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PHYTOGEOGRAPHY OF BERKSHIRE COUNTY, MASSACHUSETTS[1]

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ABSTRACT

Origin of the present vegetation of Berkshire County, Massachusetts, is discussed, with emphasis on glaciation, refugia of floristic elements during glaciation, migration patterns of taxa, and the effect these factors may have had on the present composition of the flora. The vegetation can be divided into five affinity groups: Eastern Deciduous Forest Region including a Southern and Midwestern sub-group, Alleghanian (Glaciated northeast and Appalachian Mountains), Boreal, Coastal Plain and Alien. Many taxa in the county are at or near their northern, southern, or eastern range limits. Selected state-listed rare taxa and common species are used to illustrate possible patterns of migration and limitations of distribution.

Key Words: Plant geography, flora, affinities, rare plants, Berkshire County, Massachusetts

I. FLORISTIC PROVINCE

Berkshire County lies within the Appalachian Province of the Atlantic North American Region as defined by Takhtajan (1986) and Cronquist (1982). This province corresponds generally to the area described by Braun (1950) as the Eastern Deciduous Forest and to the Eastern Deciduous Forest Province of Gleason and Cronquist (1964). The most widespread and characteristic type of vegetation is the deciduous forest which, in Berkshire County, includes such species as *Acer saccharum, A. rubrum, Fagus grandifolia, Quercus rubra, Q. alba, Betula papyrifera, B. lenta, B. alleghaniensis, Carya ovata, C. cordiformis, Tilia americana, Fraxinus americana, Prunus serotina, Juglans cinerea, Populus deltoides,* and *P. grandidentata.* Authorities of these and other species are given in Table 1. Important evergreen components of this Region are the conifers *Pinus strobus* and *Tsuga canadensis.* An abundant understory layer, an herbaceous ground cover, and, in favorable soils, a rich vernal flora are an integral part of the deciduous forest.

Since Berkshire County is situated in the northeastern section of the Appalachian Province, where it is relatively close to the

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Table 1. Phytogeographic affinities of rare plants of Berkshire County. E = Endangered, T = Threatened, SC = Special Concern, H = Historical.

Widespread. Species follow approximately the boundaries of the Eastern Deciduous Forest.

Ophioglossum vulgatum L. T
Sagittaria cuneata Sheldon T
Eragrostis frankii C. A. Meyer SC
Panicum gattingeri Nash SC
P. philadelphicum Bernh. SC
Sphenopholis nitida (Biehler) Scribn. T
Carex hitchcockiana Dewey SC
C. sterilis Willd. T
C. typhina Michx. T
Eleocharis intermedia (Muhl.) Schultes T
Scirpus pendulus Muhl. SC
Corallorhiza odontorhiza (Willd.) Nutt. E
Morus rubra L. E
Claytonia virginica L. T
Waldsteinia fragarioides (Michx.) Tratt. SC
Linum medium (Planch.) Britt. T
Acer nigrum Michx. SC
Hypericum ascyron L. (*H. pyramidatum* Ait.) T (H in county)
Panax quinquefolius L. SC
Sanicula gregaria Bickn. T
Gentiana andrewsii Griseb. T
Verbena simplex Lehm. E
Blephilia ciliata (L.) Benth. E
B. hirsuta (Pursh) Benth. E
Veronicastrum virginicum (L.) Farw. SC
Hedyotis longifolia (Gaertn.) Hook. (*Houstonia longifolia* Gaertn.) T
Symphoricarpos albus var. *albus* (L.) Blake (H in county)
Lobelia siphilitica L. T

Southern and midwestern. Species centered to the south and midwest and are at or near their northern or eastern limits in the county.

Lygodium palmatum (Bernh.) Sw. SC (H in county)
Asplenium montanum Willd. E
A. ruta-muraria L. T
Elymus villosus Muhl. T
Carex alopecoidea Tuckerm. E
C. bushii Mack. E
C. davisii Schw. & Torr. E
C. formosa Dewey E
C. grayi Carey T
C. schweinitzii Dewey E
C. tetanica Schkuhr T
C. trichocarpa Muhl. T
Arisaema dracontium (L.) Schott T

Table 1. Continued.

Chamaelirium luteum (L.) Gray E
Quercus macrocarpa Michx. SC
Q. muhlenbergii Engelm. SC
Minuartia michauxii (Fern.) Farw. (*Arenaria stricta* Michx.) SC
Cimicifuga racemosa (L.) Nutt. E
Hydrastis canadensis L. E
Cardamine douglassii (Torr.) Britt. E
Agrimonia pubescens Wallr. T
Ilex montana Torr. & Gray T
Hydrophyllum canadense L. E
Trichostema brachiatum L. T
Veronica catenata Pennell E
Lonicera hirsuta Eat. E
Viburnum rafinesquianum Schultes T
Aster prenanthoides Muhl. T

Alleghanian. Species centered in glaciated district with extension south in Appalachian Mountains.

Thuja occidentalis L. E
Milium effusum L. T
Potamogeton hillii Morong SC
Sporobolus neglectus Nash E
Carex baileyi Britt. E
Rhynchospora capillacea Torr. E
Sisyrinchium mucronatum Michx. T
Arethusa bulbosa L. T (H in county)
Cypripedium calceolus L. var. *parviflorum* (Salisb.) Fern. E
Cypripedium reginae Walt. SC
Platanthera flava (L.) Lindl. var. *herbiola* (R. Br.) Luer T (H in county)
Clematis occidentalis (Hornem.) DC. SC
Adlumia fungosa (Ait.) Greene T
Arabis lyrata L. T
Amelanchier sanguinea (Pursh) DC. SC
Rhododendron maximum L. T
Calystegia spithamaea (L.) Pursh (*Convolvulus spithamaeus* L.) (H in county)

Boreal, including Circumpolar. Species that have a center in the Canadian Biome.

