



Taxonomic, phylogenetic and functional homogenization of bird communities due to land use change

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ABSTRACT

Biotic homogenization, the increasing similarity of biotas over time, is an important topic in biodiversity conservation and has been widely linked to anthropogenic factors, e.g., land use change and climate change. However, so far few studies have simultaneously tested the taxonomic, phylogenetic and functional homogenization caused by human activities. Here, we analyzed the effects of land use change on biotic homogenization of bird communities in these three biodiversity dimensions in the steppe region in Inner Mongolia, China. The results showed that taxonomic, phylogenetic and functional similarities were significantly lower in relatively natural grassland than in the other disturbed habitats, i.e., planted woodland, farmland and village. In addition, there were also higher associations between bird community similarities and climate distances in natural grassland than in the other disturbed habitats. These results suggest that more intense land use types result in consistent taxonomic, phylogenetic and functional homogenization of bird communities, while at the same time diminish community turnover across climate gradients. These findings indicate that anthropogenic activities in this steppe region may not only cause biodiversity loss in taxonomic level, but also in other biodiversity dimensions, highlighting the important role of natural steppe in biodiversity conservation.

1. Introduction

Biotic homogenization, the process of an increasing similarity of biotas over time, is an important challenge for biodiversity management and conservation, and is primarily driven by two processes, i.e., environmental modification and species introduction (McKinney and Lockwood, 1999; Olden, 2006). Massive anthropogenic activities, e.g., urbanization, land use change, damming and eutrophication, have greatly altered the nature habitats at the regional and global scales, creating similar environment with homogenized biological communities (Karp et al., 2012; Petsch, 2016; Ibáñez-Álamo et al., 2017). These homogenized communities would further generate serious ecological and evolutionary consequences (Olden et al., 2004; van der Plas et al., 2016; Nowakowski et al., 2018).

Although biotic homogenization may operate on multiple dimensions of biodiversity, e.g., taxonomic, phylogenetic and functional diversity, few attempts have simultaneously assessed the extent to which

they are affected by homogenization. Phylogenetic diversity could reflect the evolutionary history of biotic communities and act as proxy of functional diversity, and may be linked with historical environment change and ecosystem functioning (Webb et al., 2002; Srivastava et al., 2012). Biotic communities with greater functional diversity may access more resources, leading to higher community productivity, ecosystem stability and ecosystem service (Moretti et al., 2006; Cadotte et al., 2009). Phylogenetic and functional homogenization of biotic communities may partially be driven by different ecological mechanisms from taxonomic homogenization (Olden, 2006; Devictor et al., 2008), although they are inherently connected to some extent. Overall, a combined taxonomic, phylogenetic and functional perspective will likely provide a more comprehensive understanding of the patterns and processes of biotic homogenization (Barnagaud et al., 2017; Jarzyna and Jetz, 2017).

Furthermore, climate is a key natural as well as human-influenced factor shaping biodiversity patterns at multiple scales, and it may

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interact with anthropogenic activities in doing so (Frishkoff et al., 2016; Karp et al., 2018). Notably, anthropogenic activities may erase the widely tested climate-biodiversity relationships (Karp et al., 2012, 2018). For example, a study on Neotropical birds shows that dry climate-affiliated species are more likely to occupy agricultural sites than wet climate-affiliated species, which are more likely to occur in forest (Frishkoff et al., 2016). Also, another study on Neotropical birds finds taxonomic beta diversity to be better explained by climate in natural forest than in farmland (Karp et al., 2018).

In terms of the intensity of anthropogenic activities, the temperate steppe is one of the most threatened biomes at the global scale (Hoekstra et al., 2005). Notably, a study about bird conservation in North America suggests that grassland birds experienced the greatest proportion of decreases (56% species declined significantly) from 1966 to 1998 (Brawn et al., 2001). Located in Central Asia, Inner Mongolia is an important component of the Eurasian Steppe, the world's largest grassland (Wu et al., 2015). However, in the past decades massive anthropogenic activities, e.g., irrigation, coal mining and urbanization, have significantly changed the landscapes (John et al., 2009; Tao et al., 2015). And so far, no studies have assessed the effect of these anthropogenic activities on bird diversity in this region.

