

REGIONAL DIFFERENCES IN RATES OF PLANT SPECIATION AND MOLECULAR EVOLUTION: A COMPARISON BETWEEN EASTERN ASIA AND EASTERN NORTH AMERICA

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Abstract.—The eastern Asian (EAS)–eastern North American (ENA) floristic disjunction is one of the best-known biogeographic patterns in the Northern Hemisphere. Recent paleontological and molecular analyses have illuminated the origins of the biogeographic pattern, but subsequent diversification and evolution of the disjunct floras in each of the two continents after isolation remains poorly understood. Although similar in climate and floristic composition, EAS has twice as many species as ENA in genera occurring in both regions. Explaining such differences in species diversity between regions with similar environmental conditions (diversity anomalies) is an important goal of the study of the global patterns of biodiversity. We used a phylogenetic approach to compare rates of net speciation and molecular evolution between the two regions. We first identified EAS–ENA disjunct sister clades from ten genera (*Asarum*, *Buckleya*, *Carpinus*, *Carya*, *Cornus*, *Hamamelis*, *Illicium*, *Panax*, *Stewartia*, and *Styrax*) that represent diverse angiosperm lineages using phylogenetic analyses of ITS (internal transcribed spacer of nuclear ribosomal DNA) sequence data. Species richness and substitution rate of ITS between sister clades were compared. The results revealed a pattern of greater species diversity in the EAS counterparts. A positive relationship between species diversity and ITS substitution rate was also documented. These results suggest greater net speciation and accelerated molecular evolution in EAS. The data support the idea that a regional difference in net speciation rate related to topographic heterogeneity contributes to the diversity anomaly between EAS and ENA. The close relationship between rates of ITS evolution and species richness further suggests that species production may be directly linked to rate of nucleotide substitution.

Key words.—Biodiversity anomaly, eastern Asian–eastern North American floristic disjunction, molecular phylogeny, rate of ITS evolution, rate of speciation.

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Explaining differences in species diversity between regions with similar environmental conditions (diversity anomalies) is an important goal of the study of global patterns of biodiversity and historical biogeography. Most previous studies have emphasized the relationship between species richness and local environment (Wright 1983; Currie and Paquin 1987; Adams and Woodward 1989; Currie 1991; Francis and Currie 2003; Hawkins et al. 2003). However, significant region effects on species richness have been reported in comparisons of floras and faunas between different parts of the world with comparable environments (Orlans and Paine 1983; Latham and Ricklefs 1993; Ricklefs and Latham 1993; Ricklefs et al. 1999, 2004; Qian and Ricklefs 2000; Qian 2002a), suggesting that global patterns of species richness reflect both environment and history, including differences in rate of speciation between regions.

Eastern Asia (EAS) and eastern North America (ENA) have played a prominent role in the study of diversity anomalies because the two regions are highly similar in climate and

floristics, but differ in species richness (Li 1952; Wolfe 1981; Muller 1982; Guo et al. 1998; Qian 2002b; Ricklefs et al. 2004). Approximately 60 genera of seed plants have disjunct distributions restricted to the two regions (Wen 1999; also see Wu 1983; Hong 1993). This pattern of biotic similarity between EAS and ENA is also documented for ferns, fungi, arachnids, millipedes, insects, and freshwater fishes (Wen 1999).

The prominent EAS–ENA floristic disjunction has fascinated botanists for more than 150 years and stimulated numerous studies over the past three decades (Wen 1999; Manos and Donoghue 2001). Recent paleontological and molecular phylogenetic analyses suggest that this phylogeographic pattern has a complex history (Manchester 1999; Wen 1999, and references therein; Donoghue et al. 2001; Tiffney and Manchester 2001; Wen 2001; Xiang and Soltis 2001). Paleontological evidence suggests that the disjunctions resulted from progressive fragmentation of the mid-Tertiary mesophytic forest flora, itself derived from the boreotropical flora

of the early Tertiary, which was continuously distributed across the northern continents (Wolfe 1975; Tiffney 1985a, b; Tiffney and Manchester 2001).

Analyses of molecular phylogeny, divergence times, and biogeography of selected extant lineages have revealed additional details concerning the history of the disjunct pattern. These analyses suggested that disjunctions often involved intercontinental distribution across land bridges followed by vicariance associated with continental drift, global climatic cooling, and/or other geological changes. Furthermore, the migration routes and the number and timing of dispersal and vicariance events appear to differ among lineages (Xiang et al. 1998a,b; Lu 1999; Manchester 1999; Wen 1999 and references herein; Xiang et al. 2000; Donoghue et al. 2001; Manos and Stanford 2001; Xiang and Soltis 2001; Milne and Abbott 2002). Long-distance dispersal has also been suggested to account for the disjunctions of some taxa estimated to have diverged recently (see Qiu et al. 1995, Wen 1999, Donoghue et al. 2001, and Xiang et al. 2000). Although these findings have provided new insights and generated new hypotheses for further testing, they also call for additional studies that integrate biogeography with paleontology, ecology, molecular phylogeny, and divergence time analysis for a better understanding of this striking biogeographic pattern, as well as the floristic history of the Northern Hemisphere as a whole.

