



Birds' ecological characteristics differ among habitats: an analysis based on national citizen science data

Jiří Reif^{1,2} · Zdeněk Vermouzek³ · Petr Voříšek³ · Dušan Romportl⁴ · Federico Morelli⁵

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Abstract

Variation in bird community composition across habitats may be reflected by changes in species' ecological characteristics. By their comparison between habitats, we can learn information about the factors underlying these changes. With this purpose, we used data from a nation-wide breeding bird monitoring scheme surveying birds in 15 habitat types sorted into four broad categories (forests, open, urban, and humid habitats) in a central European country, Czechia. We considered life-history strategy, migration distance, climatic niche position, European rarity, and diet niche as species' ecological characteristics and compared their mean values across the habitat types. Although habitat type explained relatively low proportion of variability in these characteristics indicating that birds widely overlap in their habitat use, we observed significant differences in ecological characteristics between broad habitat categories, as well as between habitat types within a given category. For example, urban habitats hosted species with generally lower degree of insectivory than forest habitats. Within forests, coniferous stands hosted species with colder climatic niche than deciduous stands. The greatest differences were observed among humid habitat types: species recorded in water bodies were rarer in Europe and had slower life-history strategies than species recorded in running water. Within the open habitat category, mining areas were the most specific habitat with long-migrating and warm-dwelling species. The observed patterns can be driven by various factors including habitat-specific selection pressures, biogeographic constraints and human-induced habitat changes. On their basis, we discuss our findings.

Keywords Bird assemblage · Life-history trait · Habitat · Bird · Central Europe

Introduction

The concept of habitat plays an essential role in ecological research (Chapman & Reich, 2007; Stirnemann et al., 2014). It facilitates our understanding of the division of space and energy among species (Storch & Okie, 2019) and helps to explain spatial variability in species abundances (Brown

et al., 1995). According to this concept, species differ in their habitat associations resulting in variation of community composition across habitats (Crosby et al., 2019). At the same time, ecological factors acting in different habitats select for specific values of ecological traits carried by the species sharing the same habitat preference (Cody, 1981). These species-specific trait values can be averaged across species present in a given habitat to reveal the traits characterizing the ecology of local communities (e.g., Hořák et al., 2015). Whereas the variation of community-level metrics across habitats has frequently been studied in terms of various diversity indices (e.g., Korňan, 2004) and facets such as functional and phylogenetic diversity (Morelli et al., 2018), the species' ecological characteristics were less frequently explored in different habitats (but see, e.g., Barbaro & Van Helder, 2009; Barnagaud et al., 2013; Montaña-Centellas et al., 2021). Since the ecological characteristics reflect the effects of different environmental filters (Webb et al., 2010), knowledge of their habitat-specific mean values can

✉ Jiří Reif
jirireif@natur.cuni.cz

¹ Institute for Environmental Studies, Faculty of Science, Charles University, Benatska 2, 128 01 Prague 2, Czechia

² Department of Zoology, Faculty of Science, Palacky University in Olomouc, Olomouc, Czechia

³ Czech Society for Ornithology, Prague, Czechia

⁴ Department of Physical Geography and Geoecology, Faculty of Science, Charles University, Prague, Czechia

⁵ Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Prague, Czechia

elucidate the contributions of different drivers to the community assembly.

Previous studies exploring spatial variation of bird community structure in central European landscape revealed that four habitat categories, namely forest, open habitat, urban habitat, and wetland, account for the largest part of variability in bird community composition in a central European country, Czechia (Reif et al., 2008; Storch & Kotecký, 1999). Here we recognize 15 habitat types within these broad categories and investigate the changes in bird community composition across different habitats in relation to the characteristics that are strongly linked to bird species' ecology: life-history strategy, migration distance, climatic niche position, European rarity, and diet niche.

According to the life-history strategy, species can be clustered along several axes, but the strongest gradient sorts the species from those with slow strategies—investing into their survival, having long generation time, low number of offspring, and long parental care (so-called K-selected species), to those with fast strategies—investing into their reproduction, having short generations, high number of offspring, and short parental care (so-called r-selected species) (Reznick et al., 2016). Migration is one of the most conspicuous phenomena in bird ecology being connected with species' flexibility in responses to phenological changes—the longer the migration distance, the less flexible species (Koleček et al., 2020); and can be lost or gained in response to large changes in environmental pressures—loss of migration due to winter climate amelioration, gain of migration due to colonization of new areas at the leading range edges (Berthold, 2001). Climatic niche position mirrors the climatic conditions prevailing in species geographic ranges sorting the species along a temperature gradient from the cold-adapted ones breeding in polar regions or mountains to warm-adapted species breeding in the southern regions or lowlands (Jiguet et al., 2010). European rarity is based on species' breeding population size in European continent which is underpinned by species' dispersal ability, niche breadth, and resource availability when species adapted to the common resources are more common (Gregory & Gaston, 2000). Diet is the only kind of energy input birds accept, and food availability is thus essential for their existence from individuals to populations (Gill, 2006). At the same time, food resources are diverse and different species adapted to their various types resulting in multidimensional nature of birds' diet niche (Pigot et al., 2020).

Although previous studies described relationships of some these characteristics to bird-habitat preferences, such as the association with forest habitat for cold-dwelling species (Barnagaud et al., 2013) or faster life-history strategy of birds breeding in more seasonal habitats (Hořák et al., 2015), we are not aware of any studies focusing simultaneously on a wider set of ecological characteristics across many different

habitats at the national level. To fill this knowledge gap, we perform here an exploratory analyses using data from mapping of bird occurrences in 15 habitat types collected within a nationwide citizen science bird monitoring project in Czechia. Specifically, we aim to explore how values of different characteristics vary across respective habitats.

Material and methods

Bird occurrence mapping

Birds were mapped within Breeding Bird Survey Czechia (Liniové sčítání druhů—LSD), a national breeding bird monitoring scheme launched in 2018. Within LSD, skilled voluntary fieldworkers record positions of individual birds into a map using a custom-designed application for smartphones and tablets. Fieldworkers must be able to recognize all regionally occurring bird species by both acoustic and visual detections. Localities included in LSD are selected by a stratified random sampling with a stratum corresponding to the observers' availability. In this respect, a square of 2.8 km × 3 km is chosen randomly within a radius of 10 km around a point indicated by the observer. Within the randomly selected square, the observer establishes two linear 1-km long transects situated at least 0.5 km from each other and 0.25 km from the square boundaries. Birds are mapped twice per breeding season: from 15th April to 10th May and from 15th May to 10th June to record both early and late breeders; the mapping dates correspond to the phenology patterns reported for most of the species in national literature (Kloubec & Čapek, 2012). During each early morning visit (from sunrise to 10 a.m.), the observer walks along the transects and records positions of all birds into an aerial photograph recognizing the type of detection (visual or acoustic) and the type of behavior (territorial or other) for each bird. Specific registrations are devoted to birds flying over the transect, flocks, breeding colonies, nests, and families with fledglings. The sampling effort is set to exactly one hour for one visit at one transect.