In this study, we assessed the effects of land use change (from natural grassland to planted woodland, farmland and village) on bird communities in Inner Mongolia. Specifically, we first tested whether taxonomic, phylogenetic and functional similarities of bird communities were consistently higher (equaling increasing homogenization) in the three anthropogenic habitats, i.e., planted woodland, farmland and village, as compared to the natural grassland. Secondly, we tested whether the associations between climate distance, a natural driver of community differentiation, and bird community similarity, was reduced in the anthropogenic habitats relative to the natural grassland.

2. Materials and methods

2.1. Study area

Inner Mongolia is located in North and Northeast China, running about 3000 km from northeast to southwest and covering 120 million ha (Wu et al., 2015). Because of the large longitudinal range, this region has strong east-west temperature and precipitation gradients (mean annual temperature ranges from -2 to 6°C and mean annual precipitation ranges from about 40 to 450 mm), resulting in a highly diverse vegetation types (forest, grassland and desert) and bird composition (467 known bird species) (Wu et al., 2015; Xu, 2015). The main anthropogenic activities include farming, grazing, coal mining and urbanization (Wu et al., 2015).

2.2. Bird data

Ten sites were selected across Inner Mongolia, China (Fig. 1). At each site, bird transects were sampled in four habitats, i.e., natural grassland, planted woodland, farmland and village (except one site without grassland transect). Because the 10 sites covered a large longitudinal range, the specific habitat is not quite homogeneous, e.g., the transects in grassland included forest steppe, typical steppe and desert steppe, and the transects in farmland included maize, potato, oat and other types. Planted woodlands were composed of some common tree species in Inner Mongolia, e.g., species in *Populus*, *Pinus*, *Salix* and *Ulmus*. Villages were mainly composed of farmer's house and country lane. In all, about 25 (18–30) transects were sampled at each site. Finally, a total of 246 transects were investigated, with 67 in grassland, 67 in woodland, 56 in farmland, and 56 in village. We surveyed birds seen and heard in each transect (1000×100 m) once per month during the breeding season (from May to July, each transect was surveyed three times). All transects were investigated by experienced observer at a constant speed ($1.5\text{--}2\text{ km} \times \text{h}^{-1}$) and the location of each transect

was recorded by GPS to ensure that the three surveys were conducted exactly at the same place. Surveys were performed during 3 h after sunrise and 3 h before sunset, avoiding conditions of heavy rain and high winds. For subsequent calculating, bird assemblages encompassed all species observed at a transect during the three visits. We excluded species never occurring in terrestrial habitats and also excluded transects with fewer than three species. This selection resulted in a matrix of 246 transects and 100 species. The threatened status of the 100 species were checked according to a recent publication (Jiang et al., 2016). Species numbers occurred in the four habitats were 65 in grassland, 85 in woodland, 61 in farmland, and 49 in village.

2.3. Functional dendrogram and phylogenetic data

We used body mass and trophic level to build the functional dendrogram for the following functional structure analyses. Body mass is assumed to be the most informative trait of bird species because it is directly connected with birds' extinction vulnerability and resource utilization (Ding et al., 2013). Trophic level is related with sensitivity to habitat change and resource requirements (Ding et al., 2013). Body mass data of all 100 species was compiled from the third and fourth volumes of Fauna of Inner Mongolia (Xu, 2007, 2015). Trophic level was coded as omnivores (1), granivores (2), frugivores (3), nectarivores (4), insectivores (5), piscivores (6) and carnivores (7) (Wang et al., 2018). Distance of the two traits among all species were generated using Gower's distance. The functional dendrogram was then constructed by hierarchical clustering using 'complete' method (Fig. S1).

We downloaded a distribution of 5000 phylogenies from the global phylogeny of birds (Jetz et al., 2014), including all 100 bird species in our study. We then sampled five thousand pseudo-posterior distributions and constructed the Maximum Clade Credibility tree using mean node heights by the software TreeAnnotator v1.8.2 of the BEAST package (Drummond and Rambaut, 2007). The resulting consensus phylogeny was used for all subsequent phylogenetic analyses (Fig. S2).

