This is an author produced version of a paper published in
Agriculture, Ecosystems & Environment.
This paper has been peer-reviewed but may not include the final publisher
proof-corrections or pagination.

Access to the published version may require journal subscription.
Published with permission from: Elsevier.

Epsilon Open Archive http://epsilon.slu.se

Title: Linking occurrence and changes in local abundance of farmland bird species to landscape composition and land-use changes

Authors: Åke Berg[a*], Johan Wretenberg[b,c], Michal Żmihorski[b], Matthew Hiron[b], Tomas Pärt[b]

Affiliations:
[a] The Swedish Agricultural University, Swedish Biodiversity Centre, Box 7007, SE 750 07 Uppsala, Sweden
[b] The Swedish Agricultural University, Department of Ecology, Box 7044, Se 750 07 Uppsala, Sweden
[c] Present address: Länsstyrelsen i Örebro Län, 701 86 Örebro, Sweden

Corresponding author: Åke Berg, The Swedish Agricultural University, Swedish Biodiversity Centre, Box 7007, SE 750 07 Uppsala, Sweden , Tel.: +46 18 672624 , fax.: +46 18 6734 80, E-mail address: Ake.Berg@slu.se

Abstract

Changes in agricultural policies have caused dramatic changes in land-use in agricultural landscapes. To investigate whether such changes in land-use relate to temporal changes in bird communities a repeated inventory (1994 and 2004) of farmland birds was made in 212 point-count sites in south-central Sweden.

Distinct changes in abundance of several species over the study period were recorded, abundance of the 16 studied species decreased by 23%. The decline was significant for eight species, while two species increased significantly. Persistence and colonisation models suggested similar species-habitat relationships as the snapshot models, i.e. eight of the 12 associations were in line with what could be expected from the snapshot models. Occurrence of nine species was linked to land-use whereas six species displayed links between changes in occurrence and changes in land-use. In line with previous studies positive effects of short rotation coppice and negative effects of autumn-sown crops were found, while set-asides showed fewer effects than expected. In the snapshot models several species showed links to landscape characteristics such as amount of forest (negative for five species) and landscape heterogeneity (positive for six species). The evidence for effects of the landscape variables on persistence/colonization was more restricted.

The results suggest that both land-use changes and the landscape setting may cause local changes in abundance of farmland birds, even for species displaying a general decline in numbers between years, the effects of land-use changes being, however, strongly species specific.

Keywords: Farmland birds, Landscape heterogeneity, Forest cover, Land-use changes, Population changes

1. Introduction

The polarization of agriculture, i.e. intensification of agriculture in productive areas and abandonment of farmland in less productive areas, is widespread in Europe and is causing farmland biodiversity to decline (Robinson and Sutherland, 2002). Farmland butterflies, birds and many other taxa associated with traditional low intensity farming have suffered from this polarization of agriculture (Chamberlain et al., 2000; Stoate et al., 2001; Wretenberg et al., 2006; Baldi et al., 2013; Loos et al., 2014). Most studies of farmland biodiversity declines and its relationships to landscape structure and farming practices are "snap-shot" studies, i.e. organisms are inventoried at different sites in one year to establish species-habitat relationships. While this approach often has been used to evaluate the impact of landscape changes on communities (Pickett, 1989; Sanderson et al., 2009; Chiron et al., 2010; Flick et al., 2012), it assumes that variation in spatial patterns will reflect variation in temporal patterns, e.g. when land-use changes due to changed agricultural policies. However, such space-for-time substitutions may fail, e.g. due to density-dependent bird habitat relationships (Riffell and Gutzwiller, 2009; Barnagaud et al., 2011; Wells et al., 2011) or complex community dynamics (Fukami and Wardle, 2005). Furthermore, several studies have shown that space-for-time substitutions might overestimate the effects of habitat changes on the dynamics of bird communities (Johnson and Miyanishi, 2008; Sorte et al., 2009; Bonthoux et al., 2013).

Bearing in mind the potential problems with the space-to-time substitutions mentioned above temporal dynamics in communities in response to changing environment should preferably be investigated by temporally repeated data (Adler and Lauenroth, 2003). This is especially so concerning studies in agricultural landscapes because (i) farmland habitats change drastically between years due to rotational schemes of land-uses and large-scale changes in agricultural policies (e.g. Wretenberg, 2007), and (ii) land-use changes are assumed to be the main drivers of population changes of several farmland birds due to their strong effects on abundance of individual species (e.g. negative effects of winter wheat (Chamberlain et al., 2001; Eggers et al., 2011), and positive effects of set-asides (van Buskirk and Willi, 2004) and short-rotation coppice (Berg, 2002b)).

Here we report on a repeated inventory (1994 and 2004) of farmland birds at 212 sites in a farmland-forest landscape gradient in south-central Sweden. We make use of the fact that the agricultural policy shifted dramatically between these years; 1994 was the last year of an eight year period promoting low-intensity farming because of overproduction (i.e. the set-aside period), whereas farming practices and land-use in 2004 reflected a nine year period of increased production according to the Common Agricultural Policy in the European Union (Wretenberg et al., 2007). In order to investigate the effects of land-use changes on birds two types of analyses were conducted. First, we investigated occurrence – land-use relationships and their interactions to landscape composition and landscape heterogeneity in a "snap-shot model". Second, we tested whether changes in local land-use were linked with changes in local occurrence of species, in terms of probability of (i) persistence (i.e. occurrence in both years in previously occupied patches) and (ii) colonisation (i.e. occurrence in the second year only of previously empty patches). Third, we investigated whether land-use-driven changes in local occurrence were related to surrounding landscape composition (cf. Wretenberg et al., 2010) and landscape heterogeneity and compared the results to our snap-shot models.

