Effects of grassland management on arthropod diversity

by

Tobias Frenzel (Mohr)

from Heidelberg

Accepted Dissertation thesis for the partial fulfilment of the requirements for a

Doctor of Natural Sciences

Fachbereich 3: Mathematik/Naturwissenschaften

Universität Koblenz-Landau

Reviewer:

Prof. Dr. Klaus Fischer

Prof. Dr. Thomas Wagner

Examiner:

Prof. Dr. Bernhard Köppen

Prof. Dr. Klaus Fischer

Prof. Dr. Thomas Wagner

Date of the oral examination: 21 March 2022

Table of contents

Summary

The ongoing loss of species is a global threat to biodiversity, affecting ecosystems worldwide. This also concerns arthropods such as insects and spiders, which are especially endangered in agricultural ecosystems. Here, one of the main causing factors is management intensification. In areas with a high proportion of traditionally managed grassland, extensive hay meadows that are cut only once per year can still hold high levels of biodiversity, but are threatened by conversion into highly productive silage grassland. The Westerwald mountain range, western Germany, is such a region. In this thesis, I compare the local diversity of bees, beetles, hoverflies, leafhoppers, and spiders of five grassland management regimes along a gradient of land-use intensity. These comprise naturally occurring grassland fallows, three types of traditionally managed hay meadows, and intensively used silage grassland. By using three different sampling methods, I recorded ground-dwelling, flower-visiting, and vegetation-dwelling species. The results show that in most cases species richness and diversity are highest on fallows, whereas variation among different managed grassland types is very low. Also, for most sampled taxa, fallows harbour the most distinct species assemblages, while that of other management regimes are largely overlapping. Management has the largest effect on species composition, whereas environmental parameters are of minor importance. Long-term grassland fallows seem to be highly valuable for arthropod conservation, even in a landscape with a low overall land-use intensity, providing structural heterogeneity. In conclusion, such fallows should be subsidized agri-environmental schemes, to preserve insect and spider diversity.

Zusammenfassung

Der Rückgang der Artenvielfalt ist allgegenwärtig in Ökosystemen auf der ganzen Welt. Bedroht sind auch Arthropoden wie Insekten und Spinnen, insbesondere in der Agrarlandschaft. Einer der Hauptgründe hierfür ist die Intensivierung der landwirtschaftlichen Nutzung. Zwar kann die Artenvielfalt in Gebieten mit einem hohen Anteil von traditionell bewirtschafteten, einschürigen Heuwiesen noch sehr hoch sein, diese sind aber durch die Umwandlung in ertragsoptimierte Silagewiesen gefährdet. Der Westerwald, ein Mittelgebirge im Westen Deutschlands, ist eine solche Region. Diese Arbeit beinhaltet einen Vergleich der hier örtlichen Artenvielfalt von Bienen, Käfern, Schwebfliegen, Spinnen und Zikaden auf fünf Grünland-Flächentypen, die in unterschiedlicher Intensität bewirtschaftet werden. Hierbei untersuche ich naturnahe Grünland-Brachen, drei Gruppen von extensiv bewirtschafteten Heuwiesen und intensiv bewirtschaftete Silagewiesen. Mithilfe von drei unterschiedlichen Fangmethoden konnten bodenlebende-, blütenbesuchende- und Arten der Vegetationsschicht erfasst werden. Die Ergebnisse zeigen, dass die Artenvielfalt auf den Brachen deutlich höher ist als auf den bewirtschafteten Grünlandtypen, zwischen denen nur geringe Unterschiede bestehen. Auch die Artenzusammensetzungen der Brachen unterscheiden sich deutlich von denen der anderen Flächen. Hierbei hat die Art der Bewirtschaftung einen größeren Einfluss als verschiedene Umweltparameter, welche nur eine untergeordnete Rolle spielen. Die Ergebnisse deuten darauf hin, dass Langzeit-Brachen eine positive Auswirkung auf den Schutz von Insekten und Spinnen haben, selbst in extensiv bewirtschafteten Kulturlandschaften mit hoher Artenvielfalt. Brachen sollten daher in Naturschutzverträgen berücksichtigt und gefördert werden.

1 General introduction

Extinction rates, and thus the ongoing loss of biodiversity, are higher than estimates of normal background extinction (Ceballos et al., 2015). This species decline threatens the functionality of ecosystems worldwide, and affects vertebrates and invertebrates alike (Dirzo et al., 2014; Wagner, 2020). Arthropods, especially insects, have received broader attention only in recent years (Vogel, 2017). For flying insects, a 76% decrease in biomass has been recorded over 27 years within conservation areas in western Germany (Hallmann et al., 2017). Similarly, the loss of arthropod biomass in grassland areas was reported to be at 68% over 9 years by Seibold et al. (2019). While it is often difficult to identify single causing factors for this decline, it is widely accepted that an interaction of multiple anthropogenic factors exerts pressure on arthropod species, including climate change, habitat loss and fragmentation, pollution, and nutrification (Chase et al., 2020; Wagner, 2021). Although not all insect taxa or ecosystems are affected equally severe (Crossley et al., 2020; van Klink et al., 2020), effective conservation measures have to be identified and applied to prevent further decline and collapses of important ecosystem services (Powney et al., 2019; Wagner, 2021).

