PLANT DISTRIBUTION IN RELATION TO THE GLACIAL BOUNDARY

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A consideration of plant distribution in relation to the glacial boundary involves, first, a knowledge of the present geographic distribution and edaphic requirements of species and communities, and, second, an attempt to interpret these distributions. Opinions may differ as to how extended a latitudinal area should be included, how far to the southward of the glacial boundary distributions were profoundly affected.

In a recent publication, Deevey (1949) has advanced the interesting but surprising thesis that "there has been sufficient time, and sufficient transfiguration of geography, for the pre-Pleistocene distribution pattern to be completely transformed in a very large number of cases." And, as a corollary to this, he states as a *principle* that "all distributions of species are taken to be of Pleistocene date in the absence of good proof that they are older."

I believe that each problem should be approached individually and without any preconceived "principle" concerning date when the pattern of distribution arose. There are few instances where "proof" of interpretations is possible. There is no more possibility of proof of a post-Wisconsin distribution date than of interglacial or preglacial dates, except on the area of Wisconsin drift where late-glacial and postglacial migrations are recorded in pollen diagrams.

In attacking such problems, we must obtain as accurate a picture as possible of present distribution; we must consider the environmental requirements of plants involved—for example, soil and moisture requirements, length of day (for some species require long days to initiate flowering, hence are latitudinally limited southward), and temperature range under which they are now growing naturally. We must, of course, admit the possibility that gradual changes in physiologic requirements have taken place and are taking place. We must realize that many species vary, physiologically if not morphologically, in different parts of their ranges (biotype variability). At the same time, we are justified in assuming that such changes are not of great magnitude; for example, that trees with thin more or less large leaves were mesophytes in the past as they are today, that xerophytes have not become hydro-mesophytes in the last 20,000 years or less.

We must consider events, from the present backward into geologic time as far as present or closely related species may have been living, for, except in the glaciated areas, vegetation earlier than the last ice advance, or even earlier than the onset of the first continental glacier, must be taken into consideration. The land was occupied, and occupying vegetation affects the habitat. We must consider the possible or probable shifts induced by *all* sorts of major environmental changes, physiographic as well as climatic.

All available evidence should be used—fossil evidence, and evidence concerning the environmental conditions of the past. Fossil evidence is very scanty in the unglaciated area. Evidence concerning soil-freezing phenomena is gradually becoming available. Microclimatic studies are suggestive. Chromosome studies are sometimes enlightening.

In a few instances, a genetic approach to problems of distribution has been possible. For discussion of such problems, the literature must be consulted.

Because of time limits, I shall emphasize plants of Appalachian and eastern interior range. I will include not only species occurring near to the glacial boundary, either in isolated stations or more or less generally distributed, but also certain

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species farther to the south, whose distributions have generally been conceded to be related to pre-Pleistocene physiographic history, but whose distribution patterns, according to Deevey, are a result of Pleistocene and post-Pleistocene movements.

When we consider species or communities whose ranges are in some way correlated with the glacial boundary—geographically, not necessarily causally—we find that they may be classified readily into groups, as northern, western, and southern.

A considerable number of species, general northward, appear to have a scattered distribution over the southern part of the area of Wisconsin drift, and rarely, if ever, occur south of the Wisconsin glacial boundary, except on the high northern Allegheny Plateau and Allegheny Mountains. A large proportion of plants illustrating this type of distribution are bog plants, which now remain in localized bog communities. Such distribution patterns are generally, and no doubt correctly, explained as due to northward migrations which followed the retreat of continental ice. But, does explaining bog relics as left behind during retreating migration of northern vegetation really explain them? Where did these bog plants spend the last cold period of the Pleistocene? Where, south of the glacial border, and within any reasonable distance of it, could they have found suitable edaphic environment? I consider this an unanswered problem, unless we concede the possibility that they occupied bogs in the detritus on or just within the ice margin. In northern latitudes, bog plants are growing today over permanently frozen subsoil.

