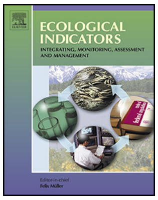
Ecological Indicators 65 (2016) 113–121

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Bird communities in agricultural landscapes: What are the current drivers of temporal trends?

Mark Frenzel*, Jeroen Everaars, Oliver Schweiger

Helmholtz Centre for Environmental Research UFZ, Department of Community Ecology, Theodor-Lieser-Straße 4, 06120 Halle, Germany

ARTICLE INFO

Article history:
Received 30 April 2015
Received in revised form
10 November 2015
Accepted 17 November 2015
Available online 21 December 2015

Keywords:
Farmland birds
Land-use change
Species traits
Biodiversity declines
Terrain analysis

ABSTRACT

Bird populations are declining in agricultural landscapes, which is ongoing for decades now. With standardized breeding bird observation data of five years within 2001–2014 from six sites in Central Germany we investigated whether trends in bird abundance are reflected by trends in species richness and whether these trends depend on the landscape context. We further analyzed whether trends and their dependencies on the landscape context differ among species groups according to their particular traits. For most of the groups (farmland birds, large birds, resident birds, short distance migrators, insectivores, granivores and birds of prey) we found declining trends in abundance. However, these trends were not reflected by species richness. In contrast to our expectations, high amounts of semi-natural habitats in the landscape did not buffer the overall negative trends. Surprisingly, bird abundance declined most in landscapes characterized by larger ranges in altitude and initially highest bird abundance in 2001. We conclude that flat landscapes in Central Germany have been utilized with high intensity already for a long time and they simply maintained their already low bird abundance. On the other hand, a recent increase in agricultural intensity in landscapes with marked altitudinal reliefs, and presumably less usability and productivity, causes the drastic declines in bird abundances. Since these strong declines are not related to habitat loss, we assume that changes in the management of agricultural fields are responsible.

1. Introduction

It is evident that birds are declining in agricultural landscapes since the last quarter of the 20th century (Donald et al., 2001, 2006), but knowledge about the underlying mechanisms and how to recover from often negative trends is still scarce (Benton, 2007). In Europe, agriculture is the dominating land use covering about 43% of the land (Eurostat, 2015) and in Germany the share is even higher (52%; Statistisches Bundesamt, 2014). While the share in land cover is impressive by itself, the dynamic component is the agricultural practice following feasibility based on technological progress triggered by economic incentives like e.g. subsidies for energy plants. From the past decades up to now, agricultural practice in the EU was characterized by intensification affecting the output per area and homogenization in terms of crops grown (Donald et al., 2006; Vickery et al., 2004). This sets the frame for the occurrence and abundance of species bound to open landscapes such as many birds. Birds are highly sensitive to agricultural intensification (Dormann et al., 2007; Billeter et al., 2008; Reif, 2013). Land transformation from semi-natural habitats to agricultural areas is usually thought to be one of the major drivers for these declines (Gaston et al., 2003). However, the rate of transformation already peaked around the 1950ies (Seppelt et al., 2014) but other drivers might gain importance. For instance, in the UK, several interrelated trends in agricultural practice have been identified with potential implications for bird populations: reduction of spring sown cereals, simplification of crop rotations, increased use of inorganic fertilizers and chemical pesticides and more intensive grassland management (Fuller et al., 1995). Further, climate change has also been shown to impact local bird communities over time (Devictor et al., 2008, 2012).

It has been suggested that increasing the amount of semi-natural habitat may act as buffer against other threats (Oliver et al., 2015) and current regulations of the EU Common Agricultural Policy (CAP) and the EU strategy for Green Infrastructure could be beneficial in this context. However, whether improving semi-natural habitats in intensively used agricultural areas is effective for a large number of species with considerably differences in their ecology still needs to be proven.

The response of species to environmental change largely depends on their traits (e.g. Öckinger et al., 2010; Webb et al., 2010), as the environment is thought to filter particular species according

---

* Corresponding author. Tel.: +49 345 558 5304; fax: +49 345 558 5329.
E-mail address: mark.frenzel@ufz.de (M. Frenzel).

http://dx.doi.org/10.1016/j.ecolind.2015.11.020
1470-160X/

to these traits. In a recent paper Reif (2013) reviewed long-term trends in bird populations in relation to species' traits. These approaches provided important insights into the drivers responsible for long-term changes in bird abundance. The trait-based approach resulted also in the common farmland birds index, an European Union agri-environmental indicator focusing on species characteristic for agricultural areas. These species are bound to open habitats by feeding and breeding habits as well. Besides habitat-related trait groupings, like in farmland bird species, several other traits are relevant to assess responses to environmental change (see review in Reif, 2013). In terms of biomass of species, smaller birds are in general more abundant but also decline stronger than larger species (Inger et al., 2015). The migratory status of species is related to the sharing of resources like territories, as these are divided between residents and early or late incoming migrants. Changes in winter and spring temperature caused by climate change alter the proportion of migratory birds within communities (Lemoine et al., 2007). Further, different feeding guilds are likely to respond in different ways to land-use change (Litteral and Wu, 2012) since anthropogenic land use influences the availability of food for different feeding guilds like insectivorous or granivorous species.

Nowadays the value of long-term data sets for detecting trends in ecosystems and components like species is evident (e.g. Devictor et al., 2012), supporting other research and monitoring projects with a long term perspective. One of these initiatives in Germany is the TERENO (Terrestrial Environmental Observatories) project of the Helmholtz Association. One issue of TERENO is biodiversity monitoring of plants, pollinators and birds. In this study, we focus on local bird communities in 'normal' landscapes in Central Germany, which are typically dominated by intensive agriculture, since the soils are among the most productive in Germany and occur on very flat, easily manageable, plains. This provides a suitable testing ground for the effects of landscape properties or intensive agriculture on the temporal trends in bird communities.

Here we analyze time-series data of local bird communities in six agricultural landscapes in Central Germany. In particular, we investigate (1) whether the same temporal trends occur in terms of both abundance and species richness. (2) We expect that landscape features affect temporal trends, in particular, that landscapes with higher proportions of semi-natural habitats can slow down declines, while declines are much stronger in intensively used landscapes. (3) Finally, we suggest that different groups of birds and their temporal trends are differentially affected by land use according to their ecological traits like habitat use (farmland birds), migratory status, feeding guild and biomass.

