Biodiversity conservation and environmental management in European farmlands

Doctor of Science Dissertation

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Table of contents

1. Introduction

1.1. Nature conservation in farmland

Agricultural intensification is considered the most important driver of terrestrial biodiversity loss from local to global scale via its effects on habitat loss, habitat fragmentation and habitat conversion (Foley et al. 2011). Although in the Middle Ages even larger areas of Europe were under agriculture than today, farmland biodiversity was very high due to a traditionally extensive management. Current European nature conservation aims at halting the on-going loss of farmland biodiversity, which has evolved during millennia of extensive management (Gaston 2010). Since the early 20th century, the development of the Haber–Bosch process for the mass production of nitrogen fertilizers, and later on the birth of pesticides, allowed more effective agricultural practices (Smil 1999). The increasing use of agrochemicals was accompanied by increasing mechanisation and gained much ground after the Second World War. This meant not only field scale intensification, but also changes at higher spatial scales, such as landscape and regional scales (Tscharntke et al. 2005a). Changes at country-wide scales happened during the beginning of the cold war, when Europe was divided into East and West. In large parts of the East the collectivisation of farms resulted in large co-operatives, where field roads, hedgerows and field margins were eliminated to merge small fields into large-scale agricultural systems within a short time period (Báldi & Batáry 2011a). Of course, this did not affect all eastern countries and regions within countries equally due to various reasons, including political or geographical differences (e.g. mountain areas). The different historical trajectories of European countries and regions led to large heterogeneity between agricultural landscapes, affecting the associated biodiversity. The “rangeland” areas in Europe, where both mechanisation and agrochemical use failed or were not possible to implement, became increasingly abandoned, especially in more economically developed areas of Europe. Therefore, farmland conservation is often confined to these remaining, often protected semi-natural areas consisting mostly of grasslands and characterized by charismatic threatened species (for example those listed in the Habitat and Bird Directives of the EU).

Implementation of agri-environment schemes (AES) is another option for farmland conservation. AES include an array of tools set up to help farmers managing their land in an environmentally-friendly way. They are important for the conservation of high nature value farmland, for the preservation of genetic diversity, for the protection of a diversity of agro-ecosystems types and for producing food with a lower environmental and ecological footprint. Historically AES were initiated to reduce the overproduction of agriculture by supporting set-aside management in the EU during the late 1980s. Meanwhile, AES aim more at mitigating negative effects of agricultural intensification. Today, a great variety of AES exist in the 28 members of the EU, as well as Switzerland and Norway. They can be classified basically in two groups: 1.) horizontal (or broad-and-shallow) schemes in all member countries, which combine environmental protection (soil, water) with nature conservation targets, such as organic management; 2.) regional (or narrow-and-deep) schemes, which target areas with high nature value for biodiversity conservation (Kleijn & Sutherland 2003). Although the effectiveness of schemes has been questioned from a nature conservation point of view (Kleijn et al. 2001), the accumulated evidence based on a meta-analysis by Bengtsson et al. (2005) showed that AES have a generally positive effect on biodiversity. Meanwhile, it has been also recognized that landscape structure may moderate the effectiveness of AES. One idea is that the schemes are more effective in regions where source populations survive in nearby natural or semi-natural habitats (Duelli & Obrist 2003). In contrast to this assumption, Tscharntke et al. (2005a) hypothesized that AES may be most effective for increasing species richness in simple, but not in complex landscapes, because farms in complex landscapes are likely to already have high species diversity. Furthermore, Attwood et al. (2008) reviewed local management effects on arthropods and found arthropod richness to be significantly higher in areas of less intensive land use.

Landscape heterogeneity has been proposed as a key tool in conserving farmland biodiversity (Benton et al. 2003). This might be true for intensively managed agricultural landscapes, but increasing landscape heterogeneity can have also a negative effect on specialist species in more near-natural and less fragmented, low-intensity agricultural landscapes (Batáry et al. 2011a). Until recently, however, most studies focusing on how management intensity affects biodiversity considered the landscape compositional heterogeneity, such as land-use type diversity (often referred to as landscape complexity), amount of remaining semi-natural area or percentage of crop area. Thus there is a need to better integrate the role of landscape heterogeneity in studies on AES (Holzschuh et al. 2010; Concepción et al. 2012). Further, studies on semi-natural fragments embedded in the agricultural matrix often focused on the effects of size and isolation of fragments as parameters of landscape configuration, but rarely investigated these effects together with the effects of landscape composition (but see Marini et al. 2010).

In agroecological studies, especially those focusing on the effects of habitat management, such as AES, the results are often explained by spillover effects, i.e. the spread of plant propagules and animal individuals from nearby natural or semi-natural areas into the more intensively used agricultural areas. Invertebrates are known to immigrate into arable fields from adjacent natural habitats (Landis et al. 2000), but evidence of the opposite process is still rare (but see Rand et al. 2006). However, as the high productivity of arable fields during the growing season locally enhances arthropod densities, a massive and large-scale spillover of organisms from crop to non-crop areas can be expected (Tscharntke et al. 2005b). The potential impact of this spillover on adjacent natural and semi-natural habitats has largely been neglected, and is a little understood topic. Spillover of insect predators and other functionally important organisms from agricultural to natural habitats and back may be underestimated (Blitzer et al. 2012).

Not all species respond in the same way to agricultural intensification (Fuller et al. 2005; Kleijn et al. 2006). As a recent study showed, there might be not only winners of extensification by AES, but also losers (Birkhofer et al. 2014). Such patterns might even change when we consider different spatial scales, since mobility of different species can be highly different (Dauber et al. 2005; Marini et al. 2012). Hence, AES effects depend on species traits, such as habitat or food specialisation, etc. Both local and landscape scale intensification select for traits, thereby shaping community composition and ecological functioning including ecosystem services, such as biocontrol or pollination (e.g. Batáry et al. 2013). This complexity needs to be considered when evaluating the role of environmental changes, such as habitat degradation, habitat fragmentation or landscape simplification.

This thesis is based on a collection of papers dealing with biodiversity conservation in European farmlands, often connected with measures of AES. These papers address gaps in the literature as outlined above and cover different habitat types, including extensively managed vast semi-natural grasslands in Hungary (“puszta”), intensively or extensively managed cereal fields and meadows, as well as semi-natural agricultural remnants, such as calcareous grassland fragments and hedgerows in Germany. The main management question behind this research is how biodiversity and associated ecosystem services can be maintained or improved with AES tools.

1.2. Structure of the thesis

The second chapter (*Role of agri-environment schemes in nature conservation*) contains one extensive synthesis paper about the European AESs, which gives a frame to the whole thesis. This chapter describes the history and heterogeneity of AESs and their economic performance. It contains two stand-alone meta-analyses about effectiveness of schemes over time, respectively, of schemes in productive versus non-productive areas. Additionally it emphasizes the importance of human factor, such as training of farmers. Finally, it shows future research directions.

The third chapter (*Managing species rich grasslands*) contains three case studies. The first paper comes from an EU project, where extensively and intensively grazed semi-natural pastures in Hungary were compared from a biodiversity point of view. It deals with the patterns of species richness and territory numbers of breeding grassland and non-grassland birds. The second paper focuses on leafhopper communities of calcareous grassland fragments in Germany by studying the effects of fragment size, their connectivity and matrix composition. The third paper deals with butterfly and bird diversity in orchard meadows and calcareous grasslands in contrasting landscape context (agricultural or forest-dominated) differing in management (regularly managed or abandoned management). There are several further closely related own papers not detailed in the thesis, e.g.: Batáry et al. 2007. Diversity and Distributions; Batáry et al. 2007. Basic and Applied Ecology; Batáry et al. 2008. Biological Conservation; Báldi et al. 2013. Agriculture, Ecosystems and Environment; Kormann et al. 2015. Diversity and Distributions; Sutcliffe et al. 2015. Biodiversity and Conservation; Rösch et al. 2015. Oecologia; Madeira et al. 2016. Agriculture, Ecosystems and Environment.

The fourth chapter (*Impact of hedgerow-forest connectivity on biodiversity and ecosystem function*) contains two papers focusing on birds, arthropods and pollination in hedgerows. The first paper compares biodiversity patters of farmland vs. woodland birds in hedges isolated from forest, hedges connected to forest and forest edges. The second paper examines the impact of oilseed rape on the pollination of wild plants and bee abundance during and after oilseed-rape bloom, including effects on crop–noncrop spillover at landscape and adjacent field scales. There are four further closely related own papers not detailed in the thesis: Ludwig et al. 2012. Acta Oecologica; Fischer et al. 2013. Journal of Insect Conservation; Haenke et al. 2014. Journal of Applied Ecology; Schlinkert et al. 2016. Wildlife Biology.

The fifth chapter (*Comparing effectiveness of agri-environment management in cropland and grassland*) contains two papers focusing on effects of agri-environment management on biodiversity in cropland and grassland. In the first paper the relative effect of management and landscape structure of arthropod communities of alkali lowland plains in Hungary is compared, using the results of two studies with similar sampling effort and study design. The second paper uses a double nested design with paired organic and conventional meadows and organic and conventional wheat fields, and investigates the effects of management, landscape composition and edge effect on plants and arthropods. There is one further closely related own paper not detailed in the thesis: Batáry et al. 2010. Biological Conservation.

The sixth chapter (*Landscape moderation and regional differences of biodiversity patterns*) contains three papers on large-scale features, such as region and landscape structure, influencing the biodiversity patterns in farmland. The first paper synthesizes the landscape moderation effects on agri-environmental management using a modern quantitative meta-analysis. The second paper deals with differences in farmland biodiversity and nature conservation in Eastern and Western Europe. The third paper addresses the ecological and economic effectiveness of organic management in two contrasting German regions, i.e. in the small-scale agriculture of Western Germany and the large-scale agriculture of Eastern Germany along the former Iron Curtain. There are couple of further closely related own multiscale papers not detailed in the thesis, e.g.: Kleijn et al. 2009. Proceedings of the Royal Society B; Batáry et al. 2010. Agriculture, Ecosystems and Environment; Tscharntke et al. 2012. Biological Reviews; Marja et al. 2014. Biological Conservation; Liu et al. 2014. Landscape Ecology; Gonthier et al. 2014. Proceedings of the Royal Society B; Clough et al. 2014. Ecology Letters; Emmerson et al. 2016. Advances in Ecological Research; Lichtenberg et al. 2017. Global Change Biology; Bosem Baillod et al. 2015. Journal of Applied Ecology; Rossetti et al. 2017. Ecology Letters; Happe et al. 2018. Agriculture, Ecosystems and Environment; Fischer et al. 2018. Journal of Applied Ecology; Hass et al. 2018. Proceedings of the Royal Society B.

The seventh chapter summarises the findings of the previous chapters and outlines new research avenues.

The thesis consists of three synthesis papers and eight primary research papers listed chronologically bellow:

Batáry, P., Báldi, A. & Erdős, S. 2007. Grassland versus non-grassland bird abundance and diversity in managed grasslands: local, landscape and regional scale effects. *Biodiversity and Conservation* 16: 871–881. [IF_{2007}: 1,421]

Batáry, P., Kovács, A. & Báldi, A. 2008. Management effects on carabid beetles and spiders in Central Hungarian grasslands and cereal fields. *Community Ecology* 9: 247–254. [IF$_{2008}$: 0,898]

Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. 2011. Landscape-moderated biodiversity effects of agri-environmental management – a meta-analysis. *Proceedings of the Royal Society B-Biological Sciences* 278: 1894–1902. [IF$_{2011}$: 5,415; Web of Science highly cited (top 1%)]

Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. & Tscharntke, T. 2012. Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agriculture, Ecosystems and Environment* 146: 130–136. [IF$_{2012}$: 2,859]

Batáry, P., Kovács-Hostyánszki, A., Fischer, C., Tscharntke, T. & Holzschuh, A. 2012. Contrasting effect of isolation of hedges from forests on farmland vs. woodland birds. *Community Ecology* 13: 155–161. [IF$_{2012}$: 1,623]

Kovács-Hostyánszki, A., Haenke, S., **Batáry, P.**, Jauker, B., Báldi, A., Tscharntke, T. & Holzschuh, A. 2013. Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecological Applications* 23: 1938–1946. [IF$_{2013}$: 4,126]

Rösch, V., Tscharntke, T., Scherber, C. & **Batáry, P.** 2013. Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology* 50: 387–394. [IF$_{2013}$: 4,754]

Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. 2015. The role of agri-environment schemes in conservation and environmental management. *Conservation Biology* 29: 1006–1016. [IF$_{2015}$: 4,267; Web of Science highly cited (top 1%)]

Sutcliffe, L.M.E., **Batáry, P.**, Kormann, U., Báldi, A., Dicks, L.V., Herzon, I., Kleijn, D., Tryjanowski, P., Apostolova, I., Arlettaz, R., Aunins, A., Aviron, S., Baležentiene, L., Fischer, C., Halada, L., Hartel, T., Helm, A., Hristov, I., Jelaska, S.D., Kaligaric, M., Kamp, J., Klimek, S., Koorberg, P., Kostiuková, J., Kovács-Hostyánszki, A., Kuemmerle, T., Leuschner, C., Lindborg, R., Loos, J., Maccherini, S., Marja, R., Máthé, O., Paulini, I., Proença, V., Rey-Benayas, J., Sans, F.X., Seifert, C., Stalenga, J., Timaeus, J., Török, P., van Swaay, C., Viik, E. & Tscharntke, T. 2015. Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity and Distributions* 21: 722–730. [IF$_{2015}$: 4,566]

Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C.F., Mußhoff, O., Császár, P., Fusaro, S., Gayer, C., Happe, A.-K., Kurucz, K., Molnár, D., Rösch, V., Wietzke, A. & Tscharntke, T. 2017. The former iron curtain still drives biodiversity-profit trade-offs in German agriculture. *Nature Ecology & Evolution* 1: 1279–1284.

Ernst, L.M., Tscharntke, T. & **Batáry, P.** 2017. Grassland management in agricultural vs. forested landscapes drives butterfly and bird diversity. *Biological Conservation* 216: 51–59. [IF$_{2016}$: 4,022]

Technical note: the thesis is based on the above eleven selected papers. Most of them contain supplementary materials, which are often very extensive. In order to keep the thesis relatively concise, the supplementary materials are not presented in the thesis, but are cited. In case of interest, all supplementary materials, including also those not cited in the thesis, but only presented in the original papers, are available electronically on this website: https://sites.google.com/site/pbatary/dsc

2. Role of agri-environment schemes in nature conservation

For this synthesis study we reviewed the history, current use and effectiveness of AES as a conservation tool in Europe. We considered the conceptual framework that has been developed to interpret the ecological findings and the implications of research on the human factors that influence farmer uptake or acceptance of the schemes. We conducted two new meta-analyses to determine whether AES are becoming more effective over time and whether changing management in productive or non-productive areas benefits biodiversity. We also identified outstanding policy-relevant research questions that cannot currently be answered using formal meta-analysis, due to data deficiency. Finally, we considered what can be learned about the use and cost-effectiveness of AES from the European experience.

2.1. History of agri-environment schemes in Europe

Although some north-western European countries had agri-environment programs predating any European regulations, most European AES can be traced back to the Agricultural Structures Regulation of 1985 (European Union EU Regulation 797/85). They were conceived as a mechanism to compensate farmers for loss of income associated with appropriate, less intensive management of environmentally sensitive areas in response to the changes described above and largely driven by a few countries of the north and west (Hodge et al. 2015). In 1987 an amendment (EU Regulation 1760/87) allowed up to 50% of the cost of environmentally sensitive areas to flow from the Common Agricultural Policy, and in 1992 AES became compulsory for all EU Member States (EU Regulation 2078/92). They are one aspect of the Rural Development pillar of the Common Agricultural Policy. Each Member State designs its own schemes. Currently, a diversity of AES exists in the 28 Member States of the EU and in Switzerland and Norway, which are not Member States (Fig. 2.1a). We confined our synthesis to 30 countries rather than the entire continent.

Because they provide income for conservation, AES have become the main tool to conserve biodiversity on European farmland and are often used to fund management in protected areas or designated sites. Within the EU, AES have always been, and remain, voluntary for land managers, although in the latest reform of the Common Agricultural Policy in 2014 certain management practices designed as AES became obligatory for farmers to quality for their basic subsidy (Pe’er et al. 2014).

Agri-environment schemes are important for conserving farmland areas designated by EU countries, Switzerland, and Norway as of “high nature value” (Lomba et al. 2014) in that they preserve genetic diversity of livestock, protect a diversity of agro-ecosystems types, and produce food with a lower environmental and ecological footprint. Many schemes have clear objectives to reduce water pollution, enhance access to the countryside and protect cultural landscapes and heritage, as well as protecting biodiversity. Almost all countries have AES that support organic farmers, based on an underlying assumption that organic farming is good for the environment (Tuck et al. 2014).

The role of AES schemes has shifted over time. Their initial purpose was to protect threatened habitats or landscapes. Over time, the emphasis changed to prevention of species’ loss, especially farmland birds, across agricultural land. More recently, emphasis is shifting to the application of AES to improve and maintain ecosystem services, such as pollination and biocontrol (Ekroos et al. 2014).

Schemes can be classified as horizontal or zonal (i.e., targeted) (Kleijn & Sutherland 2003). Horizontal schemes usually combine environmental protection with nature conservation objectives and can be applied throughout a country. They are designed to fit easily into farm management systems; they are not too demanding or directly support management farmers are doing anyway, such as organic management. Zonal schemes target areas with high nature value. They generally require bespoke management for target species or ecosystems, and farmers are often obliged to seek expert advice in developing management plans.

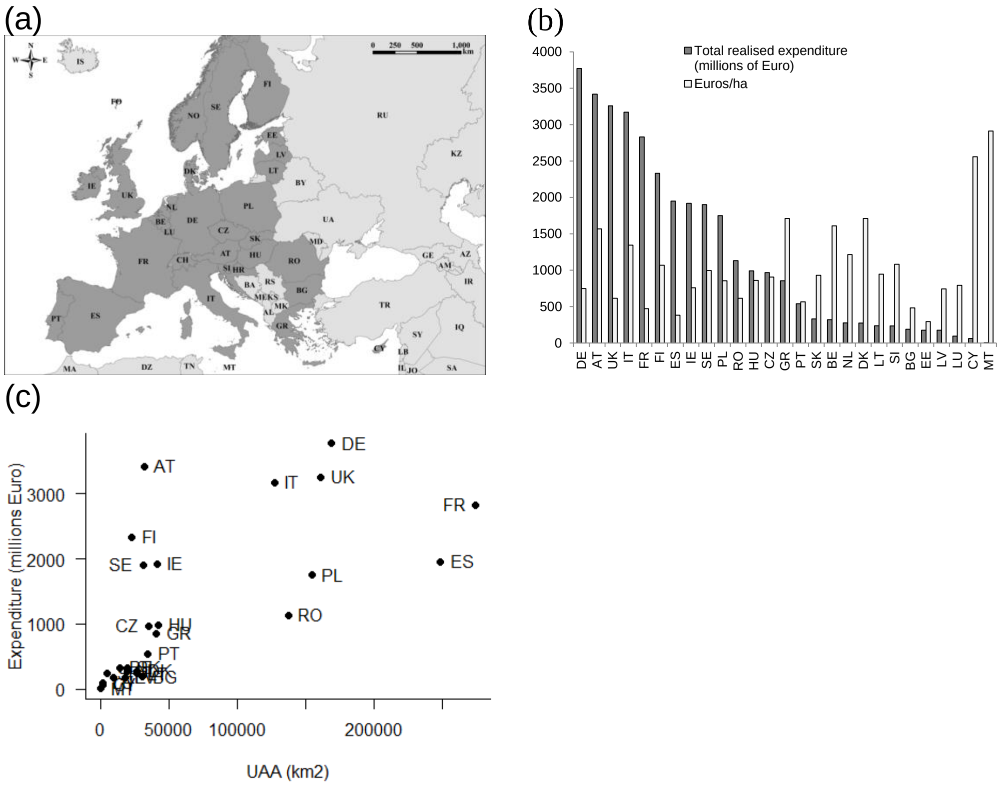


Fig. 2.1. (a) Countries in Europe where agri-environment schemes (AES) exists (dark gray). (b) Total realized expenditure spent on AES in 2007-2013 (dark gray) and total realized expenditure spent on AES in 2007-2013 per area under AES (light gray) (no data available for Croatia, Norway, and Switzerland). (c) Utilized agricultural area (UAA) relative to total realized expenditure on AES in 2007-2013. Data for (b) and (c) derived from European Network for Rural Development (2014).

2.2. Big spending for agri-environment schemes

Budgets for AES are substantial and for most countries usually equal or exceed the amounts of money spent on wildlife conservation through other routes. For example, in 2005 the Dutch budget for conservation in protected areas was 48.8 million €, while that for AES with biodiversity objectives was 42.1 million € (MNP 2007). In England, total expenditure on AES, including measures with non-biodiversity objectives, was 375 million €/year from 2007 to 2013 (European Network for Rural Development 2014). The total annual expenditure of the government’s nature conservation agency for England was much lower, around 250 million € in 2013-2014 (Natural England 2014). In new EU member states this difference can be larger. For example, in 2008 the Hungarian budget for nature conservation was roughly 41.0 million € (Hungarian Government 2009), while total expenditure on AES was 117.6 million € (Hungarian Ministry of Agriculture and Rural Development 2009). The European Commission spent 3.23 billion € on AES in 2012, a figure two orders of magnitude higher than the cost of managing Natura 2000 sites (Maiorano et al. 2015) that year, which was 39.6 million € (Pe’er et al. 2014).

The total amount of public expenditure on AES in each EU Member State for 2007-2013, including co-financing at national levels, is strongly correlated with the amount of agricultural land in each country (Fig. 2.1c) (Spearman rank rho = 0.83, $p < 0.001$), although some countries are relative outliers. Spain and France spend less than would be expected from their agricultural area, while Austria spends more. The proportion of agricultural land under the schemes varies greatly across countries, from 6 % in Denmark to 95 % in Finland. This means the intensity of spending also differs among countries, as illustrated by the amount of money spent per hectare of AES area (Fig. 2.1b); there is a tendency for more focused spending in smaller countries.

Future spending on AES is very likely to be lower in all countries, following reforms of the European Common Agricultural Policy enacted at the end of 2013 (Pe’er et al. 2014). The budget for Rural Development Programmes, of which AES are part, will be 18 % less by 2020. Moreover Member States have been given the choice to shift funds out of Rural Development to directly support farmers. In the coming years, differences among countries in AES spending will therefore increase.

2.3. Ecological effectiveness of European agri-environment schemes

Given the huge expenditure on European AES, it is important to ask whether they improve biodiversity outcomes. The first well-designed studies examining the ecological effects of AES were published in the early 2000s. Kleijn and Sutherland (2003) reviewed published peer-reviewed and grey literature on the effectiveness of AES with biodiversity targets and concluded that about half of the schemes lack positive effects on biodiversity. Successful schemes focus mainly on specific (rare) species and are often supervised by scientists or volunteers. Non-targeted schemes to enhance biodiversity usually benefit common species or have no overall impact.

Since that review there has been a wealth of published papers on the subject and a number of important Europe-wide reviews (Bengtsson et al. 2005; Batáry et al. 2011b; Scheper et al. 2013; Tuck et al. 2014). These demonstrate that AES generally enhance biodiversity locally, usually with modest increases in species richness or abundance of common species. Studies have been mainly of intensively farmed areas; little work has been done on effectiveness of schemes in areas with more extensive agriculture (Kampmann et al. 2012).

Based on these studies a theoretical framework has been developed. The effectiveness of AES at attracting wild species is influenced by landscape structure, land-use intensity, and the ecological contrast created by AES (Kleijn et al. 2011). The hypotheses on the relationship between effectiveness and landscape structure and between effectiveness and ecological contrast have both been confirmed (Batáry et al. 2011b; Scheper et al. 2013; Hammers et al. 2015). In their meta-analysis, Batáry et al. (2011b) found that in cropland areas AES are effective in simplified but not in complex landscapes. This was further confirmed in a meta-analysis on pollinators (Scheper et al. 2013) and by Tuck et al. (2014), who showed that the positive effects of organic farming on biodiversity increased as the amount of cropland increased. However, the suggested relationship between effectiveness and land-use intensity has not been confirmed, possibly because most research has been done in countries dominated by intensive farming, such as the United Kingdom and Germany (Dicks et al. 2013a), and has not specifically incorporated an intensification gradient. There is almost no evidence yet on whether this attraction of wild species to AES land represents a stabilization and increase of plant and animal populations or a local concentration of these populations with concurrent dilution in other nearby areas (but see Morandin & Kremen 2013).

We addressed two specific issues by merging the data sets of three recent meta-analyses on the effects of AES on species richness (Batáry et al. 2011b; Scheper et al. 2013; Tuck et al. 2014). We imposed the following restrictions: only studies from the 28 European Member States, Norway, and Switzerland were included; studies were excluded if the number of replicates was fewer than three experimental or control areas; studies performed at plot level (i.e., within-field experiments) were excluded. This resulted in a data set with 284 observations from 103 studies (the entire data set is in Supporting Information of the original paper).

We used the unbiased standardized mean difference (Hedges' g) as a common effect size in our analyses, originating from the above meta-analyses. Effect size was positive if species richness was higher in the AES than in the control fields. For the error estimate, we used the non-parametric variance estimates of each effect size, which is based on few assumptions and may be less constrained by the assumptions of large sample theory (Hedges & Olkin 1985). We carried out statistical analyses in the metafor package (Viechtbauer 2010) of R. Funnel plots, regressions test for funnel plot asymmetry, and calculated fail-safe numbers all showed no sign of publication bias, either in the entire data set or in the two meta-analyses presented. However, our meta-analyses shared with the three previous meta-analyses a strong geographic bias of study areas towards Northern and Western Europe. This issue was previously highlighted by Tryjanowski et al. (2011) and recently by Sutcliffe et al. (2015). They concluded that new eastern EU Member States had adopted Western European type AES designed for intensively farmed landscapes. In the extensively farmed areas in the new member states such AES seem to be ineffective or even have negative effects on biodiversity. Therefore, there is a great need for better locally adapted AES.

2.3.1. Effectiveness of schemes over time

The regular reforms of the European Common Agricultural Policy (CAP) allow countries to use novel scientific insights and modify their agri-environmental programs to increase their efficiency. As a result national agri-environmental programs change substantially every 7 years. Dicks et al. (2013b) questioned whether scientific evidence was used to improve policy efficiency during the most recent CAP reform. After 25 years of AES in Europe and almost 15 years of high-quality research on their effectiveness, it is possible to ask whether the effectiveness of the schemes has improved as policy experience and scientific evidence accrued over time.

If evidence was being taken into account, findings from studies in the early 2000s, which mostly covered AES implemented in the 2000-2006 budget period or before, would be reflected in the designs of schemes in the 2007-2013 budget periods. This may be expected to result in increased effectiveness in the second budget period. To test this, we used a mixed-effects meta-regression model in which budget period was the moderator variable.

We found that schemes implemented after 2007 were not more effective than schemes implemented before 2007 (Fig. 2.2a, summary statistics is available in Supporting Information of the original paper). Although AES were effective in both periods, there was no sign of improvement in effectiveness over time.

Of course, we cannot conclude directly from this that science is not being used to improve design of the schemes. There are other possible explanations for the lack of improvement over time. We know that biodiversity is still degrading and agricultural landscapes are still changing in Europe, and both of these could potentially decrease the effectiveness of AES as a result of the reduced pool of species available to colonize and benefit from the scheme. Alternatively, there might be a time-delay effect, meaning that the positive effect of research on AES will appear farther in the future (Weis 2001).

It is unfortunate that there is no evidence yet of AES becoming more effective over time, as such a change might have compensated to some extent for forthcoming reductions in AES budgets (Pe'er et al. 2014). Policy makers might argue that elements of AES, such as field margins left out of production, become obligatory across Europe as "compulsory greening measures" under the direct payments pillar of the Common Agricultural Policy from 2014-2020 and that this would compensate for loss of AES coverage. However, recent analyses of the compulsory greening measures show that effective elements of AES have generally not been incorporated (Dicks et al. 2013b; Pe'er et al. 2014). Rather than being obligatory, the greening measures that are similar to AES (known as ecological focus areas) apply to just over half the farmed area of Europe, due to the exemption of farms of <15 ha of arable land (Pe'er et al. 2014).

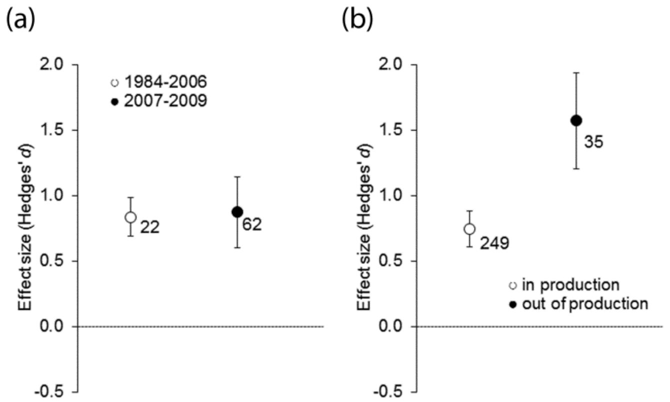


Fig. 2.2. Changes in effectiveness of agri-environment schemes over time as shown in studies published from 1984 to 2006 compared with studies published from 2007 to 2009 and (b) differences in species diversity between control areas and areas in production (such as fields under organic management) and areas out of production (such as field margins and hedgerows). Shown are mean effect sizes and 95 % CI. The mean effect size is significantly different from zero, if the CIs do not overlap with zero. Numbers near symbols indicate sample size.

2.3.2. Effectiveness of schemes in productive versus non-productive areas

Agri-environment schemes can be classified according to whether they apply to non-productive areas, such as field boundaries and wildflower strips (sometimes called off-field practices, Garibaldi et al. 2014), or productive areas, such as arable crops or grasslands (sometimes called on-field practices). Schemes targeting non-productive areas include hedgerows, sown or naturally regenerated field margins, or simply taking areas of land out of production for different conservation purposes. We call these out-of-production schemes. In contrast, in-production schemes support environmentally sensitive approaches to the management of land that is used to grow crops or feed livestock. For example, the use of agrochemicals might be reduced or prohibited or certain management actions, such as mowing grassland, might be restricted. The most widespread in-production scheme is organic farming.

In our second meta-analysis, we used a mixed-effects meta-regression model with management type as a moderator variable. We found that out-of-production schemes were much more effective at enhancing species richness than in-production schemes (Fig. 2.2b, summary statistics is available in Supporting Information of the original paper). A possible explanation may be that most of the out-of-production schemes we examined evaluated measures that take agricultural land out of production, such as the establishment of wild-flower strips. The conversion of crop monocultures to semi-natural habitat results in a much larger increase in resource availability (i.e., creates a larger ecological contrast) for a wider range of species than measures such as organic farming, reducing stocking rates, or restricting fertilizer application rates that are typical for in-production schemes. Schemes promoting the establishment of wildflower strips may also be better targeted to the conservation of a given species group than in-production schemes because they often specifically address a resource that is limiting population growth or size (e.g., floral resources for flower visiting insects). Many in-production schemes do not address specific species groups; rather, they aim to enhance biodiversity in general as one of several targets, alongside improvements in other ecosystem characteristics or services.

Targeting the needs and spatial distribution of specific species groups is most likely more important than whether schemes prescribe measures on or off land that is being used for farming. Targeted schemes tend to be more effective than untargeted schemes (Kleijn & Sutherland 2003; Wilson et al. 2009), and better spatial targeting of in-production schemes can greatly benefit rare and declining species (Pywell et al. 2012). In many countries, there is a move toward better targeting of AES, either toward particular declining species groups or landscapes where they are likely to be effective,. As this is being incorporated into AES and implemented between now and 2020, one might expect a review similar to this one in 2025 to be able to show an increase in effectiveness of AES over time.

It is important to appreciate that species richness is just one measure of diversity, although this is the one most easily understood and used by policy makers. We think that the importance of this measure is overrated and other variables characterizing biodiversity should be applied in primary studies and analyzed (if sufficient studies are available) in meta-analyses (e.g., the meta-analysis on functional diversity by Flynn et al. 2009). An additional fundamental point is that in-production and out-of-production options typically support different communities. In-production options select for species adapted to the highly disturbed, cropped areas of fields, for example, in contrast to out-of-production options (see the example of arable weeds in Storkey et al. 2012).

2.4. The human factor

In addition to research on the ecological effectiveness of AES, there is a body of work on how to ensure that AES are palatable to farmers and therefore effective at changing farmer behavior. This is important because AES are always voluntary (but see recent CAP reform Pe’er et al. 2014). Uptake of specific AES options is a key element of their success and does not always correlate with ecological effectiveness. For example, Hodge and Reader (2010) found that the vast majority of options taken up in the first 5 years of entry level stewardship (a horizontal scheme) in England were the straightforward field corner and grass margin options that require little change of management or resource investment. Evaluation of synthesized evidence shows that these are not the most effective AES options for enhancing biodiversity (Dicks et al. 2013b).

Studies on motivations of farmers to take up AES or environmental management have repeatedly demonstrated that farmer attitudes are important in explaining uptake of environmental measures (e.g., Defrancesco et al. 2008; Sattler & Nagel 2010). As well as the effect of general attitude, scheme adoption is linked to utilitarian motivations, such as payment rate and ease of fit within existing farm practice (e.g., Defrancesco et al. 2008; Sutherland et al. 2010). Many authors have pointed out that AES intended to support biodiversity should be designed with farmer circumstances and attitudes in mind (e.g., Herzon and Mikk 2007; de Snoo et al. 2013), indicating a need for ecologists and social scientists to work together. Herzon and Mikk (2007) found that views of biodiversity among Finnish and Estonian farmers were largely restricted to the realm of wild nature outside the farmed environment. This implies a need to demonstrate to farmers when they can directly benefit from measures to promote functional ecological groups of biodiversity, such as pollinators, natural enemies, or soil biodiversity.

2.5. Future research

2.5.1. Effectiveness of schemes for enhancing ecosystem services

The value of ecosystem services to agriculture has been much discussed recently (e.g., Power 2010; Kremen & Miles 2012). For some services, such as food production, pest regulation, pollination, and soil nutrient cycling, farmers themselves are direct beneficiaries because their yields and input requirements are directly affected. Other services, such as air and water quality or enjoyment of cultural landscapes, are public goods (i.e., the main beneficiaries are outside the farm business). The role AES can and should play in maintaining ecosystem services is still under discussion. There is a clear mandate for CAP to support delivery of public goods from agriculture (European Commission 2010) but not to support actions that directly increase farm income.

The effectiveness of specific AES options at delivering ecosystem service benefits has only just started to be tested. For example, a small number of studies outside Europe have demonstrated benefits to crop pollination from wildflower strips or patches (Garibaldi et al. 2014), and there is some evidence that vegetated buffer strips can enhance water quality (Zhang et al. 2010). The combined effects of specific AES options on multiple ecosystem services are still poorly understood.

2.5.2. Effectiveness of schemes in agriculturally marginal areas

In Europe agriculturally marginal areas, where the productivity of land is limited by biophysical or socio-economic constraints, are currently home to the highest concentrations of biodiversity and host the largest populations of threatened species (Tryjanowski et al. 2011). Many of them typically occur in new central and eastern Member States (Sutcliffe et al. 2015). These areas are under pressure from agricultural intensification and abandonment. Counteracting farmland abandonment in marginal areas is an important objective of AES in many countries, yet surprisingly few studies have examined the effects of AES on marginal farmland. What limited evidence there is suggests that AES can be very effective on low-intensity farmland. Schemes effectively support threatened birds in low-input cereal steppes in Central Spain (Kleijn et al. 2006), bird richness in environmentally sensitive areas in Hungary (Kovács-Hostyánszki & Báldi 2012), and species-rich plant communities in the Swiss Alps (Kampmann et al. 2012). An illustrative study is done by Weis (2001), in the German Eiffel mountain range, where many low-productive species-rich grasslands had been abandoned or afforested since the late 1960s, but then AES were introduced in 1986 that paid farmers to reintroduce sheep grazing on abandoned grasslands. Weis (2001) compared trends in plant species richness in plots where grazing had recommenced and plots where sheep were kept out. In 1999 species richness in grazed plots had increased by 20 %, while species richness in ungrazed plots had decreased by 17 %. The population size of a range of threatened orchid species increased by 50-500 % in grazed plots. However, it took 8-10 years before the first positive effects became apparent, which may explain why this has been an unpopular research topic. Previous AES were designed solely to maintain biodiversity (e.g. by reintroducing extensive management) and not to restore it completely (Kleijn et al. 2009), so it was cheaper to execute these schemes in marginal areas than in intensive areas. More studies are needed, however, before general conclusions can be drawn about the effectiveness of AES in agriculturally marginal areas.

2.5.3. Cost-effectiveness of agri-environment schemes

As a conservation strategy, AES focus on reducing the impact of agricultural activities on species that inhabit the agricultural landscape. They are not the only possible route to protect such species. Another major conservation tool is protected areas, which can also be applied in agricultural landscapes. In some countries, there are protected sites managed as working farms for farmland wildlife (e.g. Moyse 2013). Little is known about the relative efficiency of these different strategies to protect farmland biodiversity.