Other species, with much the same type of distribution pattern as the bog plants, but with different edaphic requirements, occur in a few isolated stations not far to the south of the glacial boundary. *Taxus canadensis* is one of these, with its southernmost interior station on the bluffs of Tygarts Creek in Carter County, Kentucky, about 50 miles to the south of the glacial boundary, where it is out of accord with the accompanying vegetation (fig. 2). *Acer spicatum*, in a gorge in the same geographic area, has its next nearest station (Clifton Gorge, Greene County, Ohio) within the area of Wisconsin drift (fig. 3). *Thuja* on calcareous cliffs occurs, in the interior, as far south as southern Ohio, and in the Appalachian Valley, as far south as Tennessee. Such local occurrences, often far to the south of the area of general distribution, are related to local habitats affording suitable edaphic environment or, in some instances, protection against too great competition because the habitat is unsuitable to the regional vegetation. There is no evidence that such plants were formerly widespread as far south as these outposts, or, in most instances, that they ever occurred much farther south. Fragments of *Thuja* in Pleistocene deposits along the Mississippi River in Louisiana (Brown, 1938) may or may not have come from trees in the immediate vicinity. As to climate, *Thuja* tells little, for it thrives in the heat of the Shenandoah Valley as well as farther north. Lime seems to be a requisite. *Taxus canadensis*, although more northern in distribution than any other species of *Taxus*, none-the-less now displays too wide a latitudinal range to be interpreted as indicative of a very cold climate. It is thriving under the same climatic conditions as some of the larger-leaved species of *Magnolia* (figs. 4, 5).

The occurrence of prairie plants and prairie communities far to the east of the location of widespread prairie is a well-known phenomenon which needs no discussion here. The Prairie Peninsula extends into central Ohio (see Transeau's map, 1935). Prairie communities are well represented on the Wisconsin drift, where their occurrence is explained by eastward migration during the post-Wisconsin xerothermic period. Whether or not the well developed and often more xeric prairies of unglaciated southern Ohio are of the same age is questionable (Braun, 1928, 1928a). (These are the prairies concerning which Dr. Deevey credits me with the astonishing and incorrect statement that they differ from central Ohio prairies in that they contain no western species, but instead, coastal plain species!). The problem of age of these prairies is interlocked with that of the occurrence of southern species (both xerophytes and mesophytes) and of pronounced disjuncts (fig. 6) in the same geographic area as the prairies. Information on soil freezing during Pleistocene time, when available, may help to solve these problems.[1] It