In agricultural areas, land-use intensification is the prevalent driver of species loss, favouring dominant species and resulting in biotic homogenization (Gossner et al., 2016; Raven & Wagner, 2021; Simons et al., 2014). In regions with high proportion of grassland, intensification often means conversion of traditionally managed, species-rich hay meadows into highly productive silage grassland, which affects arthropod taxa such as butterflies, bees, beetles, grasshoppers, hoverflies, leafhoppers, spiders, and true bugs (Habel et al., 2019; Humbert, Delley & Arlettaz, 2021; Woodcock et al., 2021). Specific changes in grassland management are increases in mowing frequency and fertilization (Manning et al., 2015; van Klink et al., 2019). While grassland abandonment may decrease local diversity too, it can also have the opposite effect (Hilpold et al., 2018; Queiroz et al., 2014).

In regions where extensively managed, species-rich grassland is still left, targeted conservation programs can be effective (e.g. Bonari et al., 2017). At the same time, such immediate preserving strategies render difficult renaturation measures unnecessary, which would have to be implemented after periods of intensification (Woodcock et al., 2021). Different grassland conservation management types are e.g. mowing once per year at a delayed date, low-intensity grazing, and abandoning (Batáry et al., 2010; Bonari et al., 2017). As these can produce variable outcomes, depending on regional conditions such as the levels of landscape heterogeneity and structural complexity, conservation measures have to be adapted to local conditions (Batáry et al., 2007; Tscharntke et al., 2005).

The Westerwald mountain range in mid-western Germany still includes areas with a high amount of traditionally managed grassland, where wet meadows in particular are refuges for diverse species assemblages (Westerwaldkreis, 2018). Because a substantial fraction of these meadows has never been fertilized or managed intensively, and grassland fallows were left aside, endangered grassland specialist species such as the Whinchat *Saxicola rubetra*, and the Violet Copper *Lycaena helle* were able to persist (Bauerfeind et al., 2009; Fischer et al., 2013). Although there are conservation programs in place already, in form of agri-environmental schemes, ongoing grassland intensification is a threat to local biodiversity (Fischer & Müller, 2018).

The aim of this study is to investigate local effects of grassland intensification, conservation efforts, and environmental parameters on bees, beetles, hoverflies, leafhoppers, and spiders, by comparing diversity and species assemblages between different types of grassland management that co-occur in close proximity. More specifically, these comprise five types: grassland fallows, two types of traditionally managed hay meadows cut only once per year and contracted under a federal agri-environmental scheme, hay meadows that are cut twice per year, and intensively managed silage grassland cut 4–5 times per year. For each grassland type, I investigated 9 replicate sites, resulting in a total of 45 sites. I recorded species richness and abundance using three different sampling methods, pitfall trapping, pan trapping, and suction sampling, to include ground-dwelling, flower-visiting, and vegetation-dwelling species. To quantify conservation value, I calculated both diversity (i.e. effective species number) and a red list score from the recorded data. I also assessed community structure, and, in case of beetles, habitat and diet preferences. In addition, I recorded soil parameters, plant species, and the composition of land-cover types within the direct surrounding of sites.

Specifically, I address three research questions:

- Q_1: To what extent does grassland intensification reduce arthropod diversity within the study area? Negative effects of grassland intensification on arthropods have been described in previous studies (e.g. Batáry et al., 2012), but from the Westerwald region, data on most arthropod groups is not yet available (but see Hannappel & Fischer, 2019).
- Q_2: Are traditionally managed hay meadows within the study area better for arthropod conservation than fallows? If any management type has significantly higher diversity levels, it can be considered to have a higher conservation value.

- Q_3: Are environmental parameters on-site and within the direct surrounding more important for conservation than on-site management within the study area? If management is not a significant factor, different parameters of soil, vegetation, or structural heterogeneity (i.e. proportions of different habitat types) may influence diversity instead.

From the first two research questions above, I deduced the following specific hypotheses, adjusted to the respective taxon:

- H_1: The diversity of bees, hoverflies, and leafhoppers is higher on traditionally managed hay meadows than on fallows and silage grassland. This hypothesis is based on the assumption that diversity of all three taxa usually depends on plant diversity, which is highest on traditionally managed hay meadows (e.g. Everwand et al., 2014; Wei et al., 2021).
- H_2: The diversity of beetles is lower on intensively managed silage grassland than on other grassland types. Here, the underlying assumption is that beetles, a large taxon that includes various feeding types (e.g. predatory, phytophagous, mycetophagous, detritophagous etc.; Koch, 1989), are not to the same degree dependent on plant diversity as solely phytophagous taxa.
- H_3: The diversity of spiders is lower on intensively managed silage grassland than on other grassland types. The assumption is that spiders, as predatory taxon, are also less dependent on plant diversity, and rather respond to vegetation structure (Lyons et al., 2018).

The following hypotheses are applied to all investigated taxa. As taxa may respond differently to similar conditions, no directions of effects are specified here:

- H_4: Species assemblages differ between management regimes. This allows to discover differences between grassland types that could remain undetected by the direct comparisons of diversity, as species assemblages can be distinct even when species richness and diversity are highly similar.
- H_5: On-site environmental conditions (soil, vegetation) and structural features (i.e. proportion of habitat types) of the direct surrounding influence arthropod parameters.

