

Bird-habitat associations predict population trends in central European forest and farmland birds

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Abstract Recent studies show differences in population trends between groups of species occupying different habitats. In Czech birds, as well as in many other European countries, populations of forest species have increased, whereas populations of farmland species have declined. The aim of our study was to test whether population trends of particular species were related to finer bird-habitat associations within farmland and forest birds. We assessed bird-habitat associations using canonical correspondence analysis based on data from a 400 km long transect across the Czech Republic. We calculated population trends of 62 bird species using log-linear models based on data from a large-scale annual monitoring scheme, which covers the time series from 1982 to 2005. Within forest birds, species with a closer association with lowland broad-leaved forest have had more positive population trends, whereas species with a closer association with montane and coniferous forest revealed more negative population trends. We attribute these opposite trends to the gradual replacement of coniferous forests by deciduous ones, which took place in the Czech Republic during recent decades. Our analyses revealed a hump-shaped relationship within farmland birds, species most closely associated with farmland habitat revealing the most negative trends, whereas species with intermediate association to farmland habitat showed the most positive population trends. Such a pattern can be explained by the abandonment of

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previously cultivated areas followed by the spread of unmanaged meadows and scrubland. Changes in quantity or quality of preferred habitats may thus represent major drivers of observed bird population changes.

Keywords Bird community · Canonical correspondence analysis · Czech Republic · Habitat use · Land use · Monitoring · Population changes

Introduction

Many studies have described bird population changes in recent decades. Several remarkable patterns were explored, e.g. the effect of agricultural intensification on farmland bird populations (Siriwardena et al. 1998; Chamberlain et al. 2000; Newton 2004a), the effects of land use changes on woodland birds (De Juana 2004; Schulte et al. 2005), the effects of urbanisation on the structure of bird communities (Parody et al. 2001; Veech 2006), or, in recent years, the effects of global warming and local climate anomalies on bird population growth (Julliard et al. 2003, 2004; Lemoine et al. 2007). In these analyses bird species are commonly sorted into several groups defined by ecological traits, and population trends are compared between these groups. For example, Gregory et al. (2007) defined groups according to migration strategy (long-distance migrants, short-distance migrants and sedentary species) and habitat association (farmland birds, woodland birds, other common birds). However, such classification into categories does not reflect finer habitat associations of particular species, which could have important consequences for species population changes. We argue that habitat association is a continuous rather than categorical variable, as particular species reveal different levels of preference/avoidance of different habitats (Gregory and Gaston 2000; Julliard et al. 2006). Therefore, a change of one habitat may have different impacts on species differing in their association with this habitat. The exploration of bird population trends then has to focus on the description of species habitat associations as continuous variables and analyses based on interspecific differences in this respect.

There are various approaches to describe the degree of association of particular bird species to their habitats (Wiens 1989; Gregory and Gaston 2000; Julliard et al. 2006; Whittingham et al. 2007). Among them, multivariate ordinations are intuitive techniques with easy-to-understand results (Lepš and Šmilauer 2003). They explore gradients in species-habitat associations using correlations between species abundances and environmental factors in multiple sites cross-correlations within species abundance-habitat matrix (ter Braak and Šmilauer 2002). As a result, each species obtains its position along a habitat gradient expressed by an ordination axis. Each axis defines one independent habitat gradient and thus each species reveals its association with each independent habitat. Species positions along these gradients can be used for further analyses.

Our previous analyses have revealed several patterns in population trends of common birds in the Czech Republic. We found that the proportion of bird species with different population trends varied between habitats: there was a high proportion of increasing species among forest birds, whereas declining species prevailed among farmland birds (Reif et al. 2006). Moreover, the rate of population growth differed between forest specialist and forest generalist species (Reif et al. 2007). Farmland birds decreased between 1982 and 2003 (Štastný et al. 2004) and the decline was more severe in farmland specialists (Reif et al. 2008). Given that the differences in population trends depend on the level of species specialisation (Shultz et al. 2005), we can further explore whether species with different

degrees of association with particular habitats reveal predictable differences in population trends. In this paper (i) we compare population trends of 62 bird species in the Czech Republic between forest and farmland birds; (ii) using an independent data set we reveal the main gradients in habitat associations among Czech birds; and (iii) we test whether the position of a species along the habitat gradient predicts its population trend.

