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Spatial Pattern of Vascular Plant Diversity in North America North of Mexico and its Floristic Relationship with Eurasia

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This paper reports: (1) patterns of taxonomic richness of vascular plants in North America (north of Mexico), an area accounting for 16·6% of the total world land, in relation to latitudinal and longitudinal gradients; (2) floristic relationships between different latitudinal zones, longitudinal zones, and geographic regions of North America; and (3) floristic relationships between North America and Eurasia at various geographic scales. North America was geographically divided into twelve regions, which were latitudinally grouped into four zones, each with three regions, and longitudinally grouped into three zones, each with four regions. The native vascular flora of North America consists of 162 orders, 280 families, 1904 genera and 15352 species. Along the latitudinal gradient, species richness shows a striking increase with decreasing latitude (e.g. the northernmost latitudinal zone has only 11·7% of the number of species in the southernmost latitudinal zone). However, about 63% of the species of the northernmost latitudinal zone are also present in the southernmost latitudinal zone of North America. Among the three longitudinal zones, the zone on the Pacific coast has 1·48 and 1·64-times as many species as the zones in the interior and on the Atlantic coast, respectively. About 36% of the species in the zone of the Atlantic coast also occur in the Pacific coast zone. However, each of over 40% of the species in North America occupies less than 10% of the total land area of North America. Some 48% of the genera and 6·5% of the species of North America are also native to Eurasia. In general, the number of genera common to North America and Eurasia increased from the north to the south and from the west to the east of North America, whereas the number of species common to the two continents decreased along the same two geographic gradients.

Key words: Asia, biodiversity, Europe, floristic similarity, latitudinal and longitudinal gradients, North America, taxonomic richness.

INTRODUCTION

It is well known that taxonomic richness (e.g. number of species) for an area of given size generally varies from one geographic region to another. No single species is ubiquitous on earth, nor are species found in all possible areas where they could survive (Morse *et al*., 1993). The distribution range of a species is determined by many factors and processes such as continental movements (plate tectonics), geographic configuration, environmental variables (e.g. geology, topography, climate and soil), and evolution of species (e.g. speciation and extinction). These factors and processes themselves change both temporally and spatially and some clearly exhibit their pattern on a large geographic scale. For example, mean annual temperature generally increases with decreasing latitude from the poles to the equator. As a result, patterns of species richness coincident with some patterns of environmental factors have come into existence. For instance, species richness in an area of given size also generally increases with decreasing latitude for most groups of terrestrial organisms. This is one of the most well known spatial patterns of biodiversity (Huston, 1994; Rosenzweig, 1995). Furthermore, all the factors which influence species richness of an area may eventually influence the floristic relationship between that area and the other areas under comparison.

North America north of Mexico (hereafter referred to as North America) is a vast geographic expanse—ranging from 26° to 85° N latitude and from 15° W to 173° E longitude—accounting for 16·6% of the total world land. This area stretches from the cold Arctic in the north to the warm subtropics in the south, and from the moist Atlantic coast in the east through the dry interior to the moist Pacific coast in the west. Most of the world's major vegetation formations, including tundra, boreal forest, temperate deciduous forest, tropical hardwood hammocks, semiarid desert and Mediterranean scrub can be found in North America (Barbour and Christensen, 1993). Being such a vast area with a great diversity of climates, landforms and soils, and with its long geological history, North America exhibits striking latitudinal and longitudinal patterns in climate (Brouillet and Whetstone, 1993), soil (Steila, 1993), and vegetation (Barbour and Christensen, 1993). Presumably, all these spatial patterns determine the geographic patterns of plant diversity across the continent, and hence influence floristic relationships between different geographic regions over the continent.

North America is presently separated from Europe and Asia by the Atlantic and Pacific Oceans, but geographic and fossil evidence has shown that the continent was geographically connected to Europe and Asia by two land bridges during the late Cretaceous and the Tertiary

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(McKenna, 1983*a*, *b*; Tiffney, 1985*a*, *b*; Hallam, 1994): the North Atlantic land bridges linked the northeast of North America with Europe, and the Bering land bridge linked the northwest of North America with East Asia. These overland connections played a crucial role in plant migration between North America and Eurasia in the past, particularly during the Tertiary (McKenna, 1983*a*, *b*; Tiffney, 1985*a*, *b*). Plant migration via these land bridges not only affected modern plant diversity at both the regional and the continental levels, but also influenced the similarity of both past and present floras in North America and Eurasia (see Boufford and Spongberg, 1983; Tiffney, 1985*a*, *b*). However, the roles played by the two land bridges in establishing the floristic relationships between North America and Eurasia were not equal. A number of paleontological and biogeographical studies suggest that the Bering land bridge primarily supported the migration of temperate taxa, while the North Atlantic land bridges facilitated the migration of both temperate and tropical taxa (McKenna, 1983*b*; Tiffney, 1985*a*, *b*; Taylor, 1990; Graham, 1993).

The diversity of North American vascular plants has attracted the attention of naturalists and botanists for several centuries. Several earlier studies addressed patterns of plant diversity in North America. However, they were either restricted to a relatively small group of plants or only dealt with taxa higher than the species level. For instance, Currie and Paquin (1987) used the distributions of 620 indigenous tree species to characterize the spatial pattern of tree species richness in North America. Thorne (1993) provided a map showing the familial richness of flowering plants in North America. Qian (1998) described the taxonomic richness patterns of vascular plants in North America at the levels of order, family and genus according to major plant groups (i.e. pteridophytes, gymnosperms, dicots and monocots). No attempt has been made to analyse the spatial pattern of species richness across North America and floristic relationships between different geographic regions of the continent using all the indigenous vascular plants of North America. Furthermore, because no comparison has been made between the entire floras of North America and Eurasia, the real floristic relationships between North America and Asia and between North America and Europe have not been quantified.

This study attempts (1) to determine species richness of vascular plants at various geographic scales ranging from all North America to smaller regions including only a couple of states or provinces, and the relationship between species richness and genus richness at various geographic scales; (2) to detect trends and rates of change in species and genus richness along latitudinal and longitudinal gradients across North America; (3) to examine the floristic relationship among different geographic zones or regions in North America; and (4) to quantify the floristic relationships (at both genus and species levels) between North America and Europe and between North America and Asia geographically from the regional to the continental level.

MATERIALS AND METHODS

The study area included all North America north of Mexico, an area of 21·5 million km^2. The area was geographically divided into twelve regions arrayed in a grid with three divisions east-to-west and four divisions north-to-south (Fig. 1). The demarcation lines between the regions were based on political boundaries, as the plant diversity data recorded for natural floristic regions are not available. The twelve regions were in turn latitudinally grouped into four zones (from north to south): northern (LATN, including WN, CN and EN), north-middle (LATMN, including WMN, CMN and EMN), south-middle (LATMS, including WMS, CMS and EMS), and southern (LATS, including WS, CS and ES); and longitudinally grouped into three zones (from west to east): western (LONGW, including WN, WMN, WMS and WS), central (LONGC, including CN, CMN, CMS and CS), and eastern (LONGE, including EN, EMN, EMS and ES).

