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Species turnover of amphibians and reptiles in eastern China: disentangling the relative effects of geographic distance and environmental difference

Abstract Spatial turnover of species lies at the heart of macroecology and conservation biogeography. However, our knowledge of the causes of species turnover remains poor, particularly for herpetofaunas including amphibians and reptiles. Here, using regression, variance partitioning, and hierarchical partitioning analyses, we examine the relationships of species turnover in herpetofaunas among provinces in eastern China with respect to geographic distance and environmental difference. We found that species turnover in herpetofaunas is moderately to strongly correlated with geographic distance and difference in most environmental variables examined between provinces. Geographic distance and environmental difference together explain 87.1 and 89.9% of the variance of species turnover for amphibians and reptiles, respectively. Variance partitioning analysis indicated that most variance in species turnover is explained by the joint effect of geographic distance and environmental difference. Beyond this shared variance, environmental difference is a stronger predictor of species turnover than geographic distance, particularly for reptiles. Hierarchical partitioning analysis showed that energy-related variables explained more variance in species turnover for both amphibians and reptiles, compared with water-related variables. The independent effects of water-related variables are slightly higher for amphibians than for reptiles whereas the independent effects of energy-related variables are slightly higher for reptiles than amphibians. These patterns are consistent with different ecophysiological requirements of the two taxa. Our results have important implications for predicting changes in biodiversity of herpetofaunas under climate change scenarios. Global warming will affect the immigration and local extinction of both amphibians and reptiles, and precipitation change may affect amphibians more strongly, compared with its effect on reptiles.

Keywords Beta diversity · Distance decay of similarity · Energy-related variables · Niche limitation · Water-related variables

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Introduction

Species turnover, which refers to changes in species composition among areas, lies at the heart of macroecology and conservation biogeography (Koleff et al. 2003; Whittaker et al. 2005; Gaston et al. 2007; Qian and Ricklefs 2007). Knowledge of the ecological processes that drive spatial turnover of species is critical to understanding the origin and maintenance of biodiversity (Janzen 1967; Whittaker 1972; Gaston et al. 2007; Qian and Ricklefs 2007), predicting possible biotic response to climatic and environmental changes (Buckley and Jetz 2008), and designing networks for protected areas (Whittaker et al. 2005; Pawar et al. 2007).

Species turnover among different areas may be driven by two major mechanisms: niche limitation (niche differentiation) and dispersal limitation, although they are not necessarily mutually exclusive (Harrison et al. 1992; Nekola and White 1999; Gaston et al. 2007; Qian and

Ricklefs 2007; Soininen et al. 2007). Niche limitation hypothesis assumes that different species possess different traits to respond to different biotic and abiotic conditions (Gaston et al. 2007). It predicts that assemblage composition will change along environmental gradients as a result of species-specific differences in evolved adaptive responses (Nekola and White 1999; Gaston et al. 2007). Thus, taxa with higher adaptability to environmental stress are expected to occupy more types of habitats and hence have lower rates in similarity decay along environmental gradients (Harrison et al. 1992). Dispersal limitation hypothesis assumes that distributions of individual species are purely limited by dispersal ability, and species tend to be aggregated (Gaston et al. 2007). Thus, low dispersal ability and high dispersal barriers (such as mountain ranges) increase the degree of aggregation and ultimately lead to high species turnover (Gaston et al. 2007; Qian 2009a, b). Knowledge of relative effects of niche limitation and dispersal limitation on species distributions has important implications for conservation and restoration ecology as well as for understanding global patterns of species richness.