For purposes of this study, we used all records up to 100 m of the perpendicular distance from the transects (i.e., within a 200-m wide belt), but excluded birds flying over the transects. We used the data from 2018 supplemented by the data from the transects established in 2019 ($n=206$ transects in total, Fig. 1). For further analysis, we had dataset of 151 species (Table S1).

Species' ecological characteristics

For each species, we collected literature information on the following five ecological characteristics (Table S1). *Life-history strategy* was taken as a species' position along the

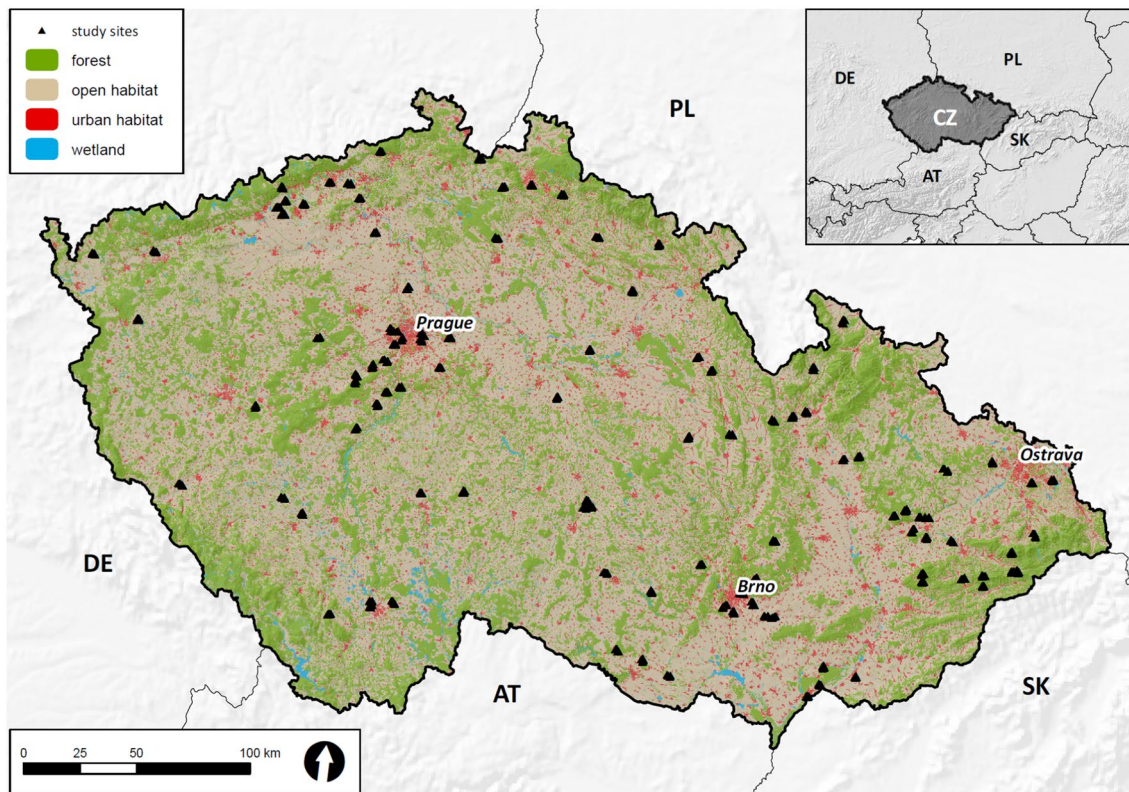


Fig. 1 Location of study sites and the distribution of the four main habitat categories in Czechia. Blue triangles—study sites used for bird counts (each represented by a square of 2.8 km × 3 km containing

two 1-km transects along that the birds were counted); green areas—forests, brown areas—open habitats, red areas—urban habitats, blue areas—humid habitats

main ordination axis obtained by PCA on six life-history traits (egg mass, clutch size, laying date, number of broods per season, incubation time, and body mass) ran by Koleček and Reif (2011). The axis sorted the species from the slow, so-called K-selected species (large eggs, large body mass, long incubation time, and small clutches), to the fast, so-called r-selected species (small eggs, small body mass, short incubation time, and large clutches). *Migration distance* was taken from Hanzelka et al. (2019) who measured the distance between centroids of species' breeding and non-breeding ranges based on maps taken from BirdLife International and Nature Serve (2014). *Climatic niche position* was extracted from Reif et al. (2016) as a mean temperature in species' European breeding range in the peak breeding season (April–June). *European rarity* was quantified as the minus logarithm of the species' relative European breeding population size. Relative European breeding population size of a given species was calculated as ratio of species' breeding abundance in Europe to the total European breeding population size of all focal bird species based on the data from European Red List of Birds (BirdLife International, 2015). *Diet niche* was expressed using two composite variables obtained by running a principal component analysis

(PCA) on nine diet types recognized by Storchová and Hořák (2018) for European bird species. PCA revealed two most important gradients (Fig. S1) explaining together 61.0% of variability in species' diet: pc1 describing increasing insectivory, and pc2 depicting a gradient from carnivorous to granivorous diet. Positions of the species along these two axes (Table S1) were taken for further analysis.

Habitat data

Habitat data come from the consolidated layer of ecosystems (CLE). CLE is a compilation of datasets on vegetation mapping, land cover and topography originating from a nationwide habitat mapping conducted between 2001 and 2005 with regular updates until 2018 (Hönigová & Chobot, 2014). CLE has a complete coverage of the country's territory into 39 non-overlapping habitat types at the scale of 1:10,000. For purposes of this study, we merged these habitat types into 15 habitat types that can be sorted into four broader habitat classes: *forests*—(1) coniferous forest, (2) mixed forest (forest stand containing both coniferous and deciduous trees), (3) deciduous forest; *open habitats*—(4) shrubland, (5) vegetation along roads, (6) cropland (arable field with

annual crops), (7) grassland (meadow, pasture), (8) mining area (opencast mine, unreclaimed slag heap), (9) rock; *urban habitats*—(10) urban green area (park, orchard, garden), (11) part of human settlement with sparse built-up area (city margin, village), (12) part of human settlement with continuous built-up area (city center, housing estate); *humid habitats*—(13) water body (fishpond, water reservoir), (14) running water (stream, river), (15) wetland (reedbed, swamp, peat bog). By that means, we created a map of non-overlapping polygons of these 15 habitats covering the whole country.