A notable exception is the case of meadow bird conservation in the Netherlands. In 2008 21 million € was spent on AES targeting meadow bird conservation on large areas of farmland. In the same year, meadow bird conservation in the spatially much more restricted protected areas cost 4 million € (van Paassen & Teunissen 2010). Settlement densities are much higher in protected areas than on farmland with meadow bird schemes, resulting, at the national level, in slightly more meadow birds breeding in protected areas than on farmland with meadow bird schemes (PBL 2009). Furthermore, on average, meadow birds show positive trends in protected areas but negative trends on farmland with meadow bird schemes (van Egmond & de Koeijer 2006). This suggests that, for this particular species group, protected areas are much more efficient than AES. However, it might be that most protected areas in the Netherlands are too small to maintain viable meadow bird populations in the long run, especially when they are bordered by inhospitable high-intensity grasslands or built-up areas that are generally avoided by these ground-nesting birds. So the apparent higher cost-effectiveness might be an illusion, hiding an extinction debt.

The comparison in cost-effectiveness between AES and protected areas is important because both are funded with public budgets and both impact the potential for food production. Investing in one strategy does not necessarily mean there is less money available for the other strategy because the source of funds for AES has a very different underlying purpose – to support farm incomes and generate public goods from agriculture. Even so, cost-effective conservation is of interest to policy makers.

2.5.4. Importance of training and advice to the effectiveness of agri-environment schemes

There has been little research on the link between farmer training or advice and the effectiveness of AES. Farmers are trained in agricultural production and have seldom experienced specific training or education in environmental management. Yet managing land for environmental outcomes requires a different set of skills and knowledge. Zonal AES schemes usually incorporate an element of training or advice. In the UK, zonal schemes are much more beneficial to bird diversity per unit cost than simplified horizontal schemes, despite the fact that a much larger proportion of the funding goes into setting up and checking the implementation rather than directly to farmers (Armsworth et al. 2012).

Horizontal AES often do not incorporate farmer training or advice (but see Marja et al. 2014), and this could be a reason for their relatively low effectiveness. One research project in the UK demonstrated that training farmers increases their confidence and develops a more professional attitude to agri-environmental management (Lobley et al. 2013). The same project also demonstrated ecological benefits; there were more flower or seed resources and higher numbers of bees or birds on AES areas managed by trained farmers relative to untrained farmers (summarized in Dicks et al. 2013a). It has been repeatedly demonstrated that farmer field schools, common in low and middle income countries, enhance uptake of beneficial integrated pest management practices, although the schools do not seem to spread practices through the farming community beyond the attendees (Waddington et al. 2014). Results-oriented AES is another approach with potential to generate long term positive behavioural change by providing incentive for farmers to improve their skills (Burton & Schwarz 2013).

3. Managing species rich grasslands

Species rich grasslands are threatened by both intensification and abandonment since they are economically not effective enough compared to improved grasslands. Thus they heavily rely on support provided by AESs or other related nature conservation schemes. This chapter focuses on insects and birds in different grassland habitats with large extent, namely the Hungarian "puszta" grasslands, respectively strongly fragmented ones, but likewise species rich, namely German calcareous grasslands and orchard meadows. The overarching idea connecting them is the importance of landscape scale effects, which can be in turn as important as local management action and amplify or neutralize that.

3.1. Grassland versus non-grassland bird diversity in "puszta" grasslands

In this study, our aims were to test the influence of a local factor (grazing intensity), landscape and regional effects on two ecological groups of bird species (grassland and non-grassland birds) and on the most frequent species (Skylark *Alauda arvensis*, Yellow wagtail *Motacilla flava*, and Corn bunting *Miliaria calandra*) of the Hungarian Great Plain. We selected extensively and intensively grazed pastures in three regions of Hungarian Great Plain (those can be categorised as solonchak alkali steppes, solonetz alkali steppes and wet meadows). In the year of the study, in 2003 were the first supports by National AES given to farmers. None of our extensively grazed fields were supported, however, all of them met the requirements of the National AES (Ángyán et al. 1999). The three regions differ in landscape structure (from simple through intermediate to complex).

3.1.1. Material and methods

Twenty-one pairs of bird census sites were selected on grasslands with high and low grazing pressure in three distinct biogeographic regions of the Hungarian Great Plain. The three regions differ in their landscape structure, although grasslands are the most extensive land-use type (over 60%) in all regions. One of our study areas is situated in the Heves Landscape Protection Area in Eastern Hungary. This region ('Simple' region) has the most simple landscape structure with the largest, least fragmented grassland patches and is dominated by mosaic-complex of dry and wet alkali grasslands and marshes on solonetz soil. An other region is situated parallel to the river Danube, in the Kiskunság National Park (KNP), has an intermediate landscape structure, and contains secondary Pannonic alkali steppe vegetation on solonchak soils ('Intermediate' region). The third region (also in the KNP) is more heterogeneous, has several marshy patches and woodlots in the grasslands, so it has the most complex landscape structure ('Complex' region). For detailed area description see Báldi et al. (2005).

We established seven pairs of 12.5 ha plots, usually square in shape, in the extensively and intensively grazed grasslands in all regions (altogether 21 pairs of fields). The extensive field and intensive field in a pair had the same soil type and groundwater level and were situated in similarly structured landscapes, therefore the effects of confounding environmental variables were diminished. Cattle density was about 0.5 cows/ha on extensive and >1 cow/ha on intensive fields. None of the fields were fertilised, cut or re-seeded. The extensive field and intensive field in a pair had the same soil type and groundwater level and were situated in similarly structured landscapes, therefore the effects of confounding environmental variables were diminished. Some of the study fields were not exactly 12.5 ha. In these cases we cut down the hang out piece on a randomly chose side of the larger field, because of the paired study design. This made possible to compare equally sized parts of a pair.

Breeding birds were surveyed using the territory mapping approach (Bibby et al. 1992). Altogether we made four censuses, two in April and two in May of 2003. Censuses were carried out under good weather conditions (no wind and rain), from sunrise to 9-10 a.m. The extensive and intensive fields of each pair were censused in the same morning by the same observer. The order in which sites were sampled was changed in the consecutive censuses. All observations registered by sight or sound were plotted on maps of the fields. Birds just flying through and not foraging in flight were excluded from the analysis. Territories were then drawn around complementary observations made during the four visits. Nest sites were allocated to the site where the observation most indicative of a territory was made (e.g. singing or displaying male, actual nests). To draw a territory in the case of breeding birds, we took two observations within about 10-20 m, with exception of late migrants (e.g. Grasshopper Warbler *Locustella naevia*, where observations occurred only in May. In the case of territories located along the borders of study plots, we counted them, if we got at least one contact within the plot. Species whose territories are larger than the target plots (e.g. great bustard *Otis tarda*, raptors) or that use the plots for feeding and clearly nested outside them (e.g. some small passerines such as tree sparrow *Passer montanus*, white stork *Ciconia ciconia* and corvids) were also mapped. Two occurrences of them meant one territory independently the number of individuals and of their places on the map.

Table 3.1.1. List of grassland and non-grassland species.

Grassland species	**Non-grassland species**
Black-tailed godwit *Limosa limosa*	Barn swallow *Hirundo rustica*
Corn bunting *Miliaria calandra*	Bee-eater *Merops apiaster*
Curlew *Numenius arquata*	Common black-headed gull *Larus ridibundus*
Grasshopper warbler *Locustella naevia*	Common buzzard *Buteo buteo*
Great bustard *Otis tarda*	Cuckoo *Cuculus canorus*
Lapwing *Vanellus vanellus*	Great white egret *Casmerodius albus*
Montagu's harrier *Circus pygargus*	Greylag goose *Anser anser*
Partridge *Perdix perdix*	Hooded crow *Corvus corone cornix*
Pheasant *Phasianus colchicus*	Hoopoe *Upupa epops*
Quail *Coturnix coturnix*	Kestrel *Falco tinnunculus*
Redshank *Tringa totanus*	Lesser grey shrike *Lanius minor*
Skylark *Alauda arvensis*	Magpie *Pica pica*
Stone curlew *Burhinus oedicnemus*	Mallard *Anas plathyrhynchos*
Stonechat *Saxicola torquata*	Marsh harrier *Circus aeruginosus*
Tawny pipit *Anthus campestris*	Nightingale *Luscinia megarhynchos*
Whinchat *Saxicola rubetra*	Red-backed shrike *Lanius collurio*
Yellow wagtail *Motacilla flava*	Red-footed falcon *Falco vespertinus*
	Roller *Coracias garrulus*
	Rook *Corvus frugilegus*
	Sand Martin *Riparia riparia*
	Savi's warbler *Locustella luscinioides*
	Sedge warbler *Acrocephalus schoenobaenus*
	Starling *Sturnus vulgaris*
	Tree sparrow *Passer montanus*
	White stork *Ciconia ciconia*
	Wood pigeon *Columba palumbus*

We divided the species for habitat specialist and generalist, because specialist species usually react in a different way to factors than generalist species (e.g. Siriwardena et al. 1998; Magura et al. 2000; Imbeau et al. 2003; Virkkala et al. 2004). We considered those species as habitat specialists (i.e. grassland birds), which breed on the ground of grasslands, whereas the remaining was considered as habitat generalist (non-grassland birds) (Table 3.1.1). Our previous analysis on the effect of grazing intensity on birds showed that species richness might increase due to increasing grazing pressure – a rather unexpected result (Báldi et al. 2005). However, this result was based solely on the local scale (grazing effect), and we explained it with the changing landscape structure of study fields. This paper in contrast to the earlier one is based on territories of grassland and non-grassland bird species and not on occurrences of all bird species, uses a pair-wise statistical design and a multi-scale approach, thus more comprehensive.

We used aerial photographs (Institute of Geodesy, Cartography and Remote Sensing; Air project 2000; 0.5 m/pixel resolution) from the study fields to digitise land-use types. First we searched the middle point of the 12.5 ha field and around this centre we used a buffer of 500 m radius. We digitised the following land-use types: 1) grasslands; 2) arable fields; 3) forests; 4) built-up areas; 5) marshes, reeds and bogs and 6) ditches, streams and lakes. Area percentages, mean areas and patch densities were measured for land-use types within the buffer. Further we also measured the total length of boundaries within buffers. All fields were situated only on grasslands and did not contain boundaries inside at all.

We analysed the local effect (extensive or intensive grazing regime), the effect of landscape and region and the interaction between management and landscape on the species number and on the abundance of grassland and non-grassland bird species in linear mixed models with the Restricted Maximum Likelihood method. To control for confounding effects of region on landscape influences (regions were selected based on their landscape structure, but differed also in soil type and vegetation structure), we built models with and without landscape factors. As landscape variable the total length of all boundaries was used, which reflects well the landscape complexity of the three regions (mean of total length of all boundaries within 500 m buffer areas in 'Simple' region: 4.74 km; in 'Intermediate' region: 6.25 km; in 'Complex' region: 8.53 km). The cause, why this variable was used is that the amount of boundaries or edges is one of the most important factors determining the nest success of ground nesting birds (Batáry & Báldi 2004). This landscape variable correlates with most other important landscape metrics – e.g. positively with total patch density (r_{42} = 0.895, p = 0.001), negatively with area and percent of grassland (r_{42} = –0.810, p = 0.001 and r_{42} = –0.475, p = 0.001) and positively with habitat diversity (r_{42} = 0.454, p = 0.003). Models contained only management, landscape, region and interaction between management and landscape as fixed factors and pair as random factor. Further we used the same models for the most abundant species, namely for Skylark, Yellow wagtail and Corn bunting as well. In the case of two latter species, data of one region was not included in the models, because both species occurred nearly only in two regions (for Yellow wagtail the 'Intermediate' region, for Corn bunting the 'Simple' region was not included into the models).

Table 3.1.2. Linear mixed models on the effects of management (intensive vs. extensive grazing [M]), of landscape (total length of boundaries in surrounding landscape [L]) and of region [R] on bird communities and species of Hungarian grasslands. Model 1 contains management and region, whereas in model 2 landscape and management × landscape interaction were included.

	Model 1				**Model 2**							
	M		**R**		**M**		**L**		**R**		**M x L**	
	F	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Species richness												
Grassland species	6.936	**0.016**	4.338	**0.029**	0.419	0.524	0.135	0.716	2.548	0.103	0.088	0.770
Non-grassland species	1.337	0.261	0.481	0.626	0.098	0.758	2.120	0.154	1.281	0.299	0.006	0.940
Territories												
Grassland species	40.030	**0.001**	1.492	0.251	7.613	**0.012**	4.671	**0.038**	0.492	0.619	0.215	0.647
Non-grassland species	1.333	0.262	0.119	0.888	0.001	0.984	1.427	0.240	0.557	0.581	0.189	0.667
Skylark	9.033	**0.007**	11.354	**0.001**	9.734	**0.005**	5.088	**0.030**	8.154	**0.003**	4.534	**0.045**
Yellow wagtail	11.039	**0.003**	1.616	0.510	0.913	0.350	2.402	0.132	2.306	0.157	0.346	0.562
Corn bunting	1.174	0.294	0.325	0.616	7.499	**0.014**	1.937	0.178	0.044	0.840	10.470	**0.005**

3.1.2. Results

Overall 748 bird territories belonging to 43 species were recorded at the 42 study sites. Intensively and extensively grazed fields had nearly the same species richness (13 grassland and 22 non-grassland species on intensively grazed grasslands, while 14 grassland and 22 non-grassland species on extensively grazed grasslands).

Investigating management (extensive vs. intensive grazing) and regional effects on species richness, we showed both effects on grassland birds, but no effect on non-grassland birds (Table 3.1.2). The species richness of grassland birds was significantly higher on extensively grazed fields, and the 'Intermediate' region proved to be the most species rich. When we included landscape (total length of boundaries) in the models, no effect was found either on grassland or non-grassland birds (Table 3.1.2).

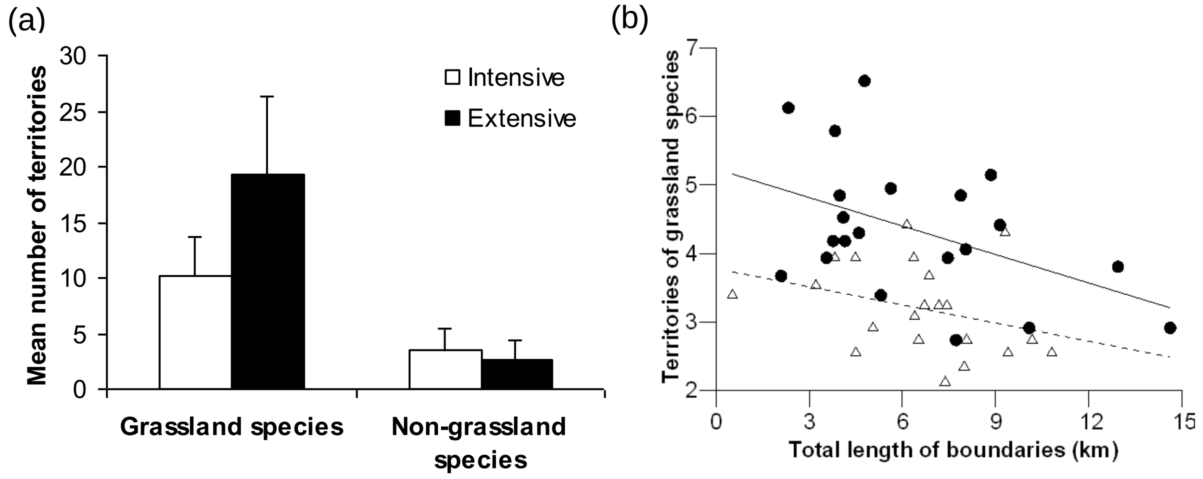


Fig. 3.1.1. (a) Mean territory number of grassland and non-grassland bird species of intensively and extensively grazed grasslands of Hungarian Great Plain (n = 42 fields); bars show 1 SE. (b) Correlation between the total length of boundaries (km) and mean territories of grassland bird species on differently managed grasslands. Dashed line indicates correlation for intensive fields, while continuous line indicates correlation for extensive fields.

Abundance of grassland species was higher on extensive than on intensive fields (Table 3.1.2; Fig. 3.1.1a), in contrast to the abundance of non-grassland species. In the case of grassland birds, management effect was shown in both models (with and without including landscape). Further, investigating the significant landscape effect, the abundance of grassland species was negatively related to total length of boundaries (Table 3.1.2; Fig. 3.1.1b; intensive fields: $r_{21} = -0.328$, $p = 0.146$; extensive fields: $r_{21} = -0.462$, $p = 0.035$). No effect of region and no interaction effect were found on the abundance of grassland and non-grassland bird species.

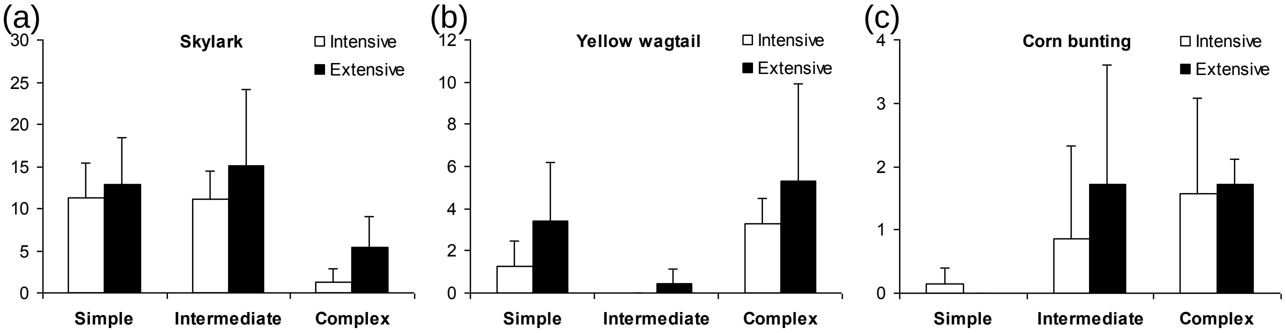


Fig. 3.1.2. Mean individual number of the most abundant grassland bird species on Hungarian grasslands. Landscape complexity increases from the 'Simple' region to 'Complex' region. Filled bars indicate extensive grazing, open bars indicate intensive grazing. (a) Skylark, (b) Yellow wagtail, (c) Corn bunting.

At the species level, the effect of management was significant for the commonest species, the Skylark (in both models), which was more abundant on the extensive fields in all regions (Table 3.1.2; Fig. 3.1.2a). Additionally, Skylark abundance was also negatively related to total length of boundaries and occurred more frequently in the 'Simple' and 'Intermediate' region than in the 'Complex' region (Table 3.1.2; Figs 3.1.2a and 3.1.3; intensive fields: $r_{21} = -0.456$, $p = 0.038$; extensive fields: $r_{21} = -0.713$, $p = 0.001$). The effect of management and landscape on Skylark abundance was also manifested by a significant interaction between management and landscape – Skylark abundance was more sensitive to boundary length on extensively grazed fields than intensive fields (Fig. 3.1.3). In the case of two other frequent species management effects were found, the abundance of these species tended to be higher on the extensive fields than on the intensive ones (Table 3.1.2; Fig. 3.1.2b,c). Further, no landscape effects were shown for the Yellow wagtail and the Corn bunting, but in the case of Corn bunting a significant management × landscape effect was found (Table 3.1.2).

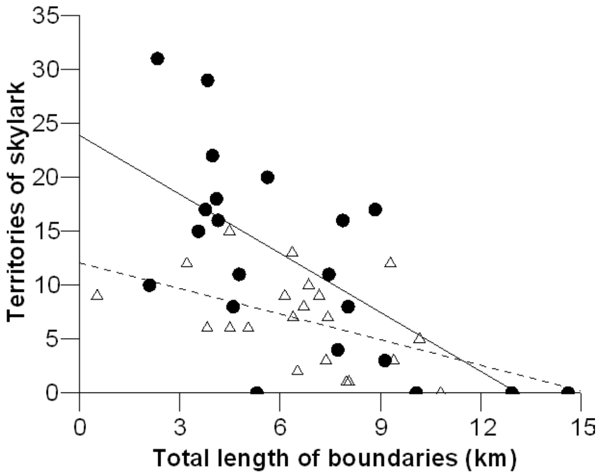


Fig. 3.1.3. Correlation between the total length of boundaries and territories of Skylark on differently managed grasslands. Dashed line indicates correlation for intensive fields, while continuous line indicates correlation for extensive fields.

3.1.3. Discussion

The relative importance of local farming management (intensive versus extensive grazing), landscape context and region was analysed on grassland and non-grassland bird diversity. In the case of community analysis region had no confounding effects on landscape influences. In recent decades great attention have been paid to the population declines of farmland birds attributed to intensive agricultural management (Vickery et al. 2001). Grazing generally has negative effect on bird species richness or abundance (Dobkin et al. 1998; Fuller & Gough 1999; Verhulst et al. 2004; Maron & Lill 2005). In the present study we showed effect of management on species richness and abundance of true grassland birds with higher species richness and abundance on the extensive sites, while on non-grassland species no effect was found. This could be explained probably by that true grassland birds are more specialised on grassland habitats than non-grassland birds, which only feed and not nest there. Grazing can impact on bird populations through changes in vegetation structure, food resources and predation pressure (Vickery et al. 2001). Alteration of the vegetation structure will affect the suitability of the sward for nesting and feeding (Milsom et al. 1998). Intensive grazing may increase nest losses due to predation and trampling (Ammon & Stacey 1997; Wilson et al. 1999; Pavel 2004).

Tscharntke et al. (2005a) concluded in their recent review that agri-environment schemes need to broaden their perspective and to take the different responses to schemes in simple (high impact) and complex (low impact) agricultural landscapes into account. Furthermore, Benton et al. (2003) reviewed that several studies have shown heterogeneity to be associated with diversity. In the present study we found landscape effect on grassland bird abundance, however with increasing heterogeneity (increasing total length of boundaries) the abundance of grassland birds declined. The conclusion of Benton et al. (2003) is probably valid only in highly managed regions. Here we have to emphasise that our study sites contained more than 60% grasslands in all regions and generally are less intensively managed (non-fertilised and pesticide free) than in Western Europe. This, and other studies warn that the understanding of biodiversity in agricultural landscapes need a more comprehensive approach (Kleijn & Báldi 2005; Tscharntke et al. 2005a). In contrast to our results, the model of Virkkala et al. (2004) explained a moderate proportion of the variation in the total density of farmland birds in the landscape. Söderström et al. (2001) emphasised the importance of landscape composition for mobile organisms such as birds and found that species richness of grassland birds decreased with increasing proportion of urban elements and arable fields in a 1000 m landscape area centred on each pasture. In a similar multi-scale study, like ours, examining the farmland management on assemblages of grassland wintering birds in Portugal, Moreira et al. (2005) found that species richness was primarily influenced by landscape context, whereas field management mostly determined abundance. Finally, we could separate regional and landscape effects with building models with and without a landscape metric. The results showed that the regional effect on species richness was not due to landscape complexity differences between regions, but probably differences in e.g. soil type and/or vegetation structure and composition.

At species level our analyses were limited to the most abundant birds (Skylark, Yellow wagtail and Corn bunting), which are important contributors of the Hungarian grassland bird assemblages. All three species underwent smaller or larger declines during the recent decades mostly in West Europe, but the key eastern populations remained stable (Siriwardena et al. 1998; Brickle et al. 2000; Burfield & van Bommel, 2004; Newton 2004; Gregory et al. 2005). In our study significant management effect was shown for all species, while landscape effect was only found in the case of Skylark. For Skylark regional effect was not separable from landscape effect, which at species level is not surprisingly, because species react individually for landscape, management, vegetation, etc. (Bradbury et al. 2004). Our results confirm that Skylarks avoid smaller fields (Donald et al. 2001; Perkins et al. 2000; Moreira et al. 2005). This is consistent with the theory that abundant generalist species should be less affected by fragmentation than (habitat) specialist species (Braschler & Baur, 2005). The significant interaction between management and landscape reflect that the increased Skylark density was confined to extensively grazed fields, of which surrounding landscapes contained less boundaries.

3.1.4. Conclusions

The ongoing changes in the agriculture threaten the rich eastern European ecosystems. However, the agri-environmental schemes open up new views to protect the biodiversity there. But as other researchers, we also have to emphasise that conservation of biodiversity and ecosystem services in agricultural systems requires a landscape perspective (Bengtsson et al. 2003; Tscharntke et al. 2005a). Finally, we conclude that both local management and landscape structure has significant effects on grassland bird abundance, but not on non-grassland abundance when analysed together, and that such effects depend on the ecology of each bird species.

3.2. Effects of grassland fragmentation on insect communities

Calcareous grasslands are among the most species rich habitats in Europe, but are increasingly threatened due to abandonment and fragmentation. Little is known about how the surrounding landscape influences fragmentation effects. Here we focus on the interaction of habitat fragmentation and landscape composition on leafhoppers, a highly diverse group of insects, including many species that are likely to be vulnerable to changes in their environment.

3.2.1. Material and methods

The study area was located in the vicinity of the city of Göttingen in southern Lower Saxony in central Germany (51.5°N, 9.9°E). The landscape is characterised by intensively managed agricultural areas with a dominance of cereal and rape fields and fertile meadows, interspersed with forests on hilltops and patchily distributed fragments of semi-natural habitats like calcareous grasslands, belonging to the plant association *Mesobrometum erecti* Koch 1926 (Ellenberg & Leuschner 2010). These grasslands are frequently located on steep slopes and are managed by mowing or grazing with sheep, goats, cattle or horses. Many smaller fragments have been abandoned, leaving them to succession (pers. obs.).

By analysing digital maps (ATKIS-DLM 25/1 Landesvermessung und Geobasisinformationen Niedersachsen 1991-1996, Hannover, Germany) with the geographical information system ArcGIS 10.0 (ESRI Geoinformatik GmbH, Hannover, Germany) and subsequent extensive field surveys in the study area, we selected 14 small (0.1-0.6 ha) and 14 large (1.2-8.8 ha) fragments of calcareous grassland (an overview of the study area is available in Supporting Information of the original paper) along two orthogonal gradients: a landscape composition gradient, i.e. an increasing percentage of arable land within a radius of 500 m around the fragments (27-77 %, mean = 47 %), and a habitat connectivity gradient, measured by a connectivity index described by Hanski, Alho & Moilanen (2000): $CI_i = \sum \exp(-\alpha d_{ij}) A^{\beta}_j$, where A_j is the area of the neighbouring fragment j (in m^2) and d_{ij} is the edge to edge distance (in m) from the focal fragment i to the neighbouring fragment j. α is a species specific parameter describing a species' dispersal ability and β is a parameter that describes the scaling of immigration. Since we applied the connectivity index to an entire community, both scaling parameters α and β were set to 0.5. The values of the connectivity index varied between 20 and 849 (mean = 244), with large values indicating high levels of connectivity. All calcareous grassland fragments within a radius of 2000 m around each study site were taken into account, to assure that for every fragment the connectivity index was greater than zero. In addition we measured the edge to edge distance to the nearest neighbouring fragment for each study fragment, which ranged from 30 to 1900 m. In order to be classified as separate, there had to be a distance of at least 30 m from the focal fragment to the nearest one. If the nearest fragment was smaller than 0.1 ha, the next nearest fragment larger than that was used. Both connectivity measures were strongly correlated (Spearman correlation, rho= 0.78, S = 6501.6, $p < 0.001$).

It was difficult to select fragments of similar quality, because management differed from fragment to fragment. Some were grazed, whereas on others, management had been abandoned. If fragments were mown, this could happen at different times throughout the season, although never before the first sampling, i.e. the beginning of June. Fragments that were managed for the conservation of rare plants (orchids in particular) were not cut before August to ensure that the seeds could fully ripen. In order to assure that the fragments exhibited the characteristics of calcareous grasslands, we only included fragments that harboured more than ten of the plant species that are characteristic for calcareous grasslands in the study area (Krauss et al. 2004). We did not try to avoid differences in habitat quality and management, since we intended to mirror the actual condition of calcareous grasslands in the study area.

Leafhoppers were sampled by sweep netting (Heavy Duty Sweep Net, 7215HS, BioQuip, diameter: 38 cm) on six randomly distributed transects with homogeneous vegetation per fragment (20 sweeps each, i.e. 120 sweeps in total) in dry weather on three occasions in 2010 (at the beginning of June, at the end of July and at the beginning of September). Transects were approximately 10 m long, and were at least 3 m away from each other within a fragment.

The specimens caught were transferred into alcohol (70 % vol.) and identified to species level in the laboratory using Biedermann and Niedringhaus (2004) and Kunz, Nickel & Niedringhaus (2011). Specimens of species with woody host plants were excluded, except when saplings of a potential host tree were present on the transects. Otherwise it was assumed that they had been dislodged from their host tree by wind. If the species' larvae used herbs or grasses as host plants and only the imagines fed on trees, specimens were included in the analysis.

The identification to species level of female specimens of several genera is not possible (e.g. *Ribautodelphax*, *Anaceratagallia*, *Psammotettix*) (Biedermann & Niedringhaus 2004; Kunz, Nickel & Niedringhaus 2011). Thus, if male specimens were present, female specimens were assumed to belong to the same species. If not, they were only identified to genus level. If males of more than one species of a genus were present, the number of females was assumed to mirror that of males.

All leafhopper species were classified into habitat specialists and generalists according to (i) their specific habitat requirements typical for calcareous grassland (i.e. warm and dry habitat conditions, short, grazed swards, open soil) and (ii) diet preferences (i.e. utilising plants that exclusively occur on calcareous grasslands) based on Nickel & Remane (2002) and Nickel (2003). A species was classified as a habitat specialist when conditions (i) and/or (ii) were fulfilled; it was classified as a generalist when neither (i) nor (ii) were fulfilled.

Table 3.2.1. Mean ± SEM leafhopper and plant species richness on small (n=14) vs. large (n=14) sites.

	Small	Large
Leafhopper SpR	22·9 ± 1·2	22·4 ± 1·6
specialists	8·6 ± 0·8	9·5 ± 0·9
generalists	14·2 ± 1·2	12·9 ± 1·0
Leafhopper abundance	246·7 ± 22·5	258·5 ± 29·3
specialists	138·6 ± 18·1	160·8 ± 23·5
generalists	108·1 ± 19·4	97·7 ± 20·7
Plant SpR	47·6 ± 3·3	55·1 ± 1·7
specialists	23·8 ± 2·1	28·8 ± 1·1
generalists	23·8 ± 2·0	26·3 ± 2·0

In addition, they were subdivided according to their ability to fly, i.e. the length of their wings, with Biedermann & Niedringhaus (2004). If a species was wing dimorphic, i.e. it could be both long and short winged, the predominant wing type was used for categorisation.

At the beginning of June the vegetation (only vascular plants) of each transect was recorded in botanical plots (one 1 × 5 m plot per transect) according to Wilmanns (1993).Plant species identification and nomenclature follow Seybold (2009). The plant species were subdivided into habitat specialists and generalists according to Krauss et al. (2004).

Both leafhopper and plant species richness of the six transects per fragment were summed up. The leafhoppers were also summed over the three sampling occasions. Statistical analyses were conducted with R, version R 2.15.1.

For analysis of overall leafhopper species richness and species richness of specialist and generalist leafhoppers, we used generalized linear models using Poisson errors with the following explanatory variables: (i) the percentage of arable land in a 500-m buffer around each fragment, (ii) fragment size (in ha, taken as a factor, either ‘large’ or ‘small’), (iii) habitat connectivity, measured by a connectivity index described by Hanski, Alho & Moilanen (2000) (log10-transformed to achieve a better fit of the models) and (iv) plant species richness per site. The explanatory variables were essentially uncorrelated (Supplementary Material of the original paper).

In the full models, two-way interactions between all the explanatory variables were included. For all three models, we performed an automated stepwise model selection by AIC (function ‘step-AIC’ in the package ‘MASS’ (Venables & Ripley 2002)). In all analyses, there was no indication of overdispersion.

3.2.2. Results

In the 28 fragments of calcareous grassland we found 77 leafhopper species (species list is available in Supporting Information of the original paper), from 65 genera with 7073 adult specimens (with 3454 specimens caught on the small sites and 3619 specimens caught on the large sites), representing 13 % of the German leafhopper fauna (Biedermann & Niedringhaus 2004; Kunz, Nickel & Niedringhaus 2011). Species richness ranged from 14 to 31 species per fragment (Table 3.2.1). Separation into habitat specialists and generalists resulted in 29 specialist and 48 generalist species. The four most abundant specialist leafhopper species were *Turrutus socialis* (18.3 % of total abundance), *Doratura stylata* (8.5 %), *Adarrus multinotatus* (7.5 %), and *Neophilaenus albipennis* (3.5 %). The four most abundant generalist species were *Arocephalus longiceps* (5.7 %), *Philaenus spumarius* (5.1 %), *Mocydia crocea* (4.1 %) and *Verdanus abdominalis* (3.2 %). In the botanical surveys we recorded 168 plant species from 123 genera, comprising 65 specialist and 103 generalist species (including 22 tree and shrub species as saplings), with a minimum of 25 and a maximum of 65 species per site (Table 3.2.1).

Table 3.2.2. Generalized linear models on the effects of landscape context (% arable land), fragment type (large or small), connectivity (log10(CI+1), a connectivity index described by Hanski, Alho & Moilanen 2000, log10-transformed) and plant species richness on (1) overall leafhopper species richness, (2) generalist leafhopper species richness and (3) specialist leafhopper species richness. Only variables included in the final models are shown.

	SpR				Generalists				Specialists			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	11·01	3·56	3·10	0·002	14·59	4·71	3·10	0·002	2·21	0·06	35·14	<0·001
% arable land (Ar)	−0·08	0·03	−2·39	0·017	−0·11	0·04	−2·40	0·016	–	–	–	–
Fragment type (Type)	−1·07	0·76	−1·40	0·161	−2·47	0·98	−2·54	0·011	–	–	–	–
log10(CI+1) (Conn)	−3·55	1·48	−2·39	0·017	−5·49	1·97	−2·79	0·005	–	–	–	–
Plant SpR	−0·07	0·05	−1·52	0·128	−0·12	0·06	−1·94	0·052	–	–	–	–
Ar × Conn	0·04	0·01	2·49	0·013	0·05	0·02	2·52	0·012	–	–	–	–
Type × Conn	0·48	0·32	1·50	0·133	1·14	0·41	2·76	0·006	–	–	–	–
Conn × plant SpR	0·03	0·02	1·60	0·110	0·05	0·03	2·10	0·036	–	–	–	–

In the analysis of overall leafhopper species richness we found an interaction between habitat connectivity and landscape composition (Table 3.2.2). An increase in habitat isolation caused a reduction in leafhopper species richness in simple (high percentage of arable land), but not in complex landscapes (low percentage of arable land) (Fig. 3.2.1a).

Subsequent analysis of generalist and specialist leafhopper species richness separately revealed that this interaction was driven by the generalist leafhoppers (Fig. 3.2.1b). The latter showed the same pattern as the overall species richness. The generalist leafhoppers showed an additional interaction: species richness on small fragments increased with increasing habitat connectivity, whereas it remained stable on large fragments (Fig. 3.2.1c). Specialist leafhopper species richness was not affected by landscape composition or connectivity but increased with fragment size and specialist plant species richness.

Generalist species richness per site was highly correlated with the number of long winged (macropterous) species (Pearson correlation, r = 0.83, t = 7.58, df = 26, p < 0.001), while the same was true for specialist species richness per site and short winged (brachypterous) species (Pearson correlation, r = 0.61, t = 3.93, df = 26, p < 0.001).

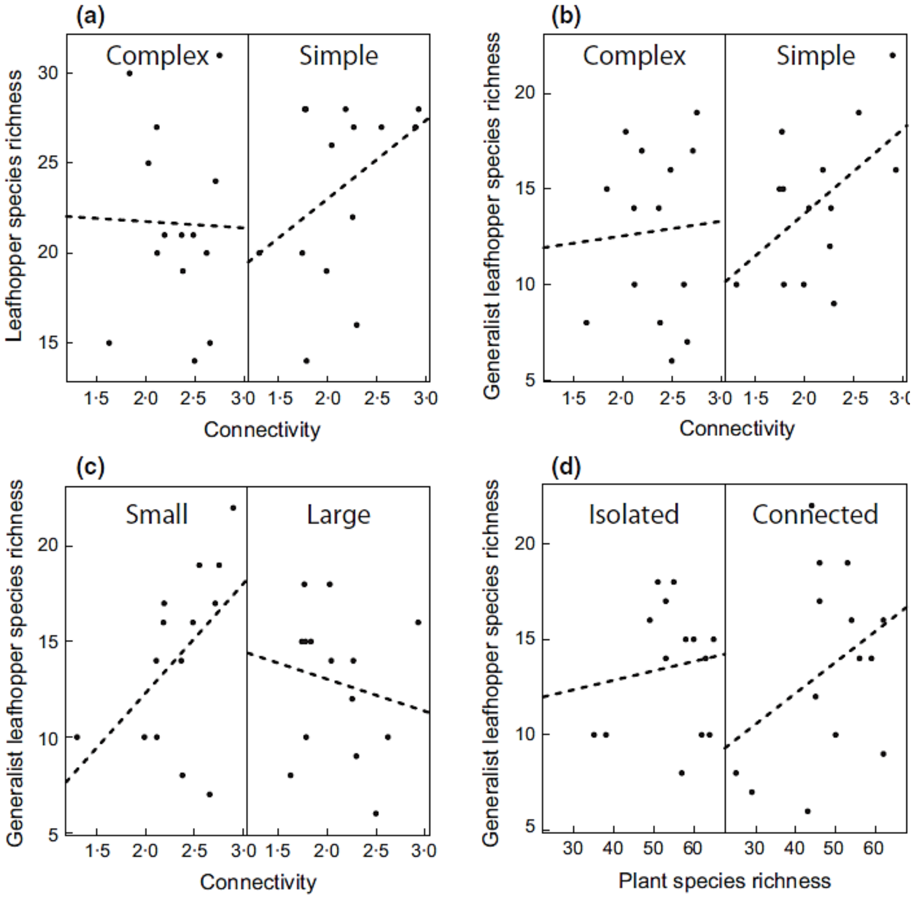


Fig. 3.2.1. Interaction plots showing the relationship between leafhopper species richness/generalist leafhopper species richness (y-axis) and the landscape parameters (x-axis). Effect of habitat isolation (measured by connectivity index (Hanski, Alho & Moilanen 2000, log10-transformed) on (a) leafhopper species richness and (b) generalist species richness in conjunction with landscape composition (Complex: 27–46% arable land, Simple: 47–77% arable land). (c) Effect of habitat isolation on generalist leafhopper species richness in conjunction with fragment type (Small: 0·1–0·6 ha, Large: 1·2–8·6 ha). (d) Effect of plant species richness on generalist leafhopper species richness in conjunction with habitat isolation (Isolated: values of the connectivity index from 19–155, Connected: values from 180–849). The dashed lines show mean squares fits (for illustration). The graphs were made with the lattice package (Sarkar 2008) in R.

