REFUGIA AND MIGRATION IN THE QUATERNARY HISTORY OF THE NEW ENGLAND FLORA

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ABSTRACT.   New data sets and analytic techniques provide the tools to build a new perception of changes in the New England flora following the retreat of the last Pleistocene continental glacier. We consider a set of 13 species for which genetic data are available in the context of 1) the fossil record when available, and 2) the evidence of the distribution of appropriate habitat in the late Pleistocene and Holocene. The current New England flora is derived from a diverse set of refugia including the High Arctic, the serpentines of the American West, and the unglaciated and now submerged North Atlantic coastal plain as well as the traditional refugia to the south, both along the coastal plain and to the west in the lower Mississippi valley. This analysis demonstrates that present-day communities are in fact transient, constantly changing assemblages of species.

Key Words: Holocene, New England flora, biogeography, genetic diversity, plant migration, refugia

One of the prominent themes in the first century of the New England Botanical Club was exploration of the biogeographic origins of the New England flora. Merritt Lyndon Fernald (1873–1950), a dominant influence in the first 50 years of the Club's history, was especially interested in the impact of Pleistocene glaciation on the flora (e.g., Fernald 1925). The present paper is based on a talk on the Quaternary biogeography of the New England flora, given by the first author at the thousandth meeting of the Club in October 2004.

Though we are accustomed to thinking of alterations in the landscape over geologic time, we often do not appreciate how dramatic the changes in the New England landscape have been since the last glacial maximum 18,000 years ago (years BP, used throughout). For New England, the major events in this period have been charted in detail in Davis and Jacobson (1985). Three geological insights from the region serve to remind us of the dynamic nature of our local landscape. First, fossil teeth of both mastodons (with a diet of woody-plant material) and mammoths (which ate mostly graminoids) have been recovered by commercial

trawlers working on the continental shelf off the New England coast (Whitmore et al. 1967). These teeth, dredged from intact sediments dating from the end of the Pleistocene and beginning of the Holocene, provide evidence for the existence of both grasslands and forests, and thus unglaciated terrain, in an extensive region now beneath the Atlantic Ocean east of Cape Cod, at least as far as Sable Island. Second, a skeleton of the beluga whale (*Delphinapterus leucas*) was recovered from late Pleistocene sediments in Charlotte, Vermont at an elevation of approximately 300 feet and over 200 miles from the nearest marine waters where the species currently occurs. The Charlotte whale is a manifest witness of the incursion of marine waters into the Lake Champlain Basin; these waters, called the Champlain Sea, were in place for about 2000 years (ca. 12,000–10,000 years BP) at the very end of the Pleistocene. Third, the two-mile-long and up to 100-foot-deep canyon in eastern New York known as Ausable Chasm has been carved in its entirety in the Holocene (beginning 10,000 years BP). This dramatic landscape, carved by the Ausable River into Cambrian Potsdam Sandstone, suggests a long erosional history. However, the Ausable River also cuts through a late Pleistocene marine delta above the gorge, so the cutting of the chasm entirely postdates the Champlain Sea interval (Franzi et al. 2002). In addition, the rate of horizontal gorge cutting in historical times is consistent with its two-mile length being cut in the Holocene. These observations attest to the dramatic and ongoing changes in the New England landscape over the last 12,000 years, the time frame for the present inquiry.

Fernald's "Persistence of plants in unglaciated areas of boreal America" (Fernald 1925) remains an elegant synthesis of plant distribution data, ecological data, and the Quaternary geological record as they were understood at the time. Fernald had spent a number of field seasons in the mountains of New England and to the northeast in Canada; he was especially interested in the ultramafic mountains of the Gaspé Peninsula and Newfoundland. From his extensive fieldwork, he was able to develop a conceptual understanding of the distribution of the Arctic flora across the southern reaches of the boreal region, especially on the alpine summits that he so loved to explore. Early on, he was impressed with and developed a strong understanding of the relation between boreal plant distribution and substrate geology (Fernald 1907). By the time he returned from his expedition to Newfoundland and

