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# INTERCONTINENTAL CORRELATION OF GEOGRAPHICAL RANGES SUGGESTS STASIS IN ECOLOGICAL TRAITS OF RELICT GENERA OF TEMPERATE PERENNIAL HERBS

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*Abstract.*—Disjunct taxa within genera of herbaceous perennial plants relict to temperate eastern Asia and eastern North America exhibit a significant correlation in area of geographical range. This relationship suggests evolutionary stasis of traits related to ecological distribution over periods of at least 10 million and possibly more than 30 million yr. Because woody taxa lack this pattern but appear to exhibit broader ecological distributions on a local scale than do herbaceous taxa, we suggest that stasis goes hand in hand with ecological specialization; some restricted subsets of ecological conditions to which herbs are specialized may persist within a changing ecological mosaic.

The fossil record presents an enigmatic picture of rates of evolution that suggests that in many lineages, episodes of rapid change punctuate long periods of relative stasis (Eldredge and Gould 1972; Gould 1982). Explanations for stasis include stabilizing selection in a constant environment (Charlesworth et al. 1982), genetic homeostasis (Lerner 1954; Eldredge and Gould 1972), and, with respect to morphological stasis, compensation of environmental selection by behavioral, physiological, and developmental plasticity (Wake et al. 1983). Punctuated equilibrium, regardless of the mechanisms involved, contrasts strikingly with the viewpoint of Rosenzweig (1973), Van Valen (1973), Hamilton (1980), Hamilton and Zuk (1982), and others that evolution of competitors, prey organisms, predators, parasites, disease organisms, and mutualists continually alters the environment of every species, which thus exerts selective pressure for continual evolutionary response (McCune 1982). Van Valen (1973) called this the "Red Queen Hypothesis."

The biological community includes a temporally and spatially shifting association of species having generally weak and changeable interactions (Gleason 1926; Davis 1965; Howe 1984; Strong et al. 1984; Delcourt and Delcourt 1987). In such a world, particularly one ruled by the Red Queen, one expects continual adaptation and change. Over time, ecological and geographical distributions of species may undergo cycles of expansion and contraction because of such factors as

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climate change, novel adaptations, species invasions, and time delays in evolutionary responses (Darlington 1957; Wilson 1961; Ricklefs and Cox 1972). At any particular time, some species may exhibit broad distributions, while close relatives occupy more restricted ecological and geographical ranges (Willis 1922).

Evolutionary changes predicted by the Red Queen Hypothesis contrast sharply with morphological stasis, but the Red Queen may be satisfied by physiological and biochemical changes not preserved in the fossil record. Although not altering the superficial appearance of the organism, such changes influence ecological relationships and may express themselves in ecological and geographical distribution. Geographical range generally reflects local ecological breadth (Willis 1922; McNaughton and Wolf 1970; Ricklefs and Cox 1978; Hanski 1982; Bock and Ricklefs 1983; Brown 1984; Hodgson 1986*a*). It follows from the Red Queen Hypothesis that the distributions of individual species should expand and contract stochastically over evolutionary time, irrespective of response to climatic or other general environmental change. To the extent that reproductively isolated populations evolve independently, correlations of the ecological or geographical breadths between ancestral and descendant taxa or between contemporary sister species should decline over evolutionary time and eventually approach zero. Conversely, if adaptations influencing ecological and geographical extent are conservative, distributions of sister taxa in geographically isolated but climatically and ecologically similar regions should vary in parallel as they respond to shifts in global climate patterns.

Jablonski (1987) demonstrated long-term stasis of distribution in gastropod and bivalve mollusks of the Cretaceous period by calculating the correlation between geographical extents of ancestral and descendant taxa. In this article, we take a similar approach by calculating the correlation between the geographical ranges of vicariantly disjunct genera of plants endemic to temperate forests of eastern Asia and eastern North America, which have been separated for 10s of millions of years.

## FLORISTIC RELATIONSHIPS BETWEEN EASTERN ASIA AND EASTERN NORTH AMERICA

The floristic similarities between temperate eastern Asia and eastern North America are well-known and have long been appreciated (Gray 1840, 1846, 1878; Anonymous 1860; Fernald 1929; Li 1952; Fryxell 1967; Graham 1972; Iwatsuki 1972; Kurokawa 1972; Thorne 1972; Good 1974; Boufford and Spongberg 1983; Ying 1983; Tiffney 1985*a*). These related vascular floras contain a large number of unique, disjunct, relict taxa, including five plant families (Camp 1947) and at least 56 genera or groups of related genera (Li 1952; Thorne 1972). Many of the disjunct taxa belong to the mixed mesophytic forest (Li 1972; Wolfe 1979), which occupies similar geographical areas in eastern Asia and eastern North America (Latham and Ricklefs 1992). However, because some members of this contemporary vegetation type have northern and some have southern affinities, it perhaps should not be considered a distinct, persistent, floristic unit (Mason 1947; Graham 1972; Thorne 1972; Wolfe 1972, 1981). Several extant genera, including some with disjunct ranges, are known from the Cretaceous period and early Paleogene epoch (Braun 1947; Graham 1972; Muller 1981; Hsü 1983; Manchester 1987). Many of the disjunct genera were formerly widespread with abundant fossil representation in western North America including Alaska (Wolfe 1969, 1979).