Kartesz's (1994) checklist was used to document geographic distribution data for each species native to North America by region. A species is defined as native to North America if there is no evidence indicating that it was introduced to the continent. To record geographic distribution (presence/absence) information and determine the native/exotic status for each species in each of the twelve regions utilized in this study, over 200 reference books (including continental, regional, state/provincial, and local floras, checklists, atlases, monographs, and theses) and more than 1000 journal papers published up to 1997 were consulted. Taxonomic scopes of species in general followed Kartesz's (1994) checklist, except for those species which were not included in his checklist (e.g. *Hasteola robertiorum* L. C. Anderson) or those species which he treated differently from the majority of other authors, in which case the majority authors' treatment was followed unless Kartesz's treatment was more compelling. Only the species native to North America (north of Mexico) were tallied. The distribution of native North American species in Eurasia was also documented, based on literature (e.g. Tutin *et al.*, 1964–1980; Czerepanov, 1995). Eurasia in this study was defined as the area including Europe, Asia and Mediterranean Africa (north of about 15° N latitude).

Taxonomic scope for each genus followed the *Phytogeographic checklist of vascular plant genera of the Northern Hemisphere* data base (VPGNH version 98; Qian, unpubl. res.). In the data base, a generic name was usually treated as an accepted name if Mabberley (1997), Brummitt (1992), Greuter *et al.* (1993) and Wielgorskaya (1995) all treated it as an accepted name for seed plants, or the first three treated it as an accepted name for pteridophytes (pteridophytes were not included in Wielgorskaya, 1995). Individual judgments were made for those genera which lacked a coincident treatment in the above four publications, in which case, continental, national and regional floras or checklists [such as Kartesz (1994) and Flora of North America Editorial Committee (1993) for North America, Tutin *et al.* (1964–80) for Europe, Czerepanov (1995) for the former USSR, and Wu (1991) for China] were consulted. The geographic distribution of each genus within North America was summarized from the species geographic distribution data base for each region. Global distribution of each native North America genus was documented from a large body of literature.

FIG. 1. The twelve regions utilized in this study.

Genera were grouped into families according to Takhtajan (1997) for angiosperms, Wielgorskaya (1995) for gymnosperms, and Brummitt (1992) for pteridophytes. Families were in turn grouped into orders according to Takhtajan (1997) for angiosperms, Wielgorskaya (1995) for gymnosperms, and Takhtajan (1986) for pteridophytes. Orders were further grouped into classes and divisions according to Takhtajan (1986).

Genus and species diversities were measured as the number of genera and species, respectively, in a region or a zone. Floristic relationships between zones or between regions in North America were assessed by two similarity coefficients, the Sørenson index (Sørenson, 1948),

$$I_{\text{Sør}} = \frac{2a}{2a+b+c} \quad (1)$$

and the Simpson index (Simpson, 1960),

$$I_{\text{Sim}} = \frac{a}{a+b} \quad (2)$$

where a is the number of taxa common to both areas, b is the number of taxa restricted to one area, and c is the number of taxa restricted to the other area ($b \leqslant c$). $I_{\text{Sør}}$ and I_{Sim} are both scaled from 0 to 1 but I_{Sim} tends to be larger than $I_{\text{Sør}}$ except when $I_{\text{Sør}}$ is 1 or 0. When I_{Sim} is multiplied by 100, the resulting value represents the percent of taxa in the area with the lower number of taxa that are shared with the area with the higher number of taxa.

The rarity and provinciality of a taxon in North America was determined as the number of zones or regions (depending on the focal spatial level) to which the taxon was restricted.

SYSTAT (Wilkinson *et al.*, 1992) was used for statistical tests where appropriate.

RESULTS

Taxonomic richness of North American vascular plants

The vascular flora of North America consists of 162 orders, 280 families, 1904 genera and 15 352 species of native plants (Table 1), which make up 61·1 % of orders, 42·9 % of families, 12·9 % of genera and 5·6 % of species of the world's vascular plants. *Aphragmus* Andrz. ex DC. was not included in this study because it was only recorded in Unalaska

TABLE 1. *Number of orders, families, genera and species of vascular plants native to North America north of Mexico according to division and class*

Division	Class	Number of taxa			
		Order	Family	Genus	Species
Lycopodiophyta	Lycopodiopsida	1	1	4	28
	Isoëtopsida	2	2	2	61
Psilotophyta	Psilotopsida	1	1	1	1
Equisetophyta	Equisetopsida	1	1	1	11
Polypodiophyta	Ophioglossopsida	1	1	2	38
	Polypodiopsida	10	21	62	296
Pinophyta	Pinopsida	3	4	16	105
Cycadophyta	Cycadopsida	1	1	1	1
Gnetophyta	Ephedropsida	1	1	1	9
Magnoliophyta	Magnoliopsida	105	186	1467	11932
	Liliopsida	36	61	347	2870
Total		162	280	1904	15352

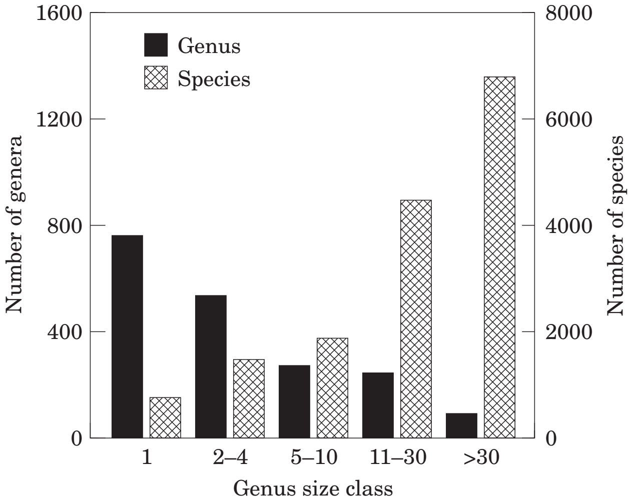

FIG. 2. The number of vascular plant genera and species in each of five genus size classes, defined according to the number of species in a genus in North America north of Mexico.

Island of Aleutian Island, for North America (Wielorskaya, 1995). Of the entire North American vascular flora, pteridophytes, gymnosperms, dicots and monocots make up 3·8, 1, 77 and 18·2 % at the genus level, and 2·8, 0·8, 77·7 and 18·7 % at the species level, respectively.

The sizes of genera were very strongly skewed towards small numbers of species per genus; 40 % of North American genera have only one native species in the study area, whereas only 5 % of genera have more than 30 species in the study area (Fig. 2). The pattern was reversed when examined from the perspective of species; only 5 % of North American species belonged to genera with only one species in the study area, while 44 % of the species belonged to genera having over 30 species in North America (Fig. 2).

The number of species in a genus in North America bore no particular relationship to the size of the genus worldwide when viewed from the perspectives of either the genus (Fig. 3A) or the species (Fig. 3B). At the genus level, the 1904 North American genera were more or less evenly distributed in each of the size classes of the world flora (Fig. 3A). About 39 % of the genera with a single species in North America were also monotypic worldwide. The rest of the genera that were monotypic in North America were more or less evenly distributed in the other four genus size classes on a worldwide basis (Fig. 3A): 31·4 % have two–four species, 23 % have five–ten species, 26·2 % have 11–30 species and 19·4 % have more than 30 species. Among all North American genera, about 30 % had more than 30 species worldwide, and another 20 % had 11–30 species worldwide. Among all North American species, 71 % belonged to genera with over 30 species in the world, and another 16 % to genera with 11–30 species in the world. However, only 2 % belonged to genera that were monotypic worldwide.

