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Indiana as a Critical Botanical Area

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The student of field botany recognizes that the plants of the present are the results of conditions of the past. He soon discovers, in comparing present with past vegetation, that Nature is not static, that even in short periods of time new colonies of a particular species may appear in a given locality, thrive for a while and even entirely disappear; that the old familiar collecting grounds take on such different aspects, if he is absent for a few years, that they are hardly recognizable; that the field which yielded crops a few years ago is, when abandoned, first a weed patch, then a briar patch and in succession thicket, mixed hard- and soft-wood forest and ultimately beech-maple or oak-hickory hard-wood forest. As topography and climates, including both temperature and rainfall, change over longer or even shorter periods of time, so does the vegetation change, even more markedly,—so that truly there is a struggle going on in Nature, a struggle which means life and death, survival and extinction; and there is evolution of vegetations just as there is evolution of structures within individuals and races.

In these struggles of the past, Indiana has often been a critical battleground, the scene of vegetational front-line trenches, the land of advance and retreat; and even today we shall see that over half of the species of ferns and seed plants occurring in the state are, in Indiana, on the borders of their present-day range and are, therefore, on critical ground. So, I have chosen to speak briefly to-night on "Indiana as a critical botanical area."

Pre-Pleistocene Uniformity

Even though our knowledge of the vegetation of past geologic time, so far as Indiana as a particular area is concerned, is exceedingly scant, what we know of the vegetation of North America in general leads us to the conclusion that Indiana has not always been the critical botanical area which it appears to have been during glacial time and from then to the present.

Available data (Berry, 2, Knowlton, 17) seem to indicate quite conclusively that the entire continent of North America was low and heavily wooded during Cretaceous time and that rainfall was abundant and climate much warmer than now, as well as quite uniform, even far into the Arctic circle. While the ancestors of our modern plants were present at this time, the flora as a whole had quite a different aspect from that of today. That the Cretaceous was a period of both great uniformity and great mildness appears certain from the fact that both temperate and subtropical species flourished side by side and occurred as far north as Greenland and Iceland. Magnolia, sassafras, willow, oak, tulip-poplar, walnut, and other temperate species grew side by side with such tropical or subtropical species as fig, palm, camphor, alligator pear, and others. These same mild and uniform conditions apparently continued far into

Tertiary time with maximum warmth being reached in early Oligocene, when temperate forests covered territory as far north as Alaska, Greenland, and Spitzbergen.

The dawn of Miocene time found our part of North America covered with a vast forest comprising many species identical with, and others very closely related to, those of our present day. Hickories (Carya), oaks (Quercus), walnuts (Juglans), sassafras, beech (Fagus), ash (Fraxinus), iron-wood (Carpinus), sycamore (Platanus), sumac (Rhus), gum (Nyssa), cypress (Taxodium), maple (Acer), elm (Ulmus), linden (Tilia), hackberry (Celtis), persimmon (Diospyros), tulip-poplar (Liriodendron), sweet gum (Liquidambar), magnolia (Magnolia), chestnut (Castanea), and many others appear to have been flourishing in what has been designated (Braun, 3) as a great Tertiary undifferentiated forest-climax, remnants of which may still be found today in the Ozarks and southern Appalachians. The continued uniformity of climatic conditions over much of the northern hemisphere is indicated by the fact that this great undifferentiated Tertiary forest was prevalent over most of North America, Europe, and Asia. The cypress (Taxodium) is known from Miocene beds of Washington and Virginia and from the same period as far south in Europe as Italy and as far north as Greenland and Spitzbergen, thus indicating a climate then at least as mild as southwestern Indiana of today, where its modern descendant reaches its present-day northern limits.

With the close of the Miocene the long period of uniform and mild climate gave way to a lowering of the temperature over the entire northern hemisphere, and by the time the Pliocene period was well advanced the elevation of the Rocky Mountains had reached sufficient height to cut off moisture-laden winds from the west, thus forcing the great undifferentiated forest eastward. This, together with the coming of the glaciers, which, in Pleistocene time, forced the temperate undifferentiated forest southward, very greatly reduced the area occupied by the forest, broke up the great uniformity of climate which had persisted from middle Mesozoic to middle Cenozoic time, and leads us to the time when Indiana presented a climatic and vegetational individuality and began to become a truly critical botanical area.

Pleistocene Battle-Ground

The coming of the glaciers was probably slow enough to permit most of the plant species to migrate southward in advance of them. In North America the pathway for this southward migration was little obstructed because the great mountain systems, then as now, lay in a direction essentially parallel to the path of the moving ice sheets, thus leaving the great valley between as an open highway for migration southward. The limits of maximum southward extension for the last two of these ice invasions occurred in Indiana. The distance beyond the ice sheet to which the temperature was lowered beyond the limits for plant growth obviously varied with the requirements of particular plant species, and in the case of many of them Indiana became the temporary limit of northern distribution. Retreats of the ice were followed by movements of plants northward, only to be forced south again by

subsequent advance of the ice. These alternate southward and northward movements of ice and plants probably occurred many times in eastern North America. Indiana was a critical area for this plant-climate struggle because the edges of maximum extension of each of the last two ice sheets (Illinoian and Wisconsin) are to be found within her borders.[1]

Post-Pleistocene Activity

The final northward retreat of the glaciers was followed by a northward migration of plants. Most of the present day flora must be looked upon as relatively recent in its occupation of the state because only the Knobs area in the south central part is entirely unglaciated; it is hardly likely that any considerable portion of this unglaciated area was suitable as a plant habitat for any of the fern or seed-plant species which now occupy it. It is probable that no point in the area was more than 50 miles from the maximum extension of the Illinoian ice-edge.