Because of the comprehensive ecological data that is available for beetles, I tested an additional hypothesis for beetles only:

- H_6: Beetle species' biotope and diet preferences, weighted by their relative abundance, differ between managed and abandoned grassland.

In summary, the goal of my thesis is to identify the best conservation strategy for preserving species-rich communities in the Westerwald region, which is still a traditionally used landscape with a high proportion of high value grassland that has never been fertilized. Planning, study design, and preparations started in December 2017. All field work was completed during the vegetation period of 2018, between May and September. Species identification was mostly finished by the end of 2019. Statistical analysis, writing, and paper submission was completed during 2020 and 2021. As of now, two papers are published, and a third manuscript is submitted, currently being peer-reviewed. All three are attached in the following section.

2 Chapters

2.1 Chapter I: Bees, hoverflies, and leafhoppers, pp. 11–24, supplementary material pp. 25–33:

Frenzel, T., Wörsdörfer, A., Khedhiri, S., Di Giulio, M., Leus, F., Lipperts, M.J., Martin, D., & Fischer, K. (2021). Grassland fallows as key for successful insect conservation. *Insect Conservation and Diversity*, 14, 837–850. https://doi.org/10.1111/icad.12525.

2.2 Chapter II: Beetles, pp. 34–43, supplementary material pp. 44–83:

Frenzel, T., & Fischer, K. (2022). Fallows benefit beetle conservation in a traditionally managed grassland landscape. *Agriculture, Ecosystems & Environment*, 327, 107829. https://doi.org/10.1016/j.agee.2021.107829.

2.3 Chapter III: Spiders, pp. 84–127, supplementary material pp. 128–133:

Frenzel, T., Rischen, T., & Fischer, K. (submitted to *Basic and Applied Ecology*). Humid grassland fallows promote spider diversity in a traditionally managed landscape.

2.1 Chapter I: Bees, hoverflies, and leafhoppers

Note by the author: This chapter is based on the following journal publication. Due to copyright issues, the text of the chapter was replaced by the reference information. Thus, the interested reader is kindly asked to read the published paper via the following reference:

Frenzel, T., Wörsdörfer, A., Khedhiri, S., Di Giulio, M., Leus, F., Lipperts, M.J., Martin, D., & Fischer, K. (2021). Grassland fallows as key for successful insect conservation. *Insect Conservation and Diversity*, 14, 837–850. https://doi.org/10.1111/icad.12525.

Abstract

There is wide scale evidence for declines in insect biodiversity at a global scale. Agricultural intensification is considered to be one of the major causes of these declines. Traditionally managed habitat types, such as hay meadows, harbour a rich diversity of plants and animals, but have been often transformed into crop fields or silage grassland.

To evaluate the role of (1) agricultural intensification for insect declines and of (2) traditionally managed hay meadows and fallows for biodiversity conservation, we here compare bee, hoverfly, and leafhopper assemblages on 45 sites along a gradient of land use intensity in western Germany. We included moist long-term grassland fallows, three types of hay meadows, and silage grasslands, each represented by 9 replicates.

Species numbers of bees and leafhoppers were significantly higher on fallows than other management types. Grassland fallows also harboured the most distinct assemblages, while those of hay meadows and silage grassland were very similar and largely overlapping.

The surprising similarity of hay meadow and silage assemblages may be due to investigating highly mobile taxa within a landscape composed of a fine-scale mosaic of traditionally managed and intensified grassland. Our results demonstrate the high importance of unmanaged areas, even when the overall land use intensity is still comparatively low.

We suggest that temporal grassland fallows (unmanaged for 3-5 years) should be subsidized in agri-environmental schemes to increase landscape heterogeneity and to preserve insect diversity.

2.2 Chapter II: Beetles

Note by the author: This chapter is based on the following journal publication. Due to copyright issues, the text of the chapter was replaced by the reference information. Thus, the interested reader is kindly asked to read the published paper via the following reference:

Frenzel, T., & Fischer, K. (2022). Fallows benefit beetle conservation in a traditionally managed grassland landscape. *Agriculture, Ecosystems & Environment*, 327, 107829. https://doi.org/10.1016/j.agee.2021.107829.

Abstract

Insect biodiversity is declining at the global scale, with agricultural intensification representing a major driver of this development. Traditionally managed grassland, such as hay meadows, can support high insect and plant diversity but is often converted into more productive cropland or silage grassland. We evaluated the effects of agricultural intensification and conservation measures on beetle assemblages in a traditional landscape dominated by grassland in western Germany. We investigated a total of 45 grassland sites including long-term (abandoned) grassland fallows with natural vegetation cover, three types of hay meadows, and intensively used silage grassland, using different sampling methods targeting ground-dwelling, flower-visiting, and vegetation-dwelling beetles. Species richness and diversity were highest on grassland fallows, while variation among different types of managed grassland was very low. Thus, fallows outperformed even unfertilized hay meadows cut after July 15th in terms of species richness. Beetle assemblages of fallows and silage grassland were both distinct from all other management regimes, while the three types of hay meadows did not differ substantially. Effects of on-site management regime were strong, but environmental parameters and surrounding land cover were of minor importance only. Our results suggest that long-term fallows are important for beetle conservation, even in landscapes with overall low land-use intensity. We suggest that grassland fallows should be considered in subsidized agri-environmental schemes.