2. Materials and methods

2.1. Study area

The study sites are situated in Saxony-Anhalt (Germany; Fig. 1) and operated as part of the TERENO project (Terrestrial Environmental Observatories; www.tereno.net) as well as part of the German and European LTER (Long-Term Ecological Research) network. The sites are embedded in agriculturally dominated landscapes. The region is characterized by a high variation in land-use intensity (from flat regions with up to 98% agriculture and large fields to regions with high levels of altitudinal heterogeneity, high cover of forests or other semi-natural habitats, less agriculture and smaller fields) and some variation in climatic conditions. The main crops are winter cereals, oilseed rape, maize and to some extent potato, sugar beet and peas. Each site covers an area of $5 \times 5\,\text{km}^2$ of which $4 \times 4\,\text{km}^2$ is treated as core area for sampling. Sampling started in 2001 at the four sites Friedeburg (FBG), Schafstaedt (SST), Greifenhagen (GFH), Wanzleben (WAN) within EU FP5 project GREENVEINS. With the start of the TERENO project in 2009 and the following surveys in 2012, 2013, 2014 the sites Harsleben (HAR) and Siptenfelde (SIP) were added (Fig. 1), resulting in 1 × 4 and 4 × 6 data points, summing up to 28 data points in five years. The monitoring program was designed to sample every three years. The years 2013–14 were taken as an additional check for variation of counts between years, also giving the opportunity for early trend analysis.

Fig. 1. Map of Germany with study sites Friedeburg (FBG), Greifenhagen (GFH), Harsleben (HAR), Schafstaedt (SST), Siptenfelde (SIP) and Wanzleben (WAN) in Saxony-Anhalt.

2.2. Bird observation

Bird surveys followed the point-stop method (Vorisek, 2008) which is most efficient when a large area has to be surveyed. According to the checkerboard grid design (Fig. 2), each of the 20 sampling points are always 500 m apart from each other, a precondition to avoid double counts in open terrain.

For reasons of accessibility, this ideal configuration had to be adopted in the field, always taking care not to count same specimens twice. A bird survey within one year was performed with three visits in the following periods: (1) 1–30 April, (2) 1–20 May, (3) 21 May–20 June. We surveyed only at favorable conditions (no rain, wind speed <4 Bft), starting at sunrise and ending about three hours later. Within this time slot we approached all points at a site. At each point all singing, calling and seen bird species were registered within a radius of 250 m for five minutes. All surveys throughout the years were performed by the same bird specialist. Based on the birds recorded in the field, the observed birds at each point were translated into territory numbers per species as an

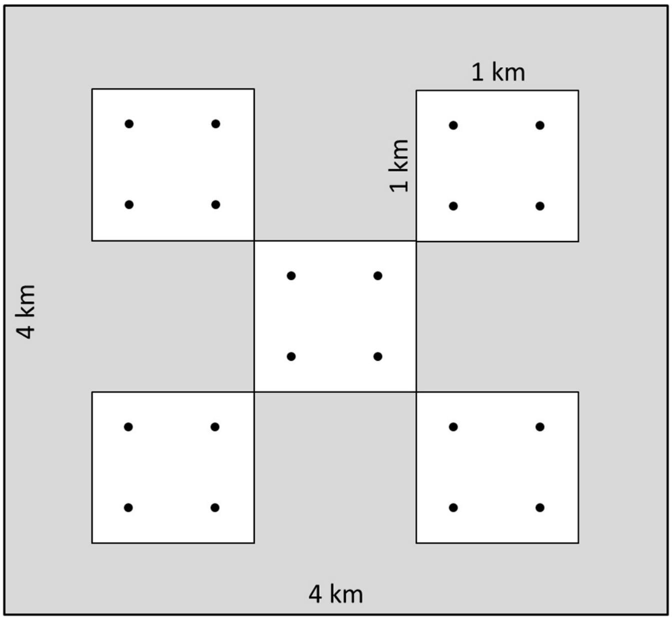


Fig. 2. Spatial sampling design for bird watching. Dots indicate stopping points in the 4 × 4 km core area.

expert guess by the same bird specialist with distinct knowledge of the habitat at each point. This was done by considering the date of the observation and the surrounding habitats (quality and size) in order to increase the reliability of the estimation. Only the maximum number of territories at a single point for a single species during the three visits within a year was taken for further analysis. The biological meaning of bird territories as an indicator for suitable habitat quality is much more relevant than singing, calling and seen birds.

2.3. *Landscape composition, habitat classification*

Based on orthorectified aerial photographs and field mapping, habitats were classified to the third level of the EUNIS classification and modified where necessary to consider linear elements in addition. Information about habitat classification, shape and extent was digitized and processed within ArcMap (10.1). The EUNIS classification was done for 2001 (four sites) and checked again in 2013 to cover the two new sites and the slightly changed land-use categories. The original EUNIS classification was aggregated to more general habitats: *Arable*, *Managed grassland*, *Forest*, *Semi-natural* and *Urban* habitats (for details see Appendix A). Semi-natural habitats include e.g. soft roads, orchards, shrubs and forest edges. Each of these five final land uses classes was calculated as percentage cover per site.

We also calculated mean arable field size and Shannon diversity (H') of EUNIS habitats. Additionally, we performed a terrain analysis based on the digital elevation model (DEM) for Germany (DGM10, grid size 10 m, accuracy in elevation ±0.5–2 m; Federal Agency for Cartography and Geodesy, © GeoBasis-DE/BKG [2012]) to represent abiotic heterogeneity which was not captured otherwise. DEM raster data were processed with QGIS 2.6.1 and SAGA geoalgorithms (SAGA 2.0.8) calculating the statistics for a given area for *elevation*, *slope*, *aspect*, *ruggedness* and *hillshade*, each with mean, standard deviation (SD), range and variance over all 10 × 10 m^2 grids of a site of 5 × 5 km^2. Due to high collinearity between these parameters, we selected standard deviation in elevation (*Elevation SD*) for the ease of interpretation. *Elevation SD* reflects the vertical structure at the landscape scale and a high *Elevation SD* is expected to support lower agricultural use, higher habitat diversity and higher variation in microclimate. The sites covered a large gradient in agricultural area and field size, landscape structure of semi-natural elements and microclimatic conditions (Table 1).

