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Original Research Article

Species traits linked with range shifts of Chinese birds

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A B S T R A C T

Range shifts are important species response to climate change and anthropogenic activities. While many studies have suggested that species traits are also important predictors of range shifts, they are mainly conducted in Europe and North America, and more importantly there are still many controversies about the roles of species traits. As far as we know, this is the first study in China linking bird species traits with range shifts. We aimed to answer two questions: 1) which order and family have most bird species with range shifts? 2) which traits are most associated with the bird species range shifts in China? A total of 204 species (14% of all bird species in China) had changed their ranges. Although passeriformes (126 species) and muscicapidae (23 species) had the most species with range shifts, the order and family with highest proportion of species with range shifts were cuculiformes (40%), rostratulidae (100%) and artamidae (100%). Our results also showed that range shifts of Chinese birds were positively correlated with geographical range size, habitat specificity, trophic level, and negatively correlated with body size. Notably, all the four traits were included in the combination of traits most associated with range shifts, suggesting that priority should be given to birds with large body size, low habitat specificity, low tropical level and small geographical size. Because these species could not adapt the effects of climate change and anthropogenic activities in time, and would then face an increased risk of extinction. As China harbors high levels of overall bird species richness, threatened and endemic bird species richness, as well as large human population, this study is of great importance for the bird diversity conservation in China.

1. Introduction

Range shifts, movement of species to track preferred conditions, are assumed to be one of the best biological responses to climate change (Parmesan, 2006; Angert et al., 2011). Species tend to move poleward or uphill in response to climate change, while others that remain unchanged or lag behind may face an increased risk of extinction (Thomas et al., 2004; Auer and King, 2014). Divergent responses among species may lead to the formation of novel communities and changed species interactions, which may have negative impacts on species populations (Auer and King, 2014). Recent global environmental

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changes are the main driver of species extinctions and range shifts (Tylianakis, 2008; Betzholtz et al., 2013). Meanwhile, species traits could also affect range shifts through their effects on the patterns of species distribution (Maclean and Beissinger, 2017). In consequence, species traits are widely used as predictors of contemporary climate-driven range shifts (Buckley and Kingsolver, 2012; Estrada et al., 2016).

Three steps are required for a species to adapt a new environment, namely dispersal, survival and reproduction. Firstly, dispersal related traits include dispersal ratio, migrant status and body size (Maclean and Beissinger, 2017; Wang et al., 2018). Studies have shown that the species with larger body size, which means greater dispersal potential, tend not to shift their ranges, because they could buffer the effects of environmental changes to survive in their original habitat (Brommer, 2008; Bradshaw et al., 2014; Maclean and Beissinger, 2017). Secondly, a broader niche, including diet and habitat breadth, may be of great benefit to species survival in new environment (Angert et al., 2011; Buckley and Kingsolver, 2012). Ecological generalist could have high possibility to shift ranges by increasing the probability for finding suitable resources and interactions, while it would be difficult for ecological specialist to establish populations in new habitats (Angert et al., 2011; Davey et al., 2013; Estrada et al., 2016). Finally, species range shifts should also depend on their reproductive abilities after arrival (Angert et al., 2011). Low annual productivity could lead to range contractions, while species with high annual productivity are more likely to expand their ranges (Amanoa and Yamaura, 2007; Moritz et al., 2008; Angert et al., 2011).

Despite plenty evidence of bird species traits affecting range shifts, there are always controversies about the role of some specific traits (Estrada et al., 2016; Maclean and Beissinger, 2017). For example, dietary breadth could promote, limit or not affect species range shifts. Specifically, a study in New Guinean shows that the upslope shifts of omnivores and frugivores tended to be larger than insectivores and nectivores in Karkar Island, but there is no relation between diet and upslope shifts in Mountain Karimui (Freeman and Freeman, 2014). Songbirds in North America with narrower diet breadths exhibit greater northward and uphill range shifts (Auer and King, 2014). Reproductive capacity could also have diverse effects on species range shifts. For example, songbirds in North America with smaller clutch sizes show greater northward shifts, while species with larger clutch sizes exhibit greater uphill shifts (Auer and King, 2014).