Separation of Asian and North American disjunct taxa probably extended over a period beginning at the end of the Eocene epoch (ca. 33–37 million yr before present [M.Y.B.P.]), when the climate of the Northern Hemisphere cooled abruptly (Wolfe 1978), and lasting until the mid- or late Miocene epoch, perhaps 10–15 M.Y.B.P., at the end of a pronounced warming and cooling cycle. The genus *Acer* (maples) contains 12 sections having Asian–North American disjunctions. Wolfe (1981) has suggested that seven of these disjunctions arose vicariantly because of climate change, three arose vicariantly because of competitive elimination of intermediate populations, and two arose through long-distance dispersal. The fossil record confirms that one of the vicariance events dates from the end of the Eocene; the others probably occurred during the Miocene.

Although Eocene floras of North America contained an abundance of tropical taxa (Berry 1937; Tiffney 1985*a*), many of the Eocene genera remain in the North American flora. By the end of the Eocene, however, the flora of the Rocky Mountains region had lost its affinities with Asia and taken on a distinctly New World character (Leopold and MacGinitie 1972). Similar changes were beginning to take place in the Far West. The early and middle Miocene floras of the northwestern United States and Alaska included 108 genera of woody plants, according to Wolfe's (1969) tabulation. Of 15 genera of trees presently having disjunct Asian–eastern North American distributions, 9 were present at that time in the Northwest (i.e., Oregon and Washington) but only 4 in Alaska. Only 1 of 10 disjunct shrub genera appears in the fossil record of the Northwest. These western populations may or may not have been continuous with conspecifics in eastern North America. But it is clear that most elements of the disjunct relict flora had become isolated by the end of the Miocene; this was a period of mountain building in the West, which led to drying and greater seasonality of rainfall and consequently to the disappearance of mixed mesophytic forest from the area. In summary, the fossil evidence suggests that disjunctions between eastern Asian and eastern North American taxa in mixed mesophytic forests arose variously from 10 to 33 M.Y.B.P.

## COMPARISON OF ASIAN AND NORTH AMERICAN RANGES

Li (1952) provided generalized outline maps of the ranges of 56 genera or groups of closely related genera (five cases), with disjunct distributions in eastern Asia and eastern North America (App. A). The distributions of genera within these areas may not be continuous, and the Asian distributions are probably less well-known than those in North America because of limited collection and the antiquity of habitat alteration. We believe it unlikely that errors in estimating geographical areas—errors that are undoubtedly greater in Asia than in North America—could produce spurious correlations between the areas occupied by disjunct congeners in the two regions. Estimated areas varied over two orders of

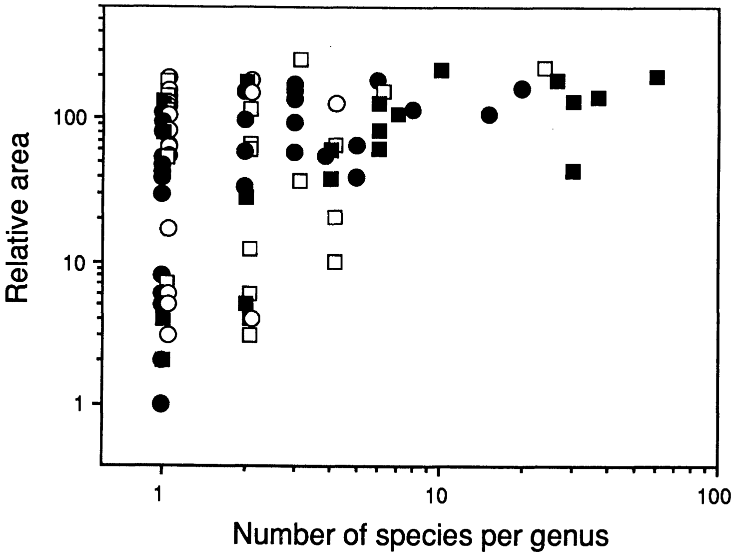

FIG. 1.—Relationship between geographical range and number of species in disjunct genera of temperate vascular plants in eastern Asia (*squares*) and eastern North America (*circles*). *Open symbols,* herbaceous genera; *filled symbols,* woody genera.

magnitude; errors certainly are much smaller than this. Li (1952) also tabulated the number of species in each region, assigned genera to categories of growth form (trees, shrub-trees, shrubs, herbs, woody vines), and distinguished genera with strictly temperate distributions ($n = 37$) from those with tropical or subtropical extensions ($n = 19$).

