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Impoverishment of the arable flora of Central Germany during the past 50 years: a multiple-scale analysis

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vorgelegt von Stefan Meyer

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Impoverishment of the arable flora of Central Germany during the past 50 years: a multiple-scale analysis

Dissertation

zur Erlangung des Doktorgrades

der Fakultät für Biologie und Psychologie

der Georg-August-Universität Göttingen

vorgelegt von

Stefan Meyer

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1

General introduction

Arable plant vegetation – the ongoing conflict between agriculture and nature conservation

There is hardly any ecosystem which is so markedly influenced by human activity as arable fields (VAN CALSTER *et al.* 2008, ELLENBERG & LEUSCHNER 2010). Since the beginning of agriculture in Central Europe in the Neolithic, the vegetation accompanying cultivated plants has changed repeatedly (BURRICHTER *et al*. 1993). Until the middle of the last century, agricultural fields were valuable habitats for a variety of animal and plant species preferring open landscapes. The diversity of the arable plant flora is a historical relic of past land management and gives testimony of the earlier increase in biodiversity through extensive land use. Therefore, agriculture has created a high number of habitat types which shape our cultural landscapes and are worth being protected (EWALD & KLAUS 2009).

In recent decades, increasing economic pressure and the resulting intensification of farming practices has led on the one hand to increasing yields of crop plants, but on the other hand to a sustained loss of species in the arable companion flora (STOATE *et al.* 2001, STORKEY *et al.* 2012). Several studies describe the partly dramatic structural changes in arable plant communities throughout Central Europe, e.g. from the Stolzenauer Wesermarsch (MEISEL 1966), Northern Hesse (HOTZE & VAN ELSEN 2006), Saxony-Anhalt (HILBIG 1985), Austria (RIES 1992), Lower Lusatia (KLÄGE 1999), Slovenia (ŠILC & ČARNI 2005) and the Czech Republic (LOSOSOVÁ & SIMONOVÁ 2008). In fact, in no other habitat type in Central Europe population sizes and diversity of the vegetation have declined as strongly as in arable land (ELLENBERG & LEUSCHNER 2010). In many regions the collapse of arable wild plant communities even exceeds the tremendous losses which were described for grasslands on mesic and wet soils (WESCHE *et al.* 2009, 2012, KRAUSE *et al*. 2011). Currently, around 120 of the approximately 350 arable plant taxa in Germany are considered endangered (HOFMEISTER & GARVE 2006).

The diversity and population sizes of arable plants have declined mainly due to increased nitrogen fertilization rates (WILSON 1992, ROBINSON & SUTHERLAND 2002), effective seed cleaning techniques (SPAHILLARI *et al.* 1999, HILBIG 2005), weed control with efficient herbicides, simplification of crop rotations (KNOX *et al.* 2011, MEDIENE *et al.* 2011) and homogenization of the landscape structure (MACDONALD & JOHNSON 2000, BAESSLER & KLOTZ 2006). Especially the widespread use of herbicides from the 1950s onwards (SALESBURY 1961, ANDREASEN & STREIBIG 2011) and the introduction of the European

Union’s Common Agriculture Policy (CAP) as a major driver of change in cropping methods (POTTER 1997, ANDREASEN & STRYHN 2008), resulted in increasingly rapid shifts in the highly dynamic agro-ecosystems (HOLZNER & IMMONEN 1982). The also ongoing abandonment of fields or conversion to grassland or forests affects those sites which were traditionally under extensive management and therefore often represent the last retreats of threatened arable wild plants (RITSCHEL-KANDEL 1988, MEYER *et al.* 2008).

Until shortly after World War II, agriculture in Germany was still characterized by a ‘low-input-agriculture system’, which changed dramatically with the beginning of agricultural industrialisation in the 1950s and early 1960s (BAUERKÄMPER 2004). Average nitrogen surplus (N) on German agricultural sites increased dramatically from 25 kg ha^{-1} yr^{-1} in the 1950s to around 110 kg ha^{-1} yr^{-1} in 2005 (ELLENBERG & LEUSCHNER 2010). N input and increased crop cover in addition to herbicide application is a key driver of vegetation change in Central European croplands. In the early 1950s, herbicides were applied on only 10% of the summer and winter cereal fields in Germany, but herbicide treatment increased to almost 100% in the mid 1980s (ELLENBERG & LEUSCHNER 2010). Herbicide sales in Germany increased by another 30% from 1994 to 2008 (UMWELTBUNDESAMT 2011).

In addition to management practices, environmental factors such as climatic and physical factors (e.g. soil properties, elevation, temperature, precipitation) can act as important determinants of arable plant diversity and species composition as identified by several large-scale phytosociological studies (e.g. LOSOSOVÁ *et al.* 2004, PINKE *et al.* 2012). However, these surveys also showed that the formerly pronounced influence of geological substrate on arable plant community composition has mostly vanished today, because uniform cultivation techniques have promoted the development of largely similar arable communities across a broad range of soil conditions.

Furthermore, numerous studies report that landscape complexity and spatial aggregation of conservation areas affect arable plant diversity (GABRIEL *et al.* 2005, ROSCHEWITZ *et al.* 2005). In Germany, a dramatic landscape homogenization has occurred that can be best exemplified by increased sizes of cropping fields. Mean field size in Germany has increased considerably, e.g. near Halle (Saale) from 1.2 ha (1953/1957) to 12.2 ha (2000; BAESSLER & KLOTZ 2006), or in the administrative district of Leipzig from 7.0 ha (1965) to 12.1 ha (1984; HORSTKÖTTER 2003). In consequence, field margins as potential refuges for arable vegetation (DE SNOO 1997, DUTOIT *et al.* 1999) become more and more unimportant from a spatial perspective. Moreover, a large fraction of the relatively high plant diversity in field margins is constituted by plants from adjacent vegetation types rather than from arable land (ROMERO *et al.* 2008, JOSÉ-MARIÁ *et al.* 2011).

The increasing fragmentation of suitable habitats in the intensively managed agricultural landscape will affect arable plant populations through reduced population size and increased isolation. It is known that increasingly smaller population sizes in most arable plant species have resulted in many species being categorised as being threatened by extinction (MATTHIES *et al.* 2004). It has been found that next to landscape effects, genetic, life history or environmental factors are the main drivers for these processes (OOSTERMEIJER *et al.* 2003, LEIMU *et al.* 2006). Changes on the population level are associated with an erosion of genetic diversity and increased interpopulation genetic divergence due to increased random genetic drift, elevated inbreeding and reduced gene flow (YOUNG *et al.* 1996, ANGELONI *et al.* 2011). Indeed, extinction threat is commonly associated with detrimental genetic structures (SPIELMAN *et al.* 2004). Lower levels of genetic variation may limit a species' ability to adapt to changing environments and thus increase the extinction probabilities (e.g. HONNAY & JACQUEMYN 2007). Formerly common species, which have become rare as the result of recent landscape transformations, may be particularly prone to the effects of habitat fragmentation (AGUILAR *et al.* 2008). Up to now, arable plant species are still underrepresented in population genetic studies, and genetic structures have just been studied in a limited number of arable plants (SCHMIDT *et al.* 2009, DÉLYE *et al.* 2010, BRÜTTING *et al.* 2012). Next to nothing is known on whether agricultural intensification has affected extant populations, and whether genetic structures vary between differently structured landscapes.

The need for long term studies to analyze shifts in arable plant vegetation in Central Europe

In Germany, the development of agricultural systems after World War II was broadly comparable to that in other European countries (specialisation of farming enterprises on either arable cropping or livestock farming), but development in western and Eastern Germany differed from each other: In Western Germany, agriculture still is dominated by private ownership and small-scale, but intensive farming systems (BAUERKÄMPER 2004). East Germany contrasted sharply, where transformation processes in the German Democratic Republic (land reform, collectivisation, industrial large-scale agriculture and privatisation of agricultural land) resulted in giant agricultural holdings with large field patches (BAESSLER & KLOTZ 2006, TIM 2008). Although agricultural systems have become more intensively managed during recent decades in both parts of Germany, there are still regional differences in habitat and species diversity (VOIGTLÄNDER *et al.* 2001). Thus, any analysis aiming at a comprehensive picture of the agricultural intensification effects on arable plant diversity in Germany must cover different regions in both parts of the country. Changes should be assessed against a common reference, when conditions were still relatively uniform; i.e. in the first phase after the Wordsl War II, before new agricultural policies were introduced. One must therefore go back at least four to five decades in time in order to establish a baseline against which the current biodiversity level can be compared to.

The nonetheless apparent loss of diversity among arable plant species in Germany highlights the need for long-term conservation activities on a national level. Unfortunately, most conservation projects for arable plants have failed after an often successful initial phase. This failure was mainly due to the lack of long-term financial coverage of the running management and administrative costs (MEYER *et al.* 2010).

Therefore, the present thesis evaluated changes in arable plant communities on various spatial scales *and* on various organisational levels from the population to the community. The objectives of the present thesis were as follows:

(1) to evaluate the impact of agricultural land use on the threat status of plants adapted to arable habitats on a European scale,

(2) to quantify the impact of agricultural intensification since the 1950s/1960s, particularly in Central Germany, on arable plant communities and on their species richness and composition,

(3) to test whether landscape structure affects the genetic structure and diversity of remnant populations of selected arable plant species and

(4) to assess both the effectiveness of current schemes and programs as well as new potential long-term strategies that aim at the conservation of arable plant diversity in Germany.

Study design and chapter outline

All empirical data were collected in Central Germany, i.e. in the federal states of Brandenburg, Saxony-Anhalt, Lower Saxony and Thuringia. These cover a range of conditions representative for northern Central Europe, with different geological substrate conditions (approximate north-south boundaries 52°61’ N to 50°78’ S; approximate west-east boundaries 9°11’ W to 13°69’ E). The study area is influenced by a subcontinental/suboceanic climate with mean annual air temperatures ranging from 7.1°C to 9.1°C, and a mean annual precipitation from 450mm up to 750mm per year.

In the following section, the approaches, methods and hypotheses of this thesis are outlined. A summary of the investigated hierarchical levels and employed methods is compiled in Table 1.1. Chapter 2 to chapter 6 present observational studies, questionnaire and literature reviews conducted within the framework of this thesis. Finally, in chapter 7, the results are synoptically presented and discussed, and general conclusions and future perspectives are outlined.

Table 1.1. Overview of the conducted studies presented in chapter 2 to chapter 6. Summarised are the investigated predictor and response variables, and methods employed.

			Methods			
	Predictor variables	**Response variables**	**No. of samples**	**Experimental methods**	**Statistical methods**	**Level of study**
Chapter 2	Wheat yield, herbicide and fertilizer use	List of threatened arable species	29	Standardized questionnaire campaign, literature survey	Descriptive analysis, generalized linear models (GLM), redundancy analysis (RDA)	Country and continental scale
Chapter 3	Temporal change (vegetation relevés)	Plant community classification, phytosociological syntaxa	1176	Observational study, vegetation analysis (100 m^2 relevés)	Descriptive analysis, Detrended Correspondence Analysis (DCA)	Community level
Chapter 4	Temporal change (vegetation relevés)	Crop composition, plant community composition and cover	1176	Observational study, vegetation analysis (100 m^2 relevés)	Detrended Correspondence Analysis (DCA), Repeated measure ANOVA, indicator species analysis	Community level
Chapter 5	Landscape complexity, Population size	Nei's genetic diversity (H_j), number and percentage of polymorphic loci (PPL)	57	Randomised block design: Population	Principal coordinate analysis (PCoA), analysis of molecular variance (AMOVA)	Population level
Chapter 6	Current policies (questionnaire and literature data)	-	85	Review study: questionnaires, literature survey	Descriptive analysis	-

In chapter 2, the impact of crop management and intensity of agricultural land use on the threat status of plants adapted to arable habitats was analysed on a continental scale. Data from Red Lists of vascular plants were compiled and assessed by national experts from 29 European countries. The experts were asked to identify vascular plant species that are particularly associated with arable habitats, and classified as threatened on the respective national Red List. In addition, a second list of species was compiled for each country, which consisted of arable plants that were either identified as ‘near threatened’ or did not appear on the national Red List at all, but still were known to be declining from on-going surveys or expert knowledge. Finally, answers were requested on possible reasons for national declines in arable plant diversity and on potential conservation measures being used to stop these declines. The relative threat status of each species was assessed using a specifically designed scoring system. National data of fertilizer and herbicide use and loss of arable land were obtained because the two factors identified in the questionnaires as the main drivers of national declines in arable plants were increased use of agro-chemicals and abandonment of arable land. It was hypothesised that (i) explanatory variables can be identified which can predict a ranking of countries in terms of the numbers of arable species that are nationally rare or threatened, and (ii) that the relative sensitivity of arable plant species to these variables can be quantified.

For chapters 3 & 4, long-term comparisons of historical and current arable plant communities were performed. Chapter 3 focuses on phytosociological shifts in arable plant syntaxa. For this study, 392 fields from ten different study areas in Central Germany that were sampled by taking phytosociological relevés in the 1950s/60s, were re-sampled in 2009. The study areas represent all main substrate types, i.e. fields on sandy, loamy and calcareous soils. On the basis of vegetation maps and precise descriptions of the study sites provided in publications or field notes, the location of 392 relevés sites could be identified at the field level and re-sampling was carried out in 2009. One observational plot of 100m² was placed at least 10 m apart from the outermost seed row at the field margin to eliminate any ecotonal effect and another plot was situated directly on the field margin. We tested the hypothesis that (i) agricultural intensification during the last 50 years leads to strong shifts in arable plant syntaxonomy and that (ii) most of the current relevés lack phytosociologically diagnostic species, and can only be classified at the level of higher syntaxa such as alliance, order, and class.

In chapter 4, changes in the arable flora of Central Germany were analysed on the level of the regional species pool and also with respect to plot-level diversity. Here, we used the same study design as in chapter 3, i. e. re-sampling of phytosociological relevés after 50-60 years. We tested if (i) agricultural intensification has resulted in a reduced diversity of crop varieties on the landscape level and denser crop stands; leading to (ii) significant shifts in the composition of the arable communities with diversity losses in archaeophytic species and increases in neophytic and Poaceae species. It was further hypothesized that (iii) the intensity of these shifts varies with the soil substrate.

For chapter 5, effects of landscape configuration on genetic structure and diversity of remnant populations of the two threatened arable plant species *Adonis aestivalis* L. and *Consolida regalis* S.F. GRAY were analysed, using dominant amplified fragment length polymorphism markers (AFLP's). These effects were investigated in six regions of 5 km² size in Central Germany, which were assigned to two different classes of landscape structural complexity, i.e. monotonous (> 95% of area being arable land) or structurally diverse (< 60% of area being arable land). Within each region, either five subpopulations of *A. aestivalis* and *C. regalis* were selected at random, or all subpopulations were investigated in case the number of populations was smaller than five. Additionally, population size was estimated for each sampled subpopulation. It was hypothesised that (i) genetic diversity is low and genetic structuring is pronounced in isolated populations of the arable plants *A. aestivalis* and *C. regalis* and that (ii) the extent of genetic structuring is related to the degree of habitat fragmentation at the landscape scale.

In chapter 6, the current status quo of activities and programs for arable plant conservation in Germany was analysed by using questionnaires and a literature survey. Questionnaires were sent specifically to institutions or to other stakeholders (e.g. nature and landscape conservation groups, open-air museums, local nature conservation authorities) involved in conservation of important arable plants areas, including establishing and maintaining special conservation sites. In addition to questions regarding data on habitat conditions and arable species present, our survey focussed on suitable cultivation practices and the financial background of the conservation activities. Country-wide data on the history of agri-environmental schemes dedicated to the conservation of arable plants in Germany were also collected. The main aim of this review was to (i) review the status quo of current conservation concepts for the arable flora in order to (ii) develop long-term strategies for conserving typical arable plant vegetation types as Important Plant Areas (WILSON 2007).

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CHAPTER

2

The impact of agricultural intensification and land use change on the European arable flora

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Abstract

The impact of crop management and agricultural land use on the threat status of plants adapted to arable habitats was analysed using data from Red Lists of vascular plants assessed by national experts from 29 European countries. There was a positive relationship between national wheat yields and the numbers of rare, threatened or recently extinct arable plant species in each country. Variance in the relative proportions of species in different threat categories was significantly explained using a combination of fertilizer and herbicide use, with a greater percentage of the variance partitioned to fertilizers. Specialist species adapted to individual crops, such as flax, are among the most threatened. These species have declined across Europe in response to a reduction in the area grown for the crops on which they rely. The increased use of agro-chemicals, especially in central and north-western Europe, has selected against a larger group of species adapted to habitats with intermediate fertility. There is an urgent need to implement successful conservation strategies to arrest the decline of this functionally distinct and increasingly threatened component of the European flora.

Keywords: rare weeds; agri-environment schemes; field margins; conservation; agro-ecosystems

Introduction

Vascular plants adapted to arable habitats are acknowledged to be among the most vulnerable groups in national floras to land-use change, particularly in western European states (KLEIJN & VAN DER VOORT 1997, BAESSLER & KLOTZ 2006, FRIED *et al*. 2009, MEYER *et al*. 2010a). For example, in the UK, of the 30 plant species that have shown the greatest decline between the 1960s and 1990s, 60 percent are associated with arable or other cultivated land (PRESTON *et al*. 2002, STILL 2007) and 24 are listed as priority species on the UK Biodiversity Action Plan (www.ukbap.org.uk). However, the conservation status of arable plants is also increasingly raising concerns in Eastern Europe, which tends to have less intensive agriculture (LOSOSOVÁ 2003, ELIÁS *et al*. 2005, PINKE *et al*. 2009). Concomitant with national extinctions and increased threat to individual species, a reduction in the overall weed seed-bank has also been observed over recent decades in a number of European countries (ROBINSON & SUTHERLAND 2002, SQUIRE *et al*. 2003) as the abundance of common species has also declined (LUTMAN *et al*. 2009).

Because the arable field is characterized by regular disturbance, the flora is dominated by annuals that rely on regular replenishment of the seed-bank for populations to persist. These plants are therefore particularly sensitive to changes in land use or management that reduce the proportion of the seed-bank germinating, seedling survival or the number of seeds per plant returning to the seed-bank (FRECKLETON & WATKINSON 1998). A number of management changes, which impact on different stages of the plant life cycle, have been implicated in the decline of national arable plant populations. These include the shift from spring to autumn sowing, increased plant density and shading by the crop canopy, decreased crop diversity, increasing fertilizer and herbicide use (KLEIJN & VAN DER VOORT 1997, WILSON & KING 2003, MOSS *et al*. 2004), and more efficient seed cleaning (FIRBANK & WATKINSON 1986). While it is likely that there has been an abundance-based mechanism to the response of arable plants to agricultural intensification, with the most infrequent species disappearing first (SUDING *et al*. 2005), there has also been a functional response. That is, changes in management have acted as filters on the arable plant community selecting against species with particular combinations of traits (BOOTH & SWANTON 2002, STORKEY *et al*. 2010). For example, the shift from spring to autumn sowing has reduced the regenerative niche for obligate spring-germinating species, such as *Galeopsis angustifolia* EHRH. ex HOFFMANN and *Valerianella dentata* (L.) POLLICH in the

UK (WILSON & KING 2003), and increased shading by the crop canopy has suppressed short species, such as *Euphorbia exigua* L. and certain *Veronica*-species.

In response to national declines in arable plant diversity, as well as evidence of their value as a resource to higher trophic groups (MARSHALL *et al.* 2003, STORKEY & WESTBURY 2007), a number of European nations have included options within subsidized agri-environment schemes that encourage the arable flora. These include conservation headlands and uncropped cultivated margins (WALKER *et al.* 2007). However, the value of these options to the conservation of arable plants has been constrained by the low uptake by farmers and limited geographical targeting to areas with high arable plant diversity (KLEIJN & SUTHERLAND 2003, STILL 2007, WILSON 2007, BUTLER *et al.* 2009). There is therefore concern that European arable plants, as a group, will continue to decline, particularly as agricultural production in Eastern Europe intensifies. This paper presents data on the threat status of arable plants from 29 European states, based on data from national Red Lists, in combination with local expert knowledge. As well as establishing a benchmark against which future national trends in arable plant diversity can be assessed at a European level, the data are analysed with respect to land-use and agricultural management statistics to address two questions. First, can explanatory variables be identified that predict the ranking of countries in terms of the numbers of arable species that are nationally rare or threatened? And, second, can the relative sensitivity of arable plant species to these variables be quantified?

Material and Methods

Data collection

An agricultural botanist was identified in each of 29 European countries and invited to complete a questionnaire. The experts were first asked to identify vascular plant species that are particularly associated with arable land and classified as recently extinct, critically endangered, endangered or vulnerable on their national Red List. In addition, a second list of species was requested from each country of arable plants that were either identified as 'near threatened' or did not appear on the national Red List but were known to be declining from on-going surveys or expert knowledge. These data were particularly valuable for states where the arable flora was traditionally under-represented in national vegetation surveys, such as in southern Europe, or where formal Red Lists were not available. Finally, information was requested on reasons behind national declines in arable plant diversity and any conservation practices being used to arrest these declines. For three countries from which completed questionnaires were not returned (Norway, Luxemburg and Ireland), the authors consulted the respective national Red Lists to obtain the data. In the case of Ireland, this was supplemented by data from an online consultation of nationally threatened plants hosted by the National Botanic Gardens of Ireland (http://www.botanicgardens.ie).

A database was compiled from completed questionnaires of all the plant species (sub-species were not included) that were identified as arable plants and were on the Red List or considered threatened in any European country. In addition, for each species, the wider European distribution was also obtained from the online Flora Europaea database (http://rbg-web2.rbge.org.uk/FE/fe.html), which was also used to standardize nomenclature. Each cell in the matrix of species x country was then assigned to a category: (1) species present in country but not on Red List or considered threatened, (2) species present in country and considered threatened but not listed as at least vulnerable on Red List, (3) species identified on Red List as vulnerable to critically endangered, and (4) species recently extinct. The relative threat status of each species was assessed using the following scoring system:

$$\text{species score} = \frac{(\text{no countries in category 2}) + (\text{no. no countries in category 3 x 2}) + (\text{no. no countries in category 4 x 3})}{(\text{total no. of countries in which species present})}$$

The following data on land-use and agricultural statistics for each European state in the survey were were obtained from the FAOSTAT database of the UN Food and Agriculture Organization (http://www.fao.org): total land surface area, proportion of land in arable production and wheat yield for 2008 (the latest year for which a full dataset was available; Table 2.1). Wheat was used as a representative crop to indicate the level of intensification as, in a previous analysis of correlates of agri-cultural statistics with farmland European bird populations, it was found to be the most widely grown crop and strongly correlated with the yields of other cereal types (DONALD *et al*. 2006). In addition, data were obtained on the two factors most commonly identified in the questionnaires as driving the national declines in arable plants: increased agro-chemical use and abandonment of arable land.

Table 2.1. Land use statistics for 29 European countries used to explain variance in the national threat status of arable plants. All data for 2008 unless indicated. Herbicide usage data calculated for all active ingredients registered for use on cereals. (-) data not available.

Country	Latitude	Land Area (1000 Ha)	Proportion arable land	Loss of arable land*	Wheat yield (t/ha)	Wheat Fertilizer (kg N/ha)	Herbicide a.i. weight (1000 kg)	Cereal area (1000 ha)	Herbicide load (kg/ha)	Number of species present in country	Number of species threatened/rare
Austria▪	47.3	8387	0.16	-0.21	5.69	97	336	845	0.40	169	102
Belgium▪	50.8	3053	0.28	-0.11	8.76	155	360	350	1.03	152	75
Bulgaria	43.0	11100	0.28	-1.98	4.17	60	128	1711	0.07	165	15
Croatia	45.2	5659	0.15	-1.75	5.48	-	154	561	0.28	182	45
Czech Republic	49.8	7887	0.38	-0.27	5.77	155	845	1561	0.54	166	84
Denmark▪	56.0	4309	0.56	-0.21	7.86	118	831	1513	0.55	115	56
Estonia	59.0	4523	0.13	-3.16	3.18	80	-	309	-	90	22
Finland	64.0	33842	0.07	0.14	3.64	85	706	1194	0.59	58	15
France▪	46.0	54919	0.33	0.06	7.10	161	4978	9618	0.52	187	69
Germany▪	51.0	35711	0.33	0.07	8.09	150	5460	7038	0.78	183	131
Greece	39.0	13196	0.16	-2.04	2.95	55	168	1189	0.14	154	13
Hungary▪	47.0	9303	0.49	-0.38	4.98	70	321	2973	0.11	168	38
Ireland	53.0	7028	0.16	0.91	9.06	150	-	314	-	64	28
Italy	42.8	30134	0.24	-0.96	3.87	85	606	4038	0.15	183	18
Latvia	57.0	6456	0.18	-1.14	3.86	75	118**	544	0.22	90	27
Lithuania	56.0	6530	0.29	-3.36	4.27	91	241**	1022	0.24	90	17
Luxemburg	49.8	259	0.24	-0.24	6.66	-	-	31	-	145	68
Netherlands▪	52.3	4154	0.26	1.75	8.73	199	267	236	1.13	131	49
Norway	62.0	32378	0.03	-0.69	4.85	120	-	309	-	74	25
Poland▪	52.0	31268	0.40	-1.10	4.07	91	2670	8599	0.31	150	17
Portugal▪	39.5	9209	0.11	-3.66	2.30	90	122	364	0.33	125	1
Romania	46.0	23839	0.37	-0.47	3.42	40	443	5182	0.09	168	10
Serbia	44.0	8836	0.37	-	4.30	-	411	1905	0.22	185	16
Slovakia	48.7	4904	0.28	-1.01	4.87	85	235	799	0.29	167	63
Slovenia	46.0	2027	0.09	-0.60	4.53	90	42	107	0.39	185	56
Spain	40.0	50537	0.25	-1.07	3.25	85	2545	6685	0.38	169	11
Sweden▪	62.0	45030	0.06	-0.43	6.11	135	338	1078	0.31	107	33
Switzerland▪	47.0	4128	0.10	-0.16	6.01	140	268	156	1.71	176	137
United Kingdom▪	54.0	24361	0.25	-0.19	8.28	194	4372	3272	1.34	127	51

▪Subsidised schemes available targeted at arable flora - *Calculated as annual change in arable land area as percentage of 1993 baseline from linear regression fitted to years 1993 – 2008 (only 2000 – 2008 data available for Belgium and Luxemberg). - **2009 data

Data on the rate of nitrogen fertilizer (kg ha^{-1}) used in wheat in 2008 across Europe was obtained from a database held by Fertilizers Europe (previously the European Fertilizer Manufacturers Association; www.fertilizerseurope.com). There is not an equivalent common metric for herbicide inputs as rates will differ according to the products used and countries cannot strictly be compared like-for-like. However, by using the weight of all active ingredients used in cereals in 2008, this effect was minimized as it included a diversity of products. These data were obtained from a commercial database of herbicide usage across Europe (AmisGlobal, www.amisglobal.com) and used to calculate a herbicide 'load' for each country by dividing by the area of cereals grown obtained from the FAOSTAT database. The change in the amount of arable land in each country was calculated using data from FAOSTAT on arable areas between 1993 (the first year with data on all countries except Belgium and Luxemburg) and 2008. The amount of arable land in each year was expressed as a proportion of the 1993 baseline and a linear regression fitted to the data to calculate the slope or annual change.

Statistical analysis

The completion of the questionnaire involved a degree of subjectivity in identifying which species on national Red Lists were particularly associated with arable habitats. To account for this variability in the assessment of habitat preference, the database was filtered to only include species that were identified as rare or threatened arable plants in at least three countries. This short list was used to analyse the relationship of land use and management with the proportion of the species present in each country that were identified as rare or threatened. For all subsets regression using generalized linear models (GLMs) was used to identify the model that explained the maximum variability in the proportion of rare or threatened species using only explanatory variables with $p < 0.05$. As well as total land area, proportion of arable land and wheat yield, the average latitude of each country was also included in the analysis. Because fertilizer and herbicide use were both significantly positively correlated with wheat yield ($r = 0.86$, $p < 0.001$ and $r = 0.67$, $p < 0.001$, respectively) and with each other ($r = 0.78$, $p < 0.001$), they were not included in the GLM. Using binomial distribution with a logit link function allowed the variability in the total number of species present in each country (ranging from 58 in Finland to 187 in France) to be accounted for. As opposed to a step-wise approach, all subset regression analysed all possible combinations of explanatory variables, using the adjusted R^2 and Mallows C_p as criteria for comparing models.

The effect of fertilizer and herbicide use on the numbers of species in different threat categories was analysed separately using variance partitioning in a redundancy analysis (RDA) using CANOCO v. 4.5 software (LEPŠ & ŠMILAUER 2003). This enabled the proportion of variance explained by collinear variables to be quantified. The counts of species in each category were log-transformed and standardized by country, to construct a similarity matrix of relative proportions, and input into an RDA with fertilizer dose and herbicide load as explanatory variables. The variance between the countries that could be accounted for by herbicide or fertilizers alone was then tested by constraining the ordination using each variable in turn while including the other as a covariate and comparing with the analysis using both as explanatory variables. Data on fertilizers were not available for Croatia, Luxemburg and Serbia, and herbicide data were not available for the small markets of Estonia, Ireland, Luxemburg and Norway. In addition, only 2009 data were available on herbicides for Latvia and Lithuania. All of these countries were excluded from the RDA, leaving a total of 21.

Finally, a hypergeometric probability function was used to test whether any plant families were disproportionately represented in the short list of rare or threatened arable plants (PILGRIM *et al*. 2004). The function calculates the probability of a number of positive results from sampling without replacement using four parameters: N, size of population; K, number of items with the desired characteristic in the population; n, number of samples drawn; and x, number of successes in the sample. The total number of species present in the Flora Europaea (excluding Pteridophytes and Gymnosperms), 10835, was input as N. For each family represented in the short list of rare or threatened arable plants, the total number of species in the Flora Europaea was obtained (WEBB 1978), n. K was calculated as the total number of species in the Flora Europaea that were on the rare or threatened arable plant list and x as the number in the family being analysed that were rare or threatened.

Results

The database of rare or threatened arable plants contained 582 species. Of these, 193 species were either on the national Red Data Lists or considered threatened in at least three of the 29 European countries from which questionnaires were returned. The most common families represented in this short list were the Caryophyllaceae, Asteraceae and Brassicaceae, of which the Caryophyllaceae and Brassicaceae were significantly over-represented when compared with the European flora as a whole. This was also the case for a number of other families (Figure 2.1), particularly the Papaveraceae. The most common genera were *Veronica* (eight species), *Silene* and *Bromus* (both six species). The factors most commonly identified as causing national declines in arable floras were increased use of agro-chemicals and the abandonment of marginal land, mentioned in 21 and 14 questionnaires, respectively. The latter was especially associated with Eastern European countries. Decreasing crop diversity was the next most commonly cited factor (in ten questionnaires), with particular emphasis placed on the decline of rye (*Secale cereale* L.) and flax (*Linum usitatissimum* L.) as major crops. Less commonly cited factors included irrigation, which was identified in the decline of species adapted to dry-land agriculture in Spain and Portugal, and loss of stubbles in the Czech Republic, with implications for species such as *Stachys annua* L.

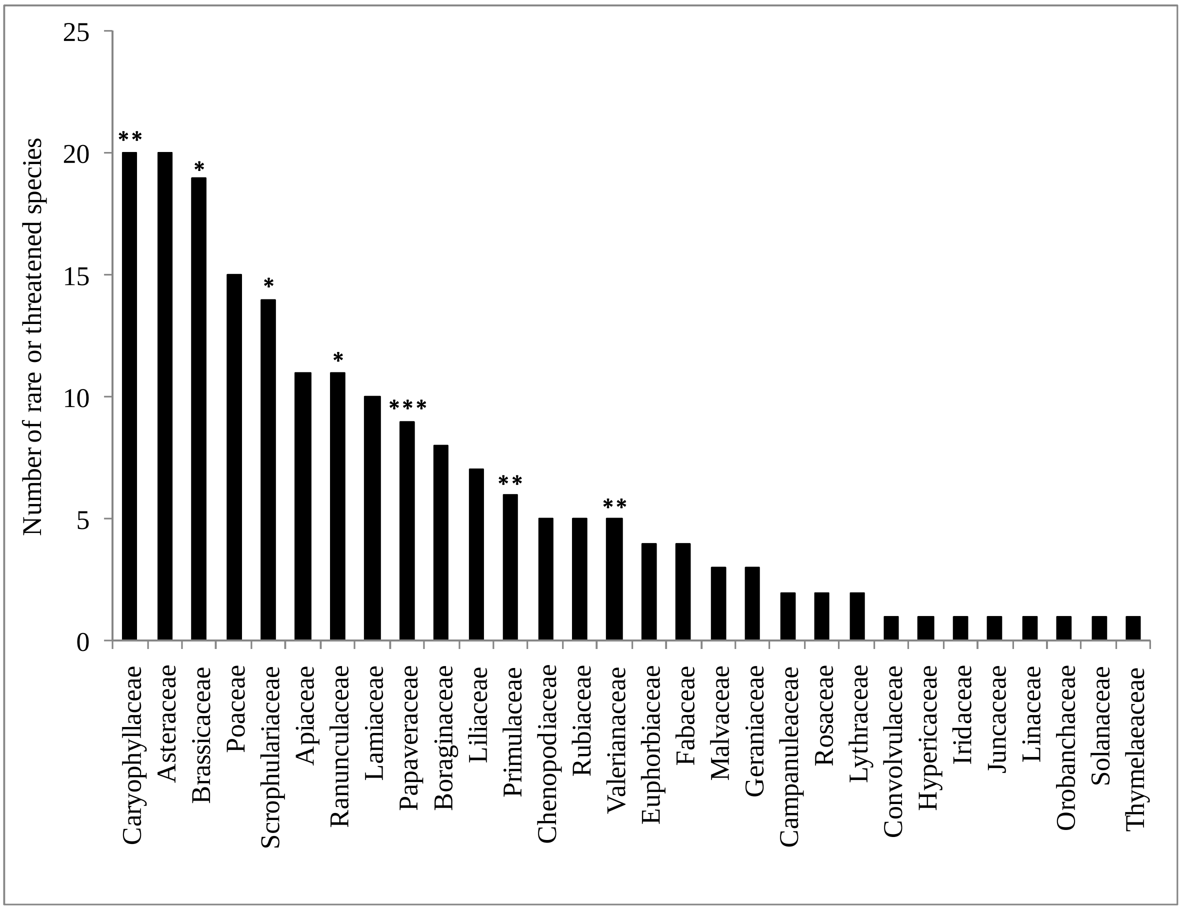

Figure 2.1. Numbers of species from each family represented in the short list of rare or threatened European arable plants (cited in questionnaires from at least three countries). The probability of the over-representation of each family in the list when compared with the European flora as a whole, calculated using a hypergeometric probability distribution, is indicated: *p < 0.05, **p < 0.01, ***p < 0.001.

The comparison of countries in terms of the proportion of species on the short list that were present in the country and identified as rare, threatened or extinct revealed a concentration of countries in central or north-west Europe with higher numbers of species (Figure 2.2). The GLM that explained the most variance between countries was wheat yield ($R^2 = 46.5$, $C_p = 2.2$, $p < 0.001$), which had a positive relationship with the proportion of nationally rare or threatened arable plants (Figure 2.3). The model was not significantly improved by the inclusion of any other explanatory variables. The only other variable that had a significant effect was loss of arable land ($p = 0.001$ when included as the only explanatory variable). However, this was negatively correlated with the proportion of nationally rare or threatened arable plants, indicating that intensification of crop production is the main threat to this group of plants. This conclusion was supported by the results of the RDA. When both fertilizer dose and herbicide load were included in the constrained analysis, 33.4 per cent of the total variance between countries in the relative proportions of species in the different threat categories was explained ($p = 0.004$; Figure 2.4). When the effect of the two variables were analysed separately, including the other as a covariate, 8 per cent of the total variance was able to be partitioned to fertilizers alone and 2.8 per cent to herbicides alone. The close correlation between the two variables meant that the remaining 22.6 per cent could not be partitioned to either.

Figure 2.2. Comparison of European countries in terms of the proportion of arable plant species occurring in the country (using the short list of 193) that were identified as rare or threatened.

Figure 2.3. Relationship between national wheat yields and the proportion of arable plant species occurring in the country (using the short list of 193) that were identified as rare or threatened (y= 0.073x – 0.081, R^2=0.51).

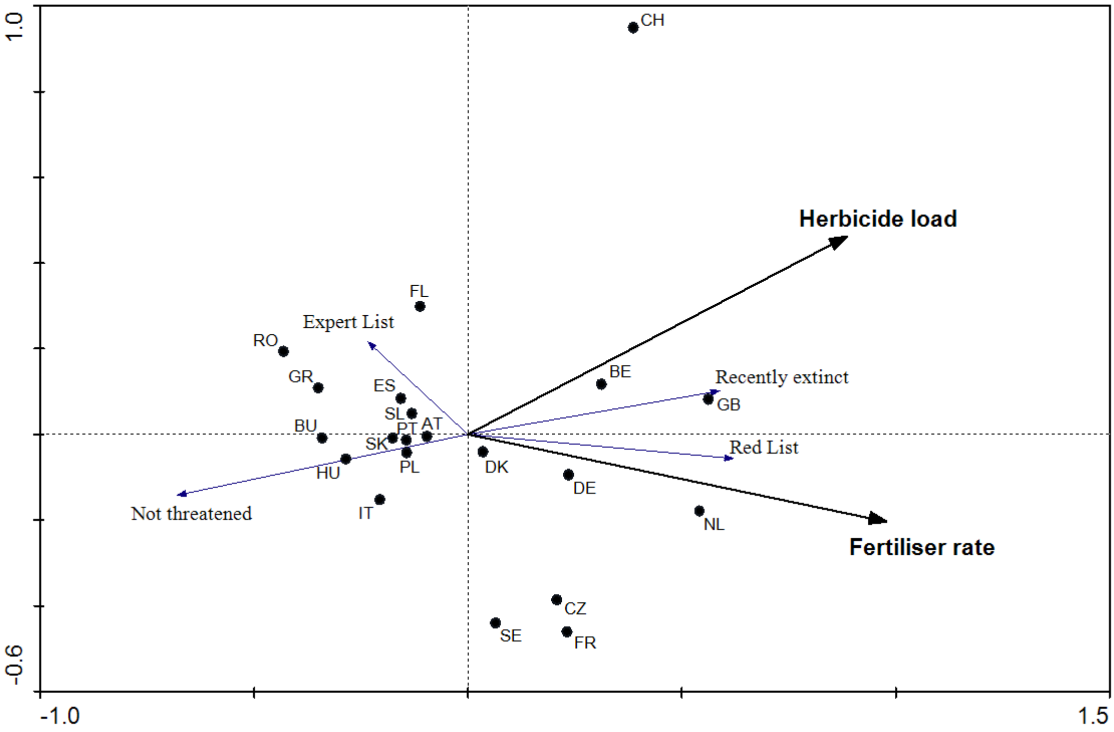

Figure 2.4. RDA analysis using fertilizer dose and herbicide load as explanatory variables on 23 countries where comparable data were available.