2.3 Chapter III: Spiders

Note by the author: This chapter is based on the following journal publication. Due to copyright issues, the text of the chapter was replaced by the reference information. Thus, the interested reader is kindly asked to read the published paper via the following reference:

Frenzel, T., Rischen, T., & Fischer, K. (submitted to *Basic and Applied Ecology*). Humid grassland fallows promote spider diversity in a traditionally managed landscape.

Abstract

Agricultural intensification is an important driver of biodiversity decline. Regarding grassland ecosystems, traditionally managed hay meadows, as opposed to highly productive silage grassland, are often of high conservation value. Here, we compare spider assemblages among five grassland management regimes along an intensification gradient, ranging from long-term fallows via traditionally managed hay meadows to high-intensity silage grassland. Humid long-term fallows harboured highest species richness and diversity, and their assemblages differed strongly from other management regimes. There was surprisingly little variation though among different types of hay meadows and silage grassland. Differences among spider assemblages were most strongly shaped by fallow-related parameters and the proportion of forests in the surroundings of study sites. The high spider diversity on fallows may result from their undisturbed vegetation structure, while management,

regardless of frequency, may have detrimental effects. Our results demonstrate the high importance of unmanaged areas even in regions with an overall low land-use intensity, such as grassland ecosystems. We thus recommend the inclusion of temporal grassland fallows (unmanaged for 3-5 years) in agri-environmental schemes to increase landscape heterogeneity and preserve spider diversity.

3 General discussion

Long-term grassland fallows were clearly the most beneficial management type for insects and spiders. The diversity of bees, beetles, leafhoppers, and spiders was significantly higher on fallows than on other management types, only hoverfly diversity was not enhanced. Species assemblages on fallows were most distinct from other management types. Also, the within-group variance of beetle and spider species assemblages was higher between fallows than between sites within other management regimes. Positive effects of fallows on different taxa (e.g. plants, insects, and spiders) have been also shown in other studies (Feng et al., 2021; Fiedler, Wrbka & Dullinger, 2017; Helden et al., 2020; Schmidt et al., 2008; Toivonen et al., 2015; Wietzke et al., 2020). Surprisingly, throughout all investigated taxa, intensively managed silage grassland performed equally to traditionally managed grassland. Since detailed results for each taxon are discussed within chapters I–III, I briefly focus on general challenges of my project in the following section, and then conclude with the synthesis of all three parts.

3.1 Challenges

Study design and sampling periods

The experimental design was constricted by availability of sites, as permission of the farmers was needed for sampling, and respective sites of management regimes were not equally dispersed within the study area. A paired block design thus was not realisable, and especially silage grassland sites accumulated in the northern area of the study region (see Fig. 1, Frenzel et al., 2021). To account for this problem, I included tests for spatial autocorrelation, and, if necessary, included corrections in the statistical analyses (Dormann et al., 2007). A second issue concerning sampling periods were the irregular mowing dates. The farmers had to align haymaking to the weather conditions, and sometimes mowing dates were scheduled on very short notice. Then, all sampling equipment had to be removed on all 45 sites, even if only few of them were cut, to ensure uniform sampling periods. Due to this occasional disassembly on short notice, and the time that was needed to visit all sites (up to 2 days, depending on the task), there were slight differences in the number of sampling days, as described in the material and methods sections above. One sampling period (out of 8 in total) of pitfall and pan trapping could not be included in the analysis, because a mowing event on all silage sites, ahead of schedule, led to a temporary loss of samples. However, small irregularities in active sampling days did not influence the results, when sampling days were included within the statistical models.

Drought

The year 2018, in which sampling took place, was exceptionally warm and dry (Buras, Rammig & Zang, 2020). The low precipitation levels in mid to late summer caused slower plant growing rates, especially in August, resulting in four instead of five cutting dates on silage grassland sites. Also, pitfall and pan trap sampling yielded lower individual numbers during these later occasions. However, the important sampling months May and June were not affected. Furthermore, since all sites were equally exposed to the dry weather conditions, a direct comparison of management regimes is still valid.

Differences between analyses

Due to constructive criticism during peer review, the principal component analyses (PCAs) are slightly different between papers. For bees, leafhoppers, and hoverflies, as well as for spiders, all 16 environmental variables (see Frenzel et al., 2021; table 1) were included in a single PCA. For beetles, two sub-sets of variables were analysed in one PCA respectively, landscape parameters (6 variables) and soil parameters (4 variables). In the subsequent models, vegetation height and plant species number were added separately, and Ellenberg values were not considered at all. Since these changes were made after I finished initial analyses of all data sets, I was able to compare both variants. When applied to the same data, the two different PCA approaches did not fundamentally change any results or the following interpretation, so both can be considered equally appropriate. Other minor differences concerned red list score, as well as biotope and habitat preference, all of which could only be calculated for beetles due to insufficient number of red list records within the other taxa. For bees, red list species number replaced red list score, since in this case, they were basically the same. For leafhoppers, hoverflies, and spiders, there were not enough red list species to justify any further calculation.