In addition, although there have been many studies on the associations between bird species traits and range shifts, most of them are investigated in Europe and North America (Estrada et al., 2016; Maclean and Beissinger, 2017). As far as we know no studies have tested this in China, which is one of the countries with richest biodiversity, harboring 1445 bird species and 33,000 vascular plant species (López-Pujol et al., 2006; Zheng, 2017). Meanwhile, unprecedented anthropogenic activities have dramatically changed the habitats of these species and threatened their survival (Feng et al., 2017; Chen et al., 2019). Climate change has also altered the bird distribution in China, presenting huge challenges for Chinese biodiversity conservation (Wu and Zhang, 2015; Wu and Shi, 2016). Notably, according to the China Vertebrates Red List, 146 species of all Chinese birds are threatened (vulnerable, endangered and critically endangered) and three species are regionally extinct (Jiang et al., 2016; Wang et al., 2018). Therefore, it's of great importance to test the associations between bird species traits and range shifts in China.

In this study, we conducted the first quantitative analyses of the relations between species traits and range shifts of Chinese birds. We aimed to answer the following two questions: 1) which order and family have most bird species with range shifts? 2) which traits are most associated with the bird species range shifts in China?

2. Materials and methods

2.1. Data collection

A list of 204 species with range shifts was compiled from two published peer review papers (Du et al., 2009; Li et al., 2013; Table S1). Among them, 120 species were from Du et al. (2009) and 109 species were from Li et al. (2013), with 25 species occurred in both papers. In Du et al. (2009), the original distribution data of Chinese birds was from two comprehensive and influential avifauna, i.e., *A Checklist on the Distribution of the Birds of China* (Cheng, 1976) and *A synopsis of the Avifauna of China* (Cheng, 1987), and the new distribution data was summarized based on the new records of bird species across China as well as the results of fieldwork by the authors in the past decades. In Li et al. (2013), the original distribution data of Chinese birds was also from an influential book, i.e., *A Field Guild to the Birds of China* (MacKinnon et al., 2000), and the new distribution data was based on the bird watching in China, i.e., China Bird Report (2003–2007) (Society, 2008).

Information of eleven life-history and ecological traits that are commonly linked to range shifts for 1205 Chinese bird species was from a recent publication (Wang et al., 2018). These traits include habitat specificity (the number of habitats a species is recorded in), body size (mm), geographic range size (km^2), trophic level (omnivores, granivores, frugivores, nectarivores, insectivores, piscivores and carnivores), nest site (cavity, tree, shrub, water and ground), hunting vulnerability (rarely/never hunted or killed, occasionally hunted or killed, and often hunted or killed), migrant status (resident, partial resident and full migrant), flocking tendency (strictly solitary, occasionally social and strictly social), dispersal ratio (mean wing length divided by the cube root of mean mass), clutch size (median number of eggs per nest) and nest type (exposed or not). A phylogeny for the 1205 species was pruned from a mega bird phylogeny composed of global species pool with the option of "Hackett All Species: a set of 10000 trees with 9993 OTUS each" (Jetz et al., 2014). 5000 pseudo-posterior distributions were sampled and the Maximum Clade Credibility tree was built using mean node height in TreeAnnotator (version 1.8.2) in the BEAST package (Drummond and Rambaut, 2007).

2.2. Statistical analyses

Because the dependent variable is binary, i.e., the species changed its range (1) or not (0), single variable generalized linear models (glm) with binomial error distribution were used to test the associations between each of the species traits and range shifts. Phylogenetic generalized linear mixed models for binary data (BinaryPGLMM) were also performed to correct for the phylogenetic effects, i.e., closely related species tend to share similar traits (Dai et al., 2018). In addition, since these traits have different dimensions, to make the regression coefficients comparable, we standardized (mean = 0 and SD = 1) the species trait data.

To test the relative importance of different combinations of species traits, we also conducted multiple variables analyses, only using the significant variables based on the previous BinaryPGLMM single variable analyses, i.e., habitat specificity, body size, geographic range size and trophic level. Because the single variable BinaryPGLMM and glm models showed similar patterns (Table 1), and BinaryPGLMM could not provide AIC values to assess the performance each combination of species traits, the multiple variables analyses were only conducted using glm models.

