

Effects of farming practice and landscape complexity on
vertebrate diversity and ecological functioning in
agroecosystems

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Christina Fischer
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1. Referent: Prof. Dr. Teja Tschardtke

2. Korreferent: Prof. Dr. Stefan Vidal

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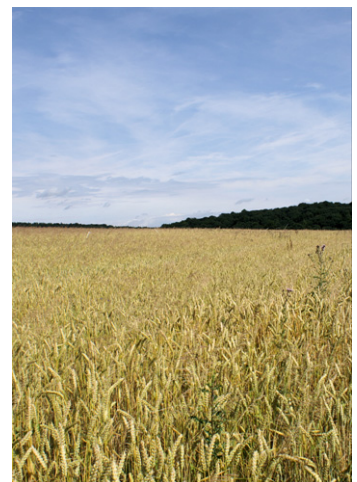
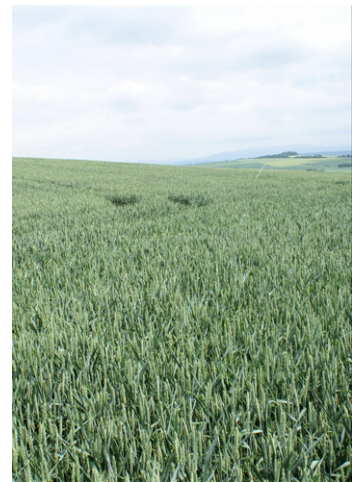
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CHAPTER 1

GENERAL INTRODUCTION



Effects of farming practice and
landscape complexity on vertebrate
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INTRODUCTION

Biodiversity research especially in agricultural landscapes has become a topic of great demand in ecology. The huge interest of science on subjects dealing with “biodiversity” and “agriculture” can be highlighted by the fact that the publication and citation output almost exponentially increased over the last 20 years, resulting in about 250 published articles and over 5000 citation in 2009 within this framework (Web of Science[®] Citation Report, 2010).

Farmland represents the major land use throughout Europe (Robinson and Sutherland, 2002). In Germany 49% of the land area is covered by agricultural land, including arable land, grassland and permanent crops (Federal Statistical Office, Germany available at <http://www.destatis.de>), harbouring many different organism groups (Scherr and McNeely, 2007). But due to agricultural intensification farmland biodiversity has become threatened during the last decades (Kleijn et al., 2006; Robinson and Sutherland, 2002; Stoate et al., 2001). Furthermore related ecosystem functions, such as pollination, pest control and disease suppression (Larsen et al., 2005; Luck et al., 2003; Tscharntke et al., 2005), are also negatively affected by an intensified agriculture (Hooper et al., 2005; Tscharntke et al., 2005). Local management such as increasing use of pesticides and mineral fertilizers (Bengtsson et al., 2005; Geiger et al., 2010; Hole et al., 2005) and the loss of semi-natural habitats at landscape scales (Benton et al., 2003; Concepción et al., 2008; Firbank et al., 2008) are the main causes for the recent species loss and the reduced efficiency of ecosystem services.

The negative effects of agricultural intensification can be compensated by high landscape complexity, characterized by high habitat-type diversity and a high amount of semi-natural habitats (shown for birds, small mammals, invertebrates, and seed predation rates see e.g. Mason and Macdonald, 2000; Michel et al., 2006; Purtauf et al., 2005; Farwig et al., 2009, respectively) and by organic farming characterized by an abandonment of pesticide applications (shown for birds, small mammals, invertebrates, and seed predation rates see e.g. Beecher et al., 2002; Macdonald et al., 2007; Navntoft et al., 2006; Menalled et al., 2007, respectively). In addition, organic farming can be expected to be most effective in enhancing biodiversity in simple, but not in complex landscapes (Concepción et al., 2008; Tscharntke et al., 2005). To facilitate farmland biodiversity and ecosystem services it is important to simultaneously consider local management and landscape context (Kleijn et al., 2004; Tscharntke et al., 2005).

STUDY ORGANISMS AND AREA

Representing a major proportion of Europe's farmland biodiversity, we focused in the first part of the present thesis on birds in agricultural landscapes. Farmland bird communities drastically declined in agroecosystems of Western and Central Europe owing to agricultural intensification during the last decades (e.g. Donald et al., 2006; Gregory et al., 2005; PECBMS, 2009; Robinson and Sutherland, 2002). In contrast, due to the abandonment of highly intensive agriculture in the course of changes in the political systems a recovery or stabilisation of farmland birds was recorded in Eastern Europe after the 1990s (Gregory et al., 2005; PECBMS, 2009).

In the second part of this thesis, we studied small mammal communities as functionally important links in food webs. In agricultural landscapes small mammals can be important as predators of seeds, non-crop plants and insects (Baraibar et al., 2009; Ness and Morin, 2008), but also as prey of larger mammals and birds (Salamolard et al., 2000), furthermore they are also agricultural pests to various crops (Brown et al., 2007).

Dealing with ecosystem functions of predators such as birds, small mammals and invertebrates (Westerman et al., 2006), we focused in the third part of the thesis on biological weed control as an important ecosystem service in agricultural fields, which can strongly affect weed population growth and recruitment (Crawley, 1992; Kolb et al., 2007) and lead to a reduced herbicide use.

Birds, small mammals and seed predation/removal rates were observed on paired organic and conventional winter wheat fields (*Triticum aestivum* L.) (Fig. 1.1) located along a gradient of landscape complexity (40 - 100% arable land within radii of 500 m around focal fields, Fig. 1.2).

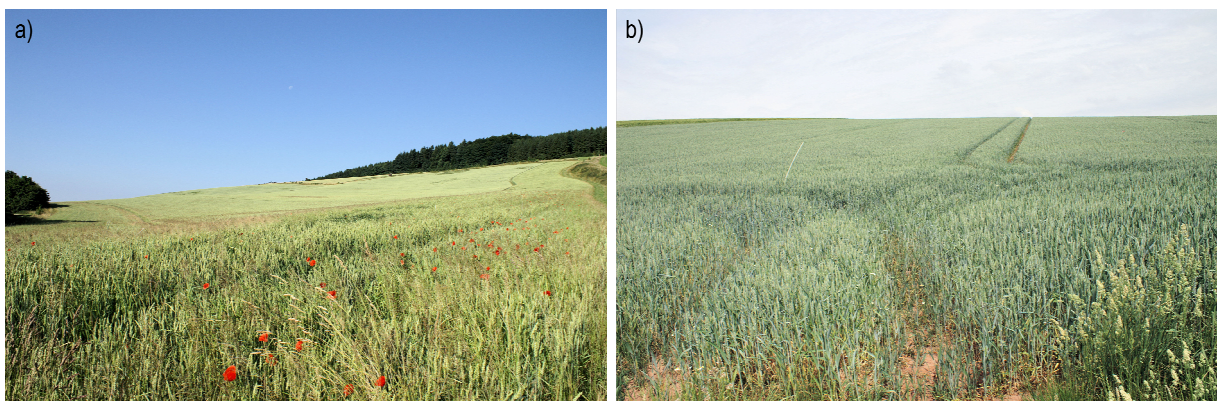


Fig. 1.1 a) organically and b) conventionally managed winter wheat field.

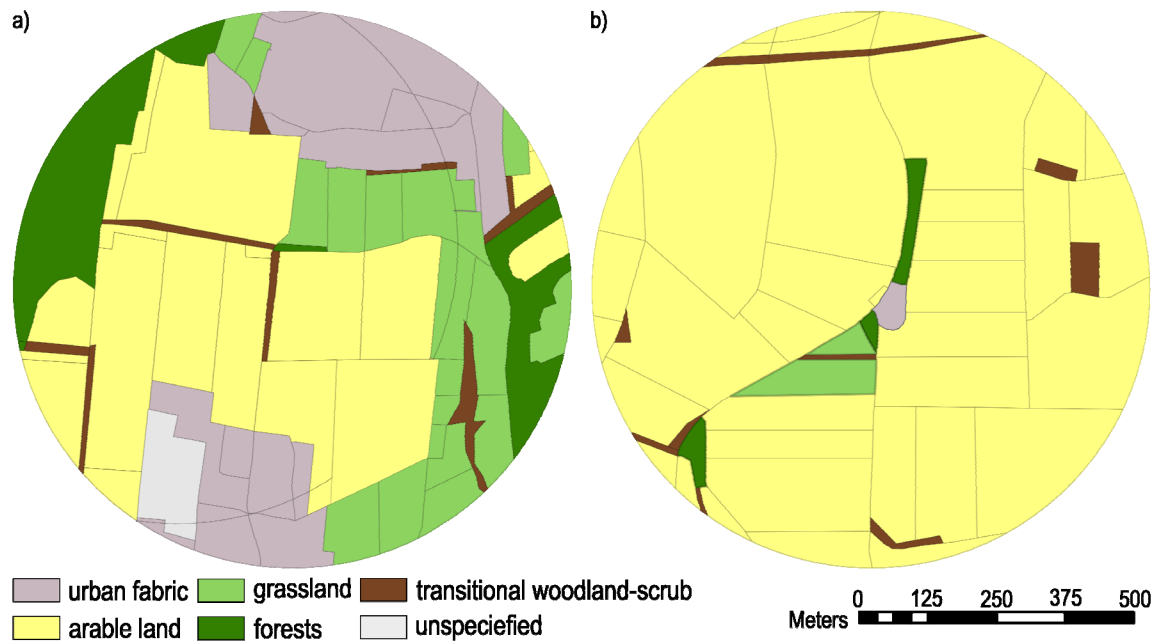


Fig. 1.2 a) complex landscape with 43% arable land and b) simple landscape with 92% arable land within a radius of 500 m around the focal wheat field.

Bird surveys were carried out in two German regions differing in land-use history: in East Germany, around the city of Bad Langensalza and in West Germany, around the city of Göttingen, with a higher habitat diversity and a lower mean field size in West Germany compared to East Germany (Fig. 1.3). All bird species were mapped on a 500 x 500 m square in and around focal fields (Bibby et al., 1992) during breeding season and in winter. Abundance, species richness, diversity, and species composition of all birds and the following bird traits were calculated: “openland species” breeding and feeding on fields; “farmland species” using fields, field edges and farmyards and “woodland species” breeding and feeding in trees and forests (Gregory et al., 2007; Herzon and O’Hara, 2007; Virkkala et al., 2004).

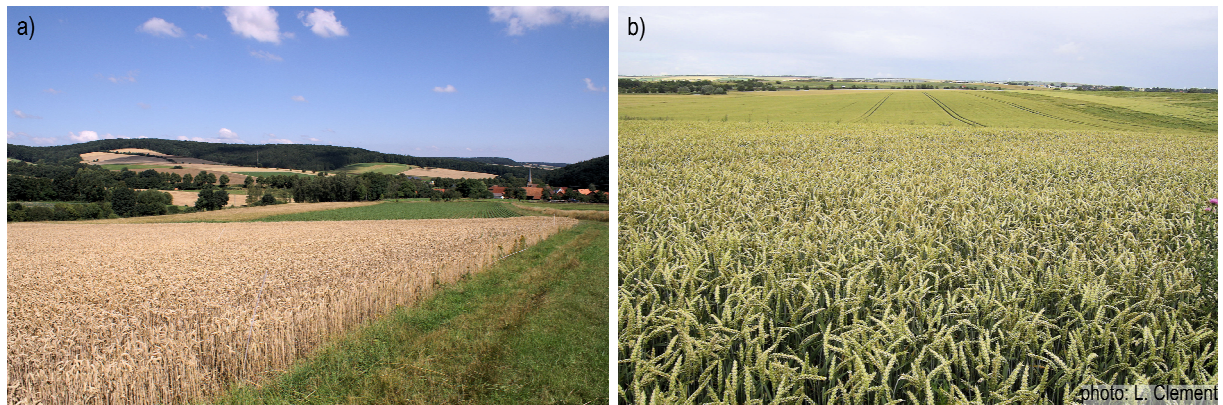


Fig. 1.3 Different study regions in West and East Germany, with a) lower mean field sizes in West Germany and b) large fields in East Germany.

Small mammal trapping and the seed predation experiment were conducted only around the city of Göttingen in West Germany between wheat flowering and ripening. Small mammals were sampled with 30 Ugglan multiple-capture live traps (240 x 60 x 90 mm; details in Lambin and MacKinnon, 1997; Fig. 1.4a) per wheat field. Individuals trapped for the first time were marked with a permanent micro-tattoo (FST Laboratory Animal Microtattoo System) at the tail base (Fig. 1.4b). Small mammal abundance was calculated as the total number of trapped animals per field, except recaptures (Michel et al., 2006). Community composition, abundance, species richness, and diversity of the total number of trapped small mammals and abundances of the three most abundant species (*Apodemus agrarius* PALLAS, *Microtus arvalis* PALLAS, *Sorex araneus* L.) were calculated.

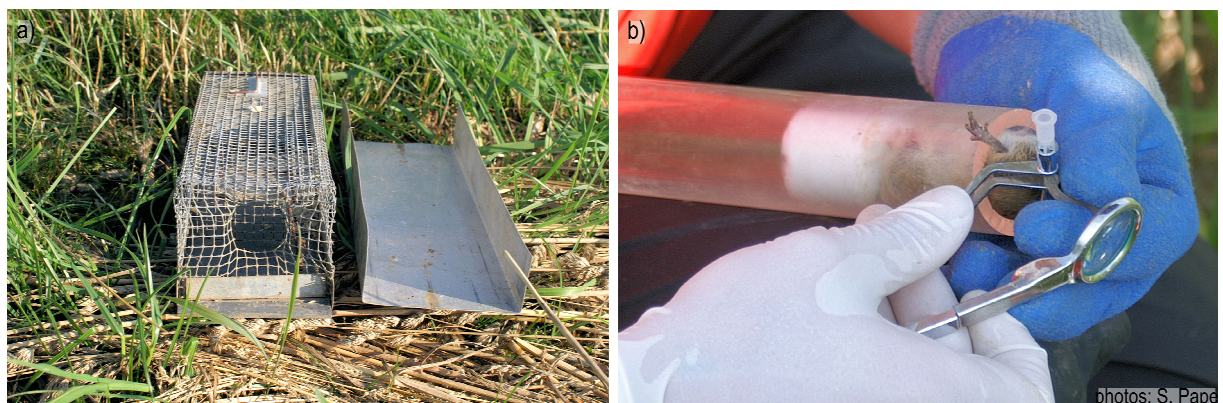


Fig. 1.4 a) Ugglan live trap for small mammal trapping; b) marking of a small mammal at the tail base using the micro-tattoo system.

Seed predation/removal of four different seed species was assessed for three different predator groups at the field edge and in the field interior by estimating seed removal rates. Therefore we exposed a defined amount of seeds of the following common weed species (Hofmeister

and Garve, 1986) into the wheat fields: *Galium aparine* L. (goosegrass), *Cirsium arvense* (L.) Scop. (creeping thistle), *Poa trivialis* L. (rough bluegrass), and *Apera spica-venti* (L.) P.B. (silky bentgrass) (Fig. 1.5).

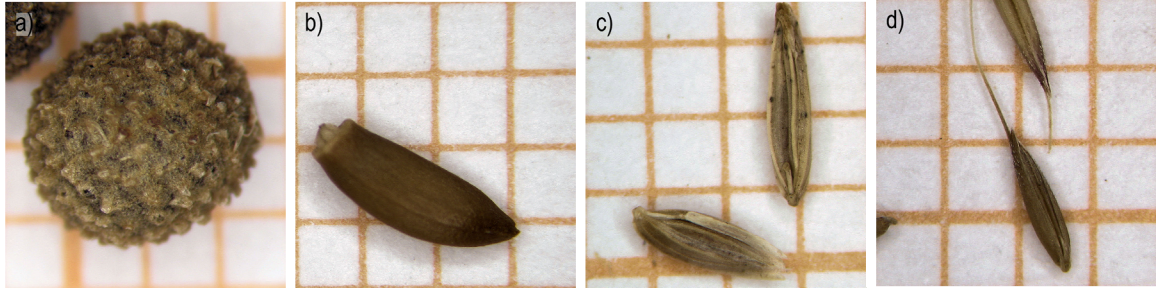


Fig. 1.5 Weed seeds used for the seed predation/removal experiment: a) *Galium aparine*; b) *Cirsium arvense*; c) *Poa trivialis*; d) *Apera spica-venti*.

We aimed to exclude a) no predators, b) vertebrates and c) vertebrates and large invertebrates by using cages with different mesh sizes (Fig. 1.6). Seed removal rates were calculated as percentage of remaining seeds from the initial seed number or seed weight. Additionally abundances of small mammals and activity densities of phytophagous carabid beetles and slugs, which are potential seed predators or dispersers (Booman et al., 2009; Honek et al., 2007; Türke et al., 2010) were measured using 30 small mammal live traps and four pitfall traps per field.



Fig. 1.6 Seed predator exclusion treatments used to exclude: a) no predators; b) vertebrates; c) vertebrates and large invertebrates.

HYPOTHESES AND CHAPTER OUTLINE

In the present thesis we analysed the relative importance of local farming practice and landscape complexity on birds, small mammals and seed predation/removal rates in agricultural landscapes. In particular, we examined the following hypotheses:

- Bird and small mammal communities, as well as seed predation/removal rates are enhanced by both organic farming and high landscape complexity (Chapter 2, 3 & 4).

- Birds specialised to farmland and woodland profit most from increasing landscape complexity, while openland species are expected to show contrasting responses because of the need to feed and breed in arable fields (Chapter 2).
- Organic farming benefits small mammal populations most in simple landscapes, while species known to profit from cereal fields show highest densities in simple landscapes (Chapter 3).
- Seed predation/removal rates vary among seed species, distance from the field edge and predator identity according to abundances and activity densities of seed predators (Chapter 4).

