Agriculture, Ecosystems and Environment 182 (2014) 37–46

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Effects of landscape, land use and vegetation on bird community composition and diversity in Inner Anatolian steppes

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ARTICLE INFO

Article history:
Received 3 August 2012
Received in revised form 6 November 2013
Accepted 7 November 2013
Available online 7 December 2013

Keywords:
Grassland birds
Agricultural landscape
Grazing
Land abandonment
Multivariate analysis
Turkey

ABSTRACT

We present here the first systematic study on drivers of bird community composition and diversity in Anatolian steppes (Turkey), an environment important for populations of threatened grassland birds yet underrepresented in conservation networks. We focused on one million hectares of mountainous land with a long and varied land use history, and collected quantitative data on breeding birds as well as environmental, vegetation, landscape and land use parameters at 32 sites. Data were analyzed by canonical correspondence analysis (CCA) and hierarchical partitioning to understand avian community structure and reveal major drivers of observed patterns. Bird communities in high-altitude steppes of inner Turkey showed patterns in species richness and community composition that were best explained by an altitudinal gradient and by human activities. Steppe birds occurred most often in cropland abandoned 20–50 years ago with good coverage of erect leafy plants while overall avian diversity tended to increase with reduced grazing pressure and with nearby presence of rural settlements. CCA results revealed a contrast between highly heterogeneous anthropogenic environments in warmer and drier land with woody elements, and treeless steppes at higher elevations that were, apart from transhumant grazing, little influenced by human activities. The former sites were characterized by the occurrence of several grassland birds along with a variety of generalist species, some of which required the presence of trees, while the latter sites were less diverse but usually with a higher proportion of steppe-dependent birds in their composition. To conserve steppes for birds, we recommend as key actions to maintain the current landscape mosaic, sustain low to moderate grazing levels and use our findings in developing a network of protected areas.

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1. Introduction

Birds of open landscapes such as grasslands, farmlands and steppic areas have declined more than other species in Europe in the last few decades (BirdLife International, 2013). Such declines are widely believed to be driven by agricultural intensification and the subsequent deterioration of habitats (Donald et al., 2001) as well as by the progressive abandonment of marginal agricultural land (Sirami et al., 2008).

Bird diversity and community composition respond strongly to productivity and its environmental drivers such as altitude and temperature at large scales (Böhning-Gaese, 1997; Waide et al., 1999). For birds of open landscapes, it has been shown that vegetation structure (Donald et al., 2001; McCracken and Tallowin, 2004; Suárez-Seoane et al., 2002), heterogeneity at habitat and landscape levels (Benton et al., 2003) and human activities such as agricultural management and grazing intensity (Atkinson et al., 2005; Batáry et al., 2007) are important drivers of species diversity and abundance.

Steppes in Turkey, represented by natural or semi-natural dry grasslands, cover an estimated 28 million hectares, which correspond to 35% of the country's territory (Kün et al., 1995). These plant species-rich communities have been maintained in a semi-natural state for centuries through grazing by domestic animals, repeated conversions to cropland and abandonment, and other management practices (Çetik, 1985). Destruction of grasslands by ploughing and degradation by excessive grazing are well-recognized threats to the ecosystem (Peart, 2008). They were experienced to an extreme between 1950 and 1980 in Turkey as a consequence of the national agricultural policies of that period (Kazgan, 2003). Accelerating emigration of the rural population since the 1950s (Akgündüz, 2008) and an increased competition from global markets (Kazgan, 2003) resulted in abandonment of marginal lands and a decline in grazing levels.

The consequences of land abandonment and changes in agricultural land management on birds are well documented in Europe (MacDonald et al., 2000; Sirami et al., 2008). However, despite the

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http://dx.doi.org/10.1016/j.agee.2013.11.006

fact that Turkey houses important populations of European and southwest Asian steppe species (Burfield, 2005), the impact of such changes is hardly known in Turkey. Many native steppe-dependent species such as great bustard (*Otis tarda*), little bustard (*Tetrax tetrax*), pallid harrier (*Circus macrourus*), saker falcon (*Falco cherrug*), and lesser kestrel (*Falco naumanni*) are species of European concern (SPEC-1) (BirdLife International, 2004). Although the conservation of Anatolian steppes is vital to achieve continental-scale conservation success, there is not yet a single protected area designated and managed specially for steppe conservation (Şekercioğlu et al., 2011).

Here we attempt to explain steppe avian diversity at a regional scale by focusing on environmental, vegetation, landscape and land use determinants of bird diversity and composition. We chose birds as target taxonomic group since they are good general indicators for wildlife (Gregory et al., 2008) and provide useful information about trends in land use change in agricultural landscapes (Donald et al., 2001). Specifically, we address the following questions: (1) What are the drivers of bird community composition and diversity in Anatolian steppes? (2) Is there a major effect of land use change on bird community composition and diversity during the past 50 years? (3) Are vegetation parameters known to be important for grassland bird community composition and diversity in other regions also valid for Inner Anatolian steppes? The answers can both fill an important information gap and provide baseline information for conservation of birds living in steppes of Turkey.

2. Materials and methods

2.1. Study area

The study area is a 1,062,554 ha mountainous land located on the transition between Central and East Anatolia in Turkey (38°20′–39°40′ N, 36°50′–38°40′ E), covering parts of Sivas and Malatya provinces (Appendix S1). The altitude of the rugged terrain varies from 850 m a.s.l. in river valleys to 2800 m a.s.l. on the mountain tops. The study area is characterized by cold, snowy winters and warm, dry summers (annual mean temperature 3.7–13.3 °C, annual mean precipitation 409–671 mm; based on Hijmans et al., 2005. The climate is classified as Semihumid Continental (İyigun et al., 2013).