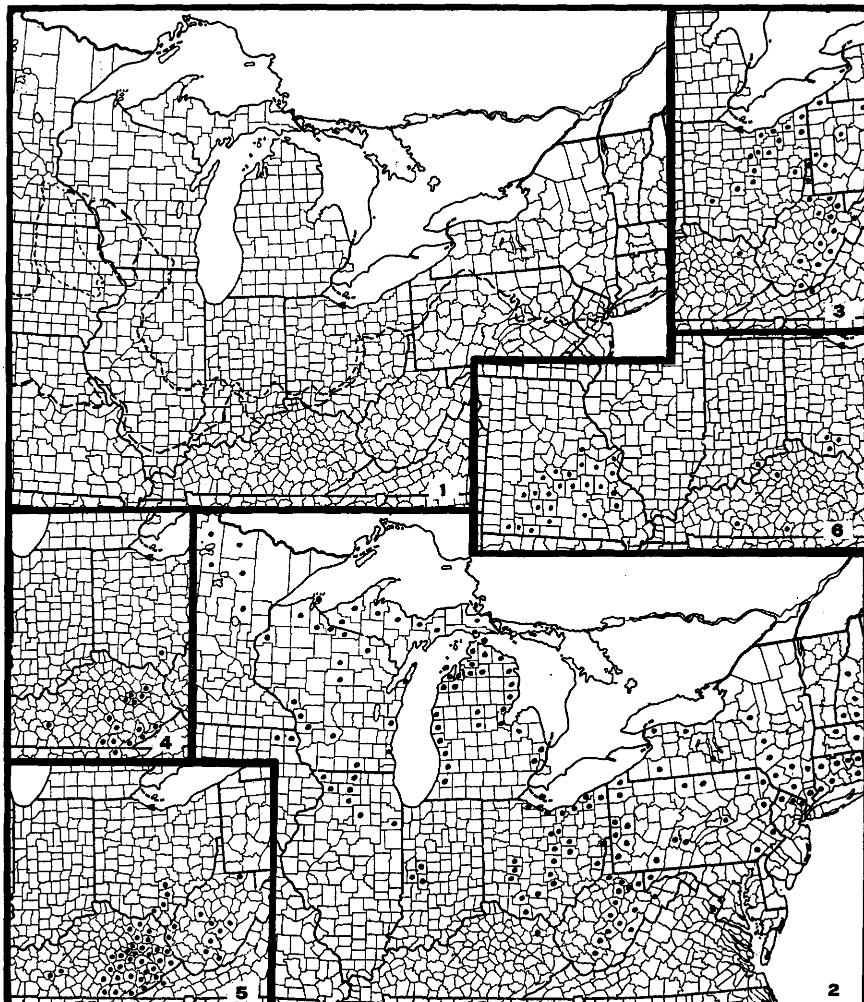


FIGURE 1. Map showing glacial boundary (long dashes) and boundary of Wisconsin glaciation (short dashes) where this is to the north of the limit of glaciation. (Iowan substage shown separate from Des Moines lobe of Wisconsin.)

FIGURES 2–6. Ranges of: (2) *Taxus canadensis* and (3) *Acer spicatum*, northern species with isolated stations south of the glacial boundary; (4) *Magnolia macrophylla;* (5) *Magnolia tripetala;* (6) *Leavenworthia uniflora*, an Ozarkian species with isolated occurrences in prairie communities of unglaciated southern Ohio, southern Indiana, and Kentucky, and in the Cedar Glades of Tennessee.

[1]This phenomenon was discussed on the field-trip which followed this symposium. Evidence of congeliturbation, although present, did not indicate severe frost action at a distance of 15 miles from the Wisconsin ice border.

must be remembered that prairie plants today, at latitude 50°N, are subjected to a rigorous climate, perhaps almost as rigorous as that of sheltered spots at latitude 39°N during a glacial age.

The interpretation of the present distribution of southern plants whose ranges overlap, reach, or fall short of the Wisconsin (or other) glacial boundaries is challenging.