We hypothesized that changes in species occurrence should be related to changes in land-use and especially land-uses earlier shown to have strong positive (set-aside, short rotation coppice) or negative (autumn sown cereals) effects on bird species-richness. Furthermore, we expected these land-use relationships to be dependent on the composition of the surrounding landscape as suggested by previous studies (Wretenberg et al., 2010) and that high landscape heterogeneity should affect population changes of most species positively.

2. Methods

We used 212 census points (i.e. sites) located in the counties of Uppland and Västmanland (approximately 59° 40' N - 60° 07' N and 16° 30' E - 18° 10' E) in south-central Sweden (total study area c. 1800 km^2). The sites were located in landscapes with different amounts of forest (e.g. median 28%, range 0 - 92% as measured within a 600 m radius from the census point). However, all sites were located in farmland habitats and the proportion of farmland within 100 m (i.e. the radius used for bird censuses) was high; 82% of the sites had more than 80% farmland within 100 m. The sites were mainly located in arable fields and the proportion of semi-natural pastures was low (1.4 % within 100 m radius). All census points were located at least 600 m apart (median 900 m, range 600 - 4000 m). In 1994 the census points were

selected in a stratified design with respect to different land-use types (i.e. spring-sown crops, autumn-sown crops, leys, cultivated pasture, set-aside fields and short rotation coppice), semi-natural pastures, occurrence of residual habitats (e.g. ditches, within-field habitat islands and field roads) and landscape composition (forest-dominated and farmland-dominated). Initially, several hundred potential census points were investigated to cover variation in land-use. Almost all sites with short rotation coppice were chosen (i.e. the rarest land-use) whereas the selection of the census points in other land-use types was random within these strata.

A detailed habitat mapping (including field types and different types of non-crop habitats) was done within 100 m (only used in site descriptions not in analyses) and within 300 m of the point centres (used in analyses) with the help of field visits, land-use maps (1:10 000) and aerial photographs. Proportions of different habitats and land-use types (see Table 1) were estimated from these detailed maps using the software ArcView, version 3.3 (Anonymous, 1992-2002) with the XTool extension (DeLaune, 2001). At the landscape level (600m radius) only the proportion of forest and the proportion of arable fields (all field types combined) was mapped.

The proportion of the landscape covered by forests within 600 m radius from the census point was used as the descriptor of landscape composition. This descriptor was strongly correlated with the proportion of arable fields (therefore not included in the analyses) at the same spatial scale (r = -0.89, P <0.001) and with the proportion of forest at smaller spatial scale (e.g. radius of 300 m; r = 0.92, P<0.001). Landscape heterogeneity was estimated by the number of transitions between crop and a group of 10 non-crop habitats (usually with trees and shrubs, e.g. farmsteads, woodlots, semi-natural pastures). The number of transitions was counted along each arm of an eight-armed ruler in a standardized manner, and the mean number of transitions per site was used as estimate of landscape heterogeneity (see Berg, 2002a). The environmental variables used in the analyses are listed in Table 1.

Table 1. Description of landscape and land-use variables included in the analyses.

Variables	Description
Forest coverage	Area (ha) of forest (coniferous, deciduous and young forest) within 600 m.
Landscape heterogeneity	Number of transitions along an eight-armed ruler between arable land and 10 other habitats (farmsteads, within-field habitat islands, semi-natural pastures, coniferous forest, deciduous forest, young forest, gardens, rivers, lakes and a class including other rare habitats) within 300 m.
Short rotation coppice	Proportion of short rotation coppice (*Salix*) among all open habitats within 300m.
Non-rotational set-aside	Proportion of fields under long-term set-aside (at least two years) among all open habitats within 300 m. Usually with dense tall vegetation.
Ley	Proportion of cultivated grassland-used for hay and silage production among all open habitats within 300m.
Cultivated pasture	Proportion of arable land under pasture among all open habitats within 300m.
Rotational set-aside	Proportion of set-aside with stubble from the previous year among all open habitats within 300 m. Usually with short and sparse vegetation.
Autumn-sown crops	Proportion of autumn-sown crops among all open habitats within 300 m. Consisted mainly of wheat.

2.1. Bird censuses

Birds were inventoried with point counts (Bibby et al., 1992). All sites were visited five times in 1994 and 2004 during early morning (mainly from sunrise, i.e. from 4:5 during first period to 3:27 in last period, to 10 am), once in each of the periods 1–10 May, 11–20 May, 21–31 May, 1–10 June and 11–20 June. Each person (all highly experienced bird watchers) visited 11-23 sites *per* morning and each observer visited the same sites across the whole study period. We carefully selected the survey points such that each observer inventoried points covering same landscape types and land-uses to avoid observer biases. Sites were inventoried in a different order at each occasion to avoid bias due to variation in diurnal activity of birds.

Birds were counted within a radius of 100 m of the census point. However, habitat structure and composition were mapped within a radius of 300 m (see above) because several species have large home ranges or are known to respond also to surrounding habitats (see e.g. Söderström and Pärt, 2000). The observer noted all bird species seen and heard during five minutes. No counts were made on mornings with strong wind or rain. Observations of singing males and pairs were used to estimate the number of territories of different species at each site and maximum number of observed territories during all visits was used as the metric of abundance. However, flocks of obviously migrating birds (usually in late April – mid May) were not included in the censuses. Sixteen common species were analysed which occurred at ≥ 20 sites in one of the census years and were considered to be farmland birds (Berg and Pärt, 1994; Pärt and Söderström, 1999a,b; Söderström and Pärt, 2000; Berg, 2002a). Full list of species recorded during the study is available in Wretenberg et al. (2010).