3.2.3. Discussion

In this study we found that generalist but not specialist leafhoppers are interactively affected by connectivity, landscape composition (complex or simple) and fragment size (large or small). Generalist leafhopper species richness increased with decreasing isolation in simple but not in complex landscapes and on small but not on large fragments. Specialist leafhopper species richness only depended on specialist plant species richness and fragment size.

According to our results we assume that the specialists persist on the fragments of calcareous grassland without much exchange between them, especially since many species have limited dispersal abilities due to their short wings. Therefore they are not affected by decreasing connectivity. In accordance with this result, Schuch, Wesche & Schäfer (2012) found no decrease in leafhopper species richness (but a marked decrease in abundance) in protected dry grasslands in Eastern Germany over the last 50 years.

Generalist leafhoppers can be assumed to move more between fragments, especially since they are more likely to be long-winged than specialists. However, the dispersal abilities of macropterous leafhoppers seem to be species dependent. In a mark and recapture experiment, Biedermann (1997) found that the froghopper *Neophilaenus albipennis*, even though able to fly, rarely moved more than 20 m from the original point of capture. Other leafhopper species are able to fly and bridge greater distances, or get passively dispersed by air currents (Waloff 1973, Nickel 2003).

Despite being referred to as generalists here, a large proportion of the species recorded in this study require low-productivity habitats, i.e. they cannot cope with the conditions that prevail in today’s intensified agricultural landscapes. Only few species are able to breed in arable fields or intensified meadows and pastures, colonising them anew every year (Nickel 2003). This leads to the assumption that calcareous grasslands are an important refuge for many leafhopper species, regardless of their degree of specialisation. So where fragments of calcareous grassland are few and scattered, even these generalist species are likely to find it difficult to locate and subsequently colonise the next suitable fragment, explaining the decrease in generalist species richness with decreasing connectivity.

Increasing isolation caused a decrease in both overall and generalist leafhopper species richness in simple (high percentage of arable land) but not in complex landscapes. In simple landscapes, leafhoppers may find it difficult to reach the next suitable site, being unable to find suitable alternative resources or habitats with a similar vegetation type or structure during dispersal. Similar to our results, Baum et al. (2004) found that dispersal of the planthopper *Prokelisia crocea* depended on the surrounding matrix habitat (pure stands of *Bromus inermis* vs. mudflat). These contrasting matrices may be comparable to arable fields vs. more natural habitats. This implies that the permeability of simple landscapes dominated by arable land may be reduced compared to more complex landscapes (Eycott et al. 2012). The reduced permeability of the matrix may become more problematic with increasing distance between suitable habitat fragments, and may explain the reduction in leafhopper species richness with decreasing connectivity in simple landscapes.

We found that generalist species richness increased with decreasing isolation in small but not in large fragments. In small fragments, a higher extinction rate due to stochastic effects in combination with a lower probability of recolonisation with increasing isolation may cause the decline in generalist species richness (Hanski, Alho & Moilanen 2000). Recolonisation of larger fragments is more probable (for a beetle species see Matter 1996), and fewer extinctions occur. Cronin (2003) found that that immigration of the planthopper P. crocea into host plant patches decreased with decreasing patch size. Nevertheless, since distances between habitat patches were much lower (up to 50 m) than in this study, immigration was not limited by increasing isolation.

In contrast to our results, Krauss, Steffan-Dewenter & Tscharntke (2002) and Meyer, Gaebele & Steffan-Dewenter (2007) found a distinct positive relationship between fragment size and species richness of butterflies, hoverflies, and bees. Butterflies as well as hoverflies and bees have more complex habitat and resource requirements than leafhoppers. This appeared to be the reason why they need larger habitat fragments. Resource requirements of butterflies and bees change during their life cycle: adult butterflies feed on nectar, whereas the caterpillars feed on plant tissue (Ebert & Rennwald 1991). Bees require nectar and pollen, both as food for themselves and to provision their brood cells, they need hollow or pithy plant stems, empty snail shells or cavities in the ground as nesting sites and nesting material like leaves, clay, small stones and plant resin (Westrich 1989). In other words, they need different resources that are often spatially separated. In contrast, leafhoppers lay their eggs directly onto the host plant and all life stages feed on plant sap, which is an ample resource throughout the growing season (Nickel 2003). This life history strategy enables them to potentially stay on the same plant stem for all their life, which is likely to reduce the minimum fragment size required for persistence. Thus, the threshold for a decrease in generalist species richness with fragment size alone might not have been reached within the range of fragment sizes chosen for this study (smallest fragment: 0.1 ha). It seems that many leafhopper species are able to cope with small fragment sizes as long as a sufficient amount of their host plant is present.

This is in accordance with Biedermann (1997) who showed a clear but species-dependent relationship between host plant patch size and the occurrence of three specialised leafhopper species. So if a dispersing individual of a specialist species reaches the next fragment but the host plant patch is too small – which is more likely to be the case in small fragments – it will not be able to establish a stable population there, causing the lower species richness of specialists on small fragments we observed in this study.

Usually, a focus on large fragments is recommended (e.g. Krauss, Steffan-Dewenter & Tscharntke 2003), but according to our results, both large and small fragments deserve to be maintained because at least for generalist leafhoppers we found no generally negative effect of small fragment size, but only in combination with decreasing connectivity.

Specialist leafhopper species richness increased with specialist plant species richness. As mentioned above, leafhoppers live in close association with their host plants (Nickel 2003), spanning from strictly monophagous to highly polyphagous species (Nickel & Remane 2002). Host plants provide feeding resources, shelter and oviposition sites and are also used for the transmission of bioacoustic signals (Nickel 2003). We therefore assume that the more specialist plant species occur per site, the more specialist leafhopper species can occur since the appropriate host plant for more species will be provided. This finding is in accordance with Siemann et al. (1998) and Scherber et al. (2010) who found an increase in herbivore diversity when the number of plant species in their experimental setups increased. So even if suitable plant resources are available, isolated fragments are less likely to be colonized than connected ones, resulting in an increase in leafhopper species richness with plant species richness that is less steep than the one on connected fragments.

3.2.4. Conclusions

Our results are the first to show that insect biodiversity on fragmented calcareous grasslands not only depends on habitat connectivity but that it is interactively affected by the four factors habitat connectivity, habitat area, landscape composition and specialist plant species richness. Isolated fragments that are either small or located in simple landscapes are less likely to receive immigrants after extinction events, leading to a gradual reduction in species richness over time. Generalist species are affected by the surrounding landscape, whereas for specialists local factors (habitat size and quality, i.e. the number of specialist plant species) are more important. These patterns should not only apply to leafhoppers but also to other insect groups as well.

Mitigating the negative effects of habitat fragmentation therefore needs to take the surrounding landscape into account. Management should be prioritised towards increasing the connectivity (i) of small, isolated fragments, (ii) of fragments in simple landscapes and (iii) towards increasing the size of fragments in order to promote specialist species. Management efforts should enhance dispersal by improving heterogeneity of both landscape composition and configuration. Moreover, extensive management of fragments by grazing or mowing, both relatively late in the season, to increase habitat quality for leafhoppers, would benefit other insect groups as well.

3.3. Butterfly and bird diversity in orchard meadows and calcareous grasslands

Calcareous grasslands and orchard meadows are among the most species-rich semi-natural habitats in Europe, but they are severely threatened by intensified land use and abandonment. Here, we focus on the effects of management vs. abandonment of these grasslands on butterfly and bird communities in agricultural vs. forest-dominated landscapes of Germany.

3.3.1. Material and methods

The study area was situated in southern Lower Saxony (Germany) in the districts of Göttingen and Northeim (about 1000 km²; for a map see Supplementary Material of the original paper). The main land use types are arable fields, intensively used meadows and semi-natural deciduous forests. The surveys were conducted in calcareous grasslands (*Mesobrometum erecti* Koch 1926) covering only 0.26 % and in orchard meadows (*Arrhenatheretum elatioris* Braun 1915) covering 0.39 % of the study area. Both semi-natural grassland habitats are patchily distributed across the landscape, and managed either by mowing or grazing with sheep, goats, cattle or horses. Many smaller fragments and party also the larger ones are in a process of abandonment with shrub encroachment and/or dye off of old fruit trees.

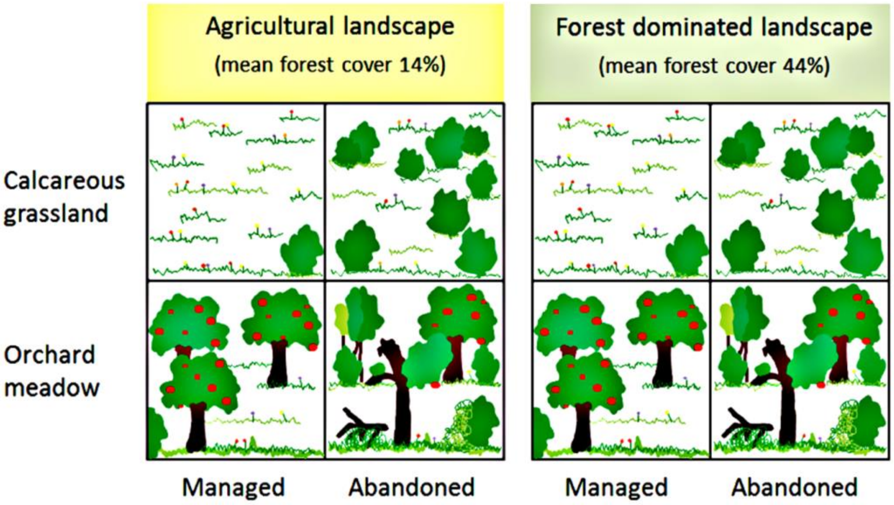


Fig. 3.3.1. Schematic figure of the study design representing the study sites. There were five replicates per treatment resulting in 20 calcareous grasslands and 20 orchard meadows located in contrasting landscape context (agricultural or forest-dominated) differing in management (regularly managed or abandoned management).

We surveyed butterfly and bird species in 20 orchard meadows and 20 calcareous grasslands in a full factorial design (mean ± SEM distance between sites: 17.9 ± 0.3 km; range of distance between sites: 0.5 – 52.0 km; fruit tree density on abandoned orchard meadows: 38.6 ± 4.4 (23.9 – 67.9) and on managed orchard meadows: 36.4 ± 5.5 (16.4 – 70.5)). The habitat fragments were selected according to differences in landscape context (forested vs. agriculture dominated landscapes) and management status (managed vs. abandoned), resulting in five replicates per treatment (Fig. 3.3.1). Within a 500 m buffer area around each habitat fragment, forest-dominated landscapes had 44 ± 2% (mean ± SEM) forest cover ranging from 28 to 63%, whereas agricultural landscapes had 14 ± 2% forest cover ranging from 0 to 28% (forest cover was measured in ArcGIS 10.4). As many semi-natural habitats are neither fully managed nor completely abandoned, we selected managed habitat fragments to be managed each year by grazing or mowing, whereas abandoned fragments to be irregularly or not managed characterised by high degree of succession to woody shrubs or dead wood. In summary, majority of the managed grasslands were grazed extensively (< 1 LUI/ha) between May and September with different livestock including cattle, sheep, goat, horse or donkey (calcareous grasslands: eight fragments grazed, one mown and one both grazed and mown; orchard meadows: eight fragments grazed and two mown). In order to minimize the effect of habitat size on species richness and abundance, fragments with a similar size were chosen, and species were surveyed on a 0.8 ha patch in each study site. The area of the selected habitat fragments was 2.64 ± 0.27 ha (mean ± SEM) for calcareous grassland (ranging from 0.90 ha to 5.38 ha) and 1.45 ± 0.15 ha for orchard meadows (ranging from 0.85 ha to 3.34 ha).

Butterflies (Lepidoptera: Hesperidae and Papilionidea) and burnet moths (Lepidoptera: Zygaenidae) were sampled from 24th of May until 19th of August 2015 with three survey rounds (roughly one survey/month) by a 20 minute zig-zag transect-walk (split into 5 four-minute sections) once on each habitat fragment (following Krauss et al., 2003; Brückmann et al., 2010). Butterflies were surveyed visually or using a butterfly net between 10.45 am and 5.30 pm, and were identified and released immediately. Surveys were conducted on a 5 m wide corridor under suitable weather conditions for butterfly activity (dry conditions, wind speed less than Beaufort scale 5, and temperature 13 °C or higher if there was at least 60 % sunshine, or more than 17 °C if overcast (Pollard, 1977)). To characterise the availability of nectar resources, the percent cover of flowering plants inside the transect corridor was estimated at the end of each transect walk. We classified butterfly species to farmland or woodland species based on literature (van Swaay et al., 2006; Plattner et al., 2010).

We recorded birds between 8th and 22nd of May and between 8th and 28th of June 2015 in two survey rounds by a 12 minute point-count on 0.8 ha patches half an hour after sunrise until 4 hours after sunrise under calm and dry weather conditions (Bibby et al., 1992). There were 22 habitat fragments with two 0.8 ha survey patches as they were larger than 1.6 ha. In the 18 remaining, smaller habitat fragments there was one 0.8 ha survey patch in each habitat fragment. Due to the high degree of heterogeneous structures and the different shape of the habitat fragments, each point-count was split into three 4-minute sections placed at points suitable to represent the study design (managed or abandoned). This guaranteed to perceive all acoustic signals of the birds and to detect them visually. To characterise the availability of nesting and foraging sites, the percent bush cover in each 0.8 ha study patch was estimated in the end of each survey. We classified bird species to farmland or woodland species based on literature (Gregory et al., 2005, 2007; Südbeck et al., 2005; Batáry et al., 2012). Species habitat affinity and specialism might change with different European regions suggesting that our classification approach may lead to different results there (see e.g. Koleček et al., 2010).

Abundance of butterflies was summed over transects and sampling occasions. For each bird species we pooled the data using the maximum abundance of the two survey rounds per patch. Species richness of birds was calculated as the number of species that were present in the particular sampling patch at least in one survey round.

For both taxa we applied linear regression models for analysing the species richness and abundance of farmland and woodland species. Habitat type (calcareous grassland vs. orchard meadow), management status (managed vs. abandoned), landscape context (forested vs. agriculture dominated landscapes) and their two-way interactions were used as explanatory design variables. In case of bird models, the survey patch within habitat fragment was used as random factor. Models were fitted with Poisson distribution or in case of overdispersion with negative binomial distribution using the MASS (for butterflies, Venables and Ripley, 2002) and lme4 packages (for birds, Bates et al., 2015) of R software (R Development Core Team, 2017). We calculated all models nested in the global model by the command ‘dredge’ in the package MuMIn (Barton, 2016), and compared them based on Akaike Information Criterion corrected for small sample size (AICc). We performed model averaging (Burnham and Anderson, 2002), if the top model and subsequent models differed less than two units in AICc. Model-averaged parameter estimates were calculated over the subset of models including the parameter (conditional average) to avoid shrinkage towards zero (Grueber et al., 2011). We present the 95% confidence intervals (CI) of parameter estimates and the relative importance of each parameter. Relative importance is 100%, when the parameter is present in all top models.

We also performed further linear regression models to test for effects of explanatory design variables on percent flowering plants and percent bush cover (both normal distribution), potentially important for butterflies and birds, respectively. The percent flowering plants was significantly higher in calcareous grasslands than in orchard meadows (Table A1; Fig. A1a). The percent bush cover was mainly determined by the management with about three times higher cover of bushes in abandoned than in managed sites. Nevertheless bush cover was also significantly higher in calcareous grasslands than in orchard meadows and in agricultural than in forested landscapes.

Furthermore, we applied redundancy analyses (RDA) to assess the variability in species composition of butterfly and bird communities explained by the environmental variables habitat type, management status and landscape context. For the bird analysis we included habitat patch as conditional variable as the study design was nested. The results were presented in ordination biplots to visualise the variability in species composition. Prior to analyses, community data matrices were Hellinger-transformed (Legendre and Gallagher, 2001). To assess for statistical significance, a permutation test based on 999 permutations was calculated using the package vegan (Oksanen et al., 2017).

3.3.2. Results

On the 20 calcareous grassland and 20 orchard meadow fragments we recorded 5182 individual butterflies belonging to 55 butterfly species (seven of them burnet moths, hereafter also called butterflies) and 1075 individuals of 55 bird species. Classification based on environmental preferences resulted in 35 farmland butterfly species with 3973 individuals and 20 woodland butterfly species with 1209 individuals as well as 22 farmland bird species with 272 individuals and 33 woodland bird species with 803 individuals (Table A2,A3). The most abundant farmland butterflies were *Maniola jurtina*, *Polyommatus coridon* and *Melanargia galathea*, whereas the most abundant woodland butterflies were *Aphantopus hyperantus*, *Pieris napi* and *Coenonympha arcania*. For birds, the most abundant farmland species were *Emberiza citrinella*, *Sylvia communis* and *Columba palumbus*, whereas the most abundant woodland birds were *Parus major*, *Turdus merula* and *Cyanistes caeruleus*.

Table 3.3.1. Summary table for generalized linear regression model results on farmland and woodland butterfly species richness and abundance testing the effects of habitat type (H: calcareous grassland vs. orchard meadow), management (M: abandoned vs. managed) and landscape context (L: agricultural vs. forest-dominated) after multimodel averaging of best candidate models. AB: abandoned, AG: agricultural, CG: calcareous grassland, FO: forest-dominated, MA: managed, OM: orchard meadow. Significant estimates are in bold characters.

Model[a]	Variable	Relative importance (%)[b]	Multimodel estimate ± 95 % CI[c]			Direction
Species richness						
Farmland	Landscape (L)	100	0.026	±	0.312	
	Habitat (H)	100	**-1.217**	±	**0.415**	CG>OM
	Management (M)	100	0.054	±	0.31	
	L × H	100	**0.702**	±	**0.448**	
	L × M	100	-0.095	±	0.403	
	H × M	100	-0.042	±	0.436	
Woodland	Landscape (L)	30	0.139	±	0.276	
	Habitat (H)	63	-0.239	±	0.278	
	Management (M)	13	0.099	±	0.276	
Abundace						
Farmland	Landscape (L)	100	0.029	±	0.481	
	Habitat (H)	100	**-1.792**	±	**0.718**	CG>OM
	Management (M)	100	0.458	±	0.465	
	L × H	62	**0.863**	±	**0.697**	
	H × M	62	**0.934**	±	**0.675**	
Woodland	Landscape (L)	20	0.138	±	0.344	
	Habitat (H)	28	-0.198	±	0.341	
	Management (M)	100	**-0.554**	±	**0.345**	CG>OM

We found habitat type to be the most important factor determining farmland butterfly species richness and abundance with higher values in calcareous grasslands than in orchard meadows (Table 3.3.1; Fig. 3.3.2a,c). Farmland species richness and abundance depended on an interaction between landscape context and habitat type; high species richness and abundance were found in both agricultural and forest-dominated landscapes of calcareous grasslands, but lower values in orchard meadows with a decrease from forested to agricultural landscapes. Additionally, farmland butterfly abundance was influenced by management in interaction with habitat type. Management increased butterfly abundances in calcareous grasslands, but decreased them in orchard meadows. In contrast, abandonment increased the abundance of woodland butterflies, but not their species richness (Fig. 3.3.2c,d).

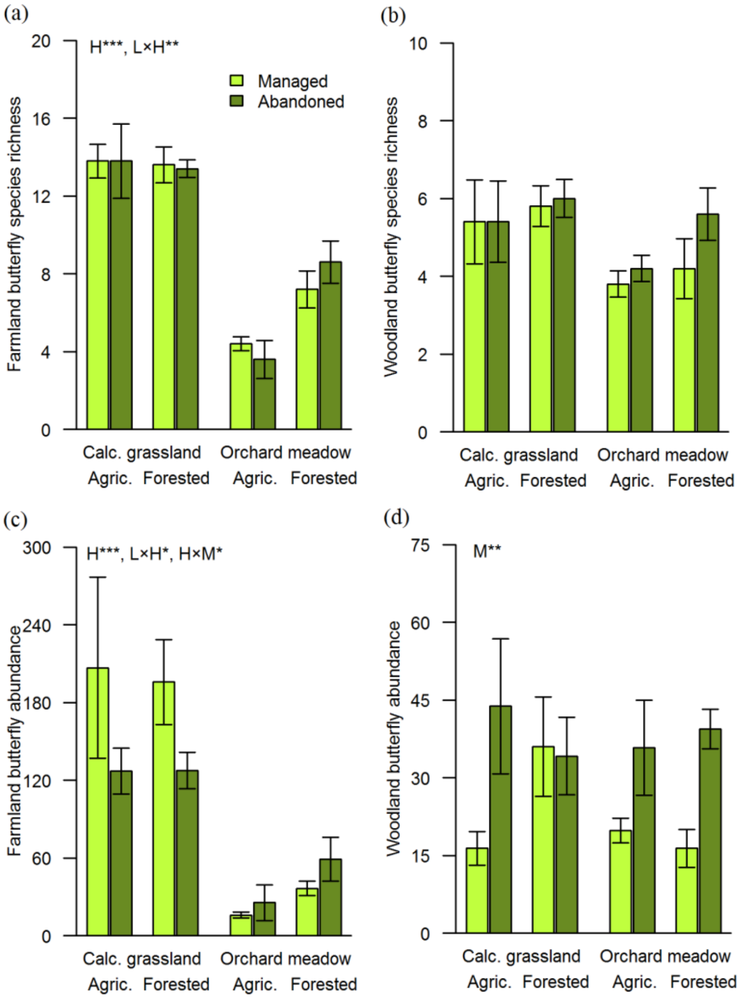


Fig. 3.3.2. Mean (± SEM) farmland (a) and woodland (b) butterfly species richness and farmland (c) and woodland (d) butterfly abundance in managed vs. abandoned calcareous grasslands and orchard meadows situated in agricultural vs. forest-dominated landscapes. Results are based on generalized linear regression models (see Table 1) with $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$ (H: Habitat type, L: Landscape context, M: Management type).

The RDA of butterfly community composition revealed significant associations with habitat type and landscape context (Table 3.3.2; Fig. 3.3.3a). In the ordination biplot, the first axis separated calcareous grasslands from orchard meadows with e.g. chalkhill blue (*Polyommatus coridon*) as characteristic species in calcareous grasslands and ringlet (*Aphantopus hyperantus*) as characteristic species in orchard meadows. The second axis separated agricultural from forest-dominated landscapes with small white (*Pieris rapae*) being a characteristic agricultural species and small skipper (*Thymelicus sylvestris*) being a species associated with forest.

Performing generalized linear mixed effects models on birds, we found that management type was the variable that most strongly explained both farmland and woodland species richness and abundance (Table 3.3.3). This was, however, in an interaction with habitat type in case of farmland species (Fig. 3.3.4a,c). Farmland birds preferred managed over abandoned fragments in orchard meadows, and abandoned over managed fragments in calcareous grassland. Additionally, they were more abundant in agricultural than forest-dominated landscapes. In contrast, woodland birds (both richness and abundance) were more common in abandoned than in managed fragments (Fig. 3.3.4b,d). Finally, woodland bird abundance was higher in orchard meadows than in calcareous grasslands.

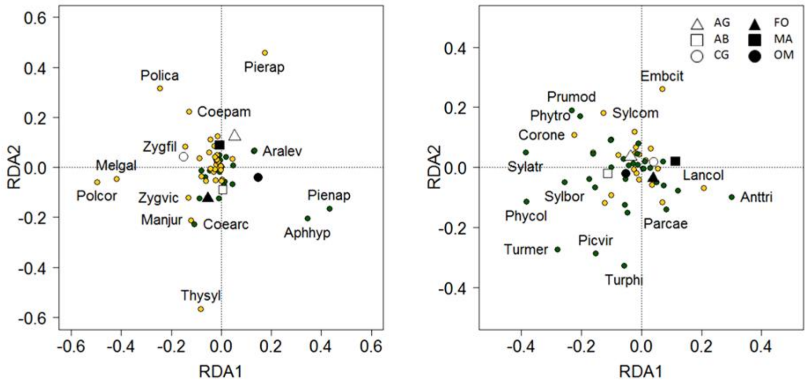


Fig. 3.3.3. Redundancy analysis biplots for all species of (a) butterfly and (b) bird communities (yellow circles: farmland species, green circles: woodland species) showing the effect of habitat type (CG: calcareous grassland, OM: orchard meadow), presence of management (AB: abandoned, MA: managed) and landscape context (AG: agricultural, FO: forest-dominated landscape). For visibility, only species with the highest fraction of variance fitted by the two first RDA axes are indicated. Species code consists of the first three letters of genus plus the first three letters of species names (Table A2, A3).

Table 3.3.2. Results of redundancy analyses to test the effect of habitat type (H: calcareous grassland vs. orchard meadow), management (M: abandoned vs. managed) and landscape context (L: agricultural vs. forest-dominated) on the community composition of all butterfly and bird species. % var.: percentage variation explained. P values < 0.05 are in bold characters.

	% var.	*F*	*P*
Butterfly			
Landscape	5.61	2.86	**0.012**
Habitat	21.33	10.88	**0.001**
Management (M)	2.49	1.27	0.229
Total constrained	29.43	5.00	**0.001**
Bird			
Landscape	2.30	1.52	**0.023**
Habitat	3.56	2.35	**0.001**
Management (M)	3.50	2.30	**0.001**
Total constrained	9.37	2.06	**0.001**

In the RDA of bird communities all three variables explained a significant part of the variation in community composition (Table 3.3.2). Landscape context explained the smallest part, followed by management and habitat type, explaining the largest part of the variation. The first axis separated in particular abandonment and management, but also orchard meadows and calcareous grasslands (Fig. 3.3.3b). For example, chiffchaff (*Phylloscopus collybita*) showed a preference for abandoned orchard meadows, whereas tree pipit (*Anthus trivialis*) was a characteristic species of managed calcareous grassland. The second axis separated agricultural from forest-dominated landscapes with green woodpecker (*Picus viridis*) as characteristic woodland species in grassland fragments of forest-dominated landscapes and yellowhammer (*Emberiza citrinella*) being a characteristic farmland species in grasslands of agricultural landscapes.

3.3.3. Discussion

We studied the effects of habitat type (calcareous grassland vs. orchard meadow), management (managed vs. abandoned) and landscape context (forested vs. agricultural landscape) in a full factorial design and found that the classification into farmland and woodland traits helps to identify key factors of diversity and abundance patterns for conservation management strategies. Farmland butterflies were more diverse in calcareous grasslands than farmland birds, which exhibited higher species richness in orchard meadows. Woodland butterfly and bird abundance increased with abandonment, whereas regular management affected farmland butterflies in calcareous grassland positively. Surprisingly, landscapes dominated by forest had a positive effect on farmland butterfly richness and abundance, but not on woodland butterflies. Farmland bird abundance was higher in agricultural landscapes, while woodland bird diversity and abundance benefited from abandonment.

Table 3.3.3. Summary table for generalized linear mixed-effects model results on farmland and woodland bird species richness and abundance testing the effects of habitat type (H: calcareous grassland vs. orchard meadow), management (M: abandoned vs. managed) and landscape context (L: agricultural vs. forest-dominated) after multimodel averaging of best candidate models. AB: abandoned, AG: agricultural, CG: calcareous grassland, FO: forest-dominated, MA: managed, OM: orchard meadow. Significant estimates are in bold characters.

Model[a]	Variable	Relative importance (%)[b]	Multimodel estimate ± 95 % CI[c]	Direction
Species richness				
Farmland	Landscape (L)	100	-0.437 ± 0.492	
	Habitat (H)	100	-0.032 ± 0.448	
	Management (M)	100	**-0.659** ± **0.518**	AB>MA
	L × H	100	0.09 ± 0.612	
	L × M	100	0.022 ± 0.61	
	H × M	100	**0.853** ± **0.602**	
Woodland	Landscape (L)	70	-0.043 ± 0.329	
	Habitat (H)	52	0.133 ± 0.261	
	Management (M)	100	**-0.381** ± **0.335**	CG<OM
	L × H	12	0.286 ± 0.418	
	L × M	49	-0.439 ± 0.443	
Abundace				
Farmland	Landscape (L)	100	**-0.518** ± **0.408**	AG>FO
	Habitat (H)	100	-0.145 ± 0.495	
	Management (M)	100	**-0.629** ± **0.49**	AB>MA
	L × H	28	0.283 ± 0.666	
	H × M	100	**1.086** ± **0.671**	
Woodland	Landscape (L)	27	-0.097 ± 0.305	
	Habitat (H)	100	**0.338** ± **0.305**	CG<OM
	Management (M)	100	**-0.545** ± **0.307**	AB>MA

Supporting our first hypothesis, species richness and abundance of farmland butterflies was highest in calcareous grasslands. Management such as mowing and grazing leads to high cover of flowering plants as feeding and reproduction resources. This positive relationship has often been reported (e.g. Krämer et al., 2012), and highlights the disproportionate high value of calcareous grassland for butterfly conservation (van Swaay, 2002).

As hypothesised, management had a negative effect on woodland butterfly abundance, but not on species richness. Woodland butterflies were more common in abandoned semi-natural grasslands, which can be explained by increasing microhabitat heterogeneity and the availability of plant communities typical for different successional stages (WallisDeVries et al., 2002). On the contrary, farmland butterfly abundance increased with management, but only in calcareous grassland, where abundances were generally higher than in orchard meadows. Abandonment appeared to provide less life-sustaining resources for farmland butterflies such as flowering plants and warm micro-climate (van Swaay, 2002). Surprisingly, in orchard meadows farmland butterfly abundance increased with abandonment. This might have been caused by the fact that management was characterised by high stocking rates, fertilisation and frequent mowing, degrading the diversity of herbs and flowers (Uchida et al., 2016). Abandoned orchard meadows were characterised by additional resources such as flowering forbs or shrubs, for example blackberries, but in the long run, late successional stages may decrease butterfly species richness and abundance (Balmer and Erhardt, 2000; Kesting et al., 2015). There is a lack of target-oriented management in orchard meadows, which should be regularly restored by clearance of shrubs and trees, opening of the canopy for light and warm micro-climate as well as reducing grazing density or intensified hay-making to facilitate larval hosts and nectar-providing plants.

In contrast to our hypothesis, farmland butterfly species richness was higher in orchard meadows when embedded in forest-dominated landscapes but not agricultural landscapes. Forest-dominated landscapes are more heterogeneous providing more resources than simple landscapes dominated by agriculture (Öckinger et al., 2012). Compared to calcareous grassland, local habitat conditions in orchard meadows were worse (less food resources) and farmland butterflies appeared to use additional resources in the surroundings (Krämer et al., 2012; Villemey et al., 2015). In this study we found more flowering plants in orchard meadows of forest-dominated than agricultural landscapes, which suggests that non-arable patches may act as buffer against intensive agricultural practices such as chemical weed control (Gonthier et al., 2014; Villemey et al., 2015).

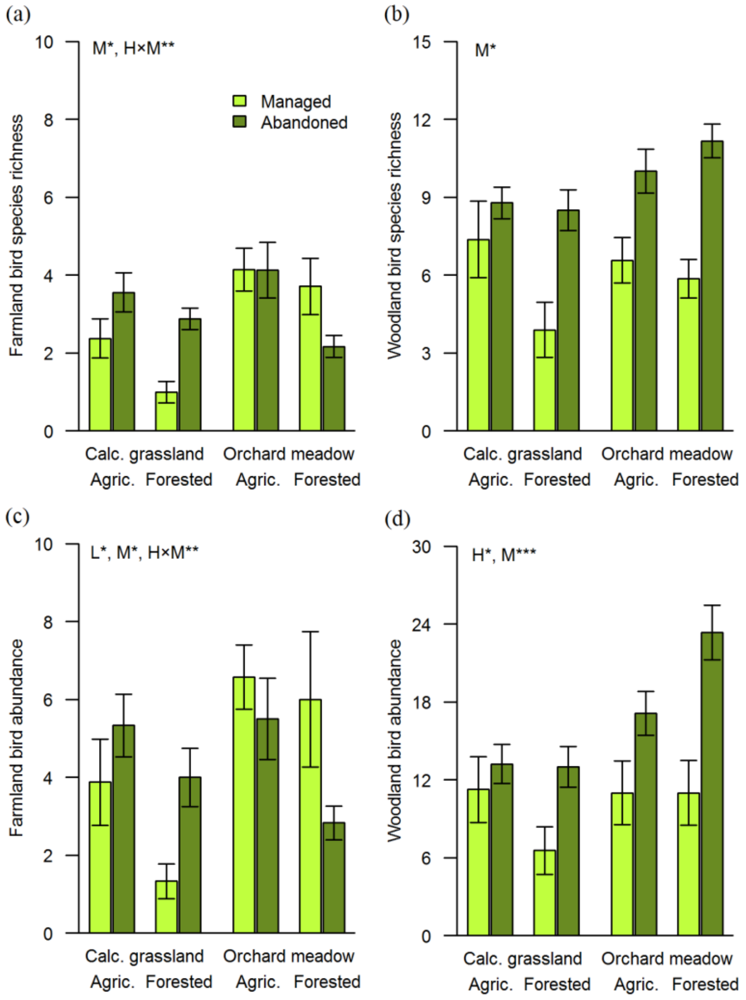


Fig. 3.3.4. Mean (± SEM) farmland (a) and woodland (b) bird species richness and farmland (c) and woodland (d) bird abundance in managed vs. abandoned calcareous grasslands and orchard meadows situated in agricultural vs. forest-dominated landscapes. Results are based on generalized linear mixed-effects models (see Table 2) with $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ (H: Habitat type, L: Landscape context, M: Management type).

As shown in the redundancy analysis, the greatest variability in community composition was explained by habitat type with most butterfly species showing a strong preference for calcareous grasslands especially by farmland species. For example, chalkhill blue is regarded as threatened in the red list of the study region (Lower Saxony, (Lobenstein, 2004)), and was the most characteristic farmland species on calcareous grasslands. The high population density of chalkhill blue is determined by the presence of the larva’s food plant *Hippocrepis comosa* (Krauss et al., 2005), which is dispersed by the hooves of livestock (Brereton et al., 2008). Hence, this result reflects the need for appropriate habitat management for specialised butterflies in the study region. Contrastingly, the community composition for orchard meadows showed that management can be important habitat for species that are associated with open woodland. For example, ringlet (*Aphantopus hyperatus*) occurred in relatively high abundances in orchard meadows. This species was often shown to be present in grasslands and mixed woodlands, but also in tree lines (van Swaay et al., 2006). Thus, orchard meadows potentially provide habitat for species that are associated with woodland edges and can be assumed to provide habitat to an even wider range of open-woodland butterfly species profiting from improved management practices. Hay-making or low-intensity grazing with reduced fertiliser use and allowance of seed maturation could restore the degraded orchard meadows in the study region.

Regarding farmland bird species richness and abundance, our first and second hypotheses were only party confirmed, because we found an interaction of habitat type and management. Abandonment caused an increase in farmland bird species richness and abundance in calcareous grasslands, but a decrease in orchard meadows. Partly abandoned calcareous grasslands were characterised by less disturbance and provided a wide range of niches, because of their heterogeneous habitat characteristics caused by higher amounts of woody vegetation and heterogeneous sward structures (Hartel et al., 2014). This supported nesting sites and foraging opportunities, e.g. for insects on the ground (Vickery et al., 2001). However, abandonment can benefit farmland birds only on a short term and further succession will exclude farmland birds (Gregory et al., 2007). Contrastingly to calcareous grasslands, farmland bird species richness and abundance were higher in managed compared to abandoned orchard meadows. Scattered trees act as keystone habitat for farmland birds and provide nesting and foraging opportunities as well as song posts (Fischer et al., 2010; Jakobsson and Lindborg, 2017). Since orchard meadows were mostly grazed by livestock, they were suitable for foraging, e.g. of insects on animal dung, or as ground-nesting sites in patches avoided by livestock. Nevertheless, some orchard meadows were frequently used and there might be a higher potential for farmland birds as the positive effect of management on biodiversity may be restricted to low levels of interference. Intensified grassland management decreases the suitability as habitat for feeding and nesting because of higher disturbance levels and a fast growing, homogeneous grassland structure as a consequence (Vickery et al., 2001). Management activities should provide feeding and nesting sites, such as breeding burrows of old trees, shelter of bushes for ground breeding birds and heterogeneous, open sward structures.

