Effects of agri-environmental measures in intensively managed farmland on the soil seed bank, butterflies and carabid beetles in Germany

Influence of local conditions and surrounding landscape on biodiversity

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Summary

Worldwide biodiversity loss is one of the biggest challenges of mankind. While agriculture historically formed heterogeneous and species rich landscapes, continuous intensification in recent decades has degraded the habitat of many plant and animal species. Homogenisation, fertilizer and pesticide use have led to the disappearance of increasing numbers of species, with serious consequences for global biodiversity, but also for important ecosystem services such as crop pollination and regulation of soil health. In response, the EU developed financial incentives, in particular agri-environmental schemes, to urge farmers to rethink their current practise and change the agricultural system towards greater sustainability.

So far agrobiodiversity loss in Europe is slowed down, but has not been halted or reversed. Many farmers hesitate to implement agri-environmental measures, as they could lead to higher workloads, expenses or sanctions if mistakes are made. Therefore, various projects have been initiated, encouraging scientists and farmer to work together developing economically acceptable, ecological beneficial and user-friendly measures. This thesis uses two such projects to provide an insight into the broader effects of agri-environmental measures under realistic conditions (e.g. differing regional species pools, farmers' management preferences): F.R.A.N.Z. ('future resources, agriculture & nature conservation'), a project using demonstration farms to promote measures within the farming community, and MEDIATE, a project dedicated to promote measures in high yielding arable landscapes in Lower Saxony.

Based on intensively managed fields, located in seven different regions in Germany, **Chapter 2** considers the effect of measures on arable plants, as the primary producers in the agroecosystem and therefore the base of the food chain. It compares above-ground vegetation with species diversity in the soil seed bank. Furthermore, a closer look is directed at enrichment of the soil seed bank in flower strips after two vegetation periods with emphasis on possible problematic weed species. Soil samples, taken in in autumn 2018, were artificially stratified, sieved and germinated. Seedlings were identified and counted. **Chapter 3** addresses butterflies as indicator for the ecological benefits provided by implemented measures. Patterns of butterfly diversity and species composition in regard to agri-environmental measures, flowering aspect and land use types are outlined, studying different measures in ten different regions in Germany. Butterflies were counted on flower strips, extensive cereals, less intensive grassland, cereal fields, conventional grassland and semi-natural habitats using the transect walk method five times between May and August between 2017 and 2019. **Chapter 4** focuses on carabids, an important organism group for pest control. Carabid beetle diversity and activity abundance on three different measures and two differing reference sites in relation to local site conditions and neighbouring land use types are compared. Changes in ecological trait and species composition, with respect to measurement, site and landscape conditions are looked into. Carabid beetle activity abundance was recorded in spring 2018 with pit fall traps.

Investigating agri-environmental measures under realistic condition paints an accurate picture of what can be achieved in intensively farmed landscapes through agricultural policy. The following three *key findings* concerning biodiversity conservation in agricultural landscapes can be derived from this study*:*

1. *Intensively farmed landscapes are characterized by a limited species pool. Insect and plant communities are dominated by a few species, some of which are classified as problematic. Due to their ecological traits ensuring (a) fast and abundant reproduction, (b) the capacity to evade unsuitable conditions and (c) development under agricultural conditions, they are adapted to frequent disturbances. Most formerly typical species of agricultural habitats are rare or missing. Therefore, conservation efforts in intensive farmland should concentrate on generalist species, maintaining ecosystem functions.*
2. *The implementation of agri-environmental measures leads to differing patterns in different organism groups. Measures promote some common and generalist plant and butterfly species, while carabid beetles show little reaction towards measures. Their effectiveness depends on the definition of success and in the present agricultural system: aiming to maintain remaining biodiversity, although limited, is a good start. With minor positive effects on biodiversity, a mix of different agri-environmental measures can at least help to prevent further decline.*
3. *Effects of agri-environmental measures on biodiversity depend strongly on several external factors, namely on-site conditions (e.g. tillage regime, vegetation structure), surrounding landscape (semi-natural habitats), and neighbouring habitats (vicinity to forests). Details of implementation schemes of agri-environmental measures need to be carefully considered, as well as the potential of the landscapes to maintain a richer biodiversity, in order to enhance effects.*

The current intensive agricultural system in Germany is not suitable to stop or reverse biodiversity loss. However, agrobiodiversity is key for sustainable land management and the remaining 'basic' biodiversity needs immediate protection, securing food production in the future. Agri-environmental measures can contribute by protecting generalist species, providing that their design is improved and that they are more widely implemented. This change can be initiated by better ecological training for famers and more financially attractive agri-environmental measures.

Zusammenfassung

Der weltweite Biodiversitätsverlust ist eine der größten Herausforderungen der Menschheit. Während Landwirtschaft in ihren Anfängen heterogene, artenreiche Landschaften geformt hat, führte die fortwährende Intensivierung zur Degradation von Habitaten vieler Pflanzen- and Tierarten. Homogenisierung, Dünger und Pestizideinsatz führten zum Verschwinden von vielen Arten mit gravierenden Konsequenzen für die Biodiversität weltweit und wichtigen Ökosystemdienstleistungen, wie Bestäubung und Bodenqualität. Als Gegenmaßnahme entwickelte die EU finanzielle Anreize, insbesondere Agrarumweltmaßnahmen, welche die Landwirte dazu ermutigen sollen, ihre jetzige Praxis hin zu einem nachhaltigen Landwirtschaftlichen System zu verändern.

Bisher konnte der Biodiversitätsverlust in Europa nur verlangsamt, nicht aber gestoppt oder rückgängig gemacht werden. Viele Landwirte zögern mit der Umsetzung von Maßnahmen, da sie zu höheren Arbeitsbelastungen und Kosten, oder zu Sanktionen bei fehlerhafter Umsetzung führen können. Deshalb wurden verschiedene Projekte initiiert um ökonomisch akzeptable, ökologisch wertvolle und einfach umzusetzende Maßnahmen zu entwickeln. Diese Arbeit nutzt zwei Projekte um einen Einblick in die breiteren Effekte von Agrarumweltmaßahmen unter realistischen Bedingungen (z. B. verschiedene regionale Artengemeinschaften, Präferenzen der Landwirte) zu geben: F.R.A.N.Z. (Für Ressourcen, Agrarwirtschaft und Naturschutz mit Zukunft), ein Projekt welches mit Demonstrations-betrieben arbeitet um Maßnahmen innerhalb der Landwirtschaft zu fördern, und MDEDIATE, ein Projekt mit dem Ziel Maßnahmen in Hochertragsstandorten in Niedersachsen zu etablieren.

Basierend auf intensiv bewirtschaftenden Felder, in sieben verschiedenen Regionen in Deutschland gelegen, vergleicht **Kapitel 2** die oberirdische Vegetation mit der Artenvielfalt in der Diasporenbank im Boden. Zudem wird die Anreicherung der Samenbank in Blühstreifen nach zwei Vegetationsperioden, mit Schwerpunkt auf problematische Ackerunkräuter, genauer betrachtet. Bodenproben wurden im Herbst 2018 genommen, stratifiziert, gesiebt und zum Keimen gebracht. Keimlinge wurden identifiziert und gezählt. **Kapitel 3** befassen sich mit Tagfaltern als Indikatoren für den ökologischen Nutzen von Maßnahmen. Muster von Tagfalterdiversität und Artenzusammensetzung im Zusammenhang mit Agrarumweltmaßnahmen, Blühaspekt und Landnutzung werden beschrieben, basierend auf Untersuchungen von Maßnahmen in zehn Regionen in Deutschland. Tagfalter wurden 2017 bis 2019 mit der Transektmethode auf Blühstreifen, extensivem Getreide, extensiviertem Grünland, konventionellem Getreide, Grünland und semi-natürlichen Resthabitaten fünf Mal zwischen Mai und August erfasst. **Kapitel 4** befasst sich mit den Laufkäfern, welche bei der Schädlingsbekämpfung eine wichtige Rolle spielen. Es werden die Laufkäferdiversität und Aktivitätsdichte auf drei verschiedenen Maßnahmen und zwei verschiedenen Referenzflächen in Bezug auf lokalen Standortgegebenheiten und den benachbarten Landnutzungsformen verglichen. Veränderungen in der ökologischen Merkmals- und Artenzusammensetzung wurden hinsichtlich der

Maßnahmen, Standortgegebenheiten und Landschaftskontext betrachtet. Die Laufkäfer Aktivitätsdichte wurden mit Barber-Fallen im Frühjahr 2018 erfasst.

Die wissenschaftliche Untersuchung von Agrarumweltmaßnahmen unter realistischen Bedingungen gibt ein akkurates Bild von dem, was in intensiven Agrarlandschaften durch die derzeitige Agrarpolitik erreicht werden kann. Die folgenden drei Schlüsselerkenntnisse für die Erhaltung der Biodiversität in Agrarlandschaften können aus dieser Arbeit abgeleitet werden.

(1) *Intensiv bewirtschaftete Agrarlandschaften zeichnen sich durch einen limitierten Artenpool aus. Insekten- und Pflanzengemeinschaften werden von wenigen Arten dominiert, welche mitunter auch als problematisch eingestuft werden. Durch ihre ökologischen Eigenschaften sind sie in der Lage (a) sich schnell und in hoher Anzahl zu reproduzieren, (b) schlechten Umweltbedingungen auszuweichen und (c) sich unter ackerbaulichen Bedingungen zu entwickeln, somit sind sie an immer wiederkehrende Störung angepasst. Viele, früher häufige und typische, Agrararten sind selten oder fehlen. Deshalb sollte der Artenschutz in intensiven Agrarlandschaften sich auf generalistische Arten konzentrieren, welche die Ökosystem-dienstleistungen aufrechterhalten.*

(2) *Die Umsetzung von Agrarumweltmaßnahmen wirkt sich unterschiedlich auf verschiedenen Organismengruppen aus. Die Maßnahmen fördern häufige Generalisten bei Pflanzen und Tagfaltern, während Laufkäfer nur wenig auf die Maßnahmen reagieren. Die Effektivität hängt von der Definition von Erfolg ab. Innerhalb des jetzigen Agrarsystems ist die Erhaltung der verbleibenden Diversität, wenn auch limitiert, ein guter Anfang. Auch bei geringen positiven Effekten auf die Biodiversität, kann eine Mischung aus verschiedenen Agrarumwelt-maßnahmen helfen, weitere Verluste zu verhindern.*

(3) *Die Effekte von Agrarumweltmaßnahmen werden von verschiedenen externen Faktoren stark beeinflusst, dazu zählen vor-Ort-Bedingungen (z. B. Bodenbearbeitung, Vegetationsstruktur), die umgebende Landschaft (z. B. Anteil von semi-natürliche Habitate) und benachbarte Habitate (z. B. Nähe zu Wald). Detailvorgaben zur Implementierung von Agrarumweltmaßnahmen müssen sorgfältig abgewogen und potentiale in der Landschaft berücksichtigt werden, um Effekte zu verstärken.*

Unser jetziges Agrarsystem ist nicht in der Lage den Biodiversitätsverlust zu stoppen. Agrarbiodiversität ist, um eine nachhaltige Bewirtschaftung unserer Landschaft zu gewährleisten, essentiell. Wir müssen die verbleibende Biodiversität schützen um die Nahrungsmittelsicherheit in der Zukunft zu gewährleisten. Agrarumweltmaßnahmen können ihren Teil dazu beitragen in dem sie Generalisten schützen. Voraussetzung ist, es kommt zu einer breiteren Umsetzung von ökologisch sinnvoll gestalteten Maßnahmen. Diese Veränderung kann durch bessere ökologische Ausbildungsinhalte für Landwirte und finanziell attraktive Maßnahmen angestoßen werden.

CHAPTER I

GENERAL INTRODUCTION

General Introduction

1.1 BIODIVERSITY LOSS IN INTENSIVELY USED AGRICULTURAL LANDSCAPES

"As we encroach on nature and deplete vital habitats, increasing numbers of species are at risk. That includes humanity and the future we want." (UN Secretary-General António Guterres, 2021). All over the globe, biodiversity is at risk and humanity is the main driver in terrestrial, freshwater and marine ecosystem destruction (IPBES, 2019). Agricultural activity is, after over-exploitation, the second most prevalent threat to biodiversity (Maxwell et al., 2016).

Biodiversity is the "variability among living organisms from all sources, including, inter alia, terrestrial, marine, and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems" (http://www.cbd.int/, 1992). One problem with biodiversity loss is, that we are dependent on ecosystem services provided by nature, for example pollination, timber, waste recycling and fuels (Daily, 1997). Therefore, they support ecosystem services especially in agricultural landscapes, which can be categorised into four groups. The first group is supporting all other services by nutrient cycling, soil formation or primary production. Second and third services are provisioning and regulation, e.g. food and fresh water, but also coastal protection or waste processing. The fourth aspect is the cultural service, agricultural landscapes are part of our cultural identity and an important part for recreation and human wellbeing (Millennium ecosystem assessment, 2005; reviewed in Jackson et al., 2007). Biodiversity loss is reducing efficiency of those services (Hooper et al., 2012). Furthermore, recent studies proved that biodiversity can assist to tackle other major man-made problems, such as climate change, by storing more carbon in biomass and soil (Lange et al., 2015; Huang et al., 2018). As biodiversity losses are dramatic and the consequences of more losses in interaction with complex and global stressors cannot be sized (Hanski, 2005; Mace et al., 2012), we need to act now and start with conserving the remaining biodiversity in our cultural arable landscapes.

In order to have stable ecosystems, we need specific sets of species. For example, in order to sustain long-term primary production, we need species-rich plant communities. Different functional groups interact and ensure sustainable plant growth (Hector et al., 1999). Dependent on species traits and interactions, ecosystem functions are maintained. In case of species decline, ecological functions can initially be compensated by other species (functional redundancy), but will eventually fail (Reich et al., 2012). Additionally, we do not yet know which species will be crucial and how biodiversity loss will interact with abiotic factors, such as global warming (reviewed in Loreau et al., 2001).

In Europe, the modernisation and industrialisation of agriculture has led to major changes in cultural landscapes and partially decoupled the traditional interdependence between agriculture and environment (Meeus, 1993). The use of chemical fertilizer and pesticides to increase production has not only caused pollution of water, soil and air (e.g. Moss, 2008; Conway and Pretty, 2013), but also simplification of the landscapes. Former mixed farms specialized into either arable or livestock, and inorganic fertilizer enabled limited crop rotation without fallows in between. Farm size increased and natural habitats, such as field margins, ponds and hedgerows gave way to larger field sizes. Therefore, arable intensification in Europe had major negative impacts on biodiversity, reducing non-crop habitats, and the biodiversity of plants and animals (Stoate et al., 2001; Benton et al., 2003; Tscharntke et al., 2005).

In Germany, arable landscapes experienced highest decline in plant, insect and bird diversity in the last 50 years (summarized by Leopoldina, 2018). The main driver of those losses, especially concerning Red List plant species, are use of agro-chemicals, abandonment of uneconomical sites and decreasing crop diversity (Storkey et al., 2012). The regional species pool of around 300 vascular plant species adapted to arable habitats declined by more than 20 % and the cover of spontaneous arable plants in fields decreased from 30 % to 3 % (Meyer et al., 2013). Biodiversity loss in plants affects the next trophic level: Arable plant diversity is essential for insect diversity. Many specialized insects, such as bees, need a variety of floral resources throughout the year (Sutter et al., 2017) for survival and reproduction (Vaudo et al., 2015). According to one study in western Germany, the biomass of flying insects declined over 75 % in the last 27 years, raising concerns not only about ecosystem functioning, but also about species depending on those insects as a food source (Hallmann et al., 2017). As the result of losses in insect diversity and affected by intensive agriculture as well, also vertebrates are decreasing. Mean population trends of farmland birds are declining (Gregory et al., 2005; Sudfeldt et al., 2013; Ryslavy et al., 2020) due to increasing cultivation of energy crops (e.g. maize and rape seed) and decreasing amount of grassland and fallows (Busch et al., 2020). Characteristic species, such as lapwing (*Vanellus vanellus*), skylark (*Alauda arvensis*) and partridge (*Perdix perdix*) have suffered population declines by up to 89 % since 1990 (Ryslavy et al., 2020).

1.2 AGRI-ENVIRONMENTAL MEASURES AND POLITICS

Over the last 50 years, there has been increasing political recognition of the need to counteract the increasing problem of biodiversity loss due to agriculture in Europe, including intensification and abandonment of farmland. In 1962, the EU initiated the Common Agricultural Policy to battle supply shortages and volatile food prices. 1985, negative impacts of agriculture on the environment were addressed in a Green Paper (Commission of the European Communities, 1985) for the first time, and reformed agri-structures policy included first measures for environmental protection. Other initiatives were taken to tackle specific problems, such as eutrophication. For example, the European Nitrates Directive was issued in 1991, with the aim to prevent further local increase of nitrate contamination of water (Musacchio et al., 2020). Since 1992, all EU member states are required to implement voluntary agri-environmental measures, co-financed by the EU (Council Regulation 1992). These measures could be quite variable and Germany initially focused on schemes to reduce agrochemical emissions and not wildlife and habitat conservation (reviewed in Kleijn and Sutherland, 2003).

Some federal states introduced programs aimed to generate additional farm income by measures with lower requirements, while others introduced restrictive measures with ecological targets. Participation in regions with good soils or high concentrations of livestock farming, however, was low. Additional measures, not funded by the EU and aiming at water protection areas and nature reserves, were also available (reviewed in Ostenburg, 1999). In 2002, payments for farmers in the EU were divided into a first and second pillar. First pillar payments were direct payments to farmers for producing different crops. The second pillar financed rural development, combining different already existing measures for coping with socio-economic and environmental needs (EU, 2000). However, funds allocated from the first into the second pillar stayed low (Dwyer et al., 2007). Since 2003 direct payments under the first pillar for farmers are linked to ‘Cross Compliance’ ensuring that standard rules in the EU, e.g. the European Nitrates Directive, are applied by farmers (Isermeyer, 2003). Other approaches try to raise awareness among farmers with respect to environmental issues, e.g. by offering training opportunities for local farmers on the subject of biodiversity (Ahrenholz et al., 2011).

In 2013, first pillar payments in the EU were tied even more to environmental issues. Farms above a certain size now only receive full payments from the first pillar if they dedicate 5 % of their arable land to so called ecological focus areas. In Germany, ecological focus areas were legally implemented in 2015. Different ‘greening measures’, including obligatory crop rotation, grassland maintenance, and more specific agri-environment measures, aimed at climate change mitigation and biodiversity conservation, were established as equivalent to ecological focus areas (BMEL, 2015). Administrative and economic considerations lead many farmers to implement measures, such as catch crops instead of buffer strips, which are considered more beneficial for biodiversity (Zinngrebe et al., 2017).

EU policy tries to balance the interests of many different groups, environmentalists, farmers and Member States. Especially the ‘5 % greening’ concept is controversial (Matthews, 2013). Many environmental ambitions got watered down during the reform process (Alons, 2017). Even though there is evidence that the continuous decline in biodiversity was slowed down for some groups (Carvalheiro et al., 2013), many measures seem to show little to no effects on biodiversity (Kleijn and Sutherland, 2003). Despite several reforms of agricultural policy, agriculture as a whole is still regarded as unsustainable in the EU (European Environment Agency, 2002; Agovino et al., 2019; Pe'er et al., 2020).

1.3 FURTHER ACTIONS ARE NEEDED

A general problem concerning agri-environmental schemes is that implementation of a measure does not guarantee that the aim of biodiversity protection will be achieved (Kleijn and Sutherland, 2003). There is clear evidence that, despite all the measures taken, intensive agriculture continues to erode environmental health (EEA, 2015). Recent studies, e.g. on grassland, attest the failure of measures on biodiversity (Kaligarič et al., 2019), while others are slightly more optimistic. For example flower strips can provide temporary nectar resources, promoting local pollinators (Aviron et al., 2006; Jönsson et al., 2015; Ouvrard et al., 2018). However, effectiveness depends on the definition of the target and then other environmental factors, such as landscape heterogeneity, play an important role (Tscharntke et al., 2005). Especially in simple cropland, measures enhance biodiversity by providing additional suitable habitats. Structurally diverse landscapes, with a variety of semi-natural habitats, are already specie-rich and additional measures often do not provide further advantages for biodiversity (Batáry et al., 2011). While the ecosystem service target can be met by promoting common species in agricultural landscapes, conservation targets of rare species are harder to achieve (Scheper et al., 2013). Locally adapted measures, aiming at specific target organism groups, might help increase effectiveness.

Furthermore, despite the introduction of different programmes to promote biodiversity in agriculture in the federal states, many farmers are reluctant to implement voluntary agri-environmental measures on their land due to administrative and regulatory barriers (Joormann and Schmidt, 2017). Farmers' attitudes towards nature and biodiversity differ, and only highly motivated farmers are willing to implement more complex, or “dark green”, measures, demanding substitutional changes in management (Wilson and Hart, 2001). Farmland accounts for 50 % of area in Germany with conventional agriculture dominating (Statistisches Bundesamt, 2021), therefore, mainstreaming of existing dark green measures is needed to reach large areas. In order to reach that goal, economic and socio-economic aspects need to be considered to remove concerns of farmers (reviewed in Pe'er et al., 2020).

In order to counteract declining biodiversity, we need (a) more measures implemented in intensive and extensive farm land (Oppermann et al., 2020), which are (b) better designed to target specific species (Batáry et al., 2015). Furthermore, measures need to be (c) better positioned in the landscape – in terms of connectivity, synergies, covering target populations (Batáry et al., 2011) – either through training of farmers or through advisors-

1.4 PROJECTS AIMING TO IMPROVE MEASURES FOR BIODIVERSITY

Various initiatives and research projects have been designed to improve the performance and acceptance of measures for agricultural biodiversity. Taking local conditions into account, e.g. landscape, farming system, legal requirements and ecological potential, scientist and farmers work together designing and implementing effective measures. In the following two projects with the ambition to develop agri-environmental measures that protect biodiversity, and at the same time easily integrate into normal farming practice and are economically viable, are outlined. Both projects were accompanied by academic research, including my thesis about agri-environmental measures and their effects on bioindicators, such as the diversity of plants in the soil seed bank, butterflies and carabids. Monitoring of different indicator species to valuate effects of measures (CBD, 2004) and simultaneously considering landscape characteristics and local management (Tscharntke et al., 2005) is recommended.

F.R.A.N.Z. Project: Future Resources, Agriculture & Nature Conservation (www.franz-projekt.de)

Ten farmers, representing the different regional farming practices in Germany (see Figure 1.1) and willing to try innovative and long-serving conservation measures, work together with environmental and socio-economical scientists from the Thünen Institute, Michael-Otto-Institute of the NABU (Nature and Biodiversity Conservation Union Germany) and the Georg-August University of Göttingen.

Participating farms

Farms were on average 460 ha large (± 467 ha; smallest 67 ha, biggest 1735 ha), including purely arable farms (7 farms), mixed farms with arable land and grassland for livestock (2 farms) and grassland farm with dairy livestock (1 farm). Main crops were sugar beet, maize, rapeseed, potatoes, and different cereals (for further information see Appendix Table A1.1). The majority of the measures implemented on the participating farms were financed and specified by the project. However, other measures relevant for biodiversity such as flower strips, grassy field margins or set-aside areas, were also present on some farms, related to agri-environmental programs, greening requirements (BMEL, 2015), crowd-funding projects, initiatives by local producers' associations, or experiments by the farmers themselves. If compatible with project specifications, these were also included in the data used in this thesis.

The farms are differently embedded into the landscape (see Figure 1.2, example of landscape section of two project farms), (1) defined by permanent crops like apples, grapes and plums, surrounded by high nature value areas (Figure 1.2 lower chart), (2) dominated by arable land, divided into large fields and surrounded by tall hedges (Figure 1.2 upper chart), (3) surrounded by highways and industrial and urban area, (4) characterized by small-scale heterogeneity, including grassland and forest, or (5) dominated by intensively used grassland (maps of all farms in Appendix Figure A1.1 to A1.8 and Table A1.2). Total area of agri-environmental measures account for 0.23 % to 6 % of the area within the landscape section depending on whether fields were compactly located or dispersed over several square kilometres (see Appendix Table A1.3). Therefore, each farm, while representing the respective region, is unique in its own way.

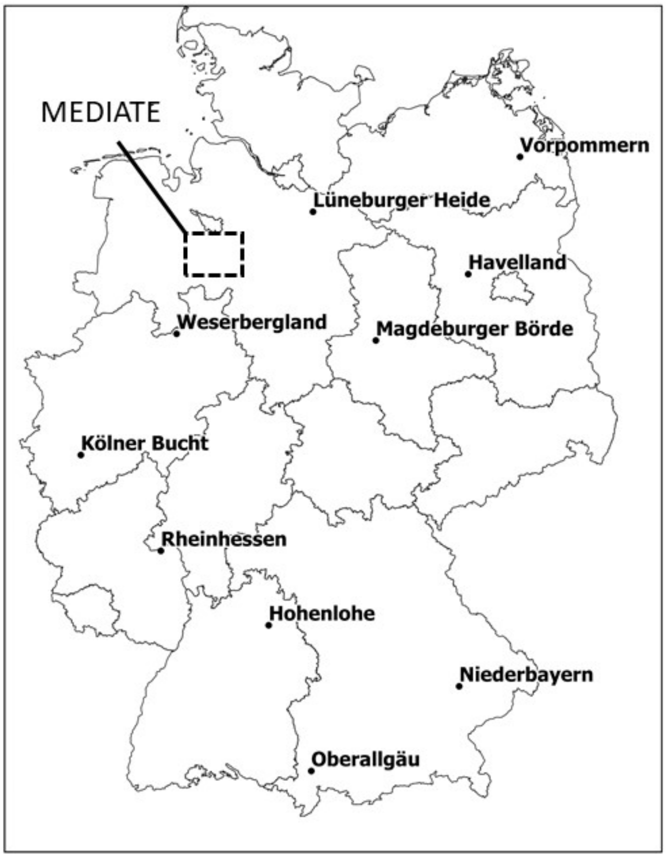

Figure 1.1: *Location of participating farms of the F.R.A.N.Z.-Project and MEDIATE landscape section.*

The study years 2017-2019 exhibited relatively extreme weather and climate conditions for Germany and mean temperature and precipitation varied between farms (see Appendix Table A1.4). In general, precipitation was highest in 2017 and lowest in 2018. The number of hot days and mean temperature was highest in 2018, followed by 2019.

Implementation of agri-environmental measures

Due to the transdisciplinary and participative nature of this project, the implementation of agri-environmental measures on each farm were adapted according to the regional context and farmer's preferences. Hence, on each farm, a variety of measures in various designs were implemented. Four groups of measures started in 2017:

(i) **flowering measures (9 farms)**: annual and perennial flower strips or areas, sown with flowering seed mixtures chosen according to preferences of the farmer and their advisors differing in size and form (smallest/largest: 0.02 ha/6.75 ha)

(ii) **integrated measures (9 farms):** cereals with increased inter-row spacing and reduced pesticide and fertiliser use, with and without undersown flowering seed mixtures and maize with green beans.

(iii) **farmland bird measures (9 farms)**: targeting mainly birds, like pea plots, strips with other crops in maize fields and skylark plots in winter cereals, but also annual fallows.

(iv) **grassland measures (5 farms):** reducing fertiliser application and mowing frequency, as well as leaving unmown strips, resulting in less intensively used grassland; exceptions: sowing of special seed mixtures and topsoil excavation.

Although not all different measures and individual sites were directly part of my studies, they were regarded within the landscape context, since in theory they provided additional nectar resources and less disturbed sites.

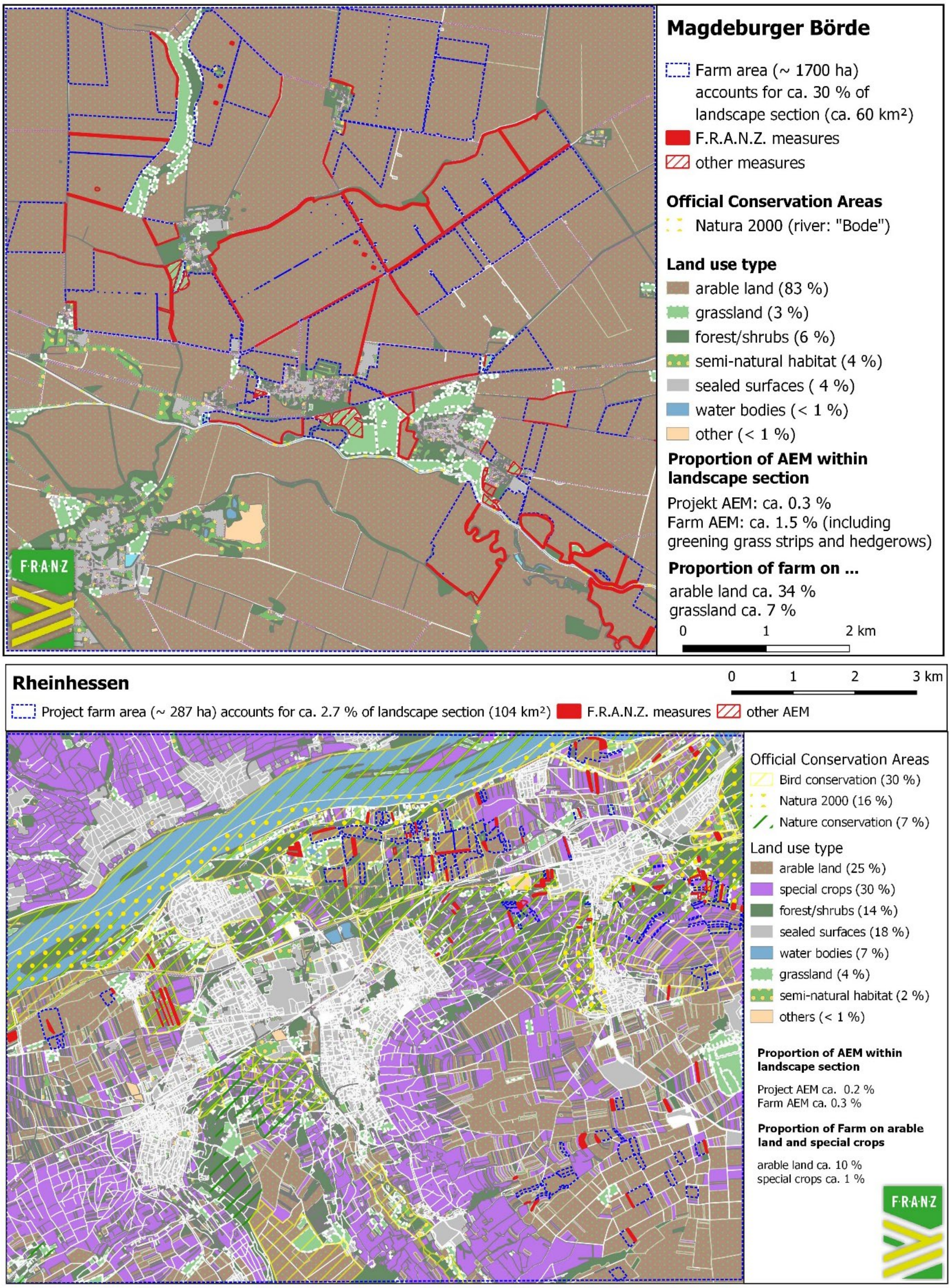

Figure 1.2: *(top) Landscape section of largest participating farm (~ 1700 ha) in the Magdeburger Börde, dominated by arable land. (down) Most dispersed farm located in fruit and wine cultivation area in Rheinhessen (areas of agri-environmental measures are displayed with bold red borders to ensure visibility).*

MEDIATE Project

The research project ‘Development of targeted and efficient schemes to increase biodiversity in agricultural landscapes (MEDIATE)’ took place from 01.01.2016 to 31.12.2019 in the districts Nienburg and Diepholz in Lower Saxony (Northwest Germany, see Figure 1.1). Funded by the German Federal Environmental Foundation, the project was led by the Thünen Institute for biodiversity and academically accompanied by the Thünen Institute for farm economics and the Department of Plant Ecology and Ecosystems Research of the University of Göttingen. On the practitioners’ side 20 local farmers and the chamber of agriculture of Lower Saxony participated. They provided part of their land and implemented different measures, all without fertilizer or pesticide use.

(i) **Conservation field margins** (Figure 1.3 right): crop cultivation with reduced sowing density (30 % to 50 %) and no fertilizer (measurement areas between 0.06 and 0.9 ha).

(ii) **Annual fallows**: annual soil disturbance (either autumn or spring, depending on neighbouring crop), no seeding (measurement areas between 0.06 and 0.7 ha).

(iii) **Alternately managed biennial flower strips** (Figure 1.3 left): sown with seed mixture containing crops, ornamental and native plant species (measurement areas between 0.04 and 0.6 ha).

The study area (Diepholz: 198,759 ha and Nienburg 139,893 ha) was dominated by intensive agriculture. More than 60 % of both districts are agriculturally used land with maize, wheat, potato, triticale and rapeseed as main crops (Landesamt für Statistik in Niedersachen). Arable field sizes ranged from 1 to 20 ha (mean field size 5.5 ha) and agri-environmental measures ranged between 0.02 and 0.9 ha. On average 5 % of the arable field was managed as agri-environmental measures. All measures were implemented on the edge of arable fields and many study sites were next to ditches or small patches of forest, however, locations of measures were dispersed.

Figure 1.3*: (left) Alternately managed biennial flower strip; (right) conservation field margin with extensive cereals.*

In order to evaluate the projects and to draw conclusion on effectiveness of implemented agri-environmental measures, monitoring of different indicator species is recommended (CBD, 2004). Furthermore, differences in landscape characteristics and local management need to be taken into account (Tscharntke et al., 2005). As part of my thesis, three studies were conducted investigating the effects of agri-environmental measures on: (1) seed accumulation in the seed bank of arable fields; (2) butterfly diversity and abundance; and (3) carabid beetle diversity and abundance.

1.5 STUDY ORGANISMS

Plants and animals combine a unique set of species, adapted to and depending on open, human made arable landscapes. For example, arable weeds are adapted and dependent on those highly disturbed environments, since termination of arable activities would ultimately lead to replacement by other plant species. Arable weed communities are sensitive to agricultural practise (Hofmeister and Garve, 2006) and, as primary producers, play a fundamental role in supporting agrobiodiversity (Marshall et al., 2003). Since soil seed banks of arable weeds reflect (1) the long-term effects of farming practice, filtering species according to their sensitivity, and (2) the weed community established in the previous seasons (Rotchés-Ribalta et al., 2020), changes in the seed bank are a good indicator for ecological effects of measures.

Another indicator for biodiversity are butterflies. They are easy to monitor using standardised methods (Pollard and Yates, 1994) and their popularity and appeal helps in the communication of biodiversity conservation (Kühn et al., 2008). Furthermore, butterfly populations, representative for other insects, react fast towards changes in their environment (Thomas, 2005). As herbivorous species, nectar and larval food plant quality and quantity are essential for butterflies (Murphy et al., 1983; Fartmann and Hermann, 2006) and agri-environmental measures have the potential to increase the availability of both.

Carabid beetles, in contrast to butterflies, are characterized by different trophic guilds, including herbivorous, omnivorous and carnivorous, reacting to other aspects of their environment es well, e.g. prey and seed availability (Lovei and Sunderland, 1996). Their usefulness as indicator is controversial, since common species present in farmland seem quite robust towards changes in agricultural management (Duelli et al., 1999). They do however react to landscape heterogeneity and especially stable overwintering sites seem to be important (Purtauf et al., 2005). Therefore, perennial measures could have an impact on the abundance of carabids.

Arable weeds, butterflies and carabid beetles display through their diversity and abundance different aspects of a healthy agroecosystem. They reflect long- and short-term changes in agricultural practise and are therefore good bioindicators to evaluate the effect of agri-environmental measures.

Arable weeds – Soil seed bank

There are around 4,305 vascular plant species in Germany (Metzing et al., 2018) of which 280 are considered as arable weed species. Some of those species are apophytic, native plants (e.g. *Juncus bufonius* or *Stellaria media*), however most are non-native, anthropochoric species, introduced by humans due to farming. Archaeophytes (e.g. *Urtica urens*) originated from the near east or Mediterranean bevor 1492, while neophytes (e.g. *Conyza canadensis*), often originating in America (Hofmeister and Garve, 2006), arrived thereafter. 'Weeds' are not only in general unwanted and harmful non-crop plants in fields, but also species characteristic for diverse plant communities within arable crops adapted to an environment, mainly characterized by human activity (Rademacher, 1948). In such highly disturbed environments, arable weeds increase their survival by specific trait combinations concerning dispersal, persistence, germination, emergence, biomass production and reproduction, sometimes adopting contrasting ecological strategies (Gaba et al., 2017). Dispersal and persistence in the form of diaspores is one strategy, how weeds survive. Their persistence in the soil seed bank is important for maintaining plant diversity in arable fields (Harper, 1977). To survive adverse conditions, plants developed two main strategies; therophytes survive through seeds and geophytes survive by means of different underground structures, such as bulbs, rhizomes and persistent roots (Hofmeister and Garve, 2006).

Arable plants have to adapt their reproduction cycle according to the short crop cultivation period. They can either form transient (less than one year), short-term (up to five years) or long-term (more than five years) persistent seed banks (Thompson et al., 1997). Many different factors influence the life story of a seed (see Figure 1.4). After harvest in summer or autumn, depending on the crop species, tillage terminates any further growth. After shedding large numbers of seeds in a short amount of time, some seeds will be translocated into deeper soil layers, e.g. through agricultural activity, while others remain on the surface. Some seeds remain dormant for a long time, spreading risk of unsuitable conditions during development in time. Other seeds germinate as soon as favourable conditions, such as rain, occurs. While germinating seeds face the risk of termination by agricultural practice (e.g. tillage, pesticides) or changing environmental conditions (e.g. drought), dormant seeds are preyed on by granivorous insects and birds (summarized by Moles and Westoby, 2006; Leck, 2012).

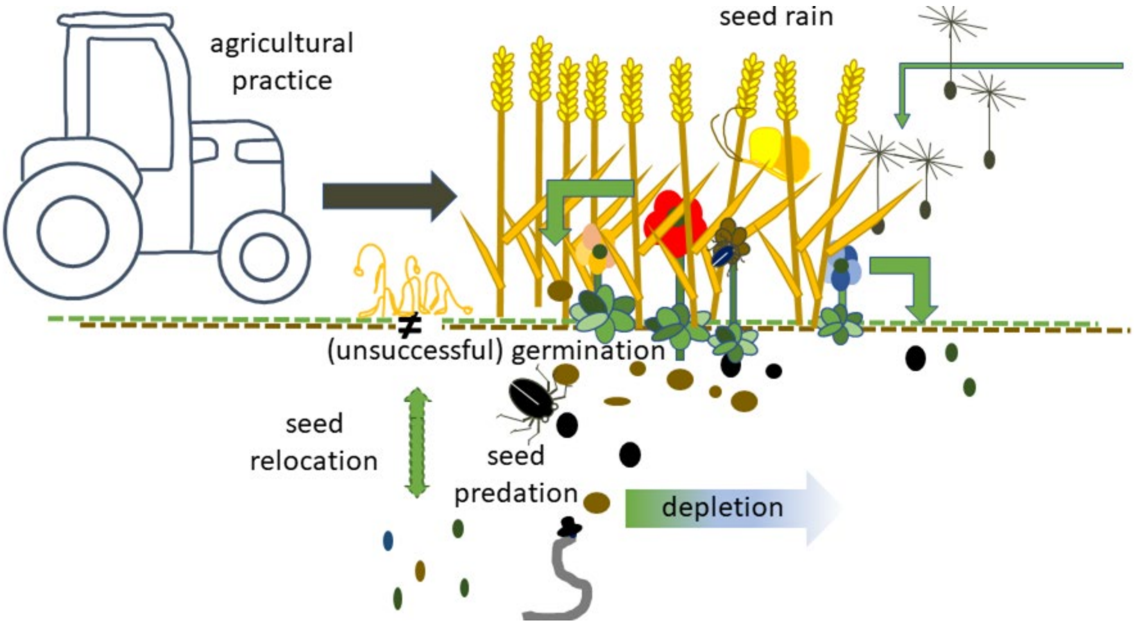

Figure 1.4: *Soil seed bank accumulation through seed rain from arable weeds on the field and neighbouring habitats. Seed bank depletion by micro- and macroorganisms, e.g. seed eating beetles. Crop cultivation, including summer or winter crops, pesticide use and date of harvest determines length of vegetation period for arable weeds. Above-ground vegetation is not identical to species composition in the weed seed bank. Many seeds get buried deep in the soil or are killed after germination due to tillage and application of pesticides.*

Arable weed species are becoming increasingly rare (see Figure 1.5). Since 1950 many specialized arable plant species have been lost (Meyer et al., 2013). Reasons are a reduced number of cultivated crops and increasing cover of cultivated crops, as well as use of pesticides, artificial fertilizer (Andreasen and Streibig, 2011) and improved seed cleaning processes during crop production (Spahillari et al., 1999) reduced arable weed diversity further. Unfortunately, not only above ground vegetation, but also the soil seed bank has become impoverished (Andreasen et al., 2018).

Soil seed banks are important for restoration and survival of plant communities (Moles and Westoby, 2006; Leck, 2012). Plants play a fundamental role in supporting agrobiodiversity, many insects and birds rely on foliage, flowers or seeds produced by arable weeds (Marshall et al., 2003), though quality, management and harvest have a high impact on the availability of seeds and foliage (reviewed in Vickery et al., 2009). Conservation of diverse arable plant communities is essential for insects, such as wild bees, butterflies and carabid beetles and also farmland birds.

Butterflies

There are more than 18,000 butterfly species (Order Lepidoptera) described world-wide (van Nieukerken et al., 2011). Most species live in the tropics, including many more non-described cryptic species (Hebert et al., 2004). Around 400 butterfly species are native to Europe and 189 species are known to inhabit forest, meadows, gardens and diverse cultural landscapes in Germany. Butterflies are popular species, well studied and not only known but mostly loved by the public. Except for a few species, e.g. *Pieris rapae* and *P. brassicae* (Hely et al., 1982), butterflies in Germany are not pest insects and prefer wild plants over cultivated crop species.

Butterflies are characterized by a complex development, including different stages with different requirements on their habitat (Fartmann and Hermann, 2006). Many lepidopteran larvae are specialist with regard to what kind of plant species or plant part they prefer. Monophagous (only eating one or a few species of the same genus), oligophagous (caterpillars eat several species of the same family) and generalists (having a broad range of food plants, but still showing preference for some plants) know without doubt, which plant to aim for with the help of their sensory system (Schoonhoven and van Loon, 2002). However, not only specific food plants are essential, but also microclimatic conditions need to be met. Sometimes, egg laying females have to choose between optimal microclimatic conditions in sparse vegetation or safe food plant resources throughout larval development in denser vegetation (Krämer et al., 2012). After larval development, caterpillars pupate and need time to metamorphose. During that time, it is crucial that the pupae are not disturbed (Huemer, 1996). When the pupal stage is successfully completed, they emerge as a butterfly and sufficient nectar resources become important for survival and further egg production (Murphy et al., 1983). Successful conservation of butterflies needs to consider the whole life cycle with its specific needs. Especially in habitats with high nutrient levels and resulting fast growth of plants in spring, microclimatic conditions might change negatively and challenge butterfly conservation in the future even further (Wallisdevries and van Swaay, 2006).