We overlaid LSD bird records and the habitat information based on CLE by restricting both datasets to the same 100 m perpendicular distance from the LSD transects obtaining the non-overlapping habitat polygons with bird records. For further analysis, we only considered polygons hosting at least two species and being larger than 100 m² at the same time because smaller areas hold only small fragments of bird territories and are thus not appropriate for studying bird communities. As a result, we obtained 2215 polygons in total sorted into focal habitat types and categories (Table 1).

For each polygon, we expressed the list of detected bird species (Table S2) and habitat identity (Table S3). Each polygon-specific species list was considered being a bird community. Then we calculated mean values for each of the ecological characteristics across the species in the bird community of a given polygon using the species-specific trait values (see above). The calculation followed the approach of Devictor et al. (2008), who obtained the community-level average by weighting the species-specific values of a

given ecological characteristic by the relative abundance of each species within a given bird community. As a result, we obtained the values of respective characteristics for every habitat polygon (Table S3).

Statistical analysis

The analyses were performed at two different levels—species level with species as replicates, and community level where the statistical units were individual habitat polygons.

For the species-level analysis, we first quantified relationships of each species to respective habitats using canonical correspondence analysis (CCA). CCA is a direct gradient analysis technique that relates species to environmental variables producing the independent gradients in species composition with respect to changes in values of environmental variables. Counts of bird species in respective habitat polygons represented the response variables (Table S2) and the habitat type (15 habitats) of polygons (Table S3) was the explanatory variable. We considered four most important habitat gradients represented by the first four canonical axes (cca1–cca4) explaining the decisive part of variability in bird–habitat relationships. Positions of individual species along these gradients were taken for further analysis. In the next step, we related species' characteristics as response variables (each variable was included in one model) to species' positions along cca1–cca4 as explanatory variables (all four axes were included together in every model) using linear models (Gaussian distribution, identity link).

Table 1 Habitat types considered in this study, their sample size, sorting into four broader habitat categories, abbreviations used in Figs. 2 and 4, and their positions along the four most important

canonical axes (cca1–cca4) revealed by a canonical correspondence analysis on bird occurrences in individual habitat types

Habitat type	No of polygons	Habitat category	Abbreviation	cca1	cca2	cca3	cca4
Coniferous forest	295	Forests	Conif_f	−0.46	0.10	−0.52	0.70
Mixed forest	122	Forests	Mixed_f	−0.23	0.06	−0.24	0.20
Deciduous forest	355	Forests	Decid_f	−0.38	0.08	−0.38	0.33
Shrubland	60	Open habitats	Shrub	−0.09	0.08	−0.08	−0.06
Vegetation along roads	94	Open habitats	Road	0.23	−0.05	−0.16	0.19
Cropland	206	Open habitats	Crop	0.16	0.84	−0.35	0.20
Grassland	503	Open habitats	Grass	0.06	0.46	−0.36	−0.06
Mining area	14	Open habitats	Mining	0.08	0.31	0.01	0.65
Rock	7	Open habitats	Rock	0.02	0.24	−0.06	0.46
Urban green area	58	Urban habitats	Urb_green	0.00	0.00	0.00	0.00
Part of human settlement with sparse built-up area	184	Urban habitats	Urb_sparse	0.43	−0.11	−0.35	0.39
Part of human settlement with continuous built-up area	217	Urban habitats	Urb_cont	0.43	−0.17	−0.32	0.39
Water body	28	Humid habitats	Water_body	0.01	0.05	0.70	0.13
Running water	47	Humid habitats	Water_run	0.00	0.03	0.15	−0.03
Wetland	25	Humid habitats	Wetland	−0.01	0.08	0.45	0.17

At the community level, we related the ecological characteristics as respective response variables to the habitat type as a factorial explanatory variable using linear mixed models (Gaussian distribution, identity link). We also included species richness of individual habitat polygons as an additional covariate. To account for possible non-independence of the habitat polygons within the same transects, we used the square (each containing two 1-km transects, see above) as a random effect. The square was nested within the large square (12 × 11.1 km) to control for a possible large-scale spatial structure in data. Model performance was expressed using pseudo-R-squared. We checked the model assumptions by plotting residuals vs. fitted values for every model (Figs. S2, S3). Moreover, we tested for the presence of spatial autocorrelation in residuals of the models used in the community-level analysis (Fig. S4). No indication of spatial autocorrelation was observed in model residuals; only the smallest distances showed slightly negative values in some models (Fig. S4).

Statistical analysis was performed in R version 3.4.3 (R Core Team, 2017) using the packages ‘nlme’ (Pinheiro, 2021) for running mixed effects models, ‘MuMIn’ (Bartoń, 2020) for producing the pseudo-R-squared values for individual mixed effects models, and ‘ncf’ (Bjornstad & Cai, 2020) for testing the spatial autocorrelation. Multivariate analyses (PCA, CCA) were ran in Canoco for Windows 4.5 (ter Braak & Šmilauer, 2002).

Results

Species level

CCA sorted the species along four most important habitat gradients together explaining 86.2% of variability in species occurrence in respect of the 15 habitat types considered (Fig. 2, Table 1, Supplementary Table S1). First axis (explaining 42.8% of variability in relationships of species to the focal habitats (Fig. 2A)) was a gradient from forest (with species such as Crested Tit *Lophophanes cristatus*, Coal Tit *Periparus ater*, Eurasian Treecreeper *Certhia familiaris*) to urban habitats (House Sparrow *Passer domesticus*, House Martin *Delichon urbicum*, Collared Dove *Streptopelia decaocto*). Second axis (28.7%, Fig. 2A) represented a gradient from urban habitats with the species mentioned above to open habitats (cropland, grassland, mining areas and rocks) with typical species including Northern Wheatear (*Oenanthe oenanthe*), Yellow Wagtail (*Motacilla flava*), Eurasian Skylark (*Alauda arvensis*), and Meadow Pipit (*Anthus pratensis*). Third axis (9.9%, Fig. 2B) was a gradient of increasing wetness represented by water body, wetland, and (to lesser extend) by running water with typical species including Common Tern (*Sterna hirundo*), Common Pochard (*Aythya*