3.2 Synthesis

The recorded data, as outlined in detail in my two published papers and one submitted manuscript above, were appropriate to answer the three initial research questions of my thesis. Patterns in the data of all three sampling methods coincided clearly, revealing the great conservation value of long-term grassland fallows. I present my overall conclusions in the following section, aligned to the initial research questions outlined in the introduction.

Low impact of grassland intensification

Q_1: *To what extent does grassland intensification reduce arthropod diversity within the study area?*

Grassland intensification within the study area was not as detrimental for arthropod diversity as expected. However, since grassland intensification is known to have negative effects on insect and spider diversity in general (e.g. Feng et al., 2021; Wersebeckmann et al., 2021), there could be implications that simply were not detected. Extinction debt for example could possibly be a reason for the rather high diversity on silage grassland, as land-use intensification in the Westerwald region has happened only in recent decades (Kuussaari et al., 2009). Specific results that support this assumption are the distinct species assemblages of beetles, separating silage sites from all other management regimes. This, together with higher individual numbers due to eutrophication by heavy fertilizing, may be hinting towards an early stage of biotic homogenization that is not yet apparent in diversity metrics (Gossner et al., 2016). If left unchecked, generalist species could be favoured over specialists in the long term (Hilpold et al., 2018). Another reason could be the common practise of real estate division, which led to small management units in the study area. Silage grassland is often located in between hay meadows, which could cause some mixing of species assemblages (e.g. Schneider et al., 2016).

High conservation value of long-term fallows

Q_2: *Are traditionally managed hay meadows within the study area better for arthropod conservation than fallows?*

Hay meadows, managed under federal conservation contracts, did not harbour higher insect and spider diversity than fallows. Rather, local fallows scored significantly better throughout all taxa, except for hoverflies. Although local fallows were already known to provide habitat for a population of the violet copper butterfly *Lycaena helle* (Bauerfeind, Theisen & Fischer, 2013), a severely endangered species, such a considerably distinct result throughout different taxa was not expected. The high diversity scores of spiders in particular seem unusual, when compared to findings of other studies, where abandonment rarely affects diversity (e.g. Wersebeckmann et al., 2021).

Minor importance of on-site environmental factors

Q_3: *Are environmental parameters on-site and within the direct surrounding more important for conservation than on-site management within the study area?*

On-site environmental conditions, i.e. soil and vegetation parameters, as well as habitat structure within the direct surrounding, were much less important than management regime, although minor effects were found. In general, environmental conditions seemed to influence individual number more than other response variables, and also could be slightly more important for leafhoppers and spiders, compared to bees, beetles, and hoverflies (Entling et al., 2007).

3.3 Conclusion

In landscapes with already high biodiversity, such as the Westerwald region, long-term grassland fallows are effective tools for insect and spider conservation (c.f. Fiedler, Wrbka & Dullinger, 2017; Helbing et al., 2017; Bucher et al., 2016). Together with traditionally managed hay meadows, which are undoubtedly important for biodiversity, they may counteract negative effects of grassland intensification (Bonari et al., 2017; Boetzl et al., 2021). The value of traditionally managed hay meadows is especially apparent when reintroduced to more intensively used landscapes like cropland areas, as practiced in restoration projects (Woodcock et al., 2021). However, mowing events can have equalising effects when all grassland within an area is cut simultaneously, even on traditionally managed hay meadows, as structural heterogeneity decreases abruptly (e.g. Cizek et al., 2012). This may explain the lack of difference between managed grassland types, as it was apparent in bees, beetles, and spiders, but especially in leafhoppers. Therefore, data from the Westerwald support the theory that spatial and temporal landscape heterogeneity may be the most important factor for biodiversity in agricultural areas (e.g. Buri, Humbert & Arlettaz, 2014; Samways et al., 2020; Sirami et al., 2019). To prevent loss of grassland biodiversity, it is essential to continue existing contracts in the Westerwald region, but additionally include fallows in agri-environmental schemes, because of their great conservation value for insects and spiders.

4 Acknowledgements

I am deeply indebted to Professor Klaus Fischer, who guided me throughout the time of my doctoral thesis. I am extremely grateful for his advice, practical help, and especially his tireless efforts in writing and correcting the manuscripts.

Many thanks also to Professor Thomas Wagner, for being my second referee, but also for verifying beetle species that I struggled to identify and his guidance.

Many thanks to Anne Wörsdörfer, for her diligence in sorting and identifying wildbees, sorting hoverflies, helping in the field, and measuring pH of soil samples, to Souha Khedhiri, for identifying leafhoppers, and to Tamara Rischen, for identifying spiders from the suction sampling. For identifying hoverflies, I thank Maurice Di Giulio, Fabienne Leus, Marie-Jo Lipperts, and Daniel Martin. Special thanks go to Jonas Köhler, for his invaluable expertise that he patiently shared whenever I struggled to identify a beetle species, and his help in the field. Many thanks also to Wolfram Remmers, Daronja Trense, Domenica Kaiser, and Roland Busch, for helping me out in the field, and with other tasks. Thanks also to Ulli Bange for his help with the soil analysis.

