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Threatened bird species are concentrated in regions with less historical human impacts

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ABSTRACT

Previous human activities have a lasting influence on modern biodiversity patterns, especially on the distribution of threatened species. China is a large country, with a high population and a long history of agriculture, but is also a megadiverse country, with over 1370 bird species and over 300 threatened bird species. As far as we know, this study is the first attempt to test the associations between distribution of proportion of threatened bird species and anthropogenic activities (changes in forest cover, cropland area and population density) over different periods (between 1700 and 1800, between 1800 and 1900, and between 1900 and 2000). We show that there are higher proportions of threatened bird species in Northern China, especially Northeastern and Northwestern China. Notably, both ordinary least squares models and simultaneous autoregressive models indicate that higher proportions of threatened bird species were largely associated with less historical anthropogenic activities, i.e., smaller changes in forest cover and cropland area in Northern China between 1700 and 1800. These findings emphasize the role of historical land use changes in shaping current distribution of threatened bird species, and highlight the importance of avoiding further anthropogenic activities in the last-of-the-wild regions for biodiversity conservation.

1. Introduction

Land use change is one of the main threats to terrestrial biodiversity (Gossner et al., 2016; Newbold et al., 2016; Polaina et al., 2018). Habitat fragmentation and habitat loss due to the expansion of cropland and urban areas into natural regions is a major threat to the continued survival of many species (Sol et al., 2014; Gossner et al., 2016; Liang et al., 2019). However, these land use changes are not just a contemporary phenomenon, but have a long history; and their historical dynamics may affect current distribution of threatened species (Dullinger et al., 2013; Feng et al., 2017; Polaina et al., 2019).

Notably, the associations between historical land use changes and distribution of threatened species are complex, depending on the extent and intensity of land use changes, as well as the species intrinsic traits (Dullinger et al., 2013; Polaina et al., 2018). Land use changes caused by anthropogenic activities not only have a direct impact on the range and abundance of species, but could also have delayed extinction debts (Kuussaari et al., 2009; Dullinger et al., 2013). Because species populations may not respond immediately to the environmental changes, time-lags between population decline, extinction and environmental forcing create a temporary disequilibrium between environmental conditions and species responses, which is known as “extinction debt” (Tilman et al., 1994; Dullinger et al., 2013). For example, the proportions of endangered vascular plants, bryophytes, mammals, reptiles, dragonflies, and grasshoppers across 22 European countries are more closely associated with historical (early 20th century) socioeconomic pressures than with recent (late 20th century) pressures, with fish being an exception (Dullinger et al., 2013).

Two major alternative hypotheses have been proposed to summarize the complex relationships between proportions of threatened species and land use changes, i.e., the *threat* hypothesis and the *shelter* hypothesis (Polaina et al., 2018). Specifically, the *threat* hypothesis assumes that vulnerable species face more threats in heavily disturbed regions than less disturbed environments, resulting in a positive association between proportions of threatened species and intensity, extent, or time of land use changes (Lenzen et al., 2009; Polaina et al., 2018). In

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contrast, the *shelter* hypothesis proposes that while vulnerable species maybe locally extinct in heavily used regions, other remaining populations may persist in regions with less human activities and higher quality habitat, resulting in a negative association between intensity, extent, or time of land use changes and proportions of threatened species (Sanderson et al., 2002; Polaina et al., 2018). In line with these two hypotheses, a previous study showed that Chinese threatened plant species are concentrated in regions with less historical, but more recent anthropogenic activities (Feng et al., 2017). Moreover, a global study exploring the association between historical anthropogenic activities and current mammal distribution classified 50% of the global land area into low-use regions, and suggested that these remaining largely intact habitats are crucial areas for biodiversity conservation (Polaina et al., 2019).

Being a country with large area, dense population, and long history of agriculture, the spatial-temporary dynamics of land use changes in China are quite complex (He et al., 2008, 2013). For example, the croplands in China increased from 1724 to 1887, but decreased from 1887 to 1949 due to natural disasters and wars (He et al., 2013). Forest cover between 1900 and 1960s significantly decreased in Southwestern China, especially in Sichuan province, but was relatively stable in other regions (He et al., 2015). In addition, China is also one most biodiverse countries globally, with at least 1371 birds in total and 312 threatened bird species (Zheng, 2011; Jiang et al., 2016). Although several studies have assessed the distribution of threatened bird species in China, few of them have quantitatively tested the effects of historical anthropogenic activities on the distribution patterns (Lei et al., 2006; Liang et al., 2018).

