

Editorial

**Intercontinental and intracontinental biogeography—
patterns and methods**

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The study of biogeography has benefited from the exponential increase of DNA sequence data from recent molecular systematic studies, the development of analytical methods in the last decade concerning divergence time estimation and geographic area analyses, and the availability of large-scale distribution data of species in many groups of organisms. The underlying principle of divergence time estimation from DNA and protein data is that sequence divergence depends on the product of evolutionary rate and time. With their molecular clock hypothesis, Zuckerkandl and Pauling (1965) separated rates of molecular evolution from time by incorporating fossil evidence. Originally, a constant rate of sequence evolution was assumed, but soon it became evident that many data sets do not obey the constant rate assumption of a strict molecular clock. In fact, many studies have revealed extreme heterogeneity of nucleotide substitution rates over time. To account for the heterogeneity, relaxed molecular clock approaches have been developed (Thorne et al., 1998; Sanderson, 2002; Yang & Yoder, 2003; Drummond et al., 2006) with the availability of computer programs such as r8s, multidivtime, and BEAST (Thorne & Kishino, 2002; Sanderson, 2003; Drummond & Rambaut, 2007; see reviews by Renner, 2005 and by Rutschmann, 2006).

Area relationships were primarily inferred using methods in phylogenetic biogeography (Brundin, 1988), cladistic biogeography (Humphries & Parenti, 1999), and panbiogeography (Craw et al., 1999) in the 1980's and 1990's. These different biogeographic methods all have some limitations. The cladistic biogeographic ap-

proach emphasizes vicariance in forming biogeographic patterns, but underestimates the impact of processes such as dispersal and extinction (Ronquist, 1996, 1997). Different groups of organisms may respond differently to biogeographic barriers, which complicate the inference of general area relationship from taxon cladograms. In response to these limitations, Ronquist (1997) proposed the dispersal-vicariance (DIVA) analysis as an alternative approach of quantification of historical biogeography. This method reconstructs the ancestral distribution in a phylogeny using a three-dimensional step matrix, while allowing for dispersal and extinction to occur. The optimal ancestral distributions are inferred by minimizing the number of dispersal and extinction events (see review by Lamm & Redelings, this issue). Many studies have employed DIVA for inferring historical biogeography in a wide range of organisms (e.g., Sanmartín & Ronquist, 2004; also see Harris & Xiang, this issue). Recent advances in ancestral area reconstruction have brought forward additional approaches, such as the Bayes-DIVA method (Nylander et al., 2008), as well as the dispersal-extinction-cladogenesis (DEC) analysis (Ree et al., 2005; Ree & Smith, 2008; also see review by Lamm & Redelings, this issue). DEC analysis uses a phylogenetic model of geographic range evolution to infer ancestral ranges and biogeographic events given rates of stochastic dispersal and local extinction estimated by maximum likelihood, and can be implemented in Lagrange version 2.0.1. (available at: <http://lagrange.googlecode.com>).

The newly developed methods have stimulated strong interests in reconstructing the intercontinental disjunctions and intracontinental patterns of biogeography. The results on the divergence times and

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area relationships have stimulated debates on the significance of vicariance and dispersal. In many cases, dispersal has been validated as an important hypothesis of the origin of many disjunctions (De Queiroz, 2005; Posadas et al., 2006; Wen & Ickert-Bond, this issue). Several important biogeographic patterns especially at the intercontinental level have been examined and reviewed, such as the northern hemisphere disjunctions (see Xiang et al., 1998; Wen, 1999; Manos & Donoghue, 2001; Donoghue & Smith, 2004), the tropical disjunctions (Givnish & Renner, 2004), and the southern hemisphere patterns (Sanmartín & Ronquist, 2004).

This special issue of *Journal of Systematics and Evolution* includes 12 papers, which examine the current intercontinental and intracontinental patterns and explore new analytical methods. Specifically, Wen and Ickert-Bond review two major patterns of intercontinental disjunctions (the Madrean-Tethyan and the North and South American amphitropical disjunctions). Harris and Xiang propose a statistical approach for analyses using DIVA without fully bifurcating trees. Lamm and Redelings provide a review of newly developed methods for reconstructing ancestral ranges. Milne explores the effects of taxon sampling on dating within-genus divergence using deep fossils. Yue et al. examine the geographic assembly of the flora of the Hengduan Mountains using the brassicaceous genus *Solms-laubachia* as a case study. Nie et al. employ *Toxicodendron* as a model genus for analyzing the biogeographic interaction of the temperate and tropical elements. Simpson et al. reconstruct the biogeographic pattern in the Andes. Ickert-Bond et al. infer the intercontinental biogeographic disjunctions between the Old and the New World in *Ephedra*. Dillon et al. explore the biogeographic patterns and diversification of the Atacama and the Peruvian deserts. Fiaschi and Pirani review biogeographic patterns and studies of Brazil. Heinrichs et al. provide an updated summary of the biogeographic disjunctions in bryophytes and the impact of molecular work on bryophyte taxonomy. Qian succinctly compares the global patterns of beta diversity among mammals, birds, reptiles and amphibians.

