26

Continental Comparisons of Temperate-Zone Tree Species Diversity

Roger Earl Latham and Robert E. Ricklefs

Biogeographers and ecologists have sought for nearly two centuries to make sense of the striking differences in tree species diversity among the major forest regions of the earth. Alexander von Humboldt and Aimé Bonpland may have been the first to comment on these differences (1807) when they remarked on the far greater species diversity among tropical tree species than in the temperate zone. With some hyperbole, they also claimed that North America had three times as many species of oaks alone as Europe had tree species. Moist tropical forests have since been found to have at least ten times as many tree species as moist forests of the northern and southern temperate zones, at several spatial scales. Biologists have proposed various explanations for the temperate-tropical disparity in tree species diversity (Pianka 1966, 1989b; Hubbell and Foster 1986; Stevens 1989). No one mechanism has found general acceptance, and several may contribute to the pattern. Within temperate latitudes, the mesic forests of eastern Asia have three times more tree species than forests in eastern North America and six times more than those in Europe. Although this pattern has been recognized for more than a century (Gray 1878), it has attracted far less attention from theorists than the temperate-tropical disparity.

Suggesting an explanation for regional disparities in temperate tree species diversity, Gray (1878) and other early authors pointed to probable differences in extinction rates due to differences between the continents in the severity of climatic cooling during the Quaternary Ice Ages. Continental ice sheets covered much of Europe's present-day temperate forest region and advanced deeply into eastern North America, but they never reached the mid-latitudes of eastern Asia (fig. 26.1). Fossil floras show that forests in Europe were far more diverse in the Tertiary than at present (Reid and Chandler 1933; Mai 1960; Kilpper 1969; van der Hammen, Wijmstra, and Zagwijn 1971; Mai 1971a, 1971b; Takhtajan 1974; Łańcucka-Środoniowa 1975; Collinson and Crane 1978; Friis 1979; Mai 1980, 1981; Gregor 1982; Friis 1985; Kvaček and Walther 1987; Mai 1987a, 1987b; Mai and Walther 1988; Sauer 1988; Kvaček, Walther, and Bužek 1989). Most, if not all, of the genera lost from Europe in the late Tertiary continue to inhabit forests of eastern Asia or North America. Plant distributions underwent severe contraction and confinement in Europe, according to some views, because most plants failed to migrate southward

beyond 40° to 45° north latitude over or around the east-west–trending mountain ranges and the Mediterranean basin (e.g., Gray 1878). The effects were less severe in eastern North America, where the barriers—the Gulf of Mexico and the Mexican highlands—lay south of 30° north latitude. For 1,200 km inland across continental eastern Asia from the eastern coast, no physical barriers would have impeded southward migration by plants well beyond the Tropic of Cancer.

Ecologists generally have invoked geographical variation in the outcome of small-scale deterministic processes to explain global-scale diversity patterns (Connell and Orias 1964; MacArthur 1972; Ricklefs 1977, 1987; Huston 1979). These hypotheses describe a world in equilibrium. Even when so-called nonequilibrial mechanisms such as natural disturbance are called into play (Huston 1979), it is assumed that disturbance and interactions between populations, such as competitive exclusion and colonization of disturbed patches, would show balance within a landscape if it were sampled at large enough spatial and temporal scales (Petraitis, Latham, and Niesenbaum 1989).

A major problem with invoking competition and other interactions to explain global diversity patterns is that the scale of the patterns is grossly mismatched to the scale of the putative causal process. It is a large step from local-scale processes to predictions of regional-scale species richness. Such predictions would require plausible hypotheses linking the expression of local processes to regional variation in the physical environment (Ricklefs 1987). Furthermore, the fossil record gives no reason to expect equilibrium in regional species richness. The global number of vascular plant species apparently has risen steadily throughout the Phanerozoic, most sharply since the radiation of angiosperms in the late Cretaceous (Crepet 1984; Niklas, Tiffney, and Knoll 1985), while the area of land in terrestrial plant communities has perhaps decreased, at least since the Oligocene, due to the growth of continental ice sheets. Local processes could determine regional species richness if the region were merely a collection of habitats and localities within which diversity were regulated. However, differences in diversity between regions with similar climate suggest that local and regional processes contribute separately to regional species richness.

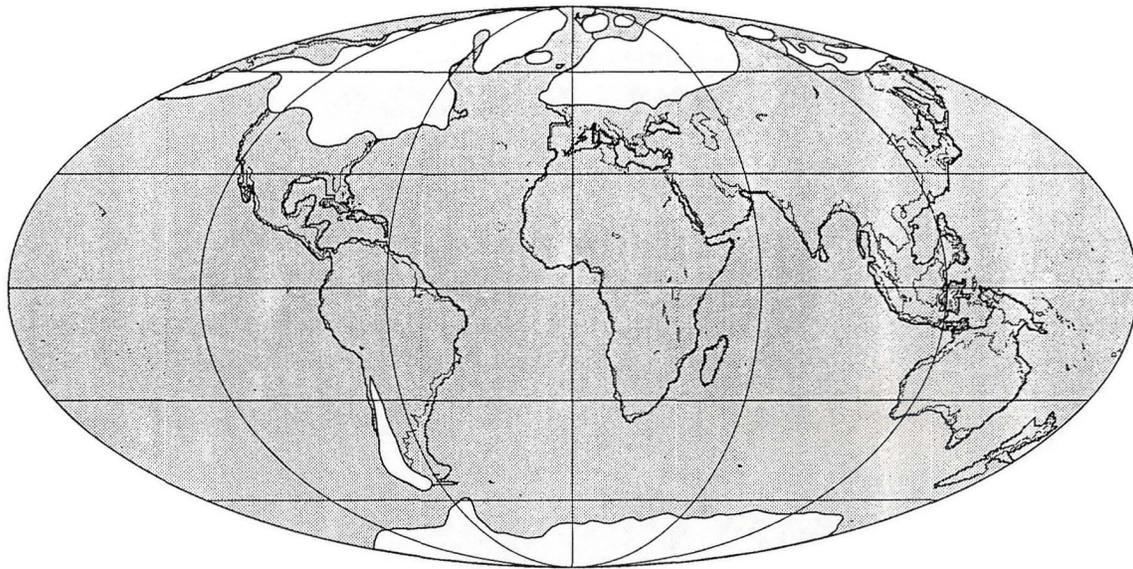In this chapter we attempt to understand geographical

Figure 26.1 Maximum Quaternary advance of continental ice sheets (white areas) superimposed on present-day coastlines (after Nilsson 1983). Maximum areal coverage has been estimated for North America (excluding Greenland), Europe (including western Siberia), and eastern Asia at approximately 16, 9.4, and 1.2×10^6 km², respectively (Nilsson 1983).

patterns in the contemporary diversity of regional tree floras in the temperate Northern Hemisphere by examining both historical and ongoing processes. We begin by comparing diversity in contemporary regional floras at several taxonomic levels. Next, we compare regional fossil floras beginning in the early Tertiary, when forests of modern aspect first appeared, with present-day regional floras, seeking patterns in the survival and extirpation (regional extinction) of genera. We then review tests of equilibrial hypotheses developed to explain local diversity. Finally, we suggest a scenario for the establishment of global patterns in tree species diversity. We infer that contemporary patterns of tree species diversity owe much to historical and evolutionary contingency, in contrast with some other authors who have interpreted the patterns as arising from, and maintained in equilibrium by, ecological interactions. We propose ancient roots for contemporary diversity anomalies, considerably older than the Pliocene and Quaternary climate cooling and resulting widespread extirpations. We conclude by discussing testable predictions suggested by our interpretation.

CONTEMPORARY GEOGRAPHICAL PATTERNS IN TEMPERATE TREE SPECIES DIVERSITY

Species Diversity in the Four Regions

In order to compare taxonomic diversities among the major moist temperate forest regions of the Northern Hemisphere, we defined the areas covered by moist temperate forest and compiled lists of all of the characteristic tree species. The regions are the four warm-temperate humid and temperate-nemoral climate biomes of Walter (1979). These mid-latitude regions extend varying distances toward mid-continent from the east and west coasts of Eurasia and North America (fig. 26.2). Appendix 26.1 pres-

ents the criteria used in compiling the tree floras and an abridged version of the floras themselves, with numbers of species tabulated by genus and region, information about the contemporary distributions of the families and genera, and Tertiary fossil data on the genera. Table 26.1 summarizes the total flora by the number of species, genera, families, orders, and subclasses occurring in each region. A total of 1,166 species make up the characteristic north temperate tree flora. Species are distributed among Europe (including the Caucasus), eastern Asia, North America's Pacific slope, and eastern North America, respectively, approximately in the ratio 2:12:1:4.

Adjoining Subtropical Forest

Of the four moist temperate forest regions, only the one in eastern Asia shares a long, common border with moist subtropical forest. Thus, it is reasonable to conjecture that the high diversity of temperate eastern Asia's tree flora may be due to the incursion of subtropical elements. Many tree species occurring in the eastern Asian temperate zone that have mainly subtropical ranges were already excluded from our list. We retallied the list also excluding those species that have mainly temperate ranges but that, nonetheless, belong to genera with predominantly tropical distributions (table 26.1). This did change the eastern Asian term in the ratio of species numbers among regions, but a large disparity between regions remained. When predominantly tropical genera were excluded, the ratio became approximately 2:9:1:4.

Area

The disparities in tree diversity among the four moist temperate forest regions cannot be explained as an area effect, because three of the regions (excluding the much smaller temperate forest zone of North America's Pacific slope) cover similar areas. The areas of the three larger regions
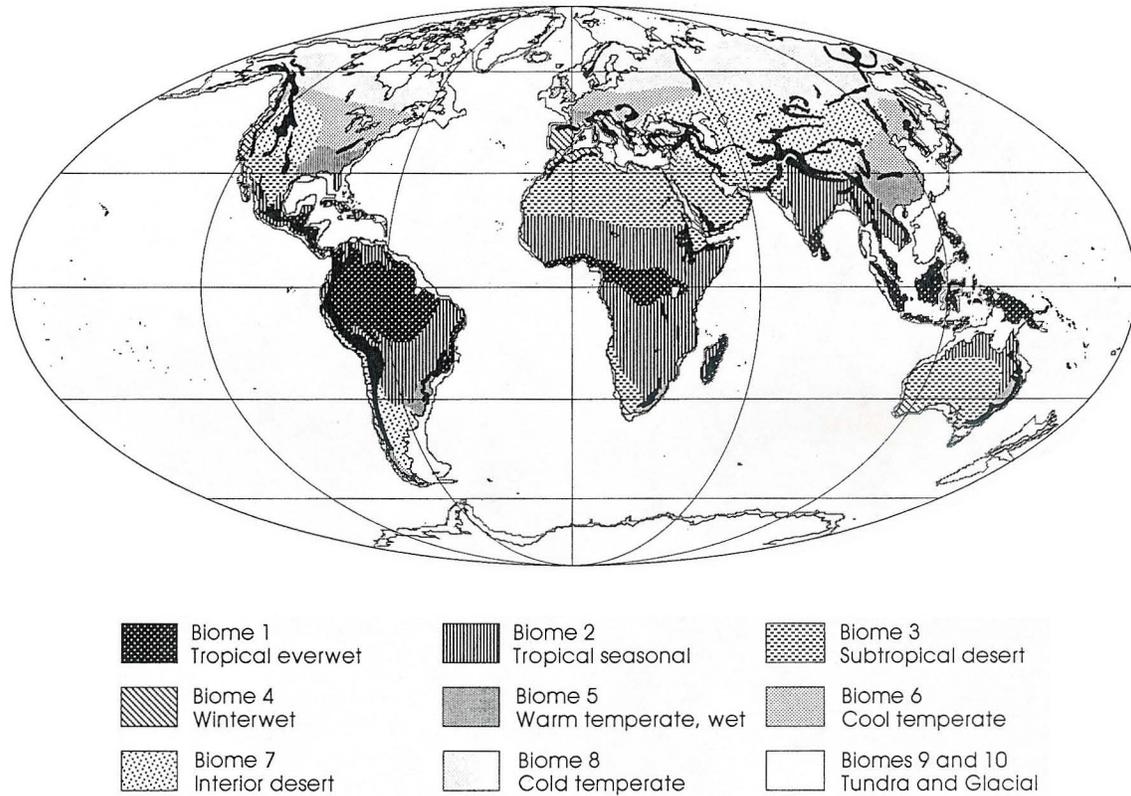
Figure 26.2   Contemporary biomes. Areas in black are major highlands. The study focuses on biomes 5 and 6. (After Walter 1979.)

Table 26.1.   Summary by Taxonomic Level and Region of Moist Temperate Forest Trees in the Northern Hemisphere

Taxonomic level	Number of tree taxa characteristic of moist temperate forests in:				
	Northern, central, & eastern Europe	East-central Asia	Pacific slope of North America	Eastern North America	Northern Hemisphere (total)
Subclasses	5	9	6	9	10
Orders	16	37	14	26	39
Families	21	67	19	46	74
Genera	43	177	37	90	213
Species	124	729	68	253	1,166
Families excluding those of predominantly tropical distribution (% of total)	18 (86%)	37 (55%)	18 (95%)	29 (63%)	41 (55%)
Genera excluding those of predominantly tropical distribution (% of total)	41 (95%)	121 (68%)	35 (95%)	77 (86%)	149 (70%)
Species exclusive of predominantly tropical genera (% of total)	122 (98%)	570 (78%)	66 (97%)	236 (93%)	987 (85%)

were estimated by transferring Walter's (1979) biome delineations to 1:12,000,000-scale Miller oblated stereographic projection maps (Rand McNally 1969) and planimetering. In Europe, eastern Asia, and eastern North America, moist temperate forest biomes were estimated by this method to cover approximately 1.2, 1.2, and 1.8 $\times$ 10^6 km^2 respectively. These estimates are generally lower than those from sources that present more detailed surveys of potential natural vegetation (roughly, preagri-

cultural vegetation) in only one region. For example, Wolfe's (1979) map of eastern Asian mid-latitude forests shows approximately 1.8 $\times$ 10^6 km^2 in forest types dominated by broad-leaved deciduous trees. Braun's (1950) map of deciduous forest associations in eastern North America indicates approximately 2.4 $\times$ 10^6 km^2 in the entire temperate forest region. Despite the discrepancies in magnitude, the ratio of these estimates—3:4—is similar to the ratio of the areas defined by Walter—2:3. (Potential
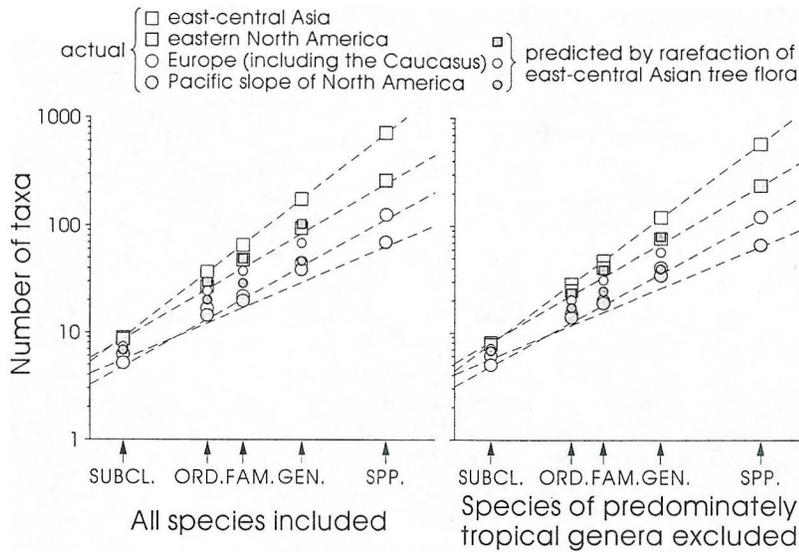
Figure 26.3 Numbers of tree taxa of the four moist temperate forest regions in the Northern Hemisphere and results of simulated rarefaction of the east-central Asian tree flora to the species numbers of the other tree floras (see table 26.1).

natural vegetation maps are common for countries or regions within Europe but are virtually nonexistent, [except for Walter 1979] for the entire temperate forest region of Europe including the Caucasus, even in the most geographically comprehensive treatments [Rubner and Reinhold 1953; Mayer 1984; Jahn 1991].) By area alone, one would expect North America's temperate forest zone to have the highest tree species diversity.