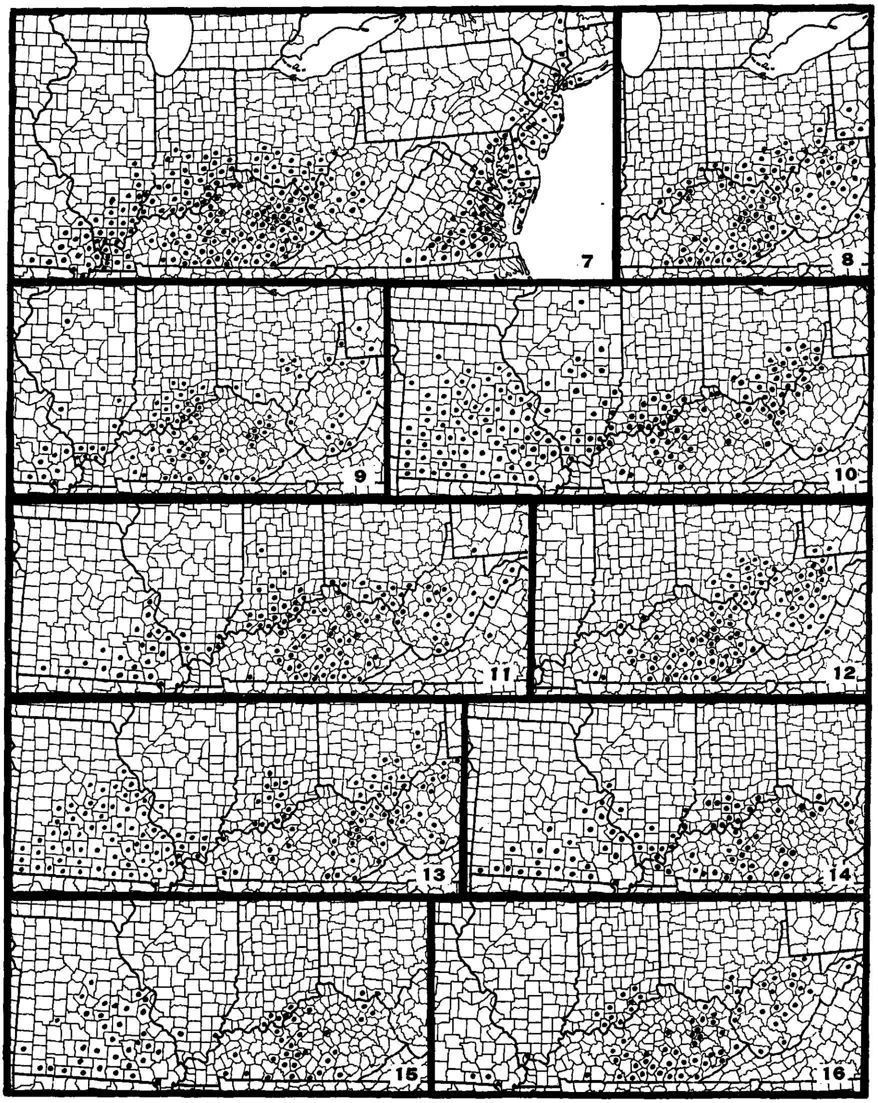
A considerable number of these southern species display evidence (based on behavior in succession) of present or very recent active migration onto the glaciated area. Sweet gum (*Liquidambar*) is one of these (fig. 7). River birch (*Betula nigra*) along most, perhaps all of its sinuous northern boundary is another. However, there are peculiar interruptions in its range in southern Ohio and Indiana (and to a lesser extent, in the range of *Liquidambar*) which correspond with places where the Ohio River was non-existent in pre-Illinoian time, and which need investigation as to possible edaphic or historical cause.

Some species, for example *Aesculus octandra* (fig. 8), have made little progress into glaciated land. This tree is a climax species whose advance must await slow changes of forest environment, and thus far it has been able to move but a short way within the Illinoian drift area, although other climax species, notably beech and sugar maple, have gone far north. A number of shrubby and herbaceous species, at least some of which (for example, *Aralia spinosa*, *Gillenia stipulata*, *Salvia lyrata*) are not climax species or are not dependent on maturity of soil, have comparable distribution patterns (figs. 9, 10, 11). Plants of immature soils or of earlier successional stages should be able to migrate sooner than climax species. For example, redbud (*Cercis canadensis*) has gone far, even though severe winter cold does kill its flower buds. Why not the ones mentioned? And why do the ranges of other such species not extend to the glacial boundary, or at least not to the Wisconsin glacial boundary, although suitable edaphic sites do exist within the glacial boundary?

Many southern plants reach the limits of their more or less continuous geographic ranges a short distance south of the glacial boundary. Others occur in isolated spots south of the glacial boundary but to the north of their area of continuous ranges. Species displaying such distribution patterns have aroused considerable discussion, and as yet there is no decisive evidence as to cause of, or date of origin of such patterns (figs. 4, 5, 12–16). Included here are the large assemblage of species, mostly Appalachian (but which Deevey calls coastal plain), species of which Transeau (1941) and Wolfe (1942) have written. Some of these species are pronounced mesophytes, some are xerophytes. If the present range, or at least its northern part, is of post-Pleistocene date, as Dr. Deevey's thesis asserts, we must account for the northward progress of mesophytes at some date (presumably during a warm moist period) and of xerophytes at some other time (presumably the xerothermic period). But, we must also explain why the ranges of a considerable number of both groups of species—species of very unlike habitats—stop at more or less the same place, and where there are no discernible climatic or soil boundaries. It is this latter feature, and the localization of disjunct occurrences in places unaffected by certain Pleistocene events, that has led to the explanation that ranges were terminated during an ice advance. When we consider the very different microclimates of rugged areas (as Dr. Wolfe has pointed out in this symposium), the existence of small local refugia seems possible, from which repopulation of the surrounding area could have taken place. This brings to mind *Sullivantia*, a plant of moist shaded cliffs near the glacial boundary in Ohio and Indiana, a plant sometimes growing near cave entrances or sinks, where temperatures vary but little.