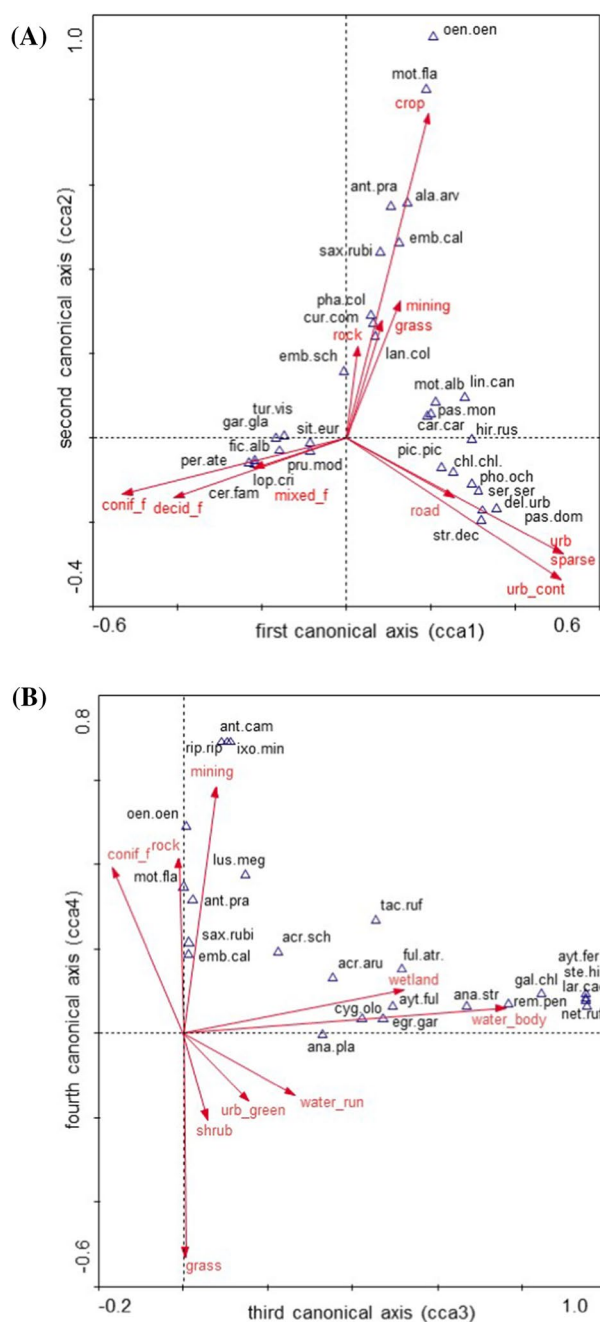


Fig. 2 Results of the canonical correspondence analysis (CCA) expressing relationships of bird species to 15 habitat types using the first four most important canonical axes (A: cca1 and cca2, B: cca3 and cca4) representing the main habitat gradients. Note that only the habitats (red arrows and labels) and species (blue triangles, black abbreviated names) showing the strongest relationships to respective axes are depicted. See Table 1 for full names of habitat types and their loadings, see Table S1 for full names of species and their scores along respective axes

ferina), and Red-crested Pochard (*Netta rufina*). Fourth axis (4.8%, Fig. 2B) was a gradient from grassland to mining areas, rocks, and coniferous forest. Species associations with

this axis were modest as also indicated by low proportion of variability explained, but Tawny Pipit (*Anthus campestris*), Sand Martin (*Riparia riparia*), and Little Bittern (*Ixobrychus minutus*) showed conspicuous positive correlations (Fig. 2B).

By relating species-specific values of the ecological characteristics to the positions of individual species along these gradients (Table 2) we revealed that species with slower life-history strategies occurred in more open (cca2, Fig. 3A) and in wetter habitats (cca3, Figure 3B). Moreover, a relationship to cca4 (Fig. 3C) indicates that species with slower life histories occurred in rocks, mining areas, and coniferous forests, while species with faster strategies were recorded in grasslands. Migration for longer distances was positively related to cca2 (Fig. 3D), indicating that species of open habitats migrate for longer distances, where species of urban habitats migrate shorter. Migration for longer distance was also characteristic for species with preference for wetter habitat (cca3, Fig. 3E). Considering European rarity, rarer species occurred in forests and commoner species in urban habitats (cca1, Fig. 3F). Moreover, increasing rarity was also associated with more open habitats (cca2, Fig. 3G), wetter habitats (cca3, Fig. 3H), and grassland (cca4, Fig. 3I). Climatic niche and descriptors of species' diet niche did not indicate significant relationships to their habitat preferences (Table 2).

Community level

Explanatory variables explained small (5–18%), but significant part of variability in values of ecological characteristics across polygons (Table 3). Whereas the polygon habitat type was significant in all models, species richness of individual polygons was only related to life-history strategy and European rarity (Table 3).

Species with faster life-history strategies occupied polygons dominated by woody plant vegetation (Fig. 4A): all three forest types, shrubland, and vegetation along roads. Moreover, these species were in parts of human settlements with sparse built-up areas. Slower life-history was characteristic in polygons with cropland, rocks, urban

Fig. 3 Significant relationships between species-specific values of ecological characteristics and positions of individual species along habitat gradients (cca1–cca4, see Fig. 2) estimated by linear models (see Table 2 for overall model fit): **A** life-history strategy and cca2 ($t = -4.50$, $p < 0.001$), **B** life-history strategy and cca3 ($t = -5.79$, $p < 0.001$), **C** life-history strategy and cca4 ($t = 4.30$, $p < 0.001$), **D** migration distance and cca2 ($t = 3.18$, $p = 0.002$), **E** migration distance and cca3 ($t = 2.07$, $p = 0.040$), **F** European rarity and cca1 ($t = -2.83$, $p = 0.005$), **G** European rarity and cca2 ($t = 4.86$, $p < 0.001$), **H** European rarity and cca3 ($t = 6.91$, $p < 0.001$), **I** European rarity and cca4 ($t = -3.08$, $p = 0.002$). Relationships are plotted as residual plots controlling for the effects of other variables included in respective models

green areas, running water, grassland, mining areas, and parts of human settlements with continuous built-up areas, although the difference was not significant in the last three habitat types (Fig. 4A). Species with much slower life-history strategies were recorded in wetland and the slowest strategies were observed in water bodies (Fig. 4A).

