Large-scale processes and the Asian bias in species diversity of temperate plants

Hong Qian* **& Robert E. Ricklefs†**

** Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada*
† Department of Biology, University of Missouri-St. Louis, St. Louis, Missouri 63121, USA

An important issue in the study of biodiversity is the extent to which global patterns of species richness reflect large-scale processes and historical contingencies[1,2]. Ecological interactions in local assemblages may constrain the number of species that can coexist[3,4], but differences in diversity in similar habitats within different regions (diversity anomalies) suggest that this limit is not firm. Variation in rate of species production could influence regional and perhaps local diversity independently of the ecological capacity of an area to support coexisting species, thereby creating diversity anomalies[5,6]. Temperate Zone genera of plants that are disjunct between similar environments in eastern Asia and eastern North America (EAS-ENA) have twice as many species in Asia as in North America[7]. Because lineages of these genera in Asia and North America are mostly sister pairs[8], they share a common history of adaptation and ecological relationship before disjunction. Thus, the diversity anomaly in EAS-ENA genera is not an artefact of taxon or habitat sampling but reflects differences in the net diversification (speciation–extinction) of the lineages in each of the continents. Here we propose that the most probable cause of the EAS-ENA anomaly in diversity is the extreme physiographical heterogeneity of temperate eastern Asia, especially compared with eastern North America, which in conjunction with climate and sea-level change has provided abundant opportunities for evolutionary radiation through allopatric speciation.

We focus on sister pairs of disjunct congeneric lineages of temperate plants in eastern Asia and eastern North America to reduce differences in age and ecology being major factors contributing to differences in diversity. Most disjunctions between Asia and North America are thought to have formed when cooling climates in the mid and late Tertiary forced temperate-climate plants south of the Bering Land Bridge, across which they formerly had continuous distributions[9,10]. Of about 100-plus disjunct genera found uniquely in temperate eastern Asia and North America[11], 58 are restricted in North America to moist environments in the eastern half of the continent (EAS-ENA disjuncts). The ecological distributions of American and Asian counterparts are more similar in EAS-ENA genera than in disjunct genera that also occur in drier environments in western North America. Our focus on EAS-ENA disjuncts is reinforced by a TWINSPAN partitioning of latitude–longitude grid cells based on the geographical occurrence of disjunct genera. This analysis identifies regions in eastern Asia and eastern North America (cluster III cells) to which most of the EAS-ENA disjuncts are restricted (Fig. 1).

Of the 58 EAS-ENA disjunct genera, 33 have more species in Asia and 10 have more species in North America, with 15 genera tied ($\chi^2 = 12.3$, $P < 0.001$ with ties deleted; $\chi^2 = 9.1$, $P < 0.001$ with ties split). Analysis of covariance of the $\log_{10}$-transformed number of species per genus, with the $\log_{10}$-transformed area (km^2) occupied by each genus included as a covariate, indicates a regional diversity bias favouring Asia by 0.30 ± 0.08 $\log_{10}$ units, which is a factor of 2.0 ($F_{1,113} = 13.5$, $P = 0.0004$). Thus, with geographical area controlled, sister lineages occupying broadly similar environments on two continents have at present twice as many species, on average, in eastern Asia as in eastern North America.

The area occupied by cluster III grid cells is physiographically more heterogeneous in eastern Asia than in eastern North America.

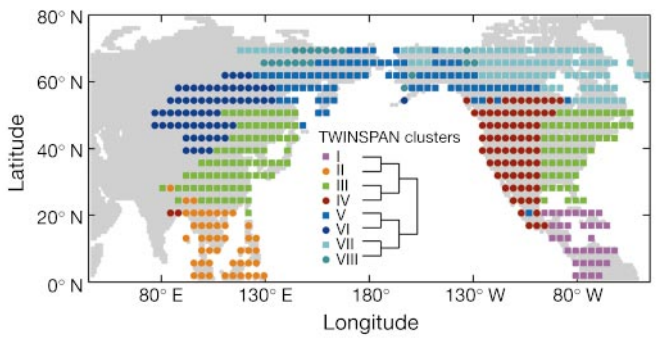

Figure 1 Geographical distribution of disjunct genera of vascular plants in eastern Asia and North America (range south of the equator not shown). Each symbol represents a grid cell with 3.75° latitude and 3.75° longitude. Symbols differentiate the eight clusters of grid cells identified by a TWINSPAN analysis. TWINSPAN divides grid cells in a dichotomous hierarchy based on ordination of the cells with respect to the occurrence of genera. Cluster III includes 79 grid cells in eastern Asia and 59 in eastern North America. Most of the species of ESA-ENA disjunct genera are restricted to cluster III grid cells.