In this study, we firstly assess the distribution patterns of proportions of threatened bird species in 214 prefectures in China. Secondly we link the distribution of proportions of threatened bird species with land use (cropland and forest cover) changes over different time-periods, i.e., between 1700 and 1800, 1800 to 1900, and 1900 to 2000, to examine whether historical anthropogenic activities are better predictors than recent anthropogenic activities.

2. Materials and methods

2.1. Data collection

Distribution of 1290 bird species in 214 prefectures in mainland China (for details see Appendix A1 and Appendix A2) was compiled from national, regional and provincial avifaunas and faunas, e.g., *A Checklist on the Classification and Distribution of the Birds of China* (Zheng, 2017), *The Avifauna of Yunnan China* (Yang, 1995; Yang and Yang, 2004), *A Checklist on the Distribution of the Birds in Xinjiang* (Ma, 2011), *Studies on Birds and Their Ecology in Northeast China* (Gao, 2006). A complete list of all the faunas used in this study can be found in Appendix A3. We collated bird distribution data by synthesizing information from these faunas (i.e., each bird species occurs in which prefectures and counted all species in each prefecture), which is based on decades of fieldwork and professional knowledge of many experienced local ornithologists (Wang et al., 2020). A list of 310 threatened bird species (critically endangered, endangered, vulnerable and near threatened) in China was compiled from Jiang et al. (2016).

The number of overall bird species and threatened bird species in each prefecture were counted. Threatened birds (310 species) were further divided into two groups, i.e., endangered birds (critically endangered, endangered, and vulnerable; 134 species) and near threatened (176 species). The proportion of all threatened birds, endangered birds, and near threatened birds was calculated as the richness of each of these three threatened groups divided by the overall bird species richness in each prefecture.

Information of historical land use in each prefecture, including cropland cover and forest cover in the past three centuries, was extracted from two land use databases (He et al., 2008, 2015; Li et al., 2016). Historical documents, modern survey and inventory data, the results of existing studies, and the data from the state forestry administration of China were used to estimate the provincial forest and cropland area over the past three centuries in China with a time resolution ranging from 5 to 60 years (He et al., 2015). The provincial cropland and forest area was then allocated into grids with a resolution of 10 km × 10 km (He et al., 2015; Li et al., 2016). Data of historical population density and pasture area was extracted from the History Database of the Global Environment, with a 5′ longitude/latitude grid resolution (HYDE 3.1; (Goldewijk et al., 2011)Goldewijk et al., 2011).

We aggregated these variables to prefecture level and then they were divided by the total area of each prefecture to represent the intensity of land use in each prefecture. Because there was a significant increase in population and land-use modification after year 1700 (Peng, 2011; He et al., 2013), we divided changes in these variables into three periods, i.e., between 1700 and 1800 (values in 1800 minus values in 1700), between 1800 and 1900 (values in 1900 minus values in 1800), and between 1900 and 2000 (values in 2000 minus values in 1900).

Finally, to test whether the threatened bird distribution could be partially affected by other potential confounding factors, e.g., contemporary climate and elevation range, mean annual temperature (MAT), mean annual precipitation (MAP) and elevation range were also included as explanatory variables in this study. MAT and MAP were downloaded from WorldClim database (Hijmans et al., 2005). Elevation data were obtained from EarthEnvDEM90 digital elevation model (Robinson et al., 2014). Elevation range was calculated as the difference between the maximum and minimum values in each prefecture.

2.2. Statistical analyses

Single variable ordinary least squares (OLS) models were used to test the associations between ratios of all threatened birds, endangered birds, and near threatened birds and each explanatory variable. In addition, to account for the spatial autocorrelation in residuals, simultaneous autoregressive (SAR) models were also performed to test these associations, and ensure that our outputs were consistent and reliable. To make the regression coefficients comparable, all the dependent and independent variables were standardized (standard deviation = 1 and mean = 0) using 'decostand' function in vegan package. All analyses were conducted in R (R Core Team, 2016).