southern Labrador in 1911, Fernald was able to propose general patterns of geographic distribution for the plants in the flora of Newfoundland (Fernald 1911). These patterns reveal that he had a modern conceptual understanding of the distribution of periglacial plants across the North American continent. His 1925 work goes one step further, in that it combines his vast experience of the northern flora with his growing understanding of substrate preference and brings to the analysis the emerging understanding of the glacial geology of northeastern North America. In this work, Fernald emphasized the strong relationship between the alpine summits of northeastern and western North America, especially among plants found on ultramafic substrates. He also espoused the then-popular argument that some alpine summits, such as Mt. Albert in the Gaspé, were unglaciated, at least during the last (Wisconsin) glaciation. Fernald's key contribution was to synthesize plant distribution data, ecological factors, and Quaternary geology to infer the historical geography of plants in and near the glaciated regions of North America.

In contrast to the time when Fernald was active, we are now able to interpret the historical geography of the New England flora in light of new and powerful data sets: palynological, macrofossil, and genetic—including isozyme data, DNA restriction-fragment length polymorphisms, and DNA sequence data. For many of the groups under study, data on morphology, habitat preference, and geographic distribution can be integrated with insights into the geographic distribution of the group's genetic variation and, in some cases, past distribution from the fossil record. Recently, an array of phylogeographic studies has combined these data sets, and it is now possible to synthesize the patterns so far encountered into a new understanding of the Quaternary biogeography of the New England flora. Of particular value are recent improvements in analysis of the geographic distribution of chloroplast DNA haplotypes, which provide unique power to interpret Holocene range change (Cruzan and Templeton 2000). This sort of analysis is already well underway in Europe (e.g., Hewitt 2000; Taberlet et al. 1998).

In this paper we characterize the patterns of refugia and migration from refugia for 13 members of the flora of New England based on 15 recent inquiries (Table 1). All of these inquiries incorporate genetic data in the context of the geographic distribution of the species. Recent genetic inquiries involving the

Table 1. New England flora included in the review of genetic diversity and Holocene biogeography.

Taxon	Data Type	Genetic Pattern	Reference
Adiantum aleuticum	RFLP of chloroplast DNA	Vermont populations sister to western North American populations	Paris 1991
Ammophila breviligulata	Ribosomal nuclear DNA ITS	Diversity greatest in the North Atlantic	Walker 1998
Asclepias exaltata	Isozymes	Appalachian forest populations most diverse	Broyles 1998
Cypripedium parviflorum	Isozymes	More diverse in previously glaciated areas, less diverse southward	Wallace and Case 2000
Dryas integrifolia	RFLP analysis of cpDNA PCR fragments	High-Arctic centers of diversity in northwest and northern North America	Tremblay and Schoen 1999
Geum peckii	RAPDs	Diverse in both western Nova Scotia and New England alpine	Paterson and Snyder 1999
Lathyrus japonicus	cpDNA sequence and isozymes	Diversity decreases away from Cape Cod and Newfoundland.	Schmitz 2002
Pinus resinosa	Chloroplast microsatellites	No variation	Echt et al. 1998
Pinus resinosa	RAPDs	No variation	Mosseler et al. 1992
Pinus resinosa	cpSSR loci	Diversity greatest in two northeast North America centers	Walter and Epperson 2001
Polygonella articulata	Isozymes	No variation	Lewis and Crawford 1995
Saxifraga oppositifolia	RFLP of chloroplast DNA	High-Arctic center of diversity (Siberia and/or Alaska)	Abbott et al. 2000
Prunus section *Prunocerasus*	Chloroplast DNA sequence data	South-central United States refugium; migration north in continent interior	Shaw and Small 2005
Trillium grandiflorum	RFLP analysis of cpDNA PCR fragments and isozymes	Diversity decreases from southwest to northeast	Griffin and Barrett 2004
Vaccinium uliginosum	Chloroplast DNA sequence data	Two lineages in New England, from different endemic centers	Alsos et al. 2005