The natural vegetation of the study area has been classified as forest-steppe, indicating the assumed naturalness of at least some of the steppes (Noirfalise, 1987; Zohary, 1973). However, other studies consider the steppes of the study area as secondary vegetation, originating from former woodlands composed of *Quercus*, *Juniperus*, *Pyrus*, *Crataegus* and *Amygdalus* species (Louis, 1939; Walter, 1956). Today, the land cover mainly consists of steppes, mostly on the slopes (49%); croplands of mostly cereal, apricot or legume cultivation on the plains (26%); woodlands of *Quercus* spp., *Juniperus* spp. and *Pinus sylvestris* with patchy distribution on uplands (9%); and sparsely vegetated, steep slopes (15%) (Kınıkoğlu, 2008).

Four district centers and 409 villages, each with less than 100 people, are inhabited by 151,767 people in total (İLEMOD, 2007). The main source of income is agriculture with a 67% share (TÜİK, 2012). About 30,000 cattle and 150,000 sheep and goats graze the region (İLEMOD, 2007) although these numbers were much higher before rural emigration started (TÜİK, 2012). Following emigration, over the last 20–60 years, the amount of cultivated land declined sharply and continues to do so. Similarly, livestock densities have decreased: the highest-known past livestock densities for sites ranged from 400 to 5357 dry sheep or equivalent (mostly sheep and various races of cattle) per 1000 ha, but have declined by 40–100% in most areas.

2.2. Data collection

2.2.1. Survey design

We adopted a cost-effective method for survey design, i.e. gradsect sampling, ending up with 32 environmentally different sites sampled for birds as well as variables related to abiotic environment, vegetation, landscape and land use (Gillison and Brewer, 1985). Gradsect sampling is similar to stratified sampling but fewer geographic transects, i.e. gradsects, are drawn across the main landscape gradients for surveying to increase cost-effectiveness (Hirzel and Guisan, 2002).

To determine the survey points, we first stratified the study area based on the environmental factors that we knew to be influential in vegetation, species distribution and land use, i.e. aridity, soil type, soil depth and geology (Böhning-Gaese, 1997; Gellrich and Zimmermann, 2007; Hamzaoğlu, 2006). We used Thornthwaite precipitation effectiveness index (Thornthwaite, 1931) calculated from relevant WORLDCLIM maps, which incorporate altitude in the models (Hijmans et al., 2005), and divided it into six aridity classes. We obtained relevant soil and geology maps from the Department of Geological Engineering of Middle East Technical University. We used five major soil types, three soil depth classes and three bedrock types; then intersected these layers to obtain ecosections, i.e. environmentally different sub-areas (Appendix S1). The resulting 58 ecosections were overlaid with the map of the steppes, and those 34 ecosections selected included at least 500 ha of steppes. We identified that two diagonals drawn across the study area represent two main gradients along which different ecosections were concentrated within short distances. We targeted to sample one site in each ecosection along the gradients but finally used only 32 of them as two were not accessible. We selected sites to be surveyed randomly within homogeneous polygons identified from satellite images for each ecosection. At each survey site, we sampled two replicates with more than 90% herbaceous coverage and separated by at least 200 m from each other.

2.2.2. Bird surveys

Bird surveys took place once on each replicate, during the breeding season, in early June 2009. We used point counts as they are commonly used for estimates of bird abundance or community composition, and for compiling useful data on bird-habitat relationships (Bonthoux and Balent, 2011). With a fixed-radius point count approach, adult birds were recorded within two distance bands (within and outside 50-m radius around replicate center point), separately in the first five and the following three minutes. Two experienced birdwatchers stood at the replicate centers, waited for birds to settle then started surveying at the same time. They identified birds visually or based on vocalizations, took additional notes about habitat use, signs of breeding, age of birds, and flyovers. We followed BirdLife Checklist Version 5.1 for bird taxonomy and nomenclature (BirdLife International, 2012).

2.2.3. Vegetation parameters

We collected vegetation data within the same 50-m radius around each replicate center point. We set 10 random quadrats of 2 m × 2 m dimensions. In each quadrat, we recorded percent cover of plant species with more than 10% coverage, considered to characterize vegetation structure and land cover best. We classified plant species into eight growth forms as short basal, semi-basal, long basal, erect leafy, cushions, tussocks, dwarf shrubs and shrubs (Cornelissen et al., 2003), and percent coverage of each growth form was used as a parameter. For vegetation structure, we recorded herbaceous vegetation cover, herbaceous vegetation height and shrub density. Since coverage and height varied much at some sites,

we preferred not to use the mean value but averages for minimum and maximum, determined visually.

We used normalized difference vegetation index (NDVI) since it is a good indicator of primary production and amount of available food for birds (Hurlbert, 2004). NDVI values were extracted from the 23 June 2009 cloud-free Landsat 174/033 image.

We observed small scale and patchy variation of vegetation due to topographical, land use or water table differences. This resulted in local heterogeneity at the site level, such as presence of small, recently abandoned fields in flat land or hydrophilic vegetation at a small patch with high water table. To indicate such patterns in our dataset, we introduced the binary parameter of local heterogeneity.

2.2.4. Other environmental parameters

Several environmental and landscape variables were either recorded in the field or calculated using remote sensing and geographical information systems. We recorded altitude in the field using a GPS device. Climate data of the survey points were derived from BIOCLIM layers (Hijmans et al., 2005). We used annual data obtained from mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation of driest quarter, which are claimed to be effective in predicting distribution of species (Hijmans and Graham, 2006). We combined altitude and correlated climatic variables in a single score using principal component analysis. We used slope (in degrees) as a parameter determining land use and land abandonment (Gellrich and Zimmermann, 2007; Mottet et al., 2006). Large rocks, which can affect bird community composition by providing nesting sites, or high stone cover on the ground were recorded and included as a binary variable.