Material and methods

Bird population changes

We used data on bird abundances collected by the Breeding Bird Monitoring Programme (organised by the Czech Society for Ornithology) in the Czech Republic over the period 1982–2005. The Breeding Bird Monitoring Programme is a large-scale generic monitoring scheme based on fieldwork by skilled volunteers. Point count transects (Bibby et al. 2000) are used as the census method, sampling plots being selected by fieldworkers (free choice). The transects are scattered throughout the Czech Republic and cover all main habitats (i.e. farmland, woodland, wetland and urban areas). Almost all transects consist of a mixture of these habitats and comprise rather representative sample of the habitats in the Czech landscape with only human settlements being slightly overrepresented (Reif et al. 2008). We included data from all 315 transects censused during 1982–2005. Each transect comprises 20 points with the distance of 300 m between points. The counting session at each point lasts 5 min, during which the observer counts all birds seen or heard without recording the distance from the point. Two counts per breeding season (late April/early May and late May/early June) are recommended to observers, but since this has not been an obligatory rule, some performed fewer or more counts at a transect per season. For this reason, we divided the total number of individuals detected at each transect in given breeding season by the number of counts at this transect to estimate abundance of each species. We excluded all species poorly detectable by the monitoring technique used (e.g. owls and raptors).

For each species, the raw abundance data from the Breeding Bird Monitoring Programme were transformed into annual indices using log-linear models in the programme TRIM 3.51 (Pannekoek and van Strien 2001). The value of the index was set at 100% in 1982 as the first year. Models with effects for each time point were used, and covariates were not included. The trend is the slope of the regression line through the logarithm of the indices across sample sites in two consecutive years. The computation of this slope takes into account the variances and covariances of the indices. The overall trend is the average of annual trends (mean relative population change) over the whole study period.

Population trends were calculated for 85 forest and farmland species (Reif et al. 2006) but we excluded 23 species with uncertain trends from further analyses. To identify the uncertain trends, we followed criteria introduced by Gregory et al. (2007), who recognize six categories of population trends based on their 95% confidence limits: strong increase (lower limit of confidence interval > 1.05), moderate increase ($1.00 < \text{lower limit of confidence interval} < 1.05$), stable (confidence interval encloses 1.00 but lower limit > 0.95 and upper limit < 1.05), moderate decline ($0.95 < \text{upper limit of confidence interval} < 1.00$), strong decline (upper limit of confidence interval < 0.95), and uncertain trend (confidence interval encloses 1.00 but lower limit < 0.95 or upper limit > 1.05). Population trends of the species are listed in Reif et al. (2006) and in Table 1.

Table 1 Population trends and habitat associations of 62 common bird species in the Czech Republic