Previous studies have documented relative contributions of environmental difference and geographic distance to species compositional changes for several taxa at large scales (Nekola and White 1999; Condit et al. 2002; Duivenvoorden et al. 2002; Tuomisto et al. 2003; Steinitz et al. 2006; Gaston et al. 2007; Qian and Ricklefs 2007; Pawar et al. 2007; Buckley and Jetz 2008; Qian et al. 2009; Leprieur et al. 2009; Linares-Palomino and Kessler 2009) and effects of species traits on dispersal (Harrison et al. 1992; Qian 2009a, b; Linares-Palomino and Kessler 2009). These studies found that environmental and geographic distance and their joint effects are important in regulating spatial turnover of species, although the relative importance of environmental and geographic distances in regulating species turnover is taxonomic- and scale-dependent (Steinitz et al. 2006; Qian and Ricklefs 2007; Buckley and Jetz 2008; Qian et al. 2009; Linares-Palomino and Kessler 2009). For instance, environmental differences among sites play a larger role in explaining variation in floristic distances than geographic distance for pteridophytes in Western Amazonian forests (Tuomisto et al. 2003). Qian et al. (2009) found that the variance in spatial turnover of mammals in North America is explained more by geographic distance and environmental differences jointly than by unique effects of geographic distance and environmental difference.

However, few studies have explored the determinants of species turnover in herpetofaunas (including amphibians and reptiles), which are sensitive to environmental changes and are declining globally due to global warming and local habitat degradation (Alford and Richards 1999; Gibbons et al. 2000; Whitfield et al. 2007). Amphibians and reptiles are ideal study taxa for relating species turnover to environmental conditions because they have remarkably different physiological requirements—both amphibians and reptiles are solar ectotherms, depending heavily on external energy input to maintain their normal metabolism (Angilletta et al. 2002) but amphibians require water to reproduce and humid environment to survive (Wells 2007). Qian et al. (2007) found that species richness of amphibians is more strongly associated with precipitation whereas temperature tends to be more important for reptiles in China. At a global extent, Qian (2010) found that temperature explains more variance in species richness for reptiles than for amphibians whereas precipitation explains more variance for amphibians than for reptiles. Thus, we may expect that the spatial distributions of amphibians are likely associated with water-related variables more strongly than reptiles.

In this study, we examine the relative effects of geographic distance and environmental difference on changes in species compositions of herpetofaunas in eastern China. Specifically, we (1) compare distance decay of similarity between amphibians and reptiles; (2) test that, compared with amphibians, species turnover of reptiles between regions is better explained by environmental difference than by geographic distance, a hypothesis formulated based on the finding of Araújo and Pearson (2005) that reptiles show closer equilibrium with current climate than amphibians in Europe; and (3) test that species turnover of amphibians is driven more by water-related variables whereas that of reptiles is determined more by energy-related variables due to their different ecophysiological requirements (Qian et al. 2007; Qian 2010).

Materials and methods

Study area

The study area is eastern China, which is defined as a region including 20 provinces or autonomous regions (hereafter referred to as provinces) of continental China (Fig. 1). This area, which is generally dominated by forest vegetation, encompasses 4.28×10^6 km^2, ranging from 21.97° to 46.63° N in latitude and from 101.79° to 128.20° E in longitude. Beijing and Tianjin were combined into Hebei Province, Shanghai into Zhejiang Province, Chongqing into Sichuan Province, and Hong Kong and Macau into Guangdong Province. The average area of each province is 217,250 km^2, ranging from 101,787 to 569,000 km^2. The number of unique province pairs is 190 for the 20 provinces (i.e., $n(n-1)/2$, where n is the number of provinces). Distances between provinces (DIS) were measured between centers of provinces.

Species data

We assembled provincial species lists of amphibians from Fei et al. (2005), and those of reptiles from Ji and Wen (2002). We updated each of the provincial species lists with information from China Species Information Service (http://www.baohu.org/cn/).