Certain features of distribution, well marked in the hilly and rugged western border of the Appalachian Plateaus, from southern Ohio southward, are not seen in sections of less relief to the east or to the west. This lends weight to the idea of

Pleistocene refugia in the hilly strip. And if there were such refugia, then a part of the vegetation is old, at least pre-Wisconsin, and if pre-Wisconsin, then just as possibly older.



FIGURES 7–16. Ranges of: (7) *Liquidambar Styraciflua*, a southern species actively migrating into glaciated territory; (8) *Aesculus octandra*, (9) *Aralia spinosa*, (10) *Gillenia stipulata*, and (11) *Saliva lyrata*, southern species whose ranges reach or extend slightly into glaciated areas; (12) *Oxydendrum arboreum*, (13) *Cunila origanoides*, (14) *Agave virginica*, (15) *Rhamnus caroliniana*, and (16) *Euonymus americana*, southern species with very unlike edaphic requirements, but whose ranges terminate south of the glacial boundary.

Examination of this rugged western margin of the plateau a little farther south discloses the presence there of at least three local endemics. One, *Conradina verticillata*, is a streambank species; the other two, a *Solidago* and a *Eupatorium*, are inhabitants of "rock-houses," the most protected sites in the entire area, sites with the least temperature range. They do not grow outside these shelters, a fact which strongly suggests their derivation from milder climate Tertiary species. It also discloses the disjunct occurrence there of a number of species commonly thought of as confined to the Southern Appalachians, and usually referred to as Tertiary relics (***Rhododendron catawbiense***, *Stewartia ovata*, *Astilbe biternata*, for example). Discussion of these under "distribution in relation to the glacial boundary" may seem far-fetched. However, as Deevey's hypothesis states "that glacial chilling in the southeastern States must have been fairly extensive, and that the warmth-loving species, including many or perhaps most of the 'Miocene relicts,' survived in peninsular Florida and in Mexico, and have subsequently migrated to their present localities," it becomes necessary to consider these Tertiary relics in connection with glacial border phenomena. There is no evidence to support the hypothesis that the "Miocene relicts" lived in Florida during the Pleistocene. In Florida peat deposits, pollens of pines, oaks, hickories, grasses, ferns, palms, etc., are found along with spruce and fir pollen (Davis, 1946), but pollens of mesophytes and Appalachian species are absent. Neither is there evidence of Mexican abode. Just because a number of widespread eastern American plants—"typical plants of the eastern United States," to use Fernald's words (1950)—have been found in the mountains of Mexico, it cannot be assumed that the rare and local "Miocene relicts" migrated there and, returning, became concentrated in or about the Southern Appalachians. Moreover, the idea of making peninsular Florida a veritable Noah's ark for plants does not take into consideration the edaphic requirements of the plants concerned. Can anyone who has seen ***Diphyllaea***, for instance, in the cool, moist coves of the Smokies, imagine it in a coastal plain environment? Deevey apparently contradicts himself in this respect, for while discussing the Pine Barrens he says that it is "doubtful that the Pine Barrens or any other part of the coastal plain constituted an ***important*** refuge for mesophytic species." However, when he wants to dispose of the "Miocene relicts" of the Southern Appalachians, he postulates that they must have gone to the Floridian section of the Coastal Plain, or, crossing a great extent of plains, to the mountains of Mexico. He inconsistently assumes that the Southern Appalachian endemics could not have stayed in this geographic area, while beech stayed in the northern Appalachians, and hickory in the Middle West. (He speaks of "beech, moving out from its center of refuge in the northern Appalachians" and of "hickory, moving eastward from centers of refuge in the middle West."). But why dispose of the Tertiary relics? Because "Cooling sufficient to permit the growth of spruce and fir forests on the summits of the Appalachians should have wiped out the remarkable relicts of the Miocene flora, some of which now occur on some of the same summits." This statement seems to imply post-Pleistocene re-entry of these "relicts of the Miocene flora." However, as spruce and fir forests ***now*** occupy the summits and upper slopes of some of the Southern Appalachians, and the Tertiary relics are there, too, it is reasonable to believe that such a combination of species could have been present in glacial ages, as now, and could have persisted since Tertiary time.[2] All of the evidence indicates that they are localized in and around the Southern Appalachians because this area was, in middle Tertiary time, the only large mountainous area of the East, and that they have continued to occupy this area to the present time (Braun, 1950, Chapters 16, 17).