2.2. Statistical methods

Redundancy analysis was used in order to visualize the associations between abundance of particular species and habitat variables. For this purpose we used RDA implemented in R program using 'vegan' package (Oksanen et al., 2013).The RDA was controlled for the forest coverage within 600 m, landscape heterogeneity and year effects.

We used two main modelling approaches. First, snapshot models (i.e. occurrence models) were based on generalized linear mixed models (GLMM) with binomial error distribution and logit link except for skylark (for Latin names of birds species see Table 2) where abundance and a Poisson error distribution with log link was used. Occurrence (i.e. presence vs. absence, for skylark abundance was used) of each bird species was used as a response variable, year as fixed categorical factor and site as random factor. Two landscape and six land-use characteristics were considered as continuous explanatory variables (Table 1) and interactions between the six land-use types and forest coverage within 600 m were also considered. Changes in area of spring-sown crops were excluded from the analyses, because this variable was redundant and correlated with other variables (r ≥ 0.53). Correlations between all other independent variables were low (r < 0.37). All possible combinations of the interactions between the six land-use types and forest coverage were considered and the main effects were always included in all these candidate models (in total 65 competing models). Model averaging within the set of competing models and averaged parameter estimates were used for further inferences. The R program was used for statistics (R Core Team, 2014) with '*lme4*' package (Bates et al., 2014) for mixed modelling and '*MuMIn*' package (Bartoń, 2013) for model averaging.

As a second step, i.e. colonization-persistence models, the processes of local colonisation and persistence were investigated separately, by dividing data by presence-absence at the site level in 1994 for each species. Probability of persistence was analysed for all sites where the species was present in 1994 and colonisation for all sites where it was absent. In both subsets occurrence of a species in 2004 was considered as a response variable and generalized linear models (GLM) with binomial error distribution and logit link were used for both colonization and persistence models. Small sample size did not allow for the forest x land-use interaction terms to be tested. In this analysis all the possible main effects, i.e. changes in land-use, expressed as a difference in coverage between 1994 and 2004, were considered as well as the two constant landscape characteristics (forest coverage and landscape heterogeneity), which were stable over the studied years. There were no sites where arable land changed into non-crop habitat and similarly no cases where non-crop habitats were turned into arable land during the study period. However, there were a few cases (n=5) when there were changes within the non-crop habitat group (i.e. pastures were abandoned and turned into shrub habitats). However, these changes did not affect the landscape measure (proportion of forest) nor the landscape heterogeneity measure used (number of transitions between arable land and a group of 10 combined non-crop habitats). AIC-based model averaging was performed within the set of competing models and averaged parameter estimates were used for further inferences.

3. Results

In total c. 6000 ha of arable land was mapped (i.e. all arable land within 300 m from the plot centres). The number of land-use types within sites in 1994 and 2004 was positively correlated (r=0.45, d.f. = 210, p<0.001) and did not differ between 1994 and 2004 (Paired t-test, t = 0.63, d.f. = 211, p = 0.529), showing that landscape structure and crop number did not change at the scale of the county between the two years. However, due to crop rotation schemes and the change in agricultural policy (see Wretenberg et al., 2007)

most sites experienced increases or decreases in areas of different land-use types across years, (i.e. all land-uses decreased or increased at ≥ 100 of the 212 sites, except short rotation coppice (changes occurred at 26 sites). The proportion of autumn sown crops showed the greatest change, increasing from 8% to 27%, whereas the proportion of cultivated pasture, ley and set-aside decreased and spring sown crops and short rotation coppice stayed roughly at the same level (Fig. 1).
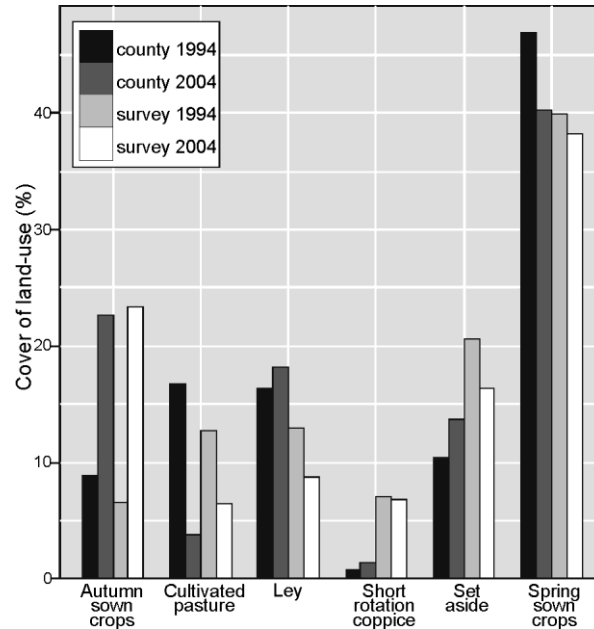

Figure 1. Proportion (%) of different land-uses of arable land within 300m of the centre of the censused plots in the survey (n=212) and in Uppsala county in 1994 and 2004.

Eight of the 16 species decreased, three species increased and five species remained fairly stable in numbers between 1994 and 2004 (Table 2). Skylark was the dominant species and was found on 83 % and 69 % of the sites in 1994 and 2004, indicating a moderate decrease in number of occupied sites. However, skylark abundance decreased drastically from 550 to 317 territories (a reduction of 42 %) across years. In addition to skylark, number of occupied sites for seven species (yellowhammer, greenfinch, whinchat, linnet, reed bunting, pheasant and red-backed shrike) decreased significantly between 1994 and 2004. Occupancy of three species (woodpigeon, white wagtail and common starling) increased with more than 40%. The other five species were more stable in numbers (Table 2).