Fig. 1 Map showing the 20
provinces used in the study
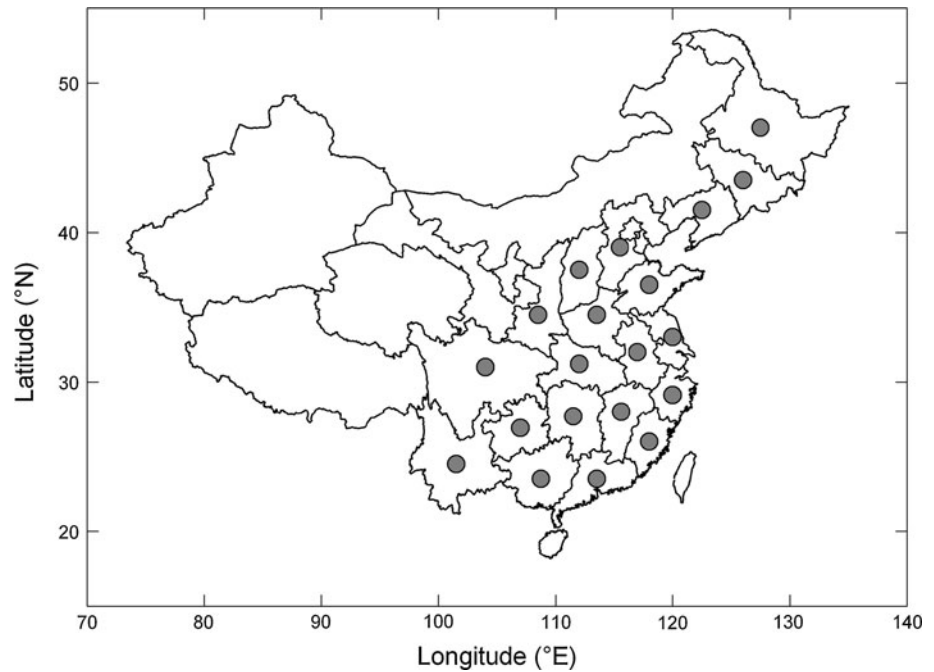
Environmental variables

To assess the relationship between species turnover and differences in climatic and physiographic conditions between each pair of provinces, we documented the following eight variables for each province: (1) mean annual temperature (TEM); (2) temperature seasonality (TS) measured as the difference between mean January temperature and mean July temperature; (3) mean annual precipitation (PRE); (4) precipitation seasonality (PS) measured as difference between the wettest month precipitation and the driest month precipitation; (5) annual actual evapotranspiration (AET); (6) annual potential evapotranspiration (PET); (7) elevation range (ELEV) measured as the difference between the highest and lowest elevations within a province; and (8) provincial area (AREA). Temperature data are widely used as a measure of ambient energy input (e.g., Qian et al. 2009). Precipitation data were used to represent water availability to organisms. The PET is also considered as a measure of ambient energy (Hawkins et al. 2003). The AET is considered as a suitable productive energy metric (Evans et al. 2005). Elevation range and sample area are generally positively correlated with habitat diversity (S. Chen et al. unpublished data).

Data for the six climatic variables were obtained from two global datasets for pixels of 0.5° of latitude and longitude; and information about sources of the datasets are available in New et al. (1999) for temperature and precipitation, and Ahn and Tateishi (1994) and Tateishi and Ahn (1996) for the evapotranspiration data. We extracted all half-degree pixels for the entirety of China from these datasets, assigned each pixel into a province according to its midpoint location, and calculated averages of the six environmental variables for each province. These averages were used to represent average

environmental conditions of the provinces. For the 20 provinces used in this study, climate data for each province was quantified using, on average, 82 half-degree pixels. The highest and lowest elevations for each province were obtained from geographical literatures (primarily provincial and national atlases) and online sources (e.g., http://www.8264.cn/19841.html for maximum elevations).

Data analyses

Many indices measuring similarity between floras and faunas have been used in the literature, but the Jaccard index was rated highly among the 39 binary similarity indices tested by Shi (1993) and is one of the most commonly used similarity indices, particularly in studies on species turnover (e.g., Buckley and Jetz 2008; Anderson et al. 2011; Beaudrot and Marshall 2011). Thus, we calculated species turnover between each pair of provinces, using the Jaccard index of similarity (J) defined as $a/(a + b + c)$, where a is the number of species shared between two localities, and b and c are the numbers of species unique to each locality (Legendre and Legendre 1998). When all species are shared, $J = 1$, and when none are shared, $J = 0$. We related the Jaccard index to geographic distance and differences in climate, elevation range, and sample area between provinces. To normalize model residuals, we used the natural logarithm of the Jaccard index (ln J); we added 0.01 to each Jaccard index so that $J = 0$ can be log-transformed.