Equisetum scirpoides Michx. SC
Lycopodium selago L. E (H in county)
Cryptogramma stelleri (Gmel.) Prantl T
Polystichum braunii (Spenner) Fee E
Woodsia glabella R. Br. E
Sparganium minimum (Hartm.) Fries E
Potamogeton friesii Rupr. E
Trisetum triflorum (Bigelow) Löve & Löve ssp. *molle* (Michx.) Löve & Löve E
Carex castanea Wahlenb. E
C. lenticularis Michx. T
C. michauxiana Boeck. E

Table 1. Continued.

C. pauciflora Lightf. E
Eriophorum gracile W. D. J. Koch T
Juncus filiformis L. T
Luzula parviflora (Ehrh.) Desv. ssp. *melanocarpa* (Michx.) Hamet-Ahti E
Cypripedium arietinum R. Br. E (H in county)
Goodyera repens (L.) R. Br. E
Malaxis brachypoda (Gray) Fern. T
Platanthera dilatata (Pursh) Lindl. T
Salix serissima (Bailey) Fern. SC
Alnus viridis (Chaix.) DC. ssp. *crispa* (Ait.) Turrill SC
Betula pumila L. T
Arceuthobium pusillum Peck SC
Moehringia macrophylla (Hook.) Fenzl E
Nuphar pumila (Timm) DC. (*N. luteum* [L.] Sibthorp & Sm. ssp. *pumilum* [Timm] E. O. Beal) T (H in county)
Ranunculus pensylvanicus L.f. T
Cardamine pratensis L. var. *palustris* Wimm. & Grab. (*C. pratensis* L.) T
Ribes lacustre (Pers.) Poir. SC
R. triste Pallas SC
Amelanchier bartramiana (Tausch) Roemer T
Rosa acicularis Lindl. E
Sorbus decora (Sarg.) Schneider E
Viola nephrophylla Greene T
Conioselenium chinense (L.) BSP. SC
Pyrola asarifolia Michx. var. *purpurea* (Bunge) Fern. E
Vaccinium vitis-idaea L. ssp. *minus* (Loddiges) Hultén E
Stachys palustris L. T
Galium labradoricum (Wieg.) Wieg. SC
Petasites frigidus (L.) Fries var. *palmatus* (Ait.) Cronq. T
Solidago macrophylla Pursh SC
S. glutinosa Nutt. ssp. *randii* (Porter) Cronq. (*S. spathulata* DC. ssp. *randii* [Porter] Cronq.) E

Coastal Plain and eastern. Species that are centered to the east.

Carex polymorpha Muhl. E (H in county)
Orontium aquaticum L. T

Atlantic-Gulf Coastal Plain Province and in close proximity to the Canadian Province (Takhtajan, 1986), it is not surprising that it contains phytogeographic elements of both these provinces. Sufficiently high mountains (up to 1064 m) in the northern part of the county provide climatic conditions that allow a southerly extension of species of the Canadian Province. Sandy outwash plains and acid, boggy marshes provide conditions suitable for a few Coastal Plain species.

One of the most interesting aspects of the Appalachian Province is the great number of taxa that are very similar to those of the Eastern Asian region. The following genera, which are found in Berkshire County, occur only in eastern United States and in eastern Asia (Li, 1952): *Camptosorus, Carya, Caulophyllum, Hydrastis, Liriodendron, Penthorum, Hamamelis, Parthenocissus, Panax, Aralia, Nyssa,* and *Epigaea.* Most of these genera, except for *Carya,* consist of one species in eastern United States and several in eastern Asia. In addition, vicariads that share this east-west distribution occur in many other more widespread genera.

II. MAJOR FOREST COMMUNITIES

The Southern Appalachians form the center of highest diversity of the Eastern Deciduous Forest (Gleason and Cronquist, 1964). As distance increases from this center, the number of species decreases. The relative abundances of species in different regions vary widely, leading to the development of a number of plant associations or communities within this great biome. Seldom does any vegetational grouping have discrete boundaries, however, except in extremes of soil or microclimatic changes. There are usually transition zones in the area where two associations are contiguous (Gleason and Cronquist, 1964).

Küchler (1964) mapped plant communities for the vegetation of the United States and based his classification on the dominant species. He also characterized them by species usually found associated with that community. Four communities are mapped for Berkshire County: Northeastern Spruce-Fir Forest (*Picea-Abies*), Northern Hardwoods-Spruce Forest (*Acer-Betula-Fagus-Picea-Tsuga*), Northern Hardwoods Forest (*Acer-Betula-Fagus-Tsuga*) and an area that Küchler designated as Transition Zone between Appalachian Oak Forest (*Quercus*) and Northern Hardwoods Forest (cf. "Transition Hardwoods" of Westveld, 1956). This classification recognizes the wide variation that occurs in the county from north to south and from high to low elevations.