RESULTS AND CONCLUSIONS

Bird abundance, species richness and diversity increased with landscape structural complexity, most pronounced for farmland and woodland bird species. Openland bird species increased with increasing percentage of arable land, indicating species-specific perception of landscape structural complexity. Organic farming practice only enhanced the species richness of openland bird species and the abundance and species richness of the whole bird community in summer. Most of the variation in community composition was explained by differences in landscape structural complexity, but not by differences in farming practice during breeding season and in winter. To enhance bird communities in agricultural landscapes, a large scale mosaic of landscapes with a high proportion of arable land for openland bird species is also needed, like landscapes with a variety of semi-natural habitats, as nesting, resting and hiding places for farmland and woodland birds. Organic farming appears to be less important especially during winter. Hence, the often stressed argument for the importance of organic farming for bird communities in agricultural landscapes has to be reconsidered.

Small mammals responded differentially to farming practice, depending on the surrounding landscape complexity. In simple landscapes organic farming increased small mammal abundance, species richness and diversity, whereas conventional farming increased it in complex landscapes. Organic fields in simple landscapes can enhance small mammals because of higher food supply compared to conventional fields, whereas conventional fields in complex landscapes may act as refuges from predator attacks, because of a higher wheat cover. Individual small mammal species increased by increasing landscape complexity, shown for *A. agrarius* abundances, while abundances of the potential pest species *M. arvalis* were positively influenced by landscape simplification especially on organic fields. Small mammals in agricultural landscapes will be enhanced by a reduction of pesticide use on

organic fields in simple landscapes providing sufficient food sources, while an increasing landscape complexity supports small mammals on conventional fields.

Patterns of weed seed predation and seed removal were determined by the identity of seed predators (vertebrates *vs.* invertebrates), with small mammals removing larger seeds, while invertebrates mainly removed small grass seeds. Seed removal was highest in seeds of intermediate size (the notorious weed *C. arvensis*) and higher on organic fields in complex landscapes and conventional fields in simple landscapes. Slug density and seed removal showed similar response to landscape complexity and farming practice, while small mammal abundances showed reverse patterns. Phytophagous carabid beetles were not affected by landscape structure, but were more abundant on organic than conventional fields. Future studies should try to separate responses of different predator groups to local and landscape management in more detail. Furthermore the relative impact of each predator group on the large range of weed species should be tested experimentally.

In conclusion, our results showed that both organic farming and landscape complexity can enhance vertebrate abundance and species richness and facilitate ecological functions but with different directions. Organic farming was less important than landscape complexity for birds especially during winter, while in interaction with the surrounding landscape complexity organic farming enhanced small mammals and seed predation/removal rates. Collectively, the results indicate contrasting responses of different vertebrate taxa and ecological functions suggesting species-specific landscape management, like organically and conventionally managed fields, surrounded by landscapes with a diversity of semi-natural habitats.

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CHAPTER 2

BIRDS



photo: A. Kovács



photo: C. Roland

Landscape structure *versus* farming
practices as predictors of bird
diversity during breeding season
and in winter



photo: J. Jurkiewicz

Fischer, C., Flohre, A., Clement, L.W., Batáry, P., Weisser,
W.W., Tschardtke, T., Thies, C.

ABSTRACT

Organic farming has been shown to enhance bird populations in agricultural landscapes, but little is known about the relative importance of local management and landscape context. We analysed abundance, species richness and diversity of bird communities on 59 plots during breeding season and 61 plots during winter (500 x 500 m around winter wheat fields) in two contrasting regions of Germany differing in land-use history (West vs. East), landscape structural complexity (40 - 100% arable land) and farming practice (organic vs. conventional). Organic farming enhanced bird abundance and species richness, but only during breeding season. In West Germany abundance, species richness and diversity were higher than in East Germany, presumably due to the higher overall habitat-type diversity, and decreased with decreasing landscape complexity, this being marked for farmland and woodland birds. In contrast, openland bird species were more abundant in East Germany during both seasons and increased with decreasing landscape complexity. During breeding season, organic farming enhanced openland bird species richness. In conclusion, bird communities in agricultural landscapes appeared to be more strongly determined by landscape complexity than by farming practices owing to the availability of nesting and sheltering places in non-crop habitats for farmland and woodland species, while openland species require arable land as breeding and feeding habitats. For bird conservation the landscape perspective has to come to the fore by providing a mixture of crop and non-crop habitats suggesting species-specific landscape management, while organic farming seems to be less important than landscape complexity for farmland and woodland birds.

KEY WORDS: farmland birds, landscape complexity, openland birds, organic farming, woodland birds

INTRODUCTION

Bird communities and particularly specialist bird species in agricultural landscapes of Western and Central Europe drastically declined owing to agricultural intensification in the last decades (Benton et al., 2003; Donald et al., 2001; Donald et al., 2006; Firbank et al., 2008; PECBMS, 2009; Reif et al., 2008; Robinson and Sutherland, 2002; Wretenberg et al., 2007). This was documented by the “European farmland bird index”, using population trends of 23 farmland birds (Gregory et al., 2005). It shows that common farmland birds decreased and woodland birds remained stable during the last 30 years. In contrast, a recovery or stabilisation of farmland birds and even an increase of woodland birds was recorded in Eastern Europe after the 1990s due to the abandonment of highly intensive agriculture in the course of changes in the political systems (Gregory et al., 2005; PECBMS, 2009).

Organic farming is often reported to counteract this trend by enhancing farmland biodiversity (e.g. Fuller et al., 2005; Hole et al., 2005; Kleijn et al., 2006), owing to abandonment of pesticide applications and a more diverse crop rotation. Also farmland birds are often facilitated by organic farming (Beecher et al., 2002; Freemark and Kirk, 2001; Lokemoen and Beiser, 1997; but see Geiger et al., 2010), while other studies reported contradicting responses of farmland bird abundance, species richness and diversity and different bird species traits to organic farming (Chamberlain et al., 2010; Filippi-Codaccioni et al., 2009; Genghini et al., 2006; Jones et al., 2005; Kragten and de Snoo, 2008; Piha et al., 2007).

Altogether, most studies addressed bird communities at the field or farm scale, but did not take into account larger spatial scales, which might be important due to the dispersal ability and behaviour of birds at landscape scale (Herzon and O'Hara, 2007; Mason and Macdonald, 2000; Sanderson et al., 2009; Walker et al., 2005; Wretenberg et al., 2010). The number of habitats, habitat-type diversity, and the percentage of semi-natural habitats, respectively, has been shown to be positively related to bird abundance (Luther et al., 2008; but see Batáry et al., 2007), species richness (McMahon et al., 2008; Piha et al., 2007; Wretenberg et al., 2010) and diversity (Laiolo, 2005). However, little is known on the relative importance of landscape structure and local farming practices.

In this study, we analyzed effects of different land-use history, landscape complexity and local farming practices during breeding season and in winter on abundance, species richness, diversity, and species composition of all birds and the following bird traits: “openland species” breeding and feeding on fields; “farmland species” using fields, field edges and farmyards and “woodland species” breeding and feeding in trees and forests (Gregory et al.,

2007; Herzon and O'Hara, 2007; Virkkala et al., 2004). Therefore we used organic and conventional wheat fields located across a gradient of landscape complexity (40 - 100% arable land) in two German regions, with smaller field sizes and high overall landscape complexity in West Germany and very large fields and a low overall landscape complexity in East Germany. We expected that bird communities are enhanced by both organic farming and high landscape complexity, most pronounced for birds specialised to farmland and woodland, while openland species are expected to show contrasting responses because of the need to feed and breed in arable fields.

MATERIALS AND METHODS

Study areas and field selection

Bird surveys were carried out in summer 2007 and winter 2007/2008 in two German agricultural landscapes on winter wheat fields, in West Germany around the city of Göttingen (51°30' N, 9°54' E) in Southern Lower Saxony and in East Germany around the city of Bad Langensalza (51°06' N, 10°38' E) in the Thuringian basin. To minimize differences in the local species pool, fields within one region were situated in an area between 30 x 30 km² and 50 x 50 km² around the study centre. Landscape complexity was quantified for an area within a 500 m radius around the centre of the focal wheat field by means of percentage of arable land, mean field size and habitat diversity (Shannon index calculated from percentage of arable land, grassland, permanent crop, forest, transitional woodland-scrub, water and urban fabric) using official digital topographical maps (ATKIS DTK 50) and the Geographical Information System ArcGIS 9.2 (1999 - 2006 ESRI Inc.). To compare different farming practices in total 39 conventionally managed wheat fields (West Germany: $n_{\text{summer}} = 14$, $n_{\text{winter}} = 15$; East Germany: $n_{\text{summer/winter}} = 24$) and 22 organically managed wheat fields (West Germany: $n_{\text{summer}} = 15$, $n_{\text{winter}} = 16$; East Germany: $n_{\text{summer/winter}} = 6$) were selected along gradients from structural simple to complex landscapes (for landscape structure parameters see Table 2.1). Minimum distance between the study fields was ~1 km. In West Germany, mean field size and percentage of arable land were lower than in East Germany, whereas habitat diversity was higher (Table 2.1, two-way ANOVA). Percentage of arable land correlated positively with mean field size (West Germany: $r_{29} = 0.41$, $p < 0.05$; East Germany: $r_{28} = 0.40$, $p < 0.05$), whereas it correlated negatively with habitat diversity (West Germany: $r_{29} = -0.97$, $p < 0.001$; East Germany: $r_{28} = -0.96$, $p < 0.001$), percentage of grassland (West Germany: $r_{29} = -0.84$, $p < 0.001$; East Germany: $r_{28} = -0.92$, $p < 0.001$) and percentage of forest (West Germany: $r_{29} = -0.69$, $p < 0.001$; East Germany: $r_{28} = -0.46$, $p < 0.01$;

$n_{\text{West Germany}} = 31$, $n_{\text{East Germany}} = 30$; Pearson's product-moment correlation), and therefore, appeared as a simple predictor of landscape complexity and was used for further investigations.

In Germany, organically managed fields are dispersed in agricultural landscapes owing to the land ownership structure, i.e. there is no concentration of organic fields or farms in structurally simple or complex landscapes such as in other countries (e.g. England: Gabriel et al., 2009; Norton et al., 2009). Between organically and conventionally managed fields there were no significant differences in mean field size, habitat diversity and percentage of arable land (Table 2.1, two-way ANOVA). Standardized questionnaires were sent out to farmers to get information about yields, pesticide and fertilizer use. Organic fields received no applications of chemical plant protections and synthetic fertilizers. In conventional fields the plant protections were applied with 5.9 ± 0.7 and 8.1 ± 0.7 applications/year (mean \pm SE) and nitrogen fertilizers were applied with 150.5 ± 11.1 and 177.6 ± 6.6 kg/ha (mean \pm SE) in West and East Germany, respectively. On organic fields the average yield per field was lower (West Germany: 3470 ± 240 ; East Germany: 4249 ± 282 kg/ha; mean \pm SE) than on conventional fields (West Germany: 7143 ± 436 ; East Germany 7021 ± 133 kg/ha; mean \pm SE).

Table 2.1 Characterisation of organic and conventional winter wheat fields in the study regions in West and East Germany. Mean field size, habitat diversity and percentage of arable land with standard errors were calculated using a radius of 500 m around the centre of each focal field. Effects of region (West vs. East Germany) and farming practices (organic vs. conventional farming) on transformed explanatory variables were calculated by using two- way analysis of variance. F-values and levels of significance of two-way ANOVA are given.

	West Germany		East Germany		Region	Farming practice
	organic (n = 16)	conventional (n = 15)	organic (n = 6)	conventional (n = 24)	F-value	F-value
Mean field size (ha) ^a	4.8 ± 0.6	5.5 ± 0.8	38.1 ± 13.0	54.9 ± 14.7	122.96 ^{***}	0.51
Habitat diversity ^a	0.8 ± 0.1	0.7 ± 0.1	0.3 ± 0.1	$0.1 \pm <0.1$	90.11 ^{***}	0.10
Arable land (%) ^b	67.9 ± 4.3	74.6 ± 4.8	81.8 ± 8.2	91.1 ± 2.3	25.61 ^{***}	0.13

^{***} $p < 0.001$; ^{**} $p < 0.01$; ^{*} $p < 0.05$; ^a log transformed, ^b arcsine-square root transformed

Bird survey

Birds were surveyed three times between April and June 2007 for breeding birds and two times in December 2007 and January 2008 for winter birds in each field. All bird species were mapped on a 500 x 500 m square in and around each focal field (Bibby et al., 1992). Starting time and direction of walking the survey route were randomized. Each survey took about two hours and was conducted from one hour after dawn until two hours before midday during the breeding season. In winter surveys could last until one hour before sunset (Bibby et al., 1992). The exact location and the number of all birds within the sampling area which were seen or heard were recorded on a map, except birds that only passed flying. Surveys were not conducted during rainy and windy weather (Bibby et al., 1992). Bird species were classified according to their habitat use in three ecological traits, namely “openland species”, “farmland species” and “woodland species” similar to those by Gregory et al. (2007), Herzon and O'Hara (2007) and Virkkala et al. (2004). We identified nine openland species breeding and feeding on fields; 21 farmland species using fields, field edges and farmyards; and 27 woodland species breeding and feeding in trees and forests. 36 other species were recorded within the sampling areas, which are breeding and feeding elsewhere (for classifications of birds according to their ecological traits see Appendix Table A2.1).

Statistical analyses

Maximum abundance of bird individuals out of the three visits in summer and the two visits in winter was calculated for all bird counts and the three ecological traits (Bibby et al., 1992). Effects of region (West vs. East Germany), landscape (percentage of arable land) and local farming practice (organic vs. conventional) on abundance, species richness and diversity (Shannon index) of the total number of observed birds and the three ecological traits were analyzed using linear models fitted by generalized least squares with a maximized log-likelihood (Pinheiro and Bates, 2000) implemented in the *nlme* package (version 3.1-96; Pinheiro et al., 2009) in R 2.9.1 (R Development Core Team, 2009). Separate analyses were done for both seasons. Response variables were either log or square root transformed, percentage of arable land was arcsine-square root transformed in order to achieve a normal error distribution and/or avoid heteroscedasticity and to get a better model fit. Different variance functions implemented in the *nlme* library were used to model the variance structure of the within-group errors. Fitted models with different within-group variances were compared by choosing the lowest value of the Akaike Information Criterion (AIC) from an

ANOVA table (Pinheiro and Bates, 2000). Model simplification was done in a stepwise model selection by AIC implemented in the R package *MASS* (Venables and Ripley, 2002) until minimal adequate model was obtained. Significance of terms in the best model was assessed by calculating the F- and p-values of an ANOVA table.

Partial redundancy analysis (RDA) implemented in the R package *vegan* (Oksanen et al., 2009) of R 2.9.1 (R Development Core Team, 2009) was used to assess influences of region (West vs. East Germany coded as factor variable), landscape (percentage of arable land coded as numeric variable) and local farming practice (organic vs. conventional coded as factor variable) on species composition of all birds and the three different ecological traits, for both seasons separately. Species matrices were Hellinger transformed to allow usage of RDA with datasets containing many zeros (Legendre and Gallagher, 2001). In the text, arithmetic means and standard errors are given.

RESULTS

Overall abundance, species richness and diversity

A total of 93 bird species were recorded (for a list of species see Appendix Table A2.1). In summer on average 13.1 ± 1.4 ($n = 38$) species were found in and around conventional fields and 23.2 ± 2.2 ($n = 21$) species in and around organically managed fields. In winter conventional fields held 6.1 ± 0.6 ($n = 39$) species and organically managed fields held 9.0 ± 1.0 ($n = 22$) species (for species richness of all birds and different ecological traits see Table 2.2). Skylarks (821 individuals) and yellowhammers (477 individuals) were the two most abundant species. In summer, total abundance, species richness and diversity of birds were higher in West than in East Germany and strongly decreased as the percentage of arable land increased, while farming practice had only an influence on abundance and species richness, but not on bird diversity. Bird abundance and species richness were higher in and around organic fields than in conventional fields (Table 2.3). In winter, species richness and abundance were higher in West than in East Germany, whereas species diversity did not differ between the regions. Total abundance, species richness and diversity decreased as the percentage of arable land increased, with no effects of farming practice (Table 2.4). Region (West vs. East Germany) and percentage of arable land explained most of the variation in the overall bird species matrix during both seasons, whereas farming practice had no significant effects (Table 2.5).

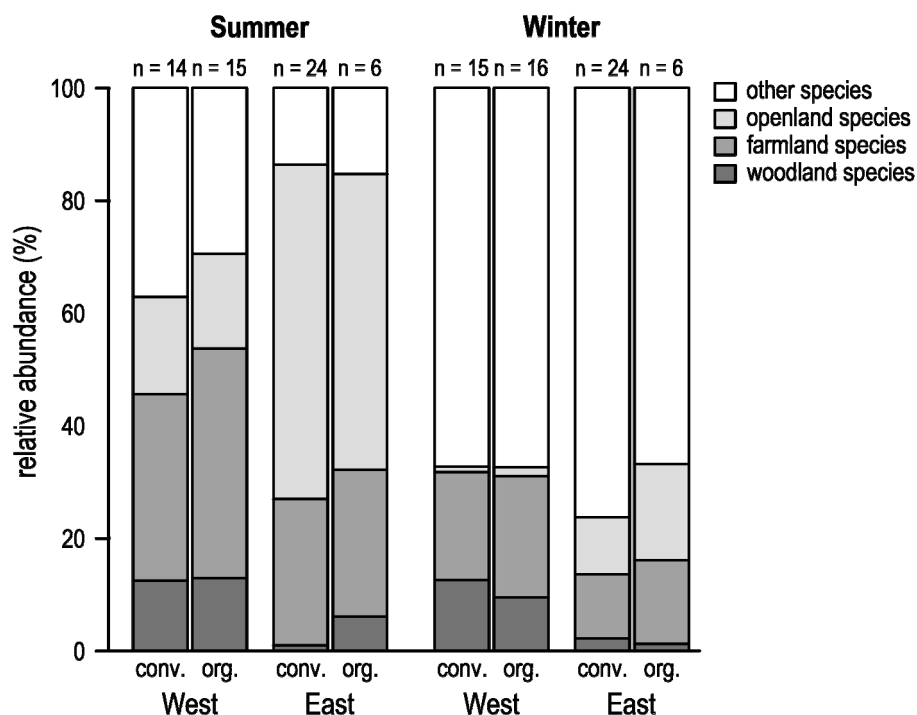


Fig. 2.1 Effects of region (East vs. West Germany) and of farming practice (organic vs. conventional) on mean relative abundance (%) of the ecological birds traits (abundance of other bird species and birds of the three traits divided by the total abundance of birds observed, averaged for organic or conventional wheat fields per study region) during breeding season (summer) and in winter.