Standardized coefficients and R^2_{pred} square of each BinaryPGLMM model were listed to assess their relative importance (Ives, 2019). Standardized coefficients and Akaike's information criterion (AIC) of each glm were also listed. BinaryPGLMM was conducted using function 'binaryPGLMM' in 'rr' R package (Ives and Li, 2018). All analyses were conducted in R (R Core Team, 2016).

3. Results

3.1. Patterns of range shifts of Chinese birds

Although passeriformes had the most species with range shifts, i.e., 126 species, accounting for 62% of all species with range shifts, the order with highest proportion of species with range shifts was cuculiformes, (40%) (Fig. 1). Also, although muscicapidae was the family having the most species with range shifts, i.e., 23 species, the family with highest proportion of species with range shifts was rostratulidae (100%) and artamidae (100%) (Fig. 2).

3.2. Correlates of range shifts of Chinese birds

Single variable phylogenetic generalized linear mixed models for binary data (PGLMM) and generalized linear models (glm) showed similar patterns about the associations between bird species traits and range shifts, i.e., the four traits with highest standardized coefficients were habitat specificity, body size, geographic range size and tropic level (Table 1). Notably, possibilities of range shifts were positively correlated with habitat specificity, geographic range size and trophic level, and negatively correlated with body size.

Multiple variable glm models showed that the combination of species traits most associated with range shifts included the four traits, i.e, habitat specificity, body size, geographic range size and tropic level (Table 2). Notably, the AIC (1072) of glm for this combination tended to be lower than the AIC (1088) of the best single variable, i.e., habitat specificity (Tables 1 and 2).

4. Discussion

In addition to climate change and anthropogenic activities, species traits are also important predictors for species range shifts, although controversies about their roles still exist. Being the first study linking bird species traits with species range shifts in China, we find that range shifts of 204 bird species are positively associated with habitat specificity, geographic range size, trophic level, and negatively correlated with body size.

Table 1
Results of single variable phylogenetic generalized linear mixed models for binary data (PGLMM) and generalized linear models (glm). The standardized coefficient (coef) of PGLMM and glm, r^2 of PGLMM and Akaike's information criterion (AIC) of glm were listed. $^{**}p < 0.01$; $^{*}p < 0.05$.

Model description	$\mathrm{Coef}_{\mathrm{-PGLMM}}$	$\mathrm{R}^2_{\mathrm{-PGLMM}}$	$\mathrm{Coef}_{\mathrm{-glm}}$	$\mathrm{AIC}_{\mathrm{-glm}}$
Body size	−0.28*	0.073	−0.21*	1094
Habitat specificity	0.25**	0.072	0.25**	1088
Geographic range size	0.24**	0.072	0.23**	1090
Trophic level	0.22*	0.056	0.23**	1091
Nest site	−0.16	0.062	−0.2	1093
Hunting vulnerability	0.15	0.075	0.02	1100
Migrant status	−0.1	0.067	−0.07	1099
Flocking tendency	−0.07	0.063	−0.12	1098
Dispersal ratio	0.07	0.064	0.12*	1097
Clutch size	−0.04	0.066	−0.07	1099
Nest type	−0.02	0.066	−0.06	1099

