n=17)	40.9 $\pm$ 0.2 (early October)	5.9 $\pm$ 0.2	61.9 $\pm$ 16.0	none	1.7 $\pm$ 0.2	31.5 $\pm$ 1.4	230
	Lentil mixed-crop (n=17)	14.7 $\pm$ 0.3 (mid of April)	5.9 $\pm$ 0.2	7.0 $\pm$ 4.1	none	0.2 $\pm$ 0.1	11.8 $\pm$ 1.9	230
Model <sup>a</sup>	F - value	Year 1.0	<b>13.6</b>	0.5	0.3	0.5	3.1	
	Crop		<b>2458.9</b>	<b>65.8</b>	<b>57.7</b>	<b>23.4</b>	<b>365.2</b>	

<sup>a</sup> All models were fitted with normal distribution.

<sup>b</sup> Square root transformed values used for model calculation.

<sup>c</sup> Only weeding between sowing and harvest counted.

<sup>d</sup> Fixed amount according to the agri-environmental scheme (AES) of the federal state Baden-Württemberg named FAKT (MLR, 2016).

### 2.3.4 Landscape analysis

We analysed landscape complexity using the Geographical Information System ArcGIS 10.2.2 (1999-2014 ESRI Inc.) and data from an area-wide classification of habitat complexes of the Biosphere Reserve Swabian Alb (see Schlager *et al.*, 2013). There was one study site outside the borders of the Biosphere Reserve Swabian Alb. Here we used aerial photographs, official digital thematic maps (ATKIS DTK 50), and official biotope mapping data of Baden-Württemberg (URL: <http://udo.lubw.baden-wuerttemberg.de/public/>, accessed 08.02.2019). We measured landscape complexity in a radius of 500 m around the midpoint of each pitfall trap transect. We used 500m radius following comparative studies (Toivonen *et al.*, 2015), because distances between study fields were small ( $0.7 \pm 0.1$  km) due to the spatially nested study design.

The most abundant land cover type was arable land with  $56.5 \pm 1.4\%$  of total cover ranging from 15.1% to 83.0% between study fields. We calculated Shannon-index as a habitat diversity measure from the percentage cover of arable land, intensively managed grassland, extensive grassland, copses, forest, wetland and urban elements (Fischer *et al.*, 2011). Arable land cover was independent of crop-use types ( $\chi^2 = 4.9$ ,  $df = 3$ ,  $P = 0.18$ ) or transect position ( $\chi^2 < 0.01$ ,  $df = 1$ ,  $P = 0.99$ ), and negatively correlated with habitat diversity (Shannon-index;  $r_{142} = -0.83$ ,  $P < 0.001$ ), as well as intensively managed grassland ( $r_{142} = -0.57$ ,  $P < 0.001$ ) or forest cover ( $r_{142} = -0.69$ ,  $P < 0.001$ ). Hence, we used arable land cover as a simple predictor of landscape complexity.

### 2.3.5 Statistical analysis

First, for describing differences in farming- and vegetation characteristics among crop-use types and study years (Table 2.1), we performed a linear mixed-effects models (GLMM) using the ‘lme4’ package (Bates *et al.*, 2015) of the R 3.4.2. software (R Development Core Team, 2017). We included ‘crop-use type’ and ‘year’ as fixed factors and ‘site’, ‘farmer’ and ‘crop type’ (cereal vs. flowering crop) as nested random factors into the model by using the following R-syntax:

“lmer(y ~ Crop-use type + Year + (1|Site/Farmer) + (1|Site/Crop type))”.

In this and all subsequent GLMMs we tested for normal distribution of model residuals by investigating normal quantile-quantile plots and plotting model residuals against fitted values to visualize error distribution and check for heteroscedasticity. For testing independence of landscape complexity from crop-use type and transect, we also used the above R-syntax with landscape complexity as response variable and ‘crop-use type’ and ‘transect’ as single and interacting fixed effects.

Third, before analysing our study organisms, we pooled data of all traps and survey periods per study transect for all taxa separately ( $N = 136$  for carabids, plants;  $N = 88$  for spiders, butterflies, wild bees). Data for cover, abundance and species richness of all taxa were ranged between 0-1 to get comparable effect sizes between taxa. GLMMs were calculated for analysing effects of landscape

complexity, crop-use type, transect position and their interactions on abundance (=number of individuals for arthropods, cover for plants) and species richness (=number of species; excluding plant species of the sown seed mixture for flowering fields). Separate models were run for each taxon and response variable. The factors ‘year’, ‘farmer’, ‘site’ and ‘crop type’ were included as nested random effects in the model, ‘landscape complexity’, ‘crop-use type’ and ‘year’ as fixed effects according to the R syntax:

“lmer(y ~ (Landscape Complexity+Crop-use type+Transect)<sup>3</sup> + (1|Year/Site/Farmer) + (1|Year/Site/Crop type)”.

We used model averaging, based on the multi-model approach of Burnham & Anderson (2002), by calculated all models nested in the global model using the dredge function of the ‘MuMIn’ package (Barton, 2017) and compared candidate models according to Akaike’s Information Criteria, corrected for small sample sizes (AICc). The models with  $< 2 \Delta AICc$  of the best model were used for model averaging applying the command model.avg of the ‘MuMIn’ package, as such models are considered to be as good as the best model (Symonds & Moussalli, 2011).

To study effects on community composition, we applied a constrained redundancy analysis (RDA) of the species-abundance matrix with ‘landscape complexity’, ‘crop-use type’ and ‘transect position’ as constraining factors and ‘year’, ‘village’, ‘farmer’ as conditional factors to account for the nested study design. We transformed species-abundance data with the Hellinger transformation prior to the RDA (Legendre & Gallagher, 2001). We calculated permutation tests based on 999 permutations to test for significant effects on community composition. We used the ‘vegan’ package in R for RDA (Oksanen *et al.*, 2015).

## 2.4 Results

In total we recorded 168 wild plant species (Table S2.4), 97 carabid species (abundance (n)= 70,814; Table S2.5), 81 species of spider (n=33,262; Table S2.6), 34 species of butterfly (n=1,551; Table S2.7), as well as 44 species of wild bees (n=1,644; Table S2.8). The wild bees were dominated by bumblebee (*Bombus* spp.) which comprised 85% (13 species) of the total abundance.

### 2.4.1 Crop-use type effects

Wild plant species richness differed between management types with higher species richness in organic (winter spelt, lentil mixed-crop) than conventional (winter wheat, flowering field) managed crop-use types. Winter wheat had lower wild plant cover and species richness as well as carabid abundance than all other crop-use types, although effects of lentil mixed-crop on carabid abundance were less pronounced (Table 2.2; Fig. 2.1a, b; Fig. 2.2a). Further, lentil mixed-crop had higher wild plant cover than flowering fields and winter spelt due to higher cover in the field interior. Crop-use type had minor effects on spider abundance and species richness of spiders and carabids (Fig. 2.1c; Fig. 2.2b, c). Flowering-crop types (flowering fields, lentil mixed-crops) but not cereal-crop types (winter wheat,

winter spelt) did strongly increase butterfly abundance and species richness (Fig. 2.1d, Fig. 2.2d). Flowering fields had much higher wild bee abundance and species richness compared to all other crop-use types (Fig. 2.1e, Fig. 2.2e). Lentil mixed-crops had higher wild bee species richness than winter wheat and winter spelt.

**Table 2.2.** Effects of landscape (% of arable cover), crop-use type (winter wheat (WW) vs. flowering field (FF) vs. winter spelt (WS) vs. lentil-mixed-crop (LMC)) and transect position (edge (E) vs. center (C)) on abundance and species richness of five taxa. Results were calculated by multi-model averaging of linear mixed-effects models. Importance of predictor variables, parameter estimates with standard error (SE) and t/z-values. Only models with  $< 2 \Delta \text{AICc}$  of the best model are shown. Landscape complexity or interaction terms were never retained among such best fit models. Bold values indicate significant effect at  $P < 0.05$ .

Response	Taxa <sup>a</sup>	Explanatory	Relative importance[%]	Multi-model estimate <sup>b</sup>	± SE	t/z- value
Cover <sup>c</sup>	<b>Wild plants</b> <sup>d</sup> (0.41/0.80;2)	Crop-use type (FF/WW)	100	0.019	0.003	<b>7.407</b>
		Crop-use type (WS/WW)	100	0.018	0.002	<b>7.156</b>
		Crop-use type (LMC/WW)	100	0.027	0.003	<b>9.792</b>
		Crop-use type (WS/FF)	100	-0.002	0.003	0.543
		Crop-use type (LMC/FF)	100	0.008	0.002	<b>3.335</b>
		Crop-use type (WS/LMC)	100	-0.010	0.003	<b>3.782</b>
		Transect (E/C)	65	0.006	0.002	<b>3.957</b>
Abundance	<b>Carabids</b> (0.13/0.59;1)	Crop-use type (FF/WW)	30.5	0.107	0.046	<b>2.319</b>
		Crop-use type (WS/WW)	30.5	0.182	0.047	<b>3.853</b>
		Crop-use type (LMC/WW)	30.5	0.102	0.056	1.806
		Crop-use type (WS/FF)	30.5	0.075	0.056	1.334
		Crop-use type (LMC/FF)	30.5	-0.005	0.047	0.107
		Crop-use type (WS/LMC)	30.5	0.080	0.045	1.758
	<b>Spiders</b> (0.17/0.58;1)	Transect (E/C)	15	-0.082	0.044	-1.848
	<b>Butterflies</b> (0.52/0.77;1)	Crop-use type (FF/WW)	0.99	0.358	0.048	<b>7.435</b>
		Crop-use type (WS/WW)	0.99	0.105	0.051	2.042
		Crop-use type (LMC/WW)	0.99	0.401	0.059	<b>6.809</b>
		Crop-use type (WS/FF)	0.99	-0.253	0.059	<b>-4.303</b>
		Crop-use type (LMC/FF)	0.99	0.043	0.051	0.831
		Crop-use type (WS/LMC)	0.99	-0.296	0.047	<b>-6.240</b>
	<b>Wild bees</b> (0.66/0.88;1)	Crop-use type (FF/WW)	100	0.432	0.033	<b>13.136</b>
		Crop-use type (WS/WW)	100	-0.013	0.041	-0.323
		Crop-use type (LMC/WW)	100	0.042	0.047	0.896
		Crop-use type (WS/FF)	100	-0.445	0.047	<b>-9.533</b>
		Crop-use type (LMC/FF)	100	-0.390	0.041	<b>-9.565</b>
		Crop-use type (WS/LMC)	100	-0.055	0.032	-1.709
Species richness	<b>Wild plants</b> (0.54/0.89;1)	Crop-use type (FF/WW)	100	11.11	1.811	<b>6.134</b>

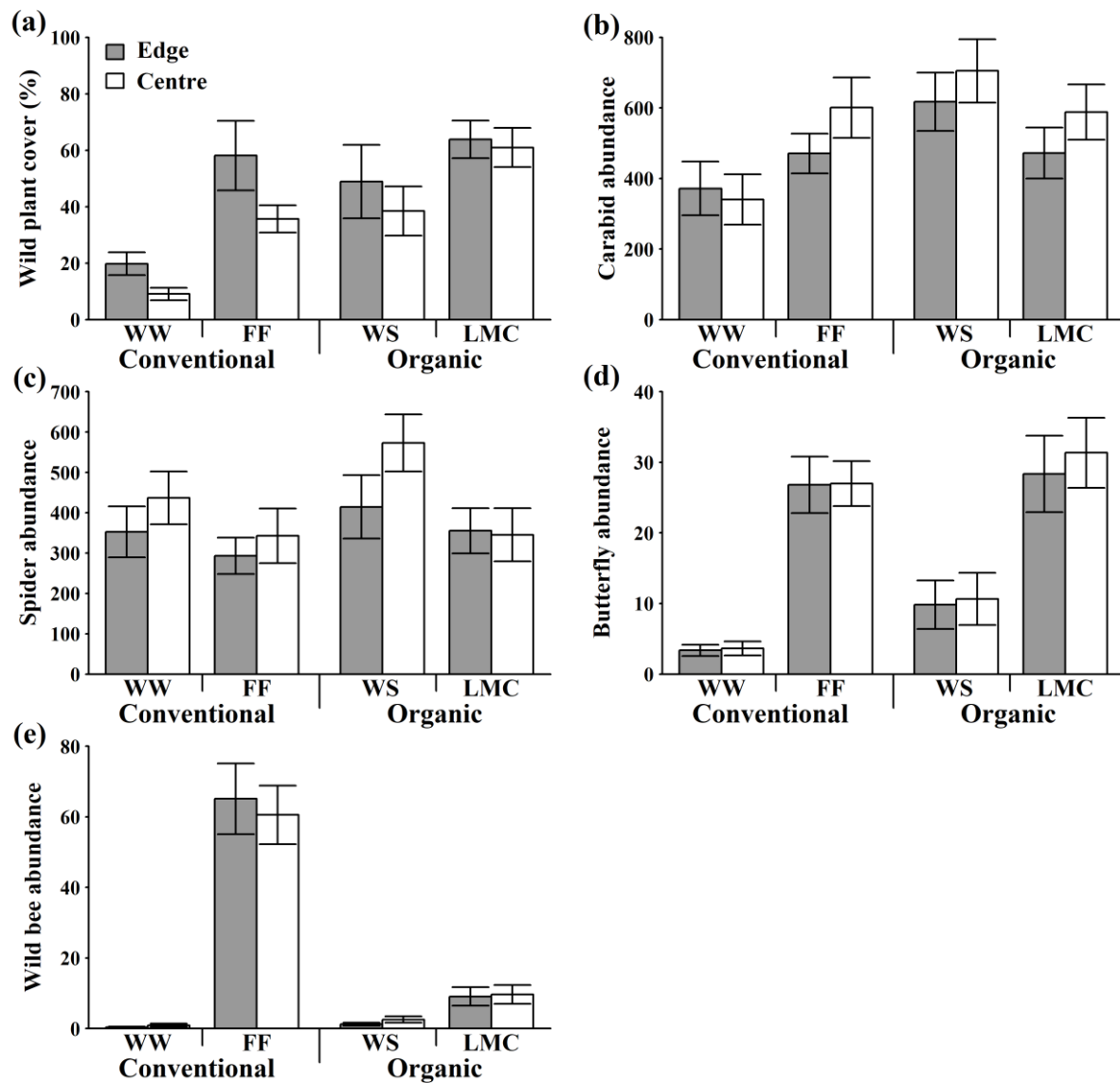
Response	Taxa <sup>a</sup>	Explanatory	Relative importance[%]	Multi-model estimate <sup>b</sup>	± SE	t/z- value
Species richness	Wild plants	Crop-use type (WS/WW)	100	18.546	1.82	<b>10.188</b>
		Crop-use type (LMC/WW)	100	22.811	2.245	<b>10.160</b>
		Crop-use type (WS/FF)	100	7.436	2.245	<b>3.312</b>
		Crop-use type (LMC/FF)	100	11.701	1.82	<b>6.428</b>
		Crop-use type (WS/LMC)	100	-4.265	1.794	-2.377
		Transect (E/C)	100	10.485	0.864	<b>12.137</b>
	Carabids (0.28/0.52;1)	Transect (E/C)	100	0.178	0.028	<b>6.410</b>
	Spiders (0.34/0.55;1)	Transect (E/C)	100	0.203	0.030	<b>6.751</b>
	Butterflies (0.58/0.77;1)	Crop-use type (FF/WW)	100	0.319	0.037	<b>8.618</b>
		Crop-use type (WS/WW)	100	0.114	0.046	2.518
		Crop-use type (LMC/WW)	100	0.430	0.047	<b>9.063</b>
		Crop-use type (WS/FF)	100	-0.204	0.047	<b>-4.306</b>
		Crop-use type (LMC/FF)	100	0.111	0.046	2.446
		Crop-use type (WS/LMC)	100	-0.316	0.036	<b>-8.696</b>
	Wild bees (0.73/0.82;1)	Crop-use type (FF/WW)	100	0.622	0.042	<b>14.848</b>
		Crop-use type (WS/WW)	100	0.056	0.042	1.336
		Crop-use type (LMC/WW)	100	0.251	0.046	<b>5.501</b>
		Crop-use type (WS/FF)	100	-0.567	0.046	<b>-12.4</b>
		Crop-use type (LMC/FF)	100	-0.371	0.042	<b>-8.873</b>
		Crop-use type (WS/LMC)	100	-0.196	0.042	<b>-4.700</b>

<sup>a</sup> All models were fitted with normal distribution (marginal/conditional R<sup>2</sup> value of full model; number of candidate models,  $\Delta$  AIC < 2).

<sup>b</sup> Positive estimates indicate higher number e.g. higher wild plant cover in flowering fields (FF) versus winter wheat (WW).

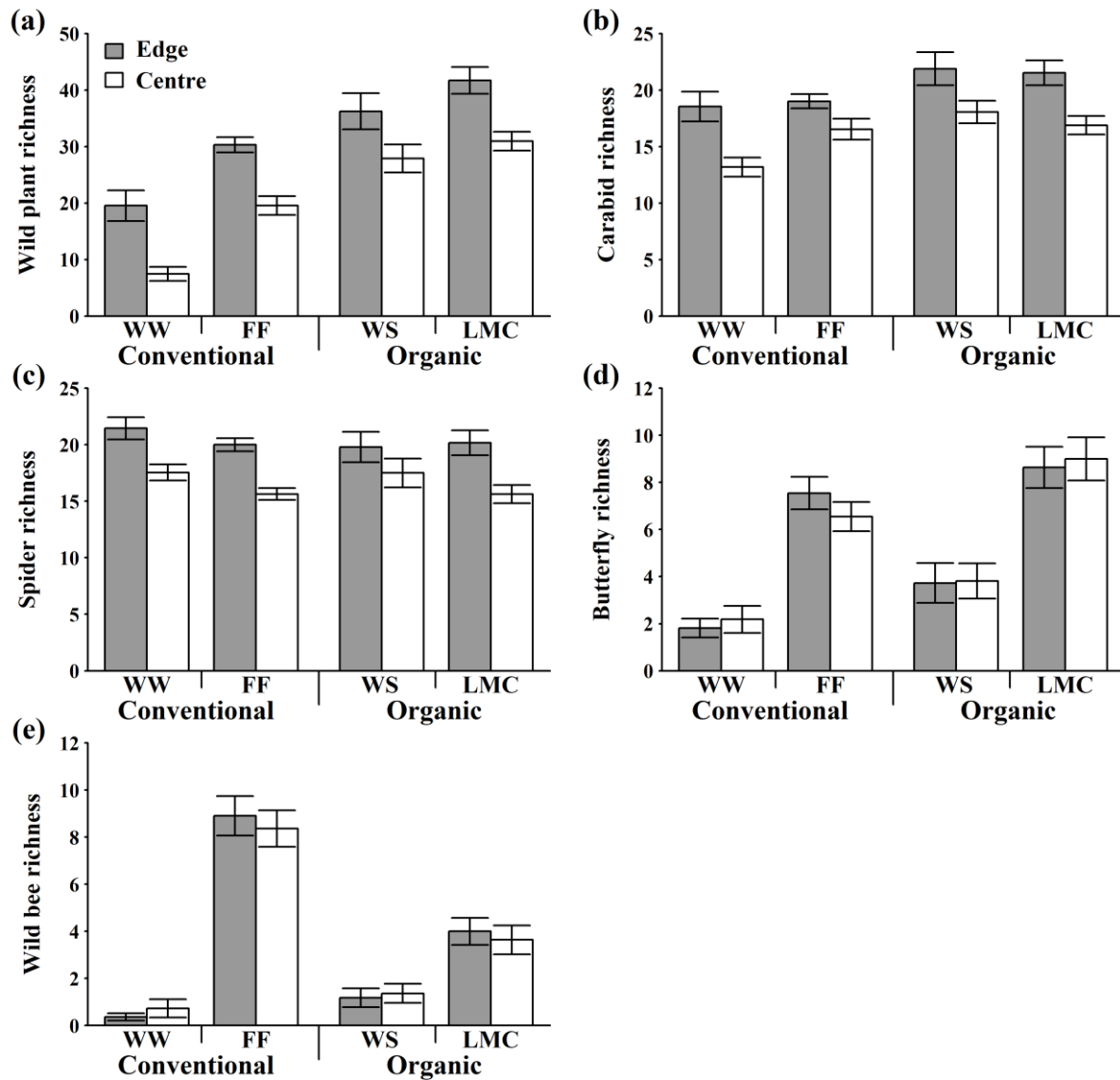
<sup>c</sup> For wild plants mean plant cover data were used, for all other taxa the number of individuals were used.

<sup>d</sup> Arcsine transformed values were used for model calculation.



**Fig. 2.1.** Effect of crop-use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil mixed-crop (LMC)) and transect position (edge, center) on wild plant cover (a) and abundance (number of individuals) of carabid beetles (b), spiders (c), butterflies (d) and wild bees (e). Bars are means  $\pm$  SE.





**Fig. 2.2.** Effect of crop-use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil mixed-crop (LMC)) and transect position (edge, center) on species richness (number of species) of wild plants (a), carabid beetles (b), spiders (c), butterflies (d) and wild bees (e). Bars are means  $\pm$  SE.

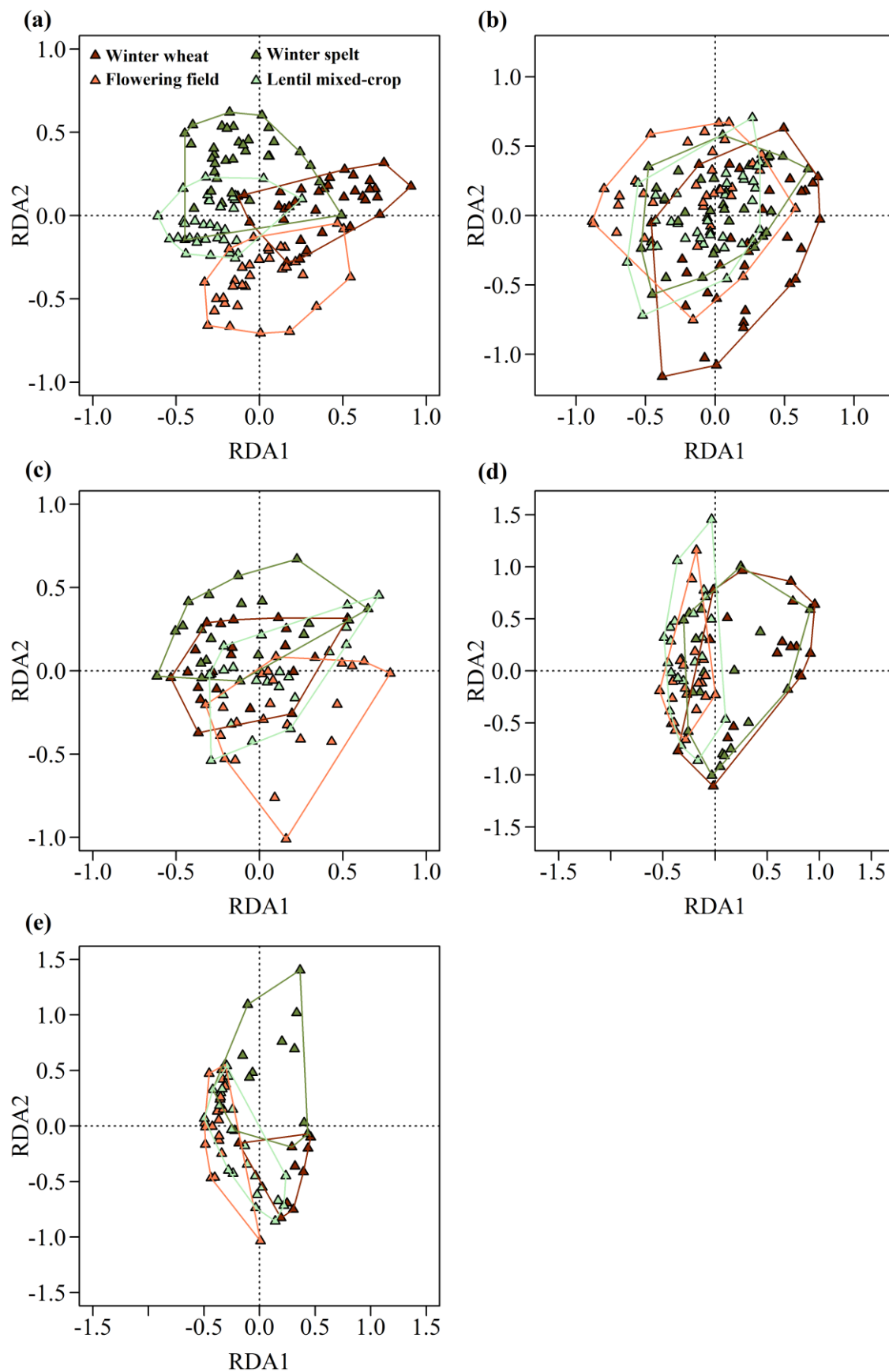
Despite differences in abundance or species richness, community composition was similar between crop-use types (Fig. 2.3), although crop-use type had significant effects and explained the highest amount of variation among the three explanatory variables for all taxa (Table 2.3). We found highest similarity between study sites for carabid as well as spider assemblages and to a lesser extend for wild plant communities (Fig. 2.3a, b, c). Similarity of butterfly as well as wild bee assemblages between study sites was also high, but community composition differed more strongly between crops of different crop types (flowering – vs. cereals crops) than between crops of the same crop type (Fig. 2.3d, e).

### 2.4.2 Edge and landscape effects

Wild plant cover was higher at the edge than in the interior of crop fields (Table 2.2), but these differences were more pronounced in both conventional managed crop-use types (winter wheat, flowering field) and absent in lentil mixed-crop (Fig. 2.1a). Abundance of carabids, spiders, butterflies and wild bees did not significantly differ between the field edge and interior (Fig. 2.1b, c, d, e). Species richness of wild plants, carabids and spiders, but not of butterflies and wild bees, was higher at the edge than the interior of fields independent of crop-use type. Transect position did significantly affect community composition of wild plants, carabids and spiders, but not of butterflies or wild bees (Table 2.3). Transect position explained high amount of variation (10.9%) for the community composition of spiders, but low amount for wild plants and spiders. Landscape complexity had no significant effect on the abundance or species richness of any taxa. It significantly affected community composition of all taxa except spiders, but with a low share of explained variation.

**Table 2.3.** Results of an RDA to analyse the effects of landscape complexity (% of arable cover), crop-use type (winter wheat, flowering field, winter spelt, lentil-mixed-crop) and transect position (edge, center) on community composition of five taxa. Percentage of explained variation, F- and P-values (bold if  $P < 0.05$ ) are given.

Taxa	Explanatory	Variation [%]	F	P
<b>Wild plants</b>	Landscape complexity	1.794	2.887	<b>0.001</b>
	Crop-use type	11.87	6.369	<b>0.001</b>
	Transect	1.480	2.383	<b>0.002</b>
<b>Carabids</b>	Landscape complexity	1.943	3.062	<b>0.002</b>
	Crop-use type	6.744	3.542	<b>0.001</b>
	Transect	3.983	6.277	<b>0.001</b>
<b>Spiders</b>	Landscape complexity	1.839	2.114	0.054
	Crop-use type	11.068	4.241	<b>0.001</b>
	Transect	10.882	12.508	<b>0.001</b>
<b>Butterflies</b>	Landscape complexity	2.671	2.759	<b>0.003</b>
	Crop-use type	7.367	2.537	<b>0.001</b>
	Transect	0.5119	0.529	0.937
<b>Wild bees</b>	Landscape complexity	2.033	2.349	<b>0.018</b>
	Crop-use type	23.52	9.059	<b>0.001</b>
	Transect	0.440	0.509	0.898



**Fig. 2.3.** Redundancy analysis ordination (RDA) plots of survey transects (triangles) for wild plants (a), carabid beetles (b), spiders (c), butterflies (d) and wild bees (e). Minimum convex polygons of the four crop-use types are shown.

## 2.5 Discussion

We found clear taxon-specific differences in response to the four crop-use types. Plants were best promoted by organic farming, in particular from lentil mixed-crops and field edges, ground-dwelling arthropods most strongly benefited from field edges with little differences between crop-use types, whereas flower-visiting arthropods solely benefited from flowering crop-types under conventional and organic management without edge effects. Despite differences in species richness and abundance, there was high similarity of species communities between crop-use types, revealing that these differences were not related to a pronounced species turnover. Landscape complexity did not affect abundance or species richness of any taxa, but showed some minor effects on community composition. Hence, there might be an additive effect of flowering fields supported by AES under conventional management, organic mono- and flowering mixed-crops as well as field edge habitats for the promotion of biodiversity in arable fields at the landscape scale.

### 2.5.1 Crop-use type effects

Responses to crop-use types were only partly in line with hypothesis (1) stating that flower-visiting arthropods are best promoted by flowering fields, whereas ground-dwelling arthropods benefit from organic farming. Although flowering fields most strongly promoted wild bees, butterflies equally benefited from flowering fields and lentil mixed-crops, whereas organic farming practices affected wild plants, but not carabids and spiders. Flowering fields had the highest flower cover (Table S2.3), including many mass-flowering forb species like phacelia (*P. tanacetifolia*), borage (*Borago officinalis*), or cornflower (*C. cyanus*), offering attractive pollen- and nectar sources for bees and butterflies (Carreck & Williams, 2002; Pywell *et al.*, 2004; Haaland *et al.*, 2011; Warzecha *et al.*, 2018). This might explain the observed positive effects on wild bees and butterflies.

Higher flower cover of lentil mixed-crops compared to both cereal crops (Table S2.3), may also have led to more wild bee species and butterfly species and individuals. This result confirmed hypothesis (2) that in organic farming systems flower-visiting arthropods can be promoted by cropping flowering mixed-crops. Positive effects of lentil mixed-crops were clearly more pronounced for butterflies than wild bees (Table S2.3). This may have been caused by stronger preferences of butterflies for native plants, in particular *Cirsium* spp. and legumes. *Cirsium* spp. are among the most frequently visited flowers by butterflies, in particular for the most abundant species of this study such as *Pieris brassicae*, *Pieris napi*, *Pieris rapae* and *Maniola jurtina* (Table S2.7) (Dover, 1989; Clausen *et al.*, 2001; Lebeau *et al.*, 2017), whereas short-tongued bee species are not well adapted to the deep corollas of *Cirsium* spp. (Warzecha *et al.*, 2018). Other frequently surveyed species such as *Polyommatus icarus*, *Polyommatus coridon* or *Colias alfacariensis* (Table S2.7) prefer legume plants as nectar and larval host plant (Settele, *et al.*, 2015). Lentil mixed-crops had highest presence of thistles, especially *Cirsium arvense*, (Table S2.4) as well as highest legume cover due to the sown lentil crop, making it a more attractive feeding habitat for butterflies than wild bees.

Despite large differences in farming practice, crop-use type effects on carabids and spiders were small. In arable fields, spiders and carabid communities are dominated by agrobiont, mainly carnivorous and omnivorous species, which are adapted to regular disturbances and crop management (Gallé *et al.*, 2018). Hence, these taxa might be less sensitive to differences in crop use. Further, the dominance of agrobiont species in the species community might have led to the observed high similarity of species communities between crop-use types. This might even apply for the communities of wild plants, bees and butterflies, which were also dominated by few agrobiont species irrespectively of crop-use type (Table S2.4-8).

Some other studies also could not show effects of organic farming on spider species richness (Mader *et al.*, 2017) or carabid diversity (Fuller *et al.*, 2005). Birkhofer *et al.*, (2014) even stated that such predatory arthropods are losers of organic farming. Nevertheless, several studies found positive effects of organic versus conventional crops (Bengtsson *et al.*, 2005; Tuck *et al.*, 2014). For flowering areas, studies showed increased abundance and species richness of carabids and spiders (Haaland *et al.*, 2011; Dietzel *et al.*, 2019), but Frank *et al.*, (2012) found that such effects may differ between perennial- and annual flowering fields.

### 2.5.2 Edge and landscape effects

In contrast to hypothesis (3), only plant cover and species richness of plants, carabids and spiders was higher at the field edge than the field interior, whereas species richness of butterflies or wild bees, as well as the abundance of all taxa did not significantly differ between the transects. The reasons may lie in the higher mobility combined with the ability of longer range detection of suitable resources by butterflies and wild bees, similar flower cover between the edge and interior of crop fields (Table S2.3), and/or different survey methods (Fig. S2.3). Higher species richness of plants and ground-dwelling arthropod taxa at the field edge was also reported by other studies, e.g. Batáry *et al.*, (2012), due to the reduced pest and weed management (Marshall & Moonen, 2002), higher microhabitat heterogeneity and closer proximity of adjacent semi-natural habitats (Schirmel *et al.*, 2016).

Last, our results did not confirm hypothesis (4), because landscape complexity did not significantly impact abundance or species richness of any of the studied taxa, although it had some minor effects on community composition with the exception of spiders. Other studies found landscape moderated biodiversity effects within crop fields, but effects may differ between simple and complex landscapes with larger effects in intensively farmed agricultural landscapes (Batáry *et al.*, 2011; Birkhofer *et al.*, 2018). Our study area consisted of a small-scale agricultural landscape with small field sizes (about 2.3 ha) and a high coverage with semi-natural habitats. Therefore, the amount of uncropped land as suitable source habitat might not be a limiting factor in the study area, which in turn might have neutralized differences in the amount of arable land in the surrounding landscape, which we used as a parameter for landscape complexity.

### 2.5.3 *Conclusions*

Our results emphasize that conventional flowering fields, organic mono- and flowering mixed-crops as well as field edge habitats have different, and thereby additive effects for the promotion of biodiversity within arable fields. Annual flowering fields established as part of AES under conventional arable agriculture were the most successful measure for promoting flower-visiting bees and butterflies, organic crops most strongly enhanced wild plants, and field edge conditions were the most important factor to enhance carabids and spiders. These findings emphasize that a diverse mosaic of different farming practices within an arable farming landscape should be applied to support a large regional species pool of different taxa.

However, farmers preferences towards environment-friendly farming practices strongly depend on monetary incentives, which are balanced against financial and labor costs for implementation. Many farmers may choose the most cost-efficient ones, resulting in a low diversity between agri-environmental measures within an agricultural landscape. Hence, future agricultural policy should provide individual farmers with incentives for the implementation of a diverse mixture of farming practices on their farmland. In addition, it should foster the coordination of agri-environmental measures between farmers at the landscape level by regional authorities and should take into account the status quo of the regional dominant farming practices to avoid an one-sided founding of single measures (e.g. if some farmers already create flowering fields within a landscape, others should be supported to create edge habitats or mixed-crops.).

## 2.6 **Acknowledgements**

We thank the farmers for their participation; Nils Engelmann, Caroline Fischer, Miriam Harper, Moritz Mayer, Nina Stork and Judith Engelke for supporting the plant survey, Theresa Faessler, Lukas Maier, Frederik Schuettler and Tobias Weiß for the sampling and identification of carabids, Róbert Horváth for the identification of spiders, and Jutta Wieland for conducting the butterfly survey. Data collection in 2017 and 2018 was funded by the Stiftung Naturschutzfonds Baden-Württemberg (73-8831.21/54691-1703GL). PB was supported by the Economic Development and Innovation Operational Programme of Hungary (GINOP-2.3.2-15-2016-00019). BW were funded by the Natural Environment Research Council (NERC) under research programme NE/N018125/1 ASSIST – Achieving Sustainable Agricultural Systems.

## 2.7 References

- Barton, K. (2017) MuMIn: Multi-Model Inference. R package version 1.40.0. <<https://CRAN.R-project.org/package=MuMIn>> 10 July 2019
- Batáry, P., Báldi, A., Kleijn, D. & Tschardtke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1894–1902. Doi: 10.1098/rspb.2010.1923.
- Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29 (4), 1006–1016. Doi: 10.1111/cobi.12536.
- Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C.F., Mußhoff, O., Császár, P., Fusaro, S., Gayer, C., Happe, A.-K., Kurucz, K., Molnár, D., Rösch, V., Wietzke, A. & Tschardtke, T. (2017) The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. *Nature Ecology & Evolution*, 1 (9), 1279–1284. Doi: 10.1038/s41559-017-0272-x.
- Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. & Tschardtke, T. (2012) Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agriculture, Ecosystems & Environment*, 146, 130–136. Doi: 10.1016/j.agee.2011.10.018.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. Doi: 10.18637/jss.v067.i01.
- Bengtsson, J., Ahnström, J. & Weibull, A.-C. (2005) The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology*, 42, 261–269. Doi:10.1111/j.1365-2664.2005.01005.x.
- Bianchi, F.J.J.A., Booij, C.J.H. & Tschardtke, 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), 1715–1727. Doi:10.1098/rspb.2006.3530.
- Birkhofer, K., Andersson, G.K.S., Bengtsson, J., Bommarco, R., Dänhardt, J., Ekbom, B., Ekroos, J., Hahn, T., Hedlund, K., Jönsson, A.M., Lindborg, R., Olsson, O., Rader, R., Rusch, A., Stjernman, M., Williams, A. & Smith, H.G. (2018) Relationships between multiple biodiversity components and ecosystem services along a landscape complexity gradient. *Biological Conservation*, 218, 247–253. Doi: 10.1016/j.biocon.2017.12.027.
- Birkhofer, K., Bezemer, T.M., Bloem, J., Bonkowski, M., Christensen, S., Dubois, D., Ekelund, F., Fließbach, A., Gunst, L., Hedlund, K., Mäder, P., Mikola, J., Robin, C., Setälä, H., Tatin-Froux, F., van der Putten, W.H. & Scheu, S. (2008) Long-term organic farming fosters below and aboveground biota: Implications for soil quality, biological control and productivity. *Soil Biology and Biochemistry*, 40, 2297–2308. Doi: 10.1016/j.soilbio.2008.05.007.
- Birkhofer, K., Ekroos, J., Corlett, E.B. & Smith, H.G. (2014) Winners and losers of organic cereal farming in animal communities across Central and Northern Europe. *Biological Conservation*, 175, 25–33. Doi: 10.1016/j.biocon.2014.04.014.

- Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference (2nd ed.). Springer, New-York, US.
- Carreck, N.L. & Williams, I.H. (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation*, 6, 13–23. Doi: 10.1023/A:1015764925536.
- Clausen, H.D., Holbeck, H.B. & Reddersen, J. (2001) Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. *Biological Conservation*, 98, 167–178. Doi: 10.1016/S0006-3207(00)00151-8.
- Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tschardtke, T. & Verhulst, J. (2012) Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, 49, 695–705. Doi: 10.1111/j.1365-2664.2012.02131.x.
- Denys, C. & Tschardtke, T. (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia*, 130, 315–324. Doi: 10.1007/s004420100796.
- Dietzel, S., Sauter M., Moosner, C., Fischer, C. & Kollmann, J. (2019) Blühstreifen und Blühflächen in der landwirtschaftlichen Praxis – eine naturschutzfachliche Evaluation. *ANLiegen Natur*, 41 (1), online preview, 14 p., Laufen, Germany.
- Dover, J.W. (1989) The use of flowers by butterflies foraging in cereal field margins. *Entomologist's Gazette*, 40, 283–291.
- Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulz, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.D. & Weisser, W.W. (2010) Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. *Basic and Applied Ecology*, 11, 473–485. Doi: 10.1016/j.baae.2010.07.009.
- Fischer, C., Flohre, A., Clement, L.W., Batáry, P., Weisser, W.W., Tschardtke, T. & Thies, C. (2011) Mixed effects of landscape structure and farming practice on bird diversity. *Agriculture, Ecosystems & Environment*, 141, 119–125. Doi: 10.1016/j.agee.2011.02.021.
- Frank, T., Aeschbacher, S. & Zaller, J.G. (2012) Habitat age affects beetle diversity in wildflower areas. *Agriculture, Ecosystems & Environment*, 152, 21–26. Doi: 10.1016/j.agee.2012.01.027.
- Fuller, R.J., Norton, L.R., Feber, R.E., Johnson, P.J., Chamberlain, D.E., Joys, A.C., Mathews, F., Stuart, R.C., Townsend, M.C., Manley, W.J., Wolfe, M.S., Macdonald, D.W. & Firbank, L.G. (2005) Benefits of organic farming to biodiversity vary among taxa. *Biology letters*, 1, 431–434. Doi: 10.1098/rsbl.2005.0357.
- Gallé, R., Császár, P., Makra, T., Gallé-Szpisjak, N., Ladányi, Z., Torma, A., Kapilkumar, I. & Szilassi, P. (2018) Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites. *Landscape Ecology*, 33, 1435–1446. Doi: 10.1007/s10980-018-0677-1.