Although recent studies have illuminated the origins of the EAS–ENA disjunct biogeographic pattern, subsequent diversification and evolution of isolated sister clades in each of the two regions is poorly understood. The United States and China are similar in area (9.4 vs. 9.6×10^6 km²), but China has a more diverse flora (ca. 18,000 vs. 29,200 species of vascular plants; Qian and Ricklefs 1999) and a higher proportion of endemic taxa (Wu 1983; Axelrod et al. 1998; Wu and Wu 1998). At a larger scale, the vascular plant flora of North America north of Mexico (~ 19.7 million km²) has only two-thirds the species richness of a similar region within the same latitudinal range covering most of eastern Asia (Qian 2002a). Three explanations have been proposed for the greater floristic richness of EAS: (1) extensive tropical rain forest in China contributes to the floristic richness; (2) the vegetational continuity between tropical, subtropical, temperate, and boreal forests, which is unique to China, has led to formation of rich plant associations; and (3) the highly dissected and elevated geography of China promote speciation, evolutionary diversification, and the persistence of local endemics (Axelrod et al. 1998; Kubitzki and Krutzsch 1998; Guo et al. 1998, Lu 1999; Qian 2002a). Although the first two factors are well established, the third remains uncertain. No clear direct evidence confirms a difference in net speciation rate between the two areas.

Qian and Ricklefs (2000) compared species diversity between EAS and ENA among 58 genera of vascular plants confined to two regions and found twice as many species in EAS. Assuming that each of the 58 EAS–ENA disjunct genera comprised equal-aged sister clades in the two regions, they related the apparent greater net speciation rate in EAS to the region's greater physiographic heterogeneity, promoting allopatric speciation and resulting in a higher rate of diversification. This explanation depends on the sister rela-

tionship of species in each disjunct genus from the two continents (i.e., the reciprocal monophyly of species from each region), which remains to be verified by phylogenetic studies (see review in Wen 1999 and Milne and Abbott 2002).

Speciation is considered to depend on genetic changes at the DNA level allowing population to diverge (Harrison 1991; Coyne 1992; Coyne and Orr 1999). However, relationship between rates of speciation and molecular evolution has long been debated, with some authors considering the two being closely linked while others remaining a view of no relationship between rates of speciation and molecular evolution (Mayr 1963; Gavrillets and Hastings 1996; Templeton 1996; Allmon 1992; Coyne 1994). Analyses in two recent studies revealed a positive correlation between rates of species diversity and molecular evolution (e.g., Barraclough and Savolainen 2001; Webster et al. 2003), providing some evidence for a link between rates of molecular evolution and speciation. In the present study, we conduct phylogenetic analyses of ITS (internal transcribed spacer of nuclear ribosomal DNA) sequences for 10 flowering plant genera to identify EAS–ENA sister clades and compare species diversity and rates of molecular evolution between the sister lineages. Our main goal was to determine whether net speciation rates differ between the two regions. A second goal of the study was to compare rates of molecular evolution between the two regions and examine whether rate of species diversification is linked with rate of molecular evolution.

MATERIALS AND METHODS

Sampling

We selected 10 genera (*Asarum*, *Buckleya*, *Carpinus*, *Carya*, *Cornus* subgenus *Mesomora*, *Hamamelis*, *Illicium*, *Panax*, *Stewartia*, and *Styrax* section *Cyrta*), each of which holds at least one pair of sister clades disjunct between EAS and ENA. Taxa were chosen based on our reanalyses of DNA sequence data published in previous phylogenetic studies (Kelly 1998 for *Asarum*; Li et al. 2001 for *Buckleya*; Yoo and Wen 2002 for Coryloideae of Betulaceae; Manos and Stone 2001 for Juglandaceae; Xiang et al., unpubl. ms. for *Cornus*; Li et al. 2000 and Wen and Shi 1999 for *Hamamelis*; Hao et al. 2000 for *Illicium*; Wen and Zimmer 1996 for *Panax*; Li et al. 2002 and Prince 2002 for *Stewartia*; and Fritsch 2001 for *Styrax*) (Table 1; for sequence information, see Appendix online only at <http://dx.doi.org/10.1554/03-712.1.s1>). These genera represent diverse lineages of flowering plants, ranging from basal angiosperms to Rosids and Asterids (APG 2003). Although other genera with species in EAS and ENA have been the subjects of molecular phylogenetic analysis (e.g., *Aesculus*, Xiang et al. 1998a; *Aralia* sect. *Aralia*, Wen et al. 1998; *Aralia* sect. *Dimorphanthus*, Wen 2000; *Boykinia*, Xiang et al. 1998b; *Cercis*, Davis et al. 2002; *Chrysosplenium*, Soltis et al. 2001; *Corylus*, Whitcher and Wen 2001; *Diervilla/Weigela*, Kim and Kim 1999; *Juglans*, Stanford et al. 2000; *Ilex*, Manen et al. 2002; *Osmorhiza*, Wen et al. 2002; *Prunus*, Lee and Wen 2001; *Tiarella*, Xiang et al. 1998b; *Trautvetteria*, Xiang et al. 1998b; and *Triosteum*, Gould and Donoghue 2000), either EAS–ENA sister clades were not resolved in these genera (most cases), or species sampling was inadequate to confirm the sister clades (e.g., *Ilex* and *Prunus*). The 10 sister pairs included in the

TABLE 1. Taxonomic information and sources of molecular data. Species richness indicates the number of species occurring in eastern Asia (EAS) and eastern North America (ENA). The numbers are based on the original studies referenced here and Mabberley (1997).