Table 2.2. Species in short list of rare or threatened European arable plants (cited in questionnaires from at least three countries) ordered according to the species score. Only the top 48 species are presented (representing the upper quartile of the list).

Species	Family	Countries in which species is present	Countries in which species is rare, threatened or recently extinct	Score
Bromus grossus	Poaceae	3	3	2.00
Silene linicola	Caryophyllaceae	6	4	1.83
Logfia neglecta	Asteraceae	5	3	1.80
Cuscuta epilinum	Convolvulaceae	25	16	1.64
Agrostemma githago	Caryophyllaceae	29	25	1.62
Adonis flammea	Ranunculaceae	18	16	1.61
Spergularia segetalis	Caryophyllaceae	9	5	1.56
Adonis aestivalis	Ranunculaceae	19	16	1.53
Scandix pecten-veneris	Apiaceae	24	17	1.46
Lolium temulentum	Poaceae	29	21	1.45
Camelina alyssum	Brassicaceae	25	16	1.44
Vaccaria pyramidata	Caryophyllaceae	23	16	1.35
Linaria arvensis	Scrophulariaceae	18	9	1.33
Conringia orientalis	Brassicaceae	20	13	1.25
Lolium remotum	Poaceae	28	14	1.21
Asperula arvensis	Rubiaceae	20	11	1.20
Bupleurum rotundifolium	Apiaceae	23	15	1.17
Caucalis platycarpos	Apiaceae	20	12	1.15
Bromus secalinus	Poaceae	28	19	1.14
Galium tricornutum	Rubiaceae	23	13	1.13
Turgenia latifolia	Apiaceae	20	10	1.10
Ajuga chamaepitys	Lamiaceae	21	12	1.10
Arnoseris minima	Asteraceae	23	12	1.09
Androsace maxima	Primulaceae	15	7	1.07
Adonis annua	Ranunculaceae	15	9	1.07
Legousia speculum-veneris	Campanulaceae	17	11	1.06
Neslia paniculata	Brassicaceae	24	13	1.04
Legousia hybrida	Campanulaceae	16	9	1.00
Roemeria hybrida	Papaveraceae	5	3	1.00
Thymelaea passerina	Thymelaeaceae	19	10	1.00
Misopates orontium	Scrophulariaceae	24	12	0.96
Valerianella dentata	Valerianaceae	23	12	0.96
Nigella arvensis	Ranunculaceae	18	9	0.94
Adonis microcarpa	Ranunculaceae	9	4	0.89
Melampyrum arvense	Scrophulariaceae	25	13	0.88
Bifora radians	Apiaceae	15	8	0.87
Filago pyramidata	Asteraceae	15	6	0.87
Valerianella rimosa	Valerianaceae	22	10	0.86
Papaver argemone	Papaveraceae	27	13	0.85
Lathyrus aphaca	Fabaceae	19	8	0.84
Centaurea cyanus	Asteraceae	29	14	0.83
Anagallis minima	Primulaceae	29	13	0.83
Ranunculus arvensis	Ranunculaceae	28	12	0.82
Gagea arvensis	Liliaceae	21	10	0.81
Silene noctiflora	Caryophyllaceae	26	13	0.81
Hypochoeris glabra	Asteraceae	28	10	0.79
Kickxia elatine	Scrophulariaceae	23	10	0.78
Bromus arvensis	Poaceae	27	13	0.78

Discussion

The analysis of the threat status of European arable plants provides further evidence of the trend, established in numerous other studies, of the negative impact of increasing intensification of crop production on the biodiversity of agro-ecosystems (KREBS *et al.* 1999, CHAMBERLAIN *et al.* 2000, ROBINSON & SUTHERLAND 2002, FIRBANK *et al.* 2008, STOATE *et al.* 2009). The ranking of species according to their score (Table 2.2) showed that those that are specialized to a single crop are particularly vulnerable, including some that have coevolved to mimic morphological or phenological characteristics of the crop (HARLAN 1965, BAKER 1974, BARRETT 1983). These include the flax specialists *Cuscuta epilinum* L. and *Silene linicola* C. C. GMELIN, and cereal specialists including *Bromus secalinus* L. and *Lolium remotum* SCHRANK in rye, or *Bromus grossus* DESF. ex DC. in spelt. A number of these species, including *S. linicola* and *B. grossus*, are anecophytes with no known natural habitats outside the cultivated field and are endemic to Europe. Several other specific factors have been identified in the literature as being responsible for the decline of individual species, including improved seed cleaning for *Agrostemma githago* L. (FIRBANK 1988), the loss of stubbles for *Stachys annua* L. (PINKE & PÁL 2009) and the drainage of wet depressions that are typically colonized by arable plants with higher moisture demand. These species have tended to decline or are already extinct across Europe, irrespective of the level of intensification, as a result of, for example, the reduction in the area of flax grown or the use of cleaner crop seed.

However, of potentially greater concern for arable plant biodiversity at the national and continental scale is the more general trend towards the intensification of agriculture with the consequent biotic homogenization of the landscape (BENTON *et al.* 2003, SMART *et al.* 2006). The results presented in this paper support the conclusions of previous studies that eutrophication, either through atmospheric nitrogen deposition or fertilizers, is one of the major drivers of decreasing habitat heterogeneity and species loss (KLEIJN *et al.* 2009, MASKELL *et al.* 2010, STEVENS *et al.* 2010), and that declining species are spread disproportionately across plant families, potentially contributing to the phylogenetic shift in the European flora (WINTER *et al.* 2009). Although greater variance in the threat status of arable plants between countries could be attributed to fertilizers alone as opposed to herbicides when they were included in the same analysis, it was not possible to fully separate the effects of the two factors. It is likely that they have acted in parallel, with herbicides reducing the overall niche for sustainable arable plant populations in the context of a functional filtering of species through increased fertility (SUDING *et al.* 2005). As well as in-field management drivers, at a regional and local scale, landscape factors such as field size, management of field margins and landscape complexity have also been shown to influence arable plant diversity (GABRIEL *et al.* 2005, BAESSLER & KLOTZ 2006, MARSHALL, 2009). It is likely that countries with less intensive agriculture would also have smaller fields and more complex landscapes, although it was not possible to obtain data on these finer-scale metrics with sufficient coverage to include them in the models used in this study. However, loss of field boundaries was identified as a driver of arable plant declines in seven questionnaires and field margins are an important refuge for declining arable plant species (FRIED *et al.* 2009). A consideration of the landscape context of conservation strategies will therefore be an important consideration at the regional scale.

As discussed above, the arable plants specialized to individual crops appear to be the most sensitive to changes in cropping patterns. If these species are removed from the list, the top of the ranking of species (Table 2.2) is then dominated by species with a similar ecological strategy, reflected in a relatively short stature and/or a large seed, indicating a specific ecological response to the drivers of disturbance and fertility (WESTOBY 1998). Increased seed size has implications for colonizing ability, being able to establish in less favourable environments (TURNBULL *et al.* 2004) and competitive ability, particularly for below-ground resources (FRECKLETON & WATKINSON 2001, STORKEY *et al.* 2010). Because of the allometric relationship between mature biomass and seed production (SUGIYAMA & BAZZAZ 1998), species with a larger seed will also be less fecund, making them less able to buffer the seedling mortality from herbicides. In addition, seed size has also been negatively correlated with persistence in the seed-bank (THOMPSON *et al.* 1993), further selecting against these species as they are less able to exploit ephemeral opportunities for growth related to failures of weed control or crop rotation. A short stature will result in a low competitive ability in dense crop canopies, where increasing fertilizer use means nutrients are non-limiting and light is the main resource limiting growth (GAUDET & KEDDY 1988, KLEIJN & VAN DER VOORT 1997). As opposed to more characteristically stress-tolerant ruderals (sensu GRIME *et al.* 1997), which may continue to persist in other disturbed, less productive environments such as coastal areas, species with a combination of short stature and large seed have been found to be adapted to habitats with intermediate fertility (STORKEY *et al.* 2010) - habitats that are declining most rapidly in response to increasing eutrophication of landscapes (SUDING *et al.* 2005).

Any continent-wide analysis of the threat status of arable plants will be limited by the fact that the procedure of compiling Red Lists does not follow a uniform protocol across different countries but involves partly subjective assessment steps by experienced botanists or state agencies that may differ. This may partly explain the very high proportions of threatened or rare species reported for Switzerland and Germany, in contrast to countries such as The Netherlands and Belgium with similar floras and comparable levels of intensification. These former countries have particularly sensitive Red List criteria, where all species that have shown recent population declines in a significant part of the country are included. However, we expect this kind of bias to be restricted to a few central European states, as the Red List criteria are more similar in other countries.

In contrast to other taxa adapted to agro-ecosystems that have suffered declines in response to agricultural intensification, particularly birds (DONALD *et al*. 2006, BUTLER *et al*. 2010), the rationale behind the conservation of arable plants is less straight-forward. This group of plants is traditionally viewed as an impediment to crop production, and a number of the species on the list compiled in this study would at one time have been serious weeds. However, two reasons can be identified to argue for the preservation of these floral elements. First, the similarity in the autecology of the most vulnerable species indicates that the factors identified in this study are systematically removing a functionally distinct component of the fabric of agro-ecosystems. Many of these plants are now restricted to arable habitats, and continuing declines in cropped fields will therefore result in a loss of plant functional diversity at a national and continental scale, with possible consequences for the specialist fauna they support (GIBSON *et al*. 2006). Second, the decline in diversity of arable plants has happened in parallel with a decrease in total abundance of plant resources in the agro-ecosystem (ROBINSON & SUTHERLAND 2002, POTTS *et al*. 2009) implicated in the decline of invertebrates and birds (CHAMBERLAIN *et al*. 2000, MARSHALL *et al*. 2003). The loss of arable plant species from the environment is therefore indicative of a wider degradation of the agro-ecosystem. Any further erosion of plant functional diversity in the agricultural landscapes of Europe may also limit the adaptability of these ecosystems to future changes in climate or land management.

Conclusion

The study has identified a suite of plant species that are already extinct or particularly vulnerable at a European scale to the increasing intensification of agricultural production. Many of these plants are still relatively common in countries where agro-chemical inputs are modest compared with those with the highest wheat yields, but these countries have still observed declines in floral diversity in response to changes in the types of crops grown, abandonment of arable land or re-intensification of former marginal arable land for the production of biofuels/bioenergy (AMMERMANN 2008). We contend that threatened arable floras have an intrinsic ecological value that justifies measures to preserve them, and the habitats with which they are associated, in the agricultural landscape. This will inevitably involve establishing refuges on marginal land, generally characterized by less-fertile soils where crop competition and agro-chemical inputs are reduced (MEYER *et al*. 2010b). Field margins in intensively cultivated landscapes, subsidized by national agri-environment schemes, will have an important role to play in this regard (MARSHALL 2002, FRIED *et al*. 2009). However, agri-environment options targeted at arable plants tend to be unpopular with farmers, and field margins are, by nature, ephemeral, and vulnerable to changes in subsidies and market forces. More extensive projects that identify the nationally important areas for arable plant communities and implement measures to conserve them on a landscape scale are therefore more likely to deliver a long-term solution (WILSON 2007, MEYER *et al*. 2010a).

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CHAPTER

3

Massive changes in Central Europe's arable plant communities since the 1950s/60s

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Abstract

In much of Europe, the intensification of cultivation practices since the mid-20th century has greatly increased crop yields but, at the same time, caused dramatic biodiversity losses in arable fields. We investigated the extent of these losses at the plant community level in ten regions in Central Germany with different soil/climate conditions and a wide range of arable plant communities.

We compared plant community inventory and composition of arable fields in the 1950s/early 1960s before the onset of agricultural industrialisation with the situation in 2009 by re-sampling 392 arable fields in the interior and at the margin. Community inventory of historical and recent fields was compared by manual classification, species composition by Detrended Correspondence Analysis (DCA), and species richness by ANOVA.

In most recent arable fields we found severely impoverished vegetation, especially in character species of lower syntaxa (associations, alliances). Only 5% of the recent relevés were assignable at the association level, and ten out of 16 associations recorded in the historical relevés could no longer be found. Instead, 76% of the recent relevés could only be classified at the level of the class Stellarietea mediae, and 7% were not assignable to any class. Although the impoverishment of vegetation was slightly less pronounced at the field margins (where 24% of the recent relevés could be assigned to associations), they could not compensate for the dramatic overall biodiversity loss. The present-day arable plant communities in the area are species-poor, consisting of common, often herbicide-tolerant generalist species, with no clear preference for cereal vs. root crops, autumn- vs. spring-sown crops, or base-rich vs. base-poor soils. This is maybe the first study which demonstrates the decline of an entire vegetation class over a large area. The present classification system for arable plant vegetation in Central Europe needs to be amended to accommodate present-day vegetation.

Keywords: agricultural intensification; arable weed communities; Germany; residual plant communities; long-term shifts; plant community turnover; relevés; segetal vegetation; species richness; Stellarietea mediae

Introduction

Since the Neolithic, a specialised flora and fauna has colonised Central Europe's agricultural fields and adapted to the conditions of low-intensity agriculture (EWALD & KLAUS 2009). Depending on the cultivation regime as well as edaphic and climatic conditions, arable vegetation has been classified and formally described as phytosociological communities, arranged in a hierarchical system (HÜPPE & HOFMEISTER 1990). This system is used for various objectives including basic ecological research, agronomic bioindication and conservation initiatives (HOFMEISTER & GARVE 2006, BELLANGER *et al*. 2012). Today, area of arable land in Germany amounts to 35% of its territory (BMELV 2010) indicating the relevance for biodiversity conservation.

The close dependence on management renders arable plant communities sensitive to land use intensification. This has led to structurally impoverished agricultural landscapes and a severe decrease in biodiversity (GABRIEL *et al*. 2005, ROSCHEWITZ *et al*. 2005). Intensification is ongoing due to further expansion of field area for e.g. bioenergy crop production (DAUBER *et al*. 2010), perpetuating the decline of taxonomic as well as functional diversity (TSCHARNTKE *et al*. 2005, KLEIJN *et al*. 2009, FRIED *et al*. 2010). Currently, about 120 of the approximately 350 arable plant taxa in Germany are considered endangered (HOFMEISTER & GARVE 2006, ELLENBERG & LEUSCHNER 2010), and arable plant communities now rank among the most threatened vegetation types (RENNWALD 2002, HILBIG 2007, MEYER *et al*. 2008).

In Europe, changes and diversity loss in arable fields were found in many studies (e.g. RIES 1992, STOATE *et al*. 2001, POTTS *et al*. 2010, STORKEY *et al*. 2012). In Germany this process has been observed since the 1950s/60s (GRADMANN 1950, TÜXEN 1962) and numerous studies examined the often dramatic species losses in arable vegetation (e.g. ALBRECHT 1989, HILBIG & BACHTHALER 1992, BAESSLER & KLOTZ 2006, KOHLBRECHER *et al*. 2012). Several reports describe changes in the arable flora from a local or regional perspective, and almost all of them compared former and recent vegetation of different fields. Very rarely have authors re-sampled the same plots as in the historical study (permanent plot design) or the same fields (semi-permanent plot design; e.g. SUTCLIFFE & KAY 2000, CONN *et al*. 2011). Large-scale studies on several hundreds of sites covering different environmental conditions are in generally rare (but see ALBRECHT 1995 and MÁJEKOVÁ *et al*. 2010 for two exceptions).

Until the 1950s, agriculture in much of Europe was based on a low input of external resources. This changed dramatically in the 1950s and early 1960s (e.g. BAUERKÄMPER 2004, KIRÁLY *et al*. 2006), when new agricultural practices such as herbicide application came into general use (SALESBURY 1961). In the same period, field size increased considerably leading to a reduction of field margins as potential refugia for arable plants (FRIED *et al*. 2009). Most associations and alliances of arable plant communities were described before agricultural practices were considerably transformed i.e. between 1930 and 1960 (RENNWALD 2002), and as a consequence, BRUN-HOOL (1966) predicted and described fragmentary arable plant assemblages as residual communities ('*Restgesellschaften*') in the mid-1960s.

In the present study, we examine shifts in arable plant communities on (semi-)permanent plots during the last five to six decades, thus covering the most recent period of agricultural intensification. Working in different regions and on different substrates, we tested the hypotheses that (i) agricultural intensification during the past 60 years has resulted in a decline in species richness and in a fundamental change in species composition; and (ii) that diversity loss in arable fields is not merely a displacement of species from the field interior to its margin. We also tested BRUN-HOOL'S (1966) prediction that (iii) species impoverishment is disproportionate; diagnostic species of the lower ranks of syntaxa (associations, alliances), considered as specialists, disappear more rapidly than those of higher-rank syntaxa (orders, classes) or other generalist species. We further assessed (iv) if the plant communities currently found in arable fields are simply the result of a degradation along the hierarchical syntaxonomic system (association → alliance residual → order residual → class residual) or represent a complete new combination of species.

Materials and Methods

Study area

This study was conducted in ten Central German regions extending about 335 km east-west and 240 km north-south, and located in four German Länder characterised by sub-oceanic (Lower-Saxony) to sub-continental (Saxony-Anhalt, Brandenburg and Thuringia) climatic conditions (Table 3.1). The mean annual air temperature at the sites ranges from 7.1° C to 9.3° C, and the mean annual precipitation from 475 mm to 727 mm (DEUTSCHER WETTERDIENST 2012; www.dwd.de). Four of the ten regions were dominated by sandy, three by calcareous and another three by loamy soils.

Sampling design

We retrieved historical vegetation records from the Reinhold Tüxen Archive (Hanover), the archives of the Herbarium Haussknecht at the University of Jena and the Department of Geobotany at the University of Halle, as well as from private relevé collections (see Table 3.1 and Acknowledgements). A total of 392 relevés from the period of 1951 to 1962 were selected and their locations identified at the level of field parcels using maps and locality descriptions provided in the original publications/manuscripts or on the relevé sheets. Re-sampling on the same field parcels was carried out in summer 2009, as with the historical relevés just before harvest when most arable plants are fully developed.

All historical records had been sampled in the field interiors. Therefore, we placed our plots at least 10 m from the field margin, and an additional plot at the field margin (up to the most marginal crop row). Recent samples were taken on nested plots of 25, 50 and 100 m² but for comparison of historical and recent plots the size of the given historical plot was decisive (mean plot size 65 m²). Relevés were sampled using the method of BRAUN-BLANQUET (1964) as in the 1950s/60s. All vascular plant species were recorded but crop species were excluded from further analysis. Nomenclature of species follows JÄGER (2011) and nomenclature of syntaxa is according to HÜPPE & HOFMEISTER (1990).

Data processing and statistical analysis

Relevés were stored in a TURBOVEG database (HENNEKENS & SCHAMINÉE 2001) and plant synonyms were merged (JANSEN & DENGLER 2008). In a few cases, plants could be determined to the genus or family level only. These were included in species richness analyses but not in the multivariate analysis of species composition. For the latter, we applied Detrended Correspondence Analysis (DCA), as suggested by a relatively high beta-diversity (gradient length on first DCA axis: 5.2 s.d. units, see MCCUNE *et al*. 2002). To calculate the median cover of each species in the historical and recent relevé subsets, the Braun-Blanquet classes were replaced by ordinal-transformed cover-abundance percentages, i.e. the median of the respective cover class with r=0.1%, +=0.2%, 1=2.5%, 2m=5%, 2a=10%, 2=15%, 2b=20%, 3=37.5%, 4=62.5%, and 5=87.5%. We tested differences in species richness between historical and recent plots separately for each community (see below) with ANOVA after ensuring normal distribution and equal variance by visually inspecting the distribution of the residuals (QUINN & KEOUGH 2002). Although multiple testing involves the risk of type-1-error inflation, we nonetheless report the uncorrected significances for the ANOVAs of the individual communities, which may

Table 3.1. Details of the ten study areas on three different soil substrates, including the number of arable fields surveyed in the 1950s/1960s and in 2009.

Area	Federal state	Coordinates (WGS 1984)	Mean annual precipitation (mm)	Mean annual temperature (° C)	Elevation (m a.s.l.)	Prevailing substrate	Year of historical records	No. of repeated relevés	Source of historical records (all unpublished)
Reese	Lower Saxony	N 52°34', E 09°03'	654	9.1	25-40	sand	1951	31	E. Preising, 1952, R. Tüxen Archive Hanover
Berkhof	Lower Saxony	N 52°36', E 09°43'	673	8.9	25-40	sand	1955	38	W. Jahns, 1957, R. Tüxen Archive Hanover
Nedlitz	Saxony-Anhalt	N 52°03', E 12°16'	565	8.8	90-120	sand	1956	46	H. Jage (Kemberg)
Luckau	Brandenburg	N 51°51', E 13°45'	560	8.5	40-125	sand	1960/61	39	W. Fischer, H.-D. Krausch & H. Illig (Luckau)
Göttingen	Lower Saxony	N 51°28', E 09°54'	727	8.7	160-225	loam	1960	37	W. Ernsting, 1961, R. Tüxen Archive Hanover
Erzhausen	Lower Saxony	N 51°53', E 09°55'	644	8.8	100-330	loam	1959	45	Anonymous, R. Tüxen Archive Hanover
Halle/Saale	Saxony-Anhalt	N 51°32', E 11°54'	475	9.1	75-140	loam	1958	40	G. Plass, 1960, Herbarium University Halle/Saale
Hachelbich	Thuringia	N 51°20', E 10°55'	542	8.3	180-320	limestone	1956/57	39	E.M. Wiedenroth, 1960, Herbarium Haussknecht Jena
Plaue	Thuringia	N 50°47', E 10°54'	487	7.1	295-520	limestone	1959-62	37	W. Hilbig, Herbarium Haussknecht Jena
Saaletal	Thuringia	N 50°58', E 11°40'	590	9.3	170-350	limestone	1959-61	40	W. Hilbig, Herbarium Haussknecht Jena

Climate data from German National Meteorological Service, DWD, based on the reference period 1961–1990.

serve as additional information in an exploratory study (ROBACK & ASKINS 2005). *Post hoc* comparisons within communities were, however, calculated with Tukey tests. All standard statistical analyses were conducted using SPSS 15; multivariate analyses were run with PC-ORD (MCCUNE & MEFFORD 2011).

Allocation of relevés to syntaxa

Our syntaxonomic reference system places the vegetation of arable fields within the class Stellarietea mediae (see Table 3.2). Impoverished arable vegetation, treated as 'residual communities', was allocated at the level of alliance, order or class, respectively. In total, our study comprises 16 out of the 20 arable plant associations in Germany listed by HÜPPE & HOFMEISTER (1990).

Table 3.2. Hierarchical reference system and ecology of arable plant communities.

- **Class**: Stellarietea mediae
  - **Order 1**: Sperguletalia arvensis: on base-poor soils
    - **Alliance 1**: Aperion spicae-venti: autumn-sown crops on base-poor and sandy soils (Ass. 1-4; see Table 3.3)
    - **Alliance 2**: Digitario-Setarion: spring-sown crops on more or less base-poor sandy soils (Ass. 5-10)
    - **Alliance 3**: Polygono-Chenopodion polyspermi: spring-sown crops on loamy soils (Ass. 11)
  - **Order 2**: Papaveretalia rhoeadis: on base-rich soils
    - **Alliance 4**: Caucalidion platycarpi: autumn sown cereal crops (Ass. 12-13)
    - **Alliance 5**: Fumario-Euphorbion: root crops or spring-sown cereals (Ass. 14-16)

Relevés were allocated manually because numerical approaches proved difficult for classification of residual communities at different ranks. Criteria were based on diagnostic species following the coherent classification system of crop vegetation in Germany by HÜPPE & HOFMEISTER (1990), slightly modified by SCHUBERT *et al.* (2001). Relevés were assigned to an association if at least one character species of the given association (AC) was present, and if at least 10% of the alliance character species (VC) and order character species (OC) were present. In rare ambiguous cases, relevés were assigned to that association with which they shared most AC species. If even this did not yield a clear result, the cover of diagnostic species was assessed as a supplementary criterion. In the absence of association character species, the allocation of relevés to a given alliance was based on the presence of at least 5% of the VC species and ≥ 5% of the OC species. Allocation of relevés to a given order required the occurrence of ≥ 5% of the listed OC species. Relevés were assigned at the level of the class if none of the above criteria was met and if at least one character species of this class (KC) was present; otherwise relevés were considered as 'non-assignable'.

Results

Changes in overall species richness and vegetation composition

The total data set comprised 466 taxa excluding taxa identified to the genus or family level only, but including crop volunteers. In the 1950s/60s, a total of 308 species were recorded, while 379 species were found in 2009; in the field interiors 235, and at the field margins 361. 222 species occurred in both inventories; 86 were restricted to the historic dataset and 158 to the recent dataset.

Plant community composition largely differed between the two sampling periods along DCA axis 2 which was strongly correlated to crop cover and height (Figure 3.1). Field interiors and margins in the 2009 data were neither differentiated along axis 1 nor axis 2. The first axis separated the historical records from sandy, loamy and lime stone substrates (data not shown). The recent relevés showed a reduced variation along axis 1.

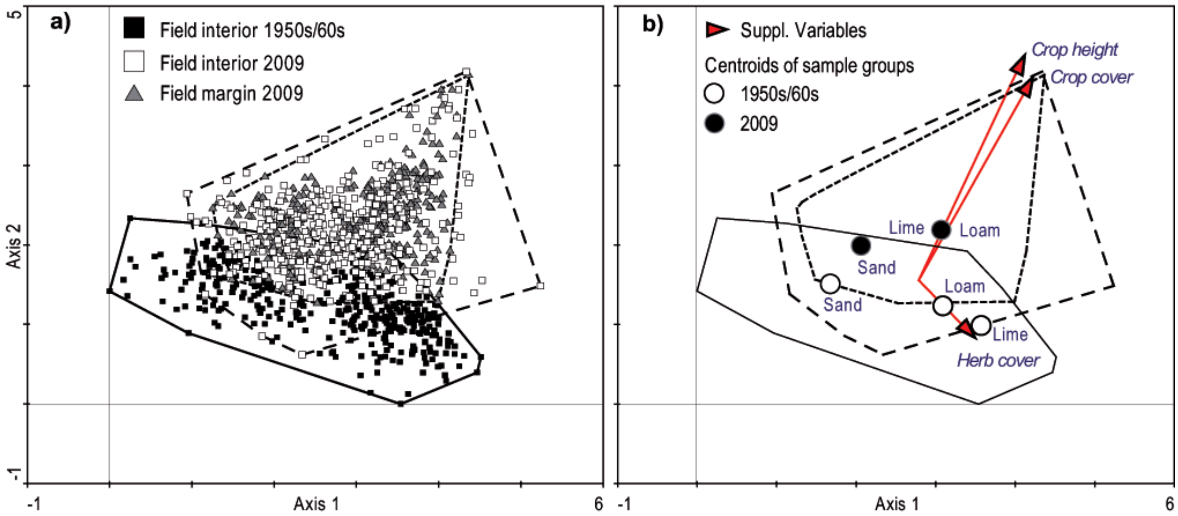

Figure 3.1. DCA of all 1176 vegetation relevés. a) Samples classified by field position and period. b) Same ordination and classification (enveloped), with supplementary soil and structural variables fitted *post hoc* (cut off value r^2=0.1) on the ordination plot (cover values transformed y=log(x+1); Eigenvalues / length of gradient: axis 1, 0.48 / 5.2; axis 2, 0.34 / 4.2; axis 3 (not shown), 0.20 / 4.7).

Shifts in syntaxa inventory

In the historical data (with only field interior records), 293 relevés (75%) were allocated at the level of associations, and a further 92 (24%) at the level of alliances (Table 3.3). In contrast, the recent data set included only 19 relevés (5%) assignable at the association level and 77 (20%) at the alliance level, while 296 relevés (76%) were more severely impoverished, among which 27 (7%) could not even be assigned to any class. For arable plant communities of base-poor soils, the ratio between relevés classified at association level and fragment communities turned from 5:1 in the 1950s/60s to 1:4 by 2009. The respective ratios for base-rich soils were 4:1 in the historical and 1:10 in the recent data set. Associations characteristic for root crops or spring-sown cereals were found in 127 historical fields but only in three recent fields, and plant communities typical for autumn-sown (cereal) crops were found in 166 historical fields but only in 16 recent fields. Of the 16 plant associations recorded in the 1950s/60s, six associations were not recorded again in 2009, and most others considerably declined in frequency (Figure 3.2, Table 3.3). Most re-sampled field interiors underwent a shift to less narrowly defined syntaxa at higher ranks, chiefly to a class-level residual community. 64% of the historical stands of the acidophytic association Teesdalio-Arnoseridetum minimae were replaced by an impoverished class-level residual community, while the basophytic Thlaspio-Veronicetum politae disappeared completely being mostly replaced by an impoverished class-level residual community (79%). Stands of the association Caucalido-Adonidetum flammeae on base-rich soils were replaced now at most sites by class-level residual stands (71%) or non-assignable assemblages (8%). The four associations with the highest transformation rates to residual communities belonged to the alliances Caucalidion platycarpae and Fumario-Euphorbion on calcareous or loamy soil. The lowest transformation rates were found in the Aperion spicae-venti and the Digitario-Setarion on sandy soil. At the alliance level, the Caucalidion platycarpae seems to be most badly affected; 77% of the historical stands were replaced by stands not assignable to this alliance today. At the field margins, syntaxon turnover was less pronounced than in the field interiors. Of sites with historical relevés assigned to association level, 24% and 39% in 2009 still represented associations and alliances, respectively. The Aphano-Matricarietum recutitae achieved the same frequency in field margins of 2009 as in the 1950s/60s field interiors. The Papaveretum argemones is nowadays more frequent in field margins than formerly in the interiors. It is the only association which increased in extent (though not in species numbers – see below), at least at field margins.

Table 3.3. Relevé numbers of arable plant communities in the 1950s/60s (field interior) and in 2009 (field interior and field margin). Plant communities are allocated to syntaxa of different hierarchical ranks: Ass. = association (lowest rank) → All. = alliance → order → class (highest rank). Communities not assignable to associations were allocated to higher-ranked syntaxa and denoted res. comm. = residual communities. Upper case values indicate the relative decrease/increase in relevé numbers assigned to a given syntaxon for field interiors between the 1950s/60s and 2009.

	1950s/60s Field interior	2009 Field interior	2009 Field margin
Communities on base-poor soils			
Autumn sown crops			
Ass. 1 – Teesdalio-Arnoseridetum minimae	59	0^{-100}	1
Ass. 2 – Papaveretum argemones	24	8^{-67}	34
Ass. 3 – Aphano-Matricarietum recutitae	19	6^{-68}	19
Ass. 4 – Holco-Galeopsietum	7	0^{-100}	1
All. 1 – residual community Aperion spicae-venti	43	40^{-7}	66
Root crops or spring-sown cereals			
Ass. 5 – Setario-Galinsogetum parviflorae	3	1^{-67}	2
Ass. 6 – Digitarietum ischaemi	11	0^{-100}	0
Ass. 7 – Spergulo-Echinochloetum cruris-galli	5	0^{-100}	1
Ass. 8 – Setario-Stachyetum arvensis	1	0^{-100}	0
Ass. 9 – Spergulo-Chrysanthemetum segetum	1	0^{-100}	0
Ass. 10 – Lycopsietum arvensis	8	0^{-100}	4
All. 2 – residual community Digitario-Setarion	9	21^{+133}	23
Ass. 11 – Chenopodio-Oxalidetum fontanae	1	1^{0}	1
All. 3 – residual community Polygono-Chenopodion	3	1^{-67}	1
Order 1 – residual community Sperguletalia arvensis	0	0^{0}	0
Communities on base-rich soils			
Cereals or autumn sown crops			
Ass. 12 – Papaveri-Melandrietum noctiflori	33	2^{-94}	15
Ass. 13 – Caucalido-Adonidetum flammeae	24	0^{-100}	4
All. 4 – residual community Caucalidion platycarpi	10	10^{0}	47
Root crops or spring-sown cereals			
Ass. 14 – Soncho-Veronicetum agrestis	4	0^{-100}	0
Ass. 15 – Thlaspio-Fumarietum officinalis	13	1^{-92}	3
Ass. 16 – Thlaspio-Veronicetum politae	80	0^{-100}	7
All. 5 – residual community Fumario-Euphorbion	27	6^{-78}	15
Order 2 – residual community Papaveretalia rhoeadis	1	15^{+1400}	43
Class residual community Stellarietea mediae	5	253^{+4960}	102
Residual community non-assignable	1	27^{+2600}	3
Total number of relevés	392	392	392

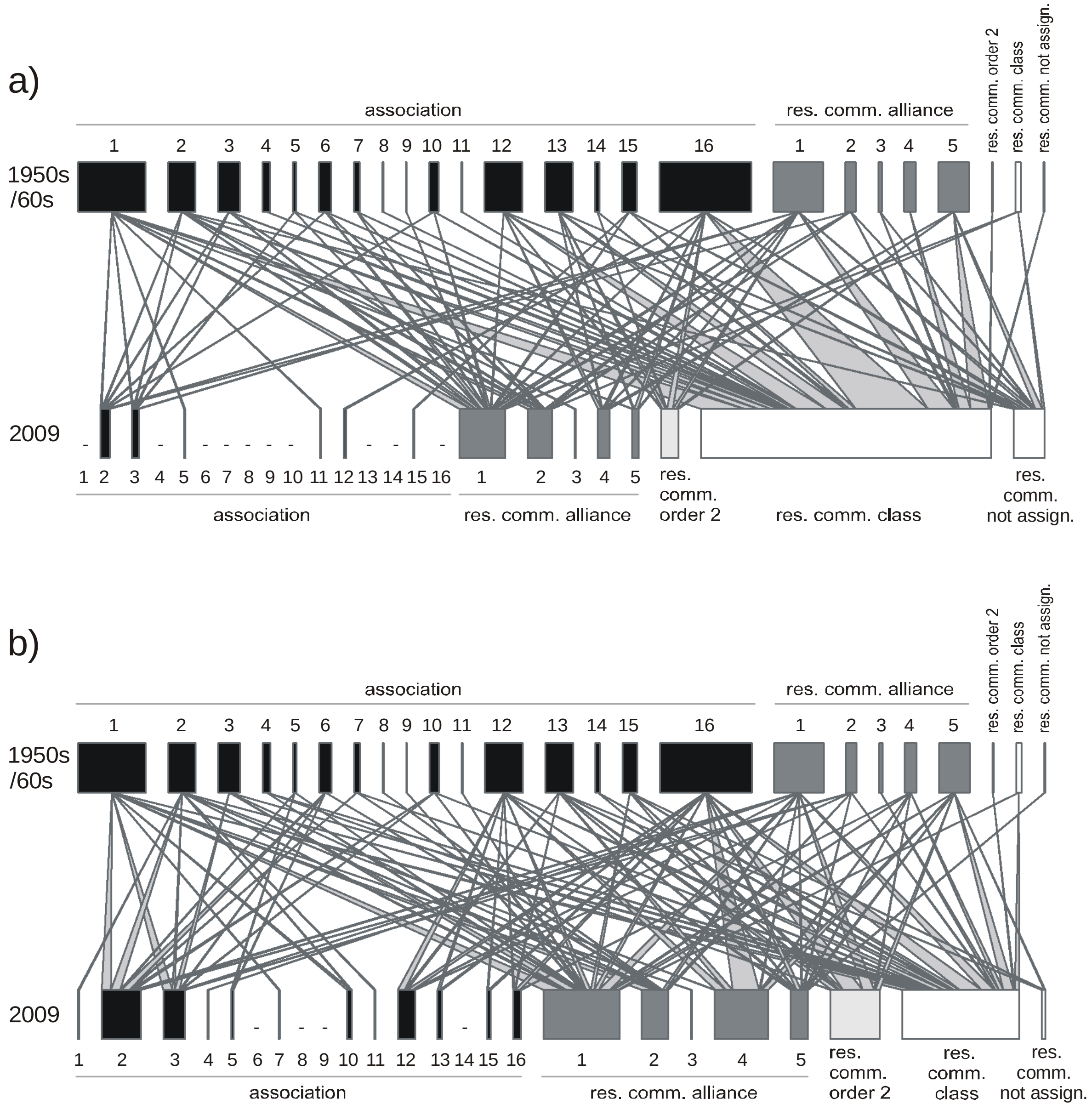

Figure 3.2. Turnover in syntaxa of arable fields between the 1950s/60s and 2009. a) Comparison of field interiors from the 1950s/60s with field interiors from 2009, and b) comparison of field interiors from the 1950s/60s with field margins from 2009. Black shading indicates associations while other levels of shading show impoverished residual communities (res. comm.) of alliances (dark grey), orders (pale grey) and the class (white) (the brighter a syntaxon the higher it is impoverished). Most strongly impoverished vegetation not assignable to any class is also indicated in white. For the hierarchical system of syntaxa and syntaxa names see Table 3.2 and 3.3.

Changes in species richness

In the field interiors, mean plot-based species richness decreased significantly for nearly all syntaxa, irrespective of whether, in the 1950s/60s, a community was already impoverished (residual community) or not (association, Figure 3.3a). Compared to historical field interiors recent margins showed a reduced richness only in associations of the order Papaveretalia rhoeadis on base rich soils (Ass. 12-16; Figure 3.3) but not in associations of the order Sperguletalia arvensis on base poor soils (Ass. 1-10 in Figure 3.3). In recent field margins representing the association Digitarietum ischaemi and the Digitario-Setarion residual community (belonging both to the alliance Digitario-Setarion), species richness was even higher than in the respective historical fields. In vegetation on base-rich soils allocated to the Papaveretalia rhoeadis (Ass. 12-16) species richness decreased by 76% ± 3.1%, while those of the Sperguletalia arvensis of base-poor soils (Ass. 1-10) decreased by 50% ± 7.5% (Figure 3.3b). In contrast, in the Setario-Galinsogetum parviflorae (Ass. 5) and the corresponding alliance residual of the Digitario-Setarion (All. 2 res. comm.), species richness was higher in field margins in 2009 than in the field interiors in the 1950s/60s indicating local species increase in spring-sown crop communities on moderately alkaline soils.

Shifts in frequency and cover of diagnostic species

The diagnostic species of the class Stellarietea mediae had declined considerably in frequency and cover across the different communities since the 1950/60s (see Appendix Table S3.1 in Supporting information). These losses were more pronounced in field interiors than at margins. Significant reductions of cover of diagnostic species were observed for the Papaveretum argemones, Thlaspio-Fumarietum officinalis, and Thlaspio-Veronicetum politae as well as in the residual communities of the alliances Aperion spicae-venti, Digitario-Setarion, Caucalidion platycarpi, and Fumario-Euphorbion, of both orders and of the class.