- Gayer, C., Lövei, G. L., Magura, T., Dieterich, M., & Batáry, P. (2019) Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats. *Agriculture, Ecosystems and Environment*, 284, 106579. Doi: 10.1016/j.agee.2019.106579.
- Haaland, C., Naisbit, R.E. & Bersier, L.-F. (2011) Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, 4 (1), 60–80. Doi: 10.1111/j.1752-4598.2010.00098.x.
- Irmeler, U. (2018) Which carabid species (Coleoptera: Carabidae) profit from organic farming after a succession of 15 years? *Agriculture, Ecosystems & Environment*, 263, 1–6. Doi: 10.1016/j.agee.2018.02.019.
- IUSS Working Group WRB (2015) World reference base for soil resources 2014, update 2015, international soil classification system for naming soils and creating legends for soil maps. *World Soil Resources Reports*, 106, UN-FAO, Roma.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G. & Tscharntke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution*, 26, 474–481. Doi: 10.1016/j.tree.2011.05.009.
- Lebeau, J., Wesselingh, R.A. & van Dyck, H. (2017) Flower use of the butterfly *Maniola jurtina* in nectar-rich and nectar-poor grasslands: a nectar generalist with a strong preference? *Insect Conservation and Diversity*, 10, 258–270. Doi: 10.1111/icad.12222.
- Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271–280. Doi: 10.1007/s004420100716.
- Mader, V., Diehl, E., Fiedler, D., Thorn, S., Wolters, V. & Birkhofer, K. (2017) Trade-offs in arthropod conservation between productive and non-productive agri-environmental schemes along a landscape complexity gradient. *Insect Conservation and Diversity*, 10, 236–247. Doi: 10.1111/icad.12220.
- Marshall, E.J.P. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment*, 89, 5–21. Doi: 10.1016/S0167-8809(01)00315-2.
- MLR (Ministerium für Ländlichen Raum und Verbraucherschutz Baden-Württemberg) (2016) Verwaltungsvorschrift des Ministeriums für Ländlichen Raum und Verbraucherschutz zum Förderprogramm für Agrarumwelt, Klimaschutz und Tierwohl. Verwaltungsvorschrift vom 27.01.2016 (Az.: 25-8872.53).
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015) Vegan: Community ecology package. R package version 2.3-0. < <https://cran.r-project.org/web/packages/vegan> > 15 June 2019
- Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbé, A., Wulf, F. & Scott, A.V. (2014) EU agricultural reform fails on biodiversity. *Science*, 344 (6188), 1090–1092. Doi: 10.1126/science.1253425.

- Pywell, R.F., Warman, E.A., Sparks, T.H., Greator-Davies, J.N., Walker, K.J., Meek, W.R., ... Firbank, L.G. (2004). Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation*, 118, 313–325. <https://doi.org/10.1016/j.biocon.2003.09.011>
- R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Reichelt, G. & Willmanns, O. (1973) Vegetationsgeographie: Praktische Arbeitsanweisungen. Westermann, Braunschweig, Germany.
- Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8–27. Doi: 10.1016/j.biocon.2019.01.020.
- Schirmel, J., Thiele, J., Entling, M.H. & Buchholz, S. (2016) Trait composition and functional diversity of spiders and carabids in linear landscape elements. *Agriculture, Ecosystems & Environment*, 235, 318–328. Doi: 10.1016/j.agee.2016.10.028.
- Schlager, P., Krismann, A., Wiedmann, K., Hiltcher, H., Hochschild, V., & Schmieder, K. (2013) Multisensoral, object- and GIS-based classification of grassland habitats in the Bio- sphere Reserve Schwäbische Alb. *Photogrammetrie - Fernerkundung - Geoinformation*, 2013, 163–172. Doi: 10.1127/1432-8364/2013/0167.
- Schröter, L. & Irmeler, U. (2013) Organic cultivation reduces barrier effect of arable fields on species diversity. *Agriculture, Ecosystems & Environment*, 164, 176–180. Doi: 10.1016/j.agee.2012.09.018.
- Settele, J., Steiner, R., Reinhardt, R., Feldmann, R. & Hermann, G. (2015) Schmetterlinge: Die Tagfalter Deutschlands. Eugen Ulmer, Stuttgart, Germany.
- Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., Snoo, G.R. de, Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21<sup>st</sup> century agricultural change in Europe—a review. *Journal of environmental management*, 91 (1), 22–46. Doi: 10.1016/j.jenvman.2009.07.005.
- Symonds, M.R.E. & Moussalli, A. (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65, 13–21. Doi: 10.1007/s00265-010-1037-6.
- The EU Commission (2008) Commission regulation (EC) No 889/2008 of 5 September 2008 laying down detailed rules for the implementation of Council Regulation (EC) No 834/2007 on organic production and labelling of organic products with regard to organic production, labelling and control.
- The EU Council (2007) Council Regulation (EC) No 834/2007 of 28 June 2007 on organic production and labelling of organic products and repealing Regulation (EEC) No 2992/91.
- Toivonen, M., Herzon, I. & Kuussaari, M. (2015) Differing effects of fallow type and landscape structure on the occurrence of plants, pollinators and birds on environmental fallows in Finland. *Biological Conservation*, 181, 36–43. Doi: 10.1016/j.biocon.2014.10.034.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein,

- A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W. H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87 (3), 661–685. Doi: 10.1111/j.1469-185X.2011.00216.x.
- Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A. & Bengtsson, J. (2014) Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. *Journal of Applied Ecology*, 51, 746–755. Doi: 10.1111/1365-2664.12219.
- Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. (2018) Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. *Insect Conservation and Diversity*, 11, 32–41. Doi: 10.1111/icad.12264.
- Woodcock B.A., Bullock J.M., McCracken M., Chapman R.E., Ball S.L., Edwards M.E., Nowakowski, M. & Pywell R.F. (2016) Spill-over of pest control and pollination services into arable crops. *Agriculture Ecosystems & Environment*, 231, 15-23. Doi: 10.1016/j.agee.2016.06.023.

## 2.8 Supplementary material

**Appendix A2.1.** Details about farming practices and the questionnaire to assess them.

Flowering fields were an specific AES type for conventional famers of the study region (federal state Baden-Württemberg) from 2015-2020 (Ministerium für Ländlichen Raum und Verbraucherschutz (MLR) 2016). They were defined as annual set-asides, where farming practices were forbidden (no pesticide, no fertilizer, no tillage) after sowing a standardized-, annual seed mixture (see Table S2.1 for species list, photo: Fig. S2.2). Twelve flowering fields were sown with seeding mixture M2 and five fields were sown with the mixture M1 (Table S2.2).

Both organic crops are not distinct AES types under the AES regime of the study region (Baden-Württemberg), but supported by standard AES support for organic farming. The lentil mixed-crop consisted of lentil, which was sparsely intercropped with a supporting crop to stabilize the lentil crop (for details see Wang, Gruber & Claupein (2012); photo: Fig. S2.2). Both were sown in the same seed row with a row spacing of 13.5-15 cm (Gruber S., Wahl E., Zikeli S., Claupein W. 2012)). Supporting crop was camelina (*Camelina sativa*, 5 sites), barley (*Hordeum vulgare*, 5 sites) or oat (*Avena sativa*; 7 sites) (Table S2.2).

Yields were considerably higher in conventional winter wheat compared to both organic crops (winter spelt, lentil mixed-crop) (Table 2.1 of the main text). Crop cover was highest in winter wheat, whereas crop height was highest in winter spelt with significant differences between study years and crop-use types (Table S2.3; for statistical analysis see the statistical analysis section of the main text). Wild plant height was highest in lentil mixed-crops and flower cover was highest in flowering fields and lentil mixed-crops compared to cereal crops.

The questionnaire to assess individual farming practices targeted fertilization practices, frequency and intensity of mechanical weed control, number of sprayed applications of herbicide, fungicide or insecticide. The sum of all mineral- and organic fertilizer applications was used to quantify annual nitrogen supply per study field (kg N ha<sup>-1</sup>). To calculate the amount (N kg) of nitrogen for organic substrates we used 4.0 kg N (m<sup>3</sup>)-1 for liquid manure and 5 kg N t<sup>-1</sup> for dung (Fritsch, 2012).

Gruber, S., Wahl E., Zikeli, S. & Claupein, W. (2012) Perspektiven und Grenzen der Unkrautregulierung bei Linsen (*Lens culinaris*) im Ökologischen Landbau. *Journal für Kulturpflanzen*, 64 (10), 365–377.

Fritsch, F. (2012) Nährstoffgehalte in Düngemitteln und im Erntegut: für die Düngplanung; für Nährstoffvergleiche. Staatliche Pflanzenberatung Rheinland-Pfalz, Germany.

MLR (Ministerium für Ländlichen Raum und Verbraucherschutz) (2016) Verwaltungsvorschrift des Ministeriums für Ländlichen Raum und Verbraucherschutz zum Förderprogramm

für Agrarumwelt, Klimaschutz und Tierwohl. Verwaltungsvorschrift vom 27.01.2016 (Az.: 25-8872.53).

Wang, L., Gruber, S. & Claupein, W. (2012) Optimizing lentil-based mixed cropping with different companion crops and plant densities in terms of crop yield and weed control. *Organic Agriculture*, 2 (2), 79–87. Doi: 10.1007/s13165-012-0028-5.

#### **Appendix A2.2.** Details about the survey of organisms.

Edge transects for surveying plants, ground beetles (Carabidae) and spiders were placed in the first crop row adjacent to a grassy field margin (except 5 cases). The interior transect was placed orthogonally to the edge transect due to the small width of some study fields. The minimum distance between edge and the interior transects was standardized to 12m in 2016 and 15m in 2017 and 2018 according to the smallest study field in each year.

We transformed plant cover estimates according to the Braun-Blanquet scale (Braun-Blanquet, 1932) into percent cover values according to the 160 percent scale of van der Maarel (2007) for data analysis and used the arithmetic mean of the three survey rounds for further analysis. We used the arithmetic mean of all plots of the same transect for cover data and pooled species within the same transect for calculating species richness. We measured additional vegetation characteristics of crop-use types by surveying crop cover, mean height of crop and wild plants as well as percent of flower cover per survey plot, although these factors were not consistently surveyed in all study years (Table S2.3).

For sampling carabids and spiders by pitfall traps, we placed a wire netting (20mm mesh size) beneath the opening to prevent vertebrate bycatch and used a coated pressboard roof for preventing flooding of traps. Carabids of all years (16,800 trap days) and all adult spiders of 2017 and 2018 (9,600 trap days) were preserved in 70 % ethanol and identified to species level. Two spider samples of the second sampling round 2017 (one edge and one centre transect of winter spelt) were lost during field work and therefore excluded from data analyses.

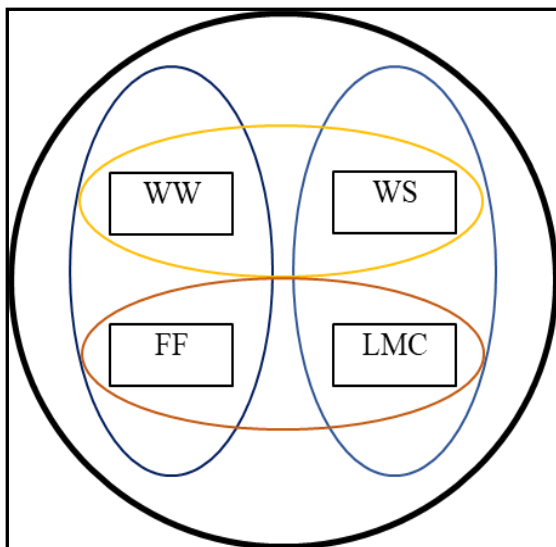
Butterflies were surveyed by walking transect lines. If species could not be identified by sight, butterflies were caught with a butterfly net and we stopped time measurement of the transect walk. Surveys were done between 8:30 and 17:00 h on days without rain, high wind speeds or temperatures less than 13 ° C. Data of the two transects per within-field position (edge vs. interior) were pooled for data analysis. Bees surveys were done between 9:30 and 16:30 h on days without rain or high wind speeds. Bees that could not be identified to species level in the field were collected and identified in the laboratory.

Braun-Blanquet, J., (1932) Plant sociology. The study of plant communities. McGraw-Hill, New-York, US.

van der Maarel, E. (2007) Transformation of cover-abundance values for appropriate numerical treatment - Alternatives to the proposals by Podani. *Journal of Vegetation Science*, 18 (5), 767–770. Doi: 10.1111/j.1654-1103.2007.tb02592.x.

**Table S2.1.** Composition of the two types of seed mixture used for establishment of flowering fields. Percentile weighting per species in the seed mixture are given as well as their origin status (native/non-native) in the study area (Germany).

Species name	Mixture M1 [%]	Mixture M2 [%]	Status
Anethum graveolens	2	2	non-native
Borago officinalis	2	3	non-native
Calendula officinalis	3	6	non-native
Centaurea cyanus	6	6	native
Coriandrum sativum	3	5	non-native
Fagopyrum esculentum	22.5	0	non-native
Foeniculum vulgare	5	5	non-native
Guizotia abyssinica	2	7.5	non-native
Helianthus annuus	12	17	non-native
Linum usitatissimum	4	10	non-native
Onobrychis viciifolia	5	5	non-native
Papaver rhoeas	0.5	0.5	native
Phacelia tanacetifolia	10	12	non-native
Raphanus sativus	2	0	non-native
Synapis alba	2	0	non-native
Trifolium incarnatum	8	10	non-native
Trifolium resupinatum	5	5	non-native
Vicia sativa	6	6	non-native
Species $\Sigma$	18	15	



**Fig. S2.1.** Cross-nested study design. The four crop-use types (winter wheat (WW), flowering field (FF), winter spelt (WS), lentil mixed-crop (LMC)) were spatially nested per study site (black circle) and nested by the two farmers managing the study fields (conventional farmer: dark-blue ellipse;

organic farmer: light-blue ellipse) and the two crop-types (cereal crop: light-orange ellipse; flowering crop: dark-orange ellipse) within each site.

**Table S2.2.** Location and farming practice before sowing of crops for each study field. For lentil crop respective mixed crop species is given.

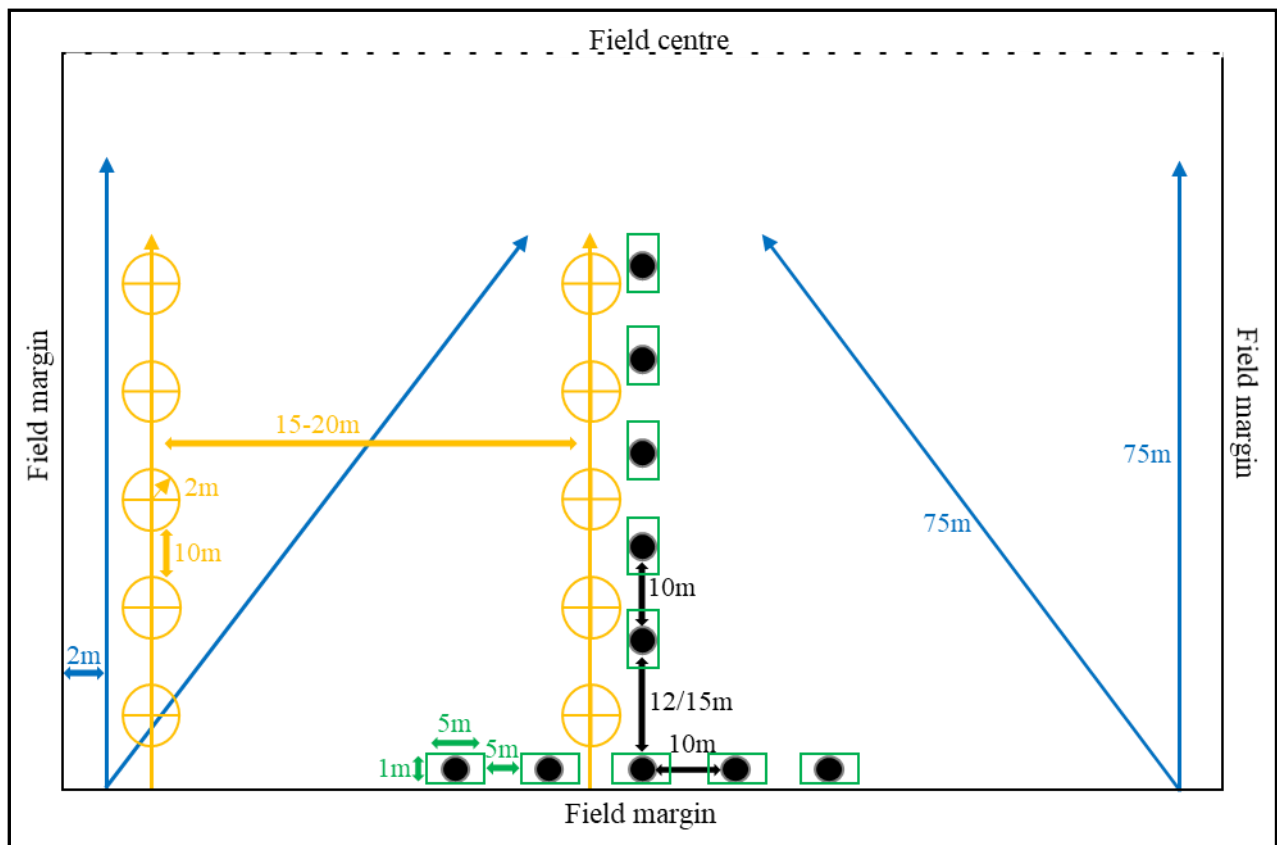
Study field ID	Nearest Village	Study year	Longitude	Latitude	Crop-use type	Mixed crop	Management	Preceding crop	Perennial crop in rotation	Tillage before sowing
ALTKB	Altsteußlingen	2016	3547902	5353724	Flowering field		Conventional	flowering field	no	ploughing
ALTKW	Altsteußlingen	2016	3548028	5353237	Winter wheat		Conventional	winter oilseed rape	no	ploughing
ALTOD	Altsteußlingen	2016	3547616	5352031	Winter spelt		Organic	field bean	yes	ploughing
ALTOL	Altsteußlingen	2016	3547735	5351768	Lentil mixed-crop	<i>Camelina sativa</i>	Organic	oat	yes	ploughing
BICKB	Bichishausen	2016	3535727	5355317	Flowering field		Conventional	flowering field	no	ploughing
BICKW	Bichishausen	2016	3535584	5355419	Winter wheat		Conventional	maize	no	ploughing
BICOD	Bichishausen	2016	3534737	5355939	Winter spelt		Organic	alfalfa-clover mix	yes	ploughless tillage
BICOL	Bichishausen	2016	3535652	5355318	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
BREKB	Bremelau	2016	3538367	5355355	Flowering field		Conventional	barley	no	ploughing
BREKW	Bremelau	2016	3538729	5355828	Winter wheat		Conventional	barley	no	ploughing
BREOD	Bremelau	2016	3538966	5356805	Winter spelt		Organic	clover	yes	ploughing
BREOL	Bremelau	2016	3539556	5355607	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
DOTKB	Dottingen	2016	3533533	5364268	Flowering field		Conventional	barley	yes	ploughing
DOTKW	Dottingen	2016	3533677	5364524	Winter wheat		Conventional	winter triticale	yes	ploughing
DOTOD	Dottingen	2016	3533965	5364221	Winter spelt		Organic	clover	yes	ploughing
DOTOL	Dottingen	2016	3533434	5365065	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
FRAKB	Frankenhofen	2016	3543774	5355366	Flowering field		Conventional	flowering field	no	ploughing
FRAKW	Frankenhofen	2016	3545277	5355444	Winter wheat		Conventional	maize	no	ploughing
FRAOD	Frankenhofen	2016	3544304	5355431	Winter spelt		Organic	alfalfa-clover mix	yes	ploughless tillage
FRAOL	Frankenhofen	2016	3543617	5356121	Lentil mixed-crop	<i>Hordeum vulgare</i>	Organic	winter spelt	yes	ploughless tillage
ZAIBB	Zainingen	2016	3541087	5372039	Flowering field		Conventional	oat	no	ploughing
ZAIBW	Zainingen	2016	3540077	5372381	Winter wheat		Conventional	maize	no	ploughless tillage
ZAIOD	Zainingen	2016	3540244	5372770	Winter spelt		Organic	clover	no	ploughless tillage
ZAIOB	Zainingen	2016	3541278	5371533	Lentil mixed-crop	<i>Camelina sativa</i>	Organic	barley	no	ploughing
BICKB	Bichishausen	2017	3535150	5354892	Flowering field		Conventional	barley	no	ploughing
BICKW	Bichishausen	2017	3536384	5354953	Winter wheat		Conventional	maize	no	ploughing
BICOD	Bichishausen	2017	3535664	5355306	Winter spelt		Organic	clover	yes	ploughing
BICOL	Bichishausen	2017	3534749	5355936	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
BREKB	Bremelau	2017	3538294	5355248	Flowering field		Conventional	winter triticale	no	ploughing
BREKW	Bremelau	2017	3541009	5354431	Winter wheat		Conventional	flowering field	no	ploughing
BREOD	Bremelau	2017	3541194	5356502	Winter spelt		Organic	clover	no	ploughless tillage
BREOL	Bremelau	2017	3541271	5356808	Lentil mixed-crop	<i>Camelina sativa</i>	Organic	winter rye	no	ploughless tillage
ERKKB	Erkenbrechtsweiler	2017	3531180	5380186	Flowering field		Conventional	maize	no	ploughing
ERKKW	Erkenbrechtsweiler	2017	3530539	5378864	Winter wheat		Organic	maize	no	ploughing
ERKOD	Erkenbrechtsweiler	2017	3529997	5377254	Winter spelt		Organic	lentil	yes	ploughing
ERKOL	Erkenbrechtsweiler	2017	3529985	5377538	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
FRAKB	Frankenhofen	2017	3544763	5354361	Flowering field		Conventional	barley	no	ploughing
FRAKW	Frankenhofen	2017	3545476	5355736	Winter wheat		Conventional	winter oilseed rape	no	ploughless tillage
FRAOD	Frankenhofen	2017	3544793	5354724	Winter spelt		Organic	alfalfa-clover mix	yes	ploughless tillage
FRAOL	Frankenhofen	2017	3545308	5355981	Lentil mixed-crop	<i>Hordeum vulgare</i>	Organic	alfalfa-clover mix	yes	ploughless tillage



Study site ID	Nearest Village	Study year	Longitude	Latitude	Crop-use type	Mixed crop	Management	Preceding crop	Perennial crop in rotation	Tillage before sowing
GRAKB	Granheim	2017	3541756	5353258	Flowering field	<i>Hordeum vulgare</i>	Conventional	flowering field	no	ploughless tillage
GRAKW	Granheim	2017	3541222	5353109	Winter wheat		Conventional	flowering field	no	ploughing
GRAOD	Granheim	2017	3541374	5353129	Winter spelt		Conventional	clover	yes	ploughing
GRAOL	Granheim	2017	3541134	5352643	Lentil mixed-crop		Conventional	winter spelt	yes	ploughing
SIRKB	Sirchingen	2017	3527885	5365745	Flowering field		Conventional	barley	no	ploughing
SIRKW	Sirchingen	2017	3528747	5366709	Winter wheat	<i>Avena sativa</i>	Conventional	flowering field	no	ploughing
SIROD	Sirchingen	2017	3529769	5368339	Winter spelt		Organic	winter wheat	yes	ploughless tillage
SIROL	Sirchingen	2017	3529946	5368524	Lentil mixed-crop		Organic	barley	yes	ploughing
ALTKB	Altsteußlingen	2018	3547613	5353918	Flowering field		Conventional	winter wheat	no	ploughing
ALTKW	Altsteußlingen	2018	3548269	5353566	Winter wheat		Conventional	winter oilseed rape	no	ploughless tillage
ALTOD	Altsteußlingen	2018	3547462	5351422	Winter spelt	<i>Hordeum vulgare</i>	Organic	clover	no	ploughing
ALTOL	Altsteußlingen	2018	3548809	5352270	Lentil mixed-crop		Organic	winter wheat	no	ploughless tillage
BICKB	Bichishausen	2018	3534483	5354971	Flowering field		Conventional	split: sunflower/sudan grass	no	ploughing
BICKW	Bichishausen	2018	3535727	5355319	Winter wheat		Conventional	maize	no	ploughing
BICOD	Bichishausen	2018	3535755	5355475	Winter spelt		Organic	clover	yes	ploughing
BICOL	Bichishausen	2018	3535249	5355118	Lentil mixed-crop	<i>Camelina sativa</i>	Organic	winter triticale	yes	ploughing
FRAKB	Frankenhofen	2018	3544812	5354302	Flowering field	<i>Hordeum vulgare</i>	Conventional	split: flowering field/barley	no	ploughless tillage
FRAKW	Frankenhofen	2018	3544379	5355683	Winter wheat		Conventional	winter oilseed rape	no	ploughless tillage
FRAOD	Frankenhofen	2018	3545324	5355980	Winter spelt		Organic	lentil mixed-crop	yes	ploughless tillage
FRAOL	Frankenhofen	2018	3544590	5355527	Lentil mixed-crop		Organic	alfalfa-clover mix	yes	ploughless tillage
HOHKB	Hohenstein	2018	3527475	5357075	Flowering field		Conventional	barley	no	ploughing
HOHKW	Hohenstein	2018	3526649	5356992	Winter wheat	<i>Camelina sativa</i>	Conventional	maize	no	ploughing
HOHOD	Hohenstein	2018	3525206	5358580	Winter spelt		Organic	winter spelt	yes	ploughless tillage
HOHOL	Hohenstein	2018	3524729	5356708	Lentil mixed-crop		Organic	winter spelt	yes	ploughless tillage
KOCKB	Kochstetten	2018	3538726	5350996	Flowering field		Conventional	oat	no	ploughing
KOCKW	Kochstetten	2018	3539373	5350974	Winter wheat		Conventional	maize	no	ploughless tillage
KOCOD	Kochstetten	2018	3539422	5350785	Winter spelt	<i>Avena sativa</i>	Organic	clover	yes	ploughless tillage
KOCOL	Kochstetten	2018	3539716	5352247	Lentil mixed-crop		Organic	winter spelt	yes	ploughing



**Fig. S2.2.** Exemplary photo of a flowering field (left) and a lentil mixed-crop field (right). Indicated in red are the lentil plant (light green) intercropped with a supporting crop (oat, dark green). © Photos: C.Gayer (left), T.Weiss (right).



**Fig. S2.3.** Sampling design indicating position and distance of pitfall traps (black dots), plant survey plots (green rectangle), butterfly survey transects (blue arrows) and wild bees transects (yellow arrows with point count locations (circles)) within a study field.

**Table S2.3.** Vegetation characteristics at the edge and centre transect of studied crop-use types sampled between 2016-2018 (mean  $\pm$  SE). Results ( $F$ -values of ANOVA table) of linear mixed-effects models are given to test for significant differences between study years, crop-use types and transects. Bold values indicate significant effect at  $P < 0.05$ .

			Crop cover [%] <sup>b,c,d</sup> (2016, 2107; n=12)	Crop height [cm] <sup>e</sup> (2107, 2018; n=11)	Wild plant height [cm] (2018; n=5)	Flower cover [%] <sup>e</sup> (2017; n=6)
Conventional	Winter Wheat	Edge	142.2 $\pm$ 1.5	67.0 $\pm$ 3.8	30.0 $\pm$ 4.4	1.3 $\pm$ 0.3
		Centre	145.8 $\pm$ 1.5	74.1 $\pm$ 4.6	32.4 $\pm$ 9.7	0.7 $\pm$ 0.3
	Flowering Field	Edge	103.6 $\pm$ 5.8	43.6 $\pm$ 4.7	34.4 $\pm$ 5.7	26.0 $\pm$ 3.5
		Centre	103.7 $\pm$ 4.9	48.7 $\pm$ 7.2	30.6 $\pm$ 5.5	29.5 $\pm$ 3.4
Organic	Winter Spelt	Edge	122.6 $\pm$ 2.8	113.6 $\pm$ 7.0	28.2 $\pm$ 4.9	4.7 $\pm$ 0.8
		Centre	122.5 $\pm$ 3.3	123.6 $\pm$ 9.3	26.4 $\pm$ 5.1	3.8 $\pm$ 0.5
	Lentil Mixed-Crop	Edge	102.8 $\pm$ 6.1	48.6 $\pm$ 4.8	40.8 $\pm$ 4.9	23.7 $\pm$ 5.8
		Centre	96.0 $\pm$ 7.5	53.6 $\pm$ 5.4	54.2 $\pm$ 8.6	26.2 $\pm$ 9.2
Model <sup>a</sup>	F - value	Year	<b>17.2</b>	<b>42.4</b>	-	-
		Crop	<b>26.1</b>	<b>65.2</b>	<b>4.0</b>	<b>30.4</b>
		Transect	0.0	3.2	0.3	0.0

<sup>a</sup> All models were fitted with normal distribution.

<sup>b</sup> Transformed Braun-Blanquet values based on 160 % scale after van der Maarel, 2007.

<sup>c</sup> Arcsine-square root transformed values used for model calculation.

<sup>d</sup> For flowering fields species of sown seed mixture was considered as crop.

<sup>e</sup> Log transformed values used for model calculation.

**Table S2.4.** List of plant species (only if identified to species level) and the respective number of transects with the plant species present at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields. Grey marked species names are plants of the seed mixture sown for the establishment of flowering fields. For plants of the seed mixture numbers refer to the study years 2017 and 2018 (without 2016).

Species name	Conventional				Organic				Total amount of transects with plant presence [%]
	Winter Wheat Edge	Winter Wheat Centre	Flowering Field Edge	Flowering Field Centre	Winter Spelt Edge	Winter Spelt Centre	Lentil Mixed-Crop Edge	Lentil Mixed-Crop Centre	
Acer campestre	1	1	0	0	0	1	0	2	3.68
Achillea millefolium	0	0	3	0	5	0	4	1	9.56
Aegopodium podagraria	1	0	0	0	1	0	0	0	1.47
Aethusa cynapium	7	2	7	4	11	11	9	8	43.38
Agrostis capillaris	1	0	1	0	1	0	1	0	2.94
Alopecurus myosuroides	13	7	16	15	14	11	14	13	75.74
Anagallis arvensis	3	0	6	4	8	5	11	9	33.82
Anthemis arvensis	0	0	0	0	1	0	0	0	0.74
Anthriscus sylvestris	2	0	0	0	1	0	1	0	2.94
Apera spica venti	2	0	0	0	1	0	1	0	2.94
Arnoseris minima	0	0	0	0	1	0	0	0	0.74
Arrhenatherum elatius	0	0	0	1	1	0	0	0	1.47
Atriplex patula	0	0	0	0	1	0	0	0	0.74
Avena fatua	2	0	2	1	0	1	4	3	9.56
Bellis perennis	0	0	0	0	1	0	0	0	0.74
Brassica juncea	1	1	0	1	3	3	2	1	8.82
Brassica napus	2	1	1	1	0	0	0	0	3.68
Brassica oleracea	0	0	0	1	0	0	1	0	1.47
Brassica rapa	0	0	1	0	0	0	0	0	0.74
Bromus arvensis	2	0	1	1	0	0	0	0	2.94
Bromus erectus	1	0	0	0	0	1	0	0	1.47
Bromus sterilis	1	0	0	0	0	0	0	0	0.74
Camelina sativa	0	0	0	0	0	0	1	1	1.47
Campanula rapunculoides	5	2	13	12	7	6	13	10	50.00
Capsella bursa-pastoris	5	2	13	12	7	6	13	10	50.00
Cardamine pratensis	0	0	0	0	1	0	0	0	0.74
Carlina vulgaris	0	0	0	0	0	0	1	0	0.74

Species name	Conventional				Organic				Total amount of transects with plant presence [%]
	Winter Edge	Wheat Centre	Flowering Edge	Field Centre	Winter Edge	Spelt Centre	Lentil Edge	Mixed-Crop Centre	
<i>Carum carvi</i>	0	0	0	0	0	0	1	0	0.74
<i>Centaurea jacea</i>	0	0	1	1	0	0	1	0	2.21
<i>Cerastium arvense</i>	0	0	0	0	1	0	0	1	1.47
<i>Cerastium brachypetalum</i>	0	0	0	0	1	1	1	1	2.94
<i>Cerastium fontanum</i>	0	0	1	0	1	0	1	0	2.21
<i>Chaenarrhinum minus</i>	0	0	0	0	2	2	0	0	2.94
<i>Chenopodium album</i>	4	3	15	13	5	4	16	12	52.94
<i>Chenopodium polyspermum</i>	1	0	3	3	1	0	2	2	8.82
<i>Cichorium intybus</i>	0	0	1	1	1	0	1	1	3.68
<i>Cirsium arvense</i>	11	8	15	9	13	13	16	16	74.26
<i>Conium maculatum</i>	0	0	0	0	0	0	1	0	0.74
<i>Convolvulus arvensis</i>	14	8	16	12	17	15	16	12	80.88
<i>Crepis setosa</i>	0	0	0	0	0	0	1	1	1.47
<i>Dactylis glomerata</i>	5	0	3	0	5	0	5	0	13.24
<i>Daucus carota</i>	1	1	0	1	2	2	2	0	6.62
<i>Echinochloa crus-galli</i>	0	0	2	0	0	0	0	0	1.47
<i>Echium vulgare</i>	0	0	0	0	1	1	1	0	2.21
<i>Elymus caninus</i>	1	0	2	0	0	1	0	1	3.68
<i>Elymus repens</i>	13	4	11	3	5	4	9	6	40.44
<i>Equisetum arvense</i>	2	3	1	1	5	3	3	1	13.97
<i>Erodium cicutarium</i>	0	0	1	0	0	0	0	0	0.74
<i>Erysimum cheiranthoides</i>	1	0	1	0	3	1	2	1	6.62
<i>Euphorbia cyparissias</i>	0	0	0	0	0	0	1	0	0.74
<i>Euphorbia exigua</i>	3	1	5	3	5	6	9	7	28.68
<i>Euphorbia helioscopia</i>	4	0	14	6	3	4	12	8	37.50
<i>Euphorbia mellifera</i>	0	0	0	0	1	1	0	0	1.47
<i>Euphorbia platyphyllos</i>	0	0	0	0	0	0	1	1	1.47
<i>Euphorbia salicifolia</i>	0	0	0	0	0	0	1	1	1.47
<i>Euphrasia rostkoviana</i>	0	0	0	0	1	0	0	0	0.74
<i>Fallopia convolvulus</i>	8	5	12	11	13	15	17	15	70.59
<i>Festuca pratensis</i>	2	0	1	0	4	0	1	0	5.88
<i>Festuca rubra</i>	2	0	0	0	2	0	2	0	4.41
<i>Fumaria officinalis</i>	3	2	3	4	3	1	4	3	16.91
<i>Fumaria vaillantii</i>	1	1	0	1	0	1	0	0	2.94
<i>Galeopsis pubescens</i>	0	0	0	0	1	0	1	0	1.47
<i>Galeopsis tetrahit</i>	3	0	3	1	14	11	15	9	41.18
<i>Galinsoga parviflora</i>	0	0	0	1	0	0	0	0	0.74
<i>Galium mollugo</i>	1	0	1	0	4	0	3	0	6.62
<i>Galium aparine</i>	15	10	9	11	17	15	13	13	75.74
<i>Gelaeopsis ladanum</i>	0	0	0	0	0	0	0	1	0.74
<i>Geranium dissectum</i>	10	3	17	12	12	13	14	13	69.12
<i>Geranium molle</i>	1	0	5	2	3	3	4	4	16.18
<i>Geranium pratense</i>	0	0	0	0	1	0	3	0	2.94
<i>Geranium rotundifolium</i>	2	1	4	2	3	1	0	0	9.56
<i>Glechoma hederacea</i>	0	0	2	0	1	0	1	0	2.94
<i>Heracleum sphondylium</i>	3	0	3	0	3	2	4	1	11.76
<i>Hypericum humifusum</i>	0	0	0	0	2	0	0	0	1.47
<i>Hypericum perforatum</i>	0	0	1	0	0	0	0	0	0.74
<i>Knautia arvensis</i>	0	0	2	0	1	0	0	0	2.21
<i>Lamium album</i>	1	0	0	0	1	0	0	1	2.21
<i>Lamium amplexicaule</i>	1	0	8	4	4	5	10	8	29.41
<i>Lamium hybridum</i>	0	0	1	0	0	0	0	0	0.74
<i>Lamium purpureum</i>	5	3	13	13	3	8	15	12	52.94
<i>Lapsana communis</i>	3	2	12	3	11	10	16	14	52.21
<i>Lathyrus pratensis</i>	0	0	0	0	3	1	1	0	3.68
<i>Lathyrus tuberosus</i>	1	1	0	0	1	1	1	1	4.41
<i>Legousia hybrida</i>	0	0	0	0	0	0	0	1	0.74
<i>Lepidium draba</i>	0	0	0	1	0	0	0	0	0.74
<i>Leucanthemum vulgare</i>	0	0	1	0	2	1	0	0	2.94
<i>Linaria repens</i>	0	0	0	0	0	0	1	0	0.74
<i>Linaria vulgaris</i>	0	0	0	0	1	0	1	0	1.47
<i>Lolium multiflorum</i>	0	0	1	1	1	1	1	0	3.68
<i>Lolium perenne</i>	7	2	4	1	10	7	4	4	28.68
<i>Lolium multiflorum</i>	0	0	1	0	0	0	0	0	0.74