Openland, farmland and woodland species

Abundance of openland species during breeding season was higher in East than in West Germany (Fig. 2.1), whereas species richness and diversity did not differ between the two study regions (Table 2.3). Openland species correlated positively with percentage of arable land, during breeding season (Fig. 2.2a), whereas no influences of landscape complexity could be found in winter (Fig. 2.2d). Organic farming had only a positive effect on species richness during breeding season but not in winter (Table 2.3, 2.4).

Abundance, species richness and diversity of farmland and woodland species were higher in West Germany than in East Germany during breeding season (Table 2.3). Same patterns could only be shown for abundance and species richness of woodland species in winter (Table 2.4). Farmland and woodland species correlated negatively with the percentage of arable land during the breeding season (Fig. 2.2b, c) and in winter (Fig. 2.2e, f). Only the abundance of woodland species was enhanced by organic farming during the breeding season. In winter no effect of farming practice could be found (Fig. 2.1; Table 2.3, 2.4).

Region and percentage of arable land explained most of the variation in the ordination analyses of openland, farmland and woodland bird species during breeding season. Farming

practice had no influence on the species composition of none of the ecological traits. In winter the openland bird species matrix was significantly constrained by differences between study regions, but not by percentage of arable land and farming practice. Variation in farmland and woodland bird species matrices were only explained by percentage of arable land in winter (Table 2.5).

Table 2.2 Species richness on 500 x 500 m squares around organic or conventional (conv.) winter wheat fields in the study regions in West and East Germany recorded during breeding season (summer) and in winter. Mean species richness and standard errors were calculated for all, openland, farmland, and woodland bird species.

	Summer				Winter			
	West Germany		East Germany		West Germany		East Germany	
	conv. (n = 14)	organic (n = 15)	conv. (n = 24)	organic (n = 6)	conv. (n = 15)	organic (n = 16)	conv. (n = 24)	organic (n = 6)
All species (n _{max} = 93)	22.1 ± 1.8	26.7 ± 2.1	7.9 ± 0.9	14.3 ± 3.6	8.8 ± 0.8	10.1 ± 1.1	4.4 ± 0.7	6.2 ± 1.6
Openland species (n _{max} = 9)	1.5 ± 0.1	1.9 ± 0.2	2.2 ± 0.2	2.7 ± 0.4	0.2 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	0.8 ± 0.3
Farmland species (n _{max} = 21)	5.9 ± 0.7	7.9 ± 0.6	2.9 ± 0.4	4.0 ± 1.4	1.2 ± 0.3	1.3 ± 0.3	0.5 ± 0.1	0.7 ± 0.2
Woodland species (n _{max} = 27)	5.0 ± 0.8	6.3 ± 1.0	0.4 ± 0.2	2.0 ± 0.7	1.4 ± 0.4	1.8 ± 0.4	0.2 ± 0.1	0.3 ± 0.3

Table 2.3 Summary of minimal adequate linear models using generalized least squares to analyse effects of A: region (West vs. East Germany), B: percentage of arable land (landscape complexity), and C: farming practice (organic vs. conventional) on abundance, species richness and diversity of all birds the different ecological traits (openland, farmland, woodland species) in agricultural landscapes recorded during the breeding season. Denominator degrees of freedom (d.f.), standardized effects referring to A: West Germany and C: conventional farming practice, F-values and levels of significance are given.

	Abundance ^a			Species richness ^a			Diversity ^b		
	d.f.	Standardized effect	F-value	d.f.	Standardized effect	F-value	d.f.	Standardized effect	F-value
All species									
A	55	-0.33	54.9 ^{***}	55	-0.52	98.9 ^{***}	56	-0.21	69.8 ^{***}
B ^c	55	-0.88	16.6 ^{***}	55	-1.14	38.2 ^{***}	56	-0.49	28.7 ^{***}
C	55	0.36	16.9 ^{***}	55	0.22	6.1 [*]	-	-	-
Openland species									
A	55	0.54	23.2 ^{***}	-	-	-	-	-	-
B ^c	55	0.99	6.5 [*]	56	0.66	18.8 ^{***}	56	0.24	6.2 [*]
C	55	0.31	3.12	56	0.19	7.9 ^{**}	56	0.07	2.2
Farmland species									
A	55	-0.54	14.4 ^{***}	55	-0.42	21.1 ^{***}	56	-0.31	34.6 ^{***}
B ^c	55	-1.69	20.0 ^{***}	55	-0.70	10.8 ^{**}	56	-0.16	2.7
C	55	0.33	2.62	55	0.20	3.0	-	-	-
Woodland species									
A	55	-1.25	160.0 ^{***}	55	-1.01	157.9 ^{***}	56	-0.47	170.1 ^{***}
B ^c	55	-1.39	14.4 ^{***}	55	-1.02	23.2 ^{***}	56	-0.45	12.8 ^{***}
C	55	0.42	6.5 [*]	55	0.31	2.8	-	-	-

*** p < 0.001; ** p < 0.01; * p < 0.05; ^a log transformed; ^b square root transformed; ^c arcsine-square root transformed

Table 2.4 Summary of minimal adequate linear models using generalized least squares to analyse effects of A: region (West vs. East Germany), B: percentage of arable land (landscape complexity), and C: farming practice (organic vs. conventional) on abundance, species richness and diversity of all birds and the different ecological traits (openland, farmland, woodland species) in agricultural landscapes recorded during winter. Denominator degrees of freedom (d.f.), standardized effects referring to A: West Germany and C: conventional farming practice, F-values and levels of significance are given.

	Abundance ^a			Species richness ^a			Diversity ^b		
	d.f.	Standardized effect	F-value	d.f.	Standardized effect	F-value	d.f.	Standardized effect	F-value
All species									
A	58	-0.73	27.0 ^{***}	58	-0.33	36.7 ^{***}	-	-	-
B ^c	58	-1.64	10.5 ^{**}	58	-1.15	24.4 ^{***}	59	-0.54	25.0 ^{***}
C		-	-		-	-		-	-
Openland species									
A	59	0.42	8.1 ^{**}	58	0.32	11.2 ^{**}		-	-
B ^c		-	-	58	-0.29	2.5	59	0.04	3.1
C		-	-		-	-		-	-
Farmland species									
A		-	-		-	-		-	-
B ^c	59	-2.09	13.5 ^{***}	59	-0.90	21.3 ^{***}		-	-
C		-	-		-	-		-	-
Woodland species									
A	58	-0.29	20.9 ^{***}	58	-0.31	37.7 ^{***}		-	-
B ^c	58	-1.38	13.3 ^{***}	58	-0.88	11.9 ^{**}		-	-
C		-	-		-	-		-	-

^{***} $p < 0.001$; ^{**} $p < 0.01$; ^{*} $p < 0.05$; ^a log transformed; ^b square root transformed; ^c arcsine-square root transformed

Table 2.5 Results of Redundancy Analyses (RDA) to analyse effects of region (West vs. East Germany), percentage of arable land (landscape complexity), and farming practice (organic vs. conventional) on species composition of overall bird assemblage (all species) and the assemblages of the different ecological traits (openland, farmland, woodland species) in agricultural landscapes. F-values (= pseudo-F-values) and p-values (significant are in bold) are given.

	Region			Arable land (%)			Farming practice		
	Variation explained in %	F	p	Variation explained in %	F	p	Variation explained in %	F	p
Summer									
All species	7.10	5.14	< 0.001	4.93	3.57	< 0.001	1.35	0.97	0.50
Openland species	3.74	2.32	0.02	3.56	2.21	0.04	1.19	0.74	0.59
Farmland species	8.27	5.65	< 0.001	3.23	2.21	0.002	1.55	1.06	0.40
Woodland species	6.65	4.76	< 0.001	3.70	2.65	0.001	1.51	1.08	0.34
Winter									
All species	5.37	3.73	< 0.001	4.50	3.13	0.001	0.65	0.45	1.00
Openland species	8.43	5.33	0.02	3.22	2.03	0.14	0.55	0.35	0.73
Farmland species	0.66	0.43	0.83	7.81	5.07	0.003	0.45	0.29	0.95
Woodland species	2.34	1.58	0.12	4.39	2.96	0.007	1.06	0.71	0.67

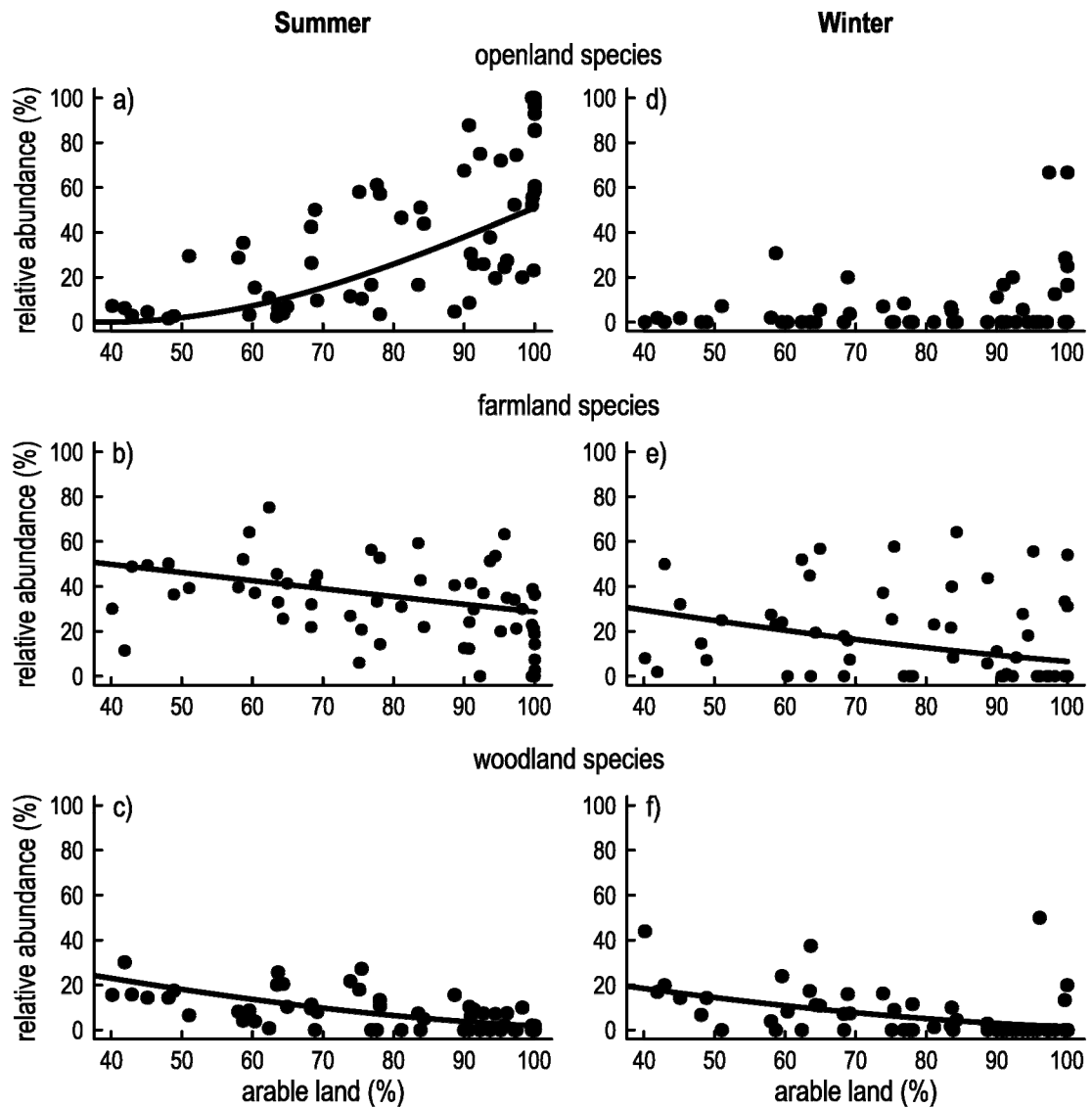


Fig. 2.2 Relation of percentage of arable land to the mean relative abundance (%) of openland, farmland and woodland bird species (abundance of birds of the three traits divided by the total abundance of birds observed, averaged over both study regions and farming systems) during summer a) – c) and in winter d) – f). Solid regression lines were used, when there was a statistical effect of percentage of arable land. For better visualisation back-transformed data are presented.

DISCUSSION

The analysis of bird communities in two contrasting regions, West and East Germany, showed a consistent increase of abundance, species richness and diversity in structurally complex landscapes, in spite of the great differences in land-use history. Organic farming was of minor importance and only enhanced bird abundance and species richness in summer, with no detectable effects in winter, thereby not supporting recent studies that ascribe great importance of organic farming for farmland birds or particular species (Beecher et al., 2002;

Chamberlain et al., 2010; Freemark and Kirk, 2001; Genghini et al., 2006; Lokemoen and Beiser, 1997; but see Filippi-Codaccioni et al., 2009; Jones et al., 2005; Kragten and de Snoo, 2008; Piha et al., 2007). Most of these studies did, however, not consider the landscape context (but see Henderson et al., 2009; Piha et al., 2007; Wretenberg et al., 2010).

The impact of landscape complexity and farming practice was the same within both study regions despite differences in mean field sizes, percentages of non-crop habitats and forests. Due to higher mean field sizes and percentages of arable land in East Germany we found higher openland bird species abundances and species richness than in West Germany, which is in line with results of Flade et al. (2008), showing same patterns for Skylark abundances, as most abundant representative for this ecological trait. Openland species that breed and feed on fields, are strongly associated with open areas like arable crops or grasslands (Erdős et al., 2009; Herzon and O'Hara, 2007; Mason and Macdonald, 2000; Sanderson et al., 2009; Virkkala et al., 2004; Wilson et al., 1997; Wretenberg et al., 2010), thereby preferring short vegetation and avoiding dense cover (Piha et al., 2007). Therefore, high openland bird densities can be expected particularly on arable fields (Chamberlain and Gregory, 1999; Sanderson et al., 2009; Virkkala et al., 2004; Wilson et al., 1997), whereas hedges and woody habitats are often negatively related to openland bird species, possibly caused by higher predator avoidance (Chamberlain et al., 1999). Also mixed farmed landscapes with winter and summer cereals as well as oilseed rape stubbles compared to farming systems dominated by winter cereals have repeatedly been emphasized to support birds in agricultural landscapes (Atkinson et al., 2002). The role of organic farming in supporting openland bird species richness appeared to be mainly related to food resources (Beecher et al., 2002; Henderson et al., 2009; McKenzie and Whittingham, 2009). Organic farming on arable fields offers diverse food resources for openland species as strong habitat specialists, resulting in higher species richness (Beecher et al., 2002; Piha et al., 2007). A high seed and invertebrate availability in organic fields (Navntoft et al., 2006; Roschewitz et al., 2005) may also lead to decreased competition between the birds and other species such as small mammals, resulting in higher bird fitness and breeding success in the next year (Siriwardena et al., 2007). In winter, variation in broad habitat differences between both study regions was a better predictor of openland bird occurrence, than variations of landscape complexity and farming system on smaller spatial scale (c.f. Chamberlain et al., 2010). As most of the openland species are migratory birds, the overall winter abundances were very low. Therefore openland birds were predominantly driven by basic habitat requirements solved through open conditions in East

Germany, whereas food availability on stubble fields (Gillings et al., 2005) played a secondary role, because of low competition between birds.

In contrast farmland and woodland birds responded negatively to decreased landscape complexity, resulting in higher farmland and woodland bird occurrence in West Germany. These two ecological traits appeared to have benefited from structural complex landscapes but not from organic farming. The availability of hedges and forests, providing nesting habitats for numerous farmland and woodland species, seems to be the main driving force of the occurrence of these ecological bird traits during breeding season and in winter (Gillings et al., 2005; Herzon and O'Hara, 2007; Mason and Macdonald, 2000; Sanderson et al., 2009; Virkkala et al., 2004; Wretenberg et al., 2010). Foraging of farmland bird species mainly takes place on farmland, field margins and other suitable habitats available in complex landscapes (Laiolo, 2005; Piha et al., 2007). Hedges and forests therefore appear to represent a basic requisite as breeding and feeding habitats for the occurrence of farmland and woodland birds, thereby enhancing the whole bird community especially in West Germany (but see Flade et al., 2008). As both species traits are not restricted to search for food within arable crops or are even specialist to other habitats like forests (Bennett et al., 2004; Heikkinen et al., 2004; Herzon and O'Hara, 2007), organic farming on wheat fields plays a minor role as high-food habitat for these species traits and their species composition (c.f. Filippi-Codaccioni et al., 2009; Genghini et al., 2006).

Conclusion

In conclusion, bird abundance, species richness and diversity increased with landscape structural complexity, while organic farming practice only enhanced the species richness of openland bird species and the abundance and species richness of the whole bird community in summer. Most of the variation in community composition was explained by differences in landscape structural complexity, but not by differences in farming practice during breeding season and in winter. Hence, the often stressed argument for the importance of organic farming for bird communities in agricultural landscapes has to be reconsidered. Furthermore, the three ecological bird traits showed contrasting responses to the landscape context. Openland bird species increased with increasing percentage of arable land, while farmland and woodland bird species decreased during both seasons, indicating species-specific perception of landscape structural complexity. To enhance bird abundance, species richness and diversity in an agricultural landscape, a large scale mosaic of landscapes with a high

proportion of arable land is also needed, like landscapes with a variety of semi-natural habitats. Structural complex landscapes with hedges and forests may play an important role as nesting, resting and hiding places especially for farmland and woodland birds, while organic farming appears to be less important especially during winter. More knowledge is needed about relative importance of factors that determine bird population densities, including landscape, local farming practice and species-specific resources.