We gathered land use data through semi-structured interviews similar to the approach of Mottet et al. (2006) for lack of available governmental resources, maps or remote sensing images of high resolution on current and historical agricultural activities at the site level. We designed the questionnaire with a mix of open- and close-ended questions. We conducted the interviews in the villages closest to survey sites with a knowledgeable person, usually a village elder or the *muhtar* (official village head). We interviewed 35 people in total and directed 27 questions about the history of the site, and the type and extent of land use. We organized data into a categorical variable for past agricultural production (no production, only cereal, cereal and legume cultivation) and three continuous variables indicating past and current livestock densities and years since cultivation abandonment (years since last ploughing). The last variable was difficult to express numerically since not all sites were ploughed in the documented past. Such sites were categorically indicated as non-ploughed. For years since abandonment, non-ploughed sites were coded as "300 years" because villagers did not remember the land use history older than 100 years, and we assume a three-century-period to be long enough for natural vegetation to fully recover in previously ploughed areas.

We used three different types of landscape variables: Landscape diversity within a radius of 2 km around each replicate, the proportion of different land cover types (grassland, cropland, woodland and settlement) in the same area, and the distances of survey sites to those habitat types, trees and water sources. Woodland patches larger than 3 ha were targeted. Flowing or standing water that supported hygrophilous vegetation were accepted as water sources. We calculated proportions and distances using CORINE Land Cover map (European Environment Agency, 2011), Google Earth and GIS tools. We obtained landscape diversity measure by the use of Shannon's diversity index (Hill, 1973) as $-\sum p_i \ln p_i$, where p_i is the proportion of each different land cover type. Additionally, we used proportions of each category as separate parameters in the analyses.

2.3. Analyses

Twelve bird species, including warblers in reedbeds heard from a distance, raptors which cover long distances for foraging, aerial species such as swifts and martins, or owls difficult to detect due to nocturnal habit were eliminated from the dataset to focus only on species related to the surveyed grassland patches and neighboring habitats. We conducted the analyses using records from within the 50-m radius as well as from the 50–100 m belt provided they were associated with grassland habitats. We included flyovers of species associated with the surveyed habitat. Analysis on bird community composition, richness and factors affecting them were performed at site level so the records of two replicates were combined and averages of two replicates were used for explanatory variables.

To address the relationship between explanatory variables and birds that depend on steppe habitats to survive, we evaluated bird species in the survey list based on their adaptations to steppe habitats. Cryptic coloration, ground nesting and reported habitat in Turkey were used as criteria. Accordingly, the birds were classified in four classes: (1) species not associated with steppes, (2) generalist species, (3) species with preference for steppic habitats or those that need specific features like rocks in steppes and (4) steppe-dependent species, absent from other habitats. We used this classification in the interpretation of CCA ordination. In addition we did hierarchical partitioning analysis using richness of steppe-dependent species as a dependent variable.

To check whether there is any relationship between the variables, nonparametric Spearman rank correlation was used since the data were not normally distributed and relationships may not be linear. We accepted results as significant at a Type-I error rate of 0.05 for all tests for significance.

We measured richness as the number of bird species observed. We calculated alpha diversity by the use of Shannon's index (Hill, 1973). We used canonical correspondence analysis (CCA) to find out the most important factors for explaining variance in species composition (Ter Braak, 1986). We used records of bird species observed at least three times during standard surveys in CCA. Due to the small number of samples, a high number of explanatory variables and multicollinearity among explanatory variables, we used partial CCA (pCCA) (Økland and Eilertsen, 1994). In order to determine the relative effect of each group of variables in turn, and to separate their effects, we introduced covariates for each explanatory variable or variable set (Table 2). Forward selection and Monte-Carlo permutation test with 1000 permutations were used to find out which variables in each group contributed significantly to explain data variance. The proportion of explained variance by each set was found by the ratio of sum of all canonical eigenvalues to total inertia similar to Wellstein et al. (2007).

To understand major factors affecting richness and diversity we used the hierarchical partitioning method of Chevan and Sutherland (1991). It is based on building all possible regression models with N independent variables to explain one dependent variable, calculating goodness-of-fit measures for the entire models, and then applying hierarchical partitioning algorithm to find out independent (I) and conjoint (J) contributions of each variable to explained variance. The advantage of this method is to provide the relative importance of variables independently and the ability to overcome multicollinearity that may cause failures in regression analyses (Mac Nally, 2000). We applied generalized linear model (GLM), used root-mean-square as goodness-of-fit measure and did randomization (300 repeated randomizations) to test the significance of the results (Walsh and Mac Nally, 2004). We tested the normality of residuals assumption of GLM with the Shapiro–Wilk test (Shapiro and Wilk, 1965). We applied hierarchical partitioning to total species richness and richness of steppe-dependent

Table 1
Summary of environmental, landscape, vegetation and land use data collected for the survey sites. NA indicates "not applicable".