A significant feature, and the one which best justifies discussion of Southern Appalachian plants in this paper is that recent investigations (King and Stupka, 1950) have shown that there was a timber-line in the Great Smoky Mountains—probably in the last cold phase of the Pleistocene; and that this timber-line was at

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[2]The fir (*Abies Fraseri*) is a Southern Appalachian endemic, *not* a northern species; the spruce (*Picea rubens*) is not a constituent of the boreal forest.

an elevation between 4000 and 5000 feet (more than that above the lowered ocean of glacial stages). The higher peaks now extend above the spruce and the spruce-fir zones, and are occupied by Fraser fir forests; they are close to a tree limit. Depression of altitudinal belts by 2000 feet, the amount indicated by recent studies, would still allow a band 1000 to 2000 feet in vertical height to serve as a refuge for plants forced to move to lower and warmer belts, belts below the spruce zone in which a number of the endemics occur. This lower band, up to an elevation of 3000 feet, more or less, and all the surrounding area in all directions, would have been suitable for the growth of deciduous forest—as it is today. The Wisconsin glacial border was less than 250 miles to the north of the Great Smoky Mountains, and if zones were depressed as rapidly as 1000 feet for every hundred miles, this would bring the deciduous forest zone to the plateau level about 50 miles south of the ice. Or, depression might have been gradual at first, more rapid as the ice margin was approached. Very few spots in the northern half of the rugged western border of the Cumberland and Allegheny Plateau reach an elevation as high as 1400 feet. A band, 50 miles wide, to the south of the southern lobe of the ice sheet in Ohio, would seem to be more than adequate, as topography in the vicinity of Morgantown, W. Va., does not appear to indicate periglacial conditions (Denny, this symposium). Morgantown is little farther from the glacial border (which is to the west as well as to the north) than is the southern tip of Ohio, and about 75 miles farther north. Furthermore, as the evidence, to date, does not "furnish unequivocal proof of the presence of permafrost" even in northern Pennsylvania, 200 miles north of and over 1000 feet higher than the Ohio and Kentucky areas where species distribution indicates Pleistocene survival, there appears to be no sound reason for postulating complete southward retreat of deciduous forest species.

We may believe, then, that the deciduous forest zone, although narrowed, maintained itself on the Appalachian Plateaus in southern Ohio and Kentucky while glaciers extended southward in Ohio. Most of its species can endure temperature extremes far greater than those in this area today. We may believe, then, that during glacial epochs, some species now showing a spotty distribution near the glacial boundary may have persisted in local favorable habitats. We may believe, also, that the ranges of many southern and Appalachian species were abruptly terminated at varying distances south of the glacial boundary. These have been able to advance greater or less distances toward or onto the glaciated area.

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(Some additional data from the author's records and from manuscript maps prepared a number of years ago by **E. N. Transeau.** Additional data from West Virginia supplied by **Nelle Ammons;** for Illinois, by **G. N. Jones;** for Missouri, by **J. A. Steyermark.**)