We estimated the area and the latitude of the geographical center of the range of each genus in Asia and in North America. All maps were drawn to the same scale. We photocopied the maps, cut out the distributions for each taxon, and weighed them to the nearest 0.1 mg on an analytical balance. The range of values was 0.1–26.1 mg, which we converted to an arbitrary scale ranging from 1 to 261. On this scale, Japan with an area of 380,000 km$^2$ had a value of 9 units. Because Li (1952) used a Mercator projection rather than an equal-area projection for his map base, areas taken directly from the maps were only relative, and geographical area was biased toward larger values at more northern latitudes. To correct this bias, we divided each range by a number ($k$) equal to the square of the scale factor for distance on a Mercator projection in which $k = 1$ at a latitude of 22° 30′ (List 1966, table 165; values of $\sqrt{k}$ interpolated between 5° intervals [10°–50°] by cubic regression and predicted values calculated for the latitude of the midpoint of the range of each genus).

In both Asia and North America, the smallest range area occupied by a genus increases with number of species per genus; the largest area appears to be independent of number of species and approximates the extent of suitable habitat for deciduous forest vegetation (fig. 1). The data suggest bimodality in range area among monotypic and ditypic genera.

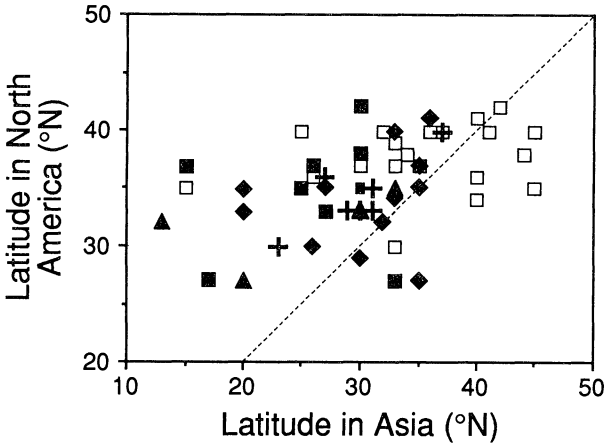

FIG. 2.—Relationship between the latitudes of the midpoints of geographical ranges of disjunct genera of temperate vascular plants in eastern Asia and eastern North America. *Diagonal line* represents identical latitudes in both regions. Symbols represent genera of trees (*filled squares*), small trees (*triangles*), shrubs (*diamonds*), woody vines (*pluses*), and herbs (*open squares*).

Latitudes of the centers of geographical distributions varied between 13° and 45°N in Asia and between 27° and 42°N in North America. Although latitudes in Asia and North America were weakly correlated (fig. 2; $F = 11.74$, df = 1,54, $P = .0012$, $r^2 = 0.18$), the fact that latitudinal distribution is closely associated with growth form ($F = 7.65$, df = 4,51, $P < .0001$, $r^2 = 0.38$ in Asia; $F = 4.03$, df = 4,51, $P = .0055$, $r^2 = 0.24$ in North America) obscures this relationship. When we statistically removed the effects of growth form on latitude in an analysis of covariance, the relationship between latitude in Asia and North America became only marginally significant ($P = .064$).

When analyzing the relationships between the areas of the disjunct genera in Asia and North America (fig. 3), we removed from consideration genera with 10 or more species in either area ($n = 11$) in order to reduce the influence of species number on geographical range in our analysis. Because range areas of speciose genera are constrained near the upper boundary of the distribution (fig. 1), their ranges appear to be determined by area of suitable climate rather than local ecological interactions. Furthermore, because numbers of species per genus are weakly correlated between Asia and North America (among herbaceous genera, $r_s = 0.36$, $n = 22$, $P = .097$; among woody genera, $r_s = 0.38$, $n = 34$, $P = .027$), biases in geographical area that arise from species number are unequally distributed between the two continents (Ricklefs 1989). Genera excluded from the analysis were woody species with tropical or subtropical distributions ($n = 8$), plus *Carya* (temperate tree), *Weigela*/*Diervilla* (temperate shrub), and *Astilbe* (temperate and tropical herbs).

Generic ranges in Asia and North America were significantly correlated among herbaceous perennials but not among other growth forms (table 1). The number of species in a genus influences its range area (fig. 1) but does not contribute to the correlation of range area between Asian and North American disjunct genera