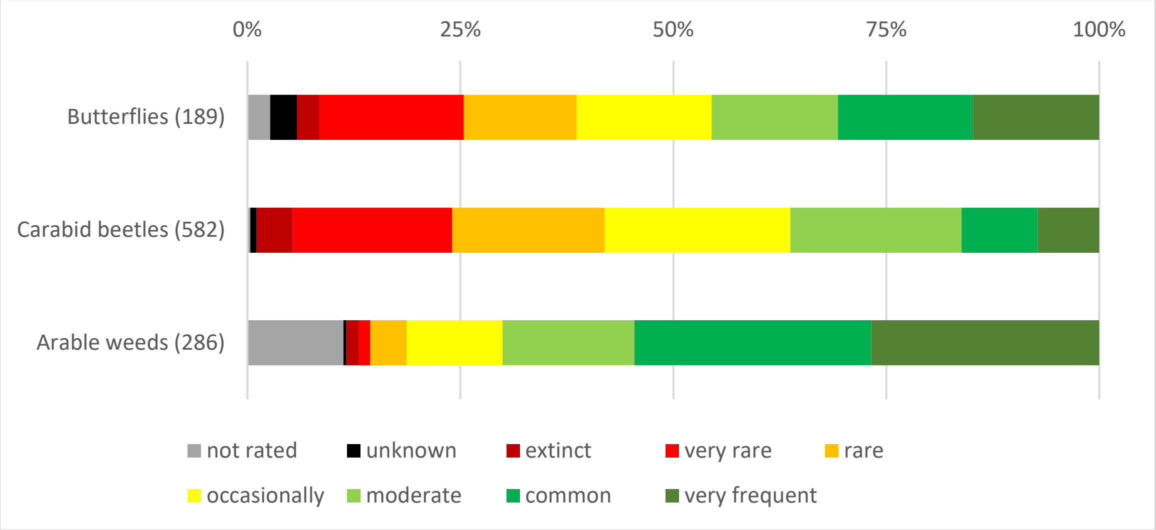

Figure 1.5.: *Proportion of butterfly, carabid and arable weed species dependent on their frequency in Germany. Data extracted from Red List sources (Reinhardt, R. and Bolz, 2011; Schmidt et al., 2016; Metzing et al., 2018) and list of arable weeds according to Hofmeister and Garve (2006).*

The strongest decline in European butterflies already happened in the 20th century (Maes and van Dyck, 2001; Wenzel et al., 2006). Major threats to butterflies in Europe are agricultural intensification, abandonment and climate change (van Swaay et al., 2010). More than 50 % of butterfly species in Germany are rare or very rare (see Figure 1.5). Due to human-made changes in landscape structures and climate, around 42 % are nowadays either extinct or endangered (e.g. *Polyommatus damon* or *Coenonympha oedippus*). Around 63 % of species are declining and only 2 % (e.g. *Pararge aegeria* or *Melanargia galathea*) show long-term increases (Reinhardt and Bolz, 2011).

Carabid beetles

Carabids populate most terrestrial habitats with about 40,000 described species. They are abundant, species-rich and can be quite colourful, making them popular research objects for professional and amateur entomologists (summarized by Lovei and Sunderland, 1996). 582 species and subspecies of carabid have been described for Germany (Schmidt et al., 2016). One of the smallest species in Germany is *Bembidion obtusum* (c. three millimetres) and *Carabus coriaceus* is the largest, reaching up to four centimetres (Trautner, 2017).

Varying carabid beetle communities develop in different habitats, depending on a variety of biotic and abiotic conditions, such as temperature and humidity, food conditions, competitors, life history and season (Lovei and Sunderland, 1996). For example, large-bodied species depend on habitats with less disturbance in order to finish their development (Kotze and O'hara, 2003). Herbivore species depend on a variety of plants and seeds (Johnson and Cameron, 1969; Talarico et al., 2016), while carnivore species hunt, for example other beetles or aphids (Forsythe, 1983). Many species, concerning their feeding guild, seem to be omnivorous and able to adapt their diet according to life stage requirements or environmental conditions. Reproduction time also varies within carabid beetles, some species reproduce in spring and are therefore most active and abundant in May, while others reproduce in autumn and have their population peak later in the year (Lovei and Sunderland, 1996). Generalist and specialist species both react to habitat changes. Therefore, they can be useful bioindicators, especially when whole species assemblages and changes within are considered. Ratio between feeding guilds, breeding time and size are indicative for habitat conditions, such as disturbance or vegetation cover (Kotze and O'hara, 2003; Rainio and Niemelä, 2003).

Ecosystem services provided by insects are essential for productivity in agriculture (Losey and Vaughan, 2006). For example, granivorous beetle species consume large amount of seeds, reducing accumulation of problematic weeds in the soil seed bank (Lundgren, 2005; reviewed in Kulkarni et al., 2015). Insect pest species, such as leafhoppers (Cicadellidae) and aphids (Aphididae) in arable crops, are reduced by carnivorous carabid species (Lang et al., 1999). In the US, the ecological services provided by insects are estimated to be around $57 billion per year (Losey and Vaughan, 2006).

Therefore, conservation of carabid beetle species in agricultural landscapes, in order to maintain those ecosystem services and reduce pesticide use is crucial.

In Germany, around 35 % of carabid species are either endangered or already extinct, while only 43 % are regarded as non-threatened nowadays (Schmidt et al., 2016). More than 60 % are rare or very rare (see Figure 1.5). So far, especially large-bodied and specialist species in open habitats associated with agriculture are declining rapidly. However, nowadays human impact on the environment puts even the species best 'equipped for survival' at risk (Kotze and O'hara, 2003). If ecosystem services are to be maintained, measures need to be taken before also common generalists are lost.

1.6 THESIS OUTLINE AND HYPOTHESES

Most studies on biodiversity measures have been conducted under experimental conditions and are highly regional, and only including 1 or 2 organism groups. Using farms participating in two applied conservation projects, I investigate the biodiversity effects of measures in real world conditions in farming systems representative for different regions of Germany. I choose different organism groups that respond to different aspects of management and landscape characteristics. The studies on seed banks and butterfly diversity took place on farms participating in the F.R.A.N.Z. project, concentrating on the effects of flower strips, extensive cereals and less intensive grassland measures. The study on carabid beetles was conducted on farms participating in the closely related MEDIATE project, comparing biennial flower strips, fallow strips and conservation field margins with cereal crops.

Chapter II: Seed bank

I tested how the seed bank developed in areas that were used as flower strips for two consecutive growing seasons in an otherwise intensively used arable landscape. Seed density and species composition were analysed to test the following hypotheses:

As crop density and pesticide dosage increase from the field edge to the field center, occurrence of weed species is suppressed with increasing distance to the edge, i.e.,

1) ***species richness and seed density decline with increasing distance to the field edge.***

Conventional tillage reduces seedling survival and leads to a continuous mixing of the soil seed bank,

2) ***species richness and seed density in the seedbank of arable land is higher in low-tilled fields, especially in the upper soil layer, compared to conventional tillage systems, with a more homogenous density distribution.***

As many plant species in a flower strip should—since the plants are generally not cut—be able to shed seeds,

3) ***the species composition and richness of flower strip seed banks differ significantly from those of arable fields after two growing seasons.***

Since plant development and seed production proceed relatively undisturbed in flower strips,

4) ***aboveground vegetation and seed banks are more similar in flower strips than in arable fields.***

Chapter III: Butterflies and agri-environmental measures

I studied the effect of agri-environmental measures implemented on ten farms located in different regions in Germany on butterfly diversity, abundance and community, taking variables like flower aspect and surrounding landscape cover into account. Furthermore, butterflies were analysed with respect to traits like mobility, flight period, voltinism and host plant specificity. My hypotheses on this topic were that:

Important food resources, such as nectar, attract butterflies towards sites with agri-environmental measures, therefore

1) ***on average more butterfly individuals and species are on sites with agri-environmental measures compared to reference areas within the intensively used landscape and species composition differs.***

Providing less disturbed and plant species-rich habitats***,***

2) ***agri-environmental measures, increase less mobile and oligophagous species with shorter flight period and fewer generations per year.***

3) ***Species diversity, abundance and composition differ among treatments. Most species and individuals occur on flower strips, followed by other agri-environmental measures such as extensive cereals and reference areas. The flowering aspect (nectar supply) generated by those measures is one main factor.***

Isolated patches surrounded by arable land only, are hard to colonize compared to measures placed in the vicinity of source habitats, such as semi-natural habitats. Therefore,

4) ***butterfly species diversity, abundance and composition are influenced by site conditions, such as small-scale habitat heterogeneity and land-use type.***

Chapter IV: Carabid beetles and agri-environmental measures

Carabid beetle activity density was measured on different agri-environmental sites, implemented as part of the MEDIATE project, and compared to reference areas in the same region. Species number, composition, activity density and trait distribution were analysed in regard to microhabitat and small-scale landscape heterogeneity. The following three hypotheses were tested:

Less disturbance, reduced input of fertilizer and pesticides after two years of implementation should have an impact on biodiversity. The applied pitfall trapping technique depends on the mobility of the beetle in the local vegetation; therefore, highly structured vegetation might lead to lower capture rates, but also to higher number of species due to higher diversity in microhabitats. Therefore,

1) ***agri-environmental measures, land-use heterogeneity and trap site conditions, such as amount of bare ground or vegetation heterogeneity, are positively correlated with species diversity and abundance (activity density).***

Measures should increase herbivore diversity, due to higher number of non-crop plant species.

2) ***Functional traits, such as food preference and size, differ between agri-environmental measures and reference sites and are also influenced by land-use and trap site heterogeneity.***

Carabid beetles immigrate, therefore neighbouring habitats, such as grassland or forest can also play a major role.

3) ***Treatments harbour different beetle communities, which are also influenced by the surrounding land-use types, heterogeneity and trap site conditions.***

In **Chapter V***,* the general state of species and trait compositions in intense farmland, the effect of agri-environmental measures and the influence of on-site and landscape conditions, concerning all three organism groups, are discussed. Similarities and differences between groups regarding their reaction towards measures are illustrated.

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APPENDIX I GENERAL INTRODUCTION

Additional information on farm characteristics

***Table A1.1:** farm size (project farm size sometimes differed from actual farm size) and main corps (% of total crop area; mean values 2017 till 2019) of participating farms; a: arable land, m: mixed, arable and grassland, g: grassland.*

Location (farm area; ha) type	Mean field size* ± sd / min; max [ha]	Rape seed	Sugar beet	Potatoes	Maize	Winter wheat	Winter barley	Spring barley	Rye	Grassland	Other
Havelland (~697) m	11 ± 10 / 0.2; 54	12			25	9	8		10	24	12
Vorpommern (~546) a	30.6 ± 31.8 / 1.1; 104.8	18	12		29	27	4			1	9
Magdeburger Börde (~1735) a	32.7 ± 31.6 / 0.1; 148.6	9	9	13	20	34	5		3	0.5	6.5
Lüneburger Heide (~187) a	6.9 ± 5 / 0.2; 18	6.6	15.6	17	2	7	7	18	4	5.3	17.5
Weserbergland (~442) m	2.4 ± 2 / 0.1; 9.6		2	5	25	8	9		1	29	21
Kölner Bucht (~395) a	10 ± 8 / 0,1; 32.1	16	13	4	4	29	0.5	30			3.5
Rheinhessen (~270) a	3.0 ± 3.2 / 0.06; 15.6	8	14			28	0.5	19	8		22*[2]
Oberallgäu (~80) g	5.5 ± 3.7 / 0.5; 17.3									100	
Hohenlohe (~184) a	4.8 ± 4.2 / 0.1; 18.4		30		3	31	28			0.5	7.5
Niederbayern (~64) a	4.9 ± 3.4 / 1.2; 10.8				32	33	20			3.3	11.7

* calculation basis are fields with crops; *[2] permanent crops

***Table A1.2:** Habitat types within area landscape section in %. SNH = semi-natural habitat. others*= water bodies and wasteland (quarries, dump sites, …) between 1-2 %; AEM: agri-environmental measures.*

	Arable land (special crops)	Grassland	Semi-natural habitat	Forest & shrubs	Sealed	Others*	AEM
Niederbayern	59	5	3	30	3	< 1	3.69
Oberallgäu		73	4	9	13	1	0.53
Hohenlohe	73	4	4	11	8	< 1	2.64
Weserbergland	41	19	5	23	11	1	4.27
Lüneburger Heide	46	5	10	29	10	< 1	6.03
Rheinhessen	25 (30)	4	2	14	19	7 % Rhein	0.39
Kölner Bucht	29	2	7	24	36	2	1.52
Magdeburger Börde	83	3	4	6	3	1	0.74
Vorpommern	59	15	4	20	2	1	1.41
Havelland	54	24	2	16	2	2	0.33

***Table A1.3:** Information to embedding of farms in the landscape, sorted by total area of landscape section in ascending order, red to green; smallest to largest values; *[1] (Numbers from 2021; partly insufficient data for 2017-2019 on non-F.R.A.N.Z. Project measures).*

	% farm area*[1]	% FRANZ measures	% AEM total	West-east [km]	Nord-south [km]	area landscape section [km^2]
Niederbayern	29.20	2.97	3.69	1.68	1.35	2.3
Oberallgäu	12.38	0.53	0.53	1.76	3.78	6.6
Lüneburger Heide	18.80	1.05	2.64	3.02	3.12	9.4
Vorpommern	42.59	3.90	4.27	3.28	4.16	13.6
Havelland	34.65	3.16	6.03	3.26	6.13	20.0
Hohenlohe	4.28	0.39	0.39	8.47	4.78	40.5
Kölner Bucht	8.69	0.70	1.52	9.15	4.90	44.8
Weserbergland	6.31	0.23	0.74	5.52	8.90	49.3
Magdeburger Börde	28.40	0.35	1.51	7.79	7.73	60.5
Rheinhessen	2.71	0.23	0.33	8.91	11.94	106.0

Landscape sections

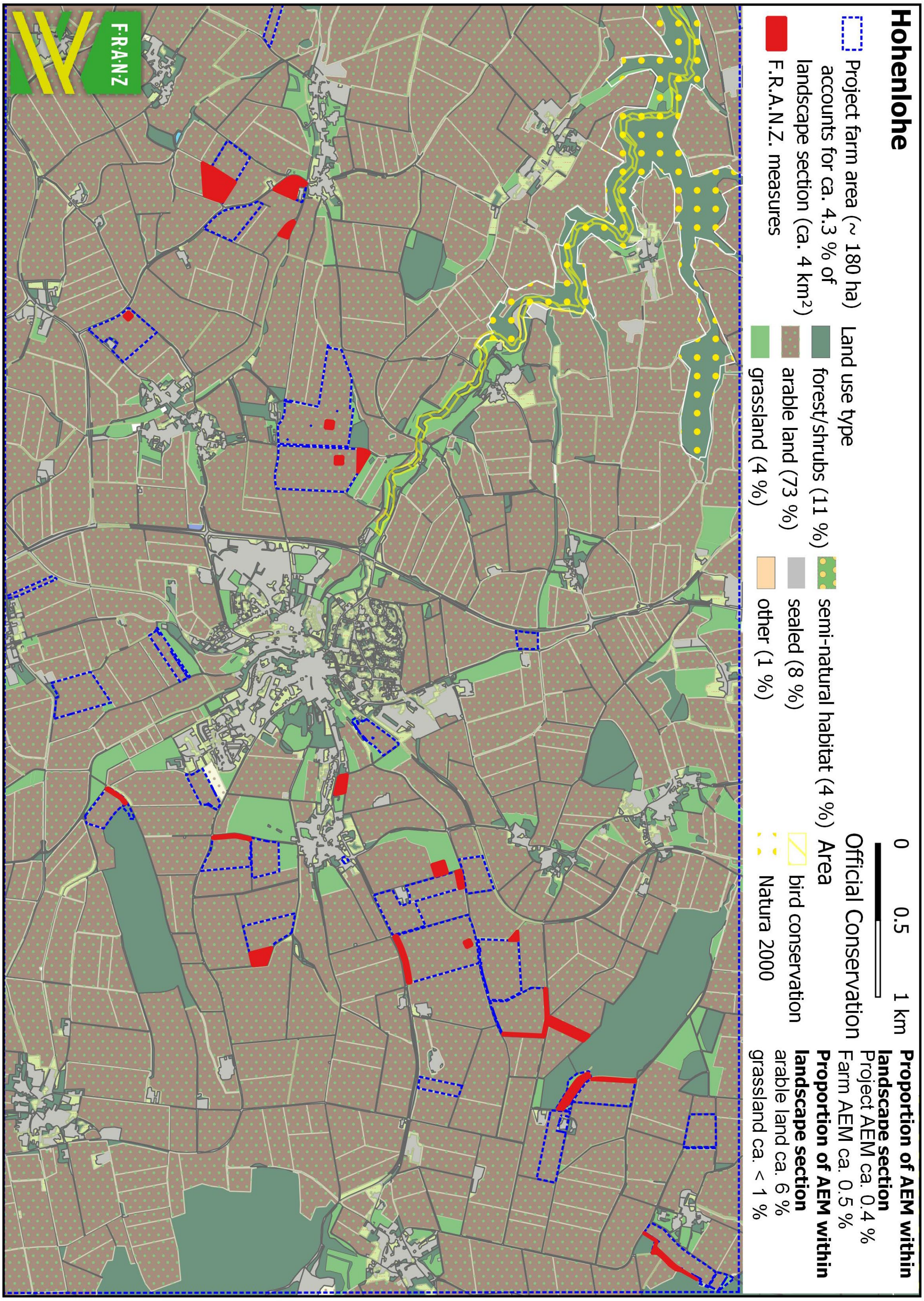

Figure A1.1: *Landscape section of F.R.A.N.Z. farm in Hohenlohe, %; AEM: agri-environmental measures, measures displayed with thick edges for better visibility.*

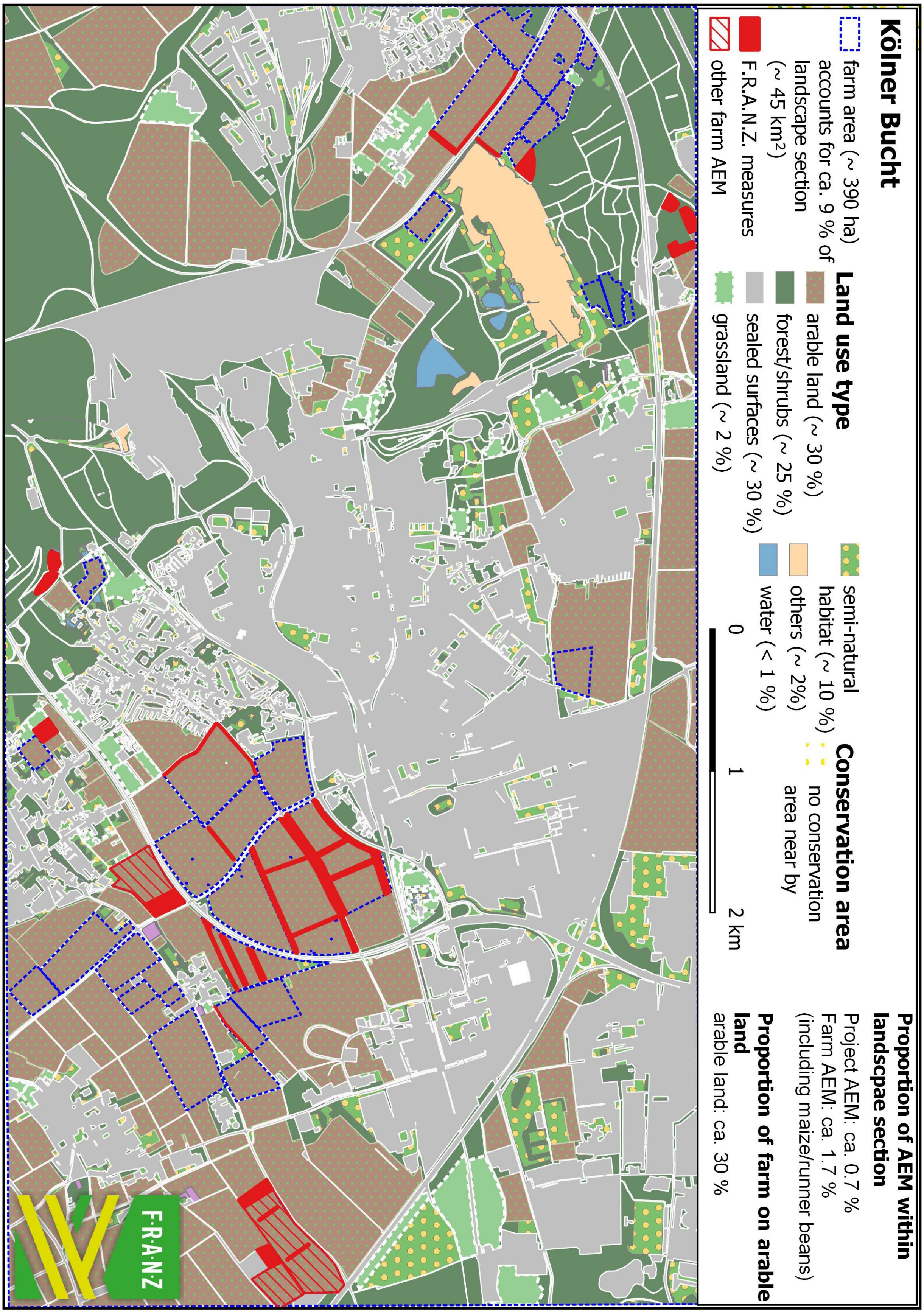

Figure A1.2: *Landscape section of F.R.A.N.Z. farm in Kölner Bucht; AEM: agri-environmental measures, measures displayed with thick edges for better visibility.*

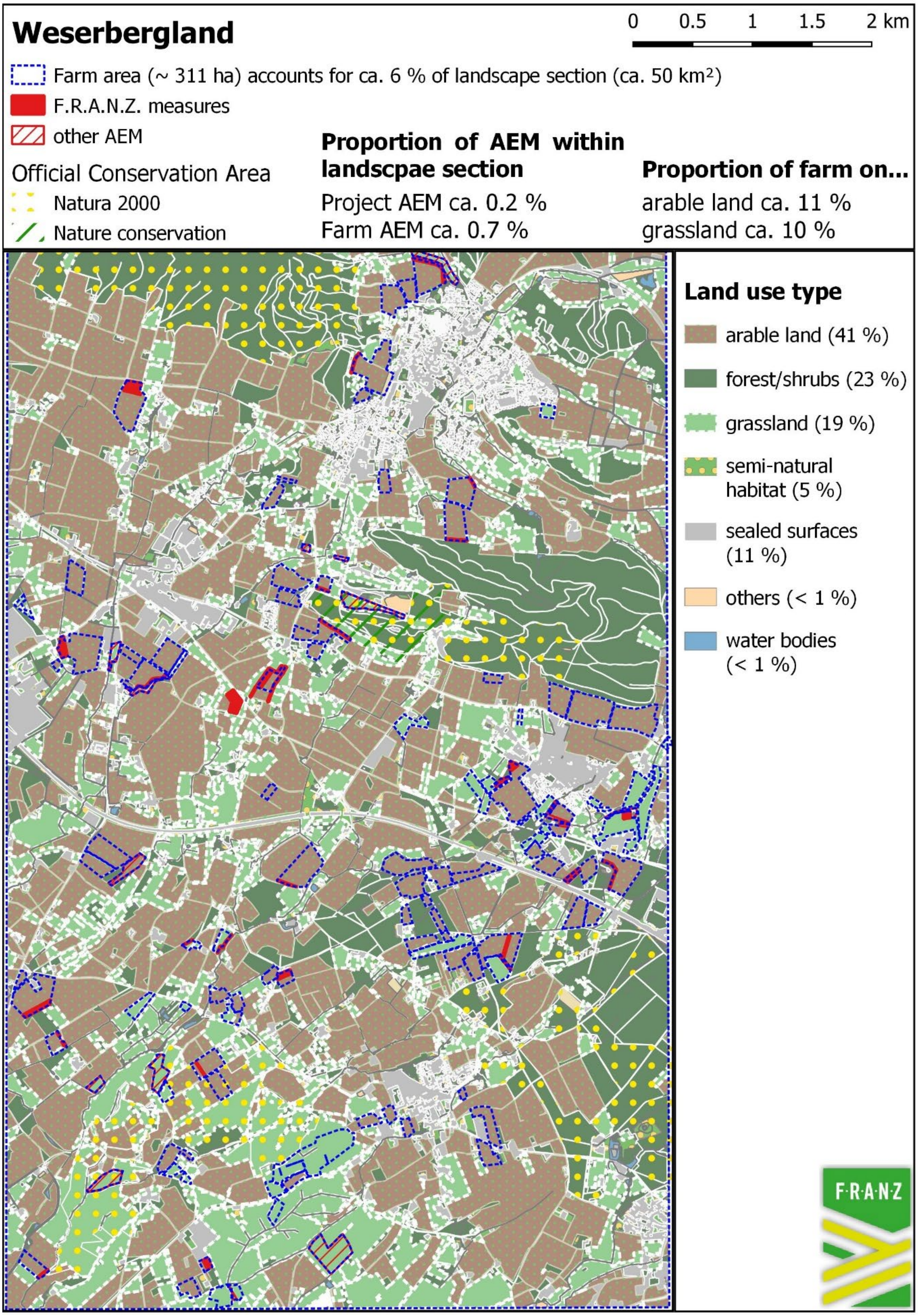

Figure A1.3*: Landscape section of F.R.A.N.Z. farm in Weserbergland, AEM: agri-environmental measures, measures displayed with thick edges for better visibility.*

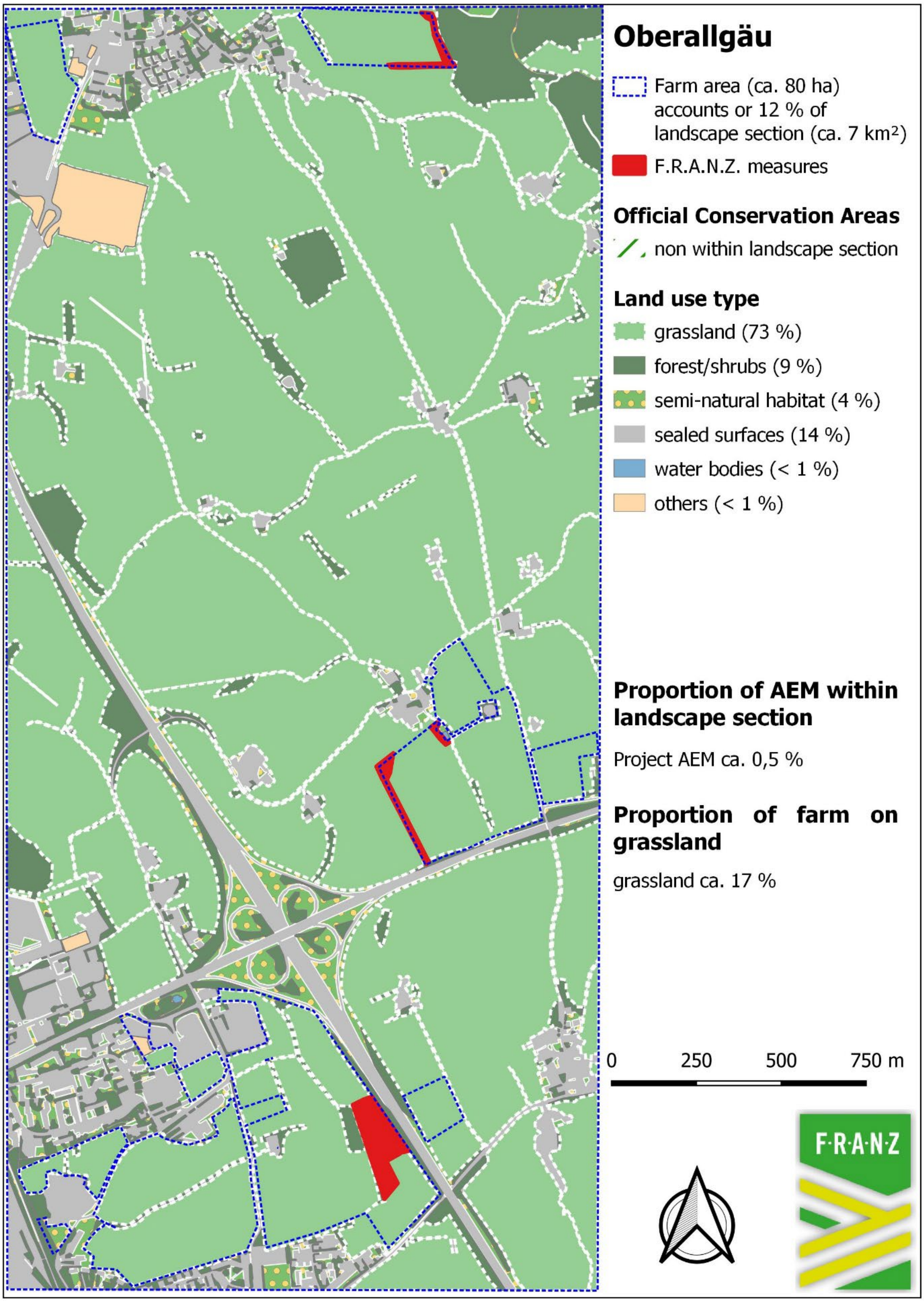

Figure A1.4: *Landscape section of F.R.A.N.Z. farm in Oberallgäu, AEM: agri-environmental measures, measures displayed with thick edges for better visibility.*

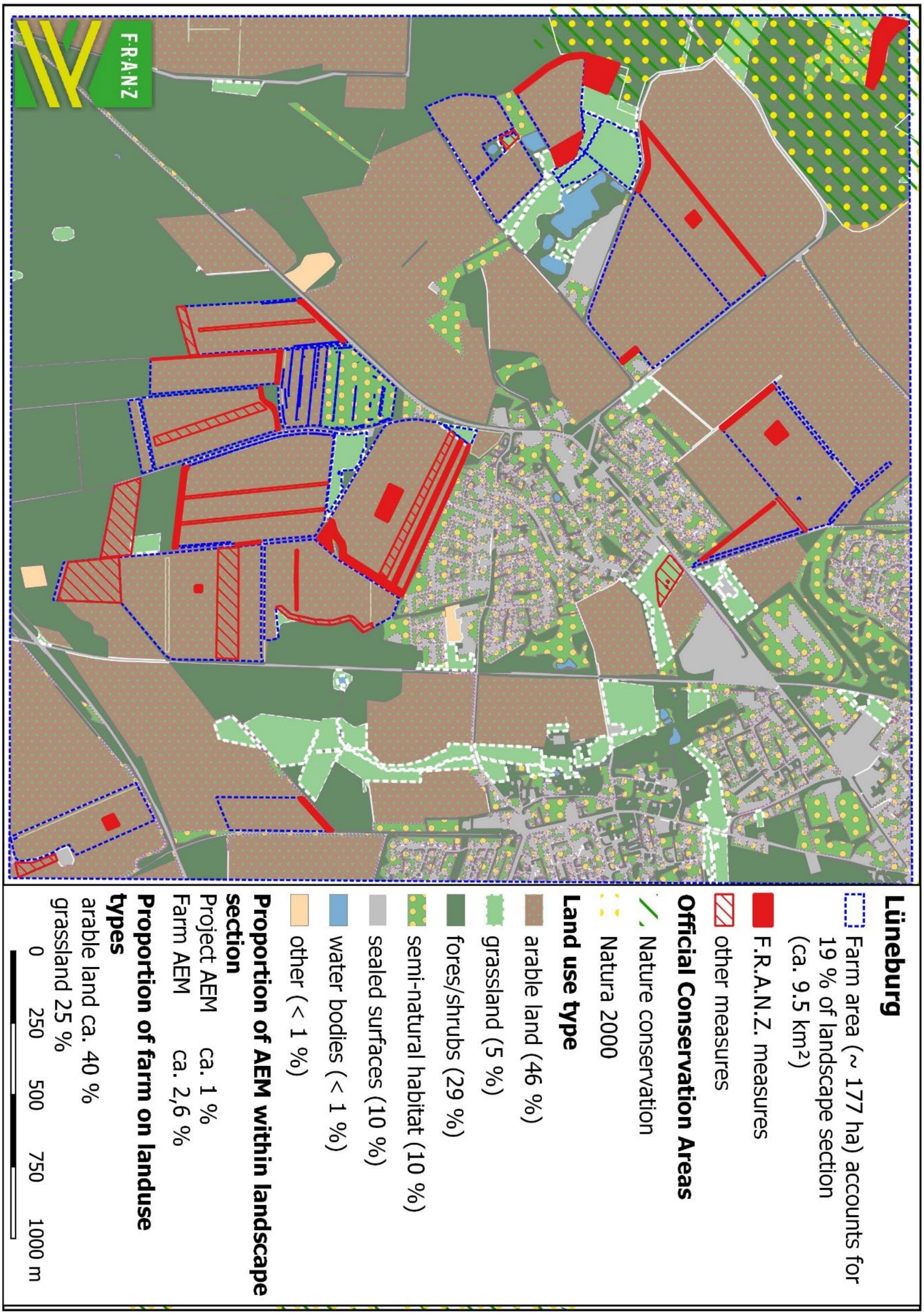

Figure A1.5: *Landscape section of F.R.A.N.Z. farm in Lüneburger Heide, AEM: agri-environmental measures, measures displayed with thick edges for better visibility.*

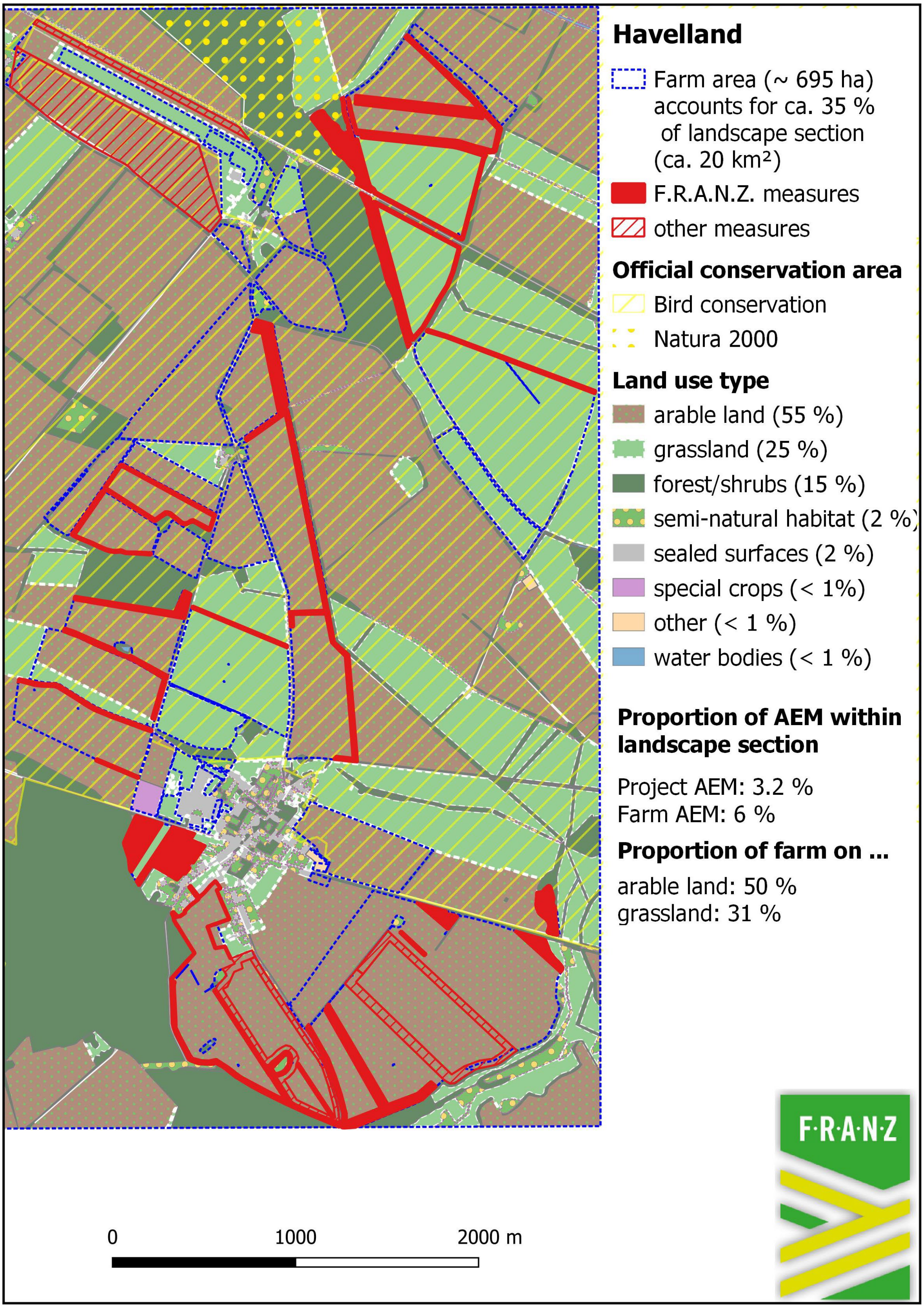

***Figure A1.6**: Landscape section of F.R.A.N.Z. farm in Havelland, AEM: agri-environmental measures, measures displayed with thick edges for better visibility.*

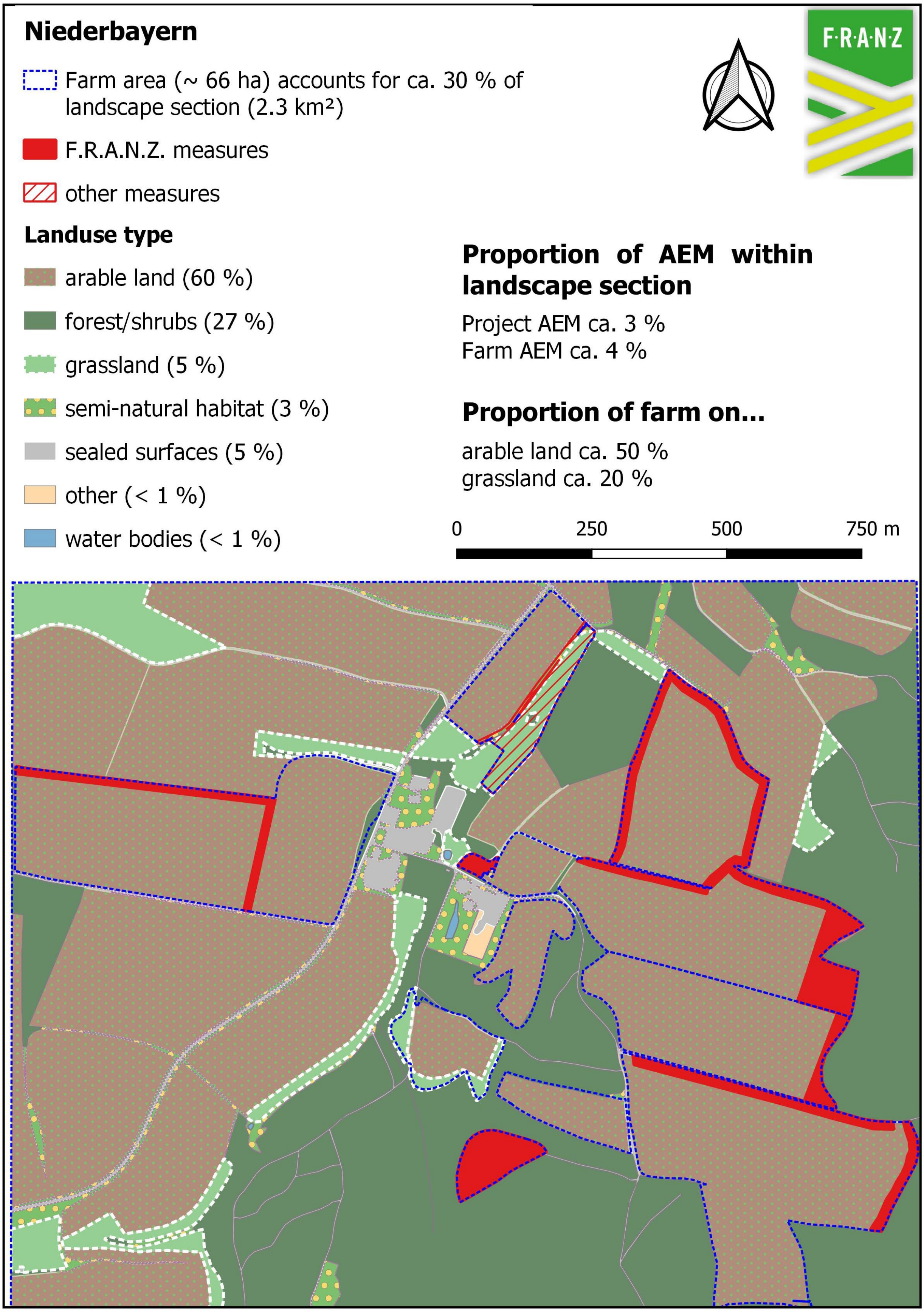

Figure A1.7: *Landscape section of F.R.A.N.Z. farm in Niederbayern, AEM: agri-environmental measures, measures displayed with thick edges for better visibility.*

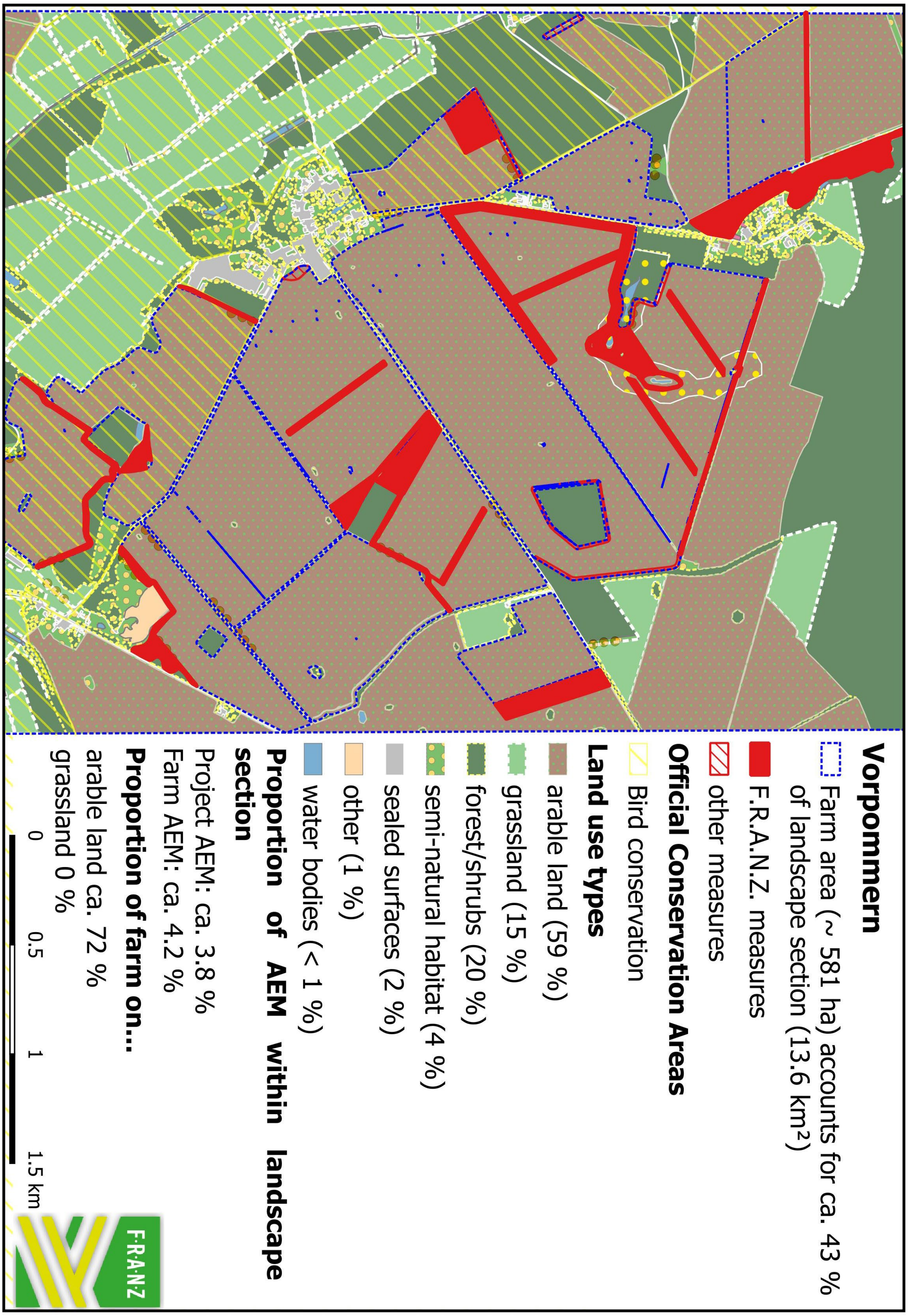

***Figure A1.8**: Landscape section of F.R.A.N.Z. farm in Vorpommern. , AEM: agri-environmental measures, measures displayed with thick edges for better visibility.*

Additional Information on climate

Table A1.4: *precipitation [mm], number of hot days (temp. > 30°C) and mean temperature [°C]; source: grid data from Deutscher Wetterdienst, climate data centre.*

	Precipitation [mm]			Number of hot days			°C mean temperature		
	2017	**2018**	**2019**	**2017**	**2018**	**2019**	**2017**	**2018**	**2019**
Niederbayern	776	627	658	14	23	16	9.2	10.4	9.9
Oberallgäu	1510	1051	1441	6	8	11	8.3	9.2	8.7
Lüneburger Heide	871	459	645	1	23	19	9.9	10.7	10.7
Vorpommern	757	370	528	1	15	12	9.4	10.1	10.5
Havelland	726	315	480	3	26	25	10.2	11.1	11.3
Hohenlohe	831	646	818	10	28	17	10	11.1	10.6
Kölner Bucht	697	529	653	11	22	19	11.6	12.2	11.9
Weserbergland	905	621	794	4	19	18	10.3	10.8	10.6
Magdeburger Börde	578	323	488	1	15	12	10.3	11.2	11.2
Rheinhessen	509	401	471	16	32	25	11.5	12.5	12
Mean values	**816**	**534**	**698**	**7**	**21**	**17**	**10.07**	**10.93**	**10.74**

CHAPTER II

WEED SEED BANKS IN INTENSIVE FARMLAND AND THE INFLUENCE OF TILLAGE, FIELD POSITION AND SOWN FLOWER STRIPS

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Weed seed banks in intensive farmland and the influence of tillage, field position and sown flower strips

2.1 ABSTRACT

Agricultural intensification has caused once diverse arable fields to become species-poor. Their seed banks, which are fundamental for re-establishment and maintenance of plant communities in such repeatedly disturbed environments, are now largely depleted. In order to advise farmers on the successful implementation of agri-environmental measures, as well as reduce potential subsequent costs of continued weed control, understanding seed bank dynamics in relation to aboveground vegetation is essential. We (1) investigated the change in seed bank composition in the field edge and the interior, and (2) analyzed the seed bank in flower strips and adjacent fields in relation to the aboveground vegetation on intensively managed arable farms across Germany. Low-tillage systems contained more plant species and higher seed densities in the seed bank than regularly ploughed fields. Species diversity at the field edge was higher than in the field interior, with a continuous decrease in the number of species and seed density within the first 2 m from the edge. Flower strips can lead to an enrichment of the seed bank, but it is driven by the strong rise in a few common species such as *Chenopodium album*. To cultivate successful flower strips, we recommend close onsite monitoring, as well as rapid intervention in the case of weed infestation.