In reality, given the diversity of bedrock, elevation, slope, soil and water regimes, these zones or communities may be found as a mosaic within a small area, along with transition zones, making it difficult at times to discern an area on the ground that corresponds exactly to any one zone. Because of the extremes of elevation encountered in the northern part of the county (1064 m to 175 m), one could map, along a transect 6 miles long, Spruce-Fir Forest and Appalachian Oak Forest, complete with *Cornus florida, Sassafras albidum* and dwarfed *Pinus rigida,* noting also, in between these extremes, the other communities as well.

Spruce-Fir Forest is found on the highest elevations in the north, from about 800 m to 1064 m. Northern Hardwood-Spruce Forest best characterizes the Berkshire Plateau (Egler, 1940), which extends along the eastern boundary of the county. Northern Hardwood Forest is perhaps the most widespread type, especially in the northern half where it is found on mid- to lower slopes and valley floors. *Quercus rubra* often is an important tree in this forest. Various types of oak forest intermix with northern hardwoods, depending on slope and soil. Toward the southern part of the county, *Pinus strobus, P. rigida, Tsuga canadensis, Quercus* spp., and *Carya* spp. become much more common as part of Küchler's Transition Zone.

Although the county is a comparatively small area, it contains a great diversity of species; factors that control or determine the limits of a species are complex. Stebbins (1980) proposed at least three such factors: genetic makeup, the environment in which the species grows, and past history of the population. It is the past history of the present vegetation, including the effects of various climatic changes and migration patterns, which is the main concern here.

III. GLACIATION AND ITS EFFECT ON VEGETATION

The greatest single factor that has determined the composition of our flora is glaciation. Glacial periods resulted in elimination or displacement of the widespread, more homogeneous, deciduous and sub-tropical flora of the Northern Hemisphere and a subsequent mixing of both northern and southern elements (Wood, 1970).

During the middle Tertiary period, at least 50 million yr. B.P. (before present), before the series of glaciations began to spread over the northern portions of the earth, a broad band of vegetation known as the Arcto-Tertiary Flora covered the Circumpolar region (Chaney, 1947). This forest contained many genera of our present deciduous forest and ranged approximately 20 degrees farther north of its present range (Larsen, 1980). Wolfe (1978) postulated that a tropical broad-leaved evergreen forest existed along the Pacific Coast in Washington from 50–34 million yr. B.P., indicating that the Arcto-Tertiary Flora was not purely deciduous or as homogeneous as once was thought. The Brandon Lignite, a Tertiary deposit dating from 32–34 million yr. B.P. (Oligocene) found in north-central Vermont, has yielded megafossils that indicate that the flora was most similar to modern floras of southeastern United States and southeastern Asia. The two species that Tiffney described, *Illicium avitum* (Tiffney and Barghoorn, 1979) and *Turpinia uliginosa* (Tiffney, 1979), belong to genera that presently inhabit warm-temperate, subtropical and tropical areas. Many species now restricted in range, such as *Liriodendron* and *Nyssa,* were widespread in the Tertiary (Wood, 1970). Herbaceous plants are not well represented in the sparse fossil record, so their presence as part of the Tertiary Flora is inferred from their existence in our own floristic assemblage (Wood, 1970).

A cooling trend in the late Tertiary, 27–2.5 million yr. B.P., resulted in a temperate deciduous forest that supplanted the warm-temperate forest at higher latitudes (Larsen, 1980), which was rapidly replaced by Arctic and Boreal species now found in the North. This cooling trend culminated in the formation of persistent ice in Polar regions.

The Quaternary Period, beginning 2.5 million yr. B.P., saw the extensions of these glaciers southward over portions of the landmasses of North America, Europe and Asia. There have been up to 18–20 glacial advances of approximately 100,000 years duration (Davis, 1983), interspersed with short interglacial warm periods of 10,000–15,000 years duration. Vegetation was repeatedly forced to migrate south during the long cold periods, which occupied 90% of the Quaternary. During the short warming intervals, the vegetation again migrated north. Climatic changes during the short interglacial periods were fairly abrupt (Davis, 1983). This oscillation resulted in much vegetational instability. Recent work based on pollen records has established that plant species migrated individually, not as plant communities (Davis, 1983; Wood, 1970). According to Davis (1983), communities formed south of the glacial border were made up of assemblages not seen today.

There are differing views as to the extent of vegetational change in unglaciated regions. Braun (1947, 1950, 1955) suggested that the deciduous forest retreated from higher elevations and was infiltrated by boreal species; additionally, boreal species reached southward along the mountain ridges. Braun suggested that a narrow band of tundra may have existed near the glacier, but the eastern deciduous forest retained its identity and most of its extent. The fact that the rather specific habitat requirements of some presently rare herbaceous species would make migration difficult was used by Braun (1955) to indicate that the deciduous forest could not have been totally displaced during the Wisconsin glaciation. Other authors (Davis, 1983; Jacobson et al., 1987) postulated that wide bands of tundra and boreal forest reached far into the south, and that most deciduous species were dispersed into scattered refugia. This viewpoint was based on extensive pollen records, but as Larsen (1980) stated, these records tell only part of the story because many species do not shed large amounts of pollen, and positive identification of species is sometimes impossible.