2.4. Taxonomic, phylogenetic, functional similarity

Sørensen index was used to calculate taxonomic similarity, which is the proportion of the shared species to the total number of species occurred in two samples (Soininen et al., 2007). Although there are many other measures of similarity index, we selected Sørensen index because it is relatively independent of species richness and comparable with Phylosor index (Soininen et al., 2007). To compute phylogenetic similarity we used the Phylosor index derived from Sørensen index, which is the proportion of shared branch length to total evolutionary branch length of two samples (Feng et al., 2012). Functional similarity was also estimated using Phylosor index based on the functional dendrogram. The standardized effect size (SES) of phylogenetic and functional similarities for each assemblage was also calculated to eliminate the effect of taxonomic similarities. $\text{SES}_{\text{phylosor}}$ was computed as

$$\text{SES}_{\text{phylosor}} = \frac{\text{Phylosor}_{\text{obs}} - \text{mean Phylosor}_{\text{rnd}}}{\text{sd Phylosor}_{\text{rnd}}}$$

where $\text{Phylosor}_{\text{obs}}$ is the observed phylogenetic or functional 'Phylosor' similarities of bird communities between two transects in each habitat, $\text{mean Phylosor}_{\text{rnd}}$ is the mean 'Phylosor' similarities of the null models (shuffle species labels in community data while maintain species richness and species shared between communities for 999 times), and $\text{sd Phylosor}_{\text{rnd}}$ is the standard deviation of 'Phylosor' similarities of the null models. Therefore, SES estimates the differences between the observed values and expected values of null models, indicating the extent of similarities after controlling the effect of taxonomic similarities.

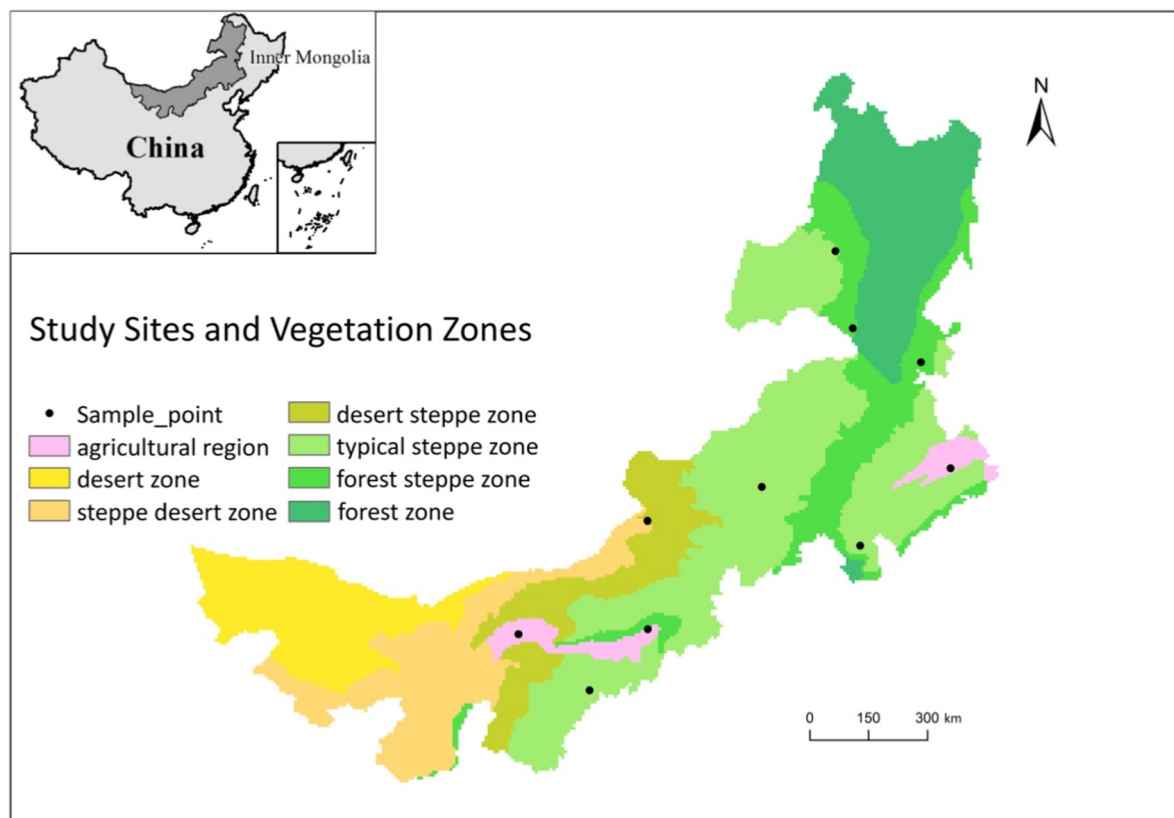


Fig. 1. Distribution of the 10 sites in Inner Mongolia. All sites are located in regions with steppe being the natural vegetation.