Species	Transects ^a	Trend ^b	SE	Habitat ^c	Lowforest ^d	Monforest ^d	Farmland ^d
<i>Perdix perdix</i>	86	0.936	0.015	Farmland	-0.493	-0.562	1.426
<i>Phasianus colchicus</i>	225	0.996	0.004	Farmland	-0.006	-0.552	0.813
<i>Vanellus vanellus</i>	172	0.901	0.009	Farmland	-0.44	-0.562	1.354
<i>Columba oenas</i>	73	1.034	0.013	Forest	-0.219	1.181	-0.652
<i>Columba palumbus</i>	293	1.028	0.005	Forest	0.241	0.435	-0.34
<i>Streptopelia turtur</i>	258	0.972	0.005	Farmland	0.046	-0.07	0.111
<i>Cuculus canorus</i>	274	0.997	0.004	Farmland	0.145	-0.321	0.215
<i>Jynx torquilla</i>	93	0.950	0.011	Farmland	0.578	-0.48	0.076
<i>Picus viridis</i>	173	1.047	0.009	Forest	0.828	-0.489	-0.252
<i>Dryocopus martius</i>	186	1.027	0.008	Forest	0.477	0.369	-0.518
<i>Dendrocopos major</i>	281	1.014	0.003	Forest	0.192	0.311	-0.287
<i>Dendrocopos minor</i>	89	1.032	0.015	Forest	1.343	-0.534	-0.344
<i>Alauda arvensis</i>	274	0.979	0.002	Farmland	-0.338	-0.429	1.028
<i>Anthus trivialis</i>	241	0.981	0.004	Forest	-0.342	0.318	0.442
<i>Anthus pratensis</i>	68	0.918	0.017	Farmland	-0.466	-0.344	1.262
<i>Troglodytes troglodytes</i>	270	1.013	0.003	Forest	0.205	0.864	-0.667
<i>Prunella modularis</i>	237	0.990	0.004	Forest	-0.128	0.394	-0.209
<i>Erithacus rubecula</i>	294	1.000	0.003	Forest	0.028	0.598	-0.348
<i>Luscinia megarhynchos</i>	96	1.044	0.013	Farmland	0.115	-0.556	0.706
<i>P. phoenicurus</i>	197	1.035	0.007	Forest	-0.312	-0.163	-0.129
<i>Saxicola rubetra</i>	153	1.032	0.008	Farmland	-0.477	-0.216	1.078
<i>Oenanthe oenanthe</i>	32	0.884	0.059	Farmland	-0.493	-0.562	1.275
<i>Turdus merula</i>	314	1.014	0.002	Forest	-0.026	0.033	-0.067
<i>Turdus pilaris</i>	179	1.000	0.005	Forest	-0.421	-0.352	0.478
<i>Turdus philomelos</i>	312	0.998	0.003	Forest	0.183	0.055	-0.113
<i>Turdus viscivorus</i>	205	1.018	0.007	Forest	-0.302	0.887	-0.226
<i>Acrocephalus palustris</i>	183	0.991	0.006	Farmland	-0.216	-0.528	0.871
<i>Sylvia communis</i>	257	1.003	0.005	Farmland	-0.158	-0.354	0.57
<i>Sylvia borin</i>	261	0.989	0.003	Forest	-0.113	-0.094	0.058
<i>Sylvia atricapilla</i>	305	1.04	0.002	Forest	0.083	0.114	-0.116
<i>Phylloscopus sibilatrix</i>	233	0.968	0.004	Forest	0.287	0.793	-0.58
<i>Phylloscopus collybita</i>	305	1.009	0.002	Forest	0.126	0.223	-0.263
<i>Phylloscopus trochilus</i>	283	0.973	0.004	Forest	-0.157	0.209	-0.158
<i>Regulus regulus</i>	222	0.987	0.004	Forest	-0.448	1.299	-0.542
<i>Regulus ignicapillus</i>	105	1.01	0.009	Forest	-0.442	1.072	-0.319
<i>Muscicapa striata</i>	165	1.039	0.008	Forest	0.781	-0.322	-0.227
<i>Ficedula albicollis</i>	118	1.034	0.007	Forest	1.171	0.102	-0.648
<i>Ficedula hypoleuca</i>	102	1.004	0.012	Forest	-0.493	-0.562	1.077
<i>Aegithalos caudatus</i>	194	0.94	0.010	Farmland	0.297	-0.173	0.118
<i>Parus palustris</i>	180	0.963	0.010	Forest	0.882	-0.263	-0.145
<i>Parus montanus</i>	116	1.003	0.012	Forest	-0.442	0.444	0.157
<i>Parus cristatus</i>	110	0.961	0.013	Forest	-0.483	1.526	-0.535
<i>Parus ater</i>	208	1.017	0.004	Forest	-0.438	1.087	-0.419
<i>Parus caeruleus</i>	286	1.002	0.003	Forest	0.35	-0.355	-0.053
<i>Parus major</i>	311	0.996	0.002	Forest	0.085	-0.027	-0.075
<i>Sitta europea</i>	267	1.013	0.004	Forest	0.521	0.167	-0.432
<i>Certhia familiaris</i>	192	1.004	0.008	Forest	0.066	0.849	-0.628
<i>Certhia brachydactyla</i>	121	0.996	0.008	Forest	1.323	-0.489	-0.529
<i>Oriolus oriolus</i>	173	1.021	0.005	Forest	0.572	-0.422	0.107
<i>Lanius collurio</i>	217	1.031	0.007	Farmland	-0.145	-0.489	0.9
<i>Garrulus glandarius</i>	282	1.035	0.005	Forest	-0.064	0.388	-0.192
<i>Pica pica</i>	181	1.017	0.008	Farmland	-0.419	-0.52	0.397
<i>Corvus corone</i>	207	0.975	0.006	Farmland	-0.204	-0.47	0.657
<i>Sturnus vulgaris</i>	280	1.024	0.005	Forest	0.44	-0.443	-0.03