Arctic element in our flora have had a broad, worldwide scope, since the species tend to be circumpolar. On the other hand, work on the North-Temperate element tends to focus on Eastern North America, as the species occur only there. Consequently, we can report a longer history—often including Pliocene and Pleistocene divergence events—for the Arctic species, but we are generally limited to identifying Wisconsin-glaciation refugia and subsequent migration events for our North-Temperate species. A key premise in interpreting periglacial distributional histories is that the regions harboring populations with the most genetic diversity are at or near Pleistocene refugia for the species (e.g., Hewitt 2000). We explore the dependability of this assumption as we review the recent work on New England plants that takes advantage of the newer data sets.

First, we consider the improvements in the fossil data. Over the past thirty years, our knowledge of Holocene changes in plant distribution based on fossils has increased substantially, inaugurated by the well-known work of Margaret Davis (e.g., Davis 1983). Davis has provided data on the return of wind-pollinated tree species to New England from pollen-core data taken across the region. Differences in both timing and route of expansion (and more recently contraction) are discernible in these data. For instance, pollen of pines such as *Pinus strobus* and *P. resinosa/ P. banksiana* (these two pollens are indistinguishable) is recorded in New England by 12,000 years BP, while tamarack (*Larix laricina*) and hemlock (*Tsuga canadensis*) pollen do not reach our region until approximately 10,000 years BP. Source as inferred from the pollen record varies: the pines and hemlock expanded into New England from the coastal southeastern United States, whereas tamarack expanded northeastward from early stations in the Midwest, suggesting that southeast coastal and Mississippi valley Pleistocene refugia harbored different assemblages of refugees from New England.

Davis's data show that broad-leaved trees reached New England more recently than the conifers. For instance, beech (*Fagus grandifolia*) expanded into New England from late Pleistocene sites in the lower Mississippi Valley about 8000 years BP, and the chestnut, *Castanea dentata*, arrived from the same region only within the last 2000 years. Finer analysis of the beech data set (presented in Clark et al. 1998) reveals a retreat from more northerly and westerly stations after 4000 years BP, correlated with

the decline in average annual temperature from a maximum at about 5000 years BP, known as the hypsithermal.

The first events in the reestablishment of non-tree vegetation in deglaciated New England have been detailed in a series of papers on micro- and macrofossils, especially from the Connecticut River Valley (e.g., Anderson et al. 1986; Miller 1989; Miller and Spear 1998; Miller and Thompson 1979). The sites studied span the period between 13,500 and 10,000 years BP (the latest Pleistocene); the recovered plant remains document a flora characteristic of present-day Arctic and alpine regions of North America. Among the fossils, there are both plants currently limited to the alpine in New England—such as *Arctostaphylos alpina*, *Harrimanella hypnoides*, *Minuartia groenlandica*, *Rhododendron lapponicum*, *Salix uva-ursi*, and *Vaccinium uliginosum*—as well as plants now known only farther north in North America. Among these fossils are remains of plants now known in northeastern North America only from the Gaspé Peninsula, James Bay, Labrador, and Newfoundland (e.g., *Parnassia kotzebuei*) Thus, at the close of the Pleistocene, at the time the Charlotte whale was stranded in the Champlain Sea, our region hosted an Arctic tundra that has since become largely restricted farther to the north and east. Remnants of this assemblage of Arctic plants have persisted only on mountaintops and ice-carved alpine notches in our region.