Table 2. Number of sites and territories occupied by different farmland bird species in 1994 and 2004. n = 212 sites. The trend in number of territories in our survey is compared with the trend in the TRIM index for the same species in the Swedish Bird Surveys (SBS) point counts during the breeding period, see http://www.zoo.ekol.lu.se/birdmonitoring/res-hackfagel.htm. Significance of the changes in number of territories is marked with asterisks.

Common name	Scientific name	1994		2004		Trend	National
		No. occupied	of No. of territorie	No. of sites occupied	No. of territorie	no. of territorie	SBS trend
Skylark***	*Alauda arvensis*	177	550	147	317	-0.424	-0.404
Yellowhammer***	*Emberiza citrinella*	165	221	103	119	-0.462	-0.305
Greenfinch**	*Carduelis chloris*	111	153	72	106	-0.307	-0.009
Whinchat**	*Saxicola rubetra*	102	130	84	93	-0.285	0.011
Linnet***	*Carduelis cannabina*	89	97	42	54	-0.443	-0.669
Common	*Sylvia communis*	77	88	65	72	-0.182	0.102
Common	*Sturnus vulgaris*	70	104	84	190	0.827	-0.264
White wagtail*	*Motacilla a. alba*	65	65	85	90	0.385	-0.153
Reed bunting**	*Emberiza*	49	60	26	29	-0.517	-0.196

Pheasant***	*Phasianius colchicus*	43	46	8	8	-0.826	-0.097
Fieldfare	*Turdus pilaris*	37	55	38	66	0.200	-0.043
Woodpigeon**	*Columba palumbus*	35	43	59	79	0.837	0.148
Magpie	*Pica pica*	34	35	22	24	-0.314	-0.068
Northern lapwing	*Vanellus vanellus*	33	69	40	57	-0.174	-0.082
Red-backed shrike*	*Lanius collurio*	25	26	10	11	-0.577	-0.371
Northern wheatear	*Oenanthe oenanthe*	22	24	29	29	0.208	-0.071

We did a redundancy analysis (Fig. 2) to display the investigated species and their relations to land-use. Further we indicated observed changes in local population size for each species (Table 2). In general, one group of species associated with short rotation coppice (and to lesser extent autumn sown crops) was clearly separated in the lower-left part of the RDA space. All these species showed decreases in population sizes whereas several species in the upper right corner (associated with ley and pasture) displayed an increase over the study period.
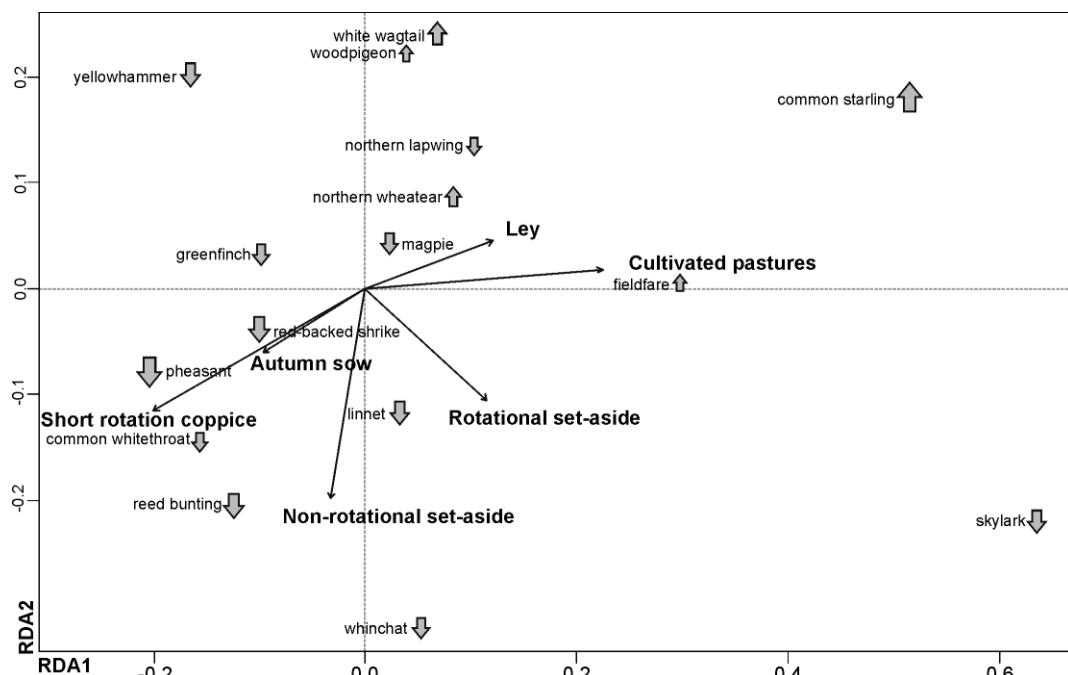

Figure 2. Redundancy analysis biplot showing association between 16 most common bird species and land-use types (controlling for the effect of forest coverage, landscape heterogeneity and year). Arrows indicate increase or decline of local population of particular species. The size of arrows is proportional to the size of the species-specific change.

3.1. Snapshot models of species occurrence

In general, landscape variables explained the variation in local occurrence of nine species, land-use variables were linked to the occurrence of nine species and seven species displayed interactions between proportion forest and land-use (Table 3, Appendix A, B). Including interactions between landscape and land-use variables gave a total of 12 species associated with arable land-use and landscape types. No effect at all was recorded for northern lapwing, woodpigeon, magpie, and red-backed shrike.