Table 1 continued

Species	Transects ^a	Trend ^b	SE	Habitat ^c	Lowforest ^d	Monforest ^d	Farmland ^d
<i>Passer montanus</i>	202	0.991	0.006	Farmland	0.065	−0.516	0.424
<i>Fringilla coelebs</i>	315	0.989	0.002	Forest	−0.001	0.313	−0.156
<i>Carduelis spinus</i>	119	0.942	0.015	Forest	−0.457	0.794	0.005
<i>Carduelis flammea</i>	37	0.961	0.015	Forest	−0.493	−0.07	0.53
<i>Loxia curvirostra</i>	93	0.96	0.016	Forest	−0.492	1.2	−0.323
<i>Pyrrhula pyrrhula</i>	157	0.971	0.009	Forest	−0.492	1.126	−0.063
<i>C. coccythraustes</i>	188	0.984	0.032	Forest	0.26	0.176	−0.198
<i>Emberiza citrinella</i>	301	0.985	0.002	Farmland	0.028	−0.3	0.404

^a Number of transects where birds were censused for population trend estimation

^b Trends with standard errors (S.E.) extracted from Reif et al. (2006)

^c A priori categorical habitat association according to Reif et al. (2006)

^d Species score at the habitat gradient revealed by the bird census at the 400 km long transect. The higher score, the tighter the association with respective habitats. Lowforest, lowland broad-leaved forest; Monforest, coniferous and montane forest; Farmland, farmland

Bird-habitat associations

For the assessment of bird-habitat associations we used data from a 400 km linear transect of 768 census points going across the whole Czech Republic. Census points were located regularly along the transect and separated by a distance ca 500 m. All birds were counted by J.R. and D.S. using the point count method (Bibby et al. 2000) within a distance limited by 150 m around each point. Birds were counted during five early morning visits in the breeding season (April–June), each visit lasting 5 min at each census point. Only maximum recorded numbers of individuals of every species from the five visits were then taken for every point to improve accuracy (see Storch et al. 2002). We highlighted the breeding activity of recorded individuals in the point abundance calculation by treating an individual showing breeding behaviour (a singing male in most cases) as one breeding pair and an individual not showing breeding behaviour as a half of a breeding pair (Janda and Repa 1986). Abundance of a species at a census point was thus expressed as a sum of breeding pairs rounded to the nearest integer.

We mapped habitat composition within a distance of 150 m around each census point recognizing 10 habitats: beech forest, mixed beech and spruce forest, mixed oak and pine forest, lowland broad-leaved forest, coniferous forest, forest clearing, field and meadow, shrubland, urban habitat and wetland. Relative areas of these habitats at particular census points were used as explanatory variables in the analysis of bird-habitat associations. Both bird and habitat data were collected in 2004 at points 1–512 and in 2005 at points 513–768.

We used canonical correspondence analysis (CCA) to relate the data on bird abundances at the points to environmental variables. CCA is a multivariate direct gradient analysis technique able to detect the patterns of variation in bird community composition that can be explained by the set of environmental variables (Lepš and Šmilauer 2003). CCA ordines the samples (census points) and the variables (bird species and habitats) along axes such that each ordination axis represents an environmental gradient along which the centroids of individual variables and samples are distributed so as to maximize differences between them (Storch et al. 2002). CCA is based on the assumption that species distribution is unimodal along environmental gradients. The score of a given species is proportional to the mean of sample scores weighted by the species abundance, and indicates the centre of the distribution of the species.

We ordinated all bird species using all 10 environmental variables by the detrended form of CCA (DCCA; detrended by the second order polynomial to factor out the arch