The first genetic inquiries we consider address plants prominent in the Late Pleistocene fossil assemblages studied by Miller and associates: *Dryas integrifolia*, *Saxifraga oppositifolia*, and *Vaccinium uliginosum*. For the first two, we couple molecular data and the fossil record to yield insights into Pleistocene and Holocene biogeographic history. Both of these taxa are limited to calcium-rich substrates, especially in the southern part of their ranges. Tremblay and Schoen (1999), using a restriction fragment length polymorphism (RFLP) analysis of chloroplast DNA (cpDNA) polymerase chain reaction (PCR) fragments, tested hypotheses for Pleistocene refugia of *D. integrifolia*—now extirpated in New England. Interpreting genetic and fossil distribution data in the light of the location of the Pleistocene ice sheets in North America, they proposed five unglaciated regions now harboring *D. integrifolia* populations as potential Pleistocene refugia: Beringia, the Canadian High Arctic, the Canadian Eastern Arctic, southeast of the Laurentide ice sheet, and the southern Rockies. Their analysis revealed high genetic diversity in the first two of their five regions,

but not in the other three or in previously glaciated regions. Tremblay and Schoen concluded that an unglaciated High Arctic region in northwest and northernmost North America most likely provided a refugium for this species in the Pleistocene. The extensive extinction of periglacial populations southeast of the Laurentide ice sheet may have destroyed the genetic evidence for a refugium there—an important limitation of the dependability of inferences about refugia advocated by Hewitt (2000).

Saxifraga oppositifolia (purple mountain saxifrage) survives today in New England in the alpine notches of Vermont, where a combination of low summer temperatures, high moisture, and lime in the substrate provide a suitable environment for the species at the southern limit of its current range. The species is circumboreal (Abbott et al. 2000; Hultén 1971); virtually all of its current distribution was glaciated in the Pleistocene, with the exception of nunataks and coastal slopes in the lee of ice flow in the Canadian eastern Arctic and northern Siberia. Phylogenetic analysis of chloroplast haplotypes from a sample representing most of the species' current range revealed that the first extant haplotypes to evolve are now endemic to north-central Siberia (Abbott et al. 2000). These results suggest an Old World high-Arctic origin or refugium for the species. The analysis also reveals early (late Pliocene or early Pleistocene) divergence of the species into two lineages, one of which is largely North American. Ancestors of this lineage evidently reached North America from Siberia across Beringia, where—based on high haplotype diversity—the species presumably found its New World Pleistocene refugium in western mainland Alaska. This lineage is also found in the high Arctic of Canada and Greenland.

The other lineage, largely European, has its greatest genetic diversity in unglaciated areas of northern Siberia, implying an Old World Arctic Pleistocene refugium. Outlying populations of this lineage are found in Eastern North America at more southern, but still Arctic, latitudes. The sole continental eastern North American accession in their sample (from southern Labrador) is in this Eurasian clade. The plants of New England alpine notches are most likely derived from these more southern populations and ultimately from Siberia via migration west across the Atlantic. Thus, judging from the inquiries into mountain avens and purple mountain saxifrage, the high-Arctic element in our flora is likely to have weathered the Pleistocene along the Arctic Ocean and migrated

south to populate the newly exposed, formerly glaciated terrain from these northern refugia.

The third species, *Vaccinium uliginosum*, was profiled from 18 chloroplast haplotypes combining the *trn*L-*trn*F and *trn*S-*trn*G spacers (Alsos et al. 2005). They presented evidence for three widespread lineages (Amphi-Atlantic, Beringian, and Arctic-Alpine), which they suggested were the result of pre-Pleistocene divergence. The New England mountains host two of these lineages, the Arctic-Alpine and Amphi-Atlantic. The location of Pleistocene refugia and Holocene migration of these lineages into New England remain obscure in spite of this work.