Concerning main effects of land-use variables, the occurrence of four species was positively associated with the cover of short rotation coppice, four species were associated with the cover of autumn-sown crops (three species showed negative associations). Fewer species were associated with the cover of non-rotational set-aside (two species), ley (two species), rotational set-aside (one species) and cultivated pasture (one species) (see Table 3, Fig. 2). Five species were associated with forest cover (all negatively) and seven species with landscape heterogeneity (six positively, one negatively; cf. Table 3).

Seven species showed significant interactions (a total of 13 interactions) between forest cover and land-use. The effects of some land-use types were more positive in landscape with high forest cover than in

more open farmland landscapes. In general land-uses classified as less intensively managed (i.e. set-asides, cultivated pasture and leys) were positively associated with the occurrence of seven species in 10 of these 13 interactions (Table 3, Appendix A) in forested landscapes, while more intensively managed autumn sown cereals only were positively associated with two species in these landscapes.

Table 3. Averaged parameter estimates (Odds Ratio; above 1 means positive effect, below 1 negative effect) for models explaining occurrences of the species in 212 count-points stations on the basis of landscape and land-use characteristics in 1994 and 2004 (skylark - Poisson model, remaining species - binomial models). Coefficients are averaged for 64 considered models and only those with 95% confidence intervals not overlapping zero are presented. Upper superscripts (^{col,pers}) indicate importance for a given habitat characteristic for colonization or persistence of a given species, marks indicate direction of the effect. Visualization of the interactions are presented in Appendix A

Species and AIC weight for the null model	Landscape factors		Land-use factors (area in ha)						Interactions with forest coverage
	Forest coverage	Land Hetero-geneity	Short rotation coppice	Non-rotational set-aside	Rotational set-aside	Ley	Cultiv. pasture	Autumn-sown crops	
Reed bunting, ω=0.00	0.970		1.511$^{col(+)}$						
Pheasant, ω=0.00		1.101	1.348$^{col(+)}$						Non-rotational set-aside (-)
Linnet, ω=0.00	0.972	1.067	1.182						Autumn sown (+), Rotational set-aside (+)
Skylark, ω=0.00	0.970$^{pers(-)}$	0.978							Non-rotational set-aside (+), Rotational set-aside (+), Ley (+), Cultivated pastures (+), Autumn sown (+)
Common whitethroat, ω=0.00	0.974		1.344						Non-rotational set-aside (+)
Whinchat, ω=0.00				1.184$^{pers(+)}$		1.177		1.086$^{col(+)}$	Cultivated pastures (+)
Common starling, ω=0.00	0.982$^{col(-)}$	1.062					0.909		
Northern lapwing, ω=0.42		col(-)							
Woodpigeon, ω=0.04									
Northern wheatear, ω=0.21							col(-)	0.629	
Fieldfare, ω=0.00		1.148		col(+)					Ley(+)
Magpie, ω=0.76									
Red-backed shrike, ω=0.00									
White wagtail, ω=0.00					0.807			0.930$^{pers(-)}$	Cultivated pastures (+), Rotational set-aside (+)
Greenfinch, ω=0.00	col(+)	1.103							
Yellowhammer, ω=0.00		1.114$^{col(+)}$	0.904			0.910	0.890		

3.2. Colonization-persistence models

We analysed whether changes in land-use were associated with presence-absence of the species in 2004 for two subsets: (i) where the species was present in 1994 (i.e. persistence model) and (ii) where the species was absent in 1994 (i.e. colonisation model).

The probability of colonisation was related to land-use changes or landscape variables in nine species (Table 3, Appendix C), while probability of persistence was only related to landscape variables or land-use change in three species. In general persistence and colonisation models often suggested similar species-habitat relationships as the snapshot models above (Table 3). Eight of the 12 associations were in line with what could be expected from the snapshot models, i.e. a positive or negative effect of a variable both in the snapshot models and in the persistence/colonisation models (reed bunting with short rotation coppice, skylark with forest cover, and yellowhammer with landscape heterogeneity; Table 3, Appendix B).

In case of four species however, the probability of colonization was related to landscape factors or land-use changes that were not selected as predictors of presence/absence of these species in snapshot models.

8

For instance, probability of colonization event in case of lapwing was negatively associated with landscape heterogeneity whilst an increase in cover of cultivated pasture was negatively associated with probability of colonisation in the northern wheatear. Change in non-rotational set-asides positively affected colonization of new sites by the fieldfare, and forest cover affected colonization by the greenfinch positively.

4. Discussion

We recorded distinct changes in abundance of several common farmland birds over the study period - in total, the abundance of the 16 species included in this study decreased by 23% (from 1753 territories in 1994 to 1353 in 2004). The decline was statistically significant for eight species of which pheasant, red-backed shrike and reed bunting displayed the most severe declines. The pheasant is an introduced species and its population in this area was mainly supported by release of captive reared birds. Thus, our study confirms the negative population trends of many Swedish farmland birds. Several decreasing bird species displayed broadly similar changes in abundance at the national level (skylark, yellowhammer, linnet, red-backed shrike, reed bunting, see Table 2), although other species (e.g. common starling, greenfinch, whinchat, white wagtail, pheasant and woodpigeon) displayed different trends at the regional and national level Table 2). Such differences between the national and local trends, however, were expected because of variation in local population trends (see e.g. Wretenberg et al., 2007), and because other suitable habitats than farmland are included in national population trend estimates (e.g. clear-cuts, mires, built up areas and alpine areas).