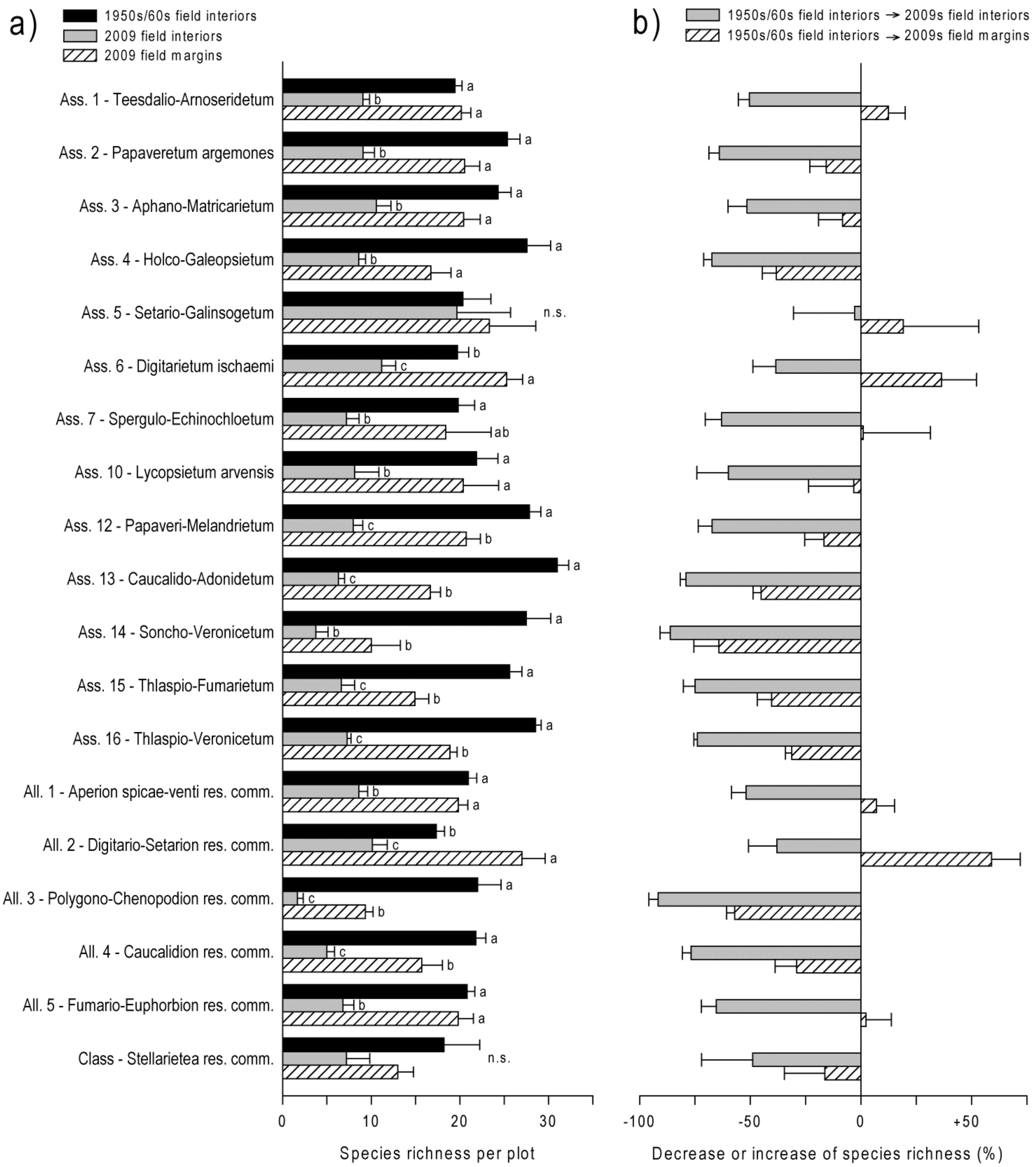

Figure 3.3. a) Species richness per plot of different arable plant communities in the 1950s/60s (field interiors) and corresponding plots in 2009 (field interiors and field margins), and b) the relative decrease/increase of species richness between the 1950s/60s (field interiors) and 2009 (field interiors and field margins). Only communities with ≥ 3 samples were compared (for sample sizes see first column of Table 3.3). Grey bars in b) show changes of species richness in field interiors between the 1950s/60s and 2009 while striped bars in b) compare 1950s/60s field interiors with 2009s field margins. Different small letters indicate significant differences at $P < 0.05$ within communities (res. comm. = residual community).

Discussion

Disproportionate species losses in arable fields

Our studied confirmed the first hypothesis, showing that vegetation of arable fields has experienced pronounced loss in species richness and also of plant communities over the last five to six decades. Floristic differences between the different soil substrates have largely vanished, and today's impoverished arable plant communities are less diverse and more homogeneous. Our results support BRUN-HOOL'S (1966) prediction that arable plants diagnostic of associations and alliances have largely disappeared, giving way to a set of only 4-5 'agrotolerant' and highly competitive generalist species such as *Chenopodium album, Galium aparine, Fallopia convolvulus, Polygonum aviculare* or *Viola arvensis* that prevail in almost every field.

This is in line with other investigations in Central Europe (e.g. HILBIG 1985, TRZCINSKA-TACIK 1991, MÁJEKOVÁ *et al.* 2010), where species diagnostic for alliances, orders and the class have been reported to decline less rapidly than species diagnostic for associations. Stenoecious (specialist) species of the alliances Caucalidion platycarpi (e.g. WAGENITZ & MEYER 1981, HILBIG 1985, KOHLBRECHER *et al.* 2012) and Aperion spicae-venti (e.g. KUTZELNIGG 1984, KULP & CORDES 1986, PILOTEK & NEZADAL 1989) disappear to a disproportionately large extent (see also GÜNTHER & VAN ELSEN 1993, LOSOSOVÁ 2003, LOSOSOVÁ & SIMONOVÁ 2008). Diagnostic species of higher-rank syntaxa or other euryoecious (generalist) species of arable fields are less strongly affected. *Arnoseris minima* as the most characteristic species of the association Teesdalio-Arnoseridetum minimae disappeared completely from both in field interiors and field margins, although in the 1950s/60s, this species had a frequency of 16% of the relevés with abundance values corresponding to 2.5% to 37.5% cover.

Some authors (HOLZNER & IMMONEN 1982, SUTCLIFFE & KAY 2000, MÁJEKOVÁ *et al.* 2010) pointed out that apparently lost arable plant species may reappear from a persistent seed bank. However, in the meantime, the seed banks are also strongly impoverished by herbicide application over decades leaving only common species (OTTE 1992, SCHMIDT *et al.* 1995). Seed banks are probably relevant for the preservation of rare arable plant species only when fallows, land set-asides or afforested former low-input fields are re-cultivated (HEYTER 1985, WÄLDCHEN *et al.* 2005).

Management-driven turnover in arable plant associations

Species richness declined in all regions irrespective of the plant community, geological substrate or position in a field (Figure 3.1 and 3.3). Margins were sometimes richer than respective historical data from field interior, probably due to an ecotonal effect (FRIED *et al.* 2009) with spill overs from adjacent non-arable vegetation (ROMERO *et al.* 2008). Former differences between fields on calcareous soil and sandy soils have largely vanished i.e. the meaning of soil reaction and soil type is today unimportant due to the all-dominant high nutrient level and herbicide pressure (HÜPPE & HOFMEISTER 1990, ALBRECHT 1989, ALBRECHT 1995). As with LOSOSOVÁ & GRULICH (2009), losses in our plot sample were most pronounced for communities of the Caucalidion platycarpi. In the following, the history of two associations exemplifies the change and species turnover.

(1) Teesdalio-Arnoseridetum minimae: This arable plant community of low-input fields on sandy, humus- and nutrient-poor, highly acidic soils (KLÄGE 1999) disappeared completely as did its diagnostic species (*Arnoseris minima, Hypochaeris glabra,* and others). The fields formerly colonized by this association show today residual plant assemblages of the class Stellarietea mediae or the alliance Aperion spicae-venti (see Ass. 1 in Figure 3.2) as a result of soil liming and application of synthetic fertilizers favouring tall fast-growing arable plants.

(2) Caucalido-Adonidetum flammeae: This plant community of shallow to medium-developed, loamy-clayey limestone soils (HÜPPE & HOFMEISTER 1990) is now confined to narrow margins of arable fields cultivated with winter cereals (HOFMEISTER & GARVE 2006). Based on records of the 1930s and 1950s, it appears that the Caucalido-Adonidetum had replaced a plant association extinct in Germany today, and already very rare in the 1950s/60s, with characteristic species such as *Asperula arvensis* and *Orlaya grandiflora*. Thus, these assiciation, still widespread in e.g. Thuringian fields in the 1960s (SCHUBERT & KÖHLER 1964), represented partly a slightly impoverished stage of the former community, perhaps due to early effects of fertilizer and herbicide application (PFÜTZENREUTER 1994). The next stage of management intensification led to the Papaveri-Melandrietum noctiflori differing from the Caucalido-Adonidetum chiefly by the absence of *Adonis aestivalis* and the presence of several more N-demanding species. Formerly an arable plant association characteristic for loess, the Papaveri-Melandrietum is now generally restricted to shallow calcareous soils. Further impoverishment will lead to replacement by residual communities. Our results indicate that nearly 90% of the former stands of the Caucalido-Adonidetum have been transformed to such residual assemblages (see Ass. 13 in Figure 3.2).

Threat and conservation of arable plant communities in Germany

Marginal arable lands have suffered dramatic diversity losses, not only through intensification of cultivation, but also due to abandonment, subsequent vegetation succession and afforestation. Although the German Red List of plant communities (RENNWALD 2002) specifies the associations of the alliances Caucalidion platycarpi and Aperion spicae-venti as the most threatened among the arable plant communities, our data suggest that the Red List assessment is still overly optimistic. Both the Teesdalio-Arnoseridetum minimae and the Caucalido-Adonidetum flammeae are listed as endangered while our data suggest that they are critically endangered.

Do we need a new syntaxonomy of arable vegetation?

Several authors discussed syntaxonomical consequences of the changes in arable vegetation some of them already decades ago (TÜXEN 1950, TÜXEN 1962, BRUN-HOOL 1966, HILBIG & KÖCK 1982, OTTE 1984, PFÜTZENREUTER 1994). There are basically two formal options to properly consider temporal and management-related processes in the phytosociological classification system. The first is to describe formally new ‘central’ associations reflecting modern species assemblages (e.g. DIERSCHKE 1994, SCHUBERT 2001, DENGLER 2003, BERG *et al*. 2004). ‘Central associations’ of species-impoverished arable fields were first described in detail by HILBIG (1973) for Thuringia and KROPÁČ (1988) for the Czech Republic/Slovakia. The second formal option would be the concept of ‘deductive classification’ as suggested by KOPECKÝ & HEJNÝ (1974, 1978; see also DIERSCHKE 1994). While the terminology suggested by the former authors apparently failed to stand the test of time, the idea of classifying plant communities with fragmentary species composition by means of different higher levels of syntaxa coincides partly with the idea of BRUN-HOOL (1966) to treat ‘residual plant communities’ of arable fields. The latter concept enables the allocation of plant assemblages representing various degrees of degradation. It appropriately reflects dynamics in plant communities; accounts for the time factor, and keeps formalism to a minimum. As our study shows, the concept of hierarchical residual communities provides a suitable basis for the interpretation of man-made dynamic processes in arable plant communities without abandoning the conventional associations which still exist at least locally. Given that vegetation classification is still needed for a wide range of theoretical and applied purposes, hierarchical community classification seems to be well positioned to cope with the difficulties of rapidly changing man-made plant assemblages.

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Supporting information

Additional supporting information may be found at the end of this document:

Appendix Table S3.1. Percentage share of fields with different crop types and crop classes in the 1950s/60s and 2009. Estimated cover values (%) of crops are given as medians and interquartile ranges (IQR). Abbreviations for cultivation period: w – winter crops (=autumn-sown crops), s – spring crops (=spring-sown crops), s/w – both spring and winter crops.

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CHAPTER

4

Dramatic losses of specialist arable plants in Central Germany since the 1950s/60s – a cross-regional analysis

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Abstract

Agricultural intensification has profoundly altered Central Europe’s arable plant communities since the 1950s. Here we present the results of a comprehensive landscape-scale study that covers ten study areas with contrasting soil conditions and compares community composition and diversity before the onset of agricultural intensification with the recent situation. We employed a semi-permanent plot design to analyse changes in 392 field interiors on sandy, calcareous or loamy soil between the 1950s/60s and 2009.

The analysis revealed a reduction in the regional species pool during the 50-year period by 23% (from 301 to 233 vascular species) and dramatic losses in plot-level diversity (medians of 24 and 7) in the ten study areas. The average cover of arable plants decreased to a tenth of its original extent (from 30% to 3%). Archaeophytes, neophytes and most Poaceae (including some aggressive weeds) showed similarly strong losses as indigenous plants, but only modest changes in their share of total arable plant cover. This contradicts the assumption that grasses and neophytes are generally profiting from agricultural intensification. Crop diversity decreased from 25 crop plants present in the 1950s/60s to only 16 in 2009 while crop cover generally increased. Winter cereals, oilseed rape and maize are dominant today, while root crops and summer cereals showed large declines. Vegetation change depended on soil substrate with once markedly different arable communities now showing more homogenized community structure. Once species-rich fields on calcareous soil were most strongly impoverished, while the formerly less diverse sandy fields suffered smaller species losses. Increasing Ellenberg Indicator Values (EIVs) for nitrogen and pH point to N fertilization as a major driver of change. Our results document tremendous diversity losses on the plot and also the species pool level. Losses did, however, differ between geological substrates and new conservation measures such as the establishment of field flora reserves and agri-environment schemes with less intensive land use are thus urgently needed especially on limestone substrates to bring an end to the decline of this functionally distinct and increasingly threatened component of the Central European flora.

Keywords: agricultural intensification; archaeophytes; calcareous soil; crop diversity; diversity loss; Ellenberg Indicator Values; fertilization; neophytes; sandy soil; weeds

Introduction

Hardly any ecosystem has been as markedly shaped by human activities as arable fields (VAN CALSTER *et al.* 2008, ELLENBERG & LEUSCHNER 2010). Until the mid-19th century, Central Europe's agro-ecosystems were characterized by a large and even increasing diversity of plants associated with crop cultivation (BURRICHTER *et al.* 1993). Species richness of these arable plants reflected variation in geological substrate, cropping type and management regime (e.g. LOSOSOVÁ *et al.* 2004, FRIED *et al.* 2008, PINKE *et al.* 2012). In terms of biogeography, indigenous plants and archaeophytes were the dominant constituents.

Agricultural intensification in recent decades has completely changed this pattern. Farmers concentrate on an increasingly limited set of crop species (KNOX *et al.* 2011), resulting in reduced diversity of crops and thus losses in associated arable plants. Stands have generally become much denser with species that are poor competitors for light increasingly being confined to field margin sites (KOHLBRECHER *et al.* 2012).

Improved seed cleaning techniques (SPAHILLARI *et al.* 1999), loss of traditional crops like flax (MIREK 1976, 1997), and increasing application of synthetic fertilizers (ROBINSON & SUTHERLAND 2002) also resulted in the homogenization of vegetation (MACDONALD & JOHNSON 2000, BAESSLER & KLOTZ 2006). Increased crop yields were paralleled by dramatic diversity losses in arable plants throughout Europe (STORKEY *et al.* 2012). Especially the widespread use of herbicides from the 1950s onwards (SALESBURY 1961, ANDREASEN & STREIBIG 2011) and the introduction of the European Union's Common Agriculture Policy (POTTER 1997, ANDREASEN & STRYHN 2008) caused an increasingly rapid impoverishment of the arable flora (RIES 1992). Losses were also dramatic in farmland birds (DONALD *et al.* 2006) and invertebrates (WILSON *et al.* 1999), and this had negative effects on ecosystem services (BIESMEIJER *et al.* 2006).

Agriculture in Central Europe represented a 'low-input-agriculture system' until the early 1950s. This changed with the beginning of agricultural industrialisation in the 1950s and early 1960s (BAUERKÄMPER 2004), when e.g. average nitrogen surplus on German increased from 25 kg N ha^{-1} yr^{-1} in the 1950s to around 110 kg ha^{-1} yr^{-1} in 2005 (ELLENBERG & LEUSCHNER 2010).

The rapid loss of phytodiversity in arable lands has received considerable attention (ALBRECHT 1995). Several studies have pointed out that the frequency of archaeophytes (immigrated before 1500 AD) has generally declined (PRESTON *et al.* 2004), while the frequency of neophytes (immigrated after 1500 AD) tended to increase (LOSOSOVÁ & SIMONOVÁ 2008). Some grass species that are now known to be problem weeds suppressing agricultural crops have also been found to increase at the expense of other herbs (ANDREASEN & STRYHN 2008).

Permanent plots with long-term monitoring are, unfortunately, non-existent in European fields. Very few re-sampling studies employed a permanent (same plot) or semi-permanent (same field) plot design (1962-1997 - SUTCLIFFE & KAY 2000, 1968-2006 - FRIED *et al*. 2009a, 1968-2005 - POTTS *et al*. 2010). These studies had limited spatial extent rendering comparisons between e.g. different geological substrates difficult. To our knowledge, MÁJEKOVÁ *et al*. (2010) from Slovakia is the only representative, large-scale resampling study (578 arable field sites, re-sampled between 1949 and 2006). This study, however, focused mainly on phytosociological changes and not on diversity patterns.

We thus still lack a reliable picture of current arable plant diversity of Central Europe. This is, however, urgently needed as funds available for arable plant conservation have dramatically declined in the last years (MEYER *et al*. 2010). Here, we analysed changes in the arable flora of 392 fields from ten different study areas in central and northern Germany between the 1950s/1960s and 2009. The study areas represent the three main geological types of sandy, loamy and limestone substrates. We tested the hypotheses that (i) agricultural intensification has resulted in a reduced diversity of crop varieties and denser crop stands; leading to (ii) large shifts in the composition of the arable communities with diversity losses in archaeophytes and increases in neophytes and Poaceae. We further hypothesized that (iii) the character of these shifts varies with the geological substrate.

Material and Methods

Study area and sampling design

The study was conducted in the German federal states of Lower-Saxony, Saxony-Anhalt, Brandenburg and Thuringia (50°78´-52°61´N; 9°11´-13°69´E, Figure 4.1). The climate changes from sub-oceanic to sub-continental from west to east with mean annual air temperatures ranging between 7.1°C and 9.1°C, and mean annual precipitation between 490 mm and 730 mm year^{-1} (HIJMANS *et al*. 2005). Four study areas were dominated by sandy soils, three by limestone substrates and three by loamy sites (Table 4.1).

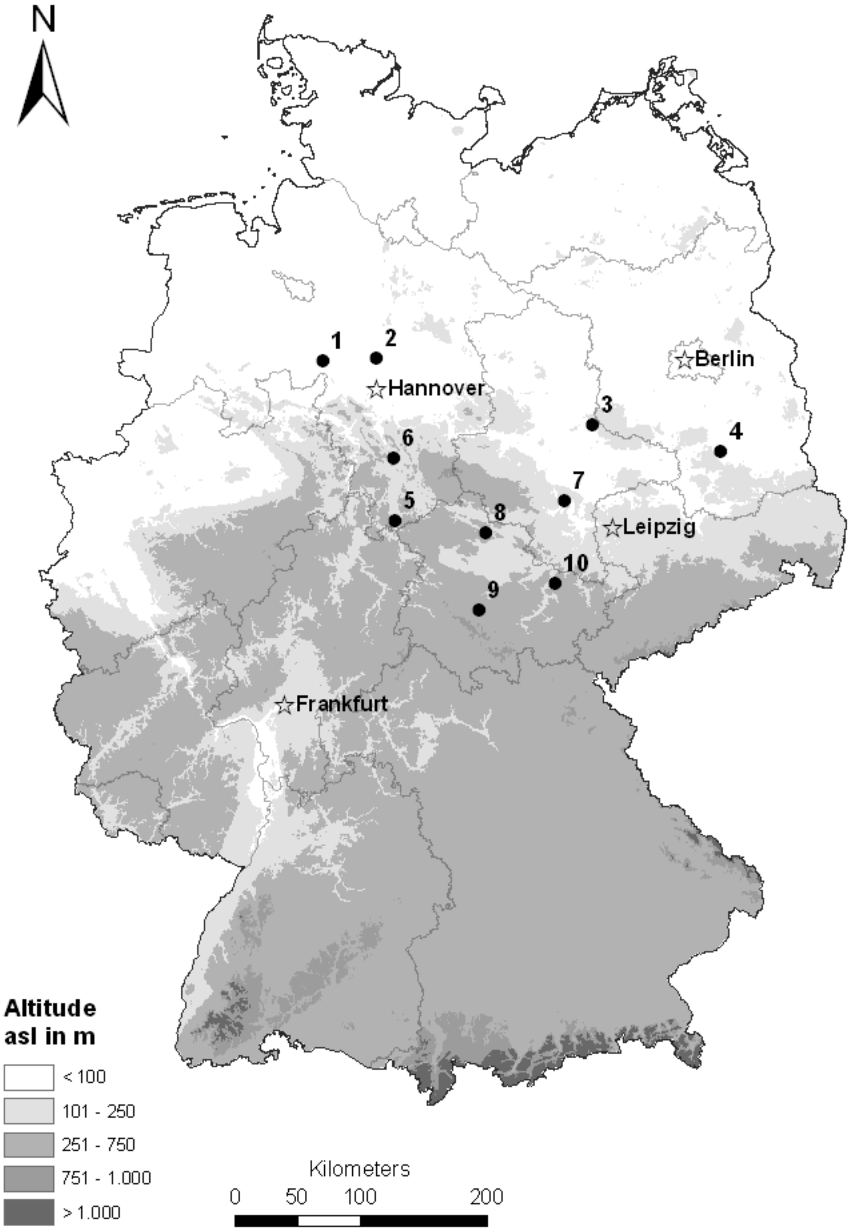

Figure 4.1. Location of the ten study areas in Central Germany (SRTM relief data).

Table 4.1. Details of the ten study areas on three different soil substrates, including the number of arable fields surveyed in the 1950s/1960s and in 2009.

Study region	Federal state	Coordinates (WGS 1984)	Annual mean precipitation (mm)	Annual mean temperature (C)	Elevation (m a.s.l.)	Prevailing substrate	Year of historical records	No. of repeated relevés	Source of historical records
Reese	Lower Saxony	N 52°34’ E 09°03’	654	9.1	25-40	sand	1951	31	Preising (unpublished data), Tüxen-Archive Hanover
Berkhof	Lower Saxony	N 52°36’ E 09°43’	673	8.9	25-40	sand	1955	38	Jahns (unpublished data), Tüxen-Archive Hanover
Nedlitz	Saxony-Anhalt	N 52°03’ E 12°16’	565	8.8	90-120	sand	1956	46	Jage (unpublished data)
Luckau	Brandenburg	N 51°51’ E 13°45’	560	8.5	40-125	sand	1960/61	39	Fischer, Krausch & Illig (unpublished data)
Göttingen	Lower Saxony	N 51°28’ E 09°54’	727	8.7	160-225	loam	1960	37	Ernsting (unpublished data), Tüxen-Archive Hanover
Erzhausen	Lower Saxony	N 51°53’ E 09°55’	644	8.8	100-330	loam	1959	45	Anonymus (unpublished data, Tüxen-Archive Hanover
Halle/Saale	Saxony-Anhalt	N 51°32’ E 11°54’	475	9.1	75-140	loam	1958	40	Plass (unpublished data), Archive University of Halle
Hachelbich	Thuringia	N 51°20’ E 10°55’	542	8.3	180-320	lime	1956/57	39	Wiedenroth (1960), Archive University of Jena
Plaue	Thuringia	N 50°47’ E 10°54’	487	7.1	295-520	lime	1959-62	37	Hilbig (unpublished data), Archive University of Jena
Saaletal	Thuringia	N 50°58’ E 11°40’	590	9.3	170-350	lime	1959-61	40	Hilbig (unpublished data), Archive University of Jena

Climate data from German National Meteorological Service (DWD), based on the reference period 1961-1990.

Historical vegetation relevés were retrieved from suitable archives (Table 4.1), and from unpublished field notes of older botanists. On the basis of vegetation maps and precise descriptions of locality initially provided, 392 relevés (154, 116 and 122 relevés for sandy, limestone & loamy substrates) could be identified at the field level. The historical information was sufficient to identify the respective field, and often a certain part of the field. However, it was not possible to find the specific plot (semi-permanent plot design). Historical vegetation samples are often biased towards well-developed stands. Today, field interiors are very homogenous; in the few cases where well developed stands were encountered during the re-sampling these were sampled preferentially. Especially in the study areas with shallow limestone or poor sandy soils, 10-15% of the fields sampled in the 1950s/60s were transformed into grasslands or forests. These were excluded from the comparisons.

Mean field size has increased considerably in the last five decades in Germany, e.g. from 1.2 ha (1953/1957) to 12.2 ha (2000) in an area near Halle (Saale) (BAESSLER & KLOTZ 2006), rendering the relative spatial share of field margins as potential refugia relatively unimportant. Because a large fraction of the field margin vegetation is constituted by plants that spill-over from adjacent vegetation types (ROMERO *et al*. 2008), we focused only on the field interior. This allows direct comparison with historical relevés which were always taken in the field interior. To eliminate any ecotonal effect (WILSON & AEBISCHER 1995, FRIED *et al*. 2009b), sample plots were placed at least 10 m apart from the field margin.

Size of historical relevés varied between 25 and 100 m²; re-sampling took place with the plot size specified by the authors of the given historical study. Historical and recent data were not systematically different in plot size (Repeated-Measures ANOVA $p<0.05$), and species richness and relevé size were not correlated. As in the 1950s/60s, relevé sampling was conducted following the method of BRAUN-BLANQUET (1964); nomenclature of species follows JÄGER (2011).

Data processing and analysis

Relevés were stored in a TURBOVEG database (HENNEKENS & SCHAMINÉE 2001) and plant synonyms were standardised using taxonomic emendation. We recorded all higher plants, including seedlings of shrubs or trees and crop volunteers. The few cases where taxa in the recent or the historical survey could be determined to the genus level only were excluded from further analysis. For consistency, all data on status (e.g. indigenous plants, archaeophytes and neophytes) follow standard lists (JANSEN & DENGLER 2008). We used Ellenberg Indicator Values (EIV) of the species (ELLENBERG *et al*. 1992) for soil reaction

(EIV-R), moisture (EIV-M) and nutrient (mainly nitrogen) availability (EIV-N) to calculate plot-level means by weighting species EIVs with the square-root of estimated cover.

Multivariate analysis included Detrended Correspondence Analysis (DCA), which indicated a relatively high β-diversity (DCA - length of gradient on first axis: 5.3 multivariate s.d., corresponding to >1 species turnover, see MCCUNE *et al*. 2002). The unimodal model in DCA was thus taken as appropriate. Changes in the occurrence of the species over time were examined with separate Indicator Species Analyses for each region (ISA, BAKKER 2008). Quantitative variables were tested for statistical differences over time by Repeated Measures Analysis of Variance (RM ANOVA); data were log-transformed where raw data graphs indicated strongly skewed distributions. Relations between numerical variables were analysed with Pearson correlation analysis. Crop types were analysed by χ^2-test; with the originally 28 recorded crop categories being aggregated to five main classes. Multivariate analyses were run with Canoco 4.5 (DCA, TER BRAAK & ŠMILAUER 2002) and PC-ORD (ISA, MCCUNE & MEFFORD 2011), univariate and bivariate data were analysed in R (R DEVELOPMENT CORE TEAM 2004) using standard packages.

Results

Change in cropping systems since the 1950s/60s

Crop diversity decreased from a total of 25 observed crop plant species in the historical surveys to only 16 today (see Appendix Table S4.1 in Supporting information). Spring cereals decreased from a share of 26% to 17%, while winter cereals increased from 41 to 61% (Figure 4.2). The main increasers were winter wheat (14 vs. 31%); winter rape (0 vs. 17%) and maize (1 vs. 9). In turn, potatoes (15 vs. 1%), oat (8 vs. 2%) and beets (5 vs. 3%) declined.

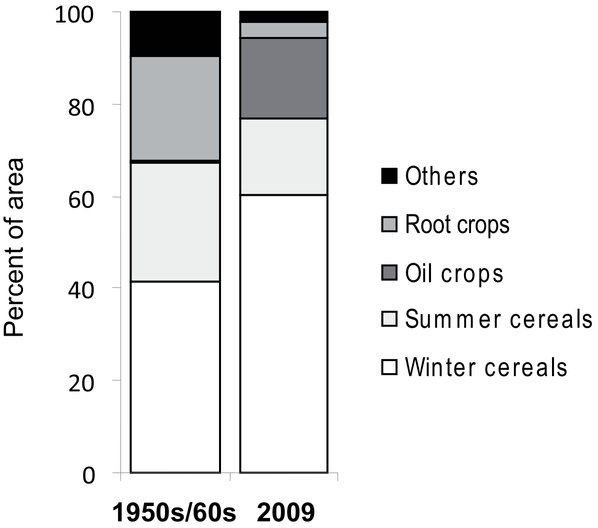

Figure 4.2. Shifts in crop species composition between the 1950s/60s and 2009 (in percent of the total number of fields investigated; means of the ten study areas) ($\chi^2=154.8$, df=4, $p<0.0001$). The main groups are winter cereals (triticale, barley, rye, wheat), spring cereals (cereal mixtures, maize, barley, rye, wheat, oat), oil crops (mustard, sunflower, oilseed rape), root crops (beets, carrots, potatoes, other vegetables), and others (beans, peas, clover-grass, lucerne, millet, buckwheat, flax, grass leys, initial fallow land, stubble, no data).

Data on historical crop cover were limited. Crop cover on sand (one study area) remained stable at a median of 80% (interquartile range 60-90%) in the 1950s/60s vs. 75% in 2009 (IQR 65-85%, RM-ANOVA $p>0.5$). In limestone regions (three study regions), crop cover increased from a $\text{median}_{1950s/60s}$ of 60% (IQR 40-70%) to median_{2009} 95% (IQR 90-95%; RM-ANOVA $p<0.0001$). Cover differed between crops ranging from a median of 20% for sunflower to a median of 90% for spring rye according to the historical data, and between 25% for carrots and a median of 90% for winter barley according to the recent data. Only two crop species were sufficiently common to directly compare historical and recent cover. Cover of winter wheat (lime) increased from a $\text{median}_{1950s/60s}$ of 60% (IQR 50-80%) to a median_{2009} of 80% (80-95%), while cover of winter rye (sand) remained essentially stable at $\text{median}_{1950s/60s}$ of 90% (IQR 70-90%) vs. median_{2009} of 85% (75-90%, see Appendix Table S4.1 in Supporting information).

Shifts in arable plant community composition

Arable plant communities differed between substrate types and sampling periods (Figure 4.3). The first DCA-axis differentiated the historical relevés with respect to samples taken on sandy soils from those taken on limestone substrates. This axis was correlated with the mean Ellenberg indicator value for soil reaction (pH value). The second axis differentiated historical from recent relevés and correlated negatively with cover, diversity and evenness of the arable communities.

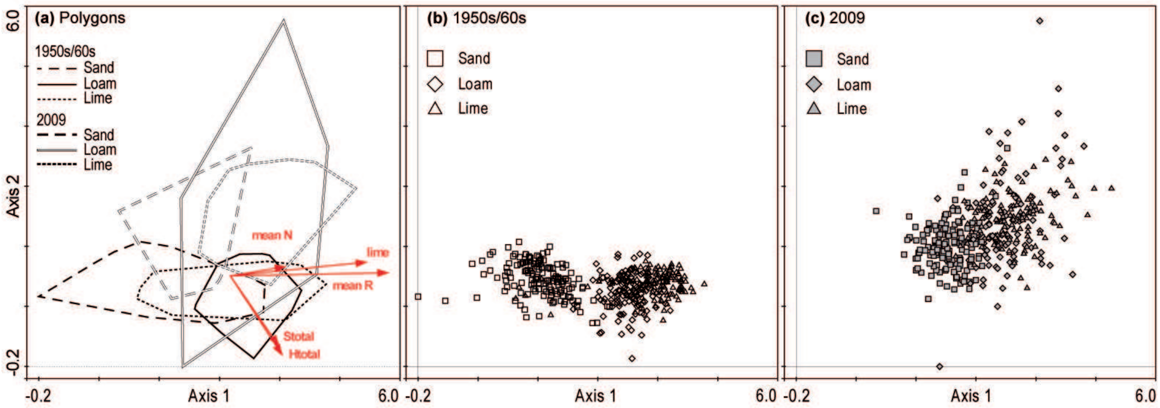

Figure 4.3. DCA of all 2 x 392 vegetation relevés, for clarity shown in three different ways (a) Samples simplified to hulls including samples of a given substrate*period class, supplementary variables fitted post hoc (cut off value r^2=0.1) on the ordination plot. (b) Same ordination, but historical samples (1950s/60s) shown as dots. (c) As b, but only recent samples (2009) shown (species with frequency < 3 deleted, cover values transformed y=log[x+1]; downweighting of rare species; Eigenvalues / length of gradient axis 1: 0.42 / 5.3; axis 2: 0.21 / 5.8; axis3: 0.15 / 4.2).

In total, 366 different species were recorded (see Appendix Table S4.2 in Supporting information); 133 were restricted to the historical data set, 65 occurred only in the 2009 data and 168 species were recorded in both surveys. None of the disappearing species was listed as nationally extinct. There was a trend towards homogenization of substrate groups. The two most dissimilar samples from historical data had a distance of 4.8 multivariate standard deviations along axis 1 of the DCA, corresponding to > 1 species turnover. Recent samples had a distance of 4.0 s.d. units along axis 1. In contrast, Whittaker's β-diversity (species pool / plot-diversity; species with frequency < 3 excluded) increased from 6 to 16 due to the tremendous decrease in plot-level diversity described below.

Median plot-level diversity decreased from 24 species in the 1950s/60s to 7 species in 2009 (Figure 4.4). Even the most well developed recent samples (95% percentile) had a median of 19 only. Substrates differed in species richness as did the sampling periods, and the magnitude of loss differed between substrates as indicated by a significant interaction term (RM-ANOVA of log-transformed data: $P_{\text{substrate}}$ $p<0.02$, P_{period} $p<0.0001$, $P_{\text{substrate*period}}$ $p<0.0001$). The cover of arable plants in the plots declined dramatically from a median of 30% to a mere 3% in 2009 (Table 4.2).

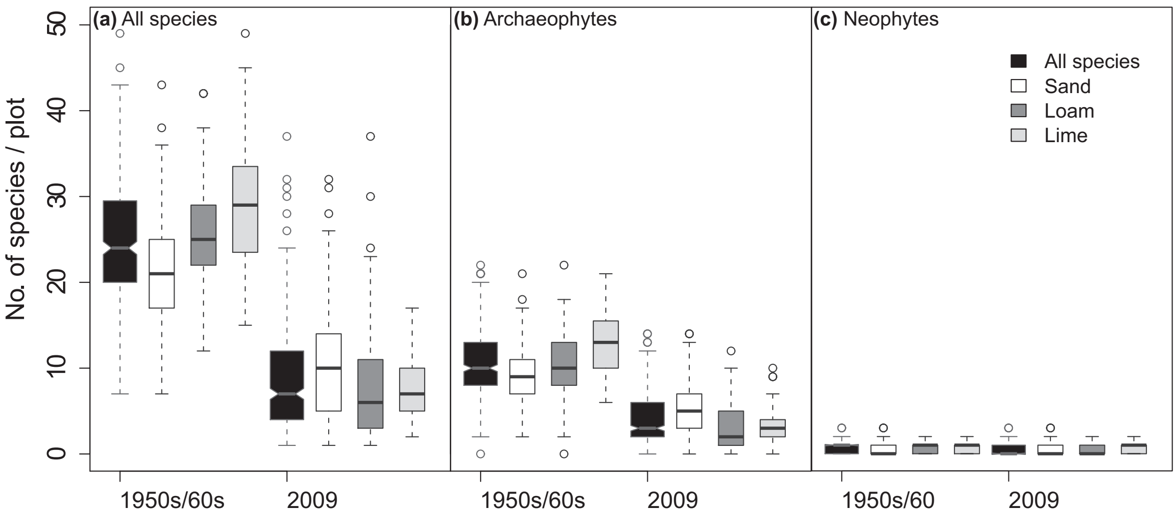

Figure 4.4. (a) Number of arable species per plot found in the historical (1950s/60s) and recent (2009) surveys, given for the entire data set (all species), (b) the archaeophytes and (c) the neophytes only. Data are given for pooled values (used for testing) and separately for substrate classes.

Table 4.2. Estimated cover values (%) of arable plant communities on three different substrate site classes in the 1950s/1960s and 2009 (data for those pairs of relevés where both recent and historical data were available). Values are given as medians and interquartile ranges (IQR).

	1950s/60s		2009		
	median	IQR	median	IQR	n
All relevés	30	20-60	3	1-10	214
Sand	50	25-80	3	4-15	58
Loam	20	10-30	1	1-6	40
Calcareous soils	40	20-50	4	1-8	116

Losses were most pronounced on limestone sites where plot-level richness dropped from a median of 29 to 7 taxa. Disappearing taxa included species associated with base-rich soils (e.g. *Adonis aestivalis*, *Lathyrus tuberosus*) and other species considered diagnostic in phytosociology (*Conringia orientalis*, *Turgenia latifolia*, see Appendix Table S4.2 in Supporting information). The losses on loamy soils were similarly high with a reduction from 25 to 6 species, where indicator species such as *Veronica polita* and *Fumaria officinalis* declined strongly. The decreases in richness on sandy soils were less pronounced (decrease in median richness from 21 to 10 taxa per relevé). The diagnostic species *Hypochaeris glabra* and *Arnoseris minima* are now very rare; *Aphanes australis* and *Teesdalia nudicaulis* disappeared completely as did species indicating fluctuations in the soil water table (e.g. *Juncus bufonius*, *Mentha arvensis*).

Our design was not aimed at keeping the crop constant, rendering the available data for paired sites with equal crop type over time limited. For winter wheat on limestone soils, historical samples had a median of 29 species (IQR 22-32), the respective recent samples had only 7 (IQR 4-9, $p<0.00001$, paired t-test, $n=10$). Winter wheat samples on loam had a median of 27 species (IQR 24-31), while the recent richness was 11 (IQR 4-24, $p<0.00001$, $n=17$). For sand, comparisons were only possible for winter rye, with a median of 25 species (IQR 12-30) in historical samples and 15 (IQR 12-20) in recent samples ($p<0.00001$, $n=33$).

Fallopia convolvulus, *Chenopodium album*, and *Viola arvensis* were the most frequent species in the historical data set. They were still among the most common in 2009 though their frequency values had dropped (*F. convolvulus*: from 84% to 34%, *C. album*: 68 vs. 44% and *V. arvensis*: 67% vs. 51%).

Changing abundance of archaeophytes, neophytes and Poaceae

Archaeophytes showed a strong decline from a $\text{median}_{1950s/60s}$ of 10 (IQR 8-13) to median_{2009} of 3 (IQR 2-6) species per relevé (Figure 4.4). Again, losses were most pronounced in limestone regions. The few exceptions were *Tripleurospermum inodorum* and *Echinochloa crus-galli*, which increased (frequency change from 11 to 28, and from 6 to 12% respectively). Neophytes were rare in the historical data and declined even further from a $\text{median}_{1950s/60s}$ of 1 species to median_{2009} 0 per relevé (Figure 4.4).