Geographic variation of taxonomic richness

Taxonomic richness in a zone increased with decreasing latitude at all taxonomic levels from order to species (Table 2), despite the fact that the land area of a zone decreased with decreasing latitude (from 75×10^5 km^2 in LATN to 38×10^5 km^2 in LATS). The same trend of increased taxonomic richness at lower latitude also appeared at the regional level in all three longitudinal zones (Table 3; data on order and family levels not listed). Across the longitudinal

TABLE 2. *Number of orders, families, genera and species of native vascular plants in each of the latitudinal and longitudinal zones of North America north of Mexico*

Zone	Number of taxa			
	Order	Family	Genus	Species
Latitudinal zones				
LATN	73	106	420	1609
LATMN	109	179	842	4064
LATMS	119	215	1234	7601
LATS	130	265	1856	13710
Longitudinal zones				
LONGW	116	203	1352	10287
LONGC	124	239	1357	6930
LONGE	123	245	1296	6257

See text for codes of zones.

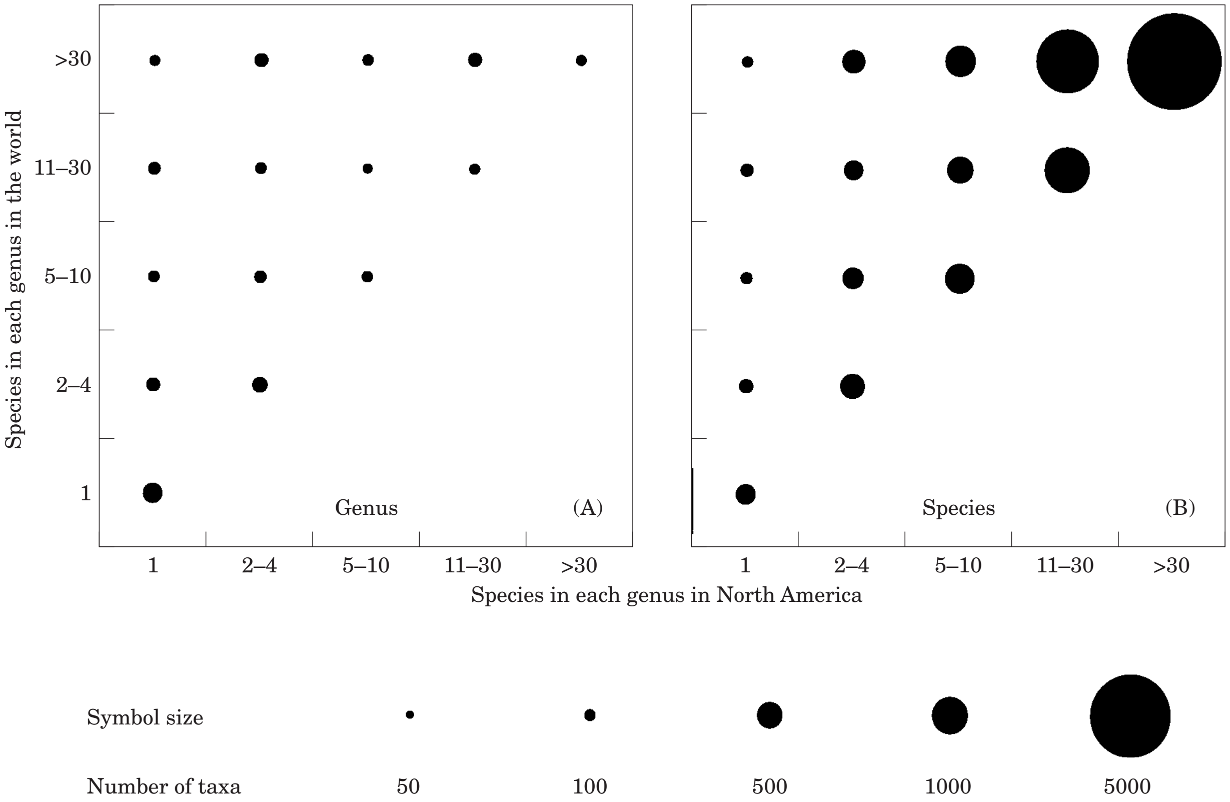

FIG. 3. Number of vascular plant genera (A) and species (B) (represented by symbol size) in each possible combination of five classes of genus size in the flora of North America north of Mexico and five classes of genus size in the flora of the world.

gradient (breadth) of North America, there was no consistent trend in the change of taxonomic richness for different taxonomic levels (Tables 2 and 3). For example, the number of families increased along the longitudinal gradient from LONGW to LONGE whereas the number of species decreased along the same longitudinal gradient, although the land area increased from 67×10^5 km^2 (in LONGW) to 76×10^5 km^2 (in LONGE). LONGW had 39 % more species than LONGE although the land area of the former was only 88 % that of the latter.

The species : genus (S : G) ratio for the flora of the whole of North America was about eight. The S : G ratio decreased from the continental level to regional level by an average of 3·8 (s.d. = 1·1, $n = 12$). A high correlation was found between S : G ratio and species richness (Pearson's correlation coefficient $r = 0{\cdot}95$, $n = 20$). At the zonal level, S : G ratio increased from the north (3·8 for LATN) to the south (7·4 for LATS) and from the east (4·8 for LONGE) to the west (7·6 for LONGW) of North America. At the regional level, S : G ratio ranged from 2·8 (in region EN) to 7 (in region WS).

Rarity and provinciality of species

The proportion of species restricted to only one of the three regions of a latitudinal zone increased from the north to the south of North America, whereas the proportion of species which occurred in all three regions of a latitudinal zone decreased strikingly along the same gradient (Fig. 4). In LATN, 19 % of its species were restricted to only one of its three regions while 60 % of its species occurred in all of its three regions. In contrast, 60 % of the total species in LATS were restricted to only one of its three regions, while only 13 % of species were present in all three regions (Fig. 4). A similar trend was found in each of the three longitudinal zones: more species were restricted to a single region than were spread across all four regions (Fig. 4). However, the

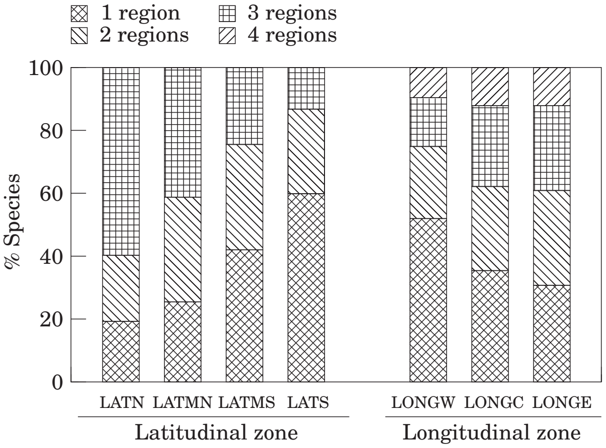

FIG. 4. Frequency (%) distribution of the vascular plant species in each zone in terms of the number of regions of a zone in which a species is present. Codes for zones are given in the text.