Taxonomic Diversity Patterns

There are many other means of detecting patterns in taxonomic diversity among regions with similar climate and vegetation besides simply comparing the numbers of species. We explored several, including comparing numbers of higher taxa (table 26.1; fig. 26.3), comparing numbers of species per genus and other ratios of lower to higher taxa, comparing numbers of genera and families consisting of only one or two species, and examining patterns in the overlap of taxa among regions. It is implicit that higher taxa are older than lower taxa. Thus, contemporary distributions of tree genera, families, and orders among regions may offer clues about the historical relationships among the regions' tree floras.

Simulated Rarefaction. Whether or not regions differ in their distributions of species among higher taxa could have broad implications for interpreting historical relationships among regional floras and possible causes of regional diversity differences. For example, suites of physiological or anatomical traits associated with plant families may have been crucial to species' regional survival or extinction during episodes of climate change that affected the regions differently. In this case, we would expect regions to differ significantly in taxonomic structure; that is, the flora of one region should diverge significantly from a random subset, containing the same number of species, of a more diverse flora in another region, in the number of families represented and in the frequency distribution of species per family.

We compared the taxonomic structures of the four re-

gions' tree floras by simulating the rarefaction (Simberloff 1979) of the most diverse floras to match the species numbers in other, less diverse floras. We performed the rarefaction tests by computer, picking randomly from the species pool of one temperate tree flora until the number present in a less diverse flora was reached. For example, in simulating the rarefaction of the 729-species eastern Asian temperate tree flora to 124—the number of species that belong to the European temperate tree flora—the program randomly picked 124 species from the eastern Asian list and tallied the genera, families, orders, and subclasses represented by those species. Each simulation was repeated 1,000 times. Rarefaction was simulated initially using the entire tree list and again using only species that do not belong to genera with predominantly tropical distributions.

The actual numbers of genera, families, and orders in the temperate tree floras of Europe and extreme western North America differ substantially from the mean numbers obtained by rarefaction of the eastern Asian temperate tree flora (tables 26.2 and 26.3; figs. 26.3 and 26.4). Statistical analysis of the rarefaction results shows that the European temperate tree flora is consistently poorer in genera, families, and orders than the eastern Asian temperate tree flora, whether or not the predominantly tropical genera are omitted. Rarefaction of the eastern North American tree flora to the numbers of species in Europe yielded similar differences, which are also highly significant. Rarefaction revealed almost no significant differences in hierarchical patterns of tree diversity between east-central Asia and eastern North America or between Europe and the Pacific slope of North America.

We assume, for the moment, that frost tolerance is a characteristic of higher taxa (we will return to this assumption later) and that frost tolerance was the key to a taxon's regional survival through Quaternary cooling. It follows that regional extinction would have been nonrandom among higher taxa. Based on these assumptions, the rarefaction results support the hypothesized link between extirpation and low tree species richness in Europe and
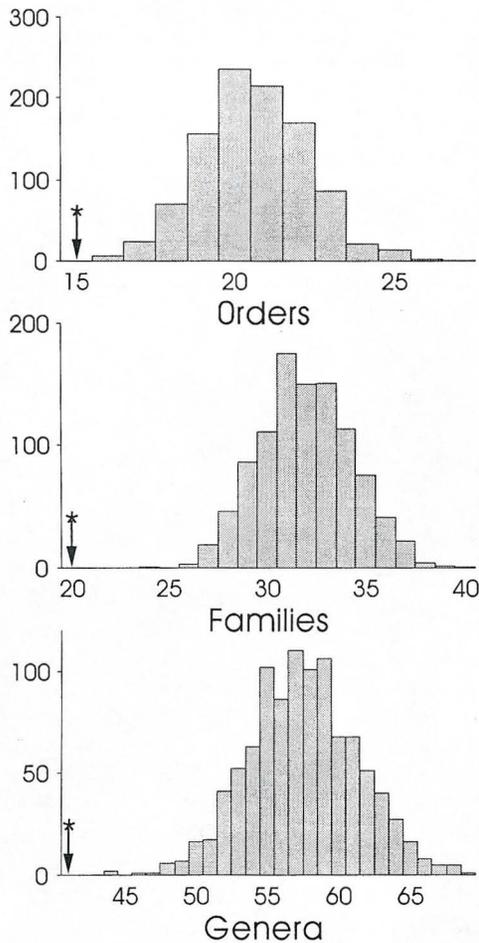
Figure 26.4 Frequency distributions of higher taxa resulting from simulated rarefaction of the east-central Asian moist temperate tree flora to the species number of the European moist temperate tree flora, with genera of predominantly tropical distribution omitted (see table 26.3). Numbers of taxa actually present in the European moist temperate tree flora are marked by asterisks (*).

western North America, since the distributions of species among higher taxa in these regions differ sharply from random subsets of the east-central Asian and eastern North American forests. However, given the same assumptions, the rarefaction results suggest that something other than differences in regional extinction rates may be responsible for the lower tree species richness in eastern North America relative to east-central Asia. To interpret these results, we seek a factor that is unbiased toward or against particular genera, families, or orders, in contrast to regional extinction based on frost tolerance or intolerance, which we assume to be phylogenetically selective.

Species per Higher Taxon. The temperate tree floras of Europe and the Pacific slope of North America clearly are depauperate at the higher taxonomic levels relative to those of eastern Asia and eastern North America. Furthermore, their higher taxa, on average, have fewer species, even though many genera and families are represented in the eastern Asian temperate forest region by only one or a few species (fig. 26.5A). While *numbers* of genera represented by one or a few species are far higher in eastern Asia than in Europe, eastern Asia and Europe have almost identically low *proportions* of these regionally low-diversity genera, lower than the corresponding proportions in North America (fig. 26.5B). In genera common to each pair of regions, Asian temperate forests are two to five times more speciose, on average, than forests in the other regions (table 26.4 columns A and B).

Globally Depauperate Genera. We examined the distribution of globally monotypic or ditypic (comprising only one or two species) tree genera among the regions (table 26.5). We were interested in the biogeography of these very low diversity genera because presumably some are relics of formerly diverse lineages, and some are autochthonous and perhaps new taxa that have not diversified. In either case they probably are more likely to go extinct

Table 26.2. Results of Simulated Rarefactions of Contemporary Tree Species

Regions compared	Taxon	Taxa present in region 1	Mean taxa in 1,000 floras drawn randomly from region 2	$t_{(df = 999)}$	Significance
1 Europe	Order	16	25.2	−4.80	**
2 East-central Asia	Family	21	38.5	−6.22	**
	Genus	43	70.2	−6.46	**
1 Pacific slope of North America	Order	14	20.7	−3.11	*
2 East-central Asia	Family	19	29.1	−3.65	**
	Genus	37	47.0	−3.16	**
1 Eastern North America	Order	26	30.4	−2.42	(NS)
2 East-central Asia	Family	46	50.4	−1.63	(NS)
	Genus	90	105.5	−3.34	**
1 Europe	Order	16	22.4	−4.58	**
2 Eastern North America	Family	21	36.5	−7.13	**
	Genus	43	58.8	−4.73	**
1 Pacific slope of North America	Order	14	18.8	−2.99	*
2 Eastern North America	Family	19	28.1	−3.80	**
	Genus	37	39.8	−0.90	(NS)
1 Pacific slope of North America	Order	14	13.5	0.46	(NS)
2 Europe	Family	19	16.8	1.51	(NS)
	Genus	37	32.6	2.01	(NS)

Note: We used *t*-tests to compare the actual numbers of taxa present with the means from 1,000 randomly generated floras in which the moist temperate tree flora of region 2 is rarified to the number of species in the moist temperate tree flora of region 1. The Type I error rate was adjusted using the Dunn-Šidák method (Sokal and Rohlf 1981): for $\alpha = .05$, $\alpha' = .0085$ and for $\alpha = .01$, $\alpha' = .0017$ (*$P < .05$, **$P < .01$).

Table 26.3. Results of Simulated Rarefactions of Contemporary Tree Species

Regions compared	Taxon	Taxa present in region 1	Mean taxa in 1,000 floras drawn randomly from region 2	$t_{(df = 999)}$	Significance
1 Europe	Order	15	20.6	−3.30	**
2 East-central Asia	Family	20	32.0	−5.07	**
	Genus	41	57.5	−4.30	**
1 Pacific slope of North America	Order	14	17.3	−1.95	(NS)
2 East-central Asia	Family	19	24.9	−2.45	(NS)
	Genus	35	40.0	−1.56	(NS)
1 Eastern North America	Order	25	23.8	0.75	(NS)
2 East-central Asia	Family	41	39.0	0.97	(NS)
	Genus	77	80.6	−0.92	(NS)
1 Europe	Order	15	21.3	−4.49	**
2 Eastern North America	Family	20	32.9	−6.41	**
	Genus	41	53.2	−4.01	**
1 Pacific slope of North America	Order	14	17.8	−2.42	(NS)
2 Eastern North America	Family	19	25.2	−2.78	*
	Genus	35	36.4	−0.47	(NS)
1 Pacific slope of North America	Order	14	12.9	0.97	(NS)
2 Europe	Family	19	16.1	2.00	(NS)
	Genus	35	31.2	1.83	(NS)

Note: Simulations were performed and tested for significance as described in table 26.2.
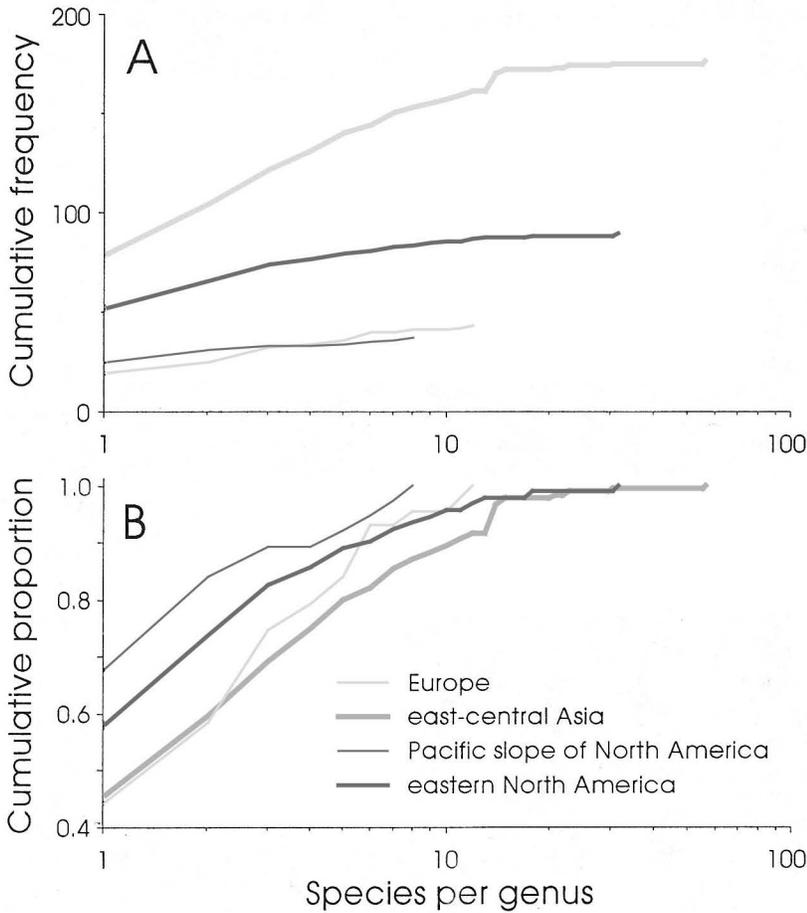

Figure 26.5 Frequency distributions of species per genus in the four regions. (*A*) Cumulative frequency; (*B*) cumulative proportion of total frequency.

Table 26.4. Comparison of Species Diversity of Tree Genera among Regions

Regions compared	(A) Mean species/ genus in region 1 of genera common to both regions	Significance of Wilcoxon T_s (H$_0$: $\bar{y}_A = \bar{y}_B$)	(B) Mean species/ genus in region 2 of genera common to both regions	Significance of Mann-Whitney U (H$_0$: $\bar{y}_B = \bar{y}_C$)	(C) Mean species/ genus in region 2 of genera extirpated from region 1
1 Europe 2 East-central Asia	3.03 $n = 39$	$P < .000001$	10.1 $n = 39$	$P < .000001$	2.69 $n = 74$
1 Pacific slope of North America 2 East-central Asia	2.00 $n = 31$	$P < .00001$	10.0 $n = 31$	$P < .0005$	3.54 $n = 35$
1 Eastern North America 2 East-central Asia	3.57 $n = 61$	$P < .000005$	7.59 $n = 61$	$P < .01$	2.00 $n = 8$
1 Europe 2 Eastern North America	3.43 $n = 30$	(NS)	5.20 $n = 30$	$P < .0005$	1.82 $n = 34$
1 Pacific slope of North America 2 Eastern North America	2.08 $n = 26$	$P < .005$	5.19 $n = 26$	(NS)	2.67 $n = 21$
1 Pacific slope of North America 2 Europe	2.27 $n = 22$	(NS)	3.64 $n = 22$	(NS)	2.50 $n = 8$

Note: We compared species diversities of tree genera currently inhabiting regions of higher overall diversity (B) with the same genera persisting in regions of lower overall diversity (A), and with genera extirpated from regions of lower overall diversity during the mid- to late Tertiary and Quaternary (C). Nonparametric methods were used to test the statistical significance of differences between groups in species numbers per genus: the Wilcoxon signed-rank test for paired samples and the Mann-Whitney test for unpaired samples. Adjusting the Type I error rate by the Dunn-Šidák method (Sokal and Rohlf 1981), for α = .05, α' = .0085 and for α = .01, α' = .0017.

