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# Global Ecology and Conservation

journal homepage: [www.elsevier.com/locate/gecco](http://www.elsevier.com/locate/gecco)

## Fragment connectivity shapes bird communities through functional trait filtering in two types of grasslands

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### ARTICLE INFO

#### Keywords:

Environmental filtering  
Functional diversity  
Habitat fragmentation  
Landscape configuration  
Species response  
Trait-based analysis

### ABSTRACT

Habitat fragmentation is considered one of the most severe threatening factors for global biodiversity. Here we assessed, how local and landscape scale environmental variables, such as fragment size (small vs. large) and landscape configuration (measured as connectivity index) relates to bird community composition, species richness, abundance and functional diversity. We surveyed 60 grassland fragments in Hungary, belonging to two different threatened grassland types, namely forest-steppes and kurgans. Forest-steppes are natural mosaics of grasslands and forests at the contact zone between closed-canopy temperate forests and steppe grasslands. Kurgans are ancient burial mounds, found on the Eurasian steppe and forest steppe zone. These fragments were embedded in plantation forestry, respectively, agricultural matrix with gradients of size and connectivity. Both habitats are threatened by forestry and agricultural intensification, though these fragments may serve as important wildlife refuges. Our findings revealed that forest-steppe birds were more diverse and abundant in large and well-connected than in small isolated fragments. High connectivity affected ground nesting birds in small forest-steppe fragments positively. Birds inhabiting kurgan area showed higher trait similarity in well-connected than in isolated fragments. Bird abundance of kurgans associated with small home range size and ground feeding habit were higher in connected compared to isolated fragments. Highly isolated kurgans filtered for more specialised bird species but not for generalists. We provide conservation implications for enhancing grassland specialist bird communities, which consist of preservation of large, well-connected grassland fragments within production landscapes and through reconsideration of the currently used intensive forestry.

### 1. Introduction

Landscape modification is the most important modern cause of habitat loss and habitat fragmentation, resulting in severe biodiversity decline throughout Europe (Tscharnitke et al., 2005). Habitat fragmentation means the breaking apart of large, contiguous areas

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<https://doi.org/10.1016/j.gecco.2021.e01687>

Received 15 December 2020; Received in revised form 15 June 2021; Accepted 15 June 2021

Available online 17 June 2021

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of habitat into several smaller fragments, which are isolated from each other. Habitat loss is a concomitant consequence of this process and occurs when a particular species loses its suitable habitat, making the area unsuitable for that species to maintain a stable population (Lindenmayer and Fischer, 2013). Furthermore, increasing management intensity results in the loss of semi-natural habitats important for several species through field size enlargement and conversion of genuine habitats by drastically changing the natural vegetation structure, deteriorating habitat quality and thereby affecting wildlife (Laiolo et al., 2004; Sanderson et al., 2013; Brandt et al., 2017).

The effects posed by the habitat fragmentation on species richness and community composition might be various depending on the local and landscape drivers (Debinski and Holt, 2000; Winter et al., 2006; Batáry et al., 2012). Coppedge et al. (2001) showed that grassland fragment size is an important determinant of grassland birds, but this effect may vary across species. Especially, open-habitat specialist bird species are most affected by fragmentation (Caplat and Fonderflick, 2009). For example, Calandra larks (*Melanocorypha calandra*) responded positively to the amount and fragment size of open habitats at landscape scale (Caplat and Fonderflick, 2009). Such edge-induced effects determine the distribution of several other bird species as well, thereby also shaping community composition (Püttker et al., 2020).

To maintain biodiversity in human-modified regions, it is important to understand the relationship between landscape-scale heterogeneity and biodiversity (Fahrig et al., 2011; Batáry et al., 2020). Spatially, landscape configurational heterogeneity is an important determinant of the landscape structure and its suitability for species. In fragmented habitats, populations are separated by barriers to movement that disrupt population dynamics, moreover the size of habitat fragments may limit species survival (Bennett et al., 2006). The importance of landscape configurational heterogeneity is well known (Teillard et al., 2014; Pedersen and Krøgli, 2017), but the actual effects are not always unequivocal. Studies investigating the effects of configurational heterogeneity on birds in agricultural and forested landscapes show mixed results. For example, Modest et al. (2016) found that size and extent of isolation of habitat fragments influence specialist and generalist birds as well. Wilson et al. (2007) showed that isolation reduces the abundance of forest specialist birds, but the species richness did not decline with reduced fragment size on more isolated habitats in particular contexts. Consequently, the overall effect of isolation on bird populations and their functional diversity still needs further investigations.