2.4. *Trait data*

Species traits are important sources for classifying ecological requirements and capability of a species in terms of e.g. mobility, feeding, or breeding. We used bird trait data available from CBS BioBase (1997) which was complemented and adapted by own expertise. To analyze potential differences in the response of birds according to their traits and ecological characteristics we used the following groups: (1) farmland birds (22 species), (2) feeding guilds (mainly insectivores – 76 species; mainly granivores – 28 species), (3) birds of prey (12 species), (4) migratory status (resident – 29 species; short distance migrant: overwintering within Europe – 43 species; long distance migrant: overwintering beyond Europe – 33 species), (5) body size (female biomass; small: up to 25 g – 48 species; medium: 26–249 g – 36 species; large: greater than 250 g – 21 species). Body size classes were grouped according to the frequency distribution considering splits at gaps (not splitting almost functionally equal species) and sufficient species numbers in each class (see histogram in Appendix B, Figure B.1). The complete table of species and their traits is provided in Appendix B (Table B.1). Groups were analyzed on the basis of summed territories across all species within a particular group (feeding guild or trait state) per site. At this stage species identity was no longer considered. No single species was particularly dominant in a group (Appendix B, Figure B.2).

2.5. *Statistical analysis*

All analyses were done with R version 3.0.1 (R Development Core Team, 2013). We used the number of territories and species richness as response variables and the initial set of explanatory variables comprised *Year (2001, 2009, 2012, 2013, 2014), Arable fields, Managed grassland, Forest, Semi-natural areas, Urban areas, Mean arable field size, Shannon diversity of EUNIS habitats* and *Elevation SD*. This set was inspected for collinearity with the varclus function from the Hmisc package (Harrell et al., 2014) and

Table 1
Site characteristics (WAN, Wanzleben; HAR, Harsleben; SIP, Siptenfelde; GFH, Greifenhagen; FBG, Friedeburg; SST, Schafstaedt).

	WAN	HAR	SIP	GFH	FBG	SST
Arable fields (%)	77	67	18	71	71	97
Mean field size (ha)	26	25	25	14	12	67
Grassland (%)	3	1	4	6	8	0.1
Forest (%)	4	13	61	12	3	0.3
Semi-natural (%)	8	17	15	6	10	2
Elevation mean (m)	113	143	423	270	122	177
Elevation SD (m)	10.0	14.1	30.6	26.6	30.8	11.2
Mean annual temperature (°C)	10.1	10.2	7.9	9.4	10.1	9.2
Mean annual precipitation (mm)	541	516	655	582	574	560

considered collinear above a value of 0.49 (Spearman p^2). *Arable* was correlated with *Forest* and *Shannon diversity of EUNIS habitats* with *Managed grassland, Mean arable field size* and *Elevation SD*. We selected *Arable* instead of *Forest* to focus on intensively used and non-intensively used landscapes. *Elevation SD* was chosen instead of *Managed grassland* and *Mean arable field size* as the primary landscape structure parameter. We discarded *Shannon diversity of EUNIS habitats* due to newly emerging collinearity with *Arable*. The remaining independent variables (*Elevation SD, Arable, Natural, Urban, Year*) were used as fixed effects and analyzed for all birds together and for each of the different bird groups separately with a generalized linear mixed effects model approach (GLMM) using the package lme4 (Bates et al., 2014). To account for possible temporal and spatial pseudoreplications, the random structure consisted of *Year* and *Site*. Models were fitted with a Poisson error structure and a log-link function.

The full model was formulated with *Year* and the interaction between *Year* and the independent variables to identify landscape features that accelerate or slow down temporal changes. We proceeded with a multimodel inference approach (R Package MuMIn, Barton, 2015), allowing only models with combinations of up to three variables to prevent overfitting. All possible combinations of one, two or three variables out of the full model were tested and evaluated by AICc values. The multimodel inference approach is becoming a valuable alternative to classical hypothesis testing (Johnson and Omland, 2004). The full model, which was too large compared to the number of observations and the resulting degrees of freedom, was then split up in different alternative hypotheses, in our case different combinations of landscape features affecting the temporal trend. We considered models with a difference in AICc (small sample unbiased Akaike Information Criterion) <2 as equally valid hypothesis-supporting models. If a model with intercept only was among the best models, all models with this response variable were discarded (for full model list see Appendix C).

3. Results

3.1. Temporal trends in territory numbers

We found a decline in the number of territories for all birds and several of the community subsets (Table 2), sometimes affected by landscape characteristics. The entire bird community shows a decline in territory numbers between 2001 and 2014, which is affected by *Elevation SD* (Fig. 3a). Landscapes with a low *Elevation SD* (topographically unstructured, flat terrain) show a generally low but rather stable number of territories (left plot) whereas the number of bird territories in landscapes with higher *Elevation SD* (more vertically structured, hilly terrain) was initially high but displayed a steep decline (right plot; note that on a non-logarithmic scale declines are even steeper). Terrain structure data are illustrated as hillshade maps in Fig. 4. When focusing on community subsets, the picture is different in some cases: (I) Farmland bird territories show a clear negative trend over time which was independent of land use and landscape structure (Fig. 3b). However, territory numbers of farmland birds are positively influenced by both the proportion of arable land (Fig. 3c) and by an increasing share of semi-natural habitats (Fig. 3d). (II) Like in farmland birds, territory numbers of large and intermediate sized birds have a negative trend independent of land use. However, they respond positively to *Elevation SD* (Fig. 4e). Similar to the entire bird community, territory numbers of intermediate sized birds are negatively influenced by the interaction of *Year* and *Elevation SD.* (III) Small birds oppose to large birds and other bird groups. They are the only group with a small positive temporal trend. Further they respond negatively to *Arable*, *Semi-natural* and *Elevation SD*. (IV) Territory numbers of resident birds and short distance migrants are affected similarly as all birds with a negative interaction effect of *Elevation SD* and *Year* whereas long distance migrants were stable. (V) Insectivorous and granivorous birds display the same trends as the whole bird community. (VI) Birds of prey exhibit strongly declining territory numbers, especially in landscapes with most arable land (Fig. 3f). None of the temporal trends in territory numbers is affected by the proportional amount of semi-natural habitats or urban habitats.