Environmental parameters (abbreviations)	Data type (unit)	Mean	S.D.	Transformation used	Data Source
Abiotic parameters					
Altitude and correlated climatic factors (Alt)	score	NA	NA	–	Principal component analysis of GPS and WORLDCLIM data
Slope	Numerical (degrees)	18	10	–	Field observation
Presence of large rocks or high stone cover (ROCK)	Binary	NA	NA	–	Field observation
Vegetation parameters					
Average minimum of herbaceous coverage (Cmin)	Numerical (%)	35	14	–	Field observation
Average maximum of herbaceous coverage (Cmax)	Numerical (%)	76	12	–	Field observation
Average minimum of herbaceous vegetation height (Hmin)	Numerical (cm)	20	4	–	Field observation
Average maximum of herbaceous vegetation height (Hmax)	Numerical (cm)	51	12	–	Field observation
Shrub density (SHBD)	Numerical	4	6	Fourth root	Plot data
Productivity (NDVI)	Numerical index	0.34	0.05	–	NDVI values of Landsat image
Local heterogeneity (HET)	Binary	NA	NA	–	Field observation
Plant growth forms (PGF)					
Percent cover of short basal plants (SB)	Numerical (%)	7	9	Fourth root	Plot data
Percent cover of long basal plants (LB)	Numerical (%)	1	6	–	Plot data
Percent cover of semi-basal plants (SEB)	Numerical (%)	2	5	–	Plot data
Percent cover of erect leafy plants (EL)	Numerical (%)	31	36	Square root	Plot data
Percent cover of cushion forming plants (CUS)	Numerical (%)	1	3	–	Plot data
Percent cover of tussock plants (TU)	Numerical (%)	18	16	–	Plot data
Percent cover of dwarf shrubs (DWSHB)	Numerical (%)	21	17	Square root	Plot data
Percent cover of shrubs (SHBC)	Numerical (%)	3	7	Fourth root	Plot data
Landscape features					
Landscape diversity (LandDiv)	Numerical index	0.47	0.34	Square root	CORINE map and Google Earth
Distance to nearest woodland (DWood)	Numerical (m)	1331	1762	Square root	CORINE map and Google Earth
Distance to nearest cropland (DCr)	Numerical (m)	998	1207	Log	Google Earth
Distance to nearest settlement (DSet)	Numerical (m)	1479	1118	Square root	Google Earth
Distance to nearest tree (Dtree)	Numerical (m)	425	491	Square root	Google Earth
Distance to nearest water source (Dwater)	Numerical (m)	578	561	–	Google Earth
Proportion of grasslands in the 2-km radius (PG)	Numerical (%)	79	18	–	CORINE map and Google Earth
Proportion of woodlands in the 2-km radius (PWood)	Numerical (%)	7	10	Angular	CORINE map and Google Earth
Proportion of croplands in the 2-km radius (PCr)	Numerical (%)	12	15	–	CORINE map and Google Earth
Proportion of total settlement area in the 2-km radius (PSet)	Numerical (%)	2	9	–	CORINE map and Google Earth
Land use					
Past livestock density (GrP)	Numerical (dry sheep equivalent)	7723	4490	Fourth root	Semi-structured interviews
Current livestock density (GrN)	Numerical (dry sheep equivalent)	914	1332	Fourth root	Semi-structured interviews
Years since abandonment for former arable fields (Ag_His)	Numerical (categorical for some analyses)	47	33	–	Semi-structured interviews
Only cereals cultivated in former arable fields (Crop1)	Binary	NA	NA	–	Semi-structured interviews
Cereals and legumes cultivated in former arable fields (Crop2)	Binary	NA	NA	–	Semi-structured interviews

species. We transformed highly skewed explanatory variables before the analysis (Table 1). Hierarchical partitioning does not provide information on whether the relationship is positive or negative, so we used results of the correlation analyses to interpret the results.

We used ArcMap 9.3.1 software (ESRI Inc., 1999–2009) for GIS work. We conducted principal component analysis, Spearman rank correlation and Shapiro–Wilk test with SPSS software, Release 18.0.0 (Polar Engineering and Consulting, 1993–2007). We used CANOCO for Windows Version 4.51 (Biometris, 1997–2003) for CCA and partial CCA analyses, the Hier.part package (Walsh and McNally, 2004) in R software (R Core Team, 2009) for hierarchical partitioning.

3. Results

3.1. Drivers of bird community composition

Standard surveys resulted in 334 records of 50 target species (Table 2). Of those, 115 came from within the 50-m radius and were thus presumed to be most closely associated with the specific surveyed habitat. A site with eight black-billed magpies came out to be an extreme outlier in the ordination diagram, and hence was removed, making survey sites better dispersed along the axes.

The results of CCA and pCCA revealed five parameters with significant explanatory power on the variance of bird community composition (Table 3). Most of the explanatory variables were