We cannot say certainly just how close to the receding ice sheet the plants followed in their return migrations northward, but if we are to judge by the behavior now shown by plants in Alaska where glaciers are today receding, the plants must have kept close pace with the withdrawing ice. It is probable that this northward 'trek' of vegetation showed a zonation not unlike that today shown by vegetation from farthest arctic regions southward; i.e., nearest the ice edge was tundra, and farther away in succession were boreal shrubs, boreal forest, northern coniferous forest, and northern hardwood deciduous forest. The latitudinal width of these zones of migration is hardly to be thought of as comparing with the latitudes shown by their present-day distribution.

The fossil records obtained from study of peat from the bogs of Indiana and adjacent territory (Sears, 28; Houdek, 16; Lindsey, 19; Artist, 1; Fuller, 12, and studies now under way in our laboratory) all bear positive evidence that the great Miocene forest, concentrated into the infinitely smaller area of the southern Appalachians by the rising cordilleras of the west and the advancing ice sheets from the north, now expanded to take on some of its former extensiveness. But the expansion was mostly in the form of differentiated associations, each segregate coming to occupy that area and climate best suited to it. The order of its extension into our territory was fir (Abies) first, followed by spruce (Picea), then pine (Pinus), and finally broad-leaved hardwoods of the forests of today.

This northward movement has continued until we find fir and spruce dominating the northern coniferous forest of southern Canada and northern New England, Michigan, Wisconsin, and Minnesota today, while the broad-leaved hardwoods have become segregated (Braun, 3) into smaller segregates, each becoming dominant and climax types adjusted to particular climatic conditions in areas farther south. The climatic uniformity of pre-pleistocene time thus became segregated into climatic zones and belts and areas whose borders (limits) have been involved in

[1]As a result of the action of this Academy and the energy of its committee on Geological Survey, the locations of these ice edges are marked by appropriate markers where they cross main highways in southern Indiana.

many changes. This has resulted in transforming vegetational uniformity into vegetational differentiation. Four or five of these segregates from preglacial uniformity are today battling for existence and competing with each other for space in Indiana, viz., beech-maple (Fagus-Acer), oak-hickory (Quercus-Carya), white pine-hemlock (Pinus-Tsuga), and oak-beech (Quercus-Fagus), fir and spruce having entirely disappeared and white pine-hemlock almost so. The fact that fir and spruce and pine once flourished in our area is shown by the records of fossil pollen from every bog so far studied in Indiana. These studies all show that from an early abundance of fir and spruce these species declined in favor of pine and broad-leaved species, finally disappearing in the order named. For these species Indiana was a critical botanical area. The fate of white pine has been a little different; reaching its greatest abundance when both fir and spruce were well on their decline and broad-leaved trees were already in dominance, it held its own for a few centuries and then declined much as did fir and spruce except that in reduced percentages it has persisted until the past few centuries and is still to be found in a few places in Indiana. For the pine, also, indiana was and, to some extent today is, a critical area. Whether pine showed forest dominance between the fir-spruce and broad-leaved dominance periods generally in Indiana remains to be determined after more bogs have been studied. Houdek (16) found a pine-dominance in Center Lake in Steuben County, but this dominance was not found by him in the Mineral Springs bog, nor by Lindsey (19) in the Merrillville bog, in Porter and Lake Counties respectively. Artist (1) has shown that farther north (in the Volo bog in Lake County, Illinois) spruce remained an element of the forest for many centuries longer; and still farther north in Minnesota the spruce-fir forest is thought to be at present invading the deciduous forest (Fuller, 12). It is therefore probable that the battle between conifer and deciduous forest, fought thousands of years ago and won in Indiana by the deciduous forest, is still being waged not far north of the former Indiana battle ground. A lowering of the general temperature only a few degrees might bring this conifer-deciduous battle-front back to Indiana soil.

Boreal and Glacial Disjuncts

Evidence of northward migrations of plants following withdrawal of the glaciers is not limited to trees whose story is told by the pollen from peat bogs but is also written on the present-day landscape in the form of disjunct colonies of northern and boreal species now in isolated and scattered sites far south of their main distribution. Time and space will here permit us to consider but a few of the most striking of these.