Taxon	Family	Order	Species richness (EAS, ENA)
<i>Asarum</i> L. (sect. <i>Heterotropis</i> /sect. <i>Hexastylis</i>) (Kelly 1998)	Aristolochiaceae	Piperales	50, 9
<i>Buckleya</i> Torr. (Li et al. 2001)	Santalaceae	Santalales	3, 1
<i>Carpinus</i> L. (Yoo and Wen 2002)	Betulaceae	Fagales	~30, 2
<i>Carya</i> Nuttall (incl. <i>Annamocarya</i>) (Manos and Stone 2001)	Juglandaceae	Fagales	3, 16
<i>Cornus</i> L. (Xiang et al., unpubl. ms).	Cornaceae	Cornales	~30, ~14
<i>Hamamelis</i> L. (Li et al. 2000; Wen and Shi 1999)	Hamamelidaceae	Saxifragales	2, 2–4
<i>Illicium</i> L. (Hao et al. 2000)	Illiciaceae	Illiciales	~36, 6
<i>Panax</i> L.	Araliaceae	Apiales	~10, 2
<i>Stewartia</i> L. (Prince 2002; Li et al. 2002)	Theaceae	Ericales	~24, 2
<i>Styrax</i> ser. <i>Cyrta</i> (Fritsch 2001)	Styracaceae	Ericales	27, 4,

present study were all identified by ITS sequence data. Although the ITS region has potential problems as a phylogenetic marker, such as the preferential amplification of ITS paralogues or recombinants (Buckler et al. 1997), no such problems were encountered in these groups. Detailed methods for ITS analyses are described below.

Phylogenetic Analyses and Branch Length Estimation

ITS sequence data for 270 species belonging to the 10 focal genera and their outgroups were obtained from the original authors or downloaded from Genbank (see Appendix online). The Genbank sequences were aligned using the Clustal X program (Thompson et al. 1997) and adjusted by eye. Phylogenetic analyses of the ITS sequence data were performed separately for each genus using the same outgroup taxa as those included in the original studies to confirm disjunct sister pairs in EAS and ENA and to reconstruct the branch lengths leading to each counterpart of the sister pairs. Branch lengths of sister lineages reflect their relative rates of sequence change. Thus, the lineage with the longer branch must have experienced a faster rate of nucleotide substitution, given that the sister lineages diverged from a common ancestor are by definition equal in age.

We used the maximum-likelihood (ML) method implemented in PAUP version 4.0b10 (Swofford 2003) to perform the phylogenetic analyses and to estimate branch lengths in sister lineages. We used Modeltest (vers. 3.06) (Posada and Crandall 1998) to determine the best model of ITS evolution for each genus. We chose ML over parsimony because it is more robust to the effect of node density in branch length estimation (i.e., estimated branch length for a clade varies in direct relation to number of taxa sampled for the clade; Sanderson 1990; also see Bromham et al. 2002). Our sampling procedure takes care of any residual artifact affecting ML branch lengths (see Statistical Analyses below). Branch lengths within each sister clade were calculated by hand using the mean path lengths method (Britton et al. 2002), which eliminates nonindependent counting of internal branches. Heuristic searches with random taxon addition of 10 replicates were conducted to find the best ML tree for each genus under

the best-fit model. ML bootstrap analyses of 100 replicates were performed for each genus to estimate the support for the sister clades.

Statistical Analyses

To assess the relationship between rate of molecular evolution (branch lengths) and species richness, we conducted a regression analysis of path length contrasts (EAS minus ENA) against contrasts in the logarithm of species number between sister clades. Significance of the association between the two variables was evaluated by least squares regression forced through the origin (Harvey and Pagel 1991). The species richness in sister lineages was the number of sampled species included in each sister clade on the phylogenetic trees without counting any unsampled species. Most of the North American species in the focal genera were included in our analysis, but the more diverse Asian clades were less well sampled (Table 2). However, this difference in sampling would not bias estimates of branch lengths or of the relationship between branch length and species richness, as explained in the Results section.

We used evidence from morphology, distribution, and other studies to assess the possible phylogenetic positions of the unsampled species, and thus evaluate their impact on species diversity estimation (see Discussion below). The potential effect of unequal and incomplete species sampling on branch length estimation in sister clades was examined by recalculating branch lengths using ML analyses with equal sampling of taxa from EAS and ENA sister pairs. For each genus except *Cornus*, in which the sister clade is represented by a single species in each region, we analyzed all combinations of species from the more diverse clade having the same number of species as the less diverse clade. The new branch lengths were compared with the original estimates to determine the level of support for the original branch asymmetry identified in the full analyses using sign tests (Table 3). The new branch length contrasts (differences in branch lengths between EAS and ENA sister clades) having the same signs as those of the full data set were considered as supporting the original analysis.

