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Short communication

Testing adaptive regime shifts for range size evolution of endemic birds of China

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A R T I C L E I N F O

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A B S T R A C T

In this brief report, adaptive regime shifts for the range size evolution of the endemic birds of China were identified. Four models with different biological meanings were tested and compared through maximum likelihood models, including the Brownian motion model, one global optimal range size model for all lineages in the phylogeny, two optimal regime model of range sizes for lineages with large and small range sizes (OU2), and three optimal regime model in which an additional regime is added to the ancestral lineages. The results of model evaluation and comparison using the maximum likelihood technique show that over 48 endemic taxa, two optimal regimes (the OU2 model) were observed for bird lineages with large and small range sizes in the country. The possible reasons for such an observation were outlined accordingly, including the different evolutionary times, which were subjected to different historical and geological conditions, heterogeneous environmental conditions, and complex climatic fluctuations. Overall, the range size evolution of the endemic taxa was subjected to multiple selective stresses. For future implications, more studies are desired to provide a holistic view of the evolution and divergence of endemic taxa.

Introduction

Both historical and contemporary factors can contribute to the community structure of species (Rabosky et al 2011). However, one interesting question is whether the adaptive ability of a species may change over the evolutionary time scale. Indeed, many previous studies have discovered adaptive regime shift patterns across different taxa (Frederich et al 2013; Santini et al 2013; Slater et al 2010).

Range size is an important ecological trait of living species (Gaston and Chown 1999; Webb and Gaston 2003). Many works have contributed to the discussion of the evolution and ecology of the range size patterns of species (Chen 2013a; Gaston and He 2002; Lee-Yaw and Irwin 2012; Machac et al 2011; Webb and Gaston 2003). For example, in a previous study (Chen 2013a), evolutionary models for the range sizes of the endemic woody plants of China were quantified, and the Brownian motion model was favored.

The endemic taxa in China have been a focus in ecological studies given that the southwestern part of the country is a biodiversity hotspot (Chen 2013a, 2013b; Chen and Bi 2007; Huang et al 2012; Myers et al 2000). In the present study, I evaluate and test whether there are possible regime shift patterns for the range sizes of the endemic birds of China. I utilize a phylogenetic tree constructed previously (Chen 2013b, 2013c) for the endemic bird taxa in the region to perform relevant phylogenetic comparative tests.

Materials and methods

Following previous studies (Butler and King 2004; Hansen 1997; Hansen and Orzack 2005), I have the following models for testing the adaptive regime shifts for the range sizes of the endemic birds of China.

As in the previous studies (Butler and King 2004; Laffe et al 2011), the following alternative regime shifting models are considered for comparison: there is no directional selection on the range sizes of bird species, following the Brownian motion model (BM); there is a single optimum of the range size for all bird lineages (OU1); there are two different optimal range sizes for large and small external species (OU2); there are three different optimal range sizes (OU3; in

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addition to large and small external species, all ancestral lineages in the tree have another optimal range size). The BM model contains one parameter, σ^2, characterizing the dispersion of the functional trait (range size, in my case). OU1 has another additional parameter, θ_1, which characterizes the global optimal value of range sizes for all lineages over the tree. Finally, OU2 has another two additional parameters to that of the BM model, θ_2 and θ_3, which indicate the optimal range sizes for the bird lineages with large and small range sizes, respectively. Lastly, OU3 has an additional parameter, θ_4, characterizing the regime optimum for the ancestors.

If after divergence, species in different subclades evolve into new regimes, the OU2 model will quantify the evolutionary dynamic of the range sizes of the bird lineages much better. Moreover, if all ancestors of the external species are adapted to a new regime different from those for small and large external taxa, then the OU3 model is the best model. In contrast, if there is no selection among the species on the range size evolution, then the BM model is favorable. Finally, if there exists selective pressure on the range size evolution of endemic birds in China but there is no selective differentiation among different species with different range sizes, then the OU1 model is the best model.

In model comparison, the modified Akaike information criterion (AICc) (Akaike 1974; Chen 2013d; Haining 2003) accounts for small samples, as follows:

$$\mathrm{AICc} = -2(n-1)\log Lik + 2k\frac{n-1}{(n-1)-k-1}, \qquad (1)$$

where $\log Lik$ is the log-transformed likelihood value; n is the number of data used for the likelihood modeling, as above; and k is the number of parameters presented in the alternative models.