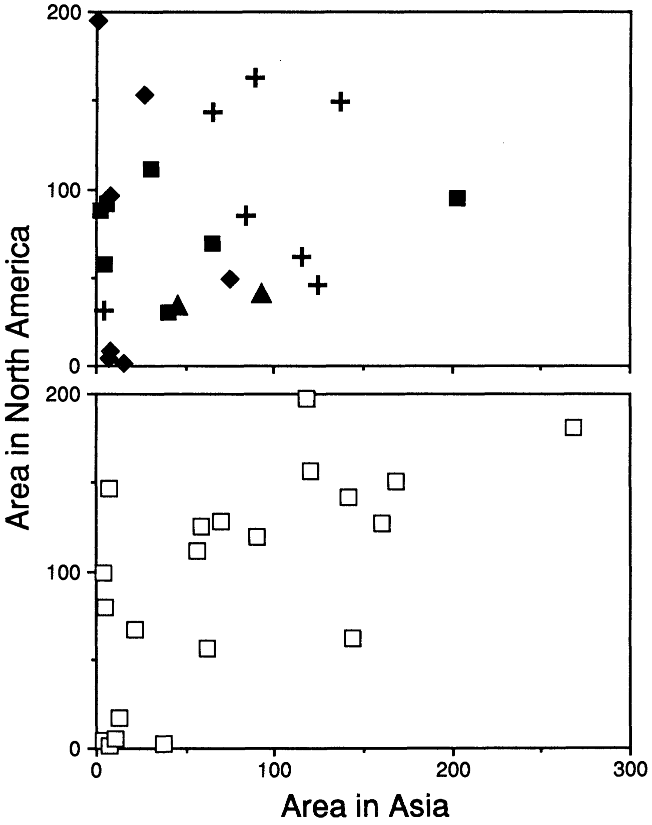

FIG. 3.—Relationships between the areas occupied by disjunct genera of temperate vascular plants in eastern Asia and eastern North America. *Above,* woody genera ($n$ = 24, $r^2$ = 0.04, $P$ = .36; see fig. 2 for symbols); *below,* herbaceous genera ($n$ = 21, $r^2$ = 0.42, $P$ = .0015). The significance of the relationship for herbaceous genera is not diminished by log-transforming areas ($r^2$ = 0.31, $P < .0086$) or by using the nonparametric Spearman rank correlation ($r_s$ = 0.64, $P$ = .002, $n$ = 21; including the one genus with more than 10 species in Asia: $r_s$ = 0.48, $P$ = .024, $n$ = 22). The partial correlation between areas in Asia and North America, with number of species per genus in each region statistically controlled, was also significant ($P < .02$). None of these manipulations altered the insignificance of the correlation between Asian and North American areas among woody genera.

TABLE 1

CORRELATIONS OF GENERIC RANGE AREAS BETWEEN ASIA AND NORTH AMERICA

| Growth Form | $n$ | $r^2$ | $P$ |
|---|---|---|---|
| Herbaceous perennials | 21 | .42 | .0014 |
| Shrubs | 8 | .00 | .93 |
| Shrub-trees | 2 | . . . | . . . |
| Trees | 7 | .04 | .69 |
| Woody vines | 7 | .08 | .54 |
| Woody genera combined | 24 | .04 | .36 |

of perennial herbs (fig. 3, legend). Areas occupied by herbaceous genera were unrelated to latitude in Asia ($F = 0.34$, df = 1,19, $P = .6$) and weakly related to latitude in North America ($F = 5.2$, df = 1,19, $P = .03$, $r^2 = 0.22$). Partialing out latitude does not affect the correlation between Asian and North American areas; thus, Rapoport's rule relating range area to latitude (Stevens 1989) does not express itself strongly in our data set, nor does it produce a fortuitous correlation in areas between continents.

Parallelism in area (i.e., persistent correlation between continents) appears to reveal long-term stasis of genus-level attributes and ecological interactions that determine geographical distribution. Either these attributes have not changed, or they have evolved in parallel over periods of 10s of millions of years. Many morphological characters have been similarly static over long periods in both herbaceous and woody plants. Generic assignments indicate that taxonomic characters have not evolved substantially in many clades since the isolation of Asian and North American taxa 10–30 M.Y.B.P. Indeed, many generic characters have persisted since the late Cretaceous period (Hsü 1983). Flowering phenology shows strong similarity between Asian and North American plants in the same families, including many disjunct taxa (Kochmer and Handel 1986). Hodgson (1986*b*) has demonstrated that ecological attributes influencing commonness and rarity of herbs in central England are conservative at the family level. One might expect independent proliferation and ecological diversification of species within genera on each continent to obscure any correlation between generic ranges, but speciation evidently produces either small or parallel effects on generic range in disjunct taxa. If geographical range expresses evolutionary relationships between plants and their herbivores, pathogens, pollinators, and seed dispersers as well as physical variation in the environment, then either the time scale of processes pertaining to the Red Queen Hypothesis must be very long or the variation in species distributions resulting from these processes is constrained within ranges set by higher-level attributes of taxa.

## A MODEL OF EVOLUTIONARY STASIS

Herbaceous genera exhibit persistent correlations (parallel change or convergence) in geographical range, but woody genera apparently do not. This difference could arise in several ways. First, the herbaceous genera may not have experienced disjunction for as long as the woody genera and thus have not had sufficient evolutionary time for divergence. Herbs do not fossilize well compared to woody plants, especially trees, so few historical records exist. The disjunct herbaceous genera as a group occur farther to the north, hence closer to the Bering and North Atlantic land bridges (Tiffney 1985*b*) than the woody genera, but they are restricted to the region of broad-leaved deciduous forest in eastern North America and clearly have been long separated from their Asian congeners. Furthermore, the shorter generation times of herbaceous perennials provide the potential for more rapid evolution compared to woody taxa.