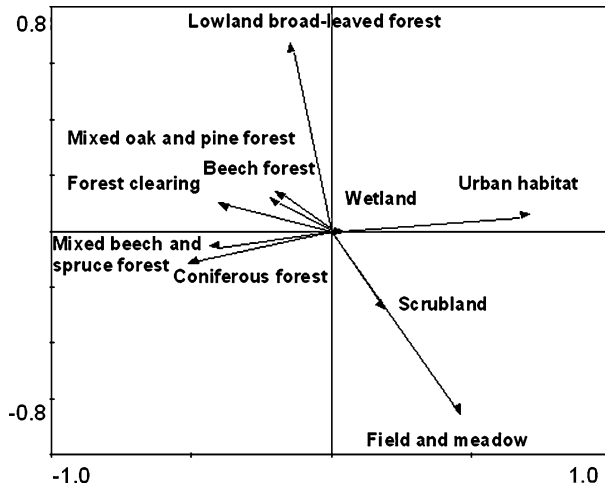


Fig. 1 Positions of particular habitat vectors on the first two canonical axes (detrended canonical correspondence analysis, DCCA) expressing the two most important environmental gradients within the bird assemblage censused along 400 km long transect throughout the Czech Republic

effect in the data, see Lepš and Šmilauer 2003). We found the most important habitat gradients in the bird community structure expressed as the first two ordination axes (Fig. 1) explaining 17.2% of all variability in bird species data and 60.0% of variability represented by the environmental variables. We created three new independent habitat variables corresponding with the first two DCCA axes: (i) montane and coniferous forest consisting of beech forest, mixed beech and spruce forest, mixed oak and pine forest, coniferous forest and forest clearing (negative part of the first axis); (ii) lowland broad-leaved forest (positive part of the second axis); (iii) farmland consisting from fields, meadows and the shrubland (negative part of the second axis). Using these new variables reduces the overall complexity of habitat associations in the studied bird community without loss of the most relevant information about habitat requirements of particular species. Despite its importance for species ordination (Fig. 1), we did not include urban habitat (i.e. the positive part of the first axis) into the analyses, as they were focused only on farmland and forest species.

In the next step, we performed separate CCAs with each of these three new habitat variables as the sole explanatory variable. The association of each species with each of these three habitats was expressed as its score along the first canonical axis in respective analysis. Five forest species (Redstart *Phoenicurus phoenicurus*, Pied Flycatcher *Ficedula hypoleuca*, Fieldfare *Turdus pilaris*, Garden Warbler *Sylvia borin* and Redpoll *Carduelis flammea*) showed negative associations with both forest types. This was probably caused by their partial association with gardens and orchards. We thus decided to exclude these five species from the analyses dealing with bird-habitat associations, as the two new habitat variables did not capture their habitat preferences precisely.

Data analysis

We divided all 62 forest and farmland species into two groups used in Reif et al. (2006) based on their habitats requirements described in local literature (Hudec 1983, Hudec and Štašný 2005): farmland birds ($n = 19$) and forest birds ($n = 43$). This arbitrary classification was

necessary as multivariate analysis provides continuous gradients in species-habitat associations and, it is thus difficult to determine such a crude category of habitat use for each species.

We compared average population trends between these groups using Mann–Whitney U -test. In the next step, we focused on the analysis of trends within each group. We defined the habitat association of each species within each group using its CCA score along the first axis from the separate CCAs mentioned above. Thus, scores at the axis determined by montane and coniferous forests and the lowland broad-leaved forest, respectively, characterized forest species, whereas farmland birds were characterized by their scores at the axis determined by farmland. We related population trends to these species-habitat associations using the least squares linear and non-linear regressions (when appropriate) within each species group. There were eight species with positive associations to both farmland and forest habitats (Table 1). We moved these species between a priori defined species groups to reveal whether their classification affect results of the abovementioned analyses and we found that their classification did not have any effects on test performance (results not shown).