The lady's Slipper, *Cypripedium reginae* Ait., (Parker, 23, Welch, 34), characteristic of wet, mossy areas of our northern woods, is found in the northern two tiers of counties, but is to be found also in three stations approximately 100 miles farther south in Montgomery, Fountain, and Henry Counties. The False Lily-of-the-Valley, *Maianthemum canadense* Desf., (Parker, 23, Welch, 34), has very similar range with a disjunct station in Putnam County. The Shin-leaf, *Pyrola americana* Sweet and *P. elliptica* Nutt. (Parker, 23), characteristic of northern

coniferous woods, is found in a few scattered localities in the northern two tiers of counties and again in disjunct colonies nearly 150 miles farther south in Monroe County. The Rough-leaved Dogwood, *Cornus rugosa* Lam., characteristic of rocky mountainous woods of the north, is limited to the northern tier of counties except for one station on a steep bluff, known as "Mill-cut Backbone", in the Pine Hills Region of Motgomery County. The Yew, *Taxus canadensis* Marsh., abundant in the coniferous woods of the northeast, occurs in Indiana in four stations, all of them steep rocky bluffs, viz., Turkey Run State Park, Pine Hills, and the Shades in Montgomery County, and along Walnut Creek in Putnam County.

The Bush Honeysuckle, *Diervilla lonicera* Mill., abundant in dry and rocky wooded slopes of the northeastern part of North America, occurs in sandy areas in the northwestern corner of the state and in Steuben County, and has two disjunct stations, one comprising but a few individuals on Bear Creek in Fountain County and the other with more numerous individuals on Turkey Backbone in the Pine Hills Region in Montgomery County.

Another species which gives us an interesting glimpse into the past is *Habenaria clavellata* (Mx.) Spreng., growing in peat moss in a bog about ten miles southeast of Bloomington. The nearest neighboring station for this little plant characteristic of northern woods is in Lake and Porter Counties. This species must have survived adverse conditions of its habitat for thousands of years, only holding its own without advance because the bog in which it occurs is not large and has been shown by Potzger (25) to be at present in a stage of advance rather than the retreat which is characteristic of most Indiana bogs. It may be that this bog has had its ups and downs through the milleniums that have passed since the northern plants migrated back over this territory, never being able to develop far but still holding on and supporting today a flora which includes a number of typically northern species such as *Alnus rugosa* (DuRoi) Spreng., *Dryopteris cristata* (L.) A. Gray, *Osmunda cinnamonea* L., *Osmunda regalis spectabilis* (Willd.) Gray, *Sphagnum*, and *Ilex verticillata* (L.) A. Gray. The club-moss, *Lycopodium complanatum flabelliforme* Fernald, shows a similar disjunct distribution though a very different type of habitat. This species, very characteristic of the northern coniferous forest, occurs in Lake, Laporte, and St. Joseph of the northern tier of counties and has been reported by Welch (33) and Welch and Price (34) for Monroe, Martin, and Putnam Counties, over 100 miles from its northern Indiana stations.

The Wintergreen, *Gaultheria procumbens* L., typical of northern forests and Appalachian highlands, occurs in the northern two tiers of counties, and then again in disjunct stations in the Pine Hills area of Montgomery County and in Monroe, Crawford, and Clark Counties. These outlying stations are each approximately 60 miles from the nearest adjacent station. The Mayflower, *Epigaea repens* L., shows a similar distribution except that disjunct areas were known only in Monroe and Brown Counties.

Every one of the disjunct stations for these relict species represents a critical botanical area in Indiana, where each of the species has

been able to survive since early post glacial times, while in territory immediately surrounding each station the species in question has lost out in the competition with others while its kin have gone on farther north. *Betula populifolia* Marsh. exhibits a peculiar distribution in Indiana. As shown by Deam, it is found in the western half of the northern tier of counties in Indiana (viz., Lake, Porter, Laporte, and St. Joseph) but is found neither west of us in Illinois, north of us in Michigan, nor east of this area in Indiana or Ohio. Apparently this Indiana distribution represents a glacial disjunct from the present-day distribution farther east and northeast in Ontario and New England.

The hemlock, *Tsuga canadensis*, is an illustration of a relict of a northern segregate of the Tertiary undifferentiated forest. In Tertiary time there was no well-marked distinction between boreal and temperate flora. Such a differentiation came later (Braun, 3), as a result of both prairie formation from the west and glacial formation from the north. As this differentiation came, we find Tsuga occupying those habitats more nearly similar to that of present-day northern coniferous forests. Glacial retreat was followed by migration of hemlock northward just as other floral elements, better suited to cooler climates, migrated northward. In this migration disjunct stations were left both in glaciated and unglaciated areas of Indiana. Miss Parker (23) maintains that Indiana was not in the main path of migration of hemlock from its southern Appalachian haven during the glacial period. This may be true, but the evidence upon which her conclusions are based is not entirely trustworthy. Her conclusions are based upon "The absence of pollen (hemlock) in the bottom of the bog" mentioned above (one in Porter County (Houdek, 16) and one in Steuben County, its scarcity in the upper part, and its absence in other peat bogs south of these two. She concludes that this indicates "that this species was not a member of the northern vegetation that retreated northward with the melting of the glacier." In the first place, it should be pointed out that data have been published for but two other bogs in Indiana. In one of these, the Merrillville bog in Lake County, no attempt was made to differentiate pollen of Tsuga from what was listed as "unknown species". In the second place, it is generally recognized by pollen workers that pollen of Tsuga was not preserved from decomposition under the conditions that prevailed in most bogs during deposition of peat. No data from Indiana are available south of the northern tier of counties. Whether Indiana was or was not in the main path of northward migration of hemlock, we were at least within the fringe of this movement, and, so, Indiana again became a critical botanical area, west of which the hemlock either did not go or at least has not survived to the present.