4.1. Land-use effects

The amount of autumn sown crops increased, and cultivated pasture and non-rotational set-aside decreased, from 1994 to 2004. However, the amount of spring-sown crops and short rotation coppice remained roughly at the same level in 1994 and 2004. We found occurrence of 12 species to be linked to land-use whereas six species displayed links between changes in land-use and changes in occurrence. In line with previous studies (e.g. Berg, 2002b; Chamberlain et al., 2001; Eggers et al., 2011) we found positive effects of short rotation coppice (four species) and negative effects of autumn-sown crops (three species, but see whinchat), while non-rotational and rotational set-asides were less important than expected from earlier studies (e.g. van Buskirk and Willi, 2004). Because these associations were strongly species specific (see also Sanderson et al., 2009) no single land-use change could be identified as the driver of the general population declines observed.

In contrast with previous results of species richness patterns (Wretenberg et al., 2010) we found a general pattern that low intensity land-uses (leys, cultivated pastures, set-asides, see Wretenberg et al., 2010) had positive (or less negative) effects on the occurrence of several species in forested landscapes (Table 2). One possible reason for these differences is that this study analysed occurrence of common species, while Wretenberg et al. (2010) analysed it on more farmland species including uncommon and rare species. Thus, rare habitats (e.g. low-intensity crops in open intensively managed farmland) might increase the probability of occurrence of uncommon species while the abundance of common species decreases.

4.2. Landscape effects

In the snapshot models several species also showed links to landscape characteristics such as amount of forest (negative for five species) and landscape heterogeneity (positive for six species), i.e. effects of landscape structure were more uniform across species than effects of land-use. The negative effects of forest on occurrence are in line with several earlier studies (Pärt and Söderström, 1999b; Berg, 2002a) showing that the amount of forest is a major factor affecting bird community composition and abundance of single species in forest-farmland mosaics. The cover of forest had negative effects on probability for colonization and persistence for two widespread farmland species (skylark and common starling). This suggests that forest cover in the surroundings had effects on probability of colonization and persistence also in other species, since our analyses of colonization and persistence (especially) suffered from restricted sample sizes. Thus, landscapes with a high amount of forest are less preferred by field-nesting species, which are avoiding vertical structures such as forest edges and farms with high predation pressure (Berg, 1992; Berg et al., 1992).

Landscape heterogeneity also had positive effects on occurrence of several non-crop nesting species, indicating that non-crop habitats and habitat elements (e.g. forest edges, habitat islands, farmsteads, semi-

natural pastures) contributing to overall landscape heterogeneity are a main factor influencing the occurrence of these species (see also Hiron et al., 2013). Concerning the colonisation/persistence models only the yellowhammer was positively affected by landscape heterogeneity, although several other species showed similar trends suggesting that non-crop nesters colonize landscapes with high landscape heterogeneity more often. In contrast, field-nesting species (here the northern lapwing and similar trends for the skylark) avoided heterogeneous areas.

4.3. Snap-shot and colonization-persistence models
Our snap-shot models and colonization-persistence models suggested similar links to land-use and landscape variables. This suggests that space-for-time substitutions may to some extent work also in the dynamic farmland landscapes. However, temporal population changes were only to a lesser extent or not at all related to corresponding changes in land-use. For example species associated with short rotation coppice declined (Fig. 2) despite the amount of this land-use was about the same in the two inventory years (Fig 1). Similarly, autumn-sown crops increased both locally and regionally (Fig. 2), but three species avoiding this habitat (i.e. common starling, white wagtail and northern wheatear) displayed either stable or increased numbers, whereas one species preferring autumn sown crops declined significantly (whinchat).
More significant associations were observed in the snap-shot than in the persistence-colonisation models and colonisation models showed more significant associations than persistence models (Table 3). These differences in statistical results between models were most likely caused by variable power of test due to sample size (largest sample in the snap-shot models, smaller in the persistence models than in the colonisation models). Another possible explanation for fewer associations in colonization/persistence models than in the snap-shot models is that transitions of land-use types were complex, i.e. an increase in a preferred/avoided land-use type might occur on the expense of another preferred/avoided land-use type. Nevertheless, colonization models showed that even several strongly declining species are still able to colonize new areas when their preferred habitat increased locally (pheasant, whinchat, reed bunting, cf. Tables 2 and 3).

6. References
Adler, P.B., Lauenroth, W.K., 2003. The power of time: spatiotemporal scaling of species diversity. Ecol. Lett. 6, 749–756.

Anonymous, 1992-2002. ArcView. Environmental Systems Research Institute, Inc.

Baldi, A., Batary, P., Kleijn D. 2013. Effects of grazing and biogeographic regions on grassland biodiversity in Hungary - analysing assemblages of 1200 species. Agric. Ecosyst. Environ. 166, 28–34.

Barnagaud, J.Y., Devictor, V., Jiguet, F., Archaux, F., 2011. When species become generalists: on-going large-scale changes in bird habitat specialization. Global. Ecol. Biogeogr. 20, 630–640.

Bartoń, K., 2013. MuMIn: Multi-model inference. R package version 1.9.13. http://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. http://CRAN.R-project.org/package=lme4

Berg, Å., 1992. Factors affecting nest site choice and reproductive success of Curlews *Numenius arquata* on farmland. Ibis 134, 44–51.

Berg, Å., Lindberg, T., Källebrink, K., 1992. Hatching success of lapwings on farmland: differences between habitats and colonies of different sizes. J. Anim. Ecol. 61, 469–476.

Berg, Å., 2002a. Composition and diversity of bird communities in Swedish farmland-forest mosaic landscapes. Bird Study 49, 153–165.

Berg, Å., 2002b. Breeding birds in short rotation coppices on farmland in central Sweden - the importance of *Salix* height and adjacent habitats. Agric. Ecosyst. Environ. 90, 265–276.

Berg, Å., Pärt, T., 1994. Abundance of breeding farmland birds on arable and set-aside fields at forest edges. Ecography 17, 147–152.