3. Results

Northern China had a higher proportion of all threatened birds and endangered birds compared with Southern China (Fig. 1A, B). The proportion of near threatened birds was higher in Northeastern China and Northwestern China than other regions of China (Fig. 1C). Notably, intensity of forest cover changes between 1700 and 1800 in Northern China was relatively smaller than Southern China, i.e., forest in Northern China was relatively better preserved during this period compared with Southern China (Fig. 1D). Changes in forest cover between 1800 and 1900 showed similar patterns with changes between 1700 and 1800, except for the rapid decrease of forest cover in some regions in Northeastern China (Fig. 1D, E). Although changes in forest cover between 1900 and 2000 in Northern China were also relatively smaller, these changes were mixed with increase and decrease of forest cover (Fig. 1F).

Cropland in Northern China increased less than Southern China between 1700 and 1800, and even decreased in some regions (Fig. 1G). In contrast, cropland in Northeastern China increased rapidly between 1800 and 1900, as well as between 1900 and 2000 (Fig. 1H, I). In addition, cropland in Northwestern China and Northern China also increased between 1900 and 2000 (Fig. 1I).

Ordinary least squares (OLS) models and simultaneous autoregressive (SAR) models showed similar patterns about the associations between the proportion of threatened birds and intensity of historical

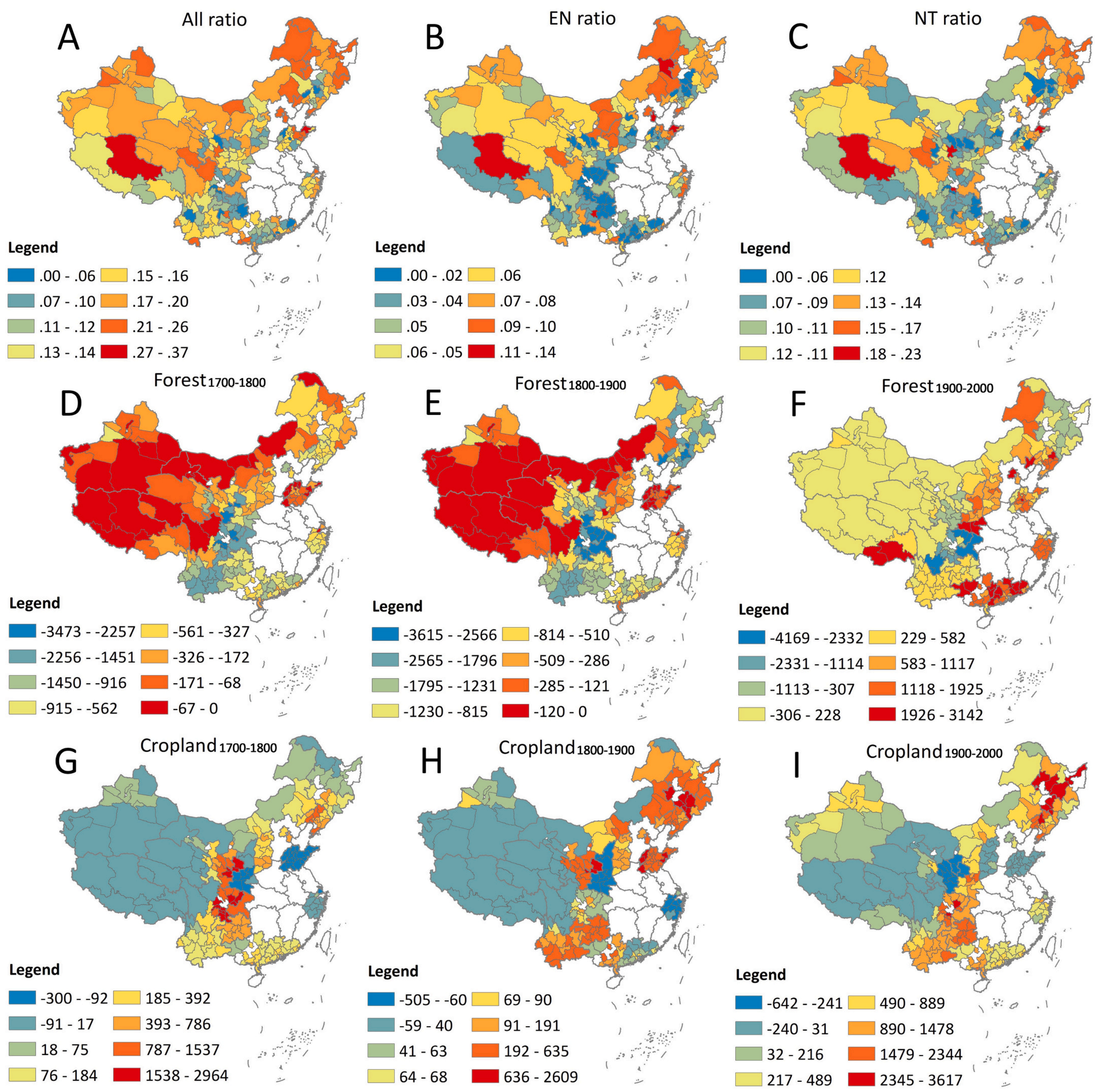