White Pine (*Pinus strobus* L.), fairly general over Indiana in early post glacial times, if we are to judge from the fossil pollen record from bogs, has left today but a few stations as mementos of its former distribution. Only one of these, that in the Pine Hills area of Montgomery County, presents any evidence of being able to maintain itself. In one other station, that near Merrillville (Lindsey, 19), it is likely to be displaced ultimately by broad-leaved trees, in this case oaks, thus giving us nearly the final scene of the drama begun thousands of years ago

when broad-leaved trees moved northward behind the phalanx of conifers following the retreating ice. Thus, not only has Indiana been a critical botanical area for these competing species in the past, but the age-old struggle is still going on, even though these relict species are fighting losing battles.

Prairie

Indiana again appears as a strongly dynamic botanical area when the limits of the prairies are studied. How many times the prairies have advanced across the state following a long dry period, only to retreat again in front of the advancing forest during a more humid period, no one can tell. But the evidence is unmistakable that in this ever-continuing struggle Indiana has been the scene of much vegetational strife in the past.

The chief evidence today is not only the striking lobate appearance of the prairie areas of Indiana, so aptly referred to by Transeau (30) as the "Prairie Peninsula", but the hundreds of small disjunct prairie patches located in many counties of the state. The strategic position of Indiana is shown in the fact that here we are on the eastern limits of present-day paririe. From the standpoint of plant geography prairies occur under two sets of conditions in Indiana. In the northwestern corner of the state they occur in a very lobate distribution and under a set of climatic conditions which make them climax for the area, and here we find the margin of the prairie today. But farther east, and in hundreds of sites scattered well throughout glaciated portions of the state and, to some extent even in unglaciated portions, we find disjunct prairie patches maintaining themselves under climatic conditions which favor the forest as a climax. These patches are able to maintain themselves for local edaphic, physiographic, or artificial (man-made) reasons and thus represent relics of a former prairie extensive over this region when much drier conditions prevailed. Farther east, in Ohio, Transeau (30) has shown that prairie communities are now limited to sites known to have been prairie at the time of the early settlers and are, thus, only relic patches. Indiana is a critical botanical area, not only on the prairie margin and on every site where relic prairie patches occur, but also we find that we are on the eastern limits of the necessary set of climatic conditions which will permit prairie indicators to invade openings in forest areas. Transeau (30) has shown that prairie species do not invade forest openings in Ohio, but farther west in Illinois and Iowa invasion of secondary forest communities by the prairie is more common. In Indiana probably the most frequent prairie invader of forest communities following cutting is *Andropogon scoparius*. Another prairie species, found much less frequently invading forest communities and limited apparently to sandy ridges dominated by black oak, is the side-oat grama grass, *Bouteloua curtipendula* (Mx.) Torr.

When soil conditions in sites occupied today by prairie indicators are taken into account, it is seen that prairie associations occur on all sorts of soil so that edaphic factors can hardly be considered as determiners. They occur on soils ranging from light sandy to heavy clay, even the extremely finely divided clay soils of the Illinoian drift, and

under physiographic conditions ranging from the level plains of the northern part of the state to upland ridges of the Knobs area in the south central part. It is apparent that civilization and climate, especially rainfall, are the chief determining factors. A study of the rainfall and relative humidity maps prepared by Visher (32) show that precipitation is less in prairie areas than in those bordering them. This is true of average annual, average winter, and average summer precipitation though the prairie area receives a greater percentage of the total rainfall during the growing season than other areas of the state. As Transeau (30) has shown, the forest climax invaded by prairie communities is always oak-hickory and never beech-maple. This is in accord with the conclusion that climatic factors are more important prairie determiners than soil factors. Oak-hickory is the most xerophytic of the forest climax associations occurring in Indiana. Beech-maple occurs on sites sufficiently mesophytic to permit other species to crowd out prairie species, and, hence, we find prairie species invading those forest areas most nearly climatically like the true prairie. Transeau has also pointed out that rainfall is notably irregular in its areal distribution in the prairie areas, some areas being affected one year and others in other years. Irregularity of rainfall is a matter of very much greater critical importance to plants than average rainfall, and this irregularity, much more than averages, becomes a determining factor in prairie limitation.

A number of plants typical of the prairie, and to be looked upon as prairie indicators, reach the eastern-most limits of their range in Indiana, i.e., *Amorpha canescens* Pursh., *Brauneria pallida* (Nutt.) Britton, *Coreopsis palmata* Nutt., *Helianthus rigidus* (Cass.) Desf., *H. Maximiliani* Schrad., *H. petiolaris* Nutt., *Petalostemon candidum* Mx., *P. purpureum* (Vent.) Rydb., *Solidago glaberrima* Martens, *S. longipetiolata* Mack. and Bush, and *Stipa comata* Trin. and Rupr.