Plot-level species richness of grasses declined from a $\text{median}_{1950s/60s}$ of 2 (IQR 1-3) to median_{2009} of 1 (IQR 0-2). Among the newly recorded species in the recent relevés were the grasses *Dactylis glomerata* (indigenous, current frequency 4%) and especially *Bromus sterilis* (archaeophyte, 15%). *Alopecurus myosuroides* (archaeophyte), *E. crus-galli* (archaeophyte) and several *Bromus* species (*B. secalinus* - archaeophyte, *B. commutatus* - archaeophyte and *B. japonicus* - neophyte) increased on a low level (see Appendix Table S4.2 in Supporting information).

Cover values of specific species groups were not estimated separately, but trends can be assessed by summing up the cover of the individual species. Expressed as a fraction of the total sum of cover values, the relative shares of archaeophytes and neophytes showed weakly positive trends (Table 4.3) as did the share of Poaceae, while the remaining species, mainly indigenous herbs, declined in proportion. Nonetheless, all species were subject to a general decrease in absolute cover as outlined above.

Table 4.3. Percentage share of different species groups (as a fraction of community cover) for communities on three different soil substrates in the 1950s/60s and 2009. Table 4.2 contains the corresponding absolute cover values. Medians and interquartile ranges (IQR) are given.

	1950s/60s		2009	
	Median	IQR	Median	IQR
Archaeophytes	0.41	0.31-0.53	0.48	0.33-0.64
Sand	0.46	0.33-0.59	0.51	0.39-0.71
Loam	0.37	0.30-0.48	0.40	0.20-0.52
Calcareous soils	0.41	0.32-0.52	0.49	0.33-0.63
Neophytes	0.01	0-0.03	0	0-0.09
Sand	0	0-0.02	0	0-0.06
Loam	0.02	0-0.03	0	0-0.06
Calcareous soils	0.02	0-0.03	0.05	0-0.15
Poaceae	0.08	0.04-0.19	0.12	0-0.29
Sand	0.16	0.07-0.31	0.11	0.04-0.24
Loam	0.07	0.03-0.15	0.18	0-0.40
Calcareous soils	0.05	0.02-0.08	0.11	0-0.25

Shifts in Ellenberg Indicator Values (EIV)

The EIV-N differed between substrates and increased over time (RM-ANOVA, P_{period} p<0.0001, $P_{substrate}$ p<0.0001). Shifts were particularly strong on plots from sandy and limestone substrates (Figure 4.5; interaction $P_{substrate*period}$ p<0.0001). Plot-level species richness on limestone and loamy soils showed no significant correlation to the EIV-N value. On sandy soils, EIV-N and mean species richness were positively correlated in the historical data set (r=0.28, p=0.001), while the correlation in 2009 was weak and negative (r=-0.16, p=0.07).

The mean EIVs for soil reaction and nutrients were positively correlated in both the historical and recent relevés (r=0.68 and 0.47, respectively) and showed strongest increases over time on sand, followed by limestone substrates, while loamy sites revealed unchanged indicator values. The mean EIV for moisture (EIV-M) did not differ between the two periods ($Median_{1950/60}$=4.8, IQR4.5-5.2; $Median_{2009}$=4.7, IQR 4.5-5.0) and was not related to species richness.

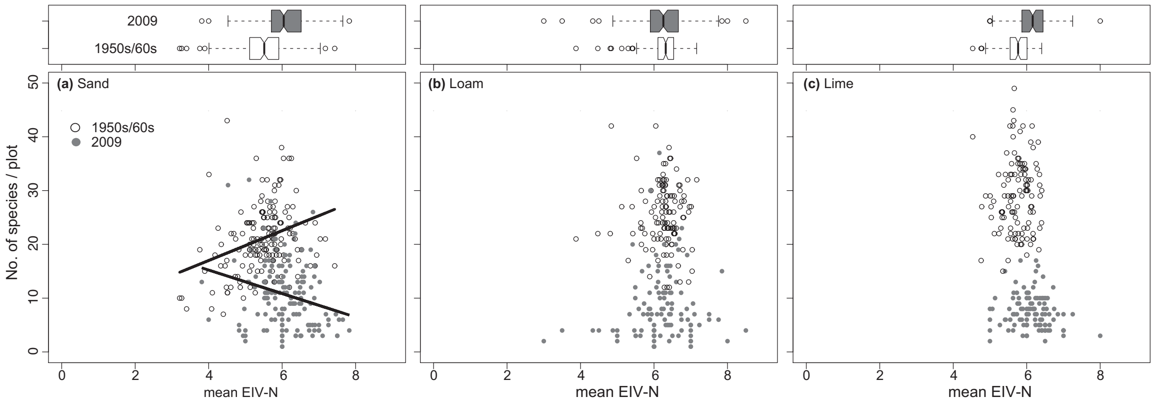

Figure 4.5. Relation between species richness (average number of species per relevé) and the weighted EIV-N for the relevés on (a) sandy, (b) loamy and (c) limestone substrate. Boxplots of EIV-N are given for the two survey periods in the top of the figure.

Discussion

Shifts in community composition

Our 50-year record of community change revealed a dramatic impoverishment since the start of agricultural intensification in the 1950s. The total number of vascular plant taxa found decreased by 23% (from 301 to 233), which resembles other reports from in Germany describing losses of the species pool in the range of 20 to 50% (ALBRECHT 1995, KOHLBRECHER *et al*. 2012). In Slovakia, where agricultural transformation started later, only 8% of the species have disappeared over the past 50 years (MÁJEKOVA *et al*, 2010).

Diversity losses at the community level were even more pronounced with a mean loss of 65% (from 24 species to only 7 in recent time). This reduction is more severe than reported in previous studies from Bavaria (-30%, i.e. plot averages of 23 vs. 16 species, ALBRECHT 1989), Thuringia/Kyffhäuser region (-45%, 24 vs. 13 species; KOHLBRECHER *et al*. 2012). A review by ALBRECHT (1995) covering 33 regions from all over Germany revealed plot-level diversity losses of 20 to 40%, with only two regions showing losses of more than 60%. Our estimate of a tenfold decline in cover of the arable plant communities (average cover of 30% in the 1950s/60s to only 3% cover in 2009) again exceeded the 75% cover loss reported in long-term surveys from Denmark and Austria (RIES 1992, ANDREASEN & STREIBIG 2011).

Land-use intensification is often associated with homogenisation (SMART *et al*. 2006). In our data set, differences between substrate groups decreased as shown by reduced spread of samples along the first DCA axis. Whittaker's β-diversity did, however, increase over time as a consequence of the dramatic decline of plot-level. This mirrors the strong differences in land use intensity found today with some sites still being under non-intensive cultivation, while most others harbour only highly agro-tolerant arable plant species (AAVIK & LIIRA 2009, FRIED *et al*. 2010).

According to the DCA analysis, the historical relevés revealed a strong differentiation between substrate types and pH classes. With the widespread liming of crop fields on poor acidic soils and modern standardised agricultural practices, floristic differences have largely disappeared, as shown by the increased overlap of substrate groups along axis 1 of the DCA. This indicates homogenisation of arable plant communities (FIRBANK *et al*. 2008) and hampers the placement of recent relevés in established phytosociological systems (MEYER *et al*. submitted).

The inner parts of arable fields are nowadays extremely species-poor with *V. arvensis*, *F. convolvulus*, *C. album*, *Polygonum aviculare* and *Galium aparine* typically being the only dominant species. In line with other studies (e.g. FRIED *et al*. 2009a), we also observed dramatic decreases in the frequency and density of formerly common arable plants such as *C. album*, *P. aviculare*, *Cirsium arvense*, and especially *Stellaria media* that had populated the fields in huge numbers. As a consequence, resources for invertebrates including pollinators and also seed-eating birds have declined (MARSHALL *et al*. 2003, STORKEY 2006).

Community change and species loss differed with substrates. In the 1950s/60s, fields on limestone bedrock were more diverse than fields on sandy deposits (HÜPPE & HOFMEISTER 1990). This has shifted due to disproportionally large species losses on limestone sites. LOSOSOVÁ & GRULICH (2009) explained these high losses with their high share of archaeophytes, a group of arable plants with predominantly Mediterranean origin and particularly high light demand (KLEIJN & VAN DER VOORT 1997). Increased crop cover, together with the wide-spread application of herbicides and the frequent abandonment of agriculture in low-productive fields are the main causes of high diversity losses in limestone regions (MEYER *et al*. 2008). Fields on loamy soils show intermediate soil conditions, and species losses were also intermediate in comparison to sandy and limestone sites.

Losses on sandy soil were less extreme, even though communities adapted to highly acidic and nutrient-poor conditions have also vanished. Less specialized species, however, still find habitats on sandy soil, which now harbour the most diverse arable plant communities in the study region. In a few regions, species numbers on sandy sites remained stable or even increased (ALBRECHT 1989). In conclusion, the overall trend in arable vegetation structure in the region is characterized by specialists disappearing while few generalists increase, reflecting the growing uniformity in crop management schemes and soil conditions in recent time.

Changes in selected species groups

Archaeophytes showed equally pronounced losses in both richness and cover, as did the indigenous plants. The total number of neophytes recorded in our sample increased slightly from 17 to 20 species. In Slovakia, MÁJEKOVÁ *et al.* (2010) found an increase in the species pool from 10 to 19 species since the 1950s. In our study, species with frequency increases included *Conyza canadensis* (on sandy substrates), *Oxalis fontana* and *Matricaria discoidea*, with the latter two not being recorded in the historical surveys. *Echinochloa crus-galli* also increased in frequency, being confined to the increasingly common maize fields. *Veronica persica*, formerly the most important neophyte on arable sites in Germany (RUMPF *et al.* 2004), decreased by 40% in frequency since the 1950s/60s. We found only one field with *Ambrosia artemisiifolia*, an invasive taxon in Central Europe's ruderal vegetation (GLADIEUX *et al.* 2011). Our results show a decreasing, and not increasing, cover of neophytes on arable fields, which is in contrast to reports on absolute and relative increase of neophyte cover in northern Germany (RUMPF *et al.* 2004) and Czech Republic (PYŠEK *et al.* 2005). In Central Europe, neophytes are suppressed by the use of certified crop seeds (ANDREASEN & STREIBIG 2011) and by modern cultivation techniques and thus suffer from similar pressures as other arable plants.

Certain Poaceae were described to benefit from current agricultural practices (ANDREASEN & STRYHN 2008, MÁJEKOVÁ *et al.* 2010). We found strong declines in the frequency and cover of most Poaceae including some species that are known to be aggressive and yield-suppressing weeds such as *Avena fatua*, *Elymus repens* and *Apera spica-venti* (see Appendix Table S4.2). Among the few increasing grasses are species known for herbicide resistance such as *A. myosuroides* with a fourfold increase presumably due to resistance development (MENNE *et al.* 2008). This species also benefits from an increased cultivation of winter cereals (KNOX *et al.* 2011). *Bromus* species showed a more or less constant frequency over time except for *B. sterilis*, which was not recorded in the historic survey and has become one of the most aggressive grass weeds since then, especially in winter cereals. It benefits from the widespread adoption of low-tillage systems, early seeding dates and winter cereal-based crop rotations (MORAY *et al.* 2003).

Erosion of crop diversity

During the last five decades, crop diversity has declined in central and northern Germany, as in other parts of Europe (e.g. MARSHALL *et al*. 2003). The recent crop systems are dominated by winter cereals, mainly winter wheat, and oilseed rape, which spread in the 1980s (HEYLAND *et al*. 2006). Maize is the sole spring-sown crop that has increased in cultivation because of biomass production (GEVERS *et al*. 2011, WALDHARDT *et al*. 2011). Arable plant communities in maize fields were largely uniform across all ten study areas and dominated by *C. album*, *F. convolvulus*, *S. media* or *E. crus-galli*.

Formerly widespread crops like flax and their associated highly specialized arable plants had already disappeared from our study area by the end of World War II, and were thus not covered by the historical surveys used here. Root crops, like beets on loamy soil or potatoes on sandy soil, are now less common than in the 1950s/1960s. An example is *Linaria arvensis* that was a highly characteristic species of potato fields (MEYER & BERGMEIER 2010), but has almost completely disappeared highlighting the fact that reduced crop diversity is one driver of diversity loss and extinction. In our data set, however, losses in arable plant diversity were also strong for the few fields where crop type remained constant over time. This suggests that altered cultivation practices had a huge effect.

Effects of site conditions

Although comparative analysis of large and sometimes heterogeneous data sets has limited power for analysing site-level effects, indicator values may still provide insight into the general impact of moisture and fertility changes. The mean moisture values remained essentially unchanged during the 50-year period, even though pronounced declines have been reported for arable plants characteristic of moist microsites (ELLENBERG & LEUSCHNER 2010). Many of the respective species indicate changing water regimes, and few of the formerly abundant ones have high indicator values for moisture. Further population decline apparently has no major impact on overall patterns. Soil pH has been identified as a major determinant of arable species composition (e.g. HÜPPE & HOFMEISTER 1990, FRIED *et al*. 2008); potentially even overriding the management effect (HAWES *et al*. 2010). Our study corroborates publications on decreasing importance of soil pH (PYŠEK & LEPŠ 1991, FRIED *et al*. 2010). Nowadays, the effect of soil pH on species composition is mainly apparent on non-intensively managed fields.

We detected a larger increase in the mean EIV-N values in communities of sandy and limestone regions which naturally have a lower fertility and thus a higher susceptibility to N fertilization than loamy soils. Fields on acidic soils have long been conditioned with liming and fertilizing, often for cultivating sugar beet (MEISEL 1969). As a consequence, indicator species for infertile conditions with EIV-N and EIV-R values of 2-4 vanished.

Atmospheric N deposition is an important driver of vegetation change in many European ecosystems (BOBBINK *et al.* 2010). With rates mostly between 20 and 40 kg N ha^{-1} yr^{-1} in Central Germany (oxidized and reduced N, UMWELTBUNDESAMT 2005), deposition accounts for less than a third of the N amount added to fields with fertilization, which has increased in croplands of Germany since 1950 from 40 to 105 kg N ha^{-1} yr^{-1} (ELLENBERG & LEUSCHNER 2010, UMWELTBUNDESAMT 2011).

The EIV-N was not correlated to species richness on limestone and loamy sites. In sandy fields, in contrast, EIV-N was positively correlated with species richness in the 1950s/60s, probably reflecting the ascending leg of the hump-shaped diversity-productivity curve. KLÄGE (1999) observed that insufficient nutrient (in particular N) causes reductions in crop yield on the poorest sandy sites, and also results in lower density of arable plant stands. This has now been reversed with elevated inputs of synthetic fertilizer, which significantly decreased species richness of plants that are poor competitors for light and thus often threatened (PYŠEK & LEPŠ 1991, STORKEY *et al.* 2010). Fifty years ago, fields on sandy soil typically were fertilized by adding solid manure and cultivating N-fixing plants such as serradella (*Ornithopus sativus*) or lupine (*Lupinus* spp.). In the 1950s, the presence of *G. aparine* and *S. media* allowed differentiation of N-richer vs. N-poorer fields on loamy sites (ELLENBERG 1950). With fertilizer levels exceeding 100 kg N ha^{-1}, these species are now widespread in all fields, regardless of soil substrate.

High fertilizer input, together with the introduction of highly productive crop varieties (ANDREASEN & STREIBIG 2011) resulted in closing of crop stands. While fields with a sparse crop cover (30-50%) were still common in the 1950s/60s, cover typically exceeds 90% today. Part of this cover increase is attributed to a shift from root crops to winter cereals, but our data show that even fields of the same species, in our case winter wheat, are now denser than they used to be. Increases in crop cover were strong on loam and limestone soil, while sandy fields remained relatively open.

Herbicide application is the third key driver of vegetation change in Central European croplands beside N input and increased crop cover. In the early 1950s, herbicides were applied in only 10% of the summer and winter cereal fields of Germany, but this increased to almost 100% in the mid-1980s (ELLENBERG & LEUSCHNER 2010). In parallel, herbicide sales increased in Germany by another 30% from 1994 to 2008 (UMWELTBUNDESAMT 2011). The herbicide effect on community composition may have been particularly large on limestone and loamy sites where fertilization effects were less pronounced, but our data allow no sound inferences on this.

Conclusions – Implications for conservation measures

Currently, around one third of approximately 350 arable plant species in Germany is considered threatened (HOFMEISTER & GARVE 2006); among them several species that have a large fraction of their distribution range in the region (e.g. *Arnoseris minima*, *Bromus grossus* and *Veronica opaca*, WELK 2002).

A further expansion of the area planted with energy crops, especially on marginal agricultural areas with high conservation value, and widespread cultivation of genetically-modified crops will most likely be associated with spreading monocultures, increasing cultivation of perennial crops, higher cropping densities and increased levels of herbicide and fertilizer application (FIRBANK 2008, DAUBER *et al*. 2010). Impoverishment of arable plant communities will thus probably continue with eventually only a few nitrophilous species persisting (GRIME 1974, STORKEY *et al*. 2010). Conservation measures for arable plants should focus on the establishment and permanent maintenance of sanctuaries that still harbour non-homogenized and species-rich plant communities with viable populations of the characteristic species in order to preserve possible source populations for future conservation and rehabilitation activities especially on limestone sites. This requires not only well-designed management regimes but also a long continuity of the measures in order to be successful (MEYER *et al*. 2010).

An initiative has been launched recently to identify new solutions for the protection of arable plants in Germany. A nationwide network of at least 100 so-called ‘conservation fields’ (‘Schutzäcker’) was designed to counteract the ongoing loss of arable plants species (MEYER *et al*. 2010). On the selected fields, crop management is carried out without application of herbicides and by taking into consideration specific management requirements of target arable plant species. Nevertheless, due to their size limitations, initiatives like the network of conservation fields can only be a first step to protect a sufficiently large part of agro-biodiversity in Central Europe.

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Supporting information

Additional supporting information may be found at the end of this document:

Appendix Table S4.1. Percentage share of different crop types and crop classes in the 1950s/60s and 2009. Estimated cover values (%) of crops are given as medians and interquartile ranges (IQR).

Appendix Table S4.2. Changes in frequency over time, given for the pooled data, and separately for the three substrate types. Change over time was tested with indicator species analysis (BAKKER 2008); significances are based on the comparison of indicator values that combine frequency and abundance. For consistency in status all data follow JANSEN & DENGLER (2008). Abbreviations indicate species status in the region: 'A' = archaeophytes; 'A/I' = unclear whether archaeophytes or neophytes; 'I' = indigenous; 'K' = crops; 'N' = neophytes; 'NA' = no data available; 'U/N' = unstable neophytes

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CHAPTER

5

Landscape complexity has limited effects on genetic structure of two arable plant species, *Adonis aestivalis* and *Consolida regalis*

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Abstract

The agricultural landscape of Central Europe has changed dramatically in recent decades due to intensified cultivation bringing many of its characteristic species to the brink of extinction. We investigated whether landscape structure affects the genetic structure and diversity of remnant populations of two arable plant species *Adonis aestivalis* and *Consolida regalis*. We used dominant amplified fragment length polymorphism markers (AFLP's), and investigated these effects in six regions of 5 km² in Central Germany assigned to two different classes of landscape structural complexity, monotonous (> 95% of area covered by arable land with low extent of field margins) or structurally diverse (< 60% of area covered by arable land with large extent of field margins). Contrary to expectation, within-population diversity levels did not significantly differ between monotonous and structurally diverse landscapes. Subpopulations from diverse landscapes tended to be more differentiated from each other than those from monotonous landscapes. However, no significant isolation-by-distance was found for either species regardless of landscape structure. These results suggest that landscape complexity as such is not as important on a local level as effects of e.g. genetic bottlenecks. Artificial transfer of material between neighbouring populations seems justified with respect to the limited genetic structuring, and the present conservation strategies should be reconsidered based on genetic variation in these species.

Keywords: Arable weeds; AFLP; conservation strategies; habitat fragmentation; landscape genetics

Introduction

Since its origin in neolithic times, the development and spread of agriculture has been accompanied by the evolution of a uniquely adapted and diverse fauna and flora (Stoate *et al*. 2001). However, agricultural land use has undergone considerable intensification and modernisation during the last half century across much of Europe (Stoate *et al*. 2009, Ellenberg & Leuschner 2010) leading to a major decline in biodiversity (Baessler & Klotz 2006, Smith *et al.* 2010, Storkey *et al*. 2012). Arable plant communities have changed dramatically during the second half of the 20th century, mainly due to the increased use of herbicides and chemical nutrient inputs (Meyer *et al*. 2013). Consequently, arable plant species have declined in numbers and diversity, with field margins partly functioning as small refugia (Marshall & Moonen 2002). Field sizes have, however, increased resulting in the removal of field margins (van Rossum *et al.* 2004, Schmidt *et al.* 2009). Agri-environment schemes have been developed to counteract the present biodiversity losses in (semi-)natural areas and also in arable fields, but the effectiveness of these agri-environment schemes is unclear (Kleijn *et al.* 2006, Meyer *et al.* 2010, Smith *et al.* 2010).

Habitat fragmentation affects populations through reduced population size and increased isolation. It is often associated with an erosion of genetic variation and increased interpopulation genetic divergence due to increased random genetic drift, elevated inbreeding and reduced gene flow (Young *et al.* 1996, van Rossum *et al.* 2004, Dittbrenner *et al.* 2005, Vandepitte *et al.* 2007). Lower genetic diversity may limit a species' adaptive ability and thus increase the extinction probabilities (e.g. Spielman *et al.* 2004, Honnay & Jacquemyn 2007). Formerly common species, which have become rare as the result of landscape transformations, are assumed to be particularly prone to the effects of habitat fragmentation (Aguilar *et al.* 2008).

Surprisingly, arable plants are rarely studied with respect to genetic structure (for exceptions see Delye *et al*. 2010, Brütting *et al*. 2012a, b). No study has explicitly considered effects of landscape structure on arable plants so far, although reduction and fragmentation should have an impact on both population sizes and gene flow and thus on genetic structure and genetic diversity. This topic has implications for both basic science and applied conservation management. Here, we tested the effects of landscape structure on genetic population structure in two rare arable plants, and compared their genetic structures for pairs of monotonous, intensively used versus less impoverished, richly structured landscapes. Pairs of sites were situated in close neighbourhoods in the states of Saxony-Anhalt and Thuringia, which are representative of the agricultural landscapes of Central Germany.

We selected the summer pheasant's-eye (*Adonis aestivalis* L.) and the Forking Larkspur (*Consolida regalis* S.F. GRAY). Both are archaeophytes that originated from the Mediterranean Basin and were introduced as seed contaminants by neolithic people to Central Europe (SCHROEDER 1969, PYŠEK *et al.* 2005). Formerly widespread until the mid-21st century, abundance of *A. aestivalis* and *C. regalis* as arable plants decreased drastically with improved seed cleaning practices, increasing use of herbicides and fertilisers, and changes in cultivation periods (WARREN *et al*. 2008). Both species are included in the Red List of Germany (KORNECK *et al.* 1996), now usually occurring in the less-well cultivated margins of fields. Populations are often already small and heavily fragmented, and still decline further especially in intensively used landscapes. In central Germany, both species are nonetheless sufficiently common to obtain reliable data, with *C. regalis* being less severely threatened on the local scale than *A. aestivalis*.

Populations are separated by mostly unsuitable habitats such as grasslands and intensively managed fields. Genetic drift should occur in the small potentially inbred populations. Gene flow in the largely selfing *A. aestivalis* (KLEIN 1926, SUTHERLAND & DELPH 1984) should be strongly limited and largely dependent on dispersal by seed, which is reduced due to current agricultural practices. *Consolida regalis* is potentially insect-pollinated and more outcrossing (HONG 1986). A previous study revealed higher gene diversity in *C. regalis*, while Φ_{st} as a proxy for fragmentation is higher in *A. aestivalis* (BRÜTTING et al. 2012a). Both arable plant species thus differ in certain aspects relevant for conservation which makes them ideal study models for our context.

We used the dominant DNA marker system AFLP (Amplified Fragment Length Polymorphism; VOS *et al.* 1995), studying (i) how genetic variation is distributed among and within populations of *A. aestivalis* and *C. regalis*; (ii) whether there is a relation between genetic structure and the degree of habitat fragmentation in *A. aestivalis* and *C. regalis* populations; (iii) and which conclusions can be drawn for the conservation of the two species.

Material and Methods

Study species

Adonis aestivalis L. (Ranunculaceae) is distributed from the Caucasus, Turkey and Iran to Russia eastwards up to Central Asia, and westwards to Northwest Africa and the Mediterranean Basin (GABRIELIAN & FRAGMAN-SAPIR 2008). In Central and Southern Europe, it is restricted to warm and dry, calcareous or loamy soils, naturally occurring in fallow and cultivated land, most often in wheat fields (winter crops), dry rocky/stony slopes, sparse oak forests and mountain steppes below 1500 m a.s.l. (ELLENBERG 1988, PARTZSCH *et al.* 2006, MEHMETI *et al.* 2009). It is a hexaploid, monocarpic herb with $2n = 48$ chromosomes (HEYN & PAZY 1989). *Adonis aestivalis* propagates by achenes with a terminal recurved or slightly curved beak, probably adapted to myrmecochory as is the case for other *Adonis* species (BASKIN & BASKIN 2001, BOJŇANSKÝ & FARGAŠOVÁ 2007). Only a minor fraction of seeds germinates immediately after seed-shedding in summer, while primary dormancy mostly delays germination until the following spring (BONN & POSCHLOD 1998). Seeds apparently have high survival rates suggested by the presence of a long-term persistent seed bank (WÄLDCHEN *et al.* 2005). Flowering in Central Europe takes place during May to August. The vermilion flowers are mostly pollinated by pollen-collecting bees and other pollen-eating insects (KLEIN 1926, BONN 2004). Flowers are proterandrous, and the species is regarded as having a mixed breeding system, i.e. self-compatible and partly outcrossing (KLEIN 1926, SUTHERLAND & DELPH 1984).

Consolida regalis S.F. Gray (syn. *Delphinium consolida* L., Ranunculaceae) has a pan-European distribution, excluding the extreme north and south, extending to Western Asia. It prefers nutrient-rich and calcareous soils, mainly occurring in crop fields, but also in rocky steppes, stony slopes and screes (PARTZSCH *et al.* 2006, BOJŇANSKÝ & FARGAŠOVÁ 2007). This monocarpic herb is diploid with a base number of $x = 8$ chromosomes (LAWRENCE 1936). It propagates by seeds enclosed in follicles adapted to semachory (BONN & POSCHLOD 1998). Most seeds germinate near the surface immediately after seed-shedding, but seeds are viable for at least 10 years, potentially building up a persistent seed bank (GÜNTER 1997, SAATKAMP *et al.* 2009). During May to August, the deep blue or violet flowers are pollinated mostly by bumblebees (RAUH 1953). Despite occasional reports on self-compatibility, *C. regalis* is usually regarded as primarily outcrossing due to proterandry (SUTHERLAND & DELPH 1984, HONG 1986).

Study sites and sampling design

We defined populations as plants occurring within areas of 5 km² and sampled six *A. aestivalis* and *C. regalis* populations from each of six regions in Central Germany differing with respect to landscape structure. All regions are mainly characterized by agricultural landscapes interspersed with grasslands, forest patches and settlements (e.g. villages and road verges). The regions Hainleite, Querfurter Platte and Witterda were very monotonous with >95% of the area being arable land; large fields resulted in a relatively low extent of field margins. The three structurally diverse study regions Kyffhäuser, Schmoner Hänge and Drei Gleichen were characterized by <60% of arable land and smaller fields with a larger extent of field margins (Figure 5.1, Table 5.1).

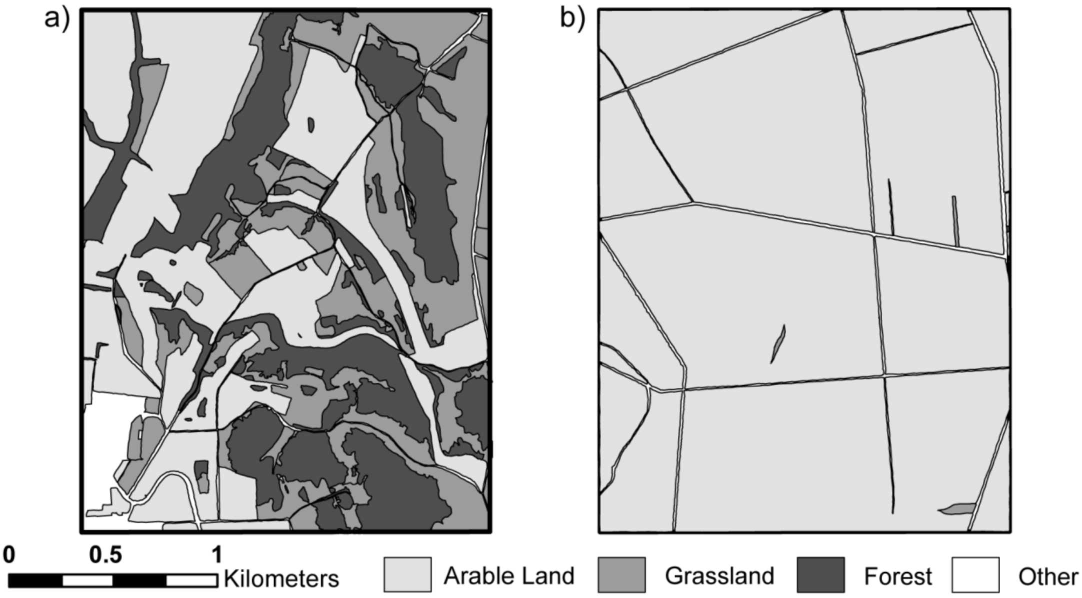

Figure 5.1. Examples for a structurally diverse region (Kyffhäuser) and a monotonous region (Hainleite) representing two of the six study regions. Shown are fields, grassland, forests and other habitat types (GIS analysis based on aerial imagery).

In all regions, we selected five subpopulations, defined as groups of plants growing in individual fields or field margins. If less than five subpopulations were encountered, all available subpopulations were sampled. Subpopulations were chosen at random with the constraint to have a minimum distance of 100 m to adjacent subpopulations. In each subpopulation, population size was estimated and fresh green leaves were stored in Silica gel for up to ten randomly selected individuals. Altogether, between 11 and 47 individuals were sampled for each population. Note that in Witterda only a single individual of *A. aestivalis* was found.

Landscape structure

The landscape structures were digitized from aerial photographs (taken in 2008) using ArcGIS (ESRI), and the percentage of all present land cover types, as well as mean field size and length of field margins were calculated (Table 5.1). Geographic coordinates of all sampled populations were obtained by GPS in order to calculate the linear distance between populations as well as the mean distance between subpopulations from the same region.

DNA extraction, AFLP analysis and scoring procedure

DNA was extracted from leaf samples using the NucleoSpin Plant Kit (Macherey-Nagel), concentration and quality was checked with a NanoDrop spectrophotometer (Thermo Scientific) and by running 1.5 % agarose gels. AFLP analysis was carried out following the method of TRYBUSH *et al.* (2006) with some minor modifications: (1) We used 5 µL instead of 2.5 µL of the digested diluted and ligated DNA template for the following preamplification and (2) for the selective amplification reactions we used 2 µL instead of 1 µL adjusting the contents at each step, respectively. Two fluorescent dye-labeled primer combinations were used: *MseI*-CAG/*Eco*RI-ACG(NED) and *MseI*-CAG/*Eco*RI-AGA(6-FAM). The resulting AFLP fragments were separated on an automated ABI 377 sequencer (PE Applied Biosystems) using the GeneScan 500 ROX labeled size standard (PE Applied Biosystems). Control samples with distilled water were included in each run.

Fragments between 100 and 600 bp were scored in an automated way using the program GeneMarker v1.91 (SoftGenetics) for the presence (1) or absence (0) of bands and assembled as a binary matrix based on the scoring protocol of WOOTEN & TOLLEY-JORDAN (2009). Local southern size call algorithm, peak saturation, baseline subtraction, pullup correction, and spike removal correction were selected with application of the size standard. A peak was considered as (1) when peak intensity was between 50 – 30000 rfu. Peaks, which could not confidently be called by the software, were denoted by “?”. Data were standardized across individuals for each primer combination by automatically creating a panel by GeneMarker. On the generated panel, electropherograms in which the size standard used in the analysis matched less than a theoretical standard of 90% as well as poor quality raw electropherograms were excluded from further analysis. Other settings, including stutter peak filter, local and global detection percentages and smoothing did not affect the scoring or performed worse and were therefore left at default values.

Mono- and polymorphic loci of *A. aestivalis* were identified from presence/absence data matrices, monomorphic loci were excluded. Only AFLP fragments that were scored in at least three individuals per species were included in the analysis. Repeatability was tested by analyzing a total of 20 *A. aestivalis* individuals from two different landscapes, Kyffhäuser and Hainleite a second time starting from the restriction step following the procedure mentioned before.

Statistical analyses

Nonparametric Mann-Whitney U tests were used to identify differences in variables of landscape structure, population size, and mean distance between populations as well as in genetic differences between the two differently structured study landscapes. The automatic scoring procedure of the AFLP fingerprint data resulted in a large number of bands, including cells with missing data. We thus analysed the full matrices, as well as subsets, where we concentrated only on those bands that were reliably detected, and bands that had a minimum frequency of 11 (minimum no. of individuals per population). These 3 sets plus the subset with 96 individuals fingerprinted the second time (see above) where subjected to the same statistical analyses.

Both band- and allele-based approaches were employed (BONIN *et al*. 2007). The presence/absence data from the AFLP samples were used to calculate genetic similarities based on the Dice coefficient (DICE 1945, NEI & LI 1979) for all possible pairwise comparisons of individuals within and among populations of *A. aestivalis* and *C. regalis*, respectively. Based on this band-based genetic similarity, dendrograms were generated by using the neighbor-joining method in the TREECON software package (VAN DE PEER & DE WACHTER 1994). Robustness of trees was evaluated by bootstrapping (1000 bootstrap replicates) using TREECON. Principal coordinate analysis (PCoA, GOWER 1966) based on the Dice similarity coefficient (DICE 1945) was performed in FAMD (SCHLÜTER & HARRIS 2006). The mean pair-wise Dice dissimilarity among individuals of a given population served as one measure of intra-population diversity (calculated with PCORD, MCCUNE & MEFFORD 2011). The number of polymorphic sites (PPL; percentage of polymorphic sites) was calculated using GenAlex 6.5 (PEAKALL & SMOUSE 2006). For a parallel allele-based approach, within population gene diversity (NEI 1987) was estimated, and analyses of molecular variance (AMOVA, GenAlex) conducted: hierarchical levels were landscape types (diverse / monotonous) and populations. A Mantel permutation test on isolation-by-distance was implemented in GenAlEx 6 using 9999 permutations to correlate pairwise

Φ_{st}-values with geographic distances. All statistical analyses were separately performed on the subsets and the repeated dataset (except for the Mantel permutation test) in the same way as for the initial data set to qualitatively assess reliability of results.

Results

Landscape and population structure

Differences in local landscape variables were significant according to non-parametric Kruskal-Wallis tests in spite of limited statistical power (n=3, Table 5.1). The share of grasslands, forests and urban areas was higher in the diverse landscapes; mean length of field margins as well as population numbers for both species were also higher. The monotonous landscapes had more arable fields and distances between subpopulations were larger. Total population sizes of *A. aestivalis* and *C. regalis* were similar in both landscapes (Table 5.2).

AFLP patterns and genetic diversity

The two primer combinations yielded a total of 393 AFLP loci for *A. aestivalis* among 163 individuals of the original dataset. The 20 individuals of the repeated dataset had 380 AFLP loci for *A. aestivalis*. For *C. regalis*, the two primer combinations yielded a total of 434 loci among 142 individuals. All these loci were polymorphic. Main data sets and respective subsets derived from the main data set (reduced no. of bands) yielded qualitatively identical results, and we thus focus our description on the main data set only.

Genetic diversity measures of *A. aestivalis* populations ranged from 0.31 to 0.35 for gene diversity (allele-based, Hj), from 0.20 – 0.33 for mean Dice dissimilarity, and from 94 to 98% for Percent Polymorphic loci (band-based, PPL Table 5.2). In *C. regalis*, H_j ranged from 0.28 to 0.32, Dice from 0.15-0.35, and PPL ranged from 77 to 93%. The landscape types did not show significant differences with respect to any of the measures of gene diversity tested.

Table 5.1. Population, region and habitat characteristics for the six study regions in Central Germany (percent cover is indicated for major land use classes, total length of field margins in km, mean field size in ha, as well as mean distances between populations in m, and number of subpopulations of *A. aestivalis* and *C. regalis*, respectively).

Population	Region	Longitude (east)	Latitude (north)	Arable Land [%]	Grasslands [%]	Forests [%]	Urban Development [%]	Length of field margins [km]	Mean field size [ha]	Mean distance between subpopulations [m]	No. of subpopulations
Diverse landscapes											
1-5	Kyffhäuser	10°57'	51°24'	38.3	29.0	28.0	4.6	34.3	6.5	941/1064	26/62
6-10	Schmoner Hänge	11°35'	51°19'	54.1	18.0	19.9	7.9	43.6	8.9	872/1047	32/66
11-15	Drei Gleichen	10°52'	50°51'	55.2	18.8	20.4	5.5	47.1	6.2	982/958	172/108
Mean (s.d.)				49.2 (9.5)	21.9(6.1)	22.8(4.5)	6.0(1.7)	41.7(6.6)	7.2(1.5)	932 / 1023 (56/57)	77/79 (83/26)
Monotonous landscapes											
16-20	Hainleite	11°02'	51°17'	96.7	0.3	0.0	2.3	28.6	78.1	790/840	20/38
21-25	Querfurter Platte	11°36'	51°19'	95.4	0.1	0.7	3.9	28.4	102.1	848/1068	8/11
26-27 (26-30)	Witterda	10°53'	51°03'	97.00	0.1	0.1	2.8	30.5	61.7	1504/1171	2/8
Mean (s.d.)				96.4(0.9)	0.2(0.1)	0.3(0.4)	3.0(0.8)	29.1(1.1)	82.7(23.5)	1047/1026 (397/169)	10/19 (9/17)
probability				<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	ns/ns	<0.05/<0.05

Table 5.2. Population size, number of analyzed individuals, Nei's genetic diversity (H_j), number of polymorphic sites and percentage of polymorphic loci (PPL) of *A. aestivalis* and *C. regalis*. (abbrevations for landscapes: D = diverse landscapes, M = monotonous landscapes - abbrevations for regions: K = Kyffhäuser, S = Schmoner Hänge, D = Drei Gleichen, H = Hainleite, Q = Querfurter Platte, W = Witterda); standard error for H_j was less than 0.01 in all cases.