Fig. 1. Distributions of threatened bird ratios and intensity of historical land use changes. All ratio, EN ratio, and NT ratio are the ratio of all threatened birds, endangered birds, and near threatened birds, respectively. $Forest_{1700–1800}$, $Forest_{1800–1900}$ and $Forest_{1900–2000}$ are the intensity of changes in forest cover between 1700 and 1800, between 1800 and 1900, as well as between 1900 and 2000. $Cropland_{1700–1800}$, $Cropland_{1800–1900}$ and $Cropland_{1900–2000}$ are the intensity of changes in cropland between 1700 and 1800, between 1800 and 1900, as well as between 1900 and 2000.

land use changes (Table 1). Specifically, for all three groups of threatened birds, intensity of land use changes between 1700 and 1800 (for both forest cover and cropland area) are more associated with the proportion of threatened species than land use changes between 1800 and 1900, as well as between 1900 and 2000 (Table 1). Notably, threatened bird ratios were positively correlated with intensity of changes in forest cover, but negatively correlated with intensity of changes in cropland (Table 1; Fig. 2). Changes in population density and pasture area, and elevation range were not significantly associated with distribution of threatened bird species (Appendix A4). Although mean annual temperature and mean annual precipitation were significantly associated with proportions of threatened bird species, these associations were lower than intensity changes of cropland and forest between 1700 and 1800, especially for the endangered birds (Appendix A4).

4. Discussion

Our results show that the proportion of threatened birds in Northern China is higher than in Southern China. Notably, the intensity of land use changes in Northern China is also lower between 1700 and 1800, i.e., the forest cover remained consistent or even increased and the cropland area did not increase. In contrast, the cropland increased in