Keywords: Agrobiodiversity, arable weeds, field edge, field interior, seed bank, segetal plants, tillage

2.2 INTRODUCTION: WEED SEED BANK IN INTENSIVE ARABLE LAND

Floral diversity stabilizes ecosystem functions and provides food for many herbivorous organism groups (reviewed in [1]). Arable fields, constantly shaped by human activities, were once species-rich ecosystems in the cultural landscapes of Central Europe [2]. However, increasing use of herbicides and mineral fertilizers, frequent disturbance by tillage, reductions in crop diversity, and the shift to more productive crops have dramatically reduced the occurrence of many arable plant species [3]. Currently, a large part of the once species-rich arable flora of Central Europe has been lost [4], and predominantly nitrogen-demanding species have persisted [5].

To counteract a further decline in agrobiodiversity, numerous agri-environmental schemes have been implemented by the European Union as part of the Common Agricultural Policy. The effect of agri-environmental schemes on plant diversity depends, among other factors, on the species pool present in the soil seed bank [6]. It has been demonstrated that flower strips, conservation field margins, and fallows can increase arable weed species in intensively farmed landscapes [7], but may also enhance insect diversity [8]. However, such measures make up only a very low proportion of the farmed area. Many farmers have voiced their reluctance to implement measures to increase biodiversity in agricultural landscapes for various reasons [9–11]. Furthermore, the ecological effects of agri-environmental schemes are debated, and it is questioned if existing schemes are sufficient to stop or even reverse biodiversity loss in intensive agricultural landscapes [12].

The currently dominating arable weed species are mostly highly competitive annual species, causing problems in agriculture. Their predominance depends on various factors of arable management, such as the tillage system, fertilizer, and herbicides applied [4,13]. For most arable species, a diaspore bank supports their persistence even in these highly disturbed environments [14,15]. The aboveground weed vegetation that develops out of the seedbank depends on crop rotation and the current management regimes [16]. Measures of weed control prevent successful establishment and seed production of arable weeds. Depending on the strength and effectiveness of weed control, the aboveground vegetation is, therefore, largely controlled by the composition of the seed bank in the soil [17].

Conventional tillage, which uses ploughing to turn the soil, and low-tillage techniques, i.e., shallow non-turning soil cultivation practices that use harrows, affect the composition and density of seed banks differently [18]. In central Europe, there has been a widespread transition from conventional tillage to low- or no-tillage systems in order to reduce carbon and soil losses through increased soil respiration and erosion [19]. This not only influences the vertical distribution of diaspores, but also leads to an increase in herbicide application that compensates for the loss of mechanical weed control measures [20]. In general, seeds are not evenly distributed in the soil whether vertically or horizontally [21]. This is particularly true for heavily disturbed ecosystems such as cropped fields. Arable weeds are particularly frequent at the field edge, which should also influence the seed rain and, therefore, composition of the soil seed bank [17,22–25]. Along field edges, arable weeds profit from lower herbicide and fertilizer input [26]. Furthermore, there should be a higher diaspore input at the field edge from neighboring habitats, such as grassy field margins, hedges, or forests [27], which may further influence the vegetation and seed bank.

The dynamics of aboveground vegetation and the related soil seed bank of arable weeds is well studied (e.g., [28]). However, their interaction with flower strips has rarely been addressed. Studies on seed banks and agri-environmental measures often focus on grassland, forest, or wetland restoration (e.g., [29,30]). Investigations on the accumulation of sown flower species in the seed bank and their possible implications for weed control and nature conservation are missing. We argue that increased acceptance of agri-environmental measures by both farmers and conservation practitioners requires a better understanding of the dynamics of the seed bank of those measures. Not only is the enrichment of problematic weed species an issue, but so is the lack of success in re-establishing certain endangered weed species [31]. We, therefore, assessed the seed bank composition of arable fields and flower strips at farms across Germany, which were part of the F.R.A.N.Z. project (https://www.franz-projekt.de/). In this way, we were able to compare the effects of different agricultural management systems and of flow-er strip establishment on seed bank composition.

Specifically, we addressed four hypotheses. Firstly, as crop density and pesticide dosage increase from the field edge to the field center, occurrence of weed species is suppressed with increasing distance to the edge, i.e., **species richness and seed density decline with increasing distance to the field edge**. Secondly, since conventional tillage reduces seedling survival and leads to a continuous mixing of the soil seed bank, **species richness and seed density in the seedbank of arable land is higher in low-tilled fields, especially in the upper soil layer, compared to conventional tillage systems**, with a more homogeneous density distribution. Thirdly, as many plant species in a flower strip should—since the plants are generally not cut—be able to shed seeds, **the species composition and richness of flower strip seed banks differ significantly from those of arable fields after two growing seasons**. Lastly, since plant development and seed production proceed relatively undisturbed in flower strips, **aboveground vegetation and seed banks are more similar in flower strips than in arable fields**.

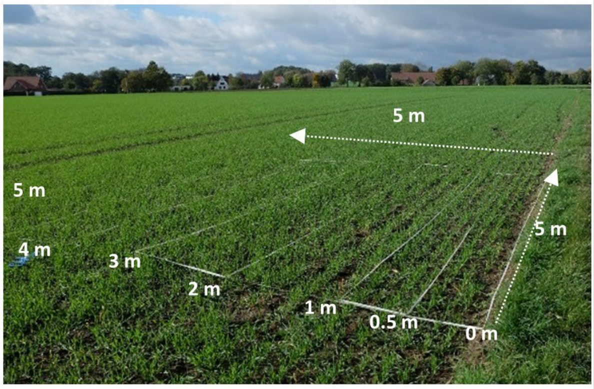
2.3 MATERIALS AND METHODS

Locations and sampling design

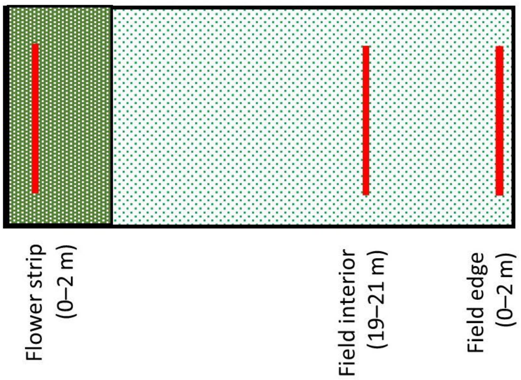
We studied intensively managed agricultural fields in seven different regions of Germany from the Baltic Sea coast to Bavaria and Baden-Württemberg in the south (see Figure 2.1a). The farms were participating in the F.R.A.N.Z. project (Future Resources, Agriculture, and Nature Conservation) which pursues a participative approach to increase farmland biodiversity in cooperation with farmers. Agri-environmental measures, established on these conventionally managed farms in different, representative agricultural landscapes of Germany, are monitored with respect to their effect on agrobiodiversity and the costs of implementation. Locations with marginal agricultural yield or known populations of species worthy of protection on farmland are identified, and options of different agri-environmental measures are assessed. In the process, issues such as accessibility, regulations, ownership (e.g., for rented land), or potential weed burden in the soil seed bank are addressed. These issues affect how the emergence of problematic and (from a conservation point of view) desirable weed species are viewed during implementation, as well as afterward, when the area is reintegrated into the normal crop rotation scheme.

All study fields were sown with winter wheat in autumn 2018 and had adjacent flower strips that varied in width (5 to 18 m) and the seed mixture used. The positioning and implementation of agri-environmental measures in the project required certain compromises in order to meet demands in terms of practicability, ecological utility, and statistical requirements.

(a) Sampling locations: Per region/farm 3 winter wheat fields with adjacent annual or perennial flower strips were sampled. Sampling scheme I (filled black dots) on three locations and sampling scheme II (dots) on all seven locations. Numbers refer to farm number in the data set.



(b) Sampling scheme I: Edge effect; 5 x 5 m plot in conventional cereals, seven transects at different distances (0 m, 0.5 m, 1 m, 2 m, 3 m, 4 m, and 5 m) to the field edge. Per transects 5 soil samples were taken (10 cm deep, 3.5 cm in diameter) and pooled.



(c) Sampling scheme II: Field position; three transects per field, each 50 m long and 2 m wide. 10 soil samples per transect, one randomly taken within every five meter subplot (20 cm deep, 3.5 cm in diameter, divided into 0–10 and 10–20 cm depth).

Figure 2.1*: Location of the seven farms in Germany (a); sampling scheme I (b) and sampling scheme II (c) in the field.*

Farms differed in size (seven farms with mean field sizes ranging from 3 to 32 ha; smallest field: 0.1 ha, largest field: 149 ha), soil quality (18–90 soil quality score), tillage regime (low-tillage N = 3, rotational tillage N = 1, and conventional tillage N = 3 farms), and main crops (cereals and maize) cultivated (see Table S1), broadly representing the spectrum of farm types and agricultural landscapes existing in Germany. Soil types in nearby unmanaged land ranged from Gleysols with poor fertility to Cambisols with relatively low to high fertility and Chernozems with very high fertility.

Winter cereals, notably wheat and barley, were cultivated on all farms, followed with lower frequency by maize and root crops such as potato and sugar beet. Low-tillage farms performed no ploughing of arable land, but used disc harrows, drag harrows, spring-tooth harrows, etc. for shallow cultivation and direct drilling in case of intercrops. Conventional tillage, practiced on three farms, implied ploughing and overturning of soil. One farm practiced rotational tillage with ploughing only after or before specific crops (not included in the analysis of tillage effects). Hereafter, diaspores of plants are referred to as seeds, although some are, in fact, fruits. Two sets of seed bank samples were taken to test the hypotheses.

Sampling scheme I edge effect: analysis of the effect of field edge

To investigate the gradient in seed density and species number from the field edge to the center of the field, sampling scheme I (Figure 2.1b) was carried out on three farms (see Figure 2.1a, black squares), located in Magdeburger Börde (farm 3), Ostwestfalen-Lippe (farm 5), and Hohenlohe (farm 6). On each farm, three freshly sown winter wheat field edges were chosen. All wheat field edges were located next to sealed roads with 0.3 to 2 m wide grassy field margins in between. Square plots of 5 m × 5 m were placed on the field edge with one square side being placed on the outermost furrow of the field. Within the plot, seven parallel transects of 5 m length and 1 or 0.5 m width were demarcated at 0, 0.5, 1, 2, 3, 4, and 5 m distance to the field edge (Figure 2.1b). Per transect, five soil samples were taken, randomly placed within each meter, using a manual steel cylinder of 10 cm length and 3.5 cm diameter (480 cm^3 soil volume). All five soil samples per transect were pooled, resulting in seven analyzed samples per field. A total area of 0.3 m^2 (to 0.1 m depth) was sampled.

Sampling scheme II field position: seed bank enrichment in flower strips

For this sampling scheme, we selected 21 winter wheat fields located on seven farms (see Figure 1.1a). On each farm, we sampled 2–3 fields with adjacent flowering strips in autumn 2018. The flower strips were established in spring 2017 and, thus, had passed their second growing season when sampled (see Figure S1). Some strips were resown in spring 2018 and were prepared during the sampling for re-seeding in spring 2019. Thus, the vegetation in these strips was removed, and soil cultivation in the form of soil-turning ploughing and chisel ploughing had been practiced. We applied a space-for-time approach and paired-sample design to account for differences between fields in terms of management history, climatic conditions, and soil properties. Seed bank sampling was conducted in three 50 m long and 2 m wide transects established in every field: one transect lay at the field edge within a flower strip, another one at a field edge without a flower strip (if possible, with similar neighboring vegetation structure), and a third one in the field interior 20 m distant to the edge (see Figure 2.1c). Each transect was divided into five subplots of 5 m × 2 m size. In each subplot, one random soil sample was taken with a cylindrical steel probe of 20 cm length and 3.5 cm in diameter. Samples were divided into depths of 0–10 cm and 10–20 cm, and then pooled for every depth within a transect, resulting in two samples per transect (960 cm^3). In scheme II, a total soil surface area of 0.6 m^2 (to a depth of 0.2 m) was sampled.

Seedling emergence method

After stratification of the samples at 5 °C in darkness in a refrigerator for 2 months, the samples were processed according to the procedure outlined by Ter Braak et al. [32]. Samples were washed through sieves (0.5 mm mesh size for gravel and twigs, and 0.02 mm mesh size for clay, while sand could not be removed); the seed material was spread out on fertilized garden soil and covered with a thin layer of sand on top. Seed germination took place in a greenhouse that was kept at 15 °C during the night and 18 °C during the day (12:12 h dark/light period). Water was added as needed. Seedlings were identified according to images given in Hanf [33] and counted. Unidentified seedlings and type individuals were repotted into separate pots for later identification and confirmation of species according to Jäger and Werner [34]. After no more new seedlings were found to emerge, watering was stopped, and samples were dried out. Six months later, a second germination procedure was started by resuming the watering cycle for an additional 10 weeks. For preparation, the topsoil layer with the samples was disturbed, and the crust was destroyed and turned over. All additionally emerging seedlings were handled in the same manner as in the previous round.

Challenges encountered in the species identification of seedlings led to the following species complexes being defined: *Matricaria spp*. and *Tripleurospermum spp*. were summarized as 'Chamomilla'; *Urtica dioica* and *Urtica urens* were classified as '*Urtica dioica/urens*'; *Papaver rhoeas, Papaver dubium*, and unidentified *Papaver spp.* were summarized as '*Papaver spp.*'; *Amaranthus spp., Epilobium spp., Euphorbia spp., Geranium spp., Juncus spp., Solidago spp*., and *Taraxacum spp*. were not determined to species level. A total of 174 seedlings remained unidentified (as they died during growth cabinet failure) and were categorized as either grass (i.e., graminoids, sedges, or rushes; 165 seedlings) or forb (i.e., non-graminoid herbaceous species; nine seedlings). Woody seedlings referred either to *Populus* or *Betula spp*., as both tree species are common within the project area. *Populus spp*. were also present with two seedlings in the control plots; however, they were not taken into account. Species were classified as forbs or graminoids, and the number of species and seedlings per group was calculated for the different localities and soil depth levels in the field.

Climatic and edaphic site factors at the sampling locations were assessed with Ellenberg indicator values of the plant species recorded [35]. To this end, we calculated abundance-weighted means. The aboveground vegetation in the transects (species composition and cover in percentage classes after Londo) was assessed by relevés recorded in summer 2018 in the 50 m × 2 m plots (for further information on sampling method, see Sutcliffe and Leuschner [36]).

Statistical analysis

To test hypotheses I and II, a subset of seed bank samples collected in scheme II was used, i.e., soil seed bank samples from three low-tillage and three conventional tillage farms. In total, these comprised 17 field edge and associated field interior plots subdivided at different soil depths. We ran linear mixed models using the '*lmer*' and '*anova*' functions of the '*lme4*' (v1.1.31) and '*lmertest*' (v3.1.3) packages [37,38] in R software [39] version 201.09.1, considering field within farm as random grouping variables, to analyze the number of species (log-transformed) and emerged seedlings (log-transformed) as a function of field location, tillage scheme, and soil depth. Subsequent pairwise comparisons using the '*emmeans*' function of the '*emmeans*' (v.1.8.2) package [40] with Tukey p-value correction for multiple testing was used to analyze differences between different soil depths. For all models, fit was evaluated with the '*simulateResiduals*' and '*plot*' functions of the '*DHARMa*' (v0.4.6) package [41]. Furthermore, in sampling scheme I (three farms with three cereal fields each), the number of species and seeds was tested for differences as a function of distance to the field edge, applying the same statistical methods to test hypothesis I. Out of the nine tested fields, one field was removed as an outlier (11 species and 167 seedings on average compared to six species and 20 seedlings per distance class; after consultation with the farmer, the plot was identified as a recent construction site), resulting in eight fields for the final analysis.

To test hypothesis III, 19 fields from seven farms investigated within sampling scheme II, which comprised transects located on field edges with flower strips or on the edge of conventional cereal fields, and in the field interior were taken. Linear mixed models using the '*lmer*' and '*anova*' functions, considering field within farm as a random grouping variable, were run to analyze the number of species (log-transformed) and emerged seedlings per m^2 (log-transformed) as a function of the field location. Subsequent pairwise comparisons using the '*emmeans*' function with Tukey p-value correction for multiple testing were conducted. The analysis was performed with all species and subsequently with the species added by the flower seed mixture excluded.

Furthermore, differences in the species composition of field edge, interior, and flower strip were analyzed employing NMDS (nonmetric multidimensional scaling [42]) using the '*metaMDS*' function from the '*vegan*' (v2.6.4) package [43] based on Bray–Curtis distances. Very abundant species were down-weighted using the Hellinger transformation [44]. Effects of farm and field location were first checked by correlation analysis using the '*envfit*' function from the '*vegan*' package, and then analyzed by pairwise PERMANOVA analysis, with Bonferroni-corrected p-values. We checked for differences in between-plot variation (beta diversity) by employing the '*betadisper*' function from the '*vegan*' package. The calculated weighted mean Ellenberg indicator values were plotted for each transect to inform about environmental conditions at the sampling site. Missing or indifferent values were substituted by average values specific for the field location. Testing of significance was performed with the ‘*envfit_cwm’* function from the ‘*weimea*’ package version 0.1.4, accounting for species abundance, and eliminating highly significant correlation values due to circular reasoning [45]. We tested for autocorrelation between individual indicator values using the ‘*cor.mtest’* function from the package ‘*corrplot*’ (v0.92) [46]. As the last step, the ‘*multipatt*’ function from the ‘*indicspecies*’ package (v1.7.12) [47] was used to identify species associated with flower strips, field edges, or the interior.

Comparisons between aboveground vegetation and seed bank (hypothesis IV) were conducted on the basis of species presence/absence data. First, the Sørensen index was calculated for every plot pair/transect (seed bank vs. flower strip). Second, the species composition was analyzed by performing an NMDS, using the ‘*metaMDS*’ function in R. Only species occurring in more than three transects were considered. On five transects, no non-crop species and, on a further four transects, only one non-crop species were found in the aboveground vegetation. Those transects were all located in the field interiors; therefore, we excluded all field interior transects from this analysis, resulting in 19 transects on flower strips and field edges, respectively. For better comparability, some plant species present in the aboveground vegetation were summed up in species complexes as were used in the seed bank analysis (e.g., *Silene spp*. and *Poa spp*.). Furthermore, tree species such as *Acer campestre* and *Alnus glutinosa* were removed. The effects of field location (flower strip vs. field edge) and data type (seed bank vs. aboveground vegetation) were tested with the ‘*envfit*’ function.

Data were analyzed with R software [39]. Graphs were generated using the ‘*ggplot2*’ (v3.4.0) package [48] and ‘*ggrepel*’ (v0.9.2) [49].

2.4 RESULTS

In the 252 soil samples, a total of 10,828 seeds germinated and could be identified to species (118) or genus (14) level. The number of species per 50 m transect sample varied between two (field interior) and 35 (flower strip), while the number of seedlings varied between three and 557, respectively. The extrapolated number of seeds expected to be pre-sent in the seed bank of 1 m^2 of the studied arable land varied between 6000 and 12,000 (flower strips on average: ~29,800, field edges: ~12,100, and field interior: ~6000).

Number of species and seeds in relation to tillage regime, soil depth, and distance to field edge

Within the seed bank sampling scheme I ‘edge effect’, a total of 1276 seedlings were counted and assigned to 58 species/groups (see Table S2). *Chenopodium album* accounted for around 40% of all seeds, followed by *Urtica dioica/urens* with 10% of the germinated seedlings. Fifteen species were present only once (e.g., *Anagallis arvensis, Linaria vulgaris, and Sagina procumbens*), while an additional 18 species were present between two and five times (e.g., *Mercurialis annua, Galium aparine,* and *Veronica hederifolia*). On average, one out of the nine present grass species was observed in the subplots of varying distance with, on average, only one individual. The transect analysis in the 5 m × 5 m plots showed a significant decrease in species numbers and seed numbers within 1 m from the edge (Figure 2.2). Forb species decreased with increasing distance to the edge from around seven to two species and from 8000 seedlings to 1000. The number of seeds decreased from around 40 at 0-1 m to 10 seeds between 2 and 5 m (mixed model: sum of squares = 18.8, F6,39 = 8.8, p < 0.0001). Five times more seedlings were present next to the field edge in the outermost sub-plot (0–0.5 m) than at the 5 m distance (0–5 m), and almost four times more seedlings were present at 0.5 m compared to the 2 to 5 m distance.

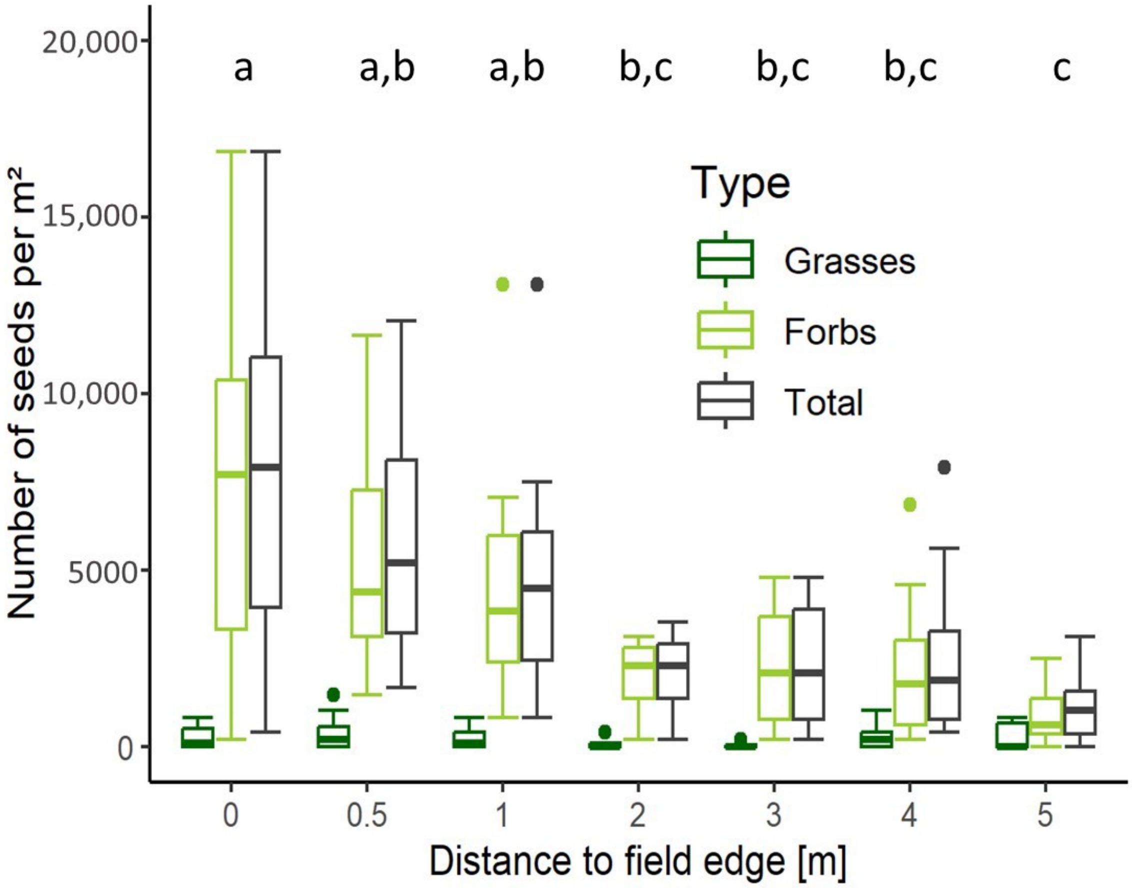


Figure 2.2*: Boxplots of extrapolated number of grass (dark green), forb (green), and total (black) seeds per m^2 in the seed bank at distances to the field edge varying between 0 m and 5 m. Different letters indicate significant differences according to distance (pairwise com-parisons, p-value ≤ 0.05, Tukey-corrected).*

With increasing distance to the field edge, the number of species in the seed bank significantly decreased (Figure 2.3; mixed model: sum of squares = 3.4, $F_{6,35}$ = 6.9, p < 0.0001). On average, seven species occurred in the seed bank between 0 and 1 m distance, and four species occurred between 2 and 5 m distance.

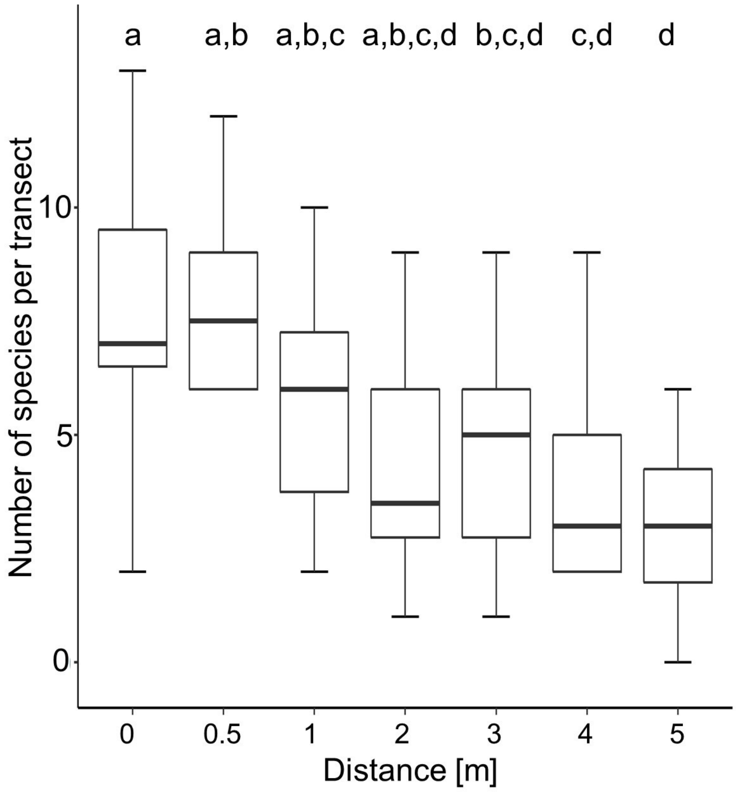


Figure 2.3: *Number of species in the seed bank as a function of distance to the field edge. Significant pairwise differences are indicated by different letters (pairwise comparisons, p-value ≤ 0.05, Tukey-corrected).*

Tillage regime and location (edge vs. field interior) both had a significant effect on the number of seeds and species present in the seed bank (Figure 2.4 and Table 2.1). In general, the number of seeds and species present was significantly higher at the field edge compared to the field interior (Table 2.2). The number of species and the number of total seeds did not significantly differ according to soil depth.

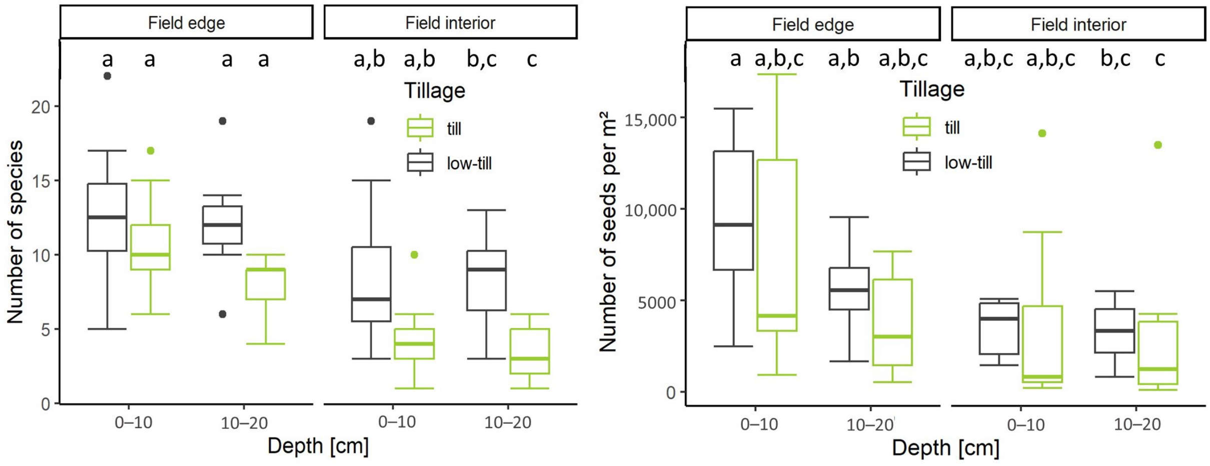


Figure 2.4: *Boxplots of the number of species (left) and seeds (right) in field interior and field edge for different soil depths on low-tillage and conventional tillage farms (tillage: n = 9; low-tillage: n = 8). Significant pairwise differences are indicated by different letters (pairwise comparisons, p-value ≤ 0.05, Tukey-corrected).*

***Table 2.1**: Effects of soil depth, field position, and tillage regime on seed and species number assessed with linear mixed models (ANOVA). Sum Sq: sum of squares; Num DF: number of degrees of freedom, Den DF: denominator degrees of freedom; F: F-value; p: probability value.*

	Sum Sq	Num DF	Den DF	F	*p*
			Number of species		
Depth	0.233	1	45	2.884	0.096
Field position	6.321	1	45	78.215	<0.001
Tillage	0.621	1	15	7.682	0.014
Depth × field position	0.0146	1	45	0.203	0.654
Depth × tillage	0.215	1	45	2.661	0.100
Field position × tillage	0.768	1	45	0.91	0.004
Depth × field position × tillage	0.008	1	1	0.101	0.752
			Number of seeds per m^2		
Depth	2.624	1	45	1.9	0.0711
Field position	13.236	1	45	10.2	<0.001
Tillage	3.651	1	15	4.3	0.046
Depth × field position	0.4122	1	45	0.5367	0.468
Depth × tillage	0.0014	1	45	0.0018	0.967
Field position × tillage	0.3966	1	45	0.5164	0.476
Depth × field position × tillage	0.0856	1	1	0.1115	0.740

Around two-thirds of seeds and species were found in the uppermost 10 cm of soil (mean number ± standard error of seeds per m^2 on average: 6048 ± 800, species 9 ± 1) and one-third at 10-20 cm depth (seeds: 3844 ± 524, species 8 ± 1). We found significantly more seeds in low-tillage fields (mean of field interior: 7598 ± 1533, field edge: 15,078 ± 2236) than under conventional tillage (field interior: 6419 ± 2996, field edge: 10,794 ± 2749).

***Table 2.2:** ANOVA results of fixed effects of linear mixed models on differences according to field interior, field edge, and flower strip in the number of species and seeds present in the soil seed bank (fls: flower strip seed mixture species).*

	Sum Sq	Num DF	Den DF	F-Value	*p*
			Number of species		
Field location (total)	8.1	2	36	34.9	<0.0001
Field location (without fls)	4.5	2	36	18.2	<0.0001
			Number of seeds		
Field location (total)	32.6	2	36	24.9	<0.0001
Field location (without fls)	30.7	2	36	23.5	<0.0001

The number of species was also significantly higher in low-tillage fields (field interior: 8 ± 1, field edge: 12 ± 1) than at conventional tillage (Figure 4 field interior: 4 ± 1, field edge: 9 ± 1).

Differences in abundance, species numbers, and species composition of the seed bank according to field location

In total, 8786 seedlings were counted (flower strip: 5445; field edge: 2166; field interior: 1175) in sampling scheme II and assigned to 113 species/groups (see Table S3). Overall, 85% of the seeds were forbs, and 15% were grasses (158 seedlings remained unidentified), with proportionally more gramineous seedlings observed in field edges (80:19) and interiors (83:15) than in flower strips (88:11).

Comparing the species composition of the seed bank of flower strips, field edges, and field interiors revealed no significant differences among the three habitat types, when taking the abundances of the 113 species/groups into account. A total of 41 species occurred in all three field locations. The most abundant species, i.e., *Chenopodium album, Urtica spp.*, and species of the 'Chamomilla' group, were also found on most transects.

Transects located in the north/northeast of Germany with low tillage and rotational tillage were concentrated in the upper part of the NMDS plot, while transects from farms in southern and southwestern Germany with conventional tillage dominated in the lower part (Figure 2.5). The NMDS further revealed that field location did not correlate with either of the axes but that the factor farm strongly correlated with the first axis ($R^2 = 0.40$, $p = 0.001$). None of the Ellenberg indicator values were significantly correlated with the NMDS axes (results not shown).

The number of species and seeds in the seed bank differed significantly across the three field locations (see ANOVA results of fixed effects in Table 2.2 and Figure 2.6).

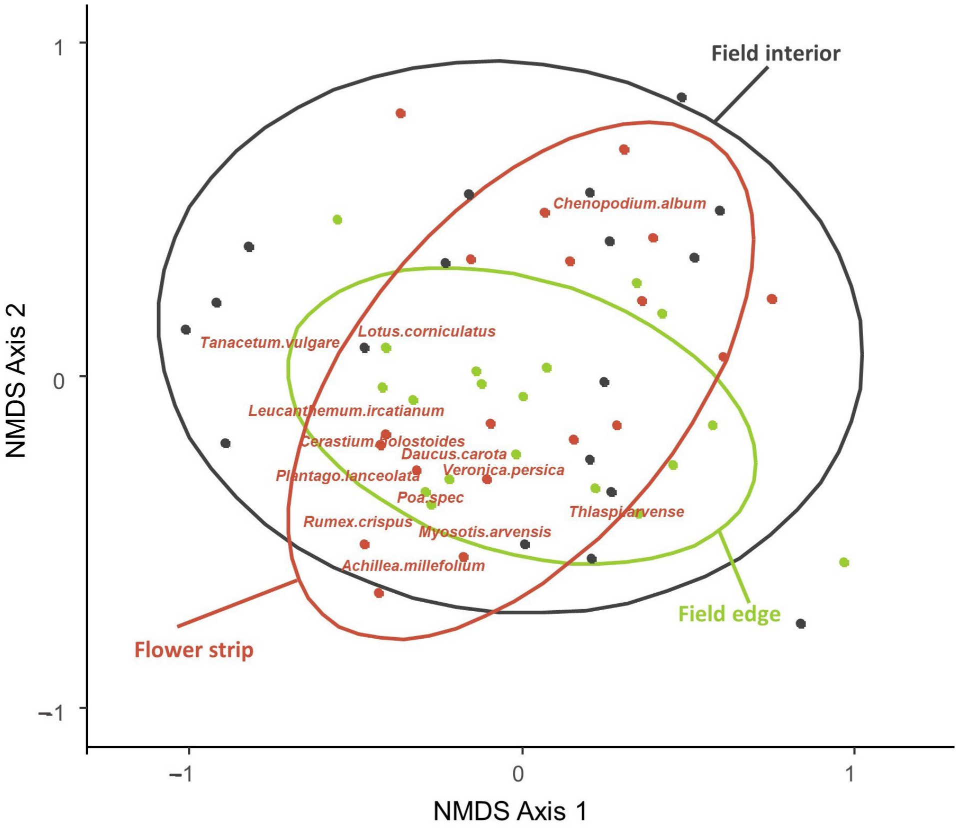


Figure 2.5: *NMDS plot with Bray–Curtis distances, abundance data Hellinger-transformed, and 85% confidence interval for field location (k = 3, stress = 0.159). Only species with a significant ecological preference for field locations are shown (in red: flower strip; in green: field edge; in yellow: flower strip and field edge; statistical results in Table S4).*

The number of seeds per m^2 was highest in the flower strips, irrespective of whether the sown species in the flower strips were included (mean ± s.e.: 29,633 ± 4369), followed by field edges (11,801

± 1632) and field interior (6420 ± 1565). The number of species, including sown species, was significantly higher in flower strips (19 ± 2) than at the field edges (13 ± 1). When excluding the sown species, the number of species in the seed bank was equal in flower strips and field edges (12 ± 1 and 11 ± 1), but still significantly higher than in the field interior (6 ± 4).

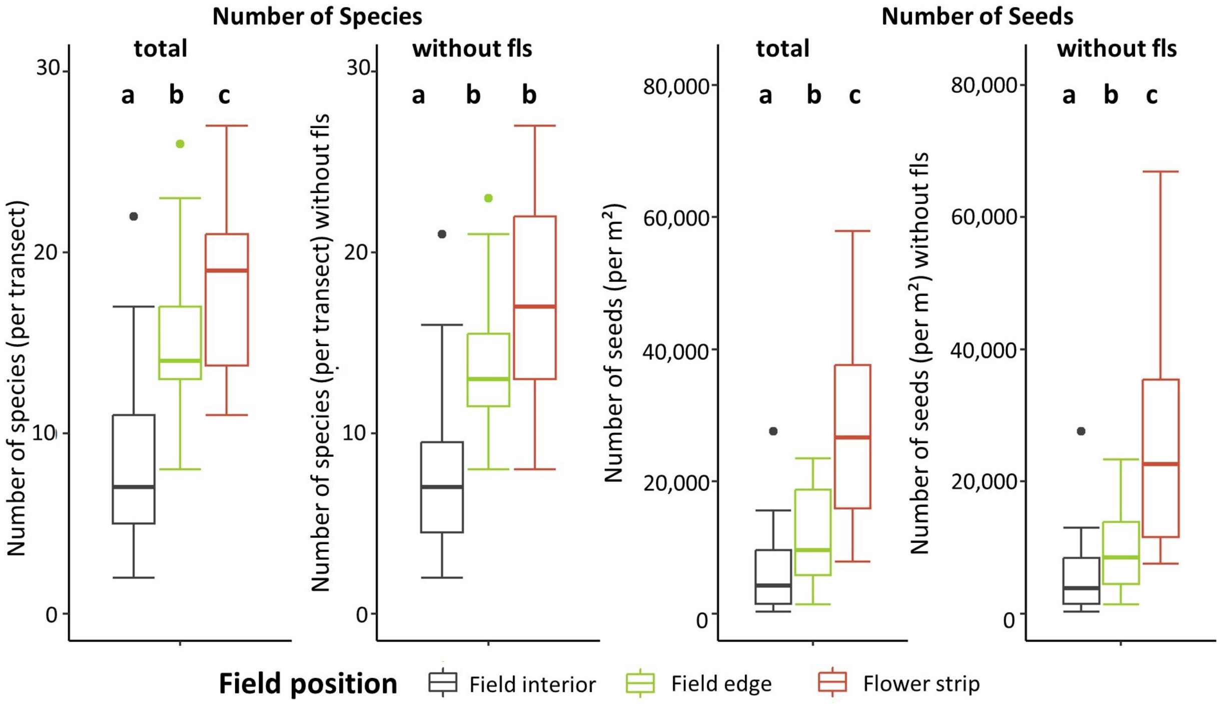


Figure 2.6: *Boxplots of the number of species and seeds (with and without species sown with flower strip seed mixture, fls) found in the seed bank in flower strips (red), field edges (green), and field interior (dark grey) (n = 19). Significant pairwise differences are indicated by different letters (pairwise comparisons, p-value ≤ 0.05, Tukey-corrected).*

Differences in the composition of seed banks and associated above-ground vegetation

We found 114 species/species complexes in the seed bank, while 176 species were present in the aboveground vegetation of the plots. A total of 71 species were shared between seed bank and vegetation, including the abundant annuals *Chenopodium album* and the 'Chamomilla' group. A total of 43 species were only present in the seed bank (e.g., *Juncus spp. and Lamium purpureum*), while 105 taxa occurred exclusively in the above-ground vegetation (e.g., *Dipsacus fullonum*, see summary in Table S3). The NDMS revealed significant differences in species composition between field edge and flower strip on the one hand, and between seed bank and aboveground vegetation on the other (Figure 2.7). Both habitats (flower strip vs. field edge: envfit analysis $R^2 = 0.19$, $p = 0.001$) and vegetation components (seed bank vs. vegetation: $R^2 = 0.38$, $p = 0.001$) were significantly correlated with the two first NMDS axes.

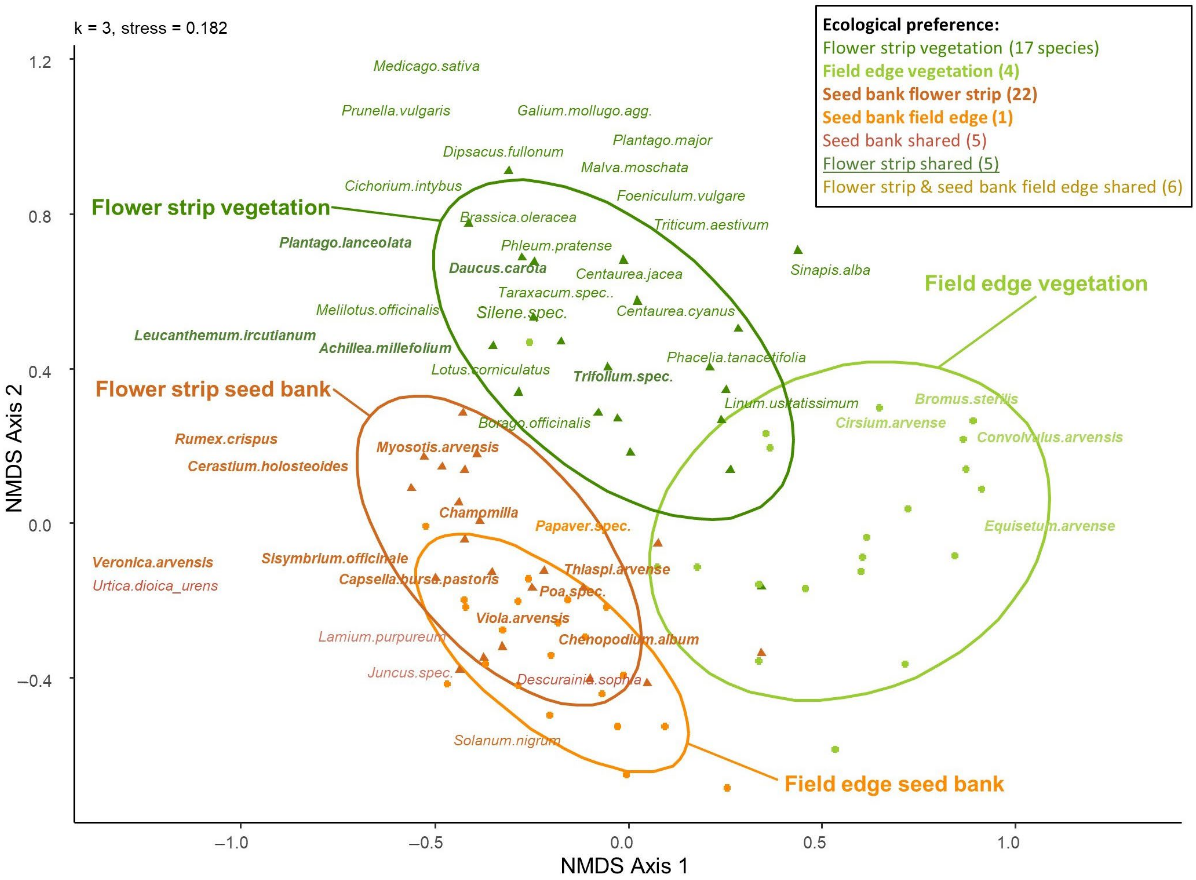


Figure 2.7: *NMDS with Jaccard distances based on species presence/absence data including 96 species/complexes (rare species excluded) (k = 3, stress = 0.182). Circles show 85% confidence interval for species composition of seed bank and vegetation on field edges and flower strips. Only species with a significant ecological preference for field locations are shown (see box top right, statistic results in Table S5).*

According to the multipattern analysis (for details, see Table S5), 25 out of the 27 species associated with flower strips originated from the seed mixture, of which five were also associated with the soil seed bank and 17 were identified as weeds. While the number of species associated with the field edge is low, no associated species were shared between the vegetation and the soil seed bank.