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

Bibby, C.J., Burgess, D., Hill, D.A., 1992. Bird Census Techniques. Academic Press, London.

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.

Chamberlain, D.E., Fuller, R.J., Garthwaite, D.G., Impey, A.J., 2001. A comparison of farmland bird density and species richness in lowland England between two periods of contrasting agricultural practice. Bird Study 48, 245–251.

Chiron, F., Filippi-Codaccioni, O., Jiguet, F., Devictor, V., 2010. Effects of non-cropped landscape diversity on spatial dynamics of farmland birds in intensive farming systems. Biol. Cons. 143, 2609–2616.

DeLaune, M., 2001. XTools. Extension for ArvView GIS. Oregon Department of Forestry, Salem.

Eggers, S., Unell, M., Pärt, T., 2011 Autumn-sowing of cereals reduces breeding bird numbers in a heterogeneous agricultural landscape. Biol. Cons. 144, 1137–1144.

Flick, T., Feagan, S., Fahrig, L. 2013. Effects of landscape structure on butterfly species richness and abundance in agricultural landscapes in eastern Ontario, Canada. Agric. Ecosyst. Environ. 156, 123–133.

Fukami, T., Wardle, D.A., 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. Proc. R. Soc. Lond. B 272, 2105–2115.

Hiron, M., Berg, Å., Eggers, S., Pärt, T., 2013. Are farmsteads over-looked biodiversity hotspots in intensive agricultural ecosystems? Biol. Cons. 159, 332–342.

Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. Ecol. Lett. 11, 419–431.

Loos, J., Dorresteijn, I., Hanspach, J., Fust, P., Rakosy, L., Fisher, J. 2014. Low-Intensity Agricultural Landscapes in Transylvania Support High Butterfly Diversity:Implications for Conservation. PLoS ONE 9(7): e103256.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H. 2013. vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Pickett, S.T.A., 1989. Space for time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.) Long-Term Studies in Ecology: Approaches and Alternatives. Springer, New York, pp. 110-135.

Pärt, T., Söderström, B., 1999a. Conservation value of semi-natural pastures in Sweden: Contrasting botanical and avian measures. Cons. Biol. 13, 755–765.

Pärt, T., Söderström, B., 1999b. The effects of management regimes and location in landscape on the conservation of farmland birds breeding in semi-natural pastures. Biol. Cons. 90, 113–123.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Riffell, S.K., Gutzwiller, K.J., 2009. Interannual variation in bird-landscape relations: understanding sources of a pervasive conservation dilemma. Oikos 118, 45–54.

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157–176.

Sanderson, F., Kloch, A., Sachanowicz, K., Donald, P., 2009 Predicting the effects of agricultural change on farmland bird populations in Poland. Agric. Ecosyst. Environ. 129, 37–42.

Söderström, B., Pärt, T., 2000. Influence of landscape scale on farmland birds breeding in semi-natural pastures. Cons. Biol. 14, 522–533.

Sorte, F., Lee, T., Wilman, H., Jetz, W., 2009 Disparities between observed and predicted impacts of climate change on winter bird assemblages. Proc. R. Soc. Lond. B 276, 3167–3174.

Stoate, C., Boatman, N., Borralho, R., Carvalho, C.R., Snoo, G.R.D., Eden, P., 2001. Ecological impacts of arable intensification in Europe. J. Environ. Man. 63, 337–365.

Wells, K., Böhm, S.M., Boch, S., Fischer, M., Kalko, E.K.V., 2011. Local and landscape-scale forest attributes differ in their impact on bird assemblages across years in forest production landscapes. Basic Appl. Ecol. 12, 97–106.

Wretenberg, J., 2006. The decline of farmland birds in Sweden. Doctoral thesis no. 2006:113. Swedish University of Agricultural Sciences, Faculty of Natural Resources and Agricultural Sciences.

Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T., Pärt, T., 2006. Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. J. Appl. Ecol. 43, 1110–1120.

Wretenberg, J., Lindström, Å., Svensson, S., Pärt, T., 2007. Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. J. Appl. Ecol. 44, 933–941.

Wretenberg, J., Pärt, T., Berg, Å., 2010. Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. Biol. Cons. 143, 375–381.