Table 26.5. Geographical Distribution of Globally Mono- and Ditypic Genera of Moist Temperate Forest Trees in the Northern Hemisphere.

	Northern, central, & eastern Europe	East-central Asia	Pacific slope of North America	Eastern North America	Entire Northern Hemisphere (total)
Genera of > 2 species worldwide	41	148	34	78	168
Genera of ≤ 2 species worldwide (% of total)	2 (4.7%)	29 (16%)	3 (8.1%)	12 (13%)	45 (21%)

Note: One ditypic tree genus, *Liriodendron*, lives in two of the regions.

than are multispecies genera. Their distribution may reflect differences among regions in rates of extirpation or production of new taxa.

There are 45 globally monotypic or ditypic tree genera native to the north temperate forest regions. Six make up globally mono- or ditypic families: four in eastern Asia (Ginkgoaceae, Eucommiaceae, Cercidiphyllaceae, Tetracentraceae) and two in eastern North America (Leitneriaceae, Cyrillaceae). The globally mono- and ditypic genera are distributed among Europe, east-central Asia, North America's Pacific slope, and eastern North America, respectively, at a ratio of approximately 1:12:1:5, compared with the ratio of total numbers of genera of approximately 1:4:1:2. We used the G-test to compare the distribution among regions of genera consisting of only one or two species worldwide with the distribution of genera with more than two species (table 26.5). The test showed the two distributions to be marginally significantly different ($G = 6.7$, df = 3, $.05 < P < .1$). Thus, globally mono- and ditypic genera may be overrepresented in eastern Asia and eastern North America relative to Europe and North America's Pacific slope.

The fossil record shows 25 globally mono- and ditypic temperate tree genera to have relict distributions; that is, they formerly ranged across at least one more of the four regions than they do currently. These genera (table 26.6)

include *Ginkgo*, 7 conifers (including *Glyptostrobus*, which ranges in eastern Asia's temperate zone but occurs primarily southward), and 11 hamamelids. The known relicts thus belong disproportionately to the older classes and subclasses. *Ginkgo* and conifers belong to the oldest surviving lineages of temperate trees, and hamamelids include the oldest known angiosperm temperate trees, members of the formerly diverse and now depauperate Platanaceae (Schwarzwalder 1986).

Of the 21 globally mono- and ditypic genera that appear to be endemic to a single region, 13 (62%) are absent from the fossil record in any of the four regions. They may have occurred sparsely in Tertiary forests, their Tertiary ranges may have been small, they may have first appeared only recently, or they may be cryptic in the fossil record owing to low pollen output, non-wind-dispersed pollen, or restriction to habitats not conducive to fossilization of leaves, flowers, fruits, or seeds. Most are probably within-region relicts or lineages that never were diverse or abundant.

Global Distribution of Genera. We tallied genera that occur in either two or three of the regions, that is, those that are neither endemic nor cosmopolitan (fig. 26.6). Of the 63 genera so distributed, 59 (94%) are present in eastern Asia. The largest tally—20 genera common only to east-

Table 26.6.   Taxonomic Distribution of Globally Mono– and Ditypic Tree Genera with Relict Distributions

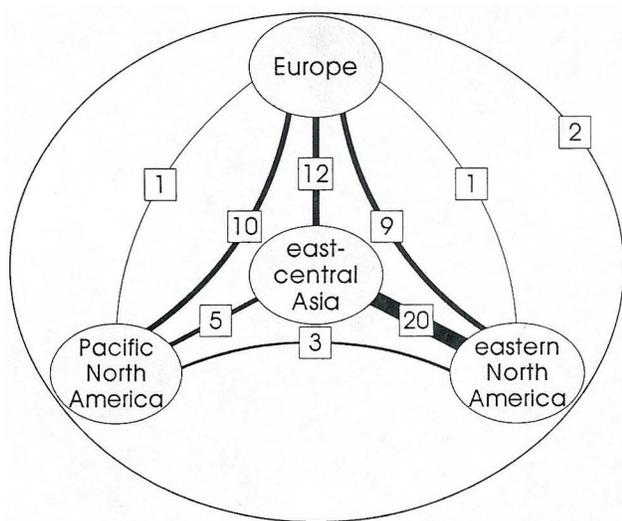| | | | Mono- and ditypic genera | |
| | | | Fossils in other regions | No fossils in other regions |
Class	Subclass	Total genera		
Ginkgoopsida		1	1	0
Pinopsida		27	7	5
Magnoliopsida	Magnoliidae	18	1	1
	Hamamelidae	45	11	2
	Dilleniidae	32	2	5
	Rosidae	67	1	7
	Asteridae	18	1	1
Liliopsida	Arecidae	3	1	0
	Commelinidae	3	0	0
	Liliidae	1	0	0

Figure 26.6   Numbers of tree genera native to either two or three of the four north temperate forest regions. Straight lines and the middle curved lines (bowing out) indicate genera that occur in two regions. The inner curved lines (bowing in) indicate genera that occur in three regions including east-central Asia. The outer ellipse indicates genera that occur in the three regions excluding east-central Asia.

ern Asia and eastern North America—reflects the well-known range disjunction displayed by many moist temperate forest plants that inhabit both regions (Li 1952; Graham 1972; Boufford and Spongberg 1983). Three tallies nearly tie for second rank: Europe and eastern Asia; Europe, eastern Asia, and Pacific North America; and Europe, eastern Asia, and eastern North America. Despite their proximity, the temperate forests at the two ends of North America share no genera uniquely, and they share the fewest genera as members of three-region groups. Eastern Asia emerges strikingly and overwhelmingly as the core area of Northern Hemisphere temperate tree genus distributions.

Exceptional Genera. A few genera run counter to the general trend of greatest diversity in eastern Asia followed, in sequence, by eastern North America, Europe, and Pacific North America. Most notable are *Carya*, the hickories, with 13 species in eastern North America and one in east-

ern Asia, and *Crataegus*, the hawthorns, with approximately 18 tree-sized species (≥ 8 m maximum height) in eastern North America, 2 each in eastern Asia and Europe, and 1 on North America's Pacific slope. Most *Crataegus* species are shrubs, but the trend in total species distribution parallels that of the few tree-sized members of the genus: approximately 220 of the global total of 306 species in a recent reexamination of *Crataegus* taxonomy (Phipps et al. 1990) are centered in the eastern North American moist temperate zone. Another genus that strikingly defies the trend is *Quercus*, the oaks, with tree-sized species numbering 32 in eastern North America, 21 in eastern Asia, 11 in Europe, and 5 in Pacific North America.

Juglandaceae, the family to which *Carya* belongs, is among the very few angiosperm tree lineages distributed widely across the north temperate zone for which there is fossil evidence that early diversification took place outside of eastern Asia, in this case in eastern North America and Europe (Manchester 1989). The tribe Querceae of the Fagaceae, including *Quercus*, may also have originated in eastern North America and Europe (Crepet and Nixon 1989). *Crataegus*, on the other hand, may have originated in southern China in the early Tertiary (Phipps 1983) despite its current locus of highest diversity in eastern North America.

CLUES FROM THE FOSSIL RECORD

In examining fossil distributions, we focused on the Paleogene, over 40 million years of warm, relatively stable climate during which forests spanned most of the present-day Arctic and covered nearly the entire breadths of Eurasia and North America, but were interrupted intermittently on both continents by north–south trending shallow seas in mid-continent (Figure 26.7). We used two different estimates of the fossil tree floras for the four contemporary north temperate forest regions: (a) genera actually represented in the fossil record of each region (Reid and Chandler 1933; Hu and Chaney 1940; Traverse 1955; Mai 1960; Kilpper 1969; van der Hammen, Wijmstra, and Zagwijn 1971; Mai 1971a, 1971b; Tanai 1972; Takhtajan 1974; Łańcucka-Środoniowa 1975; Rachele 1976; Collinson and Crane 1978; Friis 1979; Mai 1980; Potter and Dilcher 1980; Mai 1981; Gregor 1982; Freder-
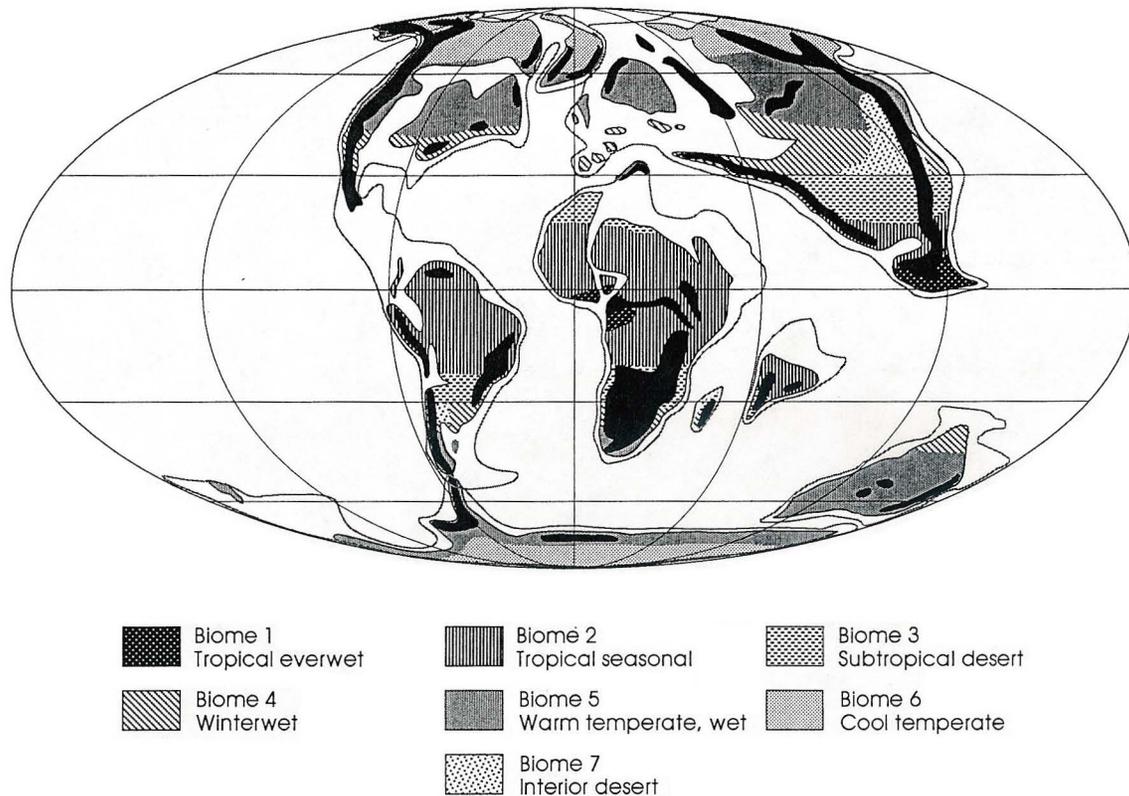
Figure 26.7   Maestrichtian (late Cretaceous) biomes. Areas in black are major highland regions. (Redrawn from Horrell 1991.)

iksen 1984a, 1984b; Wing and Hickey 1984; Friis 1985; Kvaček and Walther 1987; Mai 1987a, 1987b; Mai and Walther 1988; Sauer 1988; Kvaček, Walther, and Bużek 1989; Guo 1990; McCartan et al. 1990; Manchester, unpublished data; Friis, personal communication) and (2) an expanded list of genera also including those that are absent from the Tertiary fossil record of the region but present in its contemporary flora *and* in the Tertiary fossil record of at least one other region. The latter we term the "inferred" Paleogene tree flora of each region. We acknowledge that these are imperfect estimates of the actual regional Paleogene tree floras for many reasons, including the infrequency and nonrandom distribution of fossilization events, the scarcity of Tertiary sedimentary deposits, and the rarity of paleontologists with the skills, specific curiosity, and time to analyze Paleogene tree floras.

In comparing fossil and contemporary floras, we included some present-day occurrences of genera not included in considerations of contemporary floras alone. All such occurrences (marked (P) in Appendix 26.1) fall into one of two categories: certain trees at the edges of their ranges, and certain shrubs. We included a genus in a region's contemporary flora even if represented there only by shrubby species if the genus also includes tree-sized species in another region, because trees may not be distinguishable from non-tree congeners in fossils. For such comparisons we also included a genus in a region's contemporary flora even if its range is peripheral to the region if it is also a characteristic member of a contemporary moist temperate tree flora in another region. For example, *Larix* is a member of the moist temperate tree floras of

Europe and east-central Asia, but its occurrences in the temperate zone of eastern North America are peripheral or disjunct from the main North American range of the genus, which is boreal. For another example, *Platanus* species belong to the moist temperate tree floras of eastern and Pacific slope North America, but in Eurasia, native stands of the genus are confined mainly to seasonally arid (eastern Mediterranean), montane (the Himalayas), and tropical (Southeast Asia) regions. Such genera may have contributed to moist temperate forest fossil assemblages both in regions where they were characteristic of the moist temperate flora and in those where their presence was infrequent, signaling spillover from a neighboring biome.

Our compiled fossil data show a tally of 107 tree genera that have disappeared since the Oligocene from some, but not all, of the present-day north temperate regions (table 26.7). We sought patterns in the division of tree genera in each region into three categories: present as Paleogene fossils but extirpated, present as fossils and persisting in the contemporary flora, and known only from the contemporary flora (see Appendix 26.1).