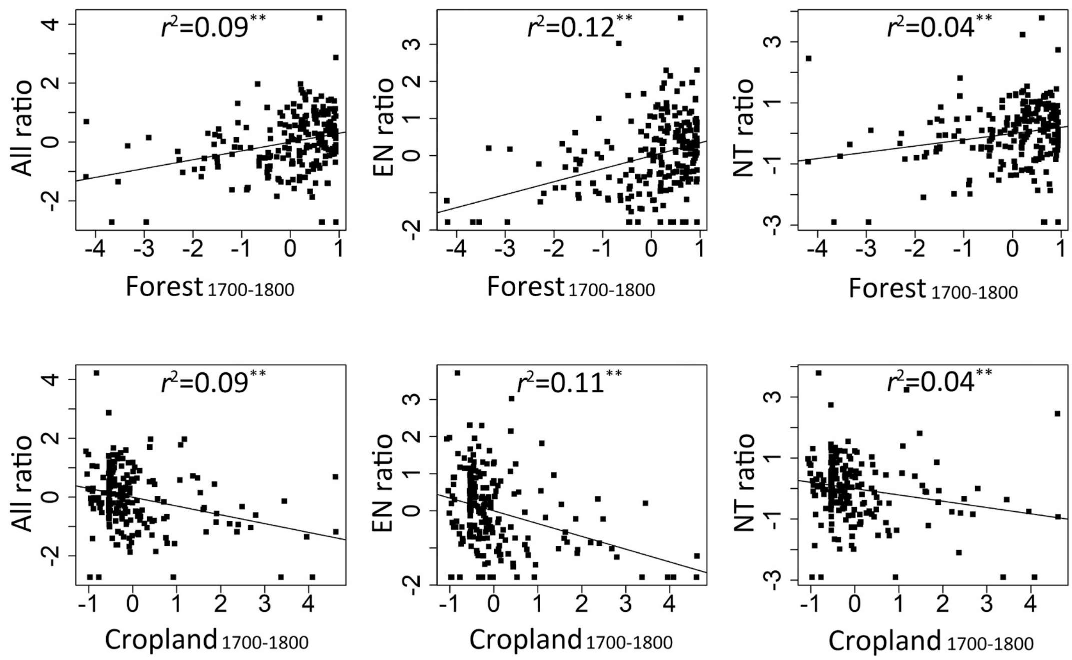

Fig. 2. Scatter plots of threatened bird ratio against intensity of land use changes between 1700 and 1800. All ratio, EN ratio, and NT ratio are the ratio of all threatened birds, endangered birds, and near threatened birds, respectively. $Forest_{1700–1800}$ is the intensity of changes in forest cover between 1700 and 1800. $Cropland_{1700–1800}$ is the intensity of changes in cropland between 1700 and 1800.

Table 1
Results of single variable ordinary least squares (OLS) models and simultaneous autoregressive (SAR) models of the proportion of threatened birds versus intensity of historical land use changes. All ratio, EN ratio, and NT ratio are the ratio of all threatened birds, endangered birds, and near threatened birds, respectively. $Forest_{1900–2000}$, $Forest_{1800–1900}$, and $Forest_{1700–1800}$ are the intensity of changes in forest cover between 1900 and 2000, between 1800 and 1900, as well as between 1700 and 1800. $Cropland_{1900–2000}$, $Cropland_{1800–1900}$, and $Cropland_{1700–1800}$ are the intensity of changes in cropland between 1900 and 2000, between 1800 and 1900, as well as between 1700 and 1800. The standardized coefficient ($Coef_{OLS}$) and r^2_{OLS} of OLS models were listed. The standardized coefficient ($Coef_{SAR}$) and Akaike information criterion (AIC_{SAR}) of SAR models were also listed. The two highest r^2 and two lowest AIC in each column were in bold. $**p < 0.01$; $*p < 0.05$.

	All ratio				EN ratio				NT ratio			
	$Coef_{OLS}$	r^2_{OLS}	$Coef_{SAR}$	AIC_{SAR}	$Coef_{OLS}$	r^2_{OLS}	$Coef_{SAR}$	AIC_{SAR}	$Coef_{OLS}$	r^2_{OLS}	$Coef_{SAR}$	AIC_{SAR}
$Forest_{1700–1800}$	0.3	**0.09****	0.28**	**582**	0.35	**0.12****	0.28**	**563**	0.2	**0.04****	0.20**	**601**
$Forest_{1800–1900}$	0.2	0.03**	0.16	589	0.3	0.08**	0.20*	568	0.08	0	0.08	606
$Forest_{1900–2000}$	0.03	0	0	592	0.07	0	0	573	−0.01	0	−0.02	607
$Cropland_{1700–1800}$	−0.3	**0.09****	−0.30**	**580**	−0.34	**0.11****	−0.31**	**561**	−0.21	**0.04****	−0.22**	**600**
$Cropland_{1800–1900}$	−0.06	0	−0.12	591	0.08	0	−0.14	571	−0.03	0	−0.06	606
$Cropland_{1900–2000}$	−0.1	0	−0.11	590	−0.17	0.02*	−0.16	570	−0.02	0	−0.04	607

Northern China between 1900 and 2000, especially in Northeastern China. Furthermore, statistical analyses suggest that there are more threatened bird species in regions with less land use change between 1700 and 1800. Taken together, our findings indicate that threatened bird species in China are sensitive to land use change, and have retained viable populations only in areas with little historic change.