Climax Forests

How really critical Indiana is as a dynamic botanical area is impressed upon the student of Indiana plant geography when an attempt is made to classify the forest types. Any classification that is not based upon detailed quantitative analysis from a successional point of view can have only temporary value because forests change as they develop from youth to maturity. In dynamic plant geography the term "climax" is applied to the ultimate type of vegetation which will be supported and permanently maintained by the climate of an area. In every case the succession moves toward the highest degree of mesophytism capable of being supported by the climate of the area. It makes no difference whether the local edaphic conditions begin with the hydrophytic side of the sequence or with the xerophytic side, the succession in either case procedes toward mesophytism. Our studies (Dr. J. E. Potzger's and mine), based upon detailed quadrat analyses and following the conceptions of Clements (7), lead us to the conclusion that all of the types of forest communities occurring in the state may be reduced to three climax forest types, viz., beech, beech-maple, and oak-hickory. In addition, we have recognized relics of the hemlock-white pine-northern hardwoods forest in the relic colonies of hemlock, hemlock-white pine, and

white pine (Friesner and Potzger 9, 10, 11) found in a few disjunct areas within the state. The presence of these northern relics of a former climatic climax are living evidence of change in climate in post-glacial times, and their continuation in the particular sites where they now occur is due to the fact that local conditions of soil and microclimate permit them to survive in competition with the sea of vegetation in which they are but isolated islands, thus making their borders critical zones in Indiana vegetation.

The best evidence of vegetational struggle and the critical character of Indiana as a plant habitat comes to light when detailed study is made of the content and environmental conditions attending the beech-maple and oak-hickory climaxes. Beech-maple occurs as the climatic climax throughout most of the southern four-fifths of the state, but, as we travel northward, we find that roughly north and west of the Tippecanoe River the forests change to chiefly oak and hickory, while beech-maple almost entirely disappears. When we plot the line of differentiation between beech-maple climax and oak-hickory climax on the map of the state, we find that this almost exactly coincides with the zone in which the annual average rainfall changes from 38 inches to 35 inches (Visher, 32), and practically half of the oak-hickory climax area receives only 33 inches of rainfall annually. Rainfall during the growing months of June, July, and August also is the lowest here of any area in the state. Summer rainfall may not be so important as total rainfall for trees in this region of little relief so far as mere survival is concerned, but it is important from the standpoint of amount of growth, and this, in turn, affects vigor and, ultimately, survival.

In the southern four-fifths of the state beech-maple occurs as the climatic climax, but as Potzger (26) has shown, oak-hickory occurs on sites which are more xerophytic and beech-maple on sites more mesophytic. In such areas oak-hickory is always preclimax. We have quadrat studies of a considerable number of oak-hickory associations in which there are to be found no beech or maple seedlings. On these more xerophytic sites oak-hickory reaches an edaphic climax which will likely remain for a long period of time until edaphic conditions change. But, since edaphic conditions change more rapidly than general climatic conditions, and since the general climate supports beech-maple as a climax, we must classify oak-hickory here as preclimax to beech-maple. The situation with regard to oak-hickory here is quite different from that in the extreme northern part of the state. Oak-hickory in the southern part of the state is there chiefly for edaphic reasons and not for general climatic reasons, while they occur in the northern part because the general climate will not support a more mesophytic association. In the northern part of the state, oak-hickory occupies most of the forest sites, and all of those which have reached the climax condition so far as mesophytism is concerned. Beech and maple are seldom found in this oak-hickory area and then only on sites which are more moist than that which is climax for the area.

On the other hand, in the southern or beech-maple area, there are sites where the mature stand may be oak and hickory and the reproduction chiefly beech and maple, in which case it is clear that oak-hickory

is preclimax, while beech-maple is climax. In no case have we observed beech-maple as a mature stand with oak-hickory reproduction. Many of the finest oak-forests in Indiana, and those as nearly virgin as any to be found, such as Nash's woods in Posey County (Cain, 6) and Donaldson's woods in the Spring Mill State Park (Cain, 5), comprise considerable beech and maple and the reproduction in them is chiefly beech and maple, indicating again that oak-hickory must be preclimax in these areas. Equally fine and equally nearly virgin oak areas on other sites, such as the Mantell woods in Dubois County, have no beech-maple reproduction, and on these sites oak and hickory will probably enjoy such a long period of dominance as to become essentially climax. Under such conditions they would be looked upon as subclimax. (Potzger and Friesner, 24).

Studies of soil moisture and evaporation show very definitely that degree of mesophytism is the chief determining factor between these two associations on soils and in climates otherwise suited for either of them. Not only is the moisture content of the soil consistently lower in oak-hickory than in beech-maple sites, but also the evaporation demands made upon the plants for water are higher in oak-hickory. Studies of herbaceous flora growing in oak-hickory and beech-maple communities also lead to the same conclusion regarding higher degree of mesophytism in beech-maple communities than in oak-hickory. The herbaceous flora of beech-maple is decidedly vernal (Esten, 8) in character, while that of oak-hickory is much more definitely aestival and even more autumnal.

The only other climax forests of any appreciable consequence in the state are modifications of the above two, i.e., beech without the maple. Beech with a long subclimax of beech and white oak are the final forest stages on the finely divided clay soil forming the Illinoian drift of the Flats areas in southern Indiana on each side of the Knobs area. Beech may also be climax on similar sites wherever they may occur when the water table is not far below the surface. As Miss Braun (4) has shown, pin oak, sweet-gum, elm, red maple, and over-cup oak form prominent earlier successional members in these Flats communities.