Comparability of Fossil Data among Regions

First, we compared total extant genera in each region with extant genera that are also represented in the fossil record for that region. This comparison provides a rough estimate of the consistency among regions of the fossil data reliability (table 26.8), assuming that most genera occurring in each of the four regions now also occurred somewhere within that region during the Tertiary. The

Table 26.7. Genera Extirpated Regionally during the Late Tertiary and Quaternary

Genera	Europe	Northern & east-central Asia	Western North America	Eastern North America
Acanthopanax	×	●		
Ailanthus^E	×	●	×	
Alangium^E	×	●	×	×
Albizia^E		●	×	
Aphananthe	×	●	×	●
Aralia	×	●		●
Asimina^N	×			●
Broussonetia	×	●		
Bumelia^E			×	●
Calocedrus	×	(P)	●	
Camellia^E	×	●		
Carpinus^N	●	●	×	●
Carya^N	×	●	×	●
Castanea^N	●	●	×	●
Castanopsis^E	×	●	●	
Catalpa	×	●	×	●
Cedrela^E	×	●	×	
Cephalanthus	×			●
Cephalotaxus^N	×	●		
Cercidiphyllum^N	×	●	×	
Chamaecyparis^N	×	●	●	●
Chionanthus^N	×	●		●
Cinnamomum^E	×	●		
Clerodendrum^E	×(?)	●		
Clethra	×	●		(P)
Cunninghamia^N	×	●		
Cyclobalanopsis^N	×	●		
Cyclocarya^N	×	●		
Cyrilla^N	×			●
Dendropanax^E		●		×
Diospyros^E	×	●	×	●
Disanthus^N	×	●		
Distylium^N	×	●		
Emmenopterys^N		●	×	
Engelhardtia^E	×	(P)		×
Enkianthus^N	×(?)	●		
Eucommia^N	×	●	×	×(?)
Euptelea^N	×	●		
Evodia^E	×	●		
Fagus^N	●	●	×	●
Fortuneria^N	×	●		
Ginkgo^N	×	●	×	
Glyptostrobus^E	×	(P)	×	×
Gordonia^E	×	(P)		●
Halesia^N	×			●
Hamamelis^N	×	●		●
Hemiptelea^N	×	●		
Hydrangea	×	●		(P)
Illicium^E	×	●		
Kalmia^N	×			●
Keteleeria^E	×	●	×	
Koelreuteria	×	●		
Lagerstroemia^E	×	●		
Leitneria^N	×	×		●
Lindera^E	×	●	×	(P)
Liquidambar^N	×	●	×	●
Liriodendron^N	×	●	×	●
Lithocarpus^E	×	●	●	
Litsea^E	×	●		(P)
Lyonia	×	(P)		●
Magnolia	×	●	×	●
Mallotus^E	×	●	×(?)	
Manglietia^E	×	●		
Meliosma^E	×	●		
Metasequoia^N	×	●	×	
Michelia^E	×	●		
Neolitsea^E	×	●		
Nyssa	×	●	×	●
Osmanthus^E	×	●		●
Ostrya^N	●	●	×	●
Paulownia	×	●	×	
Persea^E	×		×	●
Phellodendron	×	●		
Phoebe^E	×	●		
Planera^N		×		●
Platycarya^N	×	●	×	×
Poliothyrsis^N	×	●		
Pseudolarix^N	×	●		
Pseudotsuga^N	×	●	●	
Pterocarya^N	●	●	×	×
Pteroceltis^N	×	●		
Rhus	(P)	●	×(?)	●
Robinia	×	×		●
Sabal^E	×		×	●
Sapindus^E	×	●	×	●
Sapium^E	×	●		
Sassafras^N	×	●	×	●
Schefflera^E	×	●		
Sciadopitys^N	×	●		
Sequoia^N	×	×	●	
Serenoa^N	×			●
Sinowilsonia^N		●		×
Staphylea^N	×	●		●
Stewartia^N	×	●		●
Symplocos^E	×	●	×	●
Tapiscia^N	×	●	×	
Taxodium^N	×	×	×	●
Ternstroemia^E	×	●		
Tetracentron^N	×(?)	●		
Thuja^N	×	●	●	●
Tilia^N	●	●	×	●
Torreya^N	×	●	●	●
Tsuga^N	×	●	●	●
Turpinia^N	×	●		
Ulmus^N	●	●	×	●
Zanthoxylum^E	×	●		●
Zelkova^N	●	●	×	×(?)

Note: (×) indicates extirpation from a region, (●) indicates contemporary tree species existing in a region. Contemporary genera are marked (P) if they do not attain tree height or if they rarely occur in the region's flora but do inhabit an adjoining biome and are characteristic members of a moist temperate tree flora in another region. Fossil genera are marked (?) if identified only tentatively by recent authorities (cited in this chapter). Present distributions of genera are indicated by superscripts: E, predominantly tropical; N, predominantly temperate or extending into tropical latitudes mainly at high elevations. (See Appendix 26.1 for sources of fossil and distributional data.)

completeness of the fossil record for extant genera does not differ significantly among the regions ($G = 6.21$, df = 3, $P > .1$).

Persistence/Extirpation Rates among Regions

Next, we compared total fossil genera in each region with fossil genera that are also extant in that region, as an estimate of the relative survival of genera among regions (ta-

ble 26.9). The four regions differ significantly in tree genus survival rate ($G = 53.9$, df = 3, $P \ll 0.001$). Extirpation rates of tree genera were radically unequal among the four regions. Europe was especially hard hit.

Extirpated Genera

Next, we looked at contemporary floras for differences between the genera that died out regionally and those that

Table 26.8. Relative Index of Completeness of Tertiary Fossil Record, by Region, of Moist Temperate Forest Tree Genera in the Northern Hemisphere

	Europe	Northern & east-central Asia	Western North America	Eastern North America
Total extant genera[a]	53	185	42	99
Represented in fossil record[b]	38 (72%)	117 (63%)	35 (83%)	49 (49%)

[a]Includes extant genera that do not attain tree height or that rarely occur in the region's flora but do inhabit adjoining biomes and are characteristic members of a moist temperate tree flora in another region.
[b]Includes a few fossil genera identified only tentatively by recent authorities (cited in this chapter).

Table 26.9. Survival since Mid-Tertiary, by Region, of Moist Temperate Forest Tree Genera in the Northern Hemisphere

	Europe	Northern & east-central Asia	Western North America	Eastern North America
Total fossil genera[a]	130	122	75	60
Surviving[b]	38 (29%)	117 (96%)	35 (47%)	49 (82%)

[a]Includes a few fossil genera identified only tentatively by recent authorities (cited in this chapter).
[b]Includes extant genera that do not attain tree height or that rarely occur in the region's flora but do inhabit adjoining biomes and are characteristic members of a moist temperate tree flora in another region.

survived. The mean numbers of species per genus in the eastern Asian temperate tree flora are significantly greater in the genera that persist in the other regions than in the genera that were extirpated from them. A similar relationship holds between the eastern North American temperate tree flora and that of Europe (table 26.4, columns B and C; fig. 26.8). In other words, genera that are currently more speciose in eastern Asia (or eastern North America) are more likely to have survived in other regions than genera that are currently less speciose.

For random extinction to have produced this effect, species diversity would have to be a distinctive property of individual genera that endures across many millions of years and among continents. The data suggest that this is unlikely. We compared numbers of species in genera common to each pair of the six possible pairs of continental areas using the G-test (adjusting Type I error rate as in table 26.2), testing genus-by-genus whether the species numbers in the less diverse region of the pair differ significantly from expected values generated by proportionally reducing the species numbers in the more diverse region. Two of the pairs show significant differences: eastern North America and eastern Asia ($G = 255$, df = 60, $P < .01$) and eastern North America and Europe ($G = 61.1$, df = 29, $P < .01$); eastern North America and the Pacific slope of North America differ marginally significantly ($G = 49.4$, df = 26, $.05 < P < .1$).

Furthermore, extirpated genera are nonrandomly distributed among higher taxa (table 26.10). For example, in Europe all tree genera of the now mostly tropical subclasses Magnoliidae and Arecidae died out. In the subclasses Hamamelidae and Rosidae, which have radiated widely in temperate, boreal, and high-altitude habitats, nearly half of the tree genera persisted. Counter to the trend of species dropping out that belong to subclasses of mainly tropical distribution, two-thirds of the genera of conifers, which inhabit mostly temperate and boreal regions, disappeared. However, over half of these genera now are monotypic and most have very small global ranges, indicating their relictual status. In contrast, more
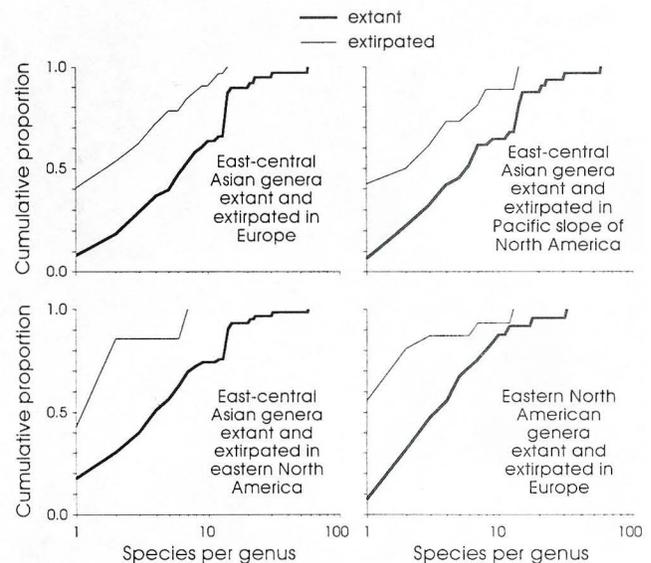

Figure 26.8 Cumulative frequency distributions (as proportions of total frequency) of species per genus in high-diversity regional tree floras for genera that are also extant in less diverse regional tree floras versus genera extirpated from less diverse regions.

than three-fourths of the conifer genera persisted on the Pacific slope of North America, the other region hit hard by extirpation. There, also, as in Europe, the magnoliids experienced the greatest attrition.

Global Distribution of Paleogene Genera

We tallied fossil genera that occurred in either two or three of the regions defined earlier for contemporary floras (fig. 26.9). In parallel with the contemporary pattern, 88 of the 95 genera in the inferred Tertiary floras that were so distributed (78 of 81 genera in the fossil-only floras) were present in eastern Asia. Of the 170 genera in our inferred Tertiary flora, 19 (11%) have been found in only one region, 95 (56%) are represented in two or three regions, and 56 (33%) are represented in all four regions.

Table 26.10. Taxonomic and Regional Distributions of Extant and Extirpated Genera of North Temperate Forest Trees Belonging to the Conifer and Dicot Classes

Class	Subclass	Europe		Northern & east-central Asia		Western North America		Eastern North America	
		Extant	Extirpated	Extant	Extirpated	Extant	Extirpated	Extant	Extirpated
Pinopsida		7	15	24	2	14	4	11	2
Magnoliopsida	Magnoliidae	0	14	15	0	1	5	7	0
	Hamamelidae	16	21	42	2	9	13	20	6
	Dilleniidae	7	13	23	0	6	4	20	0
	Rosidae	19	16	61	1	10	8	28	2
	Asteridae	4	6	15	0	2	3	9	0

Note: Includes a few fossil genera identified only tentatively by recent authorities (cited in this chapter) and extant genera that do not attain tree height or that rarely occur in the region's flora but do inhabit adjoining biomes and are characteristic members of a moist temperate tree flora in another region.

Of the 213 genera in our extant flora, 122 (57%) are endemic to one region, 63 (30%) are present in two or three regions, and 28 (13%) are in all four regions. The Tertiary and extant distributions differ highly significantly ($G = 240$, df $= 2$, $P \ll .001$). The low numbers of endemic fossil genera may be due in part to the lower likelihood of discovering fossil genera that were present in only one region. However, the pattern of decline in cosmopolitan distributions is striking. The well-known concurrence between the temperate floras of eastern Asia and eastern North America (Li 1952; Graham 1972; Boufford and Spongberg 1983) appears to be merely a vestige of the formerly even stronger affinity among the floras of these two regions and that of Europe. Most of the changes from figure 26.9 to figure 26.6 are due to extirpations in Europe.

Rarefaction of Paleogene Genera

We compared the higher taxonomic structures of the inferred Paleogene tree floras (table 26.11) by simulating the rarefaction of the eastern Asian flora to match the numbers of genera in the other regions' floras (method given above). Unlike the simulated rarefaction of contemporary floras, the analysis of Paleogene floras does not compare regions in numbers of tree *species* among genera, families, and orders because species number cannot be reliably estimated from fossil remains. Rarefaction of the eastern Asian fossil tree *genera* indicated that the distribution of fossil genera among families and orders in Europe, the Pacific slope of North America, and eastern North America did not differ from random samples of the Asian fossil genera (table 26.12). We also simulated rarefaction of the contemporary tree genera of temperate east-central Asia to contemporary numbers of tree genera in the other three regions, for comparison with the rarefactions of fossil genera and of contemporary species (table 26.13). Rarefying contemporary floras by genera paralleled the results of rarefying contemporary floras by species (see table 26.2).

CLIMATE AND TREE SPECIES DIVERSITY

Several comparative studies have revealed a direct relationship between species diversity and various climate variables, particularly precipitation or estimates of actual evapotranspiration (AET) (Richerson and Lum 1980;
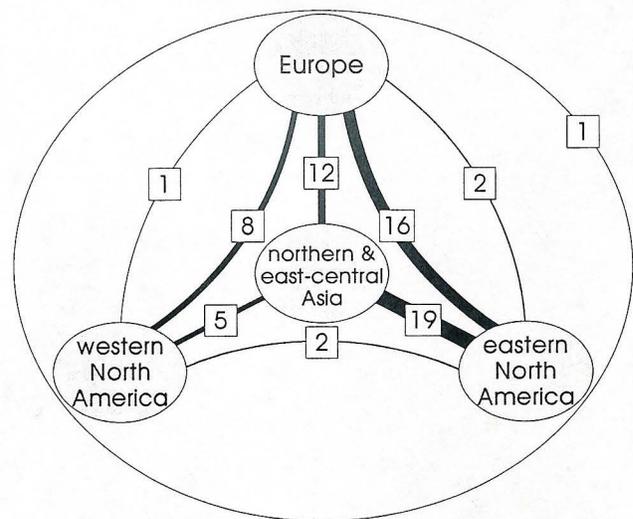

Figure 26.9 Numbers of tree genera occurring in either two or three of the four contemporary north temperate forest regions during the Paleogene (genera represented by fossil remains plus those inferred as present during the Tertiary because they are present in the region's contemporary flora *and* in the Tertiary fossil record of at least one other region). See figure 26.6 for an explanation of the lines.

Wright 1983; Turner, Lennon, and Lawrenson 1988). Patterns of this type have been demonstrated for trees in both temperate (Currie and Paquin 1987; Adams and Woodward 1989) and tropical (Gentry 1988a) regions, using sampling areas ranging from grid blocks as large as 100,000 km² to small plots of 0.1 to 1 hectare. Furthermore, several authors have cited the consistency of these relationships between regions (e.g., Adams and Woodward 1989) as evidence of convergence and determination of species richness by local physical factors.