Habitat fragmentation does not affect all species equally, since their distribution is filtered based on several traits, thus habitat loss and fragmentation alters the regional species pool and may reduce the role of birds in particular ecosystem functions (Tscharnatke et al., 2008). Several traits of species show sensitivity to habitat loss and fragmentation, e.g. large body size, resident migration status or low dispersal capacity (Blumstein, 2006; Cuervo and Møller, 2020), thereby trait-based approach is a useful method to evaluate the effects of habitat fragmentation (Barbaro and van Halder, 2009). This approach can also provide important insights because functional traits can reveal an organism's role in ecosystem functioning. Hence, studying functional traits can identify mechanisms underlying the impact of biodiversity on ecosystem processes (Wood et al., 2015). Here we focused on birds because they contribute to a great quantity of ecosystem functions and fill a diverse range of ecological niches (Sekercioglu, 2006).

In this study, we investigated two types of natural grassland fragments, namely forest-steppe grasslands and kurgans. Forest-steppes represent a transition between closed forests and mostly treeless steppes, and can be defined as a distinct vegetation belt encompassing a huge area from Eastern Europe to far East of Russia (Gallé et al., 2018). Erdős et al. (2018) defined forest-steppes as natural or near-natural vegetation complexes of arboreal and herbaceous components (distributed in a mosaic pattern) in the temperate zone, where forests and grasslands coexist. The mosaic structure of the forest-steppes is resulted from abiotic conditions, as well as the presence of herbivores and natural fires. The components of forest-steppes contribute differently to the overall conservation value of the whole landscapes due to the mosaic character. Forest patches can support grassland species in drought season, and can facilitate grassland regeneration in highly humid season (Erdős et al., 2019). Forest-steppes are considered as highly threatened ecosystems, along with the species inhabiting these habitats, due to habitat loss and fragmentation (Molnár et al., 2012).

Kurgans are unique landforms found in the steppe and forest-steppe belts from Eastern Europe to East Asia (Tóth, 2006). These are round or elliptical shaped man-made mounds, mainly made of soil, rarely stone (Sudnik-Wójcikowska and Moysiynko, 2014). Their history dates back to a period from the late Stone Age, 3300–2500 BCE (Dani and Horváth, 2012). Kurgans were originally built by ancient steppe cultures for burial purposes, and they were widespread in the steppe and forest-steppe zones from Hungary to Mongolia (Törbat et al., 2009). Their dimensions vary from several meters up to 100 m width with a height ranging from 0.5 to 15 m (Tóth, 2006). As a result of high cultural and historical importance, kurgans nowadays are considered as monumental protected sites, thereby having also nature conservation potential, despite this, agricultural production still threatens these habitats, as the law unfortunately is often not respected. Since agricultural intensification threatens these remaining natural grasslands throughout Europe, kurgans, despite their small size, have an important role in preserving farmland biodiversity (Moysiynko and Sudnik-Wójcikowska, 2008). Recent studies mainly focused on vegetation of kurgans, and found that these areas are likely to be biodiversity hotspots, but their value has not yet been widely investigated for avian communities (Deák et al., 2017).

In our study, we focused on forest-steppes and kurgans of the Hungarian Great Plain, where both habitats are severely threatened. Our aim was to investigate the effects of fragment size and configurational landscape heterogeneity (connectivity of the fragments) on bird community composition, species richness, abundance and functional diversity of the two fragmented grassland types. Since most of the fragmentation studies, which utilize birds as model organisms focuses on forest habitats, studies related to grasslands are still scarce. Our study aims to fill this knowledge gap through these hypotheses: H1: large fragments have higher bird diversity than smaller ones (Rösch et al., 2013). H2: We expect lower bird diversity with increasing habitat isolation (Kormann et al., 2015). H3: We expect moderation effects of study variables on functional traits, e.g. more negative effects for foraging specialists than for generalists (Cuervo and Møller, 2020).

## 2. Materials and methods

### 2.1. Study area

We conducted our study in the Southern Great Plain region of Hungary, in the Kiskunság and the Körös-Maros areas (Fig. 1). These areas include the two types of threatened, natural grassland habitat fragments: the forest-steppes in Kiskunság and kurgans in the Körös-Maros. Both areas are characterized by a continental climate with mean annual precipitation ranging from 500 to 550 mm and a mean temperature of 9.5 and 10 °C respectively (Kaur et al., 2019; Deák et al., 2016b).

