



Significance of pre-Quaternary climate change for montane species diversity: Insights from Asian salamanders (Salamandridae: *Pachytriton*)

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ABSTRACT

Despite extensive focus on the genetic legacy of Pleistocene glaciation, impacts of earlier climatic change on biodiversity are poorly understood. Because amphibians are highly sensitive to variations in precipitation and temperature, we use a genus of Chinese montane salamanders (Salamandridae: *Pachytriton*) to study paleoclimatic change in East Asia, which experienced intensification of its monsoon circulation in the late Miocene associated with subsequent Pliocene warming. Using both nuclear and mitochondrial DNA sequences, we reconstruct the species tree under a coalescent model and demonstrate that all major lineages originated before the Quaternary. Initial speciation within the genus occurred after the summer monsoon entered a stage of substantial intensification. Heavy summer precipitation established temporary water connectivity through overflows between adjacent stream systems, which may facilitate geographic range expansion by aquatic species such as *Pachytriton*. Species were formed in allopatry likely through vicariant isolation during or after range expansion. To evaluate the influence of Pliocene warming on these cold-adapted salamanders, we construct a novel temperature buffer-zone model, which suggests widespread physiological stress or even extinction during the warming period. A significant deceleration of species accumulation rate is consistent with Pliocene range contraction, which affected *P. granulatus* and *P. archospotus* the most because they lack large temperature buffer zones. In contrast, demographic growth occurred in species for which refugia persist. The buffer-zone model reveals the Huangshan Mountain as a potential climatic refugium, which is similar to that found for other East Asian organisms. Our approach can incorporate future climatic data to evaluate the potential impact of ongoing global warming on montane species (particularly amphibians) and to predict possible population declines.

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1. Introduction

Compared to the extensively studied Quaternary climatic fluctuations and associated genetic legacy on extant organisms (reviewed in Hewitt, 2000), the impacts of more ancient environmental changes as far back as the Pliocene and late Miocene, which witnessed remarkable shifts in global climate and continental ecosystems (Cerling et al., 1997; Zachos et al., 2001), are poorly known. Yet, those early climatic transitions may have had crucial roles in promoting diversification within radiations of Cenozoic organisms (Kozak et al., 2006; Vieites et al., 2007; Lo Presti and Oberprieler, 2009; Zheng et al., 2009; Dasmahapatra et al., 2010; Miralles and Carranza, 2010; Patel et al., 2011).

During the Quaternary glacial period, East Asia was largely not glaciated due to dry winters (Hewitt, 2000; Li et al., 2004). Species from this region may not have experienced the extreme demographic fluctuations that characterize biota from glaciated areas. Old gene lineages are more likely to be preserved, which allows us to study the evolutionary forces that acted upon organismal diversity before the glacial period. Studies have demonstrated that glacial climatic oscillations are too recent to explain some of the deep genetic divergences observed today (Dasmahapatra et al., 2010; Miralles and Carranza, 2010; Patel et al., 2011). East Asia experienced a distinctive climatic history since the late Miocene, which is characterized by development of the unique East Asian monsoon system accompanied by the accelerating uplift of the Tibetan Plateau (An et al., 2006; Harris, 2006). Seasonality increased, with most precipitation occurring in summer (An et al., 2001). The monsoon is strongly associated with East Asian terrestrial ecosystem turnover (Jia et al., 2003). On the other hand, East Asia was affected by global warming in the Pliocene (Zachos et al., 2001; Ravelo et al., 2004; Salzmann et al., 2011). This

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warm and wet period contrasts with the otherwise prevailing trend towards global cooling that existed since the late Miocene, and it could have devastated cold-adapted organisms in ways similar to current global warming (Pounds et al., 2006; Milanovich et al., 2010). Because these climatic shifts greatly altered precipitation patterns and environmental temperatures, we might expect to find signals in extant East Asian amphibians, whose life history and species richness are governed by precipitation and temperature (Buckley and Jetz, 2007). Nevertheless, few phylogeographic studies have focused on East Asia, and our knowledge of the genetic consequences of historical climatic change in this region remains sparse.

The stout newts (*Pachytriton*, also known as paddle-tailed newts) from southeastern China are an ideal system with which to investigate organismal response to historical climatic change. Earlier studies suggest that *Pachytriton* diverged from its sister genus *Laotriton* as early as the middle Miocene (Zhang et al., 2008b; Vieites et al., 2009). Such long-term persistence is essential to be able to capture climatic signatures over the last 10 million years (Ma). Species in this genus are restricted to montane habitats at high elevations (i.e., on sky islands), which were uplifted by major orogenies before the middle Eocene (Guo, 1998). Therefore, the phylogeographic pattern in *Pachytriton* evolved too recently to be explained by mountain orogeny. However, ranges of individual populations likely expanded and contracted along elevational gradients that changed as the result of climatic fluctuations, in a manner similar to that recorded in North American montane salamanders (Shepard and Burbrink, 2008). Salamanders generally have low dispersal ability and exhibit philopatry; thus, they are more sensitive than are endotherms to changes in precipitation and temperature (Buckley and Jetz, 2007; Vieites et al., 2009). Adult *Pachytriton* permanently live in small, shallow and clean montane streams (usually 1–3 m wide) and have morphological and osteological specializations associated with their aquatic habitat (Özeti and Wake, 1969; Zhao et al., 1994; Fei et al., 2006; Wu et al., 2012a). They are adapted to live in cold water, and a small increase of ambient temperature may be fatal (Zhao et al., 1994).