Furthermore, the multi-pattern analysis showed that many species contained in the flower strip seed mixtures were significantly correlated to the above-ground vegetation (e.g., *Foeniculum vulgare* and *Silene spp*.), while non-sown weed species of the aboveground vegetation, i.e., spontaneously occurring taxa, were more often correlated to the seed bank in flower strips and field edges (e.g., *Juncus spp., Chenopodium album,* and *Capsella bursa-pastoris*). Some flower strip species were common in the seed bank and the aboveground vegetation (e.g., *Leucanthemum vulgare/ircutianum, Daucus carota*, and *Achillea millefolium*). Common in the aboveground vegetation but absent from the seed bank was, for example, *Cirsium arvense*.

The number of species was higher in the aboveground vegetation than in the seed bank in flower strips (seed bank vs. vegetation; 18 vs.25), but higher in the seed bank at the field edges (13:8) and in the field interior (7:3). A similar pattern was observed for plant abundance (seed numbers and vegetation cover). When expressed in relative values (flower strip set to 100%), species numbers in the aboveground vegetation decreased from 10% in the field edge to 3% in the field interior, while the number of seeds dropped to 41% and 20% compared to the flower strips. The Sørensen similarity index indicated the highest similarity of vegetation and seed-bank in flower strips, followed by field edges and by field interiors (Table 2.3).

Table 2.3. *Sørensen similarity index, and number of species present in both seed bank and vegetation or only in seed bank or vegetation in the three habitat types. Pairwise comparisons of seed bank and vegetation in field edges and flower strips. Values per transect: n = 3 × 19.*

	Sørensen Similarity Index	**Both**	**Seed Bank Only**	**Vegetation Only**
	Mean ± SE	**Mean ± SE**	**Mean ± SE**	**Mean ± SE**
Field interior	0.17 ± 0.04	1.05 ± 0.44	6.40 ± 0.90	2.25 ± 0.67
Field edge	0.20 ± 0.02	2.40 ± 0.34	11.50 ± 0.89	5.90 ± 0.84
Flower strip	0.33 ± 0.02	8.10 ± 0.84	13.55 ± 1.36	17.85 ± 1.58

2.5 DISCUSSION

In this comparative study of the seed bank in flower strips, field edges, and field interiors in intensively used agricultural landscapes in seven regions of Germany, the extrapolated number of seeds varied between 6000 and 12,000 per m^2 of arable land. While these numbers are lower than seed densities of 47,000 per m^2 reported from sandy fields in eastern Poland [50], up to 20,000 per m^2 from Danish fields [51], and of 15,000 per m^2 from Czech fields [52], seed densities in our study matched very well seed densities from Poland [53], southern Germany (8270 per m^2 [54]), and northern Germany (approximately 8500 per m^2 [17]).

Edge effect and low-tillage increase seed bank density in arable soils

Confirming our first hypothesis, we found more species and higher total seed numbers in field edges compared to the field interior. Sampling in small distance steps from the edge confirmed that a pronounced edge effect does exist within the first 2 m of the field. This result is in accordance with several other studies from Europe, confirming that field edges can be refugia for various weed species, including rare taxa, while the field interior is much less diverse [7,23,55]. A study on the arable seed bank of dicotyledons in England found mostly arable weeds within the first few meters, while species originating from the margin vegetation, such as Galium aparine and Urtica dioica, were rather rare in that soil seed bank [22]. In line with our results, the same study revealed a decrease in seed bank diversity and density within the first few meters. Interestingly, in our study, the reduction in seed and species numbers from field edge to interior only occurred in forbs, while grasses stayed constant with on average one species and one seed per m^2 along the same gradient. The low density of grass seeds is unexpected, because we anticipated seed rain from the adjacent grassy field margins at least within

1 m of the field. One possible explanation could be the maintenance regime of the field margins, the regular cutting of which prevents successful seed production (own observation and personal communication of the farmers). In addition, seed rain from the field margins might be limited due to the very narrow field margins in our study (less than 0.5 m wide).

Our second hypothesis prediction that fields on low-tillage farms contain more seeds and species in the seed bank than fields under conventional tillage was also confirmed by our data. However, contrary to our expectations, we did not find a significant decrease in the number of seeds with increasing soil depth, i.e., from 0–10 cm to 10–20 cm, in any habitat type. This might have been caused by the fact that even low-tillage regimes disturb the topsoil layer to a depth of up to 20 cm, depending on the equipment used. Therefore, seeds will be evenly distributed within the top 20 cm, independent of the tillage system. A study on the effects of different tillage systems on the vertical distribution of seeds at three sites in England also found no vertical differences in seed numbers for conventional and low-tillage systems. In fact, accumulation of seeds in the first 5 cm of the topsoil was found only in zero-tillage systems [56]. In general, the size of the seed bank increases with conversion from conventional tillage to low-tillage systems. However, there are complex interactions of tillage system, herbicide application, and crop rotation (reviewed in [57]). Low and no tillage, combined with specific crop rotations and pesticide application schemes, might even lead to a decrease in weeds in the soil seed bank, when mechanical weed control is replaced by intensified chemical control [58,59].

In our sample of seven farms, geographical location, soil properties, and local differences in crop rotation must be taken into account as additional explanatory variables when explaining seed bank differences. This is reflected in the fact that all large farms in our sample were located in the north and northeast of Germany and were practicing low tillage, while the smaller, family-run farms characteristic for western and southern Germany carried on with conventional tillage. Taking further into account that species pools usually differed across regions [3,60], our finding that the variable ‘farm’ explained more variation in species composition than habitat type (or field location) seems to be the result of a complex interplay of these factors. Consequently, only 12 of 117 plant species occurred in the seed bank of all seven farms that were studied. The ubiquitous species included taxa such as Chenopodium album, the Chamomilla group, and Poa spp. However, all three taxa exhibit large differences in seed density between farms. This result is consistent with findings of a comparable study on weed species in the aboveground vegetation of fields located in Catalonia (Spain) and Lower Saxony (Germany), where a share of common species of only 15% was reported [61]. A study in Bavaria identified management factors, notably previous crop cover, as one of the most important factors influencing the density and composition of the seed bank [28]. In our study, the seed bank of directly neighboring fields within one farm also showed high small-scale variation.

Certainly, a more comprehensive analysis with consideration of the complexity of the surrounding landscapes [62], as well as crop rotation patterns, might help to explain differences between farms and to quantify the effect of geography on seed bank composition. Yet, despite considerable variation among fields due to crop rotation, soil type, and herbicide and fertilizer use patterns, our data show a negative effect of conventional tillage systems on seed density compared to low- or no-tillage systems.

Flower strips enrich the quality and quantity of seed banks

In line with our third hypothesis, seed banks of flower strips had higher species numbers and seed densities than adjacent fields both at the field edge and in the field interior. We found 2–3 times higher seed densities on flower strips than on field edges in equivalent positions, regardless of whether sown flower strip species were included or not. Yet, the total number of species found in the seed bank of flower strips was not elevated in comparison to the field edges, indicating that sown species seemed not to accumulate in the soil seed bank, at least within the first 2 years after sowing. The seed bank composition supports this finding, i.e., we observed a similar arable species composition in the seed bank of flower strips and conventional field edges after two vegetation periods. However, some species such as *Chenopodium album, Veronica persica, Thlaspi arvense*, and *Rumex crispus* were found to be associated with flower strips and, thus, seem to have benefited from their establishment. It is well known that these taxa can reach high densities in the seed bank due to a high seed production per plant [63,64,65]. *T. arvense*, for example, can shed up to 3000 and *R. crispus* can even shed up to 60,000 seeds per plant. Both species may also profit from the lack of pesticide application in flower strips and are, therefore, able to replenish their seed bank. Nevertheless, this did not lead to a principal difference in species composition between flower strips and field interior. If at all, we expect this differentiation to occur only several years after flower strip establishment.

In line with this finding, only a few species from the sown seed mixture, e.g., *Plantago lanceolata* or *Daucus carota*, were able to establish a seed bank. Possible causes for this might be the short lifespan of the flower strips due to flower strip management by farmers, which may have prevented the development of adult seed-producing individuals of perennial plant species. In contrast, studies on vegetation development of undisturbed flower strips with high sown wild plant diversity show that these plants are able to establish a seed bank and make reseeding superfluous [66].

We expected that higher fertilizer load and, as a result, lower light availability in the field interior compared to field edges would translate into marked differences in Ellenberg indicator values. However, no such pattern was found. Similarly, in arable fields in northeastern France, aboveground vegetation of field edges and field interiors did not differ in Ellenberg nitrogen and light values, which led the authors to the conclusion that field edges and interiors have similarly high nutrient levels [23]. Newly established flower strips did not change that matter.

Concerning the accumulation of problematic weed species in the seed bank, we observed a significant increase in some problematic species, i.e., *Chenopodium album, Rumex crispus, Poa spp.*, and *Echinochloa crus-galli*. Consequently, we observed increasing application of herbicides in the course of flower strip establishment, a phenomenon that was especially pronounced on low-tillage farms. Some farmers even decided against re-establishment of flower strips, terminated agri-environmental measures ahead of time, and re-established crop fields on the area of flower strips to suppress emerging weeds. In addition, those areas were often treated with higher amounts of herbicides to combat and prevent the spread of occurring weeds (personal communication of local farmers). Since this development calls into question the whole point of flower strip establishment, advice to farmers must improve to reduce the risk of weed infestation after the establishment of flower strips. Adapting the seed mixtures and cutting the vegetation at 25–30 cm height in the first year could help to overcome some of the problems associated with flower strip establishment [67].

The composition of the aboveground weed vegetation of conventionally managed fields made it unlikely that high-nature-value species or taxa not present in the aboveground vegetation can be still found in the seed bank [25]. In general, seed banks of farmland with a long history of intensive use, i.e., high chemical and physical stress levels, are mostly depleted [68]. As a consequence, the restoration potential of the seed bank is limited [29]. Despite the limitations of seed bank analyses to detect rare species, we found two individuals of *Myosurus minimus*, a species classified as vulnerable according to the red list of threatened plants [69].

Our study of seed bank changes in the context of short-term establishment of flower strips on fertile arable land shows that only few and common sown flower strip species, such as Plantago lanceolata or Daucus carota, were able to establish also in the seed bank after two vegetation periods. We found no general increase in seed bank diversity under flower strips, but observed an increase in some problematic weed species, which might have jeopardized the acceptance of agri-environmental measures by farmers.

Larger differences between aboveground vegetation and seed bank in the field than in flower strips

Comparison of seed bank and aboveground vegetation in the three field locations revealed a higher Sørensen similarity index for flower strips compared to field edges and field interior. A study comparing seed bank and aboveground vegetation before first herbicide application on seven spring barley fields in England found that, depending on the species, 0.4-55% of the seeds were present as seedlings in the aboveground vegetation. This highly variable relation is largely influenced by the coincidence of crop management schemes and the timing of seedling emergence [22]. The aboveground vegetation in the field interior often comprises only the cultivated crop and barely any additional weed species, while the soil seed bank may still contain some additional species. Under intensive conventional farming practices, most weed seedlings in the field will not fully develop as a consequence of herbicide use and low light availability under the crop [26], while the seed bank often is less impacted by the management regime [70,71], which can explain low similarity between aboveground vegetation and seed bank. At the field edge, where fertilizer and pesticide amounts are usually reduced, more weed species are typically able to establish themselves as plants [5]. In flower strips, with reduced to no fertilization and use of herbicides, similarity between seed bank and aboveground vegetation was highest, although many sown species were missing in the seed bank. The high similarity in flower strips is confirmed by another study investigating the established flora in sown flower strips [72]. They found that over half of species present in the vegetation were not sown. Among the most abundant plants were several common weed species, probably germinated from the seed bank. The spatial distribution of seeds in the soil is usually highly patchy [21]. In arable fields, however, regular soil disturbance may lead to a more even distribution pattern of the seed bank, which may also translate into a more evenly distributed aboveground vegetation. Consequently, when no herbicides are applied, Sørensen's similarity index between vegetation and seed bank may reach values as high as 65% [73].

2.6. CONCLUSION

In this study, we showed that the weed seed banks in conventional arable fields of seven regions of Germany were, apart from a few dominant species, largely depleted. However, species diversity and the abundance of seeds were still higher at the field edge, which may provide refugia for some arable species. Low-tillage regimes in general seemed to support higher seed densities and a greater number of species in the seed bank in the upper 20 cm of soil than conventional tillage. Regardless of tillage system, the seed bank was found to be largely dominated by nitrogen- and light-demanding competitive species. Flower strips of short duration, a widely established element of agri-environmental measures to increase biodiversity in intensive farmland, only showed a limited potential to enrich the depleted seed bank with naturally occurring or even rare arable species. The possible increase and dominance of problematic weed species on flower strips needs close monitoring, especially on fertile soil. Otherwise, increased herbicide treatment to control weed-dominated flower strips may outweigh any positive conservation benefit of flower strips.

Supplementary Materials

The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land12040926/s1 , Figure S1: Soil seed bank sampling; (a) field edge with winter cereals, (b) flower strip in autumn, (c) soil sampling and (d) seedling emergence in the green house. Table S1: Mean field size [min:max], soil quality score (SQR), tillage regime and main crops cultivated on the 7 studied farms. Table S2: Species list for distance classes (alphabetically ordered), mean values for species and seed [mean ± sd] and total number of seedlings per species. Table S3: Species list of sampling scheme II, field position, with total number of seedlings per transect (sampled area 0.01 m^2) and number of transects. Table S4: Results of multilevel pattern analysis, only significant species associations are shown. Table S5: Results of multilevel pattern analysis, only significant species associations are shown.

Author Contributions

Conceptualization, L.S. and T.W.D.; methodology, L.S. and T.W.D.; software, L.S.; validation, L.S. and L.M.E.S.; formal analysis, L.S.; investigation, L.S. and L.M.E.S.; resources, C.L.; data curation, L.S.; writing—original draft preparation, L.S.; writing—review and editing, L.S., L.M.E.S., C.L. and T.W.D.; visualization, L.S.; supervision, T.W.D. and C.L.; project administration, L.M.E.S.; funding acquisition, C.L. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

Data are available in a publicly accessible repository. The data presented in this study are openly available from the Open Science Framework (OSF) at DOI 10.17605/OSF.IO/YNQR3.

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Conflicts of Interest

The authors declare no conflict of interest.

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APPENDIX CHAPTER II WEED SEED BANK IN FLOWER STRIPS

Supplementary Materials

Table S1. *Mean field size [min:max], soil quality score (SQR), tillage regime and main crops cultivated on the 7 studied farms.*

	Mean field size (ha) [min:max] ha	SQR	Soil fertility	Tillage	Main crops
Farm 1	31 [1.1:104]	18–48	poor to moderate	low-tillage	cereals, maize, rape seed, sugar beet
Farm 2*	11 [0.2:54]	26–35	poor	low-tillage	cereals, maize, rape seed
Farm 3	32 [0.1:149]	65–90	high to very high	low-tillage	cereals, potato, maize
Farm 4	7 [0.2:18]	26–35	poor	*rotational till.*	cereals, potato, sugar beet
Farm 5*	3 [0.1:9.6]	36–65	poor to high	conventional	cereals, maize
Farm 6*	5 [0.1:18.4]	35–72	poor to high	conventional	cereals, sugar beet
Farm 7*	5 [1.2:10.8]	23–70	poor to high	conventional	cereals, maize

* fertilization: additionally, fermentation residues from biogas plants and manure

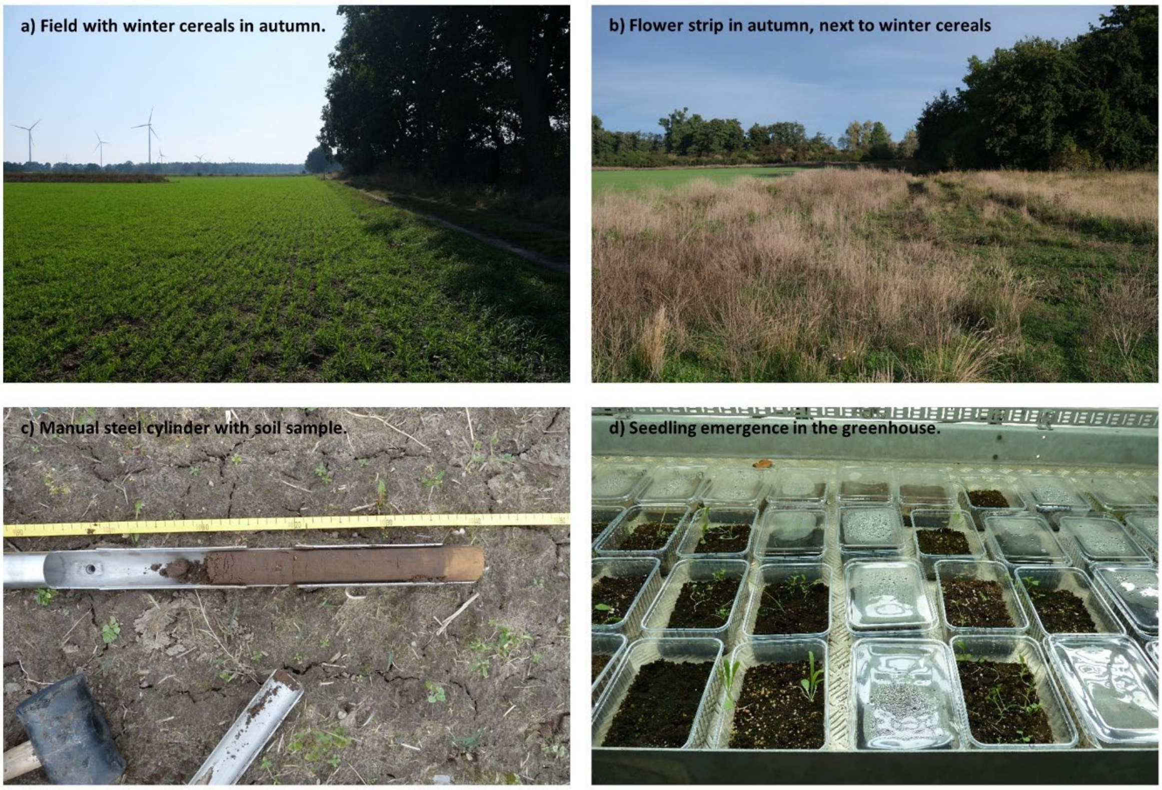

Figure S2: *Soil seed bank sampling; (a) field edge with winter cereals, (b) flower strip in autumn, (c) soil sampling and d) seedling emergence in the greenhouse.*

***Table S3**: Species list for distance classes (alphabetically ordered), mean values for species and seed [mean ± sd] and total number of seedlings per species.*

	total	**%**	**0 m**	**0.5 m**	**1 m**	**2 m**	**3 m**	**4 m**	**5 m**
Species/groups	**58**		7.6 ±3.2	7.9 ± 2	5.8 ± 2.5	4.3 ± 2.4	4.7 ± 2.4	3.9 ± 2.3	3 ± 1.9
Seedlings	**1261**		38 ± 24	56 ±74	24 ±18	10 ± 5	11 ± 8	13 ± 12	6 ± 5
"Chamomilla"	**99**	**7.9**	18	24	33	11	5	3	5
"Grasses unidentified"	**7**	**0.6**	0	2	3	0	0	2	0
"Forbs unidentified"	**1**	**0.1**	1	0	0	0	0	0	0
Achillea millefolium	**7**	**0.6**	3	1	2	0	1	0	0
Aethusa cynopium	**34**	**2.7**	2	11	7	7	5	2	0
Agrostis stolonifera	**1**	**0.1**	0	0	0	0	0	1	0
Alopecurus myosuroides	**15**	**1.2**	2	3	3	0	0	5	2
Amaranthus spp.	**64**	**5.1**	1	42	19	0	0	0	2
Anagalis arvensis	**1**	**0.1**	0	0	0	0	1	0	0
Anthriscus sylvestris	**2**	**0.2**	2	0	0	0	0	0	0
Apera spica-venti	**4**	**0.3**	0	3	0	0	0	1	0
Aphanes arvensis	**1**	**0.1**	1	0	0	0	0	0	0
Arabidopsis thaliana	**17**	**1.3**	9	1	4	2	1	0	0
Artemisia vulgaris	**1**	**0.1**	0	0	0	0	0	1	0
Brassica napus	**2**	**0.2**	0	1	0	0	0	1	0
Capsella bursa-pastoris	**28**	**2.2**	10	3	3	1	1	6	4
Centaurea cyanus	**3**	**0.2**	0	0	0	1	1	1	0
Chenopodium album	**479**	**38**	96	234	56	18	22	39	14
Conyza canadensis	**6**	**0.5**	2	2	0	0	2	0	0
Crepis biennis	**1**	**0.1**	0	1	0	0	0	0	0
Descuriana sophia	**42**	**3.3**	0	1	2	5	20	11	3
Echinochloa crus-galli	**3**	**0.2**	0	0	0	0	1	1	1
Epilobium spp.	**1**	**0.1**	0	0	0	0	0	1	0
Erigeron annua	**1**	**0.1**	0	0	1	0	0	0	0
Euphorbia spp.	**1**	**0.1**	0	0	0	1	0	0	0
Fallopia convolvulus	**3**	**0.2**	0	2	0	1	0	0	0
Festuca ovina	**1**	**0.1**	0	1	0	0	0	0	0
Galium aparine	**2**	**0.2**	0	0	2	0	0	0	0
Geranium pusillum	**5**	**0.4**	4	1	0	0	0	0	0
Geranium spp.	**1**	**0.1**	1	0	0	0	0	0	0
Holcus lanatus	**1**	**0.1**	0	0	1	0	0	0	0
Juncus spp.	**13**	**1**	2	0	1	2	1	2	5
Lactuca serriola	**19**	**1.5**	2	1	3	2	1	9	1
Lamium amplexicaule	**3**	**0.2**	1	2	0	0	0	0	0
Lamium purpureum	**11**	**0.9**	6	3	1	0	1	0	0
Linaria vulgaris	**1**	**0.1**	1	0	0	0	0	0	0
Mercurialis annua	**2**	**0.2**	0	0	1	0	0	0	1
Myosotis arvensis	**2**	**0.2**	0	0	1	0	1	0	0
Papaver spp.	**46**	**3.6**	15	11	5	4	7	3	1
Plantago lanceolata	**48**	**3.8**	17	22	4	3	2	0	0
Plantago major	**6**	**0.5**	0	1	1	3	1	0	0
Poa pratensis	**3**	**0.2**	1	0	0	2	0	0	0
Poa trivialis	**18**	**1.4**	6	7	1	0	0	1	3
Polygonum aviculare	**28**	**2.2**	12	6	7	1	1	0	1
Rumex crispus	**7**	**0.6**	6	1	0	0	0	0	0
Rumex crispus	**6**	**0.5**	5	1	0	0	0	0	0
Sagina procumbens	**1**	**0.1**	0	0	0	0	1	0	0
Sisymbrium officinalis	**4**	**0.3**	2	0	1	1	0	0	0
Solanum nigrum	**2**	**0.2**	1	0	0	0	1	0	0
Solidago spp.	**2**	**0.2**	1	1	0	0	0	0	0
Sonchus arvensis	**5**	**0.4**	0	2	2	1	0	0	0
Sonchus asper	**3**	**0.2**	0	1	1	0	1	0	0
Sonchus oleraceus	**8**	**0.6**	2	3	0	0	0	3	0
Stellaria media	**11**	**0.9**	0	2	0	2	2	4	1
Taraxacum spp.	**2**	**0.2**	0	0	0	0	2	0	0
Urtica dioica/urens	**140**	**11.1**	55	41	22	13	5	3	1
Veronica agrestis	**2**	**0.2**	0	0	1	0	1	0	0
Veronica hederifolia	**3**	**0.2**	0	0	1	0	0	2	0
Veronica persica	**18**	**1.4**	10	5	1	1	1	0	0
Viola arvensis	**13**	**1**	4	3	2	0	1	2	1

***Table S4**: Species list of sampling scheme II, field position, with total number of seedlings per transect (sampled area 0.01 m²) and number of transects.*

	Seed bank						**Vegetation**		
Species	Field interior	Field edge	Flower strip	Field interior	Field edge	Flower strip	Field interior	Field edge	Flower strip
	Number of Seedlings			**Number of Transekts**					
Acer campestre	0	0	0	0	0	0	1	0	0
Achillea millefolium	0	3	97	0	3	7	0	1	9
Achillea ptarmica	0	0	1	0	0	1	0	0	3
Aegopodium podagraria	0	0	0	0	0	0	0	0	1
Aethusa cynapium	3	0	0	1	0	0	0	0	0
Alnus glutinosa	0	0	0	0	0	0	0	0	1
Alopecurus myosuroides	2	47	4	1	5	1	1	3	4
Alopecurus pratensis	0	0	0	0	0	0	0	0	1
Amaranthus spp.	0	3	35	0	3	4	0	0	1
Anagallis arvensis	4	4	15	4	2	3	0	0	0
Anethum graveolens	0	0	0	0	0	0	0	0	3
Anthemis arvensis	0	0	0	0	0	0	0	0	3
Anthemis tinctoria	0	0	5	0	0	1	0	0	3
Anthoxanthum odoratum	0	0	1	0	0	1	0	0	0
Anthriscus caucalis	0	0	0	0	0	0	1	0	0
Anthriscus sylvestris	0	0	0	0	0	0	0	0	1
Apera spica-venti	12	61	42	3	4	6	1	2	2
Aphanes arvensis	0	0	0	0	0	0	0	1	0
Arabidopsis thaliana	4	13	11	1	3	4	0	0	0
Arctium lappa	0	0	0	0	0	0	0	2	2
Arenaria serpyllifolia	2	16	10	1	1	2	0	0	0
Arrhenatherum elatius	0	0	0	0	0	0	0	4	3
Artemisia vulgaris	13	28	59	4	5	6	1	2	8
Atriplex patula	0	0	6	0	0	3	0	0	0
Avena sativa	0	0	0	0	0	0	1	0	0
Betula spp.	9	12	37	6	7	5	0	0	0
Borago officinalis	0	1	4	0	1	2	0	0	6
Brassica napus	9	0	6	3	0	5	0	0	3
Brassica nigra	0	1	6	0	1	2	0	0	1
Brassica oleracea	0	0	0	0	0	0	1	0	6
Brassica rapa	0	0	0	0	0	0	1	0	0
Brassica spp.	0	0	0	0	0	0	0	0	1
Bromus hordeaceus	0	0	0	0	0	0	0	1	1
Bromus sterilis	0	0	0	0	0	0	0	8	8
Calendula officinalis	1	0	1	1	0	1	0	0	2
Campanula spp.	0	0	0	0	0	0	0	0	1
Capsella bursa-pastoris	56	50	171	9	12	15	0	1	7
Cardamine hirsuta	0	1	17	0	1	2	0	0	0
Carduus acanthoides	0	0	0	0	0	0	0	0	1
Centaurea cyanus	1	0	11	1	0	3	0	3	9
Centaurea jacea	0	0	0	0	0	0	0	0	5
Centaurea nigra	0	0	0	0	0	0	0	0	2
Cerastium arvense	0	0	0	0	0	0	0	0	1
Cerastium holosteoides	0	3	25	0	3	6	0	0	2
Chaerophyllum bulbosum	0	0	0	0	0	0	0	1	0
"Chamomilla"	226	293	1054	9	15	15	2	5	12
Chenopodium album	313	301	1295	12	20	20	5	8	10
Chenopodium ficifolium	0	2	0	0	2	0	0	0	0
Chenopodium hybridum	4	5	10	1	2	2	0	0	0
Chenopodium polyspermum	2	41	208	2	4	4	0	0	0
Cichorium intybus	0	0	0	0	0	0	0	0	6
Cirsium arvense	0	0	0	0	0	0	3	8	10
Cirsium vulgare	0	1	1	0	1	1	0	0	3
Clinopodium vulgare	0	0	0	0	0	0	0	0	2
Conium maculatum	0	0	0	0	0	0	0	1	0
Consolida regalis	0	0	0	0	0	0	0	0	1
Convolvulus arvensis	0	0	0	0	0	0	1	4	2

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	Seed bank						**Vegetation**		
Species	Field interior	Field edge	Flower strip	Field interior	Field edge	Flower strip	Field interior	Field edge	Flower strip
	Number of Seedlings			**Number of Transekts**					
Conyza canadensis	11	57	45	1	6	4	0	0	1
Coriandrum sativum	0	0	0	0	0	0	0	0	3
Crataegus spp.	0	0	0	0	0	0	0	0	1
Crepis biennis	0	0	0	0	0	0	1	1	2
Dactylis glomerata	1	19	8	1	2	2	0	5	4
Daucus carota	0	0	145	0	0	8	0	0	11
Deschampisia cespitosa	0	1	2	0	1	2	0	0	0
Descurainia sophia	89	112	69	6	8	7	0	0	5
Digitaria ischaemum	1	0	0	1	0	0	0	0	0
Dipsacus fullonum	0	0	0	0	0	0	0	0	4
Draba verna	0	0	0	0	0	0	0	0	1
Echinochloa crus-galli	49	64	149	3	6	5	1	3	0
Echium vulgare	0	0	0	0	0	0	1	0	2
Elymus repens	0	0	3	0	0	2	0	6	4
Epilobium ciliatum	1	23	3	1	3	3	0	0	0
Equisetum arvense	0	0	0	0	0	0	1	6	0
Erigeron annuus	1	0	0	1	0	0	0	0	1
Erodium cicutarium	0	0	0	0	0	0	0	1	0
Erysimum cheiranthoides	0	0	0	0	0	0	0	1	0
Euphorbia spp.	0	2	0	0	2	0	2	1	0
Fagopyrum esculentum	0	0	0	0	0	0	0	0	3
Falcaria vulgaris	0	0	0	0	0	0	1	0	0
Fallopia convolvulus	6	4	47	4	3	4	4	8	6
Festuca arundinacea	0	0	0	0	0	0	0	0	1
Festuca pratensis	0	0	0	0	0	0	0	0	1
Festuca rubra agg.	0	0	0	0	0	0	0	3	4
Foeniculum vulgare	0	0	1	0	0	1	0	0	8
Fragaria moschata	0	0	1	0	0	1	0	0	0
Fumaria officinalis	0	0	0	0	0	0	1	1	0
Galeopsis tetrahit	0	0	0	0	0	0	0	0	1
Galinsoga cilliata	0	1	1	0	1	1	0	0	0
Galinsoga parviflora	0	0	10	0	0	3	0	0	1
Galium aparine	2	4	3	2	4	3	5	9	8
Galium mollugo agg.	0	0	0	0	0	0	0	0	5
Galium verum	0	0	0	0	0	0	0	0	1
Geranium columbinum	0	0	0	0	0	0	0	0	1
Geranium dissectum/pusillum	1	168	38	1	10	6	2	4	7
Geum rivale	0	0	1	0	0	1	0	0	0
Geum urbanum	0	0	0	0	0	0	0	0	1
Glechoma hederaceae	3	6	1	2	3	1	0	0	0
Glyceria fluitans	0	0	0	0	0	0	0	1	0
Gnaphalium uliginosum	2	2	20	1	1	3	0	0	0
Grasses unidentified	28	68	62	7	8	14	0	0	0
Guizotia abyssinica	0	0	0	0	0	0	0	0	1
Helianthus annuus	0	0	0	0	0	0	0	0	3
Heracleum sphondylium	0	0	0	0	0	0	0	1	1
Hieracium spp.	0	0	4	0	0	2	0	0	0
Holcus lanatus	0	1	6	0	1	3	0	1	5
Hordeum vulgare	0	0	0	0	0	0	1	2	3
Humulus lupulus	0	0	0	0	0	0	0	0	1
Hypericum perforatum	0	0	1	0	0	1	0	0	1
Hypochaeris radicata	0	0	0	0	0	0	0	0	2
Juncus spp.	29	57	59	10	12	16	0	0	0
Knautia arvensis	0	0	0	0	0	0	0	0	2
Weeds unidentified	0	3	5	0	2	2	0	0	0
Lactuca seriola	0	12	1	0	2	1	0	0	0
Lamium purpureum	1	12	13	1	4	7	0	0	0

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	Seed bank						**Vegetation**		
Species	Field interior	Field edge	Flower strip	Field interior	Field edge	Flower strip	Field interior	Field edge	Flower strip
	Number of Seedlings			**Number of Transekts**					
Lapsana communis	1	10	1	1	3	1	0	0	0
Lathyrus pratensis	0	0	0	0	0	0	0	0	1
Leontodon autumnalis	0	0	1	0	0	1	0	0	0
Leonurus cardiaca	0	0	0	0	0	0	0	0	1
Lepidium sativum	0	0	0	0	0	0	0	0	1
Leucanthemum ircutianum	0	0	31	0	0	6	0	0	4
Leucanthemum vulgare	0	0	0	0	0	0	0	0	2
Linum usitatissimum	0	0	0	0	0	0	0	0	5
Lolium multiflorum	0	0	0	0	0	0	1	2	3
Lolium perenne	3	0	8	1	0	1	2	6	5
Lotus corniculatus	0	0	11	0	0	9	0	0	13
Lotus pedunculatus	0	0	0	0	0	0	0	0	2
Lychnis flos-cuculi	0	7	40	0	1	3	0	0	3
Lysimachia vulgaris	0	0	0	0	0	0	0	0	1
Malva moschata	0	0	0	0	0	0	0	0	5
Malva sylvestris	0	14	0	0	3	0	0	0	4
Medicago lupulina	1	0	18	1	0	3	0	0	7
Medicago sativa	0	0	0	0	0	0	0	0	5
Medicago varia	0	0	0	0	0	0	0	0	2
Melilotus albus	0	0	0	0	0	0	0	0	2
Melilotus officinalis	0	0	4	0	0	2	0	0	4
Mercurialis annua	0	0	1	0	0	1	1	0	1
Milium effusum	0	1	0	0	1	0	0	0	0
Myosotis arvensis	5	8	39	1	5	7	0	1	4
Myosurus minimus	0	1	36	0	1	1	0	0	1
Oenothera biennis	0	0	2	0	0	1	0	0	0
Onobrychis viciifolia	0	0	0	0	0	0	0	0	3
Origanum vulgare	0	0	0	0	0	0	0	0	1
Oxalis acetosella	0	0	0	0	0	0	0	0	1
Oxalis stricta	0	0	0	0	0	0	0	0	1
Papaver spp.	41	212	77	3	7	9	2	5	5
Parthenocissus inserta	0	0	0	0	0	0	1	0	0
Pastinaca sativa	0	0	0	0	0	0	0	0	2
Persicaria hydrapiper	0	0	5	0	0	1	0	0	0
Persicaria maculosa	2	0	119	1	0	4	1	2	3
Phacelia tanacetifolia	0	0	64	0	0	4	0	0	9
Phalaris arundinacea	0	0	0	0	0	0	0	1	3
Phaseolus (bean)	4	1	0	2	1	0	0	0	0
Phleum pratense	0	0	0	0	0	0	0	0	5
Phragmites australis	0	0	0	0	0	0	0	2	0
Picris hieracioides	0	0	0	0	0	0	0	0	1
Pisum sativum	0	0	0	0	0	0	0	0	1
Plantago intermedia	6	7	13	5	4	3	0	0	0
Plantago lanceolata	0	1	44	0	1	4	0	0	9
Plantago major	0	0	0	0	0	0	0	0	6
Poa spp.	39	117	278	6	17	11	0	9	13
Polygonum aviculare	3	39	14	2	7	11	4	8	5
Populus spec.	17	18	26	9	10	12	0	0	0
Potentilla anserina	0	0	0	0	0	0	0	1	0
Potentilla reptans	0	0	0	0	0	0	0	1	0
Prunella vulgaris	0	0	1	0	0	1	0	0	4
Quercus robur	0	0	0	0	0	0	0	0	2
Ranunculus repens	0	0	0	0	0	0	0	1	1
Ranunculus sceleratus	0	0	0	0	0	0	0	0	1
Ranunculus spp.	0	0	4	0	0	2	0	0	0
Raphanus sativus	0	0	0	0	0	0	0	0	1
Reseda lutea	0	0	0	0	0	0	0	0	2

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Seed bank **Vegetation**

Species	Field interior	Field edge	Flower strip	Field interior	Field edge	Flower strip	Field interior	Field edge	Flower strip
	Number of Seedlings			**Number of Transekts**					
Rumex acetosa	0	1	0	0	1	0	0	0	2
Rumex crispus	0	7	39	0	2	5	0	0	2
Rumex obtusifolius	0	6	10	0	2	4	0	2	8
Rumex spp.	0	1	1	0	1	1	0	0	0
Sagina procumbens	3	0	2	3	0	1	0	0	0
Salvia pratensis	0	0	0	0	0	0	0	0	1
Sanguisorba minor	0	0	0	0	0	0	0	0	1
Scropholaria spp.	0	0	1	0	0	1	0	0	0
Secale cereale	0	0	0	0	0	0	1	4	2
Secale multicaule	0	0	0	0	0	0	0	0	2
Senecio sylvaticus	0	0	1	0	0	1	0	0	0
Senecio vulgaris	0	1	0	0	1	0	0	1	2
Setaria pumila	0	0	0	0	0	0	0	2	0
Setaria spp.	0	1	0	0	1	0	0	0	0
Silene spp.	1	1	36	1	1	6	1	1	14
Sinapis alba	0	0	0	0	0	0	0	0	6
Sinapis arvensis	3	0	7	1	0	1	0	0	1
Sisymbrium officinale	34	23	57	3	4	9	2	0	5
Solanum nigrum	21	13	32	3	5	7	1	0	0
Solanum tuberosum	0	0	0	0	0	0	1	0	0
Sonchus arvensis	0	1	0	0	1	0	0	0	1
Sonchus asper	2	5	6	2	3	4	0	0	3
Sonchus oleraceus	0	0	1	0	0	1	0	0	1
Sonchus spp.	0	1	2	0	1	2	0	0	0
Spergula arvensis	0	1	0	0	1	0	0	0	0
Stachys spp.	0	1	0	0	1	0	0	0	0
Stellaria graminea	0	0	0	0	0	0	0	0	1
Stellaria media	19	66	53	6	8	12	1	3	6
Tanacetum vulgare	0	1	26	0	1	5	0	0	5
Taraxacum spp.	0	0	4	0	0	3	1	2	12
Thlaspi arvense	1	3	270	1	2	7	0	0	3
Trifolium spp.	3	1	131	2	1	10	2	2	17
Triticosecale spp.	0	0	0	0	0	0	1	0	1
Triticum aestivum	0	0	0	0	0	0	1	0	5
Tussilago farfara	0	0	0	0	0	0	0	0	2
Urtica dioica/urens	29	271	395	8	16	15	1	1	8
Valerianella spp.	2	5	2	1	3	2	0	0	0
Verbascum densiflorum	0	0	0	0	0	0	0	0	1
Verbascum nigrum	0	0	3	0	0	2	0	0	1
Verbascum spp.	0	0	0	0	0	0	0	0	1
Veronica agrestis	0	0	1	0	0	1	0	0	0
Veronica arvensis	31	2	6	2	2	2	0	0	1
Veronica hederifolia	0	4	4	0	1	2	2	1	0
Veronica persica	10	43	111	2	6	9	0	1	2
Vicia angustifolia	0	0	0	0	0	0	0	0	2
Vicia cracca	0	0	0	0	0	0	0	3	0
Vicia hirsuta	0	0	0	0	0	0	0	1	2
Vicia sativa	0	0	0	0	0	0	0	0	3
Vicia villosa	0	0	0	0	0	0	0	0	2
Viola arvensis	37	22	102	7	7	10	1	3	5
Zea mays	0	0	0	0	0	0	0	1	0

Table S5: *Results of multilevel pattern analysis, only significant species associations are shown.*

Species	stat	p-value	
Lotus corniculatus	0.534	0.005	**
Daucus carota	0.483	0.005	**
Chenopodium album	0.372	0.010	**
Cerastium holosteoides	0.364	0.015	*
Poa spp.	0.358	0.030	*
Leucanthemum ircutianum	0.357	0.005	**
Thlaspi arvense	0.351	0.005	**
Plantago lanceolata	0.325	0.030	*
Tanacetum vulgare	0.301	0.020	*
Veronica persica	0.299	0.050	*
Achillea millefolium	0.284	0.010	**
Rumex crispus	0.281	0.025	*
Myosotis arvensis	0.267	0.040	*

Table S6: *Results of multilevel pattern analysis, only significant species associations are shown.*

Group field edge seed bank

	stat	p-value
Papaver spp.	0.292	0.035

Group field edge vegetation

	stat	p-value
Equisetum arvense	0.368	0.005
Cirsium arvense	0.348	0.005
Bromus sterilis	0.315	0.020
Convolvulus arvensis	0.239	0.030

Group flower strip vegetation

	stat	p-value
Foeniculum vulgare	0.469	0.005
Cichorium intybus	0.415	0.005
Lotus corniculatus	0.395	0.005
Sinapis alba	0.386	0.005
Taraxacum spp.	0.386	0.010
Brassica oleracea	0.384	0.005
Silene spp.	0.322	0.015
Borago officinalis	0.322	0.030
Melilotus officinalis	0.313	0.025
Galium mollugo agg.	0.301	0.005
Medicago sativa	0.300	0.005
Phleum pratense	0.299	0.010
Prunella vulgaris	0.292	0.040
Phacelia tanacetifolia	0.291	0.030
Centaurea cyanus	0.282	0.035
Malva moschata	0.276	0.010
Centaurea jacea	0.267	0.005
Linum usitatissimum	0.267	0.005
Plantago major	0.265	0.005
Dipsacus fullonum	0.210	0.030
Phalaris arundinacea	0.201	0.045
Triticum aestivum	0.194	0.010

Group flower strip seed bank

	stat	p-value
Chenopodium album	0.486	0.005
Viola arvensis	0.390	0.005
Thlaspi arvense	0.369	0.005
Cerastium holosteoides	0.360	0.025
Poa spp.	0.349	0.020
Chamomilla	0.337	0.020
Veronica persica	0.333	0.010
Capsella bursa pastoris	0.305	0.005
Myosotis arvensis	0.288	0.015
Solanum nigrum	0.285	0.035
Rumex crispus	0.273	0.035
Sisymbrium officinale	0.268	0.040

Group field edge & flower strip seed bank

	stat	p-value
Juncus spp.	0.388	0.005
Urtica dioica/urens	0.312	0.015
Stellaria media	0.303	0.005
Lamium purpureum	0.288	0.030
Descurainia sophia	0.266	0.045

Group flower strip seed bank & vegetation

	stat	p-value
Daucus carota	0.374	0.010
Trifolium spp.	0.309	0.030
Plantago lanceolata	0.308	0.035
Achillea millefolium	0.278	0.025
Leucanthemum ircutianum	0.266	0.050

CHAPTER III

AGRI-ENVIRONMENTAL MEASURES SUPPORT FARMLAND BUTTERFLY DIVERSITY IN INTENSIVELY USED AGRICULTURAL LANDSCAPES

Agri-environmental measures support farmland butterfly diversity in intensively used agricultural landscapes

3.1 ABSTRACT

Agrobiodiversity is declining worldwide due to the intensification of agricultural practices, leading to the loss and degradation of the habitats of many plants and animals. Agriculture plays an important role in Germany, with around 50 % of its land area used for farming. Recently, the role of conventional agriculture in the decline in insect populations has been receiving increasing attention in Germany. The implementations of agri-environmental measures are seen as one solution to provide essential resources for important insect groups such as butterflies. We investigated butterfly diversity in three such agri-environmental measures (flower strips, extensive cereals, and less intensive grassland) and three reference habitats (conventional cereals, conventional grassland, and semi-natural habitats, i.e., grassy strips next to fields) on ten conventional farms distributed across Germany between 2017-2019. Butterfly diversity and abundance was highest on flower strips, followed by semi-natural habitats and low-intensity cereals, and lowest on conventional cereals and grassland. Trait composition did not differ between sites with and without measures, and species with life strategies adapted to high disturbance prevailed. The overall species pool was dominated by a few common species (e.g., *Pieris rapae*, *P. napi, Maniola jurtina*), while rare species (e.g., *Lycaena dispar, Boloria dia*) were only seldomly observed in semi-natural habitats.