In general, tree species richness increases in direct relation to precipitation and AET, suggesting that a positive relationship exists between diversity and productivity of the habitat (but see Tilman and Pacala, chap. 2, and Rosenzweig and Abramsky, chap. 5 for evidence that diversity declines at high habitat productivity). This relationship forms the basis of "species-energy theory" or energy-diversity theory (Wright, Currie, and Maurer, chap. 6), which relates diversity to energy flux by means of several possible mechanisms. In general, high produc-

Table 26.11. Summary by Taxonomic Level and Region of Forest Trees in "Inferred" Tertiary Floras

	Number of tree taxa in inferred Tertiary floras of:				
Taxonomic level	Europe	Northern & east-central Asia	Western North America	Eastern North America	Total
Subclasses	8	7	8	7	8
Orders	33	33	24	26	34
Families	61	63	43	49	67
Genera	140	156	81	98	170

Table 26.12. Results of Simulated Rarefactions of Tertiary Tree Genera

Region	Taxon	Taxa in early Tertiary tree flora of region	Mean taxa in 1,000 floras drawn randomly by genus	$t_{(df = 999)}$	Significance
Europe	Order	33	31.2	2.25	(NS)
	Family	61	59.4	1.04	(NS)
Western North America	Order	24	26.5	−1.45	(NS)
	Family	43	44.1	−0.39	(NS)
Eastern North America	Order	26	28.2	−1.50	(NS)
	Family	49	49.0	0.02	(NS)

Note: We used *t*-tests to compare the numbers of tree taxa inferred to have inhabited high-latitude forest regions during the Tertiary with the means from 1,000 randomly generated floras in which the Tertiary tree flora of northern and east-central Asia is rarified to the number of genera in the Tertiary tree flora of each of the other regions (see text for method of inferring paleofloras). The Type I error rate was adjusted using the Dunn-Šidák method (Sokal and Rohlf 1981): for $\alpha = .05$, $\alpha' = .017$ and for $\alpha = .01$, $\alpha' = .0033$ (*$P < .05$, **$P < .01$).

Table 26.13. Results of Simulated Rarefactions of Contemporary Tree Genera

Region	Taxon	Taxa in present-day tree flora of region	Mean taxa in 1,000 floras drawn randomly by genus	$t_{(df = 999)}$	Significance
Europe	Order	16	21.6	−2.78	*
	Family	21	30.5	−4.14	**
Pacific slope of North America	Order	14	19.9	−3.00	**
	Family	19	27.3	−4.00	**
Eastern North America	Order	26	30.0	−2.16	(NS)
	Family	46	48.2	−0.82	(NS)

Note: We used *t*-tests to compare the actual numbers of taxa present with the means from 1,000 randomly generated floras in which the moist temperate tree flora of contemporary east-central Asia is rarified to the number of genera in the moist temperate tree flora of the other regions. Simulations were performed and tested for significance as described in table 26.12.

tivity maintains larger numbers of individuals per species and thus reduces the probability of stochastic extinction. High production in habitats with little stress may also increase the total variety of microhabitats and permit greater microhabitat specialization. For certain types of organisms, notably trees, high precipitation and temperature may be associated with the occupation of a greater variety of habitats, thereby increasing sample diversity through increased habitat heterogeneity on a regional scale and through spillover or mass effects on a habitat scale. Regardless of the mechanism, the correlation between diversity and physical factors suggests that the outcome of species interactions depends on the physical conditions of the environment.

Alternative viewpoints must be entertained when one identifies diversity anomalies, in which habitats with similar physical conditions are occupied by different numbers of species in different regions (Schluter and Ricklefs, chap. 21). Such is the case in both local and regional comparisons of mangrove species between the depauperate Caribbean and species-rich Indo-Pacific regions (Ricklefs and Latham, chap. 20). It is also certainly the case in the regional comparisons of species richness in north temperate deciduous broad-leaved forests presented here. The evi-

dence for a parallel diversity anomaly at the local level (1- to 10-ha plots) is weak due to inadequate sampling in Asia, but appears to be consistent with the regional trend between Europe and eastern North America (Latham and Ricklefs 1993). Lacking contrary evidence, we accept the possibility that eastern Asian temperate forests contain markedly more species at the local level than do temperate forests elsewhere.

Both Currie and Paquin (1987) and Adams and Woodward (1989) claimed general similarity among eastern Asia, Europe, eastern North America, and temperate regions of the Southern Hemisphere in species richness of temperate forests. We have reviewed and criticized these conclusions in detail elsewhere (Latham and Ricklefs 1993). Briefly, in these comparisons Asian data cited by Adams and Woodward (1989) were restricted to boreal and island localities. Moist temperate continental Asia, where regional tree species diversity is higher by far than anywhere else in the earth's temperate zones, was not sampled. Although diversity in Europe was claimed to be comparable to that in eastern North America, seven out of eight European sampling areas fell below the North American regression of species richness on AET. In these studies, species richness was tabulated for large grid

blocks (51,000 to 100,000 km²), which introduces unspecified contributions of habitat heterogeneity to species diversity. In arid regions, for example, in which average climate conditions do not support forest vegetation, tree species were recorded only from riparian habitats. Furthermore, both Currie and Paquin (1987) and Adams and Woodward (1989) mixed broad-leaved and needle-leaved (including boreal) forests, perhaps making direct comparisons inappropriate. Latham and Ricklefs (1993) found that tree species richness in 0.5- to 10-ha samples of temperate broad-leaved forests was unrelated to AET. Because the outcome of any ecological interaction that may restrict local coexistence of species is determined at the local scale, we feel that our analysis more directly tests the relationship between species richness and energy flux within the temperate broad-leaved deciduous forest biome of eastern North America.

The increase in tree species richness from temperate to tropical latitudes is generally thought to reflect parallel gradients of physical conditions (Ricklefs 1977; Gentry 1988a), with temperature and moisture generally higher toward the equator at low elevation. While species richness of trees, large shrubs, and lianas on 0.1-ha plots in the tropics appears to increase with annual precipitation up to 300 to 500 cm (Gentry 1988a), Latham and Ricklefs (1993) failed to find a relationship between species number of trees alone and AET on 1-ha plots in tropical forests. A latitudinal gap of at least 15° separates broad-leaved forests in the Neotropics and in temperate North America. As noted by Latham and Ricklefs (1993), a corresponding discontinuity exists in tree species richness. In an analysis of covariance of tree species richness and AET on 0.5- to 10-ha plots, temperate and tropical plots differed significantly between each other (by an order of magnitude) but independently of AET, even though the ranges of temperate and tropical AET values overlapped. Thus, the latitudinal difference in tree species diversity is not a direct consequence of a latitudinal difference in physical conditions, because tree species diversity is statistically unrelated to AET within latitudinal belts.

In general, we conclude that regional effects influence tree species richness independently of, and in addition to, local effects of climate. Diversity-climate correlations among large sampling blocks may reflect increased variety of habitats suitable for trees as productivity increases (increased beta diversity). Temperate-tropical differences in diversity in the Americas and Europe/Africa may represent discontinuities in diversity along continuous environmental gradients. Greater sampling, particularly of temperate and subtropical forests in eastern Asia, will be required to clarify these relationships. But for the present, we feel that a simple, continuous relationship between diversity and local climate does not provide an adequate description of contemporary patterns of tree species diversity.

THE HISTORICAL DEVELOPMENT OF TEMPERATE TREE FLORAS

North temperate broad-leaved deciduous tree floras present the following patterns. First, a large proportion of these floras, particularly in the northerly parts of the biomes, belong to families that are characteristic of north temperate regions, primarily Betulaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Salicaceae, Cornaceae, Rosaceae, and Aceraceae. Toward the southern parts of the biomes, representatives of more tropical families appear, but generally not in large numbers.

Second, the difference in diversity between tropical and temperate floras, and between temperate floras in different regions, resides at high taxonomic levels. There are roughly 11 species per family in temperate eastern Asia and half that number in temperate eastern North America, which has about a third the total number of species (see table 26.1). Rarefaction of the Asian species indicates that the distribution of North American species among higher taxa does not differ from that in a random sample of the Asian taxa. On 0.1-ha plots, temperate floras exhibit about 1.4 to 2.3 species per family, while lowland tropical floras, having up to 10 times as many species, exhibit species/family ratios of between 2 and 4, with as many as 58 families represented at a single site (Gentry 1988a). Thus, patterns of diversity are expressed at a high taxonomic level (Ricklefs 1989b). This suggests that contemporary patterns were established long ago by colonization and cladogenesis, which played roles at least as important as that of extinction.

Third, temperate flora diversity and the proportion of species belonging to predominantly tropical families and genera are both highest in eastern Asia, where there is and perhaps has been since before the Tertiary a continuous corridor of mesic forest connecting tropical and temperate latitudes. Colonization of temperate biomes in Asia from the tropics over long time periods has probably played an important role in the development of temperate forest communities there.

Fourth, although both European and western North American temperate floras suffered extinctions during the mid- to late Tertiary, the primary temperate diversity anomaly, that distinguishing eastern Asia from other temperate regions, is old and probably was established primarily by regional differences in colonization and autochthonous production of new taxa.

We propose that the differences in diversity of temperate tree floras among continents reflect the history of colonization of temperate biomes, which appears to have occurred more frequently in Asia, and the subsequent production of new autochthonous taxa and their geographical spread within temperate biomes. Furthermore, we propose, as have Farrell, Mitter, and Futuyma (1992) for insects, that differences between temperate and tropical floras reflect a physiological barrier to colonization of temperate zones that can be crossed only by the evolution of freezing tolerance mechanisms. Thus, the relatively low diversity of angiosperm trees in temperate areas arises because of the difficulty of colonizing temperate regions, rather than, or in addition to, any intrinsic limits either on species production or on coexistence of species within temperate areas. Accordingly, explanations for latitudinal gradients (actually disjunctions) in diversity can be traced to historical and evolutionary factors rather than to contemporary ecological interactions. We discuss these ideas in more detail below. It is not our purpose here to provide a balanced evaluation of alternative models. Rather, we

advocate a particular model that must be properly evaluated in the future.

Most angiosperm families arose during the late Cretaceous and Paleogene. During this time, frost-free climates covered much of the world's land surface (see fig. 26.7). The oldest fossils of contemporary moist temperate zone tree families in the Northern Hemisphere date from over 100 mya to less than 15 mya, with most falling within the range 30 to 90 mya (fig. 26.10). During the early part of this period, eastern Asia was the only region in the Northern Hemisphere where a more or less continuous zone of forest vegetation might have existed between the tropics and high latitudes (see fig. 26.7). Fossil data from the late Cretaceous to the mid-Tertiary indicate an arid zone covering most inland fossil collection sites between subtropical moist forests in northeastern Asia and tropical moist forests in southeastern Asia (see figure 26.7; Song, Li, and He 1983; Horrell 1991). However, moist conditions are likely to have existed near the coast throughout this period, as they do today (A. M. Ziegler, personal communication). Europe was isolated from tropical Africa by the Tethys Sea and from eastern Asia by large inland seas during much of this period. North America was isolated by water from extensive tropical areas in South America. The southern portions of the north temperate regions were separated from each other by two oceans and two shallow mid-continental seas, but their northern portions were at least intermittently connected via Greenland, Ural, Bering, and mid-Canadian land bridges (Tiffney 1985a). Because several of the most prominent temperate families of trees have fossil records dating back to the late Cretaceous (Betulaceae, Fagaceae, Juglandaceae) or early Paleogene (Hamamelideceae, Nyssaceae), we presume that the development of temperate floras occurred at this time.

In our scenario, the development of north temperate forests involved the crossing of a major physiological boundary—the evolution of freezing tolerance—and reflected routes of colonization and dispersal from frost-free areas into various areas north of the frost boundary. Initially, areas of the Northern Hemisphere exposed to freezing were very restricted and distributed far to the north. Most angiosperm families, including those restricted to frost-free areas at present, inhabited what are now mid-temperate latitudes. Palynological data demonstrate that the replacement of gymnosperms by angiosperms during the Cretaceous began in equatorial latitudes but quickly spread far to the north (Crane and Lidgard 1990). The broad latitudinal distribution of forest vegetation in eastern Asia would seem to have been especially conducive to the evolution and spread of tree taxa.

With cooling beginning in the Oligocene and the expansion of the frost zone, most angiosperm families vacated the high-latitude areas that now make up the temperate zone. At the same time, the separation of Eurasia from Africa and India by the Tethys Sea and a wide separation between North and South America continued to limit any possible connection between moist tropical and moist temperate regions solely to eastern Asia (see fig. 26.7). By the Miocene, the two biomes shared 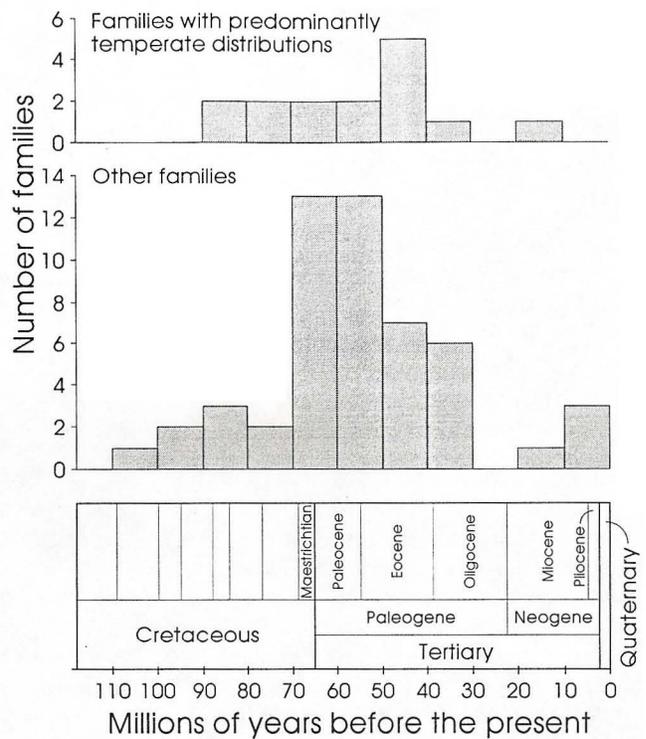a common boundary or transition zone in east-central Asia extending more than 1,500 km westward from the coast (Song et al. 1981).

Figure 26.10 Frequency distribution of earliest known fossil ages of angiosperm plant families represented in contemporary moist temperate tree floras of the Northern Hemisphere. (Data from Cronquist 1981 and Muller 1981, using the greater age where the two sources disagree.)