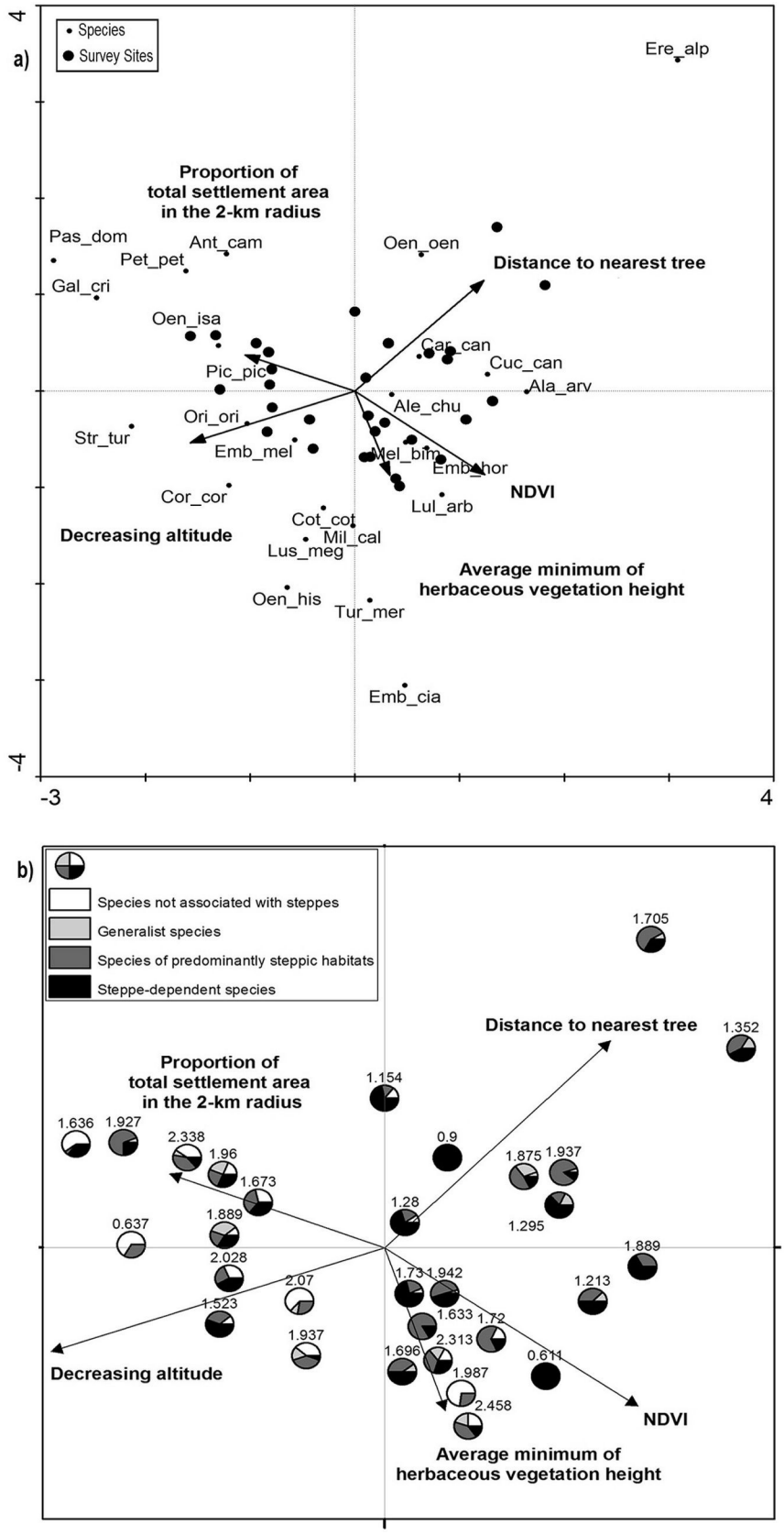

Fig. 1. Ordination space by first (horizontal) and second (vertical) axes of CCA analysis of bird data with environmental parameters with significant contribution. (a) Triplot of sites, bird species and environmental variables. See Table 2 for abbreviations of species names. (b) Biplot showing sites represented as pie charts according to abundance of bird species with different degree of steppe dependence and environmental variables. Sites are labeled with Shannon's diversity values.

aligned along the diagonals of the diagram indicating them to be important on both axes (Fig. 1, see Appendix S2 for weighted correlation matrix among axes and environmental variables of CCA). Altitude (and related climatic factors), distance to nearest tree, productivity, and proportion of total settled area in a 2-km radius had highest loadings on the first axis, describing 43% of the species–environment interaction. The positive extremity of the first axis was characterized by treeless, productive grassland at high altitudes in landscapes with no settlements, i.e. sites around 2000 m a.s.l. where the nearest tree was c. 1000 m away. Interviews with the local people revealed that the majority of the survey sites (below 2500 m) had been forested in the past (60 and more years ago). Horned lark and northern wheatear were largely associated with such sites. Eurasian skylark, Eurasian linnet, and their probable brood parasite, common cuckoo, were recorded at similar sites but also at lower altitudes and in increased proximity (i.e. 100–800 m) to trees.

At the negative end of the first axis were sites at lowest altitudes (down to 1200 m a.s.l.) where productivity was lower due to a drier climate, and where proportion of settlements and associated cropland were higher. Species such as house sparrow, crested lark, tawny pipit, and Isabelline wheatear formed a group that depended on either disturbed land for foraging or anthropogenic structures for nesting. Similar sites but with trees within 150 m were used by European turtle-dove, Eurasian golden oriole, hooded crow, and black-headed bunting.

Parameters with highest loadings on the second axis (describing 26% of the species–environment related variation) were found to be distance of the site to nearest tree and average minimum height of herbaceous vegetation. At the negative end of the second axis were sites less than 100 m away from the next tree, and where herbaceous vegetation was taller, i.e. a minimum of 20–25 cm. Such sites were shrubby steppes, where the herbaceous layer was dominated by various forbs and perennial grasses. Eurasian blackbird,

Table 2
List of bird species recorded during standard surveys. Species are listed in order of scientific name. Score indicates dependency to steppes 1: species not associated with steppes; 2: generalist species; 3: species of predominantly steppic habitats or those that need specific features like rocks in steppes and 4: steppe-dependent species, not seen in other habitats. *f*: frequency (i.e. number of occupied sites among 32 study sites), Abnd.: Abundance (i.e. total number of observed individuals across all sites).