Second, the geographical ranges of woody taxa may not have regained ecological equilibria following glaciation, particularly in North America (Wright 1964;

Davis 1976). Thus, their present distributions may include the influence of Pleistocene refugia and subsequent migration following rapid climate change. Whether these factors might have affected woody taxa to a greater extent than forest herbs cannot be resolved by us. However, the similar relative sizes of ranges of woody and herbaceous taxa in eastern North America (average woody/average herbaceous = 0.78) and eastern Asia (0.67) suggest that the two groups have not differed markedly in the reestablishment of geographical distributions during the last 18,000 yr. Furthermore, Webb (1986) and Huntley and Webb (1989) have argued that migrations of plants in Europe and North America following the retreat of the glaciers were sufficiently rapid to maintain geographical ranges in approximate climatic equilibrium. The apparent independence of migrations of species presently coexisting in temperate forest associations resulted, according to Webb and Huntley, from "individualistic responses . . . to the different regional patterns of temperature and precipitation change" (Webb 1986, p. 75) rather than from slow migration from isolated refuges occupied by chance during the late Pleistocene epoch.

Third, many of the disjunct woody genera have ranges extending into the tropics in Asia; in North America, this does not occur because of the interposition of arid northern Mexico and the Gulf of Mexico (Latham and Ricklefs 1992). The differential extension of temperate woody genera into the tropics may cause the correlation among the ranges of woody genera to break down, whereas the same geographical constraints do not affect the more northern distributions of the disjunct herbaceous genera. Nonetheless, because the average range area of woody genera bears a similar relationship to the average of herbaceous genera in Asia as it does in North America (see above), the extension of temperate woody genera into the oriental tropics appears to have resulted from shifts rather than expansions of ranges.

Fourth, herbaceous and woody genera may be sensitive to different scales of spatial heterogeneity in the environment in their response to general change in the environment. We present a simple model of this difference in figure 4, which portrays herbs as specialized with respect to their occupancy of niche space and woody plants as generalized. When rapid change in the environment causes the boundaries of the niche space to shift, the relatively narrow niche requirements of herbaceous genera will either fall outside of the new niche space, in which case the genus will go extinct, or they will continue to be included within the new niche space, in which case the environment need not exert directional selective pressure. For woody genera having broad niche occupancy, environmental change will more likely apply strong directional selection, which will thus cause evolutionary response but rarely extinction or stasis; that is, some portion of the niche space occupied by each woody species will persist. The hypothesized difference between the niche spaces of woody and herbaceous taxa may arise from woody taxa averaging over and therefore not recognizing small-scale heterogeneity in the environment (particularly edaphic factors to which herbs are sensitive), responding to environmental variables with larger spatial scales of heterogeneity (e.g., climate vs. edaphic factors), or both.

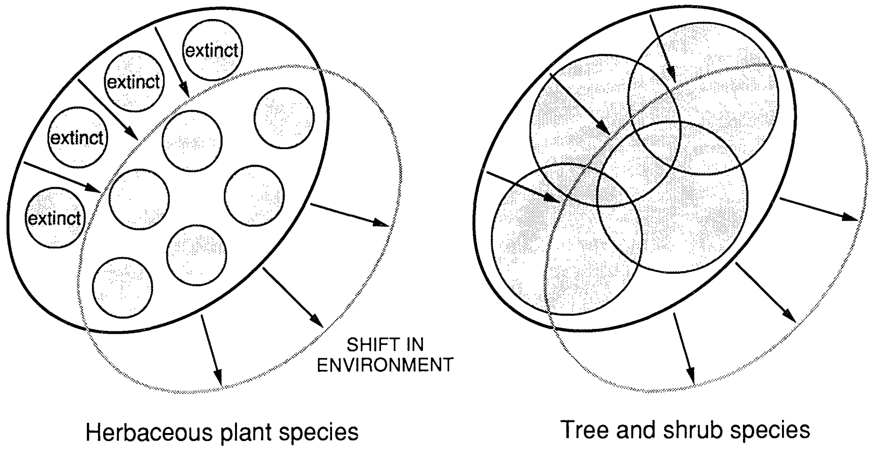

FIG. 4.—A model of response to environmental change based on degree of ecological specialization. *Left*, specialized herbs either remain static or go extinct as the environment shifts; *right*, more generalized woody species persist but respond to strong selection.

The distributions of herbaceous and woody genera both among and within habitats on the Piedmont of North Carolina support the hypothesis that herbs occupy smaller, more specialized niche spaces than do woody plants, whether shrubs or trees (fig. 5). In Oosting's (1942) study of plant distribution on the Piedmont of North Carolina, nearly 60% of genera of perennial herbs but only about 20% of woody genera were restricted to a single one of nine localities. Within localities, more than 50% of perennial herbaceous genera but less than 20% of woody genera were restricted to a single 1 of 10 quadrats sampled. Restricted distribution over samples need not result from specialized ecological requirements or tolerances, but this proposition may be investigated experimentally.