Species name	Conventional				Organic				Total amount of transects with plant presence [%]
	Winter Edge	Wheat Centre	Flowering Edge	Field Centre	Winter Edge	Spelt Centre	Lentil Edge	Mixed-Crop Centre	
<i>Lotus corniculatus</i>	1	0	0	0	1	0	1	0	2.21
<i>Malva sylvestris</i>	0	0	0	1	0	0	0	0	0.74
<i>Matricaria recutia</i>	0	0	0	0	1	0	0	0	0.74
<i>Medicago falcata</i>	0	0	1	0	1	1	0	0	2.21
<i>Medicago sativa</i>	2	0	4	1	8	10	10	5	29.41
<i>Medicago lupulina</i>	1	0	6	1	5	4	9	6	23.53
<i>Melampyrum arvense</i>	0	0	1	0	1	0	0	0	1.47
<i>Myosotis arvensis</i>	4	1	8	8	16	15	15	14	59.56
<i>Neslia paniculata</i>	0	0	0	0	0	0	0	3	2.21
<i>Odontites vernus</i>	0	0	0	0	2	1	1	0	2.94
<i>Papaver dubium</i>	2	1	0	0	9	8	4	4	20.59
<i>Pastinaca sativa</i>	0	0	0	0	0	0	1	0	0.74
<i>Persicaria amphibia</i>	1	0	0	0	0	0	1	0	1.47
<i>Persicaria lapathifolium</i>	3	0	13	10	8	4	13	11	45.59
<i>Persicaria maculosa</i>	1	0	6	5	5	3	10	9	28.68
<i>Phleum pratense</i>	11	1	9	4	15	12	15	5	52.94
<i>Pimpinella major</i>	0	0	0	0	1	0	0	0	0.74
<i>Pimpinella peregrina</i>	0	0	0	0	1	0	0	0	0.74
<i>Pisum sativum</i>	0	0	0	0	1	2	0	0	2.21
<i>Plantago lanceolata</i>	4	0	9	0	6	1	6	1	19.85
<i>Plantago major</i>	4	0	10	3	6	4	9	3	28.68
<i>Plantago media</i>	0	0	0	0	0	0	1	0	0.74
<i>Poa annua</i>	2	2	1	1	0	0	0	0	4.41
<i>Poa pratensis</i>	10	2	6	0	7	3	4	0	23.53
<i>Poa trivialis</i>	6	0	0	0	3	0	0	0	6.62
<i>Polygonum aviculare</i>	11	7	16	11	16	14	16	16	78.68
<i>Potentilla reptans</i>	1	0	0	0	2	0	1	0	2.94
<i>Potentilla verna</i>	0	0	1	0	0	0	1	1	2.21
<i>Prunus domestica</i>	0	0	0	0	0	0	1	0	0.74
<i>Prunus spinosa</i>	0	0	0	0	1	0	0	0	0.74
<i>Ranunculus acris</i>	0	0	1	0	2	1	1	0	3.68
<i>Ranunculus arvensis</i>	0	0	0	0	1	0	0	0	0.74
<i>Ranunculus bulbosus</i>	0	0	1	0	0	0	0	0	0.74
<i>Ranunculus repens</i>	0	0	3	0	9	3	6	2	16.91
<i>Rhinanthus alectorolophus</i>	1	0	1	1	10	7	2	1	16.91
<i>Rubus fruticosus</i>	0	0	0	0	0	1	0	0	0.74
<i>Rubus ideaus</i>	0	0	0	0	1	0	1	0	1.47
<i>Rumex acetosa</i>	1	0	0	0	1	1	0	1	2.94
<i>Rumex crispus</i>	0	0	6	1	7	5	4	4	19.85
<i>Rumex longifolius</i>	0	0	1	0	2	4	0	1	5.88
<i>Rumex obtusifolium</i>	2	2	5	2	8	7	10	6	30.88
<i>Scandix pecten-veneris</i>	0	0	0	0	1	0	0	0	0.74
<i>Secale cereale</i>	1	1	0	0	1	2	0	0	3.68
<i>Sedum telephium</i>	0	0	0	0	1	0	1	1	2.21
<i>Setaria pumila</i>	0	0	1	0	0	0	0	0	0.74
<i>Sherardia arvensis</i>	6	1	9	6	8	8	10	6	39.71
<i>Silene latifolia</i> subsp <i>alba</i>	0	0	0	1	0	0	1	0	1.47
<i>Silene noctiflora</i>	2	1	7	3	9	9	12	10	38.97
<i>Silene vulgaris</i>	0	0	0	0	1	1	1	0	2.21
<i>Sinapis arvensis</i>	2	0	5	2	3	2	12	7	24.26
<i>Solidago virgaurea</i>	0	0	0	0	1	0	0	0	0.74
<i>Sonchus arvensis</i>	4	2	10	7	7	8	11	12	44.85
<i>Sonchus asper</i>	6	3	16	13	11	7	16	14	63.24
<i>Spergula arvensis</i>	0	0	0	0	1	1	0	0	1.47
<i>Stellaria media</i>	5	1	11	7	10	13	16	12	55.15
<i>Taraxacum officinale</i> agg	10	5	14	11	13	8	13	10	61.76
<i>Thlaspi arvense</i>	2	0	15	14	13	8	16	15	61.03
<i>Thlaspi perfoliatum</i>	0	1	0	1	0	1	0	0	2.21
<i>Tragopogon pratensis</i>	1	0	0	0	0	0	0	0	0.74
<i>Trifolium alexandrinum</i>	0	0	1	1	0	0	0	0	1.47
<i>Trifolium arvense</i>	0	0	0	0	0	0	1	0	0.74
<i>Trifolium pratense</i>	2	0	3	3	7	6	7	6	25.00
<i>Trifolium repens</i>	3	1	6	6	14	14	14	13	52.21
<i>Tripleurospermum inodorum</i>	4	2	4	4	11	10	12	9	41.17

Species name	Conventional				Organic				Total amount of transects with plant presence [%]
	Winter Edge	Wheat Centre	Flowering Edge	Field Centre	Winter Edge	Spelt Centre	Lentil Edge	Mixed-Crop Centre	
<i>Tussilago farfara</i>	0	0	0	0	1	2	0	1	2.94
<i>Urtica dioica</i>	0	0	0	0	2	0	1	0	2.21
<i>Valerianella dentata</i>	0	0	0	0	0	0	2	1	2.21
<i>Valerianella locusta</i>	0	0	4	0	7	3	8	6	20.59
<i>Veronica agrestis</i>	0	0	1	0	1	1	1	2	4.41
<i>Veronica arvensis</i>	0	0	1	0	2	0	0	3	4.41
<i>Veronica hederifolia</i>	0	0	0	0	1	0	3	1	3.68
<i>Veronica persica</i>	12	10	16	14	13	14	16	15	80.88
<i>Vicia cracca</i>	0	0	1	1	5	4	4	1	11.76
<i>Vicia hirsuta</i>	0	0	0	0	4	3	1	0	5.88
<i>Vicia sepium</i>	0	0	1	0	3	0	2	1	5.15
<i>Viola arvensis</i>	8	5	17	14	15	16	17	16	79.41
<i>Anethum graveolens</i>	1	0	11	11	0	0	1	0	27.27
<i>Borago officinalis</i>	1	0	11	11	1	0	2	0	29.55
<i>Calendula officinalis</i>	0	0	10	9	0	0	1	0	22.73
<i>Centaurea cyanus</i>	3	0	11	11	4	1	2	2	38.64
<i>Coriandrum sativum</i>	1	0	11	11	1	0	1	0	28.41
<i>Fagopyrum esculentum</i>	0	0	2	4	1	0	0	0	7.95
<i>Foeniculum vulgare</i>	0	0	10	9	0	0	0	0	21.59
<i>Guizotia abyssinica</i>	0	0	11	11	1	1	1	1	29.55
<i>Helianthus annuus</i>	0	0	10	11	0	0	1	1	26.14
<i>Linum usitatissimum</i>	1	0	11	10	1	0	0	1	27.27
<i>Onobrychis viciifolia</i>	1	0	10	6	1	0	0	0	20.45
<i>Papaver rhoeas</i>	2	0	7	4	9	7	11	7	53.41
<i>Phacelia tanacetifolia</i>	2	1	11	11	1	0	1	0	30.68
<i>Raphanus sativus</i>	0	1	3	3	0	0	3	2	13.64
<i>Sinapis alba</i>	0	0	7	4	1	0	5	3	22.73
<i>Trifolium incarnatum</i>	1	0	11	11	1	2	2	3	35.23
<i>Trifolium resupinatum</i>	0	0	11	11	1	1	5	3	36.36
<i>Vicia sativa</i>	0	0	12	14	3	6	14	13	70.45

**Table S2.5.** List of carabid species and the respective number of individuals sampled at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields.

Species name	Conventional				Organic				Total number of individuals
	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		
	Edge	Centre	Edge	Centre	Edge	Centre	Edge	Centre	
Abax carinatus	1	0	0	0	0	0	1	0	2
Abax ovalis	0	0	0	1	2	0	0	0	3
Abax parallelepipedus	4	3	8	7	4	6	3	3	38
Abax parallelus	1	0	1	1	1	0	0	0	4
Acupalpus meridianus	0	0	1	0	0	0	0	0	1
Agonum muelleri	50	19	22	11	63	66	35	33	299
Agonum sexpunctulatum	1	0	1	1	1	3	2	1	10
Amara aenea	11	1	17	16	65	5	60	75	250
Amara apricaria	0	0	1	0	0	0	0	0	1
Amara aulica	7	0	22	9	19	3	8	2	70
Amara bifrons	0	0	4	6	6	0	1	2	19
Amara communis	8	0	7	3	46	10	12	21	107
Amara consularis	1	1	4	1	4	0	2	1	14
Amara convexior	4	0	2	2	0	0	1	1	10
Amara curta	0	0	4	1	6	0	4	3	18
Amara eurynota	0	0	29	21	2	1	14	0	67
Amara familiaris	1	0	12	17	28	42	22	28	150
Amara fulva	0	0	0	0	2	0	0	0	2
Amara fulvipes	1	0	0	0	0	0	0	0	1
Amara littorea	11	0	37	178	13	18	76	124	457
Amara lucida	0	1	1	0	2	2	2	0	8
Amara lunicollis	3	1	4	1	48	5	9	0	71
Amara nitida	0	0	1	0	0	0	0	0	1
Amara ovata	4	2	14	21	3	1	19	13	77
Amara plebeja	58	7	6	2	9	3	9	0	94
Amara similata	5	6	47	34	9	2	30	196	329
Anchomenus dorsalis	1591	477	759	381	1209	545	902	768	6632
Anisodactylus binotatus	6	1	1	2	4	2	12	0	28
Badister bullatus	3	1	1	0	0	1	1	1	8
Badister sodalis	2	1	2	1	0	0	1	0	7
Bembidion guttula	0	0	0	0	0	0	1	1	2
Bembidion lampros	70	30	71	38	123	42	97	108	579
Bembidion lunulatum	0	0	0	0	1	0	0	0	1
Bembidion obtusum	0	0	5	1	3	3	2	3	17
Bembidion properans	8	2	18	6	63	21	17	6	141
Bembidion quadrimaculatum	15	17	50	26	8	5	33	22	176
Brachinus crepitans	27	1	363	1255	81	122	70	8	1927
Brachinus explodens	1	0	0	1	3	25	0	0	30
Calathus erratus	1	0	0	0	1	0	0	0	2
Calathus fuscipes	75	76	111	68	240	62	70	24	726
Calathus melanocephalus	2	0	0	1	6	1	0	0	10
Carabus auratus	27	41	46	42	248	221	105	115	845
Carabus cancellatus	1	0	0	0	0	0	2	2	5
Carabus convexus	14	2	9	8	12	12	1	0	58
Carabus granulatus	87	96	80	88	147	218	71	96	883
Carabus monilis	1	0	1	0	0	1	0	1	4
Carabus violaceus	4	1	0	3	13	7	3	7	38
Clivina collaris	0	0	0	0	1	0	1	0	2
Clivina fossor	10	23	8	23	8	19	10	11	112
Diachromus germanus	2	1	0	0	24	6	2	0	35
Dyschirius globosus	2	4	0	0	0	0	2	2	10
Epaphius secalis	47	383	0	1	1	0	0	1	433
Harpalus affinis	124	15	193	96	212	99	245	108	1092
Harpalus calceatus	0	0	1	0	2	0	0	0	3
Harpalus dimidiatus	0	0	2	12	2	0	1	0	17
Harpalus distinguendus	0	0	0	0	1	0	0	0	1
Harpalus latus	4	1	2	2	10	3	4	2	28
Harpalus luteicornis	0	0	0	0	1	1	0	0	2
Harpalus rubripes	0	0	1	1	1	0	2	1	6

Species name	Conventional				Organic				Total number of individuals
	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		
	Edge	Centre	Edge	Centre	Edge	Centre	Edge	Centre	
Harpalus rufipes	805	360	969	1037	1706	1496	719	726	7818
Harpalus signaticornis	0	1	1	0	0	0	0	0	2
Harpalus tardus	1	0	4	5	2	2	5	4	23
Leistus ferrugineus	0	0	0	0	1	0	0	0	1
Limodromus assimilis	7	35	1	2	12	13	2	0	72
Loricera pilicornis	41	28	20	4	77	27	13	7	217
Microlestes minutulus	0	0	3	2	2	0	4	1	12
Molops piceus	0	1	0	1	0	0	0	0	2
Nebria brevicollis	11	13	6	2	38	17	28	5	120
Nebria rufescens	0	0	0	0	0	1	0	0	1
Notiophilus aestuans	2	0	1	2	0	1	2	1	9
Notiophilus biguttatus	5	6	1	1	3	2	1	2	21
Notiophilus palustris	1	2	0	0	0	0	0	0	3
Ophonus azureus	1	0	2	5	10	20	24	15	77
Ophonus laticollis	0	0	0	0	1	0	18	0	19
Ophonus puncticollis	0	0	3	2	3	0	2	0	10
Ophonus rufibarbis	0	0	0	0	1	0	0	0	1
Panageus bipustulatus	0	0	0	0	0	0	1	0	1
Patrobus atrorufus	2	13	1	0	2	7	8	6	39
Poecillus cupreus	954	587	1796	2300	1794	2497	1907	2148	13983
Poecillus versicolor	52	18	120	76	230	187	85	86	854
Pterostichus anthracinus	22	44	7	29	8	38	4	9	161
Pterostichus cristatus	1	1	1	0	0	0	0	0	3
Pterostichus madidus	19	78	210	259	173	166	23	27	955
Pterostichus melanarius	1861	3071	2496	3607	3396	5587	3110	4995	28123
Pterostichus melas	29	12	363	456	32	100	50	122	1164
Pterostichus minor	0	0	1	0	2	3	6	0	12
Pterostichus niger	14	10	3	11	12	11	13	7	81
Pterostichus nigrिता	0	0	0	1	0	0	0	0	1
Pterostichus ovoideus	4	6	4	4	27	13	10	8	76
Pterostichus strenuus	9	13	3	0	9	16	3	0	53
Pterostichus vernalis	4	3	4	1	15	13	5	3	48
Stomis pumicatus	4	0	1	1	4	3	4	10	27
Syntomus truncatellus	0	0	1	0	0	0	0	0	1
Synuchus vivalis	3	6	2	3	23	15	9	7	68
Trechoblemus micros	1	0	1	0	0	1	0	0	3
Trechus quadristriatum	170	265	10	9	151	159	6	19	789
Trichotichnus nitens	0	1	0	0	0	0	0	0	1

**Table S2.6.** List of spider species (only if identified to species level) and the respective number of individuals sampled at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields.

Species name	Conventional				Organic				Total number of individuals
	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		
	Edge	Centre	Edge	Centre	Edge	Centre	Edge	Centre	
Agroeca brunnea	1	0	0	0	0	0	0	0	1
Agyneta affinis	0	0	0	0	8	0	0	0	8
Agyneta rurestris	164	91	170	109	103	46	108	75	866
Agyneta saxatilis	0	1	0	0	0	0	0	0	1
Alopecosa pulverulenta	1	1	5	2	2	2	2	1	16
Araeoncus humilis	21	51	16	34	26	13	36	32	229
Araneus sturmi	0	0	0	0	0	0	0	1	1
Arctosa lutetiana	0	0	1	0	3	0	6	0	10
Aulonia albimana	3	0	1	1	3	0	4	0	12
Bathypantes gracilis	15	2	1	0	2	0	2	0	22
Coelotes terrestris	0	0	0	0	0	0	0	1	1
Collinsia inerrans	10	6	3	0	6	3	2	1	31
Dicymbium nigrum	2	0	0	0	0	0	0	0	2



Species name	Conventional				Organic				Total number of individuals
	Winter Edge	Wheat Centre	Flowering Edge	Field Centre	Winter Edge	Spelt Centre	Lentil Edge	Mixed-Crop Centre	
Diplocephalus cristatus	2	0	0	0	0	1	0	0	3
Diplocephalus latifrons	0	0	0	0	0	1	0	0	1
Diplostyla concolor	35	42	30	2	50	20	27	5	211
Drassodes lapidosus	0	0	0	0	0	1	0	0	1
Drassodes pubescens	0	0	0	0	0	0	1	0	1
Drassyllus praeficus	2	0	1	1	1	2	3	0	10
Drassyllus pusillus	4	0	3	3	2	4	11	3	30
Enoplognatha thoracica	0	0	1	0	0	0	1	0	2
Eratigena agrestis	0	0	0	0	0	0	1	0	1
Erigone atra	39	76	104	64	66	27	73	76	525
Erigone dentipalpis	165	145	508	440	161	80	280	412	2191
Euophrys frontalis	0	0	0	1	1	0	0	0	2
Haplodrassus signifer	0	0	1	0	0	0	0	1	2
Histopona torpida	0	1	3	0	4	1	3	1	13
Maso sundevalli	0	0	1	0	0	0	0	1	2
Mermessus trilobatus	3	2	0	1	0	2	1	0	9
Micaria pulicaria	5	0	1	1	3	1	1	2	14
Micrargus subaequalis	5	3	1	0	2	0	6	0	17
Microlinyphia pusilla	0	0	2	0	0	0	0	0	2
Neottiura bimaculata	0	2	0	0	0	0	0	1	3
Oedothorax apicatus	1784	3231	1287	2369	2226	4135	1428	2331	18791
Oedothorax fuscus	0	0	1	0	0	0	0	0	1
Oedothorax retusus	1	2	2	0	0	2	0	0	7
Ozyptila simplex	0	2	0	0	0	0	2	0	4
Ozyptila trux	0	0	0	0	1	1	0	0	2
Pachygnatha clercki	1	0	0	0	1	3	1	1	7
Pachygnatha degeeri	188	173	118	39	188	175	80	54	1015
Panamomops sulcifrons	0	0	0	0	1	0	0	0	1
Pardosa agrestis	111	45	123	142	45	51	142	131	790
Pardosa amentata	39	9	20	12	13	5	26	24	148
Pardosa bifasciata	2	1	3	0	0	3	1	0	10
Pardosa lugubris	5	3	8	3	5	2	18	7	51
Pardosa palustris	440	146	418	121	564	447	609	275	3020
Pardosa pullata	9	1	7	2	39	13	12	8	91
Pardosa riparia	11	3	5	1	6	2	9	2	39
Pelecopsis parallella	0	0	0	0	0	1	0	1	2
Phrurolithus festivus	1	0	1	0	1	1	6	1	11
Phylloneta impressa	1	0	0	0	0	0	0	0	1
Piratula latitans	5	5	2	0	3	5	7	2	29
Piratula uliginosa	0	0	0	0	0	0	1	0	1
Pisaura mirabilis	1	0	0	0	0	0	0	0	1
Pocadicnemis juncea	0	0	0	0	0	0	1	0	1
Porrorhoma microphthalmum	5	4	4	5	6	2	8	5	39
Robertus arundineti	1	0	0	0	0	0	0	0	1
Robertus neglectus	6	1	2	4	1	0	2	2	18
Saaristoa abnormis	0	0	1	0	0	0	0	0	1
Tapinocyba insecta	0	0	0	0	0	0	1	0	1
Tenuiphantes tenuis	18	23	13	7	6	5	8	5	85
Tetragnatha extensa	0	1	0	0	0	0	0	0	1
Tiso vagans	6	2	3	1	1	0	1	0	14
Trichopterna cito	0	0	0	0	0	0	0	1	1
Trachyzelotes pedestris	1	0	0	0	0	0	0	0	1
Trochosa ruricola	68	53	55	45	76	76	110	39	522
Trochosa terricola	6	0	2	1	5	1	4	0	19
Walckenaeria atrotibialis	2	1	0	0	2	0	0	0	5
Walckenaeria furcillata	0	0	1	0	0	0	0	0	1
Walckenaeria nudipalpis	0	2	0	0	0	0	0	1	3
Walckenaeria vigilax	8	11	7	4	8	12	3	5	58
Xerolycosa miniata	9	0	7	3	4	0	1	1	25
Xysticus audax	0	0	2	0	0	0	0	0	2
Xysticus bifasciatus	0	0	0	0	0	0	1	0	1
Xysticus cristatus	1	2	3	0	0	0	1	0	7
Xysticus kochi	4	15	7	3	2	8	3	1	43

Species name	Conventional				Organic				Total number of individuals
	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		
	Edge	Centre	Edge	Centre	Edge	Centre	Edge	Centre	
Xysticus lanio	0	0	0	0	0	0	2	0	2
Zodarion italicum	2	0	0	0	0	0	0	0	2
Zelotes latreillei	0	0	1	0	1	0	0	0	2
Zelotes subterraneus	0	0	0	0	1	0	2	0	3
Zora spinimana	1	0	0	0	0	1	0	0	2

**Table S2.7.** List of butterfly species (only if identified to species level) and the respective number of individuals sampled at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields.

Species name	Conventional				Organic				Total number of individuals
	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		
	Edge	Centre	Edge	Centre	Edge	Centre	Edge	Centre	
Aglais io	0	0	15	4	1	3	17	28	68
Aglais urticae	3	4	19	15	3	5	17	31	97
Anthocharis cardamines	0	0	0	0	0	2	0	0	2
Aphantopus hyperantus	1	1	6	7	2	1	2	3	23
Argynnis aglaia	0	0	0	0	0	5	1	1	7
Argynnis adippe	0	1	0	0	0	0	0	0	1
Argynnis paphia	0	1	1	3	0	0	2	7	14
Boloria dia	1	0	2	0	0	0	2	1	6
Coenonympha arcania	0	0	0	0	0	0	1	0	1
Coenonympha pamphilus	3	3	2	1	4	1	13	7	34
Colias alfacariensis	0	0	5	1	1	0	9	22	38
Colias hyale	0	0	2	2	0	0	0	1	5
Cupido argiades	0	0	0	0	0	0	2	2	4
Cupido minimus	0	0	3	0	1	2	9	2	17
Cyaniris semiargus	0	0	0	0	3	0	2	0	5
Gonepteryx rhamni	0	1	2	1	1	1	2	6	14
Issoria lathonia	0	0	7	4	0	0	3	5	19
Lasiommata megera	0	0	1	1	0	0	0	0	2
Lycaena phlaeas	1	1	0	0	0	0	1	2	5
Macroglossum stellatarum	0	0	2	4	0	1	3	3	13
Maniola jurtina	2	9	60	72	7	13	43	53	259
Melanargia galathea	1	2	4	8	1	1	13	18	48
Melitaea diamina	0	0	0	0	0	0	1	0	1
Nymphalis polychloros	0	0	2	2	2	0	7	3	16
Ochlodes sylvanus	0	0	0	0	1	0	0	0	1
Papilio machaon	0	0	2	1	1	0	0	2	6
Pieris brassicae	1	1	4	10	0	1	4	11	32
Pieris napi	6	2	17	22	6	15	22	31	121
Pieris rapae	12	7	108	122	26	19	71	60	425
Plebejus argus	0	0	0	0	4	0	0	0	4
Polyommatus coridon	0	0	4	0	8	18	3	2	35
Polyommatus icarus	0	0	10	5	10	3	32	25	85
Vanessa atalanta	0	0	0	0	0	1	0	1	2
Vanessa cardui	0	0	3	2	0	0	5	4	14

**Table S2.8.** List of wild bee species and the respective number of individuals sampled at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields.

Species name	Conventional				Organic				Total number of individuals
	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		
	Edge	Centre	Edge	Centre	Edge	Centre	Edge	Centre	
Andrena bicolor	0	0	1	0	0	0	0	0	1
Andrena chrysosceles	0	0	1	0	0	0	0	1	2
Andrena cineraria	0	0	0	0	0	0	1	0	1
Andrena flavipes	0	0	0	2	0	0	0	1	3
Andrena labiata	0	0	1	0	0	0	1	0	2
Andrena minutula	0	0	1	1	0	0	0	0	2
Andrena minutuloides	0	0	1	0	0	0	0	0	1
Andrena nigroaenea	0	0	1	0	0	0	0	0	1
Andrena nitidiuscula	0	1	0	0	0	0	0	0	1
Andrena subopaca	0	0	0	1	0	1	0	0	2
Bombus barbutellus	0	0	1	0	0	0	0	0	1
Bombus hortorum	0	0	14	5	3	15	2	0	39
Bombus humilis	0	0	2	8	0	0	1	0	11
Bombus hypnorum	0	0	0	1	0	0	1	0	2
Bombus lapidarius	0	1	377	350	4	3	43	52	830
Bombus lucorum s.l.	0	0	48	32	1	0	2	1	84
Bombus pascuorum	0	1	39	33	0	0	14	4	91
Bombus pratorum	0	1	14	23	1	0	2	0	41
Bombus subterraneus	0	0	0	1	0	0	0	0	1
Bombus sylvarum	1	2	42	32	2	0	10	4	93
Bombus sylvestris	0	0	0	1	0	0	0	0	1
Bombus terrestris s.l.	0	1	96	95	0	5	6	6	209
Bombus wurflenii	0	0	0	0	0	0	0	1	1
Halictus confusus	1	0	2	1	0	0	0	1	5
Halictus rubicundus	0	0	1	0	0	0	0	0	1
Halictus simplex s.l.	0	0	0	1	0	0	2	3	6
Halictus subauratus	0	0	0	1	0	0	0	0	1
Halictus submediterraneus cf.	0	0	1	1	0	0	0	0	2
Halictus tumulorum	0	0	4	3	1	1	1	1	11
Lasioglossum albipes	0	0	0	1	0	0	0	1	2
Lasioglossum calceatum	0	0	18	18	0	0	4	4	44
Lasioglossum fratellum	0	0	1	0	0	0	0	0	1
Lasioglossum fulvicorne	0	0	0	0	0	0	0	3	3
Lasioglossum laticeps	0	0	22	43	0	0	0	3	68
Lasioglossum lativentre	0	0	0	1	0	0	1	0	2
Lasioglossum malachurum	0	0	0	0	0	0	1	2	3
Lasioglossum morio	0	0	2	0	1	1	1	2	7
Lasioglossum nigripes	0	0	1	0	0	0	0	0	1
Lasioglossum pauxillum	1	3	19	11	1	2	7	14	58
Melitta haemorrhoidalis	0	0	1	0	0	0	0	0	1
Melitta leporina	0	0	0	0	0	0	0	2	2
Osmia adunca	0	0	1	0	0	0	0	0	1
Osmia bicornis	0	0	3	0	0	0	0	0	3
Sphecodes ehippius	1	0	1	0	0	0	0	0	2



### 3. CHAPTER

#### **Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats**

A version of chapter 3 is published at *Agriculture, Ecosystems and Environment*:

Gayer, C., Lövei, G. L., Magura, T., Dieterich, M., & Batáry, P. (2019) Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats. *Agriculture, Ecosystems and Environment*, 284, 106579, doi.org/10.1016/j.agee.2019.106579



© Photos: V. Bohle: top-left.; C. Gayer: bottom-right; F. Schüttler: top-right, bottom-left.

## **Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats**

Christoph Gayer<sup>1</sup>, Gábor L. Lövei<sup>2</sup>, Tibor Magura<sup>3</sup>, Martin Dieterich<sup>4</sup> & Péter Batáry<sup>5,6</sup>

<sup>1</sup>Institute of Landscape and Environment (ILU), University of Applied Science Nürtingen-Geislingen, 72622 Nürtingen, Germany;

<sup>2</sup>Department of Agroecology, Flakkebjerg Research Center, Aarhus University, 4200 Slagelse, Denmark;

<sup>3</sup>Department of Ecology, University of Debrecen, 4032 Debrecen, Hungary;

<sup>4</sup>Landscape Ecology and Vegetation Science, University of Hohenheim, 70599 Stuttgart, Germany;

<sup>5</sup>Agroecology, University of Göttingen, 37077 Göttingen, Germany;

<sup>6</sup>MTA Centre for Ecological Research, Institute of Ecology and Botany, “Lendület” Landscape and Conservation Ecology Research Group, Vácrátót, Hungary.

### **3.1 Abstract**

The continued decline in farmland biodiversity in Europe despite substantial funding for agri-environment schemes (AES) has prompted calls for more effective biodiversity conservation measures. The current AES regime allows for both holistic measures, such as organic farming, that broadly target the agricultural environment and biodiversity-specific measures, such as flowering fields, but little is known of their relative efficacies. To address this gap, we studied carabids in 48 arable fields that presented four crop types under different management practices along a gradient of landscape complexity: (a) conventionally managed crop (winter wheat), (b) biodiversity-specific AES under conventional management (sown flowering field), (c) organically managed mono-crop (winter spelt) and (d) organically managed lentil-mixed crop (lentil intercropped with cereal or camelina). For these crop-use types, we compared functional diversity of carabid assemblages at the edge and center of the fields. Using pitfall traps, we collected more than 55,000 carabids of 95 species over two years. We characterized diversity using community weighted means and functional divergence of three ecological traits – body size, feeding type, and flight ability. Conventional flowering fields and organic winter spelt, but not organic spring sown lentil-mixed-crop, increased the proportion of plant feeding carabids; moreover, trait characteristics and their divergences were most affected by field edges, with smaller, less carnivorous and more flight-enabled carabid assemblages found there than in the center. Divergence of body size and feeding type but not of flight ability was larger at the field edges than centres. Surrounding landscape complexity did not affect carabid traits. We conclude that future AES policy should avoid strict decisions between biodiversity specific- and holistic measures. Instead, priority

should be given to a diversity of different measures, targeting the enhancement of edge habitats as well as productive and non-productive measures.

**Keywords:** Agri-environmental schemes, arable fields, field margins, herbivores, landscape structure, traits.

### 3.2 Introduction

To halt the loss of farmland biodiversity in the European Union, agri-environment schemes (AES) provide financial support to farmers who follow environmentally friendly practices (Henle *et al.*, 2008). Although the EU allocates a significant portion of its budget to AES (€ 2.5 billion  $y^{-1}$ ), biodiversity continues to decline (Flohre *et al.*, 2011; Westerink *et al.*, 2017). This has led to repeated calls for more effective biodiversity conservation in agri-environment schemes (Kleijn & Sutherland, 2003; Kleijn *et al.*, 2011; Batáry *et al.*, 2015). How to create such schemes requires insight into the impact of specific agri-environment measures (AEM) on farmland biodiversity.

Recently, different types of AES have been implemented, targeting either the establishment of non-productive areas (e.g. sown flowering field schemes) or the reduction of farming intensity in productive areas (e.g. organic farming) (Mader *et al.*, 2017). Sown flowering fields, which primarily target biodiversity conservation, have become more common within arable farming regions in Europe (e.g. England, Germany and Switzerland), (Haaland *et al.*, 2011; Batáry *et al.*, 2015; Boetzel *et al.*, 2018). Organic farming, which is supported under the AES regime in Europe, follows a more holistic approach, focusing on ecologically responsible low input agriculture (IFOAM, 2005). Hence, biodiversity conservation is just one of several objectives of organic farming. Compared to organic farming systems, a history of shorter crop rotations as well as long term effects of pesticide and mineral fertilizer applications in conventional farming systems (Bruggen *et al.*, 2016) may lessen or even neutralize any beneficial effects on biodiversity from sown flowering fields. The question remains could AES that are more targeted toward biodiversity conservation deliver greater results for biodiversity than measures which focus broadly on the overall agricultural environment?

Despite high subsidies, direct comparisons of the biodiversity conservation effects of different AES measures and organic farming are rare. Most studies focus on activity density, species richness or community composition (Caro *et al.*, 2016; Labruyere *et al.*, 2016a; Mader *et al.*, 2017). Meanwhile, the central question of how different AEMs affect functional diversity based on species traits has received scant attention (Rusch *et al.*, 2013; but see Boetzel *et al.*, 2018). Focusing on functional, rather than taxonomic, diversity can provide more insight into the mechanisms by which changes in land use impact biodiversity (Rusch *et al.*, 2013; Woodcock *et al.*, 2014; Gallé *et al.* 2018a). Functional diversity also provides a more sensitive determinant of environmental changes and ecosystem processes (de Bello *et al.*, 2010; Woodcock *et al.*, 2014). Hence, it is essential to understand the effects of different AEMs and farming types on functional diversity in order to increase the effectiveness of future AES regimes.

As study organisms, we chose ground beetles (Coleoptera: Carabidae), because they are highly sensitive towards habitat change and agricultural practices, such as tillage or pesticide use (Lövei & Sunderland, 1996), and they can respond to the degree of extensiveness of farming practice (Caro *et al.*, 2016). Establishing flowering fields or organic farming can alter carabid assemblages and their trait composition, but effects vary depending on which traits and AES measures are considered. For instance, Mader *et al.*, (2017) observed no significant differences in body size distribution of carabids between organically farmed cereals and sown flowering fields, but Boetzel *et al.*, (2018) found significant effects of flowering fields on body size as well as feeding type distribution of carabid assemblages. Flight ability also responds to different farming practices (e.g. Ribera *et al.*, 2001; Caprio *et al.*, 2015).

Irrespective of local habitat management, carabids within arable fields may also be affected by edge effects from bordering non-cultivated habitats, such as grassy field margins, that provide shelter, overwintering habitat and other resources (Schirmel *et al.*, 2016; Gallé *et al.*, 2018b). Due to spillover effects, grassy field margins can shape trait characteristics of arthropod assemblages in arable fields, as they provide different ecological niches by a contrasting disturbance regime, microclimate, vegetation structure and -composition compared to arable fields (Rouabah *et al.*, 2015; Labruyere *et al.*, 2016a; Schirmel *et al.*, 2016). Consequently, functional diversity may differ considerably between the edges and the center of arable fields. The complexity of the surrounding landscape can be a further important factor in shaping both carabid assemblages and functional composition (e.g. Purtauf *et al.*, 2005a). For example, simple landscapes support smaller carabids than do complex ones (Gallé *et al.*, 2018b), and carnivorous species show a stronger response to landscape structure than do herbivorous ones (Woodcock *et al.*, 2010).

Here we aimed to study functional diversity of carabid assemblages in response to three agri-environmental measures: a biodiversity specific AES under conventional management (sown flowering fields) and mono-, as well as a mixed-crop under organic management. Conventionally managed winter wheat fields served as control. For these four crop-use types, we assessed the distribution and divergence of three ecological traits of the resident carabid assemblages: body size, feeding type, and flight ability. Specifically, we posed the following questions: (1) whether functional diversity of carabid assemblages differs between the four crop-use types, (2) whether there are differences between the edge and the centre of arable fields, irrespective of crop-use type, and (3) how the functional diversity of carabid assemblages is shaped by the complexity of the surrounding landscape.

### 3.3 Materials and methods

#### 3.3.1 Study area and study design

We studied carabid assemblages under four crop-use types: (a) conventionally managed winter wheat (*Triticum aestivum* L.), (b) conventionally managed sown flowering fields, (c) organically managed



winter spelt (*Triticum aestivum* subsp. *Spelta* L.) and (d) organically managed lentil with supporting crop (*Lens culinaris* Medic. Intercropped with cereal or camelina, *Camelina sativa* L.). Each crop-use type was sampled in 12 sites over two years (2016 and 2017) with a sample size of six in each of the two study years ( $n_{\text{total}} = 12$ ). In each study year we chose different study fields for each crop-use type due to crop rotation.

We selected 48 study fields (4 crop-use types  $\times$  6 sites  $\times$  2 years) in the Central Swabian Jurassic mountains in south-western Germany (Fig. S3.1). All sites are located within the UNESCO Biosphere Reserve Swabian Alb. The Swabian Alb is a low mountainous area situated in the center of the state of Baden-Württemberg, Germany. Due to a history of small-scale land use, the region is characterized by small field sizes. Terrain elevation of the Swabian Alb ranges between 460 and 860 m a.s.l. (Egorov *et al.*, 2017). Soils were shallow and poor luvisols or cambisols with a bedrock of White Jurassic limestone (IUSS WG WRB, 2015).

We sampled carabids along two transects per study field ( $n = 96$  transects). One transect was placed at the field edge within the first crop row, adjacent to a grassy margin (permanent meadow strip) as a standardized neighboring habitat, mostly accompanied by field paths. When no bordering grassy field margin was available, we chose a fertilized grassland as bordering habitat (4 cases). The central transect was placed orthogonally to the edge transect within the study field forming a “T” shape (Fig. S2.2); this was necessary due to the small width of some study fields (minimum width 24 m). The minimum distance between the edge and the center transects was standardized to 12 m in 2016 and 15 m in 2017 for all study fields. This minimum distance (smallest possible distance between edge and center) was always determined according to the smallest study field. The mean field size was 2.2 hectares (ha) (SE: 0.2 ha) with similar field sizes between crop-use types (winter wheat:  $2.3 \pm 0.5$  ha; flowering field:  $2.3 \pm 0.6$  ha; winter spelt:  $2.0 \pm 0.3$  ha; lentil-mixed-crop:  $2.1 \pm 0.6$  ha) and varied between study sites from  $1.4 \pm 0.3$  ha to  $3.4 \pm 1.5$  ha.

To study the impact of landscape complexity, crop-use type and transect position (field edge vs. center) on functional diversity, we applied a fully cross-nested design, spatially nesting crop-use types per study site (Fig. S3.2). Each study site spatially blocked the four crop-use types. We selected twelve study sites (six per study year) in order to standardize the effects of landscape context and local site conditions (soil and climate) across crop-use types. The mean minimum distance between study fields in the same site was much smaller ( $0.63 \pm 0.1$  km) than the minimum distance between study fields of different study sites ( $4.7 \pm 0.9$  km). Within each study site, the two conventional crop-use types (winter wheat, flowering field) as well as the two organic crop-use types (winter spelt, lentil-mixed-crop) were farmed by the same farmer (conventional or organic). The pairwise nesting of study fields within each study site minimized the potential impact of variable farming practices by different farmers. Besides this double nesting, crop-use types were also crossed over management type (conventional vs. organic), as each management type always had one flowering (flowering field, lentil-mixed-crop) and one cereal (winter wheat, winter spelt) crop associated with it. The result was a cross-nested study design.

### 3.3.2 Farming characteristics of study fields

Data on the farming practice used on each study field were collected via personal interviews with the farmers ( $n = 24$ ) using a standardized questionnaire. Annual nitrogen supply ( $\text{kgNha}^{-1}$ ) was calculated by summing the amount of applied mineral and/or organic fertilizers. While farmers gave precise information about the amount of mineral fertilizers used, information about organic fertilizer was less accurate and therefore recorded by type (liquid manure or dung) and quantity ( $\text{m}^3$  of liquid manure, kg of dung). To calculate the amount of applied nitrogen by organic substrates, we multiplied the quantity of the used substrate with standard values for nitrogen content:  $4.0 \text{ kg N (m}^3\text{)}^{-1}$  for liquid manure and  $5 \text{ kg N t}^{-1}$  for dung (Fritsch, 2012). We characterized pesticide use by the number of applications of herbicide, fungicide or insecticide.

Flowering fields were annual set-asides sown with a standard seed mixture of 15 to 18 flowering plant species, predominantly non-native, but nonetheless traditionally cultivated in German horti- or agriculture (see Table S3.1 for a species list). Nine flowering fields were sown with seeding mixture M2 and three fields were sown with the mixture M1 (Table S3.1). AES regulations do not allow management measures on flowering fields (no pesticide, no fertilizer, no tillage after sowing) for one year after their establishment (MLR, 2016).

The two organic crops were subsidized through standard AES support for organic farming. In contrast to conventional flowering fields, organic crops are not a specific AES type within the AES regime of the study area (Baden-Württemberg). The lentil crop was a flowering legume sown with a row spacing of approximately 13.5-15 cm (Gruber et al., 2012). It was sparsely intercropped (same row spacing) with camelina (three sites), barley (*Hordeum vulgare*; three sites) or oats (*Avena sativa*; six sites) in order to stabilize the lentil plants (Table S3.2, Fig. S3.3, for details about lentil mixed-cropping systems see Wang *et al.*, 2012).