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APPENDIX

Table A2.1 Bird species abundances recorded in the study regions (West and East Germany) on organic (org.) and conventional (conv.) winter wheat fields during the breeding season (summer) and in winter, with their conservational status on the red list of breeding birds in Germany 2007 (0 = extinct; 1 = critically endangered; 2 = endangered; 3 = vulnerable; NT = near threatened; PE = pre-endangered; - = least concern; Südbeck et al., 2008). Bird species were classified according to their habitat use in three ecological traits, namely openland species = O breeding and feeding on fields; farmland species = F using fields, field edges and farmyards and woodland species = W breeding and feeding in trees and forests. Other species = OTH are breeding and feeding elsewhere.

English name	Scientific name	Trait	Summer				Winter			
			West Germany		East Germany		West Germany		East Germany	
			org. (n = 15)	conv. (n = 14)	org. (n = 6)	conv. (n = 24)	org. (n = 16)	conv. (n = 15)	org. (n = 6)	conv. (n = 24)
Black Kite	<i>Milvus migrans</i>	W	0	1	0	1	0	0	0	0
Black Redstart	<i>Phoenicurus ochruros</i>	OTH	5	2	0	0	0	0	0	0
Black Woodpecker	<i>Dryocopus martius</i>	W	0	1	0	0	0	0	0	0
Blackbird	<i>Turdus merula</i>	OTH	67	43	5	3	41	25	6	7
Blackcap	<i>Sylvia atricapilla</i>	OTH	41	28	6	9	0	0	0	0
Blue Tit	<i>Cyanistes caeruleus</i>	OTH	31	18	2	7	50	22	3	7
Bluethroat ^{PE}	<i>Luscinia svecica</i>	OTH	0	1	0	1	0	0	0	0
Bullfinch	<i>Pyrrhula pyrrhula</i>	W	4	1	0	0	20	20	0	0
Buzzard	<i>Buteo buteo</i>	OTH	10	6	0	7	8	12	63	54
Carrion Crow	<i>Corvus corone</i>	OTH	40	23	4	46	103	43	28	54
Chaffinch	<i>Fringilla coelebs</i>	OTH	46	53	4	5	32	66	5	1
Chiffchaff	<i>Phylloscopus collybita</i>	W	31	25	2	1	0	0	0	0
Coal Tit	<i>Parus ater</i>	W	6	4	0	0	3	0	0	0
Collared Dove	<i>Streptopelia decaocto</i>	OTH	1	0	0	0	0	0	0	0
Common Teal	<i>Anas crecca</i>	OTH	0	0	0	0	0	0	0	4
Coot	<i>Fulica atra</i>	OTH	0	1	0	0	0	3	0	0
Corn Bunting ³	<i>Miliaria calandra</i>	O	0	0	1	3	0	0	0	0
Crested Tit	<i>Lophophanes cristatus</i>	W	0	2	0	0	0	0	0	1
Crossbill	<i>Loxia curvirostra</i>	W	2	1	0	0	0	2	0	0

English name	Scientific name	Trait	Summer				Winter			
			West Germany		East Germany		West Germany		East Germany	
			org. (n = 15)	conv. (n = 14)	org. (n = 6)	conv. (n = 24)	org. (n = 16)	conv. (n = 15)	org. (n = 6)	conv. (n = 24)
Cuckoo ^{PE}	<i>Cuculus canorus</i>	OTH	6	6	0	0	0	0	0	0
Dunnock	<i>Prunella modularis</i>	W	13	15	3	1	1	0	0	0
Fieldfare	<i>Turdus pilaris</i>	W	33	10	2	0	4	8	1	7
Firecrest	<i>Regulus ignicapillus</i>	W	13	10	0	0	0	0	0	0
Garden Warbler	<i>Sylvia borin</i>	W	27	17	2	2	0	0	0	0
Goldcrest	<i>Regulus regulus</i>	W	7	2	0	0	14	12	0	0
Goldfinch	<i>Carduelis carduelis</i>	F	9	6	6	15	9	19	2	37
Grasshopper Warbler ^{PE}	<i>Locustella naevia</i>	F	2	1	0	3	0	0	0	0
Great Grey Shrike ²	<i>Lanius excubitor</i>	F	0	0	0	0	0	0	0	1
Great Spotted Woodpecker	<i>Dendrocopos major</i>	W	7	5	1	0	4	0	0	0
Great Tit	<i>Parus major</i>	OTH	51	52	8	9	77	41	5	8
Great White Egret	<i>Ardea alba</i>	OTH	0	0	0	0	0	0	0	6
Green Woodpecker	<i>Picus viridis</i>	OTH	3	0	0	0	2	0	0	0
Greenfinch	<i>Carduelis chloris</i>	OTH	21	12	3	4	65	152	2	15
Grey Heron	<i>Ardea cinerea</i>	OTH	0	1	0	1	0	0	0	11
Grey Partridge ²	<i>Perdix perdix</i>	O	0	0	0	7	0	0	2	2
Grey Wagtail	<i>Motacilla cinerea</i>	OTH	1	1	0	0	0	0	0	0
Greylag Goose	<i>Anser anser</i>	OTH	0	6	0	0	190	143	0	0
Hawfinch	<i>Coccothraustes coccothraustes</i>	W	7	3	0	0	0	1	0	0
House Martin ^{PE}	<i>Delichon urbica</i>	F	11	3	5	62	0	0	0	0
House Sparrow ^{PE}	<i>Passer domesticus</i>	F	58	2	21	8	30	5	0	0
Icterine Warbler	<i>Hippolais icterina</i>	OTH	0	0	1	0	0	0	0	0
Jay	<i>Garrulus glandarius</i>	OTH	2	4	0	0	14	3	0	0
Kestrel	<i>Falco tinnunculus</i>	O	2	1	3	4	3	6	7	24
Lapwing ²	<i>Vanellus vanellus</i>	O	0	0	0	0	0	0	2	0
Lesser Spotted Woodpecker ^{PE}	<i>Dendrocopos minor</i>	W	1	0	0	0	0	0	0	0

English name	Scientific name	Trait	Summer				Winter			
			West Germany		East Germany		West Germany		East Germany	
			org. (n = 15)	conv. (n = 14)	org. (n = 6)	conv. (n = 24)	org. (n = 16)	conv. (n = 15)	org. (n = 6)	conv. (n = 24)
Lesser Whitethroat	<i>Sylvia curruca</i>	OTH	8	7	2	0	0	0	0	0
Linnet ^{PE}	<i>Carduelis cannabina</i>	F	21	3	4	8	0	0	0	0
Long-Eared Owl	<i>Asio otus</i>	OTH	0	0	0	0	0	0	0	1
Long-Tailed Tit	<i>Aegithalos caudatus</i>	OTH	7	0	4	0	2	0	7	0
Magpie	<i>Pica pica</i>	OTH	22	10	1	1	21	7	1	13
Mallard	<i>Anas platyrhynchos</i>	OTH	4	3	0	5	0	45	2	40
Marsh Tit	<i>Poecile palustris</i>	W	13	10	0	0	11	4	0	0
Marsh Warbler	<i>Acrocephalus palustris</i>	F	15	12	3	4	0	0	0	0
Meadow Pipit ^{PE}	<i>Anthus pratensis</i>	O	7	4	0	1	0	0	0	0
Mistle Thrush	<i>Turdus viscivorus</i>	W	8	5	0	0	0	0	0	0
Nightingale	<i>Luscinia megarhynchos</i>	OTH	1	0	3	3	0	0	0	0
Nuthatch	<i>Sitta europaea</i>	W	6	2	0	0	9	4	0	0
Pied Flycatcher	<i>Ficedula hypoleuca</i>	W	0	1	0	0	0	0	0	0
Quail	<i>Coturnix coturnix</i>	O	2	1	5	15	0	0	0	0
Raven	<i>Corvus corax</i>	OTH	5	1	2	1	0	2	18	2
Red Kite	<i>Milvus milvus</i>	W	2	3	9	2	0	0	0	0
Red-Backed Shrike	<i>Lanius collurio</i>	F	3	2	0	6	0	0	0	0
Redstart ^{PE}	<i>Tringa totanus</i>	OTH	2	0	1	0	0	0	0	0
Reed Bunfing	<i>Emberiza schoeniclus</i>	F	8	6	0	8	0	0	0	0
Reed Warbler	<i>Acrocephalus scirpaceus</i>	OTH	2	3	0	7	0	0	0	0
Robin	<i>Erithacus rubecula</i>	OTH	11	17	1	1	14	10	1	1
Serin	<i>Serinus serinus</i>	F	3	2	1	0	0	0	0	0
Short-Toed Treecreeper	<i>Certhia brachydactyla</i>	W	1	0	0	0	0	0	1	0
Siskin	<i>Carduelis spinus</i>	W	0	0	0	0	0	0	0	1
Skylark ³	<i>Alauda arvensis</i>	O	158	106	136	414	2	0	0	5
Song Thrush	<i>Turdus philomelos</i>	OTH	28	24	1	3	0	0	0	0
Sparrowhawk	<i>Accipiter nisus</i>	OTH	1	0	0	0	1	0	0	2

English name	Scientific name	Trait	Summer				Winter			
			West Germany		East Germany		West Germany		East Germany	
			org. (n = 15)	conv. (n = 14)	org. (n = 6)	conv. (n = 24)	org. (n = 16)	conv. (n = 15)	org. (n = 6)	conv. (n = 24)
Spotted Flycatcher	<i>Muscicapa striata</i>	OTH	1	2	0	0	0	0	0	0
Starling	<i>Sturnus vulgaris</i>	F	191	19	1	27	16	0	0	0
Stock Dove	<i>Columba oenas</i>	W	12	0	0	0	0	0	0	0
Swallow ^{PE}	<i>Hirundo rustica</i>	F	12	7	5	37	0	0	0	0
Swift	<i>Apus apus</i>	F	0	0	0	7	0	0	0	0
Tree Pipit ^{PE}	<i>Anthus trivialis</i>	W	9	2	1	2	0	0	0	0
Treecreeper	<i>Certhia familiaris</i>	W	6	1	0	0	5	2	0	0
Treesparrow ^{PE}	<i>Passer montanus</i>	F	135	87	23	24	11	5	0	0
Turtle Dove ³	<i>Streptopelia turtur</i>	F	2	0	0	0	0	0	0	0
Wheatear ¹	<i>Oenanthe oenanthe</i>	F	6	1	0	0	0	0	0	0
Whinchat ³	<i>Saxicola rubetra</i>	O	7	1	0	3	0	0	0	0
Whitethroat	<i>Sylvia communis</i>	F	48	29	2	1	0	0	0	0
Willow Tit	<i>Parus montanus</i>	F	1	1	0	0	5	4	0	0
White Wagtail	<i>Motacilla alba</i>	F	22	17	1	1	0	0	0	0
Willow Warbler	<i>Phylloscopus trochilus</i>	OTH	13	9	4	0	0	0	0	0
Wood Pigeon	<i>Columba palumbus</i>	F	29	17	1	6	33	7	0	0
Wood Warbler	<i>Phylloscopus sibilatrix</i>	W	0	1	0	0	0	0	0	0
Woodcock ^{PE}	<i>Scolopax rusticola</i>	W	1	0	0	0	0	0	0	0
Wren	<i>Troglodytes troglodytes</i>	OTH	19	11	1	1	15	12	0	2
Yellow Wagtail	<i>Motacilla flava</i>	O	10	1	7	28	0	0	0	0
Yellowhammer	<i>Emberiza citrinella</i>	F	106	81	14	35	92	70	42	37

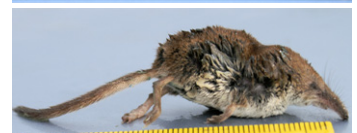
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CHAPTER 3

SMALL MAMMALS

Small mammals in agricultural
landscapes: interacting effects of
farming practice and landscape
complexity

Fischer, C., Thies, C., Tschamtkke, T.



ABSTRACT

Agricultural intensification has led to landscape changes and to declines of various taxa. Organic farming often counteracts these negative trends, but little is known about the relative importance of local management and landscape context for small mammals at different spatial scales. We observed abundance, species richness and diversity of small mammal communities on 22 organically and conventionally managed winter wheat fields located along a gradient of landscape structural complexity (41 - 94% arable land) on three spatial scales (100 m, 250 m, 500 m radii around each focal field). Organic farming increased small mammal abundance and, with marginal significance, also species richness and diversity, but only in simple landscapes, whereas in conventional fields, it increased with increasing landscape complexity (measured within a radius of 500 m around focal fields). Hence, small mammals responded differentially to farming practice, depending on the complexity of the surrounding landscape. The three most abundant species responded differentially to landscape complexity, suggesting species-specific ecological needs. *Apodemus agrarius* PALLAS was more abundant in complex landscapes at the spatial scale of 100 m, while *Microtus arvalis* PALLAS and *Sorex araneus* L. were more abundant in simple landscapes at spatial scales of 100 m and 500 m, respectively. In conclusion, organic fields in structural simple landscapes enhanced small mammal populations, presumably due to higher food supply. However, populations of potential pest species such as *M. arvalis* showed highest abundances in simple landscapes characterized by high percentages of arable land.

KEY WORDS: agricultural intensification, *Apodemus agrarius*, *Microtus arvalis*, organic farming, *Sorex araneus*

INTRODUCTION

Agricultural intensification is one of the major threats to farmland biodiversity (Kleijn et al., 2006; Robinson and Sutherland, 2002; Stoate et al., 2001). Local management such as increasing pesticide use (Bengtsson et al., 2005; Geiger et al., 2010; Hole et al., 2005) and the loss of semi-natural habitats at landscape scales (Benton et al., 2003; Concepción et al., 2008; Firbank et al., 2008) are the main causes for the recent species loss. Declines of farmland birds (Donald et al., 2001), insects (Hendrickx et al., 2007) and plants (Gabriel et al., 2005; Roschewitz et al., 2005) were detected at different spatial scales in agricultural landscapes. High landscape complexity, characterized by high habitat-type diversity and a high amount of semi-natural habitats and organic farming, can counteract the negative effects of agricultural intensification for e.g. insects and plants (Holzschuh et al., 2007; Roschewitz et al., 2005). In addition, organic farming can be expected to be most effective in enhancing biodiversity in simple, but not in complex landscapes (Concepción et al., 2008; Tschardt et al., 2005). Therefore it is important to simultaneously consider local management and landscape context (Kleijn et al., 2004; Tschardt et al., 2005).

Small mammals in agricultural landscapes are functionally important as predators of seeds, non-crop plants and insects (Baraibar et al., 2009; Ness and Morin, 2008) and they represent food resources (prey) for larger mammals and birds (Salamolard et al., 2000), but they are also agricultural pests to various crops (Brown et al., 2007). Published studies on the effects of agricultural intensification rarely consider small mammals and until now, studies on small mammal communities and particular species in agricultural landscapes focused either on local or landscape effects. Researchers tested the influences of farming practice on small mammal communities but found no or weak responses to increased agrochemical input on small mammal abundance, species richness, and diversity (Bates and Harris, 2009), the abundance of shrews (Pocock and Jennings, 2008) and voles (Jacob, 2003). However, true mice have been shown to prefer unsprayed plots (Macdonald et al., 2007; Shore et al., 1997; Tew et al., 1992). Moreover, some studies analysing the influences of landscape simplification detected no effect on small mammal species richness (Millán de la Peña et al., 2003; but see Silva et al., 2005), while others found higher abundances and a lower diversity in simple landscapes (Michel et al., 2006). Small mammals show only relationships to landscapes at small spatial scales (up to a radius of 500 m around focal fields: see Alain et al., 2006; Bowman et al., 2000; Silva et al., 2005), which indicated relatively small home ranges. Altogether, the

knowledge on small mammal population responses to agricultural intensification at local and landscape scale is fragmentary and needs to be reconsidered.

Here, we analysed the relative importance of local vs. landscape parameters at different spatial scales on small mammal community composition and abundance, species richness and diversity. We investigated organic and conventional wheat fields located along a gradient of landscape complexity (41 - 94% arable land) at three spatial scales (100 m, 250 m, 500 m radii around focal fields). We hypothesized that organic farming would benefit small mammal populations most in simple landscapes, while species known to profit from cereal fields should show highest densities in simple landscapes with high amount of arable fields.

MATERIALS AND METHODS

Study sites

Trapping was carried out in summer 2008 in winter wheat (*Triticum aestivum* L.) fields around the city of Göttingen (51°30' N, 9°54' E), Southern Lower Saxony. We selected 11 landscapes along a gradient of landscape complexity from structural simple landscapes with a high percentage of arable land (94%) to complex landscapes with a low percentage of arable land (41%; within a radius of 500 m around focal fields). To compare different farming practices, one conventionally and one organically managed winter wheat field was selected within each landscape with a maximum distance of ~1000 m between two paired fields. Landscape complexity was characterized at three spatial scales within radii of 100 m, 250 m and 500 m around the centre of each wheat field by measuring percentage of arable land, grassland, forest and habitat diversity (Shannon index calculated from percentage of arable land, grassland, forest, transitional woodland-scrub and urban fabric) using official digital topographical maps (ATKIS DTK 50) and the Geographical Information System ArcGIS 9.2 (1999 - 2006 ESRI Inc.), (for a detailed overview of landscape parameters at the three spatial scales see Table 3.1). Percentage of arable land was negatively correlated with habitat diversity (500 m: $r_{20} = -0.96$, $p < 0.001$, 250 m: $r_{20} = -0.92$, $p < 0.001$, 100 m: $r_{20} = -0.98$, $p < 0.001$), percentage of grassland (500 m: $r_{20} = -0.68$, $p < 0.001$, 250 m: $r_{20} = -0.78$, $p < 0.001$, 100 m: $R_S = -0.98$, $p < 0.001$) and percentage of forest (500 m: $r_{20} = -0.79$, $p < 0.001$, 250 m: $r_{20} = -0.61$, $p < 0.01$, 100 m: $R_S = -0.85$, $p < 0.001$; Pearson's product-moment correlation or Spearman's rank correlation). Thus percentage of arable land appeared as a simple predictor of landscape complexity. Percentage of arable land within the 100 m radius around focal fields was positively correlated with percentage of arable land of the 250 m radius ($r_{22} = 0.76$, $p < 0.001$) but not with those of the 500 m radius ($r_{22} = 0.24$,

$p = 0.26$), and percentage of arable land within the 250 m radius was also positively correlated with those of the 500 m radius ($r_{22} = 0.60$, $p < 0.01$; Pearson's product-moment correlation). To characterize local fields the size of wheat fields was measured using ArcGIS 9.2. (1999 - 2006 ESRI Inc.). Wheat height and cover were measured by using three 2 x 2 m plots which were placed 5 m apart behind the first wheat row and in a distance of 13 m within the field parallel to the field border. From the total six subplots mean wheat height and cover were calculated per field. Standardized questionnaires were sent out to farmers to get information about yields, pesticide and fertilizer use, and ploughing frequency. Carabids as food source for omnivorous and carnivorous small mammals were caught using four pitfall traps per field (90 mm diameter, filled with 50% ethylene glycol) placed 55 m apart behind the first wheat row and in a distance of 13 m within the field. Pitfall traps were opened three times for one week at the end of May, June and July 2008. Carabid activity density was calculated as the mean value per field out of the three sampling weeks (for a detailed overview of local scale parameters see Table 3.1).