Gordon (13) shows the mixed mesophytic forest identified in Ohio by Sampson (27) as a climax forest on his recent map of "major vegetation areas of Indiana". His conclusion as to the mixed mesophytic forest being climax or even dominant in the Knobs area of Indiana will not stand when based upon detailed quadrat studies. We have made detailed studies of a number of areas in the Knobs region of the state, and, while we have found areas containing linden, tulip, elm, walnut, red oak, white oak, black oak, scarlet oak, chestnut oak, beech, and maple, we have yet to find an area in which the dominants and the character of reproduction did not indicate the association to be either beech-maple or oak-hickory. Beech-maple communities contain more tulip, linden, red oak, elm, and walnut than do oak-hickory communities.

Hemlock and hemlock-pine occur in Indiana today only in a very few sites and are unquestionably relics of a former climatic climax. As such, they have been considered earlier in this paper under the heading of "relics".

Again we reach the conclusion that Indiana is today a critical botanical area in the struggle for dominance on the part climax forest associations.

Range Limits

The critical character of Indiana as a botanical area stands out strikingly also when we realize that over 45% of the present-day species are extraneous, i.e., are on the borders of their range in the state. This figure is probably much higher than actual facts would warrant if they were fully known. Unfortunately no data were available dealing with the complete flora of either Kentucky or Illinois. If such were available, no doubt the total number of species listed as occurring on the southern borders and on the western borders of their range in Indiana would be reduced. It is still more striking when we see that within the state are the critical zones marking limits of distribution for species of all types of higher vegetation: ferns, trees, shrubs, grasses, and other herbaceous forms. There are critical zones for northern species on the southern boundary of their range, for southern species on the northern boundary of their range, for western species on the eastern boundary of their range, and for eastern species, both Appalachian and coastal plain, on the western boundary of their range. Then, to climax it all, there are to be found a few endemics known only within the state.

A total of 392 species are on the southern borders of their range in Indiana in our longitude. Some of these are boreal species, but many others merely range to the north of us. Some may reach more southern latitudes either east or west of us but not in our longitude. A study of the intra-state distribution of these species shows that a number of critical zones occur marking the present-day known limits for these plants. Table I will show the critical zones for this group of species.

It will thus be noted that the Lakes area forms the critical zone for nearly three-fourths of the northern plants which are, in Indiana, on

TABLE I. NORTHERN EXTRANEOUS SPECIES

RANGE LIMITS	PERCENTAGES		
	Of Northern Extraneous Species	Of All Extraneous Species	Of All Species
Lake, Porter, and LaPorte counties only	23.00	9.81	4.50
Lakes area generally, exclusive of above	51.74	21.13	11.15
Wisconsin drift plain south of Lakes area	11.75	5.01	2.30
Illinoian drift plain	9.44	4.03	1.85
Unglaciated Area	4.08	1.24	0.80

the southern border of their range. The margins of Wisconsin glaciation and Illinoian glaciation, respectively, are critical zones for most of the remaining species of this group. Checking these critical vegetational zones with zones derived from metereological data, such as average annual rainfall, lowest and highest years of rainfall, length of average, longest, and shortest growing season, summer and winter precipitation, and temperature zones does not show any certain correlation. It appears that character of soil and amount of human interference are the most critical limiting factors. In any case, it is quite clear that somewhere in Indiana there occurs the critical zone delimiting distribution for many plant species of northern distribution.

A study of the intra-state distribution of the 297 species which are on the northern boundary of their range in Indiana shows that approximately 30% of them reach their northern limits in our longitude within the unglaciated portion of the state, chiefly in the Knobs area. Approximately 34% reach their northern limits in glaciated territory below the southern limits of the Wisconsin drift. Sixty-seven per cent of these southern species reach the northern border of their range at or below the southern edge of Wisconsin glacial drift. The remaining 33% reach the northern boundary of their range far in glaciated territory, about half of them reaching the Lakes area and the other half terminating their range in the Wisconsin drift area south of the Lakes area. These results are tabulated in Table II.

TABLE II. SOUTHERN EXTRANEOUS SPECIES

RANGE LIMITS	PERCENTAGES		
	Of Southern Extraneous Species	Of All Extraneous Species	Of All Species
Unglaciated Territory	30.24	9.81	4.50
Illinoian drift plain	34.94	11.34	5.20
Ohio and Wabash River Counties	3.36	1.09	0.50
Wisconsin drift plain south of Lakes area	11.75	3.82	1.75
Lakes area	19.48	6.32	2.90

This analysis reveals five general areas critical for these southern species, viz., (1) the borders of the unglaciated area of the state, (2) areas bordering the lower Wabash and the Ohio rivers, (3) the southern limits of Wisconsin glacial drift, (4) area of Wisconsin glaciation south of the Lakes area, and (5) the Lakes area. Rainfall belts show little correlation with these critical zones. The first four of them fall within the area of the state receiving an average annual rainfall of 40 inches or more, while the last occurs in the area receiving an average annual

rainfall of 33-35 inches. Rainfall, length of growing season, topography, and soil character probably combine to determine available moisture, and this composite of factors probably determines these critical zones.