TABLE 2. Sampling information, species richness, and relative branch lengths in sister pairs of clades. Numbers before the slash are the number of species included in the phylogenetic studies and numbers after the slash are the number of species present in the region. An asterisk indicates the number of species from the EAS–ENA disjunct subgroup of *Cornus* (*Cornus* subg. *Mesomora*).

Taxa	Sampling		No. of species in sister clades		Branch length in sister clades	
	EAS	ENA	N_{EAS}	N_{ENA}	EAS	ENA
<i>Asarum</i> (<i>Heterotrop</i> / <i>Hexastylis</i>)	13/50	5/9	13	3	0.0445	0.0175
<i>Buckleya</i>	3/3	1/1	1	1	0.0255	0.0290
<i>Carpinus</i>	14/30	1/2	4	1	0.0030	0.0200
<i>Carya</i>	3/5	6/13	3	2	0.0293	0.0075
<i>Cornus</i>	1/1*	1/1*	1	1	0.0165	0.0074
<i>Hamamelis</i>	2/2	4/4	1	4	0.0040	0.0155
<i>Illicium</i>	12/36	2/6	12	2	0.0359	0.0260
<i>Panax</i>	10/10	2/2	6	1	0.0117	0.0020
<i>Stewartia</i>	9/24	2/2	3	2	0.0300	0.0140
<i>Styrax</i> ser. <i>Cyrta</i>	15/27	4/4	15	4	0.0235	0.0097

RESULTS

The maximum-likelihood phylogenetic analyses using the best-fit model of ITS sequence evolution recovered EAS–ENA sister clades in each of the ten genera (*Asarum*, *Buckleya*, *Carpinus*, *Carya*, *Cornus* subg. *Mesomora*, *Hamamelis*, *Illicium*, *Panax*, *Stewartia*, and *Styrax* sect. *Cyrta*; Fig. 1). The nodes joining the sister pairs are the same as those found in the original studies, except in *Styrax* and *Carya*, for which the original phylogenetic analyses used parsimony rather than maximum likelihood and did not resolve a clade of EAS–ENA sisters in *Styrax* (Fritsch 2001) and resolved an EAS–ENA sister clade with different species compositions in *Carya* (Manos and Stone 2001). All of the sister pairs, except the pair in *Illicium*, involve only a portion of the species in each genus (Fig. 1), indicating that monophyly of all species from the same region in both sister clades is infrequent and that species from at least one of the two regions, usually EAS, are often paraphyletic (Fig. 1). This implies that most genera evolved and initially diversified in one region, followed by subsequent spread into the other, either by long-distance dispersal or gradual migration across a land bridge.

Except for *Cornus* and *Buckleya*, each having only one species in the identified sister clade in each of the regions, and *Hamamelis*, for which the sister pair includes more spe-

cies in ENA (four spp.) than in EAS (one sp.), species richness in the remaining seven sister pairs favors EAS by 56 to 15; overall, the difference is 59 versus 21 species. Of eight sister pairs differing in species richness between the two regions, seven favored EAS (binomial one-tailed $P = 0.035$). ITS branch lengths are greater in eastern Asia than in eastern North America in seven of the 10 disjunct sister pairs (*Asarum*, *Carya*, *Cornus* subg. *Mesomora*, *Illicium*, *Panax*, *Stewartia*, and *Styrax* sect. *Cyrta*) (Table 2; Fig. 1). In *Buckleya* the branches in each of the sister lineages are nearly equal. In *Carpinus* and *Hamamelis*, the branches of the ENA clades are longer. Random subsampling of species from the richer side of each sister pair to equalize the number of species to the less diverse clade did not change the relative branch lengths based on the full data set (Table 3). Maximum-likelihood analyses with all possible combinations of species from the richer clade with sample sizes equal to the sister clade revealed longer branches in EAS in the seven genera that favored EAS in the full analysis, but weaker support for the longer branches of ENA in the three genera that favored ENA in the full analysis (*Buckleya*, *Carpinus*, and *Hamamelis*) (see P -values in Table 3). Relative branch lengths and relative species numbers are positively related in all the genera except in *Carpinus* (binomial $P = 0.01$) (Table 2; Fig. 2).

TABLE 3. Results of tests on effects of unequal and incomplete sampling from sister clades. Maximum-likelihood analyses were performed for matrices including each possible combination with equal number of species in a pair of sister clades. N = number of combinations; R = region with higher rate of ITS evolution in analysis of complete dataset; T = times full analysis was supported; P = result of one-tailed sign test. Statistics should be viewed conservatively because combinations of species are not independent.