Using pollen profiles from bogs and ponds throughout the eastern half of North America and sediments that have been radiocarbon-dated, Davis (1983) mapped full-glacial floras and traced the return northward of some of our more important trees. Since pollen grains are produced in different amounts by different species and may be transported varying distances, the precise composition of the flora cannot be defined, but fossil pollen profiles have been compared to modern ones from various vegetational types to check their accuracy. Davis and Goodlett (1960), in a study of modern pollen deposition in Vermont, found that several tree species are over-represented, such as oak (*Quercus*), pine (*Pinus*) and birch (*Betula*). Tree species that are under-represented are maple (*Acer*), arbor-vitae (*Thuja*), fir (*Abies*), poplar (*Populus*), larch (*Larix*), and basswood (*Tilia*). Davis (1983) also stated that it is still unclear where many deciduous species survived. Given these cautions, the refugia and migration routes northward of a few of our species can be postulated.

Coniferous pollen seems to dominate the unglaciated region at full-glacial time, but fossil seeds and fruits of some deciduous species have been found near Memphis, Tennessee (Davis, 1983). *Quercus* and *Carya* were prevalent in northern Florida. Davis suggested that populations of deciduous trees may have survived in small, scattered, unusual habitats that served as refugia. Wolfe (1951) postulated similarly that sheltered, cave-like grottoes, because of their more equable climate, may have served as refugia for certain species of restricted habitat close to the glacial margin.

According to Davis (1983), spruce (*Picea* spp.) migrated north from a widespread distribution in the south into the Appalachian Mountains and northeastward into New England. Larch (*Larix laricina*) persisted only on the eastern edge of the Great Plains and moved northeast from west of the Appalachians. The jack/red pine (*Pinus banksiana/P. resinosa*) group migrated northward from refugia on the coastal plain and in the Appalachians, as did fir (*Abies balsamea*). These four genera of conifers, arriving in New England from 12,000–11,000 yr. B.P. (Davis, 1983), were among the earliest trees to appear in the recently deglaciated region, and now have northerly distributions. However, jack pine is not presently a member of the Berkshire County flora.

White pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*) persisted only along the coastal plain during glaciation. After glacial retreat, they migrated west to the Appalachians and then north into New England, arriving approximately 10,000–9000 yr. B.P. (Davis, 1983).

Deciduous trees, such as *Quercus, Ulmus, Acer, Carya* and *Castanea,* persisted in the south central portion of the United States and migrated north and eastward, but arrived in our area at widely varying times. *Quercus* reached New England about 10,000 yr. B.P., sugar maple (*Acer saccharum*) expanded into the northeast about 9000 yr. B.P., *Carya* migrated more slowly, and *Castanea* arrived only 2000 years ago, illustrating that present communities did not survive or migrate together (Davis, 1983). Our flora is made up of species which have been subjected to repeated dispersal, competition with many other species, and varying climatic conditions. Its composition undoubtedly is changing continuously, as the climate changes, as species continue to migrate, and as some perhaps become extinct in our area.

Berkshire County experienced total glaciation, the ice limit of the Wisconsin glacier being some 150 miles to the south and east. This glacial maximum occurred 20,000 yr. B.P. Climatic changes at the end of the last stadial (glacial period) resulted in rapid melting of the ice, the Berkshire County region becoming ice-free around 14,000 yr. B.P. (Davis and Jacobson, 1985; Whitehead, 1979).

Whitehead (1979) made a detailed study of the pollen profile in Berry Pond, a small natural pond in the town of Hancock, Berkshire County, Massachusetts, at 610 m elevation in the Taconic Range. He found that the sedimentary record at this site began about 14,000 yr. B.P. and that it closely parallels pollen profiles seen in other New England bogs.

The lowest zone, or level of sediment, corresponding to about 13,000–12,100 yr. B.P., showed a large percentage of non-arboreal pollen, mostly Cyperaceae, and a very small pine component, either jack or red pine. Whitehead (1979) inferred an essentially treeless vegetation, somewhat comparable to tundra or forest-tundra.

The pollen profile of the next zone, from about 12,100–10,200 yr. B.P., indicated that spruce was dominant, pine not common, and alder (*Alnus*), juniper (*Juniperus* type), larch, fir, oak (*Quercus*) and hornbeam (*Ostrya/Carpinus*) were well represented. Presence of spruce has been corroborated by cones of white spruce (*Picea glauca*) found in a bog in Egremont, that were carbon-dated to 11,630 ± 470 yr. B.P. (Moeller, 1984). However, it is not possible to determine whether white spruce was the common spruce at that time; it is not native in Massachusetts at present.

The upper portion of this zone, in Whitehead's study, showed a decline of spruce and increase of pine and birch. Pine-pollen type indicated an increase of white pine (*Pinus strobus*). At about 10,500 yr. B.P., ash (*Fraxinus*), sugar maple, hazelnut (*Corylus*) and beech (*Fagus*) occurred in very small percentages. The presence of their pollen may not, however, indicate their actual presence in the flora. Miller and Thompson (1979) stated that temperate deciduous tree pollen appeared in very small quantities in many pollen profiles of this zone and may represent long-distance wind transport or rebedding. No macrofossils of *Quercus, Acer,* or *Ostrya/Carpinus* have been found in this zone in any New England site (Miller and Thompson, 1979).

Miller and Thompson's (1979) investigation of the Columbia Bridge site, near the Connecticut River in northern Vermont, yielded macrofossils dating from 11,540–11,390 yr. B.P., representing a rich assemblage of herbs and shrubs, but a low occurrence of spruce and balsam poplar (*Populus balsamifera*). This more northern site compared well with Whitehead's characterization of the same zone in Berkshire County as open boreal forest.