		Adonis aestivalis					*Consolida regalis*				
Land-scape	Region	Pop. size	No. of analyzed plants	H_i	Mean Dice diss.	PPL [%]	Pop. size	No. of analyzed plants	H_j	Mean Dice diss.	PPL [%]
D	K	187	47	0.35	0.20	97	601	41	0.32	0.15	91
D	S	172	40	0.34	0.22	97	549	37	0.29	0.18	88
D	D	360	22	0.32	0.30	94	478	16	0.31	0.35	91
Mean		*240*		*0.34*	*0.24*	*96*	*543*		*0.30*	*0.23*	*90*
M	H	847	31	0.32	0.29	95	594	26	0.32	0.26	93
M	Q	213	23	0.31	0.33	98	120	11	0.28	0.27	81
M	W	130	-	-		-	394	11	0.30	0.21	77
Mean		*397*		*0.33*	*0.31*	*97*	*369*		*0.29*	*0.24*	*83*
P		*ns*		*ns*	*ns*	*ns*	*ns*		*ns*	*ns*	*ns*

Genetic differentiation and partitioning of molecular variance

For *A. aestivalis*, the overall Φ_{st}-value was 0.06. Mean Φ_{st}-values were Φ_{st} = 0.06 for the diverse landscape (range 0.04 – 0.10) and Φ_{st} = 0.01 for the two populations in the monotonous landscape. For *C. regalis*, the overall Φ_{st}-value was Φ_{st} = 0.07; values were mean Φ_{st} = 0.11 (range 0.08 – 0.13) for the diverse landscape and Φ_{st} = 0.04 (range 0.02 – 0.06) for the other type. For both species, both overall and pairwise values were significant, except for the pair-wise comparisons between *A. aestivalis* populations D, H, Q. The AMOVA partitioned the significantly largest fraction of variation in *A. aestivalis* within populations (94%), whereas only 5% were partitioned among populations within habitat types (Table 5.3) and 1% was partitioned among landscape types. In *C. regalis*, most variation was partitioned within populations (92%), whereas only 8% rested among populations leaving 0% for landscape types.

Table 5.3. Summary of analysis of molecular variance (AMOVA). Plants represented each five subpopulations from five regions of *A. aestivalis*. Summary of analysis of molecular variance (AMOVA). Plants represented each five subpopulations from five regions except of one region (Witterda) with three subpopulations of *C. regalis*.

	Adonis aestivalis				*Consolida regalis*			
Source	df	SS	MS	%	df	SS	MS	%
Among types	1	282.58	282.58	1	1	26.08	26.08	0
Among pops	3	647.87	215.96	5	4	171.16	42.79	8
Within pops	158	13252.01	83.87	94	136	1945.46	14.30	92
Total	162	14182.46		100	141	2142.70		100

Genetic similarity

The cluster analysis for *A. aestivalis* dataset showed no population-specific clustering (See Appendix Table S5.1, S5.2 in Supporting information). The same data were also subjected to Principal Coordinate Analysis, with the three axes of the PCoA for *A. aestivalis* accounting for 23.9% of the total variation (Figure 5.2).

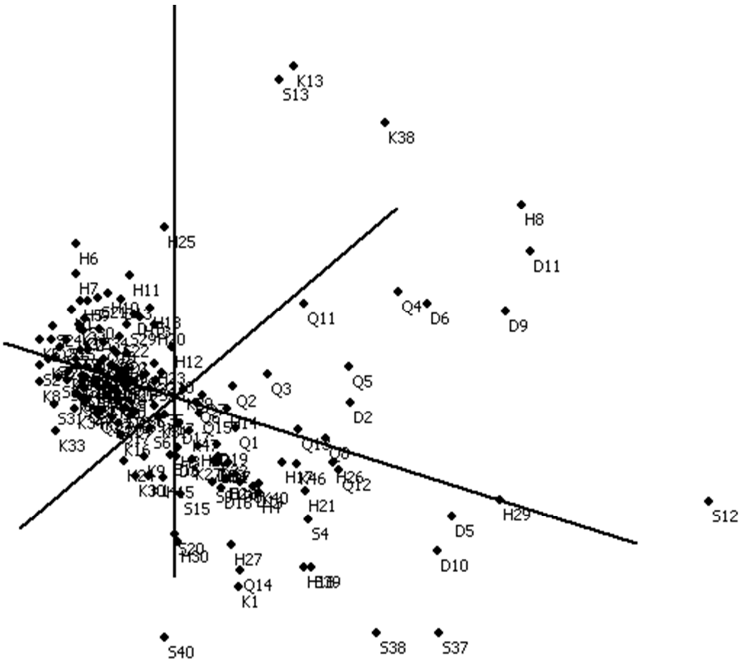

Figure 5.2. Three-dimensional plot from the Principal Coordinates Analysis (PCoA) based on Dice similarity of the AFLP data of 163 *A. aestivalis* individuals from the original dataset sampled from five regions in Central Germany (diverse landscapes: D=Drei Gleichen, K=Kyffhäuser, S=Schmoner Hänge, monotonous landscapes: H=Hainleite, Q=Querfurter Platte). The three axes explain 13.3%, 5.7% and 4.9% of the data, respectively.

Consolida regalis individuals from the Kyffhäuser region clustered separately in the neighbour joining tree, and those from the Schmoner Hänge region were also somewhat apart (aee Appendix Figure S5.3 in Supporting information). The first three axes of the corresponding PCoA accounted for 19.3% of the total variation, with individuals from Kyffhäuser and Schmoner Hänge again forming separate groups, (Figure 5.3). Pairwise Φ_{st} values also indicated for both species that populations from the Kyffhäuser are most distant to the others while populations Drei Gleichen, Hainleite and Querfurter Platte are most similar to each other.

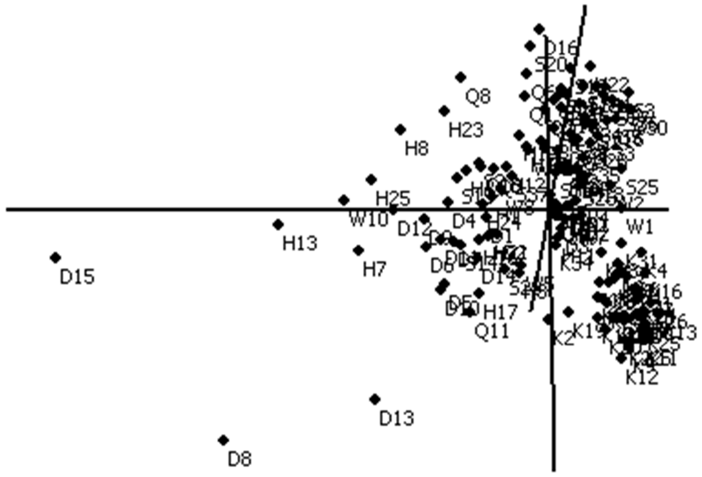

Figure 5.3. Three-dimensional plot of the first three axes from the Principal Coordinates Analysis (PCoA) based on Dice similarity of the AFLP data of 142 *C. regalis* individuals from the original dataset sampled from six regions in Central Germany (diverse landscapes: D=Drei Gleichen, K=Kyffhäuser, S=Schmoner Hänge, monotonous landscapes: H=Hainleite, Q=Querfurter Platte, W=Witterda). The axes explain 7.9%, 7.2% and 4.2% of the data, respectively.

There was no evidence for isolation-by-distance on the population level. For *A. aestivalis* the Mantel test among populations from the diverse landscapes, and among populations from the monotonous landscapes indicated no significant correlations between spatial and genetic structure (among all: $r = 0.124$, $p > 0.1$; diverse: $r = -0.07$, $p > 0.5$; monotonous: $r = -0.374$, $p > 0.6$). The pattern was qualitatively similar for *C. regalis* (among all: $r = 0.017$, $p > 0.3$; among diverse: $r = -0.002$, $p > 0.5$; among monotonous: $r = 0.123$, $p > 0.1$).

Discussion

Landscape structure and genetic differentiation

Genetic structuring in *A. aestivalis* and *C. regalis* populations was marginally higher in the diverse landscapes (Φ_{st}= 0.06 and 0.11, respectively) than in the monotonous landscapes (Φ_{st}= 0.01 and 0.04), implying equally strong, if not even somewhat stronger habitat fragmentation in the diverse landscape. Larger geographic distances between populations in the diverse landscape can be excluded as an explanation since mean population distances were not significantly different between regions and Mantel tests were also not significant. The higher proportions of unsuitable habitat in the diverse landscape such as grasslands and forests form some kind of barrier for gene flow among populations. In contrast, populations from monotonous landscapes seem to have frequent genetic exchange even between distant populations. Apart from natural barriers to gene flow, human land use patterns are likely to differ between landscapes: In the monotonous region fewer farmers (and fewer tractors) cultivate more land, thus increasing the likelihood of spreading seeds across the region. For both species, *A. aestivalis* and *C. regalis*, lack of specific adaptations to long-distance seed dispersal increases the importance of hemerochory, i.e. dispersal of plants by agricultural practice. This process contributed considerably to dispersal over large distances in former times and still does today (BONN & POSCHLOD 1998, POSCHLOD *et al.* 2005, see also WALLINGA *et al.* 2002).

Sporadic gene flow over larger distances due to human activity (e.g. BONN & POSCHLOD 1998) could also explain the lack of significant isolation-by-distance in our data sets. Weak isolation-by-distance in a comparable study of SCHMIDT *et al.* (2009) studying *Geum urbanum* in German forests was suggested to be the result of reduced connectivity between populations, but gene flow in forest species may be different from that in fields. Low differentiation was reported for the arable weed *Alopecurus myosuroides*, which is not comparable since it is wind-pollinated (DELYE *et al.* 2010). The detected levels of genetic differentiation between *A. aestivalis* and *C. regalis* populations are comparatively low (NYBOM 2004), which may indicate that either population subdivision is a rather recent event in the area or gene flow is still occurring to some small degree as suggested by BERGE *et al.* (1998). Despite that, the low differentiation should not be overemphasized since increasing the geographical distances between the sampled populations frequently increases the F_{ST}-values in population genetic studies (NYBOM & BARTISH 2000, VEKEMANS & HARDY 2004).

Indeed, larger-scale comparisons across Central Europe for our two species revealed higher levels of genetic differentiation (BRÜTTING *et al*. 2012b). In support of differentiation on the small scale, the AMOVA analysis demonstrates that the amount of variance was by far largest within the populations of *A. aestivalis* and *C. regalis* which contrasts with the findings of most studies examining species threatened by habitat fragmentation (TRAVIS *et al.* 1996, SCHMIDT & JENSEN 2000; JACQUEMYN *et al.* 2007, STANTON *et al.* 2009), again pointing to relatively frequent exchange.

Genetic diversity

Estimates of population-level gene diversity also showed no clear pattern. Compared to levels reported by HAMRICK & GODT (1989) and other studies dealing with predominantly outcrossing species (e.g. NYBOM & BARTISH 2000, CULLEY *et al.* 2007, PARISOD & BONVIN 2008), populations of *A. aestivalis* and *C. regalis* from our study show low to medium levels of genetic diversity. *Consolida regalis* showed approximately similar values to *A. aestivalis* suggesting that pollination and dispersal modes are not that different. The diverse landscape harbours a larger number of smaller but less related subpopulations, in contrast to the monotonous landscape in which populations have been homogenized across larger areas as a result of agricultural intensification and field enlargement. Low genetic differentiation of *A. aestivalis* and *C. regalis* populations, which did not differ significantly in population sizes, may be a result of a single or few colonization events accompanied by inbreeding (JACQUEMYN *et al*. 2004). Loss of genetic variation after colonization depends on the degree of spatial isolation from other sources, and on the incoming diversity of pollen and seed (SORK & SMOUSE 2006). Whether the current levels of genetic variation are caused by increased inbreeding or founder effects cannot be concluded from our results. Inbreeding should lead to a reduction in heterozygosity within populations (YOUNG *et al.* 1996, KELLER & WALLER 2002), which cannot directly be assessed from dominant markers such as AFLP in contrast to codominant markers (e.g. microsatellites). Nevertheless, inbreeding may arise from increased self-pollination (YOUNG *et al.* 1996), which may become more important with declining pollinator populations (POTTS *et al.* 2010). Alternatively, remaining partners may be related through recent common ancestry (YOUNG *et al.* 1996), probably as a result of historical founder effects or small population sizes of *A. aestivalis* and *C. regalis*. Thus, census population size may not be very effective in evaluating survival chances of populations. This is in line with studies demonstrating that rare species may harbour similar levels of genetic diversity as more widespread species (GITZENDANNER & SOLTIS 2000).

Conclusions - Conservation implications

Maintaining genetic diversity has become a major issue in conservation biology. Despite much effort by the European Union since the mid-1980s, e.g. through agri-environment schemes, it is doubtful whether existing efforts are effective in protecting agricultural biodiversity (KLEIJN *et al.* 2001, 2006). Regarding arable plant communities, a range of measures has been introduced in European countries, including Germany (MEYER *et al.* 2010), Switzerland (AGROFUTURA 2011), Great Britain (CARSTAIRS 2006, STILL &BYEFIELD 2007), Belgium (LEGAST *et al.* 2008) and France (CHARDÉS 2011), to stop the decline of arable plant species. Because management practices that allow survival within fields lead to considerable economic forfeits, such efforts have mainly focussed on field margins that are economically unimportant (e.g., 'Ackerrandstreifenprogramm'). Most existing programmes solely considered the species level and not the community (WILSON 1994, MEYER *et al.* 2010). If the goal is to secure the long-term survival of endangered species such as *A. aestivalis* and *C. regalis,* strategies that maintain genetic variation must be initiated.

Our results demonstrated that (i) landscape structure had only a small effect on the amount of genetic variation among and within populations of *A. aestivalis* and *C. regalis*, but whether this was related to landscape structure per se, the history of agricultural practice or the size of suitable habitats, cannot be decided by our study. Our findings do not support the assumption that a higher landscape heterogeneity always improves the viability and increases the genetic diversity of arable plant population. (ii) The *A. aestivalis* and *C. regalis* populations of all studied regions exhibited hardly any genetic differentiation. This indicates that there should be no problem enriching populations by transferring plants from other populations on this scale. (iii) In both species, most of the genetic variation was located within populations irrespective of landscape structure. Furthermore, on small spatial scales, we found no indication of isolation-by-distance, possibly pointing to occasional dispersal by human activity throughout central Germany. Studies on larger spatial scales are needed to test this idea.

In many areas of Central Europe, the remaining population sizes, in particular on isolated arable field margin strips maintain similar genetic variation to larger fields, but isolation and small habitat size make populations vulnerable. Since our data reveal only minor differences in the genetic constitution of the different populations, we suggest that active seed transfer and thus the deliberate mixing of gene pools from different populations is an acceptable and straightforward means of increasing genetic exchange in these threatened species.

As a first step we started to establish permanent so-called ‘important arable plant areas’ (IAPA) or ‘sanctuary fields’ (MEYER *et al.* 2008, 2010) to save the remnant populations of the arable vegetation in Central Europe. In a second step, seed exchange by transferring plant material from selected IAPA locations to other potential sanctuary fields or field margin areas is recommended on a regional level where the within-population genetic diversity is found to be moderate or low. It is important that such arable plant conservation measures are accompanied by genetic analyses and monitoring activities to document the success or failure.

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Supporting information

Additional supporting information may be found at the end of this document:

Appendix Figure S5.1. Neighbor joining phenogram of *A. aestivalis* individuals from the original dataset using Nei-Li (=Dice) distances from 5 regions in Central Germany (D=Drei Gleichen, H=Hainleite, K=Kyffhäuser, Q=Querfurter Platte, S=Schmoner Hänge).

Appendix Figure S5.2. Neighbor joining phenogram of *A. aestivalis* individuals from the repeated dataset using Nei-Li distances from 2 regions in Central Germany (H=Hainleite, K=Kyffhäuser).

Appendix Figure S5.3. Neighbor joining phenogram of *C. regalis* individuals using Nei-Li distances from 6 regions in Central Germany (D=Drei Gleichen, H=Hainleite, K=Kyffhäuser, Q=Querfurter Platte, S=Schmoner Hänge, W=Witterda).

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CHAPTER

6

Are current agri-environment schemes suitable for long-term conservation of arable plants? – A short review of different conservation strategies from Germany and brief remarks on the new project ‘100 fields for diversity’

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Abstract

In Germany, arable plant communities are among the most threatened vegetation types; formal legal protection of the associated rare species/communities is, however, virtually non existent. Using questionnaires and a literature survey, we assessed the history and the current status quo of arable plant conservation in Germany. Results revealed that most conservation projects fail after an often initially successful phase, which is mainly due to complicated and insecure funding. Agri-environment schemes, such as protection of field-margin strips, have started losing attractiveness for farmers due to constantly changing regulations and conditions for grants, and increasingly complex bureaucratic procedures. In addition, current schemes usually last only 5 years, and thus provide no permanent protection, even if contracts should happen to be extended. Here, we present the new conservation project ‘100 fields for diversity’, which aims to establish a nationwide network of Important Arable Plant Areas (IAPA) in Germany.

Keywords: arable plants; conservation schemes; nationwide network; sanctuary sites; Germany

Introduction

There is scarcely any ecosystem in Europe which has been as markedly influenced by human activities as farmland (ELLENBERG & LEUSCHNER 2010). For this reason, arable plants belong to the most threatened plant species associations in the whole of Central Europe (HILBIG & BACHTHALER 1992, HILBIG 2007). Increasing economic pressures are driving farmers to optimize yields, such that population sizes and diversity of arable plant communities and the related fauna have decreased more severely and rapidly than in any other habitat in our cultural landscape (ŠILC & CARNI 2005, TSCHARNTKE *et al*. 2005, BAESSLER & KLOTZ 2006, STILL 2007, LOSOSOVÁ & SIMONOVÁ 2008, FRIED *et al*. 2009).

Levels of threat are high for the German arable flora – currently around 120 of the approximately 350 arable plant taxa in Germany are considered endangered and at least 15 species are already extinct (HOFMEISTER & GARVE 2006). In regions such as northern Germany, the impoverishment of arable plant communities even exceeds the losses described for grasslands on mesic and wet soils (WESCHE *et al*. 2009). The main reason is that grasslands are at least partly subject to conservation efforts, and a large number of conservation projects for grasslands have been implemented (FRIEBEN 2005, ROSENTHAL & HÖLZEL 2009). In contrast, the arable flora is poorly covered by ongoing conservation schemes in Germany, and there is no formal legal protection for its rare species or plant communities (MEYER *et al*. 2008).

Here, we review the status quo of current conservation concepts for arable flora and vegetation in Germany briefly describing the development of these concepts over the last decades and putting a special focus on field-margin strips as the single most wide-spread conservation tool. This forms the basis for introducing the project ‘100 fields for diversity – the development of a nation-wide reserve network for important sites of arable plant communities in Germany, which was started in 2007. Its main aim is to develop long-term strategies for conserving typical segetal vegetation types as Important Arable Plant Areas (WILSON 2007) and ensure their adaptability in future decades. A special focus is on identifying economically sustainable and long-term effective financial schemes for maintaining the reserves.

Materials and Methods

Using questionnaires and a literature survey, we analyzed the current status quo of activities in the task of arable plant conservation in Germany (for more details see MEYER *et al*. 2008). Questionnaires were sent specifically to institutions or other stakeholders (e.g. nature and landscape conservation groups, open-air museums, local nature conservation authorities) who are involved in conservation of important arable plants areas by establishing and maintaining special sanctuaries or so-called 'Field Flora Reserves', where rare arable plants are sown in suitable sites (usage of local seed provenances is unfortunately not mandatory here). In addition to standard data on habitat conditions and species present, our survey focussed on suitable cultivation practices and the financial background of the conservation activities.

We tried to collect country-wide data on the history of agri-environment schemes dedicated to the conservation of arable plants in Germany. Unfortunately, no reliable key data (protected areas in hectares, financial assets) for field margin strip programs are available at the federal level; therefore we contacted the ministries of agriculture and environment of the respective federal states individually.

Results and Discussion

The history of arable plant conservation projects

First considerations of the need to conduct specific measures for preserving arable plants can be traced back in the German literature to the early 1950s. It was the phytosociologist Robert GRADMANN (1950) who proclaimed that the '*the flower-filled cornfields have nearly vanished from our surrounding landscape, and very soon small reserves will have to be established where our traditional three-step crop rotation system is still practised using only unpurified seeds*'. Consequently, the first preservation schemes for arable plants were established during the 1960s. In the beginning, efforts concentrated on the preservation of selected species (ex situ conservation in botanical gardens, open-air museums or gene banks). Conservation of entire communities in situ or on farm was, however, neglected in those times.

This task was adopted only from the early 1970s onwards when so-called field flora reserves were increasingly implemented (SCHLENKER & SCHILL 1979). The objective was to protect the regionally typical arable flora and vegetation on the ecosystem level under conditions of low-input cultivation. The establishment of field flora reserves was often linked to the cultivation of ancient or regionally distributed crop varieties, and has been particularly pursued by the ‘Arable plant conservation working group’ in the former Eastern Germany. By 1989, almost 25 so called Important Arable Plant Areas had been established (ILLIG 1990). Unfortunately, only 4–5 of these sanctuaries are still subject to appropriate management, and thus currently in reasonable condition (MEYER *et al*. 2008).

The implementation of conservation headlands in Germany

The goal of conserving viable populations of the arable flora in situ or on farm may also be achieved by the concept of establishing extensively managed field margins. Here, field edges are left untreated by herbicides, and the resulting additional labour effort needed and the reductions in crop yield are financially compensated by governmental funds. In 1978, a field margin strip program for arable plants - probably the first agri-environment scheme in the former West Germany - was established in the federal state of North-Rhine-Westphalia (Table 6.1; SCHUMACHER 1980). In the last three decades, numerous studies have investigated the positive effects on the arable field flora of herbicide-free conservation areas in the farmland (an overview of around 50 studies published before 1994 can be found in VAN ELSEN 1994). This type of conservation measure has been discussed extensively ever since it’s first implementation. Environmentalists have criticised compensatory payments for avoiding environmentally damaging measures such as herbicide use to be absurd (DAHL 1987, KOCH 1991), whilst agrochemical companies advertise crop margins as being ‘*prime examples of how economy and ecology can harmoniously co-exist in agriculture*’. In any case, untreated crop margins can play an important role in the conservation of rare plant species and their communities, provided that the field margins are selected according to criteria that highlight their value in terms of threatened species present. The conservation success of the field margin scheme thus depends heavily on the involvement and dedication of local experts on biodiversity. Unfortunately, support by experts is lacking in many cases, and the selection of field margins to be included in the programme is not based on floristic richness or similar criteria, but on suggestions by the farmers themselves, who have often the interest in the programme in that they want the money but may not have the most appropriate areas for conservation. The most severely threatened locations of rare species are thus only accidentally included in the protection measures, and the ultimate goal of the scheme, i.e. to effectively protect threatened arable plants, is rarely achieved.

Table 6.1. Key features of the implementation of the headland program for conservation of arable plants in Germany (according to SCHUMACHER 1980).

Unsprayed conservation headlands for arable plants

... established 1978 as a pilot project by Prof. Wolfgang Schumacher (University of Bonn) in the northern Eifel region (North-Rhine-Westphalia).

The basic idea: 'To protect and support rare segetal species through targeted avoidance of chemical weed control along the edges of managed fields.'

- Under otherwise identical cultivation methods a zone between 3-5 metres wide will be left unsprayed along the edges of the cultivated field;
- the farmers who volunteer to participate will get financial compensation for reduced yields;
- in order to prevent the growth of weeds, a reduced application of fertilizers (and of lime in sandy soils) is recommended

The success of conservation headland programs crucially depends...

- on an appropriate site selection which is targeted on the presence of rare and endangered arable plants and plant communities,
- on the mentoring of the participating farmers,
- on the engagement of biodiversity experts on-site.

In most cases, local authorities cannot be criticised for this practise, as they often lack sufficiently experienced personnel. For this reason, the German state of Bavaria occasionally awards contracts to self-employed biologists to undertake the professional evaluation and monitoring of field margins in terms of biodiversity. A positive example also comes from the district of Euskirchen in North Rhine-Westphalia, where the first unsprayed field margins (as part of the previously mentioned pilot programme) were established in 1978. The crop margin programme was supervised by two full-time agricultural engineers from the governmental agriculture agency until the beginning of the 1990s, providing very effective protection for threatened species. Threatened species were thus effectively protected. In contrast, despite the preparation of comprehensive reports with recommendations for sites of high conservation interest (VAN ELSEN & SCHELLER 1995), the states Hesse and Thuringia failed to stop the rapid declines in rare arable plant populations that were still common in the Eichsfeld region and northern Hesse. Unfortunately, this seems to be the rule rather than the exception in Germany, particularly as available publications tend to report the successful conservation endeavours and not the failures.

The ‘unsprayed conservation headlands’ programme was a long-term favourite among conservation agencies and reached its climax during the 1980s and ‘90s when several thousands of hectares were covered by the programme throughout Germany. However, in the last decade agri-environment schemes for arable plant conservation started to lose their attractiveness for farmers for several reasons:

- the risk-aversion of weed spreading (MANTE & GEROWITT 2009)
- the regulations and conditions for grants were modified,
- the prices for agricultural products - especially cereals - increased,
- new programs like the establishment of sown strips of mixed wildflowers offered higher income options (VAN ELSEN *et al*. 2005, MANTE & GEROWITT 2009) and
- the agricultural policy at the EU and national changed rapidly and bureaucratic procedures became increasingly complex (WHITFIELD 2006, MEYER *et al*. 2008).

Even in some federal states known for ‘good practice’ like Lower Saxony (WICKE 2007) and Thuringia (REISINGER *et al*. 2005) (Table 6.2), the area covered by headland programs for arable plants declined dramatically during the last 2-3 years (Figure 6.1). In addition, current agri-environment schemes usually run for 1-5 years only, and thus provide no long-term protection perspective which is required to preserve the arable flora. Even if the contracts are extended, farmers are allowed to move the less intensively managed strip to another part of the field which drastically reduced the benefit for biodiversity.

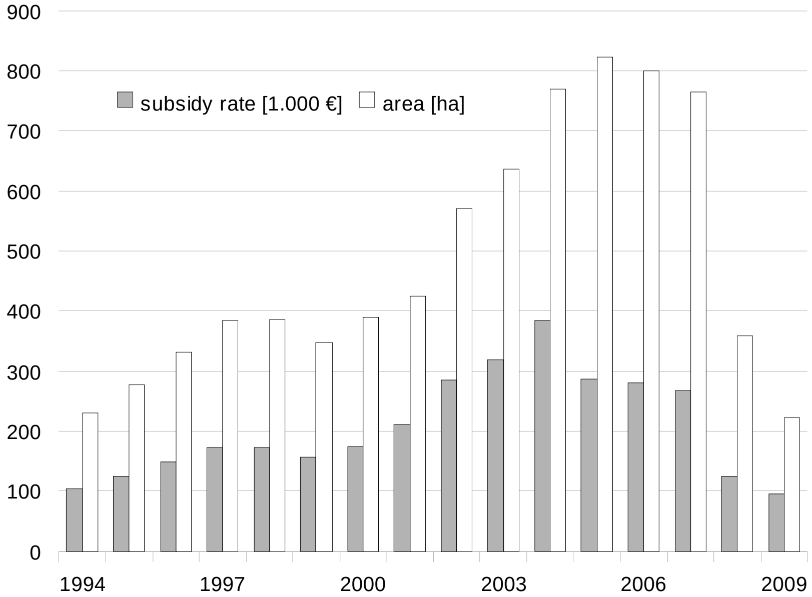

Figure 6.1. The development of subsidy rates (in 1.000 Euro) and area sizes (in ha) of field-margin strips in the federal state of Thuringia from the year 1994–2009.

Table 6.2. Review of agri-environmental schemes for arable plants as they are offered in some federal states of Germany (data as of 12/2009).

What will be subsidised?	**Requirements**	**Subsidy rates**
Bavaria 1.1 Extensive agricultural cultivation for farmland birds and arable plants	● no usage of maize, clover, clover-grass, lucerne, potatoes , sugar beets ● no usage of catch crops ● no cultivation between 15.04. and 30.06. every year ● reduced seed density (row spacing at least 20 cm) ● yield index (a measure of average site-specific crop output) < 4.500 → ● yield index > 4.500 → ● optionally: no application of fertilizer and →	150 €/ha 350 €/ha 310 €/ha
Lower Saxony Conservation oriented management of agriculturally used sites 1.1 Arable plants	● field margin strips at least 6 and at most 24 m in (along field edges) ● only grain crops, no other catch crops ● rape may be sown, maize not ● no pesticides nor fertilizers ● double row spacing (at least 18 cm) ● fields with high conservation valuable are eligible for complete or partial protection ● subsidy rates for field-margin strips → ● subsidy rates for entire fields or parts of fields →	425 €/ha 275 €/ha
North Rhine-Westphalia nature conservation of fields /field margins, cultivation for conservation of arable plants	● sites may rotate (total area covered must be retained) during allowance period ● without rotation: grasses may be controlled with selective herbicides twice during the allowance period ● no usage of mechanical, thermal and electrical controls of arable plants **1. option** → ● no application of pesticides, growth regulators and acidic fertilizers ● no cultivation of perennial forage crops **2. option** → ● no application of synthetic chemical nitrogen fertilizers ● no application of pesticides, growth regulators and acidic fertilizers ● no cultivation of perennial forage crops	350 €/ha 475 €/ha
Rhineland-Palatinate Arable plants	● field strips between 5 and 20 m in width. Fields have to be ploughed each year, but may be left unsown with crops every second year → ● double row spacing (at least 20 cm) or/and half sowing intensity ● no usage of fertilizers ● no usage of plant protection and weed control methods ● alternatively: late stubble processing →	650 €/ha 45 €/ha
Saxony A4 – nature conservation field cultivation with reduction of pesticides and guidelines for cultivated plants	● grain may be cultivated at most 3 times in 5 respectively 6 years, or 4 times in 7 years ● no cultivation of maize, rape and sunflowers ● no catch crops ● usage of organic fertilizers only (liquid manure, stall manure), at most every second year ● stubble processing at the earliest from the 15th September onwards ● no application of herbicides, rodenticides, insecticides and growth regulators →	304 €/ha
Thuringia L32 – Field margin strips	● only on agricultural sites with significant populations of arable plants, which are still used for agricultural production: ● field margin strips between at least 3 and at most 24 m in width (along field edges) → ●sowing of the same species of cultural plants as on the rest of the field ● no application of pesticides and fertilizers ● no mechanical processing other than sowing of fields ● no cultivation of perennial forage crops and root crops ● implementation is regularly monitored by the local nature conservation authority	452€/ha

Conclusions and Outlook

Status quo of arable plant conservation projects

Against the background of ongoing climate change, conservation should aim to 'provide' communities which are as diverse as possible. This is the only means of ensuring adequate functional, taxonomic and genetic diversity to cope with the need of adaptation to changing environmental conditions (HAMPICKE *et al*. 2005). In addition, Germany has a high level of responsibility for the protection of some arable species and their metapopulations, e.g. *Arnoseris minima* SCHWEIGG. et KOERTE, *Bromus grossus* DESF. ex. DC. and *Veronica opaca* FR. (WELK 2002, CZYBULKA *et al*. 2009), which can only be met by ensuring appropriate management of selected sites. In that sense, prospects for conservation of arable plants in Germany are disappointing and the status of the arable flora is alarming. The results of the questionnaire campaign revealed that most conservation projects for arable plants fail after an often initially successful phase, which is mainly due to the lack of long-term financial coverage of the running costs. Remarkably, half of those agencies or persons questioned had not had any exchange of views with those involved in similar conservation activities in other regions, although 95% of respondents expressed an interest in an exchange of ideas and experience. The respondents hoped that a national network would provide better public relations, give new ideas for further activities and result in a general improvement in conservation the status of arable plants. The existing initiatives would benefit from a supra-regional exchange and/or coordination, which could also help to gather advice on management in order to optimise conservation measures. Summarising the pros and cons, those questioned felt that the few long-term initiatives for conserving arable plants are mostly positive in terms of species protection although economic constraints are a permanent issue (MEYER *et al*. 2008). Another principal problem of the aforementioned agri-environment conservation schemes is that they just tackle the species level, while genetic, community and ecosystem levels are widely ignored. We therefore believe that the actual agri-environment schemes with their strong focus on headlands are not the most effective tool, with a principal reason being that communities along field margins are always subject to edge effects with the possible consequence that 'edge communities' in many cases do not harbour the target plants (i.e. threatened arable field species) but in fact are dominated by species from other habitats (e.g. grasslands or hedges). The lack of long-term options (with contracts only ranging from one to five years) adds to these problems and renders strip protections schemes insufficient to preserve the 'hot spots' of arable flora communities in Germany.

The conservation initiative '100 fields for diversity'

The project '100 fields for diversity', which has been funded by the Deutsche Bundesstiftung Umwelt (DBU) since 2007, attempts to cope with the shortcomings discussed above and to meet the needs of long-term preservation in the agricultural landscape by establishing a nation-wide system of arable field sanctuaries for the segetal flora and associated fauna. The regulations for field management are stricter in this programme than in earlier schemes of arable plant protection in order to increase the success in biodiversity conservation. The overall project goal is that management aimed at preserving and fostering arable plants is to be guaranteed in the long term (up to 25 years) on at least 100 particularly suitable arable sites throughout Germany. In that context, a suitable field has to meet the following criteria: high floristic value in terms of species composition, and the signing of long-term contracts with farmers and/or legally binding long-term commitments that guarantee long-term protection. In addition, the coverage of running costs for the next few decades has to be ensured. Only a long-term financial commitment will ensure the support of farmers. This is one of the main causes of the failure of earlier field margin strip schemes which are dependent on agri-environmental programmes with limited continuity. In addition, networking and the exchange of ideas are of crucial importance, because even under conditions of low-input farming practice, inappropriate management can lead to the partial or full loss of the characteristic species assemblages. Finally, the 100-fields initiative has the goal to conduct a long-term monitoring of these sanctuary sites by regional landscape conservation groups. In 2010, the first phase of the project will be finalised with at least 30 sanctuaries being already put in place and having secured management over the next decades. Additional information on this project is available in MEYER & VAN ELSEN (2007), MEYER *et al.* (2008), MEYER *et al.* (2010) and at project's website: www.schutzaecker.de

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CHAPTER

7

Synopsis

Key lessons learnt

The present study has shown that arable plant communities are under a dramatic threat, and this refers to all major organisational levels. The key objectives named in the introduction spanned a wide range from the European scale to the population level; the respective chapters demonstrated that the initially stated concerns were justified. The magnitude of the problem becomes apparent by a quick look on the key findings.

Threat status of arable plants – an European level assessment

The following key hypotheses were tested: (i) explanatory variables can be identified which can predict a ranking of countries in terms of the numbers of arable species that are nationally rare or threatened, and (ii) that the relative sensitivity of arable plant species to these variables can be quantified.

For the first time a suite of arable plant species was identified that are threatened at a continental scale due to the increasing intensification of agricultural production. Hypothesis (i) was supported as we found a positive relationship between national wheat yields and the numbers of rare arable plant species in a given country. The survey established that for every extra tonne/hectare of wheat produced approximately ten more plant species become nationally threatened. Many arable plants are still relatively common in countries where agro-chemical inputs are modest; examples include the new EU-member states or the southern European states. In comparison, the share of threatened plants is much higher in countries with highest wheat yields found in Central and North-Western Europe such as Germany, Switzerland or Austria. There, threats continue to increase due to changes in the abandonment or transformation of arable land, types of cultivated crops or re-intensification of former marginal arable land for the cultivation of biofuels/bioenergy crops.

Ranking species according to their threat level supported hypothesis (ii); species that are specialized on a single crop (e.g. flax specialists) are particularly vulnerable, including several taxa that have coevolved to mimic morphological or phenological characteristics of their host crop (HARLAN 1965). Some of these species are anecophytes with no known natural habitats outside the cultivated field and are endemic to Europe. For no clear reason, they are nonetheless not listed on any of the annexes of the Natural Habitats Directive of the European Union.

The European scale study has also demonstrated increased use of agro-chemicals, especially in central and north-western Europe, which caused losses for a group of species adapted to intermediate fertility. They share a similar ecological strategy, reflected in a relatively short stature and/or a large seeds, indicating a specific ecological response to the drivers of disturbance and fertility (WESTOBY 1998). A short stature will result in a low competitive ability in dense crop canopies, where increasing fertilizer use resulted in non-limited nutrient availability and intense competition with light becoming the main resource limiting growth (GAUDET & KEDDY 1988, KLEIJN & VAN DER VOORT 1997). As opposed to more characteristically stress-tolerant ruderals (sensu GRIME *et al.* 1997), which may continue to persist in other disturbed, less productive environments, species with a combination of short stature and large seed have been found to be adapted to habitats with intermediate fertility (STORKEY *et al.* 2010) - habitats that are declining most rapidly in response to increasing eutrophication of landscapes within Europe (SUDING *et al.* 2005).

Turnover in arable plant communities – do we need a new syntaxonomy of arable vegetation?

The hypotheses were tested that (i) after five to six decades of agricultural intensification the composition and richness in arable plant communities was altered drastically and (ii) that plant associations have been largely replaced by fragmented communities, with diagnostic species for the association level disappearing faster than diagnostics on higher levels.

Moving to a finer spatial scale, we assessed changes in arable plant communities by comparing historical relevés from the 1950s/60s with resampled relevés taken at the same fields in 2009. In a first step, communities were compared with respect to the occurrence of diagnostic species that allow classification of stands with respect to established phytosociological syntaxonomy. Hypothesis (i) was confirmed as our supra-regional comparative study indicated fundamental shifts in composition and richness of the Central German arable plant communities over recent decades. In particular, the diagnostic species of the alliances are disappearing to a disproportionately large extent. This is in line with other investigations within Central Europe (e.g. HILBIG 1985, TRZCINSKA-TACIK 1991, MÁJEKOVÁ *et al.* 2010), where diagnostic species on alliance, order and class level are declining less rapidly than association character species.

Nowadays, floristic differences between community types have largely disappeared, which indicates homogenization of arable plant communities and renders placement of recent relevés in established phytosociological systems, as already described above, difficult. This supports hypothesis (ii); field interiors are nowadays almost 'free' of plants and often only a limited set of 4-5 'agrotolerant' highly competitive and therefore common species such as *Chenopodium album* L., *Polygonum aviculare* L. or *Galium aparine* L. occur everywhere. In accordance with other studies (e.g. FRIED *et al.* 2009a), losses affected species that always have been rare but also common species decreased in density and frequency. Our results indicate that the main direction of this transformation process is towards the development of fragment communities that lack any diagnostic species for the association level. Our results imply that a countrywide effort to update classification of extant arable plant communities is urgently needed.

Dramatic impoverishment of biodiversity in arable plant communities

The key hypotheses were that (i) agricultural intensification has resulted in a reduced diversity of crop varieties and in denser crop stands; paralleled by (ii) significant shifts in the composition of the arable communities with diversity losses in archaeophytic species and increases in neophytic species and Poaceae. (iii) These shifts differ in intensity among different geological and thus soil substrate.

The long-term comparison spanning 5-6 decades showed that crop diversity decreased while crop cover generally increased confirming hypothesis (i). Winter cereals, oilseed rape and maize are most common today, while root crops and summer cereals showed large declines in cultivation. Analysis of Ellenberg Indicator Values pointed to increasing nutrient availability in the fields, which mirrors the general trend in croplands of Germany where fertilizations level have increased since 1950 from 40 to 105 kg N ha^{-1} yr^{-1} (ELLENBERG & LEUSCHNER 2010, UMWELTBUNDESAMT 2011).