TABLE 3. *Matrix presenting number of taxa (values in bold on the diagonal), Sørensen indices (lower-left), and Simpson indices (upper-right) for pair-wise comparisons of the twelve regions at the genus (G) and species (S) levels*

Region	Taxonomic level	WN	CN	EN	WMN	CMN	EMN	WMS	CMS	EMS	WS	CS	ES
WN	G	**389**	0·91	0·97	0·97	0·81	0·86	0·95	0·83	0·86	0·92	0·63	0·69
	S	**1412**	0·84	0·85	0·84	0·54	0·59	0·71	0·44	0·44	0·61	0·15	0·18
CN	G	0·85	**337**	0·99	0·96	0·90	0·93	0·93	0·87	0·90	0·91	0·66	0·70
	S	0·74	**1102**	0·90	0·85	0·71	0·76	0·70	0·55	0·55	0·61	0·18	0·24
EN	G	0·56	0·63	**157**	0·96	0·91	0·99	0·94	0·83	0·92	0·92	0·62	0·71
	S	0·41	0·52	**442**	0·79	0·71	0·92	0·62	0·45	0·56	0·56	0·12	0·21
WMN	G	0·74	0·67	0·38	**632**	0·89	0·75	0·96	0·81	0·80	0·95	0·67	0·66
	S	0·60	0·52	0·24	**2530**	0·78	0·47	0·87	0·49	0·44	0·76	0·24	0·22
CMN	G	0·70	0·72	0·43	0·80	**511**	0·91	0·91	0·95	0·94	0·91	0·78	0·78
	S	0·50	0·57	0·31	0·61	**1630**	0·81	0·76	0·83	0·73	0·70	0·43	0·43
EMN	G	0·63	0·61	0·37	0·72	0·78	**683**	0·75	0·93	0·97	0·81	0·81	0·85
	S	0·41	0·44	0·26	0·46	0·61	**2686**	0·45	0·73	0·86	0·44	0·50	0·60
WMS	G	0·61	0·54	0·30	0·83	0·70	0·68	**826**	0·72	0·69	0·96	0·64	0·58
	S	0·34	0·28	0·11	0·63	0·40	0·34	**4487**	0·45	0·31	0·82	0·22	0·16
CMS	G	0·50	0·48	0·25	0·67	0·69	0·80	0·69	**891**	0·90	0·81	0·86	0·82
	S	0·26	0·27	0·10	0·42	0·53	0·65	0·39	**3402**	0·79	0·53	0·69	0·63
EMS	G	0·50	0·47	0·26	0·64	0·66	0·81	0·65	0·87	**948**	0·73	0·82	0·86
	S	0·23	0·23	0·11	0·33	0·42	0·68	0·30	0·72	**4101**	0·36	0·60	0·72
WS	G	0·42	0·38	0·20	0·62	0·51	0·56	0·75	0·66	0·62	**1293**	0·71	0·57
	S	0·16	0·13	0·05	0·33	0·21	0·20	0·54	0·29	0·23	**8994**	0·44	0·22
CS	G	0·31	0·29	0·15	0·46	0·47	0·59	0·52	0·74	0·73	0·68	**1186**	0·76
	S	0·06	0·06	0·02	0·16	0·20	0·34	0·20	0·54	0·53	0·33	**5318**	0·60
ES	G	0·35	0·32	0·17	0·47	0·48	0·63	0·49	0·72	0·78	0·53	0·74	**1144**
	S	0·09	0·09	0·04	0·16	0·22	0·44	0·16	0·53	0·67	0·15	0·56	**4705**

Codes for regions are given in the text. Regional division of North America is shown in Fig. 1.

ratio of the numbers of species restricted to only one region compared to the number of species spanning all four regions in a longitudinal zone decreased from 5·5 in LONGW to only 2·5 in LONGE. That is, latitudinal distributions were greater in eastern than in western North America.

At the regional level, over 40 % of North American species were restricted to only one of the twelve regions and no species occurred in all twelve regions (Fig. 5). Less than 30 % of the species in North America occurred in more than three of the twelve regions. In general, the frequency distribution of species with respect to number of geographic regions exhibited a reverse J-shape, i.e. the number of species which were present in a given number of regions decreased as the number of regions increased (Fig. 5).

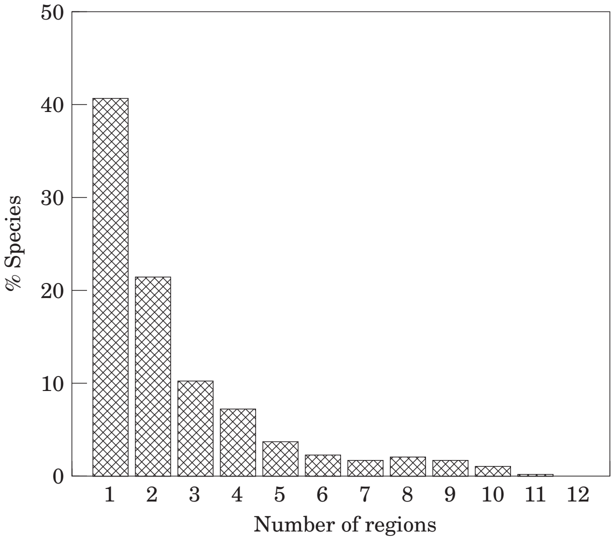

FIG. 5. Frequency (%) distribution of the vascular plant species in North America north of Mexico in terms of the number of regions of North America in which a species is present.

Floristic relationships among zones or regions in North America

Among all possible pair-wise comparisons of the four latitudinal zones of North America, the highest $I_{\text{Sør}}$ was found between LATMN and LATMS (0·8 at the genus level, 0·64 at the species level), and the lowest $I_{\text{Sør}}$ was found between LATN and LATS (0·34 at the genus level, 0·13 at the species level) (Fig. 6A). I_{Sim} had much higher values but narrower ranges than $I_{\text{Sør}}$ (Fig. 6A). I_{Sim} ranged from 0·93 to 0·99 at the genus level and from 0·63 to 0·92 at the species level (Fig. 6A). These values indicate that no less than 93 % of genera or 63 % of species in the zone which has the smaller number of taxa also occurred in the zone which has the greater number of taxa in any pair of latitudinal zones. Although LATN was separated from LATS by two latitudinal zones and their climatic conditions differed greatly, about 93 % of genera and 63 % of species in LATN were shared with LATS.

In pair-wise comparisons between longitudinal zones, the highest $I_{\text{Sør}}$ and the highest I_{Sim} were both found when comparing LONGE and LONGC, while the lowest $I_{\text{Sør}}$ and the lowest I_{Sim} were both found in the pair LONGW and