We conclude that the studied agri-environmental measures provide an important but temporary increase in essential flower resources in conventionally farmed landscapes, but with a limited effect only on generalist butterfly species. To further increase populations and the species spectrum, we recommend changes to agri-environmental measures management to provide complementary functions, such as providing suitable habitat for overwintering, larval development, and pupation. This requires not only better design of measures, but also greater awareness among practitioners of the complex ecological requirements of insects.

Keywords: agrobiodiversity, species composition, species traits, flower strips, Lepidoptera

3.2 INTRODUCTION

Agriculture, once creating open and diverse habitats in Europe (Bignal and McCracken, 2000), is now one of the main drivers of species decline due to habitat homogenisation, fertilizer, and pesticide use (Baessler and Klotz, 2006). The negative impact of this intensification of agriculture and the accompanied loss, degradation, and fragmentation of habitats on biodiversity is a well-known problem (Stoate et al., 2001; Benton et al., 2002; Tscharntke et al., 2005; Warren et al., 2021). Germany has one of the largest and most highly intensified agricultural sectors in Europe. Around 35 % of Germany is arable land and used for crop cultivation, and 15 % are permanent grassland, whereby 90 % of that agricultural area is conventionally managed (Statistisches Bundesamt, 2021). Mainstreaming of conservation into agriculture is thus of utmost interest for these agricultural landscapes. Since 1985, various agri-environmental measures have been developed and implemented in the EU to attempt to counteract the causes of biodiversity loss (reviewed in Batáry et al., 2015). However, their effectiveness is questioned (Kleijn and Sutherland, 2003) when not carefully designed and targeted (Batáry et al., 2015).

The effects of agri-environmental measures depend on a variety of local site and landscape characteristics, and it is known that landscape heterogeneity is a crucial factor in the agricultural landscape concerning biodiversity (Tscharntke et al., 2005; Aviron et al., 2011). Heterogeneity in time and space on different scales on farmland may be the most important element to stop and reverse biodiversity loss in European agricultural landscapes (Benton et al., 2003). Many studies have shown that butterfly species abundance and composition depends on small- and large-scale heterogeneity and the amount of habitat types like forests or grasslands (Weibull et al., 2000; Weibull and Östman, 2003; Bergman et al., 2004). However, some studies found other relationships with site and landscape conditions and questioned whether there are unmeasured environmental factors on a regional level (Aviron et al., 2011), such as bio-geographical conditions important for increasing insect diversity (Schweiger et al., 2005). This might influence effectiveness of agri-environmental schemes for insect biodiversity.

Butterflies are a well-studied insect group and popular within the public (e.g., Kühn et al., 2008). They play minor roles are pollinators, but are important for some plant species, such as *Dianthus* spp. or *Viscaria* spp (Jennersten, 1984). Furthermore, they are susceptible to environmental change and have not only high but also changing demands on their habitat during their life cycle, as caterpillars and butterflies require different resources (Fleishman and Murphy, 2009). Therefore, they are a valuable indicator group for the agricultural landscape. Furthermore, the decline in common and widespread butterflies continues, indicating that efforts taken so far, including implementation of agri-environmental measures, are not effective (van Dyck et al., 2009; Wallisdevries et al., 2012). Intensification and abandonment of farmland are problematic for butterflies (Settele et al., 2009b). One challenge in butterfly conservation is that adult nectar resources are not only different from larval food plants, they can also vary in space, and flight ability, and weather conditions determine dispersal (Dennis et al., 2006). In intensively used farmland, butterflies are directly and indirectly affected by fertilizer and pesticide use, e.g. due to the removal of arable weeds (Longley and Sotherton, 1997). Thus, survival and reproduction are, for example, restricted by limited floral resources (Lebeau et al., 2016). Furthermore, disturbances such as cutting or overgrazing increase adult and larval mortality

(Dover et al., 2010; van Noordwijk et al., 2012). Therefore, butterfly populations inhabiting agricultural landscapes are directly influenced by human activity.

Some butterfly species, exhibiting specific traits, are better in coping with man-made disturbances. Butterfly species with more than two generations per year and several potential host plants are less negatively impacted by increasing human disturbance, compared to oligovoltines and diet specialists (Kitahara et al., 2000; Börschig et al., 2013). Polyphagous species, with the possibility to switch between host plants, can compensate for plant species loss, while monophagous species cannot (Wenzel et al., 2006). High mobility and long flight periods are also necessary traits to survive in frequently disturbed landscapes, enabling butterflies to find new suitable patches with nectar resources or larval host plants (Börschig et al., 2013).

We used butterfly species richness and abundance data from monitoring between 2017-2019 on 10 conventional farms scattered across Germany. Those were participating in the F.R.A.N.Z. project to promote biodiversity. The data was collected on three agri-environmental measures (flower strips, extensive cereals and less intensive grassland) and three reference habitats (conventional cereals, conventional grassland and semi-natural habitats, i.e., grassy strips next to fields) to test the following four hypotheses.

Important food resources, such as nectar, attract butterflies towards sites with agri-environmental measures, therefore (1) ***on average more butterfly individuals and species are on sites with agri-environmental measures compared to reference areas within the intensively used landscape. Additionally, species composition differs.*** Providing less disturbed and plant species-rich habitats***, (2) agri-environmental measures, increase less mobile and oligophagous species with shorter flight period and fewer generations per year. (3) Species diversity, abundance and composition differ among treatments. Most species and individuals occur on flower strips, followed by other agri-environmental measures such as extensive cereals and reference areas. The flowering aspect (nectar supply) generated by those measures is one main factor.*** Isolated patches surrounded by arable land only, are hard to colonize compared to measures placed in the vicinity of source habitats, such as semi-natural habitats. Therefore, ***(4) butterfly species diversity, abundance and composition are influenced by site conditions, such as small-scale habitat heterogeneity and land-use type.***

3.3 MATERIAL AND METHODS

Study area

This study was performed as part of the F.R.A.N.Z. project (https://www.franz-projekt.de/website/english-summary), which aims at uncovering and communicating the effectiveness of different agri-environmental measures on biodiversity. For this purpose, the project collaborates with ten conventional farms, located across Germany (Figure 3.1). Farms were on average 460 ha large (s.d.: ± 467 ha; smallest 67 ha, biggest 1735 ha), including purely arable/cropping farms (n = 7), mixed farms with arable land and grassland for livestock (n = 2) and one grassland farm with dairy livestock (n = 1). Main crops (> 10 % cultivation area per farm) were sugar beet (n = 5), maize (n = 5), rapeseed (n = 3), potatoes (n = 2), and different cereals (n = 9). Due to the transdisciplinary nature of this project, the implementation of agri-environmental measures on each farm were adapted according to the regional context and farmer´s preferences. Hence, on each farm, a variety of measures in various designs were implemented.

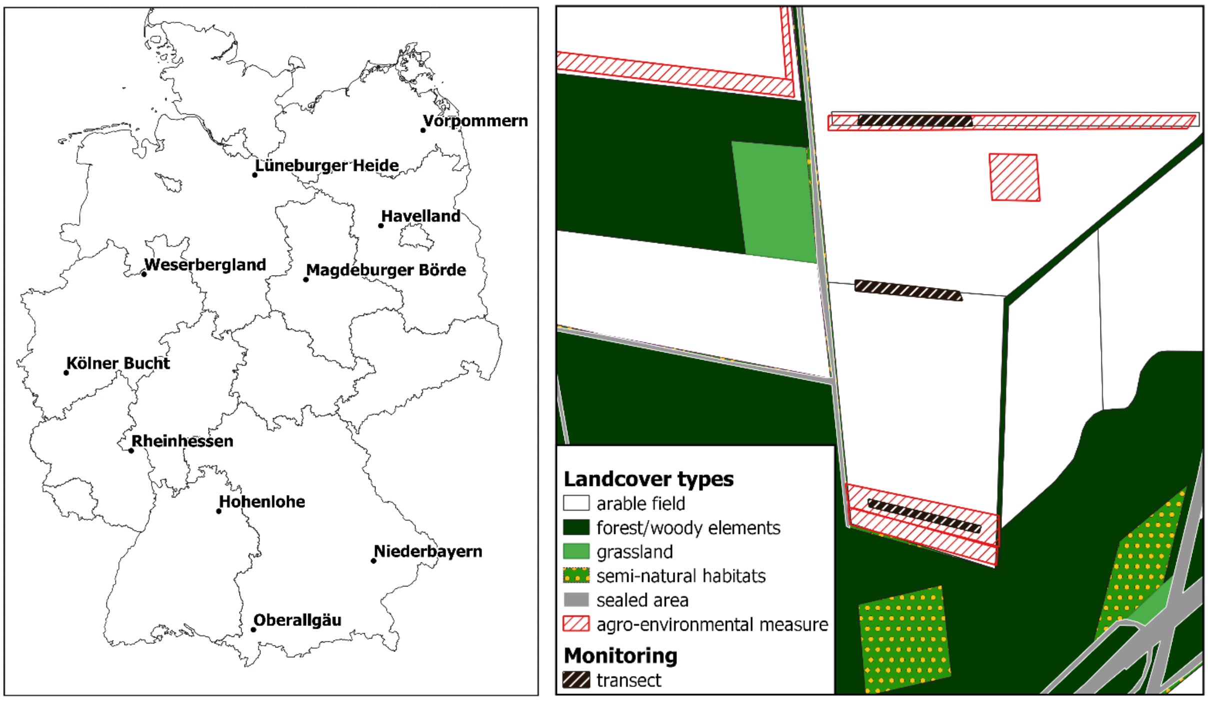

Figure 3.1: *(left) Locations of investigated farms across Germany and (right) example of transect locations within a farm.*

Study design

On each farm, we surveyed butterflies (Papilionidae and Zygaenidae) within the different agri-environmental measures over the duration of three years (2017-2019). On average, we surveyed 18 transects per farm (+/- 5) and year, resulting in 237 different surveyed transects. Transects representing the same treatment and sampled in the same year were located at least 200 m apart from each other.

Butterfly monitoring took place on six different treatments (see Figure 3.2) representing two groups. The first group contained three types of agri-environmental measures. **(i) Flowering strips (n=67):** Autumn- or spring-sown flower strips, between 3 and 18 m wide and 100 to 1700 m long, with seed mixtures containing 1 plant species (black medick) up to 41 species (crop and wild species mixtures). The flower strips and their vegetation were of varying age at the time of monitoring (between 1 month and 2 years). **(ii) Extensive cereals (n=32):** Strips (between 15 m and 27 m wide) or areas (0.7 ha – 1 ha) with different winter and summer cereals, sometimes containing additional under sown seed mixtures with different clover species. Areas differed in sowing density and ranged from wide row spacing with reduced sowing densities to normal conventional sowing density. The cereal crops were typically harvested between the 4th and 5th survey.

(iii) extensive grassland (n=10): Different grassland areas or strips with reduced mowing frequencies or less grazing. In all agri-environmental measures, use of fertilization and crop protection products were reduced compared to the reference areas conventional cereals and grassland. Measures were either stationary or rotated with the crops, depending on the type of farm.

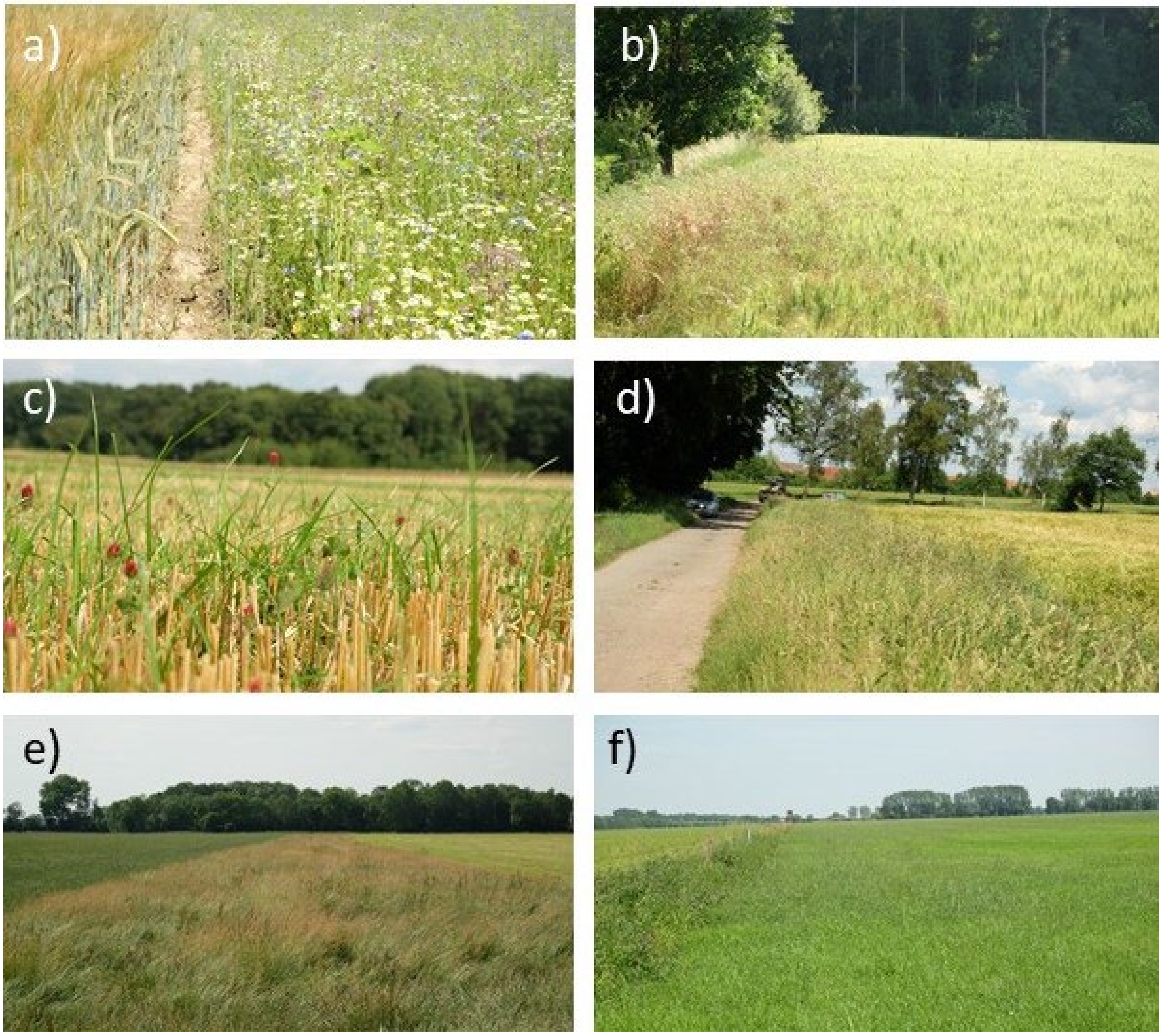

Figure 3.2*: left side: agri-environmental measures (a: flower strip, c: extensive cereals with undersown clover seed mixture in August after harvest, e: less intensive used grass strip); right side: reference areas (b: edges of cereal fields, d: semi-natural habitats, such as grassy field margins, f: conventionally used grassland)*

The second group of treatments consisted of three classes of reference areas: **(iv) Cereals (n=59):** Field edges with no agri-environmental measures, but conventional cereals. **(v) Grassland (n=10):** Conventionally used grassland (meadows with and without grazing)**. (vi) Semi-natural habitats (n=56):** Mostly linear field margins, but also smaller areas, such as grass strips with occasionally shrubs or small residual habitats, including grassland with no significant use for the farmers and therefore not conventionally used.

Survey walks and butterfly identification

Butterflies were counted according to the method of Pollard and Yates (1994). 100 m long transects were placed in agri-environmental measurement areas and corresponding reference areas and walked for 10 minutes each (walking speed around 0.6 km/h). Transect walks were repeated 5 times between May and August with three weeks interval in 2017, 2018 and 2019 between 9:30 and 18:00. The flowering aspect of each transect was estimated for every walk on a scale of zero to four (flower coverage between 0 – 5 % was categorized as 0; 5 – 25 %: 1; 25 – 50 %: 2; 50 – 80 %: 3; > 80 %: 4). Monitoring took place on days with suitable weather conditions (clouds less than 100 %; at min. air temperatures of 13°C (highest was 35°C); wind not more than four Bft (wind speed around 20 km/h). Photographic documentation and occasionally hand netting, with subsequent release, were used for species determination. Whenever individual species could not be determined, they were included in the protocols as species complexes (*Pieris rapae/napi, Thymelicus lineola/sylvestris, Colias hyale/croceus*) or families (Lycaenidae). For taxonomic determination we used Settele et al. (2009c) as well as Tolman and Lewington (2012).

Due to annual changes in management, some transects needed to be relocated between years. Particular attention was paid to the following aspects during transect placement: (i) reuse of transect from past year (e.g., semi-natural habitats and flower strips, to account for differences between the years), (ii) if possible, at least three transects per treatment and farm were selected (aim: local differences at farm level as random factor/nested with enough replicates per farm), (iii) requirement of minimum distance of 200 m between transects of same treatment within one year was to be met.

Species traits

Species traits of butterflies were obtained from Middleton-Welling et al. (2020). For species complexes, mean values of occurring species were calculated and information on two day-flying burnet moths (*Zygaena filipenduae* and *Z. loti*) were obtained from Rheinhardt et al. (2020). Number of individuals exhibiting a specific trait were calculated for each transect. The following traits were analysed: (i) host plant specificity: species were classified according to their host plant range. No monophagous species were identified, but 12 narrow oligophagous, 27 broad oligophagous and 16 polyphagous species (see Appendix Table A3.1). (ii) Voltinism (nr. of generations per year): maximum number of generations per year was chosen to categorize 20 univoltine, 7 bivoltine and 27 multivoltine species with up to three generations per year. For reasons of simplicity three species with 1.5 generation per year (*Coenonympha arcania, Melitaea athalia* and *Polyommatus semiargus*) were categorized as univoltine. (iii) Mobility: we plotted the wing index of all occurring species. The resulting histogram showed three distinguishable size groups (see bar chart Appendix Figure A3.1). Therefore, we defined three mobility classes based on wing index; less mobile (Wing index between -0.075 and -0.025; 18 species), mobile (-0.025 to 0.05; 23 Species) and highly mobile (0.05 to 0.125; 9 Species).

(iv) Flight period: same method for grouping as mobility data was applied, resulting in two classes. In total, 20 species with flight periods shorter than 4.5 months were categorized as short and 34 species with flight periods exceeding 4.5 months as long. For species complexes (e.g., *Pieris rapae/napi*) mean values of traits were calculated and used for analysis.

Land use heterogeneity

We obtained information on land use heterogeneity at the transect level, by placing buffers with 250 m radius around all transects in 2019 (buffer area ~24 ha). First, proportion of each land use type of the following seven land cover types in the surrounding landscape was determined (for further description of types see Table 3.1): arable land, grassland, sealed surfaces, woody vegetation, semi-natural habitats, water bodies and permanent crops (see Figure. 3.3 for example). Second, to derive land use heterogeneity Shannon diversity index for every transect was calculated.

Table 3.1: *Description of land use within 250 m buffer around transects including agri-environmental measures.*

land use type	description
arable land	all areas cultivated with annual crops like cereals, potatoes, or sugar beet
permanent crops	vineyards, orchards (only present on one farm)
measures on fields	measures implement on arable land, like flower strips or extensive cereals
grassland	conventionally used grassland
measures on grassland	measures implemented on grassland, like less intensive use or top soil removal
woody elements	shrubs, small clusters of trees, alley trees, forest
water	ditches, water filled hollows and rivers
others	construction sites, quarries, manure heap

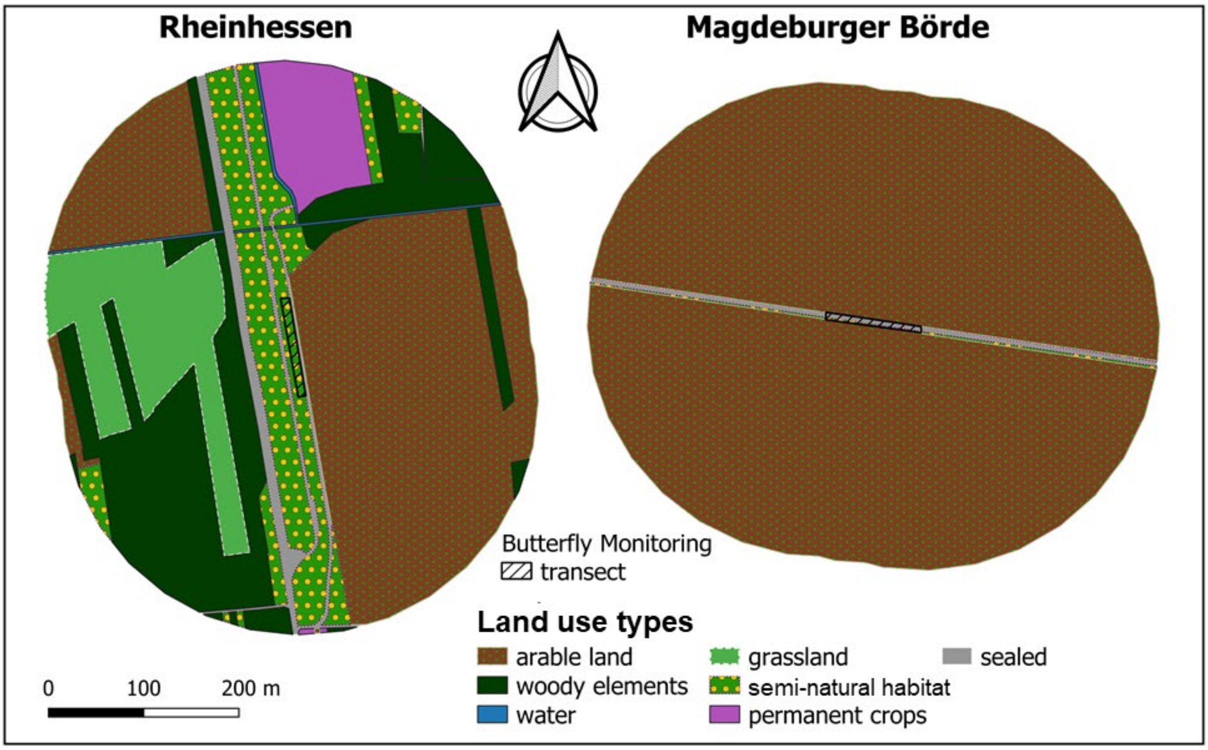

Figure 3.3: *Land use heterogeneity on two different farms. 250 m buffer around the transects, both located on semi-natural habitats.*

Statistical Analysis

Data of the five walks per year was pooled for every transect. *Vanessa cardui* was removed from the analysis due to mass migration in 2019 (2017 and 2018: < 1 % observations and present on 12.5 % of transects; 2019: 25 % of all observations and present on 83 % of transects). Furthermore, species complexes (*Pieries rapae/napi*, *Thymelicus lineola/sylvestris* and *Colias hyale/croceus*) were used for most analyses, except when number of species was calculated. In this case, individual species were counted if possible and complexes only when none of the individuals was identified. Farm location had an impact on diversity and abundance of butterflies and due to an imbalanced implementation of agri-environmental measures, three different data sets were generated to test the hypothesis.

Data set one: calculated mean values for transect surveyed two or three times within the three years study period from all ten participating farms. Furthermore, transects were categorized according to their group, either agri-environmental measure (n = 109) or reference area (n = 125). *Data set two*: in order to account for the effect of farm (problems arising due to insufficient number of replicates for specific treatments on individual farms) data was grouped into two subsets. Subset one included data from five farms and four different treatments (flower strips: 41, extensive cereals: 27, conventional cereals: 34 and semi-natural habitats: 31). Subset two included data from three farms and two treatments (less intensive: 10; and conventional grassland: 10). For both subsets mean values for transects surveyed two or three times within the study period were calculated. *Data set three*: Data from 2019 of all participating farms, 158 transect (including 6 without any butterfly observations at all).

To answer hypothesis one and check for difference between the two groups, we used *data set one* and performed a linear mixed model for negative binomial data using the '*glmer.nb'* function from the *'GLMMadaptive'* package (Dimitris Rizopoulus, 2021), with "farm" as random factor. The response variables were species number and abundance with flowering aspect, group and their interaction as explanatory variable. Model residuals were tested for overdispersion (Pearson chi² Test, with *overdisp_fun* from PsychHelperFunctions) and spatial auto-correlation with the '*corelog*' function of the '*ncf*' package (Bjornstad, 2020). We checked the variance inflation factor for both predictors in each model with the *'vif'* function from the '*car*' package (Fox and Weisberg, 2019). Differences in species composition were analysed by permutational multivariate analysis of variance using distance matrices (derived from square root transformed species abundance data) form the '*vegan*' package (Oksanen et al., 2020), controlling permutations for farm. The same data set was used for hypothesis two with the '*lmer*' function from the '*lme4*' package (Bates et al., 2007) was used and weighted proportion for species traits were generated per transect and log transformed (log(1+x)) for better model fit. To test hypothesis three and check for difference between treatments, *data set two* was used for detailed comparison between flower strips, extensive cereals, and cereals and semi-natural habitats, as well as differences between less intensive and intensive grassland. For analysing number of species and abundance generalized mixed models using the '*nb.glmer'* function of the R package '*GLMMadaptive*' followed by pairwise comparisons (Lenth et al., 2021) were performed. Species composition was analysed by permutational multivariate analysis of variance followed by subsequently permutational MANOVAs and Bonferroni p-value correction. Cross comparison between grassland groups and arable land groups was not possible due to the specific farm characteristics and their uniqueness (lack of comparability).

To test hypothesis four and identify major variation patterns in species composition due to local landscape characteristics, we used *data set three* to perform a non-metric multidimensional scaling (NMDS) using the '*metanmds*' function from the '*vegan*' package. Before performance of NMDS species abundance data was log transformed (log(1+x)), reducing influence of very abundant species. Rare species were not removed, ensuring that especially species sensitive to anthropogenic impact are considered (Poos and Jackson, 2012). Six transects were removed due to missing butterfly occurrence. The '*envfit*' function was used to get the p-values of correlation of each variable with the overall butterfly communities. Impact of landscape characteristics on number of species and abundance was tested with linear mixed model. Landscape cover types with less than 5 % cover in more than 70 % of transect (112 of 158) were not considered for analysis. Remaining cover types (field, grassland, woody elements, and area of agri-environmental measure) as well as transect conditions, such as flowering aspect and landscape cover diversity were analysed. Backward model selection for analysing effects on species number and abundance was used.

Statistics were done using R Studio (RStudio Team, 2021) version 201.09.1 Build 372 “Ghost Orchid” Release; all graphics were created with '*ggplot2*' package (Wickham, 2016). For all models, fit was evaluated with the '*simulateResiduals*' and '*plot'* function of '*DHARMa*' package (Hartig, 2021).

3.4 RESULTS

We observed a total of 8674 butterfly individuals from 48 species (Appendix Table A3.1). Transect-level species richness ranged between 0 and 16 (mean ± sd: 8.1 ± 3), number of individuals between 0 and 121 (mean ± sd: 23 ± 25) per transect and year. More than 50 % of all individuals belonged to *Pieris* spp. represented by the small cabbage white (*Pieris rapae)*, the green-veined white (*P. napi*) and the big cabbage white (*P. brassicae*). Twenty percent of all individuals composed grassland butterflies, including the meadow brown (8 %, *Maniola jurtina*), small heath (5 %, *Coenonympha pamphilus*) and ringlet (4 %, *Aphantopus hyperantu*s) and the peacock (4 %, *Aglais io*). Only the *Pieris* species were observed on more than 50 % of the transects. 24 species were counted less than ten times on six or fewer transects. The scarce swallowtail (*Iphiclides podalirius*), black hairstreak (*Satyrium pruni*) and the pearly heath butterfly (*Coenonympha arcania)* were detected only once within the three-year study period.

Agri-environmental measures increase observed butterfly abundance and diversity

On average more individuals and species occurred on transects with agri-environmental measures compared to transects in reference areas (Table 3.2). Flowering aspect had a significantly positive relationship with both individual and species richness. 44 species occurred on transects within agri-environmental measures and 41 on transects within reference areas. Seven species occurred exclusively on transects with agri-environment measures, and four species occurred exclusively on reference areas and thus 37 species occurred on both. Species composition differed between measures and reference and depended on flowering aspect as well. Both, measures and reference, and flowering aspect explained around 6 % of the observed variance. Multilevel pattern analysis detected nine species and three species complexes significantly associated with agri-environmental measures (ordered, beginning with strongest association: *Pieris* complex*, Polyommatus* complex*, Pieris brassicae, Colias* complex*, Pontia edusa, Aglais io, Papilion machaon, Maniola jurtina, Gonepteryx rhamni, Carcharodus alceae, Issoria lathonia, Aglais urticae*, for further details see Appendix Table A.3.2). No significant indicator species for reference areas were identified, however, species such as *Ochlodes sylvanus* and *Lycaena dispar* were associated with those areas.

Table 3.2: ***R****esults of linear mixed model, testing differences between reference areas and AEMs with farm as random factor.*

Number of species

Fixed effects	**Estimate**	**s.e.**	**Z value**	**p-value**
(intercept)	1.37	0.13	10.71	<0.001*
Measures vs. reference	-0.22	0.11	-1.98	0.048*
Flowering aspect	0.29	0.06	5.05	<0.001*
Measures vs. reference *flowering aspect	0.20	0.13	1.56	0.12

Number of observations

Fixed effects	**Estimate**	**s.e.**	**Z value**	**p-value**
(intercept)	2.67	0.18	14.88	<0.001*
Measures vs. reference	-0.48	0.17	-2.84	0.004*
Flowering aspect	0.57	0.10	5.78	<0.001*
Measures vs. reference*flowering aspect	0.57	0.24	2.40	0.016*

Species composition

Fixed effects	**DF**	**SumsOfSqs**	**MeansSqs**	**F. Model**	**R²**	**p-value**
Measures vs. reference	1	2.13	2.13	15.08	0.06	0.001*
Flowering aspect	1	1.89	1.88	13.32	0.06	0.001*
Residuals	227	0.14	0.14		0.88	
Total	228	36.00			1.0	

Most common butterfly species in intensively used agricultural landscapes were oligophagous, mobile species and short reproduction cycle

We analysed whether butterfly species react differently to agri-environmental measures depending on their ecological traits, such as food plant specialization, mobility, number of generations per year and flight period duration. Monophagous species were not present, but 12 narrow and 29 broad oligophagous, as well as 17 polyphagous species. Oligophagous, mobile species and long flight periods (consequently with up to three generations per year) were more common in intensively used agricultural landscapes compared to less mobile species with limited flight periods and narrow hostplant range, as trait proportion analysis showed (see Figure 3.4). This pattern for butterflies holds true irrespective of treatment or reference area. Proportion within trait characteristic was different, but trait characteristics did not differ between agri-environmental measures and reference areas (see Table 3.3).

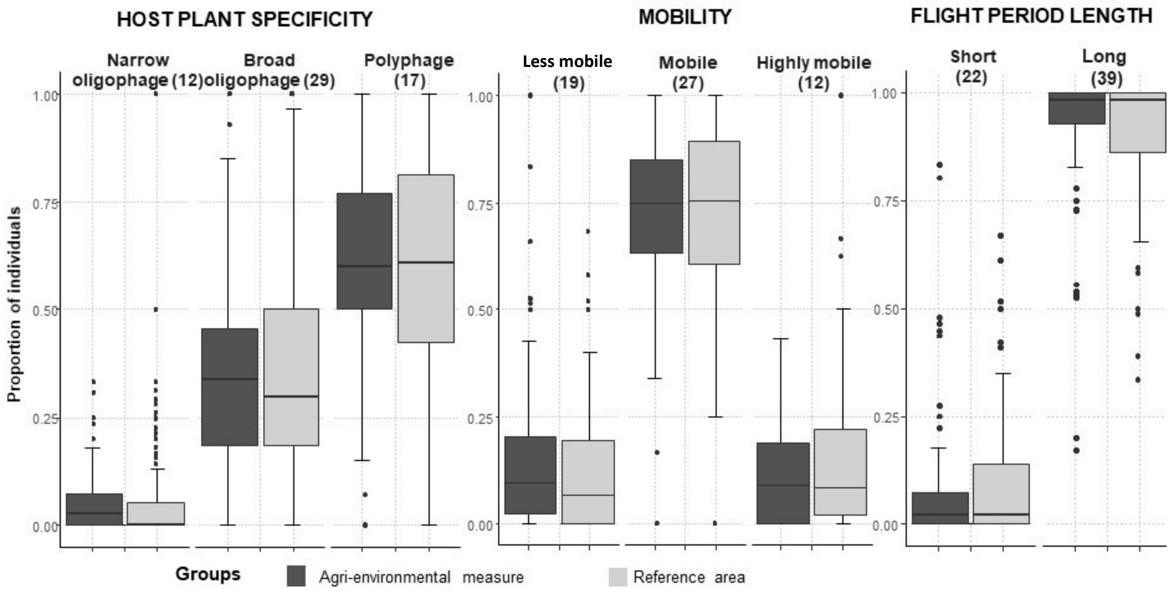

***Figure 3.4**: Boxplots illustrating proportion of traits for host plant specificity, mobility and flight period (number of generations not shown, due to trait relationship with flight period; species with long flight periods also have two or three generations per year, whereas species with short flight periods only have one generation).*

Significant interactions between flight period and group due to higher mean values for proportion of short flight periods for agri-environmental measures (0.07 vs 0.01), were not confirmed by subsequent pairwise tests.

Table 3.3: *Test results of four linear mixed models with proportion of specific traits as dependent variable with group (agri-environmental measure or reference area), trait and their interaction as explanatory variables (farm as random factor).*

Type III Analysis of Variance Table with Satterthwaite's method

	Sum Sq	**Mean Sq**	**NumDF**	**DenDF**	**F**	**p-value**
Group	0.004	0.004	1	681	0.173	0.678
Host plant specificity	19.394	9.697	2	681	441.848	< 0.001*
Group*host plant specificity	0.006	0.003	2	681	0.1319	0.877
Group	0.001	0.001	1	681	0.056	0.814
Mobility	27.906	13.953	2	681	905.820	< 0.001*
Group*mobility	0.043	0.021	2	681	1.402	0.247
Group	0.000	0.000	1	681	0.017	0.895
Nr. of generations	43.428	21.713	2	681	1597.229	< 0.001*
Group*nr. of generations	0.003	0.001	2	681	0.118	0.888
Group	0.003	0.003	1	454	0.303	0.582
Flight period	37.246	37.245	1	454	3539.380	< 0.001*
Group*flight period	0.041	0.041	1	454	3.931	0.048*

Flower strips exhibited more individuals and species compared to other agri-environmental measures

Number of species and observations differed significantly between flower strips and extensive and conventional cereals, as well as between extensive and conventional cereals and semi-natural habitats and cereals (generalized linear mixed model results in Appendix Table A3.2). On average, highest flowering aspect and most species and individuals occurred on flower strips, followed by less intensive grassland, semi-natural habitats and extensive cereals (see Table 3.4 and 3.5 and Figure. 3.5). Conventional cereal fields displayed the least flowering aspect and only two to three species and seven butterfly individuals were counted on average per transect. The same pattern was true for the average number of individuals occurring on different treatments. Less intensive and conventional grassland - represented by a limited number of replicates did not significantly differ in number of butterflies or species (see Figure. 3.5, left side).

Table 3.4: *Mean values for number of individuals, species and flowering aspect (sd: standard deviation), as well as smallest (min) and largest (max) value for individuals and species.*

	Individuals				**Species**				**Flowering**	
Treatment (n)	mean	sd	min	max	mean	sd	min	max	**aspect**	sd
Flower strips (39)	40.10	± 23.56	3	105	7.07	± 2.91	1	13	1.46	± 0.69
Extensive cereals (27)	14.48	± 12.84	1	47	3.89	± 2.65	1	11	0.65	± 0.62
Conventional cereals (34)	6.42	± 6.67	0	32	2.37	± 1.41	0	7	0.15	± 0.38
Semi-natural habitats (29)	18.13	± 14.74	3	62	5.37	± 2.25	1	10	0.42	± 0.50
Less intensive grassland (9)	28.19	± 28.99	5	100	5.19	± 2.88	2	11	0.16	± 0.21
Intensive grassland (10)	16.70	± 14.64	3	47	3.67	± 1.44	2	6	0.13	± 0.19

***Table 3.5**: Results of pairwise comparisons of species composition; significant differences marked *.*

SPECIES	Estimate	SE	Z-ratio	p-value
Flower strip vs. extensive cereals	0.363	0.129	2.822	0.025*
Flower strip vs. conventional cereals	0.825	0.153	5.406	<0.001*
Flower strip vs. semi-natural hab.	0.071	0.122	0.584	0.937
Extensive cereals vs. conventional cereals	0.462	0.151	3.059	0.012*
Extensive cereals vs. semi-natural hab.	-0292	0.128	-2.278	0.103
Conventional cereals vs. semi-natural hab.	-0.754	0.139	-5.419	<0.001*
Extensive grassland vs. conventional grassland	0.329	0.219	1.500	0.134

ABUNDANCE	Estimate	SE	Z-ratio	p-value
Flower strip vs. extensive cereals	0.646	0.189	3.424	0.003*
Flower strip vs. conventional cereals	1.106	0.222	4.985	<0.001*
Flower strip vs. semi-natural hab.	0.240	0.197	1.218	0.615
Extensive cereals vs. conventional cereals	0.461	0.196	2.351	0.087
Extensive cereals vs. semi-natural hab.	-0.405	0.186	-2.179	0.129
Conventional cereals vs. semi-natural hab.	-0.866	0.186	-4.658	<0.001*
Extensive grassland vs. conventional grassland	0.397	0.221	1.795	0.070

Results are given on the log (not the response) scale.
P value adjustment: tukey method for comparing a family of 4 estimates

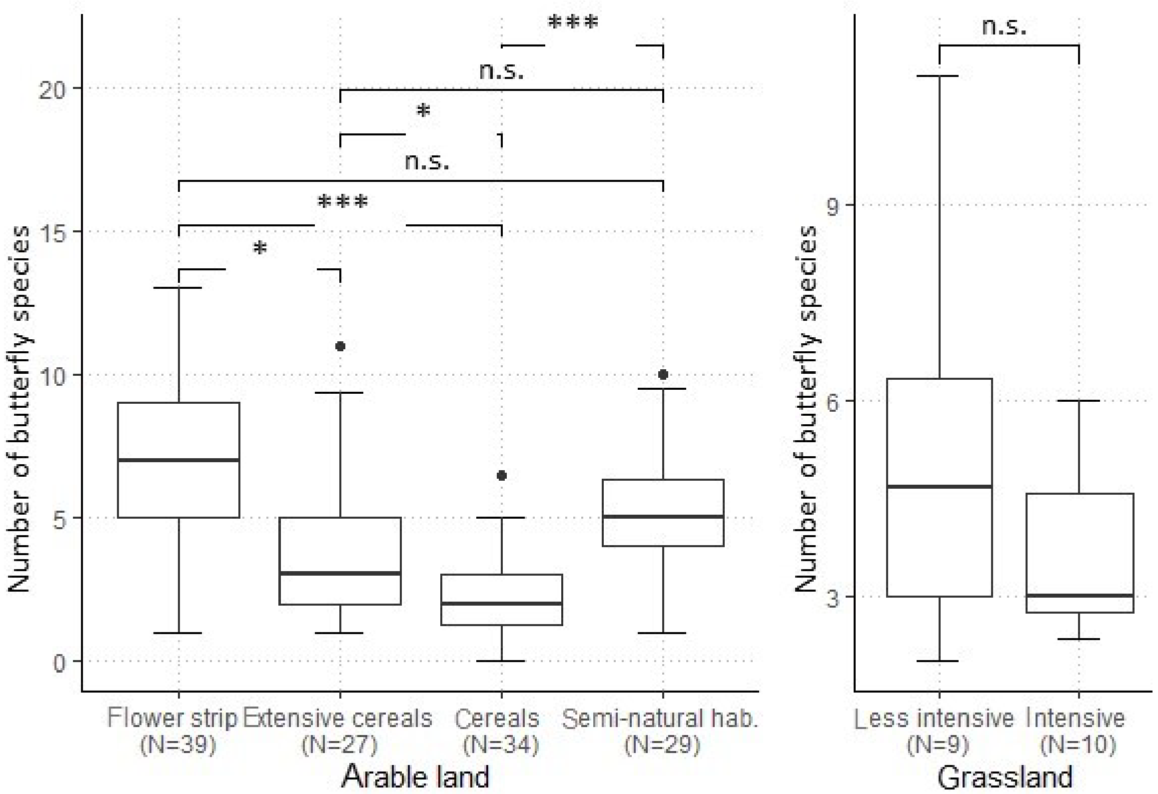

***Figure 3.5:** Boxplots: (right) Number of butterfly species for flower strips and extensive cereals as most common agri-environmental measure and cereals and semi-natural habitats as reference area. Flower strips vs. extensive cereals: Z = 2.8, p = 0.02*; flower strip vs. cereals: Z = 5.4, p = <0.001; flower strip vs. semi-natural habitat: Z = 0.6, p = 0.94; extensive cereals vs. cereals: Z = 3.1, p = 0.01*; extensive cereals vs. semi-natural habitat: Z = -2.3, p = 0.1, cereals vs. semi-natural habitat: Z = -5.4, p = <0.001, significance levels from pair wise comparisons of estimated marginal means, calculated from the mixed model. (left) Comparison between species counted on low intensive and conventional grassland: Z = 1.5, p = 0.1; (N = total number of transects).*

Species composition differed between treatments on arable land, accounting for ~ 20 % of variation. Grassland transects with and without agri-environmental measures exhibited the same species composition, however small sample size reduces explanatory power. Flowering aspect (influenced by factors, such as development of vegetation, seed mixture, drought and local management) had a significant influence and explained in grassland ~ 10 % and in arable land ~ 4 % of variation in species composition (see results in Table 3.6, terms added sequentially and flowering aspect additionally to treatment). Species composition differed significantly between all pairs, except for extensive cereals and semi-natural. Five species and three species complexes were significantly associated with flower strips only (in order of importance: *Pieris* complex*, Polyommatus* complex*, Pieris brassicae, Gonepteryx rhamni, Issoria lathonia, Pontia edusa, Carcharodus alcaea, Colias* complex). An additional seven species were characteristic for both flower strips and semi-natural habitats (*Aglais io, complex Thymelicus, Maniola jurtina, Coenonympha pamphilus, Aglais urticae, Lycaena phlaeas*). Other species could not be assigned significantly to specific treatments due to insufficient number of observations (see statistical results in Appendix A3.4).