In the next zone in Whitehead's (1979) study, 10,200–8250 yr. B.P., pine and birch (*Betula*) were abundant. White pine predominated, but there was also some pitch pine (*Pinus rigida*) present.

Hemlock (*Tsuga canadensis*) made an appearance here as well and oak and the other deciduous trees increased in abundance.

Whitehead (1979) characterized the last zone, from 8250 yr. B.P. to the present, as the Oak-birch-beech-hemlock zone. Hemlock suffered a dramatic decline in his pollen profile, which corresponds to a similar decline noted all over the northeast around 4800 yr. B.P. (Davis et al., 1980). It was originally thought to be an effect of the Hypsithermal Period, but since only hemlock was affected, a disease or insect may have been the cause (Whitehead, 1979; Davis et al., 1980). Chestnut (*Castanea dentata*) arrived much later, about 2000 yr. B.P. in southern New England, and became an important part of the forest at Berry Pond along with white pine, pitch pine, hickory (*Carya*) and oak; this was a more southern type of assemblage than is seen today.

At present, red maple (*Acer rubrum*), red oak (*Quercus rubra*), and beech (*Fagus grandifolia*) are dominant in the forest around Berry Pond, reflecting historical disturbance, with sugar maple, yellow birch (*Betula alleghaniensis*), black cherry (*Prunus serotina*), paper birch (*Betula papyrifera*), and ash (*Fraxinus americana*) also common. Whitehead (1979) stated that the modern shrub and herbaceous layers of that site are not represented at all in his pollen profile. Other trees that do not produce abundant pollen or are less common today are also absent. A pollen profile reliably reflects only trees and shrubs that produce abundant pollen and are found within 15 km of the site of deposition (Davis, 1983). Whitehead (1979) also noted that since the Berkshires contain diverse topography and bedrock types, plant associations other than those described in his paper may have been present in the corresponding zones in different sections of the county.

IV. FLORISTIC AFFINITIES

Repeated displacement of species during the Pleistocene, their migration back into regions of bare soil, and the subsequent mixing of species from quite different regions, from the boreal to the southern, and of different vegetational associations, has resulted in a present-day flora that may appear to be a confusing mixture. Davis (1983) termed the Eastern Deciduous Forest a "grab-bag of species" which was selected for colonization and competitive abilities. Perhaps this is one reason why the forest is able to renew itself after repeated clearing for timber and agriculture.

Each species exhibits an individual distribution, but patterns emerge that allow species with similar distributions to be assigned to a floristic group. Each group possesses a geographic "center" which gives it its name or affinity. The following floristic groups are recognized for Berkshire County: 1. the Eastern Deciduous Forest element (including a southern and midwestern element), 2. the Alleghanian element, 3. the Boreal element (including Circumpolar plants), 4. the Coastal Plain element and 5. an Alien element.

Examples of some common and characteristic species and of some rare plants are used to define each grouping. Affinities and migration patterns of the selected rare species are discussed more fully to illustrate the floristic relationships of Berkshire County flora. The use of the word "rare" is restricted to only those taxa listed by the Massachusetts Natural Heritage and Endangered Species Program (Sorrie, 1989) as rare in Massachusetts. Rare taxa that are found in the county are listed in Table 1, and are arranged according to affinity.

Eastern Deciduous Forest Element

Since Berkshire County lies within Braun's (1950) Eastern Deciduous Forest, it is to be expected that plants of this phytogeographic element would be the most common and most important to the general character of the vegetation. These species have the wide distribution exemplified by *Corallorhiza odontorhiza* (Figure 1), although many extend farther north. They include most of our deciduous trees such as *Acer saccharum, A. rubrum, A. saccharinum, Quercus rubra, Q. alba, Prunus serotina, Tilia americana, Fagus grandifolia, Carya* spp., *Liriodendron tulipifera, Fraxinus americana, Ulmus* spp., and *Carpinus caroliniana.* On favorable soils a rich vernal flora is found typically with this forest. Fifteen common, spring wildflowers have approximately the same distribution, including *Hepatica nobilis* var. *obtusa* (*H. americana*), *Sanguinaria canadensis, Dicentra cucullaria, Erythronium americanum, Dentaria laciniata, Asarum canadense, Arisaema triphyllum, Thalictrum dioicum, Hydrophyllum virginianum, Geranium maculatum, Viola pubescens,* and *Thalictrum* (*Anemonella*) *thalictroides* (Gleason and Cronquist, 1964). The shrub *Dirca palustris* also has a similar distribution.

The plants of this widely distributed element that are consid-

Figure 1. Eastern Deciduous Forest element: distribution of *Corallorhiza odontorhiza* (after Luer, 1975).

ered rare (Sorrie, 1989), are so because they may require a more specialized habitat, or suffer from habitat elimination and commercial exploitation. Some, such as *Carex hitchcockiana* and *Blephilia hirsuta,* require a rich, mesic, calcareous soil. *Claytonia virginica,* rare congener of the common *C. caroliniana,* has narrower habitat requirements of rich, open floodplains. *Verbena simplex* and *Blephilia ciliata* occupy dry, calcareous open situations. The somewhat rich, open woods habitat of *Corallorhiza odontorhiza* (Figure 1) is fairly common, but the plant is scarce; what its particular needs are, are not fully known. Plants that inhabit an early successional vegetational type, such as a calcareous wet meadow, are easily shaded out by taller growth. *Ophioglossum vulgatum* and *Veronicastrum virginicum* are possible examples of rarity due to this process. *Panax quinquefolius,* while requiring rich sites, undoubtedly was more common before it became extensively hunted and the roots dug for herbal uses.