We hope this collection of papers will stimulate future biogeographic analyses on intercontinental and intracontinental patterns and facilitate collaborations of colleagues from different continents. It is important to explore new analytical methods, which may bring better synthesis of data from different fields such as phylogenetics, paleontology and ecology (Donoghue & Moore, 2003; Crisci, 2006). More model-based techniques are needed for rigorous statistical test of hypotheses pertain-

ing to historical biogeography (Ree & Sanmartín, 2009). Robust data using multiple loci including cytoplasmic and nuclear markers are needed in molecular biogeographic studies, especially for groups with frequent interspecific hybridization (Peng & Wang, 2008). Many intercontinental disjunct patterns are particular to either the northern hemisphere or the southern hemisphere. It is nevertheless important to characterize the biogeographic interactions between the northern and the southern hemispheres. Comprehensive biogeographic analyses at the global scale are clearly needed in the future. Recent biogeographic analyses have provided important insights into intercontinental patterns, yet we need to rigorously explore the intracontinental patterns of different regions using comparative phylogeographic and ecological approaches (Soltis et al., 2006). In particular, phylogeographic studies are helpful for understanding intracontinental disjunctions (Yang et al., 2008). It is an exciting period for biogeography, and we hope to see important syntheses that will lead to better understanding of both intracontinental and intercontinental biogeographic dynamics.

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Materials and Methods. Taxon Sampling. Ingroup species from Anacardiaceae and Burseraceae were chosen on the basis of assembling the most complete biogeographic coverage possible from all major lineages. Origins of Terebinthaceae and Patterns of Diversification in Anacardiaceae and Burseraceae. The Cretaceous age of the stem and crown lineages of Terebinthaceae (95–127 Ma) coincides with several episodes of continental vicariance that may have contributed to their early widespread distribution and spurred their diversification through allopatric speciation. Keywords: biogeography, biome shifts, continental vicariance, diversification, long-distance dispersal, phylogenetic niche conservatism. When analytical methods are used in biogeography, patterns may prove to be neither wholly historical nor wholly ecological, and testing and reasoning are needed if the effects of the processes causing these patterns are to be distinguished (148). We believe that disciplinary boundaries between ecological and historical biogeography are circumstantial and that they can be fruitfully unified into a single research program (94). Flying in historical biogeography and coevolution: methodological and theoretical approaches. *Current Biology* 3: date. Intercontinental relationships of African and South American Asteraceae: a cladistic biogeographic approach. *Journal of Systematics and Evolution* 47(5):327-329. These different biogeographic methods all have some limitations. The cladistic biogeographic approach emphasizes vicariance in forming biogeographic patterns, but underestimates the impact of processes such as dispersal and extinction (Ronquist, 1996, 1997). Different groups of organisms may respond differently to biogeographic barriers, which complicate the inference of general area relationships from taxon cladograms. In response to these limitations, Ronquist (1997) proposed the dispersal-vicariance (DIVA) analysis as an alternative approach of quantification of historical biogeography. 2009. Intercontinental and intracontinental biogeography: patterns and methods. *Journal of Systematics and Evolution* 47: 327-330. [Link]. 2009. Contrasting patterns of plant distribution in Beringia. *Proceedings of the Arctic Alaska Park Science Symposium and Beringia International Conference*. *Alaska Park Science* vol. 8 (2): 26-32. If biogeographic distribution does play a significant role in influencing the outcome of extinction events, then geographic variability in extinction intensity should be mirrored by patterns of endemism. A comparison of data for the terminal Cambrian extinction indicates that survival of trilobite families in Kazakhstan was significantly greater than in North America. As predicted, the Kazakh sequence was characterized by a significantly larger number of pandemic families. Larval ecology, life history strategies and patterns of extinction and survivorship among Ordovician trilobites. *Paleobiology* 15:118–132. CrossRef Google Scholar. Chugaeva, M. N., and Apollonov, M. K. 1982.