Abbreviation	Scientific name	English name	Family	Score	*f*	Abnd.
Ala arv	*Alauda arvensis*	Eurasian skylark	Alaudidae	4	10	40
Ale chu	*Alectoris chukar*	Chukar	Phasianidae	3	5	7
Ant cam	*Anthus campestris*	Tawny pipit	Motacillidae	4	8	12
Ant spi	*Anthus spinoletta*	Water pipit	Motacillidae	3	1	1
Cal bra	*Calandrella brachydactyla*	Greater short-toed lark	Alaudidae	4	1	1
Car can	*Carduelis cannabina*	Eurasian linnet	Fringillidae	3	13	36
Car car	*Carduelis carduelis*	European goldfinch	Fringillidae	1	1	1
Cla gla	*Clamator glandarius*	Great spotted cuckoo	Cuculidae	1	1	1
Col pal	*Columba palumbus*	Common wood-pigeon	Columbidae	1	2	3
Cor cor	*Corvus cornix*	Hooded crow	Corvidae	1	8	14
Cor mon	*Corvus monedula*	Eurasian jackdaw	Corvidae	1	1	2
Cot cot	*Coturnix coturnix*	Common quail	Phasianidae	4	3	3
Cuc can	*Cuculus canorus*	Common cuckoo	Cuculidae	2	8	12
Den syr	*Dendrocopos syriacus*	Syrian woodpecker	Picidae	1	1	1
Emb cia	*Emberiza cia*	Rock bunting	Emberizidae	3	4	7
Emb cir	*Emberiza cirlus*	Cirl bunting	Emberizidae	1	1	1
Emb hor	*Emberiza hortulana*	Ortolan bunting	Emberizidae	3	15	28
Emb mel	*Emberiza melanocephala*	Black-headed bunting	Emberizidae	3	19	39
Ere alp	*Eremophila alpestris*	Horned lark	Alaudidae	3	4	10
Gal cri	*Galerida cristata*	Crested lark	Alaudidae	4	6	10
Gar gla	*Garrulus glandarius*	Eurasian jay	Corvidae	1	1	1
Lan col	*Lanius collurio*	Red-backed shrike	Laniidae	1	1	5
Lul arb	*Lullula arborea*	Wood lark	Alaudidae	3	7	11
Lus meg	*Luscinia megarhynchos*	Common nightingale	Muscicapidae	1	4	5
Mel bim	*Melanocorypha bimaculata*	Bimaculated lark	Alaudidae	4	8	17
Mel cal	*Melanocorypha calandra*	Calandra lark	Alaudidae	4	2	3
Mil cal	*Miliaria calandra*	Corn bunting	Emberizidae	4	9	16
Mon sax	*Monticola saxatilis*	Rufous-tailed rock-thrush	Muscicapidae	1	1	1
Mot fla	*Motacilla flava*	Yellow wagtail	Motacillidae	2	1	1
Oen fin	*Oenanthe finschii*	Finsch's wheatear	Muscicapidae	2	1	1
Oen his	*Oenanthe hispanica*	Black-headed wheatear	Muscicapidae	2	5	7
Oen isa	*Oenanthe isabellina*	Isabelline wheatear	Muscicapidae	4	6	9
Oen oen	*Oenanthe oenanthe*	Northern wheatear	Muscicapidae	4	13	24
Ori ori	*Oriolus oriolus*	Eurasian golden oriole	Oriolidae	1	3	3
Pas dom	*Passer domesticus*	House sparrow	Passeridae	1	4	19
Pas his	*Passer hispaniolensis*	Spanish sparrow	Passeridae	1	1	1
Per per	*Perdix perdix*	Gray partridge	Phasianidae	4	1	1
Pet bra	*Petronia brachydactyla*	Pale rock sparrow	Passeridae	3	1	2
Pet pet	*Petronia petronia*	Rock sparrow	Passeridae	3	4	11
Pho och	*Phoenicurus ochruros*	Black redstart	Muscicapidae	2	2	3
Pic pic	*Pica pica*	Black-billed magpie	Corvidae	2	5	17
Pte ori	*Pterocles orientalis*	Black-bellied sandgrouse	Pteroclididae	4	1	1
Rho san	*Rhodopechys sanguineus*	Asian crimson-winged finch	Fringillidae	3	1	2
Sit neu	*Sitta neumayer*	Western rock-nuthatch	Sittidae	1	1	4
Str tur	*Streptopelia turtur*	European turtle-dove	Columbidae	1	4	4
Stu vul	*Sturnus vulgaris*	Common starling	Sturnidae	1	2	8
Syl com	*Sylvia communis*	Common whitethroat	Sylviidae	2	1	1
Syl cur	*Sylvia curruca*	Lesser whitethroat	Sylviidae	1	2	2
Tur mer	*Turdus merula*	Eurasian blackbird	Turdidae	1	4	6
Upu epo	*Upupa epops*	Eurasian hoopoe	Upupidae	2	2	2

Table 3
Results of CCA and pCCA for bird community composition. Explanatory variables with significant explanatory power ($P < 0.05$) are indicated in bold. Eigenv., sum of all canonical eigenvalues, a measure for explanatory power of the explanatory variables; %, percentage of explained variance; *F*, *F*-ratio for the test of significance of all canonical axes (test on the trace); *P*, corresponding probability value obtained by the Monte-Carlo-permutation test (1000 permutations). Asterisks indicate significance levels: *$0.01 \leq P < 0.05$; **$0.001 \leq P < 0.01$; ***$P < 0.001$; sp and sp-env are cumulative percentage of variance explained by each CCA analysis for species data and species–environmental relationship, respectively. Codes for explanatory variables are given in Table 1.

Explanatory variables	Covariates	Eigenv.	%	*P*	*F*	sp	sp-env
Alt	–	0.337	8.2	0.001***	2.58	43	100
DWood, DSet, DCr	Alt	0.467	11.3	0.151	1.22	25	100
DTree	Alt, Ag_His, GrP, Dwood	0.312	7.6	0.009**	2.15	51	100
DWater	–	0.232	5.6	0.053	1.72	41	100
PG, PWood, PCr, **PSet,** LandDiv	Alt	0.754	18.3	0.011*	1.55	20	100
Ag_His	Alt, DSet, ROCK, Slope	0.388	9.4	0.147	1.28	42	100
GrP, GrN	DSet, NDVI	0.411	10.0	0.097	1.38	40	100
HET	–	0.173	4.2	0.192	1.27	41	100
ROCK	–	0.186	4.5	0.138	1.37	42	100
Slope	–	0.195		0.101	1.44	42	100
Hmin, Hmax	Alt, GrN	0.465	11.3	0.023*	1.56	40	100
Cmin, Cmax	Alt, GrN, ROCK	0.313	7.6	0.429	1.02	39	100
NDVI	Alt, ROCK	0.223	5.4	0.020*	1.77	42	100
SHBD	Alt, Ag_His, GrP, GrN, DWood	0.223	5.4	0.097	1.51	49	100
PFT	Alt, Ag_His, GrP, GrN	1.374	33.3	0.135	1.24	36	75
All significant factors	–	0.976	25.0	0.001	1.60	24	94