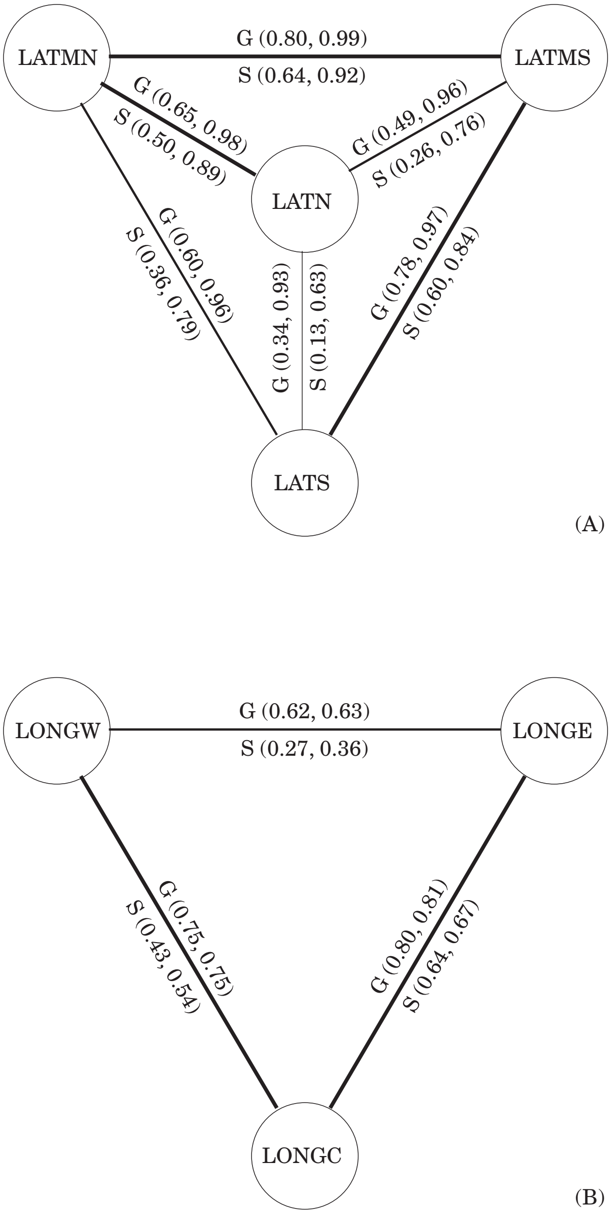

FIG. 6. Sørenson index ($I_{\mathrm{Sør}}$, the first value in parentheses) and Simpson index (I_{Sim}, the second value in parentheses) between each pair of the latitudinal zones (A) or between each pair of the longitudinal zones (B) in North America at the genus (G) and species (S) levels. Thick lines link two zones connected geographically to each other; medium lines link two zones separated geographically by one zone; and thin lines link two zones separated geographically by two zones. Codes for zones are given in the text.

LONGE (Fig. 6B). The biggest difference in $I_{\mathrm{Sør}}$ was 0·18 at the genus level and 0·37 at the species level, and the biggest difference in I_{Sim} was 0·18 at the genus level and 0·31 at the species level. LONGE shared 63 % of its genera and 36 % of its species with LONGW.

Compared with latitudinal zones, longitudinal zones had narrower ranges of $I_{\mathrm{Sør}}$ and I_{Sim} at both genus and species levels (Fig. 6). In addition, the difference between $I_{\mathrm{Sør}}$ and I_{Sim} in a comparison of any two longitudinal zones was very much reduced at both genus and species levels. For example, the biggest difference between $I_{\mathrm{Sør}}$ and I_{Sim} was 0·01 at the genus level and 0·11 at the species level. The reduction in the difference between $I_{\mathrm{Sør}}$ and I_{Sim} from latitudinal to longitudinal zones was largely due to the reduction in the difference of the size of the two floras under comparison.

The similarity indices of pair-wise comparisons between regions ranged from 0·15 to 0·87 for $I_{\mathrm{Sør}}$ and from 0·57 to 0·99 for I_{Sim} at the genus level, and ranged from 0·02 to 0·74 for $I_{\mathrm{Sør}}$ and from 0·12 to 0·9 for I_{Sim} at the species level (Table 3). Along a geographic gradient from the north to the south of North America, I_{Sim} between a Pacific region and an Atlantic region in the same latitudinal zone decreased. The sequences of I_{Sim} between Pacific and Atlantic regions from the north to the south (i.e. WN *vs.* EN, WMN *vs.* EMN, WMS *vs.* EMS and WS *vs.* ES) were 0·97, 0·75, 0·69 and 0·57 at the genus level, and 0·85, 0·47, 0·31 and 0·22 at the species level. $I_{\mathrm{Sør}}$ showed the same trend as I_{Sim} along the same north-south gradient except for that in the LATN zone due to the dramatic difference in flora size between WN and EN regions (389 *vs.* 157 at the genus level and 1412 *vs.* 442 at the species level) (Table 3). I_{Sim} between a region of LATN zone and a region of LATS zone in the same longitudinal zone was the lowest in LONGC among the three longitudinal zones (Table 3). The percentage of genera and species in a region of LATN which were also present in a region of LATS in the same longitudinal zone was 92 and 61 % for LONGW, 66 and 18 % for LONGC, and 71 and 21 % for LONGE at the genus level and the species level, respectively.

Floristic relationships between North America and Eurasia

Relationships at the genus level. A total of 908 (or 48 %) of the native North American genera are also native to Eurasia. Among these genera, 75·3 % were present in both eastern and western Eurasia (hereafter referred to as NA-EUAS), 18·3 % only in eastern Eurasia (NA-AS), and 6·4 % only in western Eurasia (NA-EU). The number of genera shared between North America and Eurasia increased along both the latitudinal gradient from the north to the south and the longitudinal gradient from the west to the east of North America for all three categories (i.e. NA-EUAS, NA-AS and NA-EU) (Fig. 7A and B). For example, the number increased from 361 in LATN to 876 in LATS (Fig. 7A), and from 670 in LONGW to 813 in LONGE (Fig. 7B). When the percentages of genera shared between North America and Eurasia were compared, an opposite trend was found along the same latitudinal gradient; however, the trend along the same longitudinal gradient did not change. For example, the percentage of genera shared between North America and Eurasia decreased from 86 % in LATN to 47 % in LATS, while it increased from 50 % in LONGW to 63 % in LONGE.

At the regional level, trends in the number of genera shared by North America and Eurasia along latitudinal and longitudinal gradients were the same as those at the zonal level except for the trends along longitudinal gradients within the LATN and LATMN zones (Fig. 7C–F).

It is worthwhile to note that: (1) the number of genera belonging to the NA-AS category was higher than the