### 2.2. Forest-steppe fragments

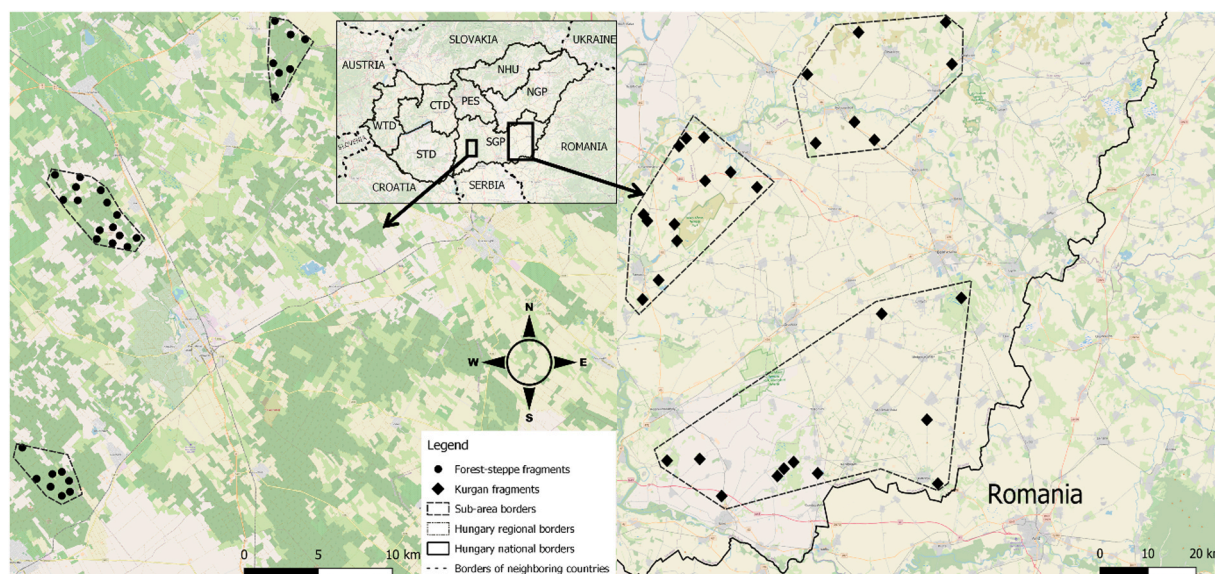
Sandy silt and loess rich soil characterize the forest-steppe area (Kaur et al., 2019). Forest-steppe grassland vegetation consists of drought tolerant tall grass species (e.g. *Festuca vaginata* and *Stipa borysthenica*, Erdős et al., 2018) and xeric tree and shrub species (e.g. *Populus alba*, *Crataegus monogyna*, *Juniperus communis*) (Erdős et al., 2018). Forest-steppe fragments are embedded in forest plantation monoculture matrix composed mainly by *Pinus sylvestris* and *P. nigra*, not native in the study area (Rédei et al., 2020), and native tree species (e.g. *Populus alba*), characterized by an even-age structure, and managed with clear-cut harvest system (pers. obs.). Almost all the selected forest-steppes were occasionally slightly grazed by sheep herds.

### 2.3. Kurgans

Kurgan area is characterized by fertile chernozem soil (Deák et al., 2016a). The heterogeneous topography of kurgans, in many cases, results in a different vegetation composition with drought tolerant species on the top and closed loess, alkali or sandy grassland on the slope and foot (Deák et al., 2016a). On kurgans, woody species can occur including trees (e.g. both native, *Pyrus pyraeaster*, and non-native, *Robinia pseudacacia*) and shrubs of abandoned loess steppic grassland (e.g. *Prunus spinosa*, *Sambucus nigra*) (Deák et al., 2016b). At the landscape scale, kurgans are embedded in a mosaic of agricultural matrix with maize, sunflower, alfalfa, and wheat as main crops. The selected kurgan fragments are annually mown with the exception of a few unmanaged fragments.

### 2.4. Study design

We performed digital map analysis (Google Satellite) with the geographical information system QGIS 3.6.1 Noosa, and extensive field survey of few hundred potential fragments in the two study areas to select 15 small (0.16–0.48 ha for forest-steppe; 0.01–0.10 ha for kurgan) and 15 large (0.93–6.88 ha for forest-steppe; 0.20–0.44 ha for kurgan) grassland fragments for each habitat type (total of



**Fig. 1.** Study area in the Southern Great Plain region of Hungary. West part of the map represents the Kiskunság area and forest-steppe fragments (black dots), whereas the East part represent the Körös-Maros area and kurgan fragments (black rhombus). The seven regions of Hungary are labelled with a code of three characters: WTD (Western Transdanubia), CTD (Central Transdanubia), PES (PEST), NHU (Northern Hungary), NGP (Northern Great Plain), SGP (Southern Great Plain), STD (Southern Transdanubia). Dark green: forest; Light yellow: farmland; Light green: grassland; Grey: urban area; Light blue: water surface. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Map source: ©Open Street Map 2020.

60 fragments). While kurgans are well and evenly distributed in a larger area due to cultural reasons, forest-steppe fragments are typically clumped on the sandy soil of the former Danube valley (Kiskunság area). We calculated connectivity index described by Hanski et al. (2000) as a landscape configuration gradient within a radius of 500 m for forest-steppe and 1000 m for kurgan fragments, measured by:

$$CI_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^\beta$$

$\alpha$  is a species-specific parameter describing a species' dispersal ability, and  $\beta$  is a parameter that describes the scaling of immigration. We set both parameters to 0.5 since we applied the connectivity index to an entire community (Rösch et al., 2013).  $A_j$  is the area of neighbouring natural grasslands  $j$  ( $m^2$ ) and  $d_{ij}$  is the edge-to-edge distance (in m) from the focal fragment  $i$  to the neighbouring fragment  $j$ . Large values of the index indicate high levels of connectivity between fragments. The values ranged from 0 to 2637 for kurgan (mean  $\pm$  SEM =  $689 \pm 748$ ) and 24–811 for forest-steppe (mean  $\pm$  SEM =  $394 \pm 206$ ). Since we found that the landscapes of kurgan and forest-steppe have two different spatial resolutions (grain size), we used 1000 m scale for connectivity in kurgan, whereas 500 m scale for forest-steppe (large-scale landscape of kurgan with large agricultural fields in the matrix and small-scale landscape of forest-steppes with very heterogeneous matrix dominated by forest plantations). Prior analyses, we first square root transformed connectivity to normalize the variable, then we ranged the values between zero and one for better indirect comparability of the two habitat types, which were analysed separately. Based on the location of each fragments within each habitat, we grouped the fragments in three sub-areas (see Fig. 1).

## 2.5. Bird survey and functional traits

We performed bird surveys through point counts (Bibby et al., 1992). We visited all fragments two times in 2019 during early morning (from 5:00 a.m. to 10:00 a.m.) once in each period (late April-early May and late May-early June) under calm and dry weather conditions. Two observers (F.M. and T.L.) visited 5–8 fragments per day together during the whole study period. To avoid possible bias due to variation in diurnal activity of birds, we visited each fragment in a different order during the second survey period.

We recorded all bird contacted, visually and acoustically, within 5 increasing radius from the centre of the fragment (0–25 m, 25–50 m, 50–75 m, 75–100 m and >100 m) whilst standing still for 10 min. Birds flying over (i.e. aerial hunters like swallows), aquatic birds (i.e. Ardeidae species), raptors, and migrating bird species based on the EBCC Atlas of European Breeding Birds (Hagemeyer and Blair, 1997) (mainly during the first survey period), were excluded from the analysis, because they were either inadequately sampled by our approach or because they were outside of their characteristic breeding habitat.

To classify the surveyed bird species, we selected a set of five functional traits: (i) foraging habit (ground prober, ground gleaner, understory gleaner, bark forager and canopy foliage gleaner or hawk, representing elevation gradient); (ii) diet (granivore, mixed diet and insectivore, representing a carnivory gradient); (iii) nest location (open on ground, reed nester/open in shrub, open in tree and cavity, representing an elevation gradient); (iv) home range size (small, medium, large) and habitat specialisation (grassland, generalist, woodland) (Table A1). Data on the trait attributes were taken from Cramp et al. (1994) except for the habitat specialisation for which the attributes were derived from Gregory et al. (2007). Number of categories for each trait was based on the work of Barbaro and van Halder (2009). To account for the different number of categories, all traits were ranged in values between 0 and 1. A comprehensive list of species recorded, including the values of each trait per species, is available in Table A2 of the Appendix. Correlations between selected functional traits were lower than 0.50 both for forest-steppe ( $\tau \leq 0.33$ ) and kurgan ( $\tau \leq 0.230$ ; see Table A3).

## 2.6. Statistical analysis

For abundance of each bird species, we pooled the data using the maximum abundance recorded between the two survey periods per fragment. Regarding species richness, we used the number of species that were present in the particular fragment at least in one survey period.

We calculated community weighted mean (CWM) for all traits, a single-trait functional diversity (FD) index, and also the RaoQ coefficient, a multiple-trait FD index, to characterize our fragments using the FD package in R (Laliberté et al., 2015). We have chosen RaoQ as representative functional diversity index of the studied communities, because this index is useful for detecting patterns of trait convergence or divergence compared to a random expectation (Ricotta and Moretti, 2011). Then we used linear mixed-effects models (GLMM) with normal errors and maximum log-likelihood method to test whether species richness, abundance and trait CWMs and RaoQ of birds were significantly affected by the following explanatory variables: (i) connectivity index (landscape configuration parameter), (ii) fragment size (either 'large' or 'small', as a local scale parameter). We analysed the two habitat types (forest-steppe and kurgan) separately, because their landscape matrix and its spatial resolution (both grain size and area extent), but also their size, are completely different. As random effect, we used a categorical variable representing the sub-area location of each fragment to consider spatial autocorrelation of bird survey points (see Fig. 1). In both areas, based on Moran's I test, response variables were spatially independent (see Table A4). In the full model we accounted for two-way interactions between the two explanatory variables. Akaike's Information Criteria was calculated to rank candidate models. Models with  $< 6 \Delta AICc$  (model with the lowest AICc) were used for model averaging (Richards, 2008) using the R package MuMIn (Barton, 2016). Furthermore, we identified potential influential outliers using both graphical methods (quantile-quantile plot) and Cook's distance  $> 1$  (Berghlund, 2018). Models were run with and without outliers of response variables as sensitivity analyses and compared by their AICc. We considered two models equivalent, if the  $\Delta AICc$

was lower than 2 (Burnham and Anderson, 2002; Table A5) prioritizing models without outliers.