I want to thank the farmers Thomas Bader, Anton Boerkamp, Karl-Martin Gros, Manfred Milnikel, Gregor Theisen, Benjamin Türk, and Joachim Uhr for their permission to conduct the study on their land, and Markus Kunz, who established the contacts.

Further, I would like to thank Professor Martin Entling, Verena Rösch, and Laia Mestre, who helped me during the planning phase, for answering methodical questions and teaching me how to identify spiders. Many thanks also to Volker Hartmann and Theo Blick, who provided their expertise by verifying my spider records and answering questions, to Herbert Nickel, for his correspondence on my leafhopper records, and to Axel Schmidt, who filed the sampling permissions.

I am very grateful to have such nice professors and colleagues, Markus Ackermann, Daniela Boecker, Maximilian Dehling, Franziska Deppe, Professor Eberhard Fischer, Katrin Friedemann, Alena Hantzschmann, Anna Hitzler, Petra Kapellen, Dorothee Killmann, Jutta Meier, Daniela Mewes, Claudia Nehls, Eva Plath, Ange Raharivololoniaina, Ronny Richter, Professor Ulrich Sinsch, Michael Tempel, Laura Tensen, Jean de Dieu Uwizelimana, Elfriede van der Zalm, Valentina Zizzari, it was a pleasure to work with all of you.

Especially I want to thank Brigitte Nilow-Lange and the late Dagmar Savelsberg-Stauth, for the warm welcome at the institute when I started there, and for all their help.

Lastly, with all my heart, I would like to thank my wife Melina Frenzel and all of my family for their love and support.

5 References

Batáry, P., Báldi, A., Szél, G., Podlussány, A., Rozner, I., Erdos, S., (2007). Responses of grassland specialist and generalist beetles to management and landscape complexity. Biodiversity research. *Diversity and Distributions*, 13, 196–202. https://doi.org/10.1111/j.1472-4642.2006.00309.x.

Batary, P., Baldi, A., Sarospataki, M., Kohler, F., Verhulst, J., Knop, E., Herzog, F., & Kleijn, D. (2010). Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agriculture, Ecosystems & Environment*, 136, 35–39. https://doi.org/10.1016/j.agee.2009.11.004.

Bauerfeind, S. S., Theisen, A. & Fischer, K. (2009). Patch occupancy in the endangered butterfly *Lycaena helle* in a fragmented landscape: Effects of habitat quality, patch size and isolation. *Journal of Insect Conservation*, 13, 271–277. https://doi.org/10.1007/s10841-008-9166-1.

Boetzl, F.A., Krauss, J., Heinze, J., Hoffmann, H., Juffa, J., König, S., Krimmer, E., Prante, M., Martin, E.A., Holzschuh, A., & Steffan-Dewenter, I. (2021). A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. *Proceedings of the National Academy of Sciences*, 118. https://doi.org/10.1073/pnas.2016038118.

Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., Kočárek, P., Konvička, O., Uřičář, J., & Chytrý, M. (2017). Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of heterogeneity and tradition. *Agriculture, Ecosystems & Environment*, 246, 243–252. https://doi.org/10.1016/j.agee.2017.06.010.

Bucher, R., Andres, C., Wedel, M.F., Entling, M.H., & Nickel, H. (2016). Biodiversity in low-intensity pastures, straw meadows, and fallows of a fen area - A multitrophic comparison. *Agriculture, Ecosystems & Environment*, 219, 190–196. https://doi.org/10.1016/j.agee.2015.12.019.

Buras, A., Rammig, A., & Zang, C.S. (2020). Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. *Biogeosciences*, 17, 1655–1672. https://doi.org/10.5194/bg-17-1655-2020.

Buri, P., Humbert, J. Y., & Arlettaz, R. (2014). Promoting pollinating insects in intensive agricultural matrices: field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees. *PloS One*, 9, e85635. https://doi.org/10.1371/journal.pone.0085635.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., & Palmer, T.M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1, 9–13. https://doi.org/10.1126/sciadv.1400253.

Chase, J.M., Blowes, S.A., Knight, T.M., Gerstner, K., & May, F. (2020). Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature*, 584, 238–243. https://doi.org/10.1038/s41586-020-2531-2.

Cizek, O., Zamecnik, J., Tropek, R., Kocarek, P., & Konvicka, M. (2012). Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. *Journal of Insect Conservation*, 16, 215–226. https://doi.org/10.1007/s10841-011-9407-6.

Crossley, M.S., Meier, A.R., Baldwin, E.M., Berry, L.L., Crenshaw, L.C., Hartman, G.L., Lagos-Kutz, D., Nichols, D.H., Patel, K., Varriano, S., & Snyder, W.E. (2020). No net insect abundance and diversity declines across US Long Term Ecological

Research sites. *Nature Ecology & Evolution*, 4, 1368–1376. https://doi.org/10.1038/s41559-020-1269-4.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406. https://doi.org/10.1126/science.1251817.

Dormann, C. F., McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., Carl, G., Davies, R. G., Hirzel, A., Jetz, W., Kissling, W. D., Kühn, I., Ohlemüller, R., Peres-Neto, P. R., Reineking, B., Schröder, B., Schurr, F. M., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30, 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x.