The four crop-use types differed in sowing time (autumn vs. spring sown crop), crop type (cereal vs. flowering plant) and management type (conventional vs. organic farming) (Table 3.1, Table S3.2). Cereal crops (winter wheat and winter spelt) were always sown in the autumn of the preceding year, while flowering crops (flowering field and lentil-mixed-crop) were sown in the spring. Herbicides, fungicides, insecticides and mineral fertilizers were applied only to winter wheat; mechanical weed control was only used in winter spelt. Compared to the conventional crop-use types, organic crop-use types had a more diverse crop rotation, more perennial crops (mainly clover-mixtures), and more plow-free soil tillage before sowing (Table 3.1, Table S3.2). Organic farming practices followed the European standards (The Council of the European Union, 2005), and all organic farmers were certified by the Bioland Association, with the exception of one certified by the Demeter Association. Yields as well as subsidies under AES differed between the crop-use types (Table 3.1).

**Table 3.1.** Farming practice characteristics, achieved yield and subsidy amount of studied crop-use types sampled in 2016 and 2017 (mean  $\pm$  SE; n=48). Results (F-value of ANOVA table) of linear mixed-effects models are given to test for significant differences between crop-use types. Bold values indicate significant effect at  $P < 0.05$ .

		Sowing date (calendar week)	Crops in rotation (number)	Fertilizer (kg N ha <sup>-1</sup> )	Pesticide application (number)	Mechanical weeding <sup>b</sup> (number)	Yield (dt ha <sup>-1</sup> )	Subsidy by AES <sup>c</sup> (€ ha <sup>-1</sup> )
Conventional	Winter Wheat (n=12)	40.2 $\pm$ 0.4 (early October)	3.9 $\pm$ 0.2	184.6 $\pm$ 11.5	2.3 $\pm$ 0.4	0.1 $\pm$ 0.1	68.8 $\pm$ 3.6	none
	Flowering Field (n=12)	18.2 $\pm$ 0.3 (early May)	3.9 $\pm$ 0.2	1.9 $\pm$ 1.9	none	none	none	710
Organic	Winter Spelt (n=12)	40.7 $\pm$ 0.3 (early October)	5.8 $\pm$ 0.2	71.2 $\pm$ 21.4	none	1.7 $\pm$ 0.3	29.9 $\pm$ 1.7	230
	Lentil-mixed-crop (n=12)	14.7 $\pm$ 0.5 (mid of April)	5.9 $\pm$ 0.2	4.9 $\pm$ 3.4	none	none	9.8 $\pm$ 2.2	230
Model <sup>a</sup>	F – value	Year 0.8	<b>23.8</b>	0.1	0	0.1	0.2	
		Crop	<b>1403.9</b>	<b>12.6</b>	<b>47.6</b>	<b>38</b>	<b>15.3</b>	<b>201.8</b>

<sup>a</sup> All models were fitted with normal distribution.

<sup>b</sup> Only weeding between sowing and harvest counted.

<sup>c</sup> Fixed amount according to the agri-environmental scheme (AES) of the federal state Baden-Württemberg named FAKT (MLR, 2016).

### 3.3.3 Landscape analysis

To take into account potential landscape effects, we analyzed landscape complexity within a radius of 500 m around the midpoint of each study transect ( $n = 96$ ). Arable land was the most abundant land cover type, with  $56.7 \pm 1.8$  % of total cover (mean  $\pm$  SEM) showing a distinct gradient between study fields ranging from 15.1% to 83.0% of arable land cover. Arable land cover was independent of crop-use types ( $\chi^2 = 5.4$ ,  $df = 3$ ,  $P = 0.15$ ) or transect position ( $\chi^2 < 0.01$ ,  $df = 1$ ,  $P = 0.99$ ). Arable land cover was significantly negatively correlated with land use diversity (Shannon index;  $r_{94} = -0.83$ ,  $P < 0.001$ ) and forest cover ( $r_{94} = -0.68$ ,  $P < 0.001$ ). This allowed us to use arable land cover as a simple predictor of landscape complexity. The Shannon index was calculated from the percentage cover of arable land, intensively managed grassland (e.g. fertile meadow), extensive grassland (e.g. calcareous grassland), copses (hedges, shrubs, single trees), forest, wetland (including water bodies) and urban elements. Landscape data were obtained from the project „Flächendeckende Biotop und Nutzungstypenkartierung im Biosphärengebiet Schwäbische Alb mittels Fernerkundungsdaten als Basis für ein Landschaftsmonitoring“, which provided an area-wide classification of habitat complexes of the Biosphere Reserve Swabian Alb, based on multisensoral remote sensing and environmental geodatasets (for details see Schlager *et al.*, 2013). Landscape analysis was conducted using the Geographical Information System *ArcGIS* 10.2.2 (1999-2014 ESRI Inc.).

### 3.3.4 Carabid and plant survey

We sampled carabids by pitfall traps consisting of a polyvinylchlorid (PVC) tube (diameter 7.2 cm, height 10 cm), into which a fitting 200 ml polyethylene beaker was inserted and filled with approx. 100 ml of a 30% ethylene glycol solution. A drop of non-scented detergent was added to reduce surface tension. To prevent vertebrate bycatch, a wire netting (20 mm mesh size) was installed approx. 3 cm beneath the opening. To prevent flooding, we placed a coated pressboard roof (approx. 15 cm  $\times$  15 cm) supported by a pair of 10 cm long iron nails. In each study field, we placed five traps at the edge and another five in the center, yielding 10 traps per study field, for a total of 240 traps per year. Distance between traps within each transect was standardized to 10 m to minimize spatial autocorrelation. During sampling collection, trap contents were pooled within each transect. A sampling round lasted for 10 consecutive days. Between each sampling round, traps were kept closed for 10 days before the next sampling round started.

In the first study year, we conducted carabid trapping in three sampling rounds between 15 June and 3 August 2016, while in the second year, we used two sampling rounds between 15 June and 16 July 2017. In both years, we finished trapping immediately before crops were harvested or plowed. The overall sampling represented 12,000 trap days (240 traps  $\times$  50 trapping days). All trapped carabids were preserved in 70% ethanol and later further identified to species level.

As vegetation structure and composition can strongly influence habitat conditions for carabids (Rouabah *et al.*, 2015), we surveyed plant cover and species richness in order to examine differences between crop-use types. For details see the supplementary material (Appendix A3.1, Table S3.3).

During the sampling period, mean temperature and rainfall was 14.7 °C with 195.9 mm rain in June and 17.0 °C with 83.7 mm rain in July 2016. In 2017, the means were 17.2 °C and 96.9 mm in June and 16.5 °C and 199.9 mm in July (dates from nearest meteorological station Münsingen-Apfelstetten, URL: <https://cdc.dwd.de/>, accessed 15.08.2018). For further analysis, we pooled data of all sampling occasions per transect per year.

### 3.3.5 *Carabid trait analysis*

To assess the functional diversity of carabids, we collected three functional trait values – body size, feeding type and flight ability – for each species according to the literature (Table S3.4.). Body size was calculated as the geometric mean of minimum and maximum values in Homburg *et al.*, (2014), followed by standardization to a range between 0 and 1 to decrease the effect of high values from large species (Gallé *et al.* 2018a). Feeding type was classified as herbivorous (including spermophagous), omnivorous or carnivorous based on the literature (Larochele, 1990; Ribera *et al.*, 2001; Purtauf *et al.*, 2005a). Flight ability was categorized using wing morphology as fully winged, dimorphic or short winged/wingless using data from Hurka (1996).

We used community weighted means (CWM) of trait values to determine if specific trait characteristics of carabid assemblages were shaped by landscape complexity, crop-use type or transect position (Lavorel *et al.*, 2008; Ricotta & Moretti, 2011). Further, we calculated functional divergence (Fdvar) as a measure of functional trait distribution within carabid assemblages. Fdvar values are higher when the abundance is higher towards either one or both margins of the trait distribution, and lower when abundance is concentrated towards the average trait value (Pla *et al.*, 2012). We calculated Fdvar indices according to Leps *et al.*, (2006) and used the R package ‘FD’ to calculate CWM values (Laliberté *et al.*, 2014).

### 3.3.6 *Statistical analysis*

We used linear mixed-effects models to statistically test for differences in farming practices between crop-use types and study years using the ‘lme4’ package (Bates *et al.*, 2015) in the R program environment (R Development Core Team, 2017). To take into account the cross-nested design, we included the factors ‘site’, ‘farmer’ and ‘crop type’(cereal vs. flowering crop) as nested random effects and ‘crop-use type’ and ‘year’ as fixed effects in the models by using the following R-syntax:

“lmer(y ~ Crop-use type + Year + (1|Site/Farmer) + (1|Site/Crop type))”.

We performed model diagnostics to test for normal distribution of model residuals, by investigating normal quantile-quantile plots and plotting model residuals against fitted values to visualize error

distribution and check for heteroscedasticity. We applied the same approach to test for differences in vegetation characteristics between years, crop-use types and transects.

We used the above R-syntax for testing differences in arable land cover over a 500 m radius around study fields with ‘crop-use type’ and ‘transect’ (edge and center) as single and interacting fixed effects in the model. In order to assess significant differences between crop-use types and transects, we performed a type-II Wald Chi-squared test using the R package ‘car’ (Fox *et al.*, 2012). Habitat diversity was characterized by the Shannon index and calculated using the ‘vegan’ package in R (Oksanen *et al.*, 2015). Pearson’s product-moment correlation was calculated for testing correlations between arable land cover and habitat diversity, as well as forest cover.

Linear mixed-effects models and model averaging methods were applied to test for significant effects of landscape complexity, crop-use type, transect position and their interactions on carabid functional diversity (CWM, Fdvar). Species richness and activity density of carabids did not differ significantly between study years, therefore ‘year’ was used as an additional random factor. We included the factors ‘year’, ‘farmer’, ‘site’ and ‘crop type’ as nested random effects, as well as ‘landscape complexity’, ‘crop-use type’ and ‘year’ as fixed effects in the model according to the R syntax:

“lmer(y ~ (Landscape Complexity+Crop-use type+Transect)<sup>3</sup> + (1|Year/Site/Farmer) + (1|Year/Site/Crop type)”.

We generated a set of all possible linear combinations of predictor variables for the above model, using the function ‘dredge’ of the ‘MuMIn’ package in R (Barton, 2017), which ranks candidate models according to Akaike’s Information Criteria, corrected for small sample sizes (AICc). The models with < 2 ΔAICc of the best model (i.e. the model with the lowest AICc) were selected for model averaging using the function ‘model.avg’ of the ‘MuMIn’ package. If only one model was left after model selection, we calculated a linear mixed-model with just one explanatory factor (the one from the remaining model) without model selection or averaging.

### 3.4 Results

In total, we collected 55,165 carabid individuals of 95 species (listed in Table S3.3). The four most abundant species *Pterostichus melanarius* (39.1%), *Poecilus cupreus* (20.1%), *Harpalus rufipes* (11.3%), and *Anchomenus dorsalis* (9.8%) accounted for 80.2 % of the samples. We collected 8,894 carabids representing 62 species from conventional winter wheat fields, 13,327 carabids from 72 species from conventional flowering fields, 17,563 carabids from 76 species from organic winter spelt fields and 15,381 carabids from 67 species from organic lentil-mixed-crop fields.

Crop-use type had high importance on feeding type but not body size or flight ability of the carabid assemblages (Table 3.2 and Fig. 3.1). Conventional flowering- and organic winter spelt fields, but not spring sown organic lentil mixed-crop fields, had a higher proportion of plant-feeding (omnivorous and herbivorous) carabids than that found in winter wheat fields. Feeding type distribution was not considerably different in organically managed winter spelt compared to lentil-mixed-crop

fields, but more plant-feeding carabids were found in flowering fields compared to lentil mixed-crops. Landscape complexity did not affect any trait characteristic or its variance (Fdvar) (Table 3.2).

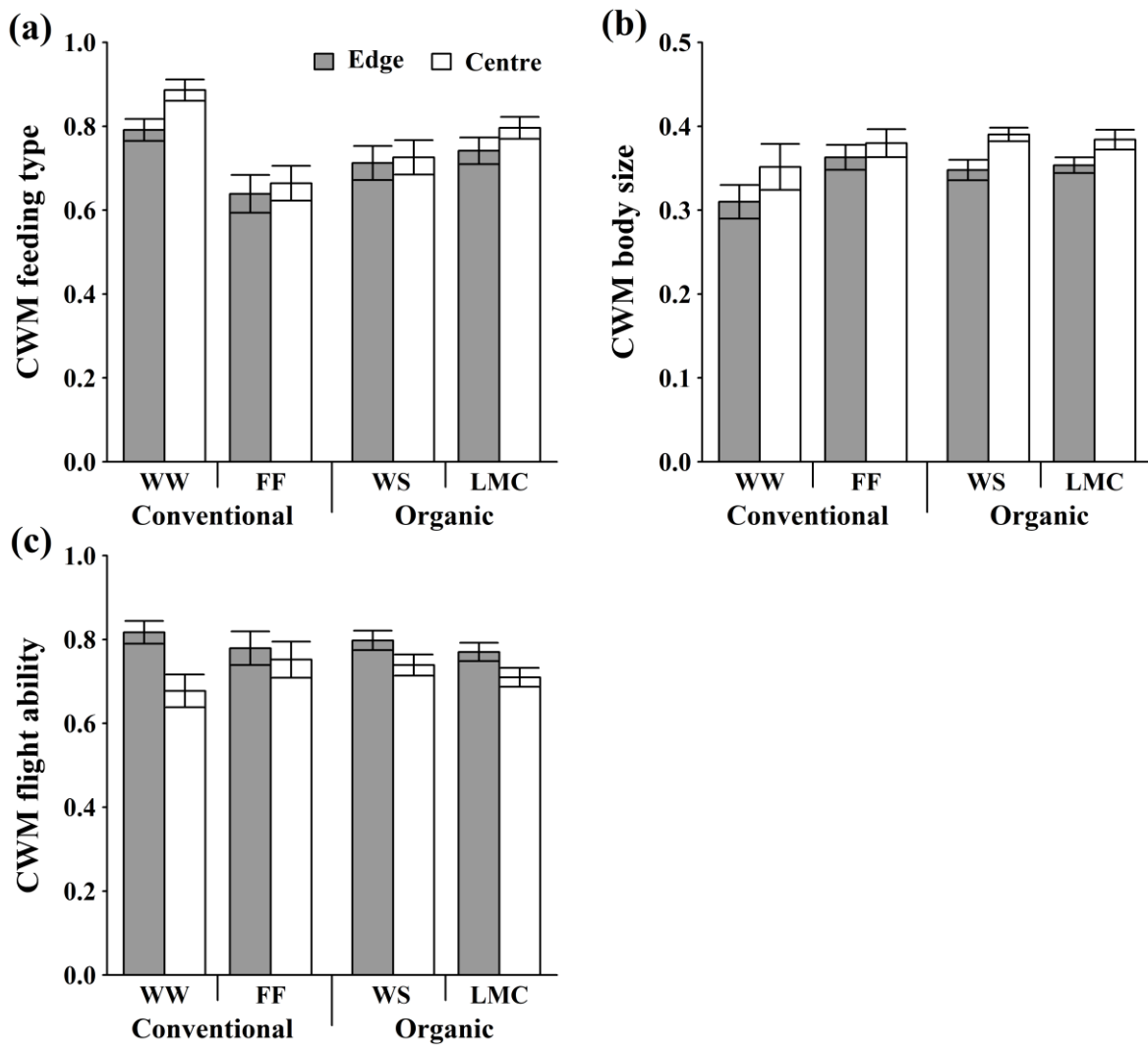
Transect position had strong effects on all traits studied (Table 3.2). Compared with those in field centers, carabid assemblages at the field edges were on average smaller, had more plant-feeding carabids and showed increased flight ability. These mean differences were independent of landscape complexity or crop-use type. The variance of body size and feeding type distribution (Fdvar) was higher within carabid assemblages at the field edges than at field centres (Table 3.2, Fig. S3.4a,b). No such difference was found in flight ability (Fig. S3.4c). The edge effects on feeding type, flight ability and variance in feeding type were most pronounced in winter wheat fields, showing a stronger increase in carnivorous species (Fig. 3.1a), and a stronger decrease in variance of feeding types (Fig. S3.4a) as well as in flight ability (Fig. 3.1c) than elsewhere, although interactions between transect position and crop-use type were not included in the averaged models.

**Table 3.2.** Effects of landscape (% of arable cover), crop-use type (winter wheat (WW) vs. flowering field (FF) vs. winter spelt (WS) vs. lentil-mixed-crop (LMC)) and transect position (edge vs. center) on community weighted mean (CWM) and functional divergence (Fdvar) of carabid traits (body size, food-type, flight ability). Results were calculated by multi-model averaging of linear mixed-effects models. Importance of predictor variables, parameter estimates with standard error (SE) and t/z-values. Only models with  $< 2 \Delta \text{AICc}$  of the best model are shown. Bold values indicate significant effect at  $P < 0.05$ .

Response <sup>a</sup>	Explanatory	Relative importance[%]	Multi-model estimate <sup>b</sup>	± SE	t/z- value
CWM size (0.19/0.82; 1)	Transect (E/C)	99	-0.033	0.007	<b>-4.91</b>
CWM feeding type (0.29/0.76; 2)	Crop-use type (FF/WW)	100	-0.187	0.031	<b>6.022</b>
	Crop-use type (WS/WW)	100	-0.120	0.031	<b>3.823</b>
	Crop-use type (LMC/WW)	100	-0.070	0.035	1.946
	Crop-use type (WS/FF)	100	0.068	0.035	1.881
	Crop-use type (LMC/FF)	100	0.117	0.031	<b>3.750</b>
	Crop-use type (WS/LMC)	100	-0.050	0.031	1.603
	Transect (E/C)	29	-0.047	0.017	<b>2.696</b>
CWM flight ability (0.18/0.77; 1)	Transect (E/C)	100	0.716	0.014	<b>5.073</b>
Fdvar size (0.29/0.59; 1)	Transect (E/C)	3	0.010	0.005	<b>2.164</b>
Fdvar feeding type (0.18/0.77; 1)	Transect (E/C)	27	0.030	0.010	<b>2.819</b>
Fdvar flight ability (0.04/0.55; 1)	Landscape	3	0.019	0.035	0.595

<sup>a</sup> All models were fitted with normal distribution (marginal/conditional  $R^2$  value of full model; number of candidate models,  $\Delta \text{AIC} < 2$ ).

<sup>b</sup> Negative estimates indicate lower number e.g. lower CWM size in edge vs. center.



**Fig. 3.1.** Effect of crop-use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil-mixed-crop (LMC)) and transect position (edge, center) on community weighted mean (CWM) of feeding type (a), body size (b) and flight ability (c). Bars are means  $\pm$  SE.

### 3.5 Discussion

Our study revealed that conventional flowering fields and organic winter spelt, but not spring sown organic lentil mixed-crops, altered the distribution of feeding traits of carabid assemblages, by increasing the proportion of plant-feeding carabids over that found in conventional winter wheat fields. Furthermore, trait characteristics and their divergence were mostly influenced by a distinct difference between field edges and centres, with smaller, less carnivorous and more flight-enabled assemblages at the field edges. The complexity of the surrounding landscape did not influence the functional diversity of carabids within crop fields. These results underline the importance of local farming practices and edge habitats to maintaining the functional diversity of carabid assemblages in arable fields.



### 3.5.1 *Effects of crop-use type*

Although both biodiversity specific (flowering fields) and holistic (organic farming) agri-environmental measures led to considerably higher wild plant cover and species richness than did conventionally farmed winter wheat (Table S3), only flowering fields and organic winter spelt increased the proportion of plant feeding carabids within the ground beetle assemblages. The effectiveness of flowering fields in promoting plant-feeding carabids might be associated with the highest total plant species richness, mainly because they were sown with a diverse seed mixture of 15/18 forb species (Table S1), whereas other crop-use types were sown with just one (wheat or spelt) or two (lentil-mixed-crop) plant species. In addition, the species of forb used in the flowering seed mixture varied strongly in origin (many non-native species from different areas) and traits (e.g. size, growth rate, taxonomic distinctness). The overall vegetation structure in flowering fields was thus probably more heterogeneous than elsewhere. Vegetation heterogeneity as well as higher plant species richness can promote plant feeding carabids, as they prefer diverse food resources (Harvey *et al.*, 2008; Woodcock *et al.*, 2009; Rouabah *et al.*, 2015).

Higher wild plant cover and species richness may also explain the positive effects of organic winter spelt crops compared to conventional winter wheat. Winter spelt crops had lower wild plant cover and species richness than lentil mixed-crops (Table S3.3), but only the former had higher proportion of plant-feeding carabids compared to conventional farming systems (conventional winter wheat). This may be explained by the different sowing time of the two crop-use types. Winter spelt were autumn sown, whereas lentil mixed-crops were spring sown (Table 3.1). Hence, ripened wild plant seeds, which are an important food resource for plant-feeding carabids (Kulkarni *et al.*, 2015), were present earlier and for a longer period in winter spelt compared to lentil mixed-crops. The majority of plant-feeding species in our study (e.g. *Amara*, *Pterostichus*, *Poecilus*, *Harpalus*) are primarily spermophagous (Kulkarni *et al.*, 2015), which might explain our findings. Herbivorous carabids are more sensitive to agricultural management than carnivores (Purtauf *et al.*, 2005b; Woodcock *et al.*, 2009), because the latter can still find abundant prey even in intensively farmed fields as they are able to feed on soil-living prey (Haddad *et al.*, 2000). In contrast, herbivores are more dependent on the above-ground resources, such as a diversity of weeds, leading to constrained food resources under intensive farming. Our study confirmed these findings, revealing the lowest proportion of herbivorous carabids in the most intensively farmed crop-use type (winter wheat), which had by far the lowest wild plant cover and species richness. The positive effects of flowering fields for promoting plant-feeding carabids are confirmed by recent studies (Mader *et al.*, 2017; Baulechner *et al.*, 2019). Other studies confirm the positive effects of organic compared to conventional winter cereals on carabid functional diversity as well as on the activity density and richness of plant-feeding carabids (Batáry *et al.*, 2012; Gallé *et al.* 2018a). Nonetheless, direct comparisons between flowering fields and organic crops in relation to conventional crops are currently missing. Our results point to similar effects between conventional flowering fields and organic winter cereals, but through different mechanisms. Spring sown flowering fields most likely increased proportion of plant-feeding carabids due to higher vegetation heterogeneity,

whereas the earlier sowing time of winter compared to spring crops might be the determining factor in organic farming. Effects of flowering fields may appear quickly (Boetzl *et al.*, 2018), are easier to implement than conversion from conventional to organic farming, and are often preferred by farmers as they allow greater flexibility and a higher level of weed control due to regular plowing. On the other hand, farmers of non-productive measures such as flowering fields cannot gain crop yield, therefore the subsidy costs under the AES are much higher compared to productive measures such as organic farming (in our study area more than three times higher, Table 3.1). As both showed positive effects for plant-feeding carabids, case specific balancing between costs and implementability of different agri-environmental measures may be most suitable in order to increase herbivorous carabid numbers in arable fields.

### 3.5.2 *Edge and landscape effects*

Trait characteristics varied strongly between the edge and the center of arable fields, consistent with other studies (Birkhofer *et al.*, 2014; Molina *et al.*, 2014; Rouabah *et al.*, 2015). This was most likely caused by spillover effects between the bordering grassy field margin and the crop field. Grassy field margins are permanent grassland strips that provide season-long food resources and shelter, as they remain relatively undisturbed by agricultural activities. They are important habitats for carabids, which often (but not always, Mansion-Vaquié *et al.*, 2017) disperse into arable fields with a distance-decay effect (Boetzl *et al.*, 2018; Gallé *et al.*, 2018a,b). Compared to crop fields, grassy margins have higher vegetation density, more complex structure, a more temperate microclimate and lower soil disturbance (Schirmel *et al.*, 2016). This in turn can affect carabid assemblages (Rouabah *et al.*, 2015; Labruyere *et al.*, 2016a). The proximity of undisturbed grassy field margins, which benefits herbivorous carabids (Birkhofer *et al.*, 2014), as well as higher plant species richness at the field edges, explains the higher share of plant feeding carabids as well as higher feeding trait diversity at field edges than in the centers.

Higher vegetation heterogeneity and density at the field edge may also have caused distinct differences in carabid body size distributions. The activity density of large carabids positively correlates with homogenous vegetation and low vegetation density, whereas small carabids prefer high plant functional diversity and heterogeneous vegetation (Rouabah *et al.*, 2015). In addition, larger carabids are more mobile than small ones (Homburg *et al.*, 2013), and can therefore disperse further into the crop fields from bordering habitats (Boetzl *et al.*, 2018). These findings can explain our observations of smaller carabids with more diverse size distribution at field edges than centers.

We also found the flight ability of the carabid assemblage higher at the edges than centers, which may be influenced by an interaction of traits. In general, brachypterous carabids in Europe are medium to large carnivores, whereas macropterous species are often small (den Boer, 1970; Ribera *et al.*, 2001). As we found larger and more carnivorous species, that are often wingless or wing-dimorphic (such as the most abundant species *Pterostichus melanarius* or the *Carabus* spp.), in the field centers, the observed differences in flight ability could be explained by an interaction with other traits. As we

studied single ecological traits, we were unable to assess possible interactions between traits, although this would be a promising research direction for future studies.

The most pronounced edge effect for feeding type distribution was found in the most intensively farmed crop-use type – winter wheat. Within the field center, the high crop density paired with extreme shortage of other plants reduced the available plant resources, thereby creating suboptimal conditions for herbivorous species. The presence of pest species able to cope with intensive agricultural management, such as aphids or soil-living species, may still provide suitable food resources for carnivorous carabids (Collins *et al.*, 2002; Rouabah *et al.*, 2015). Our results suggest that such habitat conditions may remain sufficient for larger, mobile, carnivorous carabids, but not for species belonging to other functional groups, that can disperse to a lesser extent from the field edges into the centres.

Finally, local effects (crop-use type, transect position) had stronger effects on carabid trait distribution than landscape effects, consistent with other studies analysing species richness and activity density (Tuck *et al.*, 2014; Caro *et al.*, 2016; but see Concepción *et al.*, 2012; Purtauf *et al.*, 2005a). Several studies revealed effects of the surrounding landscape on carnivorous and seed eating carabids (Labruyere *et al.*, 2016b) or body sizes (Gallé *et al.*, 2018b), but others failed to detect significant landscape effects on carabid traits (Mader *et al.*, 2017). Within our study region, the biosphere reserve Swabian Alb, soils are poor and stony, therefore land use may be less intensive compared to regions with rich soils. The differences in landscape complexity within our study area were possibly too limited to affect carabid traits more strongly (Caro *et al.*, 2016).

### 3.5.3 Conclusions

This study highlights the importance of edge habitats, i.e., grassy field margins, for promoting the functional diversity of carabids in crop fields. Furthermore, we showed that conventional flowering fields and organic winter cereals are equally effective for enhancing the amount of plant-feeding carabids, which may increase essential ecosystem services in arable fields, such as weed seed control. Because non-productive flowering fields are easier to implement, but require higher amount of subsidy payments compared to organic farming, a strict decision between biodiversity specific non-productive measures and productive measures may be of little benefit for the successful implementation of more effective AES for biodiversity conservation. Instead, future AES policy should aim at a diversity of different measures, targeting the enhancement of edge habitats as well as productive and non-productive measures with proven biodiversity benefits, such as flowering fields and organic winter cereals.

## 3.6 Acknowledgements

We thank the farmers for their participation; Nils Engelmann, Caroline Fischer, Miriam Harper, Moritz Mayer and Nina Stork for supporting the plant survey, and Theresa Faessler, Frederik Schuettler and Tobias Weiß for the sampling and identification of carabids. We also thank Emmiline N. Topp for linguistic corrections of the manuscript. Data collection in 2017 was funded by the Stiftung

Naturschutzfonds Baden-Württemberg (73-8831.21/54691-1703GL). PB was supported by the Economic Development and Innovation Operational Programme of Hungary (GINOP-2.3.2-15-2016-00019).

### 3.7 References

- Barton, K. (2017) MuMIn: Multi-Model Inference. R package version 1.40.0. <<https://CRAN.R-project.org/package=MuMIn>> 25 May 2018
- Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29 (4), 1006–1016. Doi: 10.1111/cobi.12536.
- Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. & Tscharntke, T. (2012) Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agriculture, Ecosystems & Environment*, 146, 130–136. Doi: 10.1016/j.agee.2011.10.018.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. Doi: 10.18637/jss.v067.i01.
- Baulechner, D., Diekötter, T., Wolters, V. & Jauker, F. (2019) Converting arable land into flowering fields change functional and phylogenetic community structure in ground beetles. *Biological Conservation*, 231, 51–58. Doi: 10.1016/j.biocon.2019.01.005.
- Birkhofer, K., Wolters, V. & Diekötter, T. (2014) Grassy margins along organically managed cereal fields foster trait diversity and taxonomic distinctness of arthropod communities. *Insect Conservation and Diversity*, 7, 274–287. Doi: 10.1111/icad.12051.
- Boetzl, F.A., Krimmer, E., Krauss, J. & Steffan-Dewenter, I. (2018) Agri-environmental schemes promote ground-dwelling predators in adjacent oilseed rape fields: Diversity, species traits and distance-decay functions. *Journal of Applied Ecology*, 56, 10–20. Doi: 10.1111/1365-2664.13162.
- Bruggen, A.H. van, Gamliel, A. & Finckh, M.R. (2016) Plant disease management in organic farming systems. *Pest Management Sciences*, 72, 30–44. Doi: 10.1002/ps.4145.
- Caprio, E., Nervo, B., Isaia, M., Allegro, G. & Rolando, A. (2015) Organic versus conventional systems in viticulture: Comparative effects on spiders and carabids in vineyards and adjacent forests. *Agricultural Systems*, 136, 61–69. Doi: 10.1016/j.agsy.2015.02.009.
- Caro, G., Marrec, R., Gauffre, B., Roncoroni, M., Augiron, S. & Bretagnolle, V. (2016) Multi-scale effects of agri-environment schemes on carabid beetles in intensive farmland. *Agriculture, Ecosystems & Environment*, 229, 48–56. Doi: 10.1016/j.agee.2016.05.009.
- Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M. & Chaney, K. (2002) Influence of beetle banks on cereal aphid predation in winter wheat. *Agriculture, Ecosystems & Environment*, 93, 337–350. Doi: 10.1016/S0167-8809(01)00340-1.
- Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T. & Verhulst, J. (2012) Interactive effects of

- landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, 49, 695–705. Doi: 10.1111/j.1365-2664.2012.02131.x.
- de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Silva, P.M. da, Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A. & Harrison, P.A. (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, 19, 2873–2893. Doi: 10.1007/s10531-010-9850-9.
- den Boer, P.J. (1970) On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia*, 4, 1–28. Doi: 10.1007/BF00390612.
- Egorov, E., Gossner, M.M., Meyer, S.T., Weisser, W.W. & Brändle, M. (2017) Does plant phylogenetic diversity increase invertebrate herbivory in managed grasslands? *Basic and Applied Ecology*, 20, 40–50. Doi: 10.1016/j.baae.2017.03.004.
- Fischer, C., Thies, C. & Tschardtke, T. (2011) Mixed effects of landscape complexity and farming practice on weed seed removal. *Perspectives in Plant Ecology, Evolution and Systematics*, 13, 297–303. Doi: 10.1016/j.ppees.2011.08.001.
- Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L.W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M.B., Onate, J.J., Pärt, T., Weisser, W.W., Winquist, C., Thies, C. & Tschardtke, T. (2011) Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecological Applications*, 21, 1772–1781. Doi: 10.1890/10-0645.1.
- Fritsch, F. (2012) Nährstoffgehalte in Düngemitteln und im Erntegut: für die Düngemanagement; für Nährstoffvergleiche. Staatliche Pflanzenberatung Rheinland-Pfalz, Germany.
- Fox, J., Weisberg, S., Bates, D. & Fox, M. (2012) Package “car”. R package version 2.1-4. <<https://CRAN.R-project.org/package=car>> 5 June 2018.
- Gallé, R., Császár, P., Makra, T., Gallé-Szpisjak, N., Ladányi, Z., Torma, A., Kapilkumar, I. & Szilassi, P. (2018b) Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites. *Landscape Ecology*, 33, 1435–1446. Doi: 10.1007/s10980-018-0677-1.
- Gallé, R., Happe, A.-K., Bøsem Baillod, A., Tschardtke, T. & Batáry, P. (2018a). Landscape configuration, organic management and within-field position drive functional diversity of spiders and carabids. *Journal of Applied Ecology*, 56, 63–72. Doi: 10.1111/1365-2664.13257.
- Gruber, S., Wahl, E., Zikeli, S. & Claupein, W. (2012) Perspektiven und Grenzen der Unkrautregulierung bei Linsen (*Lens culinaris*) im Ökologischen Landbau. *Journal für Kulturpflanzen*, 64 (10), 365–377.
- Haaland, C., Naisbit, R.E. & Bersier, L.-F. (2011) Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, 4 (1), 60–80. Doi: 10.1111/j.1752-4598.2010.00098.x.

- Haddad, N.M., Haarstad, J. & Tilman, D. (2000) The effects of long-term nitrogen loading on grassland insect communities. *Oecologia*, 124, 73–84. Doi: 10.1007/s004420050026.
- Harvey, J.A., van der Putten, W.H., Turin, H., Wagenaar, R. & Bezemer, T.M. (2008) Effects of changes in plant species richness and community traits on carabid assemblages and feeding guilds. *Agriculture, Ecosystems & Environment*, 127, 100–106. Doi: 10.1016/j.agee.2008.03.006.
- Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F.A., Niemelä, J., Rebane, M., Wascher, D., Watt, A. & Young, J. (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—A review. *Agriculture, Ecosystems & Environment*, 124 (1), 60–71. Doi: 10.1016/j.agee.2007.09.005.
- Homburg, K., Homburg, N., Schäfer, F., Schuldt, A. & Assmann, T. (2014) Carabids.org – a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity*, 7, 195–205. Doi: 10.1111/icad.12045.
- Homburg, K., Schuldt, A., Drees, C. & Assmann, T. (2013) Broad-scale geographic patterns in body size and hind wing development of western Palaearctic carabid beetles (Coleoptera: Carabidae). *Ecography*, 36, 166–177. Doi: 10.1111/j.1600-0587.2012.07488.x.
- Hurka, K. (1996) Carabidae of the Czech and Slovak Republics. Ing. Vit Kabourek, Zlin, Czech Republic.
- IFOAM (2005) Principles of organic agriculture, IFOAM International Federation of Organic Agriculture Movements, Bonn, Germany, 4 p.  
<[https://www.ifoam.bio/sites/default/files/poa\\_english\\_web.pdf](https://www.ifoam.bio/sites/default/files/poa_english_web.pdf)> 10 March 2018.
- IUSS Working Group WRB (2015) World reference base for soil resources 2014, update 2015, international soil classification system for naming soils and creating legends for soil maps. *World Soil Resources Reports*, 106, UN-FAO, Roma.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G. & Tscharntke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution*, 26 (9), 474–481. Doi: 10.1016/j.tree.2011.05.009.
- Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, 40 (6), 947–969. Doi: 10.1111/j.1365-2664.2003.00868.x.
- Kulkarni, S.S., Dosdall, M.S. & Willenborg, J. C. (2015) The role of ground beetles (coleoptera: carabidae) in weed seed consumption: a review. *Weed Science*. 63, 355–376. Doi: 10.1614/WS-D-14-00067.1.
- Labruyere, S., Ricci, B., Lubac, A. & Petit, S. (2016a) Crop type, crop management and grass margins affect the abundance and the nutritional state of seed-eating carabid species in arable landscapes. *Agriculture, Ecosystems & Environment*, 231, 183–192. Doi: 10.1016/j.agee.2016.06.037.

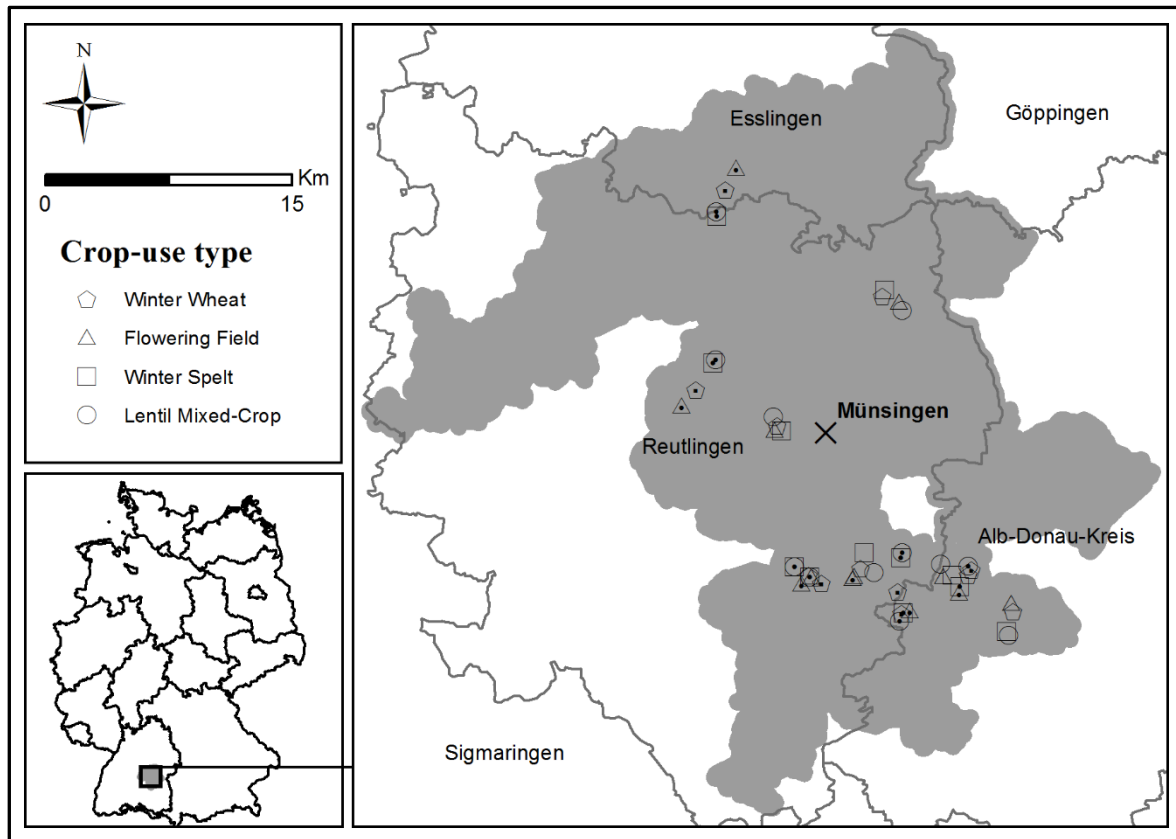
- Labruyere, S., Bohan, D.A., Biju-Duval, L., Ricci, B. & Petit, S. (2016b) Local, neighbor and landscape effects on the abundance of weed seed-eating carabids in arable fields: A nationwide analysis. *Basic and Applied Ecology*, 17 (3), 230–239. Doi: 10.1016/j.baae.2015.10.008.
- Laliberté, E., Legendre, P. & Shipley, B. (2014) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R Foundation for Statistical Computing, Vienna, AT.
- Larochelle, A. (1990) The Food of Carabid Beetles: (coleoptera: Carabidae, Including Cicindelinae). Association des entomologistes amateurs du Québec, Fabriques Supplement 5, 1-132.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A. & Bonis, A. (2008) Assessing functional diversity in the field – methodology matters!. *Functional Ecology*, 22, 134–147. Doi: 10.1111/j.1365-2435.2007.01339.x.
- Leps, J., de Bello, F., Lavorel, S. & Berman, S. (2006) Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia*, 78, 481–501.
- Lövei, G.L. & Sunderland, K.D. (1996) Ecology and Behavior of Ground Beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, 41, 231–256. Doi: 10.1146/annurev.en.41.010196.001311.
- Mader, V., Diehl, E., Fiedler, D., Thorn, S., Wolters, V. & Birkhofer, K. (2017) Trade-offs in arthropod conservation between productive and non-productive agri-environmental schemes along a landscape complexity gradient. *Insect Conservation and Diversity*, 10, 236–247. Doi: 10.1111/icad.12220.
- Mansion-Vaquié, A., Ferrante, M., Cook, S.M., Pell, J.K. & Lövei, G.L. (2017) Manipulating field margins to increase predation intensity in fields of winter wheat (*Triticum aestivum*). *Journal of Applied Entomology*, 141, 600–611. Doi: 10.1111/jen.12385.
- MLR (Ministerium für Ländlichen Raum und Verbraucherschutz Baden-Württemberg) (2016) Verwaltungsvorschrift des Ministeriums für Ländlichen Raum und Verbraucherschutz zum Förderprogramm für Agrarumwelt, Klimaschutz und Tierwohl. Verwaltungsvorschrift vom 27.01.2016 (Az.: 25-8872.53).
- Molina, G.A.R., Poggio, S.L. & Ghera, C.M. (2014) Epigeal arthropod communities in intensively farmed landscapes: Effects of land use mosaics, neighbourhood heterogeneity, and field position. *Agriculture, Ecosystems & Environment*, 192, 135–143. Doi: 10.1016/j.agee.2014.04.013.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015) Vegan: Community ecology package. R package version 2.3-0. < <https://cran.r-project.org/web/packages/vegan> > 15 May 2018
- Pla, L., Casanoves, F. & Di-Rienzo, J. (2012) Quantifying functional biodiversity. Series: Springer Briefs in Environmental Science. Springer Editorial, Berlin, DE.
- Purtauf, T., Dauber, J. & Wolters, V. (2005b) The response of carabids to landscape simplification differs between trophic groups. *Oecologia*, 142, 458–464. Doi: 10.1007/s00442-004-1740-y.

- Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tschantke, T. & Wolters, V. (2005a) Landscape context of organic and conventional farms: influences on carabid beetle diversity. *Agriculture, Ecosystems & Environment*, 108, 165–174. Doi: 10.1016/j.agee.2005.01.005.
- R Development Core Team, 2017. R: a language and environment for statistical computing. R Version 3.4.2. R Foundation for Statistical Computing, Vienna.
- Ribera, I., Dolédec, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, 82, 1112–1129. Doi: 10.1890/0012-9658(2001)082[1112:EOLDAS]2.0.CO;2.
- Ricotta, C. & Moretti, M. (2011) CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia*, 167, 181–188. Doi: 10.1007/s00442-011-1965-5.
- Rouabah, A., Villerd, J., Amiaud, B., Plantureux, S. & Lasserre-Joulin, F. (2015) Response of carabid beetles diversity and size distribution to the vegetation structure within differently managed field margins. *Agriculture, Ecosystems & Environment*, 200, 21–32. Doi: 10.1016/j.agee.2014.10.011.
- Rusch, A., Bommarco, R., Chiverton, P., Öberg, S., Wallin, H., Wikteli, S. & Ekbom, B. (2013) Response of ground beetle (Coleoptera, Carabidae) communities to changes in agricultural policies in Sweden over two decades. *Agriculture, Ecosystems & Environment*, 176, 63–69. Doi: 10.1016/j.agee.2013.05.014.
- Schirmel, J., Thiele, J., Entling, M.H. & Buchholz, S. (2016) Trait composition and functional diversity of spiders and carabids in linear landscape elements. *Agriculture, Ecosystems & Environment*, 235, 318–328. Doi: 10.1016/j.agee.2016.10.028.
- Schlager, P., Krismann, A., Wiedmann, K., Hiltcher, H., Hochschild, V., & Schmieder, K. (2013) Multisensoral, object- and GIS-based classification of grassland habitats in the Bio- sphere Reserve Schwäbische Alb. *Photogrammetrie - Fernerkundung - Geoinformation*, 2013, 163–172. Doi: 10.1127/1432-8364/2013/0167.
- The Council of the European Union (2005) Council Regulation (EC) No 1698/2005 of 20 September 2005 on Support for Rural Development by the European Agricultural Fund for Rural Development (EAFRD).
- Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A. & Bengtsson, J. (2014) Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. *Journal of Applied Ecology*, 51, 746–755. Doi: 10.1111/1365-2664.12219.
- Wang, L., Gruber, S. & Claupein, W. (2012) Optimizing lentil-based mixed cropping with different companion crops and plant densities in terms of crop yield and weed control. *Organic Agriculture*, 2 (2), 79–87. Doi: 10.1007/s13165-012-0028-5.
- Westerink, J., Jongeneel, R., Polman, N., Prager, K., Franks, J., Dupraz, P. & Mettepenningen, E. (2017) Collaborative governance arrangements to deliver spatially coordinated agri-environmental management. *Land Use Policy*, 69, 176–192. <https://doi.org/10.1016/j.landusepol.2017.09.002>.



- Woodcock, B.A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A.J., Heard, M.S., Roy, D.B. & Pywell, R.F. (2014) National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. *Journal of Applied Ecology*, 51, 142–151. Doi: 10.1111/1365-2664.12171.
- Woodcock, B.A., Potts, S.G., Tscheulin, T., Pilgrim, E., Ramsey, A.J., Harrison-Cripps, J., Brown, V.K. & Tallowin, J.R. (2009) Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. *Journal of Applied Ecology*, 46, 920–929. Doi: 10.1111/j.1365-2664.2009.01675.x.
- Woodcock, B.A., Redhead, J., Vanbergen, A.J., Hulmes, L., Hulmes, S., Peyton, J., Nowakowski, M., Pywell, R.F. & Heard, M.S. (2010) Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. *Agriculture, Ecosystems & Environment*, 139, 181–186. Doi: 10.1016/j.agee.2010.07.018.

### 3.8 Supplementary material



**Fig. S3.1.** Location of study fields (center transect) according to crop-use type and study year (unfilled symbols: 2016, symbols with black dot: 2017) in southwest Germany. All fields were located near the city of Münsingen in the administrative districts (solid lines) Alb-Donau-Kreis, Esslingen or Reutlingen within the Biosphere Reserve Swabian Alb (grey area).

#### Appendix A3.1. Plant survey.

We surveyed plants by estimating plant cover according to the Braun-Blanquet scale (Braun-Blanquet, 1932) in five plots ( $5 \times 1$  m, 5 m from each other) per transect ( $n = 480$  plots). Plant and carabid surveys were conducted within the same transects. In 2016, we conducted one survey for each plot between 25 June and 4 August, while in 2017 we surveyed each plot three times: In mid-June, early July, and late July. We used the mean of the three survey rounds for further analysis. We transformed the Braun-Blanquet values to percent cover according to the 160 percent scale of van der Maarel (2007).

We found significant differences between years and crop-use types in crop cover, wild plant cover and plant species richness (Table S3.3). Wild plant richness was highest in lentil-mixed-crop fields, whereas total plant richness was the highest in flowering fields. Edge and center transects differed only in plant species richness. Conventional winter wheat had higher crop and lower wild plant cover and species richness than any of the other crop-use types. The underlying statistical analysis is described in the section “statistical analysis” of the main text.

Braun-Blanquet, J., (1932) Plant sociology. The study of plant communities. McGraw-Hill, New-York, US.

van der Maarel, E. (2007) Transformation of cover-abundance values for appropriate numerical treatment - Alternatives to the proposals by Podani. *Journal of Vegetation Science*, 18 (5), 767–770. Doi: 10.1111/j.1654-1103.2007.tb02592.x.

**Table S3.1.** Composition of the two types of seed mixture used for establishment of flowering fields. Percentile weighting per species in the seed mixture are given as well as their origin status (native/non-native) in the study area (Germany).

Species name	Mixture M1 [%]	Mixture M2 [%]	Status
Anethum graveolens	2	2	non-native
Borago officinalis	2	3	non-native
Calendula officinalis	3	6	non-native
Centaurea cyanus	6	6	native
Coriandrum sativum	3	5	non-native
Fagopyrum esculentum	22.5	0	non-native
Foeniculum vulgare	5	5	non-native
Guizotia abyssinica	2	7.5	non-native
Helianthus annuus	12	17	non-native
Linum usitatissimum	4	10	non-native
Onobrychis viciifolia	5	5	non-native
Papaver rhoeas	0.5	0.5	native
Phacelia tanacetifolia	10	12	non-native
Raphanus sativus	2	0	non-native
Synapis alba	2	0	non-native
Trifolium incarnatum	8	10	non-native
Trifolium resupinatum	5	5	non-native
Vicia sativa	6	6	non-native
Total no. of species	<b>18</b>	<b>15</b>	

**Table S3.2.** Location (geographical coordinates) and farming practice before sowing of crops for each study site. For lentil crop respective mixed crop species is given.

Study site ID	Study year	Longitude	Latitude	Crop-use type	Mixed crop	Management	Preceding crop	Perennial crop in rotation	Tillage before sowing
ALTKB	2016	3547902	5353724	Flowering field		Conventional	flowering field	no	ploughing
ALTKW	2016	3548028	5353237	Winter wheat		Conventional	winter oilseed rape	no	ploughing
ALTOD	2016	3547616	5352031	Winter spelt		Organic	field bean	yes	ploughing
ALTOL	2016	3547735	5351768	Lentil mixed-crop	<i>Camelina sativa</i>	Organic	oat	yes	ploughing
BICKB	2016	3535727	5355317	Flowering field		Conventional	flowering field	no	ploughing
BICKB	2017	3535150	5354892	Flowering field		Conventional	barley	no	ploughing
BICKW	2016	3535584	5355419	Winter wheat		Conventional	maize	no	ploughing
BICKW	2017	3536384	5354953	Winter wheat		Conventional	maize	no	ploughing
BICOD	2016	3534737	5355939	Winter spelt		Organic	alfalfa-clover mix	yes	ploughless tillage
BICOD	2017	3535664	5355306	Winter spelt		Organic	clover	yes	ploughing
BICOL	2016	3535652	5355318	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
BICOL	2017	3534749	5355936	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
BREKB	2016	3538367	5355355	Flowering field		Conventional	barley	no	ploughing
BREKB	2017	3538294	5355248	Flowering field		Conventional	winter triticale	no	ploughing
BREKW	2016	3538729	5355828	Winter wheat		Conventional	barley	no	ploughing
BREKW	2017	3541009	5354431	Winter wheat		Conventional	flowering field	no	ploughing
BREOD	2016	3538966	5356805	Winter spelt		Organic	clover	yes	ploughing
BREOD	2017	3541194	5356502	Winter spelt		Organic	clover	no	ploughless tillage
BREOL	2016	3539556	5355607	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
BREOL	2017	3541271	5356808	Lentil mixed-crop	<i>Camelina sativa</i>	Organic	winter rye	no	ploughless tillage
DOTKB	2016	3533533	5364268	Flowering field		Conventional	barley	yes	ploughing
DOTKW	2016	3533677	5364524	Winter wheat		Conventional	winter triticale	yes	ploughing
DOTOD	2016	3533965	5364221	Winter spelt		Organic	clover	yes	ploughing
DOTOL	2016	3533434	5365065	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
ERKKB	2017	3531180	5380186	Flowering field		Conventional	maize	no	ploughing
ERKKW	2017	3530539	5378864	Winter wheat		Organic	maize	no	ploughing
ERKOD	2017	3529997	5377254	Winter spelt		Organic	lentil	yes	ploughing
ERKOL	2017	3529985	5377538	Lentil mixed-crop	<i>Avena sativa</i>	Organic	winter spelt	yes	ploughing
FRAKB	2016	3543774	5355366	Flowering field		Conventional	flowering field	no	ploughing
FRAKB	2017	3544763	5354361	Flowering field		Conventional	barley	no	ploughing
FRAKW	2016	3545277	5355444	Winter wheat		Conventional	maize	no	ploughing
FRAKW	2017	3545476	5355736	Winter wheat		Conventional	winter oilseed rape	no	ploughless tillage
FRAOD	2016	3544304	5355431	Winter spelt		Organic	alfalfa-clover mix	yes	ploughless tillage
FRAOD	2017	3544793	5354724	Winter spelt		Organic	alfalfa-clover mix	yes	ploughless tillage
FRAOL	2016	3543617	5356121	Lentil mixed-crop	<i>Hordeum vulgare</i>	Organic	winter spelt	yes	ploughless tillage
FRAOL	2017	3545308	5355981	Lentil mixed-crop	<i>Hordeum vulgare</i>	Organic	alfalfa-clover mix	yes	ploughless tillage
GRAKB	2017	3541756	5353258	Flowering field		Conventional	flowering field	no	ploughless tillage
GRAKW	2017	3541222	5353109	Winter wheat		Conventional	flowering field	no	ploughing
GRAOD	2017	3541374	5353129	Winter spelt		Conventional	clover	yes	ploughing
GRAOL	2017	3541134	5352643	Lentil mixed-crop	<i>Hordeum vulgare</i>	Conventional	winter spelt	yes	ploughing
SIRKB	2017	3527885	5365745	Flowering field		Conventional	barley	no	ploughing
SIRKW	2017	3528747	5366709	Winter wheat		Conventional	flowering field	no	ploughing
SIROD	2017	3529769	5368339	Winter spelt		Organic	winter wheat	yes	ploughless tillage

Study site ID	Study year	Longitude	Latitude	Crop-use type	Mixed crop	Management	Preceding crop	Perennial crop in rotation	Tillage before sowing
SIROL	2017	3529946	5368524	Lentil mixed-crop	<i>Avena sativa</i>	Organic	barley	yes	ploughing
ZAIBK	2016	3541087	5372039	Flowering field		Conventional	oat	no	ploughing
ZAIKW	2016	3540077	5372381	Winter wheat		Conventional	maize	no	ploughless tillage
ZAIOD	2016	3540244	5372770	Winter spelt		Organic	clover	no	ploughless tillage
ZAiol	2016	3541278	5371533	Lentil mixed-crop	<i>Camelina sativa</i>	Organic	barley	no	ploughing

**Table S3.3.** Vegetation characteristics at the edge and centre transect of studied crop-use types sampled in 2016 and 2017 (mean  $\pm$  SE; n=48). Results ( $F$ -values of ANOVA table) of linear mixed-effects models are given to test for significant differences between study years, crop-use types and transects. Bold values indicate significant effect at  $P < 0.05$ .

			Crop cover [%] <sup>b,c</sup>	Wild plant cover [%] <sup>b</sup>	Wild plant species richness	Total plant species richness <sup>d</sup>
Conventional	Winter Wheat	Edge	87.8 $\pm$ 2.3	7.4 $\pm$ 0.9	14.2 $\pm$ 0.9	15.2 $\pm$ 0.9
		Centre	91.3 $\pm$ 1.8	3.1 $\pm$ 0.7	5.8 $\pm$ 1.2	6.8 $\pm$ 1.2
	Flowering Field	Edge	65.3 $\pm$ 5.3	27.5 $\pm$ 5.7	28.7 $\pm$ 1.2	43.8 $\pm$ 1.7
		Centre	64.7 $\pm$ 7.1	27.1 $\pm$ 5.9	18.6 $\pm$ 2.0	32.8 $\pm$ 2.3
Organic	Winter Spelt	Edge	75.3 $\pm$ 3.8	19.3 $\pm$ 2.6	29.8 $\pm$ 2.5	30.8 $\pm$ 2.5
		Centre	76.3 $\pm$ 4.8	17.3 $\pm$ 3.2	23.8 $\pm$ 2.1	24.8 $\pm$ 2.1
	Lentil Mixed-Crop	Edge	63.8 $\pm$ 4.9	32.9 $\pm$ 3.9	37.2 $\pm$ 2.3	39.2 $\pm$ 2.3
		Centre	60.8 $\pm$ 5.2	33.7 $\pm$ 6.7	29.2 $\pm$ 1.9	31.1 $\pm$ 2.0
Model <sup>a</sup>	F – value	Year	<b>16.3</b>	<b>13.9</b>	<b>11.1</b>	<b>10.7</b>
		Crop	<b>21.2</b>	<b>32.0</b>	<b>36.3</b>	<b>63.4</b>
		Transect	0.1	3.6	<b>57.4</b>	<b>60.9</b>

<sup>a</sup> All models were fitted with normal distribution.

<sup>b</sup> Arcsine-square root transformed values used for model calculation.

<sup>c</sup> For flowering fields species of sown seed mixture was considered as crop.

<sup>d</sup> Including crop species and species of seed mixture for flowering fields.

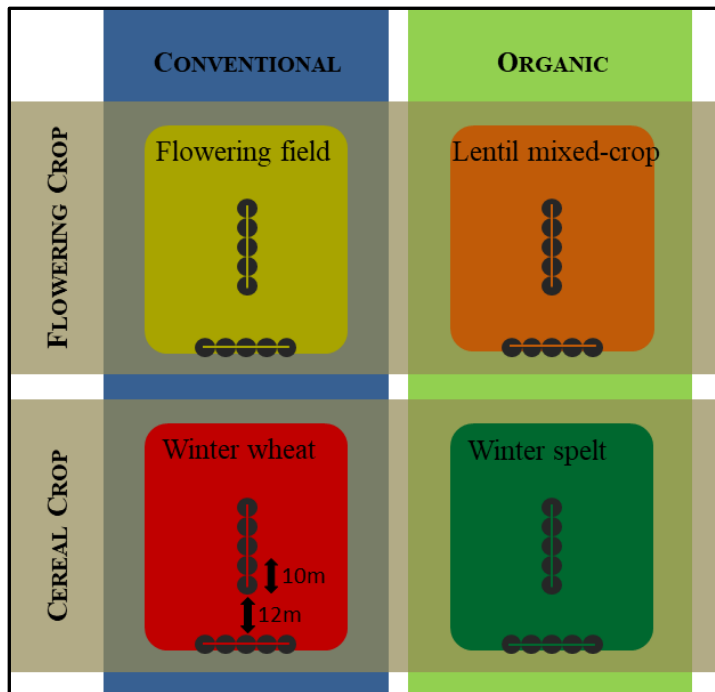
**Table S3.4.** List of sampled carabid species and their trait classification according to body size (geometric mean), feeding type and their flight ability according to wing morphology. Further number of individuals per carabid species recorded at the edge and centre of conventionally farmed winter wheat and flowering fields as well as organically farmed winter spelt and lentil mixed-crop fields.

	Trait			Conventional				Organic				
Species name	Body size [mm]	Feeding type	Flight ability	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		Total number of individuals
				Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	
Abax carinatus	15.3	carnivorous	short winged/wingless	1	0	0	0	0	0	1	0	2
Abax ovalis	12.8	carnivorous	short winged/wingless	0	0	0	1	0	0	0	0	1
Abax parallelepipedus	18.8	carnivorous	short winged/wingless	3	2	5	6	3	5	0	1	25
Abax parallelus	15.3	carnivorous	short winged/wingless	0	0	0	1	0	0	0	0	1
Acupalpus meridianus	3.5	carnivorous	winged	0	0	1	0	0	0	0	0	1
Agonum muelleri	7.3	carnivorous	winged	44	16	15	8	51	57	31	28	250
Agonum sexpunctatum	7.3	carnivorous	winged	1	0	1	0	1	2	2	1	8
Amara aenea	6.9	omnivorous	winged	6	1	16	16	61	3	52	60	215
Amara apricaria	7.3	omnivorous	winged	0	0	1	0	0	0	0	0	1
Amara aulica	12.2	omnivorous	winged	5	0	15	6	18	3	8	2	57
Amara bifrons	5.9	omnivorous	winged	0	0	4	1	6	0	1	1	13
Amara communis	5.9	omnivorous	winged	3	0	1	2	9	1	4	2	22
Amara consularis	7.9	omnivorous	winged	1	1	3	1	3	0	0	0	9
Amara convexior	7.9	omnivorous	winged	4	0	2	2	0	0	1	1	10
Amara curta	5.9	carnivorous	winged	0	0	4	1	6	0	4	3	18
Amara eurynota	10.8	herbivorous	winged	0	0	29	21	2	1	14	0	67
Amara familiaris	6.7	omnivorous	winged	1	0	12	16	24	39	16	16	124
Amara fulva	8.9	herbivorous	winged	0	0	0	0	2	0	0	0	2
Amara fulvipes	10.4	herbivorous	winged	1	0	0	0	0	0	0	0	1
Amara littorea	7.5	herbivorous	winged	3	0	36	82	8	18	56	108	311
Amara lucida	4.9	herbivorous	winged	0	1	1	0	2	2	2	0	8
Amara lunicollis	7.3	omnivorous	winged	3	0	1	1	47	5	9	0	66
Amara nitida	7.9	herbivorous	winged	0	0	1	0	0	0	0	0	1
Amara ovata	8.4	omnivorous	winged	2	2	6	13	3	1	7	13	47
Amara plebeja	6.9	omnivorous	winged	57	3	6	1	9	3	9	0	88
Amara similata	8.4	omnivorous	winged	3	0	35	26	9	2	19	43	137
Anchomenus dorsalis	6.3	carnivorous	winged	1377	445	358	165	1119	417	813	691	5385
Anisodactylus binotatus	10.4	omnivorous	winged	6	0	1	1	4	2	12	0	26
Badister bullatus	4.9	carnivorous	winged	3	1	1	0	0	1	0	1	7
Badister sodalis	3.5	carnivorous	winged	2	1	2	1	0	0	1	0	7
Bembidion guttula	2.4	herbivorous	winged	0	0	0	0	0	0	1	1	2
Bembidion lampros	2.8	carnivorous	dimorphic	54	23	42	24	108	21	73	70	415
Bembidion lunulatum	3.5	carnivorous	winged	0	0	0	0	1	0	0	0	1
Bembidion obtusum	2.4	omnivorous	short winged/wingless	0	0	5	0	3	1	2	2	13
Bembidion properans	3.5	carnivorous	dimorphic	5	0	12	5	47	21	14	6	110
Bembidion quadrimaculatum	2.4	carnivorous	winged	9	14	16	15	7	4	24	17	106
Brachinus crepitans	7.7	omnivorous	winged	5	0	329	1230	76	8	44	8	1700

Species name	Trait			Conventional				Organic				Total number of individuals
	Body size [mm]	Feeding type	Flight ability	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		
				Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	
Brachinus explodens	5.3	carnivorous	winged	0	0	0	1	3	2	0	0	6
Calathus erratus	9.8	carnivorous	dimorphic	1	0	0	0	1	0	0	0	2
Calathus fuscipes	11.8	carnivorous	dimorphic	54	43	78	63	140	50	39	11	478
Calathus melanocephalus	7.3	omnivorous	dimorphic	1	0	0	0	5	0	0	0	6
Carabus auratus	23.2	carnivorous	short winged/wingless	24	39	38	22	174	154	35	68	554
Carabus cancellatus	25	carnivorous	short winged/wingless	1	0	0	0	0	0	2	2	5
Carabus convexus	16.7	carnivorous	short winged/wingless	8	1	2	1	11	8	0	0	31
Carabus granulatus	19.7	carnivorous	winged	34	39	27	36	101	93	62	79	471
Carabus monilis	23.9	carnivorous	short winged/wingless	0	0	1	0	0	1	0	0	2
Carabus violaceus	28.9	carnivorous	short winged/wingless	4	1	0	3	10	5	3	7	33
Clivina collaris	4.5	carnivorous	winged	0	0	0	0	1	0	1	0	2
Clivina fossor	5.9	omnivorous	dimorphic	10	21	8	20	7	17	10	11	104
Diachromus germanus	8.4	herbivorous	winged	2	0	0	0	24	6	2	0	34
Dyschirius globosus	2.4	carnivorous	dimorphic	2	4	0	0	0	0	2	2	10
Epaphius secalis	3.5	carnivorous	short winged/wingless	47	383	0	0	1	0	0	1	432
Harpalus affinis	9.8	omnivorous	winged	89	2	150	78	143	78	190	79	809
Harpalus calceatus	12.2	herbivorous	winged	0	0	0	0	2	0	0	0	2
Harpalus dimidiatus	12.4	herbivorous	winged	0	0	2	12	1	0	1	0	16
Harpalus distinguendus	8.8	omnivorous	winged	0	0	0	0	1	0	0	0	1
Harpalus latus	9.4	herbivorous	winged	4	1	2	1	4	2	2	2	18
Harpalus luteicornis	6.5	omnivorous	winged	0	0	0	0	1	1	0	0	2
Harpalus rubripes	9.8	omnivorous	winged	0	0	0	1	1	0	1	0	3
Harpalus rufipes	13.3	herbivorous	winged	647	259	783	793	1312	1208	623	597	6222
Harpalus signaticornis	6.5	herbivorous	winged	0	0	1	0	0	0	0	0	1
Harpalus tardus	8.8	herbivorous	winged	0	0	0	4	1	1	2	4	12
Leistus ferrugineus	6.3	carnivorous	short winged/wingless	0	0	0	0	1	0	0	0	1
Limodromus assimilis	11.4	carnivorous	winged	5	25	0	2	10	13	0	0	55
Loricera pilicornis	6.9	carnivorous	winged	32	18	15	2	73	22	9	5	176
Microlestes minutulus	2.4	carnivorous	dimorphic	0	0	3	0	0	0	0	0	3
Molops piceus	11.2	carnivorous	short winged/wingless	0	1	0	1	0	0	0	0	2
Nebria brevicollis	11.2	carnivorous	winged	11	13	6	2	38	15	25	5	115
Nebria rufescens	10.8	carnivorous	winged	0	0	0	0	0	1	0	0	1
Notiophilus aestuans	4.5	carnivorous	winged	2	0	1	2	0	1	2	0	8
Notiophilus biguttatus	4.2	carnivorous	dimorphic	2	4	0	1	3	2	0	2	14
Notiophilus palustris	4.9	carnivorous	dimorphic	1	0	0	0	0	0	0	0	1
Ophonus azureus	7.3	herbivorous	dimorphic	0	0	2	5	6	13	20	10	56
Ophonus laticollis	9.4	herbivorous	dimorphic	0	0	0	0	0	0	2	0	2
Ophonus puncticollis	7.7	herbivorous	winged	0	0	3	2	3	0	0	0	8
Ophonus rufibarbis	7.3	herbivorous	winged	0	0	0	0	1	0	0	0	1
Panagaeus bipustulatus	6.9	carnivorous	winged	0	0	0	0	0	0	1	0	1
Patrobus atrorufus	8.4	carnivorous	dimorphic	2	13	1	0	2	7	8	6	39
Poecillus cupreus	10.8	omnivorous	winged	643	266	1265	1903	1563	1853	1760	1833	11086
Poecillus versicolor	9.8	carnivorous	winged	26	9	84	49	200	114	36	36	554

Species name	Trait			Conventional				Organic				Total number of individuals
	Body size [mm]	Feeding type	Flight ability	Winter Wheat		Flowering Field		Winter Spelt		Lentil Mixed-Crop		
				Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	Edge (number of individuals)	Centre (number of individuals)	
Pterostichus anthracinus	10.4	carnivorous	dimorphic	4	21	7	29	8	31	4	6	110
Pterostichus madidus	16.1	carnivorous	dimorphic	9	60	161	220	163	147	18	13	791
Pterostichus melanarius	14.7	carnivorous	dimorphic	1413	1967	1650	2374	2743	4204	2747	4457	21555
Pterostichus melas	15.9	carnivorous	short winged/wingless	21	1	347	421	29	32	44	104	999
Pterostichus minor	6.9	carnivorous		dimorphic	0	0	0	0	1	1	2	0
Pterostichus niger	18.2	carnivorous	winged	13	9	0	5	8	10	12	7	64
Pterostichus ovoideus	6.9	carnivorous	dimorphic	4	6	4	4	27	13	9	8	75
Pterostichus quadrifoveolatus	9.4	carnivorous	winged	2	9	0	0	2	0	2	0	15
Pterostichus strenuus	5.9	omnivorous	dimorphic	9	11	2	0	9	14	3	0	48
Pterostichus vernalis	6.5	carnivorous	winged	4	2	4	0	15	11	4	2	42
Stomis pumicatus	6.9	carnivorous	short winged/wingless	3	0	0	1	4	3	4	9	24
Syntomus truncatellus	2.4	carnivorous		dimorphic	0	0	1	0	0	0	0	0
Synuchus vivalis	6.7	carnivorous	dimorphic	1	4	1	2	21	14	9	3	55
Trechoblemus micros	4.5	carnivorous	winged	0	0	1	0	0	1	0	0	2
Trechus quadristriatus	3.5	carnivorous	winged	166	252	5	5	144	151	6	15	744

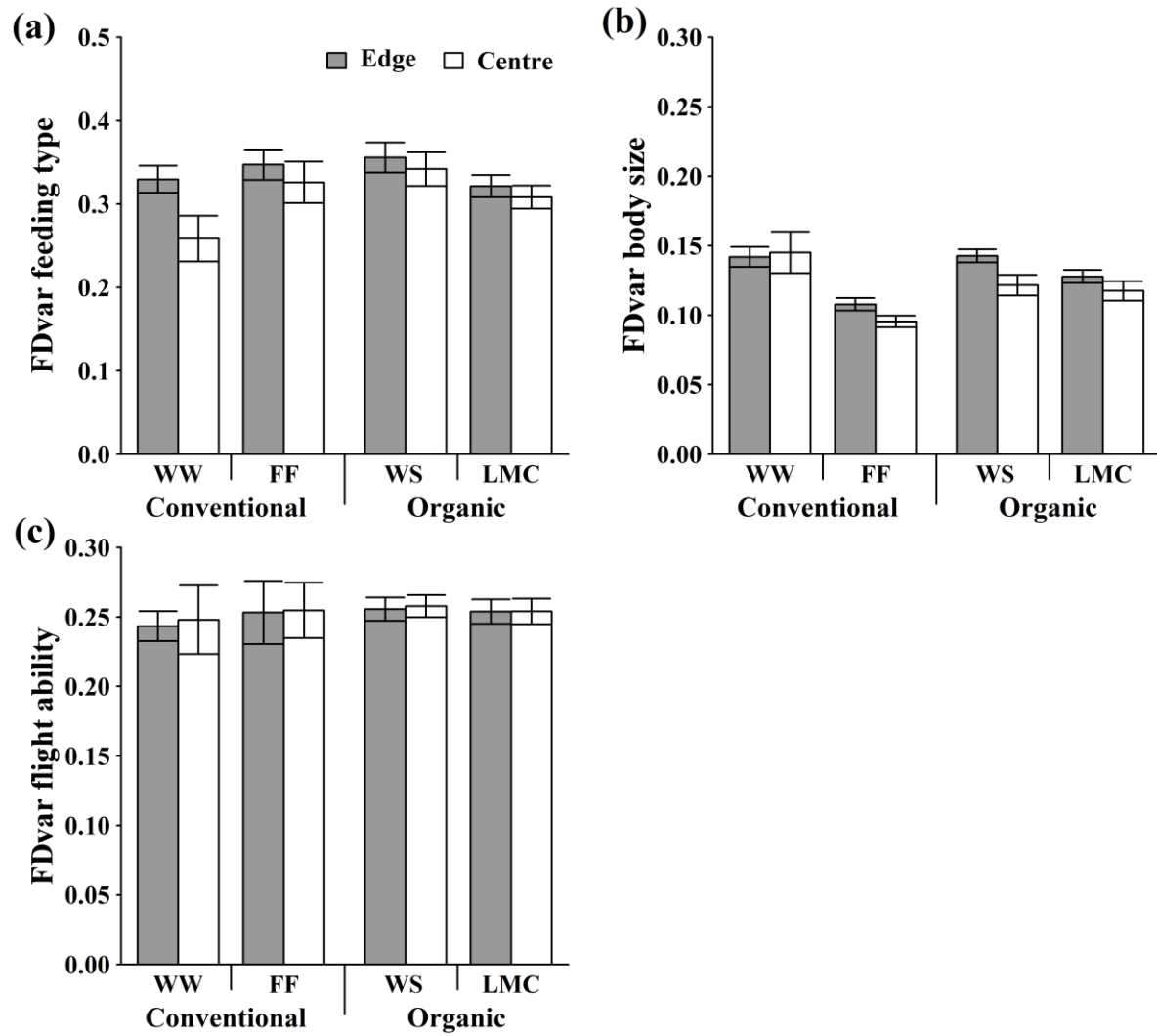




**Fig. S3.2.** Cross-nested design of crop-use types and experimental set-up of pitfall traps. Five traps were placed at the edge and another five at the centre transect, in a distance of 10m between traps. Distance between edge and centre transect was 12 m in 2016 and 15 m in 2017.



**Fig. S3.3.** Exemplary photo of a lentil mixed-crop field. Indicated are the lentil plant (light green) intercropped with a supporting crop (oat, dark green). © Photo: T. Weiss.



**Fig. S3.4.** Effect of crop- use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil mixed-crop (LMC)) and transect position (edge, centre) on functional divergence (FDvar) of feeding type (a), body size (b) and flight ability (c). Bars are means  $\pm$  SE.

## 4. CHAPTER

### **Landscape-wide attraction of flowering fields and vicinity to organic winter cereals support bumblebee colonies in agricultural landscapes**

A version of chapter 4 was submitted to *Insect Conservation and Diversity*:

Gayer, C., Biermann, A., Dieterich, M., Reidl, R. & Batáry, P. (2020) Landscape-wide attraction of flowering fields and vicinity to organic winter cereals support bumblebee colonies in agricultural landscapes. Submitted to *Insect Conservation and Diversity*.



© Photos: A. Biermann.

## Landscape-wide attraction of flowering fields and vicinity to organic winter cereals support bumblebee colonies in agricultural landscapes

Christoph Gayer<sup>1</sup>, Alina Biermann<sup>2</sup>, Martin Dieterich<sup>3</sup>, Konrad Reidl<sup>1</sup> & Péter Batáry<sup>4</sup>

<sup>1</sup>Institute of Landscape and Environment (ILU), University of Applied Sciences Nürtingen-Geislingen, 72622 Nürtingen, Germany;

<sup>2</sup>University of Applied Sciences, Weihenstephan-Triesdorf, Markgrafenstr. 16, 91746 Weidenbach, Germany;

<sup>3</sup>Landscape Ecology and Vegetation Science, University of Hohenheim, 70599 Stuttgart, Germany;

<sup>4</sup>MTA Centre for Ecological Research, Institute of Ecology and Botany, “Lendület” Landscape and Conservation Ecology Research Group, Vácrátót, Hungary.

### 4.1 Abstract

The loss of flower resources is a major reason for declining pollinator populations in farmland.

Measures to increase flower resources on arable land include non-productive approaches like sown flowering fields as well as production-integrated approaches like organically farmed crops sustaining flowering arable wild plants, but little is known about their relative efficacy for bumblebee conservation. We observed weight gain, foraging activity, worker body size, queen brood cell number and analysed stored pollen types of *Bombus terrestris* colonies experimentally exposed at arable fields farmed under four crop-use types: (a) flowering fields under conventional farming, (b) organic cereal mono-crops (winter spelt), (c) organic flowering mixed-crops (lentil mixed-crop) and (4) a conventional control crop (winter wheat). Additionally, we analysed effects of flower cover in the surrounding landscape. Colonies exposed at organic winter spelt fields had higher foraging activity and larger body sizes, whereas other colony performances were unaffected by local crop-use type. *Phacelia tanacetifolia*, which was only cultivated in flowering fields, accounted for about 50 % of the total pollen amount irrespectively of crop-use type indicating a landscape-wide attraction of flowering fields for *B. terrestris*. Flower cover in the surrounding landscape did not affect colony development, but negatively affected pollen diversity. We conclude that establishing flowering fields might be an appropriate measure where flower resources quantity is the crucial limiting factor, but in landscapes containing mass-flowering crops, local bumblebee populations could be more efficiently supported by increasing flowering wild plant diversity, such as with flower-rich organically farmed winter cereals.

**Keywords:** Agri-environment schemes, *Bombus terrestris*, colony growth, mass-flowering crop, organic farming, pollinator.

## 4.2 Introduction

The ongoing decline of insect pollinators is a major threat to the conservation of biodiversity and associated pollination services for wild plants and insect-pollinated crops, which are fundamental to the maintenance of global crop production (Potts *et al.*, 2010; Potts *et al.*, 2016). In Europe, bumblebees (*Bombus spp.* L., Hymenoptera, Apidae) are abundant pollinators in agricultural landscapes, but severe declines have been reported for several species as a result of local and landscape-wide farming practice intensification, leading to habitat loss and sharp decrease of flower resources (Goulson, 2003; Goulson *et al.*, 2008). The availability of flower resources, which provide carbohydrates by nectar and proteins, lipids and micronutrients by pollen (Vaudo *et al.*, 2015), limit the survival, growth and reproduction of bumblebee colonies (Goulson *et al.*, 2002; Westphal *et al.*, 2006). Beside the decreased flower quantity, the lack of flower diversity in consequence of monoculture dominated arable land can negatively affect bumblebees colony development through pollen diversity loss (Hass *et al.*, 2019). Hence, increasing the amount and diversity of flower resources is a key task for the promotion of bumblebee populations in agricultural landscapes.

To increase flower resource supply on arable land, productive and non-productive approaches exist. The establishment of flowering fields (planted seed mixture of flowering forbs on fallow arable land) is a popular agronomically non-productive measure, which is publicly supported through agri-environmental schemes (AES) in several European countries (Haaland *et al.*, 2011; Dietzel *et al.*, 2019). It removes whole fields from crop production to create mass-flowering habitats with highly rewarding nectar and pollen resources. Other studies found positive effects of mass-flowering crops such as oilseed rape (OSR), red clover or patches sown with a flower mixture on the colony growth or reproduction success of bumblebee populations (Westphal *et al.*, 2009; Carvell *et al.*, 2015; Rundlöf *et al.*, 2014; Westphal *et al.*, 2006), although effects of flowering fields have been rarely studied directly. In contrast, organic farming of arable crops is a common production-integrated approach, combining continued crop use with environmental friendly farming practices such as permanent ban of chemical pesticides, - mineral fertilizers and reduced crop plant density (Batáry *et al.*, 2017), which in turn can increase flower cover and species richness of flowering forbs compared to conventional farmed crops (Happe *et al.*, 2018). Increased and more diversified floral resources in organically farmed crops were shown to increase abundance and species richness as well as colony growth and reproduction of bumblebees (Rundlöf *et al.*, 2008; Carrié *et al.*, 2018; Adhikari *et al.*, 2019). In addition, the positive effects of organic crops might be further increased by growing flowering legumes such as lentils instead of cereal crops, as it offers higher amount of flower resources. However, previous studies did not compare the relative efficacy of establishing flowering fields and organically farmed crops to support bumblebee populations.

Besides, most studies considering either the effects of mass-flowering-, or organically farmed crops surveyed the activity density of bumblebees, but did not take into account effects on bumblebee colony development (e.g. Rundlöf *et al.*, 2008; Scheper *et al.*, 2015). It has therefore not been clear, if

observed positive effects on bumblebee abundance and species richness were simply caused by the transiently attraction to flower-rich locations, leading to redistribution of the present population within a landscape (Holzschuh *et al.*, 2016), or if it resulted in higher colony growth, reproduction success or individual fitness, factors which are essential for the long-term conservation benefit (Spiesman *et al.*, 2017).