3.2. Temporal trends in species richness

We found a total of 105 species breeding at the six sites. Changes in species richness could not be explained by a temporal trend for the entire bird community or in any of the bird groups (Table 2). However, species richness is positively influenced by the land use categories *Urban* in intermediate sized birds, short and long distance migrants and *Semi-natural* in intermediate sized birds and long distance migrants. While *Arable* had a positive effect on long-distance migrants, its influence on short-distance migrants was adverse. *Elevation SD* affected only intermediate sized birds positively.

4. Discussion

With respect to our first question, we found that there are strong declining trends in the overall number of bird territories as well as in many species groups but these trends were not reflected by changes in species richness. Our second question aimed at the role of landscape features affecting temporal trends. The decrease in territories was affected by the terrain structure, rather than by land use. To our knowledge this work demonstrates for the first time the effect of a DEM-derived measure on breeding birds. The third question focused on differences in temporal trends when analyzing bird community subsets built on ecological traits. The picture looks different when switching from the general view including all species to trait-based species subsets. The interaction between terrain structure and year appeared in intermediate sized species, resident species, short distance migrants, insectivores and granivores, but not in farmland birds. Besides in small birds, the effect of year on the number of territories was negative in all groups, indicating a decline in territory numbers. An interaction with land use was evident only in birds of prey, which responded negatively to increasing arable land cover. Semi-natural habitats had no temporal effect at all on the number of territories in any species group.

4.1. Trait-based species groups

The overall negative temporal trend in the number of territories in farmland birds in our data is in line with the general trend of farmland birds in German agricultural landscapes (Sudfeldt et al., 2013) and at the European level as well (Eurostat, 2012). In terms of bird species biomass we found contrasting results. Intermediate sized and large birds declined, while small birds show a small positive trend. One possible explanation with size-related life history traits is that small species can more easily adapt to environmental changes (Stearns, 1992). This is supported by ‘fast strategies’ typical for small species compared to ‘slow strategies’ in large species (Blackburn and Gaston, 1996). In a recent paper, Inger et al. (2015) analyzed European-wide bird data from 1980 to 2009 with a focus on abundance and biomass. They found that the common birds which are often the smaller species declined from 1980 to 2000 and remained stable or slightly recovered afterwards. These findings point in a similar direction like the ones in our study, where the small birds are also the most frequent ones (Appendix B, Figure B.1). The migratory status of birds revealed an interesting pattern: The absence of a temporal trend of long distance migrants is somewhat surprising, given their long term and recent declines in

Table 2
Passed models with a difference in AICc <2 for all combinations of two response variables (Territories, Richness), five independent variables and four interactions (indicated by ×). Models are arranged by species subsets and best models (lowest delta, difference in AICc value). Df: degrees of freedom, logLik: log likelihood, AICc: small sample unbiased Akaike Information Criterion, delta: differences of AICc to the best model. The complete set of models including intercept only models is provided in Appendix C.

Subset	Response	Intercept	Elevation SD	Arable	Semi-natural	Urban	Year	Elevation SD × Year	Arable × Year	Semi-natural × Year	Urban × Year	df	logLik	AICc	delta
All birds	Territories	5.76	0.10				−0.08	−0.05				6	−149.17	314.35	0.00
Farmland birds	Territories	4.53					−0.19					4	−120.34	250.42	0.00
Farmland birds	Territories	4.53		0.18	0.18		−0.19					6	−117.95	251.89	1.47
Large birds	Territories	3.14	0.19		0.12	0.23						6	−84.35	184.69	0.00
Large birds	Territories	3.13	0.21			0.20	−0.18					6	−84.54	185.09	0.40
Intermediate sized birds	Territories	4.90	0.09				−0.15	−0.06				6	−124.84	265.69	0.00
Small birds	Territories	5.05		−0.17		0.13						5	−136.53	285.78	0.00
Small birds	Territories	5.05		−0.22	−0.07	0.13						6	−135.53	287.07	1.28
Small birds	Territories	5.05		−0.17		0.14	0.02					6	−135.72	287.45	1.66
Small birds	Territories	5.05	−0.06	−0.21		0.14						6	−135.83	287.65	1.87
Residents	Territories	4.16	0.27				−0.01	−0.10				6	−111.57	239.13	0.00
Short distance migrants	Territories	5.19		−0.20		0.13	−0.11					6	−136.23	288.46	0.00
Short distance migrants	Territories	5.20	0.14				−0.12	−0.04				6	−136.84	289.69	1.23
Long distance migrants	Territories	4.21		0.26	0.18	0.08						6	−108.75	233.50	0.00
Long distance migrants	Territories	4.20		0.26	0.16							5	−110.99	234.71	1.21
Insectivores	Territories	5.53	0.08				−0.07	−0.04				6	−149.14	314.28	0.00
Granivores	Territories	4.51	0.18				−0.09	−0.08				6	−114.66	245.33	0.00
Birds of prey	Territories	1.43				−0.19	−0.29					5	−59.68	132.09	0.00
Birds of prey	Territories	1.45					−0.26					4	−61.63	133.00	0.91
Birds of prey	Territories	1.40		0.13			−0.14		−0.26			6	−58.66	133.33	1.24
Intermediate sized birds	Richness	2.81			0.13	0.13						5	−70.04	152.82	0.00
Intermediate sized birds	Richness	2.81	0.05		0.12	0.13						6	−69.40	154.80	1.98
Short distance migrants	Richness	3.08		−0.11								4	−73.06	155.86	0.00
Short distance migrants	Richness	3.08		−0.12		0.07						5	−71.63	155.98	0.12
Long distance migrants	Richness	2.71			0.13	0.16						5	−70.32	153.37	0.00
Long distance migrants	Richness	2.71		0.09	0.18	0.16						6	−69.48	154.95	1.58
Long distance migrants	Richness	2.72				0.15						4	−72.73	155.21	1.84