The AICc weights (Burnham and Anderson 2002) are calculated for each model to evaluate its favorability probability in model tests. Obtaining the weights requires the difference between the raw AICc of each model and the lowest AICc value, as follows:

$$\Delta AICc(i) = AICc(i) - \min(AICc). \qquad (2)$$

Then, the weights for the models are calculated as

$$w_i(AICc) = \frac{\exp(-\Delta AICc(i))}{\sum\limits_i \exp(-\Delta AICc(i))}. \qquad (3)$$

The probability that a candidate model is favored increases when the model has a higher weight value. All the analyses are done using R statistical software (R Development Core Team, Vienna, Austria) and the extension package Ouch (Butler and King 2004).

Results

The species list and corresponding range sizes (log-transformed; original unit: km^2) for the endemic birds of China used for the present study are outlined in Table 1. The determination of large and small range sizes is based on the mean value of the log-transformed range sizes across all external species (11.95).

Diagrams of the optimal range sizes over the phylogenetic branches for each alternative model (BM, OU1, OU2, and OU3) are presented in Figure 1. The diagrams for OU1 and BM are the same, but the numbers of parameters to be estimated are not. OU1 has the same diagram as the BM model because both assume no regime shifts among the lineages.

The results of maximum likelihood estimation, as shown in Table 2, suggest that OU2 is the best model in comparison with the OU1, OU3, and BM models, as evidenced by the lowest AICc (122.69) and the highest weight ($w(AICc) = 0.78$). Although the AICc of the OU1 model is not remarkably different from the second best model (OU3; AICc = 125.18), the AICc weight implies that the OU2 model has a remarkably higher probability of being selected as the best model than the others.

Discussion

The present study suggests that the OU2 model is the best among the four candidate models, implying that there are two

Table 1. Species list and original range sizes (km^2) used for the present study. The number of each species indicates the position of the species in the phylograms presented in Figure 1 from top to bottom.

ID	Endemic birds	Range size	ID	Endemic birds	Range size
1	*Arborophila gingica*	7700	25	*Garrulax maximus*	562,000
2	*Arborophila rufipectus*	13,200	26	*Garrulax davidi*	1,090,000
3	*Arborophila ardens*	396,000	27	*Babax koslowi*	44,400
4	*Urocynchramus pylzowi*	628,000	28	*Aegithalos fuliginosus*	215,000
5	*Emberiza koslowi*	78,100	29	*Leptopoecile elegans*	1,380,000
6	*Latoucheornis siemsseni*	112,000	30	*Phylloscopus kansuensis*	172,000
7	*Carpodacus eos*	864,000	31	*Phylloscopus hainanus*	13,200
8	*Carpodacus roborowskii*	194,000	32	*Phylloscopus emeiensis*	8900
9	*Phoenicurus alaschanicus*	243,000	33	*Parus venustulus*	1,620,000
10	*Certhia tianquanensis*	32,000	34	*Parus davidi*	56,800
11	*Sitta yunnanensis*	170,000	35	*Parus superciliosus*	547,000
12	*Alcippe variegaticeps*	15,500	36	*Oriolus mellianus*	27,600
13	*Paradoxornis paradoxus*	137,000	37	*Perisoreus internigrans*	143,000
14	*Paradoxornis conspicillatus*	277,000	38	*Podoces biddulphi*	283,000
15	*Paradoxornis przewalskii*	32,700	39	*Alectoris magna*	625,000
16	*Paradoxornis zappeyi*	41,100	40	*Tragopan caboti*	397,000
17	*Alcippe striaticollis*	428,000	41	*Lophophorus lhuysii*	176,000
18	*Chrysomma poecilotis*	261,000	42	*Tetraophasis obscurus*	118,000
19	*Rhopophilus pekinensis*	1,710,000	43	*Bonasa sewerzowi*	394,000
20	*Liocichla omeiensis*	6800	44	*Chrysolophus pictus*	970,000
21	*Garrulax bieti*	23,400	45	*Crossoptilon auritum*	513,000
22	*Garrulax sukatschewi*	28,500	46	*Crossoptilon mantchuricum*	147,000
23	*Garrulax elliotii*	815,000	47	*Syrmaticus ellioti*	471,000
24	*Garrulax lunulatus*	214,000	48	*Syrmaticus reevesii*	532,000

ID = identification number.