Results

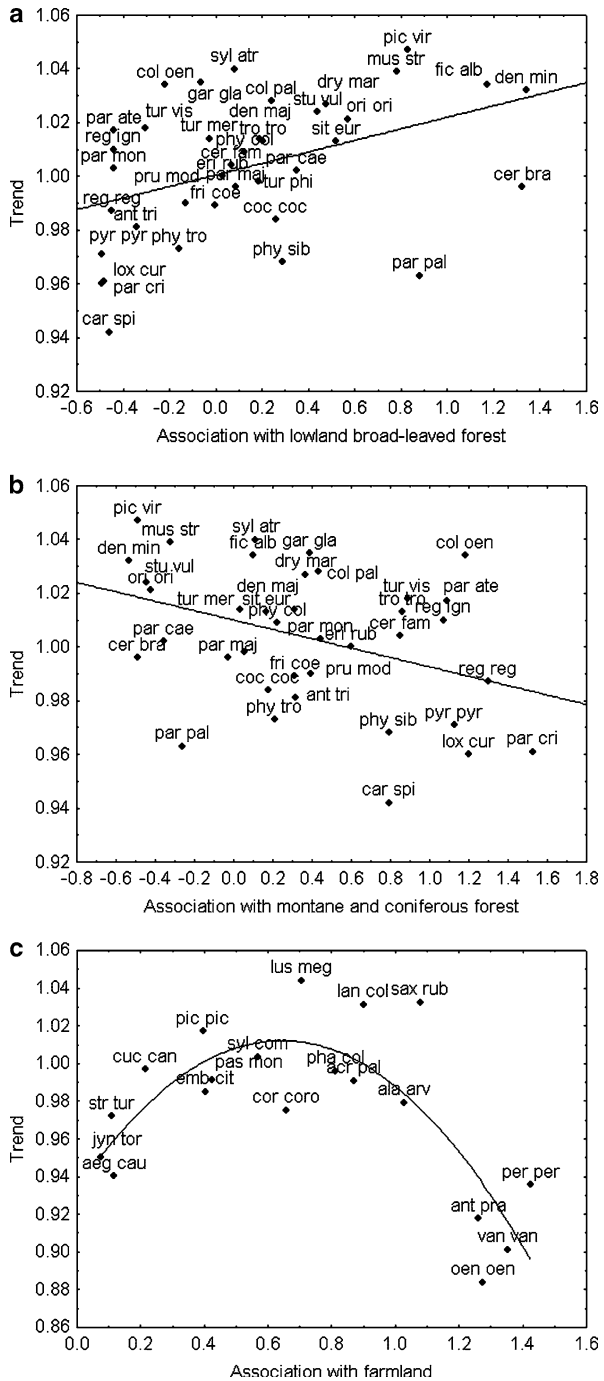
Habitat gradients expressed by CCA scores were intuitive and agreed with habitat requirements of Czech birds described in local literature (Table 1). For instance, Grey Partridge *Perdix perdix*, Northern Wheatear *Oenanthe oenanthe* and Lapwing *Vanellus vanellus* were the species most closely associated with farmland; Crested Tit *Parus ater*, Goldcrest *Regulus regulus* and Common Crossbill *Loxia curvirostra* were the species the most closely associated with coniferous and montane forest; Collared Flycatcher *Ficedula albicollis*, Short-toed Treecreeper *Certhia brachydactyla* and Lesser-spotted Woodpecker *Dendrocopos minor* were the species most closely associated with lowland broad-leaved forest. Forest and farmland birds differed in their associations with forest and farmland habitats, respectively. Although all farmland species had positive association to farmland, many forest species expressed negative associations with one of the forest habitats (Table 1). The majority of species with a negative association to one forest type showed a positive association to the other forest type. These species thus lie on the opposite sites of the gradient “from lowland broad-leaved forest to montane and coniferous forest”.

Comparison of mean population trends between our pre-defined species groups revealed that forest birds had significantly higher population trends than farmland birds (Mann–Whitney U -test: $Z_{1,60} = -2.34$, $P = 0.019$). Analyses which used species CCA scores along respective habitat-determined axes revealed further relationships between trends and habitats (Fig. 2). Among forest birds, the species which were more closely associated with lowland broad-leaved forest revealed more positive population trends ($r = 0.42$, $n = 38$, $P = 0.008$; Fig. 2a). On the contrary, the association with montane and coniferous forest was negatively correlated with population trend ($r = -0.38$, $n = 38$, $P = 0.018$; Fig. 2b). Among farmland species, the relationship between association with farmland habitat and population trend was non-linear and hump-shaped ($r = 0.79$, $t_{18} = 148.28$, $P < 0.001$; Fig. 2c). However, species with the highest CCA scores had the lowest population trends (Fig. 2c).