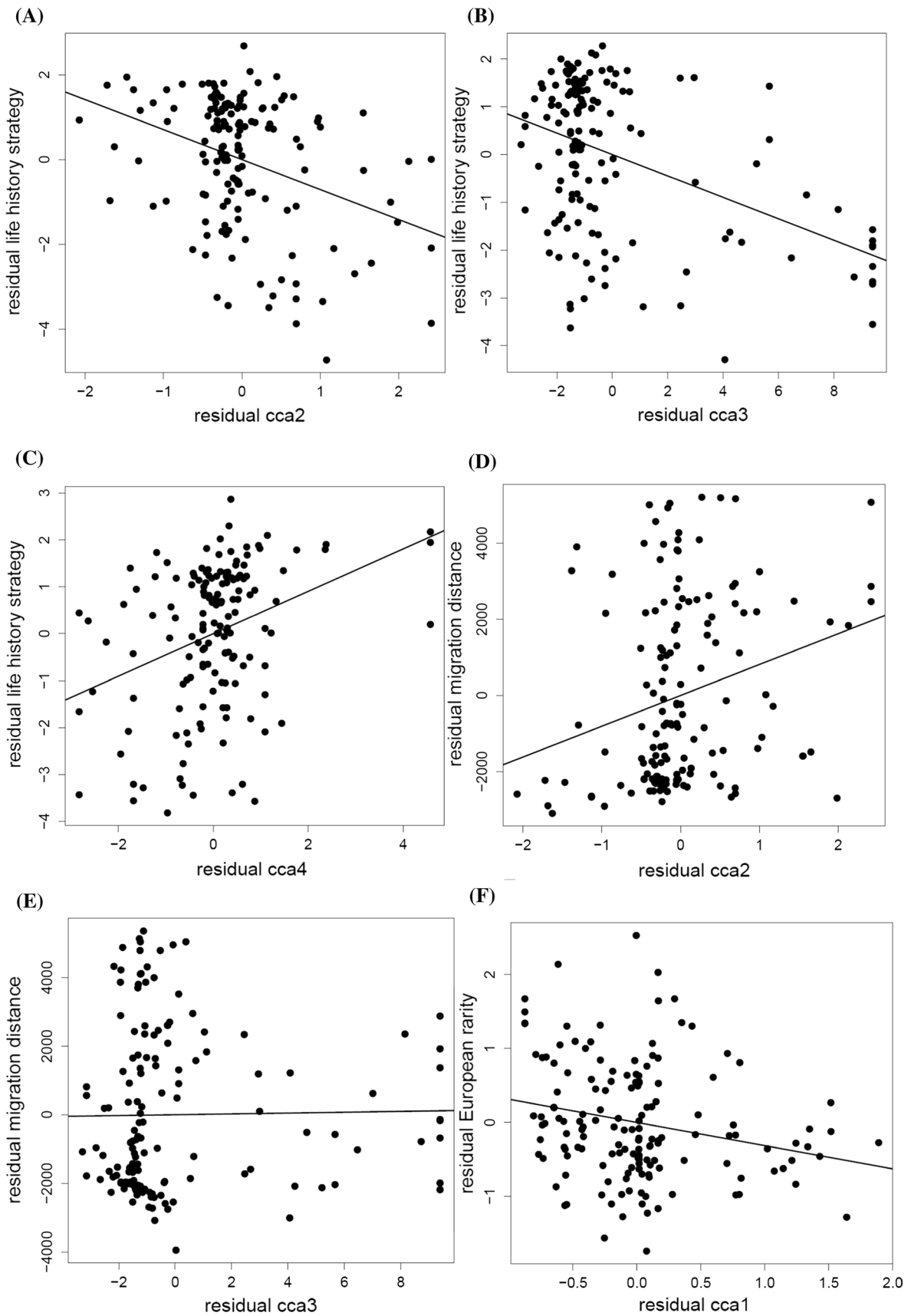
Bird communities containing the species with the longest migration distances were in polygons of mining areas, water bodies, rocks, and wetlands, but the migration distance of the species in the latter two habitats did not differ significantly from the other habitat types (Fig. 4B). In contrast, species occupying coniferous forest, deciduous forest, vegetation along roads, parts of human settlements with continuous built-up areas, and running water had the shortest migration distances (Fig. 4B). Bird communities of the other habitat types can be considered as those with migration distance being intermediate between the above-mentioned habitat groups (Fig. 4B), but the differences were insignificant with the exception of grassland that showed the intermediate position significantly (Fig. 4B).

In respect of the climatic niche position, species breeding in the coldest climate of Europe were those recorded in coniferous forest (Fig. 4C), whereas the species recorded in mining areas were those breeding in the warmest climate. Preference for warm climate had also species recorded in all types of urban areas, whereas relatively colder-dwelling species were observed in grassland (Fig. 4C). Remaining habitat types showed considerable overlap in respect of climatic niche values of bird communities (Fig. 4C).

Wetlands and water bodies were occupied by species being the rarest in Europe (Fig. 2D). Species with relatively high European rarity values (but being significantly lower than in the above-mentioned habitats) were recorded in cropland, mining, and rock areas and in running water (Fig. 4D). On the other hand, all types of forests, polygons situated in urban areas, along roads, in shrubland, and in grassland were characterized by bird communities with the lowest rarity values (Fig. 4D). However, within this group of habitats, shrubland, grassland, and parts of human settlements with sparse built-up areas hosted relatively rarer species (Fig. 4D).

Table 2 Overall fit of the linear models relating species-specific values of ecological characteristics to their positions along the four most important habitat gradients revealed by the canonical correspondence analysis (cca1–cca4, see Table 1, Fig. 2)

Ecological characteristic	$F_{4,146}$	P	R^2
Life-history strategy	11.83	<0.001	0.22
Migration distance	4.81	0.001	0.09
Climatic niche position	2.14	0.079	0.03
European rarity	17.65	<0.001	0.28
Diet pc1	2.34	0.058	0.03
Diet pc2	1.16	0.332	<0.01