Table 3.6: *Results of permutational multivariate analysis of variance, effect of treatment and flowering aspect on species composition for treatments on (upper part) arable land (flower strips, extensive and conventional cereals and semi-natural habitats) and (lower part) grassland.*

Species composition

Arable land	**DF**	**SumsOfSqs**	**MeansSqs**	**F. Model**	**R²**	**p-value**
Treatment	3	3.975	1.325	10.919	0.199	0.001*
Flowering aspect	1	0.718	0.718	5.919	0.036	0.001*
Residuals	126	15.291	0.121		0.765	
Total	130	19.984			1.000	
Pairwise comparison						p.adjusted
Flower strip vs. extensive cereals	1	1.760		9.64	0.13	0.006*
Flower strip vs. cereals	1	4325		24.79	0.26	0.006*
Flower strip vs. semi-natural habtat	1	1.799		10.90	0.13	0.006*
Extensive cereals vs. cereals	1	0.652		3.166	0.05	0.042*
Extensive cereals vs. semi-natural hab.	1	0.449		2.300	0.04	0.120
Cereals vs. semi-natural habitat	1	1.416		7.670	0.11	0.006*

Grassland	**DF**	**SumsOfSqs**	**MeansSqs**	**F. Model**	**R²**	**p-value**
Treatment	1	0.123	0.123	0.866	0.046	0.153
Flowering aspect	1	0.261	0.261	1.843	0.099	0.021*
Residuals	16	2.265	0.142		0.855	
Total	18	2.648			1.000	

Land use heterogeneity and butterfly abundance, diversity and species composition

In 2019 we observed a total of 3118 butterfly individuals from 39 species (for species composition analysis four species complexes were formed, resulting in 36 "species"). Mean flowering aspect and land use heterogeneity significantly influenced butterfly abundance and diversity in 2019 (see model results Table 3.7). Other environmental factors such as percentage of woody elements or grassland did not contribute substantially to explaining the number of species and observation according to backward model selection.

Differences in species composition depending on environmental factor, such as habitat heterogeneity, and percentage of woody elements within a 250 m radius are displayed in non-metric multidimensional scaling (Figure 3.7, *Vanessa cardui* removed): The green veined and small cabbage white (*Pieris rapae/napi*) were most abundant and occurred on 146 of 159 monitored transects. Both species grouped together as "*complex_Pieris*" stand apart from all other species. They accounted for 43 % of all observations, followed by meadow brown (*Maniola jurtina*) and the small heath (*Ceononympha pamphilus*) with 10 % each. 21 species were observed less than ten times on six or less transects. Butterflies, such as the black hairstreak (*Satyrium pruni*), black-veined white (*Aporia crataegi*), southern small white (*Pieris mannii*) and violet fritillary (*Boloria dia*) occurred only once (see Appendix Figure A3.2).

Table 3.7: *Results of backward selection of linear mixed models for effect of land use variables (response variable log data of species and abundance.*

SPECIES	Value	Std.error	df	T-value	p-value
Intercept	0.76	0.15	146	4.82	<0.001*
Flowering aspect	0.35	0.05	146	7.00	<0.001*
Land use heterogeneity	0.51	0.12	146	4.22	<0.001*

ABUNDANCE	Value	Std.error	df	T-value	p-value
Intercept	1.50	0.30	145	5.03	<0.001*
Flowering aspect	0.50	0.10	145	5.01	<0.001*
Land use heterogeneity	0.81	0.20	145	3.98	<0.001*

The variable 'field' (% of arable land) displayed opposing effect on composition compared to 'woody_element' (forest, shrubs, patches of trees), habitat heterogeneity ('Sh_Het': Shannon index of land cover types) and amount of agri-environmental measure in arable land ('AEM_field'). Flowering aspect ('flower') as well, was directed in opposing direction with most species occurring on sites with increasing flowering aspect.

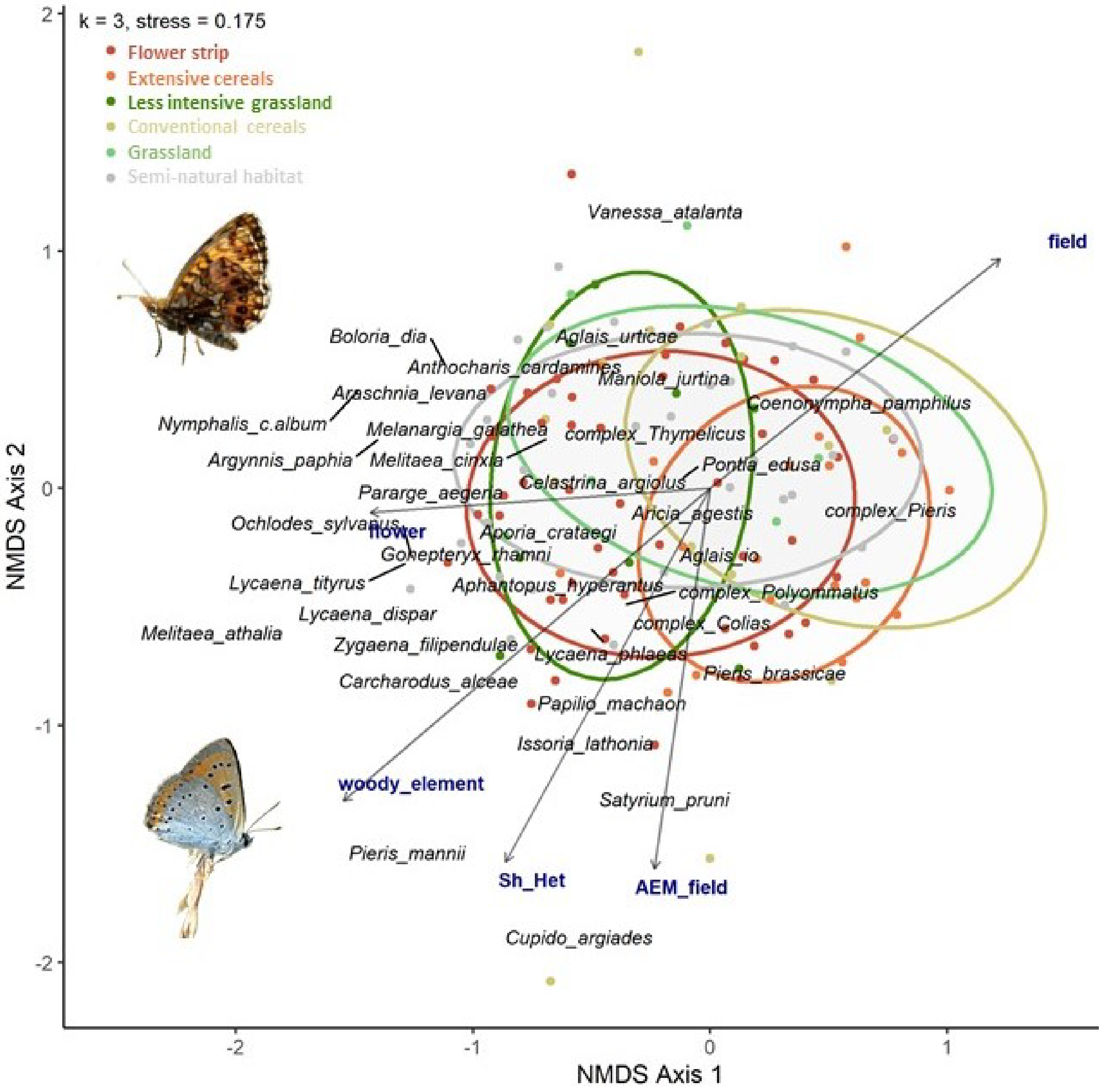

Figure 3.7: *Non-metric multidimensional scaling (NMDS) of butterfly species composition in 159 transects, grouped in ten farms. Scores from the NMDS ordination were plotted. Significant environmental factors according to a model of multiple regression with the ordination axes are displayed as arrows (Sh_Het: habitat heterogeneity, $R^2 = 0.10$, $p = 0.002$, AEM_field: proportion of total area of agri-environmental measures on arable land, $R^2 = 0.8$, $p = 0.002$; woody_element: forest and hedged, $R^2 = 0.13$, $p = 0.001$; flower: flowering aspect, R^2 0.06, $p = 0.003$. Polygons (confidence level: 0.65): treatments: R^2 0.17, $p = 0.005$ (statistical interference due to unbalanced design, different farms did not implement all measures), farm (not depicted): $R^2 = 0.17$, $p = 0.001$; Butterflies: (top) Boloria dia; (bottom) Lycaena dispar*

3.5 DISCUSSION

We investigated patterns of butterfly diversity with regard to agri-environmental schemes, embedded into an otherwise intensively used agricultural landscape in context of the F.R.A.N.Z. Project (www.franz-projekt.de). This study is one of the first attempts to capture the effectiveness of agri-environmental measures by studying butterfly diversity in a real-world farming context over the period of three years on farms located in different regions in Germany. While acknowledging that due to the transdisciplinary nature of the project the study design might come along with limitations, the findings of these investigations still show robust evidence for the limited effectiveness of agri-environmental measures for butterfly conservation.

Agri-environmental measures are characterized by higher diversity and abundance compared to reference areas, but overall species pool is limited

More individuals and species occurred at sites with agri-environmental measures compared to reference areas. Moreover, species composition differed between sites with agri-environmental schemes and reference areas. These findings confirm the first hypothesis with regard to butterfly diversity, abundance and composition. A meta-analysis on bees, hoverflies and butterflies supported that in general agri-environmental measures in Europe promote species richness and abundance (Scheper et al., 2013). In our study, the effect of the agri-environment measures was highly dependent on the flowering aspect, and we observed more butterfly individuals on sites with more flowers. However, the significant interaction between group (agri-environmental measures vs. reference area) and flowering aspect for effect on butterfly abundance, raises the question of whether there is an actual increase in butterflies or if we just observe one due to the monitoring method. Butterflies, pulled away from the landscape might spend more time on sites with agri-environmental measures ("vacuum cleaner effect") due to foraging behaviour and therefore, only probability of observing more butterflies increases. This effect is described for light pollution and insects active during the night (Eisenbeis et al., 2009). A study on foraging behaviour of the meadow brown (*Maniola jurtina*) comparing intensive and extensively used landscapes, observed many more individuals on introduced flower patches in intensive landscapes although overall butterfly density was lower compared to extensive landscapes (Lebeau et al., 2016). Neither we nor most of the studies analysed by a meta-analysis measured if actual population density increased. Therefore, we cannot rule out that the observed patterns are due to spatio-temporal concentrations (Scheper et al., 2013). Nonetheless, limited floral resources are problematic in intensively used landscapes and were identified as one possible reason for declines in specialist and generalist butterflies (Maes and van Dyck, 2001; Wallisdevries et al., 2012). Studies, for example on the meadow brown (*Maniola jurtina*) demonstrate that lifespan under limited and low-quality nectar availability is reduced as well as flight activity (Lebeau et al., 2016). A study on agricultural compensation areas in Switzerland observed caterpillars of the same butterfly species in flower strips and more adult individuals compared to extensively used meadows. They concluded that, flower strips implemented in high densities, with appropriate seed mixtures and minimum time span (at least 5 years) can support specific species (Haaland and Bersier, 2011). Agri-environmental measures can support present butterfly communities by providing additional nectar resources during the summer. However, those resources, e.g., flowers, are temporarily restricted and effective butterfly protection need to entail the entire lifespan (Dennis et al., 2006), and additionally provide overwintering places, larval food plants and shelter.

Our data confirm that mobile species with long flight periods, several generations per year and a high number of food plants are more common in agricultural landscapes compared to less mobile species with limited flight periods and narrow hostplant range. Differences in trait probability, however did not differ between agri-environmental sites and reference areas, contradicting our second hypothesis. Studies on increasing land use intensity, life-history and ecological traits confirm that general pattern. In areas with high land use intensity, species exhibit traits often associated with generalists. Traits such as long flight periods and high dispersal rate and several generations per year, help to survive in a frequently disturbed landscape (Börschig et al., 2013). We detected no monophagous species and while there was twice the number of oligophagous than polyphagous species, polyphagous individuals dominated. Most polyphagous species have larval host plants likewise adapted to disturbance or high nutrient conditions, so both, plants and butterflies can survive (Dennis et al., 2004). Other studies confirm that monophagous species are most affected and the first ones to vanish if disturbance increases, while polyphagous species can compensate for plant species loss by foraging on other plants (Wenzel et al., 2006). Habitat specialists like monophagous species also react stronger to fragmentation and are even rare on extensively used calcareous grasslands (Steffan-Dewenter and Tscharntke, 2000). Therefore, our results represent the general pattern in an intensively used landscape and, in contrast to our hypothesis, agri-environmental measures are not able to compensate negative effects and promote mono- or oligophagous specialist species (Aviron et al., 2011). As observed in other studies, species benefiting from agri-environmental schemes are common and widely distributed (Pywell et al., 2004).

One possible reason for this pattern in our study is, that some participating farmers were reluctant to use autochthone wild flower seed mixtures. Despite our recommendations, high costs of wildflower seed mixtures lead to rejection, and around half of the participating farmers decided on cost efficient mixtures. These mixtures were characterized by cultivar plant species such as sunflower, phacelia, fodder radish and marigolds. Therefore, many flower strips could provide nectar resources for generalists, but were not suitable as foraging habitat for specialized butterflies. Furthermore, those flower strips showed problems with establishment and often had to be reseeded every year. Tests with different seed mixtures in lower Saxony, showed that high quality wildflower seed mixtures establish themselves better and promote a higher species diversity compared to seed mixtures with cultivars (Schmidt et al., 2020).

Based on our results, a positive pattern can be seen on areas with agri-environmental schemes, but intensively used agricultural landscapes are and will be dominated by only a few generalists, including pest species like the cabbage white (*Pieris rapae/napi*). In general, we see a relatively limited common species butterfly assemblage. Long term trends of many butterfly species in Germany are still declining (Habel et al., 2019; Kühn et al., 2019). Whether agri-environmental schemes are able to stop and reverse butterfly diversity loss in regions with intensive agriculture, considering all other ongoing changes, like pollution, climate change and land use for example, remains to be seen.

Different agri-environmental measures show different effects on butterflies

Most butterfly individuals occurred on flower strips, followed by extensive cereals and semi-natural habitats. Flower strips and semi-natural habitat also hosted most species, followed by extensive cereals and conventional cereals. Furthermore, species composition differed: 20 % of variance was explained by treatment effects in arable land. This confirms our third hypothesis. Again, flowering aspect impacts differences in number of species and observations, as well as species composition.

Flower strips are most effective in providing additional nectar resources and enhancing diversity

Flower strips provide additional floral resources in an otherwise flower limited surrounding, therefore providing a foraging habitat for adults (see discussion to flowering aspect in hypothesis 1). A review comparing effects of sown wildflower strips in the EU confirms those agri-environmental measures are beneficial for insect diversity. However, effects depend among other things on seed mixtures and management (Haaland et al., 2011; Schmidt et al., 2022). In our study, annual flower strips were dominated by sunflowers (*Helianthus annuus*), cornflower (*Centaurea cyanus*), phacelia (*Phacelia tanacetifolia*), marigold (*Calendula arvensis*) and buckwheat (*Fagopyrum esculentum*). Perennial flower strips were characterized by plants such as golden buttons (*Tanacetum vulgare*), different campion species (*Silene* spec.) and teasel (*Dipsacum fullonum*). Flower richness in flower strips is important for butterfly diversity, however, not all flower strips establish well (Scheper et al., 2021) - a pattern we also observed in our study. Although, sometimes non-planted and by farmers undesirable (weed) species, such as creeping thistle (*Cirsium arvense*), attracted large numbers of butterflies as well. Weed species in general and thistle especially are beneficial for many insects (Balfour and Ratnieks, 2022). Flower strips illustrated the predicament between official requirements, farmers preference and considerations of requirements for plant establishment and butterflies. Cutting in late June is important for controlling undesirable weed species, especially if low budget seed mixtures have been used, and helps maintain the flowering aspect over a longer time period. Unfortunately, it has negative effects on butterfly abundance and diversity, shown by a study in England on flower strips on fertile soil (Pywell et al., 2011). In our study, a number of flower strips were mulched, either due to official requirements, such as minimum of agricultural activity or because farmers regarded them as too weedy. Mulching in July and August reduced flowering aspect and consequently number of observations and species. Mulching in winter (around February) had no observable impact on butterflies, but destroyed valuable overwintering habitat (Ganser et al., 2019). Furthermore, especially low budget flower strips had to be re-sown frequently, resulting in continuous disturbance in those areas. Flower strips, as implemented in this study, provide additional floral resources in an otherwise flowerless environment. In order to detect long-term population trends, e.g.

increases, as reported by other studies (Aviron et al., 2011; Kolkman et al., 2022) monitoring strictly insect friendly flower strips (only partial moving, no re-sowing), continuing monitoring of farms is needed.

Flower resources in extensive cereals not used by butterflies

Some of the extensive cereals surveyed were under-sown with flowering plant species (mostly clover), with mean flowering aspect reach values up to 2 (flowers covering between 20 to 50 %). However, own observations in the field showed that "hidden" flowers were not of interest for butterflies. Although, we observed some crossing the area, they did not dip into the cereals. Only after cereals were harvested and mostly clover species flowers were freely available, butterflies were interested in the measure, resulting in higher counts for the last monitoring. Though, many areas were ploughed shortly afterwards and monitoring in August sometimes took place on bare soil. Cereals without under-sown seed mixtures showed limited flowering aspect. Most, until now intensively used areas, exhibited dense cereals and non-flowering weed species like black grass (*Alopecurus myosuroides*) or goosefoot (*Chenopodium album*). Some areas had flowering species such as chamomile (*Matricaria* spec.) and some thistle (*Cirsium* spec.). Especially the thistle flowers attracted butterflies and led to high counts when in full blossom. For example, *Maniola jurtina* prefers thistle flowers over other flowers, demonstrated by a study on the nectar preference (Lebeau et al., 2017). However, thistles are problematic for farmers and in case of large patches, areas were mulched or pesticides used. We conclude that extensive cereals, as implemented in this project, are not a suitable measurement for butterfly conservation.

Limited data on grassland measures indicate no positive effects on butterflies

Implementation of measures in grasslands did not significantly influence butterfly diversity. Most sites were high-yielding locations, dominated by forage grass species and the reduced mowing frequency associated with the extensive grassland measure resulted in some cases in a decrease in habitat quality due to excessive biomass production. The flowering aspect did not improve within the three-year study period. Butterfly diversity on conventional grassland and low-input grassland as part of ecological compensation areas in Switzerland did not differ (Aviron et al., 2007), confirming our results. Other studies also conclude that less intensive grassland as such is not suitable as a butterfly conservations measure. Rather, expensive steps are needed, for example increasing plant diversity due to scarification and wildflower seeds (Blake et al., 2011), or implementation of sophisticated local management regimes, resulting in a mosaic landscape providing mown and unmown vegetation throughout the year (Settele et al., 2009a). Meadows, without additional cutting in summer provide major potential for hibernating insects (Unterweger et al., 2018). Efforts made to establish sites with alternating mowing frequency, were only partly successful within the project. Communication of alternating mowing regimes and no fertilization with employees and contractors sometimes failed and one farm considered it as not practicable at all. Mowing not only removes nectar resources, but also increases egg destruction and larval mortality (Johst et al., 2006). Research and interaction with farmers need to continue to find suitable measures for high yielding grasslands to support biodiversity. Although, the negative trend of grassland species was slowed down, further action is needed, including measures in intensive grassland as well as support for less intensive sites, preventing abandonment (van Swaay et al., 2015).

Ditches, forest and other semi-natural habitats enhance biodiversity in arable landscapes

Environmental variables like flowering aspect and habitat heterogeneity positively influence butterfly diversity, abundance and composition. Additional factors, such as proportion of woody elements, area under agri-environmental measures and arable land influence species composition. This confirms the fourth hypothesis. A study on butterfly diversity with comparable landscape sections (200 m radius) confirms the importance of woody elements for butterflies (Aviron et al., 2007). Woody elements provide shelter, e.g. by reducing wind speed (Dover et al., 1997). They also provide additional nectar resources. Trees like the common wayfaring tree (*Viburnum lantana*), or the small leaved lime (*Tilia cordata*) and shrubs, such as blackberries (*Rubus* spp.) or wild roses (*Rosa* spp.) were common in those elements. Furthermore, flowering herbaceous plants like ground ivy (*Glechoma hederacea*) and butterfly host plant species like stinging nettle (*Urtica dioica*), viola species (*Viola* spp.) and different grasses occurred in the undergrowth. However, not to be disregarded, woody elements are also positively correlated with habitat heterogeneity and amount of agri-environmental measures. Individual effects of specific factors were not distinguishable in our case. Not only in our project, but also for example in the Swiss plateau, compensation areas were in general placed close to hedgerows or forests (Aviron et al., 2007). From the perspective of both farmers and nature conservation, placement near or along woody elements is in most cases desirable. Positive influences of individual aspects interact, promoting butterfly diversity.

Other studies also identified agricultural management (cultivated crops, pesticide use, quality of field margins) and landscape aspects like heterogeneity, proportion of grassland or forest as factors influencing butterfly diversity (Feber et al., 1997; Kuussaari et al., 2007; Billeter et al., 2008; Haaland and Gyllin, 2010). In our study, the amount of grassland and semi-natural habitats did not affect diversity. Several reasons are possible. Due to the project design, most transects were located in arable land with no or little grassland nearby (in 56 % of transects buffer grassland covered < 5 % of the area). Especially flower strips with higher number of species and individuals compared to grassland sites often had no grassland in the immediate vicinity. Semi-natural habitats were also sparsely represented, covering in 95 % of transect less than 5 % of buffer area. Therefore, the effect might not be adequately tested. Second, the effects of structural variables measured may vary because definition of variables differ (reviewed by Tews et al., 2004). In our study grassland was often characterized by highly intensive use. Fertilizing, mowing, reseeding and chemical plant protection measures were conducted. But also, less intensive, from the perspective of agriculture farms, uninteresting small grassland areas were characterized as grassland. A better differentiation was not possible due to lacking information and limited number of replicates. The same pattern was observed in semi-natural habitats. Their quality varied, some were several meters wide, with bushes or ditches, while others were 1 m wide short kept grassy field margins next to tarred roads. Although, road side verges can enhance butterfly communities, quality plays an important role (Munguira and Thomas, 1992). Effects, ought to exist, might not have been detected. Nonetheless, all structural variables, whether it is field, grassland, semi-natural habitats or forest and hedgerows contribute to habitat heterogeneity and therefore play a role in butterfly diversity. Successful butterfly conservation needs to consider the resources different habitats provide for butterflies, e.g. larval habitat, shelter or roosting places. On landscape level all these requirements have to be met (Dennis et al., 2006).

Butterfly diversity, abundance and composition were in all data sets highly influenced by the factor farm, indicating that differences in bio-geographical aspects on a larger scale play a role (Schweiger et al., 2005). Some of the above-mentioned variables might differ between regions as well as cultivated crops, measurement types implemented and climatic conditions. However, monitoring design was not considering all those factors and missing information hide distinct patterns. Nonetheless, we recommend in agriculturally intensively used areas, to implement agri-environmental measures in combination or in proximity with other potentially suitable structures, such as hedges and ditches.

Merits and limitations

This study is one of very few investigations of the relation between butterfly diversity and agri-environmental schemes on conventional farms located in different agricultural regions in Germany. In contrast to many previous studies, the approach in the F.R.A.N.Z. project was to involve farmers in conservation practices directly. Studies show that perceptions of agricultural biodiversity are different for farmers compared to ecologists and that more dialog and knowledge transfer is needed to increase high quality area with agri-environmental measures (Maas et al., 2021). Based on this approach, following detailed discussions, farmers chose what, where and how to implement the respective measures, therefore generating the framework of the study design (see Appendix CHAPTER III 'Statistical limitations' for detailed discussion). This approach leads to limitations in our ability to relate agri-environmental measures to actual effects on butterfly diversity.

However, the merits of this study are that we gain insights in general pattern of butterfly diversity related to agri-environmental measures implemented by different farmers. Those farmers represent different attitudes towards biodiversity and regional challenges present in the agricultural landscapes in Germany. For example, several farmers lost arable land to road and urban development during the study period. In Germany, 53 ha per day are used for streets, houses, and industrial areas (Statistisches Bundesamt, 2021), increasing the pressure on farmers to increase productivity on the remaining fields and additionally destroying valuable habitats. Lease agreements sometimes prevented implementation of measures on ecologically meaningful sites, or lead to premature termination of measures. These incidents picture the reality in agricultural landscapes, and our findings help to get a better understanding on what, is achievable for butterfly conservation in intensively used agricultural landscapes under the present system. It also hints at reasons why, agri-environmental schemes were unable to halt biodiversity loss in the agricultural landscape despite the attempt to counteract the negative impacts of intensive agriculture on biodiversity by implementing different policies on EU level (Kleijn and Sutherland, 2003; Pe'er et al., 2014).

3.6 CONCLUSION

Our study demonstrates that voluntarily implemented agri-environmental measures promote common and widespread butterflies. Those measures provide additional nectar sources in an otherwise flowerless intensively used agricultural landscape. However, minimum time span and intensity of maintenance/harvest regimes could be optimized to improve the beneficial effects of those measures. In order to maintain and improve conditions for biodiversity in the agricultural landscape, more areas with high quality agri-environmental measures, are needed, taking the whole life cycle into account.

Ethics Statement

We obtained the necessary permits for surveying butterflies within the farming area of the ten participating farms, located across Germany from the respective regional nature conservation authorities. We also had the permission of the landowners to access the survey areas.

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APPENDIX CHAPTER III BUTTERFLY DIVERSITY

Table A3.1: *Species list with mean values of number of observation and ecological traits: hostplant specificity (poly.: polyphagous, broad oligo.: broad oligophagous, narrow oligo.: narrow oligophagous, no monophagous species present), number of generations per year (nr. of gen.), mobility (less mobile, mobile and highly mob.: highly mobile species) and fight period (short < 4.5 months > long). Mean values of observation for agri-environmental measures (AEM) and reference areas (ref. area).*

	Mean		Hostplant	Nr. of		Flight
Species	AEM	ref. area	specificity	gen.	Mobility	period
Hesperiidae						
Carcharodus alceae	0.051	0.008	poly.	3	less mobile	long
Carterocephalus palaemon	0	0.004	broad oligo.	1	less mobile	short
Ochlodes sylvanus	0.097	0.149	poly.	2	less mobile	short
Pyrgus armoricanus	0.005	0.004	poly.	2	less mobile	long
Thymelicus lineola	0.267	0.364	poly.	1	less mobile	short
Thymelicus lineola/sylvestris	0.355	0.182	broad oligo.	1	less mobile	short
Thymelicus sylvestris	0.018	0.017	broad oligo.	1	less mobile	short
Lycaenidae						
Aricia agestis	0.051	0.029	poly.	3	less mobile	long
Celastrina argiolus	0.055	0.008	poly.	2	less mobile	long
Cupido argiades	0.129	0.025	broad oligo.	2	less mobile	long
Favonius quercus	0.005	0	narrow oligo.	1	less mobile	long
Lycaena dispar	0.005	0.041	narrow oligo.	3	mobile	long
Lycaena phlaeas	0.088	0.099	narrow oligo.	3	less mobile	long
Lycaena tityrus	0.032	0.045	poly.	3	less mobile	long
Polyommatus icarus	1.419	0.335	broad oligo.	3	less mobile	long
Polyommatus semiargus	0.009	0.008	broad oligo.	1 (1.5)	less mobile	long
Polyommatus spec.	0.018	0.017	narrow oligo.	3	less mobile	long
Polyommatus thersites	0	0	narrow oligo.	3	less mobile	long
Satyrium pruni	0.005	0	narrow oligo.	1	less mobile	short
Thecla betulae	0	0	poly.	1	mobile	short
Nymphalidae						
Aglais io	1.401	0.537	poly.	3	highly mob.	long
Aglais urticae	0.323	0.132	narrow oligo.	3	mobile	long
Apatura ilia	0	0	broad oligo.	2	highly mob.	short
Apatura iris	0	0	broad oligo.	1	highly mob.	short
Aphantopus hyperantus	1.47	0.649	poly.	1	mobile	short
Araschnia levana	0.221	0.289	narrow oligo.	3	mobile	long
Argynnis paphia	0.194	0.194	narrow oligo.	1	highly mob.	short
Boloria dia	0.009	0	narrow oligo.	3	mobile	long
Brenthis daphne	0.005	0	narrow oligo.	1	mobile	short
Coenonympha arcania	0	0.004	broad oligo.	1 (1.5)	mobile	short
Coenonympha pamphilus	1.258	1.025	broad oligo.	3	less mobile	long
Hyponephele lycaon	0.005	0.012	broad oligo.	1	mobile	short
Issoria lathonia	1.014	0.289	narrow oligo.	3	mobile	long
Lasiommata megera	0	0	broad oligo.	3	mobile	long
Limenitis camilla	0	0	broad oligo.	1	highly mob.	short
Maniola jurtina	2.687	1.649	broad oligo.	1	mobile	long
Melanargia galathea	0.332	0.24	broad oligo.	1	mobile	short
Melitaea athalia	0	0.008	poly.	1 (1.5)	mobile	short
Melitaea cinxia	0.028	0.004	broad oligo.	2	mobile	short
Nymphalis c.album	0.051	0.025	poly.	3	mobile	long
Pararge aegeria	0.005	0.017	broad oligo.	3	mobile	long
Vanessa atalanta	0.226	0.252	broad oligo.	3	highly mob.	long
Vanessa cardui	0.106	0.07	poly.	3	highly mob.	long
Papilionidae						
Iphiclides podalirius	0	0.004	broad oligo.	3	highly mob.	long
Papilio machaon	0.175	0.033	poly.	3	highly mob.	long
Pieridae						
Anthocharis cardamines	0.046	0.008	broad oligo.	1	mobile	short
Aporia crataegi	0.005	0	broad oligo.	1	highly mob.	short
Colias croceus	0.023	0	broad oligo.	3	mobile	long

to be continued on next page

Species	Mean AEM	Ref. area	Hostplant specificity	Nr. of gen	Mobility	Flight period
Colias hyale	0.161	0.054	broad oligo.	3	mobile	long
Colias spec	0.092	0.033	broad oligo.	3	mobile	long
Gonepteryx rhamni	0.576	0.178	broad oligo.	1	highly mob.	long
Leptidea sinapis/juvernica	0.018	0.008	broad oligo.	2	mobile	short
Pieris brassicae	2.009	0.665	broad oligo.	3	highly mob.	long
Pieris mannii	0.005	0	broad oligo.	3	mobile	long
Pieris napi	1.816	0.946	broad oligo.	3	mobile	long
Pieris rapae	7.382	2.012	poly.	3	mobile	long
Pieris rapae/napi	8.097	4.426	broad oligo.	3	mobile	long
Pontia edusa	0.604	0.021	poly.	3	mobile	long
Zygaenidae						
Zygaena filipendulae	0.018	0	NA	NaN	less mobile	NA
Zygaena loti	0.014	0	NA	NaN	less mobile	NA

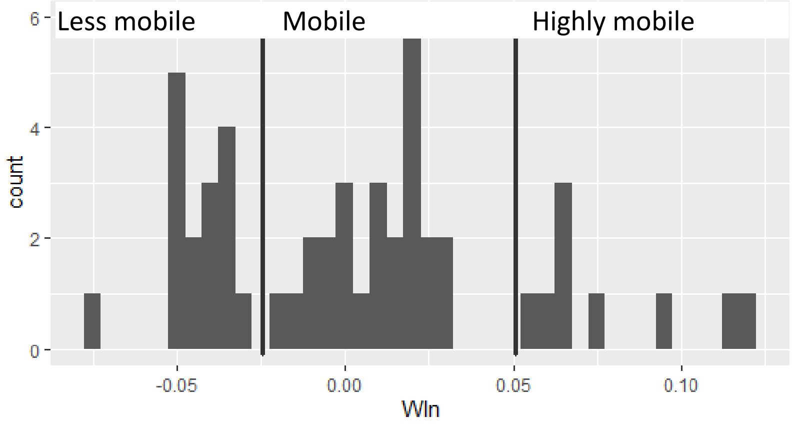

Figure A3.1: *Mobility classes; number of butterfly species for different wing index (Win), classification in three mobility classes due to three distinct size groups.*

Table A3.2: *Multilevel pattern analysis, only significant results are shown.*

Species	**Statistic**	**p-values**	**Species**	**Statistic**	**p-values**
Complex *Pieris* spp.	0.37	0.005*	*Papilion machaon*	0.19	0.005*
Complex *Polyommatus* spp.	0.33	0.005*	*Maniola jurtina*	0.18	0.005*
Pieris brassicae	0.26	0.005*	*Goneperyx rhamni*	0.17	0.005*
Complex *Colias* spp.	0.23	0.005*	*Carcharodus alceae*	0.16	0.015*
Pontia edusa	0.22	0.005*	*Issoria lathonia*	0.15	0.005*
Aglais io	0.20	0.005*	*Aglais urtica*	0.13	0.030*

Table A3.3: *Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) for number of species and observations.*

NUMBER OF SPECIES

Fixed effects:	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept) flower strip	1.663	0.135	12.256	< 0.001
Extensive cereals	-0.363	0.128	-2.822	0.005
Conventional cereals	-0.825	0.152	-5.406	< 0.001
Semi-natural habitat	-0.071	0.121	-0.584	0.559
Flowering aspect	0.183	0.065	2.821	0.005

NUMBER OF OBSERVATIONS

Fixed effects:	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept) flower strip	2.872	0.200	14.323	< 0.001
Extensive cereals	-0.645	0.188	-3.424	0.001
Conventional cereals	-1.106	0.222	-4.985	< 0.001
Semi-natural habitat	-0.240	0.197	-1.218	0.223
Flowering aspect	0.515	0.109	4.708	< 0.001

Tabelle A3.4: *Multilevel pattern analysis; out of 52 species 37 were selected and associated to one to four groups.*

	Flower strip	Extensiv cereals	Less intensive grassland	Conventional cereals	Grassland	Semi-natural habitats	p-value
Aglais io	**x**						**0.01***
Aglais urtica	x						n.s.
Anthocharis cardamine	x						n.s.
Aphantopus hyperantus			**x**				**0.005***
Aporia crataegi	x						n.s.
Araschnia levana			x		x	x	n.s.
Argynnis paphia						x	n.s.
Aricia agestis		x		x			n.s.
Bolori dia	x						n.s.
Carcharodus alceae	x						n.s.
Celastrina arigolus		x					n.s.
Coenonympha pamphilus			**x**		**x**		**0.01***
complex Colias	x						n.s.
complex Pieris	**x**						**0.005***
complex Polyommatus	**x**						**0.02***
complex Thymelicus	**x**					**x**	**0.05**
Cupido argiades	x			x			n.s.
Gonepteryx rhamni	**x**					**x**	**0.045***
Issoria lathonia	x						n.s.
Leptidea spec	x					x	n.s.
Lycaena dispar						x	n.s.
Lycaena phlaeas			x			x	n.s.
Lycaena tityrus	x			x		x	n.s.
Maniola jurtina	x				x	x	n.s.
Melanargia galathea						x	n.s.
Melitaea athalia						x	n.s.
Melitaea cinxia	x						n.s.
Nymphalis c.album						x	n.s.
Ochlodes sylvanus						x	n.s.
Papillio machaon	x						n.s.
Pararge aegeria					x		n.s.
Pieris brassicae	x	x	x			x	n.s.
Pieris mannii	x						n.s.
Pontia edusa	**x**						**0.035***
Satyrium pruni		x					n.s.
Vanessa atalanta	x					x	n.s.
Zygaena filipendula	x						n.s.

SPECIES DOMINANCE CHART (Data 2019)

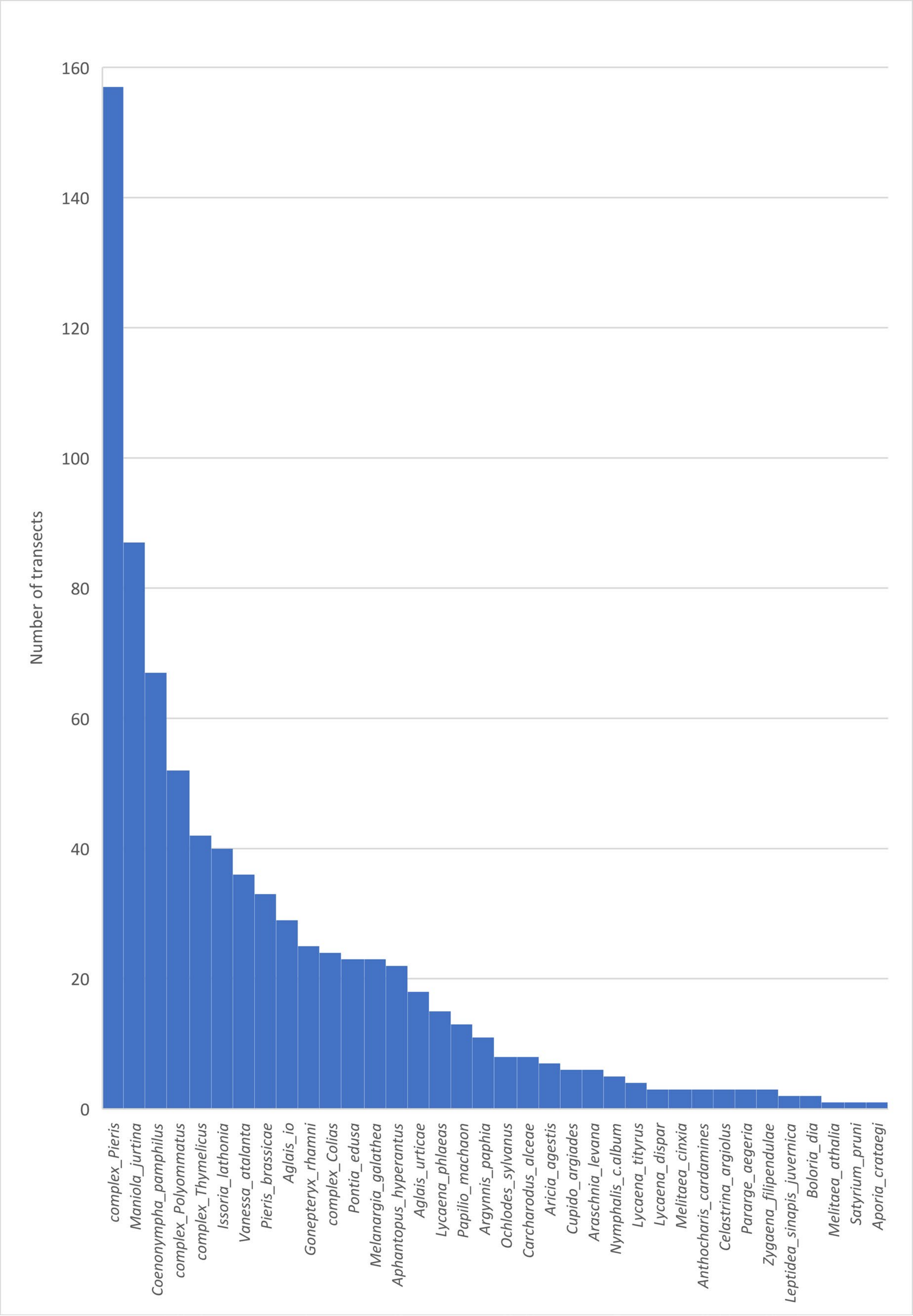

Figure A3.2: *Species dominance chart. Species ordered according to number of transects present (total number of transects: 165).*

STATISTICAL LIMITATIONS

Results of this study need to be viewed especially with respect to the study design, including 10 farms, located all over Germany and representative for their specific region. Therefore, most German agricultural systems were covered, but unknown “farm” effects could not be accounted for. All transects per region were located on fields, cultivated by one farm. Farm areas were dispersed within landscape windows ranging from 2 to 110 km². Although, individual transect of one treatment were placed at least 250 m apart, butterflies are mobile species and pseudoreplication needs to be considered. Pseudoreplication is an old problem in ecological field experiments (Hurlbert, 1984) and a controversially debated topic (Oksanen, 2001; Hurlbert, 2004; Oksanen, 2004; Davies and Gray, 2015). Nonetheless, monitoring, and analysing effects of agri-environmental measures under real conditions are necessary to understand how their ecological benefit can be influenced by other variables. This knowledge than can be used to consult farmers by the implementation, in order to increase the ecological benefit, e.g., due to recommendations concerning placement, maintenance and seed mixture. I decided to follow the recommendations mentioned by Davies and Gray (2015) and dealt with pseudoreplication by using different statistical techniques (see section *Statistical Analysis*).

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CHAPTER IV

EFFECT OF HABITAT HETEROGENEITY AND LOCAL MANAGEMENT PRACTICE ON CARABID BEETLE DIVERSITY, ABUNDACNE, SPECIES COMPOSTION AND ECOLOGICAL TRAITS IN INTENSIVE FARMLAND

Effect of habitat heterogeneity and local management practice on carabid beetle diversity, abundance, species composition and ecological traits

4.1 ABSTRACT

The intensification of agricultural practices in Europe has led to a devastating loss of biodiversity, including many insect groups. Schemes offering financial compensation to farmers for implementing biodiversity measures aim to reverse this trend. In this study, we investigate the effects of three such measures - flower strips, fallow strips and extensive cereals - in Lower Saxony (northern Germany) on ground beetles (Carabidae), a large and diverse insect group occupying a range of important niches in agroecosystems. Using pitfall traps placed in measures and reference areas, such as conventional cereals and grass dominated field margins, we collected data in early summer 2018 on number of species, activity density, trait and species composition.

Different treatments had no significant influence on number of species and activity density. However, the amount of bare soil was positively correlated to activity density and habitat heterogeneity to number of species. In general, predatory, medium-sized (between 6.5 and 11 mm) carabids, such as *Bembidion lampros* dominated. However, especially in flower, fallow and field margin strips, more herbivorous carabids were collected, compared to extensive and intensive cereals. Herbivorous species presumably benefited from the presence of non-crop plant species on these sites. NMDS analysis also confirmed this pattern, showing differences in species composition between treatments and with variation in site characteristics, such as the amount of bare ground or plant cover. We found no effect of land use heterogeneity.

In contrast to patterns found in other organism groups, we show that ground beetle abundance or species richness is not increased in agri-environment measures compared to intensive agriculture. However, the measures show positive effects for biodiversity by supporting different trophic guilds, thus widening the species pool of the agricultural landscape. This is particularly relevant in the context of the ecosystem services provided by ground beetles such as weed seed predation.

Keywords: biodiversity, pitfall traps, ground beetles, Carabidae, conventional agriculture, agri-environmental measure

4.2 INTRODUCTION

The negative impact on biodiversity due to intensification in agriculture is well documented. Not only the use of fertilizer and pesticides, but also the homogenization of landscapes have led to a decline in many plant and animal species (Tscharntke et al., 2005; Geiger et al., 2010; Tscharntke et al., 2012). Different groups of organisms have varying demands on habitats. Sometimes biodiversity depends on the occurrence of specific structures in the landscape, e.g. temporary wetlands in fields (Tews et al., 2004). Arable fields, planted with different crops, dominate intensively used agricultural areas. Non-crop or semi-natural habitats, such as hedges, grassy field margins and ditches are rare. Heterogeneity, on different spatial and temporal scales, is needed to prevent further decline in species numbers and abundances (reviewed in Benton et al., 2003). To counteract negative impacts of intensive agriculture, the EU decided to introduce different measures (European Economic Community, 1992). Since the Agenda 2000 reform of the Common Agricultural Policy, environmental and landscape protection schemes have been mandatory for all EU members (European Union, 1999).

The aim of these measures is to counteract negative impacts of intensive farming on the environment, while farmers receive financial support. Different measures, reflecting the complex and varying interaction within agroecosystems, are integrated in agricultural policy and farming practice with the aim to protect biodiversity in agricultural landscapes (Science for Environmental Policy, 2017). Agri-environmental measures are either categorized as non-productive (e.g. flower strips, area of the field taking out of active production) or production-integrated (e.g. extensive crop production with reduced fertilizer and usage of plant protection). In general, non-productive measures seem better suited to promote diversity (Batáry et al., 2015). However, integrated measures are able to promote rare specialist species of agricultural habitats (Pywell et al., 2012). In general, positive effects on biodiversity of EU agri-environmental measures are still debated, and many studies on ecological benefits lack adequate statistical and experimental designs, for example taking into account the surrounding landscape (Kleijn and Sutherland, 2003).