Corresponding to our hypotheses, woodland bird species richness and abundance were higher in abandoned compared to managed grassland fragments and abundance was also higher in orchard meadows than in calcareous grassland. Abandoned habitat fragments are structurally more similar to forest as they contain a high bush and tree cover. Orchard meadows were characterised by high, old fruit trees representing structurally rich stands important for birds nesting in treetops and hollows (Tworek, 2002), which can be compared with forest structures as well, but being more open. Thus, habitat structural diversity might be reasonable for some parts of the habitat, but probably favours primarily forest species and not characteristic semi-open woodland species. Long-term abandonment should be avoided as orchard meadows would develop into forest.

In accordance with the third hypothesis, farmland bird abundance increased in semi-natural grassland located in agricultural landscapes. Similar results were found by Wretenberg et al., (2010) with a positive effect of low-intensity land use on farmland birds in open landscapes with low forest cover. This indicates that farmland birds are using resources from different semi-natural grasslands, but also the surrounding agricultural landscape. Birds experience the landscape at a large scale, which also enables them to react fast to local habitat changes (Tscharntke et al., 2012a). Hence, semi-natural grassland can be regarded as a valuable landscape element for landscape-wide conservation management.

Analysing the bird community composition, habitat type and management explained the greatest part of its variation. For abandoned orchard meadows, for example, chiffchaff (*Phylloscopus collybita*) was a characteristic woodland species nesting on the ground or in herbaceous woody vegetation structures (Südbeck et al., 2005; Gregory et al., 2007). However, for orchard meadows there are also some semi-open woodland bird species regarded as characteristic due to their ecological requirements (Herzog et al., 2005), but only two of them were found in this study (*Phoenicurus phoenicurus*; *Picus viridis*) and one of them, namely *P. phoenicurus*, only with one individual. This indicates that the ecological requirements of many characteristic species for orchard meadows cannot be fulfilled by the current habitat status, e.g. for ortolan (*Emeriza hortulana*) and hoopoe (*Upupa epops*), which are regarded as threatened in the red list of the study region (Lower Saxony, (Krüger and Nipkow, 2015)). This shows the importance of orchard meadows for a wide range of bird species, but emphasises the urgent need for conservation management to work more target-oriented with land owners. Thus, abandoned orchard meadows should be taken into low-intensity management again, while nest-holes and heterogeneous structures must be preserved at the same time. Another rare open woodland species is tree pipit (*Anthus trivialis*), which is specialised on open semi-natural grassland with single trees and characteristically occurred in managed calcareous grassland of forest-dominated landscapes. High solitary trees are used as perches, and an increasing shrub cover was shown to negatively affect the occurrence (Kumstátová et al., 2004). This suggests that the tree pipit, being in a sharp decline across Europe (Gregory et al., 2007), was favoured by open semi-natural grassland with single perches and would be disadvantaged by abandonment.

3.3.4. Conclusions

Our results show that the classification of species into farmland and woodland traits can help to disentangle the complex local and landscape effects on butterflies and birds in semi-natural grasslands. Results of this study detail the relative importance of local and landscape management and their complex interaction for understanding and applying best conservation measures. Woodland birds and butterflies appeared to be less affected by habitat type, management or landscape context than farmland species. Calcareous grasslands were much more important for butterfly diversity than orchard meadows, but suitability of orchards for butterflies was improved when embedded in forested landscapes. In contrast to butterflies, bird diversity benefited more from orchard meadows than calcareous grasslands, which had higher diversity when management was abandoned. Hence, short-term abandonment can improve habitats for birds and butterflies, but of course, long-term abandonment would destroy the identity of these openland habitats and their associated community. Landscape context can shape communities in these two grassland habitat types, so conservation management should consider reserves in both agricultural and forest landscapes and thereby, diversify regional biota.

4. Impact of hedgerow-forest connectivity on biodiversity and ecosystem function

Most landscape ecological studies in farmland focus on the effects of landscape composition, i.e. how the variety and abundance of patch types modulates species populations and community composition. However, landscape configuration, i.e. the spatial character and arrangement, position, or orientation of landscape elements, in farmland has received less attention. Here we focused on the effect of configuration of hedgerows (adjoined to forest or isolated in agricultural matrix) on birds and pollinators, whereby also taking forest edges as a reference.

4.1. Effect of isolation of hedges from forests on birds

In this study, we investigated the response of farmland vs. woodland birds at two degrees of isolation of hedges from forest. Hence we studied farmland and woodland birds by comparing forest edges with hedges of different connectivity to forests, namely hedges directly connected to forest and hedges isolated in the agricultural areas. Farmland species were expected to be mostly ecotonic forest birds depending on tracts of woody vegetation for nesting and on open habitats for foraging (sensu Díaz et al. 1998). In contrast woodland bird species needed woody vegetation for both nesting and foraging.

4.1.1. Material and methods

The study sites were situated in the surroundings of the city of Göttingen in southern Lower Saxony, Germany (51.5° N, 9.9° E; a map is available in Supplementary Material of the original paper). The main land-use types of the study area are arable lands, followed by forests and grasslands. Arable fields and grasslands (generally 2-5 ha in size) occur in a mosaic, and surround or intermix with forests (mainly beech), which can have a size from few up to several hundreds of hectares. These beech forests are managed in a nature-oriented way often by selective logging and with a preference of native precious hardwoods. There are still quite a lot of hedges in the farmland area surrounding the forest fragments; however, one can also find extremely simplified agricultural landscapes without hedges or trees (Batáry et al. 2010a). In order to study the effects of hedge isolation from forests on birds, we selected study sites representing three degrees of habitat isolation: forest edges, hedges connected to the forest and isolated hedges. Isolated hedges were situated in the agricultural landscape, and had a minimum distance of 300 m to the nearest forest. None of the selected hedges was part of a larger hedge network system (mean ± SE of length of connected and isolated hedges: 272 ± 31 m and 225 ± 11 m, respectively). The most characteristic woody plants of hedges and forest edges were blackthorn (*Prunus spinosa*), hawthorn (*Crataegus spp.*) and rose (*Rosa spp.*), while further frequent woody plants include maple (*Acer spp.*), willow (*Salix spp.*), common dogwood (*Cornus sanguinea*), ash (*Fraxinus excelsior*), elder (*Sambucus nigra*) and hazel (*Corylus avellana*).

All selected study sites had a continuous dense shrub layer for at least 200 m, where the birds were surveyed. The connected hedges directly adjoined perpendicular to forest. We avoided selecting green lanes (parallel hedges on both sides of a road or track) and sites along regular water-bearing ditches, which may influence bird abundance and community composition (Walker et al. 2005). We further excluded sites bordering busy roads, but study sites along roads with only agricultural traffic were included. The distance between study sites was at least 500 m to avoid spatial autocorrelation. All hedges and forest edges were bordered by cropland, mainly winter cereal and oilseed rape fields.

Taking into account all above constrains (especially minimum length of hedges and spatial independence), we were able to select six forest edges, six hedges connected to forest and six isolated hedges. In all sites, the surveyed 200 m transects of forest edges and hedges were divided by 50 m sections, where birds were surveyed. In order to provide an overview of the landscape structure of the study sites, Table 4.1.1 shows some landscape structural parameters (arable %, forest %, forest edge length and hedge length), which were calculated for buffer areas with a 500 m radius around the study sites. All four landscape parameters were significantly different among the three degrees of habitat isolation owning to their different configuration (one-way ANOVAs, $p > 0.05$).

Birds were surveyed three times from April to June 2009 in the early morning (from sunrise within 4 hours) in windless and rainless weather. In case of a connected hedge the 200 m section always started at the forest. For bird survey we followed the method of Green et al. (1994). All bird contacts, visual and acoustic, were recorded whilst standing still at one end of a 50 m section for one minute. Birds located in sections beyond the one immediately ahead were recorded for the relevant section. In the end of the one-minute observation period, the surveyor (PB) walked slowly along the section (in two minutes), noting any new contacts. The procedure was repeated for the next 50 m section. If birds were known to move between sections, they were recorded only in the section where first seen in order to reduce the rate of pseudo-replicated data. The order in which sites were sampled was changed in the consecutive censuses. At the forest edges birds were also recorded on the trees above the shrub layer. We separated bird species characteristic for farmland or woodland based on the literature (Table 4.1.2; Tucker and Heath 1994, Gregory et al. 2005, 2007).

	Forest edge	Connected hedge	Isolated hedge
Width (m)	5.0 ± 0.5	4.4 ± 0.4	5.7 ± 0.5
Height (m)	3.5 ± 0.1	3.7 ± 0.1	4.0 ± 0.1
Arable %	52.1 ± 5.3	48.3 ± 3.9	82.6 ± 4.4
Forest %	38.6 ± 5.2	30.8 ± 3.3	2.4 ± 1.9
Forest edge length (km)	2.9 ± 0.3	2.8 ± 0.2	1.0 ± 0.5
Hedge length (km)	1.4 ± 0.2	1.2 ± 0.2	2.5 ± 0.4

Table 4.1.1. Summary data of environmental variables describing local characteristics and landscape structure of forest edges, connected and isolated hedges in central Germany. Width and height of edges and hedges (only the shrub layer) were measured at eight points per site. Landscape structure parameters were calculated for buffer areas with a 500 m radius around the study sites. Means ± SEM are given.

Vegetation parameters potentially important for birds were surveyed during June. We measured the width at ground level and height of hedges and edges (only the shrub layer) with 0.5 m precision (hereafter referred as width and height) at two points per section (at 12.5 and 37.5 m), which then were averaged for hedges and edges. Width and height were independent of isolation (linear regression models; width: $F_{2,15} = 0.65$, $p = 0.534$; height: $F_{2,15} = 1.37$, $p = 0.283$; Table 4.1.1).

In order to calculate the maximum abundance out of the three visits, we always took the highest abundance value for each bird species in each site (Bibby et al. 1992), i.e. section data were pooled per hedge or edge ($n = 18$). For analysing the species richness and abundance of all birds, farmland and woodland birds, we applied linear models. Isolation, width and height were used as explanatory variables. We also tested all possible two-way interactions. However, non-significant interactions ($p > 0.05$) were discarded using a manual stepwise backward selection procedure. The normality of model residuals was checked with normal quantile-quantile plots, and dependent variables were log-transformed to achieve normal residuals, if necessary. Differences between degrees of isolation, whenever significant in the model, were further investigated using multiple pair-wise comparisons of means by Tukey contrasts in order to be able to present all three possible comparisons (forest edge vs. connected hedge; forest edge vs. isolated hedge; connected hedge vs. isolated hedge). Calculations were made using the nlme (version 3.1, Pinheiro et al. 2011) and the multcomp (version 1.2, Hothorn et al. 2008) packages for R 2.11.1 software.

To measure the influence of the above described explanatory variables on bird species composition, we applied partial redundancy analyses (RDA). The species matrix was constrained by isolation, width or height. Prior the analyses the species matrix was transformed with the Hellinger transformation (Legendre and Gallagher 2001). This transformation allows the use of ordination methods such as PCA and RDA, which are Euclidean-based, with community composition data containing many zeros, i.e. characterised by long gradients. Pseudo-F values with the corresponding p values were calculated by permutation tests based on 999 permutations. Calculations were performed using the vegan package (version 2.0, Oksanen et al. 2011) for R.

Table 4.1.2. Bird species abundances recorded in the study region (surroundings of the city of Göttingen in southern Lower Saxony, Germany) in forest edges, hedges connected to the forest and isolated hedges in agricultural landscape (maximum abundance of three visits per habitat). Bird species were classified according to their habitat use in two ecological traits (farmland or woodland) based on the literature (Tucker and Heath 1994; Gregory et al. 2005, 2007).

Scientific name	English name	Trait	Forest edge	Connected hedge	Isolated hedge
Acrocephalus palustris	Marsh Warbler	Farmland	0	1	1
Aegithalos caudatus	Long-tailed Tit	Woodland	4	0	0
Anthus trivialis	Tree Pipit	Woodland	2	0	0
Carduelis cannabina	Linnet	Farmland	0	2	6
Carduelis carduelis	European Goldfinch	Farmland	0	0	2
Carduelis chloris	Greenfinch	Farmland	2	10	9
Coccothraustres coccothraustes	Hawfinch	Woodland	1	1	0
Corvus corone	Carrion Crow	Farmland	0	4	2
Cyanistes caeruleus	Blue Tit	Woodland	9	0	3
Dendrocopos minor	Lesser Spotted Woodpecker	Woodland	1	0	0
Emberiza citrinella	Yellowhammer	Farmland	8	18	35
Erithacus rubecula	Robin	Woodland	1	0	0
Fringilla coelebs	Common Chaffinch	Woodland	1	1	0
Luscinia megarhynchos	Nightingale	Woodland	1	1	0
Oenanthe oenanthe	Wheatear	Farmland	0	0	2
Parus major	Great Tit	Woodland	15	4	2
Passer domesticus	House Sparrow	Farmland	0	0	1
Passer montanus	Tree Sparrow	Farmland	0	2	2
Phylloscopus collybita	Common Chiffchaff	Woodland	9	0	0
Phylloscopus trochilus	Willow Warbler	Woodland	1	0	0
Pica pica	European Magpie	Farmland	0	1	1
Prunella modularis	Dunnock	Woodland	4	0	8
Pyrrhula pyrrhula	Eurasian Bullfinch	Woodland	1	1	0
Sitta europaea	Eurasian Nuthatch	Woodland	3	0	0
Sturnus vulgaris	Starling	Farmland	0	1	0
Sylvia atricapilla	Blackcap	Woodland	16	4	2
Sylvia borin	Garden Warbler	Woodland	1	4	2
Sylvia communis	Common Whitethroat	Farmland	2	22	24
Sylvia curruca	Lesser Whitethroat	Farmland	2	5	5
Turdus merula	Blackbird	Woodland	5	13	8
Turdus philomelos	Song Thrush	Woodland	0	1	0
Turdus pilaris	Fieldfare	Woodland	0	0	4

4.1.2. Results

We recorded 32 bird species including 13 farmland and 19 forest species (Table 4.1.2). The two most abundant species were Yellowhammer (*Emberiza citrinella*) and Common Whitethroat (*Sylvia communis*).

Analysing the species richness and abundance of all bird species, we did not find a significant difference among forest edges, connected and isolated hedges (Table 4.1.3). Performing linear models separately for farmland and woodland birds, both species richness and abundance in hedges were different from forest edges (Table 4.1.3). The groups showed contrasting results: farmland birds were more abundant in hedges, while woodland birds were more abundant in forest edges (Fig. 4.1.1a,b). We did not find any significant difference between isolated and connected hedges. Neither width, nor height of hedges and edges influenced the species richness and abundance of farmland or woodland birds. No interactions proved to be significant at all.

In the ordination analysis, isolation explained a significant part of the variation in the bird species matrix (20.18%, pseudo-F$_{2,13}$ = 2.00, p = 0.006; Fig. 4.1.2). The first axis separated forest edges from hedges with characteristic woodland species attributed to forest edges and farmland birds attributed to hedges. The second axis separated the two hedge types, i.e. the connected and isolated hedges. For example, Yellowhammer was more abundant in the latter. Width and height of hedges and edges did not have a significant effect on bird community composition (5.31%, pseudo-$F_{1,13}$ = 1.05, p = 0.411; 4.25%, pseudo-$F_{1,13}$ = 0.84, p = 0.611 respectively).

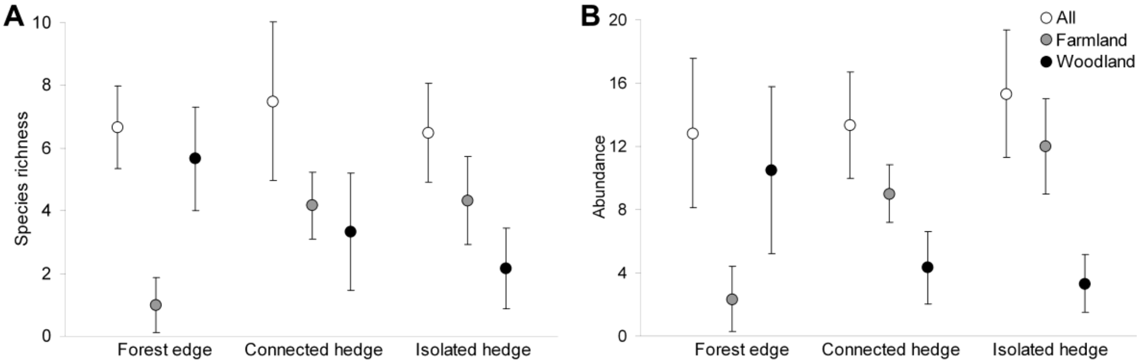


Fig. 4.1.1. Species richness (A) and abundance (B) of all birds, farmland and woodland birds in 200 m sections of forest edges, connected hedges and isolated hedges (mean ± 95% CI are shown).

Table 4.1.3. Effects of habitat type (FE: forest edges; CH: hedges connected to the forest; IH: isolated hedges in agricultural landscape), width and height of hedges and edges on species richness and abundance of all, farmland and woodland birds. In case of habitat type all pairwise comparisons are shown. Bold estimates (effect sizes) with 95% CI indicate significant effects at $p < 0.05$.

	Parameter	Estimate ± CI	t
All bird richness	(Intercept)	5.47 ± 10.48	1.02
	FE – CH	1.42 ± 2.65	1.05
	FE – IH	-0.37 ± 2.70	-0.27
	CH – IH	-1.80 ± 2.51	-1.40
	Width	0.67 ± 0.77	1.70
	Height	-0.60 ± 3.66	-0.32
All bird abundance	(Intercept)	12.55 ± 24.86	0.99
	FE – CH	1.56 ± 6.28	0.49
	FE – IH	2.37 ± 6.41	0.72
	CH – IH	0.81 ± 5.97	0.27
	Width	1.11 ± 1.83	1.19
	Height	-1.48 ± 8.67	-0.33
Farmland bird richness	(Intercept)	1.56 ± 6.50	0.47
	FE – CH	**3.61 ± 1.64**	4.31
	FE – IH	**3.36 ± 1.68**	3.93
	CH – IH	-0.25 ± 1.56	-0.31
	Width	0.43 ± 0.48	1.77
	Height	-0.77 ± 2.27	-0.66
Farmland bird abundance	(Intercept)	-0.66 ± 14.04	0.90
	FE – CH	**7.73 ± 3.55**	4.27
	FE – IH	**10.09 ± 3.62**	5.46
	CH – IH	2.36 ± 1.72	1.38
	Width	0.89 ± 1.03	1.70
	Height	-2.42 ± 4.90	-0.97
Woodland bird richness	(Intercept)	3.91 ± 10.28	0.75
	FE – CH	-2.19 ± 2.60	-1.65
	FE – IH	**-3.74 ± 2.65**	-2.76
	CH – IH	-1.55 ± 1.26	-1.23
	Width	0.24 ± 0.75	0.61
	Height	0.16 ± 3.59	0.09
Woodland bird abundance	(Intercept)	0.96 ± 1.03	1.83
	FE – CH	**-0.28 ± 0.26**	-2.10
	FE – IH	**-0.43 ± 0.26**	-3.19
	CH – IH	-0.15 ± 0.13	-1.21
	Width	0.05 ± 0.08	1.26
	Height	-0.05 ± 0.36	-0.30

4.1.3. Discussion

We found higher species richness and abundance of farmland birds and lower species richness and abundance of woodland birds in hedges than in the forest edges. None of these variables differed significantly between connected and isolated hedges. Width and height of hedges and edges did not affect the species richness and abundance of either farmland or woodland birds. Finally, we showed that bird community composition was highly determined by the habitat type (forest edge or hedge) and the degree of isolation (connected or isolated hedge).

While woodland species were more abundant in the forest edges, farmland birds were more abundant in hedges. Only few woodland birds used hedges; this means that they may perceive hedges only as secondary or alternative habitat and/or as corridor (Krebs 1971). Farmland birds appeared to be present in both hedge types, including those that are isolated in the agricultural landscape. Several studies showed that the presence, density or length of hedges are critical for many farmland birds (Fuller et al. 2001, Whittingham et al. 2009), or even they may be more important than the direct limiting effects of agricultural production intensification (Bas et al. 2009, Batáry et al. 2010a), such as depletion and/or decreased availability of food supply (Siriwardena et al. 2008). We did not find any effect of isolation (i.e. no difference between connected and isolated hedges) on species richness and abundance of both farmland and woodland birds. For the farmland birds, this suggests that both types of hedges are important. Even hedges closer than 300 m to the nearest forest provided a nesting resource for several farmland birds (e.g. for Yellowhammer and Common Whitethroat).

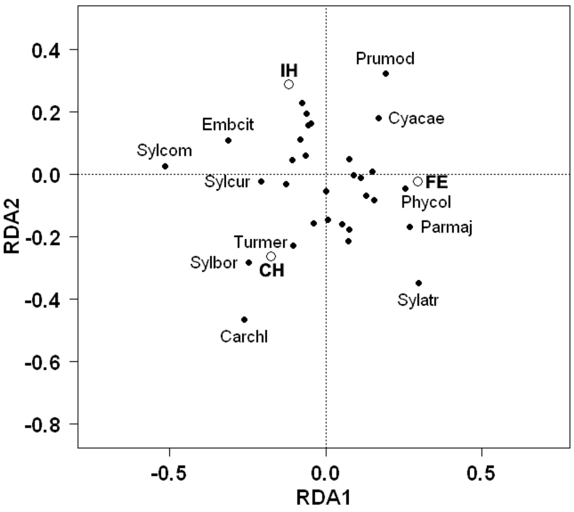


Fig. 4.1.2. RDA ordination diagram with bird species (black points) and habitat types (open circles; CH: connected hedge, FE: forest edge, IH: isolated hedge). For visibility, only bird species with the highest fraction of variance fitted by the two first factorial axes are indicated (Carchl: *Carduelis chloris*, Cyacae: *Cyanistes caeruleus*, Embcit: *Emberiza citrinella*, Parmaj: *Parus major*, Phycol: *Phylloscopus collybita*, Prumod: *Prunella modularis*, Sylatr: *Sylvia atricapilla*, Sylbor: *Sylvia borin*, Sylcom: *Sylvia communis*, Sylcur: *Sylvia curruca*, Turmer: *Turdus merula*; for English names see Table 4.1.2).

The partial redundancy analyses also showed an effect of habitat type on the birds' community composition. As expected, forest edges and hedges supported different communities and showed segregation along the first axis (Fig. 4.1.2). While some species showed a stronger response to habitat type (mainly those signed by name in Fig. 4.1.2), others did not. Fuller et al. (2001) also found that farmland and woodland plots supported distinctive bird communities, but there was considerable overlap between them in species composition. Community dissimilarity is a consequence of species-specific preferences for hedge vs. forest edge characteristics (Berg & Pärt 1994, Sparks et al. 1996), as some bird species are specialist, while others are generalist for these characteristics (Villard et al. 1999). Furthermore, some species responded differently to hedge type, i.e. they were influenced by isolation from forest. While Yellowhammer occurred mainly in isolated hedges (Bradbury et al. 2000), other species, such as Blackbird (*Turdus merula*) or Garden Warbler (*Sylvia borin*), were often recorded in connected hedges. Batáry et al. (2010a) showed a concentration effect on Yellowhammer in hedges in those landscapes, where relatively low amount of alternative semi-natural areas, such as forests, were available. Fuller et al. (2001) found that Blackbirds rather prefer hedges than woodlands, but not so extremely as Yellowhammers. Probably, this is why we registered most Blackbirds in the connected hedges, where forest habitats are nearby. Elle (2003) investigating the habitat choice of *Sylvia* species showed that Blackcap (*Sylvia atricapilla*) and Common Whitethroat do not occur syntopically in most habitats. He found Common Whitethroats mostly in shrub areas, whereas Blackcaps seemed to be more a woodland species (Cramp 1992). Our results support this finding, since Blackcaps were more abundant in forest edges than in hedges and Common Whitethroats occurred mainly in hedges regardless of hedge type. Finally, our results also suggest that the habitat requirements of Garden Warbler can be intermediate between the two former Sylvia species.

Investigating the local parameters of habitats, i.e. width and height, we did not find any significant effect, however, hedge width tended to affect slightly the woodland bird abundance. Woodland species might probably perceive wider hedges as similar to forests because of the better development of a dense understorey/herb layer there. A previous study showed that from 12 local parameters, the width of hedges was the most important for enhancing the abundance of bird species, especially that of woodland species (Barkow 2002). The height of the shrub layer did not have a high variability in our study, which was probably the reason why it did not affect the bird responses in this case (but see the review of Hinsley and Bellamy 2000).

4.1.4. Conclusions

Based on our results we emphasize the importance of hedges in conserving farmland birds in western and central Europe (Batáry et al. 2010a, but see Bas et al. 2009), but maybe not in those areas of southern or eastern Europe, where most farmland birds still depend on open habitats both for nesting and foraging (Frank and Battisti 2005, Concepción and Díaz 2010, Báldi and Batáry 2011b, Batáry et al. 2011a). Therefore we encourage German policy makers to support hedge creation and maintenance with landscape-wide management strategies supporting a diverse hedge structure, which could be part of agri-environment schemes, like in the UK (Fuller et al. 2001). Though we did not find an isolation effect of hedges on bird species richness and abundance, we showed that both connected and isolated hedges are important and benefit different species. However, we also have to emphasize that it is not enough to provide nesting sites for these birds in agricultural landscapes, but it is also necessary to consider their food diversity, amount and availability (Siriwardena et al. 2008), e.g. by grass margins next to the hedges (Perkins et al. 2002). According to Bennett et al. (2004), higher hedge density around woodlots and forests may enhance the abundance of woodland species also within the forests.

4.2. Effects of mass-flowering crops on pollination of hedge plants

In this study we aimed to assess the impact of oilseed rape on the pollination of wild plants and bee abundance during and after oilseed-rape bloom, including effects on crop–noncrop spillover at landscape and adjacent field scales. We focused on two shrub species (hawthorn *Crataegus spp.*, dog rose *Rosa canina*) and adjacent herb flowering in forest edges, connected hedges, and isolated hedges in Lower Saxony, Germany.

4.2.1. Material and methods

The study took place in the vicinity of the city of Göttingen (51.5°N, 9.9°E) in southern Lower Saxony, Germany, in 2009 (a map is available in Supplemental Material of the original paper). The area is dominated by arable fields (2-5 ha in size on average), intermingled with grasslands and remnants of deciduous forests. The most widely sown crops are winter wheat and winter oilseed rape. The forests are dominated by common beech (Fagus sylvatica), used for timber production. The agricultural matrix is characterized by hedges, which are often close to or connected to forests, but can also be situated alongside arable fields, isolated from forests. Most of the hedges and forest edges are managed regularly by pruning (every 8-15 years). The most characteristic woody plants in hedges are blackthorn (*Prunus spinosa*), hawthorn and dog rose, however, one can also find dogwood (*Cornus sanguinea*), European ash (*Fraxinus excelsior*), common hazel (*Corylus avellana*), silver birch (*Betula pendula*), elderberry (*Sambucus nigra*), European mountain ash (*Sorbus aucuparia*), etc.

To study the effects of habitat isolation of the semi-natural habitats (i.e. hedges) on pollinators and pollination success, three different habitat types were selected, representing different levels of how strongly they are embedded in the open crop landscape: forests edges (n=12), hedges connected to forests (n=11) and isolated hedges (n=12) (Fig. 4.2.1). Connected hedges were directly adjoined to forests. Isolated hedges were separated from forest patches, with a minimum distance of 300 m representing an adequate isolation for wild bees (Steffan-Dewenter and Tscharntke 1999, Gathmann and Tscharntke 2002). To consider the effects of the adjacent crop fields, half of the forest edges and hedges were selected next to winter cereal fields, the other half next to winter oilseed rape fields on at least one side. Length of connected and isolated hedges ranged from 100 to 300 m. None of the hedges was part of a longer hedge network or of green lanes with two hedges bordering dirt roads. The selected study sites had a minimum distance of 300 m to each other. Hedges and forest edges had a similar species composition of shrubs and trees, and were surrounded by similar landscape matrices, characterized by arable fields, grasslands and forest patches. Limitations in the availability of the suitable habitats precluded choosing equally oriented habitats. However, there was a random mix of hedge orientation across treatments and the great majority of the samplings and observations were done on the south or south-west orientated sides of the hedges and forest edges, getting the highest amount of sunshine during the day.

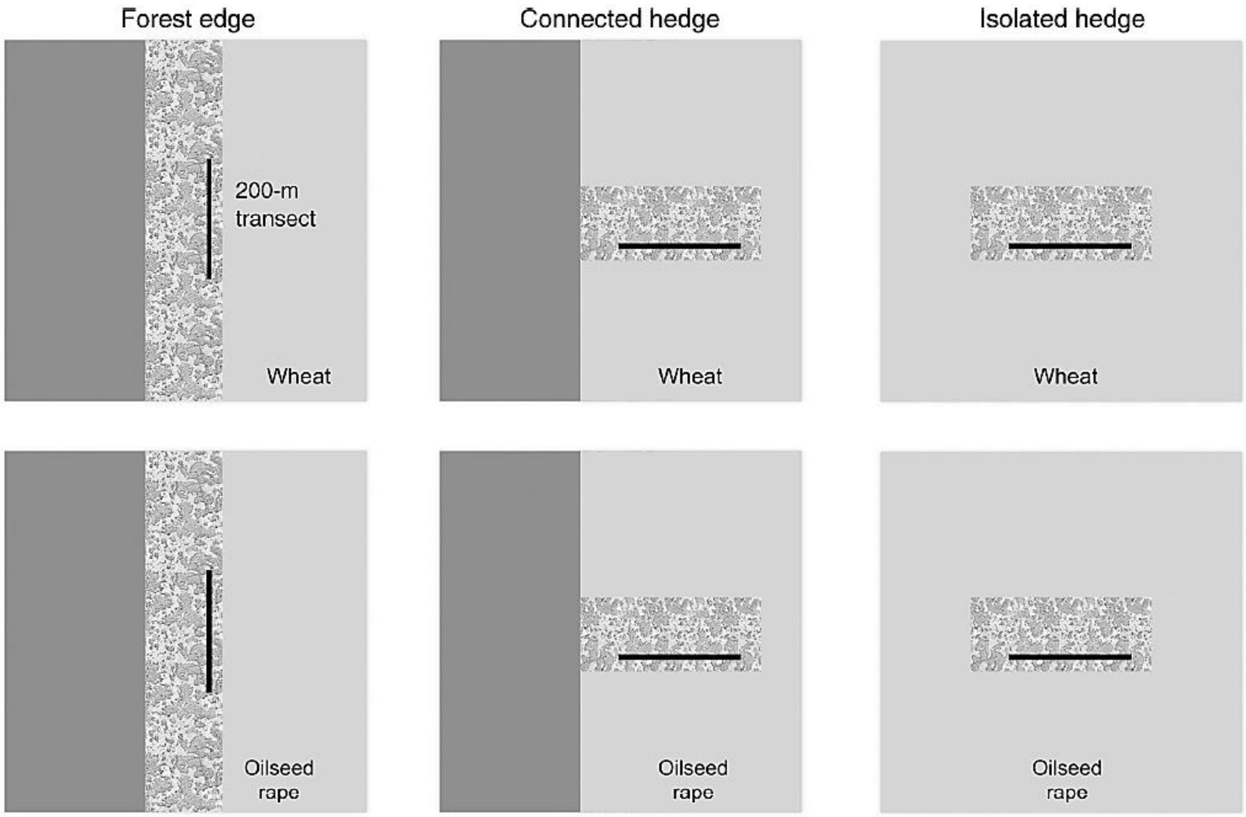


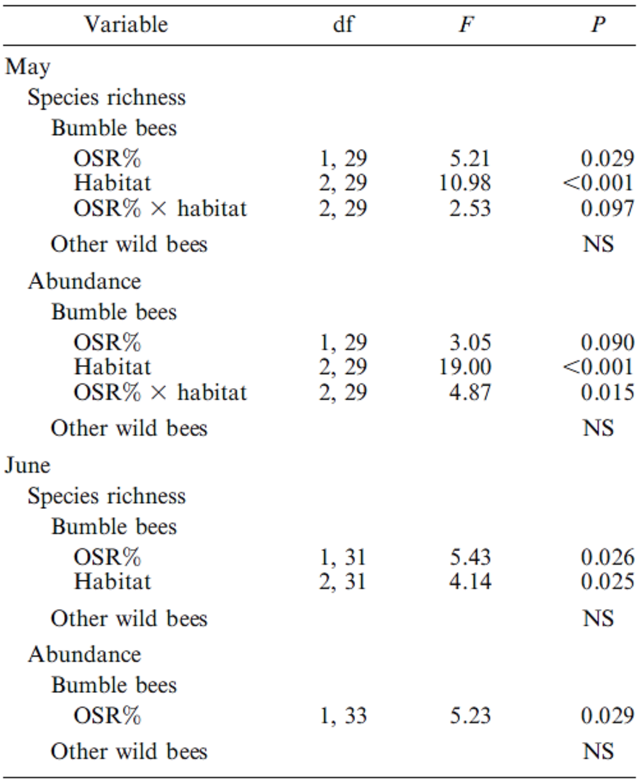
Fig. 4.2.1. The study design: spatial arrangement of the forest edges (left), connected (middle), and isolated hedges (right). Dark gray=forest, dotted gray=study site, light gray=landscape matrix: wheat (top) or oilseed rape (bottom). Flowering plants were assessed along a 200-m-transect in each study site.

Bees were sampled by coloured pan traps of 15 cm diameter and 10 cm depth during two one-week long periods in the first part of May, and also during two one-week long periods in the middle of June. Two painted white, yellow and blue pan traps, respectively, were exposed on three woody posts (two traps of the same colour on one post) along forest edges, connected and isolated hedges, ca. 100 cm above ground level and ca. 10 m apart from each other. The traps were filled with ethylene glycol-water mixture (1/4, v/v) and a small amount of detergent to reduce surface tension and enhance the effectiveness of sampling. Collected bees were taken to the laboratory and identified to species level. Data from the two sampling periods within a month and from pan traps of different colours were pooled. May data represent the period of oilseed rape flowering and June data were those collected after oilseed rape flowering. Wild bees were divided into two groups: bumble bees (i.e. *Bombus spp.*) and other wild bees (all the remaining species except honey bees).

The effectiveness of pollination was measured by determining fruit set of flowers and the seed number per fruit on one individual of hawthorn and dog rose in each site. Hawthorn was flowering in the first half of May and dog rose in the first half of June. Two branches per plant and approximately 50 flowers per branch were marked and exposed to open pollination. To test whether insect pollination adds to self-pollination, two branches per plant with similar numbers of marked flowers were bagged with a mesh bag before the beginning of the flowering period to exclude pollinators. The bags were removed after the flowering period and all mature fruits of the two bagged and the two open branches were harvested in early autumn. Due to hedge cutting in the autumn three bagged and three open dog rose branches were lost. The fruits were dried at 35°C for two weeks and then weighed. Afterwards seeds were extracted and counted. The pollination success was compared between the bagged and open branches using the following parameters: fruit set (number of fruits divided by the number of flowers of the two branches per treatment), fruit mass (average weight of dried fruits), seed number (average number of seeds per fruit) and aborted seed number (average number of immature seeds, only important in the case of dog rose). Flower-visitors were investigated on one individual (same as used in the pollination success measurements) of hawthorn and dog rose in each site during the shrub species' flowering period. Methods and results are included in Supplemental Material of the original paper.

Transects of 200 m length (if possible) were assigned in all habitat types along the hedges and forest edges (Fig. 4.2.1). The overall number of herb flowers along the transects was assessed once per pan trap sampling period and during flower-visitor survey. Flower density was assessed along the transects by estimating the number of flower heads at species level in the (h)edges and the adjacent grassy herbaceous margin of maximum 0.5 m width (only one side of the hedges, for pan trap data analyses on that side of the hedge, where traps were exposed, for flower visitor data analyses on the shrubs from the sunny side of the hedge, where samples were taken). Data from the two consecutive sampling periods within a month were pooled, taking the average number of flowers. During the flowering of hawthorn and dog rose shrubs the following flower data were assessed: abundance of conspecific flowers in the observed 2×2 m patch, and the pooled number of herb flowers. Flower species richness and the number/cover of blossoms are suitable proxies of foraging resources of bees (e.g. Ebeling et al. 2008).

Table 4.2.1. Local- and landscape-scale effects on species richness and abundance of bumble bees and other wild bees in forest edges and in connected and isolated hedges, in the vicinity of Göttingen, Germany, in May and June 2009, according to the final ANCOVA models after backward selection.



Variable	df	*F*	*P*
May			
Species richness			
Bumble bees			
OSR%	1, 29	5.21	0.029
Habitat	2, 29	10.98	<0.001
OSR% × habitat	2, 29	2.53	0.097
Other wild bees			NS
Abundance			
Bumble bees			
OSR%	1, 29	3.05	0.090
Habitat	2, 29	19.00	<0.001
OSR% × habitat	2, 29	4.87	0.015
Other wild bees			NS
June			
Species richness			
Bumble bees			
OSR%	1, 31	5.43	0.026
Habitat	2, 31	4.14	0.025
Other wild bees			NS
Abundance			
Bumble bees			
OSR%	1, 33	5.23	0.029
Other wild bees			NS

Landscape parameters were measured within a 1000 m radius around each site based on official digital thematic maps (ATKIS DTK 50) and mapping of the arable fields (based on Steffan-Dewenter et al. 2002). We calculated the percent area of oilseed rape fields (OSR%) and the percent area of non-crop habitats excluding forest interiors (i.e. grasslands and 10 m wide forest boundaries). The percent area of non-crop habitats was significantly related to habitat type (ANOVA: df=32, F=3.91, p=0.03), with lower values around the connected (Tukey post-hoc: t=-2.15, p=0.095) and higher around the isolated hedges (Tukey post-hoc: t=2.61, p=0.035) than around forest edges. Therefore we decided not to include this landscape parameter in the models. OSR% was not significantly related to the adjacent crop type (Anova: df=33, F=2.48, p=0.125).