We regressed the natural logarithm of Jaccard index against geographic distance to determine the distance decay of similarity. When the presence of a species in two areas reflects only dispersal between the areas, one

would expect the intercept of the ln *J*-distance regression to be 0 (i.e. *J* = 1, complete faunal similarity) at 0 distance (Buckley and Jetz 2008). A randomization procedure described by Nekola and White (1999) and Steinitz et al. (2006) was performed to test the differences in the rate of decay in similarity with geographical distance between amphibians and reptiles. We conducted a simple Mantel test with 999 permutations to determine the significance of the relationship between faunal similarity and geographic distance (Mantel 1967; Legendre and Legendre 1998). Simple Mantel tests were also conducted to assess the relationship between similarities and climatic differences between provinces, and to evaluate the relationship in faunal similarities between amphibians and reptiles.

We used a variation partitioning approach (Legendre and Legendre 1998) to distinguish between the effects of variables determining dispersal limitation (geographical distance) from those pertinent to niche limitation (environmental difference). Variation partitioning analyses decompose the total variance in species similarity into four fractions: (1) variance explained uniquely by geographic distance, (2) variance explained uniquely by environmental difference, (3) variance explained jointly by geographic distance and environmental difference, and (4) unexplained variance (Steinitz et al. 2006; Qian et al. 2009).

We used the hierarchical partitioning analysis (HP) to assess the relative importance of each environmental variable on species turnover (Chevan and Sutherland 1991; Mac Nally 2000; Quinn and Keough 2002). In our case, HP determined improvement in the fit (R^2 in a multiple regression on distance matrices) of all models with a focal variable (predictor) to all possible models without the focal predictor, and the improvement in fit was then averaged across all possible models with the focal predictor (Quinn and Keough 2002; Lichstein 2007). This method allows us to partition explanatory power of each predictor variable into the independent effect by the variable and the joint effect with other variables. We conducted multiple regressions in R (R Development Core Team 2009).

Results

There are 270 amphibian species and 327 reptile species analyzed in this study. Each province has, on average, 43.4 ± 33.4 (SD) amphibian species and 67.9 ± 43.7 (SD) reptile species. The mean range size estimated by the number of provinces occupied by each taxon was larger for reptiles (4.6 provinces) than for amphibians (3.2 provinces), and the mean faunal similarity was higher for reptiles (0.279 ± 0.181) than for amphibians (0.227 ± 0.175) (*t* test, $p < 0.001$), suggesting a higher species turnover for amphibians than for reptiles. Moreover, there was a significant correlation in faunal similarity between amphibians and reptiles (Spearman's $r = 0.918$, $p < 0.001$).

Table 1 Pearson correlation coefficient between the natural logarithm of Jaccard index and geographic and environmental predictors between provinces in eastern China

Predictors	Amphibians	Reptiles
DIS	−0.870***	−0.887***
TEM	−0.586**	−0.704**
TS	−0.806**	−0.877***
PRE	−0.565**	−0.602**
PS	−0.142[NS]	−0.229*
PET	−0.700***	−0.812**
AET	−0.668**	−0.734**
ELEV	−0.163[NS]	−0.026[NS]
AREA	−0.191[NS]	−0.064[NS]

Levels of statistic significance were determined by Mantel tests (999 permutations in each test) as follows: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and [NS]$p > 0.05$
DIS distance between provinces, *TEM* mean annual temperature, *TS* difference between mean January temperature and mean July temperature, *PRE* annual precipitation, *PS* difference between mean January precipitation and mean July precipitation, *PET* potential evapotranspiration, *AET* actual evapotranspiration, *ELEV* elevation range (maximum elevation minus minimum elevation), *AREA* area of a province

Climatic differences between provinces were, in general, strongly and significantly correlated between different climatic variables (Table S1). Compositional similarities of amphibians and reptiles were highly correlated with geographic distance and climatic difference; and correlations tended to be stronger for reptiles than for amphibians (Table 1). However, compositional similarities of amphibians and reptiles were not significantly correlated with differences in elevation range and differences in sample area ($p > 0.05$; Table 1). As a result, we excluded these two variables from further analyses.