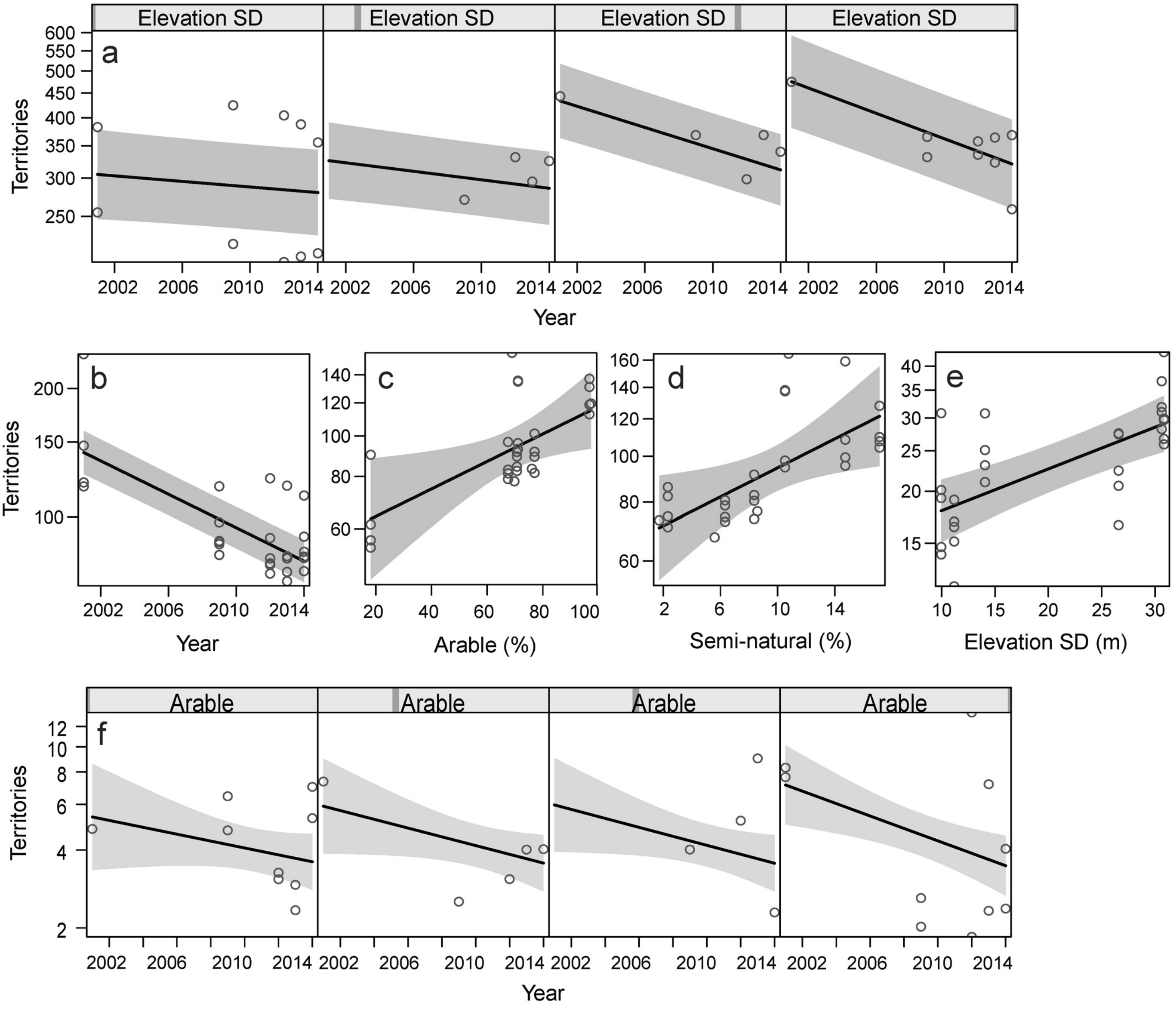


Fig. 3. Effect plots for territory numbers (log scale) and explanatory variables. Regression lines correspond to the best model for the considered variable; gray bands indicate 95% confidence intervals; open circles depict partial residuals of the plotted variable when other variables were in the respective model. (a) To visualize the interaction effect of *Year x Elevation SD* on all bird territories, regression lines were predicted for four levels of *Elevation SD* (levels indicated at the top of each plot: minimum values, values indicated by vertical bars and maximum values); (b–d) farmland birds in response to (b) *Year*, (c) *Arable* land and (d) *Semi-natural* habitats; note the different ranges in residual-adjusted *Territories* for farmland birds; (e) large birds in response to *Elevation SD*; (f) birds of prey in response of *Year x Arable* (four levels, for explanation see (a)).

other European studies (Lemoine et al., 2007; Vickery et al., 2014). It may be explained by the prevalence of mortality factors during the migration and in the wintering grounds (McCulloch et al., 1992; Reif, 2013; Klaassen et al., 2014). These factors may change from year to year making it difficult to filter for temporal trends at the regional scale. The two categories of feeding guilds, insectivores and carnivores, did not respond differently to the factors tested. As dietary niche proved to influence population trends at the country level with a decline in herbivores and an increase in insectivores (Reif, 2013; Reif et al., 2011), this indicates that the categories used in our study may have not been enough differentiated. The strong decline for birds of prey is somewhat surprising, since most of them are generally recovering in Germany since the 1990s (Sudfeldt et al., 2013). While birds of prey at the investigated agricultural dominated sites are generally favored by open habitats like arable fields (Table 2), oilseed rape and maize cultures may counteract by protecting prey like small mammals (Hötker et al., 2009). About 62% of Saxony-Anhalt is covered by arable fields (Statistisches Bundesamt, 2014) which changed considerably since 2001 by almost a doubling in the cultivation area of oilseed rape and maize, while the area covered by e.g. legumes decreased by more than 50% (Statistisches Landesamt Sachsen-Anhalt, 2014; Appendix D, Figure D.1). Moreover, we observed that after the harvest of oilseed rape the remaining stubbles are quite long preventing birds of prey from catching prey on the ground. The decline of birds of prey may also be attributable to Buzzard alone, the most common bird of prey in our data set. Interestingly, a recent study fosters the idea of prey protection in oilseed rape fields as these supports a larger portion of vole populations than other crops (Panek and Hušek, 2014). However, the authors concluded that in turn the breeding success of Buzzards increased due to the larger vole populations. This could be an indirect effect caused by large vole populations with a lot of individuals emigrating and being caught when they leave the oilseed rape shelter.

