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Original article

Modeling contemporary range size patterns of endemic birds in China: Testing the relative importance of phylogeny, space, and environment

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ABSTRACT

The contemporary range size of endemic birds in China was investigated by studying the relative deterministic importance of phylogeny, space, and environment using a novel maximum likelihood model. The results show that space plays the most influential role in structuring the contemporary range sizes of endemic birds by explaining 39.1% of the total variance alone, followed by phylogeny alone, which explains 12.3% of the variance. In contrast, environment alone plays no role in structuring the range sizes of endemic birds. However, the interaction between space and environment can explain 24.8% of the total variance. Therefore, although all three mechanisms can affect the ranges of the endemic birds of China, the role of environment only emerges when it interacts with space. This study shows that the range sizes of species are ubiquitously affected by space, irrespective of the taxonomic groups studied. In conclusion, the novel maximum likelihood model developed in this study allows the study of the sole and interactive effects of phylogeny, environment, and space on determining the evolution of trait patterns.

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Introduction

The evolutionary and ecological control of the range size of species (Gaston and Fuller, 2009) has been of interest in macroecological studies in recent years (Gaston and Chown, 1999; Holt, 2003; Webb and Gaston, 2003; Abellan and Ribera, 2011). The contemporary range size patterns of species are affected by multiple factors including, but not limited to, historical cladogenesis and heritage (Ree and Smith, 2008; Cooper et al., 2011; Jetz and Fine, 2012; Pigot et al., 2012), contemporary ecological conditions (Buckley and Jetz, 2007), space (Freckleton and Jetz, 2009), and random drift (Vellend, 2010).

The global and regional range size patterns of mammals have been well characterized in some previous studies (Freckleton and Jetz, 2009; Cooper et al., 2011). However, the contemporary range size patterns of birds and the underlying driving mechanisms have not yet been quantified. The range size of species is thought to be related to

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the dispersal abilities of the species (Birand et al., 2012). As birds can migrate over large distances, it is expected that the determinants influencing the range size patterns of birds might be different from those for mammals. As such, this study applied and extended previous maximum likelihood models (Freckleton and Jetz, 2009; Cooper et al., 2011) to measure the relative importance of phylogeny, space, and environment to reveal their roles in structuring the contemporary range size patterns of endemic birds in China.

Endemic species are an ideal model to test and evaluate different evolutionary models of the trait evolution of species (Ree and Smith, 2008). The endemic birds of China consist of at least 50 species with their full distributional range limited to the terrestrial boundary of China (Lei et al., 2002; Zhang, 2004; Lei and Lu, 2006). Endemic birds were used as the study model because the range sizes of these species have been well quantified for conservation purposes (The World Conservation Union, 2010). The range sizes of endemic birds could be driven by a number of factors. The central purpose of this study was to determine the independent and interactive roles of different ecological or evolutionary mechanisms on structuring the range sizes of birds and to compare the results obtained with those for mammals (Freckleton and Jetz, 2009; Cooper et al., 2011).

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Materials and methods

Data set

An endemic bird species list of mainland China was gathered from previous studies (Lei et al., 2002, 2007; Lei and Lu, 2006) and the World Bird Database (http://avibase.bsc-eoc.org/). Some species were excluded from this study because their phylogenetic relations with other species are not known or because their range size information is unclear, resulting in 44 endemic birds being used for the analyses.

The phylogenetic relationship between the 44 endemic birds of China was extracted from the BirdTree.org database (http://www.birdtree.org), which was derived from a full phylogeny of the global bird species in a previous study (Jetz et al., 2012). A total of 3000 trees for the possible phylogenetic affinities of these endemic birds were retrieved and the resultant consensus tree with average branch lengths was obtained using the DendroPy Python library

(Sukumaran and Holder, 2010). Molecular dating of the tree was fulfilled using a penalized likelihood method (Sanderson, 2002). The resultant dated tree (Figure 1) was used for all subsequent analyses.

The associated range size information for each endemic bird was obtained from an online database (http://www.birdlife.org/). Detailed historical distributional records of each species were obtained from the China Species Information Service (http://www.baohudi.org/). The original range sizes (in km²) of the species were subjected to log-transformation prior to maximum likelihood inference (Figure 1).

Likelihood model for disentangling the relative importance of phylogenetics, space, and environment

Under the Brownian model, the expected distribution of a trait (here the log-range size) follows a simple multi-normal distribution in which the mean of the trait at the root, μ , and the variance of the trait across the phylogenetic tree, σ^2 , can be estimated



Figure 1. Phylogeny and associated log-transformed range sizes (km²) of endemic birds of China.

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