Bumblebees forage on local flower resources in close proximity to their nest site, but also exploit landscape wide food resources in a distance of up to several kilometers (Chapman *et al.*, 2003; Westphal *et al.*, 2006; Redhead *et al.*, 2016). The spatial distribution of flower resources at the landscape level as well as their nutritional quality (e.g. greater pollen diversity) determine the forage flight distance and -duration, as well as the nectar and pollen intake of worker bumblebees (Westphal *et al.*, 2006; Redhead *et al.*, 2016; Vaudo *et al.*, 2018). Hence, bumblebee colony development can also be affected by the amount of flower resources in the surrounding landscape, irrespectively of the local flower resource supply (Williams *et al.*, 2012; Bukovinszky *et al.*, 2017).

In this study we compared the colony development and the diversity of pollen stores of *Bombus terrestris* L. colonies, which were experimentally sited at arable fields farmed as (a) flowering fields under conventional management, (b) non-flowering mono-crop (organic winter spelt) and (c) flowering mixed-crop (organic lentil mixed-crop) under organic management. As control we also compared *B. terrestris* colonies exposed at (d) conventional winter wheat fields. For these four crop-use types we measured colony development by four parameters, i.e. maximum weight gain of colonies, foraging activity, body size of workers and total amount of queen brood cells. In addition, we compared the effects of the relative flower cover in the surrounding landscape on colony development and pollen diversity, irrespectively of crop-use type. We hypothesized that (1) direct vicinity of conventional flowering fields would most strongly promote colony development through short flight distance to highly rewarding, mass-flowering plants leading to higher nectar and pollen intake by workers. (2) Direct vicinity of organically farmed crops would improve colony development and diversity of pollen stores compared to conventional winter wheat thorough higher amount and diversity of flowering wild plants in short flight distance and that (3) organic lentil mixed-crops would further improve colony development compared to organic winter spelt crops. (4) We expected that colony development would be positively related to the amount of flower cover in the surrounding landscape.

### 4.3 Materials and methods

#### 4.3.1 Study area and design

We conducted the study in a small-scale agricultural landscape within or close to the border of the UNESCO Biosphere Reserve Swabian Alb in southwest Germany (map see Fig. S4.1). Elevation of study fields ranged between 630-754 m a.s.l., with a mean temperature of 18.1° C and a total precipitation rate of 55.5 mm during the study period (July 2018). For this region, it was considerable

warmer and dryer than usually in July (mean of 2008-2017:  $16.7 \pm 0.5^\circ \text{C}$  (mean  $\pm$  SEM),  $131.1 \pm 14.0$  mm; data from nearest meteorological station Münsingen-Apfelstetten, URL: <https://cdc.dwd.de/portal/>, accessed 18.08.2019).

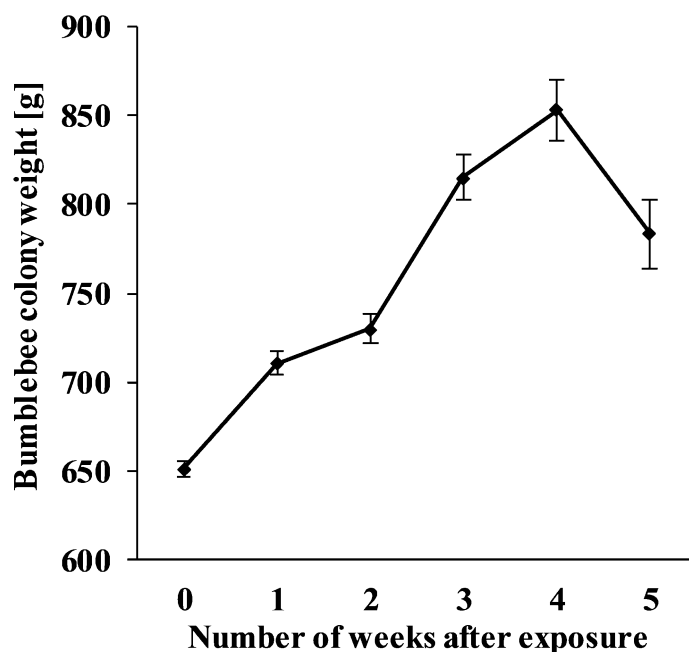
We exposed two nest boxes of commercially purchased colonies of the buff-tailed bumblebee (*B. terrestris*) per study field (=nest box location, photo see Fig. S4.2). Nest box locations were situated at the edge of 24 arable fields farmed under four crop-use types, which were conventional flowering field (sown seed mixture, Fig. S4.2), organic winter spelt (*Triticum aestivum* subsp. *spelta* L.), organic lentil (*Lens culinaris* Medic.) intercropped with a supporting crop (cereal or camelina (*Camelina sativa* L.)) and conventional winter wheat (*Triticum aestivum* L., except one field with winter triticale). We spatially nested the four crop-use types in six study sites (4 crop-use types  $\times$  6 sites = 24 study fields), which compromised the four crop-use types in spatial proximity (Fig. S4.1). Within each study site the two conventionally managed crop-use types (winter wheat, flowering field) were farmed by the same farmer (except two study sites with two different farmers for winter wheat and flowering fields) and the same applied to both organically farmed crop-use types (winter spelt, lentil-mixed-crop). Besides, each farmer managed one flowering- (flowering field, lentil-mixed-crop) and one cereal- (winter wheat, winter spelt) crop type, resulting in a threefold nested (landscape, farmer, crop type) and crossed (between farmer and crop type) study design (see Fig. S4.3 for an illustration; details about the study design in Gayer *et al.*, 2019).

The mean study field size was  $2.6 \pm 0.3$  ha with minor differences between crop-use types (conventional winter wheat:  $3.5 \pm 0.9$  ha; conventional flowering field:  $2.5 \pm 0.5$  ha; organic winter spelt:  $2.4 \pm 0.6$  ha; organic lentil mixed-crop:  $2.2 \pm 0.5$  ha). The mean minimum distance between nest box locations within each study site was  $865 \pm 106$  m and  $4521 \pm 558$  m between nest box locations of different study sites. Although *B. terrestris* is able to fly several kilometer, flower resources in close proximity to the nest are most important (Hass *et al.*, 2019; Redhead *et al.*, 2016). Hence, it is possible to compare even spatially nested study fields within the forage flight distance of *B. terrestris*. The mean minimal distance of nest box locations to the next studied flowering field was  $1510 \pm 153$  m. However, during field work we recognized additional flowering fields (same crop-use type) of other farmers in the surrounding landscape, which we mapped in a buffer of 500 m around each nest box location. Only 8 of 24 surrounding landscapes had no additional flowering field. The mean number of additional flowering fields was  $1.4 \pm 0.35$ . The mean minimum distance of nest box locations to the next flowering field (studied or additional flowering field) was  $458 \pm 90$  m.

#### 4.3.2 Bumblebee experiment

We placed two *B. terrestris* colonies (Apidae, Hymenoptera) next to each other (approx. 20 cm distance) at the field edge of each study field (2 colonies  $\times$  24 fields = 48 colonies). All bumblebee colonies were even-aged, bred and sold by STB Control in Aarbergen, Germany, and consisted of one founding queen and approximately 30-40 workers per colony. The cultured strain of *B. terrestris*

originated from Germany according to the breeder. Each colony was housed in a cardboard box with a ventilated inner plastic cage and a Plexiglas tube allowing free outdoor access. Nest boxes were placed on wooden pallets to avoid moisture from ground vegetation and light green rigid foam roofs of 5cm depth, fixed with tensioning strap, protected colonies from rain and sun exposure. Although *B. terrestris* naturally nests below ground, its nest site selection is highly adaptable (Fussell & Corbet, 1992). Bumblebee colonies were set up for five weeks between 26.06. – 03.08.2018. At that time flower cover was already low in the study area, because oilseed rape blooming and the first mowing round of grassland habitats ended. During the first week, each colony was provided with sugar syrup to support environmental adaptation of the colonies. The sugar syrup tank was removed after one week. We weighted each colony before opening the entrance for the first time and continued to weight each colony at an interval of seven days, using weight gain as an indicator for colony growth following previous studies (Hass *et al.*, 2019; Westphal *et al.*, 2009). Colonies were weighted in the field at daytime after closing the entrance. Weight measures might have been slightly underestimated, as some foraging workers could have been absent from the nests during measuring time, but such measures are still good indicators of colony growth (Hass *et al.*, 2019; Westphal *et al.*, 2009). Colonies continually gained weight during the first four weeks of exposure and started to lose weight in the last week of exposure (Fig. 4.1).



**Fig. 4.1.** Mean ( $\pm$  SE) colony weight of *Bombus terrestris* colonies (n=37) over the course of five week exposure at study fields.

Furthermore, we measured foraging activity of bumblebees by sitting 1 m apart from the colony entrance and counting the amount of worker bumblebees entering or leaving the colony during a 15 min observation period (Goulson *et al.*, 2002). We conducted two observation rounds in the second and third



week after colony set up, between 09:00 a.m. and 05:00 p.m. in the absence of rain, strong wind or low temperatures (below 15° C). Observations were always conducted by the same person (AB) to standardize observations.

After five weeks we collected all colonies and froze them. From each colony we randomly selected 15 workers and measured their inter-tegular width with digital callipers to estimate body sizes of worker bumblebees (Stanley *et al.*, 2016). Additionally, we counted the number of queen brood cells in each colony as a proxy for its reproduction success (Westphal *et al.*, 2009; Williams *et al.*, 2012). Queen brood cells are larger than other brood cells (Williams *et al.*, 2012), therefore we determined a threshold by measuring the diameter of the ten smallest and the ten largest brood cells per colony out of ten well developed, randomly selected colonies using a digital calliper. Finally, we considered a diameter of 11.3 mm as minimum size for queen brood cells. As some queen brood cells contained dead larvae, we only took intact queen brood cells into account which were either closed (with intact larva) or open (already hatched imago).

Last, we collected ten pollen pots per nest box location (pooled from both colonies at one study field, due to the limited amount of pollen pots in some colonies) for pollen grain analysis. For that, the ten pollen pots were pooled per sample and 1000 mg of it were mixed with 10 mL of distilled water. 1 mL of the solution were put on a microscope slide and dried at 40 ° C. Afterwards, the dried pollen were covered with Kaiser's glycerol gelatine using glass slips. From the dried preparation 500-600 pollen grains were identified under a microscope at 200-400 × magnification. All pollen analysis were conducted by Dr. Raghdan Alkattea of the Apicultural State Institute of the University of Hohenheim.

### 4.3.3 Farming practice- and vegetation characteristics

We collected information about farming practice characteristics by personal interviews with farmers (n=13) using standardized questionnaire. We quantified the amount of applied fertilizer per study field (kg N ha<sup>-1</sup>) by taking into account mineral- as well as organic fertilizer applications, and used 4.0 kg N (m<sup>3</sup>)<sup>-1</sup> as fixed value for liquid manure and 5 kg N t<sup>-1</sup> for dung (Fritsch, 2012). Pesticide application was measured by the total number of herbicide, fungicide or insecticide applications.

Differences in farming practices between the four crop-use types were characterised by the type of crop (cereal (winter wheat, winter spelt) vs. flowering plant (flowering field, lentil mixed-crop)), the sowing time (autumn (winter wheat, winter spelt) vs. spring sown crop (flowering field, lentil mixed-crop)) and management system (conventional (winter wheat, flowering field) vs. organic farming (winter spelt, lentil mixed-crop)). Flowering fields were a specific measure under the AES program in the study region (Baden-Württemberg), whereas the two organic crops were only subsidized by standard AES support for organic farming according to European standards (The Council of the European Union, 2005), but not a specific measure of the AES program. Flowering fields were arable fields sown with an annual standardised seed mixture of 15 to 18 flowering plants (Table S4.1) and treated as annual set-aside without farming practices (tillage, mechanical weeding, fertilizer- or pesticide application)

allowed after sowing. The lentil mixed-crop consisted of the lentil plant, a flowering legume, sparsely intercropped with camelina (two sites), barley (*Hordeum vulgare*; two sites) or oat (*Avena sativa*; two sites) to stabilize the branching lentil plant (for details about lentil mixed-cropping systems see (Wang *et al.*, 2012)). Pesticides and mineral fertilizers were only applied in conventional winter wheat, whereas mechanical weed control was mainly applied in organic winter spelt crops (Table S4.2). Organic crops had a more diverse crop rotation than conventional crops. Crop yield was highest in conventional winter wheat and subsidy amount was highest for conventional flowering fields in order to compensate for complete yield loss.

Wild plant cover and plant species richness was higher in the three extensively used crop-use types (flowering field, winter spelt, lentil mixed-crop) compared to conventional winter wheat, with highest species numbers of wild plants in both organically farmed crops (Table S4.3; for statistics see the section statistical analysis). Flower cover as well as species richness of flowering forbs was much higher in flowering fields compared to all other crop-use types. Organic winter spelt and lentil mixed-crops had similar amount of flower cover and species richness of flowering forbs, but higher flower cover and richness compared to winter wheat crops. For details about the vegetation survey see Appendix A4.1.

#### 4.3.4 Landscape analysis

We analysed the surrounding landscape in a buffer of 500m around each nest box location using the Geographical Information System ArcGIS 10.2.2 (1999-2014 ESRI Inc.). Arable land was the most abundant land cover type accounting for  $57.5 \pm 3.6$  % of total land cover, followed by intensively managed grassland ( $19.0 \pm 3.6$  %), forest ( $14.7 \pm 3.6$  %), urban areas ( $4.8 \pm 1.2$  %), copses ( $2.3 \pm 0.3$  %) and extensively managed grassland ( $1.7 \pm 0.4$  %). We used percentage cover of these six land cover types to calculate land use diversity (Shannon index). None of the land cover types or land use diversity did significantly differ between crop-use types (arable land:  $\chi^2 = 1.6$ ,  $df = 3$ ,  $p = 0.67$ ; intensive grassland:  $\chi^2 = 0.55$ ,  $df = 3$ ,  $p = 0.91$ ; forest:  $\chi^2 = 1.7$ ,  $df = 3$ ,  $p = 0.63$ ; urban areas:  $\chi^2 = 3.46$ ,  $df = 3$ ,  $p = 0.33$ ; copses:  $\chi^2 = 2.55$ ,  $df = 3$ ,  $p = 0.47$ ; extensive grassland:  $\chi^2 = 1.34$ ,  $df = 3$ ,  $p = 0.72$ ; land use diversity:  $\chi^2 = 1.78$ ,  $df = 3$ ,  $p = 0.62$ ). Hence, effects of crop-use types were independent of the surrounding land use cover. For land cover analysis we used data of an area-wide classification of habitat complexes of the Biosphere Reserve Swabian Alb (for details see Schlager *et al.*, 2013). Aerial photographs, official digital thematic maps (ATKIS DTK 50), as well as official biotope mapping data of Baden-Württemberg (Landesamt für Umwelt Baden-Württemberg (LUBW), URL: <http://udo.lubw.baden-wuerttemberg.de/public/>, accessed 08.02.2019) were used for study sites outside of the biosphere reserve Swabian Alb.

Further, we estimated percent flower cover in 500m radius around each nest box location by estimating flower cover area for each land use patch (e.g. 10% flower cover of an arable field of 10,000 m<sup>2</sup> = 1000m<sup>2</sup> flower cover), calculated the sum and divided it with the total area (785398m<sup>2</sup>). We

conducted two survey rounds for estimating flower cover (beginning and end of July 2018) and used the arithmetic mean of both rounds for further analysis. Percent flower cover in 500m was low ( $3.8 \pm 0.4$  %) with significant differences between crop-use types (conventional winter wheat:  $4.1 \pm 1.0$  %; conventional flowering field:  $5.0 \pm 0.4$  %; organic winter spelt:  $2.9 \pm 0.7$  %; organic lentil mixed-crop:  $2.7 \pm 0.4$  %;  $\chi^2 = 22.7$ ,  $df = 3$ ,  $p < 0.001$ ). Hence, these two explanatory factors (flower cover in 500m and crop-use type) were not independent from each other, therefore we analysed them with separate statistical models.

#### 4.3.5 Statistical analysis

From the total amount of 48 bumblebee colonies eleven had to be excluded from data analysis, because they were either damaged by animals or there was no additional weight gain (= colony development) after the sugar syrup was taken out at the end of the first week. Overall a total of 37 colonies were used for data analysis, with ten colonies of six study landscapes located at conventional winter wheat fields, eleven colonies of six landscapes at conventional flowering fields, nine colonies of five landscapes at organic winter spelt fields and seven colonies of four landscapes at organic lentil mixed-crop fields.

We calculated the maximum colony weight gain by the difference between the initial weight (before opening the nest box entrance in the field) and the highest measured weight during the field experiment following Hass *et al.* (2019). For analysing foraging activity, we used the arithmetic mean of the two observation rounds. The amount of entering and leaving bumblebee individuals was significantly positive correlated (Pearson's  $r$  correlation index.:  $r_{35} = 0.94$ ,  $p < 0.001$ ), as well as the total amount of individuals (entering + leaving) with entering ( $r_{35} = 0.98$ ,  $p < 0.001$ ) and leaving ( $r_{35} = 0.98$ ,  $p < 0.001$ ) individuals. Hence, we used the total amount of individuals (entering + leaving the nest box) as proxy for foraging activity. We used the sum of all intact, closed and open queen brood cells per colony for measuring reproduction success. For testing effects on body size, we used the arithmetic mean of 15 inter-tegular distances of workers.

We applied linear mixed-effects models using the 'lme4' package (Bates *et al.*, 2015) of the R software (R Development Core Team, 2017) to test for differences in farming practice- and vegetation characteristics (separate model for each response variable), taking into account the cross-nested study design. We treated the factors 'study site', 'farmer' and 'crop type' (cereal vs. flowering crop) as nested random factors and 'crop-use type' as well as 'flower cover in 500 m' as fixed factors in the models (separate models for both fixed factors). We tested for normal distribution of model residuals and heteroscedasticity by visual model diagnostics plotting normal quantile-quantile plots as well as model residuals against fitted values. We applied the same model approach for testing differences between crop-use types regarding the six land cover types and land use diversity (Shannon index) in 500 m radius around each nest box location. Shannon index was calculated applying the 'vegan' package in R (Oksanen *et al.*, 2015).

To test for differences in colony development (maximum weight gain, foraging activity, body size, queen brood cells) or pollen diversity between crop-use types, we also applied linear mixed-effects models with the above mentioned random structure but including the factor ‘pair’ (two colonies per study field) as additional random factor in the model using the following R-syntax:

“lmer(y ~ crop-use type+ (1|Study site /Farmer) + (1|Study site/Crop type) + (1|Study site/Pair))”.

The same R-syntax was used for flower cover in 500 m as explanatory variable to test its effect on pollen diversity, but without the random factor ‘pair’ as pollen pots of both colonies were pooled per nest box location for pollen analysis.

#### 4.4 Results

The 37 *B. terrestris* colonies included in the analysis developed well with a maximum weight gain of  $216.3 \pm 17.1$  g during the five weeks of exposure. There was no significant difference in maximum weight gain of bumblebee colonies between the four crop-use types, although colonies exposed at organic winter spelt fields had slightly higher weight gain (Table 4.1, Fig. 4.2a). Foraging activity of worker bumblebees was higher at organic winter spelt fields compared to all other crop-use types (Fig. 4.2b). Colonies exposed at organic winter spelt fields produced largest workers with significant larger body sizes than those found in colonies at conventional winter wheat fields (Fig. 4.2c). Workers at conventional flowering fields and organic lentil mixed-crop had also larger body sizes compared to conventional winter wheat fields, but these differences were only marginal significant. The total number of queen brood cells did not differ between crop-use types (Fig. 4.2d). Finally, percent flower cover in 500 m around colonies did not significantly affect colony weight gain, foraging activity, body size of workers, or the total number of queen brood cells (Table 4.1).

**Table 4.1.** Effects of crop-use type (winter wheat (WW) vs. flowering field (FF) vs. winter spelt (WS) vs. lentil-mixed-crop (LMC)) and percental flower cover in 500m radius on maximum weight gain, foraging activity (entering+leaving individuals), body size of workers (inter-tegular width), the total amount of queen brood cells and pollen diversity (Shannon index) of pollen stores of *Bombus terrestris* colonies. Results were calculated by separate linear mixed-effects models for the two explanatory variables. Parameter estimates with standard error (SE) and t- values are given. Bold values indicate significant effect at  $P < 0.05$ .

Response <sup>a</sup>	Explanatory <sup>b</sup>	Estimate <sup>c</sup>	± SE	t- value
<b>Maximum weight gain</b>	Crop-use type (FF/WW)	-10.71	39.11	-0.274
	Crop-use type (WS/WW)	40.01	41.22	0.971
	Crop-use type (LMC/WW)	-17.81	44.61	-0.399
	Crop-use type (WS/FF)	50.71	40.87	1.241
	Crop-use type (LMC/FF)	-7.11	44.60	-0.159
	Crop-use type (WS/LMC)	57.82	45.70	1.265
	Flower cover in 500 m	-67.97	381.30	-0.178

Response <sup>a</sup>	Explanatory <sup>b</sup>	Estimate <sup>c</sup>	± SE	t- value
<b>Foraging activity <sup>d</sup></b>	Crop-use type (FF/WW)	4.37	2.80	1.559
	Crop-use type (WS/WW)	19.08	2.95	<b>6.461</b>
	Crop-use type (LMC/WW)	-0.50	3.20	-0.157
	Crop-use type (WS/FF)	14.72	2.94	<b>5.013</b>
	Crop-use type (LMC/FF)	-4.87	3.21	-1.518
	Crop-use type (WS/LMC)	19.58	3.28	<b>5.976</b>
	Flower cover in 500 m	-38.75	54.16	-0.715
<b>Body size</b>	Crop-use type (FF/WW)	2.08	1.07	1.933
	Crop-use type (WS/WW)	4.78	1.41	<b>3.399</b>
	Crop-use type (LMC/WW)	1.69	1.49	1.132
	Crop-use type (WS/FF)	2.70	1.39	1.948
	Crop-use type (LMC/FF)	0.022	1.47	-0.263
	Crop-use type (WS/LMC)	3.09	1.24	2.491
	Flower cover in 500 m	-12.23	13.64	-0.897
<b>Queen brood cells <sup>e</sup></b>	Crop-use type (FF/WW)	0.95	0.99	0.956
	Crop-use type (WS/WW)	0.54	1.05	0.515
	Crop-use type (LMC/WW)	0.95	1.13	0.833
	Crop-use type (WS/FF)	-0.41	1.04	-0.393
	Crop-use type (LMC/FF)	-0.01	1.13	-0.005
	Crop-use type (WS/LMC)	-0.40	1.16	-0.348
	Flower cover in 500 m	3.24	9.24	0.350
<b>Pollen diversity</b>	Crop-use type (FF/WW)	-0.12	0.20	-0.604
	Crop-use type (WS/WW)	0.13	0.17	0.750
	Crop-use type (LMC/WW)	-0.05	0.23	-0.206
	Crop-use type (WS/FF)	0.25	0.21	1.186
	Crop-use type (LMC/FF)	0.08	0.19	0.401
	Crop-use type (WS/LMC)	0.18	0.23	0.756
	Flower cover in 500 m	-3.36	1.59	<b>-2.118</b>

<sup>a</sup> All models were fitted with normal distribution.

<sup>b</sup> For flower cover in 500 m arcsine transformed values used for model calculation.

<sup>c</sup> Negative estimates indicate lower number e.g. lower maximum weight gain in flowering fields vs. winter wheat

<sup>d</sup> Simplified random structure (without farmer and crop type) used to avoid overfitting of the model.

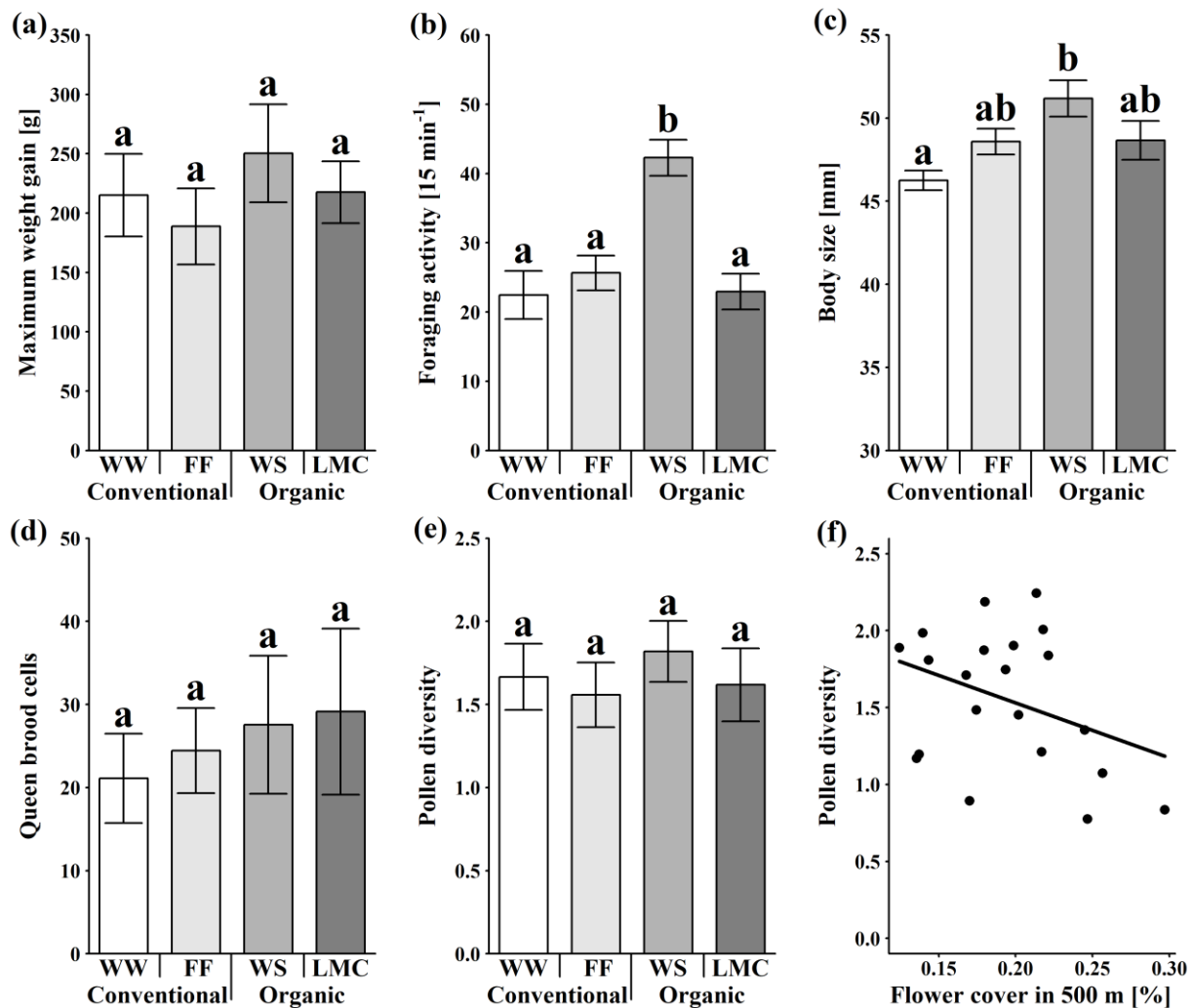
<sup>e</sup> Square root transformed values used for model calculation.

We identified 64 pollen morphotypes in the pollen stores of the colonies, but only 11 pollen types had a share of minimum 1 % of the total pollen amount and those pollen types accounted for 92 % of the total pollen amount (Table 4.2). *Phacelia* (*Phacelia tanacetifolia*, Benth.) was by far the most abundant pollen type accounting for 52 % of the total pollen amount, irrespectively of crop-use type (Table 4.2). Only *Centaurea cyanus* (L.) and *Medicago* pollen types did significantly differ among crop-use types, but with small percentage share. Bumblebee colonies located at flowering fields did not have a higher amount of pollen types of plants, which were only present in flowering fields (plants sown in the seed mixture but not growing wild in the study area, such as *P. tanacetifolia*). Pollen diversity did also not differ significantly between crop-use types (Table 4.1, Fig. 4.2e), but was negatively related to the amount of flower cover in 500 m around colonies (Table 4.1, Fig. 4.2f).

**Table 4.2.** Most abundant pollen types ( $\geq 1\%$  of the total amount of pollen grains) found in *Bombus terrestris* colonies placed at four different crop-use types (conventional winter wheat (WW; n=6), conventional flowering field (FF; n=6), organic winter spelt (WS; n=5), organic lentil mixed-crop (LMC; n=4)). Bold pollen types indicate plant species sown in the seed mixture for establishing flowering fields. Percental pollen amount (mean  $\pm$  SE) per crop-use type are given as well as results (F-value of ANOVA table) of linear mixed-effects models to test for significant differences between them. Bold F-values indicate significant effect at  $P < 0.05$ .

Pollen type	Total amount [%]	WW [%]	FF [%]	WS [%]	LMC [%]	F-value <sup>a</sup>
<b><i>Phacelia tanacetifolia</i></b>	51.9	49.5 $\pm$ 7.7	55.2 $\pm$ 9.8	47.2 $\pm$ 9.9	61.4 $\pm$ 6.8	1.9
<i>Trifolium pratense</i> group	7.4	11.3 $\pm$ 4.3	6.9 $\pm$ 4.4	4.2 $\pm$ 0.9	5.6 $\pm$ 1.6	1
<i>Balsaminaceae</i>	6.6	2.3 $\pm$ 1.2	6.8 $\pm$ 6.8	14.9 $\pm$ 7.2	1.4 $\pm$ 1.3	1.9
<i>Plantago</i>	6.3	7.4 $\pm$ 5.6	6.2 $\pm$ 4.3	6.9 $\pm$ 3.9	0.8 $\pm$ 0.3	0.9
<b><i>Borago officinalis</i></b>	4.7	4.1 $\pm$ 1.9	5.7 $\pm$ 2.1	2.7 $\pm$ 1.4	6.9 $\pm$ 2.9	1.9
<b><i>Centaurea cyanus</i></b>	3.8	2.6 $\pm$ 1	3.9 $\pm$ 0.8	3.4 $\pm$ 1.4	6.2 $\pm$ 1.8	<b>2.9</b>
<i>Medicago</i> type	2.9	4.8 $\pm$ 3.6	1.4 $\pm$ 1.1	2.3 $\pm$ 1.2	3.2 $\pm$ 1.5	<b>2.9</b>
<i>Trifolium repens</i> group	2.3	3.1 $\pm$ 1.6	1.5 $\pm$ 0.5	2.3 $\pm$ 0.7	1.8 $\pm$ 0.6	0.3
<i>Papaver</i>	2.1	1.5 $\pm$ 0.9	2 $\pm$ 1.5	3.2 $\pm$ 2.3	1.2 $\pm$ 1	0.2
<i>Anthriscus</i> group	1.6	2.3 $\pm$ 1.9	0.7 $\pm$ 0.2	1.6 $\pm$ 1.4	1.5 $\pm$ 0.3	0.3
<b><i>Helianthus annuus</i></b>	1.4	0.9 $\pm$ 0.3	0.8 $\pm$ 0.3	2.3 $\pm$ 0.6	2.4 $\pm$ 0.8	2.1
<i>Brassica</i> group	1.4	2.6 $\pm$ 2.6	0.9 $\pm$ 0.8	0.4 $\pm$ 0.3	1.9 $\pm$ 1.9	1

<sup>a</sup> Arcsine transformed values used for model calculation.



**Fig.4.2.** Differences (mean  $\pm$  SE) in (a) maximum weight gain, (b) foraging activity (number of individuals entering and leaving the colony), (c) body size of workers (inter-tegular width), (d) total amount of queen brood cells, and (e) pollen diversity (Shannon index) of pollen stores between *Bombus terrestris* colonies placed at arable fields of four crop-use type (winter wheat (WW), flowering field (FF), winter spelt (WD), lentil-mixed-crop (LMC)). Further effects of percental flower cover in 500 m radius (arcsine transformed values) on pollen diversity (f) with a regression line based on a linear model. Different letters indicate significant differences between crop-use types at  $P < 0.05$ .

## 4.5 Discussion

This study revealed that crop-use type in direct vicinity to the nest affected the individual fitness of workers by a larger body size and higher foraging activity of workers at organic winter spelt fields, but colony growth and reproduction success of *B. terrestris* colonies were neither affected by the crop-use type nor by the amount of flower cover in the surrounding landscape. Furthermore, abundance distribution and diversity of pollen stores did not differ between crop-use types and was dominated by phacelia in all crop-use types, although this plant species was only present in conventional flowering fields. These findings suggest that the overall quality and quantity of the food resource intake (pollen,

nectar) was similar between crop-use types, but local farming practices in direct vicinity to the nest can still be important drivers affecting the individual fitness of worker bumblebees indicated by an altered foraging activity and body size.

Contrary to hypothesis (1), we found that colonies directly located at conventional flowering fields did not have enhanced colony development, although flower resource supply in conventional flowering fields was much higher compared to all other crop-use types (Table S4.3). Workers of *B. terrestris* can have large foraging ranges, if there are highly rewarding- and easy to handle flowers such as phacelia (Walther-Hellwig, 2000; Westphal *et al.*, 2006), which can act as pollinator magnets attracting generalist bumblebees from the surrounding landscape (Gilpin *et al.*, 2019). For instance, Walther-Hellwig (2000) reported that high percentage of *B. terrestris* workers were foraging in a distance between 500-1750 m from the colony nest in response to phacelia fields, but Wolf & Moritz (2008) found mean foraging distances of  $267 \pm 180$  m (max. 800 m), if rewarding forage resources were available in close vicinity to the nest. As there were conventional flowering fields within the foraging distance of *B. terrestris* (mean distance to the next flowering field was  $458 \pm 90$  m) for all colonies in the study areas, *B. terrestris* workers most likely conducted foraging flights into the next conventional flowering field in the surrounding landscape, irrespectively of crop-use type. This large-scale attraction to bumblebee colonies in the surrounding landscape might have weakened the local effects of crop-use types. Nevertheless, these colonies had much shorter flight distances and reduced searching time for this rewarding flower resource, but our findings reveal that the direct spatial vicinity did not result in increased colony growth, reproduction success or individual fitness of workers, which was also found by other studies for colony growth (Osborne *et al.*, 2008) and foraging activity (Dramstad *et al.*, 2003) of *B. terrestris*. However, the high amount of phacelia pollen throughout all colonies suggests that conventional flowering fields are still an important food resource for all colonies located within the usual foraging flight distance of this species.

Higher cover and diversity of flowering forbs in both organically managed crop-use types compared to conventional winter wheat crops (Table S4.3) did not increase colony growth and reproduction success as predicted in hypothesis (2), but foraging activity and body size of workers was higher for colonies next to organic winter spelt fields. The positive effects of organic winter spelt might be due to nutritional requirements of bumblebees for a diverse- and nutritional balanced diet, which can be achieved by collecting pollen and nectar from a high diversity of plant species (Vaudo *et al.*, 2015). Such poly-floral food resources were shown to provide healthier diets to bumblebee larvae and adults compared to mono-floral food resources (Tasei & Aupinel, 2008; Moerman *et al.*, 2017). To obtain an optimal nutrition, bumblebees are able to regulate their nutrient intake by selectively collecting pollen and nectar from specific plant species to achieve a nutritional balance (Behmer, 2009; Vaudo *et al.*, 2015). Although conventional flowering fields did provide a large quantity of flower resources, worker bumblebees mainly collected phacelia, resulting in a low diversity of actually collected pollen types from the sown flowering mixture (only four of 15-18 seed mixture species were recorded in pollen



stores). Warzecha *et al.* (2018) also showed that the attractiveness of such flowering mixtures for wild bees mainly depend on only few key plant species. The higher cover and species richness of wild plants within organic winter spelt fields compared to both conventionally managed crop-use types, possibly made it easier to achieve a diverse diet for colonies there, due to shorter flight distances to diverse wild plant resources. Hence, the physical costs for individual workers (i.e. energy costs for distance and duration of foraging trips) to provide a nutritional balanced resource supply to their colony, might be lower for those colonies, which were close to organic winter spelt fields, resulting in higher individual fitness of their workers.

Furthermore, we found no evidence that organic lentil mixed-crops could improve colony development compared to organic winter spelt (hypothesis 3). Other studies report positive effects of flowering legumes to enhance abundance and diversity of short- and long-tongued bumblebee species (Wood *et al.*, 2013), but our findings might be biased by the study time in the late flowering season (July 2018) during a considerable warmer and dryer summer than usual in the study area. Warmer temperatures might have caused earlier development, and increased densities of the lentil crop, which can increase wild plant suppression (Wang *et al.*, 2012) and led to similar wild plant cover and richness as found in winter spelt crops (Table S4.3). The access for bumblebees to wild plant flowers between the crop plants might have been better in winter spelt crops, because the lentil mixed-crop was characterised by a finely branched and denser vegetation structure in the late phase of the crop plant development. However, future studies are needed to test if our findings are generally applicable or if lentil mixed-crops might have more pronounced effects for bumblebee colonies in earlier stages of their vegetation development.

Last, in contrast to our expectations increased flower cover in the surrounding landscape did not influence colony performances. This finding was in accordance with the results of Hass *et al.* (2019) for OSR, who also found no effects of increased OSR blooming on the landscape scale on colony growth of *B. terrestris*, but in contrast, we even found a negative relationship between landscape-wide flower cover and the collected pollen diversity. During the study time in the late flowering season, landscape-wide flower cover differences were mainly driven by the amount and size of flowering fields, because the flowering period of other mass-flowering crops (mainly OSR in the study area) already ended and was significantly reduced in other habitats (e.g. semi-natural habitats such as grassland or hedge rows). Therefore, this negative relation might be explained by an increased attraction of flowering fields to bumblebees, if higher cover of flowering fields were present in the surrounding landscape (Marja *et al.*, 2018). Due to the high attraction to flowering fields, bumblebees might have less strongly exploited other wild plants (as shown by Holzschuh *et al.*, 2011 for OSR), as they might have more strongly focused on single, highly rewarding and easily to handle flowers like phacelia (Westphal *et al.*, 2006), which in turn could explain the negative relation with pollen diversity.

This study suggests that both the establishment of conventional flowering fields as well as organically farmed winter cereals such as winter spelt fields, can positively impact colonies of highly mobile- and generalist bumblebee species such as *B. terrestris* through different effects, if both crop-use types are established within the foraging flight distance of the species (minimum 500 m). Flowering fields were the most abundant pollen source for all colonies in the surrounding landscape due to the presence of the highly attractive phacelia plant, whereas direct vicinity of organic winter spelt fields positively affected individual fitness of workers indicated by higher foraging activity and larger body size. The promotion of the individual fitness of workers within a colony might increase its pollination performance for insect-pollinated crop- and wild plants as well as its resilience in response to environmental changes such as land use-, or climate change.

We conclude that the establishment of non-productive flowering fields on arable land can be an appropriate measure to support generalist bumblebee populations in agricultural landscape, where the overall amount of flowering resources is the limiting factor. But to establish additional flowering fields in landscapes with already existing flowering fields or other mass-flowering crops might be of little conservation value. Instead, in landscapes with sufficient quantity of flower resources, bumblebee populations could be more efficiently supported by increasing the amount of less intensively farmed arable land with high wild plant diversity such as organically farmed winter cereals, which even cause less compensation costs for farmers compared to non-productive measures such as flowering fields. Hence, conservation- and agricultural authorities should carefully take into account the landscape-wide flower resource offer, to decide if non-productive flowering fields or production-integrated measures are more efficient to support bumblebee populations and thereby pollination services in arable land dominated landscapes.