The present high diversity of the temperate Asian tree flora, particularly at the family and genus levels, combined with the strong representation of modern taxa in the fossil record of eastern Asia, indicates Asian origins for much of the north temperate flora. Contemporary distributions of cosmopolitan elements of this flora give no clues to the locations of their origins. Several cases are known in which the present distribution of a taxon does not include its fossil distribution. For example, *Platycarya* is restricted at present to temperate and subtropical eastern Asia (one species) but is known from the fossil record only in North America and Europe (Manchester 1987). Whether its presence in Asia is relictual (as in the case of *Cyclocarya*) rather than representing a recent colonization depends on whether it occurred historically in the region, which cannot be ruled out. Details of this sort cannot be adequately resolved, even for the best-known of families like the Juglandaceae, owing to the inadequacies of the fossil record.

By all measures, eastern Asia's forests claim most of the diversity of the north temperate tree flora. All but 4 families of the total flora—95%—live in temperate eastern Asia (all but 7 of the families include tree-sized species there); the exceptions are the primarily tropical Cyrillaceae and Sapotaceae, the Leitneriaceae (a family in southeastern North America without clear relationships), and the more widespread Platanaceae, which currently inhabits tropical Southeast Asia and occurs as fossils at higher

latitudes in Asia. In total, these account for only 8 temperate species—less than 1% of the total flora. Of the genera, 87% live in eastern Asia (most include tree-sized species there). The 28 genera that are absent from eastern Asia account for only 3% of the total species. The pattern still holds when families or genera of predominantly tropical distributions are omitted: 95% of the nontropical families and 85% of the nontropical genera occur in eastern Asia.

We presume that the dispersal of cosmopolitan families and genera occurred early in the evolution of the north temperate tree flora, and that most higher taxa restricted to eastern Asia originated there at a later time. If exchanges between the regions were possible throughout the Tertiary, we would have expected less endemism in the eastern Asia temperate flora, particularly its southerly elements. By Manchester's (1987) account, the cosmopolitan distribution of the Juglandaceae, including most of its modern genera, was established by the mid- to late Eocene. This particular case would seem to go against the general rule. The fossil record indicates an origin for the Juglandaceae in North America in the Paleocene, with nearly contemporary distribution of most of the genera in Europe, followed by their somewhat later appearance in eastern Asia. The family is also unusual in having roughly equal numbers of species in eastern North America and eastern Asia, primarily owing to the thirteen species of tree-sized *Carya* (hickories) in North America.

While cosmopolitan north temperate genera might have originated anywhere in the Northern Hemisphere, the distributions of more restricted genera clearly place east-central Asia at the center of dispersal (see fig. 26.6). The corresponding distributions of Tertiary fossil genera (see fig. 26.9) give approximately equal weight to east-central Asia and Europe as possible centers of origin. These patterns, together with the presence of a high diversity of endemic Asian taxa, point strongly to a Eurasian—most likely an eastern Asian—origin for much of the temperate flora. The scarcity of evidence for extirpation of genera in eastern North America suggests that the Asia bias reflects origination and not contraction of global ranges to relictual distributions (although, admittedly, fewer Tertiary fossil assemblages have been discovered so far in eastern North America than elsewhere in the contemporary north temperate zone).

In addition to the larger number of higher taxa in eastern Asia, widespread genera also tend to be more species-rich in that region. Conspicuous examples include *Carpinus,* with 14 tree-sized species in eastern Asia and 1 in eastern North America, *Alnus* (12/2), *Populus* (14/3), *Malus* (15/5), *Prunus* (32/10), *Sorbus* (15/2), *Acer* (58/9), and *Fraxinus* (14/7). The only exceptions of note are *Quercus* (21/32), *Carya* (1/13), and *Crataegus* (2/18). These genera are typically northern in distribution, and we therefore assume that the diversity differences represent differential proliferation and perhaps survival of species within temperate clades, rather than a differential frequency of invasion of temperate biomes by groups of mainly southern distribution. We are not comfortable speculating on the conditions in eastern Asia that might promote cladogenesis, although these might be associated with the varied topography of the region. Nor are we

ready to conjecture about the possible role of the age of taxa within each of the regions, although we presume that genera present in more than one region have had relatively long independent histories in each. Based on paleobotanical data, Wolfe (1981) has suggested that the Asian–eastern North American connection within *Acer*'s range was severed by the end of the Eocene, with a connection between eastern Asia and western North America persisting into the early Miocene.

The diversity anomaly in temperate tree floras between eastern Asia and other temperate regions appears to have arisen in part from the more frequent invasion of temperate biomes by tropical and subtropical vegetation in that region. If this is true, it also sheds light on the origin of the diversity contrast between tropical and temperate tree floras. We presume that the invasion of contemporary temperate biomes required the acquisition of frost tolerance, which involves extensive (and presumably costly) elaboration of biochemical mechanisms to protect stems and dormant buds from freezing (Sakai and Larcher 1987). Thus, frost tolerance presents a physiological barrier to dispersal that precludes most higher taxa of tropical and subtropical plants from the frost zone and has resulted in their withdrawal from temperate latitudes with recent cooling and more pronounced latitudinal stratification of temperature. Several of the taxa that crossed the frost barrier early in the Tertiary or perhaps in the Cretaceous have proliferated tremendously and achieved family status. Many taxa in typically tropical and subtropical families and genera have also crossed the barrier to varying degrees, but have not proliferated to the same extent nor penetrated the temperate biomes so extensively. Of genera from typically tropical families, only *Magnolia,* several genera in the Lauraceae (*Cinnamomum, Lindera, Litsea, Machilus*), and *Tilia* have achieved even moderate levels of diversity in temperate zones, and then primarily in eastern Asia and southern portions of eastern North America.

As expected, high-latitude subtropical Tertiary floras show strong taxonomic affinities with modern low-latitude subtropical floras (Sharp 1951). However, many plant families represented in subtropical Tertiary floras unearthed in the present-day temperate zone still have species living there. One possible explanation is that most temperate taxa may have dispersed and diversified globally under frost-free conditions across northern (but subtropical) latitudes, and then invaded the frost zone within each continent. This scenario suggests that there may have been "preadaptation" among certain subtropical groups for frost tolerance when global cooling near the end of the Eocene expanded the area of temperate climate in the north. Alternatively, the temperate flora may have invaded the frost zone at relatively few times and places and then dispersed and diversified globally, mainly within the frost zone. This hypothesis receives support from the simulated rarefaction of the Paleogene fossil tree genera of eastern Asia to match the numbers of fossil tree genera found in the other three regions, which showed no significant differences between the smaller fossil floras and random samples of the Asian fossil flora.

Phylogenetic analysis would provide a test of these

hypotheses and might offer clues about the relative ease or difficulty of evolving frost tolerance. Such a test would focus on genera with species inhabiting temperate areas and species inhabiting frost-free areas on two or more continents, or families with genera similarly distributed. The aim would be to determine which are more closely related: frost-tolerant and frost-sensitive sister species or genera from a single continent (consistent with taxa dispersing globally across the subtropics, then invading the frost zone) or frost-tolerant sister species or genera from different continents (consistent with taxa invading the temperate zone, then dispersing globally across it).

Our hypothesis concerning the historical development of temperate tree floras can be applied more widely whenever a major physiological barrier must be crossed. Farrell, Mitter, and Futuyma (1992) make a similar case for the lower diversity of insects in temperate zones relative to the tropics. Certainly the invasion of mangrove habitat by angiosperms requires a comparable evolution of new physiological capabilities (Tomlinson 1986). The hypothesis is consistent with the distribution of diversity among habitat types within temperate biomes as well. If habitat shifts require any level of physiological adaptation, then the highest diversity will likely occur in the habitat where species invaded the temperate zone. This is likely to be the oldest habitat occupied and the closest to the habitat type of the external source of colonists. In the case of trees, if colonization of temperate habitats occurred from the wet tropics or seasonally moist subtropics, we might expect diversity in temperate biomes to be highest in those habitats with warmer and more moist conditions. Productivity in such habitats ranks among the highest in the temperate zone. Thus, the observed correlation between species diversity and energy flux in temperate biomes could as well represent the historical origins of the biota as it could variation in the outcome of local interactions under different physical conditions.

Conclusions

The diversity anomaly in temperate forest tree species between east-central Asia and other regions of the Northern Hemisphere appears to be ancient and to have arisen from differences between the regions in colonization history and perhaps in subsequent rates of proliferation of endemic taxa. The fossil record also supports the old hypothesis that the low diversity of temperate tree species in Europe and North America's Pacific slope (but not the intermediate diversity of tree species in eastern North America) resulted from extinctions during the Neogene period of cooling climate and glaciation. These extinctions were nonrandom, being centered on old, relictual taxa of gymnosperms and old, primarily tropical families of angiosperms.

Geographical distributions and the fossil record suggest that most cosmopolitan taxa of temperate trees originated in eastern Asia and dispersed to Europe and North America, with conspicuous exceptions in the Juglandaceae and, probably, the Fagaceae. Additional temperate taxa appeared in Asia after dispersal routes to other temperate regions were largely closed off, giving rise to a large number of endemic temperate taxa there, many with tropical affinities.

This pattern of colonization of temperate regions suggests that the disjunction in diversity between temperate and tropical tree species may have arisen in part due to physiological constraints on crossing the freezing tolerance barrier. Thus, diversity patterns may have significant evolutionary as well as biogeographical and ecological bases.

Further resolution of the causes of diversity patterns will require new paleontological, biogeographical, and taxonomic data and synthesis. It must also be based on increased understanding of the physiological basis for the relationship of species' distributions to the physical environment.

Appendix 26.1
Regional Distribution of Tree Species Inhabiting Northern Hemisphere Moist Temperate Forests

Tree is defined as a self-standing woody perennial that reaches a maximum height of eight meters or more. The four regions are the Northern Hemisphere warm-temperate humid and temperate-nemoral climate biomes of Walter (1979). Taxonomy and range information are from Bailey and Bailey (1976), Braun (1950), Camus (1936–1938), Chi'ên (1921), Cronquist (1981), Elias (1980), Kartesz and Kartesz (1980), Krüssman (1979, 1984), Li (1935, 1973), Meyen (1987), Mirov (1967), Mitchell (1974), Ohwi (1965), Petrides (1972), Rehder (1940), Uphof (1968), Walter (1979), Wang (1961), and Zheng (1983, 1985). Taxonomy follows the most recent source for genera and species and Cronquist (1981) and Meyen (1987) for families and higher taxa of angiosperms and gymnosperms, respectively. Sources of fossil data are: Europe: Reid and Chandler (1933), Mai (1960), Kilpper (1969), van der Hammen, Wijmstra, and Zagwijn (1971), Mai (1971a, 1971b), Takhtajan (1974), Łańcucka-Środoniowa (1975), Collinson and Crane (1978), Friis (1979), Mai (1980, 1981), Gregor (1982), Friis (1985), Kvaček and Walther (1987), Mai (1987a, 1987b), Mai and Walther (1988), Sauer (1988), Kvaček, Walther, and Bužek (1989), and Friis (personal communication); eastern Asia: Hu and Chaney (1940), Tanai (1972), Takhtajan (1974), and Guo (1990); western North America: Wing and Hickey (1984), Sauer (1988), and Manchester (unpublished data); eastern North America: Traverse (1955), Rachele (1976), Potter and Dilcher (1980), Frederiksen (1984a, 1984b), and McCartan et al. (1990).

Northern tree species with pan-continental distributions and southern tree species with more than 50% of their ranges extending into subtropical or mediterranean areas were omitted from the list, even if they inhabit substantial fractions of the moist temperate forest regions. Omitted species that live in moist temperate forests only at high latitudes or high elevations often are more widespread in the biome poleward from the moist temperate forest zone which, in the Northern Hemisphere, also extends much farther east or west across the continent; examples include *Betula papyrifera* Marsh. (paper birch),

Picea mariana (Mill.) B.S.P. (black spruce), and *Populus tremuloides* Michx. (quaking aspen) in North America and *Betula pubescens* Ehrh. (downy birch), *Picea abies* (L.) Karst. (Norway spruce), and *Populus tremula* L. (aspen) in Eurasia. Omitted species that grow in moist temperate forests only at low latitudes, often on protected sites, represent incursions from the moist subtropics or from the mediterranean winter rain biome. Many subtropical tree species occur in scattered locations along the southern fringes of the moist temperate forest zone in China, including species of *Mangletia* and *Michelia* (Magnoliaceae), *Actinodaphne, Cinnamomum, Lindera, Litsea, Machilus, Neolitsea,* and *Phoebe* (Lauraceae), *Cyclobalanopsis, Lithocarpus,* and *Quercus* (Fagaceae), *Elaeocarpus* and *Sloanea* (Elaeocarpaceae), and numerous other genera (Wang 1961). Examples in the eastern North American moist temperate forest zone—far rarer than in eastern Asia—include *Pinus clausa* (Chapm.) Vasey (sand pine) and *Quercus chapmanii* Sarg. (Chapman oak).

Also omitted from the list were some cold-weather deciduous tree species in eastern Asia that occur mainly in the mountains in the subtropics and more sparsely northward into the temperate forest. Examples include *Bretschneidera sinensis* Hemsl. (of the monotypic Bretschneideraceae), which occurs at elevation 800 to 1,500 m in China's Guizhou, Yunnan, and Hunan provinces (Li 1935); *Cathaya argyrophylla* Chun & Kuang (Pinaceae), from elevation 920 to 1,800 m in Guangxi, Sichuan, Hunan, and Guizhou (Zheng 1983); and *Rhoiptelea chiliantha* Diels & Hand.-Mazz. (of the monotypic Rhoipteleaceae),

from elevation 500 to 1,400 m in Yunnan, Guangxi, Guizhou, and south beyond the borders of China (Li 1935). A large number of cold-hardy deciduous and evergreen species with ranges mainly in the mountains of China's western Sichuan and Yunnan provinces and the eastern Himalayas also were omitted, including scores of tree-size *Rhododendron* species.

Tree species that commonly dominate the moist temperate forest canopy on North America's Pacific slope were included on the list even if their ranges lie mainly outside the moist temperate forest region. Examples include *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir), *Abies grandis* (Dougl. es D.Don) Lindl. (grand fir), and *Populus balsamifera* L. subsp. *trichocarpa* (Torr. & Gray) Brayshaw (black cottonwood). Dominance of communities across several biomes is common among species inhabiting this smallest of the north temperate forest regions, as one might expect from the so-called "mass effect" of spillover among habitats and the larger ratio of this region's perimeter to its total area.

The filters applied to the total floras to derive our regional tree species lists result in underestimation of the true tree species richness in all four regions. However, we believe that our lists for Europe, the Pacific slope of North America, and eastern North America closely approximate the total numbers of native tree species actually present in those regions. Our list for east-central Asia, by contrast, substantially underestimates the total number of native tree species actually present due to spillover from subtropical, tropical, and montane forests along the southern and southwestern margins of the region.