Another well-known New England alpine species, Peck's avens (*Geum peckii*), presents evidence of a nearby refugium and recent vicariance. Paterson and Snyder (1999) have recently addressed the geography and genetics of this species and its close ally *G. radiatum* using random amplified polymorphic DNA (RAPDs). Currently, *G. peckii* has a distribution disjunct between wet meadows and streamsides on the alpine summits of the White Mountains in New Hampshire and a single sea-level bog in Nova Scotia. This disjunct distribution provides an elegant illustration of the tendency for New England Arctic-Alpine species to be distributed both on summits and along the coast from Maine's Casco Bay east into the Canadian Maritimes [as exemplified by, among others, black crowberry (*Empetrum nigrum*), see the map in Fernald 1925]. The cool summer temperatures and high moisture availability in the coastal region presumably are enough like the climate on the alpine summits to explain this pattern. In Paterson and Snyder's analysis of these plants, samples from the single Nova Scotia population of *G. peckii* and the various accessions from the White Mountains were undifferentiated—different individuals from Nova Scotia were sister to various accessions from the White Mountains. These data for *G. peckii* suggest that the history of these two regions is intimate, that recent vicariance with Holocene climatic change has led to the loss of populations between the White Mountains and coastal Nova Scotia. Coastal bogs in unglaciated regions of the Maritimes may have provided the Pleistocene refugium for *G. peckii*, a hypothesis that seems likely, given that the White Mountain populations now grow well within the region previously covered by the continental glacier, while the Nova Scotia population lies near the region proposed to have been ice-free continental shelf tundra and forest (Pielou 1991).

The flora of the New England sea beaches is the place to search for evidence of plants persisting in refugia now lost to rising sea level. In our lab, we have explored the Holocene history of New England's sea beach flora, as several species are also found on relict dune systems along Lake Champlain. Most prominent in this community is the beachgrass (*Ammophila breviligulata*). This grass is widely distributed from North Carolina northward along the Atlantic Coast to Newfoundland and Labrador and inland along the Saint Lawrence Seaway, as well as around Lake Champlain and the Great Lakes. Walker (1998) used nuclear ribosomal DNA sequence data from the internal transcribed spacers ITS1 and ITS2 to explore the divergence and biogeographic history of beachgrass. He demonstrated that there are four clades with strong geographic integrity; these were: 1) Southern Atlantic, 2) Northern Atlantic, 3) Great Lakes, and 4) Lake Champlain. Walker showed the Lake Champlain and Great Lakes clades to be sister to each other, consistent with their divergence being recent, that is following the isolation of the Champlain Basin from salt water at approximately 10,000 years BP. His data on genetic diversity within the four clades provide insight into the location of a Pleistocene refugium for this species. The greatest nucleotide diversity was found in populations from the northern Atlantic (Long Island to Nova Scotia); lower diversity was encountered on the southern Atlantic (North Carolina to New Jersey) and inland (Lake Champlain and the Great Lakes). These data suggest that there was a Pleistocene refugium for beachgrass in the North Atlantic, north of the southernmost extension of the Laurentide glacier. A plausible location for this refugium would be the extensive sandy shores of the exposed and ice-free continental shelf extending east from Cape Cod.

We have uncovered a similar but more complex history for the beachpea (*Lathyrus japonicus*) in North America (Schmitz 2002). Analysis of isozyme data yielded evidence of two distinct centers of genetic diversity in the North Atlantic, one on Cape Cod and a second, less diverse, on Newfoundland. These two centers have almost all of the narrowly localized allozymes, and they have the most allozyme diversity among the sampled regions. Allozyme diversity decreases away from the Cape Cod center, with the ranges of geographically widespread allozymes almost always including the ranges of more restricted allozymes (i.e., the restriction of allozymes is nested or geographically congruent). These data suggest a refugium for the New England beachpea populations on the exposed

sandy shores from Cape Cod east, just as with *Ammophila breviligulata*.

The beachpea is in fact circumboreal. Sequence data for the chloroplast spacer between *trn*H and *psb*A from throughout the range of the species (from Japan to Scandinavia) revealed five haplotypes. One haplotype was widely distributed in the North Atlantic, and along the shores of the Gulf of St. Lawrence, Lake Champlain, and the Great Lakes. This haplotype closely follows the distribution of allozymes found in the Cape Cod center of diversity. A second widely distributed haplotype was distributed from the Straits of Belle Isle north and west across Canada and Alaska; it was also the haplotype retrieved from the Japanese populations sampled. This haplotype closely follows the distribution of the allozymes found in the Newfoundland center of diversity, suggesting a second refugium for the species in the Arctic. Nested clade analysis (Templeton 1998, and references therein) of these data suggest an earlier fragmentation of the two widely distributed haplotypes, followed by isolation of local peripheral haplotypes in Lake Champlain and at the southern limit of the Atlantic and eastern Pacific range of the species.