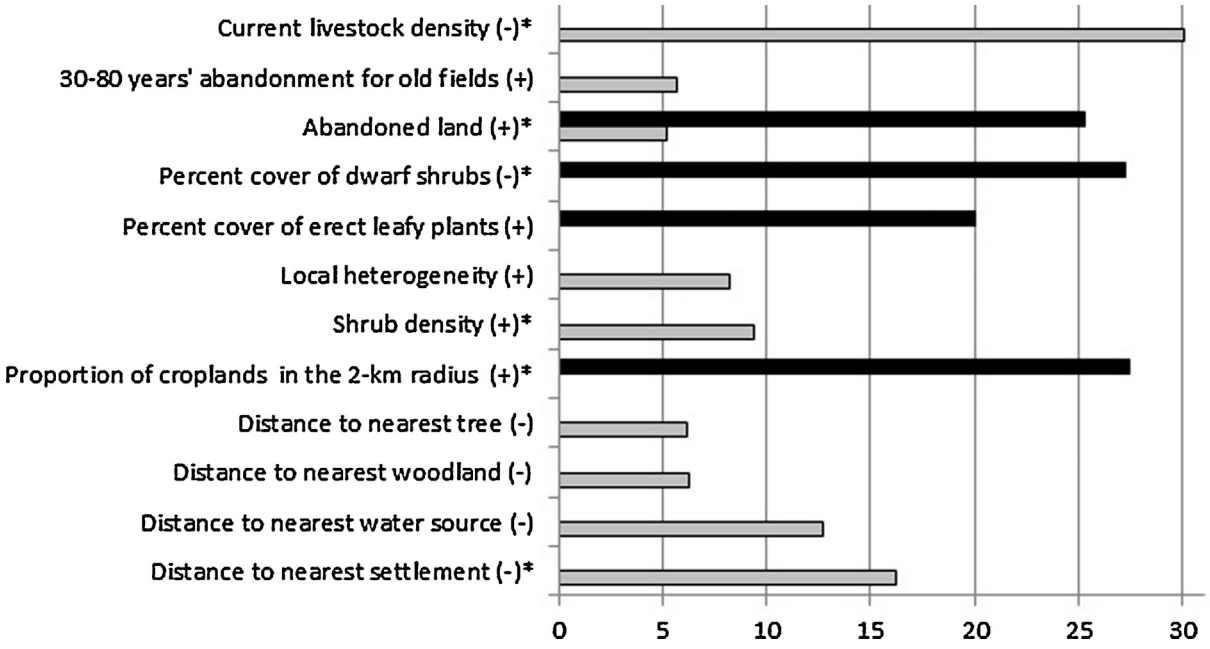

Fig. 2. Results from the hierarchical partitioning, explaining the total species richness (gray bars) and steppe-dependent species richness (black bars). The relationship between each variable with richness is indicated in parenthesis as positive (+) or negative (−). The significances of the independent contributions of each of the explanatory variables are indicated (*$0.01 \leq P < 0.05$; **$0.001 \leq P < 0.01$; ***$P < 0.001$).

common nightingale, black-headed wheatear, rock bunting, corn bunting and common quail were frequently recorded there.

A redrawing of the CCA diagram with proportional abundance of species groups categorized by degree of steppe dependence did not reveal a clear division of species groups in ordination space (Fig. 1b). At many sites, species with different levels of steppe dependence occurred together. However, sites with abundant steppe-dependent birds were located along the positive half of the first axis. This means treeless, productive steppes at high altitudes supported steppe-dependent birds, which represented 37% of the avian assemblages at sites. Species not typical of steppes were abundant at sites along the negative end of the first axis where settlements were more frequent and trees were nearby. The other two species categories, including more generalist species and those that needed other features (e.g. rocks) were recorded at majority of survey sites, leading them to be widely dispersed in the ordination space.

3.2. Drivers of bird diversity

The species richness of a site ranged from 2 to 13 with an average of 6.8 (±0.5). Shannon's diversity values ranged from 0.611 to 2.458 with an average of 1.663 (±0.082). Steppe-dependent birds or species of predominantly steppic habitats that can be seen in other habitats or in need of specific features (categories 3 and 4 in Table 2), represented 71%. Values of species richness and Shannon's diversity were highly correlated; therefore in the following we present only the findings for richness.

Nine parameters with significant correlation with bird richness that contributed to explained variance were selected for hierarchical partitioning of species richness. Among those, randomization test revealed four of them as significant (Fig. 2). Current livestock intensity and distance to nearest settlement were the major factors with 30% and 16% independent explanatory power on variance in species richness, respectively. Hierarchical partitioning and

correlation both showed that species richness was high in sites with low livestock density and sites near settlements. They were usually close to woodlands, trees, or water sources (less than 250 m), and with high shrub density and local heterogeneity in the herbaceous vegetation. Mostly they consisted of cereal and legume fields abandoned within the last 30–80 years.

The richness of steppe-dependent species at a site ranged between 0 and 5 with an average of 2.7 (±0.3). Steppe-dependent species with highest frequencies were Eurasian skylark and northern wheatear (Table 2). Other common species were tawny pipit, bimaculated lark, corn bunting and crested lark. Four parameters with significant correlation with steppe-dependent bird richness that contributed to explained variance were selected for hierarchical partitioning of steppe-dependent species richness. Three of them had a significant independent contribution to explained variance at a magnitude of 23–31% (Fig. 2). Sites with high richness of steppe-dependent species were mostly abandoned fields, located in landscapes with high proportion of croplands. Percent cover of dwarf shrubs had a negative relationship on steppe-dependent species richness whereas high percent cover of erect leafy plants had positive relationship with steppe-dependent species richness.

4. Discussion

The survey design of this first study had to be limited to one site per ecosection, one visit per site, and a low number of total survey sites. This resulted in a lower sample size, and perhaps, lower values for total species richness compared to similar studies (Delgado and Moreira, 2000; Guerrero et al., 2010). In consequence, the explanatory power of most tests was somewhat limited.

4.1. Factors shaping species composition

Species groups typical of open environments such as larks, buntings and wheatears were most frequently recorded at our sites. Although the species composition in our study area is similar to those from steppes in similar latitudes (e.g. Spain, Tellería et al., 1988), there are also differences, and evidently, a more subtle partitioning of habitat resources. For example, while both Eurasian skylark and northern wheatear occurred in treeless, homogenous high-altitude steppes, the former was often found at more productive sites with a taller, even sward, and the latter at more degraded sites with shorter, sparser vegetation (Fig. 1a). Eurasian skylark, one of the commonest bird species in agricultural mosaics (Chamberlain and Gregory, 1999), does not commonly occur in arable fields in Turkey unlike in western and central Europe, but is more of a bird of upland steppe and wetland margins (Roselaar, 1995; also see Nikolov, 2010). Regardless of altitude, ortolan bunting, wood lark and bimaculated lark preferred productive (high NDVI) steppes with a tall sward, although the latter two species were rarely recorded from the same locality. Horned Lark behaves as a truly alpine species, never occurring below 1700 m a.s.l.