Supporting hypothesis (ii), our resampling of historical vegetation relevés revealed tremendous losses on the plot level during the 50-yr period, when species richness declined by c. 65% (a median loss of 17 species per relevé). The magnitude of loss is in the upper range of values previously reported from Central Europe (30 – 90%, review by ALBRECHT 1995). In our sites, cover of the arable plant communities declined to about a tenth of its original extent (from 30% to 3%), corresponding to 75% of cover loss reported for other European countries (sensu RIES 1992, ANDREASEN & STREIBIG 2011). Archaeophytes showed pronounced losses in both richness and cover, which were, however, in the same order of magnitude as the losses in indigenous plants. The total number of neophytes recorded in our sample increased slightly. Losses on the plot level were partly mirrored at the level of the regional species pool, where 70 taxa corresponding to 23% of all previously occurring species disappeared. This adds further support to hypothesis (ii) and corroborates studies describing 20-50% losses in species pools of other regions in Germany (ALBRECHT 1995). In Eastern Europe (e.g. in Slovakia), where agricultural transformation processes started later and arable farming is less intensive, less than 10% of the species have disappeared during the past 50 years (MÁJEKOVÁ *et al.* 2010).

As hypothesised (iii), losses differed between geological substrates with sandy sites being less severely affected, where some specialized species still find habitats. Losses were most pronounced on calcareous soils. A study from the Czech Republic (LOSOSOVÁ & GRULICH 2009) explained the high losses in these communities with their high share of archaeophytes, a group of arable plants with predominantly Mediterranean origins and particularly high light demand and thus particular sensitivity to increasing crop cover. Nowadays, the vegetation of calcareous sites shows a similar community composition as that on sandy on fertile loamy soil, where species losses were intermediate in comparison to sandy and calcareous soils. Thus, we observed a clear trend towards homogenization in community composition where specialists have disappeared and generalists have increased, reflecting the growing uniformity in crop management schemes and soil fertility levels in recent time.

The influence of habitat fragmentation on the genetic structure of rare arable plants

It was hypothesised that (i) genetic diversity is low and genetic structuring is pronounced in isolated populations of the arable plants *A. aestivalis* and *C. regalis* and that (ii) the extent of genetic structuring is related to the degree of habitat fragmentation at the landscape scale.

Although minimum levels of genetic diversity are regarded as essential (SPIELMANN *et al.* 2004, JUMP & PEÑUELAS 2005), population genetic studies are widely lacking for rare arable plant species (BRÜTTING *et al.* 2012a). So far, only common species were assessed in this respect (SCHMIDT *et al.* 2009, DÉLYE *et al.* 2010). Consequently, little is known on whether agricultural intensification affects rare and small arable plant populations, and whether genetic structure varies among species in different landscape scenarios. Comparing three intensively used, and three extensively used regions of Eastern Germany, we surveyed populations of *Adonis aestivalis* L. and *Consolida regalis* S.F. GRAY using dominant amplified fragment length polymorphism markers (AFLP's). In contrast to hypothesis (i), within-population diversity levels in *A. aestivalis* and *C. regalis* were significantly higher and genetic evidence for fragmentation was significantly lower in populations located in the homogenous landscape than in populations of the structurally diverse landscape. The lack of evidence for isolation by distance suggests that population structures still reflect genetic bottlenecks caused by recent and historical habitat fragmentation and founder effects. A likely explanation is that higher proportions of unsuitable habitats in the diverse landscape such as grasslands and forests form some kind of barrier for gene flow among populations. Apart from barriers to natural gene flow, barriers to gene flow by human activity may differ between the landscapes, since in the monotonous region (fewer farmers and fewer tractors cultivate more land), thus increasing the likelihood of spreading seeds across the region. Such sporadic gene flow over larger distances by human activity (e.g. BONN & POSCHLOD 1998) in combination with population differentiation could also explain the lack of significant isolation-by-distance in our data sets.

In support of hypothesis (ii), genetic diversity was generally low in both species, with structures being slightly more favourable in the outcrossing *C. regalis*. This corresponds to results from another study jointly conducted with colleagues from the University of Halle-Wittenberg, where the genetic structure of six arable plant species was analysed with RAPD fingerprints (BRÜTTING *et al.* 2012a). Levels of genetic diversity proofed generally to be low, and were especially detrimental in species listed as threatened on the German Red List. Again, *C. regalis* still had the (relatively) highest genetic diversity, with *A. aestivalis* being intermediate.

Effectiveness of current schemes and programs

We hypothesized that (i) the status quo of current conservation concepts for the arable flora is insufficient and that consequently (ii) new long-term strategies for conserving arable plant communities are needed.

Our nationwide survey about current efforts on promoting arable vegetation supports the hypothesis (i) that there is a further need for intensifying efforts in the conservation of arable field plants in Germany. Previous activities, such as the creation of field flora reserves, were often restricted to short-term and single initiatives without any regular exchange of experience between experts. Therefore, many projects fail shortly after an initial success phase due to a lack off long-term financial coverage of the running costs.

Furthermore, agri-environment schemes (AES) are losing their attractiveness due to modified regulations and conditions for grants, successive changes on programming complex bureaucratic procedures and a general increase in revenue farmers can obtain from standard intensive agriculture. Finally, most of the reviewed conservation initiatives fail to tackle the increasing fragmentation of arable plants in Germany (as already described above).

The participants in our survey pointed out that initiatives for the protection of arable vegetation can only be successful if sound funding is available as well as regional supervision and support. As hypothesised, the respondents hoped (ii) that a national network of arable plant experts would provide better public relations, could foster development of new ideas for further activities and result in a general improvement in conservation of arable plants. The existing initiatives would benefit from such a supra-regional exchange and/or coordination, which could also help to gather advice on management in order to optimise conservation measures. More practical perspectives are listed in the last subchapter below.

Examples: Trends in selected characteristic species

Modern high-intensity agriculture puts strong filters on species' presence in arable fields. The current management regimes select against arable species with short stature, large seeds, and late flowering which are nowadays traits of rare and threatened arable plants (STORKEY *et al.* 2010). The few 'agrotolerant' arable species benefit from high fertilizer inputs in a similar manner as do crops, are often herbicide-resistant and have adapted their life-cycles to that of the crops allowing them to become ubiquitous weeds (FRIED *et al.* 2010). Further expansion of the area planted with energy crops and widespread cultivation of genetically-modified crops in future times may result in even further impoverishment of arable plant communities with eventually only a few highly stress-tolerant generalist species persisting.

Numerous arable plant species are already considered threatened and have shown a very sharp reduction in frequency on the regional level. One third of the species remained stable and only a handful of species (mostly *Bromus* species, some of them now erroneously red-listed) have increased slightly during the last decades in Central Germany. Negative trends in even formerly common species were reported from southern England (SUTCLIFFE & KAY 2000), and add support to concerns that common species and thus associated functions such as pollination webs are also affected (GIBSON *et al*. 2006). The results of the presented studies generally confirm reference surveys from many other countries in Europe (e.g. FRIED *et al.* 2009b). Most strongly affected are arable plants of fields with extreme soil reaction and only a moderate supply of nutrients. For example, *Anagallis foemina* MILL., a diagnostic species of the Caucalidion platycarpae alliance was not encountered at all in 2009. *Agrostemma githago* L., which by 1950s/1960s was only sporadically found due to effective seed cleaning techniques (HILBIG 2007), has also vanished. Even formerly common species such as *Consolida regalis* S.F. GRAY often completely disappeared form field interiors, and are nowadays restricted to field margins. Formerly rare species, such as *Bupleurum rotundifolium* L., remained stable on a low level, or disappeared entirely like *Turgenia latifolia* (L.) HOFFM. Finally, we also found a sharp decline in the frequency and cover of most Poaceae including those species that are known to be aggressive and yield-suppressing weeds elsewhere such as *Alopecurus myosuroides* HUDS. or *Bromus sterilis* (L.) NEVSKI. Neophytes also declined with the exception of the neophytic grasses *Anthoxanthum aristatum* BOISS. that showed slight increases. In the following, seven of these species are briefly discussed (for pictures see Appendix Figure S7.1 in the Supporting information).

(1) *Agrostemma githago* L. – Common Corncockle

In the 19th century, this Caryophyllaceae was still commonly found in the cereal fields, covering all kind of different soils (e.g REICHENBACH 1844, VOCKE & ANGELRODT 1886). Its seeds are large and black, and *A. githago* is a prime example for the influence of improved seed cleaning techniques (FIRBANK 1988). This plant was adapted to the life cycle of cereal plants and had to rely each year on spreading with the ‘contaminated’ seeds. In our study areas, the corncockle was already rare in the 1950s/1960s and restricted to fields used for subsistence agriculture (5% in frequency of occurence), but disappeared from today’s fields. To our knowledge, today less than ten ‘autochthonous’ populations remain within Germany, most of them on special conservation sites, (e.g. Schellenzipf, Wolferode, Tauer).

(2) *Bupleurum rotundifolium* L. – Thorow Wax

The archaeophytic *B. rotundifolium* (Apiaceae) is restricted to extremely warm soils and can in Central Germany be only found on calcareous sites. The plants are very beautiful; the flowers are yellowish and are self-pollinated or insect-pollinated. In Germany, the species has experienced severe losses; more than 80% of formerly occupied raster cells have been abandoned in the last 5 decades (BfN 2011). Thorow wax is now one of the rarest arable plants within Germany and is therefore listed as threatened with extinction (KORNECK *et al.* 1996). We studied the genetic structure of *B. rotundifolium* in Germany and neighbouring states (BRÜTTING *et al.* 2012b). Values of genetic diversity were very low; gene diversity and structure implied that selfing plays an important role in the reproduction. The proportion of polymorphic loci per population varied between 9.4% and 38.7%, with those from Eastern Germany being significantly less diverse (mean 19.1%) than those of the other group (mean 25.5%). Most of the populations of the eastern part of Germany formed one cluster, and most of the Western German populations as well as populations from outside Germany built another group. The ϕ_{ST}-value was very high (0.65) and there was evidence for isolation-by-distance with strong effects particularly in Eastern Germany. Consequently, *B. rotundifolium* populations should be closely monitored over the coming decades, and restoration plans should take the presence of the two main *B. rotundifolium* cluster groups into account.

(3) *Consolida regalis* S.F. GRAY – Forking Larkspur

This Ranunculaceae has a beautiful violet-blue colour (red or white larkspurs specimens also occur rarely), which is not commonly found in our wild plants. *Consolida regalis* is considered as a diagnostic species of of the Caucalidion platycarpae alliance and was formerly widespread on calcareous fields. In our study areas, its frequency declined dramatically from 22% up to only 3% in the last five decades. As a result, *C. regalis* is listed as endangered on the German Red List (RL 3, KORNECK *et al.* 1996). Own genetic investigations on Central German populations revealed a higher within-population diversity of *C. regalis* compared to other arable plants, differentiation between populations is relatively low (BRÜTTING *et al.* 2012a, chapter 4 above). Forking Larkspur is exceptional in not being self-pollinating (SVENSSON & WIGREN 1986), which may explain that it is less affected by isolation than other arable plants.

(4) *Anagallis foemina* MILL. – Blue Pimpernel

This Primulaceae is in phytosociology regarded as a characteristic species of the Caucalidion platycarpae alliance and still occurred at a frequency of 5% in frequency some decades ago. In the resampling survey of 2009, we did not observe *A. foemina*. A possible reason for that could be the loss of stubble fallows, because stubbles are nowadays often cultivated immediately after harvest. With its short stature *A. foemina* needs open conditions, which in today's dense grain stocks are only available after crop harvesting. We found a high differentiation among populations and very low within-population diversity in *A. foemina* populations (BRÜTTING *et al.* 2012a). Although rare and genetically impoverished, the species is not red-listed and was the sole example where the red-list status did not match the genetic structure. Red-list status should thus be raised. Most likely, the abundance of *A. foemina* is overestimated because it is often confused with the rare blue-flowering form '*azurea*' of the more common *A. arvensis*. A reliable determination is possible because the latter has many three-celled glandular hairs on the smooth margin of the petals vs. few four-celled glandular hairs on the serrated margin of the petals of three-cell glandular hairs at fringe of the otherwise smooth petals (*A. foemina*).

(5) *Bromus sterilis* (L.) NEVSKI – Barren brome

During the last few years, a rapid increase in the number of *Bromus* strains with herbicide resistance has been observed in Germany (RUIZ-SANTAELLA 2011, personal communication), and consequently the Poaceae *B. sterilis* is now one of the most aggressive weeds on German fields (MORAY *et al.* 2003). In the historical dataset of the 1950s/60s it was still absent from field interiors, where it is relatively common today (frequency 15%); in field margins in can be considered aggressive (54%). The recent spread of barren brome is next to the fact of herbicide resistance also linked to the widespread adoption of low-tillage systems, early seeding dates and winter cereal-based crop rotations (MORAY *et al.* 2003). Furthermore, *Bromus* species have been found surviving in grass-rich boundary strips between fields, which serve as a major seed source for continuous re-infestation of the fields (THEAKER *et al.* 1995). An investigation by REW *et al.* (1996) has shown that under natural dispersal over 80 % of the Barren brome seeds were scattered within 1m of the mother plants, while seed dispersal of *B. sterilis* by combine harvesters was observed up to a distance of 50m.

(6) *Alopecurus myosuroides* HUDS. – Black grass

Among the few grass species experiencing an increase in frequency are several taxa known to have developed herbicide resistance such as *A. myosuroides*, which locally had a fourfold increase presumably due to resistance development (MENNE *et al.* 2008). This species also benefits from an increased abundance of winter cereals and earlier sowing dates (KNOX *et al.* 2011). From Great Britain SUTCLIFFE & KAY (2000) reported that Black grass, which was mainly limited to loamy soils in the 1960s, is now also found on calcareous soils. In contrast, we found a sharp decline in frequency (2 to 8% today) and cover of *A. myosuroides*. Interestingly, *A. myosuroides* was strongly restricted to loam and lime substrates. It was a common plant species in western Germany in the 1980's (HAEUPLER & SCHÖNFELDER 1989), while it was considered a rare plant in Eastern Germany (HILBIG 2010, personal communication). *Alopecurus myosuroides* is among the few arable plants species that had been studied genetically before. DÉLYE *et al.* (2010) observed an efficient gene flow between populations.

(7) *Anthoxanthum aristatum* BOISS. - Annual vernalgrass

This grass, with its distinctive cumarine smell, is neophytic on nutrient-poor and sandy fields (KLÄGE 1999). In the current phytosociological syntaxonomy, Annual vernalgrass is regarded as a diagnostic species in the association of Teesdalio-Arnoseridetum, together with *Arnoseris minima* SCHWEIGG. et KOERTE, *Hypochaeris glabra* L., *Galeopsis segetum* NECK., *Teesdalia nudicaulis* (L.) R. BR. and *Aphanes inexspectata* W. LIPPERT. As the other diagnostic species, *A. aristatum* is now rare and one the few examples of arable neophytes being red-listed as endangered in some federal states (e.g. Thuringia, KORSCH & WESTHUS 2011). In our study, the grass was only observed on sandy soils and slightly increased in frequency (from 1 up to 6%) within the last decades. Most other sampled neophytes were already rare in the historical data set and, to our surprise, declined even further between the 1950s/60s and 2009. Thus, we found no evidence that neophytes as a group profited from modern land use practices, instead they showed similar losses or remained essentially stable on a low level as did other groups of arable plants described above.

Effective conservation measures for arable plants

The present studies once again highlighted that there is an urgent need to conserve communities which are as species-rich as many other Central European ecosystems, because this is the only means of providing adequate genetic diversity for allowing the necessary adaptations to changing environmental conditions (SPIELMAN *et al.* 2004, HAMPICKE *et al.* 2005). In recent years, scientific and public concern has also arisen questioning whether the observed losses in agro-ecosystems on both flora and fauna will effect ecosystem functioning and services (JORDAN & VATOVEC 2004, TSCHARNTKE *et al.* 2005). Studies from cultivated areas in Switzerland (DUELLI & OBRIST 1998, OBRIST & DUELLI 1998) have clearly demonstrated direct effects of a higher diversity of the flora on the diversity of the fauna. Consequently, trends in the number of plant species are an appropriate indicator of losses in other taxonomic groups.

Results of functional biodiversity research have been conducted primarily in grasslands but, numerous recent studies have pointed out that a diverse arable flora is not only of importance for conservation of biodiversity, but also plays a key role for the functioning of agro-ecosystems (ISSELSTEIN *et al.* 1991, ALTIERI 1999, ALBRECHT 2003, FRANKE *et al.* 2009). Arable plants have been identified to provide beneficial ecosystem services (GEROWITT 2003), e.g. mineral N storage in periods of oversupply (MAHN 1992, BLANK & YOUNG 2004, MAJUMDER *et al.* 2008) can develop a more dense rootsystem and reduce soil erosion (BROCK 1982, WEIL 1982, SWANTON 1996), offer pollen for pollinating insects (GABRIEL & TSCHARNTKE 2006, GIBSON *et al.* 2006) or promote an increase in the diversity of soil organisms (NENTWIG *et al.* 1998, NENTWIG 1999). Arable plants host a wide variety of phytophagous insect species which are an important food resource for farmland birds (CHAMBERLAIN *et al.* 2000, MARSHALL *et al.* 2003, STORKEY & WESTBURY 2007). Furthermore, arable plants play an important role for biological control, because they offer shelter, feeding sites and reproduction opportunities for natural enemies of pests (WELLING *et al.* 1988, SCHELLHORN & SORK 1997, BÀRBERI *et al.* 2010). In this context, for example, HEYDEMANN & MEYER (1983) reported 1200 different phytophagous insect species on 102 arable plant species in Northern Germany.

There is much concern about conservation concepts for farmland birds in Germany (e.g. SUDFELDT *et al.* 2010), but arable plants are surprisingly neglected although they are essential primary resources for all higher trophic levels (ALTIERI 1999, MARSHALL *et al.* 2003, HAWES *et al.* 2010, EVANS *et al.* 2011). In this context, until now only few studies (e.g. PETIT *et al.* 2010) investigated the ecological function of individual arable plant species and consequently future research in this direction is urgently required.

The current state of arable plant conservation in Germany

The results show that losses in population sizes and diversity have been stronger in arable plant vegetation than in any other habitat type in the Central German cultural landscape (ELLENBERG & LEUSCHNER 2010). Currently, around one third of approximately 350 arable plant species in Germany is considered endangered (HOFMEISTER & GARVE 2006). Germany has a high level of responsibility for the protection of some of these species (WELK 2002), including *Arnoseris minima* SCHWEIGG. et KOERTE, *Bromus grossus* DESF. ex DC. and *Veronica opaca* FR. which can only be conserved by ensuring appropriate management of selected sites.

The effectiveness of current agri-environment schemes (AES), as the most important conservation measure on arable land, has been questioned (KLEIJN *et al.* 2001, 2006, MEYER *et al.* 2010a, SMITH *et al.* 2010). Several studies demonstrated that agri-environment schemes generally increase the richness of arable plants (KLEIJN *et al.* 2006, BUTLER *et al.* 2009). In most of the federal states of Germany, previously successful AES-measures for the conservation of arable plants, such as the establishment of field margin strip programmes, have unfortunately stopped due to changes in funding, lack of regional support or increased levels of administrative requirements (MEYER *et al.* 2008, 2010a). Another principal problem of the aforementioned AES is that they just tackle the species level, while genetic, community and ecosystem levels are widely ignored. Therefore, the AES with their strong focus on headlands are not the most effective tool, with a principal reason being that communities along field margins are always subject to edge effects with the possible consequence that 'edge communities' in many cases do not harbour the target plants (i.e. threatened arable plant species) but in fact are dominated by species from other habitats (e.g. grasslands or hedges, see also results in chapter 2).

Our results together with the findings of BRÜTTING *et al.* (2012a, b) confirm that after only 5-6 decades of intensified agriculture, most arable plants already show detrimental genetic structure. Habitat fragmentation nowadays has already affected extant populations, and provenance issues become of fundamental importance for possible restoration schemes. In the future, conservation schemes for arable plants need to tackle genetic aspects and to promote efficient gene flow within and between populations. Examples are increased connectivity of field margin strips and conservation fields, or seed transfer due to grazing by e.g. sheep (local nomadic shepherds).

Options for improved conservation measures

An initiative has been launched recently to identify new solutions for the protection of arable plants in Germany. A nationwide network of at least 100 so-called 'conservation fields' ('Schutzäcker') was designed to counteract the ongoing loss of arable plants species (MEYER *et al.* 2010b). On the selected fields, crop management is carried out without any application of herbicides and by taking into consideration specific management requirements of target arable plant species. These 'conservation fields' can constitute an important element of biodiversity conservation in Germany's intensively used agricultural landscape and may help to preserve highly endangered plant species and their communities for the future. Nevertheless, due to their size limitations, initiatives like the network of conservation fields can only be a first step to protect a sufficiently large part of agrobiodiversity in Central Europe.

In 2007, the German federal government passed the National Biodiversity Strategy (NBS), which is in accordance with the guidelines of the International Conference on Biological Diversity (Convention on Biological Diversity [CBD], (BMU 2011). For the agricultural sector, the NBS aims at a significant enhancement of biodiversity by 2020; to that end populations of the majority of species in agricultural ecosystems should increase from 2015 onwards. For the implementation of these targets, the design of the Common Agricultural Policy of the European Union (CAP) after 2013 will be of major importance. Currently, important agricultural policy principles are discussed at European and national levels.

The proposed CAP reform so far includes no specific requirements or targets for the EU or individual member states to include plant conservation measures or agri-environment schemes. The implementation of such schemes depends on the interest of the member states and on the willingness of farmers to adopt these schemes. However, among the potential actions that are currently discussed regarding the CAP reform are some that may also concern the conservation of arable plant diversity. The so called ‘greening‘ of the CAP basically implies that, in addition to the basic agricultural subsidy payments (Pillar I), each agricultural holding will receive a payment per hectare for respecting certain agricultural practices beneficial for the climate and the environment. Among others, these beneficial agricultural practices should include maintenance of an ‘ecological focus area’ of at least 7% of farmland (excluding permanent grassland) – i.e. field margins, extensively used arable sites, hedges, fallow land, landscape features, biotopes or buffer strips. The implementation of such a minimum ecological focus area also aims at slowing down the decline in farmland biodiversity, most notably in intensive farming areas (ROSCHEWITZ *et al*. 2005, CROWDER *et al.* 2010, GABRIEL *et al.* 2010).

In addition to the described possible ‘greening’ of the Pillar I, the CAP reform might also affect the future design and financial resources of agri-environment schemes under Pillar II. Regardless of whether they are included as potential measures in Pillar I or II, future conservation programs for arable plant diversity need to be more effective in yielding benefits for plant conservation, e.g. Payments for Environmental Services (PES) schemes (ULBER *et al.* 2011). In this context, it will be necessary to compile a list of indicator species which can be used for monitoring and evaluating the actual benefits of certain measures for arable plant conservation. A model is provided by the European Farmland bird index (GREGORY *et al.* 2005) which has been widely established as a useful indicator on a European basis. A similar arable plant index could be a useful tool to monitor trends on a continental scale in other elements of biodiversity in this habitat. In any case, future approaches to arable plant conservation have to be more comprehensive in several aspects: extensive research is still needed, and conservation must translate this research into practice. The focus must shift from the field-level to the farm-level and the still rarely utilised whole farm approach of conservation advice to farmers (OPPERMANN *et al.* 2006, JEDICKE 2009, ROCHA 2009) should be expanded more strongly. Only this will ensure that our cultural landscapes will still host sufficient biodiversity and are able to provide crucial ecosystem functions and services.

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Summary

Since the first creation of arable land a crop-adapted flora and fauna has developed as a by-product of low-intensity agriculture. Intensification and economic optimization of agricultural production during the last few decades have led to simplified agricultural landscapes and a decrease in spatial heterogeneity, resulting in a dramatic loss of species diversity and population decline of arable plants. In this context, numerous recent studies have pointed out that a diverse arable flora plays a key role in the functioning of agricultural systems, acting to maintain beneficial ecological functions (e.g. support of higher trophic levels or provision of ecosystem services).

The aim of this thesis is to provide insights into the influence of agricultural intensification processes on shifts in arable vegetation from the continental to the population level for evaluating existing arable plant conservation schemes and proposing future strategies. Within the framework of this thesis, all observational studies were carried out in Central Germany.

This study demonstrates a dramatic impoverishment of the arable vegetation on all major organisational levels. At the continental European scale, we found a positive relationship between national wheat yields and the numbers of rare, threatened or recently extinct arable plant species in each European country. It was found that for every extra tonne/hectare of wheat produced approximately ten more plant species become nationally threatened. Specialist species adapted to certain crops were among the most threatened. The results from this study showed that the increased use of agro-chemicals, especially in the EU Member States in Central and North-Western Europe, has selected against a larger group of arable species adapted to habitats with intermediate fertility.

Moving to finer scale on the community level, this study clearly demonstrates that the European-wide intensification of arable habitat use has led to massive shifts in the arable plant community composition. In the 1950s/60s, most of the relevés could be easily assigned on association level, while the recent relevés could often only be classified at the level of higher syntaxa such as alliance, order, class or ‘fragmental’ floristically-impoverished communities. In this context, our analysis revealed a reduction of 23% in the number of species in the regional species pool during the 50-yr period, dramatic losses in plot-level diversity (median loss of 17 species per relevé) and decreasing population sizes of rare and diagnostic species. The results also indicate that vegetation changes depended

on geological substrate, with sandy sites being less severely affected. Furthermore, the average cover of arable plants has dramatically decreased to a tenth of its original extent, while crop cover generally increased and crop diversity decreased. Archaeophytes, neophytes and most Poaceae (including some highly competitive weeds) showed large frequency losses similar to that of indigenous herbarceous plants, but only modest changes in their share of total arable plant cover. The observed increasing Ellenberg indicator values (EIV) for nitrogen and pH indicate that N-fertilisation may, in combination with increasing usage of herbicides and denser crop stands, act as a major driver of change in the arable vegetation. Consequently, the reported clear trend towards homogenization in community structure, where specialists and diagnostic species have disappeared and generalists increased is reflecting the growing uniformity in crop management schemes and soil fertility levels in recent time.

The reported decreasing population sizes, especially in rare species with small populations (in this case *Adonis aestivalis* L. and *Consolida regalis* S.F. GRAY), are shown to affect their genetic diversity. In this context, also landscape complexity plays an important role because genetic structure varies among species and populations. However, contrary to expectation, within-population diversity levels of the species were significantly higher in populations located in monotonous landscapes than in populations of structurally diverse landscapes. Populations from diverse landscapes differed more significantly from each other than those from monotonous landscapes. Furthermore, we observed high within-population diversity for the outcrossing *C. regalis*, but low within-population diversity for the self-pollinating *A. aestivalis*. However, neither *A. aestivalis* nor *C. regalis* showed a significant isolation-by-distance regardless of landscape structure.

In conclusion, the present study shows that arable plant communities are under dramatic threat, affecting all major organisational levels from the European scale to the population level. The rapid shifts in the highly dynamic agro-ecosystems within the last few decades have strongly influenced community structure, plant diversity, population sizes and genetic variation. To achieve the defined target of increasing the population size of the majority of species in agricultural ecosystems by 2015, new, effective and innovative schemes and programs are urgently required. Especially the design of the Common agricultural policy (CAP) after 2013 will be of major importance for the task to halt the loss of arable plant biodiversity in the agricultural landscape.

Zusammenfassung

Seit Beginn des Ackerbaus hat sich eine an die Kulturarten angepasste Ackerbegleitflora und -fauna entwickelt. Intensivierungsprozesse der landwirtschaftlichen Produktion führten in den letzten Jahrzehnten zu einer stetig voranschreitenden Umstrukturierung vieler Agrarlandschaften und einer Abnahme der Habitatdiversität. Diese Entwicklung war verbunden mit einem dramatischen Verlust der Artenvielfalt und einem drastischen Rückgang der Populationsgrößen von Segetalarten. Eine Reihe von Studien zeigt aber, dass eine artenreiche Segetalflora eine entscheidende Rolle bei der Erhaltung der Funktionsfähigkeit von Agrar-Ökosystemen spielt, z.B. durch Förderung höherer trophischer Ebenen oder durch die Bereitstellung von Ökosystemdienstleistungen.

Die vorliegende Arbeit untersucht die Auswirkungen der ackerbaulichen Intensivierung auf die Segetalvegetation in Mitteldeutschland sowohl auf Landschafts- als auch auf Populationsebene. Die Ergebnisse dieser Untersuchungen wurden zur Evaluierung bestehender Projekte zur Förderung der Segetalflora genutzt und liefern eine Grundlage für zukünftige Schutzstrategien.

Die Ergebnisse der Untersuchungen zeigen eine dramatische Verarmung der Segetalvegetation auf allen wichtigen Hierarchiestufen. Auf europäischer Ebene konnte für alle europäischen Länder nachgewiesen werden, dass ein höherer Weizenertrag auch mit einer erhöhten Zahl gefährdeter Segetalarten einhergeht. So hatte jede zusätzlich produzierte Tonne Weizen/ha eine Gefährdung von etwa zehn weiteren Segetalarten Ländern zur Folge. Dabei scheinen die an bestimmte Kulturarten angepassten Spezialisten am stärksten vom Aussterben bedroht zu sein. Die Untersuchungen belegen, dass der verstärkte Einsatz von Herbiziden in den EU-Mitgliedstaaten in Mittel-und Nord-Westeuropa zu einer Selektion ausgewählter Segetalarten geführt hat, die an die heutigen nivellierten Standortbedingungen angepasst ist.

Auf Gesellschaftsniveau, zeigen unsere Untersuchungen deutlich, dass die Intensivierung der Nutzung von Agrar-Ökosystemen zu massiven Verschiebungen in der Zusammensetzung von Segetalgesellschaften geführt hat. In den 1950er/60er Jahren konnte die Mehrzahl der Vegetationsaufnahmen noch auf Assoziationsebene zugeordnet werden, während sich aktuelle Vegetationserhebungen oft nur noch auf der Ebene höherer Syntaxa wie Verband, Ordnung, Klasse oder als floristisch stark verarmte Fragment-Gesellschaften einstufen ließen. In diesem Zusammenhang kann in den letzten fünf Jahrzehnten auch eine

Verringerung des regionalen Artenpools um 23 %, ein dramatischer Artenverlust auf Plot-Ebene (mittlerer Verlust von 17 Arten pro Aufnahme) sowie stark zurückgehende Populationsgrößen kennzeichnender Arten belegt werden. Die Ergebnisse verdeutlichen auch, dass die Intensität der Veränderungen in der Vegetationszusammensetzung zwischen den unterschiedlichen Böden variierte, wobei sandige Standorte weniger stark betroffen waren. Des Weiteren hat sich der mittlere Deckungsgrad der Segetalarten drastisch auf ein Zehntel des früheren Wertes reduziert, wohingegen der Deckungsgrad der Kulturpflanzen anstieg und die Kulturpflanzenvielfalt abnahm. Archäophyten, Neophyten und die meisten Grasartigen zeigten zum Teil starke Frequenzverluste ähnlich denen von einheimischen krautigen Pflanzen, aber nur geringe Veränderungen in ihrem Anteil an der Gesamtdeckung der Segetalarten. Der beobachtete Anstieg der „Ellenberg-Zeigerwerte“ für Stickstoff und Bodenreaktion deutet darauf hin, dass die höhere Düngergaben in Kombination mit der heute üblichen Anwendung von Herbiziden und den sehr dicht stehenden Kulturpflanzenbeständen als Hauptursachen für Veränderungen in der Segetalvegetation angesehen werden können. Der beobachtete Trend einer Vereinheitlichung der Gesellschaftstrukturen von Segetalarten, bei der Spezialisten und diagnostisch wichtige Arten zurückgehen und die Anzahl und Abundanz der Generalisten zunimmt, spiegelt die Vereinheitlichung von Anbausystemen und der Optimierung des Nährstoffangebotes in den letzten Jahrzehnten wider.

Der beobachtete Rückgang der Populationsgröße, insbesondere bei selten gewordenen Arten mit geringer Populationsgröße (*Adonis aestivalis* L. und *Consolida regalis* SF Gray), wirkten sich auf die genetische Vielfalt dieser Populationen aus. Da die genetische Struktur zwischen den Arten und Populationen variiert, ist in diesem Zusammenhang auch die Komplexität der Landschaftsstruktur entscheidend. Anders als erwartet war die genetische Diversität innerhalb einzelner Populationen in weniger stark strukturierten Landschaften wesentlich höher als innerhalb von Populationen in strukturreichen Landschaften. Populationen aus strukturreichen Landschaften unterschieden sich genetisch zudem stärker voneinander als Populationen strukturärmerer Landschaften. Darüber hinaus wurde bei der fremdbefruchtenden *C. regalis* eine höhere Diversität innerhalb der Populationen festgestellt, während die selbstbefruchtende *A. aestivalis* eine geringere Diversität innerhalb der Populationen aufwies. Allerdings zeigten weder *A. aestivalis* noch *C. regalis* eine signifikante „Isolation-by-Distance“ unabhängig von der Landschaftsstruktur.

Zusammenfassend zeigt die vorliegende Arbeit, dass auf allen Hierarchiestufen von der kontinentalen Ebene, über die Phytocoenosen bis hin zu Populationen einzelner Arten starke Veränderungen in den Segetalgesellschaften stattgefunden haben. Um das nationale Ziel der Erhöhung der Populationsgrößen der Mehrzahl der Arten in landwirtschaftlich genutzten Ökosystemen bis 2015 zu erreichen, sind neue, effektive und innovative Maßnahmen dringend erforderlich. Um den fortwährenden Biodiversitätsverlust in der Agrarlandschaft entgegenzuwirken ist vor allem eine entsprechende Ausgestaltung der Gemeinsamen Europäischen Agrarpolitik (GAP) für die Förderperiode 2014-2020 von zentraler Bedeutung.

List of Publications

Peer reviewed journal publications

Meyer S, Wesche K, Krause B, Leuschner C (2013) Dramatic losses of specialist arable plants in Central Germany since the 1950s/60s – a cross-regional analysis. *Diversity and Distributions*. in press.

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Appendix - Supporting Information

Appendix Table S3.1. Percentage share of fields with different crop types and crop classes in the 1950s/60s and 2009. Estimated cover values (%) of crops are given as medians and interquartile ranges (IQR). Abbreviations for cultivation period: w – winter crops (=autumn-sown crops), s – spring crops (=spring-sown crops), s/w – both spring and winter crops.

Appendix Table S4.1. Percentage share of different crop types and crop classes in the historical (1950s/60s) and recent (2009) surveys. Abbreviations for cultivation period: w – autumn sown crops, s – spring sown crops, s/w – both winter and spring sown crops.

Appendix Table S4.2. Changes in frequency over time, given for the pooled data, and separately for the three substrate types. Species with significant changes according to Indicator Species Analysis (ISA, considering abundance and frequency) are given first; these are further differentiated according to their habitat preferences (ISA on historical data alone). Grey shadings indicate frequency increases from 1950s/60s to 2009. For consistency in status all data follow JANSEN & DENGLER (2008). Abbreviations indicate species status in the region: 'A' = archaeophytes; 'A/I' = unclear whether archaeophytes or neophytes; 'I' = indigenous; 'K' = crops; 'N' = neophytes; 'NA' = no data available; 'U/N' = unstable neophytes.

Species are marked as threatened (x) if listed in the red lists of Germany (LUDWIG & SCHNITTLER 1996), or the federal states of Lower-Saxony (GARVE 2004), Saxony-Anhalt (FRANK *et al*. 2004), Brandenburg (RISTOW *et al*. 2006) and Thuringia (KORSCH & WESTHUS 2011).

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Appendix Figure S5.1. Neighbor joining phenogram of *A. aestivalis* individuals from the original dataset using Nei-Li (=Dice) distances from 5 regions in Central Germany (D=Drei Gleichen, H=Hainleite, K=Kyffhäuser, Q=Querfurter Platte, S=Schmoner Hänge).

Appendix Figure S5.2. Neighbor joining phenogram of *A. aestivalis* individuals from the repeated dataset using Nei-Li distances from 2 regions in Central Germany (H=Hainleite, K=Kyffhäuser).

Appendix Figure S5.3. Neighbor joining phenogram of *C. regalis* individuals using Nei-Li distances from 6 regions in Central Germany (D=Drei Gleichen, H=Hainleite, K=Kyffhäuser, Q=Querfurter Platte, S=Schmoner Hänge, W=Witterda).

Appendix Figure S7.1. Photo documentation.

Appendix

Appendix Table S3.1. Percentage changes in frequency and median cover over time. Data are given for the different periods (1950s/60s and 2009), and the sample localities of 2009 (interior and margin). Diagnostic species of the respective syntaxa are given first; other species are listed alphabetically.