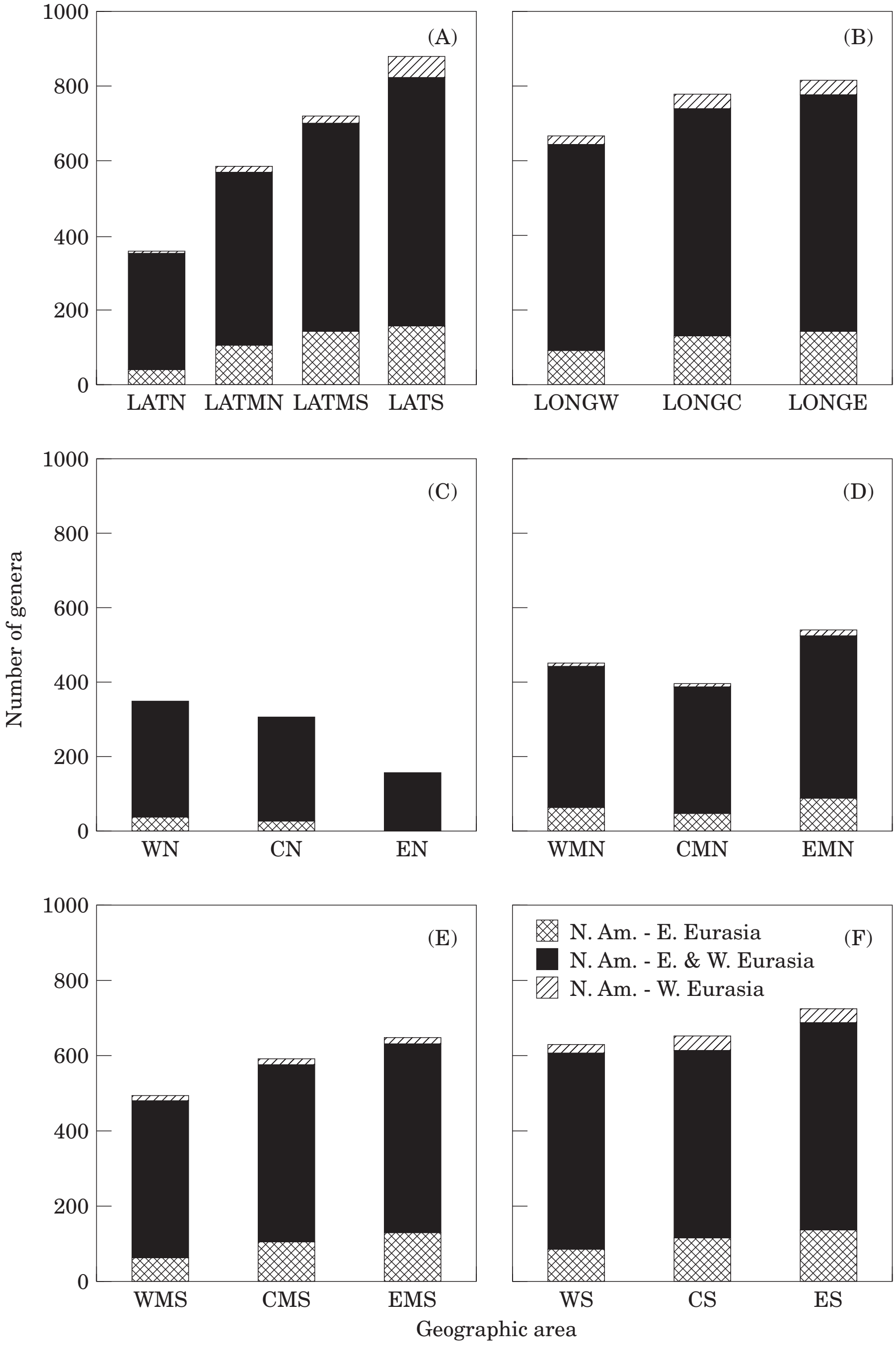

FIG. 7. Number of vascular plant genera shared between North America north of Mexico and Eurasia in each latitudinal zone (A), each longitudinal zone (B), and each region (C–F) in North America. Codes for zones and regions are given in the text.

number of genera belonging to the NA-EU category, and the number of genera in NA-EUAS was the highest among all three categories in all zones and all regions of North America; and (2) the number of genera belonging to the NA-AS category was lower in the regions of LONGW than those in LONGE in the same latitudinal zones except for LATN, despite the fact that LONGW was much closer to East Asia than LONGE (Fig. 7C–F).

Relationships at the species level. No fewer than 991 (or 6·5%) of the native North American species were also native to the modern flora of Eurasia. This number does not include a few species which were present in Iceland but absent from other parts of Eurasia. Among the shared species, 47·2% were present in both eastern and western Eurasia, 30·2% only in eastern Eurasia, and 22·6% only in western Eurasia. The total number of species shared by North America and Eurasia within a zone decreased along both the latitudinal gradient (from the north to the south) and the longitudinal gradient (from the west to the east) of North America (Fig. 8A and B). The number of shared

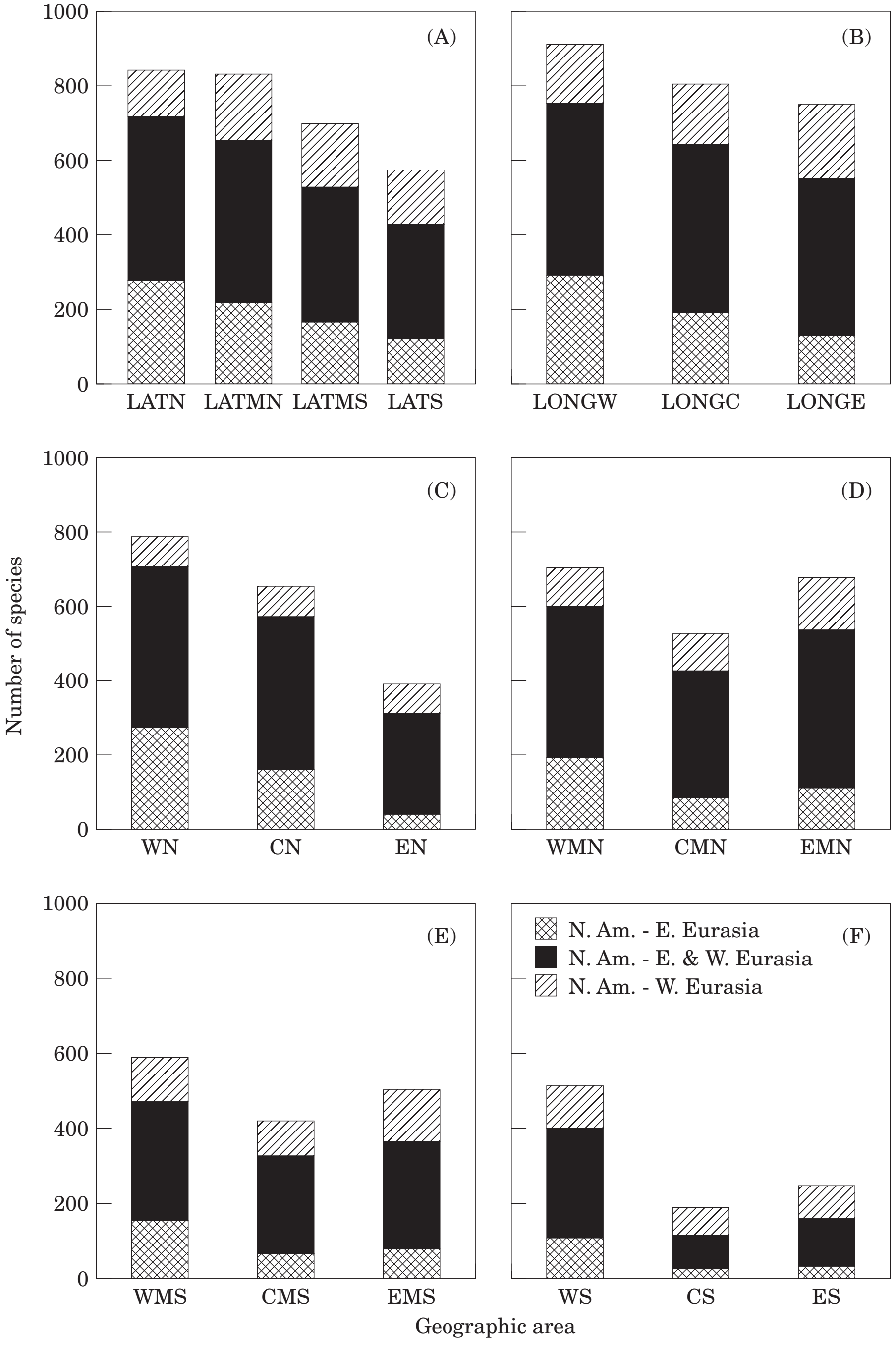

FIG. 8. Number of vascular plant species shared between North America and Eurasia in each latitudinal zone (A), each longitudinal zone (B), and each region (C–F) in North America north of Mexico. Codes for zones and regions are given in the text.

species in both NA-EUAS and NA-AS categories within a zone decreased from the north to the south and from the west to the east of North America. The number of shared species in the NA-EU category tended to decrease from the north to the south (except for less species in LATN than in LATMN, primarily due to the effect of flora size), but increased from the west to the east of North America (Fig. 8A and B).