Linear regressions of the ln *J* on distance, which describe the exponential or proportional decline in faunal similarity with distance, are characterized by a slope (*b*) and an intercept [ln *J*(0)]. Intercepts were −0.345 and −0.144, respectively, for amphibians and reptiles. A greater absolute value of intercept for amphibians than for reptiles indicates a higher species turnover over short distances for the former than the latter. The ln *J* decreased significantly with increasing geographic distance for both amphibians and reptiles, and the slope of the relationships per 1000 km was −1.145 for amphibians and −1.107 for reptiles (Fig. 2), indicating that species turnover over distance among areas was greater for amphibians than for reptiles in eastern China.

Geographic distance and environmental difference together explained 87.1 and 89.9% of the variance in the natural logarithm of the Jaccard index of amphibians and reptiles, respectively. Most of the variance in similarity for amphibians (68.0%) and reptiles (75.7%) was explained by the joint effect of climatic difference and geographic distance. The proportion of the variance uniquely explained by climatic difference and by geographic distance was, respectively, 11.4 and 7.7% for amphibians, and 11.2 and 3.0% for reptiles (Fig. 3).
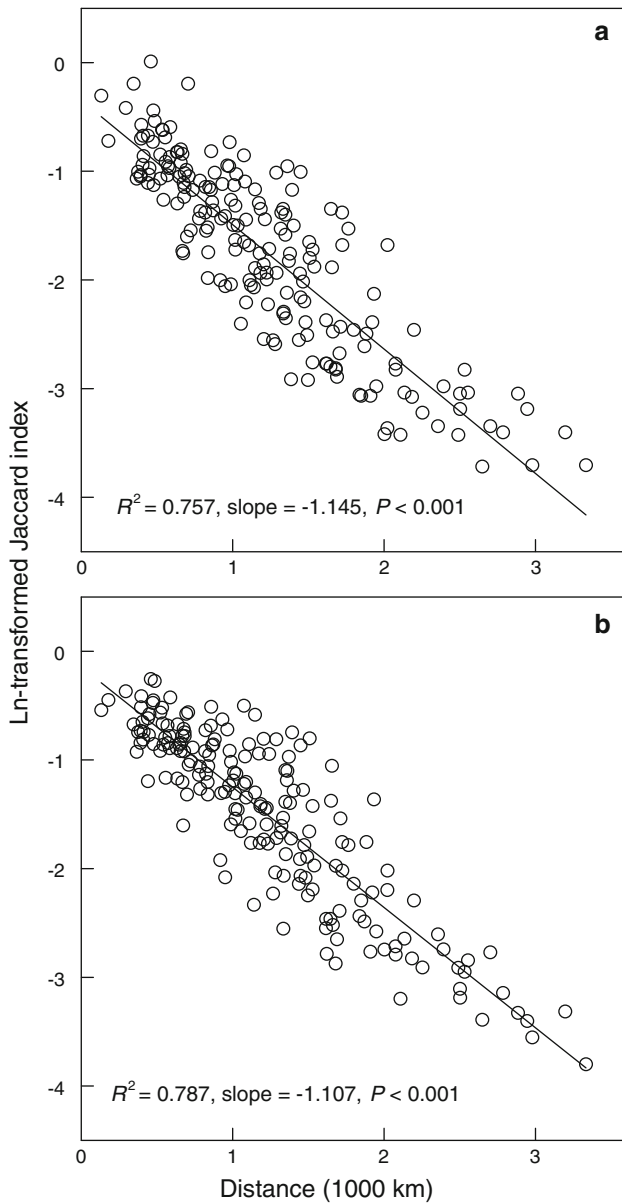
Fig. 2 Distance decay of similarity for **a** amphibians and **b** reptiles estimated using the Jaccard index