Figure 2. Southern-Midwestern element: distribution of *Quercus macrocarpa* (after Little, 1971).

A sub-group of the Eastern Deciduous Forest element has, from the point of view of the Berkshire County Flora, a distinctly southern and midwestern center (Figure 2). Most of these species are among the more uncommon or rare plants of the county as they are at or near the northeastern limits of their ranges, and most are found in the southern half of the county. Among these species are *Quercus macrocarpa, Q. muhlenbergii, Staphylea trifolia, Zanthoxylum americanum, Ilex montana, Solidago speciosa, Andropogon gerardii, Sorghastrum nutans* and *Chamaelirium luteum.*

Since the refugium of the deciduous forest species was centered in the south-central United States, migration spread northward and eastward. This sub-group probably migrated into Berkshire County along rivers, either from the Hudson River via the Hoosac River, and east along the Green and Williams Rivers, or north along the Housatonic River, since there apparently existed little favorable habitat in the mountain ranges bounding the county.

Those plants that are at the eastern limits of their ranges may still be in the process of migrating eastward or northward as part of a continuing adjustment to the post-glacial period (Griggs, 1914). The rare *Ilex montana,* which occurs only in the southwest corner of the county, occupies a common type of acidic, rocky woodland. Its non-disjunct distribution may illustrate a continuing migration northeastward.

Certain species, such as *Quercus macrocarpa,* have outlying discontinuous distributions beyond their continuous area (Figure 2). Davis postulated (1965) that this species may have expanded its range during the Hypsithermal Period, 5000–4000 yr. B.P., then retreated as environmental conditions changed, leaving stranded populations.

Continued migration eastward may be impeded by several factors. Good (1974) indicated that a mountain range "athwart" the trend of migration is a more formidable barrier than one that is in the same alignment. The rare plant *Aster prenanthoides* reaches its easternmost limit in Berkshire County, where it is found primarily on the floodplains of two different rivers with separate watersheds: the Green River which flows east from New York State through the towns of Egremont and Great Barrington, and the Green River in Williamstown and Hancock, which rises near the New York–Massachusetts border. However, this species appears to be quite common on the western flanks of the Taconic Range, indicating that the two rivers provide migrational routes across the montane barrier. *Acer nigrum* may also migrate along rivers, since it is most often found in rich floodplain soil.

Other factors may affect migration. Increasingly unfavorable climate northward may impede further migration. *Asplenium montanum,* a rare fern, has no competition in its acidic, rocky-outcrop environment, which is not rare in the northeast, yet it is near its northeastern limit in Berkshire County. Habitat availability may limit *Chamaelirium luteum, Trichostema brachiatum* and *Lonicera hirsuta,* all rare species, since they need more sunlight than is found in the mature deciduous forest. *Chamaelirium luteum* inhabits more open, secondary woods, while the latter two species survive on open calcareous ledges. As Griggs (1940) suggested, many rare plants occupy natural pioneer habitats.

Edaphic conditions may form a barrier to migration. The many calcicolous species at their eastern limit here in the county may be barred from migrating farther eastward by the acidic soils of the high, north-south trending Berkshire Plateau, as described by Egler (1940). Certain rare sedges found in calcareous fens, such as *Carex tetanica* and *C. schweinitzii,* or species of rich floodplains, such as *C. trichocarpa,* would find it difficult to spread eastward over this terrain which is not traversed by any suitable major river.

Alleghanian Element

Some species that are now an integral part of our flora belong to the Alleghanian element (Figures 3 and 4). They are confined to the area of the northeast and midwest which was once covered by the last glaciation, and extend southward along the Appalachian Mountains. Their refugia may have been on the coastal plain (Davis, 1983) and/or the Appalachian Mountains. Of this group, *Pinus strobus, Tsuga canadensis,* and *Betula alleghaniensis* are important members of the forest. *Betula alleghaniensis* is a co-dominant tree in the Northern Hardwoods Association (Küchler, 1964), particularly on the upper slopes. *Pinus strobus* is more prevalent at present in the southern half of the county, possibly due to greater abundance of well-drained soils and extensive agricultural disturbance associated with low, gentle topography. *Tsuga canadensis,* in the northern half of the county, occupies moist rocky ravines, north-facing slopes and poorly drained areas, while in the southern half of the county it is more widely distributed. Küchler (1964) indicated much of this southern section to be in a transition zone. *Pinus resinosa* occupies only a few mountain ridges in the southern half.

Trees of dry, sandy soil or rocky summits, *Pinus rigida* and *Quercus ilicifolia,* have similar, quite limited distributions in the Appalachian Mountains and in the northeast, especially near the coast. The pollen profile of Berry Pond indicated that *Pinus rigida* was more abundant around 4800 yr. B.P., during the Hypsithermal Period.

Because many Alleghanian species are largely restricted to areas formerly covered by the Wisconsin ice sheet, some authors (Braun, 1955) infer that the deciduous forest remained extant near the glacial edge, presenting a closed community that could not be

Figure 3. Alleghanian element: distribution of *Thuja occidentalis* (after Little, 1971).

invaded. An alternative explanation might be that many of these Alleghanian species could more easily colonize poor, poorly developed and bare soil than could typical Eastern Deciduous Forest species. In addition, the Eastern Deciduous Forest species, with their refugia in the south-central United States, were able to migrate rapidly northward into the unglaciated soil of the northern midwest (Davis, 1983). It may have then presented a closed community to the Alleghanian species spreading out from Appalachian refugia.