Carabid beetles are a large and important organism group: they inhabit all major habitats, are well studied and abundant in the European agricultural countryside (reviewed in Lövei and Sunderland, 1996). However, over half of the 582 carabid beetle species in Germany are currently categorized as threatened (Schmidt et al., 2016). In recent decades, beetle species reacted differently to changing environmental conditions. Some species became more common, while many others disappeared (Desender et al., 1994). Carabid abundance, species number and composition respond to different disturbance levels and habitat heterogeneity. Management practice in arable land can directly or indirectly affect reproduction or hibernation and therefore survival. Carabid beetles are therefore often used as suitable bioindicators to evaluate the quality of different habitats (Niemelä, 2001; Rainio and Niemelä, 2003).

The number of species and densities of carabid beetles alone do not comprehensively describe communities. To understand communities and how they react, information regarding the ecology of species and classification of assemblages are essential (Whittaker, 1970). Trophic guild, body size, and breeding time are traits commonly used to characterize and differentiate carabid beetle species. According to their trophic guild they can be categorized as carnivores, herbivores and omnivores (e.g.

Lövei and Sunderland, 1996). Herbivorous species act as important seed consumers in agricultural landscapes with the potential of reducing weed seed density in the soil (Honek et al., 2013; Kulkarni et al., 2015), while predators are essential in controlling other pest species (reviewed in Kromp, 1999; Lang et al., 1999). The body size of European species ranges from several millimetres to up to four centimetres (Freude et al., 2004). Density of adult individuals peaks at different times in the year depending on the species and if they reproduce in spring or autumn (Holland et al., 2009). Ecological traits of carabid beetles can be related to environmental factors, such as intensity of agricultural practice (Ribera et al., 2001). To evaluate the habitat quality, information of ecological traits is hence essential.

We investigated the effect of different agri-environmental measures on abundance, diversity and trait composition on carabid beetles. We had the following three hypotheses.

Less disturbance, reduced input of fertilizer and pesticides after two years of implementation should have an impact on biodiversity. The applied pitfall trapping technique depends on the mobility of the beetle in the local vegetation; therefore, highly structured vegetation might lead to lower capture rates, but also to higher number of species due to higher diversity in microhabitats. Therefore, **(1)** ***agri-environmental measures, land-use heterogeneity and trap site conditions, such as amount of bare ground or vegetation heterogeneity, are positively correlated with species diversity and abundance (activity density).*** Measures should increase herbivore diversity, due to higher number of non-crop plant species. **(2)** ***Functional traits, such as food preference and size, differ between agri-environmental measures and reference sites and are also influenced by land-use and trap site heterogeneity.*** Carabid beetles immigrate, therefore neighbouring habitats, such as grassland or forest can also play a major role. (3) ***Treatments harbour different beetle communities, which are also influenced by the surrounding land-use types, heterogeneity and trap site conditions.***

4.3 MATERIAL AND METHODS

Study area and design

The study took place in the northern part of Lower Saxony in the districts Nienburg and Diepholz (see Figure 4.1a). This intensively agriculturally used area is characterized by arable fields, covering around 55 % of the area and an additional 14 % with grassland (including intensively and extensively used areas). Forest and woody elements accounted for around 16 %, while urban area (streets, industry and houses) covered around 10 %. Semi-natural habitats, such as grassy strips along streets and ditches, but also gardens and parks accounted for 5 % of the area. The implementation of agri-environmental measures was part of the MEDIATE project (www.mediate-projekt.de).

The project started in 2017, and in 2018 several farmers implemented three different measures in the study area. Those measures were (1) alternately managed biennial flower strips, sown with seed mixtures containing cultivated plants (15 species) and wild flowers (12 species) typical for the region. Reseeding took place every year on 50 % of the area, resulting in two neighbouring sections with old and new vegetation. (2) Extensively used field margins contained crops sown with reduced seed rate. (3) Annual fallow strips along the field edge were ploughed once a year and otherwise left undisturbed. Participating farmers did not use fertilizers or pesticides on any areas with measures.

We selected only agri-environmental measures implemented on fields with cereals to minimize the effect of cultivated crop type. As unimproved reference, we chose grassy field strips with comparable neighbouring habitats as the agri-environmental measures and margins of fields with conventional cereals. This resulted in five different treatments, (1) flower strips, (2) extensive cereals, (3) fallow strips, (4) conventional cereals and (5) grassy field margins. Sixty-meter-long transects were established (see Figure 4.1c,d), each three meters away from the edge to standardize edge effects, since the narrowest agro-environmental measures were six meters wide. Grassy field margins (semi-natural habitats) were only between one and three meters wide, so transects were placed in the middle. Eight fields for each studied agri-environmental measure, and eight for each control (conventional cereals and grassy field margins) were chosen. Measures accounted for around 5 % of field area, which differed between 1.8 and 10 ha. The most northerly field was around 60 km apart from the most southerly field. Distance between fields with same agri-environmental measure were at minimum 1 km. Fields were located in three clusters, one in the north by Weyhe, one around Bruchhausen-Vilsen and one north of Nienburg/Weser.

Carabid beetle sampling

We sampled carabid beetles using the commonly applied pit-fall trap method. Behaviour and locomotory activity influence trapping probability of individual species, therefore the number of trapped individuals reflects activity densities rather than population densities. Nonetheless, the method has proven to be a reliable relative measure (e.g. Baars, 1979). On each transect, we installed three traps in the ground, the rim of the container flush with the surface. The diameter of the opening was 6 cm and a wire mesh (mesh size 1.9 x 1.9 cm) kept small mammals and other vertebrates from falling in. A small rooftop made of a transparent but dull square plexiglas plate (20 x 20 cm) placed around 5 cm atop every trap protected against flooding by rain. Containers were half-filled (~250 ml) with a mixture of ethylene glycol and water (1:1), a killing and preserving solution. Unscented soap, used as detergent, reduced surface tension of the preserving solution. The traps were active for seven successive days from 4.5.2018 to 13.5.2018. Samples were transferred into 70 % alcohol for further conservation. Determination of specimens was done using Freude et al. (2004) and Schaefer (2009).

Species traits

We classified the carabid species according to body size and trophic guild. Traits were compiled from www.carabids.org (Homburg et al., 2014) and Trautner (2017). Species were classified in three body size classes: small (< 6.5 mm, 25 species, mean size 4.8 ± 1.2; [min. – max.] 3.1 - 6.5 mm), medium (6.5 > 11 mm, 25 species, mean size 8.3 ± 1.1 mm; 6.7 – 10 mm) and large (> 10 mm, 20 species, mean size 13.8 ± 4.3; 10.2 - 24.5 mm). They were additionally classified according to three categories of trophic guild: herbivore, omnivore or carnivore.

Trap site and landscape cover characteristic

Around each trap the following characteristics of the vegetation structure were recorded within 2 x 2 m (Figure 4.1e): percentage of bare ground, litter cover and plant ground cover in the four height categories: ground cover plants (< 10 cm), small (10 > 30 cm), medium (31 > 50 cm), tall plants (> 50 cm). Average and maximum height of vegetation (in cm) was noted as well. Treatments differed in vegetation structure (Table 4.1) and the first six variables (bare, litter and height categories) were used to calculate a local micro-habitat heterogeneity index (Shannon index), hereinafter referred to as trap site heterogeneity.

Around each transect land use type within a 250 m radius was recorded to assess the influence of the surrounding area (Figure 4.1b). The landscape was classified into the following types: (a) agricultural area (conventional arable land), (b) grassland (differently used grassland), (c) forest (larger forest, but also small patches of shrubs or field copses), (d) semi-natural habitats (mostly grassy field strips, but also not cultivated remaining area next to water channels), (e) sealed surface (streets and houses), (f) water (ditches, water channels and perennial water bodies), (g) agri-environmental measure (arable land managed according to the project measure specifications). All variables were used to calculate a small-scale habitat heterogeneity index (Shannon index), hereafter referred to as landcover heterogeneity.

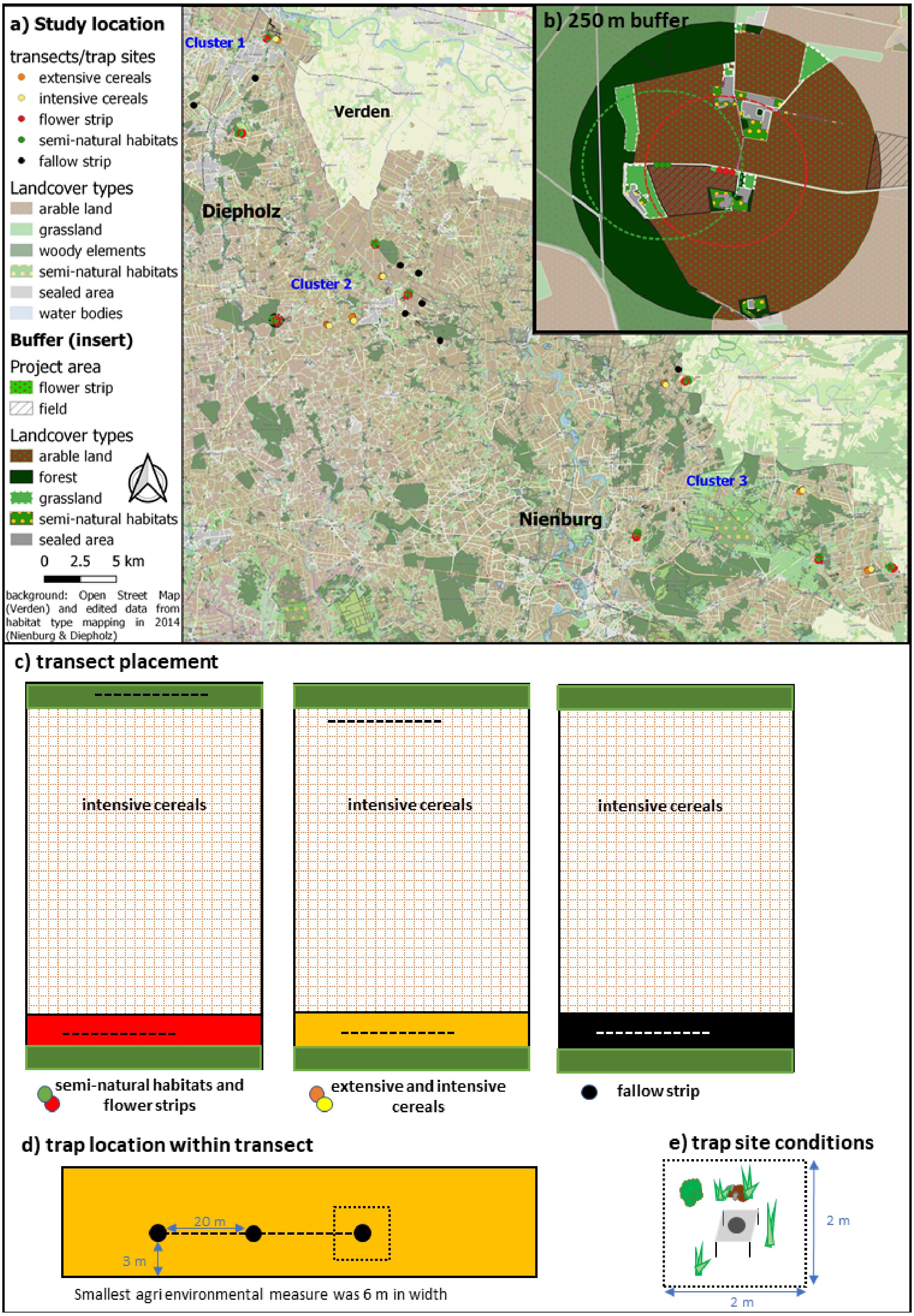

Figure 4.1: *a) Agri-environmental measures located in Lower Saxony in the districts Diepholz and Nienburg. b) Buffer around transects and land use types. c) Placement of transect within agri-environmental measures and reference transect in grassy field strips (semi-natural habitats) next to fields with flower strips and reference transect in conventional cereals, opposite to extensive cereal strips. d) trap placement: three traps, each 3 m apart from the edge and 20 m apart from following trap. e) trap site conditions: within in a four-square meter area, around each trap, vegetation site conditions were noted.*

Statistical analyses

We analysed carabid species richness and activity density at each transect by pooling all three traps. For further analysis, we used total number of species and individuals per transect, as well as log transformed (‘*log(x+1)’*) proportion of species and individuals per trait class.

Correlation plots of all explanatory variables were generated with the ‘*cor*’ and ‘*corrplot*’ function from the ‘*corrplot*’ package (Wei et al., 2017) to check for multicollinearity. Within site and land use heterogeneity several variables were correlated. When analysing the number of species and activity density we included the amount of bare soil, treatment and habitat heterogeneity. When analysing trait composition, the heterogeneity index for trap site and land use type were included. Differences in species composition were analysed by taking a reduced set of variables into account (only non-correlated variables, results of correlation analysis in Appendix Figure A4.1).

Linear mixed models were used to analyse the effects of site, treatment and landscape conditions on species diversity, abundance and trait composition using the ‘*lmer*’ function of the ‘*lme4*’ package (Bates et al., 2007) and the ‘*anova*’ function from the ‘*lmerTest’* package (Kuznetsova et al., 2017) to obtain p-values. The clustered distribution of study sites was taken into account by adding a random cross-nested factor (Krzywinski et al., 2014). Each field was given a unique ID number (same number for paired transects on the same field) and assigned to one of three clusters (Weyhe, Bruchhausen-Vilsen and Nienburg). Distribution of residuals was checked for model fit and model with lowest AIC value chosen.

Species occurring at less than three transects were removed prior to analyses of species composition in order to reduce noise. For the analysis of species composition NMDS with three dimensions with subsequent fit of environmental variables with the function ‘*metaNMDS*’ and ‘*envfit*’ from the ‘*vegan*’ package (Oksanen et al., 2007) were used. Furthermore, the ‘*adonis*’ function in the ‘*vegan*’ packages was used to run permutational multivariate analysis of variance for pairwise species composition testing. The ‘*multipatt*’ function from the ‘i*ndicspecies*’ package (Caceres et al., 2016) was used to identify species that were associated with specific treatments. The correlation index calculated, reveals the ecological preference of species among the set of studied treatments.

All models were checked for multicollinearity of factors by looking for incorrect coefficients, instability of coefficients and calculating variance inflation factor with the ‘*vif*’ function of the ‘*car*’ package (Fox et al., 2012).

Statistics were done using RStudio (RStudio Team, 2021) version 201.09.1 Build 372 “Ghost Orchid” Release, all graphics were created with ‘*ggplot2*’ (Hadley Wickham, 2016) and some help from the ‘*ggrepel*’ package (Slowikiwski et al.). Summary and overview tables were generated with the ‘table1’ and ‘stargazer’ packages (Rich, 2006; Hlavac, 2015).

4.4 RESULTS

In total, we collected 4226 individuals that belonged to 65 carabid species (Appendix, Table A4.1). 22 species were present on all treatments (three genera could only be identified to genus level, *Micropestes* spec*.*, *Acupalpus* spec*.*, and *Dyschirius* spec.), 17 were unique for sites with agri-environmental measures, 11 occurred on reference areas. The most abundant species was *Bembidion lampros*, which was present on all but one transect and made up 20 % of all identified beetles. Other frequent species were *Poecilus versicolor* on 34 of 40 transects, accounting for 13 % of individuals, followed by *Bembidion tetracolum* and *Poecilus cupreus* with 13 and 7 %, respectively. Together those four species accounted for more than 50 % of all trapped individuals. 20 species occurred with three or less individuals on no more than three transect (e.g. *Badister lacertosus* or *Agonum sexpunctatum*).

Number of individuals and species

Activity density was highest in extensive and intensive cereals, followed by fallow and flower strip. Intensive cereals were characterized by highest variation with minimum 18 trapped individuals and maximum 348 within two different transect (see mean, minimum and maximum values Table 4.1). The mean number of species varied between 13 ± 5 and 15 ± 6 for treatments and 5 ± 2 and 28 ± 8 for transects.

Table 4.1: *Means, standard deviations, minimum and maximum values (three traps per transect pooled, 8 transects per treatment) of dependent variables number of individuals and number of species and explanatory variables site and land cover heterogeneity (Shannon Index) for different treatments.*

	Dependent variables				**Explanatory variables**			
Treatment.	**Individuals**		**Species**		**Bare soil (%)**		**Land use heterogeneity (SI)**	
	mean ± s.d.	[min:max]	mean ± s.d.	[min:max]	mean	[min:max]	mean ± s.d.	[min:max]
Extensive cereals	129 ± 79.8	[39:241]	15 ± 6	[6:28]	29 ± 18	[10:60]	0.58 ± 0.3	[0.06:1.0]
Fallow strip	93 ± 36.9	[50:151]	14 ± 4	[5:21]	52 ± 26	[5:95]	0.67 ± 0.3	[0.21:0.11]
Flower strip	89 ± 33.4	[34:146]	15 ± 3	[10:21]	23 ± 15	[0:155]	0.64 ± 0.3	[0.32:1.32]
Intensive cereals	148 ± 112	[18:348]	13 ± 5	[5:16]	30 ± 20	[1:70]	0.62 ± 0.2	[0.35:0.99]
Semi natural habitat	66.8 ± 26.9	[28:112]	13 ± 3	[10:18]	3 ± 7	[0:25]	0.68 ± 0.3	[0.29:0.99]

Table 4.2*: Results of linear mixed models with log number of species (top) and individuals (bottom) as the response variable and treatment, amount of bare ground and land use heterogeneity as predictors. For number of species, the best model included the interaction between treatment and bare soil.*

Type III Analysis of Variance Table with Satterthwaite's method

N species	Sum Sq	Mean Sq	d.f.	F-value	p-value
Treatment	0.12	0.03	4	0.97	n.s
Bare soil	0.05	0.05	1	1.53	n.s
Land use heterogeneity	0.15	0.15	1	4.41	0.05
Treatment*bare soil	0.26	0.07	4	1.99	n.s

N individuals	Sum Sq	Mean Sq	d.f.	F-value	p-value
Treatment	0.38	0.09	4	0.67	n.s
Bare soil	0.74	0.74	1	5.27	0.03
Land use heterogeneity	0.26	0.26	1	1.83	n.s

The amount of bare soil significantly differed between treatments (ANOVA: df = 4, Sum Sq = 9964, Mean Sq = 2491, F = 8.1, p < 0.001) and land use index did not (ANOVA: df = 4, Sum Sq = 0.054, Mean Sq = 0.013, F = 1.666, p = 0.954). Neither number of species, nor number of individuals differed significantly between treatments. However, number of species was influenced by land use heterogeneity and number of individuals by amount of bare soil (see model results in Table 4.2).

Trait correlations and composition

Carabid beetle species differed in their life-history traits, but traits were correlated. Size class of a species was significantly related to its trophic group (Fischer's test, p=0.003). Large and small species were mostly predators, while medium sized species evenly represent all three trophic levels. Differences in size classes depended on treatment (Table 4.3, Figure 4.2) with proportionally more small species in cereals (extensive and conventional) and more medium sized species in fallows, flower strips and grassy field margins. Neither site nor land use heterogeneity had an influence on abundance of specific size classes.

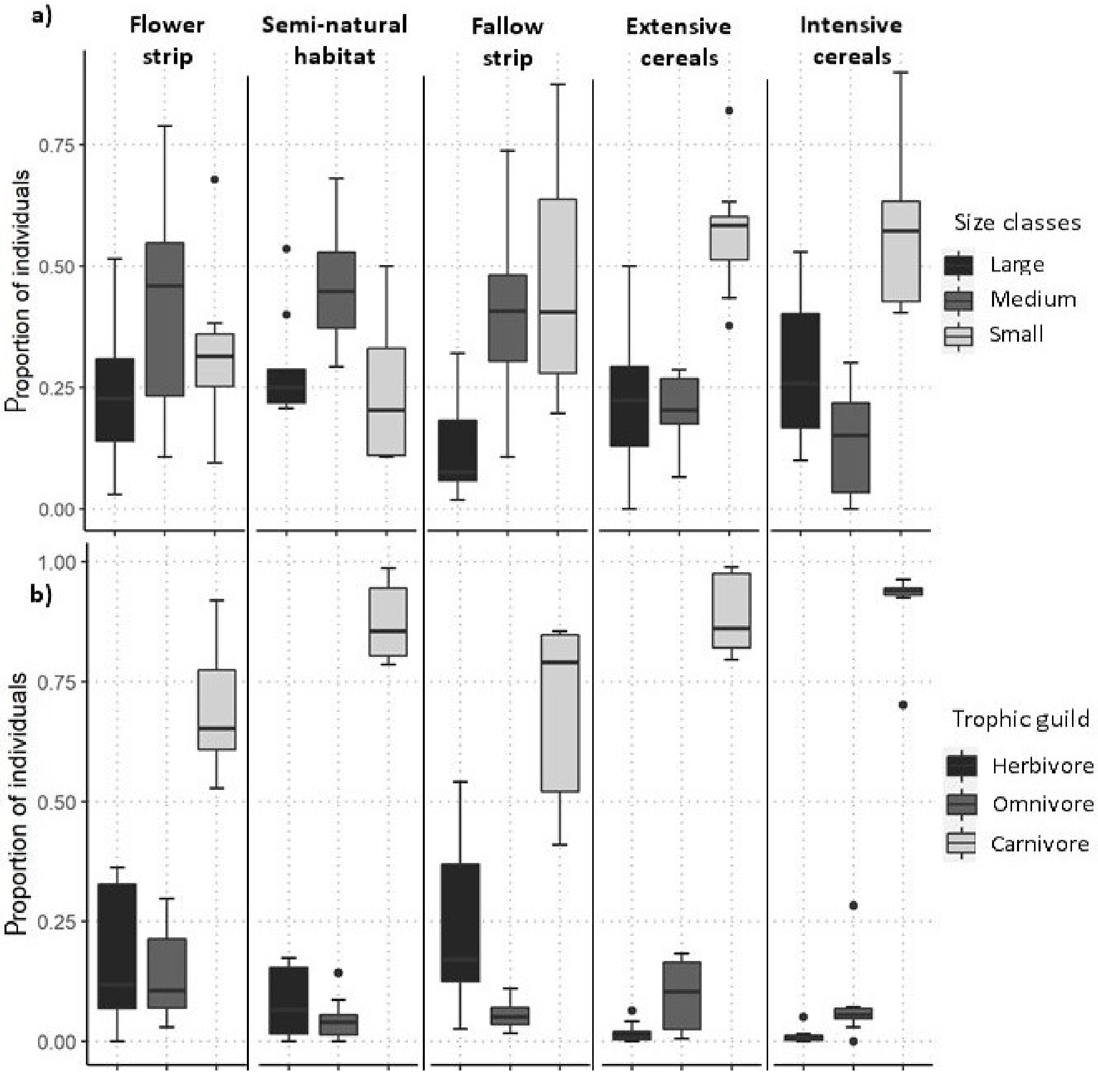

Figure 4.2: *Boxplots of proportion of individuals belonging to different ecological trait groups, separately for the studies treatments. a) Size classes were small (< 5 mm), medium (5 < 10 mm) and large (> 10 mm). b) trophic guild.*

Around 80 % of individuals were predators and only five to ten percent omnivores or herbivores (see Figure 4.2b). Differences in trophic guild depended on treatment (see Table 4.3 model results for trophic guild). Herbivores, primarily caught in flower strips, semi-natural habitats and fallow strips, were rare in extensive and intensive cereals. Site and land use heterogeneity did not affect trophic guild.

Table 4.3: *Results of linear mixed models with proportion of size class and trophic ecology as dependent variable.*

Type III Analysis of Variance Table with Satterthwaite's method

Size classes	Sum Sq	Mean Sq	d.f.	F-value	p-value
Treatment	0.001	0.000	4	0.022	0.999
Size class	0.076	0.038	2	2,638	0.076
Site heterogeneity	0.001	0.001	1	0.112	0.739
Land use heterogeneity	0.000	0.000	1	0.002	0.970
Size class*treatment	0.633	0.079	8	5.512	<**0.001**
Size class*site heterogeneity	0.025	0.012	2	0.870	0.422
Size class*land use heterogeneity	0.032	0.015	2	1.100	0.337

Trophic guild	Sum Sq	Mean Sq	d.f.	F-value	p-value
Treatment	0.006	0.001	4	0.245	0.912
Trophic guild	0.371	0.185	2	31.438	**<0.001**
Site heterogeneity	0.000	0.000	1	0.007	0.930
Land use heterogeneity	0.000	0.000	1	0.040	0.841
Trophic guild*treatment	0.302	0.038	8	6.400	**<0.001**
Trophic guild*site heterogeneity	0.002	0.001	2	0.177	0.838
Trophic guild*land use heterogeneity	0.016	0.008	2	1.360	0.262

Trap site conditions and surrounding land use

Treatments were characterized by different site conditions, while land use types within a 250 m buffer were similar (see Table 4.4: trap site conditions). The percentage of bare ground was lowest in semi-natural habitats and varied between 50 and 20 %, but did not differ significantly between intensive and extensive cereals and flower and fallow strips. Litter cover was highest in flower strips, whereas it did not differ significantly between the other treatments. Ground cover plants, less than 10 cm in height, were least abundant in semi-natural habitats and differed significantly compared to flower and fallow strips. Small plants, between 10 and 30 cm, did not differ significantly between treatments after Bonferroni correction. Percentage of tall plants, mean height and maximum height did not differ between treatments. High standard deviation values in all measured variables show high variation within treatments.

Within each buffer, agricultural land made up around 80 ± 10 % (see Table 4.4: land use type). Grassland, forest and semi-natural habitats accounted for around 6 % each, while sealed surfaces and water covered up to around 2 %. Area with agri-environmental measures made up around 1 % of the area within the 250 m buffer around each transect.

Table 4.4: *(top) Mean values (± standard deviation) for site conditions and p-values for significant differences between treatments (Kruskal-Wallis-test and subsequent pair-wise Wilcoxon (Appendix Table A4.2), different letters indicate significant differences between treatments. (bottom) Mean values for land use types [%] within 250 m buffer around all transects. Due to correlations between variables, only underlined once were considered in MANOVA analysis.*

Trap site conditions	**Extensive cereals**	**Intensive cereals**	**Flower strip**	**Semi-natural habitat**	**Fallow strip**	**p-value**
Bare soil [%]	29 ± 18^{a}	31 ± 18^{a}	23 ± 12^{a}	3.5 ± 5.3^{b}	53 ± 27^{a}	**<0.001**
Litter cover [%]	8.2 ± 10^{a,c}	2 ± 3^{a}	38 ± 22^{b}	14 ± 15^{c}	0.3 ± 0.4^{a}	**<0.001**
Plants < 10 cm	18 ± 24^{a,c}	10 ± 20^{a,c}	19 ± 18^{a}	2 ± 3^{b,c}	22 ± 24^{a}	**0.01**
Small plants (10-30 cm)	22 ± 32	12 ± 29	22 ± 13	36 ± 20	18 ± 20	**0.01**
Medium plants (31-50 cm)	23 ± 30	39 ± 39	19 ± 9	54 ± 22	9.3 ± 9	**0.03**
Tall plants (> 50 cm)	26 ± 40	29 ± 34	12 ± 15	7.8 ± 11	8.9 ± 17	n.s.
Mean height [cm]	46 ±21	50 ± 13	35 ± 15	37 ± 7.5	27 ± 25	n.s.
Maximum height [cm]	58 ± 20	56 ± 14	74 ± 11	58 ± 12	54 ± 23	n.s.

Land use type	**Extensive cereals**	**Intensive cereals**	**Flower strip**	**Semi-natural habitat**	**Fallow strip**	**Landscape mean**
Agricultural area	80 ±10	80 ±7	70 ±10	70 ±10	70 ±20	80 ±10
Grassland	5 ±10	4 ±6	4 ±5	8 ±9	10 ±10	6 ± 9
Forest	6 ±4	10 ±7	9 ±8	10 ±7	7 ±10	8 ± 7
Semi-natural habitat	7 ±6	4 ±2	8 ±8	4 ±2	5 ±4	6 ± 5
Sealed surface	2 ±3	1 ±0.9	2 ±3	0.9 ±0.9	2 ±2	2 ± 2
Water	1 ±1	2 ±3	0.7 ±0.9	1 ±1	0.5 ±0.4	1 ± 2
Agri-environmental measure	1 ±0.5	0.9 ±0.8	2 ±1	1 ±1	1 ±0.5	1 ± 0.8

Species composition

Species composition differed between treatments and was influenced by environmental variables (Figure 4.3 NMDS). Species composition differed significant between semi-natural habitats (snh) and extensive cereals (ext) as well as intensive cereals (int) and fallow strips (fal) (pairwise comparisons between treatments snh vs. ext: df = 1, S Sq = 0.59, F = 2.94, R^2 = 0.17 p = 0.04*; snh vs. int: df = 1, S Sq = 0.92, F = 4.13, R^2 = 0.23 p = 0.01; snh vs. fal: df = 1, S Sq = 0.72, F = 3.48, R^2 = 0.20, p = 0.04). Furthermore, extensive cereals and fallow strips differed significantly (df: 1, S Sq = 0.59, F = 2.94, R^2 = 0.17 p = 0.04*) and species composition in intensive cereals were almost significantly different from fallow and flower strips (int vs. fal: df =1, S Sq = 0.62, F = 2.84, R^2 = 0.17, p = 0.06; int vs. flo: df = 1, S Sq = 0.67, F = 2.95, R^2 = 0.17, p = 0.07).

Significantly correlated with the first NMDS axis were bare soil and ground cover plants and percentage of medium plants and mean height in opposing directions. Trap site heterogeneity, maximum vegetation height and water were correlated with the second NMDS axis.

Eight species showed significant ecological preferences for specific treatments (full list of species associations in Appendix Table A4.3: correlation index for indicator species analysis). *Harpalus tardus* was associated with flower strips, while *Microlestes* sp. and *Carabus nemoralis* with semi-natural habitats next to the fields. *Amara aenea* and *Amara familiaris* were associated with fallow strips and *Bembidion lampros* with fallow strips, extensive and intensive cereals. *Harpalus rubripes* and *Bembidion properans* preferred extensive cereals strips and *Limodromus assimilis* intensive cereals.

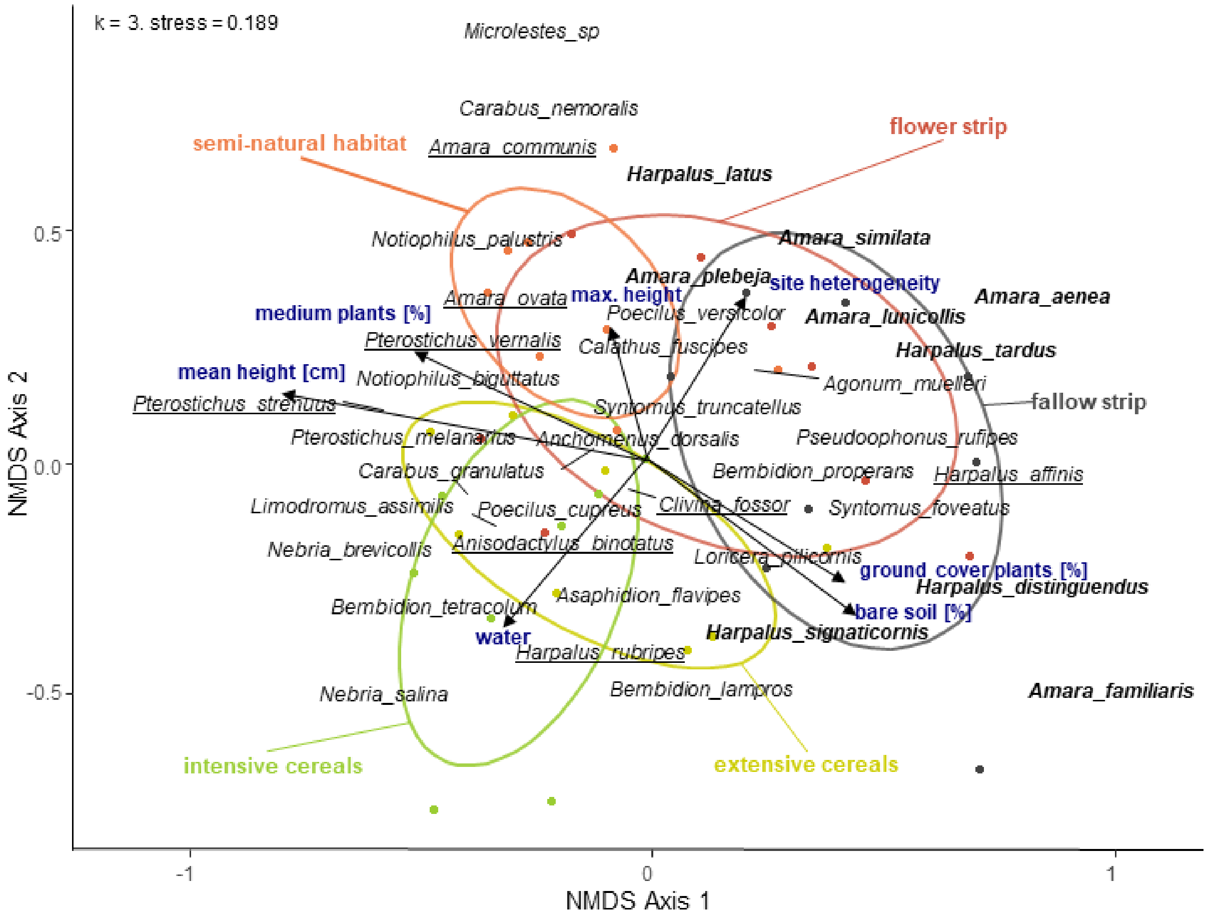

Figure 4.3: *Non-metric multidimensional scaling (NMDS) of carabid beetle species composition in 40 transects. Scores from the NMDS ordination were plotted. Trophic ecology illustrated as follows:* ***herbivorous species*** *(**bold**),* *<u>omnivore species</u>* *(<u>underlined</u>) and predatory species. Significant environmental factors according to a model of multiple regression with the ordination axes are displayed as arrows (site heterogeneity, $R^2 = 0.17$, $p = 0.03$*, max. height: $R^2 = 0.20$, $p = 0.01$*; medium plants (between 10 and 50 cm): $R^2 = 0.20$, $p = 0.01$; mean height of vegetation: $R^2= 0.38$, $p = 0.002$, bare soil: $R^2 = o.19$, $p = 0.02$*, ground cover plants: $R^2 = 0.18$, $p = 0.02$* and water: $R^2 = 0.18$, $p = 0.02$*. Ellipses (confidence level: 0.65): treatments: $R^2= 0.47$, $p = 0.001$.*

4.5 DISCUSSION

In this study, we investigated patterns of carabid beetle diversity in relation to agri-environmental measures embedded into an otherwise intensively used agricultural landscape. In general, our results confirm that agri-environmental measures increase trait diversity in carabid beetles, by providing further habitat especially for herbivorous species. Most abundant species, such as *Bembidion lapros*, *Poecilus versicolor*, *Bembidion tetracolum* and *Poecilius cupreus* are known species in arable land across Europe (Thiele, 1977).

Agri-environmental measures did not increase carabid beetle activity density or diversity

Carabid beetle activity density and diversity did not differ between treatments, thus rejecting our first hypothesis that it would be higher in the agri-environment measures. Results in the literature on the effects of biodiversity measures on carabids are also mixed (see results of meta analysis in Marja et al., 2022): for example, a study investigating the effect of different intensities of agri-environmental measures, extensive and conventional cereals found 20 % more carabid beetles in extensive managed sites. However, this was only the case under the most restrictive management, including conservational tillage (Caro et al., 2016). Pesticide use on field edges seem not to influence carabid beetles (Frampton and Dorne, 2007), although negative effects of insecticides on carabids are known (Geiger et al., 2010). Therefore, differences in management in our study might not be strong enough to impact carabid beetle diversity and activity density. This is in accordance with a study on different agri-environmental measures next to oil seed rape fields. No differences in species diversity and activity density between agri-environmental measures, such as old and new flower strips and set-aside greening and calcareous grassland were observed (Boetzl et al., 2019). Another study comparing flower strips, grassy field margins and cereals also found no differences in total number of species, but higher activity density in cereal fields (Anjum-Zubair et al., 2015). In our study, variation within the eight tested study sites per treatment was high, and we analysed only one trapping period in spring. To get a better understanding of carabid beetle communities, it is advised to sample at least several times a year (Baars, 1979). Therefore, the analysis of a second trapping period in August and more replicates might enhance possible differences or similarities.

Another explanation for lacking differences in activity density between the different treatments might be differently biased capture rates in treatments due to differences in vegetation structure. Especially in habitats with dense vegetation, activity density, measured by pitfall traps is not correlated to actual population density (Thomas et al., 2006). For example, in traps located in grass dominated habitats the number of trapped carabid beetles is downwardly biased (Harvey et al., 2008). In the present study, this could have resulted in underestimated carabid beetle abundances in grassy field margins. This problem of (micro)vegetation structure biasing trapping efficiency is also reflected by the here observed positive correlation of activity density with the amount of bare soil. Although this confirms part of our hypothesis, it reinforces the assumption that the applied catching method might not be ideal for comparing abundances in differently structured habitats. Several other studies on different types of habitats in agricultural landscapes also concluded that vegetation density and amount of bare soil influences the number of trapped individuals and species. Dense vegetation hinders free movement of carabid beetles on the ground and results in different microclimatic conditions (Greenslade, 1964; e.g. Jarosìk et al., 2000; Lang, 2000; Anjum-Zubair et al., 2015). Nevertheless, pitfall traps are suitable for comparing species assemblages (Spence and Niemelä, 1994), which will be discussed in a later section. With regard to the questions whether agri-environmental measures enhance density of carabid beetles, the results of the present study need to be considered with care.

While small scale heterogeneity, like amount of bare soil, increased the number of trapped individuals, large scale heterogeneity in the surrounding habitat was positively related to number of species. This confirms part of our second hypothesis and is somewhat surprising as the habitat heterogeneity gradient in our study area was small. All sites were located in a landscape dominated by agriculture, this is represented by around 80 ± 10 % of agricultural land within each buffer around our trap sites. Still, some transects were located closely to ditches, woody elements or small patches of grassland. Habitat heterogeneity is important, as a study comparing conventional and organic farming practise, discovered. In that study, not farming practice but the occurrence of landscape features, such as grassland, was positively correlated to carabid beetle diversity (Purtauf et al., 2005). Another study found that small-scale landscape heterogeneity or an increase in the length of field margins promote not only beetle diversity but also butterfly and plant diversity (Weibull et al., 2003). Our results also highlight the importance of field margin, ditches and other non-agriculturally used habitats for biodiversity.

Agri-environmental measures influence trait composition

Trait composition of carabid beetles in different treatments differed, supporting our second hypothesis. The two most abundant species in our samples, *Bembidion lampros* and *B. tetracolum,* were small sized predators. A study on different management intensities confirms that especially carnivorous species dominate in agricultural land and disturbance intensity is negatively correlated with size (Hanson et al., 2016). Supporting that observation, a study in England detected more smaller sized carabid species, such as *Nebria brevicollis, Loricera pilicornis*, or *Amara communis* in disturbed grassland habitats, while large *Carabus* species were rare. Reasons discussed are the lack of stable resources for a longer time during larval development, which are needed for larger beetles (Blake et al., 1994). In the present study extensive, as well as conventionally managed cereals are characterized by wheat as cover plants and bare soil on the ground, explaining the high proportions of carnivores. An experimental study on abandoned agricultural land investigating the effect of secondary vegetation succession on carabid trophic guild showed that carnivorous carabids prefer habitat with canopy layer and at the same time bare ground at the ground level (Harvey et al., 2008). High numbers of carnivores support the general statement that generalist predators are effective as biocontrol (Symondson et al., 2002).

Agri-environmental measures influenced the occurrence of herbivorous species. Especially on fallows and flower strips, as well as on semi-natural habitats as reference, more herbivorous carabid beetles were caught. All three treatments are dominated by a variety of non-crop plant species (see Wietzke et al., 2020) providing various food sources for different herbivorous beetle species. Herbivorous species are known to feed on crop species but not on cereals (Eyre et al., 2013), explaining low activity density of herbivore in extensive and conventional cereals in this study. Furthermore, conversion of arable land into flowering fields can increase the occurrence of closely related medium-sized herbivorous species (Baulechner et al., 2019). In our study, especially herbivorous members of the genus *Amara* were more common in flower strips. This underlines that environmental measures are able to enhance ecological trait diversity in beetle communities on arable land.

Trap site conditions in agri-environmental measures influence species composition

Species compositions differed between some agri-environmental measures and was influenced mainly by trap site conditions, such as the amount of bare ground and plant cover. Land use types in the surrounding area had no effect, except for the presence of water courses or bodies. The core species assemblage was identical for all treatments. The five most common species, all predators, (*Bembidion lampros, B. tetracolum, Poecilus versicolor, P. cupreus* and *Anchomenus dorsalis*) accounted for more than 60 % of all captures and were present on most sites and all treatments. Carabid beetle species composition is highly influenced by roaming individuals from neighbouring environments, especially in small habitat patches (reviewed in Niemelä, 2001). In our study, most agri-environmental measures were only six meters wide and grassy field margins only up to one meter. More distinct species communities are therefore not to be expected. An investigation of carabid species communities in winter wheat fields already concluded that cultivation leads to limited species composition, with a few dominant species, such as *B. lampros, P. cupreus* and *Harpalus tardus* (Kromp, 1989).

Although the most common species were present on all treatments, they seemed to prefer specific habitats reflected in their varying activity density. The predator *B. lampros* was less abundant on semi-natural habitats, while *P. versicolor* dominated in grassy margin strips, as well as in flower strips. *B. tetracolum, P. cupreus* and *A. dorsalis* dominated in intensive and extensive cereals. *B. lampros* was associated with extensive and intensive cereals as well as fallows, treatments with high amounts of bare ground. Studies on the behaviour of *B. lampros* showed that they prefer bare ground (Mitchell, 1963). Furthermore, cereal fields are optimal habitats for reproduction and larval development for this species (Wallin, 1989). Fallow strips and semi-natural habitats, such as grassy margins, while both showed overlapping carabid beetles species compositions towards flower strips, differed in disturbance. Grassy field margins are stable environments regarding the soil with permanent vegetation cover and are only mowed. Fallows, on the other hand are ploughed every year, resetting the vegetation cover. In flower strips, established in the previous year, species composition was a mixture of the species compositions of field margins and fallows. Herbivorous species, especially of the genus *Amara*, were more common on those sites. *A. communis*, associated with flower strips and semi-natural habitats, characterized by grasses in our study, is a common species in grassland or grass dominated habitats (Trautner, 2017).

While species composition was influenced by different site conditions and treatment, out of the six land cover types only the proportion of water influenced species composition. This pattern is contrary to the roaming behaviour of carabid beetles (reviewed in Niemelä, 2001). Although several sites were located next to or near forest patches, almost no exclusively forest species were caught. Both large *Carabus* species (*C. nemoralis, C. granulatus*), formally classified as forest species, are known to inhabit open agricultural used areas as well (Weber and Heimbach, 2001). Habitat edges resulting from human activities, such as agricultural practice, often block the movement of some species. Especially for forest species, high disturbance levels in agricultural habitats are detrimental to beetle survival. Therefore, diversity is not substantially higher on fields located next to forests, as a meta-analysis on studies investigating carabid beetles in regard to habitat heterogeneity revealed (Magura et al., 2017). This might explain why other types of land use, such as forest, did not influence species composition. Local variables, such as agri-environmental measures, affect species community and trait composition more, compared to landscape variables (Caro et al., 2016).

Limited species assemblage reflects high disturbance in agricultural habitats

In general, our results show that a few common species dominate in intensively used agricultural landscapes. This is in line the previous results of the impact of changing land use and climate on carabid beetles in Belgium. Scientists concluded that a few common species are more common at the expense of a large number of rare species due to intensification of agriculture (Desender et al., 1994; Desender et al., 2010). The lack of specialist species, e.g. large forest species, might be also due to high disturbance levels (Halme and Niemelä, 1993) in the agricultural environments. Furthermore, xerophilous seed eater preferer open vegetation and warm bare soil with a variety of short-lived annuals. A condition missing in intensified arable land due to fertilisation (Desender and Bosmans, 1998). A review on data of carabid bevor and after the shift in production intensity in Germany confirms loss and decline of many species (Kromp, 1999). Alarming is a similar trend in a nature reserve in northern Germany. While biomass stayed the same within the last 24 years, number of specialist species declined (Homburg et al., 2019). With potential species rich source habitats, also experiencing a homogenisation of species assemblage, more effort is needed, otherwise species will be lost permanently.