#### 4.6 Acknowledgements

We thank the farmers for participation and Judith Engelke and Rosa Witty for conducting the plant survey. Data collection was funded by the Stiftung Naturschutzfonds Baden-Württemberg (73-8831.21/54691-1703GL). PB was supported by the Economic Development and Innovation Operational Programme of Hungary (GINOP-2.3.2-15-2016-00019).

#### 4.7 References

- Adhikari, S., Burkle, L.A., O'Neill, K.M., Weaver, D.K. & Menalled, F.D. (2019) Dryland organic farming increases floral resources and bee colony success in highly simplified agricultural landscapes. *Agriculture, Ecosystems & Environment*, 270-271, 9–18. Doi: 10.1016/j.agee.2018.10.010.
- Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C.F., Mußhoff, O., Császár, P., Fusaro, S., Gayer, C., Happe, A.-K., Kurucz, K., Molnár, D., Rösch, V., Wietzke, A. & Tschamtké, T. (2017)

- The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. *Nature Ecology & Evolution*, 1 (9), 1279–1284. Doi: 10.1038/s41559-017-0272-x.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. Doi: 10.18637/jss.v067.i01.
- Behmer, S.T. (2009) Insect herbivore nutrient regulation. *Annual Review of Entomology*, 54, 165–187. Doi: 10.1146/annurev.ento.54.110807.090537.
- Bukovinszky, T., Verheijen, J., Zwerver, S., Klop, E., Biesmeijer, J.C., Wäckers, F.L., Prins, H.H.T. & Kleijn, D. (2017) Exploring the relationships between landscape complexity, wild bee species richness and reproduction, and pollination services along a complexity gradient in the Netherlands. *Biological Conservation*, 214, 312–319. Doi: 10.1016/j.biocon.2017.08.027.
- Carrié, R., Ekroos, J. & Smith, H.G. (2018) Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies. *Biological Conservation*, 227, 48–55. Doi: 10.1016/j.biocon.2018.08.022.
- Carvell, C., Bourke, A.F.G., Osborne, J.L. & Heard, M.S. (2015) Effects of an agri-environment scheme on bumblebee reproduction at local and landscape scales. *Basic and Applied Ecology*, 16 (6), 519–530. Doi: 10.1016/j.baae.2015.05.006.
- Chapman, R.E., Wang, J. & Bourke, A.F.G. (2003) Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. *Molecular Ecology*, 12 (10), 2801–2808. Doi: 10.1046/j.1365-294X.2003.01957.x.
- Dietzel, S., Sauter M., Moosner, C., Fischer, C. & Kollmann, J. (2019) Blühstreifen und Blühflächen in der landwirtschaftlichen Praxis – eine naturschutzfachliche Evaluation. *ANLiegen Natur*, 41 (1), online preview, 14 p., Laufen, Germany.
- Dramstad, W.E., Fry, G.L.A. & Schaffer, M.J. (2003) Bumblebee foraging—is closer really better? *Agriculture, Ecosystems & Environment*, 95 (1), 349–357. Doi: 10.1016/S0167-8809(02)00043-9.
- Fox, J., Weisberg, S., Bates, D. & Fox, M. (2012) Package “car”. R package version 2.1-4. <<https://CRAN.R-project.org/package=car>> 5 June 2018.
- Fritsch, F. (2012) Nährstoffgehalte in Düngemitteln und im Erntegut: für die Düngeplanung; für Nährstoffvergleiche. Staatliche Pflanzenberatung Rheinlald-Pfalz, Germany.
- Fussell, M. & Corbet, S.A. (1992) The nesting places of some British bumble bees. *Journal of Apicultural Research*, 31 (1), 32–41. Doi: 10.1080/00218839.1992.11101258.
- Gayer, C., Lövei, G.L., Magura, T., Dieterich, M. & Batáry, P. (2019) Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats. *Agriculture, Ecosystems & Environment*, 284, 106579. Doi: 10.1016/j.agee.2019.106579.
- Gilpin, A.-M., Denham, A.J. & Ayre, D.J. (2019) Are there magnet plants in Australian ecosystems: Pollinator visits to neighbouring plants are not affected by proximity to mass flowering plants. *Basic and Applied Ecology*, 35, 34–44. Doi: 10.1016/j.baae.2018.12.003.
- Goulson, D. (2003) Bumblebees. Behaviour and Ecology. Oxford University Press, New York, US.

- Goulson, D., Hughes, W., Derwent, L. & Stout, J. (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia*, 130 (2), 267–273. Doi: 10.1007/s004420100803.
- Goulson, D., Lye, G.C. & Darvill, B. (2008) Decline and conservation of bumble bees. *Annual Review of Entomology*, 53, 191–208. Doi: 10.1146/annurev.ento.53.103106.093454.
- Haaland, C., Naisbit, R.E. & Bersier, L.-F. (2011) Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, 4 (1), 60–80. Doi: 10.1111/j.1752-4598.2010.00098.x.
- Happe, A.-K., Riesch, F., Rösch, V., Gallé, R., Tschardtke, T. & Batáry, P. (2018) Small-scale agricultural landscapes and organic management support wild bee communities of cereal field boundaries. *Agriculture, Ecosystems & Environment*, 254, 92–98. Doi: 10.1016/j.agee.2017.11.019.
- Hass, A.L., Brachmann, L., Batáry, P., Clough, Y., Behling, H. & Tschardtke, T. (2019) Maize-dominated landscapes reduce bumblebee colony growth through pollen diversity loss. *Journal of Applied Ecology*, 56 (2), 294–304. Doi: 10.1111/1365-2664.13296.
- Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J.B., Wickens, V.J., Bommarco, R., Kleijn, D., Potts, S.G., Roberts, S.P.M., Smith, H.G., Vilà, M., Vujić, A. & Steffan-Dewenter, I. (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecology Letters*, 19 (10), 1228–1236. Doi: 10.1111/ele.12657.
- Holzschuh, A., Dormann, C.F., Tschardtke, T. & Steffan-Dewenter, I. (2011) Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B: Biological Sciences*, 278 (1723), 3444–3451. Doi: 10.1098/rspb.2011.0268.
- Marja, R., Viik, E., Mänd, M., Phillips, J., Klein, A.-M. & Batáry, P. (2018) Crop rotation and agri-environment schemes determine bumblebee communities via flower resources. *Journal of Applied Ecology*, 55 (4), 1714–1724. Doi: 10.1111/1365-2664.13119.
- Moerman, R., Vanderplanck, M., Fournier, D., Jacquemart, A.-L. & Michez, D. (2017) Pollen nutrients better explain bumblebee colony development than pollen diversity. *Insect Conservation and Diversity*, 10 (2), 171–179. Doi: 10.1111/icad.12213.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015) Vegan: Community ecology package. R package version 2.3-0. < <https://cran.r-project.org/web/packages/vegan> > 15 June 2019.
- Osborne, J.L., Martin, A.P., Carreck, N.L., Swain, J.L., Knight, M.E., Goulson, D., Hale, R.J. & Sanderson, R.A. (2008) Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, 77 (2), 406–415. Doi: 10.1111/j.1365-2656.2007.01333.x.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neuman, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25 (6), 345–353. Doi: 10.1016/j.tree.2010.01.007.

- Potts, S.G., Imperatriz, V.L., Ngo, H.T., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., Aizen, M.A., Cunningham, S.A., Eardley, C., Freitas, B.M., Gallai, N., Kevan, P.G., Kovács Hostyánszki, A., Kwapong, P.K., Li, J., Li, X., Martins, D.J., Nates-Parra, G., Pettis, J.S., Rader, R. & Viana, B. (2016) Summary for Policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) on pollinators, pollination and food production. Post-print hal-01946814, HAL. <<https://ideas.repec.org/p/hal/journal/hal-01946814.html>> 10 August 2019.
- R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Redhead, J.W., Dreier, S., Bourke, A.F.G., Heard, M.S., Jordan, W.C., Sumner, S., Wang, J. & Carvell, C. (2016) Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. *Ecological Applications*, 26 (3), 726–739. Doi: 10.1890/15-0546.
- Rundlöf, M., Nilsson, H. & Smith, H.G. (2008) Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation*, 141 (2), 417–426. Doi: 10.1016/j.biocon.2007.10.011.
- Rundlöf, M., Persson, A.S., Smith, H.G. & Bommarco, R. (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation*, 172, 138–145. Doi: 10.1016/j.biocon.2014.02.027.
- Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J. & Kleijn, D. (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, 52 (5), 1165–1175. Doi: 10.1111/1365-2664.12479.
- Schlager, P., Krismann, A., Wiedmann, K., Hiltcher, H., Hochschild, V., & Schmieder, K. (2013) Multisensoral, object- and GIS-based classification of grassland habitats in the Biosphere Reserve Schwäbische Alb. *Photogrammetrie - Fernerkundung - Geoinformation*, 2013, 163–172. Doi: 10.1127/1432-8364/2013/0167.
- Spiesman, B.J., Bennett, A., Isaacs, R. & Gratton, C. (2017) Bumble bee colony growth and reproduction depend on local flower dominance and natural habitat area in the surrounding landscape. *Biological Conservation*, 206, 217–223. Doi: 10.1016/j.biocon.2016.12.008.
- Stanley, D.A., Russell, A.L., Morrison, S.J., Rogers, C. & Raine, N.E. (2016) Investigating the impacts of field-realistic exposure to a neonicotinoid pesticide on bumblebee foraging, homing ability and colony growth. *Journal of Applied Ecology*, 53 (5), 1440–1449. Doi: 10.1111/1365-2664.12689.
- Tasei, J.-N. & Aupinel, P. (2008) Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae). *Apidologie*, 39 (4), 397–409. Doi: 10.1051/apido:2008017.

- The Council of the European Union (2005) Council Regulation (EC) No 1698/2005 of 20 September 2005 on Support for Rural Development by the European Agricultural Fund for Rural Development (EAFRD).
- Vaudo, A.D., Farrell, L.M., Patch, H.M., Grozinger, C.M. & Tooker, J.F. (2018) Consistent pollen nutritional intake drives bumble bee (*Bombus impatiens*) colony growth and reproduction across different habitats. *Ecology and Evolution*, 8 (11), 5765–5776. Doi: 10.1002/ece3.4115.
- Vaudo, A.D., Tooker, J.F., Grozinger, C.M. & Patch, H.M. (2015) Bee nutrition and floral resource restoration. *Current Opinion in Insect Science*, 10, 133–141. Doi: 10.1016/j.cois.2015.05.008.
- Walther-Hellwig (2000) Foraging Distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae): Sehr gut für Flugdistanz von Erdhummeln. *Journal of Insect Behavior*, 13 (2), 239–246.
- Wang, L., Gruber, S. & Claupen, W. (2012) Optimizing lentil-based mixed cropping with different companion crops and plant densities in terms of crop yield and weed control. *Organic Agriculture*, 2 (2), 79–87. Doi: 10.1007/s13165-012-0028-5.
- Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. (2018) Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. *Insect Conservation and Diversity*, 11 (1), 32–41. doi: 10.1111/icad.12264.
- Westphal, C., Steffan-Dewenter, I. & Tschardtke, T. (2006) Foraging trip duration of bumblebees in relation to landscape-wide resource availability. *Ecological Entomology*, 31 (4), 389–394. Doi: 10.1111/j.1365-2311.2006.00801.x.
- Westphal, C., Steffan-Dewenter, I. & Tschardtke, T. (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, 46 (1), 187–193. Doi: 10.1111/j.1365-2664.2008.01580.x.
- Williams, N.M., Regetz, J. & Kremen, C. (2012) Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology*, 93 (5), 1049–1058. Doi: 10.1890/11-1006.1.
- Wolf, S. & Moritz, R.F.A. (2008) Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae). *Apidologie*, 39 (4), 419–427. Doi: 10.1051/apido:2008020.
- Wood, T.J., Smith, B.M., Hughes, B., Gill, J.A. & Holland, J.M. (2013) Do legume-rich habitats provide improved farmland biodiversity resources and services in arable farmland? *Aspects of Applied Biology*, 118, 239–246.

## 4.8 Supplementary material

### Appendix A4.1. Vegetation survey.

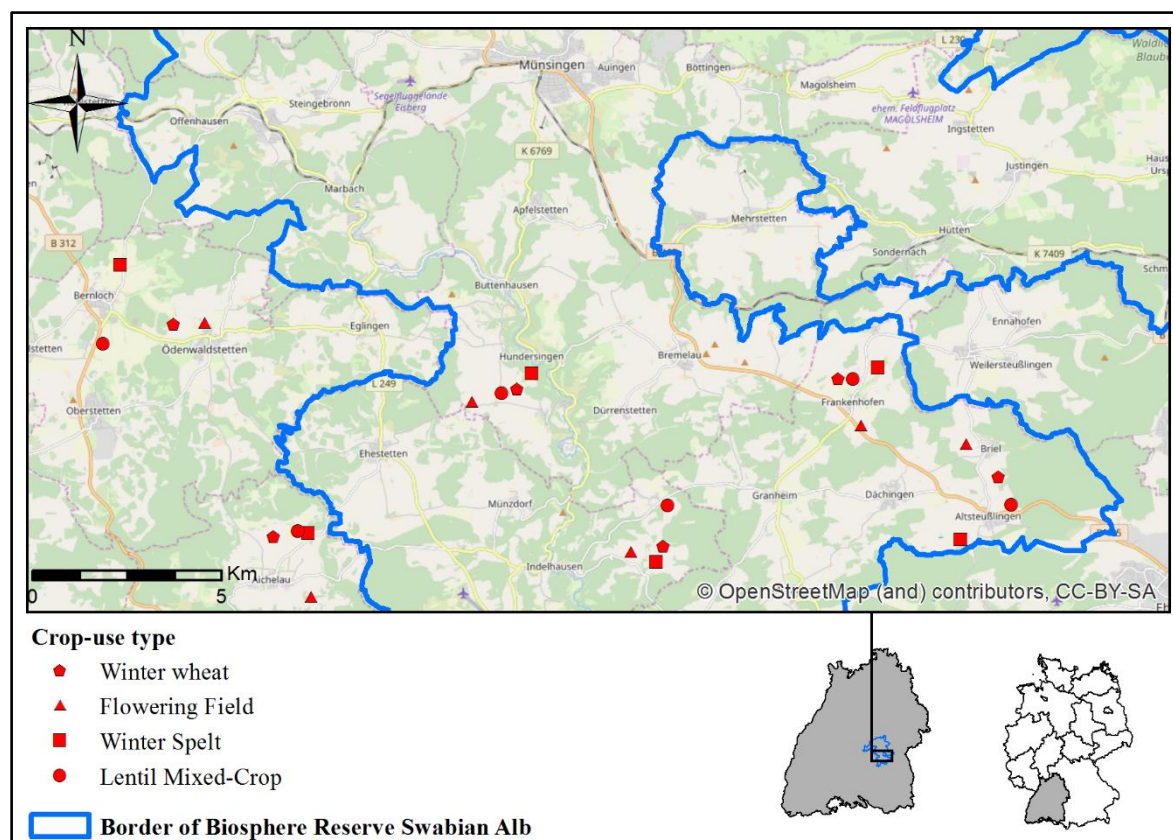
We surveyed plants at the edge and interior of study fields with five plots ( $5 \times 1\text{m}$  in size and 5m distance between them) per transect (= 10 plots per study field; 15m distance between transects). For each plot we estimated cover per wild plant species according to the Braun-Blanquet scale (Braun-Blanquet, 1932). We further recorded flower resources for each survey plot, by recording each forb species flowering at the survey time and estimating the total amount of flower units (classification according to Rundlöf *et al.* 2014)  $\times$  the mean surface area (in  $\text{cm}^2$ ) of the flower unit, following Scherper *et al.* (2015). We surveyed each plot two times (early July, late July) in 2018. We transformed plant cover estimates according to the Braun-Blanquet scale (Braun-Blanquet, 1932) into percent cover values according to the 160 percent scale of van der Maarel (2007) for data analysis and used the arithmetic mean of the two survey rounds for further analysis. We also used the arithmetic mean of all plots per study field for plant cover and flower cover data analysis. In the case of two study fields (one conventional winter wheat, one organic winter cereal) plant survey was not conducted at the same study field of bumblebee nest box locations, but on a separate field of the same farmer and crop-use type to avoid direct neighbourhood with flowering fields. In one case (conventional winter wheat) bumblebee nest boxes were placed at a separate field of a different farmer. Here we excluded the plant survey data for the analysis.

Braun-Blanquet, J., (1932) Plant sociology. The study of plant communities. McGraw-Hill, New-York, US.

Rundlöf, M., Persson, A.S., Smith, H.G., Bommarco, R. (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation*, 172, 138–145. Doi: 10.1016/j.biocon.2014.02.027

Scherper, J., Bommarco, R., Holzschuh, A., Potts, S. G., Riedinger, V., Roberts, S. P., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, V. J., Kleijn, D. (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, 52(5), 1165-1175. Doi: 10.1111/1365-2664.12479.

van der Maarel, E. (2007) Transformation of cover-abundance values for appropriate numerical treatment - Alternatives to the proposals by Podani. *Journal of Vegetation Science*, 18 (5), 767–770. Doi: 10.1111/j.1654-1103.2007.tb02592.x.



**Fig. S4.1.** Bumblebee nest box locations according to the crop-use type at the Biosphere Reserve Swabian Alb within the federal state Baden-Württemberg (below left) in southwest Germany (below right).

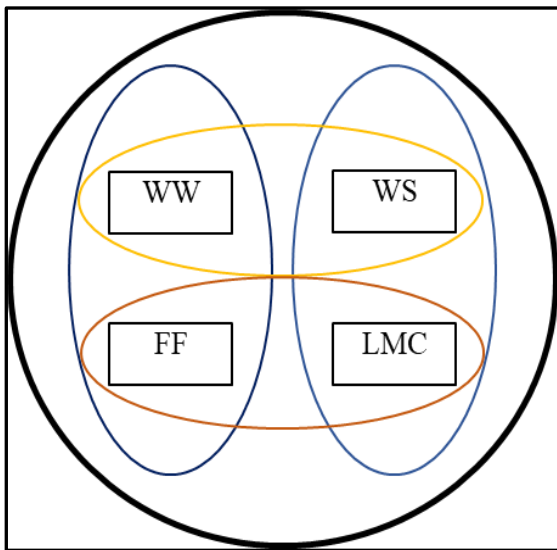
**Table S4.1.** Composition of the two types of seed mixture used for establishment of flowering fields. Percentile weighting per species in the seed mixture are given as well as their origin status (native/non-native) in the study area (Germany).

Species name	Mixture M1 [%]	Mixture M2 [%]	Status
<i>Anethum graveolens</i>	2	2	non-native
<i>Borago officinalis</i>	2	3	non-native
<i>Calendula officinalis</i>	3	6	non-native
<i>Centaurea cyanus</i>	6	6	native
<i>Coriandrum sativum</i>	3	5	non-native
<i>Fagopyrum esculentum</i>	22.5	0	non-native
<i>Foeniculum vulgare</i>	5	5	non-native
<i>Guizotia abyssinica</i>	2	7.5	non-native
<i>Helianthus annuus</i>	12	17	non-native
<i>Linum usitatissimum</i>	4	10	non-native
<i>Onobrychis viciifolia</i>	5	5	non-native
<i>Papaver rhoeas</i>	0.5	0.5	native
<i>Phacelia tanacetifolia</i>	10	12	non-native
<i>Raphanus sativus</i>	2	0	non-native
<i>Synapis alba</i>	2	0	non-native
<i>Trifolium incarnatum</i>	8	10	non-native
<i>Trifolium resupinatum</i>	5	5	non-native
<i>Vicia sativa</i>	6	6	non-native
Species $\Sigma$	18	15	





**Fig. S4.2.** Exemplary photo of a nest box location with two colonies of *Bombus terrestris* placed on a wooden palette and sheltered by a styrodur roof (© Alina Biermann).



**Fig. S4.3.** Cross-nested study design. The four crop-use types (winter wheat (WW), flowering field (FF), winter spelt (WS), lentil mixed-crop (LMC)) were spatially nested per study site (black circle) and nested by the two farmers managing the study fields (conventional farmer: dark-blue ellipse; organic farmer: light-blue ellipse) and the two crop-types (cereal crop: light-orange ellipse; flowering crop: dark-orange ellipse) within each site.

**Table S4.2.** Farming practice characteristics, achieved yield and subsidy payment of studied crop-use types in 2018 (mean  $\pm$  SE; n=23). Results (F-value of ANOVA table) of linear mixed-effects models are given to test for significant differences between crop-use types. Bold values indicate significant effect at  $P < 0.05$ .

Management	Crop-use type	Sowing date (calendar week)	Crops in rotation (number)	Fertilizer <sup>c</sup> (kg N ha <sup>-1</sup> )	Pesticide application (number)	Mechanical weeding <sup>d</sup> (number)	Yield (dt ha <sup>-1</sup> )	Subsidy by AES <sup>e</sup> (€ ha <sup>-1</sup> )
Conventional	Winter Wheat (n=5 <sup>b</sup> )	40.6 $\pm$ 0.5 (early October)	4.2 $\pm$ 0.2	185.4 $\pm$ 25.9	2.1 $\pm$ 0.5	none	75.8 $\pm$ 3.6	none
	Flowering Field (n=6)	18.2 $\pm$ 0.3 (early May)	4.0 $\pm$ 0.3	none	none	0.2 $\pm$ 0.2	none	710
Organic	Winter Spelt (n=6)	41.3 $\pm$ 0.3 (early October)	6.0 $\pm$ 0.3	33.2 $\pm$ 15.4	none	1.8 $\pm$ 0.5	34.5 $\pm$ 1.7	230
	Lentil-mixed-crop (n=6)	14.8 $\pm$ 0.3 (mid of April)	6.0 $\pm$ 0.3	10.0 $\pm$ 10.0	none	0.3 $\pm$ 0.2	15.2 $\pm$ 3.6	230
Model <sup>a</sup>	F - value	<b>1573.6</b>	<b>64.2</b>	<b>26.9</b>		<b>12.1</b>	<b>215.3</b>	

<sup>a</sup> All models were fitted with normal distribution.

<sup>b</sup> Data of one winter wheat farmer are missing.

<sup>c</sup> Square root transformed values used for model calculation.

<sup>d</sup> Only weeding between sowing and harvest counted.

<sup>e</sup> Fixed amount according to the agri-environmental scheme (AES) of the federal state Baden-Württemberg named FAKT (MLR, 2016).

**Table S4.3.** Vegetation characteristics of studied crop-use types (mean  $\pm$  SE). Results (F-values of ANOVA table) of linear mixed-effects models are given to test for significant differences. Bold values indicate significant effect at  $P < 0.05$ .

Management	Crop	Wild plant cover [%] <sup>b,c</sup>	Wild plant species richness	Plant species richness <sup>d</sup>	Flowering forb species richness	Flowering forb cover [cm <sup>2</sup> ] <sup>e</sup>
Conventional	Winter Wheat	28.2 $\pm$ 4.8	22.4 $\pm$ 3.6	22.4 $\pm$ 3.6	1.5 $\pm$ 0.5	22.3 $\pm$ 9.4
	Flowering Field	69.7 $\pm$ 19.6	28.1 $\pm$ 2.1	44.0 $\pm$ 2.0	8.9 $\pm$ 0.4	817.4 $\pm$ 106.1
Organic	Winter Spelt	74.6 $\pm$ 27.2	45.1 $\pm$ 3.2	45.1 $\pm$ 3.2	4.9 $\pm$ 0.7	81.8 $\pm$ 36.9
	Lentil Mixed-Crop	75.6 $\pm$ 11.9	44.3 $\pm$ 2.1	44.3 $\pm$ 2.1	5.1 $\pm$ 0.7	99.9 $\pm$ 29.1
Model <sup>a</sup>	F - value	2.4	<b>16.3</b>	<b>48.9</b>	<b>32.3</b>	<b>41.4</b>

<sup>a</sup> All models were fitted with normal distribution.

<sup>b</sup> Transformed Braun-Blanquet values based on 160 % scale after van der Maarel, 2007.

<sup>c</sup> Arcsine-square root transformed values used for model calculation.

<sup>d</sup> Including species of the sown seed mixture for flowering fields.

<sup>e</sup> Square-root transformed values used for model calculation.

## 5. CHAPTER

### General Discussion

#### 5.1 Overview of results

Overall, this thesis revealed that there are different and thereby complementary biodiversity effects of conventional flowering fields, organically farmed mono-crops (winter spelt) as well as flowering mixed-crops (lentil mixed-crops), as each crop-use type can promote specific components of biodiversity compared to conventional farmed crops (winter wheat). Neither the taxonomical-, nor the functional diversity, nor the population development of bumblebee colonies did solely benefit from just one specific crop-use type. Positive effects appeared to be taxon-specific as shown in chapter 2, whereas chapter 3 highlights similar effects of conventional flowering fields and organic winter spelt on carabid functional diversity. Regarding bumblebee population development different crop-use types did support different determinants of the population development. Conventional flowering fields were shown to be the main pollen source, whereas the exposure at organic winter spelt fields increased body size and foraging activity of worker bumblebees (chapter 4). Effects of conventional flowering field exceeded the positive effects of both organically farmed crop-use types only in terms of abundance and species richness of wild bees. All other considered biodiversity components did maximally reach similar effect sizes than organic crops. Growing of lentil mixed-crops in organic farming systems enhanced wild plant cover, butterflies and wild bees (chapter 2), but organic winter spelt crops can more strongly enhance carabid functional diversity by increasing the proportion of plant-feeding carabids (chapter 3) and the population development of generalist bumblebee populations (chapter 4).

The diversity of ground-dwelling arthropods was more strongly affected by positive edge effects within crop fields than by crop-use type, which could be shown for the species richness of carabids and spiders (chapter 2), but also for the trait diversity of carabid species assemblages (chapter 3). These findings point to the importance of bordering field edge habitats such as grassy field margins as well as supporting a high field edge density within arable-dominated landscapes. In contrast, over all studies we did not find any significant effect of the surrounding landscape, except small effects on the species composition of some taxa (chapter 2) and a negative correlation with the diversity of pollen collected by bumblebee colonies (chapter 4). Interaction effects of landscape complexity, crop-use type and within-field position (edge vs. interior) did not significantly affect taxonomical or functional diversity, because they were included in the analyses, but never retained among the best fitting models (chapter 2 and 3). Hence, within the scope of this thesis biodiversity responses were in general more strongly driven by local effects of crop-use type and field edges than by landscape effects or interaction effects among explanatory variables. Nevertheless, due to the different and taxon-specific effects of conventional flowering fields, organic winter spelt and lentil mixed-crops as well as field edge habitats,

the simultaneous presence of these local measures within an agricultural landscape might contribute to the promotion of regional species diversity.

## 5.2 Biodiversity effects of annual flowering fields in conventional farming

Within three studies, we found clear evidence that the establishment of annual flowering fields on former conventional farmed arable land can considerably increase wild plant and arthropod diversity in conventional farming systems. Although the considered flowering fields were only established for a short period of time (two to three months) before we studied biodiversity effects, they already supported several taxa (abundance and species richness of wild plants, butterflies and wild bees, carabid abundance; chapter 2), increased the proportion of plant-feeding carabids (chapter 3), and provided important pollen sources by offering mass-flowering resources like phacelia for generalist pollinators in the surrounding landscape (chapter 4). Nevertheless, other studies reveal that perennial flowering fields might be more effective for biodiversity conservation compared to annual ones, especially for less mobile taxa such as ground-dwelling arthropods, which are sensitive to mechanical soil disturbances (Haaland *et al.*, 2011). For instance, higher biodiversity benefits with increasing habitat age of flowering fields or strips have been shown for the diversity and evenness of beetles (Frank *et al.*, 2012), the reproduction and nutritional condition of carabids (Barone & Frank, 2003; Frank *et al.*, 2007), the abundance of spiders (Denys & Tschardt, 2002) and the abundance of bees and butterflies (Pywell *et al.*, 2007).

Furthermore, because annual flowering fields on arable land are usually ploughed in within the same- or at the beginning of the next year after establishment, the intensive farming practices in the following year might neutralize any positive effects for biodiversity in the long term. Annual flowering fields can even act as ecological trap for arthropods overwintering there and do not survive detrimental effects of ploughing during the overwintering period or even later. This was shown in annual flowering strips for carabids and spiders, which were reduced in numbers by 67% and 69% respectively (Ganser *et al.*, 2019). Thorbek & Bilde (2004) also showed that soil tillage in arable crops caused increased mortality and emigration of ground-dwelling arthropods, especially in case of spiders. As all studied crop-use types were annually ploughed, these findings might explain why we found no differences for the spider- and little differences for the carabid fauna and in general similar species communities between crop-use types (chapter 2). Even for flower-visitors, for which we found strong increase in abundance and species richness on flowering fields, the studied type of annual flowering fields can be considered as important food habitat, but represent a poor overwintering or reproduction habitat, as tillage is allowed in late autumn within the year of establishment (21<sup>st</sup> of November, or 1<sup>st</sup> of September if a winter crop follows in crop rotation). Because the negative effects of annual soil tillage also apply for the studied organically farmed crops, effects of perennial flowering fields probably would have been exceeded the effects of organic farming more strongly, although we did not test for it within the scope of this thesis.

Altogether it can be assumed that the local biodiversity effects of flowering fields would have been more pronounced, if they were established over more than one year, even though some species groups such as arable wild plants or agrobiont species adapted to regular farming practices might benefit more strongly from annually established flowering fields (Tscharntke *et al.*, 2011). Because species community composition can change during succession of older flowering fields (Frank & Künzle, 2006), the implementation of various flowering fields of different age within the agricultural landscape matrix would most likely maximize the biodiversity benefit of this conservation measure. However, further studies are needed to compare biodiversity effect of perennial flowering fields compared to organically farmed crops (but see Mader *et al.*, 2017). Future studies should also address landscape-wide effects of establishing several flowering fields of different age compared to flowering fields of the same age within a landscape.

Beside habitat age the effectiveness of sown flowering fields for biodiversity conservation might strongly depend on the type of sown seed mixture, as it determines the flower abundance, -diversity and vegetation structure. According to Haaland *et al.*, (2011), there are mainly three different kind of seed mixtures. There are seed mixtures containing native flowering forbs and grasses, mixtures with native flowering forbs without grass seeds and mixtures particularly rich in non-native but nectar and pollen rich plant species (e.g. agricultural cultivars of legumes) (Isaacs *et al.*, 2009) which are attractive to generalist flower-visitors (Haaland *et al.*, 2011; Woodcock *et al.*, 2014). In this thesis, we studied a pollen and nectar rich seed mixture which consisted mainly of non-native flowering forbs without grasses. In accordance to the literature, our results indicate that this mixture was highly attractive for generalist butterflies and wild bees, in particular bumblebees (chapter 2, 4). But many species of the native fauna, especially more specialised and rare species, depend on native plant species as larval and adult food plants (e.g. due to adaptations to secondary plant metabolites of host plants) as well as on the provision of resources and habitats during all stages of their life history (Isaacs *et al.*, 2009; Haaland *et al.*, 2011; Tscharntke *et al.*, 2011; Jain *et al.*, 2016). For that reasons a regional seed mixture of native plants is recommended to be of higher biodiversity conservation value than sowing non-native plants (Tscharntke *et al.*, 2011). To increase the share of native flowering plants within the seed mixture of the studied flowering fields would therefore most likely increase the revealed positive effects on flower-visiting and other arthropod taxa. As this would probably more strongly address rare than common species, it would mainly affect total species richness rather than total abundance. Abundance responses might be more strongly affected by the presence of single highly rewarding plant species, such as phacelia in case of generalist bee species, than by the origin of the species (native or non-native). Additional research is still needed to test which type of seed mixture and management practice is most appropriate to target the support of rare species more strongly than the commonly applied type of non-native, but flower-rich flowering fields which mainly favour common species (Haaland *et al.*, 2011).

### 5.3 Biodiversity effects of lentil mixed-crops in organic farming

This thesis could show that the cultivation of lentil mixed-crops is an appropriate measure to further enhance biodiversity benefits of organic farming by supporting in particular arable wild plant cover, wild bees and butterflies. These findings most likely result from the slow initial growing of the crop plants allowing establishment of arable wild plants and the higher amount of flowering resources (at least if intercropped with a flowering companion crop such as camelina) compared to organic winter cereal crops. Other biodiversity components like the body size and foraging activity of worker bumblebees (chapter 4) as well as the functional diversity of carabid assemblages (chapter 3) benefited more strongly from organic winter spelt than organic lentil mixed-crops. Insertion of lentil mixed-crops into the crop rotation can therefore contribute to the overall support of biodiversity within an organically managed farm, but in general cannot be considered as more beneficial for biodiversity than other organically farmed crop-use types based on our findings.

The flowers of the lentil plant are small, inconspicuously (about 5 mm) and mostly self-pollinated (only 5 % allogamy) (Horneburg, 2006). The flower resources supply of lentil mixed-crops might be more strongly driven by their increased cover of flowering arable weeds (e.g. *Cirsium arvense* or *Convolvulus arvensis*) than by the lentil plant itself. Additionally, the mass-flowering companion crop camelina, which was used as one of three mixed-crop companions in the study area (5 of 17 studied lentil mixed-crop fields had camelina as companion crop) was shown to be an attractive flower resource for flower-visiting insects (Groeneveld & Klein, 2014). Therefore, the magnitude of effects regarding flower-visiting insects might be smaller for lentil mixed-crops, if they do not include attractive flowering companion crops such as camelina. Further studies are needed in order to assess if the biodiversity effects of organic lentil mixed-crops differ between different companion crops. As we already compared a high amount of different levels and were mainly interested in the overall effect of lentil mixed-crops irrespectively of the specific companion crop, it was beyond the scope of this thesis to include possible companion crop effects.

Globally, lentil cropping can markedly differ in its farming characteristics such as the lentil cultivar and companion crop, the seeding rate, sowing depth or row spacing. Lentils are also grown as mono-crops (Gruber *et al.*, 2012; Wang *et al.*, 2012). Due to the variation between different lentil cropping methods and the expectable differences between the study area of this thesis and other biogeographical regions (the main producers of lentils are India, Turkey and Canada, in Europe the main production areas are in France and Spain (Erskine *et al.*, 2009)), the findings of this thesis mainly depict the effects of the specific type of lentil cropping in the study area. Due to the current lack of other biodiversity studies, there is still the need for a plethora of additional studies focusing on biodiversity responses of lentil cropping under different farming practices and in different biogeographical regions to be able to draw general conclusions. Future studies should also compare the relative biodiversity effects of lentil mixed-crops compared to other commonly grown legume crops such as faba bean (*Vicia faba*)

or field pea (*Pisum sativum*). The currently limited distribution of other legume crops in the study area did not allow for a direct comparison with other flowering legumes within the scope of this thesis.

Moreover, as the effects of management (organic vs. conventional farming) and crop type were not disentangled according to the applied study design, it is not possible to assess the effects of conventional farmed lentil mono- or mixed-crops. The main ecological contrast of the studied lentil mixed-crops compared to mono-crops was their increased vegetation heterogeneity and the higher amount of arable wild plants. Because the application of herbicides in conventional farming systems have detrimental effects on these vegetation characteristics, similar biodiversity effects of conventional farmed lentil mono- or mixed-crops cannot be expected, but future studies should specifically address this question. However only 1.8 % of the European arable land is currently cropped with grain legumes (Mahmood *et al.*, 2018) and about 69% of the protein-rich feed material is imported to the EU (de Visser *et al.*, 2014). Hence, increasing the amount of protein-rich and nitrogen fixing legumes such as lentils within the crop rotation could still be an ecologically valuable improvement towards a more sustainable agriculture (e.g. reducing greenhouse gas emissions), despite possible weak effects for biodiversity conservation. Currently, the studied organic lentil mixed-crops are not specifically supported under the AES regime in the study region. If further studies will confirm their positive effects for biodiversity conservation, it should be taken into account as valuable agri-environmental measure for organic farmers in future funding periods.

#### **5.4 Comparison with similar studies**

Currently there are only few studies which simultaneously compared biodiversity effects between flowering fields and organically managed crops directly. An exception is Mader *et al.*, (2017) regarding carabid and spider responses as well as Mader *et al.*, (2018) for the trophic niche size and diet of common carabid species. Both studies compared organically farmed cereals with conventional managed, two year old flowering fields in Central Germany (in the federal state Hessen, Germany). They found higher carabid species richness (Mader *et al.*, 2017) as well as reduced activity density and altered trophic responses of four common carabids (Mader *et al.*, 2018) in flowering fields compared to organic cereal crops. These findings are in contrast to this thesis, which did not reveal significant differences of carabid species richness, activity density or feeding type diversity between flowering fields and organic cereals (winter spelt) (chapter 2 and 3). As vegetation composition and -structure of flowering fields may change over time since establishment, the different findings might be caused by the fact that we studied annual flowering fields, whereas Mader *et al.*, (2017, 2018) studied two year old flowering fields. Older flowering fields might be more suitable habitats for those carabid species which are more sensitive towards farming practices (e.g. regular soil tillage) probably explaining the higher carabid species richness in older flowering fields. Negative impacts of denser vegetation in perennial compared to annual flowering fields on the activity density of agrobiont species might explain why Mader *et al.*, (2018) found higher activity densities in organic cereals than flowering fields. Differences

to Mader *et al.*, (2018) regarding carabid diet responses might appear, because that study only considered single species responses of the four most abundant species (which were also the most abundant ones of this thesis), whereas this thesis considered changes in the overall species community (chapter 3). Mader *et al.*, (2017) also report that the surrounding landscape complexity affected spider community composition and was positively correlated with spider richness. Even though we used the same predictor of landscape complexity than Mader *et al.*, (2017), i.e. arable land cover in 500 m radius, we did not find effects of landscape complexity on spider richness or community composition (chapter 2). It might be due to regional different landscape structures, which might affect arthropods on larger spatial scales than the considered 500 m radius around study fields. Despite the described differences there are also similar findings. In accordance with these studies (Mader *et al.*, (2017, 2018)), our results confirm that species richness of spiders and mean body size of carabid assemblages (CWM) do not differ between flowering fields and organic cereals and all studies showed that carabid responses were unaffected by the surrounding landscape complexity.

For flower-visiting arthropods direct comparisons to other studies are more difficult, as comparable studies (biodiversity effects of flowering fields and organic crops) are based on different study approaches and designs. Holland *et al.*, (2015) found that wild bees and butterflies were promoted by the establishment of wildlife habitats on conventional farms including flowering areas for insects, but organic farms had little effect on wild bees and butterflies. The pollination rates of insect-pollinated plants were also shown to be positively affected by flowering strips, but did not differ between conventional or organic farms (Chateil & Porcher, 2015). These results are in line with the results of the thesis, as wild bees and butterflies did also profit more strongly from conventional flowering fields than organic crops (lentil mixed-crop were not assessed by the other studies) (chapter 2). However, both studies made comparisons on the farm-level (comparing whole farms), not on the field-level which was the assessed spatial scale in this thesis. In contrast to our findings, Hardman *et al.*, (2016), who compared organic farms to conventional farms conducting different types of wildlife-friendly schemes (including measures for pollen- and nectar rich habitats), found no difference in bee and hoverfly diversity and density between schemes at the point or farm-level, but higher pollination service in organic farms. Pfiffner *et al.*, (2018) found no differences in wild bee abundance or species richness between flowering strips under organic management and organic cereal fields, but positive effects of organic low-input meadows. Altogether, our findings regarding wild bee and butterfly responses are partly but not consistently in line with the findings of other studies which had slightly different study approaches and designs. Further studies are therefore needed to be able to draw ultimate conclusions.