Picea rubens, now largely restricted to the Northeastern Spruce-Fir Forest (Küchler, 1964), is found on the highest mountain tops and ridges, and is associated there with *Abies balsamea,* a Boreal Forest species. The small tree or shrub *Rhus typhina* shows a typical Alleghanian distribution, as does the rare tree *Thuja occidentalis* (Figure 3). The rare plant *Clematis occidentalis* may

Figure 4. Alleghanian-Ozarkian element: distribution of *Rhynchospora capillacea* (after Gale, 1944).

occupy its habitat of open limestone ledges partly because, being a trailing woody vine, it cannot compete with typical deciduous forest growth.

Three rare plants, *Arabis lyrata, Cypripedium reginae* and *Rhynchospora capillacea,* illustrate an Ozarkian and Alleghanian distribution. These three species may have had refugia in both the Ozarks and the Appalachians during glaciation. The separate populations perhaps merged once they migrated northward, as in the case of *Arabis lyrata* and *Cypripedium reginae.* The Ozarkian population of *Rhynchospora capillacea* (Figure 4) may have migrated north to form the western stations while eastern stations may have derived from Appalachian refugia. *Arabis lyrata* is restricted to calcareous open ledges while *R. capillacea* and *C. reginae* are found only in calcareous fens, both uncommon habitats in Berkshire County.

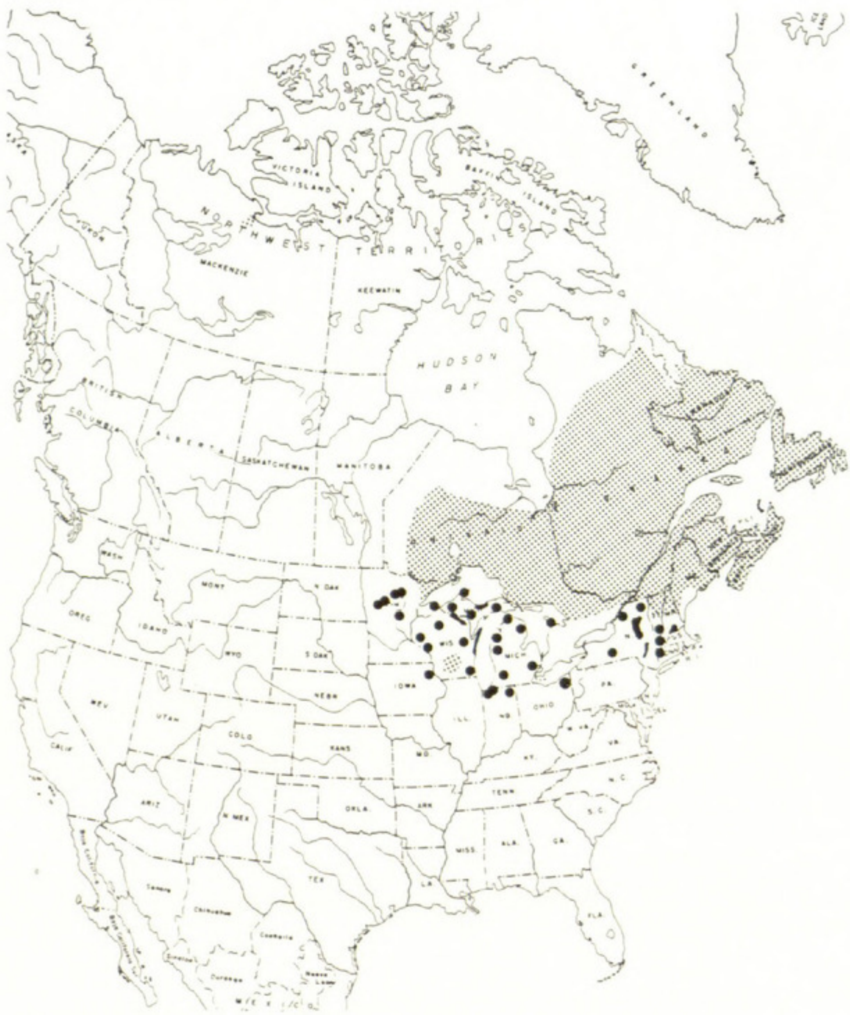

Figure 5. Boreal element: distribution of *Sorbus decora* (after Little, 1977).