Appendix A. Visualisation of the interaction terms from generalized linear mixed models presented in Table 2. Contours indicate expected probability of occurrence (abundance in case of the Skylark) of species in relation to variability of two interacting habitat variables.
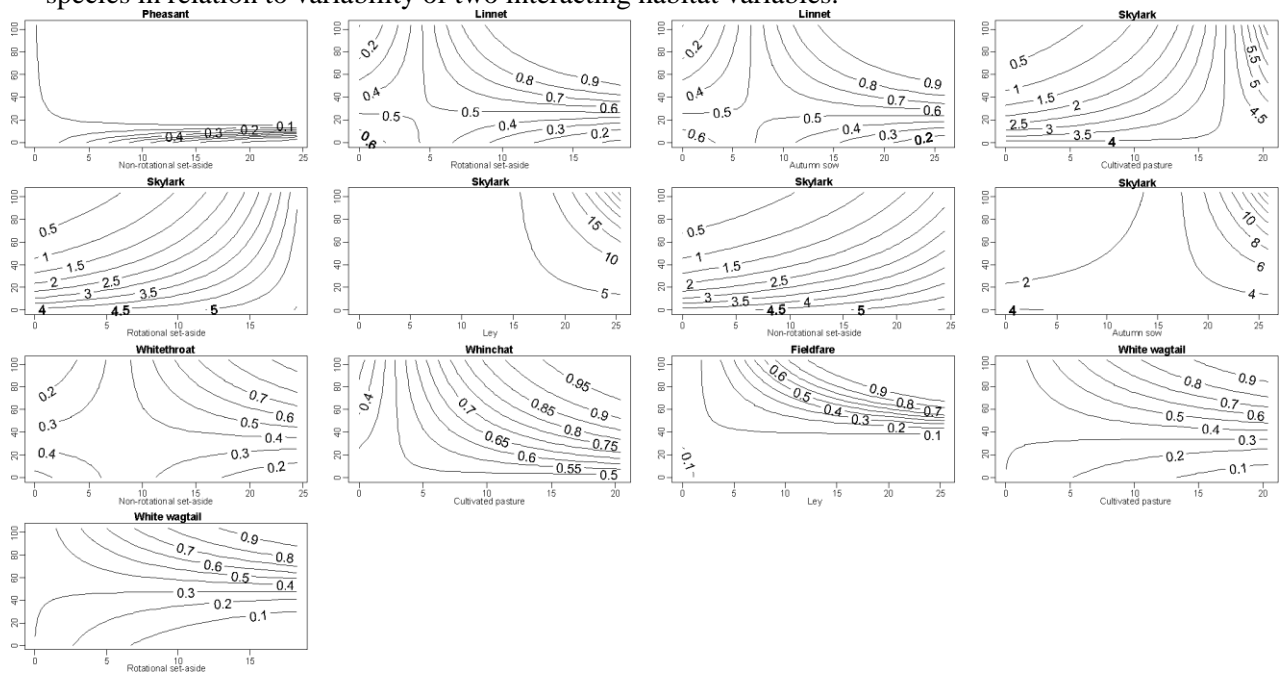
Appendix B. Visualization of the main effects of landscape variables (forest cover and landscape heterogeneity) and cover of different land-uses (short rotation coppice, set-aside, autumn-sown crops, ley and cultivated pasture) on abundance (skylark) and probability of occurrence (all other species) in the snap-shot models. The curves were drawn using the coefficients estimated with the help of model averaging for the full set of models considered. Each curve indicates one species, curves at one panel are specific in term of style, thickness and colour combination to be easy to distinguish. Order of species labels (from top to down) follows the order of values of particular curves in place indicated by dashed vertical line.
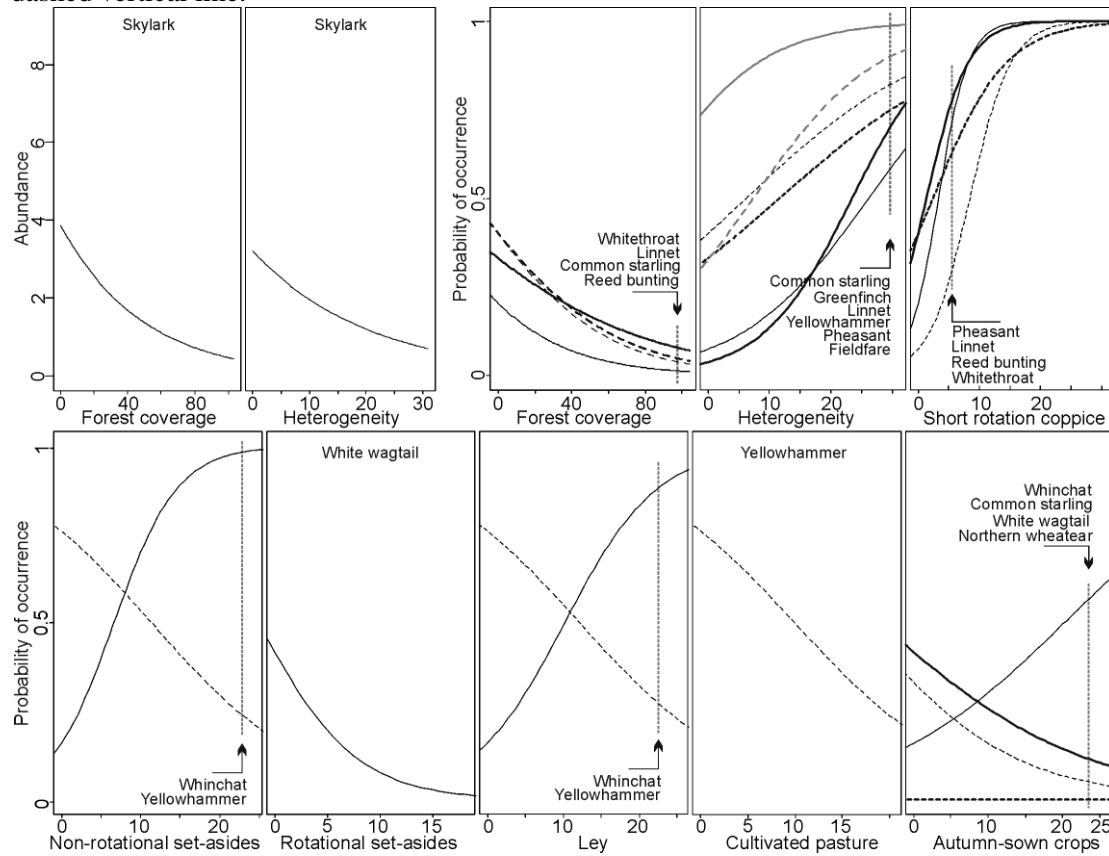
Appendix C. Probability of persistence and colonization as a function of the landscape variables (forest cover and landscape heterogeneity) and change in cover of different land-uses (short rotation coppice, set-aside, autumn-sown crops and cultivated pasture) between 1994 and 2004. Sample size for each species is given in brackets. Other explanations as in Fig. 2.