In this paper, we use *Pachytriton* to understand the likely impact of late-Miocene monsoon intensification and Pliocene warming on montane species diversity in East Asia. First, we evaluate the hypothesis that the substantial intensification of the East Asian summer monsoon in the late Miocene (7–10 Ma) triggered range expansion in *Pachytriton*, which subsequently promoted initial speciation in the genus. By sampling throughout the known geographic range of *Pachytriton*, we employ a coalescent method to generate a species tree along with divergence times and test whether speciation occurred after monsoon intensification. During the monsoon season, we have encountered *Pachytriton* in temporary waterways after heavy rains or in puddles with signs of a recent flood (unpublished personal observations). Given that this genus is the most aquatic in the family Salamandridae (Özeti and Wake, 1969; Titus and Larson, 1995), floods that connect neighboring stream systems could facilitate colonization of new habitats and lead to range expansion. Recent studies suggest a critical role for range expansion in promoting speciation (Moyle et al., 2009; Van Bocxlaer et al., 2010). Speciation could occur followed by vicariance that reduces gene flow across a barrier formed after expansion. Second, we follow the rationale of ecological niche-modeling to examine likely physiological constraints on *Pachytriton* and the extent to which Pliocene warming (3–5 Ma) may have affected their survival. Because these salamanders are sensitive to high temperatures and restricted to specific montane habitats, they may experience range contraction toward higher elevations or even habitat collapse under a climatic warming scenario (Wake and Vredenburg, 2008; Wake, 2009, 2012). Third, we reconstruct historical demography using a multi-locus coalescent model to assess how population size may have fluctuated under different

climatic conditions. We predict no population growth in species that were most stressed by Pliocene warming and stable demographic growth in species for which areas of suitable habitat persisted. Fourth, we test the tempo of diversification in the genus against a null model of constant rate of lineage accumulation. A detrimental impact of Pliocene warming would favor rate deceleration over constancy.

2. Material and methods

2.1. Taxon sampling and sequence preparation

We conducted extensive fieldwork throughout southeastern China and acquired specimens and tissues from 6 of the 8 species in *Pachytriton*: 4 populations of *P. archospotus*, 6 populations of *P. brevipes*, 7 populations of *P. granulatus*, 1 population of *P. feii*, 5 populations of *P. inexpectatus* and 1 population of *P. xanthospilos* (Fig. 1; Supplementary Table S1). Samples of the recently described *P. moi* from Guangxi province and *P. changi* (described from two salamanders obtained from a Japanese pet store with unknown origin) were unavailable for this study.

Total genomic DNA was extracted from ethanol-preserved liver or muscle tissue by using a QIAGEN DNeasy Blood and Tissue Kit (Valencia, CA, USA). We amplified from all specimens two mitochondrial fragments (*ND2* and the *cytb* with flanking tRNAs, each with ~1200 base pairs, bp) and two nuclear fragments that cover the 3' end of the *RAG-1* (~1200 bp), as well as a non-coding region of the tyrosinase gene (*NCRT*, 600 bp). The first three markers are widely used in phylogenetic studies; *NCRT* is used for the first time and developed following the anonymous-loci development method described in Espregueira Themudo et al. (2009). The *NCRT* fragment was amplified using the forward primer TYR-F (5'AGC GGT AGA CCT GTG GCT TC3') and reverse primer TYR-R (5'TGC ACA CTG ATG GGG TTG GT3'). Other PCR primers and thermal cycle protocols are the same as Wu et al. (2010). Nucleotide sequences were manually aligned in Se-Al 2.0 (Rambaut, 1995). Sequences are deposited in GenBank (Supplementary Table S1).

2.2. Individual gene-trees estimation

We inferred separate gene genealogies from *RAG-1*, *NCRT* and the concatenated mitochondrial DNA (mtDNA). We utilized the Bayesian criterion in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001) and the maximum-likelihood (ML) criterion in RAxMLv7.4.3 (Stamatakis, 2006). The concatenated mtDNA was partitioned by codon positions, but nuclear DNAs were not partitioned due to limited variable sites. Substitution models in Bayesian inference were determined by the Akaike Information Criterion (AIC) in MRMODELTEST 2.2 (Nylander, 2004). Bayesian Markov Chain Monte Carlo (MCMC) was run for 10-million generations sampled every 100 generations. In the ML analysis, the GTRGAMMA model was used for each gene partition, and 1000 nonparametric bootstrap replicates were performed to calculate node support.

2.3. Species-tree and divergence-time estimation

It is a common practice to assume that a species phylogeny equals a single-gene genealogy (including trees derived from gene concatenation). However, a gene tree represents only one realization of the stochastic process embedded inside the species tree (Ho and Shapiro, 2011). Discrepancies between species trees and gene trees can arise if lineage sorting is incomplete among recently diverged species (Pamilo and Nei, 1988). Therefore, we used a multispecies coalescent model to estimate the species tree based on multi-locus data under the Star BEAST (*BEAST) option implemented in BEAST v1.6.1 (Drummond and Rambaut, 2007; Heled and

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