Western species occurring in Indiana on the borders of their range form the smallest group of extraneous species found within the state. When the intra-state distributions of the 98 species comprising this group are studied, we find several critical zones marking the termini of distribution. Table III will reveal these critical zones and their relative importance.

TABLE III. WESTERN EXTRANEOUS SPECIES

RANGE LIMITS	PERCENTAGES		
	Of Western Extraneous Species	Of All Extraneous Species	Of All Species
Dunes and sandy areas	38.76	4.14	1.90
Lakes area, exclusive of above	16.32	1.74	0.80
Wisconsin drift south of Lakes area	12.24	1.31	0.60
Illinoian drift area	15.30	1.64	0.75
Unglaciated	4.08	0.44	0.20
Western two tiers of counties, exclusive of above areas	6.12	0.65	0.30
Elsewhere, not classified in any of above groups	7.14	0.76	0.35

It is to be noted that over half of these western extraneous species terminate their ranges in our latitude in the Lakes area, most of them in sandy sites. Approximately 67% terminate their eastern ranges north of the south limits of the Wisconsin drift area, while approximately 18% terminate their range south of this drift plain. Approximately 37% terminate their range within the western two tiers of counties.

It is likely that soil character plays the primary role in determining the critical zones for these species. Rainfall appears to play a prominent secondary role because nearly 36% of these plants terminate their range near the border of the zone of 33 inches average rainfall. An additional 27% terminate their ranges near the border of the zone of 35 inches average rainfall.

Eastern species occurring extraneously in Indiana fall mostly into two groups, viz., those characteristic of the Appalachian plateau, and, hence, both eastern and southeastern, and those characteristic of the coastal plain, some of which may range throughout the extent of the Atlantic Coastal Plain. Species characteristic of the Appalachian plateau are, for the most part, trees and shrubs such as the chestnut

(Castanea dentata), scrub pine *(Pinus virginiana)*, cucumber tree *(Magnolia acuminata)*, chestnut oak *(Quercus montana)*, tulip tree *(Liriodendron tulipifera)*, mockernut *(Carya alba)*, laurel *(Kalmia latifolia)*, and deerberry *(Vaccinium stamineum)*. Additional species are given by Parker (23) in her recent analysis of the Indiana flora.

Peattie (21) has listed over 60 species of plants occurring in the Indiana Dunes and elsewhere limited to the Atlantic coastal plain. Miss Hoober (15), in a manuscript not yet published, has listed over 90 species common to Lake, Porter, and Laporte Counties and the Atlantic Coastal Plain. An even larger number of species characteristic of the coastal plain find range limits within the state as a whole. The explanation for coastal plain species finding range limits in Indiana places them in three main groups. McLaughlin (20) and Peattie (21) have pointed out the presence of early post-glacial paths of migration leading into, and terminating for the most part in, the Dunes and Lakes Region of the state. They have also pointed out a path of migration up the Mississippi River, over which a number of species characteristic of the Gulf Coastal Plain have entered the southwestern and southern parts of the state. Pennell (22) has also shown that many species of the coastal plain have migrated both eastward to the coast and westward into Indiana from the Appalachian highlands. These species have terminated their ranges in Indiana, in some cases because they found here the limit of hospitable territory, and in other cases, no doubt, because they have not yet had time to migrate farther.

When the intra-state distribution of these plants, whose western range terminates in Indiana in our latitudes, is considered, we find again a number of critical zones. The Dunes area of the northwestern corner serves as the critical zone for over one-third of the 108 species. Over 57% terminate their ranges within the Lakes area. Over 16% find

TABLE IV. EASTERN EXTRANEOUS SPECIES

RANGE LIMITS	PERCENTAGES		
	Of Eastern Extraneous Species	Of All Extraneous Species	Of All Species
Sand areas in northwestern corner of state	37.00	4.36	2.00
Lakes area generally, exclusive of above	19.97	1.53	0.70
Eastern lobe of Illinoian drift	5.56	0.65	0.30
Unglaciated territory	16.67	1.96	0.90
Western lobe of Illinoian drift	7.41	0.87	0.40
Western border of State	6.48	0.76	0.35
Wisconsin drift plain south of Lakes area	6.41	0.87	0.40
Elsewhere	6.48	0.76	0.35

their critical zone in the unglaciated area of the Knobs region, and these are mostly trees and shrubs. The extremely finely divided clay soils of the Illinoian drift serve as the critical zone for an additional 12%, nearly all of which are herbs. Table IV presents these critical zones and their relative prominence.

Approximately 52% of these species have the western limits of their range in Indiana north of the limits of Wisconsin glaciation, while 30% have their western limits south of this zone.

Lindsey (18) has shown that 41% of our tree species are on the limits of their range in Indiana, and only 10% are found in all botanical areas of the state. This means that one area or another of Indiana becomes the critical limiting zone in the distribution of many of our common tree species. Twenty-six per cent of the tree species are exclusive to single botanical areas of the state.