Table 3.1 Characterisation of local scale parameters on organic ($n = 11$) and conventional ($n = 11$) winter wheat fields and landscape scale parameters in a radius of 100 m, 250 m and 500 m around all focal fields ($n = 22$). Shannon habitat diversity was calculated from percentage of arable land, grassland, forest, transitional woodland-scrub and urban fabric. Mean values with standard errors are given.

Local scale		organic	conventional	
	Field size (ha)	5.21 ± 1.56	7.11 ± 1.23	
	Yield (kg/ha)	4019 ± 445	8136 ± 565	
	Wheat height (m)	0.86 ± 0.03	0.73 ± 0.03	
	Wheat cover (%)	74.09 ± 2.11	87.19 ± 3.45	
	Ploughing frequency (No./Year)	0.91 ± 0.09	0.63 ± 0.18	
	Nitrogen fertilizer (kg/ha)	-	169.59 ± 8.10	
	Herbicide applications (No./Year)	-	3.63 ± 0.42	
	Carabid activity density	16.44 ± 3.56	15.27 ± 4.70	
Landscape scale		spatial scale		
		100 m	250 m	500 m
	Arable land (%)	86.03 ± 2.87	79.14 ± 3.29	68.62 ± 3.95
	Grassland (%)	5.33 ± 1.95	10.87 ± 2.80	12.53 ± 2.30
	Forests (%)	4.84 ± 1.63	5.32 ± 1.27	11.79 ± 2.70
	Shannon habitat diversity	0.42 ± 0.07	0.62 ± 0.07	0.85 ± 0.07

There were no significant differences between organically and conventionally managed fields regarding the percentage of arable land in the surroundings (500 m: $t = -0.09$, d.f. 20,

$p = 0.93$; 250 m: $t = 0.48$, d.f. 20, $p = 0.64$; 100 m: $t = 0.20$, d.f. 20, $p = 0.84$) as well as the mean field size ($W = 84$, $p = 0.13$), but wheat cover was higher ($W = 109$, $p < 0.01$) and wheat height was lower ($W = 27$, $p = 0.03$; paired-sample t-tests or Wilcoxon rank sum test) in conventional fields compared to organic fields.

Small mammal trapping

Each winter wheat field was sampled two times in June and July 2008. Trapping was carried out for three consecutive trap nights per field, with one additional pre-baiting day before each trapping session over the total course of three weeks. 30 Ugglan multiple-capture live traps (240 x 60 x 90 mm; details in Lambin and MacKinnon, 1997) were placed in two trap lines, 15 traps each, spaced every 5 m behind the first wheat row and in a distance of 13 m within the field parallel to the field border. Starting point of each trap line was 10 m apart from the field border. Traps were baited with rolled oats in the evening before sunset and checked in the morning. Individuals trapped for the first time were marked with a permanent micro-tattoo (FST Laboratory Animal Microtattoo System, green tattoo paste, sterile hypodermic needles 27 G x 1/2") at the tail base. Captured small mammals were weighed, identified to species and sexed.

Statistical analyses

Abundance was calculated as the total number of trapped animals per field, except recaptures (Michel et al., 2006). The predator *Mustela nivalis* L. (least weasel) was trapped three times, but excluded from further analysis because of the different trophic level. *Microtus agrestis* L. (field vole), *Myodes glareolus* SCHREBER (bank vole) and *Neomys fodiens* PENNANT (Eurasian water shrew) were trapped only once and therefore also excluded from the data set, as they are associated to specific environmental conditions (dense ground vegetation, woody structures, aquatic habitats).

Community composition was described using non-metric multidimensional scaling (NMDS) implemented in the R package *vegan* (Oksanen et al., 2009) of R version 2.9.1 (R Development Core Team, 2009), which is a robust unconstrained ordination method to plot community compositions (Minchin, 1987). Local and landscape environmental variables (Table 3.1) were overlaid separately over the ordination diagram. For the NMDS a field-species-matrix, summed-up abundances over both trapping sessions and Bray-Curtis dissimilarity were used. Environmental vectors were fitted and p-values were assessed using

1000 permutations. Mantel tests with Euclidean dissimilarities based on Pearson's product-moment correlation were performed, to test if the species and environmental matrices were correlated.

The relative importance of local *vs.* landscape parameters at different spatial scales was analyzed using linear mixed-effects models (Pinheiro and Bates, 2000) with a maximized log-likelihood implemented in the R package *nlme* (Pinheiro et al., 2009) of R version 2.9.1 (R Development Core Team, 2009). For each radius around focal fields (100 m, 250 m, 500 m) effects of landscape (percentage of arable land), local farming practice (organic *vs.* conventional) and two-way interactions on abundance, species richness, and diversity (Shannon index) of the total number of trapped small mammals and the three most abundant species (*Apodemus agrarius* PALLAS, *Microtus arvalis* PALLAS, *Sorex araneus* L.) were analyzed. Landscape (11 sites) and study field (22 fields, 2 trapping sessions) nested in landscape were included as random effects. Response variables were either log- or square root-transformed, percentage of arable land was arcsine-square root-transformed to achieve a normal error distribution and/or to avoid heteroscedasticity. Different variance functions implemented in the *nlme* library were used to model the variance structure of the within-group errors. Fitted models with different within-group variances were compared by choosing the lowest value of the Akaike Information Criterion (AIC) from an ANOVA table (Pinheiro and Bates, 2000). Model simplification was done in a stepwise model selection by AIC implemented in the R package *MASS* (Venables and Ripley, 2002) until minimal adequate model was obtained. Significance of terms in the best model was assessed by calculating the F- and p-values of an ANOVA table. In the text, arithmetic means and standard errors are given.

RESULTS

In total 410 small mammals out of ten species were trapped in 3960 trap-nights. Three true mice *A. agrarius* (striped field mouse), *Apodemus flavicollis* MELCHIOR (yellow-necked field mouse), and *Apodemus sylvaticus* L. (wood mouse), as well as one vole *M. arvalis* (common vole), and three shrews *Crocidura leucodon* HERMANN (bicolored shrew), *S. araneus* (common shrew), and *Sorex minutus* L. (pygmy shrew) were recorded (for total abundances, species richness and diversity in organic and conventional fields see Table 3.2).

	conventional		organic	
	Mean \pm SE	Total	Mean \pm SE	Total
Abundance	20.00 \pm 3.56	218	17.27 \pm 2.88	189
Species richness	4.09 \pm 0.28	7	4.00 \pm 0.38	7
Diversity	1.09 \pm 0.11	1.50	1.00 \pm 0.08	1.62
<i>A. agrarius</i>	5.73 \pm 3.10	63	5.18 \pm 1.66	57
<i>A. flavicollis</i>	0.73 \pm 0.38	8	1.18 \pm 0.52	13
<i>A. sylvaticus</i>	1.27 \pm 0.51	14	2.09 \pm 0.74	23
<i>C. leucodon</i>	1.00 \pm 0.49	11	0.64 \pm 0.45	7
<i>M. arvalis</i>	8.18 \pm 2.59	90	5.27 \pm 2.12	58
<i>S. araneus</i>	2.64 \pm 0.87	29	2.64 \pm 1.42	29
<i>S. minutus</i>	0.27 \pm 0.27	3	0.18 \pm 0.12	2

Table 3.2 Abundance, species richness and diversity of the small mammal community and abundances of captured species on organic (n = 11) and conventional (n = 11) winter wheat fields. Mean values with standard errors and total values of both trapping sessions are given.

Community composition

Sites and species were plotted with the NMDS in a two-dimensional species space (two dimensions, stress = 14.984, two convergent solutions found after 9 tries). No significant effects of any of the local scale parameters (Table 3.1) on the field-species-matrix were found. Community composition could not be explained by the fine-scale local parameters (Mantel statistic r : -0.10, p = 0.80). Fitting landscape parameters within a radius of 100 m around focal fields into the species space, habitat diversity (goodness of fit statistic: r^2 = 0.37, p < 0.01), percentage of arable land (r^2 = 0.37, p < 0.01), and percentage of grassland (r^2 = 0.25, p = 0.06) explained ordination (Mantel statistic r : 0.24, p < 0.05, Fig. 3.1). On the smallest spatial scale (100 m radius) three groups of small mammal functional composition could be identified by interpreting environmental variables. True mice (*A. flavicollis*, *A. sylvaticus*, *A. agrarius*) occurrence tended to be positively related with grassland. Voles (*M. arvalis*) occurred in areas with low habitat diversity and shrews (*C. leucodon*, *S. araneus*, *S. minutus*) were more generalistic in their habitat requirements as they occurred as well in areas with high habitat diversity as in areas with low amount of arable land and grassland. For the 250 m radius (Mantel statistic r : 0.19, p = 0.06) and the 500 m radius (Mantel statistic r : 0.01, p = 0.45) landscape parameters did not significantly contribute to the explanation of community composition.

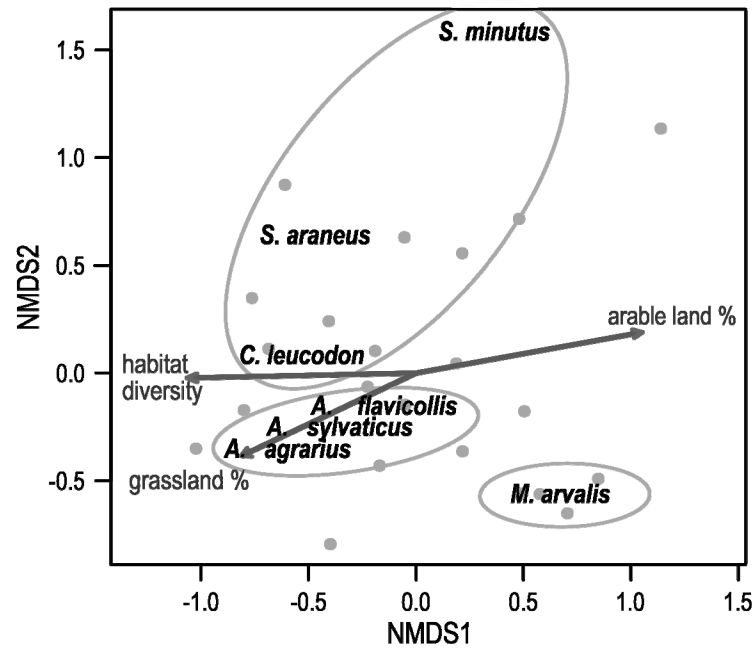


Fig. 3.1 Graphical interpretation of small mammal community dissimilarities calculated from the overall abundance per species by plotting site scores (grey points) with NMDS. Significant environmental parameters (habitat diversity, percentage of arable land) and marginal significant values (percentage of grassland) sampled within a radius of 100 m around focal fields were fitted to the dataset. Small mammal functional composition was grouped according to their ecological needs and taxonomic classification.

Relative importance of local vs. landscape parameters on total abundance, species richness and diversity

Farming practice in interaction with landscape complexity had a significant effect on small mammal abundance on the 250 m and 500 m radius around focal fields. Species richness and diversity held same patterns, but with only marginal significance on the 500 m radius (Table 3.3). Small mammal abundance, species richness and diversity were higher on organic fields in simple landscapes (> 80% of arable land), whereas small mammals on conventional fields decreased with increasing percentage of arable land (Fig. 3.2).

No main effects of organic farming and landscape complexity on any spatial scale on total abundance, species richness and diversity of small mammals were found.

Table 3.3 Summary of minimal adequate linear mixed-effects models to analyse effects of A: landscape complexity, B: farming practice (organic vs. conventional) and A x B: two-way interaction within a radius of 100 m, 250 m and 500 m around focal fields on abundance, species richness and diversity of the small mammal community and on abundance of the three most abundant species. Degrees of freedom (d.f.), F-values and p-values are given. Bold values show significant or marginal significant results.

	100 m			250 m			500 m		
	d.f.	F- value	p- value	d.f.	F- value	p- value	d.f.	F- value	p- value
Abundance^b									
A ^c	1, 10	4.47	0.06	1, 8	0.69	0.43	1, 8	0.06	0.81
B		-	-	1, 8	1.91	0.20	1, 8	1.86	0.21
A ^c x B		-	-	1, 8	5.48	0.04	1, 8	5.98	0.04
Species richness									
A ^c		-	-		-	-	1, 8	0.14	0.72
B		-	-		-	-	1, 8	0.92	0.36
A ^c x B		-	-		-	-	1, 8	4.19	0.07
Diversity									
A ^c	1, 8	0.11	0.75		-	-	1, 8	0.02	0.89
B	1, 8	0.16	0.70		-	-	1, 8	1.06	0.33
A ^c x B	1, 8	1.99	0.20		-	-	1, 8	3.55	0.09
<i>A. agrarius</i>^a									
A ^c	1, 10	8.92	0.01	1, 8	4.99	0.06	1, 8	0.72	0.42
B		-	-	1, 8	0.28	0.61	1, 8	0.02	0.88
A ^c x B		-	-	1, 8	5.48	0.04	1, 8	3.79	0.09
<i>M. arvalis</i>^a									
A ^c	1, 8	4.40	0.07	1, 8	4.08	0.08		-	-
B	1, 8	3.00	0.12	1, 8	2.38	0.16	1, 10	2.36	0.16
A ^c x B	1, 8	4.40	0.07	1, 8	3.92	0.08		-	-
<i>S. araneus</i>^a									
A ^c	1, 10	2.04	0.18		-	-	1, 10	7.63	0.02
B		-	-		-	-		-	-
A ^c x B		-	-		-	-		-	-

^a log transformed; ^b sqrt transformed, ^c arcsine-square root transformed

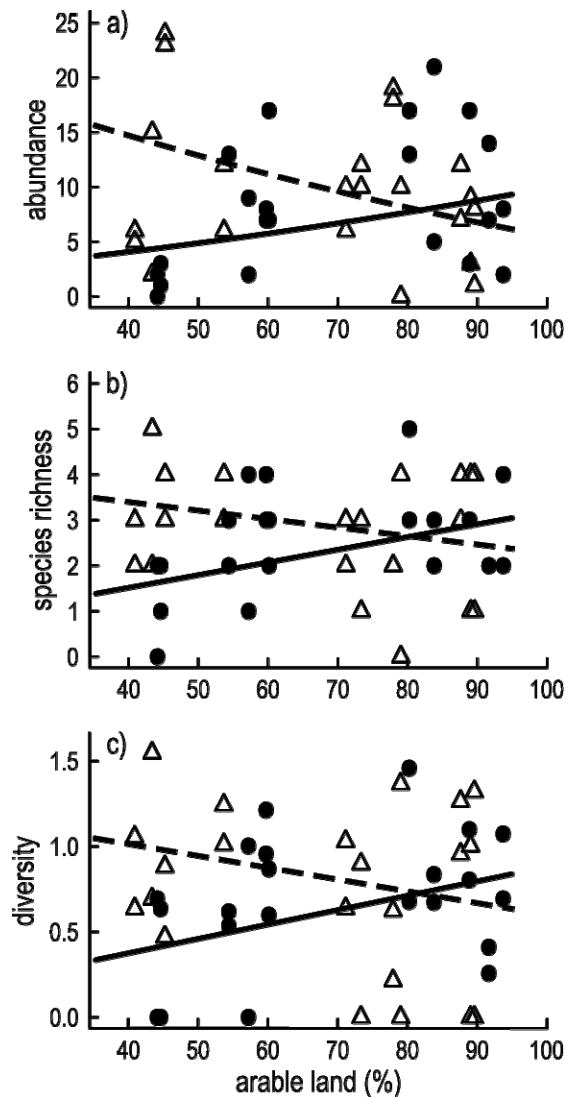


Fig. 3.2 Relation of percentage of arable land to small mammal community parameters a) abundance, b) species richness and c) diversity within a radius of 500 m around focal fields. Open triangles and dashed lines (conventional fields), filled circles and solid lines (organic fields). Statistical significant interaction between landscape context and farming practice was found for small mammal abundance; species richness and diversity held same patterns, but with only marginal significance. For better visualisation back-transformed data are presented.

Relative importance of local vs. landscape parameters on abundances of the three most abundant species

Individual species showed different responses to landscape complexity on different spatial scales (Table 3.3). *A. agrarius* abundance increased with increasing landscape complexity, most pronounced for the 100 m radius around focal fields (Table 3.3; Fig. 3.3a). Within a radius of 250 m around focal fields *A. agrarius* abundance was higher on organic fields in simple landscapes, whereas abundance decreased on conventional fields with decreasing landscape complexity.

M. arvalis abundance showed reverse patterns, as it increased marginal significantly with decreasing landscape complexity. On conventional fields *M. arvalis* abundance remained to be stable independently from landscape structure, but increased on organic fields with

decreasing landscape complexity, most pronounced for the 100 m radius around focal fields (Table 3.3; Fig. 3.3b).

S. araneus abundances were not different between organic and conventional fields, but increased with decreasing landscape complexity within a radius of 500 m around focal fields (Table 3.3; Fig. 3.3c).