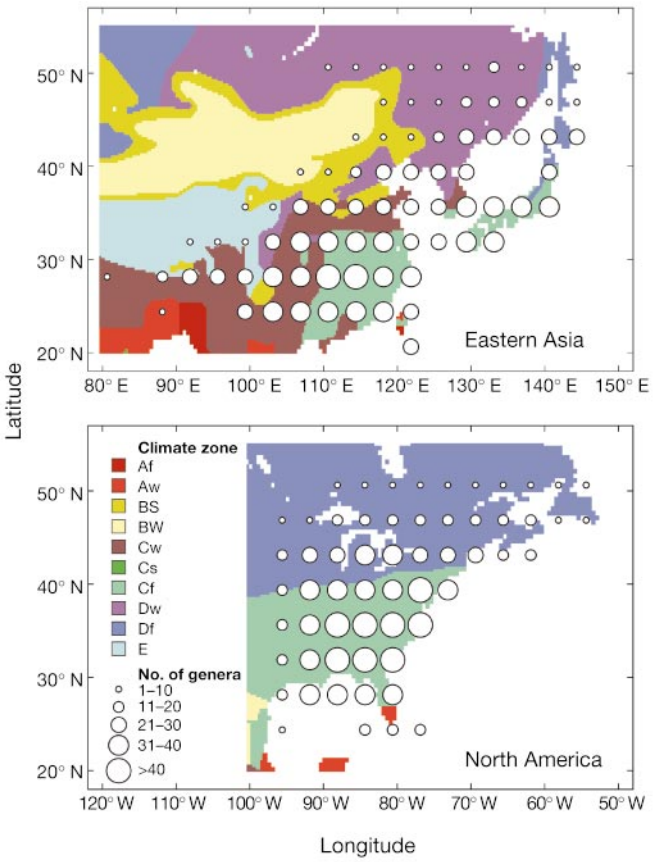

Figure 2 Maps showing climate heterogeneity and spatial patterns in the number of EAS-ENA disjunct genera of vascular plants for grid cells in TWINSPAN cluster III. Climate classification is according to ref. 12. Climate zones: Af, tropical rainforest climate; Aw, tropical savanna climate; BS, steppe climate; BW, desert climate; Cf, warm temperate climate with all seasons moist; Cw, warm temperate rainy climate with dry winter; Cs, warm temperate rainy climate with dry summer; Dw, cold snowy forest climate with dry winter; Df, cold snowy forest climate with all seasons moist; E, ice climates.

Table 1 Distribution of genera in North America according to size classes of species richness

Number of species	1	2	3–5	6–10	11–20	21–50	51–100	>100
East only (EAS-ENA)	31	10	12		2	3		
East and west			5	3	3		1	1

The Asian region includes four Köppen climate zones[12], supporting temperate forest (warm and cool temperate climate groups C and D), distributed in 13 geographically distinct patches, including areas isolated by water on the Korean Peninsula and Japan (Fig. 2). Extensive tropical and subtropical forests at lower elevation separate temperate forests at higher elevations in southern mainland China. The comparable floristic region in North America includes only two climate zones distributed in two large adjoining areas.

The contemporary fragmentation of temperate forest in eastern Asia combined with fluctuations of climate and sea level could create conditions for generating diversity through allopatric speciation. During cooler 'glacial' climates in the Pleistocene, temperate forests would have extended to lower elevations in the south of China, as they did elsewhere in the world[13], allowing isolated patches to join together; warmer climates would have forced temperate forest back to 'refugia' at higher elevation. Shallow seas lying between mainland China, peninsular Korea and Japan create additional isolated areas of temperate forest in Asia. During Pleistocene periods of lowered sea level associated with glacial maxima, the Yellow Sea was largely drained and these areas were connected by dry land with a climate suitable for temperate forest. CLIMAP reconstruction (http://ingrid.ldgo.columbia.edu/SOURCES/.CLIMAP/.LGM/.vegetation/) of plant formations during the glacial maximum 18 thousand years ago, which is probably representative of glacial maxima throughout the Pleistocene, places deciduous forest in coastal areas between present-day China, Korea and Japan, and over much of coastal China. Eustatic fluctuations in sea level that would have alternately separated and joined plant distributions also occurred well before the Pleistocene, with pronounced sea-level highs at about 15 million and 5 million years (Myr) ago and frequent excursions between high and low levels during the past 10 Myr[14,15]. The larger proportion of species-rich genera among those whose distributions include Korea or Japan suggests a potential role of sea-level fluctuations in species production. Of the 18 EAS-ENA genera restricted to mainland China, only 2 have more than 5 species; of 40 genera including Korea, Japan or both in their distributions, 21 have more than 5 species (likelihood-ratio $\chi^2 = 10.0$, $P = 0.002$) and 11 have more than 10 species.