First, we used ANCOVAs to test which predictors affected the pollinators recorded in the pan traps samples. In the models of the pan-trap analyses, response variables were the species richness and the abundance of bumble bees and of other wild bees. Predictors in all full models were adjacent crop type (oilseed rape vs. cereal), habitat type (forest edge vs. connected hedge vs. isolated hedge) along with the proportion of oilseed rape in 1000 m radius and total flower abundance (number of herb flowers along the 200 m transect) included as covariates. Pan trap data were tested separately for May and June. Abundance data were square root transformed to reach normal residual distribution.

Second, we assessed the reproductive success of hawthorn and dog rose. Reproductive success was measured as fruit set, fruit mass, seed number or number of aborted seeds (only in case of dog rose), which were used as response variables in the following analyses. T-tests for paired samples were used to assess the effect of open pollination vs. self-pollination of bagged flowers on reproductive success. ANCOVAs were used to test the effect of the predictors OSR%, adjacent crop, habitat type, total flower abundance and conspecific flower abundance in the patch on the reproductive success of open-pollinated flowers. Fruit set values of hawthorn were arcsine-transformed to reach normal residual distribution.

In all the above-mentioned analyses, two-way interactions were tested between habitat type and adjacent crop type, habitat type and OSR%, respectively. Non-significant variables (p>0.05 from F-test) were excluded in backward stepwise selection, except being part of a significant interaction. Multivariate comparisons by means of Tukey contrasts were performed between habitat types. Analyses were performed using the nlme (Pinheiro et al. 2010), multcomp (Hothorn et al. 2008) and mvtnorm (Genz et al. 2010) packages of R 2.10.1 software. An overview on all the described ANCOVA models is provided in Supplemental Material of the original paper.

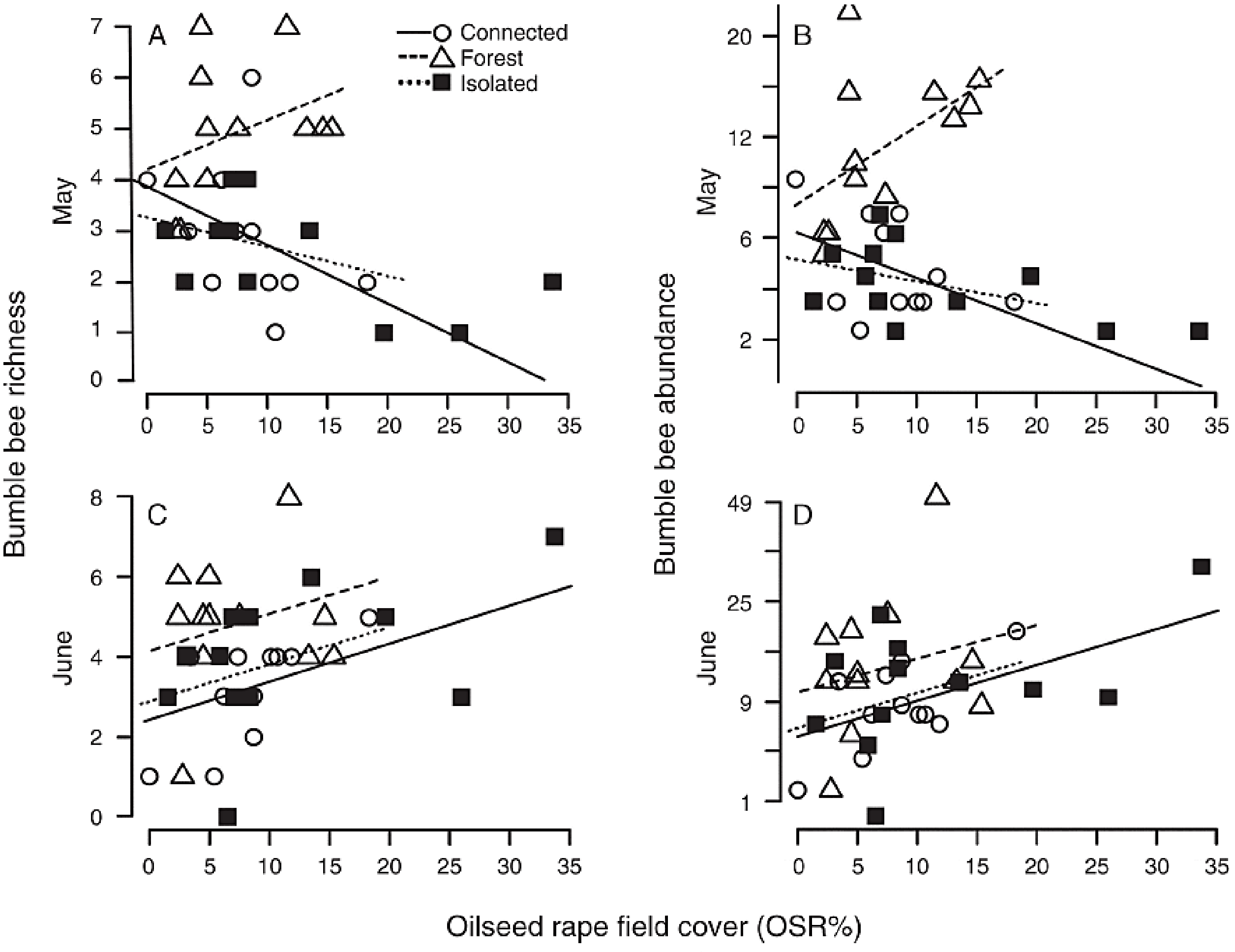


Fig. 4.2.2. Species richness (A) and abundance (B) of bumblebees in May 2009 and (C) species richness and (D) abundance of bumblebees in June 2009 in relation to percent area of oilseed rape fields in 1000 m radius.

4.2.2. Results

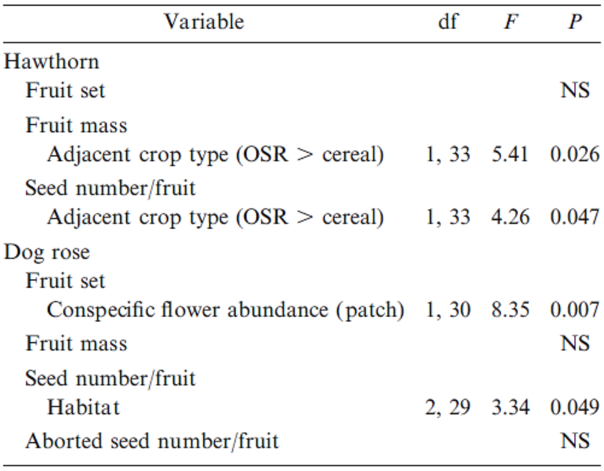
Pan traps sampled 235 individuals of 11 bumble bee species and 1315 individuals of 51 other wild bee species in May, and 421 individuals of 11 bumble bee species and 1117 individuals of 45 other wild bee species in June (abundance and species list of bees is available in Supplemental Material of the original paper). The most abundant bumble bee species were *Bombus lapidarius*, *B. pascuorum*, *B. pratorum*, and *B. terrestris agg.* in both May and June. The oilseed rape fields in the landscape (OSR%) had contrasting effects on bumble bees in May (during rape flowering) compared to June (after rape flowering). There was a significant interaction between the effects of OSR% and habitat type on bumble bee abundance in May, and a marginally significant interaction for bumble bee species richness in May (Table 4.2.1). Bumble bee abundance and species richness increased with increasing OSR% in the forest edges, and decreased with increasing OSR% in connected and isolated hedges (Fig. 2). Both species richness and abundance of bumble bees were higher in forest edges than in connected and isolated hedges in May, with differences being small for low OSR% and large for high OSR%. In June, species richness of bumble bees was also higher in forest edges than in the connected hedges (t=2.784, p=0.024), while the isolated hedges did not differ from the other two habitat types (Fig. 4.2.2). In June, OSR% had a positive effect on species richness and abundance of bumble bees in all habitat types. We found no significant difference in the abundance of bumble bees between the habitats in June. Species richness and abundance of other wild bees were not found to be influenced by any of the tested variables. The adjacent crop had no effect on the bees sampled by pan traps.

The fruit set, fruit mass and seed number per fruit of hawthorn were significantly higher for open than for bagged branches (tables in Supplemental Material of the original paper). There was no difference in fruit set of dog rose between the two treatments, however, higher fruit mass, more seeds and less aborted seeds were found in fruits from open than from bagged branches (data in Supplemental Material of the original paper).

The fruit mass and seed number per fruit of hawthorn were higher next to oilseed rape fields than next to cereal fields (Table 4.2.2; Fig. 4.2.3a, b).The seed number per fruit of dog rose was slightly higher in connected than in isolated hedges (Tukey; t=-2.37, p=0.061); the forest edges did not differ from the other two habitat types (Tukey; forest edge-connected hedge: t=-2.05, p=0.119; forest edge-isolated hedge: t=-0.27, p=0.959). Fruit set of dog rose was positively related to the number of dog rose flowers in the observed patch.

4.2.3. Discussion

In this study we focused on the effects of flower resources on overall species richness and abundance of bees in hedges and forest edges and pollination success of three shrub species at three spatial scales: effects of oilseed rape at the landscape and adjacent crop field scale, and the local scale effects of hedge plants. At the landscape scale, effects on bumble bees in hedges and forest edges depended on whether oil seed rape was flowering at the time or had ceased flowering and on the habitat types forest edges and hedges. At the adjacent field scale, oilseed rape had positive effects on fruit mass and seed number per fruit in hawthorn growing in forest edges and hedges. The abundance of local wild flowers of hedge plants enhanced the fruit set of dog rose, particularly of conspecific flowers in the direct surrounding of the focal shrubs.



Variable	df	*F*	*P*
Hawthorn			
Fruit set			NS
Fruit mass			
Adjacent crop type (OSR > cereal)	1, 33	5.41	0.026
Seed number/fruit			
Adjacent crop type (OSR > cereal)	1, 33	4.26	0.047
Dog rose			
Fruit set			
Conspecific flower abundance (patch)	1, 30	8.35	0.007
Fruit mass			NS
Seed number/fruit			
Habitat	2, 29	3.34	0.049
Aborted seed number/fruit			NS

Table 4.2.2. Final ANCOVA models on the different parameters of pollination success of hawthorn and dog rose flowers available to pollinators in forest edges and in connected and isolated hedges.

Our study showed strong and mixed landscape-scale effects of percent area of oilseed rape fields on bumble bees recorded in pan traps. During oilseed rape flowering in May, a higher percent area of oilseed rape had a negative effect on bumble bee species richness and abundance in hedges, but a positive effect in forest edges. In June, when oilseed rape had ceased flowering, percent area of oilseed rape had a positive effect on bumble bee species and individuals in all three habitat types (hedges and forest edges).

We suppose that the negative landscape-scale effect of oilseed rape on bumble bees in our hedges during oilseed rape flowering is due to of the dramatically enhanced resources supplied by mass-flowering oilseed rape. Our results suggest that the distribution of pollinators depends on the amount of oilseed rape in bloom: in landscapes with high amounts of oilseed rape, pollinator abundances per area hedge decline because pollinators are attracted to the oilseed rape fields. Thus, our results suggest that competition between oilseed rape and wild shrubs is higher in landscapes with high amounts of oilseed rape. Bumble bee abundance declined in oilseed rape fields, when the percent area of oilseed rape was high at the landscape scale during oilseed rape flowering (Holzschuh et al. 2011). Here, we show that competition for bumble bee pollinators results in a transient decline in visitation to flowers or captures in pan traps in semi-natural habitats like hedges, when oilseed rape is flowering.

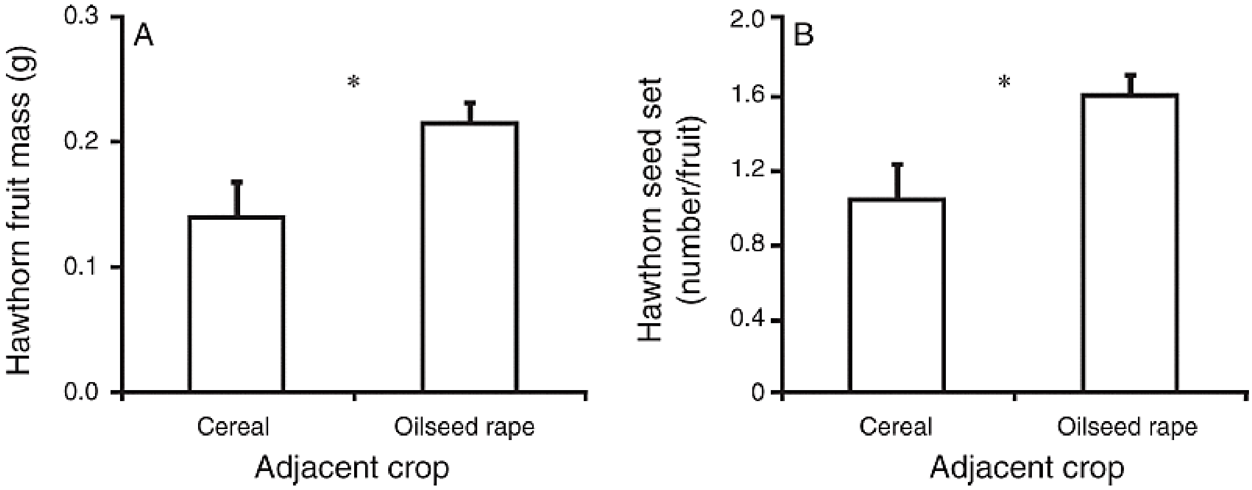


Fig. 4.2.3. The (A) seed number per fruit and (B) fruit mass of hawthorn in relation to crop type (oilseed rape vs. wheat). Stars indicate significant differences.

In contrast to hedges, bumble bee abundance in forest edges increased with increasing percent area of oilseed rape in the landscape, and was generally higher in forest edges than in hedges. Forest edges might provide more extended nesting and foraging habitat compared to hedges. An increased abundance of bumble bees in forest edges surrounded by high percent area of oilseed rape suggests increased nesting activity and enhanced growth of new colonies due to the increased availability of nectar and pollen resources in the landscape (Westphal et al. 2009).

After oilseed rape flowering, species richness and abundance of bumble bees in both the hedges and forest edges were positively affected by percent area of oilseed rape in the landscape. Semi-natural habitats represent continuous foraging resources for bumble bees when flowering crops are not available (Corbet 2000), resulting in spillover and concentration of bumble bees in the semi-natural habitat patches. Our result corresponds with former studies, which showed great benefits of mass-flowering crops, especially oilseed rape, in terms of subsequent bumble bee densities in semi-natural habitats (Westphal et al. 2003, Herrmann et al. 2007, Diekötter et al. 2010a, Goulson et al. 2010), deviating from the general assumption that social wild bees do not profit from annual crops because of the short flowering time (Corbet 2000).

In contrast to bumble bees, we did not find a landscape-wide oilseed rape effect on the species richness and abundance of other wild bees. Other wild bee species, most of them of smaller body size, forage in the vicinity of their nesting sites, being more dependent on local conditions and less sensitive to landscape-scale crop structure (Gathmann and Tscharntke 2002). Therefore, solitary bees are more likely to be influenced by intermediate-scale oilseed rape effects, showing increased diversity and abundance in semi-natural grasslands adjacent to oilseed rape fields (Holzschuh et al. 2011).

The fruit mass and the seed number per fruit of hawthorn were higher adjacent to oilseed rape fields than next to cereal fields. Hawthorn was flowering simultaneously with oilseed rape, therefore the adjacent flowering oilseed rape fields might have had a facilitation effect on the reproductive success of hawthorn. Hanley et al. (2011) described higher bumble bee visitation rate to wild flowers in field margins next to mass-flowering bean fields than adjacent to wheat, suggesting that mass-flowering crops facilitate pollinator spillover into adjacent semi-natural habitats during their flowering. However, Hanley et al. (2011) did not study the effects of pollinators on plant reproduction. Our study supports Cussans et al. (2010) finding positive local effects of oilseed rape during its flowering on the reproductive success of a simultaneously flowering wild plant species. Adjacent oilseed rape in flower might have served as a highly attractive magnet plant as it is known from abundantly flowering invasive plants, which can also facilitate the visitation and pollination of neighbouring native plants by attracting high numbers of pollinators (Bartomeus et al. 2008).

Considering the right spatial scale and differences in pollinator guilds, however, it is important to access the effects of oilseed rape on the reproduction success of co-flowering plants. In contrast to the positive adjacent field scale effects of oilseed rape that we found on directly adjacent hawthorn, Holzschuh et al. (2011) found a negative landscape-scale effect of oilseed rape on the mainly bumble bee-pollinated cowslip (*Primula veris*). During mass flowering, oilseed rape might have positive (magnet) effect on pollinator abundance and pollination success at adjacent field scale, but negative (competition) effect at the landscape scale. Whether pollinators and pollinator-dependent plants are influenced on the adjacent field or the landscape scales, might depend on the mobility of the pollinators. Therefore, wild plant species like cowslip, which are mainly pollinated by large mobile bumble bees, might be affected at landscape scales, while plant species like hawthorn, which are also frequently visited by small solitary bees, are rather affected at smaller scales.

We found higher fruit mass, more seeds and fewer aborted seeds in fruits from open than from bagged branches, however, the higher abundance of pollinators in hedges and forest edges adjacent to oilseed rape fields did not translate to increased fruit and/or seed production of dog rose. Spillover of arthropods subsidized by a managed agricultural land to the adjacent semi-natural habitats has already been described in the case of insect natural enemies (Rand et al. 2006) and pollinators (Hanley et al. 2011). However, a positive effect on pollinators of a wild plant flowering after the mass-flowering crop has not been described yet. Hanley et al. (2011) compared bumble bee activity along hedgerow transects adjacent to mass-flowering field bean and wheat fields, but they found no difference two weeks after bean flowering.

The conspecific flower abundance had a positive effect on the fruit set of dog rose, which might be attributed to the increased flower-visitation by the higher abundance of flower-visiting insects. The higher number of flowers and the amount of available pollen might increase fruit set, showing a facilitation effect (Bjerknes et al. 2007). However, differences in pollinator generalization levels and main pollinators result in species-specific response of the focal shrub species to the co-flowering neighbourhood (Lazaro et al. 2009). The self-compatible flowers of dog rose set fruits even without pollinators, while the self-incompatible flowers of hawthorn set no fruits without insect pollination. The fruit set of hawthorn was significantly enhanced by the abundance of flower-visitors, in correspondence with findings of Jacobs et al. (2009).

4.2.4. Conclusions

We conclude that considering the right scale is important when effects of mass-flowering crops on pollinators and pollination success of wild plants are evaluated. At the landscape scale, flowering of oilseed rape resulted in a lower number of bumble bees in the hedges. However, at the adjacent field scale, pollinators show crop-noncrop spillover. Our results on hawthorn suggest that the consequent higher number of bees might increase the pollination success of wild plants in the neighbourhood hedges and forest edges. However, this has to be tested for further plant species. After the flowering of oilseed rape, the value of wild flower resources in hedges and forest edges for foraging bees increases as demonstrated by their general spillover from the oilseed rape fields and increase in these still flower-rich semi-natural habitats.

The total area planted in oilseed rape has considerably increased due to the increased demand for bioenergy. Understanding the effects of this mass-flowering crop on biodiversity is therefore critical. Given the potential impacts of oilseed rape on wild plants high amounts of mass-flowering fields in the landscape around nature reserves are critical to the preservation of wild species. Future agri-environmental management should consider the pros and cons in evaluations of landscape-scale configuration and composition of crops. Conservation measures should give on the one hand more attention to the allocation and maintenance of semi-natural habitat elements like forest edges and hedges in the agricultural landscape and provide through continuous flower resources for pollinators even after the flowering of mass-flowering crops. On the other hand enhancement of the diversity of flowering plants is recommended due to reasonable hedge management in the form of diverse shrub communities and wide grassy margins along the hedges and forest edges.

5. Comparing effectiveness of agri-environment management in cropland and grassland

Most landscape ecological studies in farmland focus on only one target habitat or land use type. In this chapter, however, we explore similarities and differences in local management actions and landscape scale effects in two broadly available, but from several aspects very different agroecosystems, namely grasslands and cereal fields.

5.1. Management effects on arthropods in Hungarian grasslands and cereal fields

Modern agriculture is one of the main anthropogenic threats to biodiversity. To explore the effects of agricultural intensification we investigated carabids and spiders in two studies; in 2003 in grasslands and two years later in cereal fields in the same region. Both aimed to study the effect of management on arthropod diversity and composition at local and landscape scales.

5.1.1. Material and methods

In 2003 extensively and intensively grazed grasslands were compared in three different biogeographical regions of the Hungarian Great Plain. In the current study we analyse only one region (middle third of Danube valley, Kiskunság NP, Báldi et al. 2005), where two years later a study in cereal fields was performed (Kovács et al. 2007, Fig. 5.1.1). The whole region, the so called Upper-Kiskunság Plain, is a part of the vast alkali lowland plain of the Great Hungarian Plain. The most important parts of the region from a nature conservation point of view are the large grasslands (up to many hundreds of hectares), termed as “puszta”, where traditional grazing methods still persist. The “puszta” habitat is characterised by common grass species like the false sheep’s fescue (*Festuca pseudovina*) and bermudagrass (*Cynodon dactylon*), and is scattered with large croplands (up to many tens of hectares), roads, canals and built-up areas, resulting in a large-scale habitat mosaic.

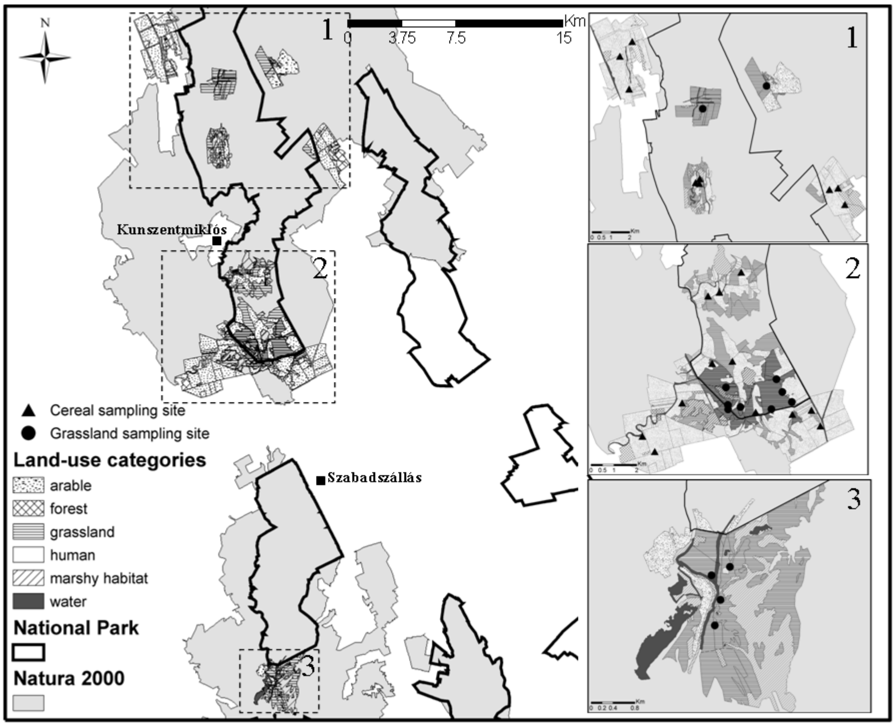


Fig. 5.1.1. Map of the study areas showing the sampling sites of the grassland and cereal field studies, land-use types, National Park and Natura2000 borders.

In the grassland study seven pairs of extensively (max. 0.5 cows/ha) and intensively (min. 1 cow/ha) grazed grasslands were compared in a paired design. None of the grasslands were fertilised, sprayed or reseeded. Both ‘intensive’ and ‘extensive’ grassland types are managed at a relatively low intensity level compared to Western European standards, where the stocking rates even on extensive sites exceed 1 cow/ha (e.g. Kruess and Tscharntke 2002, Grandchamp et al. 2005). Carabids and spiders were sampled using funnel traps opened for three 2-week collecting periods during spring and early summer in 2003 (for trapping method see Obrist and Duelli 1996, Batáry et al. 2007a). On each field, samples were taken with two traps: one at the edge (but within the grassland) and the other 50 m away in the interior (altogether 7 pairs × 2 fields × 2 traps × 3 periods = 84 trap samples). For all analyses in-field (edge and interior) traps were pooled.

In the cereal field study in 2005 we used a gradient design. Seven land-use intensity categories within five farms were chosen. The farmers were asked to fill out a questionnaire about the use of fertilisers (nitrogen input in kg/ha/year with seven intensity options: 0, 34, 68, 92, 100, 113 and 270) and pesticides (no insecticide was used before the field samplings). In all intensity categories we chose three autumn-sown cereal fields, with the exception of two categories, in which samples were taken from only one (0 N kg/ha/year) or two (113 N kg/ha/year) fields, due to the limited number of the available fields. In both cases the same number of traps as in the other intensities was used (the minimum distance between pairs of traps were at least 200 m). On each field, samples were taken with two funnel traps using the same procedure as for the grassland study, with two 2-week collecting periods (altogether 7 intensities × 3 fields × 2 traps × 2 periods = 84 trap samples). For all analyses in-field traps were pooled. In both studies adult carabids and spiders were identified to species level (Heimer and Nentwig 1991, Ádám 1996).

In both studies five local factors were measured along 95 m long transects (Báldi et al. 2007, Kovács et al. 2007). All fields had one transect in the edge and one 50 m away from the edge. In each transect ten 1 × 5 m plots were established at five meter intervals. In June 2003 and June 2005 we estimated the cover of each plant species (in the analyses total plant cover, total weed cover and species richness were used), bare ground (%), and height of vegetation (cm). In the cereal field study the weed plus wheat cover was measured, and in the grassland study the plant litter cover (%) (Table 5.1.1). In the cereal field study we had the questionnaire data about the amount of fertiliser and pesticide application, whilst in the grassland study we distinguished between levels of grazing intensity (extensive vs. intensive).

Table 5.1.1. Environmental variables at local and landscape scales used as explanatory variables in the analyses on biodiversity. Landscape scale variables were grouped according to landscape composition and landscape configuration.

Group of variables	Variable	Description
Local	Plant species richness	Species richness of plants in grassland study
		Species richness of weeds in cereal field study
	Cover	Cover of plants, bare ground and litter in grassland study
		Cover of vegetation (weed+wheat), weeds and bare ground in cereal field study
	Vegetation height	Mean grass height in grassland study
		Mean vegetation height in cereal field study
	Management	Grazing intensity (extensive/intensive) in grassland study
		Fertiliser amount in cereal field study
Landscape composition	% of land-use types	% of arable, built-up area, forest, grassland, marshland and open water
	Diversity of land-use types	Shannon diversity of land-use types
Landscape configuration	Patch density of land-use types	No. of arable, built-up area, forest, grassland, marshland and open water
	Mean area	Mean area of arable, forest, grassland and marshland
	Length of boundaries	Total length of all boundaries

Eighteen landscape parameters were measured within 500 m circles around every fields based on aerial photographs (for more details see Batáry et al. 2007b). Six land-use types were considered: arable field, grassland, forest, marshland, built-up area and open water. On the landscape scale we distinguished parameters according to landscape composition and configuration as in other studies (Batáry et al. 2008, Concepción et al. 2008). Landscape composition variables describe the actual amount of each land use type within the landscape, without being spatially explicit. The landscape configuration shows the physical distribution or spatial character of patches within the landscape (Concepción et al. 2008). Percentage area and Shannon diversity of these land-use types were defined as landscape composition metrics (Table 5.1.1). The number of patches of the above mentioned land-use types, mean area of arable, forest, grassland and marshland and total length of boundaries were grouped as landscape configuration metrics.

To analyse the species richness and abundance of the two taxa, general linear mixed models were applied, using similar models for both studies. From the local scale variables, grazing intensity (extensive vs. intensive) in the grassland study was used as a fixed factor, and N input (kg/ha/year) in the arable study as a fixed covariate. From the landscape scale variables land-use diversity was used as a fixed covariate. In both studies we applied a nested design. In the grassland study the trapping period was the first random factor and field pair was the second. In the case of the cereal field study we used the random factors of period/farmer/field. The normality of the distribution of the model residuals was assessed using normal quantile plots, and raw data were log-transformed when necessary (see Kéry and Hatfield 2003). The calculations were made using R (version 2.2.1; R Development Core Team 2006) and the nlme package for R (version 3.1; Pinheiro et al. 2007).

Table 5.1.2. Mean ± SE of species richness and abundance of carabids and spiders detected in the grassland and cereal field studies in the Kiskunság Plain, Hungary.

	Species richness		Abundance	
	Grassland study	**Cereal field study**	**Grassland study**	**Cereal field study**
Carabids	6.48 ± 0.47	9.50 ± 0.64	20.67 ± 2.50	33.45 ± 4.89
Spiders	10.07 ± 0.56	13.26 ± 0.68	58.52 ± 4.99	34.38 ± 2.52

To measure the influence of environmental variables on different farmland beetle and spider species composition constrained ordinations were performed. We conducted separate analyses for the two taxa and for the two studies. Only those species which occurred in more than five traps from the total 42 traps were included in the analyses. Abundance data were log-transformed prior to analysis to improve normality of response variables. We conducted separate DCA (Detrended Correspondence Analyses) for all four species dataset to decide which constrained ordination model should be applied (Lepš and Šmilauer 2003). In all cases the redundancy analysis (RDA) proved to be the appropriate method.

Table 5.1.3. General linear mixed models on the effects of management intensity (extensive or intensive grazing regime in the grassland study and fertiliser use (kg N/ha/year) in the cereal field study) and landscape (land-use diversity) of Hungarian grasslands and autumn-sown cereal fields. Type: direction of the significant effect. df: denominator degrees of freedom.

	Management				**Landscape**			
	F	***df***	***p***	**type**	***F***	***df***	***p***	**type**
Species richness								
Grassland carabids	64.868	19	< 0.001	+	1.957	19	0.178	
Grassland spiders	0.343	19	0.565		0.800	19	0.382	
Cereal field carabids	1.197	25	0.284		0.021	5	0.891	
Cereal field spiders	4.442	25	0.045	–	1.036	5	0.355	
Abundance								
Grassland carabids	5.834	19	0.026	+	19.426	19	< 0.001	+
Grassland spiders	1.511	19	0.234		0.053	19	0.820	
Cereal field carabids	3.273	25	0.083		0.359	5	0.575	
Cereal field spiders	2.877	25	0.102		0.065	5	0.809	

In all four indirect gradient analyses (grassland beetles, grassland spiders, cereal field beetles, cereal field spiders) we performed separate analyses to eliminate those environmental variables that do not explain variation (based on Monte Carlo permutation tests with 999 permutations; Jeanneret et al. 2003a,b, Aviron et al. 2005). Separate analyses were done for local variables, for landscape composition variables and for landscape configuration variables. Variables that contributed significantly ($p < 0.05$) to the pattern of species composition were included in the global ordination. From the used variables which showed strong correlation ($r > 0.7$) with each other, only those which had the highest correlation values with RDA axes were selected for partial RDA. Finally, in the partial RDA, the variance explained by each variable and its significance (Monte Carlo permutation tests with 999 permutations) was obtained after eliminating the variance explained other variables, which were used as co-variables (partial variables). Since differences in species composition caused by different sampling periods were not the focus of this study, sampling periods were used as dummy co-variables. DCA and RDA calculations were performed using Canoco 4.54 (ter Braak & Šmilauer 2002).

5.1.2. Results

Spiders and carabids species richness was higher in the cereal fields than in the grasslands (Table 5.1.2, for complete species list see Supplementary Material of the original paper). Abundance of carabids was also higher in the cereal fields, whilst spider abundance trapped was higher in the grasslands.

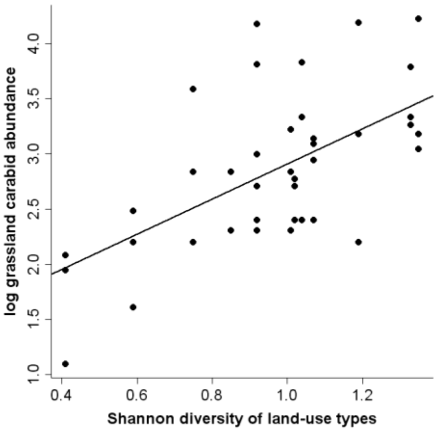


Fig. 5.1.2. Fitted regression line of general linear model on the relationship of land-use diversity within 500 m buffer area of grassland study sites and grassland carabid abundance on logarithmic scale ($Y = 1.32 + 1.59 * Lg(X)$, $F_{1,19} = 19.426$, $p = 0.0003$, $n = 42$).

In the grassland study, the higher grazing pressure had a significant positive effect on species richness and abundance of carabids (Table 5.1.3). Further, the increasing land-use diversity had a significant positive effect on the abundance of carabids (Fig. 5.1.2). Spider abundance and diversity in the grassland study was neither affected by management nor by land-use diversity. The same was true for the spider abundance in the cereal field study, however here the increased fertiliser had a significant negative effect on species richness (Fig. 5.1.3).

After variance partitioning with partial RDA for the grassland carabids, one landscape configuration variable (mean area of marshlands) and two local variables (management and bare ground cover) explained the greatest part of variation (Fig. 5.1.4). Among the landscape composition variables, the only significant variable was the land-use diversity. Contrary to the grassland carabids, in grassland spider communities the landscape composition variables (% arable and % forest) were the most important. However, local variables (plant species richness and plant cover) and landscape configuration variables (built-up area density and total length of boundaries) also explained a significant part of variation. In the case of cereal field carabid communities, landscape composition variables (% grassland, % forest and % open water) also explained most of the variation, but the local variable wheat height and the landscape configuration variable mean area of forests also had significant effects. Finally, the cereal field spider communities were affected mostly by local variables (weed species richness and wheat height). Two landscape configuration (grassland density and area of forests) and one landscape composition (% forest) variables also had significant effects.

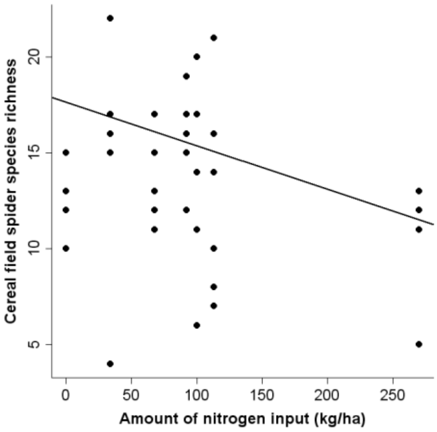


Fig. 5.1.3. Fitted regression line of general linear model on the relationship of fertiliser use (kg N/ha/year) and cereal field spider species richness on autumn-sown cereal fields ($Y = 17.65 – 0.02 * X$, $F_{1,25} = 4.442$, $p = 0.0453$, $n = 42$).

5.1.3. Discussion

In the present study we analysed the effects of land-use intensification at local and landscape scales on the carabid and spider fauna of Central Hungarian farmlands. In 2003, grassland sampling with paired fields was performed in which we found effects on species richness and abundance of carabids, but not on spiders at either scales (Batáry et al. 2007a, Batáry et al. 2008). Direct gradient analyses showed the importance of environmental variables at both scales on both taxa. The latter situation was true for the cereal field study performed two years later in the same biogeographical region with the same sampling effort, but with a gradient design. However, analyses on species richness and abundance in the cereal field study showed changes only for spiders at the local scale.

Looking at our GLM results in more detail, the interesting positive effect of higher grazing pressure found on carabid species richness and abundance could most probably be explained by the very small difference in grazing intensity between the intensive (min. 1 cow/ha) and extensive (~0.5 cow/ha) paired fields compared to Western European standards. In a study by Kruess and Tscharntke (2002), the grazing intensity in Germany defined intensive as 5.5 cows/ha and extensive as 1.4 cows/ha, whilst average grazing intensity in a study by Grandchamp et al. (2005) comparing mown vs. grazed plots in the Swiss Pre-Alps, was deemed to be 1.4 cows/ha. In contrast to these, all of the grasslands investigated in this study were pesticide and fertiliser free, i.e. can be termed as "semi-natural" habitats. Analysing all three regions together, we found no management effects either on specialist or generalist carabids (Batáry et al. 2007a), therefore the positive effect found in this study is region specific. These grasslands probably require this level of grazing disturbance to attain such an elevated level of species richness and abundance. Similar to the present result, Grandchamp et al. (2005) showed that cattle density was positively related to the number of carabid species in grazed montane meadows in the Pre-Alps.

