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Multiscale Patterns of Phylogenetic Community Structure and Distributional Aggregation for Endemic Mammals of China

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Abstract.- In the present study, the multiscale phylogenetic community structure and distributional aggregation patterns of endemic mammals of China are revealed. The results show that, when spatial resolution is scaled up, the distributional aggregation degree of endemic species is increasing, while the phylogenetic community structure is turning to show emerging clustering patterns. The present study might offer some new insights into phylogenetic community structure studies.

Key words: Evolutionary ecology, mammalian endemism, scale-dependence, community ecology

INTRODUCTION

Phylogenetic community structure (Webb *et al.*, 2002, 2008; Cavender-Bares *et al.*, 2004; Kraft *et al.*, 2007) has now become widely appreciated in community ecology by considering the impacts of phylogenetic history of species on structuring species composition patterns. Typically there are three types of phylogenetic community structure found in the contemporary literature: clustering, overdispersion and randomness (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2004; Kraft *et al.*, 2007). For phylogenetic clustering pattern, it is expected that phylogenetically closely related species tend to distribute aggregately. In contrast, phylogenetic overdispersion pattern shows that closely related species tend to avoid each other, leading to segregating distribution patterns among species. Phylogenetic randomness is a kind of pattern without phylogenetic signals. Thus, phylogenetic history plays no roles on structuring species distribution and associated community composition patterns.

Many empirical studies have been reported over different taxonomic groups of species for their phylogenetic community structure patterns (Cavender-Bares *et al.*, 2004; Chen, 2013b; Qian *et al.*, 2013,2014). However, it seems less studied that how the spatial scales would influence observed phylogenetic community structure. Thus, it is interesting to reveal the association between scale and phylogenetic community structure so as to better understand the mechanisms determining ecological assemblies. When spatial scales are changed, the resultant phylogenetic community structure patterns are expected to change because species inside a quadrat vary greatly.

Distribution of species in a studied landscape is not homogeneous (Zillio and He, 2010; He and Hubbell, 2011). Typically, aggregation of its distribution is a prevailing pattern in real world (Chesson and Neuhauser, 2002; Zillio and He, 2010; He and Hubbell, 2011; Hui *et al.*, 2012; Chen, 2013a; Gao, 2013). In a previous study, it is found that increasing spatial scales could decrease the distributional aggregation patterns of species (Chen, 2013a). Please note that the original argument made in that previous study was wrong, as the aggregation parameter *k* value is high, the aggregation of species distribution should be low. If the change of spatial resolution will result into the change of phylogenetic relatedness patterns of species, then one might expect that there might be some associations between phylogenetic relatedness patterns of species and their distribution aggregation patterns.

When many species are found to inhabit a sample area concurrently, their distributions should be aggregate. Then, we would expect that phylogenetic overdispersion pattern should be observed. This is because these species in that area are likely to come from different clades in phylogenetic trees based on the principle of limiting similarity (Abrams, 1983; Abrams and Rueffler,

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2009): strong competition between closely related species drives the distribution of these closely related species to be not overlapped. Thus, the likelihood of observing phylogenetic clustering pattern is reduced. However, this expectation is not always true. When the habitat heterogeneity is large enough to obscure the influence of interspecific competition, we may still observe the phylogenetic clustering patterns even the distribution of species is very aggregate. As such, the present study could test the above contrasting hypotheses and identify the mechanisms driving the distribution patterns of species.

In the present study, by utilizing the distribution of endemic mammals of China, its aim is to describe the phylogenetic relatedness patterns across various spatial scales. The influence of distributional aggregation would be analyzed and the potential ecological mechanisms determining phylogenetic community structure of these endemic taxa would be elucidated.

MATERIALS AND METHODS

Distributional data and phylogenetic tree for endemic mammals of China

Distributional records of endemic mammals of China are derived from China Species Information Service (http://www.baohu.org/) and literature related to the mammalian fauna of China (Wang, 2003; Smith and Xie, 2008). The phylogeny of these mammal species is constructed from the well established meta-phylogeny for global mammals (Bininda-Emonds *et al.*, 2007). In our study, 61 endemic mammal species are considered. When referring to multi-scale analysis, the maps which are used for measuring phylogenetic community structure and distributional aggregation patterns of species have the following twelve spatial resolutions: 0.25°x0.25°, 0.5°x0.5°, 0.75°x0.75°, 1°x1°, 1.25°x1.25°, 1.5°x1.5°, 1.75°x1.75°, 2°x2°, 3°x3°, 4°x4°, 5°x5° and 10°x10°, respectively.