Climate and geography have evidently had a much smaller role in speciation in EAS-ENA disjunct genera in the topographically more homogeneous region of eastern North America, where only 5 of 58 EAS-ENA genera have more than 5 species. Because physiographic heterogeneity is greater in western North America than in the east, however, we would expect greater species richness in genera that include western North America (TWINSPAN cluster IV) in their geographical distributions. Thirteen eastern Asia/North America herbaceous disjunct genera that occur in temperate eastern North America extend their ranges throughout the west. Of these, 8 have more than 5 species (likelihood-ratio $\chi^2 = 18.3$, $P < 0.001$; Table 1). This difference is independent of range size. In an analysis of covariance of the $\log_{10}$-transformed number of species per genus, with the $\log_{10}$-transformed area (in km^2) occupied by each genus included as a covariate, the species richness of genera distributed widely across North America exceed that of genera restricted to the east (EAS-ENA disjuncts) by $0.55 \pm 0.14 \log_{10}$ units, a factor of 3.5 ($F_{1,68} = 15.6$, $P = 0.0002$). Most of the diversity in these genera is concentrated in the western half of North America. The 13 genera distributed continuously from east to west across North America have 40 species restricted to the east, 23 species occurring in both the east and the west, and 298 species restricted to the west[16].

The conclusion that EAS-ENA disjuncts are more diverse in Asia than in North America depends on the application of uniform taxonomic practices in the two continents. It is possible that taxonomists have split Asian disjunct species more than those in North America by applying names to poorly differentiated allopatric populations. Three observations argue against this being a factor in the Asia diversity bias among EAS-ENA disjuncts. First, disjunct genera in boreal environments (TWINSPAN clusters V–VIII) are more diverse in North America than in Asia[17,18]. Second, greater diversity is associated with greater geographical heterogeneity in North America, as it is between eastern North America and eastern Asia. Third, much of the diversity in eastern Asia occurs within small regions of sympatry and thus is unlikely to represent artificial splitting. Using accounts in volumes published to date of the Flora of China[29], we examined the geographical distribution of species in four species-rich disjunct genera among the 33 provinces of China. These accounts indicate that individual species occupy 20–50% of the province-level distribution of each species in China and that up to 40–100% of the congeneric species coexist in a single province (Table 2).

The hypothesis that geographical heterogeneity combined with climate and sea-level change have had a major role in the diversification of the eastern Asian flora assumes allopatric mechanisms of species production. Plants are well known for sympatric production of new species through autopolyploidy and allopolyploidy. However, relative uniformity of chromosome numbers in genera, indicates that sympatric speciation is a minor factor in the diversification of the Asian and North American disjunct floras. A brief survey showed that chromosome numbers for 57 primarily Asian species in 14 EAS-ENA disjunct genera were the base number ($2N$) for 43 species, $4N$ for 9 species and $6N$ for 5 species. Thus, a minority of speciation events has involved autopolyploidy or hybridization.

Compared with the allopatric speciation hypothesis, two alternative explanations for the Asian diversity bias seem less likely. First, if Asian species were more frequently paraphyletic with respect to congeners in North America, then the Asian diversity bias could be attributed to the longer occurrence of presently disjunct genera in Asia as compared with North America. Asian paraphyly has been reported in molecular phylogenetic studies of some non EAS-ENA disjunct genera, such as *Aesculus*[19] and *Gleditsia*[20]; however, the fossil record suggests that most EAS-ENA disjuncts have longer histories in North America than in Asia. Of nine woody EAS-ENA disjunct genera[21], all appear earlier in the fossil record of North America than in that of Asia.