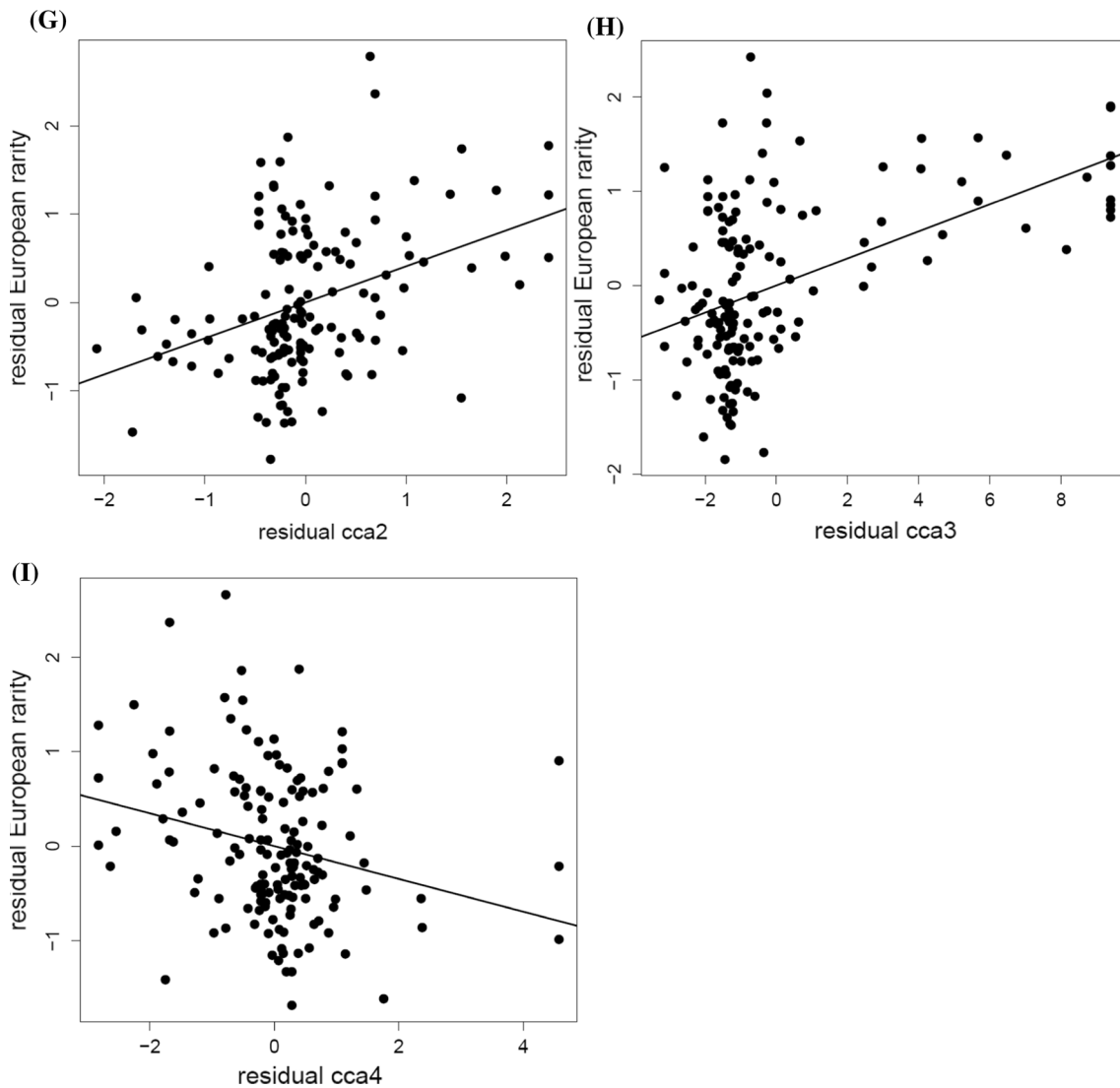


Fig. 3 (continued)

Diet expressed as pc1 reflecting the degree of insectivory showed that this trait is characteristic for bird communities of all forest types, shrubland, cropland, grassland, and wetland (Fig. 4E). In contrast, birds in vegetation along roads, all urban habitat types, running water polygons, and water bodies were less insectivorous (Fig. 4E). Diet expressed as pc2 (carnivory vs. granivory) did not show much differences among habitats (Fig. 4F). Continuous built-up urban areas and urban green areas hosted more granivorous species, whereas coniferous and deciduous forest and mining areas are more carnivorous species (Fig. 4F).

Discussion

Our dataset was based on bird occurrences in habitat polygons represented by 15 habitat types from four broad habitat categories (forests, open habitats, urban habitats, and humid habitats). Across these habitats, we compared various ecological characteristics of birds (life-history strategy, migration distance, climatic niche position, European rarity, and diet niche) by the analyses performed both at the species and the community level. Habitat type explained relatively low proportion of variability in these characteristics because birds are relatively large and mobile organisms that often use a wider spectrum of habitats in contrast to more specialized (e.g., insects) or sedentary (e.g., plants) taxa (Roth et al., 2014; Thomas, 1995). Despite their relative habitat

Table 3 Overall fit (A) and performance of respective explanatory variables (B) in linear mixed models relating mean values of species' ecological characteristics in habitat polygons to the habitat type (recognizing 15 habitats, see Table 1) and species richness of individual polygons

		Life-history strategy			Migration distance			Climatic niche position			European rarity			Diet pc1			Diet pc2		
		log Lik	pseudo- R^2	P	log Lik	pseudo- R^2	P	log Lik	pseudo- R^2	P	log Lik	pseudo- R^2	P	log Lik	pseudo- R^2	P	log Lik	pseudo- R^2	P
(A) Overall model fit		1594.5	0.15		18,314	0.08		652.36	0.11		667.94	0.18		132.6	0.12		965.85	0.05	
		F	P		F	P		F	P		F	P		F	P		F	P	
Habitat type	14, 2097	20.56	<0.001		3.04	<0.001		8.70	<0.001		19.49	<0.001		12.61	<0.001		3.79	<0.001	
Species richness	1, 2097	15.06	<0.001		0.46	0.496		2.00	0.155		54.00	<0.001		1.79	0.182		0.02	0.877	

generalism, we found that birds clustered along several main habitat gradients that corresponded to the bird–habitat associations previously reported from Central Europe (Reif et al., 2008; Storch & Kotecký, 1999) and to our a priori defined broad habitat categories. According to the species-level analysis, species' positions along these gradients were related to life-history strategy, migration distance, and European rarity, but unrelated to climatic niche position and diet. Community-level analysis provided additional insights by detecting differences in several characteristics across the 15 habitat types both within and between the broad habitat categories. Below we interpret the main findings.

The most conspicuous pattern in respect of species' life-history strategy was the association of slow strategies with humid habitats which particularly concerned water bodies and wetlands. The pattern was driven by frequent occurrence of numerous large-bodied water birds such as waterfowl (e.g., Mute Swan *Cygnus olor*), herons (e.g., Gray Heron *Ardea cinerea*), and gulls (e.g., Caspian Gull *Larus cachinans*) with these habitats. In the case of water bodies that were typically represented by fishponds in our dataset, this association was facilitated by high stocks of Carp (*Cyprus carpio*) (Pechar, 2000) providing superabundant food resource for the large-bodied fish eaters (gulls, herons, Great Cormorant *Phalacrocorax carbo*). At the opposite end of life-history continuum, we found an interesting association of fast life-history strategies with habitats dominated by wood plants. They were represented not only by various forest types, but also by shrubland and vegetation along roads. Faster life-history strategy of species in those habitats may be partly driven by cavity nesting passerines that have large clutches (Jetz et al., 2008) due to investment in the current breeding attempt after finding a suitable nest site which may be scarce (Martin & Li, 1992). Another possibility may be small body size as an adaptation to maneuverability in dense woody vegetation (Norberg, 1979, 1995).