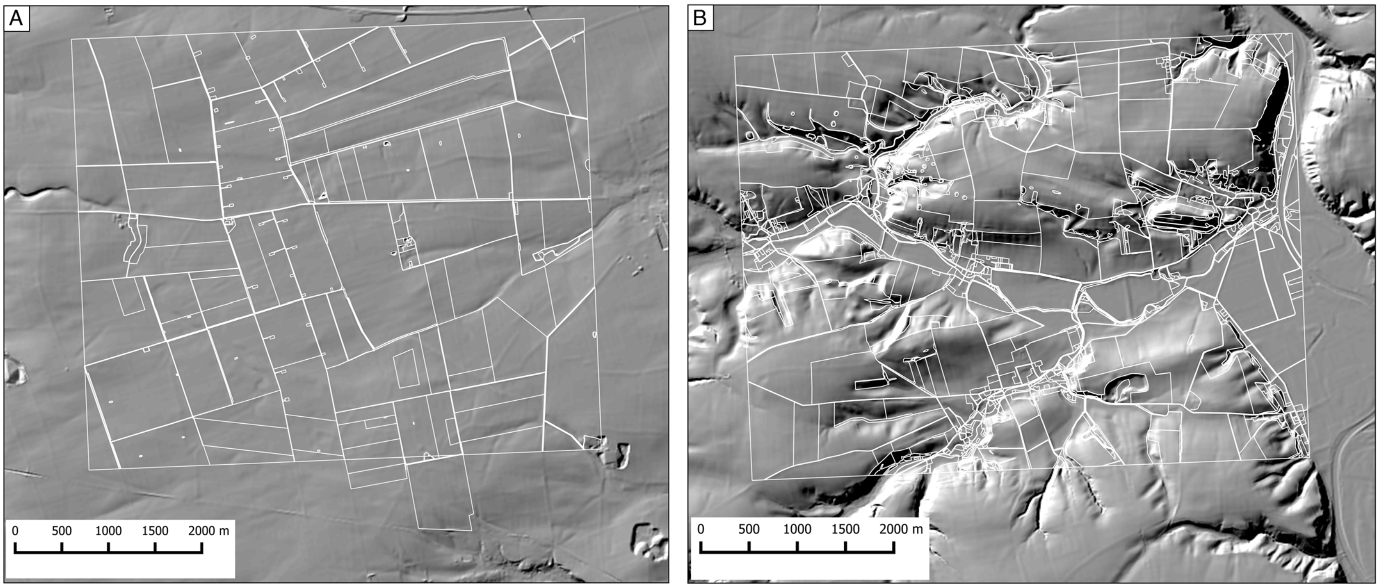


Fig. 4. Hillshade maps based on Digital Elevation Model (DEM) data with borders of different land use categories: (a) flat terrain (SST), (b) vertically structured terrain (FBG).

4.2. *Species richness*

The lack of temporal trends or a low contrast in species richness in analyzed time series is common in other bird studies (Böhning-Gaese and Bauer, 1996; Doxa et al., 2010) and species richness of birds shows rather spatial than temporal patterns (Bonthoux et al., 2013). But the clear decrease in territory numbers in our study implies that there may be a time lag for species richness decline or even extinction debt (Metzger et al., 2009; Tilman et al., 1994). A possible explanation for a lack of temporal trends in species richness in our study is that a major turnover of species caused by agricultural intensification has taken place before our study started in 2001. This is supported by Donald et al. (2001) who analyzed population trends in farmland birds across Europe in the period of 1970–1990. They stated that the increase of cereal yield alone accounted for over 30% of the variation in population trends. This was reinforced by a follow-up study focusing on European farmland birds between 1990 and 2000 (Donald et al., 2006)

4.3. *Impact of terrain structure*

Focusing on the interaction of landscape features with temporal trends, we found that terrain structure (*Elevation SD*) affects the decline in territory numbers. Surprisingly, in landscapes with a distinct altitudinal relief, indicated by a higher deviation in elevation, the decline was strongest. It appears that landscapes with high levels of altitudinal heterogeneity had the highest territory densities in 2001, and bird populations in all landscapes now leveled off to a similarly low number of territories (Fig. 3a), suggesting a large spatial homogenization of low bird densities. Due to collinearity with *Elevation SD* it can also be argued that bird territory numbers were previously higher in landscapes with a high *Shannon diversity of EUNIS habitats* ($r^2 = 0.71$), a low *Mean arable field size* ($r^2 = -0.63$) or a high share of *Managed grassland* ($r^2 = 0.84$), and now show the strongest temporal declines there. The negative effect of *Elevation SD* on the temporal trend was missing in farmland birds. The reason may be that these species are adapted to open habitats, being positively influenced by the share of arable fields and natural habitats as well, whereas terrain properties like *Elevation SD* play no role (Table 2).

The fact that terrain structure rather than land use affected the temporal decline was somewhat surprising. For example, we expected that landscapes with intensive use (high proportion of arable land) would have stronger bird declines than less intensively used ones, or that a high amount of semi-natural habitats would have reduced declines. We did not find the strongest declines in landscapes with more arable land, or a consistent negative effect of arable land. Despite the strong gradient of arable land at the investigated sites (18–97%) a negative correlation with territory numbers was only found once in short distance migrants. Hence, arable land per se seems not cause the decline of birds, in any case not after 2000 in our region. It is likely that land-use intensification in the decades before 2000 has also impoverished the bird communities (Donald et al., 2001; Sudfeldt et al., 2013). Although the positive correlation between territories of farmland birds and arable land could reflect the affinity of this group to farmland, we think that in our case it could also be a sampling effect since we selected the landscapes for their difference in arable land cover. Hence sampling within each landscape is not random with respect to the frequency of territories near or in arable fields. We did not find a mitigating effect of semi-natural habitats on bird declines. Even our model selection approach, allowing multiple models with varying parameter combinations to be selected, could not show this in a single case. However, a direct positive effect of semi-natural habitats was found in farmland birds (Fig. 3d), large birds and long distance migrants, suggesting that these habitats supply food or breeding facilities not provided by arable fields. There was no landscape feature that accelerated or mitigated bird declines, nor did we find a consistent negative effect of arable land or a consistent positive effect of semi-natural habitats. This may indicate that bird declines follow a pattern at a higher spatial scale applying to our sites equally. In terms of food, a large scale reduction of invertebrates is suspected as cause of general bird declines (Wilson et al., 1999), possibly invoked by high neonicotinoid application (Hallmann et al., 2014). Also changes in crops grown can affect birds, e.g. maize and oilseed rape reduces food levels and nesting opportunities (Hötker et al., 2009, 2005). This applies to Saxony-Anhalt, as the area under cultivation for oilseed rape was doubled from 2003 to 2007 (Statistisches Landesamt Sachsen-Anhalt, 2014; Appendix D, Figure D.1). However, the impact needs to be considered species specific and can be especially harmful for farmland birds when applied in large field aggregations resulting in large (several km^2) monocultures of oilseed rape and maize (Everaars et al., 2014; Sauerbrei et al., 2014). The study sites lacked a sharp decrease in set-aside fields, which is sometimes regarded as driver of declines since 2008 when the EU wide set-aside obligations were abolished (Kovacs-Hostyanszki and Baldi, 2012). A combination of all these changes in the management of crops, when applied to agricultural regions at large spatial scales, may induce nation-wide population changes, rather than detectable land-use effects at the site level. Alternatively, climate change may be getting more important than land use (Lemoine et al., 2007).