Within the flora of the Carolinas as a whole (Radford et al. 1968), the proportions of disjunct genera belonging to different growth forms also suggest that woody species, especially trees, have been less vulnerable to extinction: 14% of 69 genera of dicotyledonous trees, 10% of 106 genera of shrubs, 15% of 55 genera of vines, but only 5% of 321 genera of perennial herbs belong to disjunct eastern Asian–eastern North American taxa (within woodland habitats these proportions were 16%, 13%, 21%, and 11%, respectively). White (1983) came to a similar conclusion based on an analysis of the flora of Great Smoky Mountains National Park. The smaller area surveyed by Oosting (1942) included seven disjunct woody genera (16% of 45 genera) but only two disjunct herbaceous genera (4% of 49). Similarly, the "metasequoia" flora of China, which contains 184 genera of dicots in 94 families, includes 12 of the disjunct woody genera (trees, shrubs, and vines) but only one herbaceous genus (Chu and Cooper 1950; Hu 1980; Bartholomew et al. 1983). Alternatively, the small proportion of disjunct genera among perennial herbs could result from a proliferation of such taxa since the origin of the

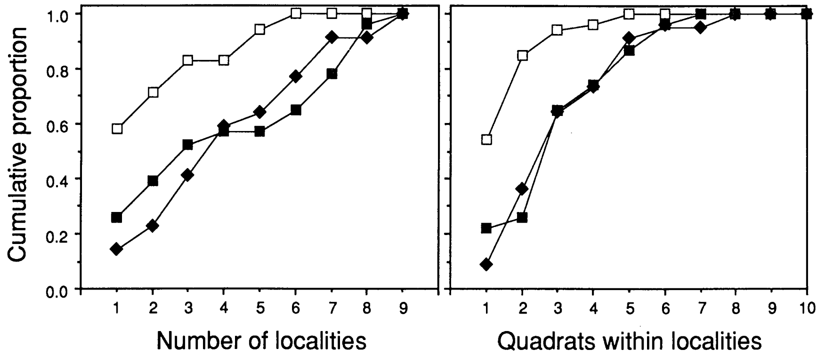

FIG. 5.—*Left,* cumulative frequency distributions of number of localities (1–9) occupied by genera of perennial herbs (*open squares;* $n = 48$), shrubs and vines (*diamonds;* $n = 22$), and trees (*filled squares;* $n = 23$) on the Piedmont of North Carolina (from data in Oosting 1942). Kolmogorov-Smirnov tests revealed significant differences between herbs and both trees ($P < .05$) and shrubs ($P < .001$), which did not differ among themselves ($P > .1$). *Right,* cumulative frequency distributions of average number of quadrats (1–10) within localities occupied by each genus. Values were calculated by summing the number of quadrats occupied by each species separately within a genus and dividing the total over all species in the genus by the total number of occupied localities. Kolmogorov-Smirnov tests revealed significant differences between herbs and both trees ($P < .001$) and shrubs ($P < .001$), which did not differ among themselves ($P > .3$). Recalculating frequencies for species rather than genera did not alter the general pattern or levels of significance of statistical tests.

disjunctions. Most woody tree genera are known from Eocene or earlier times; herbaceous taxa in general may be younger and more diverse at present than in the past (Tiffney 1981), which would thus dilute the number of older, disjunct taxa. However, forest understory herbs tend to be much older, probably as old as woody taxa (Tiffney 1985*a*), and their history should be regarded as distinct from that of the herbaceous flora of fields and disturbed sites.

Among perennial herbs of the Carolinas, disjunct taxa account for 12 of 112 genera of forested habitats but none of 102 genera of fields and roadsides (Radford et al. 1968; see also White 1983). This pattern supports the idea of ecological conservatism in the herbaceous perennials; they presumably evolved in association with temperate forest habitats and have not escaped them. Most of the herbaceous perennial taxa associated with field habitats may have evolved after the disjunction of Asian and North American temperate biomes.

Ecological traits influencing geographical range appear to have a long persistence in herbaceous taxa but not in woody taxa isolated for similar periods, in spite of the shorter generation time of herbaceous taxa. The correlation of geographical range among disjunct herbaceous genera indicates either stasis in or parallel evolution of ecologically important attributes of genera for periods of 10s of millions of years (Hodgson 1986*b*). Parallel evolution would require constraints on the direction of evolution of physiological tolerances and antiherbivore and antipathogen mechanisms at the level of the genus. Variation in such traits among species within genera argues against such constraints being a general feature of plant evolution. Evolutionary stasis provides a more parsimonious explanation for parallelism in area of geographical range.

Variation within genera also casts doubt on a role for genetic homeostasis. Wake et al.'s (1983) model of morphological stasis compensated by physiological flexibility might apply to the persistent correlation between the ranges of disjunct herbaceous taxa if area were directly related to capacity for phenotypic or genotypic response, which itself exhibited stasis. Our point is that such responses in woody species have led to changes in the relative areas occupied by genera independently in Asia and North America. We contend that in herbaceous genera, these characters have remained unchanged over very long periods because of the absence of directional selection. Unlike woody taxa, herbs can select small microhabitat patches, some of which have persisted over very long periods. Among woody plants, either the combinations of patches to which taxa are adapted have been more labile, or the geographical ranges of taxa are determined by a different set of factors with larger scales of heterogeneity and change, compared to those of herbaceous taxa.