2.5. Climate data

Both contemporary and paleo climate may have influence on current biodiversity patterns (Currie et al., 2004; Svenning et al., 2015). Therefore, we used the following four climate variables, i.e., mean annual temperature (MAT), mean annual precipitation (MAP), temperature in Last Glacial Maximum (MAT in LGM), and precipitation in Last Glacial Maximum (MAP in LGM), which were downloaded from WorldClim (Hijmans et al., 2005). MAT in LGM and MAP in LGM were obtained from the Community Climate System Model version 3 (CCSM3; Otto-Bliesner et al., 2006) and the Model for Interdisciplinary Research on Climate version 3.2 (MIROC3.2; Hasumi and Emori, 2004). We then respectively calculated the mean values of MAT in LGM and MAP in LGM by averaging the two models. Change in MAT and change in MAP were then calculated as contemporary values minus mean LGM values.

2.6. Statistical analyses

Because bird transects in each site were close to each other, linear mixed effects (lmer) models were used to control the spatial autocorrelation of these bird transects, with site as a random factor. Tukey's multiple comparisons based on lmer models were conducted to test the differences of taxonomic, phylogenetic and functional similarities among the four habitats, i.e., grassland, woodland, farmland and village. Differences of SES phylogenetic and functional similarities among the four habitats were also assessed using tukey's multiple comparisons.

Single variable ordinary least squares (ols) and lmer models were conducted to estimate the associations between each climate variable distance (MAT, MAP, MAT_{Change}, MAP_{Change}) and bird community similarity in different habitats. Multiple regression of ols and lmer models were also used to find the best combination of variables for explaining the community similarities. The normal distribution of ols and lmer

residuals was assessed using the Kolmogorov-Smirnov test. Akaike weight (w), which indicates the probability of each model being the best model and the relative advantage of the competing models, was used to select the optimal combination of variables (Wagenmakers and Farrell, 2004). Akaike weight of each climate variable distance in all lmer models was also used to describe its relative importance. Each climate variable distance (MAT, MAP, MAT_{Change}, MAP_{Change}) was computed as the Euclidean distance. Correlations among these four climate variable distances in each habitat were smaller than 0.7 (Table S1). Because of the discrepancy of magnitude of climate variables, all climate distances and community similarities values were standardized (mean = 0 and standard deviation = 1).

Taxonomic, phylogenetic and functional similarities were computed using the function 'betadiver' and 'phylosor' in vegan and picante package. The 999 random phylogenetic and functional similarities were generated using 'phylosor.rnd' function in picante package. Multiple comparisons were carried out using the function 'glht' in multcomp package. Lmer multiple regressions were performed using 'lme4' R package. All calculations were performed in R statistical software version 3.3.0 (R Core Team, 2016).

3. Results

There were two vulnerable species, five near threatened species and one data deficient species in the 100 species found in our investigation. Notably, seven of the eight species occurred in natural grassland (65 species in total), while four species occurred in woodland (85 species in total) and farmland (61 species in total), and only one species occurred in village (49 species in total) (Table S2).

Taxonomic, phylogenetic and functional similarities were significantly different among the four habitats, i.e., grassland, woodland, farmland and village (Fig. 2). Similarity was lowest in grassland (0.24, 0.42 and 0.70 for species, phylogeny and functional traits,