Genus	N	R	T^*	P	Average branch length in sister clades	
					EAS	ENA
<i>Asarum</i>	15	EAS	15	0.00003	0.0415	0.0177
<i>Carya</i>	9	EAS	9	0.0020	0.3017	0.0072
<i>Illicium</i>	78	EAS	78	3×10^{-24}	0.0345	0.0261
<i>Panax</i>	6	EAS	6	0.016	0.0128	0.0020
<i>Stewartia</i>	4	EAS	4	0.06	0.0960	0.0466
<i>Styrax</i>	6	EAS	6	0.016	0.0224	0.0105
<i>Buckleya</i>	2	ENA	1	0.75	0.0260	0.0280
<i>Carpinus</i>	4	ENA	3	0.31	0.0023	0.0200
<i>Hamamelis</i>	4	ENA	3	0.31	0.0053	0.0140

* Branch length contrasts having the same sign as that of the full dataset were considered as supporting the original analysis. *Cornus* was not included because it was represented by one species in each region; the relative branch lengths favored EAS.

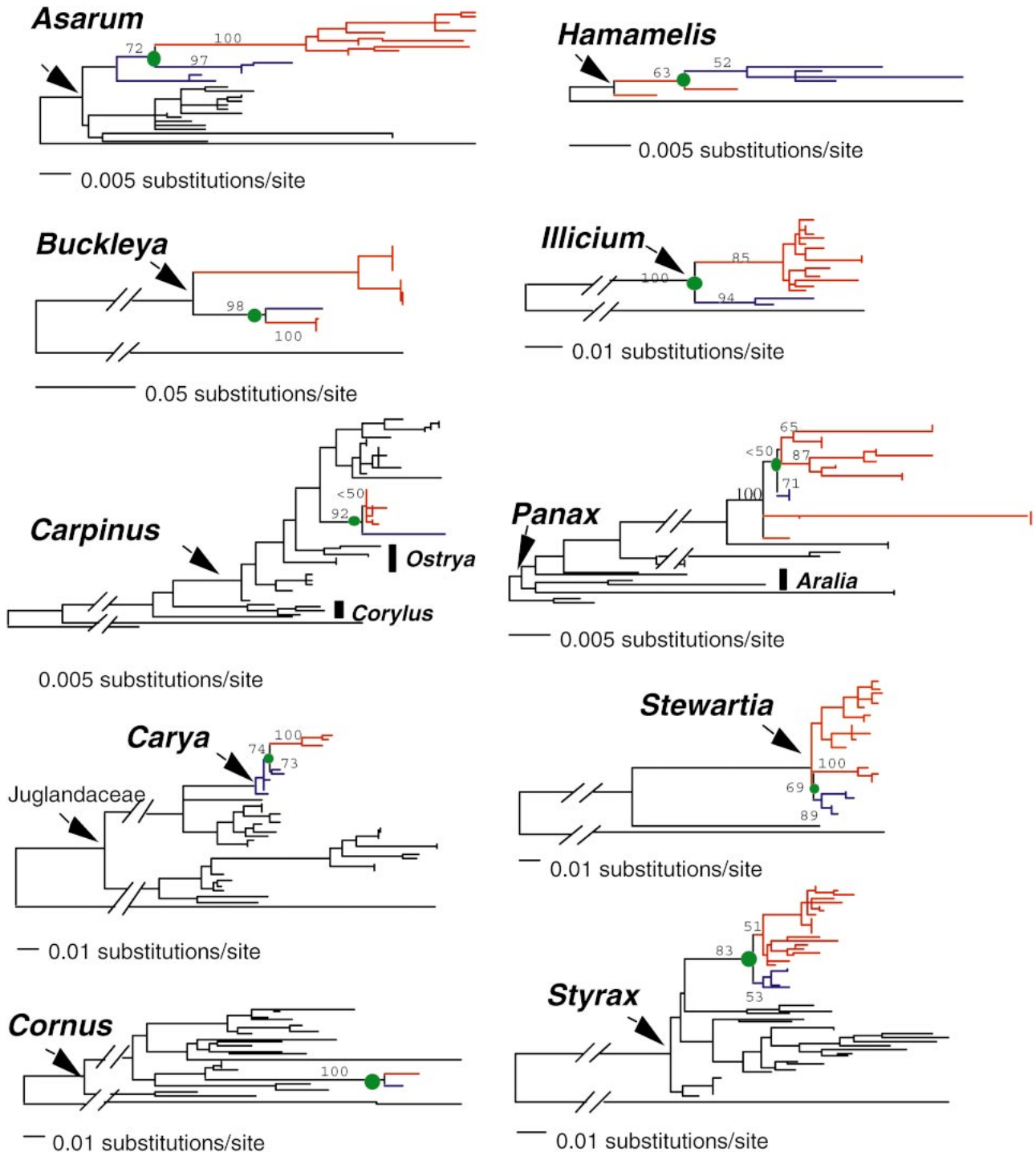


FIG. 1. Phylogenies showing EAS–ENA sister clades. For each genus, the EAS species are presented in red and ENA species are in blue. Nodes uniting the sister clades are indicated by solid circles. Relative branch lengths between the sisters correspond to relative ITS rates. Bootstrap support is indicated for the node uniting the sister pairs and for the basal node uniting species within each sister clade.