Recent work on the population biology of the well-known white-flowered trillium (*Trillium grandiflorum*) used both isozyme and DNA sequence data to yield insights into the Holocene biogeography of this common forest-floor species (Griffin and Barrett 2004). Using RFLP analysis of cpDNA PCR fragments, Griffin and Barrett were able to discern five haplotypes, evidencing a strong geographic pattern in eastern North America. Nested clade analysis of the five haplotypes argued for grouping them into two clades established by fragmentation and long-distance colonization. These comprised a southern Appalachian upland group of three haplotypes concentrated in Tennessee and North Carolina and a northern group of two haplotypes that mapped to the limestone terrain to the west of the Appalachians from Vermont to Michigan. Since the southern clade is the less derived relative to allied *Trillium* species, Griffin and Barrett argued that it is ancestral.

Griffin and Barrett also did an isozyme sample of the same plants. Our analysis (data not shown) of geographic restriction of allozymes in their isozyme data suggests a single refugium, as populations having either unique allozymes or the greatest number of allozymes are confined to the west and south of the sampled set of populations. Davis's (1983) plotting of late Pleistocene popula-

tions of canopy tree species likely to have sheltered *Trillium grandiflorum* (such as *Fraxinus americana* and *Acer* species) in Arkansas and Alabama suggests a refugium for the trillium (Griffin and Barrett 2004) there, near the highest concentration of allozyme diversity. We suggest that the haplotypes retrieved in this study evolved as the species migrated east and north following glacial retreat, with haplotypes now adapted to southern, more montane habitats early giving rise to the haplotypes now largely confined to limestone country in the north. The emerging portrait from these considerations is that the New England populations of *T. grandiflorum* appear to be outliers of a northern, limestone-country lineage that diverged from the lineage found in the present-day southern Appalachians at the beginning of the Holocene, as the species was dispersing from its Pleistocene refugium in Alabama and Arkansas.

The history of the poke milkweed (*Asclepias exaltata*) appears to be similar. Like *Trillium grandiflorum*, this milkweed is distributed in the Appalachians and across the Great Lakes basin; in New England it is found in drier habitats at woodland borders on alkaline substrates. Broyles (1998) inferred features of the post-glacial migration of this milkweed from allozyme variation. Broyles found that the northern populations (north of glaciation), which are smaller and more fragmented, have less allozyme diversity than the large southern populations, with the greatest diversity of all concentrated at the southeastern limits of the species distribution. This pattern points to a refugium in the south, but perhaps farther to the east than that of *T. grandiflorum*. The New England plants, far from the apparent refugium in the south and confined to small populations at distance from one another, are among the most genetically depauperate.

Work on species in *Prunus* section *Prunocerasus* (Shaw and Small 2005) reveals evidence for a similar refugium for cherry species in the south-central United States, and their subsequent migration north in the interior of the continent. However, the historical signal is largely hidden by recent hybridization among the genetic lineages.

In contrast to *Trillium, Asclepias,* and *Prunus,* the common northern New England species *Polygonella articulata* and *Pinus resinosa* present depauperate genetic profiles. An isozyme analysis of *Polygonella* species revealed the sand-jointweed, *P. articulata*, to be without genetic variation (Lewis and Crawford 1995). The remaining eastern North American polygonellas all have restricted

distributions in the south, especially in Texas and peninsular Florida. Of these, seven of ten species have at least three times the allelic diversity of *P. articulata*, leading Lewis and Crawford to propose the southeast as a genetic refugium for the genus.