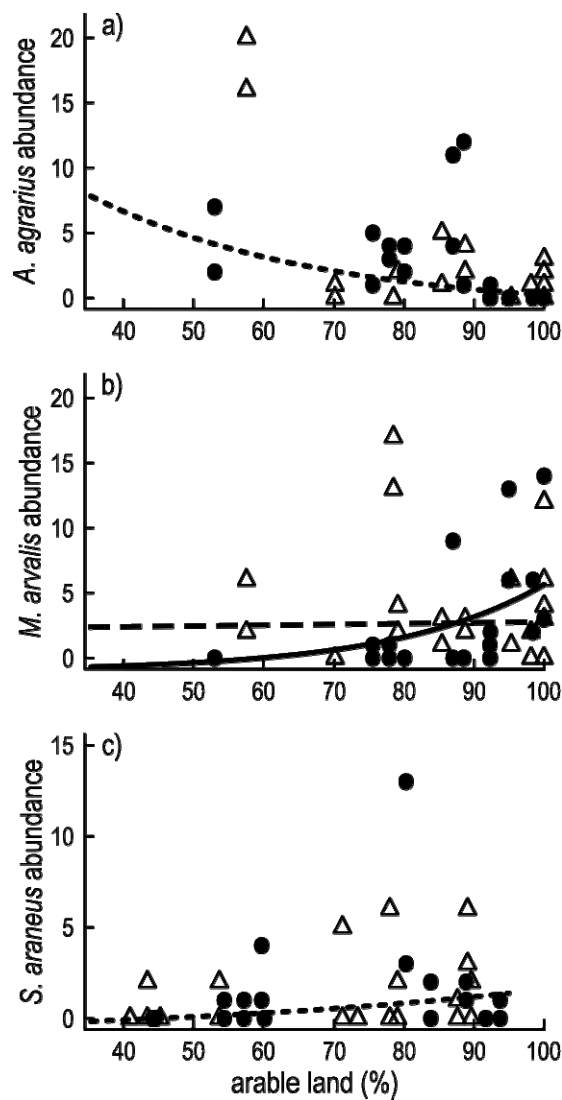


Fig. 3.3 Relation of percentage of arable land to single species abundance at spatial scales with strongest correlations (Table 3.3). a) *A. agrarius* within a radius of 100 m, b) *M. arvalis* within a radius of 100 m, and c) *S. araneus* within a radius of 500 m around focal fields. Open triangles and dashed lines (conventional fields), filled circles and solid lines (organic fields). Dotted lines were used, when farming practices was excluded from the minimal adequate model. Statistical significant effects were shown for *A. agrarius* and *S. araneus* abundance in relation to percentage of arable land. An interaction between landscape context and farming practice was found for *M. arvalis* abundance, but with only marginal significance. For better visualisation back-transformed data are presented.

DISCUSSION

In this study we analysed the influence of local farming practice and landscape complexity on small mammal communities. The study design of paired organic and conventional fields situated in landscapes differing in structural complexity allowed analysing local and landscape effects independently and to test the hypothesis, that organic farming benefits small mammal populations most in simple landscapes.

Community composition

Small mammal community composition was determined by landscape context on small spatial scales (100 m radius around focal fields), while fine-scale parameters related to local farming practice had no influence on small mammal communities (but see Shore et al., 1997; Tew et al., 1992 showing negative effects of agrochemicals on true mice populations). In the landscape context true mice are known to be associated with a variety of semi-natural habitats (*A. sylvaticus*: Montgomery and Dowie, 1993; Schlitter et al., 2008), forests and forest edges (*A. flavicollis*: Amori et al., 2008), and grassland and cultivated areas (*A. agrarius*: Kaneko et al., 2008), which is consistent with our results, showing true mice to be associated with grassland and a high habitat diversity. In contrast voles are specialist to agricultural areas (*M. arvalis*: Delattre et al., 1996; Huitu et al., 2003), shown for *M. arvalis* which was related to low habitat diversity and high percentage of arable land. Shrews are more generalistic, inhabiting various, mainly extensive habitats like forests (*S. araneus*: Hutterer et al., 2008a; *S. minutus*: Hutterer et al., 2008b; Mortelliti and Boitani, 2009), and open fields (*C. leucodon*: Shenbrot et al., 2008). The clear separation of true mice, voles and shrews within the species space, can therefore be explained by environmental variables according to small mammals' degree of specialisation and species specific ecological needs but not by fine-scale habitat changes related to local farming practice. Pattern could only be found on small spatial scale, supporting findings of Alain et al. (2006); Bowman et al. (2000) and Silva et al. (2005) who observed relationships to landscape context only within radii of 100 m to 500 m around focal fields.

Relative importance of local vs. landscape parameters on total abundance, species richness and diversity

Organic farming increased small mammal abundance in simple landscapes (250 - 500 m radii around focal fields), whereas on conventional fields, the abundance decreased with increasing percentage of arable land. Species richness and diversity showed same patterns (500 m radius), but with only marginal significance, since four out of seven species were common to all sites, which is in line with results of e.g. Michel et al. (2007). Small mammal density is driven by a higher food supply on organic fields caused by an abandonment of agrochemicals, like molluscicides and reduced herbicide applications (Shore et al., 1997; Tew et al., 1992). So, small mammals can be expected to actively move to organic fields in simple landscapes. Accordingly, we found higher abundances, most pronounced by the potential pest species *M. arvalis*. In complex landscapes, predator abundance is higher (Delattre et al., 1999) because of more suitable habitats such as forests, hedgerows, grassland and villages (Magrini et al., 2009; Zub et al., 2008), increasing predation pressure on small mammals. Better and more hiding places, realized through higher wheat cover and lower wheat height in the studied conventional fields, appeared to be responsible for enhancement of small mammal abundance (already reported for *A. sylvaticus* in Ouin et al., 2000; Torre et al., 2007). Furthermore dense cover on conventional fields increases habitat connectivity (Alain et al., 2006) and explains a shift of small mammals from hedges to crop fields (Ouin et al., 2000). Our results suggest that the mobility of small mammals (Jacob and Hempel, 2003; Lambert et al., 2008) makes an active selection of the best habitats, which provide food and shelter, possible (Briner et al., 2005; Tew et al., 2000).

Relative importance of local vs. landscape parameters on abundances of the three most abundant species

In our study individual species showed different response to landscape context suggesting that species differ in terms of home range size and mobility. As landscape compositions in a radius of 100 m and 500 m around focal fields were not correlated, these scales can be discussed separately. Farming practice had no or minor effects on single species abundance, which is in line with previous results (Bates and Harris, 2009; Pocock and Jennings, 2008; but see Macdonald et al., 2007).

The abundance of *A. agrarius* was mainly explained by landscape complexity within a radius of 100 m around focal fields, going along with home range size of 585 m² for females and 716 m² for males (Vukićević-Radić et al., 2006). The negative correlation with percentage of arable land in our study can be interpreted by positive correlations to woodlot size in other studies, where *A. agrarius* searches for sheltering places (Kozakiewicz et al., 1999).

Populations of the potential pest species *M. arvalis* with stable home ranges of 200 m² (Briner et al., 2005, Jacob and Hempel, 2003) were enhanced by decreasing landscape complexity on the small spatial scale (100 m radius around focal fields). In an open arable landscape colonization of empty habitat patches is faster than in a hedgerow network (Delattre et al., 1996) and can explain higher abundances in simple landscapes.

S. araneus with home ranges of more than 800 m² (Wang and Grimm, 2007) was also in our study related to largest scale measured (500 m around focal fields) and positively correlated with decreasing landscape complexity. In a modelling study Wang and Grimm (2007) found that *S. araneus* adapted their home range sizes to environmental conditions. In areas with low-food habitats, such as cereal fields, home ranges were larger than in high-food habitats. Further, the trapping success might have been lower in complex landscapes due to the lower mobility because of high food availability than in simple landscapes which may be a methodological artefact making reliable estimates for this species difficult. *S. araneus* seems to be relatively resistant to disturbances: Schmidt et al. (2009) found no differences in population densities between ungrazed and little grazed meadows.

Conclusions

Small mammals responded differentially to farming practice, depending on the surrounding landscape complexity. In simple landscapes organic farming increased small mammal abundance and, with marginal significance, also species richness and diversity, whereas in conventional fields it increased with increasing landscape complexity (measured within a radius of 500 m around focal fields). Small mammal density is driven by food supply, thus high-food habitats in simple landscapes such as organic fields can enhance small mammals as an important link of food webs. Conventional fields in complex landscapes, with a high wheat cover, may act as refuges from predator attacks. To enhance individual small mammal species, landscape structural complexity with more forests, hedges and grassland will lead to an increase of *A. agrarius* abundances, while abundances of the potential pest species *M. arvalis* were positively influenced by landscape simplification especially on organic fields.

Findings suggest that for the conservation of small mammals in agricultural landscapes sufficient food sources provided by a reduction of pesticide use on organic fields in simple landscapes are needed. In contrast, an increasing landscape complexity will enhance small mammals especially on conventional fields. Furthermore, species-specific needs on landscape scale should be considered to allow reliable recommendations for conservation.

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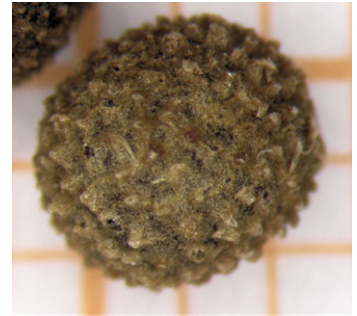
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CHAPTER 4

SEED PREDATION



Mixed effects of landscape
complexity and farming practice on
weed seed removal

Fischer, C., Thies, C., Tschamtkke, T.

ABSTRACT

Agricultural intensification has negatively affected farmland biodiversity and related ecosystem services such as biological weed control through seed predation at local and landscape scale. Landscape complexity (with large areas of semi-natural habitats) and organic farming (with an abandonment of pesticides and mineral fertilizers) can counteract this negative trend, but little is known on their relative importance. We experimentally tested seed removal rates of four weed seed species by excluding different predator groups using cages at the field edge and in the interior of 22 organically and conventionally managed winter wheat fields, which were located along a gradient of landscape structural complexity (41 - 94% arable land in a radius of 500 m around fields). Seed predation and removal was mainly determined by large invertebrates and increased with decreasing landscape complexity in conventional fields, but decreased in organic fields. Slug density showed a similar response to landscape complexity and farming practice, while small mammal density decreased with decreasing landscape complexity in conventional fields, but increased in organic fields. Phytophagous carabid beetles were not affected by landscape structure, but more abundant in organic than conventional fields. Seed identity was a major factor driving seed removal with *Cirsium arvense* being more affected than *Poa trivialis*, *Apera spica-venti*, and *Galium aparine*. In conclusion, patterns of weed seed removal were not only determined by weed and predator identity, but also by farming practice and landscape structure, which exhibited complex interaction effects and could be related to activity patterns and foraging behaviour of diverse seed predators.

KEY WORDS: post-dispersal seed predation, small mammals, carabids, slugs, ecosystem services

INTRODUCTION

Ecosystem services in agroecosystems, such as pollination, pest control and disease suppression, are linked to farmland biodiversity (Landis et al., 2000; Larsen et al., 2005; Luck et al., 2003). Agricultural intensification during the last decades has led to a serious decline in farmland biodiversity (Kleijn et al., 2006; Robinson and Sutherland, 2002; Stoate et al., 2001) and therefore negatively affects ecosystem services (Hooper et al., 2005; Tscharntke et al., 2005a). Main causes for the decline of farmland biodiversity and the reduced efficiency of ecosystem services are the replacement of natural and semi-natural habitats by cropland (Benton et al., 2003; Concepción et al., 2008; Firbank et al., 2008) and the intensification of agricultural practices with an increasing pesticide use (Bengtsson et al., 2005; Geiger et al., 2010; Hole et al., 2005).

One important ecosystem service in agricultural fields is the biological weed control by predators such as birds, small mammals and invertebrates (Westerman et al., 2006), which can strongly affect weed population growth and recruitment (Crawley, 1992; Kolb et al., 2007). Weeds can reduce crop yields seriously. Therefore, expensive herbicides are regularly used to reduce weed cover within fields (Geiger et al., 2010). On the other hand, herbicide applications are environmentally unfriendly, as they do not only reduce plant species richness (Roschewitz et al., 2005), but also predator abundances, like small mammals, phytophagous carabid beetles or ants by reducing food sources (Baraibar et al., 2009; Menalled et al., 2007; Shore et al., 1997; Tew et al., 1992). Organic farming, characterized by an abandonment of pesticide applications, enhances predator abundances and thereby counteracting negative effects of agricultural intensification (for birds, small mammals and invertebrates see e.g. Filippi-Codaccioni et al., 2009; Macdonald et al., 2007; Navntoft et al., 2006, respectively). In addition to local management predator abundances and distribution patterns are also driven by the landscape scale (Farwig et al., 2009). In particular, semi-natural habitats adjacent to crop fields like grassy strips and hedgerows act as refuges for birds, small mammals and invertebrates and thereby contribute to higher seed predation rates (Jacob et al., 2006; Navntoft et al., 2009). High landscape complexity, characterized by high habitat-type diversity or a high amount of semi-natural habitats, can also increase seed predator populations (for birds, small mammals and invertebrates see e.g. Mason and Macdonald, 2000; Michel et al., 2006; Purtauf et al., 2005, respectively). To facilitate ecosystem services such as biological weed control by certain predator species, it is important to consider local management and the landscape context simultaneously (Kleijn et al., 2004; Tscharntke et al.,

2005a). Previous studies analysing influences of agricultural intensification on weed seed predation considered either local management or landscape scale effects. Studies on the influence of farming practices on seed predation rates found higher predation rates in organic and non-till fields compared to conventionally managed fields (Baraibar et al., 2009; Menalled et al., 2007; O'Rourke et al., 2006), often interacting with the distance from the field border (Navntoft et al., 2009). Moreover, predation rates have been found to be higher in complex, compared to simple landscapes (Farwig et al., 2009; Matías et al., 2009; Menalled et al., 2000; but see Breitbach et al., 2010; García and Chacoff, 2007). Altogether, the knowledge about seed predation and removal at local and landscape scales is fragmentary, controversial and needs to be reconsidered.

Here, we simultaneously analysed the relative importance of local farming practice and landscape complexity within a radius of 500 m around focal fields on weed seed removal and predation rates and abundances of potential seed predators. We compared organic with conventional wheat fields located along a gradient of landscape complexity (41 - 94% arable land). Removal rates were estimated for four different economically relevant weed seed species at the field edges and in the field interior. To account for predator identity and preferences exclusion treatments, using cages with different mesh sizes, were established. We wanted to quantify the relative importance of local *versus* landscape parameters, seed preferences, distance from the field edge and predator identity on seed removal rates. Concurrently, seed predators, namely small mammals and carabids and potential seed dispersers such as slugs, were monitored.

MATERIALS AND METHODS

Study sites

Experiments were carried out in summer 2008 on winter wheat (*Triticum aestivum* L.) fields around the city of Göttingen (51°30' N, 9°54' E) in Southern Lower Saxony. We selected 11 landscapes along a gradient of landscape complexity from structural simple landscapes with a high percentage of arable land (94%) to complex landscapes with a low percentage of arable land (41%). Landscape complexity was characterized within a radius of 500 m around the centre of each wheat field by measuring percentage of arable land, grassland, forest and habitat diversity (Shannon index) using official digital topographical maps (ATKIS DTK 50) and the Geographical Information System ArcGIS 9.2 (1999 - 2006 ESRI Inc.) (for a detailed overview of landscape parameters see Table 4.1). The percentage of arable land was negatively correlated with habitat diversity ($r_{20} = -0.96$, $p < 0.001$), percentage of grassland

($r_{20} = -0.68$, $p < 0.001$) and percentage of forest ($r_{20} = -0.79$, $p < 0.001$; Pearson's product-moment correlation; Fig. 4.1). Thus percentage of arable land appeared as a simple predictor of landscape complexity.

Table 4.1 Characterisation of local and landscapes scale parameters in a radius 500 m around organic ($n = 11$) and conventional ($n = 11$) winter wheat fields. Shannon habitat diversity was calculated from percentage of arable land, grassland, forest, transitional woodland-scrub and urban fabric. Mean values with standard errors are given.

Local scale		organic	conventional
	Field size (ha)	5.21 ± 1.56	7.11 ± 1.23
	Species richness of non-crop plants	20.27 ± 1.34	6.73 ± 0.94
Landscape scale			
	Arable land (%)	68.97 ± 5.71	68.28 ± 5.73
	Grassland (%)	12.30 ± 2.89	12.75 ± 3.73
	Forests (%)	12.26 ± 3.26	11.31 ± 4.46
	Shannon habitat diversity	0.87 ± 0.11	0.83 ± 0.09

To compare different farming practices one conventional and one organically managed winter wheat field was selected within each landscape with a maximum distance of ~1000 m between two paired fields. To characterize local fields, size of wheat fields was measured using ArcGIS 9.2 (1999 - 2006 ESRI Inc.). Non-crop plant species richness was determined by using three 2 x 2 m plots which were placed 5 m apart behind the first wheat row and in a distance of 13 m within the field parallel to the field border. From the total six subplots total plant species richness was calculated per field. Between organically and conventionally managed fields there were no significant differences in percentage of arable land in the surrounding landscape ($t = -0.09$, d.f. 20, $p = 0.93$) and mean field size ($W = 84$, $p = 0.13$). However, species richness of non-crop plants was lower in conventional fields compared to organic fields ($t = -8.31$, d.f. = 20, $p < 0.001$; paired-sample t-tests or Wilcoxon rank sum test, for a detailed overview of local parameters see Table 4.1).