Measurement of phylogenetic relatedness

We calculate two indices, the standardized net relatedness index (NRI) and the nearest taxon index (NTI) for the distribution of endemic bird species across different grid cells of China to measure their phylogenetic relatedness. These two indices (Webb *et al.*, 2002, 2008) have been widely applied to phylogenetic community structure analysis:

$$NRI = -\frac{MPD - rndMPD}{sd(rndMPD)}, \quad (1)$$

$$NTI = -\frac{MNTD - rndMNTD}{sd(rndMNTD)}. \quad (2)$$

Where MPD represents the mean pairwise phylogenetic distance in which it finds the average distance to all other taxa in the sample for each taxon and MNTD is to calculate the nearest phylogenetic neighbor in the sample for each taxon (Webb *et al.*, 2008). The rndMPD and rndMNTD represent the mean MPD and mean MNTD from randomly generated assemblages. Negative values of both metrics indicate overdispersion, while positive values of both metrics indicate clustering (Pei *et al.*, 2011). These two standardized indices should follow the unit normal distribution with mean=0 and variance=1. As such, if any of the indices is larger than 1.96 (or less than -1.96), the clustering (or overdispersion) pattern identified is regarded to be statistically significant.

However, *NRI* is found to be biased when detecting overdispersion pattern (Kembel and Hubbell, 2006; Swenson *et al.*, 2006), thus the ratio NRI/NTI is used to quantify overdispersion or clustering patterns by comparing the observed ratio to the random ones. If no more than 5% of randomly simulated NRI/NTI values larger than the observed one (that is, P (simulated<observed) >0.95), phylogenetic clustering is recognized for the community. In contrast, if no more than 5% of random NRI/NTI values less than the observed one (P (simulated>observed) >0.95), phylogenetic overdispersion is suggested accordingly (Cooper *et al.*, 2008).

For describing the phylogenetic relatedness pattern presented in the distribution map of endemic mammals under the new spatial resolution, we use the following simple indices, including the percentage of the number of positive NRI and NTI (pnri and pnti); the percentage of the number of negative NRI and NTI (nnri and nnti); the percentage of the number of significantly large NRI/NTI ratio (P(simulated<observed)>0.95) (psratio); and the percentage of the number of significantly small NRI/NTI ratio (P(simulated>observed)>0.95) (nsratio). These metrics reflect different aspects of phylogenetic community structure, and thus should be compared to see if they can consistently identify the phylogenetic community structure for the present study.

Measurement of distributional aggregation of species

Following a previous study (Chen, 2013a), instead of using the negative binomial distribution (Boswell and Patil, 1970; Pielou, 1977; Taylor *et al.*, 1978; Perry and Taylor, 1985), we used the finite version of negative binomial distribution (Zillio and He, 2010; Chen, 2013a) to measure distributional aggregation of species.

The finite negative binomial probability of species distribution reads,

$$P_{FNBD}(n)=\frac{\binom{n+k-1}{n}\binom{N-n+k/a-k-1}{N-n}}{\binom{N+k/a-1}{N}} \quad (3)$$

Estimation of aggregation parameter k follows the previous work (Zillio and He, 2010):

$$\begin{cases}\hat{k}=\dfrac{(1-a)\bar{n}^2-as^2}{s^2-(1-a)\bar{n}} \\ \bar{n}=\dfrac{1}{m}\sum n_i \\ s^2=\dfrac{1}{m}\sum (n_i-\bar{n})^2\end{cases} \quad (4)$$

Where m is the number of quadrats, a is the ratio between smallest spatial unit size and the whole range, $\{n_i\}$ is the abundance vector in a set of sampled quadrats. A high (or low) k value indicates that the species will have a low (or high) aggregation on its spatial distributional pattern.

Because in the present study we have only presence information for each species over the studied qudrats, we take the overall aggregation parameter k to represent the community aggregation status, which is measured on the species richness over the sampling quadrats.

RESULTS

As seen in the Figure 1, there are tight relationships between the six phylogenetic relatedness indices, overall distributional aggregation and spatial resolutions. Increasing spatial resolutions of the sampling quadrats would result into increasing aggregation patterns of species distribution.

In contrast, increasing spatial resolution would increase the likelihood of phylogenetic clustering patterns over the sampling quadrats. This can be evidenced by the increasing trends for the indices pnri, pnti and psratio and the decreasing trends for the indices nnri, nnti and nsratio (Fig. 1).

As such, it can be showed that there is a positive association between aggregation of species distribution and the likelihood to find more grids showing phylogenetic clustering patterns (as indicated by pnri, pnti, psratio) (Fig. 1).

DISCUSSION

Based on the results, there is a positive relationship between the sampling sizes of the quadrats and phylogenetic clustering structure for the endemic mammalsin China. Thus, increasing the sampling size will lead to the reduction of total number of sampling quadrats, which in turn would increase the chance to find more quadrats showing phylogenetic clustering patterns (that is, species found in these quadrats will tend to be closely related for their evolutionary relationships).