Fig. 3 Proportion of the variance in the ln-transformed Jaccard index explained by geographic distance and environmental difference between sample areas

Fig. 4 Independent and joint effects of each explanatory variable on species turnover (measured as ln-transformed Jaccard index) of amphibians (*left column*) and reptiles (*right column*). Variable names are as in Table 1

Thus, environmental distance explained uniquely 1.5 and 3.7 times more variance in the species turnover of amphibians and reptiles, respectively, than did geographic distance. Hierarchical partitioning analysis showed that geographic distance and temperature seasonality were the two most important predictors determining species turnover of both amphibians and reptiles (Fig. 4).

Discussion

Our study found that the mean range size of amphibians is smaller than that of reptiles, the compositional similarity between provinces is lower for amphibians than
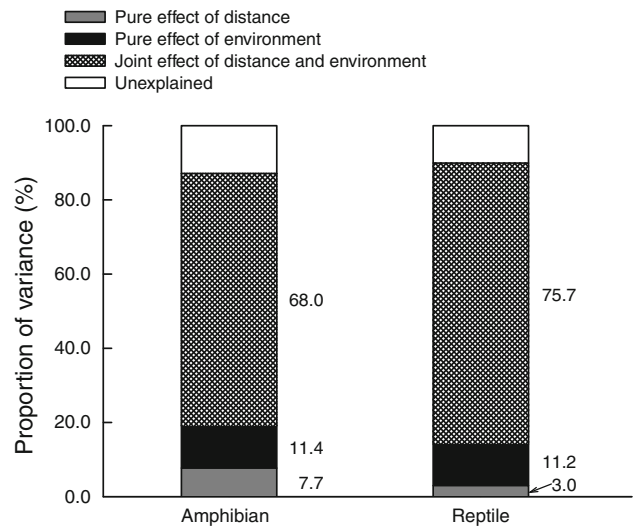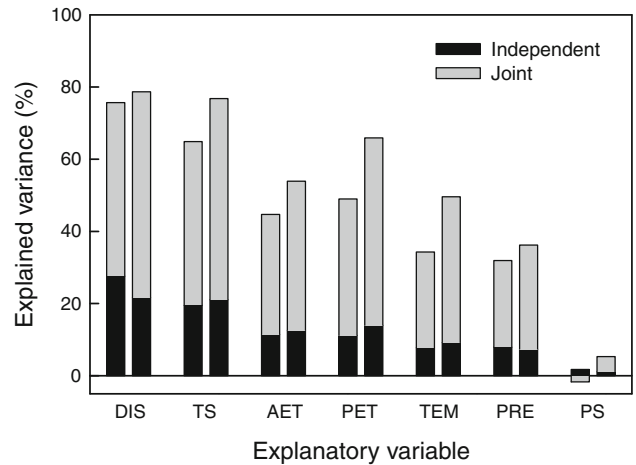
for reptiles over the shortest distance used in this study, and the rate of distance decay of similarity is greater for amphibians than for reptiles. All these findings are in agreement with one another and indicate that species turnover (i.e., beta diversity) is higher for amphibians than for reptiles in eastern China. Our results are consistent with that of Laurencio and Fitzgerald (2010), who found that beta diversity is higher for amphibians than for reptiles between the Atlantic and Pacific lowland rainforests in Costa Rica. Previous studies have documented that more vagile species have a lower level of beta diversity (Nekola and White 1999; Steinitz et al. 2006; Qian 2009a, b). For example, Qian (2009a) found that, in North America, pteridophytes with vagile propagules have lower beta diversity than spermato-

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phytes with less vagile propagules. Buckley and Jetz (2008) compared species turnover of amphibians with that of birds, which disperse more readily than amphibians, and they found a greater species turnover for amphibians than for birds. A lower species turnover for amphibians than for reptiles may suggest that reptiles as a group have better dispersal ability than amphibians.