At the regional level, the total numbers of the North America-Eurasia shared species in the regions of the LONGC zone were lowest in all latitudinal zones except for LATN where EN (a region of LONGE zone) had the lowest value (Fig. 8C–F). The number of species belonging to the NA-AS category was higher in all regions of LONGW than those of LONGE in the same latitudinal zones (Fig. 8C–F), while the number of species belonging to the NA-EU category was higher in the regions of LONGW than in those of LONGE within the same latitudinal zones except for those in the LATS zone (Fig. 8 C–F). The number of genera in NA-EUAS was the highest among the three categories in all zones and regions of North America (Fig. 8 A–F).

DISCUSSION

Geographic trends in taxonomic diversity

The trends in taxonomic diversity along spatial gradients such as latitude and longitude have been reported for many groups of organisms. Among them, the latitudinal diversity gradient is most frequently reported and has been considered as one of the most striking patterns on earth. For most groups of organisms, taxonomic diversity (e.g. the number of species) in an area of a given size tends to increase with decreasing latitude from the poles towards the equator (Schluter and Ricklefs, 1993; Huston, 1994; Rosenzweig, 1995; Qian, 1998). For example, the number of plant species at 0·1-ha scale increases as the latitude decreases from about 41° N in North America to the equator (Rosenzweig, 1995), while the number of tree species at scales of $5{\cdot}1 \times 10^4$–10×10^4 km^2 increases from nearly monospecific boreal forests of the subarctic to the fairly diverse forests in southern North America (Currie and Paquin, 1987). The rate of increase in taxonomic diversity from pole to equator depends on many factors such as organism group, taxonomic level, size of a study area, landmass configuration, and distance of a study area to the ocean. For example, the southern latitudinal zone of North America (LATS, this study) has 1·8, 2·5, 4·4 and 8·5-times as many orders, families, genera and species of vascular plants, respectively, as the northern latitudinal zone of North America. This trend suggests that the rate of increase in taxonomic richness from the north to the south of North America increases with decreasing taxonomic level.

Longitudinal gradients in taxonomic diversity have been less studied, relative to latitudinal gradients. Because climates differ with respect to precipitation and continentality from coastal to interior areas in all the continents of the world, longitudinal gradients of taxonomic diversity also exist in all of the continents. Because climate change along a latitudinal gradient is, in general, more marked than it is along a longitudinal gradient, longitudinal patterns of taxonomic diversity may not be as striking as latitudinal patterns; longitudinal patterns may also have a modal trend, which can be either U-shaped or humped. For example, at the regional level of this study, regions in the central (longitudinal) zone of North America have fewer species than regions in both western and eastern zones of North America at the same latitude, except for the northern zone. However, Qian, Klinka and Kayahara (1998) found that the number of vascular plant species at a spatial scale of 9 ha was higher in central North America than in both western and eastern North America along a transect in boreal spruce-fir forests from the Pacific to the Atlantic coast.

Our understanding of the cause of patterns in taxonomic diversity along latitudinal and longitudinal gradients is still incomplete. Although many of these patterns are correlated with climatic variables such as mean annual temperature, annual actual (or potential) evapotranspiration, insolation, and frost-free days, all of which tend to increase from the poles towards the equator (MacArthur, 1972; Stevens, 1989; Morse *et al.*, 1993; Qian, 1998), the mechanisms that regulate diversity patterns have not been well understood. Abiotic processes such as glaciation, and biotic processes such as speciation, immigration, extinction and competition between species have all been involved in the formation of diversity patterns at various geographic scales. Several hypotheses have been proposed to explain spatial patterns of taxonomic diversity on earth, especially the latitudinal gradient. Species-energy theory, time theory, spatial heterogeneity theory, climatic stability theory, competition hypothesis, predation hypothesis, and productivity hypothesis encompass some of the proposed mechanisms (Pianka, 1966; Wright, 1983). However, no single hypothesis can explain all of the taxonomic gradients on the earth.

The most recent (Quaternary) continental glaciations were one of the major abiotic factors to shape modern latitudinal gradients in taxonomic diversity in North America. Some species in northern North America either shifted their distributions southward or went extinct in advance of expanding glaciers. In addition, the geographic ranges of some plant species may not have regained ecological equilibria after glaciation because they have only recently arrived in northern forest regions from the southern unglaciated regions (Wright, 1964; Davis, 1976; Webb and Bernado, 1977; Delcourt and Delcourt, 1987; Webb, 1987), although the glaciers started their retreat to the north about 10000 years ago, and the continental ice sheets in North America retreated north of latitude 60° by 6000 years B.P. (Delcourt and Delcourt, 1993).

Differences in the dispersal ability of plant species between temperate and tropical zones are an example of a biological process that may help to create the latitudinal gradient in taxonomic diversity. Wind transport of seeds and pollen is an effective means of long distance dispersal for many plant species. The proportion of wind-dispersed species, however, decreases towards the tropics (Huston, 1994). Due partly to this fact, the geographic ranges of tropical species tend to be smaller than those of temperate species (Huston, 1994). In general, the more species there are with small geographic ranges in an area, the higher the proportion of endemic species in that region. Thus, the number of endemic species in the tropics is much higher than in temperate regions. For example, the number of endemic plant species (species with distributions of 50000 km^2 or less) generally increases from the north to the south of the United States (Gentry, 1986). Although a larger spatial scale was used in this study, a similar trend has been shown, i.e. the proportion of species with narrow distribution ranges increases from northern North America (LATN) to southern North America (LATS) by about 40%. High endemism in a region tends not only to increase α- and γ-diversity (i.e. the number of taxa) in that region but also to increase β-diversity (e.g. floristic dissimilarity) among regions. For example, β-diversity [represented by 1 − Sørenson index] of plant species between a Pacific region and an Atlantic region at the same latitude increases from 0·37 in north-middle latitudinal zone (LATMN) to 0·7 in south-middle latitudinal zone (LATMS) and 0·85 in south latitudinal zone (LATS) (Table 3).

Origin of floristic similarity between North America and Eurasia

The modern floristic similarity between North America and Eurasia arose through movements of taxa in the geologic past (Tiffney, 1985*a*), when the two landmasses were geographically linked with each other. Although North America is currently separated from Eurasia by the Atlantic Ocean in the east and by the Pacific Ocean in the west, geological data have shown that these two landmasses were connected in the past. Their connection can be traced as far as the late Carboniferous/Permian (around 300 million years ago, Ma) when the two protocontinents, Gondwana and Laurasia were united as a single supercontinent, Pangaea (Emery and Uchupi, 1984; Hallam, 1994). During Carboniferous times (just before the formation of Pangaea), North America shared a common flora with other continents of the earth (Gómez, 1982). In the Mesozoic and early Cenozoic, Pangaea fragmented progressively to give rise to the present-day continents (Hallam, 1994). Although the coalescence of the individual continents of Pangaea has contributed to a certain extent to the current floristic relationships between North America and Eurasia, it has been widely accepted that the land bridges between North America and Eurasia during the late Cretaceous-early Quaternary have played a significant role in the current floristic relationships of the two landmasses (McKenna, 1983*a*, *b*; Tiffney, 1985*a*, *b*; Hallam, 1994).