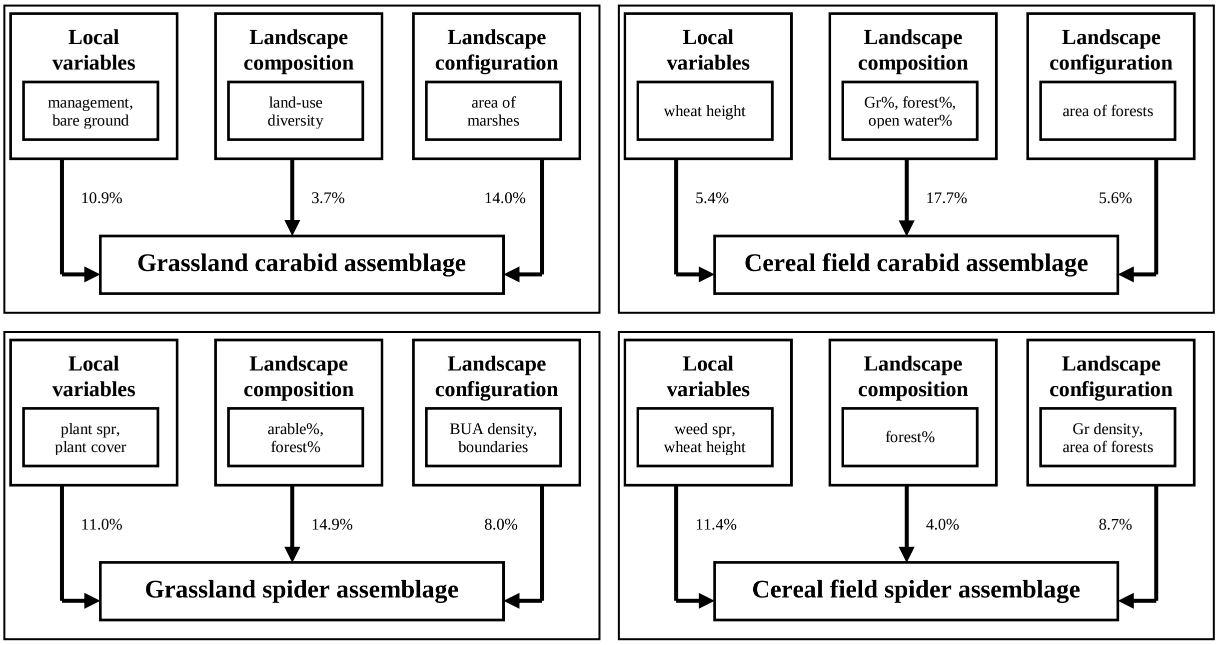


Fig. 5.1.4. Four synthetic models of correlative relations between environmental variables and carabid and spider assemblages of grasslands and cereal fields, based on partial RDA. Abbreviations: Gr: grassland; spr: species richness; BUA: built-up area.

The absence of management and landscape scale effects on cereal field carabids is intriguing, especially taking that into account that there was a relatively large variation in the amount of fertiliser applied and a similar range in land-use diversity to the grassland study. The most probable explanation is that the studied cereal fields surround the above mentioned semi-natural grasslands, from where strong immigration is presumed, i.e. mass and spillover effect (Shmida and Wilson 1985, Zonneveld 1995, Tscharntke et al. 2005b). Considering the spillover of predator arthropods from grasslands to cereal fields we would suspect that with increasing landscape diversity this spillover effect would intensify. We could not demonstrate this intensification of spillover effect at landscape scale, however, at a finer edge scale we found significantly higher species richness and higher abundance of both taxa in the cereal field edges than in the interiors (Kovács et al. 2007).

Among spiders only the species richness was significantly negatively affected by management in the cereal field study. Clough et al. (2005) did not show management effect on spiders comparing organic and conventional wheat fields (despite the large difference in N fertilisation: organic: ~40 kg/ha and conventional: ~175 kg/ha; for fertiliser amount in Germany and other countries see Kleijn et al. 2006), but found a positive effect of non-crop area. Schmidt et al. (2008) also reported that local species richness was enhanced by non-crop habitats on a landscape scale. In our case the absence of landscape scale effect in the cereal field study could be linked with the strong spillover effect from neighbouring grasslands. Considering the local scale management results of the current analyses, we found that in the grassland study the "increased" management intensity has neutral or positive effects on arthropod richness and abundance. Turning these grasslands into low intensity arable fields surrounded with semi-natural grassland could further increase these numbers up to a point, after which they will decrease. However, we have to emphasize that the land conversion from grassland to low intensity arable fields would probably result in a serious loss of stenotypic and specialist grassland fauna (Duelli and Obrist 2003, Tscharntke et al. 2005a, Batáry et al. 2007a).

The species richness, abundance and community composition of grassland carabid assemblages were affected by grazing management and land-use diversity. Aviron et al. (2005) investigating the carabid communities in different agricultural landscapes, found that landscape units (25 km2 areas of contrasting landscape structure) and habitat types had higher effects on community composition than landscape composition, similar to our result. This was not the case in the cereal field study, where no effects were found on carabid species richness and abundance at either scales, however landscape composition scale variables were the most important factors influencing carabid community composition. Similarly to Aviron et al. (2005), Jeanneret et al. (2003a,b) found that habitat type is a very important explanatory factor of community composition for both beetles and spiders. The type of land-use in the surroundings also had significant effect, but only on carabids. Looking at the local variables of both cereal field taxa, we found that both plant and weed species richness are important factors, supporting the results of Jeanneret et al. (2003a). In our case, plant cover and wheat height were also significant. Dennis et al. (2001) also found that besides stocking rate and botanical composition, the vegetation height determines the arachnid composition in Scotland. Finally, with exception of grassland beetle communities, in the other three cases the importance of forests is conspicuous. Öberg et al. (2007) argued that forests could serve as important source habitats for lycosid spiders in Swedish agroecosystems. Isaia et al. (2006) showed that landscape heterogeneity, mostly related to the presence of woods, seem to be the most important environmental factor for spider communities of Italian vineyards. Finally, we think that the similar environmental variables affecting the alkali grassland and cereal field arthropod communities could be connected with their common annual dynamics: both are productive in springtime, and both are disturbed until summer, either by harvest or by drying out (Samu and Szinetár 2002).

5.1.4. Conclusions

Summarizing our results, increasing management intensity affected the richness and the abundance of grassland carabids positively and the richness of cereal field spiders negatively. It also affected the species composition of grassland carabids. We consider that the recently introduced national agri-environmental schemes to be potential tools, which could contribute to the conservation of valuable fauna in this region. Although this is a correlative study, we think that current and future agri-environmental schemes should be concentrated on cereal field extensification to compose a buffer zone around the semi-natural grasslands, at least in this biogeographic region. Further, agri-environmental schemes should support the maintenance of extensive grazing. To conclude, we agree with Tscharntke et al. (2005a) that in diverse and complex landscapes (> 20% non-crop habitat) extensive farming appears to have a minimal or non-measurable enhancement effect on species diversity compared to intensive farming, therefore it should be implemented in more monotonous landscapes.

5.2. Responses of plants and arthropods to management in crops and grasslands

There are more and more multitaxa and multiscale studies performed in agricultural landscapes investigating management and landscape effects (see above). However, most of them focus on one agroecosystem (e.g. Diekötter et al., 2010b; Rundlöf et al., 2010). Here we investigated both cereal fields and grasslands at the same time, and tested the effectiveness of organic farming along a gradient in landscape management intensity.

5.2.1. Material and methods

Nine landscapes were selected along a landscape scale management intensity gradient (percent intensively used agricultural area, IAA%) within a 35 km radius of the city of Göttingen, Lower Saxony, Germany (for a map see Supplementary Material of the original paper; for landscape structure parameters, see Table 5.2.1). In each landscape, a pair of conventional and organic winter wheat fields and a pair of conventional and organic meadows were chosen in close vicinity to each other (within-pair distance of wheat fields (mean ± SEM): 716 ± 185 m; within-pair distance of meadows: 715 ± 185 m; distance between wheat fields and meadows within the same landscape: 1101 ± 109 m). The two pairs per landscape resulted in 36 fields and belonged to 24 farmers (most farmers managed mixed farms). This double paired design allowed comparing organic and conventional managements of the two most frequent agroecosystem types.

Table 5.2.1. Summary data of environmental variables describing land-use and landscape structure of organic and conventional wheat fields (n = 9+9) and meadows (n = 9+9) in central Germany. Land-use (arable %, grassland %, intensive agricultural area %) was calculated for buffer areas with a 500 m radius around the study sites. Means ± SEM are given.

	Wheat		Meadow	
	Organic	Conventional	Organic	Conventional
Fertiliser (kgN/ha)	44 ± 22	209 ± 22	29 ± 19	116 ± 30
No. pesticide application	0	4.8 ± 1.0	0	0.3 ± 0.1
Cereal yield (dT/ha)	44 ± 5	80 ± 7	–	–
Mowing frequency	–	–	1.7 ± 0.3	2.8 ± 0.3
No. grazed fields[a]	–	–	6	4
Field size (ha)	2.9 ± 0.8	3.1 ± 1.1	2.2 ± 0.3	2.4 ± 0.3
Arable %	74.6 ± 6.8	73.9 ± 5.6	62.1 ± 6.9	62.1 ± 5.3
Grassland %	11.1 ± 3.0	16.4 ± 4.2	18.5 ± 3.4	25.1 ± 4.0
Intensive agricultural area %	79.3 ± 6.0	87.0 ± 3.9	72.5 ± 6.0	80.5 ± 4.0

The study area was characterised by an agricultural mosaic of mostly intensively used arable crops and fertile meadows, which also contained forest remnants and small fragments of semi-natural habitats such as naturally developed fallows, field margin strips and hedges. Based on official digital thematic maps (ATKIS DTK 50) the landscape surrounding each field was characterized within a circle of 500 m radius using ArcGIS 9.2 (ESRI, 2006). This distance has been found suitable to analyse landscape effects on species richness and abundance for a wide range of taxa (Concepción et al., 2008; Schmidt et al., 2008). The centre of the 500 m radius buffer was in the mid-point of the rectangle formed by the two transects in each field (see section 2.2). The proportion of arable land, grassland and intensively used agricultural area (IAA %, proportion of conventionally managed crop fields and grasslands) in a 500 m radius area did not differ significantly between organic and conventional fields for wheat fields or for meadows (Table 5.2.1; t-test for paired samples, p > 0.05).

The selected organic and conventional wheat fields received twice as much nitrogen fertiliser as meadows, while conventionally managed fields received about four times more fertiliser than organic ones (Table 5.2.1). Organic fields were all managed without pesticides and synthetic fertilisers. Management of meadows included mowing 1–4 times from mid-May. Conventional meadows were in a few cases treated with herbicides and were mown more often than organic meadows, while on the latter ones, grazing by cattle occurred more frequently (Table 5.2.1).

On each field one edge (in the first wheat row or in the meadows next to the edge) and one field interior transect (30 m into the centre and parallel to the edge) were surveyed in June 2008. In each transect four 5×1 m plots (288 plots in total) were established, spaced 12 m apart. Field edges were bordered by grassy field margins. Cover of each plant species (%), bare ground (%) and cover of cereal (%) were estimated in each plot. Subsequently, relative cover of each species and the total number of plant species (i.e. species richness per 20 m2) were determined for each transect. Relative cover (%) per species was calculated by dividing the cover of the given species by total plant cover plus bare ground cover and also wheat cover in case of wheat fields. Plant species were grouped into grasses and forbs.

Ground beetles (Carabidae) and spiders (Araneae) were sampled using funnel traps (10 cm diameter). Funnel traps are a modification of more conventional pitfall traps, and have a funnel reducing escape rates. They are up to three times more efficient per centimetre trap diameter in catching ground beetles (Obrist and Duelli, 1996). One funnel trap was placed in the centre of each botanical plot and was opened over a one week sampling period (9 June 2008, ± 2 days). The trapping fluid was ethylene glycol (antifreeze) diluted with water (1/2 v/v). All carabids and adult spiders were identified to species level. Carabid species were sorted to functional groups according to their feeding type following Purtauf et al. (2005). Criteria for dividing species into functional groups were reports of adult beetles feeding solely on animal material (carnivore) or feeding additionally on plant material (non-carnivore: phytophagous and omnivorous; Larochelle, 1990; Ribera et al., 2001; Purtauf et al., 2005). Further classification of non-carnivorous carabids to phytophagous and omnivorous species was not meaningful due to the low number of phytophagous species. On the basis of their family identity spiders were placed into one of two guild categories: hunting or web-building spiders (Uetz et al., 1999). This classification is well-founded, since spiders using these two distinct predatory behaviours are separated both in the resources they utilise and the mode of predation (Nyffeler, 1999). For all analyses within-transect funnel trap data were pooled.

Orthopterans were surveyed once by sweepnetting in the meadows in late August and early September 2008. Since one of the organic meadows was ploughed in order to turn it to an arable field, this pair of meadows was not surveyed. One sweepnet sampling was made per transect and each consisted of 4×15 sweeps with a heavy duty sweep net (38 cm internal diameter, 7215HS, BioQuip). The orthopteran individuals caught were identified to species in the laboratory. Due to the low number of caught orthopteran individuals, species could not be classified in functional groups.

In order to analyse the effects of landscape scale management intensity (IAA %), agroecosystem type (winter wheat vs. meadow), local field management (organic vs. conventional) and within-field position (edge vs. interior) on species richness and abundance (in case of plants the relative cover) of the studied taxa, general linear mixed models (GLMM) were applied with the Restricted Maximum Likelihood method. The following random factors were used: landscape (9 landscapes) and field (36 fields). Separate models were built for the following functional groups: grasses and forbs (plants), carnivore and non-carnivore carabids as well as hunter and web-building spiders. In case of plant cover data, separate analyses were performed for meadows and wheat fields, because it was not possible to test the effect of agroecosystem type on plant cover data due to their strong bimodal distribution between meadows (generally high plant cover) and wheat fields (generally low plant cover excluding wheat cover). Additionally all possible two-way interactions of explanatory variables were also tested. Non-significant interactions ($p > 0.05$) were discarded using a manual stepwise backward selection procedure. The normality of model residuals was assessed using normal quantile-quantile plots, and data were either log or square root transformed, when necessary. Plant cover data were either logit or arcsine transformed prior to analysis, when necessary. In order to avoid heteroscedasticity, different variance functions were implemented in the models, if necessary. For a better overview, non-transformed data are presented in the figures.

Calculations were made using the nlme package (version 3.1, Pinheiro et al., 2009) of R 2.10.0 software (R Development Core Team, 2009).

5.2.2. Results

In total 83 vascular plant species in the wheat fields (including 20 grass and 59 forb species) and 102 species in the meadows (among them 28 grass and 66 forb species) were recorded (for species list see Supplementary Material of the original paper). Significantly more plant species were found in the meadows than in the wheat fields (for statistics see Supplementary Material of the original paper). In both agroecosystem types, organic management significantly enhanced the number of plant species, and more plant species occurred in the edges than in the interiors of both agroecosystem types. Performing the same GLMM separately on forbs and grasses, very similar results were found with the exception that there was no effect of organic management on grass species richness, but a negative effect of IAA % (proportion of conventionally managed crop fields and grasslands in a 500 m radius area; for figures see Supplementary Material of the original paper). Forb richness was highest under organic management and in field edges.

Plant cover (excluding cereal in wheat field) was, as expected, much higher in meadows than in wheat fields; therefore the two agroecosystem types were analysed separately. Organic management increased the plant cover in the wheat fields, whereas in meadows, plant cover was higher in the conventional fields (for statistics see Supplementary Material of the original paper). This latter result was due to the grass cover, which was significantly higher in conventional than in organic meadows (Fig. 5.2.1a). Forb cover was increased by organic management in both wheat fields and meadows (Fig. 5.2.1b). Furthermore, there was an interaction between landscape scale management intensity (IAA %) and local field management on plant cover in meadows: in conventional meadows plant cover increased, in organic meadows it slightly decreased with increasing IAA %. Finally, in the edges of wheat fields plant cover, especially grass cover, was higher than in the interiors.

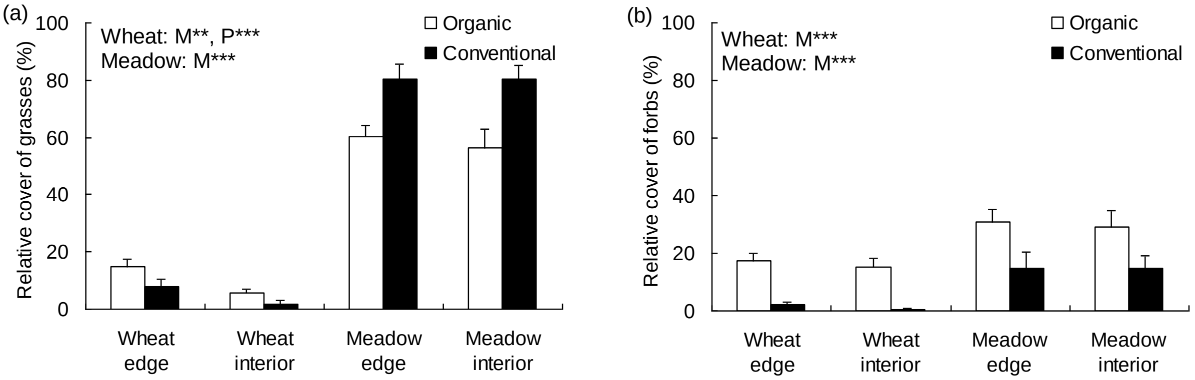


Fig. 5.2.1. Mean relative cover of grasses (a) and forbs (b) in relation to agroecosystem type (winter wheat vs. meadow), local management (organic vs. conventional) and position in field (edge vs. interior). Relative plant cover (%) was calculated by including bare ground cover and wheat cover. Error bars represent SEM. *p < 0.05, **p < 0.01, ***p < 0.001 (M: effect of management; P: effect of position in field). Plant cover was analysed separately for wheat fields and meadows.

In total 50 carabid species in the wheat fields (including 19 carnivore and 28 non-carnivore species) and 45 species in the meadows (among them 16 carnivore and 28 non-carnivore species) were trapped (for species list see Supplementary Material of the original paper). Carabid overall species richness and richness of non-carnivore species was higher in the edges than in the interiors of habitats (for statistics and figures see Supplementary Material of the original paper). Organic management enhanced the richness of non-carnivore carabids. Finally, richness and abundance of non-carnivore species and richness, but not the abundance, of carnivore carabids, were shown to be higher in wheat fields than in meadows (Fig. 5.2.2a,b).

In total 29 spider species in the wheat fields (including 16 hunting and 13 web-building species) and 29 species in the meadows (among them 17 hunting and 12 web-building species) were trapped (for species list see Supplementary Material of the original paper). Spider species richness (and that of hunting species) was higher in the edges than in the interiors of the habitats and it was negatively affected by IAA % (for statistics and figures see Supplementary Material of the original paper). The richness of hunting spider species, but not that of web-building spider, was enhanced by organic management. Spider abundance was higher in meadows than in wheat fields. There was a significant interaction effect between agroecosystem type and position in field on spider abundance – interestingly more spider individuals were captured in the field interiors than in the edges in case of wheat fields, whereas the opposite relationship was observed in the meadows. This interaction was also found in the case of web-building spider abundance (Fig. 5.2.3b). Furthermore, web-building spiders occurred in significantly higher numbers, and hunting spiders in significantly lower numbers, in wheat fields than in the meadows (Fig. 5.2.3a,b). Finally, hunting spider abundance was higher in organic fields and was negatively affected by IAA %, especially on conventionally managed fields (Fig. 5.2.3a).

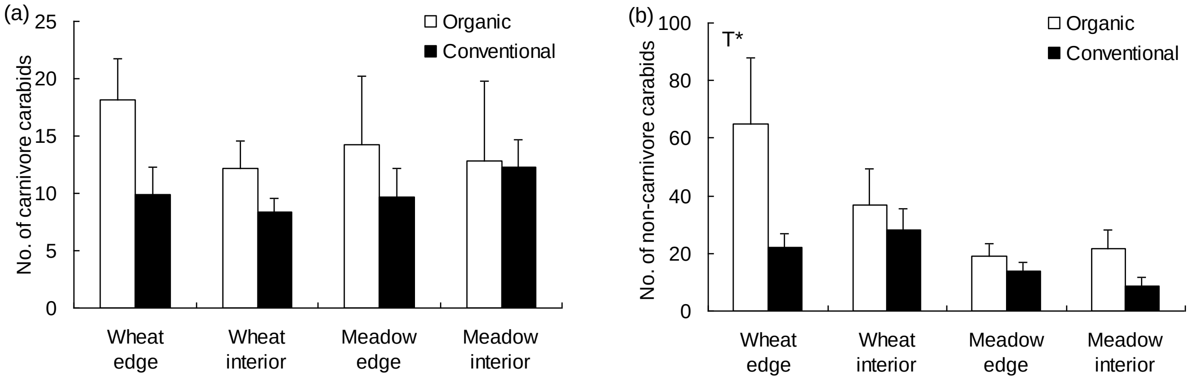


Fig. 5.2.2. Mean abundance of carnivore (a) and non-carnivore (b) carabids in relation to agroecosystem type (winter wheat vs. meadow), local management (organic vs. conventional) and position in field (edge vs. interior). Error bars represent SEM. *p < 0.05, **p < 0.01, ***p < 0.001 (T: effect of agroecosystem type; M: effect of management; P: effect of position in field).

Altogether 216 individuals of orthopterans were sampled in the meadows, which belonged to only six species (for species list see Supplementary Material of the original paper). No effect of landscape composition, management or position in field could be detected either on orthopteran richness or on abundance (p > 0.1 in all cases).

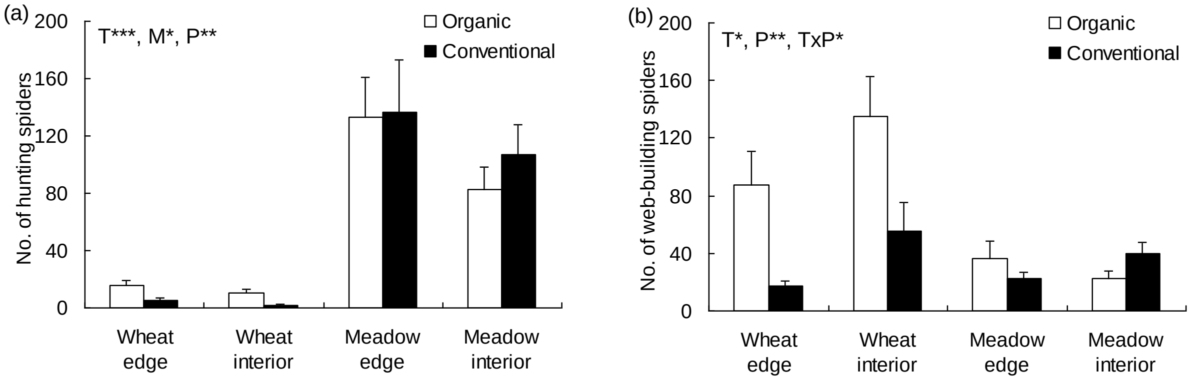


Fig. 5.2.3. Mean abundance of hunting (a) and web-building (b) spiders in relation to agroecosystem type (winter wheat vs. meadow), local management (organic vs. conventional) and position in field (edge vs. interior). Error bars represent SEM. *p < 0.05, **p < 0.01, ***p < 0.001 (T: effect of agroecosystem type; M: effect of management; P: effect of position in field).

5.2.3. Discussion

Diversity patterns of the taxa considered in this study were affected by the local variables (field management intensity, agroecosystem type and within-field position) and by landscape scale management intensity, depending on functional groups of plants, carabids and spiders, while orthopterans did not respond at all.

Grass species richness decreased with increasing IAA% (landscape scale management intensity gradient measured as the proportion of conventionally managed crop fields and grasslands in a 500 m radius area). This was probably because conventional farmers typically sow a low diversity seed mix dominated by competitive grass species, while at the same time spray herbicides against grasses in cereal fields. Therefore at landscape scale this leads to a reduced species pool of grasses when the landscape scale management intensity increases (Roschewitz et al., 2005a). Furthermore, meadows harboured more forb and grass species than wheat fields (as found by Gabriel et al., 2010). Organic management increased forb richness regardless of agroecosystem type. Several studies have previously found such positive effects of organic management in cereal fields (e.g. Fuller et al., 2005; Romero et al., 2008; Ekroos et al., 2010) and in grasslands (e.g. Marini et al., 2008, but see Batáry et al., 2010b). Dietschi et al. (2007) compared Swiss low-intensity meadows with 30 kg N ha-1 year-1 and one cut after 15 July (also part of an agri-environment scheme) and high-intensity meadows with 200 kg N ha-1 year-1 and three or four cuts. These Swiss management types are close to the organic and conventional management types of the present study, with the exception of only late mowing in low intensity meadows. They also found that the high amount of N fertiliser together with the frequent mowing regime greatly reduced the diversity of plants. Finally, confirming our expectations (Romero et al., 2008), species richness of forbs and grasses was significantly higher in the edges than in the interiors of both management types. This can be explained by the increased spillover of weed seeds from the surrounding habitats, which affect edges more than interiors (Rundlöf et al., 2010), and by the fact that management activities are usually less effective at the edges of fields (Kovács-Hostyánszki et al., 2011).

In wheat fields, organic farming enhanced cover of both grasses and forbs as found in other studies (e.g. Roschewitz et al., 2005a; Clough et al., 2007a; Ekroos et al., 2010), but in meadows there were contrasting effects of management on grasses and forbs. Nutrient enrichment together with a reduced chance of establishment of less competitive forbs in conventional meadows enhances the performance of competitive, agronomically desirable grass species (Mayer et al., 2008). This was reflected in the findings, which showed higher grass and lower forb covers in conventional compared to organic meadows. Furthermore, increased plant cover (primarily grass cover) in the edges compared to the interiors was observed only in wheat fields. In meadows dense vegetation cover was observed regardless of within-field position, probably because of a lack of herbicide application, which affects centres usually more than edges.

Non-carnivore carabids were more abundant in wheat fields than in meadows, which may be caused by the wheat fields providing high productivity and large areas of bare soil for these ground-dwelling soil arthropods. Preference of carabids for wheat fields over grasslands has been also shown by French and Elliott (1999). Non-carnivore species benefited from organic farming, possibly because organic wheat fields maintain more weeds, which are their major food resource. However, no correlation was found between richness or cover of forbs and non-carnivore carabids in organic fields (Spearman's rank correlation test, rho < 0.25, $p > 0.1$). Management did not affect species richness of all carabids, which points to the need to separate functional groups (Clough et al., 2007a; Dahms et al., 2010; Diekötter et al., 2010b; Ekroos et al., 2010; but see Shah et al., 2003). Like in the case of plants, strong edge effects were found for carabid diversity, especially due to the edge preference of non-carnivore species (Clough et al., 2007a). The edge of both agroecosystem types provides not only more food resources, but due to the increased number and diversity of plants an elevated number of niches, which makes those microhabitats suitable for more species.

In the present study a negative effect of IAA% was found on species richness and abundance of hunting spiders. Schmidt et al., (2008) studying the effect of percentage non-crop habitats on various families of spiders in wheat fields showed similar results: i.e. a positive effect of percentage non-crop habitats on lycosid spiders and no effect on linyphiid spiders, the two most abundant taxa of (low-dispersive) running and (highly dispersive) web-building groups respectively. According to the results, the negative effect of IAA% on hunting spider abundance was more pronounced in conventional than in organic fields, which appeared to be due to the higher mechanical disturbance and agro-chemical use under conventional management. Therefore, we emphasize the importance of landscape-wide reduced management intensity for conserving and maintaining these important biocontrol agents (Pluess et al., 2010). Furthermore, also agroecosystem type had a contrasting effect on web-building and hunting spiders; web-builders had a higher activity density in wheat fields, whereas the ground-dwelling hunters in meadows. This increased density of web-builders in wheat fields was mainly due to a dominant species, *Oedothorax apicatus*, belonging to Erigoninae subfamily, which builds small webs on the ground surface. Frequent mowing impedes the spread of web-building spiders in the meadows (Thomas and Jepson, 1997).

Organic management enhanced the species richness of hunting, but not web-building spiders. One possible explanation could be that increasing richness of forbs enhanced indirectly the richness of hunting spiders through providing more herbivorous prey for them (significant correlation between richness of forbs and non-carnivore carabids in organic fields and no such correlation with cover of forbs; Spearman's rank correlation test, rho = 0.37, $p = 0.025$, respectively rho < 0.25, $p > 0.1$). Studies investigating species richness and abundance of the total spider community often failed to find any difference between organic and conventional management (for cereals: Diekötter et al., 2010b; for grasslands: Kleijn et al., 2006; Batáry et al., 2008; Dahms et al., 2010). Feber et al. (1998) found positive effects in one region studied, but not in two other regions. The higher activity density of hunting spiders in conventional fields can mainly be attributed to the high density of *Pardosa palustris* in the conventional meadows, which differs from results of some other studies (see e.g. Öberg, 2007 for a cereal field study). Richness of hunting spider showed an opposite response to local field management than their abundance, which may be due to the smaller number of competitor or intraguild predator species in conventional fields that might have resulted in a competitive release effect for *P. palustris* (Rypstra and Samu, 2005). Finally, a positive edge effect was observed on richness of hunting spiders, independent of management or agroecosystem type. The less intensive management in the edges and the spillover from the neighbouring habitats should have caused this pattern. In the case of abundance, again a contrasting response of the two functional groups was observed. Hunting spider abundance increased along edges, but web-building spider abundance decreased. *O. apicatus* was the dominant species among web-building spiders in wheat fields (> 80%) and occurred about twice as frequently in wheat interiors than in wheat edges. Schmidt et al. (2008) showed that this arable (agrobiont) spider species, which is often the most abundant species in Central European crop fields (Samu and Szinetár, 2002), was negatively influenced by the high percentages of non-crop habitats in the surrounding landscape. In contrast, the dominant hunting spider, *P. palustris* (> 85% in meadows) showed a positive edge effect having about 37% more individuals in meadow edges than in the meadow interiors, obviously benefiting from source habitats outside the field.

No effect of organic meadow management was found on diversity or abundance of grasshoppers. The orthopteran assemblages of both management types were composed of a few generalist species (*Chortippus spp.*) and were poor in terms of species richness compared to semi-natural grassland studies (e.g. Batáry et al., 2007b; Marini et al., 2010). This phenomenon was most probably observed because not only the conventional, but also the organic meadows were managed intensively, in the sense that several organic meadows were mown twice or more per year depending on the weather conditions. Some organic farmers were also observed harrowing and overseeding their meadows in order to decrease the amount of forbs, thereby achieving higher yields. The main limiting factor for several of the grasshopper species was probably the frequent mowing by heavy machinery in the most sensitive period of their life cycle, which also led to a homogenous vegetation structure that was less supportive of species diversity (Humbert et al., 2009).

5.2.4. Conclusions

Our results show that high-intensity management, which included agrochemical use and ploughing in wheat fields and mowing and grazing in meadows, influenced our study organisms both at local and landscape scales. Organic farming enhanced forb richness and cover, species richness of non-carnivore carabids and hunting spiders, showing that effects of organic management differ between functional groups. However, organic management can result in contrasting responses depending on agroecosystem type: grass cover increased in wheat fields, but decreased in meadows. Agri-environmental schemes including organic management support only certain functional groups contingent on the investigated agroecosystem type. In general we suggest the following management conclusions: 1.) Grasshoppers were the only group, which was not affected by organic management at all, but may benefit from reducing mowing frequency. 2.) Functional groups that were not enhanced by organic farming presumably need other management practices such as reduced mowing frequency or decrease in landscape scale management intensity. 3.) Decreasing field sizes, enlarging the edge area, will enhance hunting spiders, non-carnivore carabids, grasses, herbs in both organic and conventional fields.

6. Landscape moderation and regional differences of biodiversity patterns

Landscape scale effects can moderate the positive effects of agri-environment management. Additionally there might regional differences in their performance. Hence to get a more robust and holistic overview, it is better to study not only several outcome variables (i.e. multi-taxa or multi-service study), but it would be ideal to study contrasting or replicated regions (i.e. multi-region studies) as well as replicated periods (i.e. multi-year studies, which is rarely done). Beside primary research studies, qualitative review studies and especially the more powerful meta-analysis studies can capture and consider heterogeneities among studies originating from different regions, years, etc. In this chapter we present a meta-analysis study on landscape moderation effect on AES, an overview paper on great regional differences of farmland biodiversity conservation between Central and Eastern vs. Western Europe, and a primary study on ecological and economic performance of organic farming in two neighbouring and contrasting regions with different land use history, i.e. West vs. East Germany.

6.1. Landscape-moderated biodiversity effects of agri-environmental management

Agri-environmental management (AEM) is heralded as being key to biodiversity conservation on farmland, yet results of these schemes have been mixed, making their general utility questionable. Here we aimed to test whether the benefits of AEM for species richness and abundance are determined by the surrounding landscape context in the frame of a meta-analysis.

6.1.1. Material and methods

We tested our research hypotheses using a meta-analysis. In ecology there is a growing need for quantitative research synthesis to generate higher-order conclusions (Gurevitch et al. 2001; Stewart 2010). In contrast to qualitative and descriptive traditional reviews, meta-analysis allows the quantitative analysis and summary of the results of several independent studies examining the same question (Hedges & Olkin 1985; Gurevitch et al. 1992; Arnqvist & Wooster 1995; Gurevitch & Hedges 1999; Cooper et al. 2009). In meta-analysis, the magnitude of effects (effect size) is quantified from each individual study, and these are then used to calculate the combined (overall) magnitude and significance of the effect under the meta-analytical study (Hedges & Olkin 1985). Therefore, meta-analysis is an appropriate method for examining the general evidence for or against a specific hypothesis (Bengtsson et al. 2005).

We conducted a systematic literature survey using key-word searches in the ISI Web of Science database (until July 2008) and by searching the reference lists of previous syntheses on related topics (Kleijn & Sutherland 2003; Hole et al. 2005; Bengtsson et al. 2005; Attwood et al. 2008). The combinations of the following key-words were used: agri*, biodiversity, farming, integrated, intensity, management, organic and species. We included only those studies, which fulfilled the following criteria: (1) Studies, which compared the species richness (Shannon diversity in case of Genghini et al. (2006)) and/or the abundance of terrestrial taxa (invertebrates, vertebrates and plants) between farming systems managed at different intensity levels (hereafter intensive vs. extensive agricultural systems; for detailed classification see next section). Set-aside studies were excluded, because set-aside is usually not an actively managed farming system (Kleijn & Báldi 2005). (2) Studies, which were carried out at the landscape scale and included at least two separate fields in each category, i.e. in intensive and extensive agricultural systems (field-scale studies were excluded). (3) Studies, which reported means, standard deviations (SD), standard errors of means (SEM) or confidence limits (CI) and sample sizes for both management systems. Observations of multiple taxa and/or of different geographical regions per individual studies were included separately in the dataset and considered independently. This may not strictly meet the assumption of meta-analysis that each observation is independent of all others (Arnqvist & Wooster 199; Langellotto & Denno 2004), but it allowed us to more fully explore the effects of landscape composition on the studied systems (Gurevitch et al. 1992; Bancroft et al. 2007). If a paper reported more than two management intensity levels or several survey periods, we selected the two management systems with the highest contrast in land-use intensity and the most recent survey. We used unpublished means and standard deviations of Kleijn et al. (2006) to include observations from this study and included unpublished data from a recent study by the first author to increase the sample size (see Batáry et al. unpublished data in Supplementary Material of the original paper) and the statistical power of the analyses.

Altogether, we found 109 observations of 47 case studies for species richness and 114 observations of 46 case studies for abundance (for datasets see Supplementary Material of the original paper). The majority of the studies compared conventional with organic management, and the latter was often part of AES. Hereafter we refer to these local extensification of farming practices as AEM. AEM includes environmentally friendly agricultural practices on the field or farm level, such as reductions in agrochemical input, soil cultivation, mowing frequency or cattle density, as well as enhancement of organic farming or field margin strip cultivation. In Europe (European studies dominate our datasets), many of these practices are facilitated by national and EU subsidies (Kleijn & Sutherland 2003; Kleijn et al. 2009).

To test the dependence of the effect of AEM on landscape context we classified studies as having been carried out in simple or complex landscapes. Landscapes with high proportions of semi-natural grasslands, forests, hedgerows, tree lines or wetlands (i.e. semi-natural areas) were referred to as 'complex' (> 20% cover of semi-natural habitat), while landscapes with few of these habitats as 'simple' (0–20% semi-natural habitat). The 20% threshold was based on earlier studies (Andrén 1994; Tscharntke et al. 2002; Bianchi et al. 2006). In addition to simple and complex landscapes, Tscharntke et al. (2005a) distinguished cleared landscapes (< 1% non-crop habitat). However, very few studies were found that had been done in cleared landscapes. We therefore included studies from landscapes with less than 1% non-crop habitat in the simple landscape category. No such analysis was possible using semi-natural area % as a continuous variable (i.e. continuous meta regression), because relatively few studies provided exact geographical codes for all study fields, and the distribution of the proportion of semi-natural area of these studies was unbalanced.

We used the landscape data provided in the papers and checked the study areas using the software Google Earth. The categorisation was done independently by two authors (PB and AB). For a subset of studies, for which Corine Land Cover 2000 datasets (hereafter CLC 2000; (Büttner et al. 2002)) and the exact location of study sites (GIS coordinates, accurate maps or settlement designations) were available, we measured the total proportion of semi-natural areas (within a radius of 1000m of the locations) with ArcGIS 9.2. Corine (Co-ordination of Information on the Environment) is a programme developed by the European Environment Agency, which has generated Europe-wide environmental data, including land-cover data for 26 European countries. CLC 2000 data are available for 26 European countries and distinguish 44 land cover (or habitat) categories. The 17 categories starting with CLC 2000 codes 3 or 4 indicate semi-natural habitats and were used to calculate the proportion of these within a radius of 1000m.