Discussion

Our analyses focused on more-detailed exploration of relationships between bird-habitat associations and population trends, and revealed several undescribed patterns, although the

Fig. 2 Relationships between population trends and habitat associations of particular species within pre-defined species groups of Czech birds (forest birds in (a) and (b), and farmland birds in (c)). Habitat associations are expressed as species scores along the first CCA axis represented by lowland broad-leaved forest (a), montane and coniferous forest (b) and farmland (c), respectively



results in general concur with findings of other studies from various European and North American regions describing recent changes of bird populations (e.g. Peterjohn and Sauer 1994; Donald et al. 2006). We found that forest birds, which are increasing in the Czech

Republic (Reif et al. 2007) as well as in some other parts of Europe (e.g. Spain (De Juana 2004), Germany (Flade and Schwarz 2004) or some of new EU-countries (Gregory et al. 2007)), reveal contrasting population trends depending on their habitat preferences. Species more closely associated with lowland broad-leaved forest had on average more positive population trends, whereas species more closely associated with coniferous forest had on average more negative population trends. Within farmland birds there was a hump-shaped relationship between population trend and species association with farmland habitat, partially reflecting severe decline of most typical farmland bird species (e.g. Partridge *Perdix perdix*, Lapwing *Vanellus vanellus* or Northern Wheatear *Oenanthe oenanthe*), which was found throughout Europe (Donald et al. 2001; Gregory et al. 2005; Wretenberg et al. 2006). However, the species expressing a weak association with farmland habitats (e.g. Wryneck *Jynx torquilla*, Turtle Dove *Streptopelia turtur* and Long-tailed Tit *Aegithalos caudatus*) revealed population decline of almost similar magnitude. We argue that the relationships detected within focal groups of species differing in habitat requirements can be easily explained by long-term changes in land cover. In this respect, we recognise three most important events that took place in the Czech landscape during last decades.

First, tree species composition of Czech forests changed over the last 35 years. The area of deciduous trees increased by 20% between 1970 and 2004 from 500,000 ha to more than 600,000 ha (Anonymous 2005). At the same time, the area of coniferous forests decreased and these opposite changes often took place in the same forest plots (Anonymous 2005). Therefore, we can say that coniferous forests were replaced by deciduous ones and such a process could have been the most important cause of detected trends of various forest bird species. Moreover, the Czech forests act (effective from 1977) states that each forest plot must host some proportion of soil-firming and meliorating wood (in fact deciduous trees) even in coniferous plantations. Such scattered trees could support populations of some species originally dependent on deciduous forests such as Nuthatch *Sitta europea* or Blue Tit *Parus caeruleus*, even within coniferous forests. This type of forest management could therefore contribute to the population increase of species associated with deciduous forests. Marked changes in forest structure resulted also from the destruction of coniferous trees by acid rain, which took place mainly during 1980s in large areas in northern part of the Czech Republic (Führer 1990). The damaged areas were then colonized by deciduous tree species and such changes in vegetation composition were subsequently tracked by changes in bird community structure (Štátný and Bejček 1985; Flousek 1989).

Second, the total forested area increased over the last 40 years as a result of managed afforestation, as given in official statistics, but also as a result of spontaneous succession in unmanaged grasslands and fields. Large areas of cultivation were abandoned in various regions of the Czech Republic in mid-elevations since World War II (Lipský 1995). Secondary succession recruits mostly from deciduous trees and bushes in such areas as these species form local potential vegetation cover (Prach et al. 2001). In a more general sense, we can speculate about a recent recovery of the Czech landscape to its more natural state. Such a process also reflected by population increases of forest species living in deciduous habitats and in population declines of species living in coniferous forests. Moreover, abandoned fields overgrown by grass with scattered shrubs prevented breeding of species most tightly associated with farmland. At the same time, resulting scrubland can be occupied by species such as Red-backed Shrike *Lanius collurio*, Nightingale *Luscinia megarhynchos* or Whinchat *Saxicola rubetra*, i.e. species with intermediate association with farmland habitat, which revealed most positive population trends within farmland birds. In contrast, species most closely associated with farmland habitat (e.g. Lapwing *Vanellus vanellus* or Partridge *Perdix perdix*) can suffer not only from the reduction of the total area of arable

land, but also from agricultural intensification on remaining areas (Chamberlain et al. 2000; Báldi and Faragó 2007), and both factors can contribute to their strong negative population trends.

Third, during the 20th century the age structure of Czech forests has changed towards the prevalence of older cohorts (Anonymous 2005), and moreover, forest pastoralism as well as other traditional types of management which maintained forests with sparse trees and dense undergrowth (Martin and McIntyre 2007) has disappeared (Konvička et al. 2004). The enlargement of the area of dense forest with closed tree canopy during the last 80 years in the Czech Republic probably resulted in the decline of species associated with open forests (see Šťastný et al. 2006). Our analyses recognized such species as farmland birds with the lowest association with farmland habitat, which revealed population declines of almost similar magnitude to the true farmland species.