DISCUSSION

Comparisons of Rate of Molecular Evolution and Species Diversity between EAS–ENA Sister Clades

Our study detected longer branch lengths and greater species richness in the eastern Asian counterparts for a majority

of the pairs of EAS–ENA sister clades examined (seven out of 10 pairs (70%) and six out of eight pairs (75%, not including two ties), respectively). In one of the exceptions (*Hamamelis*), both branch length and species richness were greater in ENA. Given that sister lineages are by definition equal in age, and branch lengths in sister lineages reflect the

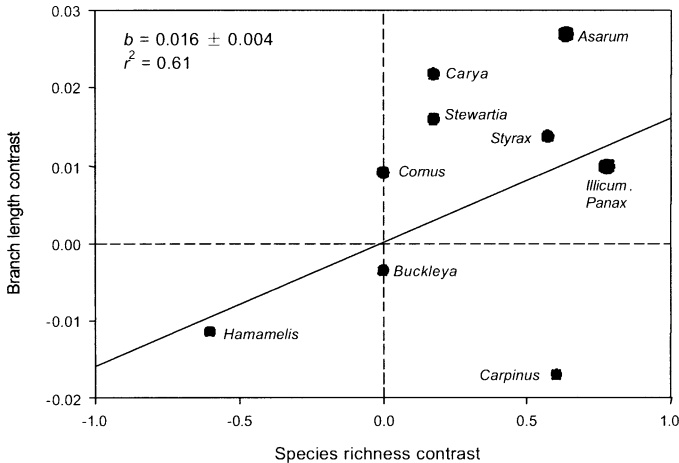


FIG. 2. Positive relationship between species richness contrasts ($\log_{10}[N_{EAS}/N_{ENA}]$) and branch length contrasts ($L_{EAS}-L_{ENA}$) ($F_{1,9} = 14.3$, $P = 0.0044$). Statistics are for a linear regression weighted by the negative log of the binomial probability that the branch length contrast is supported when samples are balanced (Table 3). Symbol size is related to weight: small (<0.6), medium (1–3), large (>4).

relative rates of their sequence changes, the longer branches in EAS taxa indicate more rapid molecular evolution in EAS.

Although incomplete sampling and extinction in either area might bias branch length and diversity estimates, we found no evidence that these factors affected the observed patterns. Our tests of sampling effects indicated that the estimates of relative branch length between the sister clades are robust to unequal and incomplete sampling of species from sister clades (Table 3). Incomplete sampling primarily involved the more diverse clades from eastern Asia (Table 2). Evidence from distribution and morphology suggests that the incomplete sampling from EAS is unlikely to influence the observed diversity bias between EAS and ENA. Instead, including the missing species in the analyses would likely strengthen the observed pattern (see discussion below).

The genera with incomplete sampling in the study were *Asarum*, *Carpinus*, *Carya*, *Illicium*, *Stewartia*, and *Styrax* ser. *Cyrta*, all of which have more species in EAS sister clades (Table 2). Most of the unsampled species were eastern Asian.

In *Asarum*, the sister clade is sect. *Heterotropa* (EAS) versus the Virginian sect. *Hexastylis* (ENA). This relationship is consistent with previous morphological and ITS sequence analyses by Kelly (1997; 1998). Several morphological synapomorphies and many nucleotide substitutions support the monophyly of the more speciose *Heterotropa*, whereas no morphological synapomorphies unite the eastern North American *Hexastylis* (Kelly 1998). This indicates that the unsampled *Heterotropa* species (all in EAS) would likely belong to the EAS clade (*Heterotropa*), which would strengthen the diversity bias toward EAS (Table 2). A combination of morphological and molecular data suggests that *Hexastylis* is paraphyletic, with the Virginian species being sister to *Heterotropa* (see Kelly 1998).

Carpinus has two sections: sect. *Carpinus* with a wide distribution in the Northern Hemisphere, and sect. *Distegocarpus* endemic to eastern Asia. Within sect. *Carpinus*, three subsections are recognized: *Carpinus*, *Monbeigiana*, and *Pol-*

lyneurae. Subsect. *Carpinus* is disjunct between eastern Asia (*C. laxiflora*, *C. londoniana*, *C. tientaiensis*, and *C. viminea*) and eastern North America (*C. caroliniana*). We sampled all species of the monophyletic subsection. The nonsampled EAS species do not belong to the sister clades and should have no impact on the diversity estimation. In *Carya*, the two unsampled species from EAS likely belong to the EAS clade based on their morphology. The seven unsampled species from ENA cannot be confidently placed, although they likely align outside the sister clades given that no clear morphological synapomorphies unite the ENA species (P. S. Manos, pers. comm.) and our ML analysis of the ITS data suggests paraphyly of the ENA *Carya* (74% ML bootstrap; Fig. 1).

In *Illicium*, characters from seed structures support a major division between New World and Old World species, as suggested by the ITS data (Oh et al. 2003). The unsampled species from each region (14 from EAS; four from ENA) would not influence the diversity asymmetry observed in our analysis. An unpublished phylogenetic study using ITS and other molecular regions, and including more species of *Illicium* from ENA than our analysis, similarly identified a primary disjunction between the EAS–ENA species (Morris et al. 2003, abstract of BSA meeting in Mobile, AL at: www.2003.botanyconference.org/). In *Stewartia* both ENA species were sampled. The unsampled EAS species are closer morphologically to the sampled EAS species, thus are likely to fall within the EAS clade. Similarly, in *Styrax* ser. *Cyrta*, both ENA species were included in the analysis and the 14 unsampled EAS species are probably part of the EAS subclade based on morphological considerations in conjunction with the molecular data (P. W. Frislich's lab, unpubl. data; pers. comm.). Therefore, including unsampled species of the ten genera would not likely change the general diversity-molecular evolution pattern observed in this study.