4.4. Management implications and conclusions

Despite all efforts to protect birds, especially farmland birds, population trends of breeding birds still appear to be negative (at best stable, but never positive). We suggest that the major depletion of bird populations and species richness took place in the last decades of the last century, especially in flat areas with low altitudinal heterogeneity suitable for intensive agricultural practice. Except for the crops grown, which we did not investigate systematically, the investigated landscapes changed only little during the period 2001–2014.

We conclude that (1) although restoration of green infrastructure is likely to improve the situation for some animal taxa (e.g. butterflies, Oliver et al., 2015), this may not work for birds in agricultural landscapes. (2) We need to identify the main causes of declines at higher spatial scales from a large list of present impacts on biodiversity (Sutherland et al., 2008). A special focus needs to be laid on agricultural intensification, as pointed out by e.g. Chamberlain et al. (2000) and the positive effect of set-aside land (Van Buskirk and Willi, 2004).

The federal government of Saxony-Anhalt recently announced (April 2015) to invest 4 million € in large scale restoration of hedgerows in the agricultural landscape of Saxony-Anhalt, to set an example for the rest of Germany. This goes much further than most restoration attempts and the EU CAP reform (Pe'er et al., 2014) and gives hope for a more sustainable coexistence of biodiversity and agriculture in the future, although our results do not indicate this will affect bird abundances in a positive way.

Acknowledgements

We are grateful to our 'bird detector' René Höhne who accompanied us during field work, did the estimation of territory numbers and provided a lot of valuable information about the ecology of bird species. Moreover we would like to thank two anonymous reviewers and the guest editor for the time they spent and their valuable input which helped to improve our manuscript a lot.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.11.020.

References

Barton, K., 2015. MuMIn: Multi-Model Inference. R package version 1.13.4.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1., pp. 1–7.

Benton, T.G., 2007. Ecology – managing farming's footprint on biodiversity. Science 315, 341–342.

Blackburn, T.M., Gaston, K.J., 1996. Abundance-body size relationships: the area you census tells you more. Oikos 75, 303–309.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., Van Wingerden, W.K.R.E., Zobel, M., Edwards, P.J., 2008. Indicators for biodiversity in agricultural landscapes: a pan-European study. J. Appl. Ecol. 45, 141–150, http://dx.doi.org/10.1111/j.1365-2664.2007.01393.x.

Böhning-Gaese, K., Bauer, H.-G., 1996. Changes in species abundance. Distribution, and diversity in a central European bird community. Conserv. Biol. 10, 175–187.

Bonthoux, S., Barnagaud, J.Y., Goulard, M., Balent, G., 2013. Contrasting spatial and temporal responses of bird communities to landscape changes. Oecologia 172, 563–574.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl. Ecol. 37, 771–788.

CBS, 1997. Biobase 1997. Register Biodiversiteit (CD-Rom). Centraal Bureau voor de Statistiek, Voorburg/Heerten.

Devictor, V., Julliard, R., Couvet, D., Jiguet, F., 2008. Birds are tracking climate warming, but not fast enough. Proc. Biol. Sci. 275, 2743–2748, http://dx.doi.org/10.1098/rspb.2008.0878.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliola, J., Herrando, S., Julliard, R., Kuussaari, M., Lindstrom, A., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I., Jiguet, F., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nat. Clim. Chang. 2, 121–124.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. B: Biol. Sci. 268, 25–29.

Donald, P.F., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J., 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agric. Ecosyst. Environ. 116, 189–196.

Dormann, C.F., Schweiger, O., Augenstein, I., Bailey, D., Billeter, R., De Blust, G., Defilippi, R., Frenzel, M., Hendrickx, F., Herzog, F., Klotz, S., Liira, J., Maelfait, J.P., Schmidt, T., Speelmans, M., Van Wingerden, W.K.R.E., Zobel, M., 2007. Effects of landscape structure and land-use intensity on similarity of plant and animal communities. Glob. Ecol. Biogeogr. 16, 774–787, http://dx.doi.org/10.1111/j.1466-8238.2007.00344.x.

Doxa, A., Bas, Y., Paracchini, M.L., Pointereau, P., Terres, J.M., Jiguet, F., 2010. Low-intensity agriculture increases farmland bird abundances in France. J. Appl. Ecol. 47, 1348–1356.

Everaars, J., Frank, K., Huth, A., 2014. Species ecology and the impacts of bioenergy crops: an assessment approach with four example farmland bird species. GCB Bioenergy 6, 252–264.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. Conserv. Biol. 9, 1425–1441.

Gaston, K.J., Blackburn, T.M., Klein Goldewijk, K., 2003. Habitat conversion and global avian biodiversity loss. Proc. Biol. Sci. 270, 1293–1300, http://dx.doi.org/10.1098/rspb.2002.2303.

Hallmann, C.A., Foppen, R.P.B., van Turnhout, C.A.M., de Kroon, H., Jongejans, E., 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511, 341-+.

Harrell, F.E.J., with contributions from C. Dupont and many others, http://CRAN.R-project.org/package=Hmisc.

Hötker, H., Bernardy, P., Cimiotti, D., Dziewiaty, K., Joest, R., Rasran, L., 2009. Maisanbau für Biogasanlagen–CO$_2$-Bilanz und Wirkung auf die Vogelwelt. Berichte zum Vogelschutz 46, 107–125.