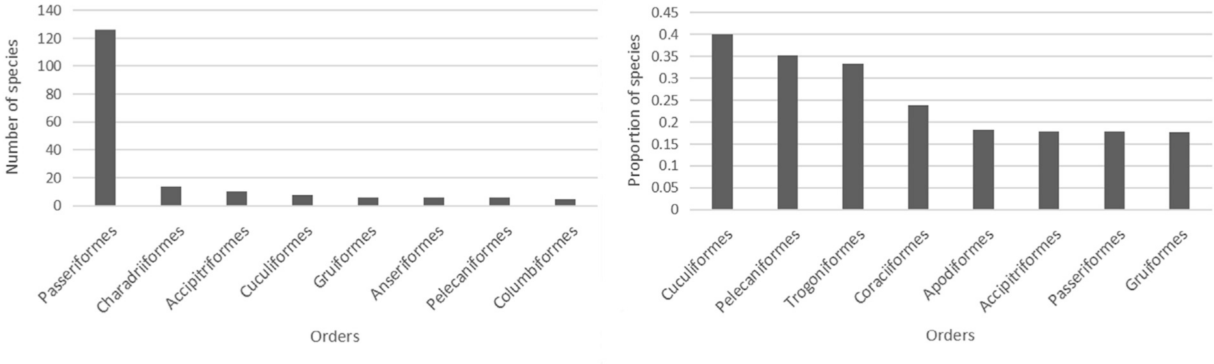

Fig. 1. The number and proportion of bird species with range shifts in different orders. Only the eight orders with highest values were showed.

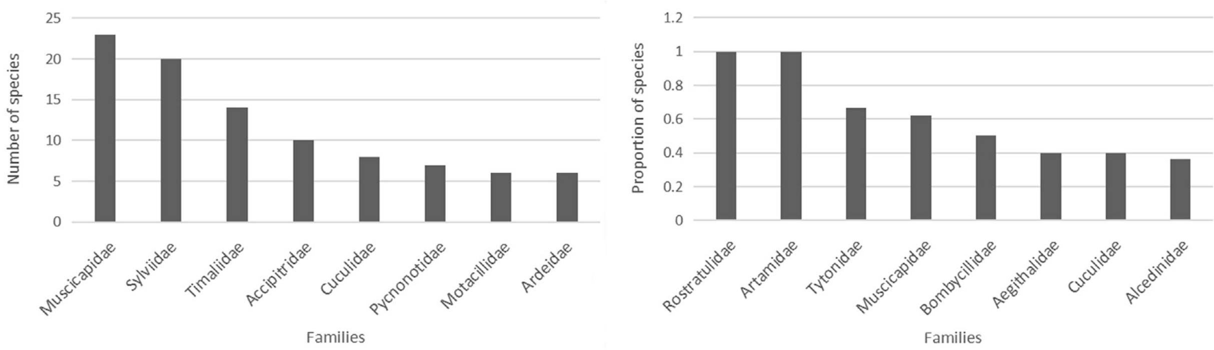

Fig. 2. The number and proportion of bird species with range shifts in different families. Only the eight families with highest values were showed.

Table 2
Results of multiple variables generalized linear models (glm). The standardized coefficient and Akaike's information criterion (AIC) of glm were listed. $^{**}p < 0.01$; $^{*}p < 0.05$.

glm	
Model description	AIC
Habitat specificity(0.22**) + Body size(-0.30**) + Geographic range size(0.15) + Trophic level(0.26**)	1072
Habitat specificity(0.28**) + Body size(-0.28**) + Trophic level(0.28**)	1073
Body size(-0.30**) + Geographic range size(0.23**) + Trophic level(0.24**)	1078
Habitat specificity(0.20**) + Body size(-0.26**) + Geographic range size(0.18*)	1080
Trophic level(0.23**) + Habitat specificity(0.26**)	1081
Habitat specificity(0.21**) + Geographic range size(0.12) + Trophic level(0.21**)	1081
Body size(-0.23*) + Habitat specificity(0.27**)	1083
Body size(-0.25**) + Geographic range size(0.26**)	1084
Body size(-0.26**) + Trophic level(0.27**)	1085
Habitat specificity(0.19*) + Geographic range size(0.15)	1086
Trophic level(0.20*) + Geographic range size(0.20**)	1086

4.1. Habitat specificity

Generally, a broader niche, including habitat breadth, may facilitate species to survive better in new environments by increasing the probability of finding suitable habitat with plenty resources and biotic interactions (Angert et al., 2011; Buckley and Kingsolver, 2012). Although a study in Giant Mountains, central Europe finds that birds with narrower habitat breadth shift more than species with wider habitat breadth (Reif and Flousek, 2012), most studies support the hypothesis, i.e., broader habitat breadth promotes species range shifts (Maclean and Beissinger, 2017). For example, bird studies in South Africa, Sweden, Spain, France and other countries in Europe and North America suggest that ecological generalisation would have positive effects on species range shifts (Hockey et al., 2011; Davey et al., 2013; Estrada et al., 2016). Consistent with these studies, our results also showed positive association between bird species range shifts and habitat specificity, the number of habitats a species is recorded in. This finding in China provides strong supplementary evidence for the role of habitat specificity in affecting the patterns of bird species range shifts.