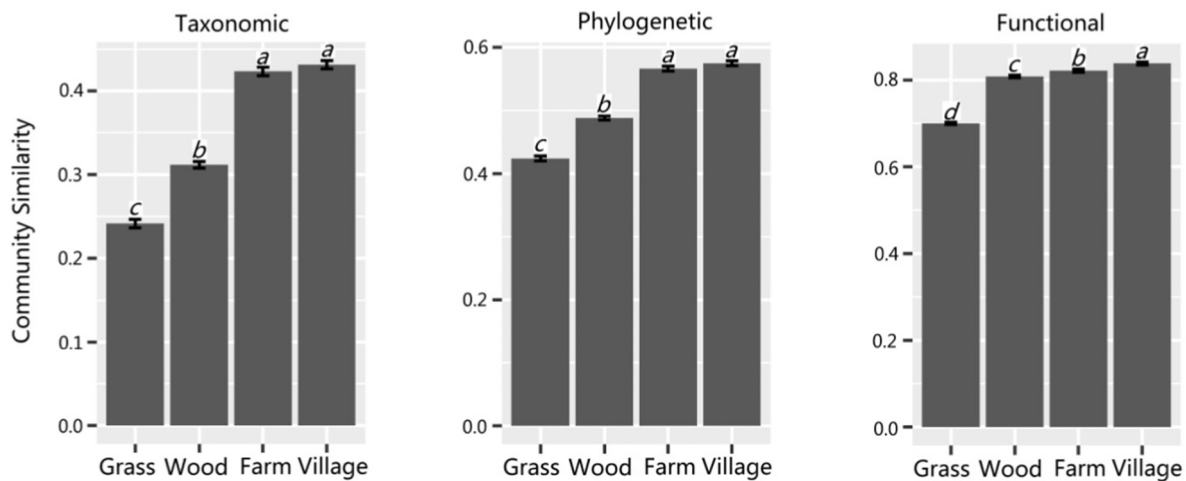


Fig. 2. Results of Tukey's multiple comparisons for the taxonomic, phylogenetic and functional similarities (Sørensen index) of bird communities in four habitats, i.e., grassland (Grass), woodland (Wood), farmland (Farm) and village, based on linear mixed effects models. Grassland, the relative natural habitat, has the lowest values for taxonomic, phylogenetic and functional similarities.

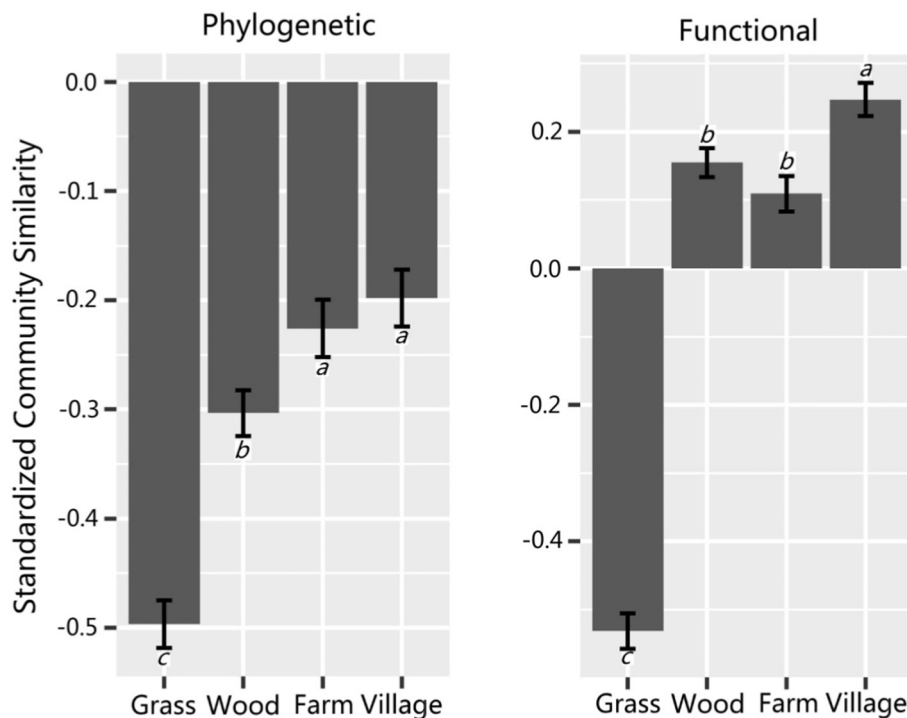


Fig. 3. Results of Tukey's multiple comparisons for the standardized effect size (shuffle species labels in community data while maintain species richness and species shared between communities for 999 times) of phylogenetic and functional similarities of bird communities in four habitats, i.e., grassland (Grass), woodland (Wood), farmland (Farm) and village, based on linear mixed effects models. Again, grassland tended to have the lowest values for phylogenetic and functional similarities.

respectively), followed by woodland (0.31, 0.49, 0.81), farmland (0.42, 0.57, 0.82) and village (0.43, 0.57, 0.84) (Fig. 2). Furthermore, SES phylogenetic and functional similarities showed similar patterns, i.e., grassland tended to have the lowest similarities (Fig. 3).