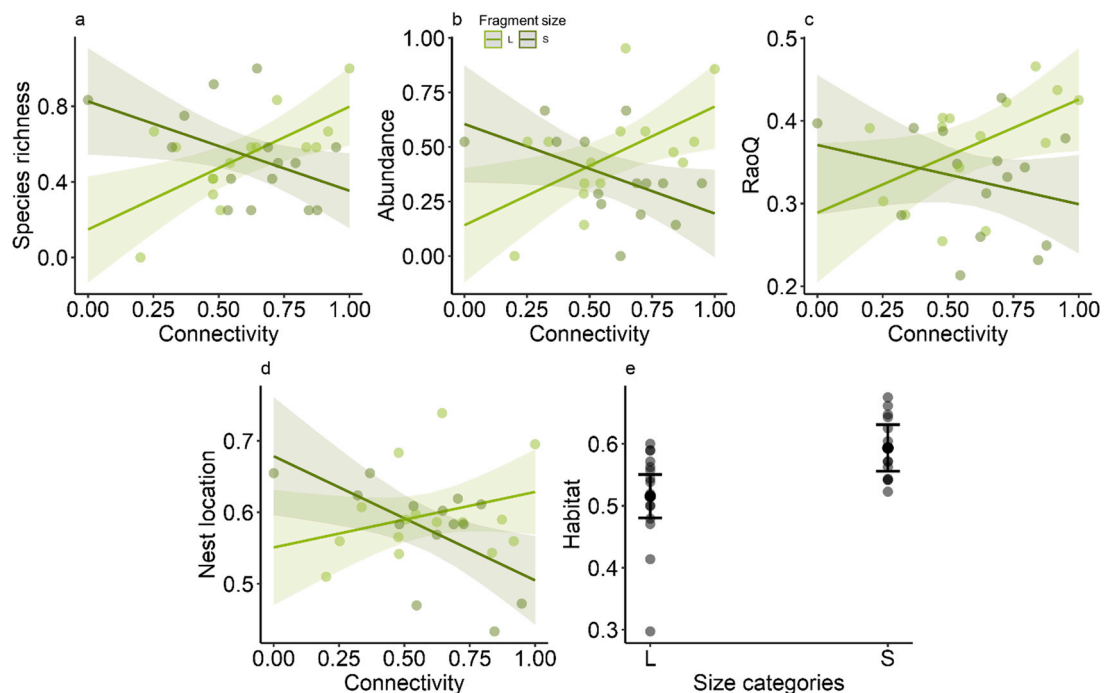
Finally, we performed redundancy analysis (RDA) to assess the effect of connectivity index and fragment size on the species composition of bird communities. Prior to the analyses, we applied a Hellinger transformation on the community data matrices (Legendre and Gallagher, 2001). Then we calculated a permutation test based on 9999 permutations to assess statistical significance of predictor variables using the package *vegan* (Oksanen et al., 2017).

### 3. Results

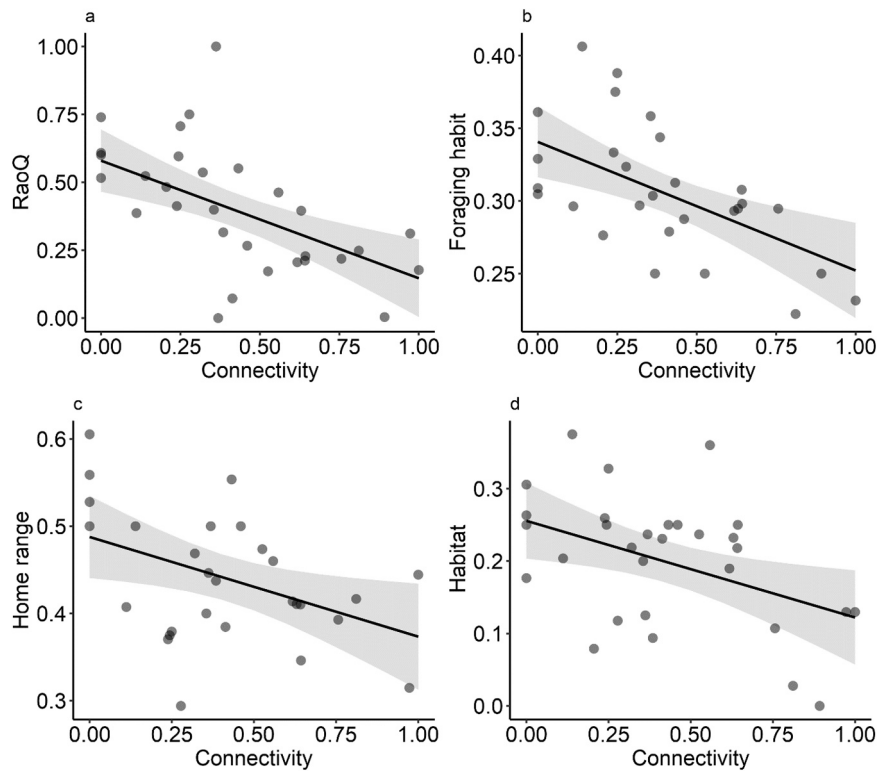
In the 60 survey points, we observed a total of 1485 birds belonging to 61 species (Table A2). In the forest steppes 784 individuals were present from 42 species, whereas the kurgans harboured 701 individuals of 42 species. The most abundant species on the forest steppe were common startling (*Sturnus vulgaris*), common chaffinch (*Fringilla coelebs*) and great tit (*Parus major*) (33.7% of all observed birds). The most common species in the kurgan region were Eurasian skylark (*Alauda arvensis*), common starling (*Sturnus vulgaris*) and common pheasant (*Phasianus colchicus*) (35.8% of all observed birds).