Hötker, H., Thomsen, K.M., Köster, H., 2005. Auswirkungen regenerativer Energiegewinnung auf die biologische Vielfalt am Beispiel der Vögel und der Fledermäuse. BfN-Skripten 142, 1–83.

Inger, R., Gregory, R., Duffy, J.P., Stott, I., Voříšek, P., Gaston, K.J., 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. Ecol. Lett. 18, 28.

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends Ecol. Evol. 19, 101–108.

Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.-M., Bairlein, F., Alerstam, T., 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. J. Anim. Ecol. 83, 176.

Kovacs-Hostyanszki, A., Baldi, A., 2012. Set-aside fields in agri-environment schemes can replace the market-driven abolishment of fallows. Biol. Conserv. 152, 196–203.

Lemoine, N., Bauer, H.-G., Peintinger, M., Böhning-Gaese, K., 2007. Effects of climate and land-use change on species abundance in a central European bird community. Conserv. Biol. 21, 495–503.

Litteral, J., Wu, J.G., 2012. Urban landscape matrix affects avian diversity in remnant vegetation fragments: evidence from the Phoenix metropolitan region, USA. Urban Ecosyst. 15, 939–959.

McCulloch, M.N., Tucker, G.M., Baillie, S.R., 1992. The hunting of migratory birds in Europe: a ringing recovery analysis. Ibis 134, 55.

Metzger, J.P., Martensen, A.C., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Teixeira, A.M.G., Pardini, R., 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biol. Conserv. 142, 1166.

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S., Bommarco, R., 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol. Lett. 13, 969–979, http://dx.doi.org/10.1111/j.1461-0248.2010.01487.x.

Oliver, T.H., Marshall, H.H., Morecroft, M.D., Brereton, T., Prudhomme, C., Huntingford, C., 2015. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. Nat. Clim. Chang., 1–6, http://dx.doi.org/10.1038/nclimate2746.

Panek, M., Hušek, J., 2014. The effect of oilseed rape occurrence on main prey abundance and breeding success of the Common Buzzard *Buteo buteo*. Bird Study 61, 457–464.

Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Baldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbe, A., Wulf, F., Scott, A.V., 2014. EU agricultural reform fails on biodiversity. Science 344, 1090–1092.

R Development Core Team, 2013. A language and environment for statistical computing, 3. 0. 1. ed. R Foundation for Statistical Computing, Vienna, Austria.

Reif, J., 2013. Long-term trends in bird populations: a review of patterns and potential drivers in North America and Europe. Acta Ornithol. 48, 1–16.

Reif, J., Böhning-Gaese, K., Flade, M., Schwarz, J., Schwager, M., 2011. Population trends of birds across the iron curtain: brain matters. Biol. Conserv. 144, 2524–2533.

Reif, J., Vorisek, P., Stastny, K., Bejcek, V., Petr, J., 2008. Agricultural intensification and farmland birds: new insights from a central European country. Ibis 150, 596–605.

Sauerbrei, R., Ekschmitt, K., Wolters, V., Gottschalk, T.K., 2014. Increased energy maize production reduces farmland bird diversity. GCB Bioenergy 6, 265–274.

Seppelt, R., Manceur, A.M., Liu, J., Fenichel, E.P., Klotz, S., 2014. Synchronized peak-rate years of global resources use. Ecol. Soc. 1, 9, http://dx.doi.org/10.5751/ES-07039-190450.

Stearns, S., 1992. The Evolution of Life Histories. Oxford University Press.

Sudfeldt, C., Dröschmeister, R., Frederking, W., Gedeon, K., Gerlach, B., Grüneberg, C., Karthäuser, J., Langgemach, T., Schuster, B., Trautmann, S., Wahl, J., 2013. Vögel in Deutschland – 2013. DDA, BfN, LAG, VSW, Münster, pp. 62.

Sutherland, W.J., Bailey, M.J., Bainbridge, I.P., Brereton, T., Dick, J.T.A., Drewitt, J., Dulvy, N.K., Dusic, N.R., Freckleton, R.P., Gaston, K.J., Gilder, P.M., Green, R.E., Heathwaite, A.L., Johnson, S.M., Macdonald, D.W., Mitchell, R., Osborn, D., Owen, R.P., Pretty, J., Prior, S.V., Prosser, H., Pullin, A.S., Rose, P., Stott, A., Tew, T., Thomas, C.D., Thompson, D.B.A., Vickery, J.A., Walker, M., Walmsley, C., Warrington, S., Watkinson, A.R., Williams, R.J., Woodroffe, R., Woodroof, H.J., 2008. Future novel threats and opportunities facing UK biodiversity identified by horizon scanning. J. Appl. Ecol. 45, 821–833.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66.

Van Buskirk, J., Willi, Y., 2004. Enhancement of farmland biodiversity within set-aside land. Conserv. Biol. 18, 987–994.

Vickery, J.A., Bradbury, R.B., Henderson, I.G., Eaton, M.A., Grice, P.V., 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biol. Conserv. 119, 19–39.

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J., Gregory, R.D., 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156 (1), 1–22.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., Poff, N.L., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecol. Lett. 13, 267–283.

Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B., 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agric. Ecosyst. Environ. 75, 13–30.

Web references

Eurostat, Data from November 2012, http://ec.europa.eu/eurostat/statistics-explained/index.php/Agri-environmental_indicator_-_population_trends_of_farmland_birds (accessed 30.4.15) 2012. Agri-environmental indicator – population trends of farmland birds.

Eurostat, Data from March 2015, http://ec.europa.eu/eurostat/statistics-explained/index.php/Land_cover,_land_use_and_landscape (accessed: 30.04.15) 2015. Land cover, land use and landscape.

Statistisches Bundesamt, 2014. Data from 2014, https://www.destatis.de/EN/FactsFigures/EconomicSectors/AgricultureForestryFisheries/LandUse/Tables/Areas.html (accessed: 30.04.15).

Statistisches Landesamt Sachsen-Anhalt, 2014. Daten und Fakten – Anbauflächen ausgewählter Fruchtarten in Sachsen-Anhalt nach Jahren auf Basis der Agrarstrukturerhebung (ASE) und Landwirtschaftszählung 2010, http://www.statistik.sachsen-anhalt.de/Internet/Home/Daten_und_Fakten/4/41/412/41241/Anbauflaechen_ausgewaehlter_Fruchtarten_nach_Jahren.html (accessed: 30.04.15).