Moreover, single variable regression results showed that distances of mean annual precipitation (MAP) and change in MAP were the two variables most associated with taxonomic, phylogenetic and functional similarities in natural grassland, and their associations decreased in the other disturbed habitats (Table 1). Akaike weight of each climate variable distance in all lmer models also indicated that climate variable were more important in natural grassland (Table 1). Generally, distances of most climate variables were negatively correlated with community similarities (Table 1). Lmer multiple regression results showed that the taxonomic, phylogenetic and functional similarities in natural grassland were better explained by climate variable distances than in other three disturbed habitats, i.e., woodland, farmland and village

(Table 2). Specifically, for taxonomic similarities, r^2 of the model with highest Akaike weight ($w = 1$) in grassland was 0.53, higher than other three habitats, i.e., 0.38 in woodland ($w = 0.88$), 0.30 in farmland ($w = 0.93$), and 0.32 in village ($w = 0.41$) (Table 2). And the patterns were similar for phylogenetic and functional similarities (Table 2). Ols multiple regression showed similar patterns (Table S3). r^2 , AIC and w of all combinations of variables based on lmer models were listed in Tables S4–S15.

4. Discussion

Transects in the natural grassland harbored most of the vulnerable, near-threatened and data deficient species, indicating the important role of natural steppe in bird diversity conservation in this region. Our results also showed consistently less taxonomic, phylogenetic and functional homogenization of bird communities in natural grassland

Table 1

Standardized coefficients of ordinary least squares (Coef_{ols}) and linear mixed effects models (Coef_{lmer}) for single climate variable distance to explain the taxonomic, phylogenetic and functional similarities in the four habitats. Akaike weight (w) of each variable based on all lmer models was also listed. MAT and MAP is the distance of mean annual temperature and precipitation. MAT_{Change} and MAP_{Change} is the distance of contemporary-Last Glacial Maximum change in MAT and MAP. *p < 0.01.

	Grassland			Woodland			Farmland			Village		
	Coef _{ols}	Coef _{lmer}	w	Coef _{ols}	Coef _{lmer}	w	Coef _{ols}	Coef _{lmer}	w	Coef _{ols}	Coef _{lmer}	w
Taxonomic												
MAT	-0.46*	-0.18*	1	-0.56*	-0.54*	1	-0.50*	-0.42*	1	-0.50*	-0.51*	1
MAP	-0.49*	-0.24*	1	-0.27*	-0.24*	1	-0.22*	-0.16*	1	-0.05	0.01	0.33
MAT _{change}	-0.28*	0.07*	1	-0.19*	-0.12*	0.88	-0.29*	-0.16*	0.03	-0.23*	-0.15*	0.30
MAP _{change}	-0.53*	-0.30*	1	-0.21*	-0.13*	1	-0.24*	-0.11*	0.04	-0.11*	0.02	0.15
Phylogenetic												
MAT	-0.38*	-0.08*	1	-0.39*	-0.36*	1	-0.40*	-0.29*	1	-0.34*	-0.36*	1
MAP	-0.52*	-0.31*	1	-0.25*	-0.21*	1	-0.20*	-0.15*	1	-0.13*	-0.07*	0.09
MAT _{change}	-0.27*	0.07*	1	-0.18*	-0.12*	0.02	-0.29*	-0.15*	0.08	-0.25*	-0.18	0.07
MAP _{change}	-0.51*	-0.26*	1	-0.23*	-0.18*	0.03	-0.22*	-0.10*	0.04	-0.15*	-0.06	0.04
Functional												
MAT	-0.16*	-0.03	0.85	-0.10*	-0.09*	0.99	-0.03	0.09*	0.99	-0.10*	-0.10*	0.05
MAP	-0.31*	-0.23*	1	-0.02	0.00	0.02	-0.11*	-0.10*	0.11	-0.01	-0.01	0.17
MAT _{change}	-0.14*	0.02	0.05	-0.04	-0.03	0.03	-0.18*	-0.11*	0.99	-0.15*	-0.16*	1
MAP _{change}	-0.24*	-0.13*	0.07	-0.07*	-0.05	0.08	-0.16*	-0.15*	0.99	-0.11*	-0.11*	0.80

than in disturbed habitats, i.e., woodland, farmland and village. While biotic homogenization of bird communities driven by anthropogenic activities has been documented in taxonomic, phylogenetic and functional dimensions, respectively (Morelli et al., 2016; Barnagaud et al., 2017), to our knowledge, simultaneous incorporation of all the three facets remain scarce. Moreover, we found higher associations between bird community similarities and climate variable distances in natural grassland than in disturbed habitats. Taking together, these findings suggest that anthropogenic activities in this steppe region may cause biodiversity loss not only in taxonomic level, but also in other biodiversity dimensions, emphasizing the crucial role of natural steppe in biodiversity conservation in this region.