Entling, W., Schmidt, M.H., Bacher, S., Brandl, R., & Nentwig, W. (2007). Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography*, 16, 440–448. https://doi.org/10.1111/j.1466-8238.2006.00305.x.

Everwand, G., Rösch, V., Tscharntke, T., & Scherber, C. (2014). Disentangling direct and indirect effects of experimental grassland management and plant functional-group manipulation on plant and leafhopper diversity. *BMC Ecology*, 14, 1. https://doi.org/10.1186/1472-6785-14-1.

Feng, L., Arvidsson, F., Smith, H.G., & Birkhofer, K. (2021). Fallows and permanent grasslands conserve the species composition and functional diversity of carabid beetles and linyphiid spiders in agricultural landscapes. *Insect Conservation and Diversity*, *14*, 825–836. https://doi.org/10.1111/icad.12520.

Fiedler, K., Wrbka, T., & Dullinger, S. (2017). Pluralism in grassland management promotes butterfly diversity in a large Central European conservation area.

Journal of Insect Conservation, 21, 277–285. https://doi.org/10.1007/s10841-017-9974-2.

Fischer, K., Busch, R., Fahl, G., Kunz, M., & Knopf, M. (2013). Habitat preferences and breeding success of Whinchats (*Saxicola rubetra*) in the Westerwald mountain range. *Journal of Ornithology*, 154, 339–349. https://doi.org/10.1007/s10336-012-0898-z.

Fischer, K., & Müller, K. (2018). Schlechter Erhaltungszustand wertgebender Vogelarten in EU-Vogelschutzgebieten des Westerwaldes: Dramatischer Rückgang von Braunkehlchen *Saxicola rubetra* und Wiesenpieper *Anthus pratensis*. *Vogelwelt*, *138,* 17–28.

Gossner, M.M., Lewinsohn, T.M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S.C., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., Diekötter, T., Jorge, L.R., Jung, K., Keyel, A.C., Klein, A.M., Klemmer, S., Krauss, J., Lange, M., Müller, J., Overmann, J., Pašali, E., Penone, C., Perovic, D.J., Purschke, O., Schall, P., Socher, S.A., Sonnemann, I., Tschapka, M., Tscharntke, T., Türke, M., Venter, P.C., Weiner, C.N., Werner, M., Wolters, V., Wurst, S., Westphal, C., Fischer, M., Weisser, W.W., & Allan, E. (2016). Land-use intensification causes multitrophic homogenization of grassland communities. *Nature*, 540, 266–269. https://doi.org/10.1038/nature20575.

Habel, J.C., Samways, M.J., & Schmitt, T. (2019). Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. *Biodiversity and Conservation*, 28, 1343–1360. https://doi.org/10.1007/s10531-019-01741-8.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & De Kroon, H.

(2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, 12, e0185809. https://doi.org/10.1371/journal.pone.0185809.

Hannappel, I., & Fischer, K. (2019). Grassland intensification strongly reduces butterfly diversity in the Westerwald mountain range, Germany. *Journal of Insect Conservation*, 24, 279–285. https://doi.org/10.1007/s10841-019-00195-1.

Helbing, F., Fartmann, T., Löffler, F., & Poniatowski, D. (2017). Effects of local climate, landscape structure and habitat quality on leafhopper assemblages of acidic grasslands. *Agriculture, Ecosystems & Environment*, 246, 94–101. https://doi.org/10.1016/j.agee.2017.05.024.

Helden, A. J., Chipps, J., McCormack, S., & Pereira, L. (2020). Is grazing always the answer to grassland management for arthropod biodiversity? Lessons from a gravel pit restoration project. *Journal of Insect Conservation*, 24, 655–670. https://doi.org/10.1007/s10841-020-00243-1.

Hilpold, A., Seeber, J., Fontana, V., Niedrist, G., Rief, A., Steinwandter, M., Tasser, E., & Tappeiner, U. (2018). Decline of rare and specialist species across multiple taxonomic groups after grassland intensification and abandonment. *Biodiversity and Conservation*, 27, 3729–3744. https://doi.org/10.1007/s10531-018-1623-x.

Humbert, J.Y., Delley, S., & Arlettaz, R. (2021). Grassland intensification dramatically impacts grasshoppers: Experimental evidence for direct and indirect effects of fertilisation and irrigation. *Agriculture, Ecosystems & Environment*, 314, 107412. https://doi.org/10.1016/j.agee.2021.107412.

Koch, K., 1989–1991. Die Käfer Mitteleuropas Ökologie, Bände 1–3, Goecke & Evers, Krefeld.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., & Stefanescu, C. (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution*, 24, 564–571. https://doi.org/10.1016/j.tree.2009.04.011.

Lyons, A., Ashton, P.A., Powell, I., & Oxbrough, A. (2018). Epigeal spider assemblage responses to vegetation structure under contrasting grazing management in upland calcareous grasslands. *Insect Conservation and Diversity*, 11, 383–395. https://doi.org/10.1111/icad.12287.