Trefz (31), in a similar study of our shrubs, has shown that 56% of them are on the limits of their range in Indiana, while 23% occur in all botanical areas of the state. Forty per cent of them are exclusive to single botanical areas. A smaller percentage of the total shrub species than of tree species occur in each botanical area of the state.

Approximately 20 species and varieties appear to be endemic to Indiana. Of these 55% occur only in the Lakes area, 70% are limited to areas north of the southern limits of Wisconsin glaciation, and 15% occur only south of the limits of Wisconsin glaciation.

Comparative Degree of Criticalness in Each Botanical Area

The Dunes and Lakes area possess a larger percentage of the total flora of the state than any other botanical area. This area also is the critical limiting zone for approximately 50% of the extraneous flora of the state, the most of which are species of northern distribution occurring here on the southern border of their distribution. Miss Hoober (15) has shown that approximately 15% of the total Indiana flora is limited in Indiana to this botanical area. The strongest affinities for the flora of this area lie toward the north and northeast with next strongest similarity to the Appalachian mountain flora.

The southern boundary of Wisconsin glacial drift is the critical limiting zone for approximately 25% of the extraneous flora. These species are southern, reaching their northern boundary just south of the Wisconsin glacial boundary or northern, reaching their southern boundary just north of the glacial boundary. Approximately 14% of the extraneous species reach their limits in the Knobs or unglaciated area of the state. The most of these are southern species. Miss Guss (14) has shown that approximately 74% of the Knobs flora occurs in all other botanical areas of the state. Approximately 5% of the total flora of the state is limited in Indiana to this area. These exclusive species are chiefly Appalachian mountain species.

The lower Wabash Valley acts as a critical limiting zone for approximately 2% of the extraneous flora of the state. Most of these are southern and southwestern species, reaching their northern limits here; a few of them are western, reaching their eastern limits here; while a very small number are northern, reaching southern limits here.

The comparative criticalness of these botanical areas of the state is shown in Table V.

TABLE V. COMPARATIVE CRITICALNESS

	Species Reaching Range Limits	Percentage of This Group of Extraneous Species	Percentage of All Extraneous Species
Lakes Area—			
Northern species	293	74.74	31.94
Eastern species	54	57.00	5.89
Western species	54	55.08	5.88
Southern species	58	19.48	6.32
Endemics	11	55.00	1.20
Total	470		51.23
Wisconsin Glacial Boundary—			
Northern species	46	11.73	5.02
Southern species	194	65.18	4.93
Unglaciated Area—			
Northern species	16	4.08	1.24
Eastern	18	16.67	1.96
Western	4	4.08	0.44
Southern	90	30.24	9.81
Endemic	3	15.00	0.33
Total	131		13.78
Lower Wabash Valley—			
Northern	9	2.09	0.45
Eastern	8	7.40	0.40
Western	12	8.57	0.60
Southern	9	2.68	0.45
Endemics			
Total	38		1.90

Summary

1. Prior to glacial time, Indiana formed a part of the area covered by the great Tertiary forest and apparently was not a critical botanical area.

2. With the coming of the glaciers, Indiana became a critical vegetational area because at least the last two ice sheets reached their southern terminals within the state.

3. As the glaciers withdrew to the north and vegetation likewise

returned northward, successive zones in Indiana marked the temporary termini of distribution of many species and hence became temporary critical botanical zones.

4. Fossil pollen obtained from bogs gives us more concrete evidence of the vegetational battle in early post glacial times. From this study we learn that our forests were once strongly coniferous, but, as climates became warmer, deciduous trees advanced from the south crowding out the fir, spruce, white pine, and hemlock in the order named. Indiana was a critical botanical area for these species.

5. The critical character of Indiana as a botanical area stands out strongly in four ways: (a) it is critical today in many places toward the disjunct stations of nearly 50 relic boreal species; (b) it contains critical zones marking the eastern limits of the present-day prairies and also contains many smaller critical areas marking the borders of hundreds of relic prairie colonies; (c) it is critical ground in the determination of borders of forest climatic climaxes, containing the boundary between beech-maple and oak-hickory climatic climaxes as well as hundreds of critical zones of lesser extent marking the borders between oak-hickory pre-climax and beech-maple climax, and (d) finally, within the state are found critical zones marking the boundaries or ranges of over 45% of the species of ferns and seed plants.

6. Southern range boundaries of northern species, northern range boundaries of southern species, eastern range boundaries of western species, and western range boundaries of eastern species all occur within the state and mark zones critical for these species.

7. The Lakes area forms the critical zone for approximately 75% of the northern extraneous species, 57% of the eastern extraneous species, 55% of the western extraneous species, and 20% of the southern extraneous species. The area is critical for approximately 50% of the total extraneous flora.

8. The limits of Wisconsin glaciation constitute the critical zone for approximately 12% of the northern extraneous species, and 65% of the southern extraneous species. More than 67% of these southern extraneous species fail to extend north of the southern limit of Wisconsin glaciation.

9. The Lower Wabash Valley constitutes a limiting zone for approximately 2% of the total extraneous flora.

10. Of the total extraneous flora, 42% is on southern limits of its range, 31% is on northern limits, 11% is on western limits, and 12% is on eastern limits of its range. A little more than 2% is endemic.

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