The GLMM showed that the interaction between fragment size and connectivity, affected the species richness, abundance, and nesting location of birds in forest steppes. Increasing connectivity increased species richness and abundance in case of large fragments, but decreased them in case of small fragments (Table A6; Fig. 2a and b). In forest-steppes, functional diversity (RaoQ) and CWM nest location (Fig. 2c and d) changed with size and connectivity. On small forest steppe fragments, community composition changed from species nesting at higher elevations to species nesting closer to ground. On large forest steppe fragments, the opposite pattern was observed. In small fragments, CWM habitat showed more woodland specialists compared to large fragments where more generalist species were present (Fig. 2e). In case of kurgans, we found that neither size, nor connectivity affected species richness or abundance (Table A7; Fig. 3). However, with increasing connectivity of the fragments, the overall functional diversity (RaoQ) decreased (Fig. 3a). Based on the CWM analysis, connectivity of kurgans entailed a change in functional traits. There was a change in bird community composition, species foraging at higher elevation changed to species foraging at lower elevations (Fig. 3b). The CWM values of home range trait also changed with increasing connectivity: here we observed a decrease from larger to smaller home range (Fig. 3c). The CWM habitat trait values changed from generalist species to grassland specialist species due to higher connectivity (Fig. 3d).

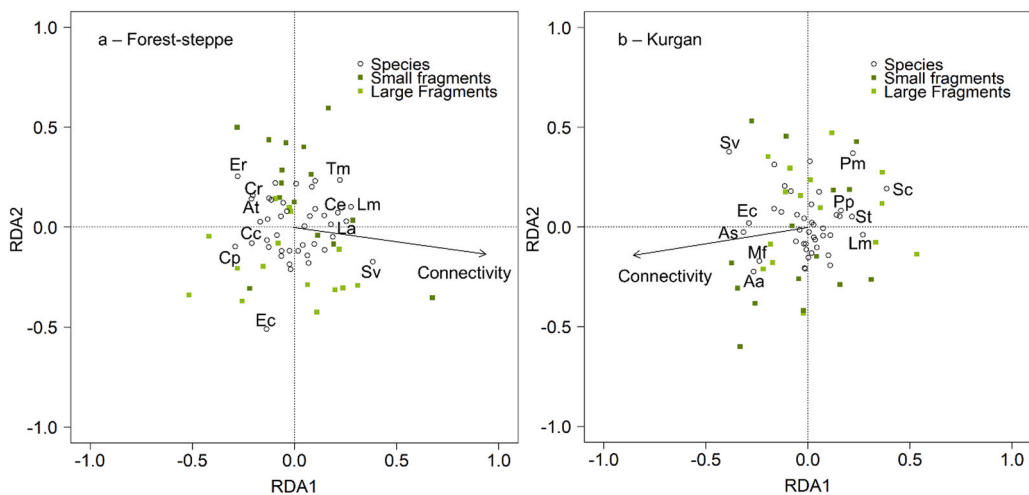
According to the RDA of forest steppe, we found a marginal effect of connectivity on bird community composition. In the case of



**Fig. 2.** The interacting effect of connectivity and size on (a) species richness (sample size = 30), (b) abundance (sample size = 29), (c) RaoQ (sample size = 30), (d) CWM nest location trait (open on ground, reed nester/open in shrub, open in tree and cavity, representing an elevation gradient; sample size = 29) and (e) CWM habitat trait (grassland, generalist, woodland; sample size = 30) in forest-steppe fragments. From a to d, dots represent the predicted values per each fragment (dark green: small fragments, light green: large fragments). Regression lines represent the fragments (dark green: small fragments; light green: large fragments). 95% CIs for the regression lines are showed (dark green: small fragments; light green: large fragments). In (e) black dot represent the median value and grey dots represent large and small fragments predicted values per each fragment. Lower black lines represent the 1st quartile of the predicted values, upper lines represent the 3rd quartile of the predicted values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** The effect of connectivity on the (a) RaoQ (sample size = 30), (b) CWM foraging habit trait (ground prober, ground gleaner, understory gleaner, bark forager and canopy foliage gleaner or hawkker, representing elevation gradient; sample size = 28), (c) CWM home range trait (< 1 ha, 1–4 ha, > 4 ha; sample size = 28) and (d) CWM habitat trait in kurgan fragments. Dots represent the predicted values. 95% CIs for the regression lines are showed.