Boreal or Northern Element

The Northern or Boreal element (Figure 5) contributes both important common species and rarer ones. Our common *Betula papyrifera,* although possessing a somewhat Alleghanian distribution southward, ranges far to the north where its distribution is transcontinental. *Betula cordifolia* is a member of the Northeastern Spruce-Fir Forest (Küchler, 1964) with *Abies balsamea,* the dominant tree species at the highest elevations (914–1064 m). *Larix laricina* and *Picea mariana* are found in cold bogs and fens. Many of our Boreal plants have a wide circumpolar distribution (Hultén, 1970), including *Epilobium angustifolium, Galium trifidum, Moehringia lateriflora, Circaea alpina, Chamaedaphne calyculata, Linnaea borealis, Menyanthes trifoliata* and *Viola selkirkii.*

As the Late Pleistocene climate warmed and the Wisconsin

Figure 6. Coastal Plain element: distribution of *Orontium aquaticum* (after Grear, 1966).

glacier retreated, Boreal species migrated upward in elevation and northward, resulting in some Boreal species being stranded as disjuncts, persisting today as rare plants in colder ravines, cold bogs and mountain tops in Berkshire County. *Vaccinium vitis-idaea* exists only as a single plant on a high exposed ledge. A few plants of *Polystichum braunii* occupy only in deep, cold ravines where there is a calcareous influence. *Woodsia glabella* inhabits a cool, high, shaded limestone ledge, of which there are few in the county. *Rosa acicularis* ssp. *sayi* is found on one open limestone ledge. The existence of these plants is tenuous since they occupy small habitat "islands" where they are subject to chance extinction. As Reznicek (1989) noted, many rare northern species occupy disjunct stations at their southern limit, as these species do. The probability of recolonization of such limited habitats is low because these sites are far from any replenishing source of propagules. *Moehringia macrophylla* is absolutely restricted to serpentine outcrops, where it is locally abundant. *Amelanchier bartramiana, Sorbus decora* (Figure 5) and *Luzula parviflora* var. *melanocarpa* are components of the Boreal Forest on the summit of Mt. Greylock. *Solidago macrophylla* is found there as well as on several other mountain tops over 792 m.

Many of the plants considered to have northern affinities or to be circumboreal do not occupy strictly boreal habitats, but mix with more southern or widespread species. As discussed earlier, repeated displacement of vegetation by glacial advances has resulted in a flora derived from several affinities.

Coastal Plain Element

The few members of the Coastal Plain element (Figure 6) that occur in Berkshire County are generally found in the southern part of the county, although suitable soil and exposure also influence distribution. During the Wisconsin Glacial Period, the wide Continental Shelf was exposed between the ice sheet and the greatly lowered Atlantic Ocean. This area served as a refugium for many plants (Davis, 1965), some of which remained centered on the Coastal Plain after the glacier retreated and sealevel rose.

Taxa that exhibit Coastal Plain affinities are *Rhynchospora capitellata, Xyris difformis, Bartonia virginica, Utricularia radiata, Thelypteris simulata, Viola lanceolata, Juncus militaris,* and *Potamogeton confervoides.* The rare *Orontium aquaticum* (Figure 6), more typically found in Coastal Plain ponds, exists at one station in a sandy pond, as does *Juncus militaris.* These species chiefly occur in wet sands, acidic bogs or acidic waters of shallow ponds common on the Coastal Plain.

Coastal Plain species were undoubtedly able to migrate north readily from the Coastal Plain along the valleys of the south-flowing Housatonic, Farmington, and Westfield Rivers. Some species, particularly the aquatic taxa, may have been distributed by birds.

Alien Element

The Alien element of our flora is an important one, comprising approximately 25% of our species. Many were introduced purposely for pasture grass (*Phleum pratense, Dactylis glomerata*), for herbal use (*Thymus serpyllum, Origanum vulgare*), for food (*Pastinaca sativa, Daucus carota*) and undoubtedly many for decorative use in gardens. Other species arrived by chance in grain, seed, wool, packing, ballast, clothing, railroads, automobiles, and food shipments; most were adapted to growing in disturbed soil and spread rapidly in the wake of tree clearance and agriculture. Many species, such as *Rhamnus cathartica* and *Alliaria petiolata,* have become more abundant since Hoffmann (1922) published his flora.

Additional species, not noted by Hoffmann, are still arriving and spreading rapidly; these include *Impatiens glandulifera, Rhinanthus minor, Euphrasia nemorosa, E. micrantha, Rhamnus frangula,* and a variety of grasses.

Removed from their own native competitors and predators, many species, such as *Lonicera morrowii, Alliaria officinalis, Lythrum salicaria, Rhamnus cathartica* and *R. frangula,* become pests and often choke out native vegetation. Others, such as *Leucanthemum vulgare* (*Chrysanthemum leucanthemum*), *Cichorium intybus, Centaurea maculosa, Ranunculus acris, Galium mollugo, Vicia cracca, Hieracium* spp., *Trifolium pratense* and the early-blooming *Tussilago farfara,* provide welcome color to meadows, roadsides and newly disturbed areas.

Several species, native to midwest or western North America, have expanded their range eastward into our region in response to extensive clearing by European settlers. *Rudbeckia hirta* var. *pulcherrima* is a common weed in pastures (Fernald, 1950), and *Penstemon digitalis* is occasional in moist meadows (Pennell, 1935; Fernald, 1950).

V. SUMMARY

A variety of factors have influenced Berkshire County's floristic composition. Most important has been glaciation, which eliminated all pre-existing vegetation from the county and displaced the boreal and temperate vegetation southward. Many species may have been extirpated during repeated displacements. The survival of species in Pleistocene refugia and their post-glacial migration routes have largely determined the composition of our flora, which is a mixture of species with a variety of affinities. Species composition is undoubtedly still changing in response to this massive disturbance, and species may still be in the process of either expanding their range or possibly becoming extinct in the county. Other factors affecting the composition and distribution of our flora are topography, bedrock geology, drainage and climate; these combine to provide diverse habitats for species with different affinities. These factors may also limit or promote plant migration. Certain taxa are at their southern, eastern or northern limits in the county.

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