Class /subclass	Order	Family	Genus	Number of tree species			
				Northern, central, & eastern Europe	East-central Asia	Pacific slope of North America	Eastern North America
Ginkgoopsida	Ginkgoales	Ginkgoaceae*[N]	*Ginkgo**[N]	†	† 1	†	
Pinopsida	Pinales	Cephalotaxaceae[N]	*Cephalotaxus*[N]	†	3		
		Cupressaceae[N]	*Calocedrus*	†	(P)	† 1	
			Chamaecyparis[N]	†	2	† 2	1
			Cupressus	1	2	† 3	
			Juniperus	3	† 4	† 1	3
			Platycladus*[N]		1		
			Thuja[N]	†	† 3	† 1	1
			Thujopsis*[N]		† 1		
		Pinaceae[N]	*Abies*[N]	† 4	† 14	† 6	† 2
			Keteleeria[E]	†	1	†	
			Larix[N]	† 1	† 5		† (P)
			Picea[N]	† 2	† 9	† 2	† 1
			Pinus	† 6	† 14	† 7	† 12
			Pseudolarix*[N]	†	† 1		
			Pseudotsuga[N]	†	† 3	† 1	
			Tsuga[N]	†	† 7	† 2	† 2
		Taxaceae[N]	*Taxus*[N]	† 1	† 3	† 1	(P)
			Torreya[N]	†	† 4	† 1	1
		Taxodiaceae[N]	*Cryptomeria**[N]		† 1		
			Cunninghamia*[N]	†	† 1		
			Glyptostrobus*[E]	†	† (P)	†	†
			Metasequoia*[N]	†	† 1	†	

Codes: E (Equatorial), family or genus is predominantly tropical in distribution; N (Nemoral), family or genus is predominantly temperate in distribution or extends into tropical latitudes mainly at high elevations; *, globally monotypic or ditypic family or genus; †, genus is represented in the Tertiary fossil record of the region; (P), geographical range of the genus is peripheral to the region and/or the maximum height of the largest species in the genus occurring in the region is less than 8 m (given only for those genera for which Tertiary fossil information is included); (?), fossil genera identified only tentatively by recent authorities (cited above).

(continued)

Class /subclass	Order	Family	Genus	Number of tree species							
				Northern, central, & eastern Europe		East-central Asia		Pacific slope of North America		Eastern North America	
			Sciadopitys*[N]	†			1			†	
			Sequoia*[N]	†		†		†	1		
			Sequoiadendron*[N]					†	1		
			Taiwania*[N]			†	1				
			Taxodium*[N]	†		†		†		†	2
Magnoliopsida /Magnoliidae	Illiciales	Illiciaceae	Illicium[E]	†			3				
	Laurales	Lauraceae[E]	Actinodaphne[E]			†	3				
			Cinnamomum[E]	†		†	11				
			Lindera[E]	†		†	8	†			(P)
			Litsea[E]	†		†	9				(P)
			Machilus[E]			†	10				
			Neolitsea[E]	†		†	5				
			Nothaphoebe[E]				1				
			Persea[E]	†				†			1
			Phoebe[E]	†		†	11				
			Sassafras[N]	†		†	1	†			1
			Umbellularia*[N]					†	1		
	Magnoliales	Annonaceae[N]	Asimina[N]	†							1
		Magnoliaceae	Liriodendron*[N]	†		†	1	†		†	1
			Magnolia	†		†	14	†			7
			Manglietia[E]	†			4				
			Michelia[E]	†			3				
	Ranunculales	Sabiaceae[E]	Meliosma[E]			†	5				
Magnoliopsida /Hamamelidae	Daphniphyllales	Daphniphyllaceae	Daphniphyllum[E]				2				
	Eucommiales	Eucommiaceae*[N]	Eucommia*[N]	†		†	1	†		†(?)	
	Fagales	Betulaceae[N]	Alnus[N]	†	3	†	12	†	1	†	2
			Betula[N]	†	3	†	14	†	(P)	†	5
			Carpinus[N]	†	1	†	14	†		†	1
			Corylus[N]	†	3	†	3			†	(P)
			Ostrya[N]	†	1	†	4	†		†	1
		Fagaceae[N]	Castanea[N]	†	1	†	4	†		†	2
			Castanopsis[E]	†		†	7	†	1		
			Cyclobalanopsis[E]	†		†	4				
			Fagus[N]	†	3	†	6	†		†	1
			Lithocarpus[E]	†		†	5	†	1		
			Quercus[N]	†	11	†	21	†	5	†	32
	Hamamelidales	Cercidiphyllaceae*[N]	Cercidiphyllum*[N]	†		†	1	†			
		Eupteleaceae[N]	Euptelea[N]	†			2				
		Hamamelidaceae[N]	Altingia[E]				1				
			Disanthus*[N]	†		†	1				
			Distylium[N]	†		†	1				
			Fortuneria*[N]	†		†	1				
			Hamamelis[N]	†		†	2			†	1
			Liquidambar[N]	†		†	2	†		†	1
			Loropetalum*[N]				1				
			Sinowilsonia*[N]				1			†	
		Platanaceae	Platanus[N]	†	(P)	†	(P)	†	1	†	1
	Juglandales	Juglandaceae[N]	Carya[N]	†		†	1	†		†	13
			Cyclocarya[N]	†		†	1				
			Engelhardtia[E]	†		†	(P)			†	
			Juglans	†	1	†	6	†	1	†	2
			Platycarya*[N]	†		†	1	†		†	
			Pterocarya[N]	†	1	†	6	†			
	Leitneriales	Leitneriaceae*[N]	Leitneria*[N]	†		†					1
	Myricales	Myricaceae	Myrica	†	(P)		1		1	†	1
	Trochodendrales	Tetracentraceae*[N]	Tetracentron*[N]	†(?)		†	1				
	Urticales	Moraceae[E]	Broussonetia	†		†	1				
			Cudrania[E]				1				
			Maclura*[N]								1
			Morus	†	(P)		7			†	1
		Ulmaceae	Aphananthe	†			1	†			
			Celtis[N]	†	3	†	8	†	(P)	†	4
			Hemiptelea*[N]	†			1				
			Planera*[N]			†				†	1
			Pteroceltis*[N]	†		†	1				
			Ulmus[N]	†	6	†	8	†		†	6
			Zelkova[N]	†	2	†	2	†		†(?)	
		Urticaceae[E]	Villebrunea[E]				1				

Class /subclass	Order	Family	Genus	Number of tree species			
				Northern, central, & eastern Europe	East-central Asia	Pacific slope of North America	Eastern North America
Magnoliopsida /Dilleniidae	Ebenales	Ebenaceae[E]	Diospyros[E]	†	† 3	†	1
		Sapotaceae[E]	Bumelia[E]			†(?)	3
		Styracaceae	Halesia[N]	†			3
			Pterostyrax[N]		2		
			Styrax[E]	† (P)	† 7	† (P)	1
		Symplocaceae[E]	Symplocos[E]	†	† 2	†	† 1
	Ericales	Clethraceae[E]	Clethra	†	† 1		† (P)
		Cyrillaceae[E]	Cliftonia[*N]				1
			Cyrilla[*N]	†			† 1
		Ericaceae	Arbutus	1		† 1	
			Elliottia[*N]				1
			Enkianthus[N]	†(?)	1		
			Kalmia[N]		†		1
			Lyonia	†	† (P)		† 1
			Oxydendrum[*N]				† 1
			Rhododendron[N]	† (P)	† 6	† 1	† 2
			Vaccinium[N]	(P)	(P)	(P)	† 1
	Malvales	Elaeocarpaceae[E]	Sloanea[E]		1		
		Sterculiaceae[E]	Firmiana[E]		† 1		
		Tiliaceae[E]	Tilia[N]	† 5	† 14	†	† 3
	Primulales	Myrsinaceae[E]	Ardisia[E]		1		
			Myrsine[E]		1		
	Salicales	Salicaceae[N]	Populus[N]	† 2	† 14	† 1	† 3
			Salix[N]	† 4	† 23	† 8	† 8
	Theales	Theaceae[E]	Camellia[E]	†	† 2		
			Franklinia[*N]				1
			Gordonia[E]	†	† (P)		† 1
			Stewartia[N]	†	† 4		1
			Ternstroemia[E]	†	† 1		
	Violales	Flacourtiaceae[E]	Idesia[*N]		† 1		
			Poliothyrsis[*N]	†	1		
			Xylosma[E]		† 1		
Magnoliopsida /Rosidae	Apiales	Araliaceae	Acanthopanax	†	2		
			Aralia	†	† 2		1
			Dendropanax[E]		2		†
			Evodiopanax[*N]		1		
			Kalopanax[*N]		† 1		
			Schefflera[E]	†	1		
	Celastrales	Aquifoliaceae	Ilex	† 1	† 14		† 5
		Celastraceae[E]	Euonymus	1	† 6		† 1
	Cornales	Alangiaceae[E]	Alangium[E]	†	† 2	†	†
		Cornaceae[N]	Aucuba[N]		1		
			Cornus[N]	† 1	† 7	† 1	† 3
			Macrocarpium[N]		2		
			Torricellia		1		
		Nyssaceae[N]	Davidia[*N]		1		
			Nyssa	†	† 1	†	† 3
	Euphorbiales	Buxaceae	Buxus	† 2	† (P)		
		Euphorbiaceae[E]	Mallotus[E]	†	† 3	†(?)	
			Sapium[E]	†	† 1		
	Fabales	Caesalpiniaceae[E]	Cercis[N]	1	† 3		1
			Gleditsia		† 5		† 2
			Glymnocladus[N]		† 1		1
		Fabaceae	Cladrastis[N]		† 5		1
			Dalbergia[E]		1		
			Erythrina[E]				1
			Laburnum[*N]	2			
			Maackia[N]		† 2		
			Ormosia[E]		1		
			Robinia	†	†		2
			Sophora		† 1		† (P)
		Mimosaceae[E]	Albizia[E]		† 3	†	
	Myrtales	Lythraceae[E]	Lagerstroemia[E]	†	2		
		Myrtaceae[E]	Szyzygium[E]		† 1		
	Rhamnales	Rhamnaceae	Hovenia[N]		† 2		
			Rhamnus[N]	(P)	2	† 2	† (P)
			Ziziphus[E]	1	† 1		
	Rosales	Hydrangeaceae[N]	Hydrangea	†	† 1		(P)

Class /subclass	Order	Family	Genus	Northern, central, & eastern Europe		East-central Asia		Pacific slope of North America		Eastern North America	
						Number of tree species					
		Rosaceae^N	Amelanchier^N		1		1		1		2
			Chaenomeles^N				1				
			Crataegus^N	†	2	†	2	†	1		18
			Eriobotrya^E			†	1				
			Malus^N		3	†	15		1		5
			Mespilus*^N		1						
			Photinia				3				
			Prunus^N	†	6	†	32	†	2	†	10
			Pyrus^N		4		10				
			Sorbus^N	†	8	†	15		1		2
	Santalales	Olacaceae^E	Schoepfia				1				
	Sapindales	Aceraceae^N	Acer^N	†	12	†	58	†	3	†	9
			Dipteronia*^N				1				
		Anacardiaceae^E	Choerospondias*^N				1				
			Cotinus^N								1
			Pistacia^E		1	†	1				
			Rhus	†	(P)	†	4	†(?)		†	3
			Toxicodendron^N				2			†	1
		Hippocastanaceae	Aesculus^N	†	1	†	3	†	1		4
		Meliaceae^E	Cedrela^E	†		†	1	†			
		Rutaceae^E	Evodia^E	†		†	5				
			Phellodendron	†		†	5				
			Ptelea						(P)	†	1
			Zanthoxylum^E	†		†	3				2
		Sapindaceae^E	Koelreuteria	†		†	2				
			Sapindus^E	†		†	1	†			2˙
		Simaroubaceae^E	Ailanthus^E	†		†	3	†			
			Picrasma^E				1				
		Staphylaceae	Staphylea^N	†			1				1
			Tapiscia*^N	†			1	†			
			Turpinia^E	†			1				
Magnoliopsida /Asteridae	Dipsacales	Caprifoliaceae^N	Sambucus	†	1		2		1		1
			Viburnum	†	(P)	†	2				4
	Lamiales	Boraginaceae	Ehretia^E			†	3				
		Verbenaceae^E	Clerodendrum^E	†(?)			1				
			Premna^E				1				
	Rubiales	Rubiaceae^E	Adina^E				1				
			Cephalanthus	†							1
			Emmenopterys*^N				1	†			
			Pinckneya*^N								1
			Randia^E				1				
	Scrophulariales	Bignoniaceae^E	Catalpa	†		†	3	†			2
			Paulownia	†			4	†			
		Oleaceae	Chionanthus^N	†		†	1				1
			Forestiera^E								1
			Fraxinus^N	†	6	†	14	†	1	†	7
			Ligustrum		(P)	†	1				
			Osmanthus^E		†	†	4				1
			Syringa^N				1				
Liliopsida /Arecidae	Arecales	Arecaceae^E	Sabal^E	†				†			1
			Serenoa*^N	†							1
			Trachycarpus^E				2				
Liliopsida /Commelinidae	Cyperales	Poaceae	Arundinaria				3				1
			Phyllostachys^N				12				
			Semiarundinaria				1				
Liliopsida /Liliidae	Liliales	Agavaceae	Yucca^E								1

REFERENCES

Adams, J. M. and F. I. Woodward. 1989. Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature* **339**: 699-701.

Bailey, L. H. and E. Z. Bailey. 1976. *Hortus Third.* Macmillan, New York.

Boufford, D. E. and S. A. Spongberg. 1983. Eastern Asian-eastern North American phytogeographical relationships — a history from the time of Linnaeus to the twentieth century. *Annals of the Missouri Botanical Garden* **70**: 423-439.

Braun, E. L. 1950. *Deciduous Forests of Eastern North America.* Hafner, New York.

Camus, A. 1936-1938. Les Chênes: *Monographie du Genre Quercus.* Paul Lechevalier, Paris.

Chi'ên H. 1921. *Chinese Economic Trees.* Commercial Press, Shanghai.

Collinson, M. E. and P. R. Crane. 1978. *Rhododendron* seeds from the Palaeocene of southern England. *Botanical Journal of the Linnean Society* **76**: 195-205.

Connell, J. H. and E. Orias. 1964. The ecological regulation of species diversity. *American Naturalist* **98**: 399-414.

Crane, P. R. and S. Lidgard. 1990. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* **246**: 675-678.