The species richness and abundance datasets were divided into two main parts according to the investigated land-use following Rounsevell et al. (2005): croplands (arable and permanent crops for food) vs. grasslands. Croplands mainly consisted of cereal fields, but a small number consisted of vineyards, orchards, olive groves, cotton fields, cacao, coffee agroforestry and vegetable fields (share of permanent crop observations in species richness and abundance datasets: 11% and 15%). Grasslands were permanent agroecosystems for grazing or hay making, but also included a few studies performed on field boundaries or ditch banks (share of field boundary or ditch bank observations in species richness and abundance datasets: 11% and 9%).

We used Hedges' d as an estimate of the standardized mean difference (i.e. the effect size). It expresses the strength of an effect in multiples of the studies standard deviation (SD), i.e. by how much the effect is increased above the noise level. A value of 1 indicates that the treatment group was 1 SD above the value of the control group. Hedges' d has the advantage that it is not biased by small sample size (Hedges & Olkin 1985). Effect sizes and their non-parametric estimates of variance were calculated for all observations based on the mean, SD and sample size (number of studied fields) of species richness and abundance of intensively (control) and extensively (AEM) used agroecosystems. Effect size was positive if species richness or abundance was higher in the extensive than in the intensive fields. Non-parametric variance estimates use only the sample sizes from the experimental and control groups rather than incorporating the effect size into the calculation (Adams et al. 1997). This alternative estimate makes few assumptions and may be less constrained by the assumptions of large sample theory (Hedges & Olkin 1985).

Categorical meta-analysis was performed separately for species richness and abundance in croplands and grasslands. The categorical factor was based on the landscape complexity, i.e. simple or complex landscape. We used random effects models (effect sizes nested within studies) with resampling (4999 iterations) to calculate the grand mean effect size for each analysis, which allowed effect size estimates to vary not only due to sampling error, but due to biological or environmental differences between organisms and studies (Gurevitch & Hedges 1999; Bancroft et al. 2007; Rosenberg et al. 2000). The output of each statistical test consisted of the mean effect size for the analysis with an accompanying bias-corrected bootstrapped 95% confidence interval (CI) (Adams et al. 1997) and a total heterogeneity statistic (Q). The heterogeneity statistic is a weighted sum of squares and is tested against a Chi-square distribution with n – 1 degrees of freedom (Bancroft et al. 2007). Estimates of the effect size were considered to be significantly different from zero if their 95% confidence intervals did not include zero (Borenstein et al. 2009).

The total heterogeneity in categorical meta-analysis – similar to the partitioning of variance in ANOVA – can be partitioned into variance explained by the categorical factor in the model (between group heterogeneity) and residual error variance (within group heterogeneity) with Chi-square tests indicating their significance (Adams et al. 1997; Rosenberg et al. 2000). Significant between-group heterogeneity indicated support that species richness or abundance responses to AEM differed in different landscape types (Gurevitch & Hedges 1999). We considered a significant mean effect size in simple landscapes but not in complex landscapes and an additional significant between group heterogeneity as support for the hypothesis that AEM is more effective in simple than in complex landscapes (Fig. 6.1.1). To test our second hypothesis that AEM has a larger effect in croplands than grasslands of simple landscapes, we performed meta-analyses on species richness and abundance. In these analyses all observations were included, and the categorical factor was habitat type, i.e. cropland vs. grassland. Here we have to note that it was not possible to test for an interaction landscape type (simple vs. complex) and agricultural system (croplands vs. grasslands) with our meta-analysis software (MetaWin 2.0; (Rosenberg et al. 2000)).

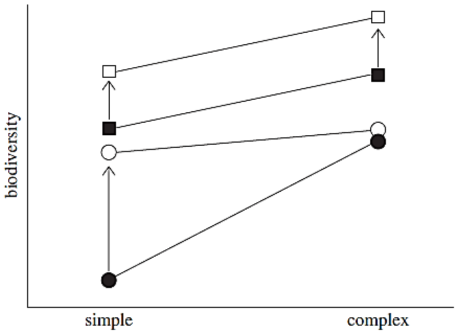


Fig. 6.1.1. Hypothesised relationship between biodiversity (species richness) and local management in dependence of the structural composition of agricultural landscapes. Agri-environmental management (AEM) is contrasted against conventional management. Landscape type is classified as simple (0–20% cover of semi-natural habitat) and complex (> 20% semi-natural habitat; see Andrén 1994; Tscharntke et al., 2002). The large black arrows indicate benefits of biodiversity, when turning conventional management to AEM.

Studies included in the analysis examined the response of many different species groups, allowing us to analyse the response of different taxonomic or functional groups separately (Supplementary Material of the original paper). This was only done for species groups for which three or more observations were available. Arthropods were further categorised in functional groups (herbivores, pollinators), but no such comparison was possible for predatory arthropods, because of data deficiency in either of the two categories (simple or complex). Within and between group heterogeneities were tested with Chi-square tests.

Studies finding a significant effect are more likely to be published than studies finding no effects. This ‘file-drawer’ phenomenon (Rosenthal 1979; Møller & Jennions 2001; Rosenberg 2005) may bias the outcome of meta-analyses. We therefore examined publication bias using Rosenthal’s technique of a fail-safe number, which calculates the number of non-significant, unpublished studies that need to be added to a summary analysis in order to change the results from significant into non-significant. Thus, the higher the fail-safe number, the more credibility a significant result has (Langellotto & Denno 2004). More precisely, a fail-safe number is often considered robust if it is greater than 5n+10, where n is the original number of studies (Rosenthal 1991). However, we have to note that random-effects model fail-safe numbers are usually quite a bit smaller than their fixed-effects model equivalents (Rosenberg 2005). Furthermore, there was a geographical bias in our dataset, whereby most studies originated from Europe and the temperate zone (like in the earlier syntheses (Hole et al. 2005; Bengtsson et al. 2005)). This bias is probably due to the many more studies performed in Europe than in other continents, which compared the biodiversity of AEM and control fields at landscape level and also fulfilled our study selection criteria. All meta-analyses were performed with MetaWin 2.0 software (Rosenberg et al. 2000).

	n	Q_B	$p(Q_B)$	Q_W	$p(Q_W)$	fail-safe
croplands						
species richness	55	4.06	0.044	63.02	0.163	529
abundance	68	0.78	0.378	74.79	0.214	747
grasslands						
species richness	54	1.19	0.276	53.02	0.434	1100
abundance	46	0.04	0.840	39.64	0.659	113

Table 6.1.1. Heterogeneity statistics and Rosenthal’s fail-safe numbers for each model of figure 2 analysing the effect of landscape type (simple vs. complex) on agricultural intensification (measured as effect size, see methods) in croplands vs. grasslands. Between (QB) and within group (QW) heterogeneities were tested with Chi-square test. n: number of individual comparisons.

6.1.2. Results

In croplands, the standardized average effect size for observations of species richness in simple but not in complex landscapes was significantly greater than zero (Fig. 6.1.2). In other words, AEM had a positive effect on species diversity in simple but not complex landscapes. This contrast was further supported by a significant between-group heterogeneity (Table 6.1.1). The average effect sizes of the abundance data differed significantly from zero in both landscape types (Fig. 6.1.2b). Sample sizes were larger for simple than for complex landscapes in croplands (Fig. 6.1.2), however, this did not appear to affect the results as the 95% CIs were similar in size and overlapped considerably (Table 6.1.1). In grasslands AEM resulted in significantly higher species richness and abundance regardless of landscape type (Fig. 6.1.2). Overall, the within-group heterogeneities of the four above categorical meta-analyses were non-significant (Table 6.1.1). Rosenthal’s fail-safe numbers were robust for all categorical meta-analyses with exception of abundance analysis in grasslands according to the definition of Rosenthal (1991) making it unlikely that the outcome was the result of publication bias (Table 6.1.1). Here we note that in the latter case (abundance analysis in grasslands based on 46 observations) it is difficult to consider a fail-safe number requiring more than 110 missing studies unrobust.

We found no significant evidence that AEM had a larger effect in croplands than in grasslands. AEM effects were positive for both species richness (between group heterogeneity: $Q_B = 1.822$, $p = 0.177$; mean effect sizes and lower–upper CIs for cropland and grassland: 0.95, 0.61–1.34, and 0.69, 0.52–0.88) and abundance ($Q_B = 1.065$, $p = 0.302$; mean effect sizes and lower–upper CIs for cropland and grassland: 0.80, 0.54–1.14, and 0.57, 0.25–0.96) regardless of land-use types (cropland vs. grassland).

In croplands, pooling of all observations of arthropods was necessary to have sufficient replicates for analysis. The effect sizes of species richness and abundance of all arthropods were significantly greater than zero in simple, but not in complex landscapes (Fig. 6.1.3a,b). However, we found significant between-group heterogeneity only in the case of all arthropod richness (Supplementary Material of the original paper). Observations on pollinators were available in sufficient number to merit separate analyses. For this functional group, AEM was effective in simple, but not in complex landscapes (Fig. 6.1.3a,b).

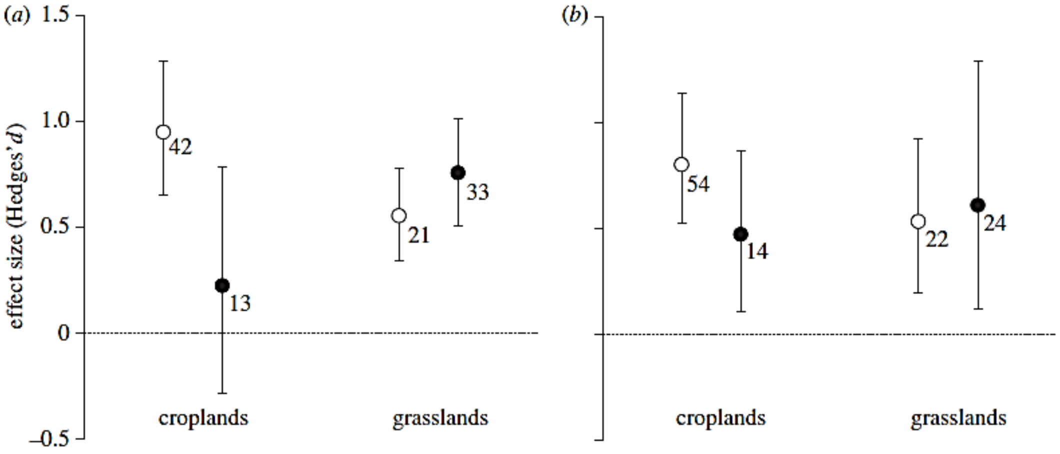


Fig. 6.1.2. The effects of agri-environmental management on (a) species richness and (b) species abundance depending on landscape type (simple vs. complex) and agricultural system (croplands vs. grasslands). Indicated is mean effect size ± 95% confidence interval. The mean effect size is significantly different from zero, if the CIs do not overlap with zero (Rosenberg *et al*., 2000). Numbers indicate sample sizes.

In grasslands, we analysed effect sizes of the species richness of plants, all arthropods, pollinators and herbivores as well as effect sizes of the abundance of all arthropods, pollinators, herbivores and birds (Fig. 6.1.4a,b). AEM had significant positive effects on the species richness of plants and all arthropods in both landscape types and on pollinators' species richness in simple landscapes only (Fig. 6.1.4a). Similar to the effects in croplands, AEM in grasslands had contrasting effects on arthropod and pollinator abundances, i.e. significant positive effects in simple but not in complex habitats, but between group heterogeneity remained non-significant. Bird abundances were significantly positively affected by AEM in the two landscape types, but herbivore abundances were not. However, the low fail-safe numbers of the two latter analyses suggest publication bias, thus questioning the strength of these results (Supplementary Material of the original paper).

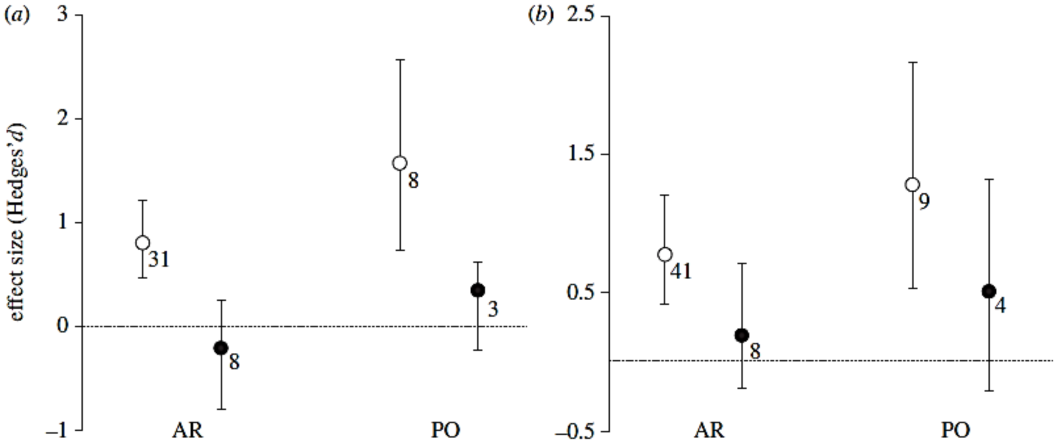


Fig. 6.1.3. The effects of agri-environmental management in croplands on (a) species richness and (b) abundance of all arthropods (AR) and pollinators (PO) depending on landscape type (simple *vs*. complex). The mean and 95% confidence interval is shown for each analysis. Numbers indicate sample sizes.

6.1.3. Discussion

The impact of landscape context on the effectiveness of agri-environmental management (AEM) that reduces management intensity on agricultural fields seems to differ between farming system and species group. In cropland AEM was more effective in enhancing species richness in simple than in complex landscapes. Furthermore, pollinators and all arthropods combined consistently showed more positive responses to AEM in croplands embedded in simple than in complex landscapes. In contrast, AEM in grasslands was equally effective in complex and simple landscapes, with positive effects on plants and birds, independent of landscape complexity; only pollinator richness and abundance and abundance of all arthropods combined responded to landscape context in cropland and grassland in a similar way. According to this meta-analysis, the hypothesis raised originally by Tscharntke et al. (2005a) that AEM is more effective in terms of species richness in simple than in complex landscapes seems to apply only for cropland, and not for grassland, which is usually less intensively managed. In addition, in grasslands taxon-specific differences can be important, and management options may depend on the specific group requiring conservation. Finally, we found no evidence that AEM had a larger effect in croplands than in grasslands.

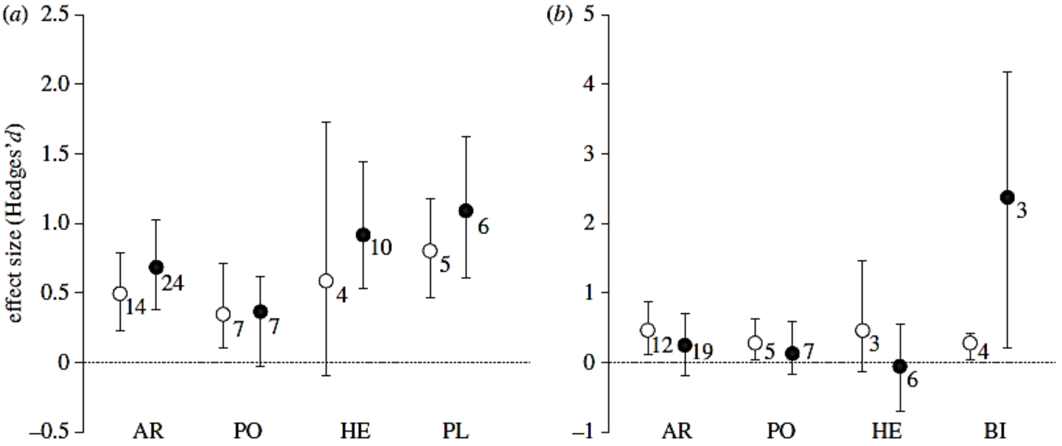


Fig. 6.1.4. The effects of agri-environmental management in grasslands on (a) species richness and (b) abundance of all arthropods (AR), pollinators (PO), herbivores (HE), plants (PL) and birds (BI) depending on landscape type (simple *vs*. complex). The mean and 95% confidence interval is shown for each analysis. Numbers indicate sample sizes.

We found that landscape context moderates effects of AEM on species richness in croplands but not in grasslands. One might argue that arthropods, which tend to be more affected by landscape complexity (Fig. 6.1.3, 6.1.4) made up a larger proportion of the studied species groups in croplands than in grasslands. However, arthropods were the investigated species group in about 70% of all studies making it unlikely that a different representation of species groups explains the observed difference in response between the two farming systems. Another explanation may be that studies in grasslands have been carried out in less intensively farmed landscapes than studies in croplands. Only a few studies synthesized in our meta-analyses reported the amount of fertilizer use in grasslands and croplands (a commonly used indicator of land-use intensity, (Kleijn et al. 2009)), which did not allow statistical analysis. However, croplands seem to receive roughly twice as much nitrogen fertilizer as grasslands. The most intriguing difference is the complete removal of the vegetation in arable systems, so spillover from semi-natural landscape elements to agricultural fields may be much more important than in grasslands (Landis et al. 2000; Rand & Louda 2006; Rand et al. 2006). Grasslands were all perennial agroecosystems that have a more stable plant and animal community (Foster et al. 2002), which hampers the establishment of invading plant and animal species from the surrounding landscape-wide species pool.

Across farmland types and for both abundance and species richness, pollinating arthropods were the only species group for which the effect sizes were consistently significant in simple and non-significant in complex landscapes indicative of landscape-mediated effectiveness of AEM (although between-group heterogeneities were not significant, possibly due to lower sample sizes at this level of analysis (Borenstein et al. 2009)). Except for very extensively managed agricultural areas, major pollinator groups such as bees or hover flies nest or hibernate in semi-natural habitats and exploit agricultural fields mainly for foraging (Kremen et al. 2004; Holzschuh et al 2008). Probably as a result, pollinator richness and the pollination services they provide, decline exponentially with increasing distance from natural or semi-natural habitats such as field margins, species-rich grasslands or forests (Albrecht et al. 2007; Kohler et al. 2008; Ricketts et al. 2008). In complex landscapes, where most fields are located at short distances from semi-natural habitats, the continuous spillover of pollinators from semi-natural habitats to agricultural fields may obscure differences caused by local management (Rundlöf et al. 2008). The complexity of the landscape in the direct vicinity (< 1 km) of the treatment fields corresponds well with the mobility of pollinators (Gathmann & Tscharntke 2002), while plant populations may be sedentary or benefit from seed rain, and bird species also greatly differ in mobility. Other species groups are often less strongly related to semi-natural habitats (Duelli & Obrist 2003). Many herbivorous arthropod species can hibernate in agricultural fields and do not need to colonize the fields from semi-natural habitats each spring, while others are colonizers. Arable or grassland plant species survive year round in agricultural fields either as perennial plants or as seeds or buds, but can be also influenced by landscape context (Gabriel et al. 2005; Gabriel et al. 2010; Roschewitz et al. 2005b). The high mobility of birds allows many species to locate and exploit fields of high resource quality independent of landscape complexity (Robinson & Sutherland 1999).

We found no evidence for AEM having larger effects on species richness or abundance in croplands than in grasslands. This supports findings of Kleijn et al. (2009), who found a similarly declining relationship between land-use intensity and plant species richness in grasslands and croplands. This suggests that schemes reducing the intensity of farming will have a similar impact in grasslands and croplands. The mechanism may lie in the fact that the disturbance regime in intensively managed grasslands is very high and is probably not very dissimilar from that in intensively managed arable fields. Agrochemical input for weed and pest control is low in extensively managed crops reducing the disturbance regime and resembling annually cut or grazed grasslands.

Although the geographic coverage of this study is somewhat better than previous reviews on related topics (e.g. Kleijn & Sutherland 2003; Hole et al. 2005; Bengtsson et al. 2005), it is still subject to considerable geographic bias. Most of the observations that were used in this study (ca. 80% for both species richness and abundance datasets) came from Europe and only few from the Americas. Africa and Australia were not included at all, while Asia was represented by studies from Indonesia alone. However, within Europe geographic coverage was fairly good, with observations from 12 and 14 countries for species richness and abundance analyses. Results should be interpreted bearing this geographic bias in mind (Kleijn & Báldi 2005).

Bengtsson et al. (2005) argued in their meta-analysis that it would be desirable to take the sampling design into account. In our study quite a lot of observations used a matched paired study design (AEM fields paired with control fields). These paired observations were though very unbalanced within landscape types (simple vs. complex) and farming systems (cropland vs. grassland), which did not allow us to perform robust meta-analyses on solely paired design observations. We agree with Bengtsson et al. (2005) that in case of matched pair studies there is a risk of producing a reduced difference between the farming practices. When conventional and organic fields are generally compared, not with pair design, differences between the systems can, in most cases, be attributed to landscape simplification rather than farming system.

6.1.4. Conclusions

This study shows that, when average effects of many studies are considered, AEM effectively enhances species abundance in croplands and species richness and abundance in grasslands regardless of landscape context. In addition, landscape complexity is moderating effects of AEM, contingent on farming system and taxonomic and functional group. In agricultural grasslands and for species groups such as plants and birds, AEM is equally effective in complex and simple landscapes, while structurally complex landscapes generally support higher biodiversity levels than simple landscapes (Tscharntke et al 2005; Hunter 2002). By contrast, in croplands and for arthropods, AEM is more effective in simple than in complex landscapes. The high effectiveness of AEM in enhancing arthropods of croplands is particularly important because of the associated ecosystem services such as pollination and pest control (Thies & Tscharntke 1999; Winfree et al. 2008). Our results clearly indicate that AEM in croplands should preferentially be implemented in structurally simple landscapes, because only in these can local AEM significantly and efficiently enhance agroecosystem functioning and services. This can be done by increasing the proportion of semi-natural habitats, or by reducing agrochemical input (Green et al. 2005; Isaacs et al. 2009). However, our study did not address effects on absolute species numbers or on endangered, red-listed species that do mostly not respond to AEM (Kleijn et al. 2006; Gabriel et al. 2010). Meta-analyses only consider relative effects between AEM and conventional agriculture. Because different studies use different sampling designs across-study comparisons of species richness in simple and complex landscapes are meaningless. Other studies, however, suggest that complex agricultural landscapes with their high amount of semi-natural areas generally have much larger species pools than simple landscapes and are inhabited by more endangered species (Kleijn et al. 2009; Batáry et al. 2010b). For this reason alone it is important to preserve these landscapes (Billeter et al. 2008). Our results suggest that in complex grassland landscapes AEM may help preserve farmland biodiversity but in complex croplands it is not a very effective tool for this purpose. This study highlights that the one-size-fits-all approach of many agri-environmental programs (Kleijn & Sutherland 2003) is not a very efficient way of spending the limited funds available for biodiversity conservation on farmland. The design of agri-environmental programs should be targeted to the nature of the landscapes of the regions in which they are implemented (Whittingham et al. 2007) and the type of species groups at which they are targeted.

6.2. Harnessing the biodiversity value of Central and Eastern European farmland

In this opinion study, we highlight the contrast between the importance of the central and eastern new member states (NMS) for farmland biodiversity in Europe on the one hand, and their poor fit with EU agricultural policy and lack of published ecological data in the international literature on the other. Addressing these problems now could help prevent a further decline in European biodiversity and ecosystem quality.

6.2.1. Legacy of communist agriculture and its implications for farmland biodiversity

Between 2004 and 2013, 11 countries from post-communist Central and Eastern Europe joined the EU in a phased enlargement process that brought it to 28 member states, sharing common policies and goals (see Fig. 6.2.1a). Despite heterogeneous in many respects, a shared characteristic of the central and eastern NMS is the legacy of communist agricultural policy during the mid and late 20th century, affecting not only on the structure and use of farmland, but also farmland biodiversity (Báldi & Faragó, 2007; Liira et al., 2008; Cousins et al., 2014). In the western EU-15, and particularly countries such as the UK, France, Germany and the Netherlands, the intensification of lowland farmland was relatively effective, carried out mainly by family farms and driven by production-linked agricultural subsidies. In contrast, although the state-imposed homogenization and intensification of farmland in Central and Eastern Europe also had severe negative impacts on biodiversity in places, this process was relatively inefficient, leaving many remaining patches of semi-natural land (Young et al., 2007). Collectivization of land in most Central and Eastern European countries also merged many private smallholdings into industrial farms of up to several thousand hectares in size. After the fall of the communist regimes around 1990, much of this land was returned to private ownership by individuals, but this had a lasting effect of creating a predominance of small semi-subsistence holdings (generally < 5 ha in size), contrasted with few but very large industrial farms (Fig. 6.2.2a; Davidova et al., 2012).

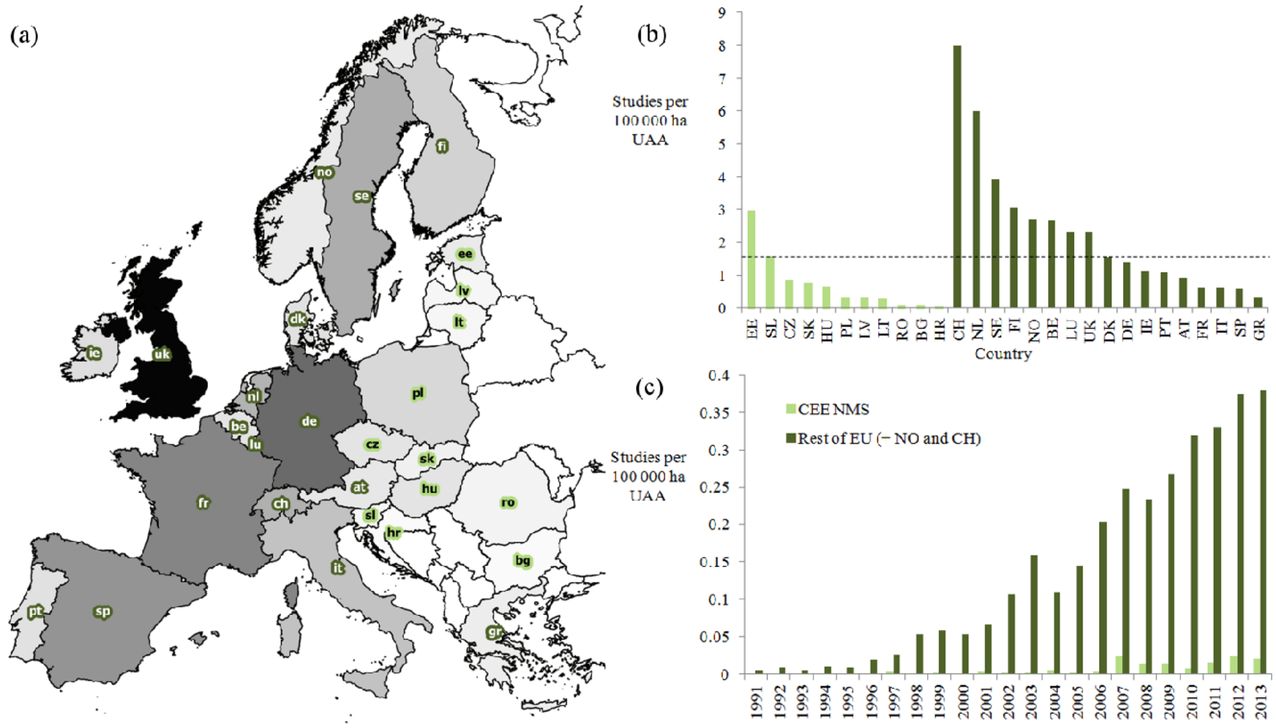


Fig. 6.2.1. (a) Map of Europe depicting the total number of studies on farmland biodiversity carried out in each EU country found in a search of the Web of Science database. A larger number of studies are indicated by a darker shade of grey. Black label text = Central and Eastern European new EU member states (CEE NMS), white label text =rest of EU + Norway and Switzerland. We have included the results for Norway and Switzerland, here grouped with the 'old' member states due to the similarities of their agricultural systems. Details of the search are given in Supplementary Material of the original paper. (b) Number of studies per 100,000 ha utilised agricultural area (UAA) carried out in each EU country (+ Norway and Switzerland) between 1991 and 2013. The dotted line depicts the average number of studies per country. (c) Number of studies per 100 000 ha UAA carried out in CEE new member states compared to the rest of the EU (+ Norway and Switzerland) in each year since 1991.

Production dropped dramatically in the east, and large areas of both cropland and grassland were abandoned in the 1990s and early 2000s, both of which allowed at least short-term population recoveries of many species (Donald et al., 2001; Keišs, 2003; Stoate et al., 2009; Kamp et al., 2011; but see e.g. some negative effects of farmland abandonment in Hungary documented by Verhulst et al., 2004). In the EU- 15 during the same period, farming intensity was maintained but with increasing regulation of environmental impacts, most notably through successive reforms of the EU Common Agricultural Policy (CAP) (see Fig. 6.2.2b,c; Stoate et al., 2009).

Through the funding structures of the EU CAP, as well as the influence of the EU market, the central and eastern NMS have experienced both large-scale reactivation and intensification of farmland since accession and continuing abandonment of marginal areas (Stoate et al., 2009; Tryjanowski et al., 2011; Sanderson et al., 2013). Nevertheless, fragmentation of land ownership is still a major hindrance in many NMS to the consolidation of farmland and agricultural intensification (Hartvigsen, 2014), and convergence of the agricultural sectors of old and new member states is limited (Csáki & Jámbor, 2013). Thus, compared to Northern and Western Europe, the NMS can be said to have (1) lower levels of agrochemical inputs, mechanization and productivity, with per hectare yields less than half of those of the EU-15 (Csáki & Jámbor, 2013; see also Fig. 6.2.2b,c); (2) farm structures polarised between a small number of very large industrial units and a large number of very small units (Fig. 6.2.2a); and (3) a predominance of subsistence and semi-subsistence farming, which is linked with positive effects on biodiversity via its promotion of mixed farming and mosaic structures (Tryjanowski et al., 2011; Davidova et al., 2013).

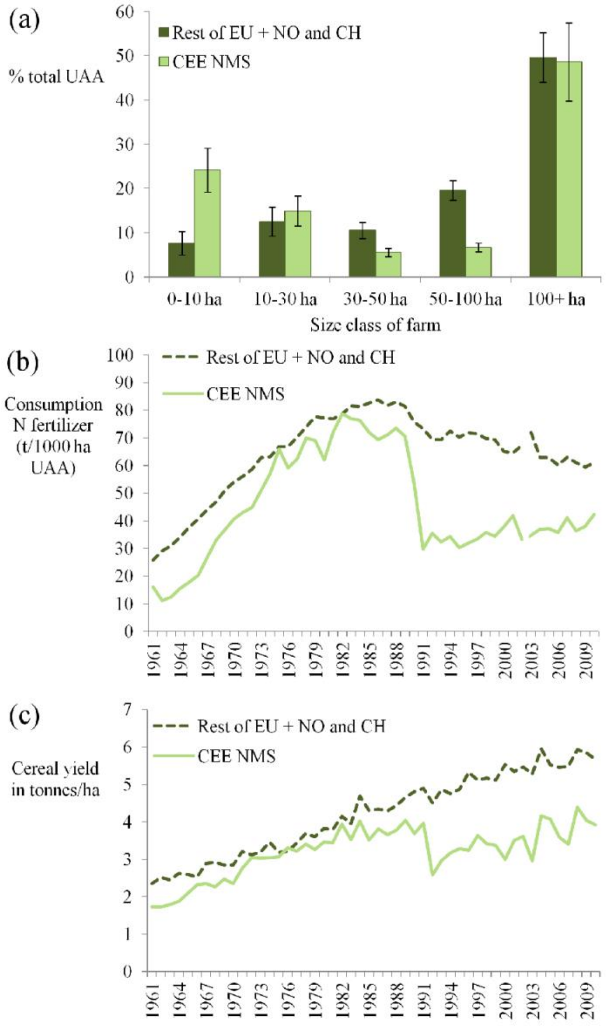


Fig. 6.2.2. Indices of agricultural intensity in the Central and Eastern EU new member states (CEE NMS) and the rest of the EU (+ Norway and Switzerland). (a) Distribution of farmland area (UAA) according to size classes of farms in 2010 (data from Eurostat, http://epp.eurostat.ec.europa.eu) showing standard error bars. (b) Consumption of N fertiliser in tonnes per 1000 ha utilised agricultural area (UAA) between 1961 and 2010 for CEE NMS and the rest of the EU (+ NO and CH) (data from FAOSTAT, http://faostat3.fao.org). The categorization N fertiliser changes slightly in 2002; therefore, difference between the years 2002 and 2003 is not comparable. (c) Cereal yield in tonnes per ha (data from FAOSTAT, http:// faostat3.fao.org). For FAOSTAT data, countries included in each category vary according to data availability, and excluding countries with incomplete data did not affect trends.

These are all major reasons why comparative studies show greater ecosystem quality for biodiversity (Reidsma et al., 2006), as well as higher levels of rare species occurrence and species richness in lowland farmland (Batáry et al., 2010b) in the NMS than in Northern and Western Europe. However, this also means that nutrient-limited yield gaps are currently larger in Eastern than in Western Europe (Mueller et al., 2012) so that the potential to intensify in the NMS is high. Whilst farmland biodiversity declines now appear to be slowing for some taxa in Northern and Western Europe, as they have already experienced their strongest losses in the mid to late twentieth century (Carvalheiro et al., 2013), the picture may be different in the NMS. For example, long-term monitoring trends in farmland birds suggest that their decline has been accelerating in the NMS in recent years. The farmland bird indices in Hungary (Szep et al., 2012), Latvia (Aunins & Priednieks, 2009) and Poland (Sanderson et al., 2013) all decreased following their accession to the EU in 2004, which the authors link to the changes in agricultural practices provoked by the CAP. General trends are difficult to measure due to the lack of standardised monitoring data from this region (notable exceptions being the Pan-European Common Bird Monitoring Scheme; Voříšek et al., 2010; and in some countries the European Butterfly Monitoring Scheme; van Swaay & Warren, 2012), as well as time-lags in species responses (Kuussaari et al., 2009; Dullinger et al., 2013). The little evidence that is available from bird monitoring suggests that the current measures in place to protect farmland biodiversity in Central and Eastern Europe seem to be insufficient, but the lack of baseline and comparative data in these regions means that we have very little idea of what is currently being lost

6.2.2. Agricultural habitats in Central and Eastern Europe underrepresented in literature

The ecological literature on European farmland biodiversity has grown steadily in the last two decades. It plays an important role not only in providing locally relevant evidence to feed into conservation management, but also for large-scale international reviews and meta-analyses to synthesise current knowledge on a topic of interest (Dicks et al., 2013b). Searching the online database Web of Science for peer-reviewed publications produced to date on farmland biodiversity in EU countries yielded 1952 studies published since 1991 (for details see Supplementary Material of the original paper). However, Northern and Western Europe dominates the literature both in terms of absolute number of studies (Fig. 6.2.1a; the UK, for example, is the focus of twice as many publications as the central and eastern EU NMS together) and proportional to the agricultural area (Fig. 6.2.1b).

Whilst the number of studies from central and eastern NMS is increasing, even when adjusted for the agricultural area in the region, they are still only the focus of a tenth of the number of studies focussed on the rest of Europe (Fig. 6.2.1c). This confirms the results of a recent literature review on European AES, in which only 3% focussed on the NMS (Uthes & Matzdorf, 2013), despite the fact that AES have been in place in most NMS for at least 4 years by the end of the analysed time period. There are many possible reasons for the disparity in the numbers of publications on farmland biodiversity. Greater perceived urgency of farmland biodiversity loss and amount of research funding available in the west is likely to play a role, although the acceptance rate by journals of submissions from Eastern Europe has also been criticised (e.g. Rotter & Gostincar, 2014). Whilst it can be assumed that ecological research from the NMS is also published in non-English language or regional journals, these are usually not detected by the international community, for example when creating large-scale reviews. This limits the accuracy of conclusions drawn from the literature, both for the general understanding of agricultural ecosystems and for the local design of conservation measures, because the responses of many species to management changes are moderated by the landscape context (Tscharntke et al., 2012a; Gonthier et al., 2014). For example, moderate intensification was found to positively affect corn bunting (*Emberiza calandra*) populations in a study in Poland (Szymkowiak et al., 2014), compared to strong evidence for the negative effects in the UK (Brickle et al., 2000; Brickle & Harper, 2002), probably due to the generally low level of intensification in the surrounding Polish landscape. For similar reasons, red-backed shrikes (*Lanius collurio*) were found to have generally low breeding site fidelity in Polish landscapes, in contrast to their high site fidelity in ‘islands’ of habitat in Western Europe (Tryjanowski et al., 2007).

6.2.3. Harnessing the biodiversity value of Central and Eastern European farmland

Of the support measures available for farmland biodiversity in the EU, the CAP has by far the greatest influence. With an average payment of 237 €/ha of farmland in the last programming period (Farmer et al., 2008), the direct payments of the CAP play an important role in supporting the viability of farming in the EU. However, it is particularly the subsistence and semi-subsistence farms making up such a large proportion of holdings in the NMS that benefit the least from this subsidy and therefore are most likely to be forced towards abandonment or intensification. Whilst it was known prior to accession that many of the smallest holdings in the NMS would have to be excluded from direct payments due to the administrative costs, this system was nonetheless adopted unaltered, exacerbating the competitive disadvantage of semi-subsistence farms (Swain, 2013). Furthermore, only few of the rural development measures so far offered by the CAP are accessible by semi-subsistence farms as they are either too small or lack the financial capital required (Davidova et al., 2012). There is, however, a planned single payment in the 2014–2020 CAP for ‘small farms’, which may improve the financial situation of these holdings (Hennessy, 2014). Nevertheless, it seems to have generally been the fate of NMS thus far to have ‘imported’ EU policies that have been designed according to the priorities of the EU-15, without being able to ‘upload’ those with a better fit to their own structures and institutions (Gorton et al., 2009; Davidova et al., 2012; Swain, 2013).