Geological data have shown the presence of two major routes connecting North America and Eurasia: the North Atlantic land bridge across the north end of the Atlantic Ocean and the Bering land bridge across the north end of the Pacific Ocean (Tiffney, 1985*a*). At the end of the Paleocene and until the early Eocene, the North Atlantic land bridge linked North America to Europe by two stages: North America to Greenland and Greenland to Europe (Tiffney, 1985*a*). The Bering land bridge was available throughout most of the Cenozoic (McKenna, 1983*b*), although with occasional breaks due to climate change (Tiffney, 1985*a*). The width of the Bering land bridge, for example during the late Cretaceous-Paleogene interval, varied from 10 to 15° between 60–75° N (Budantsev, 1992). The current discontinuity of the Bering land bridge has lasted since about 10000 years B.P. In addition to the Bering land bridge at the north end of the Pacific Ocean, a second northern Pacific bridge between Asia and North America was probably formed via the Aleutian chain at the time when Kula Ridge was subducted (McKenna, 1983*b*). Since angiosperms are first known in the early Cretaceous, about 120 Ma (Cox and Moore, 1993), it is presumable that the existence of the two land bridges during the Tertiary and also the Bering land bridge during the Quaternary allowed floristic interchanges between the two landmasses.

Based upon paleobotanical evidence Wolfe (1975, 1977) argued that the origin of the similarity of floras in North America and Eurasia involved the evolution of a great number of modern taxa in the late Cretaceous and early Tertiary. Their initial appearance in the fossil record was in the mid-latitudes of the Northern Hemisphere and they spread via the land bridges (Tiffney, 1985*a*). The newly evolved taxa spread rapidly over the Northern Hemisphere (Wolfe, 1975; Tiffney, 1985*b*). Due to the widespread, equable conditions of warm climate in the Northern Hemisphere in the early Tertiary, a large number of tropical taxa appeared at far northern latitudes (Reid and Chandler, 1933; Chandler, 1964; Wolfe, 1975; Tiffney, 1985*a*). consequently, a relatively homogeneous early Tertiary flora was ultimately formed in both North America and Eurasia. Owing to the nature of its paratropical climates and the thermophilic affinities of many of its constituent taxa, Wolfe (1975) called this assemblage the ‘boreotropical flora’. The rise of the modern floristic similarity between North America and Eurasia can be traced back at least to the time when the boreotropical flora emerged on the two landmasses, which were linked by the North Atlantic land bridge and the Bering land bridge. Most of the genera of trees found in the northern temperature zone today are known from fossil assemblages of the early Tertiary (i.e. 60 Ma) (Grubb, 1987), and thus were floristic components of the boreotropical flora.

However, the boreotropical flora underwent considerable internal variation after its establishment (Tiffney, 1985*a*). Individual species probably occupied only a portion of the range of the flora at any one time during the times of maximum land connection in the Northern Hemisphere. This internal variation resulted in allopatric speciation and increased local differentiation as time progressed and geography and climate changed (Tiffney, 1985*a*). More importantly, the changes in climate from the widespread warm conditions of the early Tertiary to the glacial maxima of the Quaternary and changes in geology such as the early Tertiary rise of the Rocky Mountains in North America undoubtedly resulted in many floristic changes, which in turn resulted in the differentiation of the floras not only between North America and Eurasia but also among different regions on the same landmass.

The reverse relationship of floristic similarities between North America and Eurasia along a latitudinal gradient at the genus and species levels suggests that the floristic relationships at these two taxonomic levels may have originated during different periods. Despite the fact that both the North Atlantic land bridge and the Bering land bridge directly linked the northern zone of North America (LATN) to Eurasia, and that the southern zone of North America (LATS) was the farthest zone from the land bridges among the four latitudinal zones, the highest number of genera shared between North America and Eurasia was found in LATS, whereas the lowest number was found in LATN (Fig. 7A). Although the number of shared genera is not independent of the total number of genera in the regions under comparison, the trend of increase in the number of shared extant genera with decreasing latitude in North America is undoubtedly related to their origin in the Tertiary boreotropical flora, some of whose constituent genera are also components of the extant flora of LATS but absent from LATN. This has been supported by numerous fossil data (e.g. Graham, 1972; Muller, 1981).

In contrast, the highest number of species shared by North America and Eurasia was found in LATN, whereas LATS had the lowest number of shared species among the four latitudinal zones (Fig. 8A). Most of the shared species are restricted to the arctic-boreal belt of the Northern Hemisphere and about 47% of the shared species have a circumpolar-circumboreal distribution. For example, among the 767 species shared between North America and East Asia, 441 species have been found in the Arctic on both sides of the Bering Strait i.e. in Alaska and Chukotka (Qian, 1993), and most are probably neo-endemics restricted to the Arctic regions. This fact suggests that many of the species shared between North America and Eurasia may have evolved in boreal-arctic floras with cool climate conditions after the boreotropical flora, which requires warm climate conditions, moved in a southerly direction as the climate of the Northern Hemisphere was cooling.

Eastern North America shares more genera with Eurasia than western North America, despite the fact that the Bering land bridge was more favourable for plant migration between North America and Eurasia because it was wider and lasted longer than the North Atlantic land bridge. More interestingly, the difference results primarily from a large number of eastern Asia–North America shared genera, rather than Europe–North America shared genera (Fig. 7B). This is particularly the case for southern North America (Fig. 7E and F). This pattern is, in part, due to the large number of plant genera with eastern Asia–eastern North America disjunct distributions, which has attracted the attention of botanists and geographers since the time of Linnaeus (Gray, 1840, 1846; Li, 1952; Graham, 1972; Boufford and Spongberg, 1983; Tiffney, 1985*a*; Ricklefs and Latham, 1992). Thorne (1972) counted no less than 74 genera which are restricted to eastern North America and Asia, among which at least 56 genera (or groups of related genera) exhibit the disjunct pattern of an eastern Asian–eastern North American distribution (Li, 1952). Many of the disjunct genera inhabit the mixed mesophytic forests (Li, 1972). Fossil evidence suggests that disjunctions between eastern Asian and eastern North America genera in mixed mesophytic forests arose from 10 to 33 million years ago (Ricklefs and Latham, 1992). The fossil evidence also indicates that many genera found now in eastern Asia and eastern North America, including some of the current eastern Asia–eastern North America disjunct genera, did exist in Europe in the Tertiary (Grubb, 1987). For example, Tertiary fossils of *Torreya* Arn., *Sassafras* Nees et Eberm., *Carya* Nutt. and *Aralia* L. have been found in Europe (Latham and Ricklefs, 1993). It has been generally accepted that the extinction of many genera in Europe during the Quaternary was due to lack of access to suitable refugia to the south during the periods of glaciation (e.g. Takhtajan, 1969; Grubb, 1987; but see Huntley, 1993). The extinction of many genera in Europe at least partly resulted in a lower floristic similarity at the genus level between North America and Europe than between North America and Asia.

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