To explain parallelism in area of geographical range of herbaceous taxa, we suggest that extant disjunct perennial herbs have exhibited stable ecological requirements and tolerances over 10s of millions of years. Although climate and other aspects of the environment have changed (Wolfe 1979), herbaceous taxa are so specialized (Antos 1988) that the narrowly circumscribed parameters of their niches may persist over a large geographical area in spite of a changing composition of microhabitat patches locally. The environment may select attributes of the taxon, but taxa also match their ecological and geographical distributions to the environment according to these attributes. So long as the particular conditions to which the taxon has become adapted persist, its evolution may become static in spite of change in the physical environment. Moreover, stasis of such population attributes as range that may express biological interactions argues strongly against the generality of the Red Queen Hypothesis.

One reviewer of this article pointed out that, if herbaceous perennials were evolutionarily static and ecologically narrow-niched, one would expect such taxa to have fewer species per genus and occupy smaller geographical ranges than do woody genera. The tendency toward reduced intrageneric diversity resulting from generic specialization might, however, be balanced by increased beta diversity (geographical replacement of species). Data presented in this article do suggest that there are fewer speciose genera among herbaceous taxa (5% have five or more species per genus) than among woody taxa (24%) (fig. 1). But geographical areas of disjunct herbaceous taxa are larger on the average than those of woody taxa (fig. 3). Ecological specialization need not be correlated with geographical distribution. Indeed, the postulated narrower niche requirements of herbaceous taxa may be satisfied over a wider geographical area than the broader requirements of woody taxa. Suppose, for example, that three localities had niche types ABC, BCD, and CDE. An herb requiring only niche type C could inhabit all three regions, whereas a perennial requiring or persisting within the combination of BCD could inhabit only one. The more extensive local distribution of woody compared to herbaceous taxa (fig. 5) suggests either that herbs do not occupy a high proportion of suitable sites or that herbs are more sensitive to finer-scale variation in the environment, as might occur if the distributions of herbs were controlled primarily by soil characteristics and those of woody plants by aboveground climate.

Our view of the ecological and evolutionary relationships of taxa to the environment, as illustrated in figure 4, allows several predictions. In particular, we would expect to observe stasis among taxa in core regions of ecological niche space and both rapid evolution and extinction among those at the periphery. Adaptive radiations should originate more frequently at the periphery of niche space than in the center (Stenseth 1984; Valentine 1984; Jablonski et al. 1985). These distinctions should be more profound among ecological specialists than generalists; among the latter, evolutionary response should be the general rule. Characterizing niche relations of taxa in such a way as to elucidate these relationships remains a challenge for the future.

## ACKNOWLEDGMENTS

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# APPENDIX A

## TABLE A1

### CHARACTERISTICS OF GENERA WITH DISJUNCT DISTRIBUTIONS BETWEEN EASTERN ASIA AND EASTERN NORTH AMERICA

| | | | AREA | | SPECIES | | TROPICAL | | LATITUDE | |
|---|---|---|---|---|---|---|---|---|---|---|
| FAMILY* | GENUS* | GROWTH FORM† | AS | NA | AS | NA | AS | NA | AS | NA |
| Saururaceae | *Saururus* | H | 58 | 126 | 1 | 1 | + | + | 25 | 40 |
| Juglandaceae | *Carya* | T | 5 | 167 | 2 | 20 | – | – | 25 | 35 |
| Santalaceae | *Buckleya* | S | 7 | 4 | 3 | 1 | – | – | 35 | 37 |
| | *Pyrularia* | S | 8 | 8 | 2 | 1 | + | – | 27 | 35 |
| Polygonaceae | *Tovara* | H | 89 | 120 | 1 | 1 | + | – | 30 | 37 |
| Ranunculaceae | *Glaucidium/ Hydrastis*‡ | H | 4 | 100 | 2 | 1 | – | – | 42 | 42 |
| Berberidaceae | *Podophyllum* | H | 69 | 129 | 4 | 1 | – | – | 32 | 40 |
| | *Jeffersonia* | H | 5 | 80 | 1 | 1 | – | – | 40 | 41 |
| | *Diphylleia* | H | 37 | 3 | 3 | 1 | – | – | 40 | 36 |
| | *Caulophyllum* | H | 144 | 62 | 1 | 1 | – | – | 37 | 40 |
| Menispermaceae | *Menispermum* | V | 136 | 149 | 1 | 1 | – | – | 37 | 40 |
| Magnoliaceae | *Liriodendron* | T | 2 | 88 | 1 | 1 | – | – | 30 | 38 |
| | *Magnolia* | T | 146 | 122 | 30 | 8 | + | + | 17 | 27 |
| Illiciaceae | *Illicium* | ST | 155 | 42 | 37 | 5 | + | + | 20 | 27 |
| Schisandraceae | *Schisandra* | V | 200 | 5 | 26 | 1 | + | – | 23 | 30 |
| Lauraceae | *Sassafras* | T | 30 | 111 | 2 | 1 | – | – | 26 | 37 |
| | *Lindera* | S | 216 | 100 | 60 | 2 | + | – | 20 | 35 |
| Papaveraceae | *Stylophorum* | H | 13 | 17 | 2 | 2 | – | – | 30 | 38 |
| Crassulaceae | *Penthorum* | H | 119 | 157 | 2 | 1 | – | – | 33 | 39 |
| Saxifragaceae | *Decumaria* | V | 4 | 31 | 1 | 1 | – | – | 30 | 33 |
| | *Astilbe* | H | 252 | 4 | 23 | 2 | + | – | 15 | 35 |
| | *Itea* | S | 230 | 56 | 10 | 1 | + | – | 20 | 33 |
| Hamamelidaceae | *Hamamelis* | S | 27 | 153 | 6 | 3 | – | – | 33 | 40 |
| Rosaceae | *Rhodotypus, Kerria/ Neviusia*‡ | S | 16 | 1 | 2 | 1 | – | – | 34 | 33 |
| Leguminosae | *Gymnocladus* | T | 5 | 92 | 1 | 1 | – | – | 30 | 42 |
| | *Cladrastus* | T | 40 | 30 | 4 | 1 | – | – | 30 | 35 |
| | *Wisteria* | V | 115 | 61 | 7 | 2 | – | – | 32 | 32 |
| | *Apios* | H | 87 | 163 | 6 | 2 | – | – | 27 | 36 |
| Buxaceae | *Pachysandra* | S | 75 | 48 | 3 | 1 | – | – | 32 | 32 |
| Vitaceae | *Parthenocissus* | V | 64 | 144 | 6 | 3 | + | – | 31 | 35 |