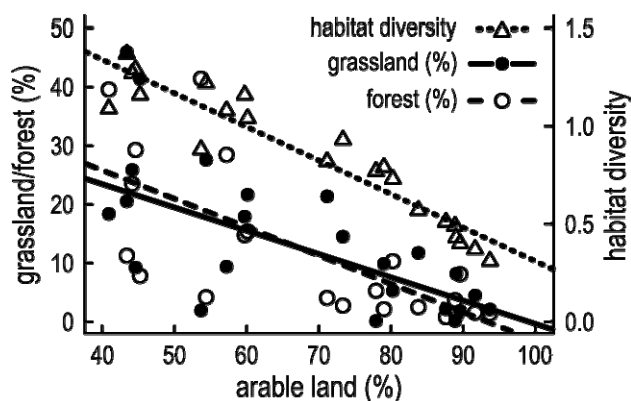


Fig. 4.1 Correlations of percentage of arable land and percentage of grassland and forest (see left axis) and Shannon habitat diversity (see right axis).

Seed removal experiment

Seed predation of four different seed species was assessed for three different predator groups by estimating seed removal. Treatments aimed to excluded (a) no predators (= “open”), using no cages for protection; (b) vertebrates (= “-vertebrates”), using cages with a mesh size of 12.7 mm; and (c) vertebrates and large invertebrates (= “control”), using cages with a mesh size of 1.0 mm. Cages had a size of 210 x 210 x 60 mm and were fixed by metal pins to the ground. To protect seeds from rainfall each treatment was protected by plastic roofs. Predator exclusion treatments were placed next to each other in a distance of 40 - 45 m from one field border. Seed removal was estimated at two distances within the focal field: at the field edge behind the first wheat row and in the field interior in a distance of 13 m parallel to the field border (Fig. 4.2). Trials were exposed to predators for two days due to high removal. Sampling took place at the end of May, June and July 2008. In case seeds became wet, they were dried for 24 h at 40°C. After field work the remaining seeds were counted and weighted in the laboratory. Seed removal was calculated as percentage of remaining seeds from the initial seed number or seed weight.

Seeds of *Galium aparine* L. (goosegrass), *Cirsium arvense* (L.) Scop. (creeping thistle), *Poa trivialis* L. (rough bluegrass), and *Apera spica-venti* (L.) P.B. (silky bentgrass) were used, as all plants are common weed species in wheat (Hofmeister and Garve, 1986). For the large seeds of *G. aparine* and *C. arvense* 50 seeds were exposed per treatment. For the small grass seeds mean weight of 10 x 50 seeds was calculated (*P. trivialis*: 0.96 ± 0.03 mg 50 seeds⁻¹ and *A. spica-venti*: 0.76 ± 0.02 mg 50 seeds⁻¹) and exposed per treatment. 35 x 10 mm (diameter x height) Petri dishes were used to store and expose each seed species separately per treatment. One treatment consisted of four Petri dishes, one for each seed species placed with the lip of the dish flushing the soil or leaf litter surface.

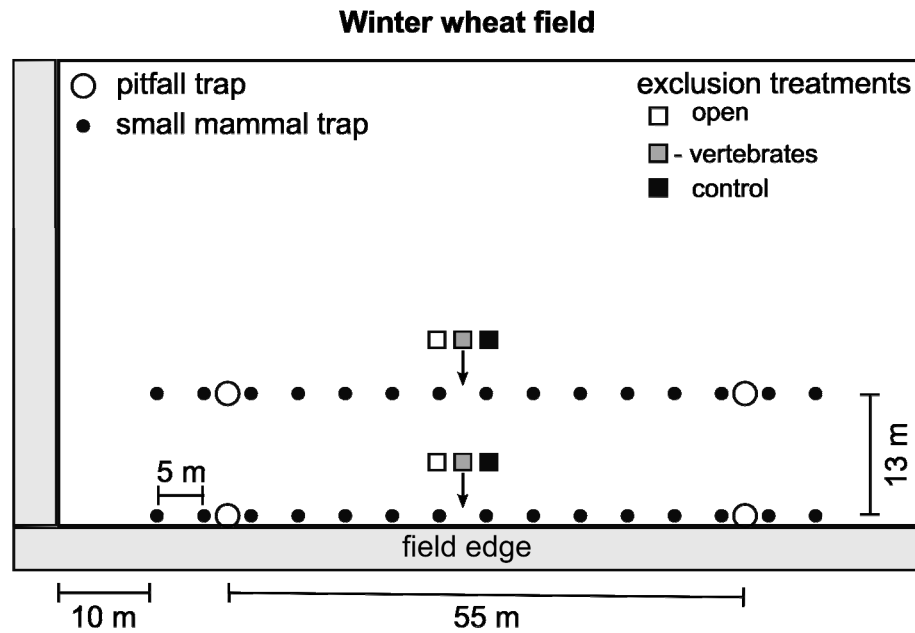


Fig. 4.2 Arrangement of the seed removal experiment, with the three different exclusion treatments, small mammal and pitfall traps in the winter wheat fields.

Seed predator sampling

Carabids and slugs were caught using four pitfall traps per field (90 mm diameter, filled with 50% ethylene glycol) placed 55 m apart at the field edge behind the first wheat row and in the field interior in a distance of 13 m within the field parallel to the field border (Fig. 4.2). They were opened three times for one week. Sampling took place at the end of May, June and July 2008 parallel to the seed removal experiment. Activity density of phytophagous carabid beetles (Laroche, 1990) and slugs (mainly *Deroceras reticulatum* and *Arion lusitanicus*) (Bohan et al., 2000; Frank, 1998) were calculated as the mean value of the two pitfall traps per distance out of the three sampling weeks. Small mammals were caught with 30 Ugglan multiple-capture live traps (240 x 60 x 90 mm; details in Lambin and MacKinnon, 1997) placed 5 m apart in two parallel trap lines, at the field edge behind the first wheat row and in the field interior in a distance of 13 m within the field parallel to the field border. Starting point of each trap line was 10 m apart from one field border (Fig. 4.2). Each winter wheat field was sampled two times in June and July 2008 before and after the second seed removal experimental round. Trapping was carried out for three consecutive trap nights per field. Traps were baited with rolled oats in the evening before sunset and checked in the morning. Individuals trapped for the first time were marked with a permanent micro-tattoo (FST Laboratory Animal Microtattoo System, green tattoo paste, sterile hypodermic needles

27 G x 1/2") at the tail base. Abundance of omnivorous and herbivorous small mammals was calculated as the total number of trapped animals, except recaptures (Michel et al., 2006) per three trap nights, field and trap line. Small mammals trapped by chance with pitfall traps (n = 2 per distance and field) were added to the data set. Mean values of both sampling rounds were calculated.

Statistical analyses

Effects of landscape (percentage of arable land), local farming practice (organic vs. conventional), distance from the field border (edge vs. interior), treatment (open, -vertebrates, control) and seed identity (*G. aparine*, *C. arvensis*, *P. trivialis*, *A. spica-venti*) with two-way interactions on percentage of seed removal were analyzed using linear mixed-effects models (Pinheiro and Bates, 2000) with a maximized log-likelihood implemented in the *nlme* package (Pinheiro et al., 2009). Landscape (11 sites), study field (22 fields) nested in landscape, distance (2 distances) nested in field and treatment (3 enclosure treatments) nested in distance were included as random effects. Additionally, individual models for each weed seed species were performed, to analyze effects of treatment on removal of single weed species. Furthermore, predator abundance and activity densities (small mammals, carabids, slugs) were also analyzed using linear mixed-effects models. As explanatory variables landscape, local farming practice, distance from the field border and interaction between landscape and farming practice were used. Landscape (11 sites) and study field (22 fields) nested in landscape were included as random effects. To achieve normal error distribution and/or avoid heteroscedasticity seed removal and percentage of arable land, as percentage data were arcsine-square root transformed, small mammal abundance was square root transformed and carabid and slug activity densities were log transformed.

Model simplification was done in a stepwise model selection by AIC implemented in the *MASS* package (Venables and Ripley, 2002) until minimal adequate model was obtained. Significance of terms in the best model was assessed by calculating the F- and p-values of an ANOVA table. Differences between treatments and seed species were further inspected on the minimal adequate model using Tukey HSD post-hoc tests implemented in the *multcomp* package (Hothorn et al., 2008). To analyze significance of correlations between seed predator abundance and percentage seed removal Pearson's product-moment correlation was used for small mammal abundance and seed removal rate of the open treatment and for carabid and slug activity density and seed removal rate of the -vertebrates treatment. All calculations were

done using R version 2.9.1 (R Development Core Team, 2009). In the text arithmetic means and standard errors are given.

RESULTS

Seed removal

Seed removal differed among weed seed species, with significantly higher removal rates in *C. arvensis* ($80.06 \pm 2.61\%$) compared to the other three species, *P. trivialis* ($42.87 \pm 3.20\%$; $p < 0.001$), *A. spica-venti* ($32.57 \pm 2.38\%$; $P < 0.001$) and *G. aparine* ($27.13 \pm 2.75\%$; $p < 0.001$; calculated for the open treatment; Table 4.2, Fig. 4.3). Overall seed removal was highest in the open treatment where vertebrates and invertebrates had access ($45.78 \pm 1.91\%$), decreased in the vertebrate exclusion treatment ($41.18 \pm 2.37\%$), and was lowest in the control treatments with no access for vertebrates and large invertebrates ($32.34 \pm 1.70\%$; Table 4.2). For large seeds of *G. aparine* and *C. arvensis* removal rates were higher in the open treatment compared to the vertebrate exclusion and control treatment, while for small grass seeds *P. trivialis* and *A. spica-venti* removal rates were higher in the open and vertebrate exclusion treatment compared to the control (Fig. 4.3).

Table 4.2 Summary of minimal adequate linear mixed-effects models to analyse effects of percentage of arable land, farming practice (organic vs. conventional), distance from the field border (edge vs. interior), predator exclusion treatment (open, -vertebrates, control), weed seed species (*G. aparine*, *C. arvensis*, *P. trivialis*, *A. spica-venti*) and two-way interaction within a radius of 500 m around focal fields on seed removal rates. Degrees of freedom (d.f.), F-values and p-values are given. Bold values show significant results.

	d.f.	F-value	p-value
% arable land ^c	1, 8	0.51	0.50
farming practice	1, 8	0.84	0.39
distance	1,21	0.48	0.50
treatment	2, 86	33.95	< 0.001
seed species	3, 389	313.43	< 0.001
% arable land ^c x farming practice	1, 8	11.28	0.01
distance x seed species	3, 389	2.07	0.10

^a log transformed; ^b sqrt transformed, ^c arcsine-square root

Seed removal was not significantly affected by distance from the field border (edge vs. interior), but differed in organic and conventional fields, depending on landscape complexity (interaction: percentage of arable land x farming practice). On conventional fields seed

removal increased with decreasing landscape complexity, while on organic fields, it decreased. (Table 4.2; Fig. 4.4a).

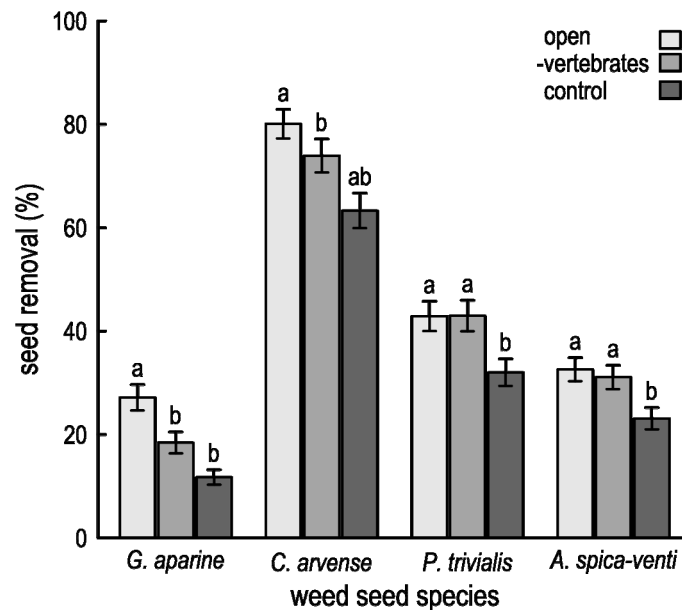


Fig. 4.3 Seed removal rate (%; mean \pm SE, $n = 22$) for the different weeds seed species, sorted by seed size and predator exclusion treatments. Different letters indicate differences between treatments within the four weed seed species (Tukey HSD post-hoc test, $p < 0.05$).

Seed predator identity

On average 4.00 ± 0.58 small mammals ($n = 44$) out of six omnivorous and herbivorous species were trapped during three consecutive trap nights per trap line (for an overview of trapped small mammals see Appendix Table A4.1). In contrast to the pattern found for seed removal, small mammal abundance was higher on organic fields in simple landscapes ($> 80\%$ of arable land), whereas it tended to decrease on conventional fields with increasing percentage of arable land (Table 4.3: small mammals; Fig. 4.4b).

On average 8.95 ± 1.91 carabids ($n = 44$) out of 21 species, which are known to feed at least partly on seeds and plant material, were trapped during one sampling period of seven days per trap line (for an overview of trapped carabids see Appendix Table A4.2). Carabid activity density tended to be higher in organic fields (11.72 ± 1.75) compared to conventional fields (6.21 ± 0.65), with no effects of landscape complexity and distance to field border (Table 4.3: carabids; Fig. 4.4c).

On average 12.13 ± 2.30 slugs ($n = 44$) were trapped during one sampling period of seven days per trap line. Slug activity densities were higher in the field edge (14.34 ± 2.95) compared to the interior (9.92 ± 2.07). Similarly to seed removal rates, slug activity densities

tended to be higher on conventional fields in simple landscapes and decreased on organic fields with decreasing landscape complexity (Table 4.3: slugs; Fig. 4.4d).

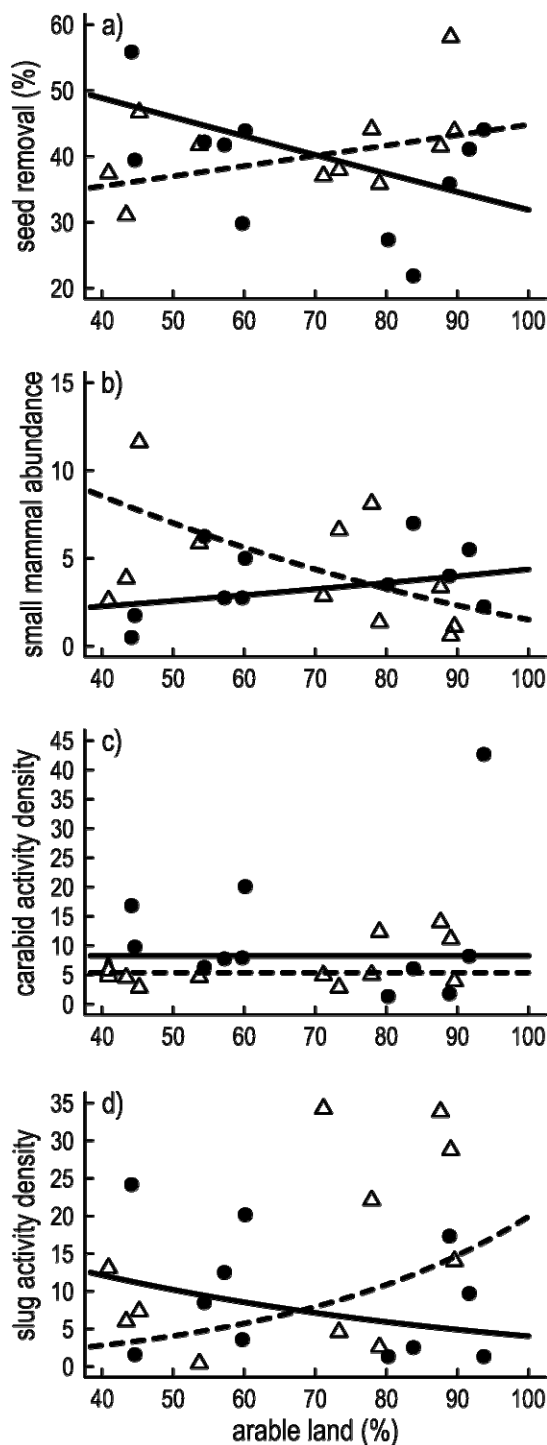


Fig. 4.4 Relation of percentage of arable land to: a) seed removal rate (%), b) small mammal abundance, c) carabid activity density and d) slug activity density within a radius of 500 m around focal fields. Open triangles and dashed lines (conventional fields), filled circles and solid lines (organic fields). Statistical significant interactions between landscape context and farming practice were found for seed removal rate and, with marginal significance, for small mammal abundance and slug activity densities. For better visualisation back-transformed data are presented.

Relationship between seed predation/removal and predator abundances/activity densities

Seed removal of *C. arvensis* decreased as small mammal abundance increased, but increased as carabid activity density increased. Seed removal of *G. aparine* increased as slug activity

density increased. Seed removal of the two grass species *P. trivialis* and *A. spica-venti* were not correlated with the observed predator groups (Table 4.4).