This situation is also found in other rural development measures, such as agri-environment schemes (AES). AES are the only instrument in the CAP directly targeting farmland biodiversity conservation, and in 2009, 20.9% of farmland in the EU was enrolled in AES (Eurostat 2012, http://epp.eurostat.ec.europa.eu), which received approximately €33.2 billion in AES support over the period 2007–2013 (ENRD, 2014). Although member states have a high degree of flexibility in the design and implementation of AES (EC, 2005), several schemes in the NMS are based on well-supported data from Northern and Western Europe that may not fit to the local or regional circumstances. For example, postponing mowing from spring to summer is a popular agri-environment measure found in a review of several Western European studies to be generally beneficial for plant and invertebrate diversity (Humbert et al., 2012; Buri et al., 2013, 2014). However, when applied to already extensively managed patches of meadow such as exist in many regions of Romania, any postponement of mowing mainly results in a synchronization of management and a loss of the mosaic of sward heights (Dahlström et al., 2013; see also Konvička et al., 2007 and Cizek et al., 2011). Even within Northern and Western Europe, the effects of AES are largely dependent on the type of landscape in which they are applied (Batáry et al., 2011b; Scheper et al., 2013), suggesting that schemes are likely to be ineffective unless they are adapted to the local context.

In contrast to much of lowland EU, the main challenge – and opportunity – for farmland biodiversity conservation in the NMS is that a large number of species of conservation concern often still coexist (e.g. in Polish field margins: Wuczyński et al., 2014). These target species may have different requirements, creating conflicts when prescribing management measures. Simple but rigid measures applied over large areas can therefore be worse than existing management (e.g. Nikolov et al., 2011; Elts & Lõhmus, 2012). Another side effect of rigid prescriptions is the disruption and eventual loss of local traditional ecological knowledge related to adaptive management (Babai & Molnár, 2014).

Many areas of HNV farmland in Central and Eastern Europe are also not eligible for AES support. As with the direct payments, a large proportion of holdings fall below the size threshold, or the vegetation does not fall into one of the categories of agricultural land defined by the EU (Kazakova & Stefanova, 2011). Actively harnessing the biodiversity value of this farmland will therefore require measures adapted to regional circumstances and allowing for variable or even idiosyncratic small-scale management using a more flexible definition of agricultural land. For this to happen, interdisciplinary research is needed on the impact of different policy options on ecology and economy of the regions. Whilst the recent reform of the CAP has failed to meet expectations regarding provisions for biodiversity conservation, the increased devolution of responsibility to member states may provide the greater flexibility needed to develop local strategies to promote farmland biodiversity (Pe’er et al., 2014).

6.2.4. Conclusions

The maintenance of HNV farmland is a policy priority for the EU, not only for the ecological, cultural and economic benefits it provides, but also for the conservation of many ‘wild’ species that over millennia of human disturbance have come to rely on these habitats. Thus, whilst there are many areas in which the promotion of low-intensity agriculture is now clearly inappropriate, the continuation of these practices should be made viable for local land managers in places where it still exists. Following Chappell & LaValle (2011), we believe that the future of food security and sustainable agriculture lies less in focussing on yield gaps, and more in increasing socio-economic access to produce, in which low-intensity and small-scale agriculture plays an important role (Tscharntke et al., 2012b). Promoting sustainable development of rural regions goes hand in hand with this, most importantly by creating a direct link between the ecological state of a landscape and the well-being of its human population (see e.g. the discussion in Fischer et al., 2012). In HNV landscapes, yields are usually limited by adverse physical conditions (altitude, substrate, climate), and biodiversity promotion as well as other functions of agriculture, such as social coherence or cultural dimensions, should be the priority rather than intensification. Although approaches to valorise HNV landscapes through high-end products and tourism are starting to make an impact in some areas, the current viability of low-intensity farmland is largely supported by payments through the EU CAP.

In this study, we have argued that the widespread low-intensity farmland and associated biodiversity in Central and Eastern European countries makes them of special conservation significance in the EU, especially given the generally poor conservation status of farmland relative to other habitat types in Europe (Halada et al., 2011). Yet these habitats are disadvantaged by the EU CAP, which is poorly adapted to their needs. This is aggravated by a lack of relevant research from the east in the international literature, leading to a bias in ecological observations in Europe towards the north-west. This not only limits the scalability and transferability of information found in the literature, but also the ability to design locally appropriate conservation measures. Whilst these problems are not unique to Central and Eastern Europe, the scale and the depth of the problem here mean that focussing more on improving the fit and evidence base of agricultural policies in the central and eastern NMS would play a disproportionately large role in sustaining European biodiversity. Promoting pan-European research and monitoring networks, as well as more research targeted on the farmland of Central and Eastern Europe, both within and outside of the EU, would help to formulate better conservation approaches to counteract the increasing pressure on farmland species in Europe.

6.3. Former iron curtain drives biodiversity-profit trade-offs in German agriculture

Agricultural intensification drives biodiversity loss and shapes farmers' profit, but the role of legacy effects and detailed quantification of ecological-economic trade-offs are largely unknown. In Europe during the 1950s, the Eastern communist bloc switched to large-scale farming by forced collectivization of small farms, while the West kept small-scale private farming (Fig. 6.3.1). Therefore, here we aimed to test the effectiveness of organic cereal management for biodiversity in large-scale vs. small-scale agriculture along the former Iron Curtain.

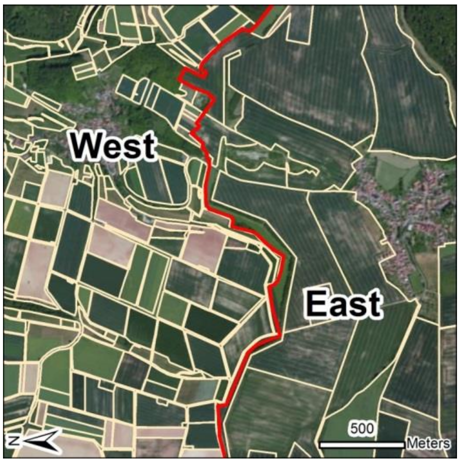


Fig. 6.3.1. Illustrative map (1:30000, date: 25.05.2012) showing field-size differences between West and East Germany along the former iron curtain (red line) in the study area (around the villages of Weissenborn and Hohes Kreuz, South-East of Göttingen, on the border of Lower Saxony (West) and Thuringia (East)). Source of the photo: ESRI, World Imagery, DigitalGlobe (date: 15.05.2015).

6.3.1. Material and methods

In 2013, we selected nine pairs of organic and conventional winter wheat fields in small-scale agricultural landscapes in former West Germany and in large-scale agricultural landscapes in former East Germany, respectively, all along the former inner German border (2 regions × 9 field pairs = 36 study fields; for a map see Supplementary Material of the original paper). These two neighbouring study regions are representative of the farmland areas of the former East and West Germany (Thiele et al. 1999; Happe et al. 2008). We aimed to explore how biodiversity patterns change from field edges to field centres with the following within-field sampling design. We designated transects at field edges (directly next to narrow grassy field margins bordering dirt roads), field interiors (15 m from field edge) and field centres (120 and 75 m from field edge in East and West, respectively). We performed our study in the agricultural matrix, minimizing the area and potential effect of non-agricultural habitats (Table 6.3.1) (Batáry et al. 2011b). Landscape structure was very different between the two neighbouring regions, with fields more than six times larger in the East, and >70% longer field edges in the West. Conventional farmers in both regions used about five times the amount of nitrogen fertilizer compared to organic farmers, applied synthetic pesticides about five times per year (vs. never), and had approximately two times higher yields than organic farmers (Seufert et al. 2012, 2017). This large difference in winter wheat yield between organic and conventional farmers is typical for the rich soils farmed in the study region (Clough et al. 2007b).

In 2013 June, we surveyed plants by estimating the relative cover per species in three plots (5 × 1 m in size and 10 m distance between them) per transect (Σ = 324 plots). Arthropods (carabids, spiders and rove beetles) were collected with two funnel traps per transect in two one-week periods from May to June (Σ = 432 funnel traps; for the trapping method see Duelli et al. 1999).

We also performed a detailed economic survey of our study farms based on farmer interviews. Total costs included expenses for mechanical field work, seeds, soil analyses, chemical plant protection, chemical growth regulators, synthetic and organic fertilizers, agricultural wage enterprises and working time. Total revenues included grain and straw revenues as well as subsidies for organic agriculture. Total profit was calculated by deducting total costs from total revenues per field per hectare.

Table 6.3.1. Landscape structure (in 500 m buffer) around and local management intensity of study fields in small (West) vs. large (East) scale agricultural systems with organic vs. conventional management (mean ± SEM) during 2013 (n=36 fields). Effects of region (R), management (M) and their interaction are shown as effect estimates ± 95% CIs from general and generalised linear mixed-effects models. Significant effects (P < 0.05) are marked in bold.

Model	West		East		Estimate ± 95% CI		
	Organic	Conventional	Organic	Conventional	Region	Management	R × M
Landscape structure							
Field size (ha)	3.7 ± 0.7	3.3 ± 0.4	21.7 ± 5.5	18.3 ± 2.1	**-14.14 ± 6.90**	2.16 ± 7.74	-1.55 ± 10.95
Edge length (km)	18.3 ± 1.3	19.5 ± 1.6	11.0 ± 0.8	10.8 ± 0.6	**8.38 ± 3.67**	0.02 ± 2.90	-1.52 ± 4.10
Grassy field margin (km)	7.2 ± 0.5	7.3 ± 0.4	5.5 ± 0.6	5.0 ± 0.9	**2.09 ± 1.90**	0.42 ± 1.73	-0.54 ± 2.45
Land-use diversity	1.4 ± 0.1	1.3 ± 0.0	0.9 ± 0.1	0.9 ± 0.1	**0.43 ± 0.26**	0.07 ± 0.22	-0.03 ± 0.31
Agricultural area (%)	73.9 ± 4.1	76.9 ± 6.2	81.0 ± 5.1	85.5 ± 4.5	-9.25 ± 16.11	-5.49 ± 13.55	2.90 ± 19.17
Management intensity							
Fertilizer (kg N/ha)	21.6 ± 10.9	199.3 ± 6.3	65.3 ± 11.7	193.6 ± 8.6	-8.47 ± 33.76	**-129.61 ± 33.76**	**-57.10 ± 22.40**
Pesticide application (#)	0.0 ± 0.0	4.3 ± 0.4	0.0 ± 0.0	5.2 ± 0.7	0.19 ± 1.03	–	–
Yield (dt/ha)	40.9 ± 2.5	85.2 ± 3.3	48.3 ± 2.5	85.3 ± 1.6	0.54 ± 8.25	**-37.91 ± 8.25**	-7.91 ± 11.67
Study field size (ha)	3.0 ± 0.5	3.1 ± 0.4	21.8 ± 3.6	20.0 ± 3.0	**-16.95 ± 7.18**	1.23 ± 5.59	-1.35 ± 7.90

The following cost factors were considered per study field: field preparation including sowing and harvesting (e.g. costs due to the use of cultivator, milling machine, plough, harrow, chipper, curry comb, seed drill, harvester and baler), seeds, soil analyses, chemical plant protection (e.g. fungicides, insecticides, herbicides, rodenticides or molluscicides), chemical growth regulators, synthetic and organic fertilizers, agricultural wage enterprises and working time. If costs of preparation, sowing (including seed costs) and harvesting were not tractable by farmers, we noted working steps and machine-data and later on calculated expenses by the use of the online plant process calculator of the agricultural advisory board for engineering and building (KTBL 2015). In doing so, we considered field size, workability of soil (medium or heavy soil), mechanization (kW, machine type, working width of machines or sowing quantity), field to farm distance (set up to 1 km) and farming system (organic or conventional). In terms of other parameters (e.g. machine costs like fuel requirement, repair costs and depreciation), we used standardized settings of the online calculator. If farmers' data did not fit exactly into the online calculator (e.g. sometimes in the case of kW, field size or machine width), we used the next closest setting. In terms of farm-saved seed, we assumed 0.40 €/kg of seed for conventional and 0.47 €/kg of seed for organic farming system (pers. comm. from Association for Technology and Structures in Agriculture), because statements of farmers showed a huge variation. Machine costs emerging through fertilization and chemical plant protection were calculated by using the default setting of the online calculator (KTBL 2015) while considering the farming system (organic or conventional), field size, workability of soil (heavy or medium) and cultivation method (direct sowing method, non-plough tillage or conventional soil cultivation with plough). If farmers only provided information about the kind and quantity of product used without prices (four farmers), then costs for chemical plant protection products and growth regulators were derived from different price lists (TopAgrar 2013; Agravis 2014; Landi 2014; Schweiger 2014). If farmers were unable to provide prices for synthetic fertilizers, cost calculation was based on individual average prices of the fertilizers in Germany for the marketing year 2013/2014 (pers. comm. Agrarmarkt Informations GmbH). Since farmers used organic fertilizers originating from their own enterprises, they were just able to tell us the quantity and the type of organic fertilizer. Average prices were derived from our own survey of regional companies (Nährstoffverwertung Oldenburger Raum Münsterland, Naturdünger Verwertungs GmbH, Agrovermittlungsdienst Emsland-Bentheim GmbH, Bioenergiedorf Jühnde), which deal with or utilize natural fertilizers. Prices for liquid manure and digested residue were generally set with 4 €/t or m³ (Lower Saxony) and 5 €/t or m³ (Thuringia), and solid dung with 10 €/t. To calculate the costs of working time, we recorded estimated working hours of each farmer (with reference to the whole winter wheat season 2013/2014). Working time was related to hectares and multiplied by 15 € (this amount was based on our own experiences as well as on a farmer's estimate) to calculate costs per hectare.

In addition to the costs, we also considered the revenue side of the winter wheat season 2013/2014. Here, we recorded grain and straw yield as well as additional state grants for organic agriculture per study field. Grain yield was multiplied by actual proceeds stated by the farmers. Grain yield was sold or used as fodder, seed or for baking purposes. If a crop was still not sold or used at the time of the survey, calculations were based on estimated proceeds of each farmer. If straw was not left on the field, we also calculated proceeds of straw (sold or used as fodder or litter). If not stated by the farmers (nine farmers), we used the average German sales price of straw (7.38 €/dt) with reference to the marketing year 2013/2014 (AMI 2015). Besides grain and straw proceeds, we also took into account state grants for organic agriculture as a source of revenue. Here, we considered federal state specific subsidy rates of the business year 2013/2014 (cultural landscape programme of Thuringia: 170 €/ha if organic farming was practised ≥ six years; Agri-environmental programme of Lower Saxony: 210 €/ha if organic farming was practised ≥ three years; pers. comm. Ministry of Food, Agriculture and Consumer Protection of Lower Saxony and Thuringian Ministry of Infrastructure and Agriculture). All matters of costs and proceeds were calculated per hectare and year for each field. To obtain total revenue (€ per ha, field and business year), aggregated costs were subtracted from overall proceeds.

Due to limited availability of organic farms in the East (fewer organic farms in the East, but with an order of magnitude larger size than in the West (Köpke & Küpper 2012)), we applied a so-called partly cross-nested design by selecting from half of the farmers two fields and from the other half only one field: in both regions we had three villages with two organic-conventional pairs and three villages with one organic-conventional pair (for a conceptual figure see Supplementary Material of the original paper). Therefore, we applied linear mixed effects models by using the 'lme4'package (Bates et al. 2015) of the statistical software R. All biodiversity data were pooled per sampling year and per transect prior to analysis by taking the mean cover for arable plants and the sum for arthropods. Response variables, if needed, were either log (carabid and rove beetle abundances) or logit (plant cover) transformed in order to achieve a normal error distribution and/or avoid heteroscedasticity and to get a better model fit. Additionally, all response data were standardized from zero to one in order to allow for direct comparisons of effects on the different dependent variables (Legendre & Legendre 1998), and to perform fixed-effect meta-analyses for getting the overall effects (see next paragraph). The partially crossed nested study design was taken into account in the random structure of the models. Accordingly, each model included the random effects: field (n = 36) nested in farm (n = 24) nested in village (n = 9) and field (n = 36) nested in pair (n = 18) nested in village. In addition, models contained the following fixed effects: region (East vs. West), management (organic vs. conventional), transect position (edge, interior or centre) and the interaction between region and management. Marginal and conditional R^2 values for species richness and abundance models were calculated using the "r.squaredGLMM" function of 'MuMIn'package (Bartoń 2016) of R. We did not simplify the models in order to be able to directly compare their effect estimates among the different taxa and to summarize these estimates in a meta-analysis (see below).

One of the main interests was, besides investigating the environmental effects on each individual group, whether these environmental effects showed an overall effect. Therefore, we performed a series of unweighted fixed effect meta-analyses for each effect type (region effect, management effect, effectiveness of organic management, edge vs. interior effect, interior vs. centre effect, edge vs. centre effect) per measure type (species richness, abundance) with the metafor package (Viechtbauer 2010) of R. Weighting was not used since data originate from the same experimental design with the same sample size per measure. This enabled us to get an effect estimate of all groups expressed as summary effect sizes with their corresponding 95% CIs presented in Fig. 6.3.2, Supplementary Material of the original paper.

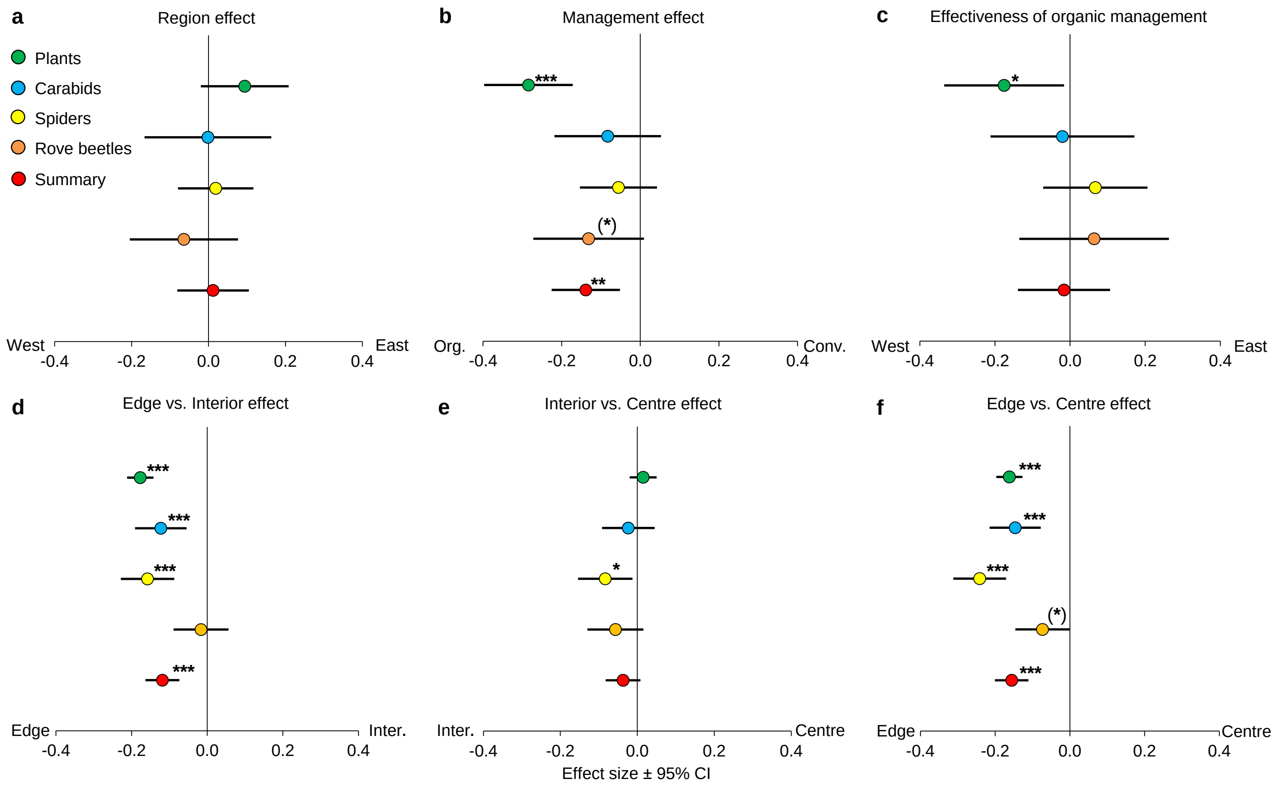


Fig. 6.3.2. Effects of region (a) and management (b), their interaction, i.e. effectiveness of organic management (c), and edge effect (edge vs. interior (d), interior vs. centre (e), edge vs. centre (f)) on plant and arthropod species richness, as well as the summary effect from meta-analysis, expressed as effect estimate ± 95% CI (n = 36 fields). Org.: organic; Conv.: conventional; Inter.: interior. Significance levels: (*): <0.1, *: <0.05, **: <0.01, ***: <0.001.

We analysed the effects of region and management and their interaction on count data from economic surveys (profit, revenue and cost) with generalized linear mixed-effects models based on a negative binomial distribution for avoiding overdispersion. Random effect terms correspond to the biodiversity analyses above without field, since that was the lowest level.

We analysed the effects of region and management and their interaction on farm size with linear regression based on a normal distribution (no random effect). Finally, we analysed the effects of region and management and their interaction, presented in Table 6.3.1 with generalized linear mixed-effects models based on a normal distribution for all non-integer continuous data based on a normal distribution. One exception was the only count variable, number of synthetic pesticide applications, which was analysed based on a negative binomial distribution for avoiding overdispersion. The structure of random effects was the same as in the case of economic survey data. In the case of number of synthetic pesticide applications, where effect of management could not be analysed (organic fields excluded because synthetic pesticides are not allowed), only village was used as a random factor.

6.3.2. Results

We found that farmers' profit from winter wheat was more than 100% higher per hectare under organic than conventional management (Fig. 6.3.3, Supplementary Material of the original paper). Subsidies for organic agriculture were 170 and 210 €/ha in East and West (AES and subsidies vary among German federal states (Batáry et al. 2015), respectively, suggesting that these subsidies contribute to the difference in profit between the two management types. Although subsidies were a substantial part of profit for organic farmers, large differences between the two management regimes still remains without these subsidies (mean values for West organic: 1181 €/ha vs. West conventional: 412 €/ha; East organic: 1663 €/ha vs. East conventional: 874 €/ha). We also found significantly higher profits per farmed area (~50-60%) in the large-scale than in the small-scale agricultural region. This is because of higher production costs in Western conventional farms due to current labour costs and higher revenues in Eastern organic farms (Hill & Bradley 2015) probably associated with better marketing possibilities (Fig. 6.3.3, Supplementary Material of the original paper).

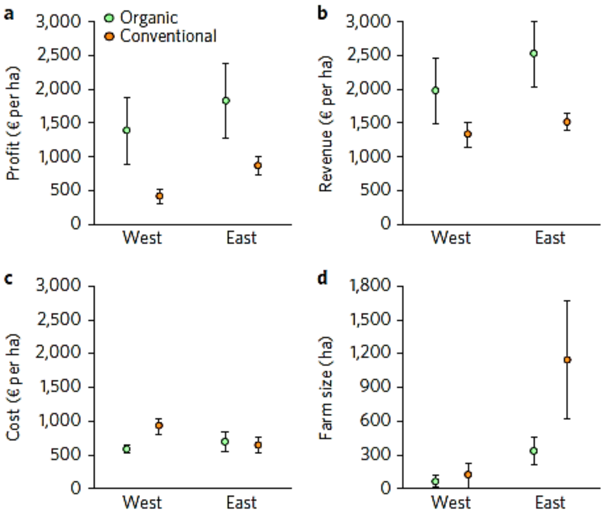


Fig. 6.3.3. Effects of region and management on farmers' profit (a), revenue (b) and cost (c) measured in Euros per hectare (n = 28 fields) and on farm size (d) (n=18 farms). Organic farmers' revenue contained the subsidy for organic farming, which was 170 and 210 €/ha in West and East. Bars represent mean ± SEM. See Supplementary Material of the original paper for test statistics.

There was no effect of region on species richness of plants and arthropods (carabids, rove beetles, spiders), as well as no overall effect of region when all groups were considered together in a fixed effect meta-analysis (Fig. 6.3.2, Supplementary Material of the original paper) (Borenstein et al. 2009). The same was true when analysing arthropod abundances and plant cover (Supplementary Material of the original paper). Organically managed fields harboured more species and individuals of all groups than conventionally managed fields. This effect was strongest for plants, which drove the overall summary effect resulting in 44% higher overall species richness in organically than conventionally managed fields. The statistical interaction of region and management was due to a higher effectiveness of organic management in the West for plant richness as well as spider abundances. Interestingly, both species richness and abundances were reduced by about 25% when comparing field edges with field interiors, but there was no further drop towards the field centres (except for spider richness). Hence, most farmland species and their populations are confined to the very edge of crop fields. This also implies that the higher biodiversity in the small-scale agricultural system in the West can be linked to the much higher amount of field edges (Benton et al. 2003; Tscharntke et al. 2005a; Fischer et al. 2008).

To further explore this pattern, we performed sample-based rarefaction curves on incidence data of all taxa in field edges combined by standardizing for field perimeter (field perimeters originate from the mean field size per region, Table 6.3.1; Gotelli & Colwell 2001; Colwell 2006). The rarefied species richness observed in different types of management (organic over conventional) and region (West over East) was significantly different (Fig. 6.3.4). Small-scale conventional management in the West supported higher biodiversity than large-scale organic management in the East (Fig. 6.3.4). Although the species richness per field was similar in both regions (Fig. 6.3.2), having only nine small fields in the West gives a much higher species richness than four large fields with the same length of field perimeter in the East regardless of management type. This means that the species richness in the fields, i.e. alpha diversity, of these two contrasting regions is similar, whereas the species turnover, i.e. between-field beta diversity, is much higher in the West than in the East. In addition, richness was higher in organic than in conventional management.

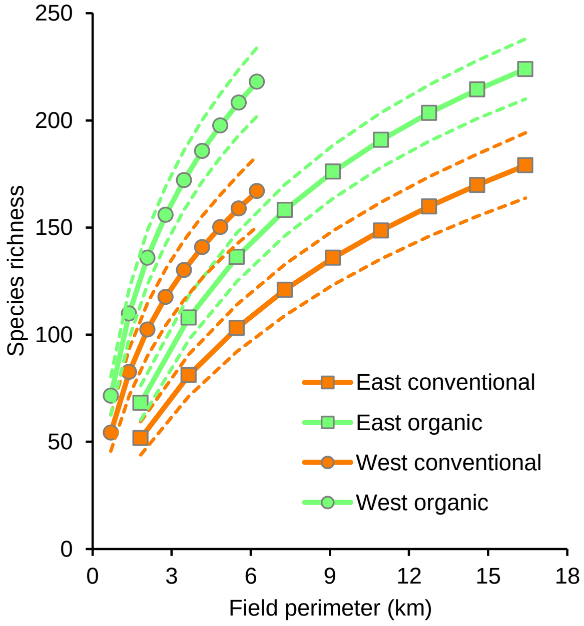


Fig. 6.3.4. Effects of region and management on overall species richness using sample-based rarefaction curves standardized for perimeter per field (n = 36 fields; dashed lines represent 95% confidence intervals).

6.3.3. Discussion and conclusions

Our study showed that large-scale agriculture in East Germany reduced biodiversity, which has been maintained in West Germany due to >70% longer field edges compared to the East. Thus we quantified the great contribution of small-scale agriculture to biodiversity, which was more important than organic management. In both regions, switching from conventional to organic farming also increased biodiversity. Yield levels were the same across the East-West divide, but large-scale agriculture led to the highest profit (despite similar yield) and organic farming even doubled profit (despite halved yield). Although large-scale farms allow higher profits, which is in line with economies of scale (Duffy 2009), future restructuring of agricultural landscapes towards small fields with field margins would probably be an economically viable option under an EU-subsidised policy on enhancing farmland biodiversity (Batáry et al. 2015).

In conclusion, EU policy should acknowledge the surprisingly high biodiversity benefits of small-scale agriculture, which are on par with conversion to organic agriculture. We emphasize the importance of quantifying ecological-economic trade-offs for a politically balanced view. Further, the long-term stability of former East-West contrasts in agricultural politics and farming practices suggests that evaluations of ecological and economic costs and benefits need to be regionally adapted, taking agricultural traditions and potential legacy effects into account (Sutcliffe et al. 2015).

7. Summary and outlook

Role of agri-environment schemes in nature conservation

We reviewed the structure of current AES across Europe. Since a 2003 review questioned the overall effectiveness of AES for biodiversity, there has been a plethora of case studies and meta-analyses examining their effectiveness (chapter 2). Most syntheses demonstrate general increases in farmland biodiversity in response to AES, with the size of the effect depending on the structure and management of the surrounding landscape. This is important in the light of successive EU enlargement and ongoing reforms of AES. We examined the change in effect size over time by merging the data sets of three recent meta-analyses and found that schemes implemented after revision of the EU's agri-environmental programs in 2007 were not more effective than schemes implemented before revision. Furthermore, schemes aimed at areas out of production (such as field margins and hedgerows) are more effective at enhancing species richness than those aimed at productive areas (such as arable crops or grasslands). Outstanding research questions include whether AES enhance ecosystem services, whether they are more effective in agriculturally marginal areas than in intensively farmed areas, whether they are more or less cost-effective for farmland biodiversity than protected areas, and how much their effectiveness is influenced by farmer training and advice? The general lesson from the European experience is that AES can be effective for conserving wildlife on farmland, but they are expensive and need to be carefully designed and targeted.

Managing species rich grasslands

The conservation of species rich semi-natural grassland is a huge challenge for the 21st century, since these grasslands cannot compete economically with the high-yield improved grasslands. Many of them still rely on traditional forms of management, such as low intensity grazing or late mowing. Our study on extensively vs. intensively grazed semi-natural pastures in Hungary showed that even slight differences in grazing intensity (0.5 vs. 1 cow/ha) can negatively influence the grassland specialist bird species (3.1).

Studies on natural or semi-natural fragments embedded in agricultural matrix often focus on the effects of fragment size and/or isolation of fragments, but rarely investigate these effects in combination with the surrounding landscape structure (but see Marini et al. 2010). In a study on leafhoppers of calcareous grassland fragments, we disentangled these effects besides considering the amount of matrix surrounding each fragment (3.2). Increasing habitat isolation reduced leafhopper species richness in simple (high arable %), but not in complex landscapes. In simple landscapes, leafhoppers may find it more difficult to reach the next suitable fragment due to a lack of alternative resources during dispersal.

In a further study we focused on the effects of management and landscape context of calcareous grasslands and orchard meadows on the two flagship taxa of nature conservation, i.e. on butterflies and birds (3.3). Calcareous grasslands were much more important for butterfly diversity than orchard meadows, but suitability of orchards for butterflies was improved when embedded in forested landscapes. In contrast to butterflies, bird diversity benefited more from orchard meadows than calcareous grasslands, which had higher diversity when management was abandoned.

Impact of hedgerow-forest connectivity on biodiversity and ecosystem function

Hedgerows are often part of cultural landscapes in Europe, and can provide habitats, corridors, refuges or even barriers for species living in agricultural landscapes (Baudry et al. 2000). We investigated the response of farmland vs. woodland birds at two degrees of isolation of hedges from forest, i.e. in hedges connected to forests and in agricultural matrix isolated hedges, and compared them with forest edges (4.1). Farmland birds were more abundant in hedges than in forest edges, while woodland birds preferred forest edges, but both groups did not differ between connected and isolated hedges. However, bird community composition differed not only between habitat types (hedge vs. forest edge), but also between hedge isolation levels (hedges connected to forest vs.

isolated hedges).

Using a similar design, but combining it with the directly neighbouring field types (oilseed rape or wheat next to the woody linear habitat), we studied the effect of a mass-flowering crop on wild bees and pollination (4.2). Adjacent oilseed rape positively affected fruit mass and seed set of hawthorn flowering simultaneously with oilseed rape, but had no effect on the later flowering dog rose. At the landscape scale, oilseed rape flowering had a negative effect on bumble bee density in the hedges due to dilution of pollinators. Our results show that oilseed rape effects on bee abundances and pollination success depend on the spatial and temporal scale considered, the habitat type, the wild plant species and the time of crop flowering.

Comparing effectiveness of agri-environment management in cropland and grassland

Studies comparing the effectiveness of agri-environment management between different crops and grasslands are rare. In the alkali region of Kiskunság NP (Hungary), we compared indirectly two similar studies on arthropods in semi-natural grasslands and two years later in cereal fields (5.1). Both aimed to study the effect of management on arthropod diversity at local and landscape scales. We showed that slightly increasing grazing intensity and landscape heterogeneity in grasslands had a positive effect on carabids, while in the case of cereal fields, the increasing local management intensity (nitrogen fertiliser kg/ha) had a negative effect on spider richness. Based on our results, we think that low intensity croplands could act as a buffer zone around the semi-natural grasslands, at least in this biogeographic region, although direct spillover effect should be further studied (Madeira et al. 2016).

We aimed to determine the relative effects of landscape complexity, agroecosystem type (wheat field or meadow) and local management (organic or conventional) on diversity patterns of functional groups of plants and arthropods in a German study (5.2). Organic management positively affected several functional groups (forbs, non-carnivore carabids, hunting spiders), mostly independently of agroecosystem type, while lower landscape scale management intensity only increased species richness of grasses and spiders. The great differences in responses of functional groups to management at the local as well as landscape scales suggest implementing more scale and group specific targets for agri-environmental schemes to improve their efficiency.

Landscape moderation and regional differences of biodiversity patterns

In a meta-analysis we tested and found evidence for the landscape complexity hypothesis showing that agri-environmental management benefits species richness only in simple, but not in complex landscapes (6.1). This was true only for studies in croplands, but not in grasslands. Therefore, we conclude that agri-environmental management should be adapted to landscape structure, agroecosystem type and the species groups at which they are targeted.

Within Europe, there is high variation in many aspects affecting farmland conservation, but particularly stark differences can be seen between the western and post-socialist eastern countries (6.2). Central and eastern new EU member states have retained relatively large areas of species-rich farmland, but despite increased investment in nature conservation here in recent years, farmland biodiversity trends appear to be becoming increasingly negative. This can be at least partly related to that measures within the EU Common Agricultural Policy are relatively poorly adapted to support biodiversity. Harnessing the benefits of the existing low intensity agriculture in Central and Eastern Europe through targeted research and monitoring to create more locally appropriate conservation strategies should be made a priority in Europe.

In a study comparing the effectiveness of organic farming in East vs. West Germany, we showed that large-scale agriculture in East Germany reduced biodiversity, which has been maintained in West Germany due to > 70% longer field edges than those in the East (6.3). In contrast, profit per farmland area in the East was 50% higher than that in the West, despite similar yield levels. In both regions, switching from conventional to organic farming increased biodiversity and halved yield levels, but doubled farmers' profits.

Outlook

The present thesis has contributed to the growing knowledge on the effects of local and landscape scale agricultural intensification from evaluation of AES effectiveness through spillover effect to effects of habitat fragmentation on species communities. In the light of this, the following new research directions are summarized. First, Kleijn et al. (2011) recently proposed in their review two different conservation initiatives. One focuses on conservation of intrinsic biodiversity values, such as structurally complex landscapes, rare or endangered species or high biodiversity values. The other focuses on ecosystem services in structurally simple landscapes independently of species identity. These are roughly equivalent to narrow-and-deep and broad-and-shallow AES. However, a stronger division in these general objectives might not only boost new research, but might also develop more effective AES. Furthermore, Macfadyen et al. (2012) highlighted in their review that actions protecting biodiversity can often indirectly help preserving ecosystem services, but actions enhancing ecosystem services does not necessarily provide good outcomes for biodiversity. A recent idea related to enhancement of ecosystem services is the so called ecological intensification, which entails the environmentally friendly replacement of anthropogenic inputs and/or enhancement of crop productivity, by including regulating and supporting ecosystem services management in agricultural practices (Bommarco et al. 2013).

Second, Fahrig et al. (2011) proposed a new framework to what extent biodiversity can be enhanced by altering landscape pattern without reducing agricultural production by considering separately crop compositional heterogeneity (the number and proportions of different land-use types) and crop configurational heterogeneity (the spatial arrangement of land-use types). Although several studies have analysed the effects of compositional heterogeneity on the effectiveness of AES, there are as yet no studies directly focusing on the potential moderation effects of configurational heterogeneity, such as by comparing small-scale vs. large-scale agriculture.

Third, most large-scale agroecological studies either focus on the generally intensively used agricultural matrix or on the remaining natural or semi-natural fragments embedded in the matrix. Instead a more holistic view is applied by a grid based sampling, which samples both the matrix and the fragments (Dormann et al. 2007; Beduschi et al. 2018). This can then provide a more thorough overview of ecological patterns and processes in and around their interfaces (Scherber et al. 2012). All these ideas may offer opportunities for future study design and better implementation of future conservation schemes including AES.

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