Species-level analysis showed an association of long-distance migration with open and humid habitats, but the community-level analysis uncovered that these patterns were driven by particularly long migration distances in species recorded in mining areas and water bodies. Mining areas were occupied mainly by species such as Tawny Pipit, Sand Martin, and Northern Wheatear that all winter in sub-Saharan Africa. Their adaptation to long-distance migration likely results from their insectivorous diet that is absent in their breeding habitat during winter. This explanation is less obvious for birds recorded in water bodies that show higher interspecific variability in diet and the winter food limitation is undoubtedly less strict in herbivores and fish eaters. However, we should bear in mind that these species often breed in northern Europe and migrate further south in non-breeding season (Keller et al., 2020) which makes the mean migration distance across the species recorded in

Fig. 4 Predicted values of respective species' ecological characteristics in individual habitat types estimated by linear mixed models (see Table 3): **A** life-history strategy, **B** migration distance, **C** climatic niche position, **D** European rarity, **E** diet pc1, **F** diet pc2. Significant differences between habitats are marked by different letters

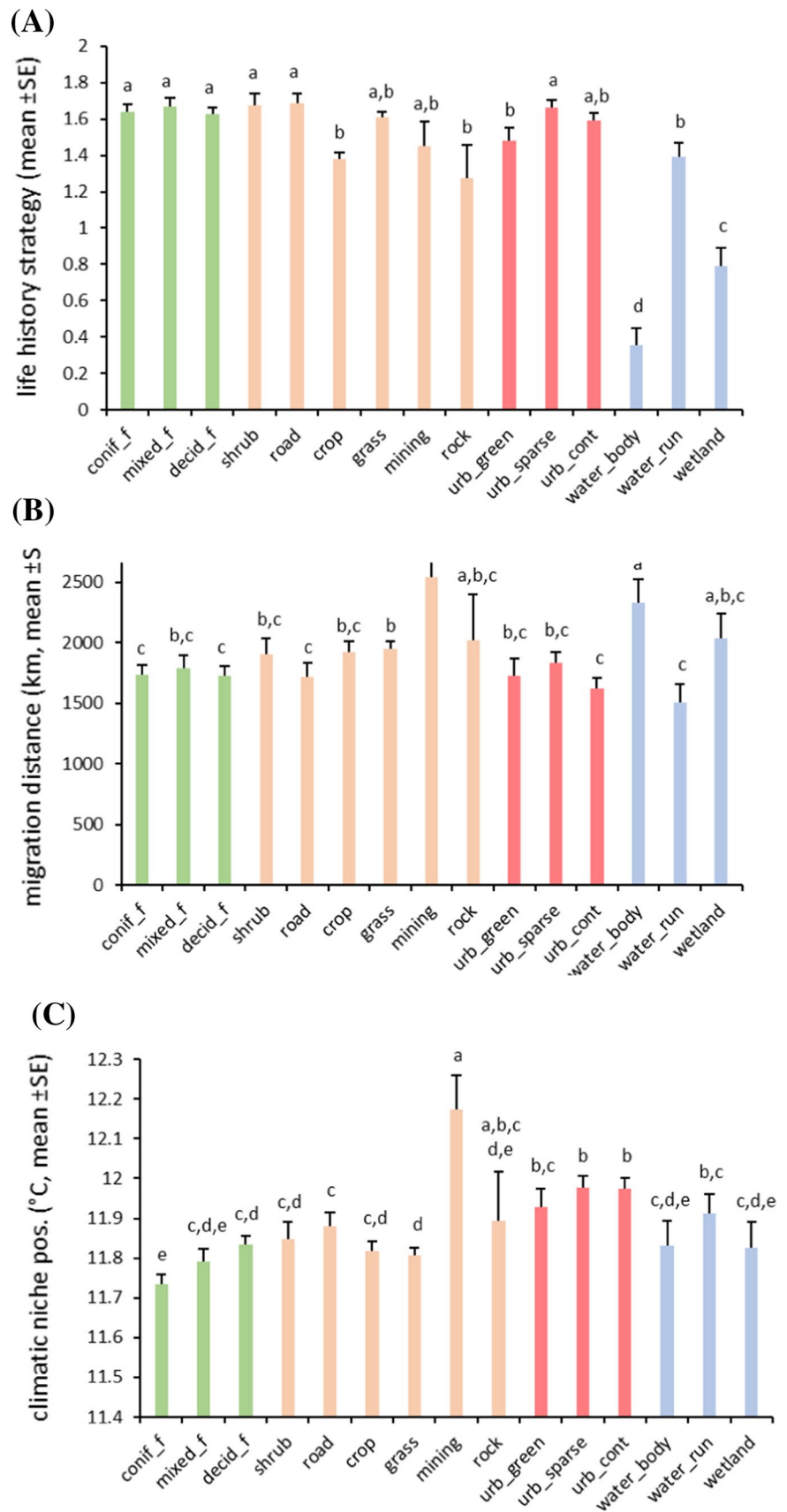
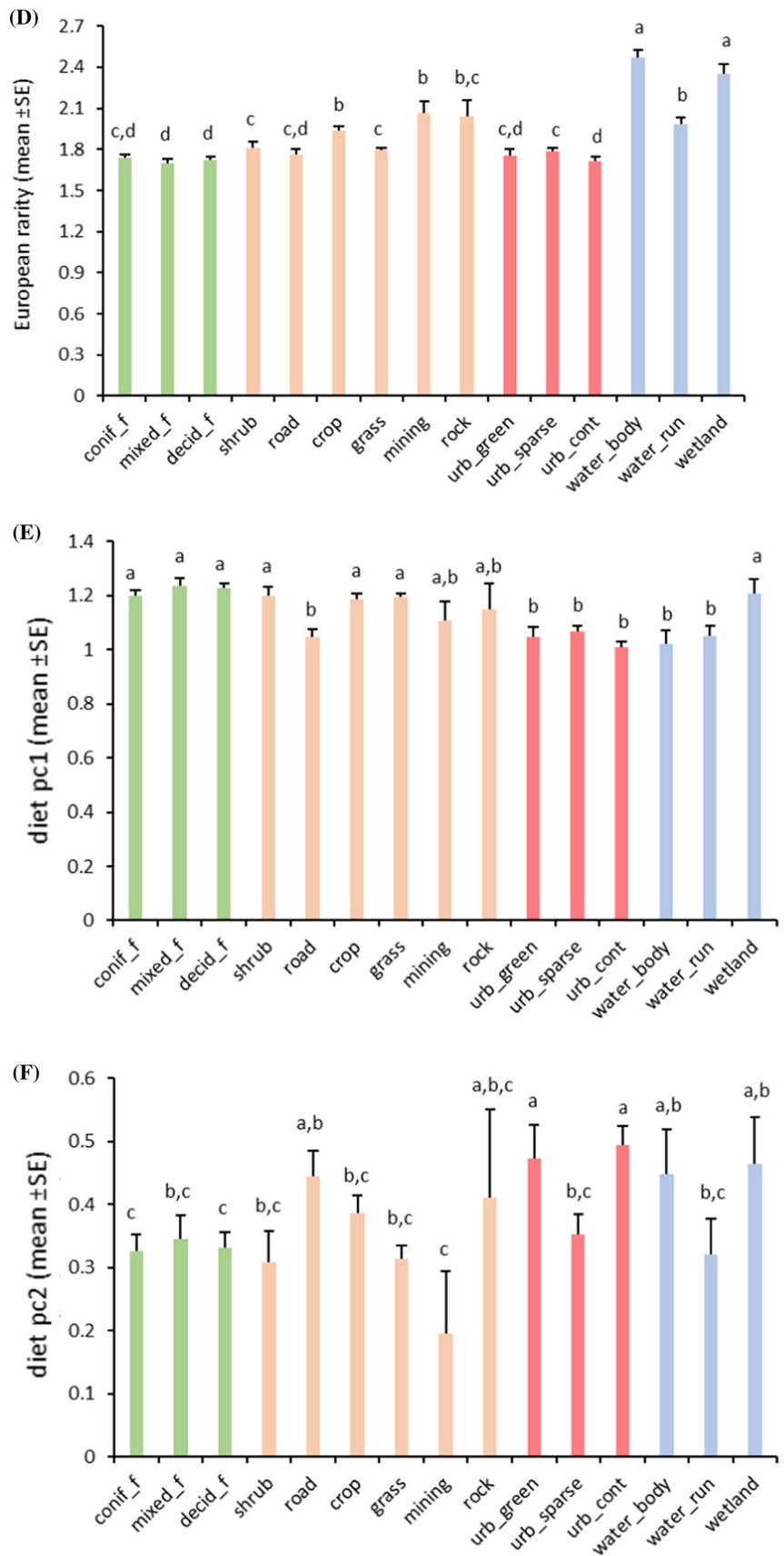