## **5.5 Landscape perspective on the implementation of local agri-environmental measures**

Overall, landscape effects had marginal impact on the within-field biodiversity. This might be related to the selected study area, the Biosphere Reserve Swabian Alb. It is a small-scale agricultural landscape (mean field sizes of about 2.3 ha) with comparatively high landscape heterogeneity due to the



heterogeneous terrain, poor soils and a relatively high amount of semi-natural habitats such as calcareous grasslands, hedges or clearance cairns. Although there was a distinct gradient in the arable land cover between study sites, it was not an extreme pronounced gradient compared to other study regions comparing simple with complex landscapes (Tscharntke *et al.*, 2005; Batáry *et al.*, 2011). Even study sites with the lowest level of landscape complexity (highest amount of arable land cover) still had an intermediate level of heterogeneity compared to cleared landscaped with minimal amount of non-crop habitats, as found in very intensively farmed, large-scale agricultural landscapes. Hence, landscape effects might be more pronounced if the gradient of landscape complexity would have been more pronounced between study sites. Besides, configurational and compositional landscape effects can be scale- as well as taxon dependent (Martin *et al.*, 2016). It is possible that the described landscape effects could potentially differ for another spatial scale (we only considered 500 m around study fields) and species groups requiring larger habitat areas than single arable fields such as birds or mammals. Other studies also state that local measures to enhance biodiversity can be more effective in simple than complex landscapes (Tscharntke *et al.*, 2005; Batáry *et al.*, 2011), although differing responses were also shown (e.g. Winqvist *et al.*, 2011; Karp *et al.*, 2018). Therefore, biodiversity effects of conventional flowering fields, organic winter spelt crops and organic lentil mixed-crops might be more pronounced if applied in more simplified agricultural landscapes than the Biosphere Reserve Swabian Alb. Further studies should therefore compare the four crop-use types in more simplified agricultural landscapes or over a more extreme gradient of landscape complexity in order to reveal relative effect sizes of local crop-use and landscape effects on the within-field biodiversity.

Furthermore, in arable-dominated landscapes, many species require a minimum amount of non-crop habitats as refuges within the agricultural landscape matrix in order to support a sufficient species pool (Landis & Marino, 1999). Irrespective of crop-use type, permanently unploughed landscape elements such as grassy field margins, hedges or other semi-natural habitats are crucial habitat refuges, especially for species groups with restricted dispersal ability, which spill-over from neighbouring non-crop habitats into the crop fields during the vegetation period (Rusch *et al.*, 2010; Schirmel *et al.*, 2016). The importance of bordering landscape elements for biodiversity and ecosystem functioning within arable fields was also revealed in this thesis by higher species richness of spiders and carabids as well as higher functional diversity of carabid assemblages found at the field edge bordered to grassy field margins than the field interior (chapter 2, chapter 3). Recommendations about the minimum proportion of non-crop habitat needed within an agricultural landscape vary between studies and considered species groups. Holland *et al.*, (2015) recommend about 7 % non-crop habitat for wild bee and butterflies, whereas Meichtry-Stier *et al.*, (2014) state 14 % for farmland birds and brown hares and Tscharntke *et al.*, (2011) recommend 20 % of non-crop habitat for sustaining overall biodiversity and associated ecosystem services. However, it is important to note that a minimum amount of non-cropped habitat (10-15% as a rule of thumb) is needed to sustain the biodiversity within farmland. The ecological importance of non-crop elements cannot be entirely compensated by promoting biodiversity friendly

farming practices such as the considered crop-use types. Hence, in addition to within-field measures, future AES regimes should more strongly support measures targeting the establishment of non-cropped semi-natural habitats within arable-dominated landscapes. Even though the creation of non-crop habitats are already an optional AES type in many European countries, the on-farm uptake and popularity among farmers for such AES types is often low, as they restrict the agricultural management of the farmer and can be more difficult to implement (Espinosa-Goded *et al.*, 2010; Batáry *et al.*, 2015). Therefore, farmers need stronger support (e.g. individual biodiversity consultation) and incentives (e.g. higher subsidies) to be able to implement such valuable measures.

Beside the presence of non-crop habitats and the implementation of biodiversity friendly crop-use types, within-field biodiversity also depends on a high landscape connectivity and permeability allowing species to move across landscapes and access different types of essential habitats (i.e. feeding, breeding, shelter and overwintering places). Such habitats are often patchy distributed especially in structural simplified agricultural landscapes. Local and temporal restricted measures, such as annual flowering fields or organic winter spelt or lentil mixed-crops, can act as important stepping stones contributing to the overall landscape connectivity, but are probably more sink than source habitats for most species groups. One approach to increase the landscape connectivity in intensively farmed landscapes is the separation of currently large farmland units into smaller ones. Landscapes with smaller farmland units (i.e. arable field sizes) and thereby higher field edge densities were shown to benefit many taxonomic groups irrespective of landscape compositional factors such as habitat diversity (Fahrig *et al.*, 2015; Batáry *et al.*, 2017; Hass *et al.*, 2018). Positive field edge effects for ground-dwelling arthropod diversity were also confirmed in this thesis (chapter 2, chapter 3). Higher field edge densities within arable-dominated landscapes are most easily achieved by reducing the size of individual crop fields. This could be done by dividing large arable fields into smaller segments of different crop-use types. However, ensuring a high level of landscape heterogeneity and connectivity between different habitat patches is essential for the long-term preservation of biodiversity and would most likely increase the effectiveness of biodiversity promoting crop-use types. The implementation of local agri-environmental measures should therefore take into account their spatial arrangement in the landscape in order to achieve an optimal distribution of biodiversity promoting stepping stones in the agricultural landscape matrix.

Altogether, the various arguments underline that future agri-environmental measures should not solely focus on local measures on the field or farm scale, even though local crop-use and edge effects were more important than effects of the surrounding landscape complexity within the scope of this thesis. On the contrary, there is broad scientific evidence that the loss of landscape heterogeneity at multiple spatial and temporal scales is a key reason for the observed loss of biodiversity (Benton *et al.*, 2003; Tscharntke, *et al.*, 2012; Landis, 2017). Single local management practices to promote biodiversity are ineffectively in landscapes, where source populations for recolonization are absent within the surrounding landscape context (Kennedy *et al.*, 2013; Tscharntke *et al.*, 2012). The

implementation of single measures should therefore be part of a landscape-wide design ensuring coordinated and collaborative agri-environmental management, which targets the overall permeability and heterogeneity of the agricultural landscape (Landis, 2017, Westerink *et al.*, 2017). The results of this thesis fit into such a landscape perspective for the implementation of local measures, as we found taxon-specific and thereby additive effects of conventional flowering fields, organic winter spelt- and lentil mixed-crops as well as field edge habitats for the promotion of overall species diversity (especially chapter 2, but also chapter 3 and 4). To ensure that a diverse mixture of different types of measures can be applied within a specific landscape, a spatially coordinated agri-environmental management is needed, which goes beyond the individual farm holding and takes into account the landscape structure and the specific type and distribution of other farming practices within the landscape.

## 5.6 Methodical limitations of the study

Although we analysed several different components and proxies of biodiversity, i.e. abundance, species richness, species composition, community weighted trait diversity and individual population development, we did not specifically analyse effects on rare, threatened (e.g. red list species) or specialist species. The latter are of higher nature conservation concern than common generalist species, even though common species can be important ecosystem service providers. In general, we found low amount of rare species and these were mostly sampled with very low consistency among study sites (often individual exemplars on a single location). Due to the strong dominance of few common species in the sampled species communities for all taxa, a statistical sound analysis was problematic to conduct and results would have been difficult to interpret. For instance, a single record of a specific rare species can easily be caused by random immigrations from a specific adjacent habitat of high nature value without reflecting the general conservation value of the sampled crop-use type. Besides, the studied crop-use types (flowering fields, organically farmed crops) can be mainly classified as ecosystem service providing schemes in contrast to biodiversity conservation schemes, which target species and habitats of conservation concern (e.g. managing low-nutrient meadows) more explicitly (Ekroos *et al.*, 2014). Hence, even though a comparison between the studied crop-use types regarding effects on rare, threatened or specialized species would be of high importance to evaluate their nature conservation potential, I did not specifically address this question within the scope of this thesis.

Further, there was an extremely low number of species and individual records in conventional winter wheat fields (especially for butterflies and wild bees), including several study fields with zero records, in comparison to considerably higher numbers in the other three crop-use types. The low sample in conventional winter wheat made it methodically difficult to analyse other metrics of species diversity such as  $\beta$ - or  $\gamma$ -diversity or the evenness of species communities (the relative abundances among species). However, if the number of individual records had been more similar distributed between crop-use types, it would have been of high interest to compare similarity of species communities, because

local enhancements of species richness do not necessarily result in higher overall species richness at the landscape scale. Other studies also underline the fact that comparing  $\alpha$ -diversity metrics can be a poor indicator for overall community diversity and spatial patterns of biodiversity (Duncan *et al.*, 2015; Lichtenberg *et al.*, 2017). For instance, Dufлот *et al.*, (2015) highlights that considering landscape-scale  $\gamma$ -diversity and taking into account the evenness within species communities helps to determine whether an increase in species richness is driven by rare or common species (Lichtenberg *et al.*, 2017). For a more holistic understanding of biodiversity effects of the studied crop-use types more studies are needed to reveal how conventional flowering fields, organic winter spelt and organic lentil mixed-crops differ in their effects regarding other metrics of biodiversity such as the similarity and evenness of species communities.

Additional studies are also needed to measure effects of the considered crop-use types on the provision of specific ecosystem services such as pollination (e.g. by phytometer plant experiments (Hass *et al.*, 2018)), biological pest- (e.g. by measuring cereal aphid parasitism (Baillod *et al.*, 2017)) or weed seed control (e.g. by measuring seed removal rates (Fischer *et al.*, 2017)) directly. For carabids we analysed specific traits which might be associated with ecosystem services. We found higher proportion of plant-feeding carabids in conventional flowering fields, organic winter spelt fields and field edges (chapter 3), which might lead to higher weed seed control in these habitats (Trichard *et al.*, 2013; Rusch *et al.*, 2016). However, weed seed control might also be affected by other factors (e.g. by total weed seed numbers or availability of alternative plant resources for herbivorous species). Therefore, direct assessments of the quantity of specific ecosystem services (e.g. weed seed removal rates) would be an important task for future studies, but additionally conducting such a study was beyond the capacities of this thesis.

Last, this thesis considered the combination of two separate explanatory factors, i.e. management effects (conventional vs. organic farming) and crop species effects (winter wheat, flowering field, winter spelt, lentil-mixed crop). Thus, it was not possible to disentangle management from crop species effects within the scope of this thesis. In order to disentangle the relative effects of both factors it would have been better to compare each crop species under both management types (e.g. conventional winter wheat vs. organic winter wheat; conventional lentil mixed-crop vs. organic lentil mixed-crop). However, the restricted number and distribution of the considered crop-use types in the study region (Biosphere Reserve Swabian Alb) did not allow for such direct comparisons. For instance, there was an extreme low number of organically farmed winter wheat fields, as winter wheat is not growing with sufficient yield on the poor soils of the study region without mineral fertilisers which are forbidden according to the regulations of organic farming. Organic farmers therefore preferred to grow winter spelt. They also did not establish flowering fields, as there was no or only difficult access to seed mixtures which were certified in accordance to organic farming regulations (personal communication of interviewed farmers). Lentil mixed-crops were also mainly grown by organic farmers and only rarely by conventional ones, due to an existing farmers cooperation in the study region - the “Öko-

Erzeugergemeinschaft Alb-Leisa". Hence, the limited availability of the specific crop-use types (especially flowering fields and lentil mixed-crops) in the study area did not allow to separate crop from management effects. If the amount of farmers establishing flowering fields and lentil mixed-crops will further expand, future studies might be able to compare the specific crop species in both management types simultaneously.

## 5.7 Conclusions and Recommendations

To summarise, the establishing of annual flowering fields enhances biodiversity in conventional farming systems, whereas lentil mixed-crops can further increase biodiversity benefits of organic farming systems. Organic lentil mixed-crops should complement rather than replace wild plant-rich winter cereals in organic crop rotations, because the later crop-use type also contributes to the promotion of biodiversity as shown for carabid functional diversity and the population development of *B. terrestris*. Even though responses of the considered biodiversity components (taxonomical-, functional diversity and bumblebee population development) were not entirely consistent, all three studies of this thesis revealed that there is no single best measure for the promotion of biodiversity on arable land. Instead, to ensure that a mosaic of different types of measures, such as conventional flowering fields, organic winter spelt, organic lentil mixed-crops as well as field edge habitats, is established within an agricultural landscape might promote overall biodiversity more effectively. In accordance to Grass *et al.*, (2019) who point to the importance of combining land sparing- and land sharing approaches within a well-connected landscape matrix in relation to natural habitats and cropland, the results of this thesis suggest that the same conclusion applies to the relation between non-productive (conventional flowering fields) and productive (organic winter spelt, organic lentil-mixed crop) measures on arable land. Both types of measures should be simultaneously applied within a heterogenous landscape matrix with high habitat connectivity between different biodiversity promoting measures.

To ensure the implementation of different measures, a landscape-wide management is needed targeting the most vulnerable species groups as well as the most limited resource gaps within a landscape. For instance, if there is a lack of flower resources for flower-visiting insects within a landscape, the establishing of conventional flowering fields might be most appropriate. But if there are already existing mass-flowering crops in close proximity, the support of organically farmed crops to promote the diversity of arable wild plant resource would be more effective. Besides, even if effects of different measures are equally effective, as shown for conventional flowering fields and organic winter spelt regarding their benefit for carabid functional diversity (chapter 3), the costs and practicability can vary between different measures dependent on the regional context, the farmers preferences and the specific subsidy regulations of the national or regional AES regime. It is therefore necessary to have a set of different, equally effective measures as a prerequisite for a case specific balancing in accordance to the regional context of implementation. Supporting individual management decisions in accordance to the targeted species group and the specific landscape setting might be more appropriate to increase

the effectiveness of future AESs, than standardised approaches in favour of a single best measure or a limited set of certain measure types.

Irrespective of the type of measure, the successful implementation of biodiversity promoting measures on arable land will depend on the participation of farmers. Farmers should be more strongly involved in the elaboration of future agri-environmental measures in order to meet their requirements and to increase the motivation to participate in the implementation of measures with proven biodiversity benefits such as establishing flowering fields, organic farming or increasing field edge density on arable land. Agricultural subsidies should provide additional incentives for farmers who implement a diverse mixture of different crop-use types on their farmland. Further, collaborations of multiple farmers and coordination between farmers regarding their individual implementation of agri-environmental measures should be strengthened. To achieve that the strict focus of current agricultural policy on the individual farm holding should be replaced by a coordinated and collaborative agri-environmental management, which coordinates the implementation of complementary measures from different farmers within the same agricultural landscape. Therefore, farmers should be provided with regional landscape coordinators, who advise and support the coordination and collaboration between farmers in order to avoid redundant measures and to ensure that individual measures fit into the targeted promotion of the regional species pool.

## 5.8 References

- Baillod, A.B., Tschamntke, T., Clough, Y. & Batáry, P. (2017) Landscape-scale interactions of spatial and temporal cropland heterogeneity drive biological control of cereal aphids. *Journal of Applied Ecology*, 54 (6), 1804–1813. Doi: 10.1111/1365-2664.12910.
- Barone, M. & Frank, T. (2003) Habitat age increases reproduction and nutritional condition in a generalist arthropod predator. *Oecologia*, 135 (1), 78–83. Doi: 10.1007/s00442-002-1175-2.
- Batáry, P., Báldi, A., Kleijn, D. & Tschamntke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceeding of the Royal Society B: Biological Sciences*, 278 (1713), 1894–1902. Doi: 10.1098/rspb.2010.1923.
- Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29 (4), 1006–1016. Doi: 10.1111/cobi.12536.
- Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C.F., Mußhoff, O., Császár, P., Fusaro, S., Gayer, C., Happe, A.-K., Kurucz, K., Molnár, D., Rösch, V., Wietzke, A. & Tschamntke, T. (2017) The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. *Nature Ecology & Evolution*, 1 (9), 1279–1284. Doi: 10.1038/s41559-017-0272-x.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18 (4), 182–188. Doi: 10.1016/S0169-5347(03)00011-9.
- Chateil, C. & Porcher, E. (2015) Landscape features are a better correlate of wild plant pollination than agricultural practices in an intensive cropping system. *Agriculture, Ecosystems & Environment*, 201, 51–57. Doi: 10.1016/j.agee.2014.12.008.
- de Visser, C. L. M., Schreuder, R. & Stoddard, F. (2014) The EU’s dependency on soya bean import for the animal feed industry and potential for EU produced alternatives. *OCL*, 21 (4), D407. Doi: 10.1051/ocl/2014021.
- Denys, C. & Tschamntke, T. (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia*, 130 (2), 315–324. Doi: 10.1007/s004420100796.
- Dufлот, R., Aviron, S., Ernoult, A., Fahrig, L. & Burel, F. (2015) Reconsidering the role of ‘semi-natural habitat’ in agricultural landscape biodiversity: a case study. *Ecological Research*, 30 (1), 75–83. Doi: 10.1007/s11284-014-1211-9.
- Duncan, C., Thompson, J.R. & Pettorelli, N. (2015) The quest for a mechanistic understanding of biodiversity-ecosystem services relationships. *Proceeding of the Royal Society B: Biological Sciences*, 282 (1817), 20151348. Doi: 10.1098/rspb.2015.1348.
- Ekroos, J., Olsson, O., Rundlöf, M., Wätzold, F. & Smith, H.G. (2014) Optimizing agri-environment schemes for biodiversity, ecosystem services or both? *Biological Conservation*, 172, 65–71. Doi: 10.1016/j.biocon.2014.02.013.
- Erskine, W., Mühlbauer, F.J., Sarker, A. & Sharma, B. (eds.) (2009) The lentil: botany, production and uses. CABI Publishing, Wallingford, UK.

- Espinosa-Goded, M., Barreiro-Hurlé, J. & Ruto, E. (2010) What do farmers want from agri-environmental scheme design ? A choice experiment approach. *Journal of Agricultural Economics*, 61 (2), 259–273. Doi: 10.1111/j.1477-9552.2010.00244.x.
- Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K.F., Mitchell, S. & Tischendorf, L. (2015) Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment*, 200, 219–234. Doi: 10.1016/j.agee.2014.11.018.
- Fischer, C., Gayer, C., Kurucz, K., Riesch, F., Tschardtke, T. & Batáry, P. (2017) Ecosystem services and disservices provided by small rodents in arable fields: Effects of local and landscape management. *Journal of Applied Ecology*, 55 (2), 548–558. Doi: 10.1111/1365-2664.13016.
- Frank, T., Aeschbacher, S. & Zaller, J.G. (2012) Habitat age affects beetle diversity in wildflower areas. *Agriculture, Ecosystems & Environment*, 152, 21–26. Doi: 10.1016/j.agee.2012.01.027.
- Frank, T., Kehrli, P. & Germann, C. (2007) Density and nutritional condition of carabid beetles in wildflower areas of different age. *Agriculture, Ecosystems & Environment*, 120 (2), 377–383. Doi: 10.1016/j.agee.2006.10.012.
- Frank, T. & Künzle, I. (2006) Effect of early succession in wildflower areas on bug assemblages (Insecta: Heteroptera). *European Journal of Entomology* (103), 61–70.
- Ganser, D., Knop, E. & Albrecht, M. (2019) Sown wildflower strips as overwintering habitat for arthropods: Effective measure or ecological trap? *Agriculture, Ecosystems & Environment*, 275, 123–131. Doi: 10.1016/j.agee.2019.02.010.
- Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., Udy, K., Westphal, C., Wurz, A. & Tschardtke, T. (2019) Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature*, 1 (2), 262–272. Doi: 10.1002/pan3.21.
- Groeneveld, J.H. & Klein, A.-M. (2014) Pollination of two oil-producing plant species: Camelina (Camelina sativa L. Crantz) and pennycress (Thlaspi arvense L.) double-cropping in Germany. *GCB Bioenergy*, 6 (3), 242–251. Doi: 10.1111/gcbb.12122.
- Gruber, S., Wahl E., Zikeli, S. & Claupein, W. (2012) Perspektiven und Grenzen der Unkrautregulierung bei Linsen (Lens culinaris) im Ökologischen Landbau. *Journal für Kulturpflanzen*, 64 (10), 365–377.
- Haaland, C., Naisbit, R.E. & Bersier, L.-F. (2011) Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, 4 (1), 60–80. Doi: 10.1111/j.1752-4598.2010.00098.x.
- Hardman, C. J., Norris, K., Nevard, T. D., Hughes, B. & Potts, S. G. (2016) Delivery of floral resources and pollination services on farmland under three different wildlife-friendly schemes. *Agriculture, Ecosystems & Environment*, 220, 142–151. Doi: 10.1016/j.agee.2016.01.015.
- Hass, A.L., Kormann, U.G., Tschardtke, T., Clough, Y., Baillod, A.B., Sirami, C., Fahrig, L., Martin, J.-L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Burel, F., Georges, R., Giralt, D., Marcos-García, M.Á., Ricarte, A., Siriwardena, G. & Batáry, P. (2018) Landscape configurational



- heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proceeding of the Royal Society B: Biological Sciences*, 285 (1872), 20172242. Doi: 10.1098/rspb.2017.2242.
- Holland, J.M., Smith, B.M., Storkey, J., Lutman, P.J.W. & Aebischer, N.J. (2015) Managing habitats on English farmland for insect pollinator conservation. *Biological Conservation*, 182, 215–222. Doi: 10.1016/j.biocon.2014.12.009.
- Horneburg, B. (2006) Outcrossing in lentil (*Lens culinaris*) depends on cultivar, location and year, and varies within cultivars. *Plant Breeding*, 125 (6), 638–640. Doi: 10.1111/j.1439-0523.2006.01290.x.
- Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M. & Landis, D. (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment*, 7 (4), 196–203. Doi: 10.1890/080035.
- Jain, A., Kunte, K. & Webb, E.L. (2016) Flower specialization of butterflies and impacts of non-native flower use in a transformed tropical landscape. *Biological Conservation*, 201, 184–191. Doi: 10.1016/j.biocon.2016.06.034.
- Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., O'Rourke, M.E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J.A., Schellhorn, N.A., Tschamntke, T., Wratten, S.D., Zhang, W., Iverson, A.L., Adler, L.S., Albrecht, M., Alignier, A., Angelella, G.M., Anjum, M.Z., Avelino, J., Batáry, P., Baveco, J.M., Bianchi, Felix J. J. A., Birkhofer, K., Bohnenblust, E.W., Bommarco, R., Brewer, M.J., Caballero-López, B., Carrière, Y., Carvalheiro, L.G., Cayuela, L., Centrella, M., Četković, A., Henri, D.C., Chabert, A., Costamagna, A.C., La Mora, A.D., Kraker, J.d., Desneux, N., Diehl, E., Diekötter, T., Dormann, C.F., Eckberg, J.O., Entling, M.H., Fiedler, D., Franck, P., Veen, F. J. Frank van, Frank, T., Gagic, V., Garratt, M.P.D., Getachew, A., Gonthier, D.J., Goodell, P.B., Graziosi, I., Groves, R.L., Gurr, G.M., Hajian-Forooshani, Z., Heimpel, G.E., Herrmann, J.D., Huseeth, A.S., Inclán, D.J., Ingrao, A.J., Iv, P., Jacot, K., Johnson, G.A., Jones, L., Kaiser, M., Kaser, J.M., Keasar, T., Kim, T.N., Kishinevsky, M., Landis, D.A., Lavandero, B., Lavigne, C., Le Ralec, A., Lemessa, D., Letourneau, D.K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K., Madeira, F., Mader, V., Cortesero, A.M., Marini, L., Martinez, E., Martinson, H.M., Menozzi, P., Mitchell, M.G.E., Miyashita, T., Molina, G.A.R., Molina-Montenegro, M.A., O'Neal, M.E., Opatovsky, I., Ortiz-Martinez, S., Nash, M., Östman, Ö., Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perović, D.J., Peterson, J.A., Petit, S., Philpott, S.M., Plantegenest, M., Plečaš, M., Pluess, T., Pons, X., Potts, S.G., Pywell, R.F., Ragsdale, D.W., Rand, T.A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.-P., Saulais, J., Schäckermann, J., Schmidt, N.P., Schneider, G., Schüepp, C., Sivakoff, F.S., Smith, H.G., Whitney, K.S., Stutz, S., Szendrei, Z., Takada, M.B., Taki, H., Tamburini, G., Thomson, L.J., Tricault, Y., Tsafack, N., Tschumi, M., Valantin-Morison, M., van Trinh, M., van der Werf, W., Vierling, K.T., Werling, B.P., Wickens, J.B., Wickens, V.J., Woodcock, B.A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A. & Zou, Y. (2018) Crop pests

- and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences*, 115 (33), E7863-E7870. Doi: 10.1073/pnas.1800042115.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalho, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Kremen, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S. & Kremen, C. (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16 (5), 584–599. Doi: 10.1111/ele.12082.
- Landis, D.A. (2017) Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, 18, 1–12. Doi: 10.1016/j.baae.2016.07.005.
- Landis, D.A. & Marino, P.C. (1999) Landscape structure and extra-field processes: Impact on management of pests and beneficials. *Handbook of pest management* (ed. by Ruberson, J.R.), pp. 79–104. Marcel Dekker Inc, New York, NY.
- Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N.A., Carvalho, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.-M., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E., Memmott, J., Morandin, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pockock, M.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardiñas, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tschamntke, T., Veselý, M., Weisser, W.W., Wilson, J.K. & Crowder, D.W. (2017) A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global change biology*, 23 (11), 4946–4957. Doi: 10.1111/gcb.13714.
- Mader, V., Diehl, E., Fiedler, D., Thorn, S., Wolters, V. & Birkhofer, K. (2017) Trade-offs in arthropod conservation between productive and non-productive agri-environmental schemes along a landscape complexity gradient. *Insect Conservation and Diversity*, 10 (3), 236–247. Doi: 10.1111/icad.12220.
- Mader, V., Diehl, E., Wolters, V., & Birkhofer, K. (2018). Agri-environmental schemes affect the trophic niche size and diet of common carabid species in agricultural landscapes. *Ecological Entomology*, 43(6), 823–835. Doi: 10.1111/een.12671.
- Mahmood, F., Shahzad, T., Hussain, S., Shahid, M., Azeem, M. & Wery, J. (2018) Grain legumes for the sustainability of European farming systems. *Sustainable Agriculture Reviews* 32 (ed. by Lichtfouse, E.), *Sustainable Agriculture Reviews*, 32, pp. 105–133. Springer International Publishing, Cham, DE. Doi: 10.1007/978-3-319-98914-3\_5

- Martin, E.A., Seo, B., Park, C.-R., Reineking, B. & Steffan-Dewenter, I. (2016) Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecological Applications*, 26 (2), 448–462. Doi: 10.1890/15-0856.
- Meichtry-Stier, K.S., Jenny, M., Zellweger-Fischer, J. & Birrer, S. (2014) Impact of landscape improvement by agri-environment scheme options on densities of characteristic farmland bird species and brown hare (*Lepus europaeus*). *Agriculture, Ecosystems & Environment*, 189, 101–109. Doi: 10.1016/j.agee.2014.02.038.
- Pfiffner, L., Ostermaier, M., Stoeckli, S. & Müller, A. (2018) Wild bees respond complementarily to ‘high-quality’ perennial and annual habitats of organic farms in a complex landscape. *Journal of Insect Conservation*, 22 (3-4), 551–562. Doi: 10.1007/s10841-018-0084-6.
- Pywell, R.F., Meek, W.M., Carvell, C., Hulmes, L. & Nowakowski, M. (2007) The Buzz project: biodiversity enhancement on arable land under the new agri-environment schemes. *Aspects of Applied Biology* (81), 61–68.
- Rusch, A., Binet, D., Delbac, L. & Thiéry, D. (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), 2163–2174. Doi: 10.1007/s10980-016-0390-x.
- Rusch, A., Valantin-Morison, M., Sarthou, J.-P. & Roger-Estrade, J. (2010) Chapter six - Biological control of insect pests in agroecosystems: effects of crop management, farming systems, and seminatural habitats at the landscape scale: a review. *Advances in agronomy* (ed. by Sparks, D.L.), pp. 219–259. Academic Press, Cambridge, US. Doi: 10.1016/B978-0-12-385040-9.00006-2.
- Schirmel, J., Thiele, J., Entling, M.H. & Buchholz, S. (2016) Trait composition and functional diversity of spiders and carabids in linear landscape elements. *Agriculture, Ecosystems & Environment*, 235, 318–328. Doi: 10.1016/j.agee.2016.10.028.
- Thorbek, P. & Bilde, T. (2004) Reduced numbers of generalist arthropod predators after crop management. *Journal of Applied Ecology*, 41 (3), 526–538. Doi: 10.1111/j.0021-8901.2004.00913.x.
- Trichard, A., Alignier, A., Biju-Duval, L. & Petit, S. (2013) The relative effects of local management and landscape context on weed seed predation and carabid functional groups. *Basic and Applied Ecology*, 14 (3), 235–245. Doi: 10.1016/j.baae.2013.02.002.
- Tscharntke, T., Batáry, P. & Dormann, C.F. (2011) Set-aside management: How do succession, sowing patterns and landscape context affect biodiversity ? *Agriculture, Ecosystems & Environment*, 143 (1), 37–44. Doi: 10.1016/j.agee.2010.11.025.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8 (8), 857–874. Doi: 10.1111/j.1461-0248.2005.00782.x.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein,

- A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., Putten, Wim H. van der & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87 (3), 661–685. Doi: 10.1111/j.1469-185X.2011.00216.x.
- Wang, L., Gruber, S. & Claupein, W. (2012) Optimizing lentil-based mixed cropping with different companion crops and plant densities in terms of crop yield and weed control. *Organic Agriculture*, 2 (2), 79–87. Doi: 10.1007/s13165-012-0028-5.
- Westerink, J., Jongeneel, R., Polman, N., Prager, K., Franks, J., Dupraz, P. & Mettepenningen, E. (2017) Collaborative governance arrangements to deliver spatially coordinated agri-environmental management. *Land Use Policy*, 69, 176–192. <https://doi.org/10.1016/j.landusepol.2017.09.002>.
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Pärt, T., Thies, C., Tschardtke, T., Weisser, W.W. & Bommarco, R. (2011) Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology*, 48 (3), 570–579. Doi: 10.1111/j.1365-2664.2010.01950.x.
- Woodcock, B.A., Savage, J., Bullock, J.M., Nowakowski, M., Orr, R., Tallowin, J.R.B. & Pywell, R.F. (2014) Enhancing floral resources for pollinators in productive agricultural grasslands. *Biological Conservation*, 171, 44–51. Doi: 10.1016/j.biocon.2014.01.023.

## 6. ACKNOWLEDGMENTS

This dissertation is the product of a long journey, which I made by small and often tiny steps during the last five years. It required endurance and patience over countless hours, but it still would have been impossible without the support of several wonderful people:

First, I sincerely want to thank PD Dr. Péter Batáry, who supported me as supervisor over many years since my master thesis and always shared his deep ecological knowledge and experiences about field studies, appropriate study designs and statistical approaches with me. Without his friendly and patiently guidance, advise and encouragement this thesis definitely would have been impossible. I also want to thank Prof. Dr. Martin Dieterich for being my first supervisor at the University of Hohenheim, his noticeable passion for nature conservation, his contribution to sample butterflies and bees in the field and for giving valuable input and advise over the course of my dissertation.

I am also grateful to my supervisors and colleagues at the University of Applied Science in Nürtingen (HfWU). Prof. Dr. Konrad Reidl for supporting me with his experiences with applied research projects, the acquisition of funds and the inclusion of project partners such as the Biosphere Reserve Swabian Alb and initial contact persons at the University of Hohenheim. Prof. Dr. Christian Küpfer, for being a very friendly and supporting superior and colleague, and without whom my numerous lectures about species conservation at the HfWU would have been hardly imaginable. I really enjoyed the company of my colleagues at the Institute of Applied Sciences (IAF), who created an open and family atmosphere with long discussions about the funny and serious problems of the world during lunch breaks or in the pub after work. Special thanks to Wolfgang Bortt and Corinna Allevato, who conducted the administrative management of research funds and to Manuel Vollrath, who shared the office with me and was always a great colleague and friend during all scientific and personal challenges.

Field and laboratory work would have been impossible without the contribution of several students, who supported the research project within their bachelor- or master thesis or as research assistant. Thanks to Theresa Fässler, Lukas Maier, Frederik Schüttler and Tobias Weiß for the sampling and identification of carabids, to Judith Engelke, Nils Engelmann, Caroline Fischer, Miriam Harper, Moritz Mayer, Nina Stork and Rosa Witty for surveying plants, to Jutta Wieland and Jochen Berger for surveying butterflies and bees and to Alina Biermann for conducting the bumblebee colony experiment. Your passion and company were essential for a joyful time during field work. You made it possible to collect such as large data base. Further, I thank Dr. Róbert Horváth for the identification of spiders and Daniel Moog for his help and introduction into the identification of carabids as well as his practical advises regarding the field work.

Further, the thesis would not exist without the participation and support of about 35 farmers, who allowed us to use their fields, shared information about their farming practices and offered hospitality for the conduction of personal interviews. I am also grateful for Dr. Rüdiger Jooß and Rainer Striebel from the head office of the Biosphere Reserve Swabian Alb for their cooperation and the

## ACKNOWLEDGMENTS

provision of information about the Biosphere Reserve as well as for hosting information events in order to present the results of the research project. I further thank the funding institutes, that was the foundation *LBBW Stiftung Umwelt und Natur*, which supported data collection in 2016 and the *Stiftung Naturschutzfonds Baden-Württemberg*, which funded data collection in 2017 and 2018.

Finally, I would like to thank my parents, who always supported me on my way and whom I can rely on. I am also thankful to my wife Victoria, our past and future ways and our common enthusiasm about nature. Last, I thank God for a never-ending passion for being outside in nature and observing and conserving the richness of wonderful ecosystems and species on earth.

*Gewidmet dem noch ungeborenen Leben,  
und unserer gemeinsamen Zeit.*

## 7. AUTHOR'S DECLARATION

Declaration in lieu of an oath on independent work according to Sec. 18 (3) sentence 5 of the University of Hohenheim's Doctoral Regulations for the Faculties of Agricultural Sciences, Natural Sciences, and Business, Economics and Social Sciences:

1. The dissertation submitted on the topic "Suitability of conventional flowering fields and organic lentil mixed-crops to promote biodiversity on arable land" is work done independently by me.
2. I only used the sources and aids listed and did not make use of any impermissible assistance from third parties. In particular, I marked all content taken word-for-word or paraphrased from other works.
3. I did not use the assistance of a commercial doctoral placement or advising agency.
4. I am aware of the importance of the declaration in lieu of oath and the criminal consequences of false or incomplete declarations in lieu of oath.

I confirm that the declaration above is correct. I declare in lieu of oath that I have declared only the truth to the best of my knowledge and have not omitted anything.

---

Ort, Datum

---

Unterschrift

## 8. CURRICULUM VITAE

**Christoph Gayer**

**Born on the 13<sup>th</sup> of July 1988 in Bad Saulgau**

**Höhenweg 8 | 72622 Nürtingen  
0160 3320256 | christoph.gayer@posteo.de**



### ACADEMIC QUALIFICATIONS

Since 03/2018	Doctoral candidate at the Faculty of Agricultural Sciences, University of Hohenheim, Germany
10/2012 - 02/2015	Bi-national, double degree Master of Science/Master of International Nature Conservation (M.Sc./M.I.N.C), Georg-August-Universität Göttingen and Lincoln University, New Zealand Master Thesis: <i>"How do landscape structure and farming practice affect bird and small mammal diversity?"</i>
10/2009 - 09/2012	Bachelor of Science., Biology Philipps Universität Marburg, Germany, Bachelor Thesis: <i>"Activity of wolves (Canis lupus) and potential prey in eastern Germany"</i>
09/1999 - 06/2008	A-levels (Allgemeine Hochschulreife), Gymnasium St.Johann, Aulendorf/Blönnried, Germany

### WORK EXPERIENCES

Since 10/2019	Employee at the nature conservation authority Baden-Württemberg
03/2015 – 09/2019	Scientific associate at the University of Applied Sciences Nürtingen-Geislingen (HfWU), Germany <ul style="list-style-type: none"><li>- Lecturer for species and habitat conservation</li><li>- Agroecological research projects</li></ul>
06/2015 - 07/2016	Freelance work as animal ecologist for the landscape planning office Stadt Land Fluss, Prof. C. Küpfer, Nürtingen <ul style="list-style-type: none"><li>- Faunistic field surveys</li><li>- Habitat potential analyses</li></ul>
08/2008 – 08/2009	Civilian service in Arusha, Tanzania <ul style="list-style-type: none"><li>- Social projects (sport, theatre) with children and youths living in poverty</li></ul>



**INTERNSHIPS**

03/2013 - 06/2013	<p>Internship semester at the planning office <i>Institut für Tierökologie und Naturbildung</i>, Laubach</p> <ul style="list-style-type: none"> <li>- Surveying and evaluating protected species for conservation planning</li> <li>- Mapping diverse species groups such as bats, wild cats or dormouse</li> </ul>
08/2012 - 10/2012	<p>Youth delegate at the 11<sup>th</sup> UN conference of the parties for the Convention on Biological Diversity (CBD) in Hyderabad, India</p>
08/2011 - 09/2011	<p>Ecological research internship during a PhD study about plant-frugivore bird networks in the Białowieża National Park, Polen</p> <ul style="list-style-type: none"> <li>- Surveying birds and their frugivorous activity in the field</li> </ul>
02/2011 – 04/2011	<p>Internship at the NABU centre for nature conservation Mettnau in Radolfszell</p> <ul style="list-style-type: none"> <li>- Management of nature conservation areas</li> </ul>

**PUBLICATIONS**

**Gayer, C., Lövei, G. L., Magura, T., Dieterich, M., & Batáry, P. (2019)** Carabid functional diversity is enhanced by conventional flowering fields, organic winter cereals and edge habitats. *Agriculture, Ecosystems and Environment*, 284, 106579, Doi: 10.1016/j.agee.2019.106579.

**Gayer, C., Kurucz, K., Fischer, C., Tschardtke, T., & Batáry, P. (2019)** Agricultural intensification at local and landscape scales impairs farmland birds, but not skylarks (*Alauda arvensis*). *Agriculture, Ecosystems & Environment*, 277, 21–24. Doi: 10.1016/j.agee.2019.03.006.

Fischer, C., **Gayer, C.**, Kurucz, K., Riesch, F., Tschardtke, T., & Batáry, P. (2018) Ecosystem services and disservices provided by small rodents in arable fields: Effects of local and landscape management. *Journal of Applied Ecology*, 55, 548–558. Doi: 10.1111/1365-2664.13016.

Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C.F., Mußhoff, O., Császár, P., Fusaro, S., **Gayer, C.**, Happe, A.-K., Kurucz, K., Molnár, D., Rösch, V., Wietzke, A., & Tschardtke, T. (2017) The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. *Nature Ecology & Evolution*, 1, 1279–1284. Doi: 10.1038/s41559-017-0272-x.

**Gayer, C** (2016) Vergleichender Einfluss der Landschaftsstruktur und landwirtschaftlicher Nutzung auf die Diversität von Vögeln und Kleinsäugetern. In: Treffpunkt Biologische Vielfalt, 15, Korn H., Bockmühl, K. (Hrsg.), *BfN-Skripten*, 436, 31-36.

**ADDITIONAL SKILLS**

<b>Software:</b>	<b>Languages:</b>
MS Office (Word, Excel, Power Point)	German (native)
Software R	English (C1)
ArcGIS	Großes Latein

---

 Ort, Datum

---

 Unterschrift