	Field interior 1950s/60s		**Field interior 2009**		**Field margin 2009**	
Species name	**Frequency (%)**	**Median Cover (%)**	**Frequency (%)**	**Median Cover (%)**	**Frequency (%)**	**Median Cover (%)**
Teesdalio-Arnoseridetum minimae						
Anthoxanthum puelii	2	0.69	1	0.01		
Aphanes australis	4	0.37			1	0.20
Arnoseris minima	16	2.01				
Galeopsis segetum	2	0.10	0	0.01	1	0.01
Hypochaeris glabra	7	0.42	0	0.00		
Teesdalia nudicaulis	1	0.02				
Papaveretum argemones						
Draba verna	3	0.08	1	0.02	2	0.03
Myosotis stricta	3	0.02	0	0.01	1	0.01
Papaver argemone	6	0.04	2	0.04	6	0.07
Papaver dubium agg.	8	0.16	3	0.05	12	0.15
Veronica triphyllos	4	0.04	1	0.01		
Vicia villosa	6	0.15	2	0.04	3	0.04
Aphano-Matricarietum						
Aphanes arvensis	17	1.40	3	0.13	11	0.78
Matricaria chamomilla	19	2.42	9	1.41	16	1.93
Holco-Galeopsietum						
Galeopsis tetrahit	19	0.78	1	0.02	6	0.07
Holcus mollis	4	0.06			2	0.76
Lapsana communis	14	0.81	4	0.07	16	0.78
Stellaria graminea	0	0.00			1	0.01
Viola tricolor agg.	29	0.43				
Aperion spica-venti						
Apera spica-venti	33	6.58	22	8.31	35	10.20
Centaurea cyanus	35	2.54	10	2.12	20	4.10
Veronica hederifolia agg.	22	2.13	2	0.11	8	0.09
Vicia angustifolia	26	0.38	9	0.16	20	0.24
Vicia hirsuta	19	1.31	11	0.62	21	0.72
Vicia sativa	7	0.55			1	0.01
Vicia tetrasperma agg.	5	0.14	2	0.05	6	0.09
Setario-Galinsogetum parviflorae						
Galinsoga parviflora	8	0.97	6	0.73	8	1.04
Digitarion ischaemi						
Digitaria ischaemum	8	1.39	1	0.08	1	0.40
Spergulo-Echinochloetum cruris-galli						
Echinochloa crus-galli	6	1.05	12	0.45	9	0.94
Setario-Stachyetum arvensis						
Stachys arvensis	1	0.03				
Spergulo-Chrysanthemetum segetum						
Glebionis segetum	3	0.14				
Lycopsietum arvensis						
Anchusa arvensis	10	0.24	3	0.05	9	0.10
Digitarion-Setarion						
Digitaria sanguinalis					0	0.00
Erodium cicutarium	17	0.54	7	0.52	17	0.71
Galinsoga quadriradiata	1	0.10	1	0.03	2	0.23
Setaria pumila	3	1.23	0	0.01	1	0.21
Setaria viridis	17	1.36	4	0.38	5	0.65
Galeopsietum speciosae						
Galeopsis speciosa					2	0.01
Chenopodio-Oxalidetum fontanae						
Cerastium glomeratum	1	0.00	0	0.00		
Chenopodium polyspermum	1	0.03			1	0.01
Erysimum cheiranthoides	6	0.10	2	0.03	2	0.03
Oxalis fontana	5	0.25			1	0.01
Rorippa sylvestris	4	0.57				
Sperguletalia arvensis						
Anthemis arvensis	5	0.46	1	0.02	1	0.01
Arabidopsis thaliana	10	0.41	4	0.53	6	0.13
Raphanus raphanistrum	15	0.60	1	0.02	1	0.01
Rumex acetosella	21	1.10	3	0.67	9	0.56
Scleranthus annuus agg.	33	3.68	2	0.03	4	0.49
Spergula arvensis	30	3.94	4	2.18	9	1.69
Papaveri-Melandrietum noctiflorae						
Euphorbia exigua	33	1.11	2	0.19	8	0.82
Silene noctiflora	21	0.67	1	0.02	1	0.01
Kickxietum spuriae						
Kickxia elatine	1	0.00				
Kickxia spuria	0	0.00				
Caucalido-Adonidetum flammeae						
Adonis aestivalis	16	1.43	1	0.02	5	0.06
Caucalis platycarpos	5	0.22	0	0.00	1	0.01
Scandix pecten-veneris	3	0.04	0	0.01		
Turgenia latifolia	0	0.00				
Caucalidion platycarpae						
Anagallis foemina	5	0.18			1	0.06
Buglossiodes arvensis	13	0.12	0	0.01	3	0.03
Campanula rapunculoides	15	1.18			1	0.02
Chaenorhinum minus	3	0.03			2	0.02
Consolida regalis	22	1.94	3	0.06	9	0.32
Falcaria vulgaris	11	0.73	2	0.03	8	0.31
Galeopsis angustifolia	4	0.31			0	0.00

Galeopsis ladanum	3	0.02	0	0.00	1	0.01
Galium tricornutum	11	0.39				
Knautia arvensis	6	0.09			3	0.03
Lathyrus tuberosus	17	0.98			5	0.76
Melampyrum arvense	1	0.00				
Neslia paniculata	8	0.10				
Ranunculus arvensis	4	0.13				
Sherardia arvensis	9	0.39	1	0.72	4	3.16
Valerianella dentata	6	0.08	2	0.03	8	0.73
Soncho-Veronicetum agrestis						
Veronica agrestis	6	0.09	0	0.01	1	0.01
Thlaspio-Fumarietum						
Fumaria officinalis	21	0.88	3	0.05	7	0.08
Thlaspio-Veronicetum politae						
Fumaria vaillantii	5	0.15	1	0.02	4	0.14
Veronica polita	15	0.69	2	0.41	5	0.26
Mercurialietum annuae						
Mercurialis annua	1	0.00	0	0.01	0	0.00
Geranio-Allietum vinealis						
Allium oleraceum			0	0.01	2	0.02
Allium vineale					1	0.02
Torilis arvensis			0	0.00		
Valerianella carinata	1	0.03				
Fumario-Euphorbion						
Chenopodium hybridum	0	0.01	1	0.01	1	0.01
Euphorbia helioscopia	34	0.89	9	0.24	19	0.73
Euphorbia peplus	4	0.27			1	0.00
Senecio vulgaris	19	0.57			1	0.01
Solanum nigrum	7	0.31	4	0.08	5	0.07
Papaveretalia rhoeadis						
Aethusa cynapium	11	0.43	6	2.58	9	2.63
Alopecurus myosuroides	2	0.25	8	1.63	17	3.33
Avena fatua	18	0.71	7	0.24	7	0.29
Geranium dissectum	2	0.03	6	0.17	16	2.51
Papaver rhoeas	35	1.98	15	1.52	36	1.80
Sinapis arvensis	43	2.89	3	0.04	6	0.06
Thlaspi arvense	36	1.41	7	0.16	19	0.50
Veronica persica	31	1.78	19	0.94	35	1.98
Stellarietea media						
Anagallis arvensis	46	1.94	8	0.31	13	0.83
Fallopia convolvulus	84	9.57	50	7.34	57	4.98
Lamium amplexicaule	28	0.86	3	0.13	7	0.09
Lamium purpureum	19	0.73	8	0.28	18	0.48
Myosotis arvensis	49	2.81	17	1.77	40	4.10
Persicaria maculosa	16	0.37	2	0.04	4	0.06
Veronica arvensis	27	0.98	9	0.24	19	0.98
Viola arvensis agg.	67	2.85	51	8.54	62	7.76
Other						
Acer campestre			1	0.01		
Acer platanoides					0	0.00
Acer pseudoplatanus					0	0.00
Achillea millefolium agg.	12	0.07	2	0.03	23	0.29
Achillea ptarmica	0	0.00				
Aegopodium podagraria					2	0.02
Agrimonia eupatoria			0	0.00	1	0.01
Agrostemma githago	2	0.01				
Agrostis capillaris	2	0.11	0	0.00	8	0.31
Agrostis gigantea	6	0.27				
Agrostis stolonifera	10	1.04				
Agrostis tenuis	2	0.10				
Ajuga chamaepitys	0	0.00				
Alliaria petiolata			0	0.00	3	0.03
Allium rotundum					0	0.00
Alnus glutinosa	1	0.03			1	0.01
Alopecurus geniculatus	1	0.03				
Alopecurus pratensis agg.			0	0.01	3	0.04
Amaranthus retroflexus	1	0.10	1	0.01	1	0.00
Anchusa officinalis			0	0.01	0	0.00
Anthemis cotula	2	0.01				
Anthemis tinctoria	1	0.18			2	0.77
Anthriscus caucalis			2	0.12	2	0.47
Anthriscus sylvestris			1	0.02	9	0.35
Arctium lappa	1	0.00	1	0.01	3	0.04
Arctium minus	0	0.00			1	0.02
Arenaria serpyllifolia agg.	17	0.75	3	0.21	10	1.36
Arrhenatherum elatius			1	0.01	36	1.50
Artemisia campestris	0	0.01			1	0.01
Artemisia vulgaris	1	0.00	3	0.04	16	0.46
Atriplex calotheca	1	0.03				
Atriplex patula	22	1.07			0	0.00
Atriplex sagittata			1	0.01	3	0.04
Ballota nigra			1	0.01	2	0.01
Barbarea stricta					0	0.00
Bellis perennis	1	0.00				
Berteroa incana			1	0.63	1	0.21
Betula pendula			0	0.00		
Bidens tripartita	2	0.10				
Bifora radians	1	0.01				
Brachypodium pinnatum agg.					0	0.00

Bromus arvensis	0	0.00				
Bromus commutatus agg.	0	0.00	1	0.01	3	1.58
Bromus erectus			0	0.01	1	0.02
Bromus hordeaceus agg.	1	0.00	2	0.04	20	0.67
Bromus inermis					0	0.00
Bromus japonicus			1	0.01	1	0.01
Bromus mollis	0	0.00			1	0.01
Bromus secalinus agg.	0	0.00	1	0.02	3	0.04
Bromus squarrosus			0	0.08	0	0.05
Bromus sterilis	0	0.08	15	1.34	55	18.39
Bromus tectorum					0	0.05
Bryonia alba					0	0.00
Bunias orientalis			0	0.00	3	0.52
Bupleurum falcatum					0	0.00
Bupleurum rotundifolium					1	0.01
Calamagrostis epigejos					1	0.01
Calystegia sepium	1	0.03	1	0.02	3	0.05
Camelina microcarpa	1	0	0	0.01	1	0.01
Camelina sativa agg.	3	0.04				
Capsella bursa-pastoris	56	1.80	25	1.02	35	1.48
Cardaria draba	1	0.03	0	0.01	3	0.23
Carduus acanthoides	0	0.00	0	0.00	4	0.04
Carduus crispus			1	0.33	3	0.03
Carex acutiformis					0	0.00
Carex hirta					0	0.00
Carpinus betulus					0	0.00
Centaurea jacea					0	0.00
Centaurea scabiosa	3	0.04			2	0.02
Centaurea stoebe	1	0.00			0	0.00
Cerastium arvense	2	0.01			2	0.07
Cerastium holosteoides	4	0.13	1	0.03	6	0.07
Cerastium semidecandrum	0	0.00	0	0.01	2	0.02
Ceratocapnos claviculata					1	0.00
Chaerophyllum bulbosum	0	0.01	0	0.00	2	0.02
Chaerophyllum temulum			1	0.01	1	0.01
Chelidonium majus					0	0.00
Chenopodium album	4	0.27	6	0.65	6	0.18
Chenopodium glaucum	0	0.00			0	0.00
Chenopodium rubrum	2	0.07	1	0.02	2	0.22
Chondrilla juncea			0	0.00	0	0.00
Cichorium intybus	1	0.00			2	0.02
Cirsium arvense	62	5.36	13	0.38	41	0.77
Cirsium eriophorum			0	0.00	0	0.00
Cirsium vulgare	0	0.00	3	0.04	5	0.05
Conium maculatum			2	0.03	3	0.04
Conringia orientalis	5	0.08			1	0.01
Convolvulus arvensis	50	6.19	11	0.38	41	7.97
Conyza canadensis	7	0.26	10	0.18	20	0.81
Cornus sanguinea					0	0.00
Coronilla varia	2	0.05			1	0.01
Coronopus squamatus	0	0.00	0	0.01	1	0.00
Corylus avellana			0	0.01	1	0.01
Corynephorus canescens	0	0.01				
Crataegus monogyna			0	0.00	2	0.02
Crepis biennis			1	0.01	2	0.02
Crepis capillaris	1	0.02	1	0.01	1	0.01
Crepis tectorum	3	0.09	2	0.04	2	0.02
Cuscuta campestris	0	0.00				
Cynoglossum officinale	1	0.03				
Dactylis glomerata	0	0.00	4	0.05	34	0.43
Daucus carota	7	0.16	4	0.08	11	0.45
Deschampsia flexuosa					1	0.01
Descurainia sophia	5	0.02	6	0.43	9	0.55
Dipsacus fullonum					1	0.00
Echinops sphaerocephalus					0	0.00
Echium vulgare	1	0.17			0	0.00
Elymus repens	50	5.41	22	5.87	60	8.23
Epilobium lamyi			0	0.01	1	0.00
Epilobium tetragonum			1	0.02	2	0.03
Equisetum arvense	26	1.39	3	0.05	16	0.77
Equisetum fluviatile					0	0.00
Equisetum palustre	1	0.00			0	0.00
Equisetum sylvaticum	1	0.10				
Eryngium campestre					1	0.01
Euphorbia cyparissias	0	0.01			3	0.03
Euphorbia esula	2	0.11			1	0.01
Euphorbia platyphyllos	1	0.00			0	0.00
Fagus sylvatica	1	0.03				
Festuca arundinacea			0	0.00		
Festuca brevipila					0	0.00
Festuca ovina agg.					1	0.01
Festuca pratensis			1	0.01	5	0.05
Festuca rubra			0	0.00	11	0.71
Festuca rupicola					0	0.00
Filago arvensis	1	0.02	1	0.03	3	0.07
Filago minima	1	0.1				
Filipendula ulmaria					0	0.00
Fraxinus excelsior			1	0.01	2	0.02
Galeopsis bifida	1	0.02				

Galium album					2	0.07
Galium aparine	36	4.10	30	2.99	59	8.39
Galium mollugo agg.					5	0.05
Galium spurium agg.	1	0.00			1	0.01
Galium verrucosum					0	0.00
Galium verum agg.					2	0.02
Geranium columbinum	0	0.00	2	0.65	3	1.22
Geranium molle	1	0.00	0	0.16	1	0.11
Geranium palustre					0	0.00
Geranium pratense					1	0.00
Geranium pusillum	12	0.13	17	1.18	43	5.98
Geranium pyrenaicum			0	0.01	1	1.55
Geranium robertianum					1	0.01
Geum urbanum					3	0.08
Glechoma hederacea	1	0.39	0	0.01	3	0.03
Gnaphalium sylvaticum	0	0.00				
Gnaphalium uliginosum	14	1.07	1	0.02	2	0.02
Gypsophila muralis	1	0.04				
Helichrysum arenarium			0	0.00	0	0.00
Heracleum mantegazzianum					1	0.01
Heracleum sphondylium	0	0.00			1	0.00
Herniaria glabra	1	0.00				
Hieracium laevigatum					0	0.00
Hieracium pilosella	1	0.00			1	0.01
Holosteum umbellatum	1	0.02			1	0.01
Hordelymus europaeus			0	0.00		
Hordeum secalinum	0	0.00				
Hylotelephium maximum	2	0.03				
Hylotelephium telephium	5	0.02			0	0.00
Hypericum humifusum	1	0.17				
Hypericum perforatum	1	0.02	3	0.04	14	0.16
Hypochaeris radicata	1	0.00	0	0.00	2	0.02
Illecebrum verticillatum	1	0.03				
Impatiens glandulifera			0	0.01	1	0.00
Impatiens noli-tangere					1	0.00
Impatiens parviflora					0	0.00
Jasione montana					0	0.00
Juncus bufonius	11	2.07	1	0.01	1	0.01
Juncus effusus	0	0.00				
Lactuca serriola			2	0.03	13	0.21
Lamium album					4	0.05
Lamium maculatum					1	0.01
Laphangium luteoalbum	0	0.00				
Lathyrus pratensis	1	0.00			1	0.02
Leontodon autumnalis	1	0.01			1	0.00
Leontodon hispidus					0	0.00
Lepidium campestre	1	0.03				
Lepidium ruderale					0	0.00
Leucanthemum ircutianum			0	0.01	0	0.00
Leucanthemum vulgare	0	0.08				
Linaria arvensis	1	0.02				
Linaria vulgaris	4	0.19	1	0.03	4	0.10
Lolium multiflorum	1	0.00	3	1.23	4	0.05
Lolium perenne	4	0.04	4	0.69	19	0.58
Lotus corniculatus					1	0.01
Lotus uliginosus	0	0.00				
Luzula multiflora	0	0.00				
Lysimachia nummularia					0	0.00
Lysimachia vulgaris	0	0.00				
Malus sylvestris			0	0.01	1	0.01
Malva neglecta	1	0.00			0	0.00
Malva sylvestris			1	0.01	2	0.02
Malva verticillata			0	0.00		
Matricaria discoidea			4	0.06	4	0.05
Medicago lupulina	16	0.29	1	0.08	4	0.05
Melilotus albus			0	0.01	0	0.00
Melilotus officinalis	1	0.00				
Mentha aquatica	0	0.01				
Mentha arvensis	24	2.55				
Misopates orontium	1	0.01				
Moehringia trinervia	0	0.00				
Myosotis ramosissima			0	0.00	1	0.01
Myosoton aquaticum	1	0.03			0	0.00
Myosurus minimus	1	0.22				
Nigella arvensis	0	0.00				
Nonea pulla	1	0.00				
Odontites vernus	1	0.03			0	0.00
Odontites vulgaris	5	0.48			1	0.01
Ononis repens	0	0.00			1	0.01
Onopordum acanthium					1	0.01
Origanum vulgare agg.					0	0.00
Ornithopus perpusillus	2	0.01	0	0.01	0	0.00
Panicum capillare	0	0.00				
Pastinaca sativa	1	0			1	0.01
Peplis portula	0	0.00	0	0.01		
Persicaria amphibia	2	0.20	1	0.02	2	0.02
Persicaria hydropiper	2	0.10				
Persicaria lapathifolia agg.	15	0.63	5	2.18	7	0.47
Phalaris arundinacea			0	0.01	1	0.01

Phleum pratense agg.			1	0.01	3	0.03
Phragmites australis	1	0.10			1	0.01
Picris hieracioides	1	0.00	2	0.03	2	0.03
Pinus sylvestris	1	0.00	0	0.00	1	0.01
Plantago lanceolata	7	0.15	2	0.03	8	0.09
Plantago major agg.	19	0.56	4	0.16	5	0.06
Plantago uliginosa	9	0.28				
Poa angustifolia					1	0.01
Poa annua agg.	19	1.50	10	1.27	13	0.49
Poa compressa					1	0.01
Poa pratensis	2	0.02	1	0.03	4	0.05
Poa trivialis	10	1.01	7	0.44	36	3.41
Polycnemum arvense	1	0.00				
Polygonum amphibium	0	0.00				
Polygonum aviculare agg.	66	3.73	38	1.76	47	2.33
Polygonum hydropiper	2	0.28				
Polygonum lapathifolium	16	0.60	2	0.12	2	0.07
Populus hybrida					0	0.00
Potentilla anserina	11	0.86			1	0.01
Potentilla argentea			1	0.02	3	0.04
Potentilla reptans	3	0.11	0	0.01	4	0.44
Prunus avium			0	0.00	1	0.01
Prunus domestica					0	0.00
Prunus mahaleb			1	0.01		
Prunus serotina			0	0.00	1	0.01
Prunus spinosa					2	0.02
Pteridium aquilinum					0	0.00
Puccinellia distans			0	0.01	0	0.00
Quercus petraea			1	0.01	2	0.02
Quercus robur	0	0.00			1	0.01
Ranunculus acris agg.	0	0.00				
Ranunculus auricomus agg.					1	0.01
Ranunculus bulbosus					0	0.00
Ranunculus rectus	0	0.00				
Ranunculus repens	25	1.05	1	0.01	5	0.06
Ranunculus sardous	0	0.00				
Rapistrum perenne	0	0.00				
Reseda lutea	2	0.01			1	0.00
Reseda luteola					1	0.01
Rhinanthus alectorolophus	1	0.00				
Rhinanthus minor					1	0.00
Robinia pseudoacacia			0	0.01	1	0.01
Rorippa palustris	1	0.00	0	0.01	1	0.01
Rubus caesius	5	0.45	1	0.01	4	0.63
Rubus fruticosus agg.					0	0.00
Rubus idaeus					3	0.03
Rumex acetosa	1	0.03	2	0.03	3	0.03
Rumex conglomeratus					0	0.00
Rumex crispus	18	0.15	2	0.03	11	0.12
Rumex obtusifolius	1	0.00	2	0.03	4	0.25
Sagina procumbens	4	0.15				
Salix viminalis			0	0.00	0	0.00
Salvia pratensis					1	0.00
Sambucus nigra			1	0.01	1	0.01
Sanguisorba minor					1	0.00
Scutellaria galericulata	1	0.00				
Sedum acre	0	0.00				
Sedum album			0	0.00		
Senecio erucifolius					0	0.00
Senecio jacobaea			1	0.01	2	0.02
Senecio sylvaticus	0	0.00			0	0.00
Senecio vernalis	1	0.02	1	0.02	1	0.01
Serratula tinctoria					1	0.01
Setaria verticillata	0	0.00				
Silene dichotoma					0	0.00
Silene dioica					1	0.00
Silene latifolia	3	0.20	4	0.08	13	0.17
Silene vulgaris	2	0.03	1	0.01	3	0.04
Sinapis alba	0	0.00				
Sisymbrium altissimum			1	0.94	1	0.01
Sisymbrium loeselii			1	0.02	3	0.23
Sisymbrium officinale	2	0.01	8	0.22	15	0.46
Sisymbrium officinale					0	0.00
Solidago canadensis					1	0.01
Sonchus arvensis agg.	27	1.90			1	0.01
Sonchus asper	22	0.91	2	0.66	5	0.10
Sonchus oleraceus	25	0.57	3	0.05	5	0.45
Sorbus aucuparia					1	0.01
Spergula morisonii	0	0.08				
Spergularia rubra x salina	0	0.00				
Spergularia rubra	6	0.72	1	0.01	0	0.00
Stachys palustris	17	0.81	0	0.00	3	0.09
Stachys recta			0	0.00	1	0.21
Stachys sylvatica					0	0.00
Stachys x ambigua					0	0.00
Stellaria media	57	7.13	16	1.55	23	0.88
Symphytum officinale	1	0.09			0	0.00
Tanacetum vulgare	1	0.00	4	0.13	15	0.23
Taraxacum officinale agg.	34	0.85	11	0.18	20	0.33

Thlaspi montanum	1	0.00				
Thlaspi perfoliatum					1	0.01
Torilis japonica					2	0.03
Tragopogon orientalis					1	0.00
Trifolium arvense	4	0.44	2	0.34	2	0.21
Trifolium campestre	0	0.00	1	0.01	0	0.00
Trifolium dubium	1	0.01	1	0.01	1	0.01
Trifolium hybridum	1	0.00				
Trifolium montanum					0	0.05
Trifolium pratense	2	0.21	3	1.21	4	0.24
Trifolium repens	7	0.16	5	0.69	5	0.06
Tripleurospermum inodorum	11	0.25	28	3.47	44	2.64
Trisetum flavescens					0	0.00
Tussilago farfara	15	1.71	1	0.01	1	0.01
Urtica dioica	0	0.00	2	0.04	25	0.90
Urtica urens	1	0.01				
Valeriana officinalis					0	0.00
Valerianella locusta					1	0.01
Verbena officinalis	0	0.00				
Veronica chamaedrys					1	0.02
Veronica dillenii	2	0.03			0	0.00
Veronica peregrina	0	0.00	2	0.06	1	0.02
Veronica praecox					1	0.00
Veronica serpyllifolia	0	0.00				
Vicia cracca	2	0.01	2	0.03	4	0.79
Vicia dumetorum					0	0.00
Vicia pannonica	0	0.00	0	0.01	1	0.06
Vicia sepium	1	0.01	2	0.03	3	0.03
Vicia tenuifolia	2	0.10			1	0.01
Viola hirta					0	0.00
Viola odorata			0	0.01	0	0.00
Viola rupestris			0	0.01		
Vulpia myuros			1	0.32	1	0.77
Crop volunteers						
Allium cepa			1	0.01		
Avena sativa	3	0.02	1	0.02		
Beta vulgaris					0	0.00
Brassica napus			11	0.18	5	0.06
Brassica oleracea			0	0.01	0	0.00
Coriandrum sativum	0	0.00				
Helianthus annuus			1	1.02	2	0.46
Hordeum vulgare	2	0.21	10	0.20	10	0.11
Humulus lupulus					1	0.00
Linum usitatissimum	0	0.00				
Lupinus luteus	2	0.01			0	0.00
Medicago sativa	1	0.00	0	0.00	0	0.00
Medicago x varia			2	0.12	2	0.11
Ornithopus sativus	3	0.09	0	0.00		
Papaver somniferum	0	0.00				
Pisum sativum	1	0.02				
Secale cereale	5	0.24	4	0.40	5	0.11
Secale cereale x Triticum aestivum			1	0.02	0	0.00
Solanum tuberosum	2	0.00	0	0.00	1	0.01
Trifolium incarnatum	0	0.01				
Triticum aestivum	1	0.09	6	0.42	9	0.70
Vicia faba	1	0.00				

Appendix Table S4.1 Percentage share of fields with different crop types and crop classes in the 1950s/60s and 2009. Estimated cover values (%) of crops are given as medians and interquartile ranges (IQR). Abbreviations for cultivation period: w – winter crops (=autumn-sown crops), s – spring crops (=spring-sown crops), s/w – both spring and winter crops.

Type/classes of crops	Cultivation period	Frequency [%]		1950s/60s		2009	
		1950s/60s	2009	median	IQR	median	IQR
Cereals – winter crops	*w*	*41.3*	*60.5*				
Triticale	w	-	1.3	-	-	80	80-80
Winter barley	w	3.3	8.4	70	70-90	94	94-97.75
Winter rye	w	24.5	20.2	90	90-90	85	85-90
Winter wheat	w	13.5	30.6	60	60-80	85	85-95
Cereals – spring crops	*s*	*26.0*	*16.6*				
Cereal mixtures	s	4.8	0.3	60	60-70	85	85-85
Maize	s	0.8	8.9	70	70-70	95	95-95
Spring barley	s	4.8	3.6	60	60-70	83	82.5-90
Spring rye	s	1.3	-	90	90-95	-	-
Spring wheat	s	6.1	1.8	70	70-80	92	92-95
Oat	s	8.2	2.0	50	50-70	90	90-95
Legumes	*s*	*2.0*	-				
Beans	s	0.5	-	-	-	-	-
Peas	s	1.5	-	45	45-47.5	-	-
Forage crops	*s/w*	*1.0*	*0.3*				
Clover-grass	s/w	-	0.3	-	-	50	50-50
Lucerne	s/w	0.5	-	75	75-75	-	-
Millet	s	0.5	-	65	65-67.5	-	-
Root/cabbage crops	*s*	*22.3*	*3.9*				
Beetroots	s	5.4	2.6	40	40-60	97	97-98.75
Carrots	s	-	0.5	-	-	25	25-32.5
Potatoes	s	15.1	0.8	40	40-85	75	75-85.5
Other vegetables	s	1.8	-	-	-	-	-
Oleaginous fruits	*s/w*	*0.6*	*17.1*				
Mustard	s	0.3	-	30	30-30	-	-
Sunflower	s	0.3	0.3	20	20-20	95	95-95
Winter rape	w	-	16.8	-	-	90	90-97.5
Other crops		*7.0*	*1.9*				
Buckwheat	s	0.3	-	90	90-90	-	-
Flax	s	0.5	0.3	60	60-60	45	45-45
Grass leys	-	0.3	-	50	50-50	-	-
Initial fallow land	-	1.5	0.8	93	92.5-95.75	63	62.5-66.25
Unidentified							
Stubble	-	3.6	0.8	90	90-95	80	80-85
No data	-	0.8	-	-	-	-	-

Appendix Table S4.2. *Changes in frequency over time, given for the pooled data, and separately for the three substrate types. Species with significant changes according to Indicator Species Analysis (ISA, considering abundance and frequency) are given first; these are further differentiated according to their habitat preferences (ISA on historical data alone). Grey shadings indicate frequency increases from 1950s/60s to 2009. For consistency in status all data follow JANSEN & DENGLER (2008). Abbreviations indicate species status in the region: 'A' = archaeophytes; 'A/I' = unclear whether archaeophytes or neophytes; 'I' = indigenous; 'K' = crops; 'N' = neophytes; 'NA' = no data available; 'U/N' = unstable neophytes*

Species		***Trend***	***Status***	***Threat Status***	***complete dataset (n=392)*** **Frequency of occurence (%)**			***sand as blocking variable (n=154)*** **Frequency of occurence (%)**			***loam as blocking variable (n=122)*** **Frequency of occurence (%)**			***lime as blocking variable (n=116)*** **Frequency of occurence (%)**		
					2009	1950s/60s	*P-value*	2009	1950s/60s	*P-value*	2009	1950s/60s	*P-value*	2009	1950s/60s	*P-value*
indicator species for sandy substrates																
Scleranthus annuus	*1*	-	**I**		2	33	0.0001	4	69	0.0001	0	13	0.0001	0	7	0.0073
Arnoseris minima	*1*	-	**I**	**x**	0	16	0.0001	0	38	0.0001				0	3	0.119
Gnaphalium uliginosum	*1*	-	**I**		1	14	0.0001	3	25	0.0001	1	6	0.0144	0	6	0.0097
Juncus bufonius	*1*	-	**I**		1	11	0.0001	1	23	0.0001	0	5	0.0307	0	2	0.4965
Viola tricolor	*1*	-	**NA**		0	8	0.0001	0	14	0.0001	0	6	0.0122	0	3	0.1246
Digitaria ischaemum	*1*	-	**A**		1	8	0.0001	1	21	0.0001						
Hypochaeris glabra	*1*	-	**I**	**x**	0	7	0.0001	1	18	0.0001				0	1	1
Rumex acetosella	*1*	-	**I**		3	21	0.0001	7	45	0.0001	1	3	0.1162	0	6	0.0119
Spergula arvensis	*1*	-	**A**		4	30	0.0001	10	69	0.0001	0	2	0.4908	2	8	0.0075
Achillea millefolium	*1*	-	**I**		2	12	0.0001	5	22	0.0001	1	2	0.2465	0	9	0.0013
Spergularia rubra	*1*	-	**A/I**		1	6	0.0001	1	14	0.0001				0	3	0.2513
Setaria viridis	*1*	-	**A**		4	17	0.0001	9	38	0.0001	0	6	0.0122			
Aphanes inexspectata	*1*	-	**A**	**x**	0	4	0.0002	0	9	0.0001				0	1	1
Vicia sativa	*1*	-	**I**		9	33	0.0001	19	58	0.0001	2	11	0.0018	1	23	0.0001
Centaurea cyanus	*1*	-	**A**		10	35	0.0001	21	55	0.0001	2	16	0.0001	5	29	0.0001
Anchusa arvensis	*1*	-	**A**		3	10	0.0001	8	21	0.0003	0	2	0.4932	0	3	0.2426
Veronica arvensis	*1*	-	**A**		9	27	0.0001	15	51	0.0001	3	20	0.0001	7	3	0.1623
Papaver dubium	*1*	-	**A**		3	8	0.0009	8	14	0.0367	0	6	0.0148	0	1	1
Arabidopsis thaliana	*1*	-	**A**		4	10	0.0001	9	20	0.0016	2	7	0.0362			
Erodium cicutarium	*1*	-	**I**		7	17	0.0001	18	39	0.0001	0	2	0.2413	0	4	0.058
Vicia hirsuta	*1*	-	**I**		11	19	0.002	28	40	0.0089	2	6	0.253	0	6	0.0112
Apera spica-venti	*1*	-	**I**		22	33	0.0018	36	58	0.0001	17	25	0.075	9	9	0.6429
Galinsoga parviflora	*1*	-	**N**		6	8	0.0198	14	15	0.1217	1	7	0.0239			
indicator species for loamy substrates																
Atriplex patula	*2*	-	**A/I**		0	22	0.0001	0	1	0.4996	0	39	0.0001	0	32	0.0001
Stachys palustris	*2*	-	**I**		0	17	0.0001	0	2	0.2581	0	36	0.0001	1	18	0.0001
Sonchus asper	*2*	-	**NA**		2	22	0.0001	3	12	0.0044	2	42	0.0001	3	16	0.0005
Lamium amplexicaule	*2*	-	**A**		3	28	0.0001	6	19	0.0001	0	38	0.0001	1	31	0.0001
Equisetum arvense	*2*	-	**I**		3	26	0.0001	3	13	0.0002	5	48	0.0001	2	19	0.0001
Veronica polita	*2*	-	**A**	**x**	2	15	0.0001				2	30	0.0001	3	20	0.0006
Fumaria officinalis	*2*	-	**A**		3	21	0.0001	3	4	0.6671	3	42	0.0001	1	22	0.0001
Plantago major	*2*	-	**I**		4	25	0.0001	5	19	0.0001	5	34	0.0001	3	24	0.0001
Aphanes arvensis	*2*	-	**A**		3	17	0.0001	5	14	0.0066	2	33	0.0001	1	3	0.315
Arenaria serpyllifolia	*2*	-	**I**		3	17	0.0001	6	12	0.0818	2	28	0.0001	1	14	0.0008
Persicaria lapathifolia	*2*	-	**I**		7	30	0.0001	8	32	0.0001	7	42	0.0001	4	13	0.0818
Euphorbia helioscopia	*2*	-	**A**		9	34	0.0001	4	8	0.0348	8	52	0.0001	16	51	0.0001
Taraxacum officinale	*2*	-	**NA**		11	34	0.0001	12	14	0.3803	8	40	0.0001	11	56	0.0001
Lamium purpureum	*2*	-	**A**		8	19	0.0002	8	10	0.1381	9	43	0.0022	7	7	0.5555
Poa annua	*2*	-	**I**		10	19	0.0003	9	16	0.0459	8	34	0.0001	13	8	0.7345
indicator species for calcareous substrates																
Silene noctiflora	*3*	-	**A**	**x**	1	21	0.0001	0	1	0.4878	0	19	0.0001	3	51	0.0001
Galeopsis tetrahit	*3*	-	**NA**		1	20	0.0001	2	12	0.0005	1	14	0.0002	0	37	0.0001
Lathyrus tuberosus	*3*	-	**I**		0	17	0.0001	0	1	1	0	11	0.0001	0	46	0.0001
Adonis aestivalis	*3*	-	**A**	**x**	1	16	0.0001							3	55	0.0001
Medicago lupulina	*3*	-	**I**		1	16	0.0001	0	5	0.0066	1	17	0.0001	1	28	0.0001
Campanula rapunculoides	*3*	-	**I**		0	15	0.0001				0	7	0.0021	0	43	0.0001
Lithospermum arvense	*3*	-	**A**	**x**	0	13	0.0001	0	1	1	1	8	0.0055	0	33	0.0001
Galium tricornutum	*3*	-	**A**	**x**	0	11	0.0001				0	1	1	0	36	0.0001
Rumex crispus	*3*	-	**I**		2	18	0.0001	1	6	0.001	2	11	0.0011	3	41	0.0001
Sherardia arvensis	*3*	-	**A**	**x**	1	9	0.0001				0	7	0.0036	4	24	0.0016
Neslia paniculata	*3*	-	**A**	**x**	0	8	0.0001	0	3	0.0566	0	3	0.1202	0	21	0.0001
Consolida regalis	*3*	-	**A**	**x**	3	22	0.0001	0	2	0.2378	6	20	0.0001	4	51	0.0001
Sedum telephium	*3*	-	**I**	**x**	0	7	0.0001				0	6	0.0105	0	19	0.0001
Knautia arvensis	*3*	-	**I**		0	6	0.0001							0	21	0.0001
Falcaria vulgaris	*3*	-	**I**		2	11	0.0001				4	5	0.2978	1	33	0.0001
Anagallis foemina	*3*	-	**I**	**x**	0	5	0.0001				0	5	0.024	0	12	0.0002
Caucalis platycarpos	*3*	-	**A**	**x**	0	5	0.0001				1	1	1	0	15	0.0001
Conringia orientalis	*3*	-	**A**	**x**	0	5	0.0001							0	16	0.0001
Fumaria vaillantii	*3*	-	**A**	**x**	1	5	0.0005				0	1	1	3	16	0.0008
Rubus caesius	*3*	-	**I**		1	5	0.0001				2	3	0.2603	0	12	0.0002

Ranunculus arvensis	*3*	-	**A**	**x**	0	4	0.0004				0	1	1	0	11	0.0004
Lapsana communis	*3*	-	**I**		4	14	0.0035	2	1	0.6193	5	7	0.416	6	40	0.0001
Centaurea scabiosa	*3*	-	**I**	**x**	0	3	0.0003							0	11	0.0003
Potentilla reptans	*3*	-	**I**		0	3	0.022	1	1	1				0	9	0.0006
Valerianella locusta	*3*	-	**A/I**		0	3	0.0007							0	9	0.0005
Avena fatua	*3*	-	**A**		7	18	0.0001				7	4	0.9984	17	55	0.0001
Tripleurospermum inodorum	*3*	**+**	**A**		28	11	0.0001	30	4	0.0001	17	11	0.5021	37	20	0.0081
Geranium pusillum	*3*	**+**	**A**		17	12	0.0164	23	5	0.0002	8	10	0.5895	18	23	0.3978
species with no specific habitat requirements																
Sonchus arvensis	*4*	-	**NA**		0	27	0.0001	0	12	0.0001	0	26	0.0001	0	47	0.0001
Ranunculus repens	*4*	-	**I**		1	25	0.0001	0	6	0.0018	2	32	0.0001	0	42	0.0001
Mentha arvense	*4*	-	**I**		0	24	0.0001	0	14	0.0001	0	42	0.0001	0	18	0.0001
Senecio vulgaris	*4*	-	**I**		0	19	0.0001	0	20	0.0001	0	24	0.0001	0	11	0.0002
Euphorbia exigua	*4*	-	**A**	**x**	2	33	0.0001	1	3	0.1121	2	33	0.0001	4	74	0.0001
Raphanus raphanistrum	*4*	-	**NA**	**x**	1	15	0.0001	1	24	0.0001	1	8	0.0035	0	10	0.0004
Tussilago farfara	*4*	-	**I**		1	15	0.0001	0	3	0.1282	2	20	0.0001	0	25	0.0001
Bromus sterilis	*4*	**+**	**A**		15	0	0.0001	3	0	0.057	17	0	0.0001	28	1	0.0001
Sinapis arvensis	*4*	-	**A**		3	43	0.0001	1	6	0.0124	3	61	0.0001	4	74	0.0001
Agrostis stolonifera	*4*	-	**I**		0	11	0.0001	0	10	0.0001	0	7	0.0063	0	16	0.0001
Potentilla anserina	*4*	-	**I**		0	11	0.0001	0	5	0.0156	0	18	0.0001	0	12	0.0002
Veronica hederifolia	*4*	-	**I**		2	22	0.0001	0	9	0.0001	5	33	0.0001	3	27	0.0001
Brassica napus	*4*	**+**	**K**		11	0	0.0001	8	0	0.0003	18	0	0.0001	7	0	0.0064
Sonchus oleraceus	*4*	-	**I**		3	25	0.0001	5	18	0.0001	2	30	0.0001	2	30	0.0001
Persicaria maculosa	*4*	-	**I**		2	16	0.0001	4	18	0.0002	0	16	0.0001	1	14	0.0003
Agrostis gigantea	*4*	-	**I**		0	6	0.0001	0	8	0.0001	0	9	0.0006	0	1	1
Veronica agrestis	*4*	-	**A**	**x**	0	6	0.0001	0	4	0.031	1	11	0.0012	0	3	0.2341
Triticum aestivum	*4*	**+**	**NA**		6	1	0.0038	0	1	1	15	0	0.0001	5	3	0.3416
Anagallis arvensis	*4*	-	**NA**		8	46	0.0001	9	37	0.0001	3	48	0.0001	10	56	0.0001
Thlaspi arvense	*4*	-	**I**		7	36	0.0001	10	6	0.7572	7	61	0.0001	5	51	0.0001
Odontites vulgaris	*4*	-	**I**	**x**	0	5	0.0001	0	5	0.0066	0	3	0.1167	0	7	0.0059
Oxalis fontana	*4*	-	**N**		0	5	0.0001	0	7	0.0011	0	2	0.2365	0	3	0.1107
Anthemis arvensis	*4*	-	**A**		1	5	0.0001	2	10	0.0007	0	3	0.1151	0	1	1
Hordeum vulgare	*4*	**+**	**K**		10	2	0.0001	1	0	0.4948	19	0	0.0001	12	6	0.1285
Cirsium arvense	*4*	-	**I**		13	62	0.0001	9	26	0.0001	18	85	0.0001	14	84	0.0001
Convolvulus arvensis	*4*	-	**I**		11	50	0.0001	1	15	0.0001	6	59	0.0001	28	87	0.0001
Rorippa sylvestris	*4*	-	**I**		0	4	0.0002	0	3	0.1228	0	10	0.0007			
Euphorbia peplus	*4*	-	**NA**		0	4	0.0001				0	10	0.0006	0	4	0.054
Galeopsis angustifolia	*4*	-	**A/I**	**x**	0	4	0.0001				0	5	0.0239	0	9	0.0011
Holcus mollis	*4*	-	**I**		0	4	0.0001	0	8	0.0006				0	3	0.12
Persicaria hydropiper	*4*	-	**I**		0	4	0.0001	0	5	0.0081	0	3	0.119	0	3	0.1197
Sagina procumbens	*4*	-	**I**		0	4	0.0001	0	8	0.0006	0	3	0.1191	0	1	1
Cerastium holosteoides	*4*	-	**I**		1	4	0.0182	1	9	0.0003	3	2	0.4989	0	1	1
Linaria vulgaris	*4*	-	**I**		1	4	0.0041	1	3	0.4034	2	3	0.3349	0	5	0.0309
Veronica triphyllos	*4*	-	**A**	**x**	1	4	0.002	1	6	0.1102	0	2	0.2437	0	3	0.1186
Sisymbrium officinale	*4*	**+**	**A**		8	2	0.0029	14	1	0.0001	7	4	0.9809	3	1	0.6178
Alopecurus myosuroides	*4*	**+**	**A**		8	2	0.0001	1	0	1	23	5	0.0001	3	0	0.253
Dactylis glomerata	*4*	**+**	**I**		4	0	0.0006	3	0	0.0607	7	1	0.0142			
Matricaria discoidea	*4*	**+**	**N**		4	0	0.0003	6	0	0.0037	4	0	0.062			
Stellaria media	*4*	-	**I**		16	57	0.0001	24	50	0.0001	11	75	0.0001	9	47	0.0001
Plantago lanceolata	*4*	-	**A**		2	7	0.0002	3	10	0.0597	0	2	0.4954	1	9	0.0021
Myosotis stricta	*4*	-	**A/I**		0	3	0.0353	0	6	0.0016	0	1	1	1	0	1
Scandix pecten-veneris	*4*	-	**A**	**x**	0	3	0.0082				0	1	1	1	8	0.0173
Ornithopus sativus	*4*	-	**U/N**		0	3	0.0076	1	6	0.0081						
Chrysanthemum segetum	*4*	-	**A**	**x**	0	3	0.0022	0	3	0.0558	0	2	0.4903	0	3	0.2394
Setaria pumila	*4*	-	**A**	**x**	0	3	0.0018	1	8	0.0008						
Galeopsis ladanum	*4*	-	**I**	**x**	0	3	0.0017	1	6	0.0043	0	1	1	0	1	1
Camelina sativa	*4*	-	**A**	**x**	0	3	0.0009				1	8	0.0063	0	3	0.2324
Chaenorrhinum minus	*4*	-	**NA**		0	3	0.0007	0	1	1	0	6	0.0125	0	3	0.1209
Agrostis capillaris	*4*	-	**I**		0	3	0.0002	1	8	0.0002						
Erophila verna	*4*	-	**I**		1	3	0.0361	2	6	0.0692				0	1	1
Persicaria amphibia	*4*	-	**I**		1	3	0.0209	0	1	1	3	7	0.0366			
Vicia villosa	*4*	-	**N**		2	6	0.0025	2	6	0.0191	2	7	0.0605	2	3	0.3906
Erysimum cheiranthoides	*4*	-	**I**		2	6	0.0006	5	6	0.2944	0	8	0.0017	0	3	0.2331
Papaver argemone	*4*	-	**A**		2	6	0.0001	4	10	0.0151	0	2	0.2437	0	6	0.0139
Lolium multiflorum	*4*	**+**	**N**		3	1	0.0156	3	1	0.4099	3	1	0.3689	3	0	0.12
Cirsium vulgare	*4*	**+**	**I**		3	0	0.0106	1	1	1	7	0	0.0053	1	0	1
Myosotis arvensis	*4*	-	**A/I**		17	49	0.0001	17	45	0.0001	19	52	0.0001	14	51	0.0001
Vicia tetrasperma	*4*	-	**I**		2	5	0.0262	3	6	0.0713	4	2	0.6039	0	5	0.0251