All of the genera included in this study have Tertiary fossil records from Eurasia and/or North America, except for *Panax* and the *Heterotropa*/*Hexastylis* clade of *Asarum* (Manchester 1999; Plant Fossil Record at <http://www.biodiversity.org.uk/ibs/palaeo/pfr2/pfr.htm>). The fossil data provide no evidence of greater extinction of species in ENA. Fossils of *Carya* occur in North America and Eurasia from the Oligocene to recent, with the earliest confirmed record from the Eocene of Colorado, but also a high diversity in the Miocene of Europe. This evidence together with the ITS phylogeny (Fig. 1) suggests a possible North American origin of the genus, as well as a secondary diversification center in Europe (Kirchheimer 1957; Mai 1981; Manchester 1999). The higher contemporary species richness of *Carya* in ENA argues against relatively higher extinction in that region.

Although *Cornus* occurs throughout the Tertiary in the Northern Hemisphere, confirmed fossils representing the EAS–ENA sister clades (Subg. *Mesomora*, the only subgroup of the genus with alternate leaves and a deep cavity at the apex of the fruit stone) have been found only in Europe (Miocene) and Japan (Pliocene) (Eyde 1988; Manchester 1999). Morphologically, the EAS species *C. controversa* is more heterogeneous, with at least two taxonomic varieties having been recognized, than the ENA sister *C. alternifolia* (Q.-Y. Xiang, pers. obs.). This is consistent with the longer ITS branch in the EAS sister clade. Fossils of *Illicium* are

known from the Eocene and Miocene of Europe, the Miocene and Quaternary of North America, and the Quaternary of Asia (Mai 1970; Tiffney and Barghoorn 1979; Manchester 1999). Because most of these fossils were not identified to species, the history of diversity in each of the regions is not resolved, in spite of the much greater contemporary diversity in EAS. *Stewartia* has a good fossil record based on fruits in the European Tertiary (Mai 1971, 1975), but has no records from North America.

In *Styrax*, the fossil seed record extends back to the upper Eocene in Europe (Chandler 1925–1926; Kirchheimer 1957; Mai 1995), and at least the Lower Pliocene (possibly the Oligocene) in Asia (Miki 1941; Mai 1995; see Fritsch 2001). Fossil fruits and seeds of *Styrax* are not known from the Americas. The reported North American fossils of *Styrax* are all leaf impressions with questionably reliable identifications (P. W. Fritsch, pers. comm.). Thus, the strong EAS diversity bias in *Styrax* appears to have a long history and does not require excessive extinction of North American forms.

Among the genera included in this study, *Hamamelis* and *Carpinus* do not follow the general pattern of species diversity and molecular rates favoring EAS sister clades. In *Hamamelis*, the ENA sister clade has more species and longer ITS branches, whereas in *Carpinus*, the ENA sister clade has fewer species, but a longer ITS branch (Table 2, Fig. 1). However, it is noteworthy that the sister clades in these two genera are relatively weakly supported by bootstrap analyses (Fig. 1). Fossils of *Hamamelis* occur extensively in the Paleocene of northeastern Asia to the later Tertiary throughout Eurasia, with only one record from the lower Eocene of Alaska and one from the Paleogene of the Atlantic Ocean (<http://www.biodiversity.org.uk/ibs/palaeo/pfr2/pfr.htm>). Thus, *Hamamelis* was probably once more diverse in Eurasia, but experienced a greater extinction there during the later Tertiary.

Fossils of *Carpinus* were also diverse in Europe and EAS throughout much of the Tertiary, but rare in North America, matching the contemporary distribution (fossil *Carpinus* has been reported only from the Tertiary of western North America; Tanai 1972; Uemura and Tanai 1993; Wehr 1995; Manchester 1999; Pigg et al. 2003). Manchester (1999) suggested that the contemporary ENA *Carpinus* likely represent a later Tertiary or Quaternary recolonization from Asia, which is supported by the ITS phylogeny. The reverse pattern of diversity versus ITS rate in *Carpinus* might be explained by (1) phylogenetic uncertainty (the more diverse EAS sister clade is supported by less than 50% bootstrap value; thus the true sister clades may contain fewer species in the EAS lineage, reducing the level of bias), and (2) differences in taxonomic practices applied to species in EAS and ENA. Morphological study of the eastern North American *Carpinus* indicated that the group is highly heterogeneous and more complex than its eastern Asian counterpart (Furrow 1987a,b), which is consistent with the longer ITS branch in the ENA clade and raises the possibility that species are too finely distinguished in the EAS *Carpinus*.