Our study found that the variance in spatial turnover of amphibians and reptiles are better explained by difference in environmental variables than by geographic distance between regions, although the difference in the explained variance between environmental difference and geographic distance is not large for amphibians and a great amount of the explained variance is due to the joint effect of environmental difference and geographic distance for both amphibians and reptiles. This suggests that niche limitation (environmental difference) is more important than dispersal limitation (geographic distance) in shaping the spatial turnover of amphibians and reptiles at the examined spatial scale in eastern China. Our finding is inconsistent with those of Qian and Ricklefs (2007) and Qian et al. (2009) who found that geographic distance generally explained about the same or more proportion of the variance of species turnover in vascular plants and mammals than did environmental difference in North America. However, this discrepancy between the present study and their studies may be partly due to different historical processes in these two regions. A larger proportion of North America was covered by thick ice sheets during the Last Glacial Maximum (Pielou 1992). The modern spatial distributions of organisms in North America may be governed by the process of postglacial colonization. According to Johnstone and Chapin (2003), northern distribution limits of some species are not in equilibrium with current climate, suggesting that species distribution ranges in North America are still expanding through dispersal processes to occupy more suitable sites. On the contrary, ice sheets only covered areas at high elevations in China during the Last Glacial Maximum. Thus, the degree to which species distributions are at equilibrium with current climate is presumably higher in China than in North America.

Compared with amphibians, the variation in species turnover of reptiles is better explained by environmental difference. This indicates that distributions of amphibians are more strongly limited by extrinsic barriers such as ranges and intrinsic dispersal ability than reptiles. If the distribution of species were at a higher degree of equilibrium with current environmental condition, one would expect a higher co-variation between assemblage composition and environmental variables, suggesting that species tend to occupy all suitable environmental spaces. Our results are consistent with that of Araújo and Pearson (2005), who found that co-variation between species composition and climate is higher for reptiles than for amphibians in Europe. This implies that amphibians are less capable of shifting distribu-

tions than reptiles, and thus are more vulnerable to extinction due to rapid climatic change (Araújo and Pearson 2005).

This study found that energy-related variables are more important than water-related variables in determining species turnover for both amphibians and reptiles. This finding is consistent with the physiology of amphibians and reptiles, both of which are ectotherms. The performance and many ecophysiological aspects of ectotherms are strongly determined by body temperature, which in turn is regulated by ambient energy input (Angilletta et al. 2002). Despite the fact that energy-related variables play a more important role than do water-related variables in determining species turnover for amphibians and reptiles, our hierarchical analyses showed that temperate tended to have a stronger unique effect for reptiles than for amphibians whereas precipitation tended to have a stronger unique effect for amphibians than for reptiles. These differential effects of energy and water on species turnover of amphibians and reptiles are consistent with differential effects of these two factors on alpha diversity, which describes species richness within single sites, of the two taxa in China (Qian et al. 2007) and in most biogeographic realms across the world (Qian 2010). Amphibians usually require water for reproduction (i.e., their eggs must be laid in water in order to survive), and amphibian adults are sensitive to desiccation in warm/dry environments and require environmental humidity/moisture plus cooler temperatures (Deullman and Trueb 1994; Qian et al. 2007; Wells 2007). In contrast, reptiles are generally more resistant to desiccation, and have higher operating temperatures than amphibians (Huey 1982).

The finding of differential effects of energy and water on distributions of amphibians and reptiles has important implications for predicting impacts of climatic change on their distributions. Because amphibians and reptiles have low dispersal ability (Blaustein et al. 1994) and thus have limited ability to track climate change through dispersal, the probability of local extinction of amphibians and reptiles, particularly rare species that are generally sensitive to environmental change, would be presumably high if their immigration rates are slower than the rate of climatic change. Both shift in distribution range of widespread species and local extinction of rare species would result in decreases in species turnover between regions, and thus result in increases in biotic homogenization (Olden and Rooney 2006). Furthermore, because amphibians prefer aquatic habitats and typically have relatively low dispersal rates (Wells 2007), whereas reptiles have a greater ability to track dryer and warmer conditions (Pough et al. 2001), amphibians may be affected more by global warming, compared with reptiles.

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