Table 4.3 Summary of minimal adequate linear mixed-effects models to analyse effects of percentage of arable land, farming practice (organic vs. conventional), distance from the field border (edge vs. interior) and interaction between percentage of arable land and farming practice within a radius of 500 m around focal fields on small mammal abundance and carabid and slug activity density. Degrees of freedom (d.f.), F-values and p-values are given. Bold values show significant or marginal significant results.

	d.f.	F-value	p-value
small mammals ^b			
% arable land ^c	1, 8	0.73	0.42
farming practice	1, 8	0.10	0.76
distance		-	-
% arable land ^c x farming practice	1, 8	5.15	0.05
carabids ^a			
% arable land ^c		-	-
farming practice	1, 10	4.80	0.05
distance		-	-
% arable land ^c x farming practice		-	-
slugs ^a			
% arable land ^c	1, 8	0.08	0.78
farming practice	1, 8	1.07	0.33
distance	1, 21	7.10	0.01
% arable land ^c x farming practice	1, 8	3.97	0.08

^a log transformed; ^b sqrt transformed, ^c arcsine-square root

Table 4.4 Pearson product-moment correlation between mean seed removal per seed species within open treatments and small mammal abundance and mean seed removal per species within -vertebrate treatments and carabid and slug activity density (n = 22). Positive pearson product-moment correlation coefficient (r) indicates positive correlations, and negative correlation coefficients indicate negative correlations. Bold values show significant correlations with levels of significance, d.f. = 20.

	small mammals ^b	carabids ^a	slugs ^a
<i>A. spica-venti</i> ^c	-0.12	0.21	0.39
<i>C. arvensis</i> ^c	-0.49*	0.58**	0.40
<i>G. aparine</i> ^c	0.25	0.15	0.53*
<i>P. trivialis</i> ^c	-0.15	0.38	0.19

*** p < 0.001; ** p < 0.01; * p < 0.05; ^a log transformed; ^b sqrt transformed, ^c arcsine-square root

DISCUSSION

The analyses of local and landscape factors on weed seed removal showed, that organic farming increased seed removal rates in complex landscapes, while conventional fields increased seed removal rates in simple landscapes. These results differentiate the current knowledge of seed predation in terms of effects of agricultural intensification, as seed removal is expected to increase with landscape structural complexity (Farwig et al., 2009; Matías et al., 2009; Menalled et al., 2000), less intensive farming practices (Baraibar et al., 2009; Menalled et al., 2007; O'Rourke et al., 2006) and decreasing distance from the field border (Navntoft et al., 2009; but see Booman et al., 2009; Marino et al., 1997). Seed removal patterns were related to weed species and predator identity, when comparing small mammals, phytophagous carabid beetles and slugs, with higher predation rates by mammalian seed predators on plant species exhibiting large seeds.

The contrasting effects of seed removal in relation to landscape complexity and farming practice and the equal removal rates in the field interior and edge can be explained by variation in abundances and activity densities, home ranges and foraging time of predators owing to food supply on the fields and the surrounding landscape. Food supply in organic fields (Roschewitz et al., 2005), at field edges (Gabriel et al., 2006) and in complex landscapes (Gabriel et al., 2005; Roschewitz et al., 2005) may be higher due to more alternative food sources and higher weed abundances, thereby reducing seed predation and removal. Seed predation rates in experimentally introduced seed patches have been shown to be lower in habitats with high-food resources, because of satiation of seed predators due to high availability of naturally occurring seeds (Honek et al., 2003; Honek et al., 2006; Marino et al., 2005; but see Hulme and Hunt, 1999 for forest ecosystems). In addition, low predator densities on conventional fields (Menalled et al., 2007) can be compensated in simple landscapes by larger home ranges (Breitbach et al., 2010; Corp et al., 1997) and an increasing foraging time in low-food habitats (MacArthur and Pianka, 1966). Predators appeared to move from conventional fields, which are low-food habitats to high-food habitats (Briner et al., 2007; Tew et al., 2000; Tschardtke et al., 2005b), resulting in e.g. higher carabid abundances on organic fields and therefore lower seed removal rates on conventional fields in complex landscapes. Vice versa, in simple landscapes predators largely exploited food patches on conventional fields because of low background food density. This mechanism might also explain the lack of differences in seed removal between field edges and field interiors. In the field interior predator abundances appeared to be lower compared to the edge (Saska et al., 2008), but exploitation of food patches (MacArthur and Pianka, 1966) and

predator home ranges might be higher (Fournier and Loreau, 2001; Jonsson et al., 2002) because of lower background food supply (Gabriel et al., 2006), resulting in equal removal rates between field interior and edge (see Marino et al., 1997; Westerman et al., 2003; but see Holmes and Froud-Williams, 2005; Jacob et al., 2006).

Our results showed that small mammal exclusion caused reduced seed removal only for larger seeds (*G. aparine* and *C. arvensis*) providing sufficient nutrient content (Booman et al., 2009; Tew et al., 2000; Wang and Chen, 2009), but not for smaller seeds (*P. trivialis* and *A. spica-venti*), indicating a changing impact of small mammals (but see Hulme, 1994; Booman et al., 2009), depending on weed seed size. Furthermore small mammal densities did not follow seed removal patterns in terms of landscape complexity and farming practice. Possibly, small mammals are only efficient seed predators, when there is a low background food supply (Edwards and Crawley, 1999; Westerman et al., 2008). In contrast large invertebrates appeared to be more important as seed predators and dispersers for small seeds most likely because of seed identity and seed preferences (Honek et al., 2007; Saska et al., 2008).

Seed removal by slugs is often not considered (but see Honek et al., 2009; Hulme, 1994; Kollmann and Bassin, 2001). In our study, activity densities of slugs followed the patterns of seed removal rates, and therefore, appeared to be most important. Slugs are known to act as seed predators feeding on many different species of weed seeds, but also can disperse seeds. For example, beech forest myrmecochores and dandelion seeds found in slug faeces could still germinate (Honek et al., 2009; Kollmann and Bassin, 2001; Türke et al., 2010). In addition, seeds adhering to sticky skin surface may also facilitate seed dispersal by slugs (C. F., pers. observations). Therefore slugs can be regarded as ecosystem disservices.

Seed identity appeared to be a major factor explaining seed removal. Such differences in seed removal rates among weed seed species according to seed size, length and weight have been reported by several studies (Booman et al., 2009; Honek et al., 2007; Matías et al., 2009). In our study *G. aparine*, which was the largest seed, has been most likely removed by slugs and predated by small mammals, as small carabids have difficulties to handle such heavy and large seeds (Honek et al., 2007). *C. arvensis* with an intermediate size among our tested seed species was predated by both small mammals and medium-sized and large carabids (Honek et al., 2007). In contrast, small grass seeds of *P. trivialis* and *A. spica-venti* are little affected by seed predators and might only be suitable for small invertebrates like ants, as seed size is positively correlated with carabid body mass (Honek et al., 2007). Nevertheless, an important proportion of seeds removed in our study appeared to result from sources such small

invertebrates (ants, isopodes and small slugs) and/or abiotic factors (rain or wind) (Jacob et al., 2006; Saska, 2008).

Conclusion

Patterns of weed seed predation and seed removal are not only determined by the identity of seed predators (vertebrates *vs.* invertebrates) and weed species, but also by landscape complexity interacting with farming practices. Seed removal was highest in seeds of intermediate size (the notorious weed *C. arvensis*) and higher on organic fields in complex landscapes and conventional fields in simple landscapes. Slug density and seed removal showed similar response to landscape complexity and farming practice, while small mammal density increased with decreasing landscape complexity on organic fields, but decreased on conventional fields. Phytophagous carabid beetles were not affected by landscape structure, but more abundant on organic than conventional fields. Future studies should try to separate responses of each predator group to local and landscape management in more detail and to experimentally test the relative impact of each predator group on the large range of weed species.

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APPENDIX

	Total
<i>Apodemus agrarius</i> (PALLAS)	120
<i>Apodemus flavicollis</i> (MELCHIOR)	21
<i>Apodemus sylvaticus</i> (L.)	40
<i>Apodemus</i> spp.	2
<i>Myodes glareolus</i> (SCHREBER)	1
<i>Microtus agrestis</i> (L.)	1
<i>Microtus arvalis</i> (PALLAS)	167

Table A4.1 Total abundance of omnivorous and granivorous small mammal species on winter wheat fields (n = 22) of both trapping sessions and trap lines per field.

	Total
<i>Abax parallelepipedus</i> (PILLER ET MITTERPACHER)	5
<i>Agonum muelleri</i> (HERBST)	95
<i>Amara aenea</i> (DEGEER)	1
<i>Amara aulica</i> (PANZER)	1
<i>Amara familiaris</i> (DUFTSCHMID)	2
<i>Amara ovata</i> (FABRICIUS)	3
<i>Amara plebeja</i> (GYLLENHAL)	6
<i>Amara similata</i> (GYLLENHAL)	13
<i>Anchomenus dorsalis</i> (PONTOPPIDAN)	1006
<i>Anisodactylus binotatus</i> (FABRICIUS)	1
<i>Bembidion obtusum</i> (SERVILLE)	2
<i>Bembidion tetracolum</i> (SAY)	8
<i>Brachinus crepitans</i> (LINNE)	33
<i>Calathus fuscipes</i> (GOEZE)	6
<i>Harpalus affinis</i> (SCHRANK)	88
<i>Harpalus rubripes</i> (DUFTSCHMID)	1
<i>Ophonus azureus</i> (FABRICIUS)	2
<i>Poecilus cupreus</i> (LINNE)	362
<i>Pseudoophonus rufipes</i> (DE GEER)	184
<i>Pterostichus melanarius</i> (ILLIGER)	430
<i>Trechus quadristriatus</i> (SCHRANK)	11

Table A4.2 Total activity density of phytophagous carabid beetle species on winter wheat fields (n = 22) of both trap lines per field, summed up over the three sampling weeks.

SUMMARY

Agricultural intensification during the last decades has led to a serious decline in farmland biodiversity and has negatively affected related ecosystem functions such as pollination, pest control and disease suppression. Main causes are the transition of natural and semi-natural habitats into cropland and the intensification of agricultural practices with, for example an increasing use of pesticides, fertilizers and soil cultivation. In contrast, organic farming, characterized by an abandonment of pesticide applications and a more diverse crop rotation, as well as increasing landscape complexity, characterized by high habitat-type diversity and a high amount of semi-natural habitats, are known to enhance farmland biodiversity. Landscape context can modulate effects of farming practice. Therefore it is important to consider both local farming practice and landscape context simultaneously in ecological studies.

Here, we analysed the relative importance of local farming practice (organic *vs.* conventional management) and landscape context (proportion of arable land). We focused on openland, woodland and farmland birds and small mammals, which are functionally important links in food webs of the agricultural landscape. We also studied weed seed removal and predation as an ecological function that can strongly affect non-crop plant population growth and recruitment rates. Bird studies were conducted on 61 winter wheat fields during the breeding season and winter in two German regions differing in land-use history (East *vs.* West Germany), with smaller field sizes and high overall landscape complexity in West Germany and very large fields and a low overall landscape complexity in East Germany. Field observations of small mammals and weed seed removal/predation of four economically relevant weed species by vertebrates and invertebrates were conducted on 22 winter wheat fields around the city of Göttingen in West Germany between wheat flowering and ripening. For each experiment we selected paired organically and conventionally managed fields located along a gradient of landscape complexity (40 - 100% arable land within radii of 500 m around focal fields).

Birds featuring different ecological traits, showed contrasting responses to the landscape context. Openland bird species richness increased with increasing percentage of arable land and responded positively to organic farming. Farmland and woodland bird species abundance and species richness decreased with increasing landscape complexity and were not related to farming practice, indicating species trait-specific perception of breeding and feeding habitats. Organic farming in simple landscapes increased small mammal abundance, species richness

and diversity, while it decreased on conventional fields. True mice abundances increased with increasing landscape complexity, while abundances of voles as potential pest species were highest in simplified landscapes with high percentages of arable land, independently of farming practice. Weed seed predation/seed removal was mainly affected by predator (vertebrates *vs.* invertebrates) and weed seed identity but also by landscape complexity in interaction with farming practice. In complex landscapes seed removal was higher on organic fields and in simple landscapes on conventional fields.

Results showed that both organic farming and landscape complexity can enhance vertebrate abundance and species richness and facilitated ecological functions but to a different extent. Organic farming was less important than landscape complexity for birds, while small mammals and seed removal/predation were enhanced by organic farming in interaction with landscape complexity. Collectively, the results indicate contrasting responses of different vertebrate taxa and ecological functions suggesting species-specific landscape management, like organically and conventionally managed fields, surrounded by landscapes with a diversity of semi-natural habitats.

ZUSAMMENFASSUNG

In den letzten Jahrzehnten hat die landwirtschaftliche Intensivierung zu einem erheblichen Verlust der Biodiversität und zu einer verringerten Effektivität von Ökosystemfunktionen, wie z.B. der Bestäubungsleistung, der natürlichen Schädlingskontrolle oder der Unterdrückung von Krankheitserregern in der Agrarlandschaft beigetragen. Hauptgründe sind dabei die Umwandlung von natürlichen und naturnahen Habitaten in landwirtschaftliche Nutzflächen und die Intensivierung landwirtschaftlicher Verfahren, wie ein erhöhter Pestizid- und Düngemiteleinsatz und eine intensivere Bodenbearbeitung. Die Biodiversität kann, im Gegensatz dazu, durch den ökologischen Landbau und eine höhere Landschaftskomplexität in der Agrarlandschaft positiv beeinflusst werden. In der Praxis kann dies durch den Verzicht auf Spritzmittel, mineralische Dünger und eine vielfältigere Fruchtfolge auf lokaler Ebene und durch eine höhere Habitatdiversität und einem höheren Anteil an naturnahen Habitaten auf Landschaftsebene realisiert werden. Da sich die die Landschaftskomplexität und die Effekte der unterschiedlichen Bewirtschaftungsformen gegenseitig beeinflussen, ist es wichtig die lokalen Bewirtschaftungsformen und den Landschaftskontext gleichzeitig zu betrachten.

In der vorliegenden Arbeit haben wir uns mit der relativen Bedeutung der lokalen Bewirtschaftungsform (ökologischer vs. konventioneller Landbau) und des Landschaftskontextes (Ackeranteil) beschäftigt. Als wichtige Bestandteile von Nahrungsnetzen in der Agrarlandschaft konzentrierte sich unsere Arbeit auf Offenland-, Wald- und Feldvögel sowie Kleinsäuger. Weiterhin haben wir die Samenverbreitungs- und -fraßraten verschiedenen Problemunkräutern untersucht, da diese Ökosystemfunktion das Wachstum und die Verbreitung vieler Pflanzenarten stark beeinflussen kann. Die Vogelstudie wurde auf 61 Winterweizenfeldern in Ost- und Westdeutschland während der Brutzeit und im Winter durchgeführt. Die zwei Regionen wurden aufgrund der unterschiedlichen Landnutzungsgeschichte ausgewählt. In Westdeutschland konnten wir kleine Felder und einer höheren Landschaftskomplexität finden, während die Untersuchungsgebiete in Ostdeutschland durch sehr große Felder und eine geringere Landschaftskomplexität gekennzeichnet waren. Die Versuche zur Untersuchung des Kleinsäugervorkommens und der Samenverbreitung/ -fraßraten wurden auf 22 Winterweizenfeldern in der Umgebung von Göttingen (Westdeutschland) zwischen der Weizenblüte und -reife durchgeführt. Für alle Experimente wurden ein ökologisch und ein konventionell bewirtschaftetes Feld innerhalb

eines Landschaftskomplexitätsgradienten (40 - 100% Ackeranteil in Radien von 500 m um das Untersuchungsfeld) ausgewählt.

Die Vögel zeigten aufgrund ihrer unterschiedlichen Habitatansprüche unterschiedliche Reaktionen auf die Landschaftskomplexität. Der Artenreichtum der Offenlandarten stieg mit zunehmendem Ackeranteil an und war auf ökologischen Feldern während der Brutzeit höher. Im Gegensatz dazu nahmen die Abundanzen und die Artenzahlen der Wald- und Feldvögel mit zunehmendem Ackeranteil ab, unabhängig von den unterschiedlichen Bewirtschaftungsformen. Eine Erklärung dafür sind die deutlich unterschiedlichen Habitatansprüche der drei Vogelgruppen. Die Abundanz, Artenzahl und Diversität der Kleinsäuger stieg auf ökologisch bewirtschafteten Flächen mit zunehmendem Ackeranteil an, während das Kleinsäugervorkommen auf konventionellen Feldern abnahm. Die Abundanzen von echten Mäusen nahm mit zunehmender Landschaftskomplexität zu, während potentielle Schädlinge, wie Wühlmäuse unabhängig von der Bewirtschaftungsform positiv auf einen zunehmenden Ackeranteil in der Landschaft reagierten. Die Samenverbreitungs/-fraßraten wurden hauptsächlich von den Unterschieden zwischen den Samenprädatoren (Vertebraten vs. Invertebraten) und der Samenart, aber auch von der Landschaftskomplexität in Interaktion mit der Bewirtschaftungsform bestimmt. Die Samenverbreitungs/-fraßraten stiegen auf ökologisch bewirtschafteten Flächen mit abnehmendem Ackeranteil an, während auf konventionellen Feldern die Samenverbreitungs/-fraßraten mit zunehmendem Ackeranteil zunahmen.

Unsere Ergebnisse konnten zeigen, dass sowohl der ökologische Landbau, als auch die Landschaftskomplexität die Abundanz und den Artenreichtum von Vertebraten und Ökosystemfunktionen beeinflussen. Für Vögel in der Agrarlandschaft war der ökologische Landbau jedoch weniger wichtig als die Landschaftskomplexität, während Kleinsäuger und Samenverbreitungs/-fraßraten von der ökologischen Bewirtschaftung in Interaktion mit der umgebenden Landschaft beeinflusst wurden. Durch entgegengesetzte Reaktionen der verschiedenen Vertebratentaxa und Ökosystemfunktionen auf die unterschiedlichen Bewirtschaftungsformen und die Landschaftskomplexität wird eine artspezifische Bewirtschaftung der Agrarlandschaften notwendig. Die Biodiversität in der Agrarlandschaft kann somit z.B. durch ökologisch und konventionell bewirtschaftete Flächen umgeben von natürlichen und naturnahen Habitaten gefördert werden.

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CURRICULUM VITAE

Christina Fischer

born 11.07.1981 in Schlema, Germany

03/2007 - 05/2010 Agroecology, Department of Crop Science, Georg-August-University,
Göttingen, Germany

PhD student

Thesis: "Effects of farming practice and landscape complexity on
vertebrate diversity and ecological functioning in agroecosystems"

Supervisors: Prof. Dr. Teja Tschardt, Dr. Carsten Thies

10/2000 - 11/2006 Friedrich-Schiller-University, Jena, Germany

Biologist (Dipl. Biol.)

Key aspects: Ecology, Zoology and Medical Microbiology

Diploma thesis: "Small mammals under influence of different land use in
an arid ecosystem in Northern Namibia"

07 - 10/2003 Okatumba Wildlife Research, Windhoek, Namibia

Voluntary research internship

work within a cheetah conservation project

09.07.2000 Clemens-Winkler-Gymnasium, Aue, Germany

Completion of school education with the "Abitur" degree (qualification
for university entrance)