4.2. Body size

Body size is always considered to be the most informative trait of bird species because it is directly linked with many other bird functional traits, e.g., dispersal potential, resource requirements, trophic levels, extinction vulnerability, reproductive strategy (Angert et al., 2011; Ding et al., 2013; Estrada et al., 2016). However, predictions and evidence of the role of body size on range shifts also varied a lot (Brommer, 2008; Angert et al., 2011; Maclean and Beissinger, 2017). For example, large birds should be easy to shift their ranges because they are ecological generalist and good dispersers (Angert et al., 2011; Maclean and Beissinger, 2017). In contrast, the short generation time and high reproductive rate of small birds may promote their ability to track environmental changes and then facilitate range shifts (Brommer, 2008; Bradshaw et al., 2014). Consistent with these studies, we also found negative associations between bird body size and probability of species range shifts in China, providing strong support for the negative effects of body size on species range shifts. Notably, the better explanatory power of body size and habitat specificity together than each of them suggests that priority should be given to species with small body size and high habitat specificity when study the effects of bird range shifts in China.

4.3. Geographic range size

Like body size, species geographic range size is also often correlated with ecological generalization, dispersal potential, and life history, which could then directly affect the possibility of species range shifts (Angert et al., 2011). Widespread species should be more likely to shift their ranges because they have already colonized and maintained viable populations across large areas, indicating that they are usually good dispersers and ecological generalist (Kunin and Gaston, 1997; Estrada et al., 2016). However, a study about North American birds suggest that range size has negative effect on species range shifts (Angert et al., 2011). In contrast, a bird study in Sweden finds positive association between distribution size and species range shifts (Davey et al., 2013). Supporting the hypothesis and this study, our results showed that geographic range size was positively associated with bird range shifts in China.

4.4. Trophic level

Previous evidence about the effects of trophic levels on species range shifts also varies a lot (Forero-Medina et al., 2011; Freeman and Freeman, 2014). For example, uphill range shifts of birds in Peru and northward range shifts of birds in New York State are similar among different tropic guilds (Zuckerberg et al., 2009; Forero-Medina et al., 2011). Notably, a study in two regions in New Guinea showed divergent effects of diet guild on range shifts, i.e., uphill shifts in Karkar Island are larger for omnivores and frugivores than for insectivores and nectivores, while no effects of diet guild are found in Karimui mountain (Freeman and Freeman, 2014). Species with higher trophic levels are suggested to be less likely to respond to climate change because they are usually constrained by prey or host availability (Buckley and Kingsolver, 2012). For example, a study in central Europe finds that species feeding on animals shift less than species feeding on plants (Reif and Flousek, 2012). In contrast, our results showed that species with higher trophic levels are more likely to shift ranges in China.

5. Conclusions

Being one of the best biological responses to climate change and anthropogenic activities, species range shifts are also affected by species traits (Estrada et al., 2016; Maclean and Beissinger, 2017). As the first study linking bird species traits with range shifts in China, a country with high biodiversity and huge anthropogenic activities, our findings provide strong supplementary evidence for the associations between species traits and range shifts. Consistent with a recent study which suggests that geographic range size, habitat specificity and body size are also correlated with the extinction risk of Chinese birds (Wang et al., 2018), this study suggests that priority should be given to birds with large body size, low habitat specificity, low tropical level and small geographical size, because these species may face high extinction risk due to their weak ability to track climate change.

However, because of the relatively short history of bird research in China compared with Europe and North America, precise estimation of bird range shifts in China is lacking, which may bias our conclusions. Further studies with more detailed information of species range shifts, e.g., range expansion or contraction, the shifting direction and distance, as well as more detailed information of climate change and anthropogenic activities would be more crucial for biodiversity conservation in China.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00874.

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