Possible Causes of the EAS–ENA Diversity Anomaly

Because comparison of phylogeny-based sister clades eliminates differences in age as a cause, the difference in

species richness between the ESA–ENA sister clades can be attributed to a greater net rate of diversification (speciation minus extinction) in eastern Asia, as previously suggested by Axelrod et al. (1998) and Qian and Ricklefs (2000). Although fossil data suggest a somewhat elevated extinction rate for tree genera in ENA relative to EAS (see Latham and Ricklefs 1993; Svenning 2003), differential extinction of species is not evident in the genera examined in this study, as discussed above. Furthermore, the higher rate of change in ITS sequences in EAS clades provides support for more rapid speciation in eastern Asia. A close link between rates of speciation and nucleotide substitution was also found in recent studies by Barraclough and Savolainen (2001) on angiosperm sister families and Webster et al. (2003) on a variety of organisms. Therefore, although we cannot completely rule out the impact of extinction and incomplete sampling in some genera, our overall evidence supports the hypothesis of higher rates of speciation in eastern Asia.

Rate of speciation is affected by both environmental (Cracraft 1985; Ricklefs and Schluter 1993; Rosenzweig 1995) and biological attributes (Farrell and Mitter 1993; Barraclough et al. 1995; Mitra et al. 1996; Hodges and Arnold 1995). Factors promoting speciation include *abundant topographic barriers* (splitting the ancestral species' range, preventing gene flow, enhancing founder effect, etc.), *strong sexual selection* (leading to divergence in mate recognition systems), *ecological specialization* (limiting population distribution and fostering divergence), *low dispersal rates* (reducing gene flow among populations), and *bottlenecks in population size* (facilitating genetic peak shifts) (Barraclough et al. 1998; Schluter 2001; Turelli et al. 2001). Although, differences in the biological attributes between the EAS and ENA sister lineages remain to be investigated, EAS does have more heterogeneous topography to provide more opportunities for allopatric speciation than ENA (Qian and Ricklefs 2000). Both natural selection and genetic drift can potentially drive allopatric speciation, although the latter has been generally considered less important (Templeton 1986; also see Turelli et al. 2001). Given that higher rates of presumably neutral molecular evolution are observed in the EAS sisters, drift, founder effects, and bottlenecks may play a substantial role in speciation in EAS. The rate of neutral molecular evolution (nucleotide substitutions) in a noncoding region such as ITS is determined by the rate of mutation and the probability of fixation (Li 1997). Because the rate of mutation of the same gene region between closely related EAS–ENA sisters is unlikely to differ, the probability of fixation of a neutral mutation will depend on population size. If drift and other random effects can contribute to the diversification of the ITS region, they might also affect gene regions responsible for the development of reproductive incompatibility between populations. Thus, the observed higher rates of ITS evolution in the EAS sisters may reflect a population structure conducive to other random changes in the genome. In addition to diversifying selection, smaller population size and more limited dispersal resulting from the complex topography of EAS may lead to more rapid establishment of reproductive isolation through random processes. Future studies examining population genetic structure across species ranges

in EAS and ENA sisters will help to test the hypotheses of allopatric speciation and its underlying mechanisms.

EAS supports mesic temperate vegetation comparable to that in ENA, although the region is topographically and climatically much more complex. The more heterogeneous physical features of EAS (e.g., the tectonically active, highly dissected and elevated geography of China) provide greater diversity of ecological habitats, particularly towards the south, where temperate and tropical floras intermingle over a broad range of longitude, compared to ENA. This ecological heterogeneity of eastern Asia makes the region an important center of survival, speciation, and evolution (Axelrod et al. 1998; Qian 2004). For example, EAS harbors 41 of the 60 families of primitive angiosperms in the world (Smith 1970) and a greater diversity of temperate elements than ENA (Lu 1999; also see above). Previous explanations for this richness of the EAS flora often emphasized the preservation of old taxa in the area (Raven and Axelrod 1974; Tiffney 1985a; Saucer 1988; Manchester 1999; but see Wu and Wu 1998). Although EAS might have provided refuges for some taxa during the Eocene-Oligocene and Pleistocene climatic deterioration, making the region a “museum” of diversity, our data clearly suggest that EAS contains an important engine of speciation in its diverse opportunities for allopatric speciation (Axelrod et al. 1998; Qian and Ricklefs 2000). It is a “cradle” of diversity for most of the disjunct genera considered in this study. Thus, a differential rate of speciation has probably played a significant role in producing the general diversity anomaly between the two regions. This result corroborates the finding from a phylogeny-based biogeographic analysis (Xiang and Soltis 2001) in suggesting that eastern Asia is likely an important center of diversification for angiosperms in the north temperate regions in the later Tertiary.

In conclusion, our study of ten diverse angiosperm lineages revealed a general pattern of more rapid ITS evolution and greater species diversity in eastern Asia than in eastern North America. This is the first phylogeny-based evidence from multiple lineages for a regional difference in rates of species diversification and molecular evolution. Additional comparisons of EAS and ENA sisters from other groups will be useful to determine the extent of the evolutionary pattern detected in our study. Studies of incipient stages of speciation in each continent also will help to identify the causes of regional differences in rates of plant diversification. Our study further indicates that assuming monophyly of species from the same region in comparative studies between EAS and ENA floras is not a safe hypothesis.

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