Although the patterns in bird population trends are consistent with long-term land use changes in the Czech Republic, there could be additional forces driving bird population changes which were not taken into account in our analysis. For example, populations of species that overwinter in non-breeding grounds could be seriously affected by conditions along their migratory routes or in winter area (Holmes 2007). Therefore, their population changes need not be connected with habitat changes on breeding grounds (Newton 2004b). However, several analyses using different subsets of Czech bird fauna (Reif et al. 2006, 2007, 2008) did not reveal migratory strategy as a significant predictor of bird population trends.

Finally, we should note that our analysis needs to be treated with some caution because sampling design of the annual monitoring scheme used for the calculation of population trends is based on the free choice of census sites. This could potentially produce biased data in some species due to preferential sampling of better habitats (Bibby et al. 2000) in which population changes could differ from the average changes. However, we do not think that this would affect the conclusions of our study. In fact, our comparison of population changes of the same species calculated on the basis of two independent data sets (the annual monitoring scheme and population size estimates based on atlas mapping) showed consistent patterns in the majority of species used for analysis in this paper (Reif et al. unpublished results).

In conclusion, we found that population trends reflect the strength of habitat associations in Czech forest and farmland birds, and the relationship between habitat associations of different species and their population trends makes very good sense in the light of our knowledge of land cover changes during recent decades. It is therefore possible that land cover changes represent the driver of long-term bird population trends which is at least as important as climate change (Lemoine et al. 2007; Seoane and Carrascal 2008). We think that the application of our technique in more comprehensive data sets could produce interesting insights as to the role of habitat selection in bird population dynamics. For instance, such an approach could be used for testing the hypothesis that habitat shifts, which are common across species ranges, are responsible for the trends differing in the same species in different regions of Europe.

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Appendix: List of abbreviations of scientific species names used in Fig. 2

per per, *Perdix perdix*; pha col, *Phasianus colchicus*; van van, *Vanellus vanellus*; col oen, *Columba oenas*; col pal, *Columba palumbus*; str tur, *Streptopelia turtur*; cuc can, *Cuculus canorus*; jyn tor, *Jynx torquilla*; pic vir, *Picus viridis*; dry mar, *Dryocopus martius*; den maj, *Dendrocopos major*; den min, *Dendrocopos minor*; ala arv, *Alauda arvensis*; ant tri, *Anthus trivialis*; ant pra, *Anthus pratensis*; tro tro, *Troglodytes troglodytes*; pru mod, *Prunella modularis*; eri rub, *Erithacus rubecula*; lus meg, *Luscinia megarhynchos*; sax rub, *Saxicola rubetra*; oen oen, *Oenanthe oenanthe*; tur mer, *Turdus merula*; tur phi, *Turdus philomelos*; tur vis, *Turdus viscivorus*; acr pal, *Acrocephalus palustris*; syl com, *Sylvia communis*; syl atr, *Sylvia atricapilla*; phy sib, *Phylloscopus sibilatrix*; phy col, *Phylloscopus collybita*; phy tro, *Phylloscopus trochilus*; reg reg, *Regulus regulus*; reg ign, *Regulus ignicapillus*; mus str, *Muscicapa striata*; fic alb, *Ficedula albicollis*; aeg cau, *Aegithalos caudatus*; par pal, *Parus palustris*; par mon, *Parus montanus*; par cri, *Parus cristatus*; par ate, *Parus ater*; par cae, *Parus caeruleus*; par maj, *Parus major*; sit eur, *Sitta europea*; cer fam, *Certhia familiaris*; cer bra, *Certhia brachydactyla*; ori ori, *Oriolus oriolus*; lan col, *Lanius collurio*; gar gla, *Garrulus glandarius*; pic pic, *Pica pica*; cor coro, *Corvus corone*; stu vul, *Sturnus vulgaris*; pas mon, *Passer montanus*; fri coe, *Fringilla coelebs*; car spi, *Carduelis spinus*; lox cur, *Loxia curvirostra*; pyr pyr, *Pyrrhula pyrrhula*; coc coc, *Coccothraustes coccothraustes*; emb cit, *Emberiza citrinella*.

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