Fig. 4 (continued)



water bodies relatively long even though many of them do not migrate to sub-Saharan Africa. Short migration distances were found in species recorded in various different habitats including built-up areas of human settlements and forests. The interpretation of these results is less clear. In the former case, it is well known that birds may benefit from the availability of food resources throughout the year in human settlements represented by various garbage the birds can feed on (Bonnet-Lebrun et al., 2020) as well as by targeted feeding by humans (Robb et al., 2008) even though important exceptions, such as urbanized aerial feeders, exist.

The differences in climatic niche position among habitats were modest which may raise concerns about biological importance of these statistically significant results. However, it is widely documented that even small changes in climatic niches have serious ecological consequences (e.g., Devictor et al., 2012) and the patterns we report here have genuine interpretations indeed. The lowest climatic niche position had the species recorded in coniferous forest. This forest type prevails in boreal zone of Europe and in higher altitudes, and it is thus not surprising that those species prefer colder climate (Barnagaud et al., 2013). Relatively northerly breeding ranges may also explain lower climatic niche positions in species of mixed forest and water bodies or wetlands (Keller et al., 2020). Community-level analysis uncovered a higher position of climatic niche in species recorded in urban areas. It may be explained by the southern origin of urbanization in some of that species such as European Serin (*Serinus serinus*), Black Redstart (*Phoenicurus ochruros*), or Eurasian Collared Dove (*Streptopelia decaocto*) which subsequently spread northward (Kinzelbach, 2004; Rocha-Camarero & De Trucios, 2002). In addition, urban habitat may act as a heat island (Taha, 1997) and thus may attract such warm-adapted species. The highest climatic niche position was found in species recorded in mining areas. They resemble xeric steppe or semi-desert habitats of southern Europe, so they host several species with a warmer climatic preference such as Tawny Pipit, Corn Bunting (*Emberiza calandra*), or European Stonechat (*Saxicola rubicola*).

European rarity was the characteristic showing considerable variation across habitats. The rarest species were recorded in water bodies and wetlands. This may be connected with reduced regional availability of these habitats because they account only for 1.5% of area in Czechia and 7.3% in Europe (Čížková et al., 2013). As a consequence, species associated with rare habitats can be regionally less common than species associated with more widespread habitats in Europe (Gregory & Gaston, 2000). In addition, large body size of water birds can also contribute to European rarity of species recorded in water bodies and wetlands since abundance is inversely linked with body mass following the metabolic scaling laws (Nee et al., 1991). On the other hand, species recorded in forest habitats and

various types of human settlements were those more common in Europe. The pattern found for forests is more difficult to interpret, but we suggest that it may be linked to generally lower habitat specialization of European forest birds (Reif et al., 2016) when less specialized species are more common at the same time (Gaston et al., 1997). On the other hand, open habitats showed generally higher rarity values, but interesting differences were observed between different open habitat types. Specifically, species recorded in mining areas and cropland were more rare than species recorded in shrubland and grassland. As noted above, mining areas resemble steppe and semi-desert habitats that are confined to southern Europe and extend further east to Asia. Due to these biogeographic constraints their bird assemblage is composed by species being relatively rare in the whole-European context (Blondel, 1997). A similar explanation may apply to cropland, but in this case we can also expect an influence of habitat deterioration. Widely reported negative impacts of agricultural intensification decrease the quality of this habitat for birds (Stoate et al., 2009). At the same time, these limitations are most likely less pronounced in shrubland and grassland.

In contrast to European rarity, changes in bird community composition across the focal habitats were only weakly related to species' diet niche showing no significant relationships in the species-level analysis and only a few patterns at the community level. We found lower degree of insectivory in both running water and water bodies, all types of urban habitats and in vegetation along roads. In the former case, lower degree of insectivory may be driven by occurrence of numerous fish eaters in both types of water habitats. In addition to the large-bodied waterbirds mentioned above, it is for example Common Kingfisher (*Alcedo atthis*) which breedings along rivers and small stream. Interestingly, wetlands showed higher degree of insectivory than water bodies, probably due to occurrence of various warbler species (*Acrocephalus* sp., *Locustella* sp.) and shorebirds (e.g., Northern Lapwing, *Vanellus vanellus*) in this habitat. Lower degree of insectivory of species recorded in human-modified habitats, most notably the urban ones, may result from their flexibility in resource use (Ducatez et al., 2015) than is linked to bird occurrence in human settlements (Evans et al., 2011; Møller, 2009). At the same time, our results indicate that urban continuous built-up areas and green areas were characterized by a higher degree of granivory. In those areas, see-eaters may benefit from feeding at dairy and poultry farms (Havlíček et al., 2021) or bird feeders (Robb et al., 2008).

In conclusion, the patterns revealed in our data are ecologically meaningful and provide further insights into the factors that govern bird community composition across habitats in Central European landscape. It would be interesting to repeat these analyses using datasets from

different European regions, for instance, boreal zone or the Mediterranean region, to show to what extent the patterns we report here hold in different landscape and biogeographical contexts.

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Author contributions JR conceived the idea; ZV, PV, and JR designed the research; ZV, PV, and JR collected data; JR, DR, and FM analyzed data; JR drafted the manuscript with inputs from all authors.

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Data availability Supplementary Tables S1–S3.

Code availability Supplementary file S5.

Declarations

Conflict of interest The authors declare they have no conflict of interests.

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