TABLE A1 (*Continued*)

| | | | Area | | Species | | Tropical | | Latitude | |
|---|---|---|---|---|---|---|---|---|---|---|
| Family* | Genus* | Growth Form† | AS | NA | AS | NA | AS | NA | AS | NA |
| Theaceae | *Stewartia* | ST | 46 | 34 | 6 | 2 | − | − | 33 | 35 |
| | *Gordonia* | ST | 142 | 6 | 30 | 1 | + | − | 13 | 32 |
| Guttiferae | *Ascyrum* | S | 1 | 195 | 1 | 6 | − | + | 26 | 30 |
| Araliaceae | *Panax* | H | 268 | 181 | 3 | 2 | − | − | 36 | 40 |
| Nyssaceae | *Nyssa* | T | 202 | 96 | 2 | 3 | + | − | 15 | 37 |
| Ericaceae | *Tripetaleia/ Elliotia*‡ | S | 6 | 4 | 2 | 1 | − | − | 35 | 35 |
| | *Pieris* | S | 113 | 62 | 10 | 3 | + | + | 35 | 27 |
| | *Lyonia* | S | 45 | 115 | 15 | 15 | − | + | 30 | 29 |
| | *Epigaea* | S | 8 | 96 | 1 | 1 | − | − | 35 | 37 |
| Diapensiaceae | *Shortia* | H | 6 | 2 | 2 | 1 | − | − | 26 | 36 |
| Styraceae | *Halesia* | T | 4 | 59 | 1 | 4 | − | − | 27 | 33 |
| Oleaceae | *Chionanthus* | ST | 92 | 40 | 1 | 1 | + | − | 30 | 33 |
| Loganiaceae | *Gelsemium* | V | 125 | 46 | 1 | 1 | + | + | 31 | 33 |
| Scrophulariaceae | *Veronicastrum* | H | 141 | 142 | 1 | 1 | − | − | 41 | 40 |
| Bignoniaceae | *Campis* | V | 84 | 85 | 1 | 1 | + | − | 29 | 33 |
| | *Catalpa* | T | 65 | 70 | 4 | 5 | − | + | 33 | 27 |
| Phrymaceae | *Phryma* | H | 117 | 198 | 1 | 1 | − | − | 33 | 37 |
| Rubiaceae | *Mitchella* | H | 7 | 148 | 1 | 1 | − | − | 35 | 37 |
| Caprifoliaceae | *Triosteum* | H | 160 | 128 | 6 | 4 | − | − | 36 | 40 |
| | *Weigela/ Diervilla*‡ | S | 140 | 167 | 12 | 3 | − | − | 36 | 41 |
| Gramineae | *Zizania* | H | 168 | 151 | 1 | 2 | − | − | 44 | 38 |
| | *Diarrhena* | H | 62 | 57 | 2 | 1 | − | − | 45 | 35 |
| Roxburghiaceae | *Croomia* | H | 3 | 5 | 2 | 1 | − | − | 33 | 30 |
| Araceae | *Symplocarpus* | H | 56 | 112 | 2 | 1 | − | − | 45 | 40 |
| Liliaceae | *Heloniopsis/ Helonias*‡ | H | 10 | 6 | 4 | 1 | − | − | 39 | 38 |
| Orchidaceae | *Tipularia* | H | 21 | 68 | 4 | 1 | − | − | 40 | 34 |

NOTE.—Data are taken from range maps in Li (1952). Area, relative area of geographical range of genus estimated from weight of range cut out of photocopied maps (1 unit equals approximately 40,000 km$^2$); species, number of species per genus on each continent; tropical, presence (+) or absence (−) of genus from tropical latitudes; latitude, latitude (°N) of midpoint of geographical range. AS, Asia; NA, North America.

* Taxonomy from Li (1952).

† H, Herb; S, shrub; ST, shrub-tree; T, tree; V, vine.

‡ Sister genera in Asia/North America.

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