4.1. Taxonomic homogenization of bird communities due to land use change

Land use change driven by anthropogenic activities may often benefit some species (i.e., widespread species/generalists) and negatively affect others (i.e., rare/endemic species), resulting in increased taxonomic similarities across sites and leading to biotic homogenization (McKinney and Lockwood, 1999). In particular, when rare species are replaced by generalists, communities would become more similar in

space and time (McKinney, 2006). Much evidence has been reported supporting this. For instance, a multi-taxa study including birds, plants and insect in Brazilian Amazon finds that land use conversion (forest to agriculture) reduces species beta diversity, leading to homogenization in a broad spatial scale (Solar et al., 2015). Moreover, a global study of terrestrial bird turnover pattern suggests that biotic homogenization in regions with higher taxonomic and trait turnover is strongly affected by human activities (Barnagaud et al., 2017).

In line with these studies, we also found a consistent increase in taxonomic similarities from grassland to village along the human disturbance gradient. Among the 56 bird transects in village, *Passer montanus* occurred in 52 transects, *Hirundo rustica* occurred in 46 transects, and *Pica pica* occurred in 40 transects. This pattern was similar in woodland (the three species occurred in 57, 45, 45 transects of 67 transects, respectively) and farmland (the three species occurred in 53, 45, 42 transects of 56 transects, respectively), which may drive the high taxonomic homogenization in these habitats. All the three species prefer habitats with intense human activities, e.g., villages and farmland (Xu, 2015). In contrast, among the 67 bird transects in grassland, *Calandrella cheleensis* only existed in 37 transects, *Passer montanus* in 31 transects, and *Galerida cristata* in 26 transects. *Calandrella cheleensis* and

Table 2

Linear mixed effects models with maximum Akaike weights (w) values for explaining the taxonomic, phylogenetic and functional similarities in the four habitats. MAT and MAP is the distance of mean annual temperature and precipitation. MAT_{Change} and MAP_{Change} is the distance of contemporary-Last Glacial Maximum change in MAT and MAP. Coefficient of each variable in the model, r^2 (fixed and random factor together) and Akaike weight (w) of each model were listed. *p < 0.01.

Type	Best Model	r^2	w
Taxonomic			
Grassland	MAT*(-0.35) + MAT _{Change} *(0.18) + MAP*(-0.17) + MAP _{Change} *(-0.24)	0.53	1
Woodland	MAT*(-0.58) + MAT _{Change} *(0.08) + MAP*(-0.25) + MAP _{Change} *(0.11)	0.38	0.88
Farmland	MAT*(-0.42) + MAP*(-0.16)	0.30	0.93
Village	MAT*(-0.51)	0.32	0.41
Phylogenetic			
Grassland	MAT*(-0.24) + MAT _{Change} *(0.13) + MAP*(-0.26) + MAP _{Change} *(-0.15)	0.40	1
Woodland	MAT*(-0.35) + MAP*(-0.20)	0.20	0.95
Farmland	MAT*(-0.30) + MAP*(-0.15)	0.22	0.88
Village	MAT*(-0.36)	0.19	0.81
Functional			
Grassland	MAT*(-0.10) + MAP*(-0.26)	0.10	0.75
Woodland	MAT*(-0.09)	0.03	0.88
Farmland	MAT*(0.14) + MAT _{Change} *(-0.15) + MAP _{Change} *(-0.14)	0.12	0.87
Village	MAT _{Change} *(-0.14) + MAP _{Change} *(-0.09)	0.04	0.61

Galerida cristata like to inhabit in grassland and semi-desert (Xu, 2015).