Manning, P., Gossner, M. M., Bossdorf, O., Allan, E., Zhang, Y. Y., Prati, D., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Hölzel, N., Jung, K., Klaus, V. H., Klein, A. M., Kleinebecker, T., Krauss, J., Lange, M., Müller, J., Pašalić, E., Socher, S. A., Tschapka, M., Türke, M., Weiner, C., Werner, M., Gockel, S., Hemp, A., Renner, S. C., Wells, K., Buscot, F., Kalko, E. K. V., Linsenmair, K. E., Weisser, W. W., & Fischer, M. (2015). Grassland management intensification weakens the associations among the diversities of multiple plant and animal taxa. *Ecology*, 96, 1492–1501. https://doi.org/10.1890/14-1307.1.

Wei, N., Kaczorowski, R. L., Arceo-Gómez, G., O'Neill, E. M., Hayes, R. A., & Ashman, T. L. (2021). Pollinators contribute to the maintenance of flowering plant diversity. *Nature*, 597, 688–692. https://doi.org/10.1038/s41586-021-03890-9.

Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., & Isaac, N.J.B. (2019). Widespread losses of pollinating insects in Britain. *Nature Communications*, 10, 1–6. https://doi.org/10.1038/s41467-019-08974-9.

Queiroz, C., Beilin, R., Folke, C., & Lindborg, R. (2014). Farmland abandonment: Threat or opportunity for biodiversity conservation? A global review. *Frontiers in Ecology and the Environment*, 12, 288–296. https://doi.org/10.1890/120348.

Raven, P. H., & Wagner, D. L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences*, 118. https://doi.org/10.1073/pnas.2002548117.

Toivonen, M., Herzon, I., & Kuussaari, M. (2015). Differing effects of fallow type and landscape structure on the occurrence of plants, pollinators and birds on environmental fallows in Finland. *Biological Conservation*, 181, 36–43. https://doi.org/10.1016/j.biocon.2014.10.034.

Samways, M. J., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch, A., Kaila, L., Kwak, M.L., Maes, D., Mammola, S., Noriega, J.A., Orfinger, A.B., Pedraza, F., Pryke, J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F., Vorster, C., & Cardoso, P. (2020). Solutions for humanity on how to conserve insects. *Biological Conservation*, 242, 108427. https://doi.org/10.1016/j.biocon.2020.108427.

Schmidt, M. H., Rocker, S., Hanafi, J., & Gigon, A. (2008). Rotational fallows as overwintering habitat for grassland arthropods: The case of spiders in fen meadows. *Biodiversity and Conservation*, 17, 3003–3012. https://doi.org/10.1007/s10531-008-9412-6.

Schneider, G., Krauss, J., Boetzl, F. A., Fritze, M. A., & Steffan-Dewenter, I. (2016). Spillover from adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural grasslands. *Oecologia*, 182, 1141–1150. https://doi.org/10.1007/s00442-016-3710-6.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., … & Weisser, W.

(2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, 574, 671–674. https://doi.org/10.1038/s41586-019-1684-3.

Simons, N. K., Gossner, M. M., Lewinsohn, T. M., Lange, M., Türke, M., & Weisser, W. W. (2015). Effects of land-use intensity on arthropod species abundance distributions in grasslands. *Journal of Animal Ecology*, 84, 143–154. https://doi.org/10.1111/1365-2656.12278.

Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., ... & Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences*, 116, 16442-16447. https://doi.org/10.1073/pnas.1906419116.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., & Chase, J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, 368, 417–420. https://doi.org/10.1126/science.aax9931.

van Klink, R., Menz, M.H.M., Baur, H., Dosch, O., Kühne, I., Lischer, L., Luka, H., Meyer, S., Szikora, T., Unternährer, D., Arlettaz, R., & Humbert, J.Y. (2019). Larval and phenological traits predict insect community response to mowing regime manipulations. *Ecological Applications*, 29, e01900. https://doi.org/10.1002/eap.1900.

Vogel, G. (2017). Where have all the insects gone? *Science*, 356, 576–579. https://doi.org/10.1126/science.356.6338.576.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. Proceedings of the *National Academy of Sciences*, 118, 1–10. https://doi.org/10.1073/PNAS.2023989118.

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual review of entomology*, 65, 457–480. https://doi.org/10.1146/annurev-ento-011019-025151.

Wersebeckmann, V., Kolb, S., Entling, M.H., & Leyer, I. (2021). Maintaining steep slope viticulture for spider diversity. *Global Ecology and Conservation*, 29, e01727. https://doi.org/10.1016/j.gecco.2021.e01727.

Westerwaldkreis (2018). *7. Umweltbericht des Westerwaldkreises*. Kreisverwaltung des Westerwaldkreises, Montabaur.

Wietzke, A., Albert, K., Bergmeier, E., Sutcliffe, L. M. E., van Waveren, C.-S., & Leuschner, C. (2020). Flower strips, conservation field margins and fallows promote the arable flora in intensively farmed landscapes: Results of a 4-year study. *Agriculture, Ecosystems and Environment*, 304, 107142. https://doi.org/10.1016/j.agee.2020.107142.

Woodcock, B. A., Pywell, R. F., Macgregor, N. A., Edwards, M. E., Redhead, J., Ridding, L. E., Batáry, P., Czerwiński, M., & Duffield, S. (2021). Historical, local and landscape factors determine the success of grassland restoration for arthropods. *Agriculture, Ecosystems & Environment*, 308, 107271. https://doi.org/10.1016/j.agee.2020.107271.