**Fig. 4.** Redundancy analysis biplot for all species of bird communities in Forest-steppe (a) and Kurgan (b). Empty dots represent the species, squares represent the fragments (dark green: small fragments; light green: large fragments). Species code consists of the first letter of genus plus the first letter of species names (a - Tm: *Turdus merula*; Ce: *Caprimulgus europaeus*; Lm: *Luscinia megarhynchos*; La: *Lullula arborea*; Sv: *Sturnus vulgaris*; Ec: *Emberiza citrinella*; Cp: *Columba palumbus*; Cc: *Cuculus canorus*; At: *Anthus trivialis*; Cr: *Corvus corax*; Er: *Erithacus rubecula*; b - Pm: *Passer montanus*; Sc: *Sylvia communis*; Pp: *Pica pica*; St: *Streptopelia turtur*; Aa: *Acrocephalus arundinaceus*; Mf: *Motacilla flava*; As: *Acrocephalus scirpaceus*; Ec: *Emberiza calandra*; Sv: *Sturnus vulgaris*). For visibility, only species with the highest fraction of variance are fitted (score > 0.2 and score < -0.2) with first RDA axes are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

kurgan bird communities, we found that a significant part of the variation was explained by connectivity, but fragment size had no effect (Fig. 4, Table A8).

#### 4. Discussion

We studied the effects of fragment size (small vs. large fragments), and configurational landscape heterogeneity (connectivity of fragments) on avian communities inhabiting two different grassland habitat types (forest-steppe and kurgan). We found that interaction between fragment size and connectivity had strong effect on birds in forest-steppes, whereas connectivity was the main driver of bird community composition in the kurgans. Forest-steppe bird species richness, abundance and trait dissimilarity increased with increasing connectivity in large fragments while decreasing in small ones, whereas low height nesting birds were associated with more connected small fragments than large ones. Birds of kurgan area showed higher traits similarity in well-connected fragments than more isolated ones and were characterized by small home range size and ground feeding habit.

##### 4.1. Forest-steppe

Our results partially support our first two hypotheses. On the one hand, species richness, abundance and functional diversity (RaoQ) of birds increased with connectivity in large fragments. On the other hand, small fragments showed an opposite trend. Since we considered the forest plantation monoculture as matrix, more connected fragments are a result of fragments surrounded by a higher amount of grassland patches. As a result, in small fragments, pine tree plantation plays a major role in diversity and abundance favouring woodland specialist species like cavity (e.g. *Dendrocopos major*) and open in tree nester species (e.g. *Fringilla coelebs*). Despite the increase of connectivity of small fragments, grassland specialist birds are negatively affected by habitat fragmentation, being better represented in large fragments than in small ones (Caplat and Fonderflick, 2009). Thus, the amplitude of forest bird loss is higher than the gain of low height nester birds (e.g. *Lullula arborea*) leading to an overall decrease in diversity and abundance even with an increase of connectivity (i.e. grassland at landscape scale). Moreover, the disturbance by forestry practice can have a higher influence on grassland (mainly ground nester) in small than in large fragments, particularly in the delicate period of the breeding season. However, compared to another study in forest-steppe habitat (see Somay et al., 2009) even large fragments did not host grassland species that would be expected in the area, like the tawny pipit (*Anthus campestris*). As reported by Cramp (1994), this species explores patches of 3–5 ha in continuous habitat, an area that was available in at least three of our studied fragments. Moreover, another expected species in forest-steppe habitat like the northern wheatear (*Oenanthe oenanthe*), was recorded only once in our surveys. Compared to the tawny pipit, this species needs smaller continuous patches (1–2 ha; Cramp, 1994), that was available in almost half of our forest-steppe fragments (13 out of 30). Caplat and Fonderflick (2009) had similar results with even larger fragment size available for the species concluding that other mechanisms (e.g. fine changes in vegetation) that were not accounted for, could have explained the species area requirements. In our case, as shown by the results on the CWM nesting trait, the increase in the height from the ground of breeding bird with increasing connectivity in large fragments, probably suggests a certain degree of encroachment (e.g. shrub). Higher shrub cover, on one hand, can enhance open in shrub nester (e.g. *Lanius collurio*), but on the other can disadvantage ground breeding species (like tawny pipit and northern wheatear) that requires a minimum continuous area for breeding (Robbins et al., 1989) not available due to the encroachment process. This hypothesis can be supported also by the evidence of higher values of CWM habitat trait in small fragments than in smaller ones, meaning a shift towards more woodland bird species. Thus, also a fine-scale environmental filtering could have occurred in our study area.