At lower altitudes, a group of species (e.g. crested lark, tawny pipit, Isabelline wheatear) appear to benefit from a drier, more disturbed grassland that is associated with higher human activity (Fig. 1a). However, when trees or shrubs were present nearby, this gave rise to a slightly different suite of birds such as European turtle-dove, hooded crow, Eurasian blackbird and black-headed wheatear (see also below). Rural settlements in inner Turkey typically transform their near environment through communal grazing, land conversion for crops, limited tree planting, and provide man-made nest sites for certain species. Similarly, the presence of trees, particularly rows of poplars along fields or streams, appear to lead to a shift in species composition toward tree-dependent, more generalist species in line with findings of Ellison et al. (2013).

4.2. Factors important for species diversity

Species linked to habitats other than steppes, i.e. small woodlands, reedbeds, or man-made structures were also commonly recorded in nearby dry grasslands as hypothesized by landscape supplementation and complementation processes (Dunning et al., 1992; Vallecillo et al., 2008). A similar study in Hungary revealed the importance of such features for high species richness (Báldi et al., 2005). Proximity to rural settlements played a major role by shaping the environment and by providing varied habitats in the village landscape. Those findings, and the fact that the proportion of steppe-dependent species consistently declined as overall richness increased, indicate that species richness was boosted by the addition of non-grassland birds or generalists, rather than the inclusion of additional steppe-dependent species.

Grazing had a significant negative impact on overall richness in our study. Similar studies found that grazing may have positive or negative effect on bird richness and abundance by modifying the vegetation structure and local heterogeneity, which in turn affects the amount, quality and accessibility of feeding and nesting opportunities; depending on the intensity of grazing and adaptations of species to grassland habitats (Batáry et al., 2007; McCracken and Tallowin, 2004; Nikolov, 2010). We found no relationship of grazing intensity either with vegetation parameters and local heterogeneity or with grassland-dependent bird richness, keeping in mind that we did not directly measure either litter depth or food availability. Instead of affecting vegetation structure at the site level, we interpret the current livestock density to behave as a composite variable, separating homogeneous treeless steppes of uplands with still high densities of livestock from steppes with trees, water sources and man-made structures at heterogeneous landscapes in lower altitude experiencing little or no grazing.

Two plant growth forms found to be important for explaining steppe-dependent species richness in this study were related to land abandonment: High percent cover of erect leafy plants and low percent cover of dwarf shrubs. The group of erect leafy plants was mainly comprised of annual weedy grasses and forbs (e.g. *Taeniatherum caput-medusae*, *Aegilops* spp., *Trifolium* spp.), typically growing in early successional stages of abandoned fields. Dwarf shrubs were represented predominantly by *Thymus* species and some tragacanthic *Astragalus* species, characteristic of grazed Anatolian steppes on mountains (Kurt et al., 2006), and their absence usually indicates that the site is a former arable field. Although land abandonment is considered to be a negative factor for grassland birds via an increase in woody elements due to succession of old fields of former forests (Moreira, 1999), we found shrub density as non-significant for steppe-dependent bird richness probably due to consecutive intensive grazing preventing woody vegetation recovery to a great extent as indicated by Gill (2006) for other regions. Kamp et al. (2011) state that fields after 5–18 years of abandonment are among the most important habitats for steppe bird species in Kazakhstan and relate this to the vegetation structure. In our study, we did not find a relationship of land abandonment with herbaceous vegetation cover and height. The most probable explanation for high steppe-dependent bird richness on abandoned sites in our study is the increased availability of safe nest sites and/or foraging opportunities due to a diverse weedy flora (including remnants of crop plants) and a rich prey base, free from herbicide, pesticide, and ploughing risks (Wilson et al., 1999).

4.3. Conclusion and conservation implications

Our study presented the first findings on relations between birds and their habitats from the little studied steppes of Inner Anatolia. We found that mid-altitude steppes, experiencing low levels of grazing and with a high heterogeneity at both landscape and local

levels, had the highest overall bird richness. Intriguingly, steppe-dependent species were also most frequent at such sites, especially if abandoned cropland (20–50 years old) was available in the neighborhood.

Two ongoing processes appear particularly relevant for the conservation of steppe birds and their habitats: the decline in grazing pressure and the increasing cropland abandonment. Grazing levels usually prove critical in shaping the vegetation structure and the presence of woody elements (Pykälä, 2000). Although higher levels of grazing seem to suppress bird richness, in the period our study was carried out most grazing was considered to be low. We expect the effects of this reduction in livestock numbers to be beneficial for the recovery of semi-natural steppes. However, it should be closely monitored since termination of grazing will help encroachment of shrubs, and if the climate and soil conditions allow, of trees in the long term (Cramer et al., 2008). As overall and steppe-dependent bird richness benefits from a diverse landscape with a good mix of arable land and abandoned fields, it is important to prevent homogenization of the landscape through large-scale land abandonment, industrial farming or land consolidation.

The lack of a conservation strategy, any protected areas or management plans for the conservation of steppes in Turkey is a serious deficiency, and one that needs to be remedied with a network of sites where all steppe biodiversity elements and gradients we revealed are adequately represented. However, any "static" conservation plan would have negative consequences in the long term since steppes are dynamic in time and space at various scales. The interaction between grazing, old field succession, and landscape diversity under the effect of climate change are areas where experimentation and long term monitoring are needed to better understand their dynamics and to provide guidance for land use and conservation actions for the future.

Acknowledgements

We thank Jürgen Dengler and three anonymous reviewers for their valuable comments on an earlier version. Soner Oruç, Süleyman Ekşioğlu, Hilary Welch and Geoff Welch have made their valuable contributions during bird data collection. We are indebted to Hüma Ülgen and Hilary Welch for review of the language. The study was supported by Rufford Small Grants Foundation, by Turan Demirarslan Grassland Research Scholarship of The Turkish Foundation for Combating Soil Erosion, for Reforestation and the Protection of Natural Habitats (TEMA), and by Nature Conservation Center (DKM) in Turkey.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.11.006.

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