Crepet, W. L. 1984. Advanced (constant) insect pollination mechanisms: pattern of evolution and implications vis-à-vis angiosperm diversity. *Annals of the Missouri Botanical Garden* **71**: 607-630.

Crepet, W. L. and K. C. Nixon. 1989. Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications. *American Journal of Botany* **76**: 842-855.

Cronquist, A. 1981. *An Integrated System of Classification of Flowering Plants.* Columbia University Press, New York.

Currie, D. J. and V. Paquin. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* **329**: 326-327.

Elias, T. S. 1980. *The Complete Guide to North American Trees.* Van Nostrand Reinhold, New York.

Farrell, B. D., C. Mitter and D. J. Futuyma. 1992. Diversification at the insect-plant interface. *BioScience* **42**: 34-42.

Frederiksen, N. O. 1984a. Sporomorph correlation and paleoecology, Piney Point and Old Church Formations, Pamunkey River, Virginia. Pages 135-149 *in* L. W. Ward and K. Krafft (editors). Stratigraphy and paleontology of the outcropping Tertiary beds in the Pamunkey River region, central Virginia Coastal Plain — guidebook for Atlantic Coastal Plain Geological Association 1984 field trip. Atlantic Coastal Plain Geological Association.

Frederiksen, N. O. 1984b. Stratigraphic, paleoclimatic, and paleobiogeographic significance of Tertiary sporomorphs from Massachusetts. U.S. Geological Survey Professional Paper **1308**: 1-25.

Friis, E. M. 1979. The Damgaard flora: a new middle Miocene flora from Denmark. *Bulletin of the Geological Society of Denmark* **27**: 117-142.

Friis, E. M. 1985. Structure and function in late Cretaceous angiosperm flowers. *Biologiske Skrifter Danske Videnskabernes Selskab* **25**: 1-37.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* **75**: 1-34.

Graham, A. 1972. *Floristics and Paleofloristics of Asia and Eastern North America.* Elsevier Publishing Company, Amsterdam.

Gray, A. 1878. Forest geography and archaeology. *American Journal of Science* **16**: 85-94, 183-196.

Gregor, H. J. 1982. *Die Juntertiären Floren Süddeutschlands: Paläokarpologie, Phytostratigraphie, Paläoökologie, Paläoklimatologie.* Ferdinand Enke Verlag, Stuttgart.

Guo S. 1990. A brief review on megafloral successions and climatic changes of the Cretaceous and early Tertiary in China. Pages 23-38 *in*: E. Knobloch and Z. Kvaček (eds.), *Proceedings of the Symposium Paleofloristic and Paleoclimatic Changes in the Cretaceous and Tertiary, 1989,* Geological Survey Publisher, Prague.

Horrell, M. A. 1991. Phytogeography and paleoclimatic interpretation of the Maestrichtian. *Palaeogeography, Palaeoclimatology, Palaeoecology* **86**: 87-138.

Hu H. and R. W. Chaney. 1940. A Miocene flora from Shantung province, China. *Carnegie Institution of Washington Publications* **507**: 1-147.

Hubbell, S. P. and R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314-329 *in* J. Diamond and T. J. Case (editors). *Community Ecology.* Harper and Row, New York.

Humboldt, A. and A. Bonpland. 1807. *Essai sur la Géographie des Plantes Accompagné d'un Tableau Physique des Régions Équinoxiales.* Schoell, Paris (repr. 1977, Arno Press, New York).

Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**: 81-101.

Jahn, G. 1991. Temperate deciduous forests of Europe. Pages 377-502 *in* E. Röhrig and B. Ulrich (editors). *Ecosystems of the World 7: Temperate Deciduous Forests.* Elsevier, Amsterdam.

Kartesz, J. T. and R. Kartesz. 1980. *A Synonymized Checklist of the Vascular Flora of the United States, Canada and Greenland.* University of North Carolina Press, Chapel Hill. North Carolina.

Kilpper, K. 1969. *Verzeichnis der im Mittleren und Unteren Rheinland Gefundenen Grossreste von Tertiärpflanzen (von 1821-1968).* Ruhrland- und Heimatmuseum der Stadt

Essen, Essen.

Krüssman, G. 1979. *Die Baüme Europas.* Parey, Berlin.

Krüssman, G. 1984. *Manual of Cultivated Broad-leaved Trees and Shrubs*, 3 vols. Timber Press, Beaverton, Oregon.

Kvaček, Z. and H. Walther. 1987. Revision der mitteleuropäischen tertiären Fagaceen nach blattepidermalen Characteristiken. *Feddes Repertorium* **98**: 637-652.

Kvaček, Z., H. Walther and C. Bužek. 1989. Paleogene floras of W. Bohemia (C.S.S.R.) and the Wiesselster Basin (G.D.R.) and their correlation. *Casopis pro Mineralogii a Geologii* **34**: 385-402.

Łańcucka-Środoniowa, M. 1975. *Hydrangea* L. (Saxifragaceae) and *Schefflera* Forst. (Araliaceae) in the Tertiary of Poland. *Acta Palaeobotanica* **16**: 103-112.

Latham, R. E. and R. E. Ricklefs. 1993. Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos* **67**. In press.

Li S. 1935. *Forest Botany of China.* Commercial Press, Shanghai.

Li S. 1973. *Forest Botany of China Supplement.* Chinese Forestry Association, Taipei.

Li, H. L. 1952. Floristic relationships between eastern Asia and eastern North America. *Transactions of the American Philosophical Society* **42**: 371-429 (repr. 1971, Morris Arboretum, Philadelphia).

MacArthur, R. H. 1972. *Geographical Ecology.* Harper and Row, New York.

Mai, D. H. 1960. Über neue Früchte und Samen aus dem deutschen Tertiär. *Paläontologische Zeitschrift* **34**: 73-90.

Mai, D. H. 1971a. Über fossile Lauraceae und Theaceae in Mitteleuropa. *Feddes Repertorium* **82**: 313-341.

Mai, D. H. 1971b. Fossile Funde von *Manglietia* Blume (Magnoliaceae). *Feddes Repertorium* **82**: 441-448.

Mai, D. H. 1980. Zur Bedeutung von Relikten in der Florengeschichte. Pages 281-307 *in: 100 Jahre Arboretum (1879-1979)*, Berlin.

Mai, D. H. 1981. Entwicklung und klimatische Differenzierung der Laubwaldflora Mitteleuropas im Tertiär. *Flora* **171**: 525-582.

Mai, D. H. 1987a. Neue Arten nach Früchten und Samen aus dem Tertiär von Nordwestsachsen und der Lausitz. *Feddes Repertorium* **98**: 105-126.

Mai, D. H. 1987b. Neue Früchte und Samen aus paläozänen Ablagerungen Mitteleuropas. *Feddes Repertorium* **98**: 197-229.

Mai, D. H. and H. Walther. 1978. Die Floren der Haselbacher-Serien im Weißelster-Becken (Bezirk Leizig, D.D.R.). *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* **28**: 1-101.

Mai, D. H. and H. Walther. 1988. Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. *Quartärpaläontologie Berlin* **7**: 55-297.

Manchester, S. R. 1987. The fossil history of the Juglandaceae. *Annals of the Missouri Botanical Garden Monographs* **21**: 1-137.

Manchester, S. R. 1989. Early history of the Juglandaceae. *Plant Systematics and Evolution* **162**: 231-250.

Manchester, S. R. Unpublished manuscript. Fruits and seeds of the middle Eocene nut beds flora, Clarno formation, north-central Oregon. Florida Museum of Natural History, Gainesville.

Mayer, H. 1984. *Wälder Europas.* Gustav Fisher Verlag, Stuttgart.

McCartan, L., B. H. Tiffney, J. A. Wolfe, T. A. Ager, S. L Wing, L. A. Sirkin, L. W. Ward and J. Brooks. 1990. Late Tertiary floral assemblage from upland gravel deposits of the southern Maryland Coastal Plain. *Geology* **18**: 311-314.

Meyen, S. V. 1987. *Fundamentals of Paleobotany.* Chapman and Hall, London.

Mirov, N. T. 1967. *The Genus Pinus.* Ronald Press, New York.

Mitchell, A. 1974. *Trees of Britain and Northern Europe.* Houghton-Mifflin, Boston.

Muller, J. 1981. Fossil pollen record of extant angiosperms. *Botanical Review* **47**: 1-142.

Niklas, K. J., B. H. Tiffney and A. H. Knoll. 1985. Patterns in vascular land plant diversification: an analysis at the species level. Pages 97-128 *in* J. W. Valentine (editor). *Phanerozoic Diversity Patterns.* Princeton University Press, Princeton, New Jersey.

Nilsson, T. 1983. *The Pleistocene.* D. Reidel Publishing Company, Dordrecht, Holland.

Ohwi, J. 1965. *Flora of Japan* (in English). Smithsonian Institution, Washington, D.C.

Petraitis, P. S., R. E. Latham and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* **64**: 393-418.

Petrides, G. A. 1972. *A Field Guide to Trees and Shrubs.* Houghton-Mifflin, Boston.

Phipps, J. B, K. R. Robertson, P. G. Smith and J. R. Rohrer. 1990. A checklist of the subfamily Maloideae (Rosaceae). *Canadian Journal of Botany* **68**: 2209-2269.

Phipps, J. B. 1983. Biogeographic, taxonomic, and cladistic relationships between east Asiatic and North American *Crataegus. Annals of the Missouri Botanical Garden* **70**: 667-700.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* **100**: 33-46.

Pianka, E. R. 1989. Latitudinal gradients in species diversity. *Trends in Ecology and Evolution* **4**: 223.

Potter, F. W. and D. L. Dilcher. 1980 Biostratigraphic analysis of Eocene clay deposits in Henry County, Tennessee. Pages 211-225 *in* D. L. Dilcher and T. N. Taylor (editors). *Biostratigraphy of Fossil Plants: Successional and Paleoecological Analyses.* Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

Rachele, L. D. 1976. Palynology of the Lagler lignite: a deposit in the Tertiary Cohansey Formation of New Jersey, USA. *Review of Palaeobotany and Palynology* **22**: 225-252.

Rand McNally. 1969. *International Atlas.* Rand McNally and Company, Chicago.

Rehder, A. 1940. *Manual of Cultivated Trees and Shrubs.* 2nd ed. Macmillan, New York (repr. 1986, Dioscorides Press, Portland, Oregon).

Reid, E. M. and M. E. J. Chandler. 1933. *The London Clay Flora.* British Museum, London.

Richerson, P. J. and K. Lum. 1980. Patterns of plant

species diversity in California: relation to weather and topography. *American Naturalist* **116**: 504-536.

Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: an hypothesis. *American Naturalist* **111**: 376-381.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**: 167-171.

Ricklefs, R. E. 1989. Speciation and diversity: integration of local and regional processes. Pp. 599-622 *in* D. Otte and J. Endler (editors). *Speciation and Its Consequences.* Sinauer Associates, Sunderland, Massachusetts.

Rubner, K. and F. Reinhold. 1953. *Das Natürliche Waldbild Europas.* Verlag Paul Parey, Hamburg.

Sakai, A. and W. Larcher. 1987. *Frost Survival of Plants.* Springer-Verlag, Berlin.

Sauer, J. D. 1988. *Plant Migration: the Dynamics of Geographic Patterning in Seed Plant Species.* University of California Press, Berkeley.

Schwarzwalder, R. N. 1986. Systematics and early evolution of the Platanaceae. PhD thesis. Indiana University, Bloomington, Indiana.

Sharp, A. J. 1951. The relation of the Eocene Wilcox flora to some modern floras. *Evolution* **5**: 1-5.

Simberloff, D. S. 1979. Rarefaction as a distribution-free method of expressing and estimating diversity. Pages 159-176 *in* J. F. Grassle, G. P. Patil, W. K. Smith and C. Taillie (editors). *Ecological Diversity in Theory and Practice.* International Cooperative Publishing House, Fairland, Maryland.

Sokal, R. R. and F. J. Rohlf. 1981. *Biometry.* Freeman, San Francisco.

Song Z., Li H., Zheng Y. and Liu G. 1981. Miocene floristic regions of China. *Geological Society of America Special Paper* **187**: 249-254.

Song Z., Li W. and He C. 1983. Cretaceous and Palaeogene palynofloras and distribution of organic rocks in China. *Scientia Sinica* **26**: 538-549.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* **133**: 240-256.

Takhtajan, A. (ed.). 1974. *Magnoliophyta Fossilia U.S.S.R. Vol. 1. Magnoliaceae-Eucommicaeae.* Nauka, Leningrad.

Tanai, T. 1972. Tertiary history of vegetation in Japan.

Pages 235-255 *in* A. Graham (editor). *Floristics and Paleofloristics of Asia and Eastern North America.* Elsevier Publishing Company, Amsterdam.

Tiffney, B. H. 1985. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the northern hemisphere. *Journal of the Arnold Arboretum* **66**: 243-273.

Tomlinson, P. B. 1986. *The Botany of Mangroves.* Cambridge University Press, Cambridge.

Traverse, A. 1955. Pollen analysis of the Brandon lignite of Vermont. *U.S. Bureau of Mines Report of Investigations* **5151**: 1-107.

Turner, J. R. G., J. J. Lennon and J. A. Lawrenson. 1988. British bird species distributions and the energy theory. *Nature* **335**: 539-541.

Uphof, J. C. T. 1968. *Dictionary of Economic Plants.* Verlag von Cramer, Lehre, Germany.

van der Hammen, T., T. A. Wijmstra and W. H. Zagwijn. 1971. The floral record of the late Cenozoic of Europe. Pages 391-424 *in* K. K. Turekian, editor. *The Late Cenozoic Glacial Ages.* Yale University Press, New Haven, Connecticut.

Walter, H. 1979. *Vegetation of the Earth.* Springer-Verlag, New York.

Wang, C. 1961. *The Forests of China* (Maria Moors Cabot Foundation Publication No. 5) Harvard University, Cambridge, Massachusetts.

Wing, S. L. and L. J. Hickey. 1984. The *Platycarya* perplex and the evolution of the Juglandaceae. *American Journal of Botany* **71**: 388-411.

Wolfe, J. A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the northern hemisphere and Australasia. *Geological Survey Professional Paper* **1106**.

Wolfe, J. A. 1981. Vicariance biogeography of angiosperms in relation to paleobotanical data. Pages 413-427 *in* G. Nelson and D. E. Rosen (editors). *Vicariance Biogeography: A Critique.* Columbia University Press, New York.

Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. *Oikos* **41**: 496-506.

Zheng W. (chief editor). 1983, 1985. *Zhongguo Shu Mu Zhi* [*Woody Plants of China*]. Chu Ban She, Beijing.