##### 4.2. Kurgan

We did not find any effect of connectivity or fragment size both on bird species richness and abundance, however (RaoQ) was higher in isolated kurgans than in more connected ones. Thus, bird communities changed with the connectivity gradient, from highly isolated kurgans (high amount of agricultural matrix) to highly connected ones (high amount of grassland patches). The amount of grassland specialists increased (e.g. *Emberiza calandra*) at the expense of non-grassland birds (e.g. *Streptotelia turtur*) in well-connected kurgans. RaoQ assesses trait dispersion in trait space (Botta-Dukát, 2005), higher proportion of grassland specialists lead to a more specialized and less variable trait state composition, maintaining their ecosystem function in grasslands. This explanation is also supported by the change in foraging habit and home range size, both decreasing with connectivity. Grassland birds observed in our study were mainly ground gleaner with small home range size. Moreover, these findings support also our third hypothesis that more isolated kurgans act as a filter for more specialised bird species (e.g. *Motacilla flava*), but not for generalists (e.g. *Corvus cornix*). Despite the capacity of many bird species to utilize landscape at large spatial scale (Tschardt et al., 2012), generalist birds with large home range, can exploit resources at larger spatial scales than specialist birds. Moreover, we found how better connected kurgans are inhabited by more grassland species than more isolated ones. Since the amount of grasslands in the landscape has a strong effect on grassland specialist birds, kurgans are not used by them if not connected to continuous grasslands.

##### 4.3. Habitat type comparison

The two grassland types considered in our study are different both in the habitat structure and bird communities. Partly due to their intrinsic abiotic characteristics, but also by the human induced alteration driven by the land-use assigned to each area. Among the 23 bird species present in both bird communities, only three were associated with grassland habitats (*Upupa epops*, *Oenanthe oenanthe* and

*Lanius collurio*), whereas the other 20 are forest associated species. We expected this ratio as kurgans are often subject to tree and shrub encroachment processes and sometimes surrounded by hedgerows delimiting agricultural fields (Deák et al., 2016b). Furthermore, conifer plantation can support as many bird species as the natural vegetation (Lantschner et al., 2008). However, when it is established in steppe areas, it leads to a change in bird community since grassland specialists cannot find suitable habitat inside the plantations (Christie et al., 2004). Thus, forest-steppe favours more woodland species than grassland and vice versa in kurgan (higher CWM for habitat trait in forest-steppe than in kurgan). Nevertheless, our findings suggest that maintaining large and well-connected grassland fragments can preserve a large part of grassland bird specialists in landscapes altered by forest management practices.

Despite kurgans play an important role for preserving steppic vegetation (Deák et al., 2016a), these grassland fragments in intensive agricultural areas are mainly too small to provide suitable habitat for grassland birds. Intensively managed agricultural landscapes dominated by cereal or maize crops has low amount of foraging resources and potential nesting sites for many birds (Morelli et al., 2018). Increasing connectivity between fragments favour grassland specialists inverting the biotic homogenization in more isolated grassland fragments due to the replacement of generalist species by specialist ones (Clavero and Brotons, 2010). Moreover, less-redundant systems that account for small number of redundant species, provide stronger association between species richness and functional richness (Farias and Jaksic, 2011), increasing the functional space, thus the trait diversity in the community (Morelli et al., 2018).

## 5. Conclusion

We studied bird communities in grassland habitat fragments embedded in agricultural and plantation forestry matrix. Bird communities responded differently to the landscape and local environmental variables in the two grassland habitat types. We showed that even in fragmented landscapes, grasslands can maintain a diverse bird community. Nonetheless, specialist grassland species like, tawny pipit or northern wheatear were absent or rare in our study area, indirectly confirming the difficulties of these species to thrive in altered habitats, as reported by other authors in Europe, where both species face a severe population decline (Hagemeijer and Blair, 1997; BirdLife International, 2015).

Despite the lack of fine-scale habitat descriptors (e.g. amount of encroachment of the fragments) could have, in some cases, hampered our results, our study importance lies not only in the fact that we accounted simultaneously for two different grassland types, but also by the fact that these habitats are embedded in intensive human altered landscapes. In fact, natural and semi-natural protected areas cannot account alone for the task of biodiversity conservation, and long-term conservation strategies need to account for the contribution of agricultural and intensive forestry areas to biodiversity (Tallis et al., 2009; Batáry et al., 2020). Conservation measures should be implemented to preserve or improve habitat quality in areas under management, like in forestry managed areas, where plantations are managed with clear-cut harvest disrupting the habitat and therefore the biotic community therein. Thus, improving matrix quality and thereby increasing grassland connectivity could ultimately support the maintenance of species and functionally diverse bird communities.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

We would like to thank Dávid Korányi for his work on GIS providing the landscape metric used in this work. This study was also supported by the Hungarian National Research, Development and Innovation Office (NKFIH KKP 133839). We thank Jiri Reif and an anonymous reviewer for their helpful comments.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01687](https://doi.org/10.1016/j.gecco.2021.e01687).

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