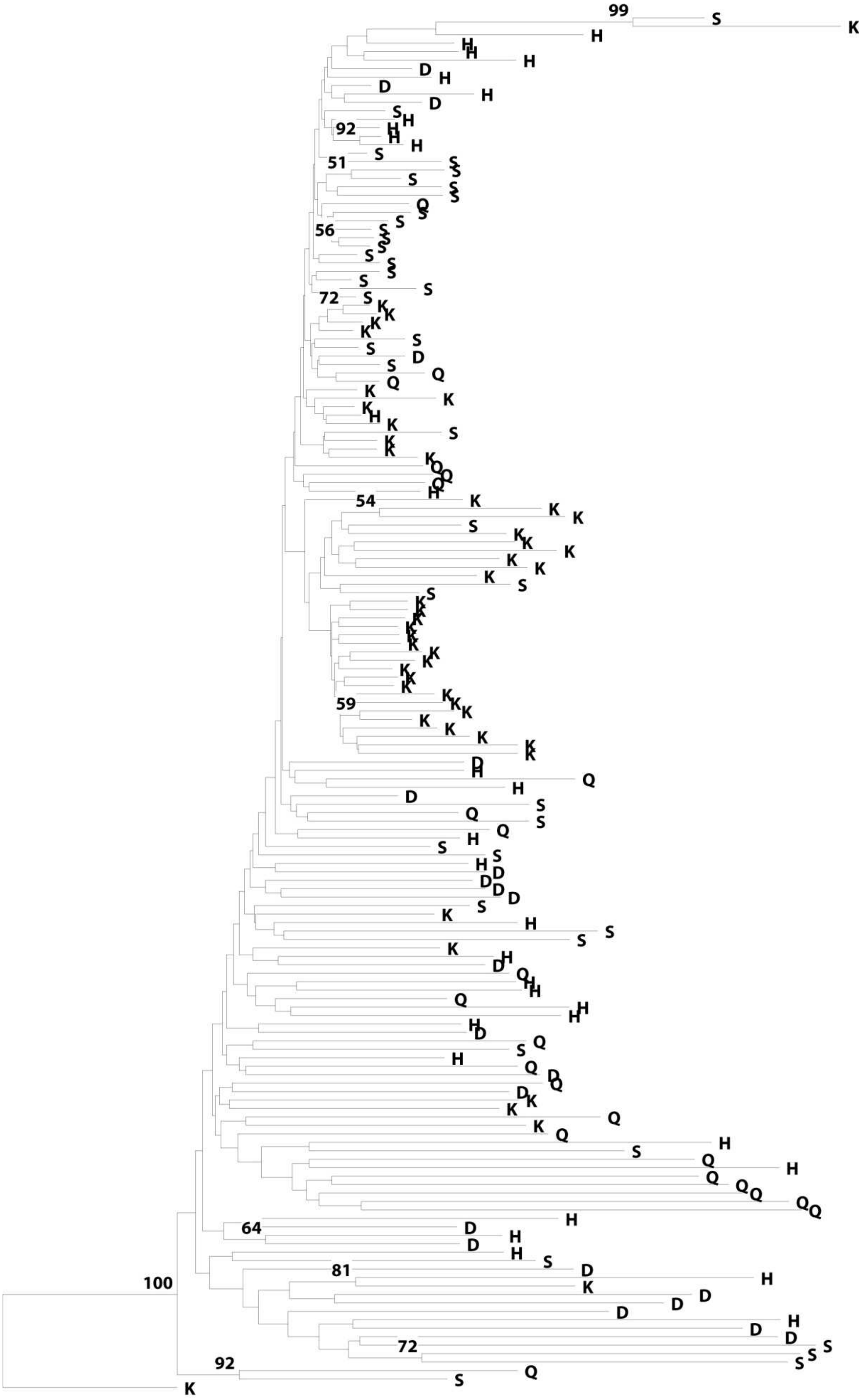
Papaver rhoeas	*4*	-	**A**		15	35	0.0001	7	4	0.3564	25	52	0.0001	16	57	0.0001
Capsella bursa-pastoris	*4*	-	**I**		25	56	0.0001	39	62	0.0001	15	65	0.0001	18	41	0.0003
Elymus repens	*4*	-	**I**		22	48	0.0001	31	40	0.2079	24	64	0.0001	7	44	0.0001
Matricaria recutita	*4*	-	**A**		9	19	0.0092	15	19	0.5872	11	34	0.0001	1	3	0.6218
Reseda lutea	*4*	-	**A**		0	2	0.0354				0	1	1	0	4	0.0578
Euphorbia esula	*4*	-	**I**		0	2	0.03				0	2	0.235	0	3	0.2445
Cerastium arvense	*4*	-	**I**		0	2	0.0292	0	3	0.0614				0	1	1
Anthemis cotula	*4*	-	**A**	**x**	0	2	0.0285							0	5	0.0312
Veronica dillenii	*4*	-	**I**	**x**	0	2	0.0271	0	4	0.0264						
Agrostemma githago	*4*	-	**A**	**x**	0	2	0.0266							0	5	0.0305
Lupinus luteus	*4*	-	**K**		0	2	0.0122	0	5	0.0132						
Bidens tripartita	*4*	-	**I**		0	2	0.0089	0	4	0.0284	0	2	0.5018			
Vicia tenuifolia	*4*	-	**I**	**x**	0	2	0.0077							0	7	0.0058
Securigera varia	*4*	-	**I**		0	2	0.0072				0	2	0.4932	0	5	0.0304
Epilobium tetragonum	*4*	+	**I**		2	0	0.0311	1	0	0.4984	3	0	0.1198			
Conium maculatum	*4*	+	**A**		2	0	0.0284				5	0	0.024			
Veronica peregrina	*4*	+	**NA**		2	0	0.0174							8	1	0.0187
Urtica dioica	*4*	+	**I**		2	0	0.0172	1	0	0.4969	6	1	0.0617			
Lactuca serriola	*4*	+	**I**		2	0	0.0164	2	0	0.2489	2	0	0.5016	2	0	0.4954
Anthriscus caucalis	*4*	+	**I**		2	0	0.0028				7	0	0.0049	1	0	1
Polygonum aviculare	*4*	-	**I**		38	66	0.0001	34	55	0.0001	34	61	0.0001	47	85	0.0001
Fallopia convolvulus	*4*	-	**A**		50	84	0.0001	71	82	0.0001	26	80	0.0001	47	91	0.0001
Chenopodium album	*4*	-	**I**		44	68	0.0001	73	69	0.0935	38	67	0.0001	10	66	0.0001
Viola arvensis	*4*	-	**A/I**		51	67	0.0001	60	65	0.1687	30	65	0.0001	60	72	0.1066
species with no significant frequency shifts																
Acer campestre	*5*	+	**I**	**x**	1	0	0.5013				2	0	0.4981			
Achillea ptarmica	*5*	**0**	**I**	**x**	0	0	1	0	1	1						
Aethusa cynapium	*5*	-	**I**		6	11	0.2506	1	0	1	4	15	0.001	15	22	0.7377
Agrimonia eupatora	*5*	**0**	**I**		0	0	1				1	0	1			
Ajuga chamaepitys	*5*	**0**	**A**	**x**	0	0	1							0	1	1
Alliaria petiolata	*5*	**0**	**NA**		0	0	1				1	0	1			
Allium cepa	*5*	**0**	**K**		0	0	1	1	0	1						
Allium oleraceum	*5*	**0**	**I**	**x**	0	0	1				1	0	1			
Alnus glutinosa	*5*	-	**I**		0	1	0.2392	0	2	0.2444						
Alopecurus geniculatus	*5*	-	**I**		0	1	0.1231				0	3	0.1183			
Alopecurus pratensis	*5*	**0**	**NA**		0	0	1							1	0	1
Amaranthus retroflexus	*5*	**0**	**N**		1	1	0.2651	1	1	1	1	2	0.241			
Anchusa officinalis	*5*	**0**	**A**	**x**	0	0	1	1	0	1						
Anthemis tinctoria	*5*	-	**A/I**		0	1	0.235				0	2	0.2428			
Anthoxanthum aristatum	*5*	-	**N**		1	3	0.056	1	6	0.0534						
Anthriscus sylvestris	*5*	+	**NA**		1	0	0.0584				4	0	0.058			
Arctium lappa	*5*	**0**	**A/I**		1	1	0.6855	1	0	1	1	2	0.4858	0	1	1
Arctium minus	*5*	**0**	**I**		0	0	1	0	1	1						
Arrhenatherium elatior	*5*	+	**I**		1	0	0.498				2	0	0.5045			
Artemisia campestris	*5*	**0**	**I**		0	0	1							0	1	1
Artemisia vulgaris	*5*	+	**I**		3	1	0.2482	6	1	0.0579	2	2	0.7482			
Atriplex calotheca	*5*	-	**I**		0	1	0.1231				0	3	0.121			
Atriplex sagittata	*5*	**0**	**N**		1	1	0.7531	1	0	0.4977	1	2	1			
Avena sativa	*5*	-	**K**		1	3	0.2897	1	5	0.3107	1	0	1	0	3	0.2436
Ballota nigra	*5*	+	**A**		1	0	0.5003				2	0	0.4988			
Bellis perennis	*5*	-	**A**		0	1	0.4899	0	1	1	0	1	1			
Berteroa incana	*5*	+	**N**		1	0	0.491	1	0	0.4943						
Betula pendula	*5*	**0**	**I**		0	0	1				1	0	1			
Biforia radians	*5*	-	**N**	**x**	0	1	0.4936							0	2	0.499
Brassica oleraceum	*5*	**0**	**I**		0	0	1				1	0	1			
Bromus arvensis	*5*	**0**	**NA**	**x**	0	0	1				0	1	1			
Bromus commutatus	*5*	+	**A**	**x**	1	0	0.258				2	0	0.4882	2	1	0.7562
Bromus erectus	*5*	**0**	**I**		0	0	1							1	0	1
Bromus horderaceus	*5*	+	**I**		2	1	0.3023	4	2	0.5628				1	0	1
Bromus japonicus	*5*	+	**NA**		1	0	0.5013	1	0	1	1	0	1			
Bromus secalinus	*5*	+	**NA**	**x**	1	0	1	1	1	1				1	0	1
Bromus squarrosus	*5*	**0**	**N**		0	0	1							1	0	1
Bunias orientalis	*5*	**0**	**N**		0	0	1							1	0	1
Calystegia sepium	*5*	**0**	**I**		1	1	1	3	0	0.1177	0	4	0.0538			
Cardaria draba	*5*	-	**N**		0	1	0.5034				1	2	0.4915			
Carduus acanthoides	*5*	**0**	**NA**		0	0	1							1	1	1
Carduus crispus	*5*	+	**I**		1	0	0.0549				4	0	0.0604			
Centaurea stoebe	*5*	-	**I**		0	1	0.4914				0	2	0.4932			

Cerastium glomeratum	*5*	-	**A/I**		0	1	1	1	0	1	0	2	0.4886			
Cerastium semidecandrum	*5*	**0**	**I**		0	0	1	1	1	1						
Chaerophyllum bulbosum	*5*	**0**	**I**		0	0	1				1	0	1	0	1	1
Chaerophyllum temulum	*5*	+	**I**		1	0	0.494	1	0	1	1	0	1			
Chenopodium glaucum	*5*	**0**	**A/I**		0	0	1				0	1	1			
Chenopodium hybridum	*5*	+	**A**	**x**	1	0	1	1	1	1	1	0	1			
Chenopodium polyspermum	*5*	-	**I**		0	1	0.2399	0	1	1	0	2	0.4932			
Chenopodium rubrum	*5*	-	**I**		1	2	0.5068	1	0	1	2	5	0.0903			
Chondrilla juncea	*5*	**0**	**I**	**x**	0	0	1	1	0	1						
Cichorium intybus	*5*	-	**I**		0	1	0.2345							0	3	0.241
Cirsium eriophorum	*5*	**0**	**NA**	**x**	0	0	1				1	0	1			
Conyza canadensis	*5*	+	**N**		10	7	0.8175	25	18	0.7319	0	1	1			
Coriandrum sativum	*5*	**0**	**K**		0	0	1							0	1	1
Coronopus squamatus	*5*	**0**	**I**	**x**	0	0	1							1	1	1
Corylus avellana	*5*	**0**	**I**		0	0	1	1	0	1						
Corynephorus canescens	*5*	**0**	**I**	**x**	0	0	1	0	1	1						
Crataegus monogyna	*5*	**0**	**NA**		0	0	1				1	0	1			
Crepis biennis	*5*	+	**A**		1	0	0.4928	1	0	0.4873						
Crepis capillaris	*5*	**0**	**A/I**		1	1	0.6206	1	1	1				0	1	1
Crepis tectorum	*5*	-	**I**	**x**	2	3	0.1079	5	6	0.1045						
Cuscuta campestris	*5*	**0**	**N**		0	0	1	0	1	1						
Cynoglossum officinale	*5*	-	**I**	**x**	0	1	0.2547				0	2	0.4878	0	1	1
Daucus carota	*5*	-	**NA**		4	7	0.0855	3	3	0.4831	2	11	0.001	5	9	0.1254
Descurainia sophia	*5*	+	**A**		6	5	0.3298	6	2	0.0698	7	9	0.7253	4	4	0.9964
Echinochloa crus-galli	*5*	+	**A**		12	6	0.4688	28	11	0.8376	3	4	0.9016			
Echium vulgare	*5*	-	**A/I**		0	1	0.4914				0	2	0.4932			
Elymus arenarius	*5*	-	**I**		1	2	0.9834	1	0	1	1	6	0.5018			
Equisetum palustre	*5*	-	**I**		0	1	0.4995				0	2	0.5018			
Equisetum sylvaticum	*5*	-	**I**		0	1	0.2415							0	3	0.244
Euphorbia cyparissias	*5*	**0**	**I**		0	0	1				0	1	1			
Euphorbia platyphyllos	*5*	-	**NA**	**x**	0	1	0.1175							0	3	0.1179
Fagus sylvatica	*5*	-	**I**		0	1	0.5019				0	2	0.4954			
Festuca arundinacea	*5*	**0**	**I**		0	0	1	1	0	1						
Festuca pratensis	*5*	+	**I**		1	0	0.5006				2	0	0.4942			
Festuca rubra	*5*	**0**	**I**		0	0	1	1	0	1						
Filago arvensis	*5*	**0**	**I**	**x**	1	1	0.5912	3	3	0.5891						
Filago minima	*5*	-	**I**	**x**	0	1	0.242	0	2	0.2455						
Fraxinus excelsior	*5*	+	**I**		1	0	0.5021	1	0	1	1	0	1			
Galeopsis segetum	*5*	-	**I**	**x**	0	2	0.1399	1	6	0.1341						
Galinsoga ciliata	*5*	**0**	**N**		1	1	0.9162	3	1	0.1244	0	3	0.1221			
Galium aparine	*5*	-	**I**		30	37	0.2465	19	2	0.0002	31	57	0.0001	44	61	0.0003
Geranium columbinum	*5*	+	**A**		2	0	0.0879	1	0	1				4	1	0.1863
Geranium dissectum	*5*	+	**A**		6	2	0.0629	3	0	0.1146	11	2	0.0135	4	5	0.6009
Geranium molle	*5*	-	**I**		0	1	1	0	1	0.4999	1	0	1			
Geranium pyrenaicum	*5*	**0**	**N**		0	0	1							1	0	1
Glechoma hederacea	*5*	-	**I**		0	1	0.1525				1	1	1	0	3	0.1281
Gnaphalium sylvaticum	*5*	**0**	**I**		0	0	1	0	1	1						
Gypsophila muralis	*5*	-	**I**	**x**	0	1	0.2488	0	1	0.4974	0	1	1			
Helianthus annuus	*5*	+	**K**		1	0	0.242	2	0	0.2494						
Helichrysum arenarium	*5*	**0**	**I**	**x**	0	0	1	1	0	1						
Heracleum sphondylium	*5*	**0**	**I**		0	0	1							0	1	1
Herniaria glabra	*5*	-	**A**		0	1	0.4991	0	1	0.4918						
Hieracium pilosella	*5*	-	**I**		0	1	0.5047	0	1	0.4905						
Holcus lanatus	*5*	**0**	**I**		1	1	1	2	1	1						
Holosteum umbellatum	*5*	-	**NA**	**x**	0	1	0.2379							0	3	0.2452
Hordelymus europaeus	*5*	**0**	**I**		0	0	1				1	0	1			
Hordeum secalinum	*5*	**0**	**I**	**x**	0	0	1	0	1	1						
Hypericum humifusum	*5*	-	**I**	**x**	0	1	0.0559	0	3	0.1195				0	1	1
Hypericum perforatum	*5*	+	**I**		3	1	0.4019	6	1	0.0775	1	1	1	0	1	1
Hypochaeris radicata	*5*	-	**I**		0	1	0.18	1	3	0.1802						
Illecebrum verticillatum	*5*	-	**I**	**x**	0	1	0.2476	0	2	0.241						
Impatiens glandulifera	*5*	**0**	**N**		0	0	1				1	0	1			
Juncus effusus	*5*	**0**	**I**		0	0	1	0	1	1						
Kickxia elatina	*5*	-	**A**	**x**	0	1	0.1241	0	1	0.4881				0	2	0.4978
Kickxia spuria	*5*	**0**	**A**	**x**	0	0	1							0	1	1
Lathyrus pratensis	*5*	-	**I**		0	1	0.4958				0	1	1	0	1	1
Leontodon autumnalis	*5*	-	**I**		0	1	0.496	0	1	0.4996						
Lepidium campestre	*5*	-	**A**		0	1	0.1048	0	3	0.1155						

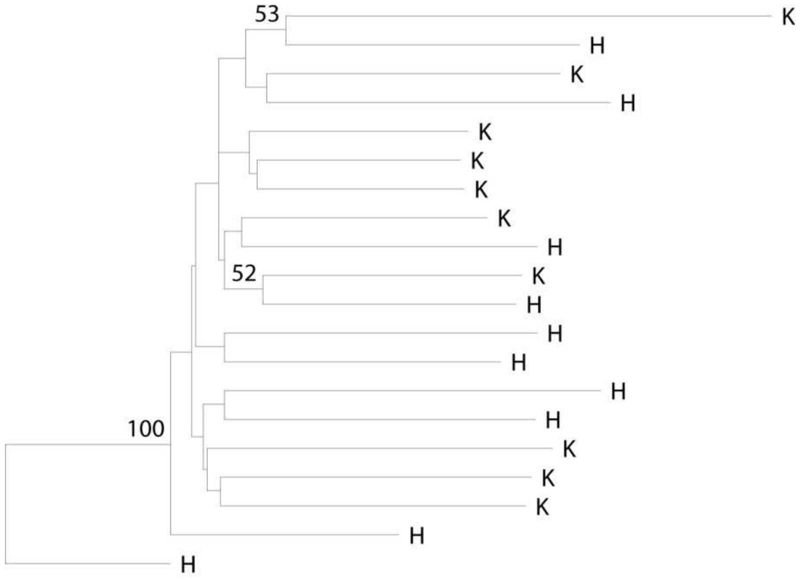
Leucanthemum ircutianum	*5*	**0**	**I**	**x**	0	0	1				1	0	1		
Leucanthemum vulgare	*5*	**0**	**I**	**x**	0	0	1				0	1	1		
Linaria arvensis	*5*	**-**	**A**	**x**	0	1	0.2449	0	2	0.2325					
Linum usitatissimum	*5*	**0**	**K**		0	0	1	0	1	1					
Lolium perenne	*5*	**0**	**I**		4	4	0.8797	3	1	0.7802	8	0	0.0018	1	11	0.0008
Lotus pedunculatus	*5*	**0**	**I**		0	0	1	0	1	1					
Luzula multiflora	*5*	**0**	**I**		0	0	1	0	1	1					
Lysimachia vulgaris	*5*	**0**	**I**		0	0	1	0	1	1					
Malus sylvestris	*5*	**0**	**I**	**x**	0	0	1				1	0	1		
Malva neglecta	*5*	**-**	**A**		0	1	0.0526	0	1	1	0	3	0.116		
Malva sylvestris	*5*	**+**	**A**		1	0	0.4948				2	0	0.4875		
Malva verticillata	*5*	**0**	**K**		0	0	1				1	0	1		
Medicago x varia	*5*	**+**	**K**		2	1	0.5033	3	0	0.1155	0	1	1	3	2	0.706
Melampyrum arvense	*5*	**-**	**NA**	**x**	0	1	0.4976							0	2	0.499
Melilotus alba	*5*	**0**	**A**		0	0	1	1	0	1					
Melilotus officinalis	*5*	**-**	**A**		0	1	0.065	0	1	1				0	3	0.1237
Mentha aquatica	*5*	**0**	**I**		0	0	1	0	1	1					
Mercurialis annua	*5*	**-**	**A**	**x**	0	1	1				1	0	1	0	2	0.4931
Misopates orontium	*5*	**-**	**A**	**x**	0	1	0.4993	0	1	0.4873					
Moehringia trinervia	*5*	**0**	**I**		0	0	1							0	1	1
Myosotis ramosissima	*5*	**0**	**A/I**		0	0	1	1	0	1					
Myosurus minimus	*5*	**-**	**A**		0	1	0.1248	0	2	0.2525				0	1	1
Nigella arvensis	*5*	**0**	**A**	**x**	0	0	1				0	1	1		
Nonea pulla	*5*	**-**	**I**	**x**	0	1	0.4917							0	2	0.4973
Odontites vernus	*5*	**-**	**I**	**x**	0	1	0.0587	0	1	1	0	2	0.2403	0	1	1
Ononis repens	*5*	**0**	**I**		0	0	1							0	1	1
Ornithopus perpusillus	*5*	**-**	**I**	**x**	0	2	0.0711	1	6	0.0677					
Panicum capillare	*5*	**0**	**N**		0	0	1	0	1	1					
Papaver somniferum	*5*	**0**	**U/N**		0	0	1				0	1	1		
Pastinaca sativa	*5*	**-**	**I**		0	1	0.2436							0	3	0.2479
Peplis portula	*5*	**0**	**I**	**x**	0	0	1	1	0	1				0	1	1
Phalaris arundinacea	*5*	**0**	**I**		0	0	1				1	0	1		
Phleum pratense	*5*	**+**	**I**		1	0	0.243				2	0	0.5001	1	0	1
Phragmites australis	*5*	**-**	**I**		0	1	0.4957				0	2	0.4894		
Picris hieracioides	*5*	**+**	**I**		2	1	0.6529	1	0	1	5	0	0.0247	0	3	0.1157
Pinus sylvestris	*5*	**-**	**I**		0	1	0.2383	1	3	0.2431					
Pisum sativum	*5*	**-**	**K**		0	1	0.2385							0	3	0.242
Poa pratensis	*5*	**-**	**I**		1	2	0.6629	3	1	1	1	0	1	0	4	0.0593
Poa trivialis	*5*	**-**	**NA**		7	10	0.1107	0	2	0.2413	17	25	0.4838	6	6	0.7266
Polycnemum arvense	*5*	**-**	**A**	**x**	0	1	0.491	0	1	0.4914					
Potentilla argentea	*5*	**+**	**I**		1	0	0.2472	2	0	0.2329					
Prunus avium	*5*	**0**	**I**		0	0	1				1	0	1		
Prunus mahaleb	*5*	**+**	**I**		1	0	0.4947				2	0	0.4859		
Prunus serotina	*5*	**0**	**N**		0	0	1	1	0	1					
Pseudognaphalium luteoalbum	*5*	**0**	**I**	**x**	0	0	1	0	1	1					
Puccinellia distans	*5*	**0**	**I**		0	0	1				1	0	1		
Quercus petraea	*5*	**+**	**NA**		1	0	0.4981	1	0	0.5034					
Quercus robur	*5*	**0**	**I**		0	0	1	0	1	1					
Ranunculus acris	*5*	**0**	**NA**		0	0	1	0	1	1					
Ranunculus creticus	*5*	**0**	**NA**		0	0	1							0	1	1
Ranunculus sardous	*5*	**0**	**I**	**x**	0	0	1	0	1	1					
Rapistrum perenne	*5*	**0**	**I**	**x**	0	0	1							0	1	1
Rhinanthus alectorolophus	*5*	**-**	**I**	**x**	0	1	0.2368							0	3	0.2474
Robinia pseudoacacia	*5*	**0**	**N**		0	0	1	1	0	1					
Rorippa palustris	*5*	**-**	**I**		0	2	0.0673	1	1	1	0	5	0.0298		
Rumex acetosa	*5*	**+**	**I**		2	1	0.6201	4	3	0.62					
Rumex obtusifolius	*5*	**+**	**I**		2	1	0.3159	2	0	0.2502	3	4	0.5675	1	0	1
Salix viminalis	*5*	**0**	**I**		0	0	1				1	0	1		
Sambucus nigra	*5*	**+**	**I**		1	0	0.2396				2	0	0.2491		
Scutellaria galericulata	*5*	**-**	**I**		0	1	0.4836	0	1	0.498					
Secale cereale	*5*	**-**	**K**		4	5	0.4846	5	5	0.7442	1	0	1	6	9	0.7378
Sedum acre	*5*	**0**	**I**		0	0	1				0	1	1		
Sedum album	*5*	**0**	**I**		0	0	1	1	0	1					
Senecio jacobea	*5*	**+**	**I**		1	0	0.2507	2	0	0.2407					
Senecio sylvaticus	*5*	**0**	**I**		0	0	1	0	1	1					
Senecio vernalis	*5*	**0**	**N**		1	1	0.6104	3	1	0.7961	0	1	1	0	2	0.4939
Setaria verticillata	*5*	**0**	**A**	**x**	0	0	1				0	1	1		
Silene latifolia	*5*	**+**	**NA**		4	3	0.5837	8	6	0.6402	4	0	0.056		

Silene vulgaris	*5*	-	**I**		1	2	0.2165	1	1	1				1	5	0.0907
Sinapis alba	*5*	**0**	**K**		0	0	1							0	1	1
Sisymbrium altissimus	*5*	**+**	**N**		1	0	0.2464	2	0	0.2524						
Sisymbrium loeselii	*5*	**+**	**N**		1	0	0.2431				2	0	0.2389			
Solanum nigrum	*5*	-	**A**		4	7	0.0758	8	6	0.7122	3	16	0.0002			
Solanum tuberosum	*5*	-	**K**		0	2	0.1816	1	4	0.3519				0	1	1
Spergularia morisonii	*5*	**0**	**I**	**x**	0	0	1	0	1	1						
Spergularia x salontana	*5*	**0**	**NA**		0	0	1	0	1	1						
Stachys arvensis	*5*	-	**A**	**x**	0	1	0.1179	0	2	0.2391	0	1	1			
Stachys recta	*5*	**0**	**I**	**x**	0	0	1	1	0	1						
Stellaria aquatica	*5*	-	**I**		0	1	0.4937				0	2	0.4925			
Stellaria graminea	*5*	**0**	**I**		0	0	1	0	1	1						
Symphytum officinale	*5*	-	**I**		0	1	0.2507				0	2	0.2533			
Tanacetum vulgare	*5*	**+**	**A/I**		4	1	0.0555	10	2	0.0029				0	1	1
Teesdalia nudicaulis	*5*	-	**I**	**x**	0	1	0.0605	0	3	0.0631						
Thlaspi montanum	*5*	-	**I**	**x**	0	1	0.4966				0	2	0.4907			
Torilis arvensis	*5*	**0**	**I**	**x**	0	0	1							1	0	1
Trifolium arvense	*5*	-	**NA**		2	4	0.1492	4	5	0.7428	0	6	0.0107			
Trifolium campestre	*5*	**+**	**I**		1	0	0.4926	2	1	0.5069						
Trifolium dubium	*5*	**0**	**I**		1	1	1	0	1	0.4913	2	0	0.4952			
Trifolium hybridum	*5*	-	**I**		0	1	0.4896				0	2	0.4937			
Trifolium incarnatum	*5*	**0**	**K**		0	0	1	0	1	1						
Trifolium pratense	*5*	**+**	**I**		3	2	0.658	4	3	0.4121	2	2	1	1	1	1
Trifolium repens	*5*	-	**I**		5	7	0.1172	7	18	0.0006	2	2	1	4	0	0.0507
Turgenia latifolia	*5*	**0**	**A**	**x**	0	0	1							0	1	1
Urtica urens	*5*	-	**A**		0	1	0.0602	0	3	0.1237	0	1	1			
Valerianella carinata	*5*	-	**N**	**x**	0	1	0.0548				0	4	0.0536			
Valerianella dentata	*5*	-	**I**	**x**	2	3	0.1496	0	1	0.5035	2	2	0.8198	3	7	0.3543
Verbena officinalis	*5*	**0**	**A**	**x**	0	0	1				0	1	1			
Veronica persica	*5*	-	**N**		19	31	0.0598	2	3	0.759	22	48	0.032	38	50	0.0092
Veronica serpyllifolia	*5*	**0**	**I**		0	0	1							0	1	1
Vicia cracca	*5*	**0**	**I**		2	2	0.3728	4	1	0.2696	0	1	1	0	3	0.1205
Vicia faba	*5*	-	**K**		0	1	0.4851							0	2	0.4924
Vicia pannonica	*5*	**0**	**N**	**x**	0	0	1	0	1	1				1	0	1
Vicia sepium	*5*	**+**	**I**		2	1	0.5516	5	0	0.0166				0	4	0.0589
Viola odorata	*5*	**0**	**N**		0	0	1				1	0	1			
Viola rupestris	*5*	**0**	**I**	**x**	0	0	1							1	0	1
Vulpia myorus	*5*	**+**	**I**		1	0	0.2433				2	0	0.2436			

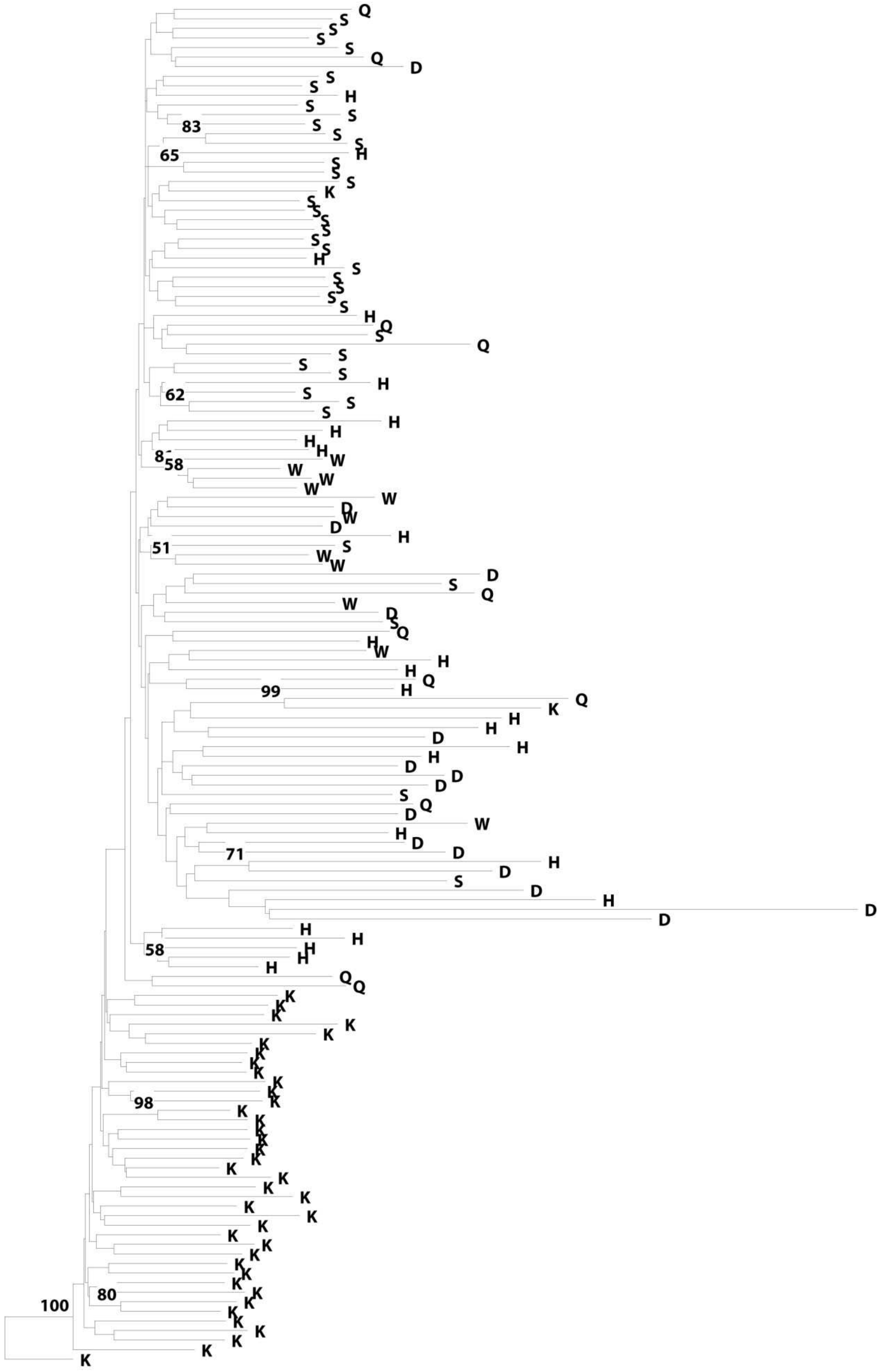
Appendix Figure S5.1. Neighbor joining phenogram of *A. aestivalis* individuals from the original dataset using Nei-Li (=Dice) distances from five regions in Central Germany (D=Drei Gleichen, H=Hainleite, K=Kyffhäuser, Q=Querfurter Platte, S=Schmoner Hänge).



Appendix Figure S5.2. Neighbor joining phenogram of *A. aestivalis* individuals from the repeated dataset using Nei-Li distances from two regions in Central Germany (H=Hainleite, K=Kyffhäuser).



Appendix Figure S5.3. Neighbor joining phenogram of *C. regalis* individuals using Nei-Li distances from six regions in Central Germany (D=Drei Gleichen, H=Hainleite, K=Kyffhäuser, Q=Querfurter Platte, S=Schmoner Hänge, W=Witterda).



Appendix Figure S7.1. Photo documentation.

(1) Common Corncockle – *Agrostemma githago* L.

(2) Thorow Wax – *Bupleurum rotundifolium* L.

(3) Forking larkspur – *Consolida regalis* S.F. GRAY

(4) Blue Pimpernel – *Anagallis foemina* MILL. (Photo by Armin Jagel)

(5) Barren brome – *Bromus sterilis* (L.) NEVSKI (Photo by Dietrich Hertel)

(6) Black grass – *Alopecurus myosuroides* HUDS. (Photo by Lena Ulber)

(7) Annual vernalgrass – *Anthoxanthum aristatum* BOISS.

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(legend top to bottom)

1 Mixed deciduous forest in the Hainich region (Central Germany)
2 Different insect taxa on the flowers of a thistle (*Cirsium* sp.)
3 *Glomeris* sp., a member of the decomposing soil fauna in forest ecosystems
4 *Pleodorina californica* (Chlorophyceae), colony-forming freshwater phytoplankton species
5 Grasshopper *Tettigonia cantans*, distributed from the Pyrenees to Northeastern China
6 *Microcebus berthae* (Cheirogaleidae), the smallest extant Primate species (Madagascar)
7 Tropical rain forest (Greater Daintree, Australia)
8 *Lethocolea glossophylla* (Acrobolbaceae), a liverwort of alpine mountain ranges in South America
9 Part of a coral reef in the Red Sea

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