Interestingly, it is found that the result for the aggregation patterns of species is totally opposite to the previous study (Chen, 2013a), which showed that increasing spatial sizes of quadrats should result into decreasing aggregation pattern (the original argument made in that previous study (Chen, 2013a) was wrong, as the parameter k value was high, the aggregation of species distribution should be low). In the present study, it is observed that global aggregation status on the distribution of all species showed an increasing trend when spatial sizes of grids are increased (Fig. 1). The difference between

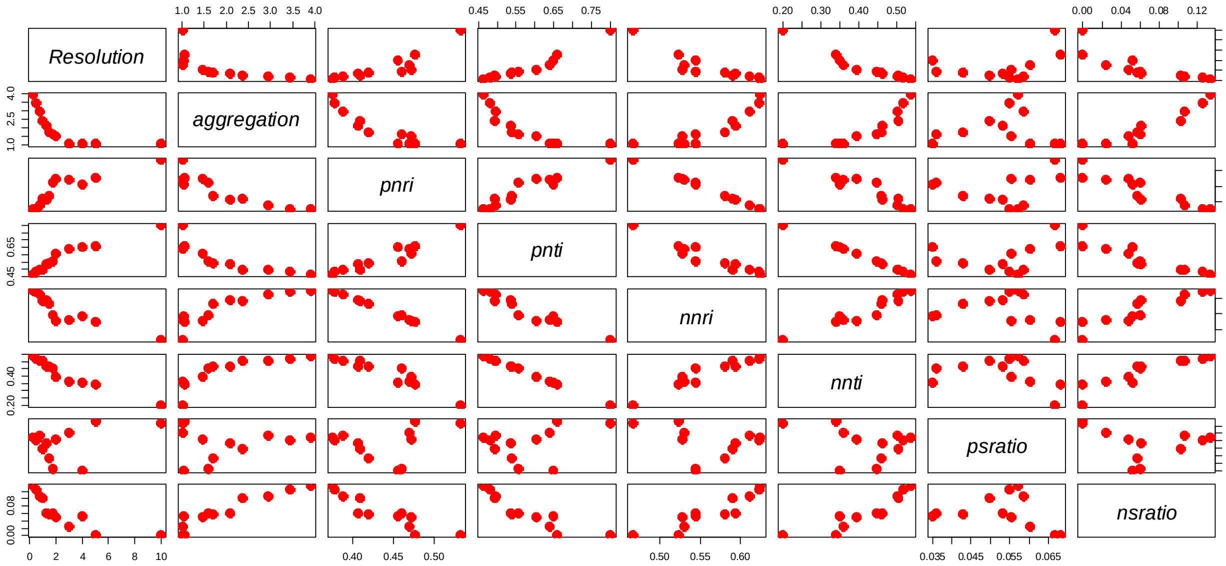

Fig. 1. Bivariate relationships between spatial resolutions, species overall aggregation, and phylogenetic relatedness indices of the quadrats for endemic mammals of China. Full names for the abbreviations in the diagonal line are: the percentage of the number of positive NRI and NTI (pnri and pnti); the percentage of the number of negative NRI and NTI (nnri and nnti); the percentage of the number of significantly large NRI/NTI ratio (P(simulated<observed)>0.95) (psratio); and the percentage of the number of significantly small NRI/NTI ratio (P(simulated>observed)>0.95) (nsratio).

the two results is derived from the measurement of overall aggregation patterns of species in the community. In the previous study (Chen, 2013a), *k* is measured as the mean for the *k* values from different species. In contrast, *k* is measured as the value which was fitted for the distributional points emerged for all the species for the present study. The reason for doing so for our present study is in that we want to reveal a general aggregation scenario for all the species, as such, we believe that the utilization of all distributional points across different species can better reveal the holistic view of aggregation status of the whole species assemblage. In the previous study (Chen, 2013a), the average of the *k* values for all the species might have the risk that if the combined distribution of all the species is random but each individual species is aggregated, the average of all *k* values might not reflect the true distributional pattern of the whole species assemblage.

Scale-dependence property of community-level aggregation and phylogenetic relatedness patterns offers a way to reveal how distributional aggregation might change the phylogenetic community structure dynamically. The previous study (Chen, 2013a) has demonstrated that species rarity pattern is tingly associated with species aggregation. The present study further showed that species aggregation pattern of the community should predict the phylogenetic relatedness pattern for endemic mammals in China as well.

Multiscale ecological patterns are now gaining wide attention in the past decade (Dray *et al.*, 2012; Blank *et al.*, 2013; Chen, 2013a,c), while the role of spatial structure of species on influencing phylogenetic community structure has been studied in recent studies (Shen *et al.*, 2013). However, as mentioned in the introduction section, no previous studies have been made to show how phylogenetic community structure may vary according to varying spatial resolutions of the sampling quadrats. Thus, the present study might be one of the first attempts to describe multiscale phylogenetic relatedness patterns of vertebrate species at regional scales. For future implications, the multiscale phylogenetic relatedness patterns for global species should be an interesting but still open question so far. Also, it is interesting to see how the influence of environment may change when evaluating their influences on species phylogenetic relatedness patterns.

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