Table 2 Distribution among Chinese provinces of species in four genera of species-rich EAS-ENA disjunct genera

Genus	Family	Number of species in mainland China	Number of provinces occupied by genus	Maximum number of species per province	Average number of provinces per species
Meehania	Lamiaceae	7	12	7	5.6
Osmanthus	Oleaceae	23	14	10	3.6
Castanopsis	Fagaceae	58	14	28	3.8
Lithocarpus	Fagaceae	123	17	79	3.0

Second, extinction of species associated with late-Pliocene and Pleistocene climate cooling and glaciation may have been more prevalent in North America than in eastern Asia, where extensive temperate refuges existed in subtropical latitudes during glacial maxima. However, although Pliocene-Pleistocene extinctions reduced the temperate woody flora of Europe considerably[22,23], extinctions were less important in eastern North America[6]. Nonetheless, greater extinction of genera in North America (18% of moist-temperate tree genera represented in the mid-Tertiary fossil record) than in Asia (4%) may translate into more pronounced extinction of species in extant genera. Thus, North American extinctions may have had a role in the diversity bias favouring eastern Asia. If so, however, they did not reverse the diversity bias favouring North America in disjunct genera with more northerly and westerly distributions in North America. Moreover, a twofold Asian diversity bias was already present with respect to genera of woody plants (122 versus 60 in eastern North America[6]) before late Tertiary climate cooling.

The role of alternate fragmentation and rejoining of geographical ranges in species production has been discussed in the past, most famously in regard to adaptive radiation in island archipelagos where fragmentation and secondary sympatry result from infrequent migration between islands. The temperate disjunct flora of eastern Asia is a superior continental model for increase in regional diversity through allopatric speciation, for several reasons. First, habitat fragmentation and rejoining are based on observed effects of climate change on elevational distribution of temperate environments[13,24] and on documented changes in sea level[14]. Second, comparisons of diversity between physiographically complex (eastern Asia) and simple (eastern North America) regions are based on sister taxa, thereby controlling for age and, to a large extent, for ecological relationships of plants to their physical environments. Third, the diversity anomaly between EAS-ENA disjunct genera occurs at the level of species in genera and is likely to have been produced by means of allopatric speciation under the influence of climate cycles associated with general climate cooling and glaciation during the late Tertiary. Distributions of temperate disjunct taxa in the fossil record suggest that temperate connections between Asia and North America were severed by the mid to late Miocene (5–10 Myr ago)[25,26]. Genetic divergence has been coupled with variously calibrated molecular clocks[8] to place ages of disjunctions between 2 and 29 Myr, with half the estimates falling between 4 and 12 Myr, providing ample time for independent diversification of lineages in each region.

The species richness of disjunct EAS-ENA genera is plausibly related to opportunities for repeated cycles of allopatry and secondary sympatry. Particularly in eastern Asia, these cycles have been driven by changes in climate and sea level within a physiographically heterogeneous region. High levels of species richness in genera are associated with distribution across currently fragmented geographical areas in eastern Asia. In eastern North America, more uniform climate and simpler geography have not fostered evolutionary radiation among the same lineages as in eastern Asia. Only among disjunct herbaceous genera that include drier environments of western North America in their habitat distribution has speciation proceeded at a rapid rate. We suggest that history and large-scale processes may explain much of the variation in species richness over the globe. □

Methods

Plant distributions

We reviewed published lists of eastern Asian/North American disjunct genera of vascular plants and included 102 genera in our analysis. Of these, 58 genera are restricted to eastern North America. Some of these extend their distributions to tropical areas in Asia and America. To document generic diversity on a smaller scale, we divided the region between 45° E and 45° W longitude and between 15° S and 75° N latitude into 1728 grid cells 3.75° on a side. Presence/absence of each disjunct genus in each grid cell was documented according to distribution maps[11,27] and additional floristic data. Within the grid area, 580 cells, 289 in eastern Asia and 291 in North America, had at least one of the 102 disjunct genera. We divided the 580 grid cells into clusters using a two-way indicator species, hierarchical, divisive cluster approach (TWINSPAN[28]). Three hierarchical levels of clustering were performed, which resulted in eight clusters (I–VIII).

Chromosome numbers

A sample of chromosome numbers for species in disjunct genera was obtained from volumes of the Index to Plant Chromosome Numbers[30]. Chromosome numbers were included only when two or more species were reported for a continent. Most of the species in the sample were eastern Asian.

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Correspondence and requests for materials should be addressed to R.E.R. (e-mail: ricklefs@umsl.edu).