The question remains, whether carabid beetles are good bioindicator to assess the ecological value of agri-environmental measures. Considering that many carabid beetles species are generalists, this group of insects might not be suitable bioindicators (Rykken et al., 1997). However, species react to environmental changes and regarding our results, changes in species and trait composition in arable landscapes happen in short time periods. There is no conclusive evidence for carabid beetles to be good indicators for ecological health (changes in carabid beetle trait composition due to environmental changes reflects changes in other species groups) or biodiversity (reflecting diversity of the overall biota), however they are good environmental indicators (changes in environment lead to changes in carabid beetle composition (reviewed in Rainio and Niemelä, 2003).

4.6 CONCLUSION

We found highest carabid species diversity in more heterogeneous landscapes. Agri-environmental measures, such as flower strips, fallow strips and extensive cereals did not increase the number of species and individuals of carabid beetles in our study. However, ecological traits and species assemblages differed between different agri-environmental measures and conventional cereals. While carnivorous species were common in general, especially herbivorous species were more abundant on flower strips and fallows. Therefore, these measures have the potential to enhance biodiversity on a larger scale by providing differently structured habitats.

Ethics Statement

We obtained the necessary permits for catching carabid beetles within the farming area of the participating farms, located in the districts Nienburg and Diepholz, from the respectively regional nature conservation authorities. No study sites were located in nature conservation or FFH areas.

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APPENDIX CHAPTER IV CARABID BEETLES AND AGRI-ENVIRONMENTAL MEASURES

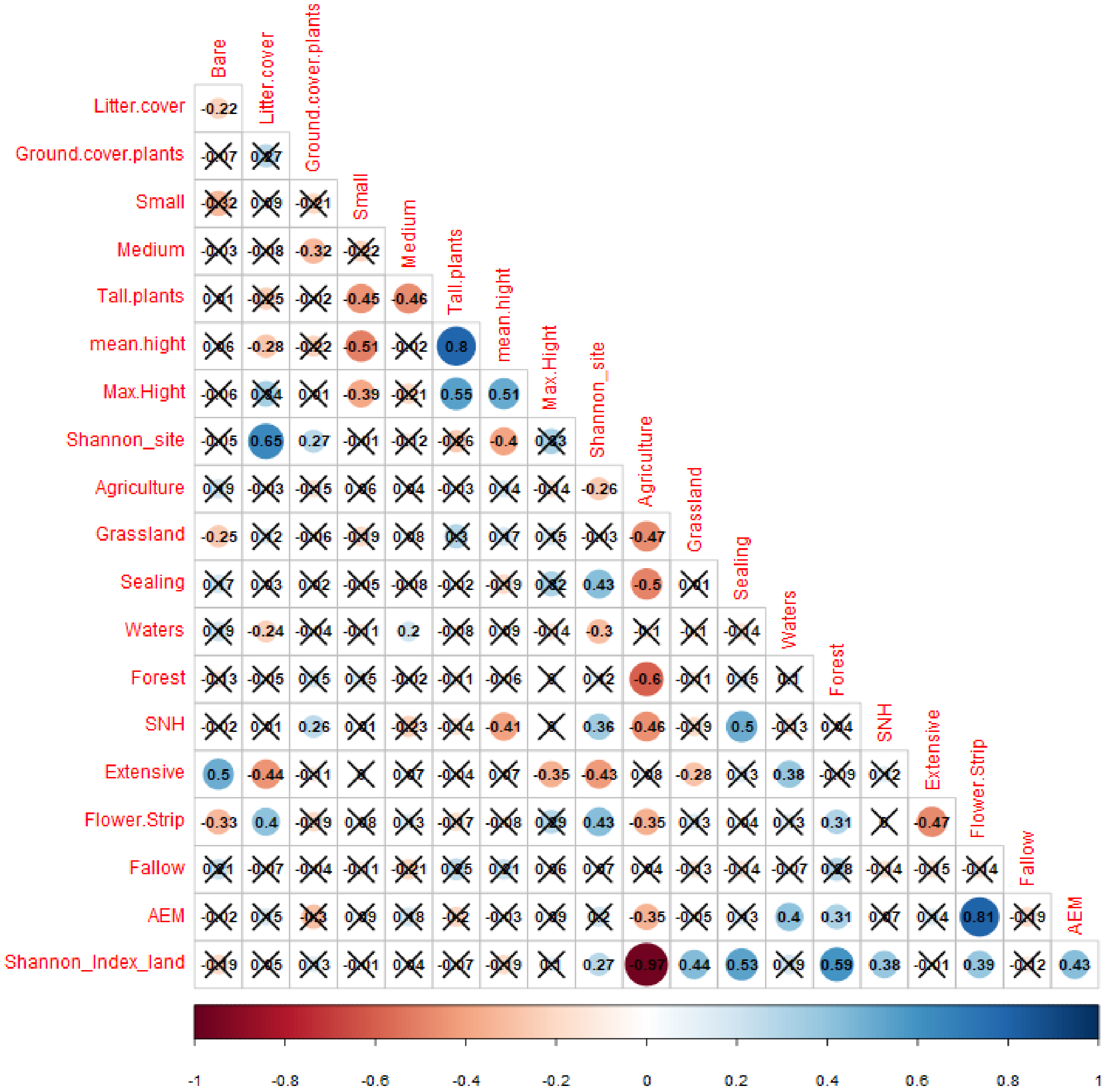

Figure A4.1: *Correlation plot of all explanatory variables, number of species and activity abundance (ground cover plants: height: < 10 cm; small: plants between 10 > 30 cm; Medium: 31 > 50 cm; Tall plants: > 50 cm; Shannon_site: Shannon index generated from site conditions; Agriculture: proportion of arable fields within 250 m radius. Sealing: sealed surfaces, such as roads and houses; Waters: ditches or small rivers; Forest: all woody structures, including small patches with trees; EAM: agri-environmental measures).*

Table A4.1: *Species in alphabetical order, information on ecological traits, total activity abundance and number of transects.*

Species	**Size category**	**Trophic guild**	**Breeding time**	**# Individuals**	**# Transects**	**Extensive cereals**	**Fallow strip**	**Flower strip**	**Intensive cereals**	**Semi natural habitat**
Abax parallelepipedus	large	predator	both	1	1					1
Acupalpus spec.	small		spring	2	1					1
Agonum gracilipes	medium	predator	spring	1	1	1				
Agonum muelleri	medium	predator	spring	10	7	2	4			1
Agonum sexpunctatum	medium	predator	spring	1	1	1				
Amara aenea	medium	herbivor	spring	101	13	2	7	2	1	1
Amara anthobia	small	herbivor	spring	5	2		2			
Amara apicaria	medium	omnivor	autumn	2	2	1	1			
Amara communis	medium	omnivor	spring	13	9	2		2	2	3
Amara consularis	medium	herbivor	autumn	1	1					1
Amara familiaris	small	herbivor	spring	15	7	1	5	1		
Amara lunicollis	medium	herbivor	spring	5	5		2	2		1
Amara ovata	medium	omnivor	spring	9	6	1	1	1		3
Amara plebeja	medium	herbivor	spring	9	7	2	2	1	1	1
Amara similata	medium	herbivor	spring	25	8		3	2	1	2
Amara spreta	medium	omnivor	spring	1	1		1			
Amara tibialis	small	herbivor	spring	4	2		1	1		
Anchomenus dorsalis	medium	predator	spring	315	27	6	5	4	6	6
Anisodactylus binotatus	large	omnivor	spring	96	14	3	1	5	4	1
Asaphidion curtum	small	predator	spring	2	2	1				1
Asaphidion flavipes	small	predator	spring	24	10	3	2	2	3	
Badister bullatus	small	predator	spring	4	3				1	2
Badister lacertosus	small		spring	1	1		1			
Bembidion lampros	small	predator	spring	837	39	8	8	8	8	7
Bembidion obtusum	small	omnivor	spring	2	1			1		
Bembidion properans	small	predator	spring	184	24	8	4	6		6
Bembidion tetracolum	small	predator	spring	546	24	6	3	4	7	4
Calathus erratus	medium	predator	both	1	1					1
Calathus fuscipes	large	predator	both	6	4		2	1		1
Calathus rotundicollis	medium	predator	both	1	1				1	
Calosoma inquisitor	large	predator	spring	3	1				1	
Carabus granulatus	large	predator	spring	64	11	3	1	2	3	2
Carabus nemoralis	large	predator	spring	24	11	2	1	3	1	4
Chlaenius tristis	large	predator	spring	1	1					1
Clivina fossor	small	omnivor	spring	74	14	4	4	2	3	1
Dyschirius spec.	small	predator		2	2				2	
Harpalus affinis	medium	omnivor	both	63	19	3	6	5	3	2
Harpalus distinguendus	medium	herbivor	spring	11	6	2	2	2		
Harpalus froehlichii	medium			11	1		1			
Harpalus latus	medium	herbivor	both	16	8	1	2	3		2
Harpalus luteicornis	medium	herbivor	spring	4	3	1		2		
Harpalus rubripes	medium	omnivor	spring	22	7	5			1	1
Harpalus signaticornis	small	herbivor	autumn	35	10		4	3	3	
Harpalus spec.	medium	omnivor	both	25	14	2	4	4	2	2
Harpalus tardus	medium	herbivor	spring	144	18	1	5	5	2	5
Limodromus assimilis	large	predator	spring	80	11	3	1	1	4	2
Loricera pilicornis	medium	predator	spring	17	12	3	1	4	3	1
Microlestes spec.	small	predator	spring	8	4	1				3

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Species	**Size category**	**Trophic guild**	**Breeding time**	**# Individuals**	**# Transects**	**Extensive cereals**	**Fallow strip**	**Flower strip**	**Intensive cereals**	**Semi natural habitat**
Nebria brevicollis	large	predator	autumn	112	18	4	1	4	5	4
Nebria salina	large	predator	autumn	106	23	7	1	3	7	5
Notiophilus biguttatus	small	predator	spring	13	8	2	1	3	2	
Notiophilus palustris	small	predator	spring	6	5	1	1		1	2
Paradromius linearis	small	predator	spring	1	1					1
Poecilus cupreus	large	predator	spring	319	29	7	5	6	6	5
Poecilus lepidus	large	predator	autumn	23	3		2	1		
Poecilus versicolor	medium	predator	spring	552	34	7	7	8	4	8
Harpalus rufipes	large	omnivor	both	24	10		4	3	3	
Pterostichus melanarius	large	predator	both	101	28	5	2	7	6	8
Pterostichus niger	large	predator	autumn	1	1			1		
Pterostichus nigrita	medium	predator	spring	2	1				1	
Pterostichus strenuus	small	omnivor	spring	49	9	2	1	3	2	1
Pterostichus vernalis	medium	omnivor	spring	7	5			1	3	1
Stomis pumicatus	medium	predator	spring	1	1			1		
Syntomus foveatus	small	predator	spring	62	11	2	4	1	2	2
Syntomus truncatellus	small	predator	spring	28	13	4	1	3	1	4
Trechus quadristriatus	small	predator	autumn	1	1	1				

Table A4.2: *Pairwise comparisons using Wilcoxon rank sum test with continuity correction, Bonferroni corrected p-values.*

	bare ground				**small plants (10-30 cm)**			
	extensive cereals	fallow strips	flower strip	intensive cereals	extensive cereals	fallow strips	flower strip	intensive cereals
fallow strip	0.824	---	---	---	1.00	---	---	---
flower strip	1.00	0.312	---	---	1.00	1.00	---	---
intensive cereals	1.00	0.827	1.00	---	1.00	0.25	0.22	---
semi natural habitat	0.013	0.019	0.027	0.037	1.00	0.28	1.00	0.12

	litter cover				**medium plants (31-50 cm)**			
	extensive cereals	fallow strips	flower strip	intensive cereals	extensive cereals	fallow strips	flower strip	intensive cereals
fallow strip		---	---	---	1.00	---	---	---
flower strip			---	---	1.00	0.649	---	---
intensive cereals				---	1.00	1.00	1.00	---
semi natural habitat					0.829	0.026	0.054	1.00

	plants < 10 cm			
	extensive cereals	fallow strips	flower strip	intensive cereals
fallow strip	1.00	---	---	---
flower strip	1.00	1.00	---	---
intensive cereals	1.00	0.391	0.90	---
semi natural habitat	0.592	0.026	0.059	1.00

Table A4.3: *Result of multipattern analysis;* **significant associations *in bold.***

Species	Extensvie cereals	Intensive cereals	Fallow strip	Flower strip	Semi-natural habitat	Index	Stat.	p-value
Abax parallelepipedus	0	0	0	0	1	4	0.32	1.00
Acupalpus sp	0	0	0	0	1	4	0.32	1.00
Agonum gracilipes	1	0	0	0	0	1	0.32	1.00
Agonum sexpunctatum	1	0	0	0	0	1	0.32	1.00
Agonum muelleri	1	0	1	0	0	6	0.41	0.07
Amara aenea	**0**	**0**	**1**	**0**	**0**	**2**	**0.63**	**0.01**
Amara anthobia	0	0	1	0	0	2	0.39	0.16
Amara apicaria	1	0	1	0	0	6	0.28	1.00
Amara communis	1	0	0	1	1	19	0.24	0.69
Amara consularis	0	0	0	0	1	4	0.32	1.00
Amara familiaris	**0**	**0**	**1**	**0**	**0**	**2**	**0.63**	**0.01**
Amara lunicollis	0	0	1	1	0	10	0.31	0.53
Amara ovata	0	0	0	0	1	4	0.38	0.20
Amara plebeja	1	0	1	1	0	16	0.16	0.97
Amara similata	0	0	1	0	0	2	0.36	0.16
Amara spreta	0	0	1	0	0	2	0.32	1.00
Amara tibialis	0	0	1	0	0	2	0.28	1.00
Anchomenus dorsalis	1	1	0	0	0	9	0.39	0.11
Anisodactylus binotatus	1	0	0	1	0	7	0.31	0.42
Asaphidion curtum	1	0	0	0	1	8	0.28	1.00
Asaphidion flavipes	1	1	0	0	0	9	0.29	0.43
Badister bullatus	0	0	0	0	1	4	0.37	0.35
Badister lacertosus	0	0	1	0	0	2	0.32	1.00
Bembidion lampros	**1**	**1**	**1**	**0**	**0**	**18**	**0.55**	**0.02**
Bembidion obtusum	0	0	0	1	0	3	0.32	1.00
Bembidion properans	**1**	**0**	**0**	**0**	**0**	**1**	**0.51**	**0.02**
Bembidion tetracolum	**1**	**1**	**0**	**0**	**0**	**9**	**0.51**	**0.01**
Calathus erratus	0	0	0	0	1	4	0.32	1.00
Calathus fuscipes	0	0	1	0	1	11	0.25	0.79
Calathus rotundicollis	0	1	0	0	0	5	0.32	1.00
Calosoma inquisitor	0	1	0	0	0	5	0.32	1.00
Carabus granulatus	0	1	0	0	0	5	0.29	0.48
Carabus nemoralis	**0**	**0**	**0**	**0**	**1**	**4**	**0.49**	**0.03**
Chlaenius tristis	0	0	0	0	1	4	0.32	1.00
Clivina fossor	1	1	0	0	0	9	0.28	0.57
Dyschirius sp	0	1	0	0	0	5	0.46	0.23
Harpalus affinis	**0**	**0**	**1**	**1**	**0**	**10**	**0.43**	**0.04**
Harpalus distinguendus	0	0	1	0	0	2	0.31	0.41
Harpalus froehlichii	0	0	1	0	0	2	0.32	1.00
Harpalus latus	0	0	0	0	1	4	0.28	0.62
Harpalus luteicornis	0	0	0	1	0	3	0.37	0.29
Harpalus rubripes	**1**	**0**	**0**	**0**	**0**	**1**	**0.60**	**0.01**
Harpalus signaticornis	0	0	1	1	0	10	0.35	0.21
Harpalus tardus	**0**	**0**	**0**	**1**	**0**	**3**	**0.51**	**0.03**
Limodromus assimilis	**0**	**1**	**0**	**0**	**0**	**5**	**0.39**	**0.05**
Loricera pilicornis	1	1	0	1	0	20	0.28	0.54
Microlestes sp	**0**	**0**	**0**	**0**	**1**	**4**	**0.53**	**0.03**
Nebria brevicollis	0	1	0	0	0	5	0.35	0.21
Nebria salina	1	1	0	0	0	9	0.42	0.08
Notiophilus biguttatus	1	1	0	1	0	20	0.21	0.86
Notiophilus palustris	0	0	0	0	1	4	0.27	0.69

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Species	Extensvie cereals	Intensive cereals	fallow strip	Flower strip	Grassy field margin	Index	Stat.	p-value
Paradromius linearis	0	0	0	0	1	4	0.32	1.00
Poecilus cupreus	1	1	0	0	0	9	0.37	0.15
Poecilus lepidus	0	0	1	0	0	2	0.42	0.17
Poecilus versicolor	0	0	0	1	1	13	0.41	0.08
Harpalus rufipes	0	1	0	0	0	5	0.33	0.35
Pterostichus melanarius	0	1	0	1	1	25	0.28	0.40
Pterostichus niger	0	0	0	1	0	3	0.32	1.00
Pterostichus nigrita	0	1	0	0	0	5	0.32	1.00
Pterostichus strenuus	1	1	0	0	0	9	0.31	0.33
Pterostichus vernalis	0	1	0	1	1	25	0.29	0.54
Stomis pumicatus	0	0	0	1	0	3	0.32	1.00
Syntomus foveatus	0	0	1	0	0	2	0.31	0.32
Syntomus truncatellus	0	0	0	0	1	4	0.31	0.35
Trechus quadristriatus	1	0	0	0	0	1	0.32	1.00

CHAPTER V

GENERAL DISCUSSION

“Habitat loss occurs in our minds”, we as a society at large must understand the consequences of biodiversity loss. Otherwise, nothing will change (Hanski, 2005).

5. General Discussion

This thesis investigated the effect of agri-environmental measures on the arable weed seed bank, butterflies and carabid beetles in a range of intensively used agricultural regions in Germany. The three studies were conducted under real life conditions, monitoring cereal fields, semi-natural habitats such as grassy field margins, and different agri-environmental measures of conventional farmers. This was not a tightly controlled scientific experiment, as not only were the farms and regional species pools quite different, but also the management of the measures differed to a certain degree depending on the farmers' preferences. Instead, it gives an insight into the broader effects of agri-environmental measures under realistic conditions, and thus paints a accurate picture of what can be achieved in intensively farmed landscapes through agricultural policy. In the section '*5.1 Key findings and conclusions*', I discuss the results of my thesis and their implications for conservation practice. Under the section '*5.2 The bigger picture*', two aspects of nature conservation in intensive agriculture, differing concepts of nature and failed communication, which I encountered, are outlined.

5.1 KEY FINDINGS AND CONCLUSIONS

Traditional, low-intensity farming once created species-rich landscapes in Europe (Bignal and McCracken, 1996; Fischer et al., 2012). Nowadays, intensive farming practice led to a drastic decline in biodiversity (Stoate et al., 2001) and several actions were taken to counteract negative effects of intensive agriculture. In the following section, I derive three overarching messages from my thesis for biodiversity conservation in agricultural landscapes, each integrating the findings from the three organism groups studied in **Chapters 2-4**.

(1) Intensively farmed landscapes are characterized by a limited species pool. Insect and plant communities are dominated by a few species, some of which are classified as problematic. Due to their ecological traits ensuring (a) fast and abundant reproduction, (b) the capacity to evade unsuitable conditions and (c) adapted to agricultural conditions, they are adapted to frequent disturbances. Most formerly typical species of agricultural habitats, such as summer pheasant's-eye or the swallowtail butterfly, are rare or missing all together. Therefore, conservation efforts in intensive farmland should concentrate on generalist species, still occurring in those landscapes and maintaining ecosystem functions.

Chapters 2, 3 and 4 demonstrate the dominance of a few species, plant or insect, in intensively used agricultural landscapes. The present species pool is limited, considering the overall species possibly occurring in open habitats. Although plant seeds and carabid beetles seem abundant, and even butterflies reach high numbers of individuals on some sites, all three organism communities are dominated by a few species. True for all three organism groups, half of the species we detected and identified, accounted in total for only two to three percent of all recorded numbers, while the five most common species accounted for more than 50 % in seed species (total: 120 species) and butterflies (50 species on transects) and 60 % in carabid beetles (65 species). This demonstrates the imbalanced species composition and the dominance of a few species. Decades of intensification in agriculture have led to reduced habitat quantity and quality all over Europe, resulting in declines in plants, birds and insects. Especially habitat specialists were affected while generalist are still common in agricultural landscapes (Desender et al., 1994; reviewed in Robinson and Sutherland, 2002; Meyer et al., 2013).

In recent decades, arable weed species experienced a dramatic decline (Fried et al., 2009; Meyer et al., 2013; Richner et al., 2015). This decline is also present in the soil seed bank where many formerly present but rare species are now missing, although the total number of seeds is high, driven by a few dominant species, that are adapted to modern cultivation practices (Andreasen et al., 2018). This pattern corresponds to my seed bank analysis. Total number of seeds in the soil of conventional arable fields in this study was high (between 6 000 and 12 000 seeds/m^2), however the number of species varied only between 2 and 22 (**Chapter 2**). This demonstrates the success of a few species to cope with the changing agricultural conditions, while many others vanished. Intensive land use depletes the soil seed bank and species being gone once, cannot be easily restored, since dispersal is limited in fragmented landscapes (Bakker and Berendse, 1999). In place of species-rich weed communities, homogenized communities, dominated by problematic yield-suppressing weeds, developed in many areas (Meyer et al., 2013).

In my study, the five most abundant species or taxa in the soil seed bank were *Chenopodium album,* Chamomilla species*, Urtica dioica/urens, Poa* spp*.* and *Papaver* spp. (**Chapter 2**). Ecological traits, to ensure survival of plants in agricultural landscapes, are for example affinity to nutrient rich environments, shade tolerance and monocotyledon growth form (reviewed in Richner et al., 2015). Most common species in my studies fit either one or two of those criteria. Furthermore, those species are known to produce high amounts of seeds. One *C. album* plant, for example is able to shed up to 72 000 seeds (Stevens, 1932) and increases in the soil seed bank fast under less intensive agricultural conditions (Albrecht, 2005). Although, in conventional fields, in the past 50 years a decrease in realised vegetation has been observed (Meyer et al., 2013), this species is regarded as one of the most problematic (causes loss in crop yield) species in European agriculture (Schroeder et al., 1993).

Butterfly density and diversity in general are declining in Europe (van Dyck et al., 2009), however biotope specialists are declining stronger than generalists, due to habitat loss and degradation (van Swaay et al., 2006; Warren et al., 2021). In Germany, some species, such as *Argynnis paphia* or *Lycaena phlaeas*, both known to use anthropogenically shaped habitats, although *A. paphia* is primarily a woodland species (Reinhardt et al., 2020), showed positive trends within the last 15 years. Unfortunately, more species are declining and many species are showing non-significant trends due to high variation between years or because they are already too rare (Kühn et al., 2019). In my thesis (**Chapter 3**), monitoring of butterflies took place between 2017 and 2019, the species loss and population decline, that already has taken place, was apparent due to the limited number of species in total and high number of single findings. Butterflies reflect the decline in other insect groups and their disappearance should be headed as warning for our deteriorating ecosystem health (Warren et al., 2021).

In my study (**Chapter 3**) most abundant butterfly species were the small white (*Pieris rapae),* the green-veined white (*P. napi*), the large cabbage white (*P. brassicae*), meadow brown (*Maniola jurtina*) and the European peacock (*Aglais io;* mass occurring of *Vanessa cardui* in 2019 not taken into account), which were also identified as most abundant species in the national wide butterfly monitoring (Kühn et al., 2019) and in case of cabbage whites (*Pieris* spec.) are dreaded pest species in vegetables (Klee, 1939). Specific life history traits allow butterfly species to react to seasonal changes due to human activity in agricultural landscapes (van Dyck et al., 2009). The mentioned species are medium-sized, mobile species, developing several generations per year and relaying on a variety of food plants (Settele et al., 2009; Middleton-Welling et al., 2020). This trait combination represents around 80 % of all butterfly counts in my study (**Chapter 3**) and is characteristic for generalists and essential for surviving in highly disturbed environments (Dennis et al., 2004; Börschig et al., 2013; Habel et al., 2019). However, even those common species, seemingly well adapted, are further declining due to missing host and nectar plants. This decline happens not only in habitats affected by intensive agriculture, but also affected by urbanisation and industrialisation. Increasing pressure from all sides leads to a decline of species even in such taxa as the small white (*P. rapae*) in some areas (van Dyck et al., 2009).

Comparable with weed species and butterflies, carabids experienced a similar trend. Activity density of carabids (**Chapter 4**) is high in agricultural landscapes. Within one week, around 100 individual carabid beetles were trapped per transect, however many species were trapped at only one site in low individual number, often only one individual. This emphasises that the species assemblage is limited and dominated by a few species. Other studies confirm the decrease in specialised species, such as xerophilous seed eaters while some generalist species increased, dominating beetle communities (Desender et al., 1994; 2010). While carabids are known to occur frequently in arable landscapes, a review on the literature of carabids before and after the shift in production intensity in Germany confirms not only the loss and decline of many species but also in overall abundances (Kromp, 1999).

The five most common carabid beetles in my study (**Chapter 4**) were *Bembidion lampros*, *Poecilus versicolor*, *Bembidion tetracolum*, *Peicilius cupreus* and *Anchomenus dorsalis*. With a size of on average one centimetre, they are small- to medium-sized carnivorous species. Being predators, they benefit from common pest species, such as cereal aphids in agriculture (Sunderland, 1975). Furthermore, being small means faster larval development, essential in a frequently changing environment (Blake et al., 1994). A limited species community in carabids is characterized by trait community homogenisation, resulting in the dominance of small polyphagous predators. Fortunately, so far the ecosystem service 'pest control' seems to be maintained (Symondson et al., 2002).

Species loss already occurred, affecting especially specialist species with particular habitat requirements, and remaining species are common generalist. Additionally, even some generalists are under pressure now (Desender et al., 1994; Thomas et al., 2004; van Swaay et al., 2006; Meyer et al., 2013; Habel et al., 2016). In order to stop further biodiversity loss (van Dyck et al., 2009; Desender et al., 2010; Richner et al., 2015; Kühn et al., 2019), actions must be taken to ensure remaining species to thrive in agricultural landscapes, maintaining functional diversity and viable populations. Generalists can provide important ecosystem services (Symondson et al., 2002) and, for example improving conditions of butterfly communities may also benefit other organism communities (Thomas, 2005), ensuring ecosystem services in intensive farmland.

Common measures to counteract negative impacts of intensive agriculture are agri-environmental schemes, implemented in the context of the Common Agricultural Policy of the EU (Pe'er et al., 2020). However, the effectiveness of measures is highly debated (Kleijn et al., 2001; van Hecken and Bastiaensen, 2010; Uthes and Matzdorf, 2013), which leads to my second key finding.

(2) The implementation of agri-environmental measures leads to differing patterns in different organism groups. Measures promote some common and generalist plant and butterfly species, while carabid beetles show little reaction towards measures. Their effectiveness depends on the definition of success and in the present agricultural system, aiming to maintain remaining biodiversity, although limited, is a good start. With minor positive effects on biodiversity, a mix of different agri-environmental measures can at least help to prevent further decline.

Agri-environmental measures affect organisms differently. This is evident when comparing the results of my studies. Measures such as flower strips promote common plant (**Chapters 2**) and butterfly species (**Chapter 3**). Carabids (**Chapter 4**), however show little reaction towards measures. Seed and butterfly abundance were several times higher in flower strips compared to reference areas in cereal fields. Meanwhile, the number of seed species did not differ whereas two times more butterfly species were present on flower strips. Furthermore, extensive cereals also increased butterfly diversity, although considerably less. Carabid activity abundance and diversity (**Chapter 4**) did not significantly differ between measures, such as fallow strips, flower strips and extensive cereals, compared to conventional cereal fields and grassy field margins. Meanwhile, at the community level, carabids and butterflies (**Chapter 3**) differed between flower strips and conventional cereals, while plant seed species community, although increased in number, remained similar (**Chapters 2**). All three organism groups have one thing in common regarding agri-environmental measures: already common species dominated.

Implementation of flower strips led to an increase of seed number but not species (**Chapter 2**). Species increasing in seed density were already common in the seed bank (see discussion of key finding 1). Our goal to increase less common representatives of the arable weed flora was not reached. Several reasons might be possible. First, although common and rare weed species are able to establish themselves in the soil seed bank, detection of rare ones is more unlikely due to the sampling methods (Thompson et al., 1998). Therefore, rare weed species might not have reached the detection threshold. Second, this pattern might be due to the already depleted seed bank. In this case, measures such as halting fertilizer use, will not change diversity (Bakker and Berendse, 1999). However, a study on the vegetation within the same project, detected such arable weeds. Though, they were not on flower strips, but on field edges with extensive cereals characterised by less dense vegetation (Sutcliffe and Leuschner, 2022), which leads to the third reason. Still present but rare species in the soil seed bank might not be competitive enough (reviewed in Albrecht et al., 2016) to establish themselves on densely vegetated flower strips (Sutcliffe and Leuschner, 2022). Besides the enormous increase of weed species (e.g., *Chenopodium album*), only a few species introduced by the flower strip seed mixture were able to established themselves in the soil seed bank. A large increase in seed numbers can also be observed during conversion from conventional to organic agriculture, however, the increase stops and decrease starts after 4 years when crops dominate and organic agriculture is established (Albrecht, 2005). A similar trend might be also true for flower strips. Especially in perennial flower strips, no further soil disturbance is intended for three to five years, limiting possibilities for annual weed species. Further research on how the soil seed bank develops after 5 years of flower strips is needed. In particular, since weed seed predation of carabids can reduce *C. album* seeds (Menalled et al., 2007).

In agricultural landscapes, activity density of carabids is relatively high (**Chapter 4**; within one week, on average 100 individuals, varying between 18 and 348 carabid beetles per transect) when compared to counts of butterflies (**Chapter 3**, on average 23 sightings per year varying between 0 and 121). While butterflies were most abundant on flower strips and less in cereals (extensive and conventional), carabids showed no significant preference. Other studies (e.g. Haaland et al., 2011) confirmed the positive impact of flower strips on butterflies, while carabids seem to prefer conventional fields (Aviron et al., 2006). This contradicting pattern can be explained by two different reasons. First, both groups have different ecological requirements. Butterflies need easily available nectar resources (Dennis et al., 2006), whereas for predatory carabids bare ground and a canopy layer for prey and protection are more important (Harvey et al., 2008). While flower strips provide flowers, aphids and a canopy layer, cereals provide, whether conventional or extensive, also bare ground and aphids. Missing differences might be due to the monitoring method, since trapping rate is correlated to vegetation density (Thomas et al., 2006). Therefore, different ecological requirements and possibly monitoring methods lead to diverging patterns in detection of ‘effectiveness’ of agri-environmental measures.

Furthermore, agri-environmental measures, although designed to provide favourable conditions for biodiversity (Geiger et al., 2010), might not meet requirements of other species. For example, former common xerophilous seed eaters might still be missing due to dense vegetation in flower strips (Desender and Bosmans, 1998). However, variation in vegetation still led to differences on the community level. Common herbivorous species, such as *Harpalus tardus* and *Amara similata*, both seed eaters not known to be field inhabitants of organic farmed agroecosystems (Thiele, 1977; Kromp, 1989), were more abundant in flower strips, fallow strips and grassy field margins, compared to conventional and extensive cereals (**Chapter 4**). Furthermore, the proportion of feeding guilds dependent on treatment and more herbivore and omnivore species were present on fallow and flower strips, as well as semi-natural habitats (Gayer et al., 2019). This indicates that measures provide other conditions supporting some additional species. Thus, a mix of measures can promote diversity on the landscape level. The increase in butterfly diversity also resulted from common species, and not specialists (**Chapter 3**), a trend reported by other studies as well (e.g. Aviron et al., 2011; Kolkman et al., 2022). Butterflies (**Chapter 3**) profited from additional resources provided by flower strips and extensive cereals. Furthermore, a few species, e.g., the small and large whites (*P. rapae*, *P. brassicae*), probably profited from larval food plants in the seed mixture leading to high numbers of those species especially in the first year. A long-term study on flower strips with strictly insect-friendly specifications (e.g. no re-sowing, only partial mowing), reported a positive population trend for several common species after 10 years, provided that for butterflies favourable climate conditions are also met (Kolkman et al., 2022). So, further monitoring of flower strips might be needed to detect trends of other species as well.

The effect of agri-environmental measures depends on the definition of success: i.e. whether they aim to enhance or maintain present biodiversity (Uthes and Matzdorf, 2013). Considering that my studies were conducted within the context of intensive agriculture, aiming at maintaining present biodiversity seems a realistic interim goal. Therefore, I conclude, agri-environmental measures can promote some generalist butterflies, plants and potentially carabids – and as a consequence – can have minor positive effects on biodiversity. Although only a few common species are promoted, they are important for preventing further declines in insect diversity (Haaland et al., 2011) and thus can be expected to have positive effects also further down the food chain. Nevertheless, more data gathering over a long time is needed to confirm if agri-environmental measures, in their current form, can counteract increasing pressure on biodiversity.

Furthermore, study region, or rather farm and local environmental conditions were as important as agri-environmental measure effecting butterflies (**Chapter 3**) and the seed bank (**Chapter 4**). Additionally, higher landscape heterogeneity and on-site conditions increased carabid diversity (**Chapter 5**). This pattern leads to my third key finding.

(3) *Effects of agri-environmental measures on biodiversity depend strongly on several external factors, namely on-site conditions, surrounding landscape, and neighbouring habitats. On-site conditions, such as tillage regime, vegetation structure and number of flowers, together with vicinity to semi-natural habitats including forest, influence the effect of measures. Details of implementation schemes of agri-environmental measures need to be carefully considered, as well as the potential of the landscapes to maintain a richer biodiversity, in order to enhance effects.*

Species pools differ between regions (Shmida and Wilson, 1985) and newly established agri-environmental measures are like bare islands. Therefore, colonisation rate and thus success of measure depend on the species pool of the surrounding landscapes (Tscharntke et al., 2005). Especially the studies of the soil seed bank and butterflies in different regions in Germany reflected that pattern, making the analysis of general patterns statistically challenging. The number of species, individuals and community composition were highly dependent on farm. Only ten percent of all seed species (**Chapter 2:** 12 species, 7 farms sampled) and around 15 % of butterfly species (**Chapter 3**: 9 species, 10 farms sampled) were present on all farms. Since local differences in the implementation of agri-environmental measures were considerable between farms (e.g., seed mixture, maintenance measures, duration of measure, field size, pesticide use) and farms differed between regions (climate, crop diversity, size, tillage regime, landscape context), classification of specific factors driving the influence of 'farm' was not possible in this study.

Especially in highly mobile organism such as butterflies, landscape predictors such as increasing land use heterogeneity and cover of woody elements were correlated with numbers of species and individuals and species composition (**Chapter 3**). In the landscape context, decreasing area of crop fields and increasing area of grassland and environmental measures are correlated with butterfly diversity (Aviron et al., 2006; 2011). The number of carabid beetle species also correlated with habitat heterogeneity, whereas individual landscape components, such as area of semi-natural habitats or woody elements, were less important in my study (**Chapter 4**).

To produce a positive effect on beetle diversity, a larger area of semi natural habitats might have been needed (Desender et al., 2010). Furthermore, human-made edges, such as forest adjacent to arable field edges, are often detrimental for certain other carabid species, limiting immigration from differing habitats (Magura et al., 2017). In general, agri-environmental measures are most effective in a simple landscape, characterized by a small proportion of only 1-20 % of non-crop habitats. Simple landscapes, still inhabited by some species, provide source pools allowing a significant response to changing management (Tscharntke et al., 2005; Boetzl et al., 2021). Differences between farms in non-crop areas, such as semi-natural habitats or grassland, varied between 10 and 50 percent (land-use analysis in a 250-m radius around transects). However, in this analysis, the quality of non-crop areas is unknown. Although transects for carabids and butterflies were always placed at the edge of fields (**Chapter 3 and 4**), large-scale landscape sections largely mirrored that distribution (see Appendix **Chapter 1**). Ecosystem services, such as pest control, are enhanced in complex landscapes (Bianchi et al., 2006).

Apart from the landscape context, local conditions and management regimes influence diversity. For example, seed density and diversity are higher on the field edge compared to the field interior (**Chapter 2**), a known edge effect pattern (Fried et al., 2009) and mirrored by established vegetation in arable fields (Sutcliffe and Leuschner, 2022). Another factor affecting the soil seed bank is the tillage regime. Low-tillage systems are characterized by more seeds in the soil compared to conventional tillage (Kladivko, 2001). Low-tillage systems generally provide higher amounts of seed in the top soil, that are available for example for carabids or farmland birds (reviewed in Holland, 2004).

Butterfly diversity and density were positively correlated with flower density (**Chapter 3**). Grassy, non-flowering ‘flower strips’ are known to have less effects on butterflies (Kolkman et al., 2022). Furthermore, temporal continuity is important for butterflies (Boetzl et al., 2021) and my study included annual and perennial strips, sometimes mulched in July or August by farmers. Agri-environmental measures with high plant species richness are needed to provide not only floral resources throughout the year, but also suitable larval food plants (Aviron et al., 2011).

The species composition of carabid communities was influenced by factors such as mean height of vegetation. Furthermore, high amounts of bare soil around the trap lead to high trapping rates (**Chapter 4**). This might be an artefact of the monitoring technique, as dense vegetation tends to lead to decreased capture rates (Greenslade, 1964). Differences in vegetation, however, also mean differences in microclimatic conditions influencing beetle communities (Kromp, 1999).

Agri-environmental schemes need to take ecological requirements of different organism groups into account, while at the same time considering the landscape context (Tscharntke et al., 2005). Different organism groups may profit from different measures (Boetzl et al., 2021). So far, many studies have been conducted, but the ecological effectiveness and social fairness of schemes and individual measures are still debated (Kleijn et al., 2001; van Hecken and Bastiaensen, 2010; Uthes and Matzdorf, 2013). A main conclusion of my study is that continued monitoring of the same sites over several years is needed to cover a larger proportion of the implementation time and include differences in weather conditions. We also need further multi-taxa assessments, including other organism groups, characteristic for farmland, such as birds and different pollinators, focusing on which measures are best suited to maintain biodiversity and ecosystem services in intensive farmland. A mix of different agri-environmental measures can help to increase spatial and temporal heterogeneity, which is important for biodiversity.

5.2 THE BIGGER PICTURE

The investigations for this thesis took place within the framework of F.R.A.N.Z. and MEDIATE, two projects aimed to develop innovative, easy-to-implement, and ecologically beneficial measures with adequate compensation for farmers and to communicate them towards politics and the farmer's community. Despite these ambitious aims, my results, however demonstrate the limits of nature conservation in intensive farmland. Thus, my thesis aligns with many earlier studies (Bakker and Berendse, 1999; Kleijn et al., 2001; Aviron et al., 2006; Aviron et al., 2011; Haaland et al., 2011; Boetzl et al., 2021), which showed limited ecological benefits of existing measures. This, combined with farmers' choices to implement the easiest but ecologically least effective measure options (Lakner et al., 2016), must be seen as the main causes of the failure of protecting biodiversity under the current Common Agricultural Policy (Pe'er et al., 2014; Pe'er et al., 2020). NGOs, the media, politicians and society are putting pressure on farmers in Germany (Ermann et al., 2017) and at the same time, protests on their side are increasing as well (e.g. "Wir haben es satt" Protest in Berlin, Fritz, 2022). Conventional farmers feel neither valued by society nor represented by politics, and idealistic and polarised discussions are not getting us any further (Heinze et al., 2021). Projects, such as F.R.A.N.Z. and MEDIATE, both mutual cooperation and communication projects, start exactly there by bringing all groups to the table.

One main difficulty in communication is that farmers' conceptualisation of 'nature' and 'nature conservation' does not fit the concept of an ecologist (Burton et al., 2008). Farmers see themselves as caring managers of nature, however in their picture 'nature' is often supposed to be clean and tidy. This contradicts the biological requirements for nature and biodiversity conservation (reviewed in Ahnström et al., 2009). Even though agri-environmental measures are recognised as good practice by the farming community, the value or benefit of them is often not recognized (Burton et al., 2008). In the past, farmers' perception of 'nature' was shaped by maximising production for food security and profit (Kropp and Wagner, 2005). Both the farming community and politics supported that focus. However, a shift in perception of agriculture has recently started; and sustainable development for the future became a main goal in agriculture (Kropp and Wagner, 2005). This shift in perception needs time to effectively influence farmers' behaviour, as a study in the Netherlands comparing actual and contingent participation in the agri-environmental measure 'fallow field margin strip' confirmed (Wossink and van Wenum, 2003). In this study, despite concessions such as quite high compensation, lower risk of weeds (less diverse seed mixture) and narrower strips, resulting in a smaller amount of land being taken out of production, still 40 % of farmers were unwilling to participate. Therefore, ecological topics need to be integrated in farmers' training, to transfer knowledge about wild animals, plants and their ecology, so farmers can envision ecological possibilities concerning their land (Mills et al., 2017). We need to change our value system away from straight and clean production landscapes towards temporally and spatially more heterogenous landscapes which support various ecosystem functions.

The change in our value system and the needed knowledge transfer can best be achieved by cooperation and communication. However, communication between farmers and environmentalists is often characterized by distrust and accusation, not acknowledging both parties as equal and knowledgeable partners (Menauer and Schweiger, 2022). Professional and trusted agricultural extension or advisory services could be part of the solution. Instead of advising against more environmental friendly measures, due to higher administrative burdens (Zinngrebe et al., 2017), these counsellors could deliver information on agri-environmental measures and increase participation (Wilson and Hart, 2000). So far, hurdles remain high and only genuinely motivated farmers take first steps in the direction of conservation (Beedell and Rehman, 2000). Projects such as F.R.A.N.Z. and MEDIATE can contribute to reducing prejudices and working for change.

The current agricultural system is not suitable to stop or reverse biodiversity loss. Since monetary compensation by itself won't lead to the necessary long-term behavioural changes (Burton and Paragahawewa, 2011; Snoo et al., 2013), we need farmers to be informed on biodiversity, seeking change through their own environmentally friendly motivation (e.g. Snoo et al., 2013; Mills et al., 2017).

5.3 OUTLOOK

Different stakeholders (farmers, the German farmers association, local cultural landscape foundations, nature conservation agencies and policy makers) are responsible for shaping the agricultural landscape (Egdell, 2000). Joint interdisciplinary projects aiming to improve existing measures for biodiversity prove the willingness to share knowledge and show mutual respect. First results of biological monitoring, as presented here, confirm achievements in improving conditions for common species. Arable weeds, butterflies and carabid beetles react differently towards different measures and are influenced by neighbouring land use types. Thus, a variety of measures should be implemented, taking the landscape context into account. Large differences in the implementation of the measures studied in this thesis affected biodiversity, indicating that further efforts are needed to transfer knowledge between different stakeholders and raise awareness about the conditions needed to promote biodiversity. Established trenches and barriers between farmers and environmentalists have not yet been overcome. Operating together, challenges of secure food supply and nature conservation can be mastered (Chappell and LaValle, 2011).

Current international crises, such as the war against Ukraine, intensify the challenges in intensive farmland. One consequence is that the EU considers to relax environmental regulations to secure food supply (Handelsblatt, 2022). However, agrobiodiversity is key for sustainable land management and the remaining ‘basic’ biodiversity needs immediate protection, since recovery can be slow and incomplete (Caro et al., 2016) which will harm food production in the future.

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THESIS DECLARATION

I hereby affirm that I have written this thesis independently and without unauthorized assistance and that I have not made use of any services that contradict the purpose of the examination procedure. Furthermore, I hereby declare that I have not used this thesis or parts thereof for the application for a doctoral degree at any other university or institution.

Liesa Schnee

Göttingen, 9.8.2022