4.2. Phylogenetic homogenization of bird communities due to land use change

Besides the effects on taxonomic diversity, anthropogenic activities could also affect the phylogenetic diversity disproportionately (Morelli et al., 2016; Thuiller et al., 2011). It has been well documented that habitat conversion by anthropogenic activities could lead to phylogenetic diversity loss and evolutionary distinctiveness reduction of bird assemblages, resulting in phylogenetic homogenization (Frishkoff et al., 2014; Ibáñez-Álamo et al., 2017). Consistent with these findings, our results also showed significantly higher phylogenetic similarities in disturbed habitats than in natural grassland, even after controlling the effect of taxonomic similarities, indicating strong phylogenetic homogenization of bird assemblages in these disturbed habitats across this region.

Strong anthropogenic activities would generally produce less stable and relative homogenized habitat, which then may favor subsets of closely related species (Frishkoff et al., 2014; Morelli et al., 2016). The mean phylogenetic distance among the three most abundant species in disturbed habitats (*Passer montanus*, *Hirundo rustica* and *Pica pica*) and other species occurred in our study is 115 myr, smaller than the mean phylogenetic distance of all species pairs (131 myr), indicating that these three species are more closely related with other species. While bird species from young clades tend to be benefit from anthropogenic impacts, evolutionarily distinctive birds species in basal lineages are less able to exploit the changed environment (Frishkoff et al., 2014; Morelli et al., 2016). Notably, the mean phylogenetic distance among the seven species unique to natural grassland (including two near threatened species and one data deficient species) is 138 myr, larger than the mean phylogenetic distance of all species pairs, suggesting that these seven species are more distantly related.

4.3. Functional homogenization of bird communities due to land use change

While there are already many studies about bird taxonomic and phylogenetic homogenization due to land use change (Frishkoff et al., 2014; Ibáñez-Álamo et al., 2017; Karp et al., 2018), bird functional homogenization, which is more directly linked with ecosystem functioning and service, has been seldom reported (Devictor et al., 2008), especially for the integration with taxonomic and phylogenetic dimensions. The increase of ecological generalists and decrease of ecological specialist due to land use change may not only cause taxonomic homogenization, but also result in functional homogenization (Olden et al., 2004; Devictor et al., 2008).

Supporting these ideas, our results also showed that functional similarities of bird communities were significantly higher in disturbed habitats than in natural habitat, even after controlling the effects of taxonomic similarities. The mean functional distance between the three most abundant species in disturbed habitats (*Passer montanus*, *Hirundo rustica* and *Pica pica*) and other species occurred in our study is 0.53, tended to be smaller than the mean functional distance of all species pairs (0.56).

4.4. Associations between climate and bird community similarities affected by land use change

Geographical distribution of biodiversity is strongly affected by both contemporary and paleo climate through their effects on net primary productivity, species range, extinction, speciation, migration and so on (Currie et al., 2004; Svenning et al., 2015). Paleo climate change could also indirectly affect terrestrial animals by causing changes in vegetation composition and structure (Jackson and Overpeck, 2000). Turnover of community composition driven by past climate change occurred across multiple terrestrial taxonomic groups and across different

continents (Nogués-Bravo et al., 2016). Supporting these studies, our results showed increasing beta diversity of bird communities with increasing distance in current climate and paleo climate change.

However, the effects of anthropogenic activities on this diversity-climate relation have recently been widely reported. For example, bird species beta diversity in Costa Rica is better explained by climate in forest communities than in agriculture ones, indicating that agriculture has erased the climate-beta diversity associations (Karp et al., 2018). Consistent with and also being an expansion of this study, we found that not only the association between climate and taxonomic beta diversity, but also the associations with phylogenetic and functional beta diversity were erased by land use change driven by anthropogenic activities. Microclimate and resources for birds in the relatively homogenized habitats, e.g., village and farmland, may be more similar across different regions than in natural grassland, resulting in the lower associations between bird community composition and climate in these homogenized habitats.

5. Conclusions

We found strong and consistent taxonomic, phylogenetic and functional homogenization of bird communities due to land use change at a regional scale. In addition we also found weaker associations between bird community similarities and climate distances in disturbed habitats. Therefore, human induced biotic homogenization of bird communities may not only act at taxonomic level, but could also strongly affect the phylogenetic and functional diversity. Our study highlights the important role of natural steppe in bird diversity conservation under the context of global land use change and biodiversity decline, providing important implications for biodiversity conservation.

Data accessibility

The data and code are available upon request from the authors.

Declaration of Competing Interest

The authors have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.05.036>.

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