4.1. Distribution of threatened birds in China

Understanding the distribution of threatened bird species facilitates the development of more effective and targeted conservation and management plans. Several previous studies have assessed the distribution of threatened bird species in China (Lei et al., 2006; Liang et al., 2018). Specifically, a national scale assessment identified six hotspots for endangered bird species in China, including the western Tianshan Mountains; the Qilian and Hengduan mountains; southern Anhui, southern Jiangsu, and the Zhejiang Hills; the Songliao Plain and the northern region of the North China Plain; the island of Taiwan; and the island of Hainan (Lei et al., 2006). A recent study based on citizen science dataset found several new hotspots for threatened birds in coastal regions, i.e., the Bohai Gulf and the Yellow Sea, the south of the North China Plain, and the lower reach of the Yangtze River (Hu et al., 2017). Contrary to this, our results showed different patterns, i.e., threatened bird species were mainly concentrated in Northern China, especially for Northeastern China and Northwestern China. Compared with Southern China, Northern China (including Northeastern China and Northwestern China) has more fragile environment and ecosystems, greater recent anthropogenic activities, as well as stronger past and future climate change (Zou et al., 2005; Wu et al., 2015). Taking together, our findings suggest that more attention should be paid for biodiversity conservation in these previously ignored regions, as they offer the last chance to maintain already threatened species which may have been lost elsewhere.

There are a number of possible reasons for the differences between previous studies and our results. Firstly, we used the proportion of threatened bird species richness to overall bird species richness, instead of the number of threatened birds (which may necessarily be higher in more species rich areas), to understand where greater proportions of species may be threatened. Southern China, especially Southwestern China, may harbor high richness of threatened bird species, but these regions also have high richness of overall bird species. Secondly, both the list of threatened bird species and the distribution data of the threatened species in our study are different with previous studies. For example, 183 threatened bird species, not assessed as the IUCN criteria, were analyzed by Lei et al. (2006). In contrast, 310 threatened bird species according to the IUCN standard were used in this study (Jiang et al., 2016). Lastly, our data on the bird distribution in Eastern China, island of Taiwan, and island of Hainan are insufficient, making it impossible to analyze the distribution of threatened birds in these regions.

4.2. Less historical anthropogenic activities preserved bird diversity

Contemporary distribution of biodiversity, especially for the threatened species with small ranges, may be the result of anthropogenic activities in past decades, centuries, and even millennia (Feng et al., 2017; Teng et al., 2019; Wan et al., 2019). However, associations between distribution of threatened species and historical anthropogenic activities are complex. Specifically, there may be more threatened species in regions with more anthropogenic activities, and in regions with less anthropogenic activities, predicted by the *threat* and *shelter* hypotheses, respectively (Polaina et al., 2018).

Similar to the prediction of the *shelter* hypotheses, our results showed that threatened bird species in China were concentrated in regions with relatively less historical anthropogenic activities. Consistent with this finding, a previous study about threatened plant species in China also suggested that there are more threatened plant species in regions with relatively small historical anthropogenic impacts (Feng et al., 2017). Similarly, Polaina et al. (2019) divided the globe into low-, recently- and steadily- used areas, classified 50% of the global land area into low-used areas, and suggested that these relatively wild regions could provide important opportunities for biodiversity conservation.

4.3. Recent anthropogenic activities threatened birds

Although the associations between distribution of threatened bird species and recent (between 1900 and 2000) anthropogenic activities were not significant, the maps indicated a trend that cropland had significantly increased between 1800 and 2000 in Northeastern China. In addition, cropland also increased in Northwestern China between 1900 and 2000. The higher proportion of threatened bird species in Northeastern and Northwestern China indicated that the strong recent anthropogenic activities may increase the risk of extinction to bird species in these regions. Similarly, threatened plant species are also concentrated in regions with strong and recent anthropogenic pressure (Feng et al., 2017).

In sum, our study provides a novel map of proportion of threatened bird species in China and identified new targets for conservation in areas where species may be particularly sensitive to change. Notably, the results indicate that threatened bird species are concentrated in regions with less historical anthropogenic activities, indicating the important role of last-of-the-wild regions in biodiversity conservation.

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CRediT authorship contribution statement

Gang Feng designed the study; Xueting Yang and Shicheng Li collected the data; Xueting Yang, Shicheng Li and Gang Feng analyzed the data and wrote the paper; all authors contributed substantially to revisions. All authors read and approved the final manuscript.

Declaration of competing interest

These authors have no conflict in interest.

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Data accessibility

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

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