Both RAPDs (Mosseler et al. 1992) and chloroplast micro-satellite (Echt et al. 1998) analysis of red pine (*Pinus resinosa*), which apparently is native in New England only on dry sandy outwash, exposed bluffs, and headlands in the northern states, yielded unusually low variation. This low variation may be the result of rapid geographic shift in, and possible limitation of, appropriate habitat. The range of red pine may have shifted rapidly with resulting loss of genetic diversity during the rapid warming in the period approaching the hypsithermal (Hewitt 2000; Ibrahim et al. 1995). Consideration of the pollen record for *P. resinosa/ P. banksiana* corroborates this view. Davis's map (Davis 1983) for this pollen shows a dramatically more rapid northern expansion of these pines than for other species she maps. *Pinus resinosa* and *Polygonella articulata* may represent a cohort of northern New England species that fit Hewitt's idea of northward-migrating species losing genetic diversity with rapid migration during the rapid climate change leading up to the hypsithermal.

However, more rapidly evolving genetic characters reveal di-versity with geographic patterning in *Pinus resinosa.* Recent analysis of chloroplast microsatellites and simple sequence repeats across the range of red pine revealed the greatest variation to be in northern New England and adjacent New Brunswick (Walter and Epperson 2001). They suggest that this anomalous diversity in a previously glaciated region is the result of the mixing of genetic diversity from two refugia, one Appalachian and the other along the Atlantic Coastal Plain. This sort of secondary development of genetic diversity as a result of the meeting of previously isolated populations is known as a suture zone (Remington 1968). These suture zones are often evoked in work on animals and plants in the European Holocene (Hewitt 2000)—and one is in fact evident in the contact zone between the two centers of diversity in our *Lathyrus* data.

Northern New England harbors another lineage—the maiden-hair ferns (*Adiantum*)—that apparently has an entirely different Holocene history. There are three species in the genus in New England, *A. pedatum*, *A. aleuticum*, and their fertile allotetraploid hybrid *A. viridimontanum* (Paris 1993; Paris and Windham 1988).

While *A. pedatum* is endemic to northeastern North America, *A. aleuticum* is disjunct between the American West and serpentine outcrops in northeastern North America. It was prominent on Fernald's list of periglacial plants disjunct between western and northeastern North America (Fernald 1925). Phylogenetic analysis of restriction fragment polymorphism data derived from chloroplast DNA reveals that the northeastern North American *A. aleuticum* populations are derived from the more broadly distributed western populations (Paris 1991). From these observations we conclude that the species migrated eastward, presumably as glacial retreat proceeded in the Holocene. Long-distance dispersal, a common process among the small-propaguled ferns (Barrington 1993; Tryon 1989), is unlikely in the case of *A. aleuticum*, because this species commonly has unisexual gametophytes (Paris 1991). Paris proposed that the western taxon arrived on serpentine substrates in northeastern North America via a series of more local dispersals across now extirpated periglacial habitats, since establishment by long-distance dispersal is unlikely for the species.

Adiantum viridimontanum, the tetraploid, is endemic to formerly glaciated serpentine substrates in Vermont and adjacent Québec. Almost certainly, the hybridization that preceded the origin of this tetraploid took place in one of these serpentine areas once the western *A. aleuticum* had arrived in the east, arguably some time in the Holocene.

Do the patterns of genetic diversity in these data sets witness the location of refugia and subsequent migration? We think they do for three reasons. First, in the studies on *Saxifraga* and *Dryas*, the genetically diverse populations are among those from unglaciated sites with fossil evidence suggesting plants were there in the Pleistocene. Second, both inquiries utilizing nested-clade analysis (*Lathyrus* and *Trillium*) yield the inference that historical factors, not ecological factors, predominate in determining the current pattern of genetic variation. Third, three isozyme data sets (*Asclepias*, *Lathyrus,* and *Trillium*) show strongly concordant distribution of allozyme diversity across loci (between isozymes). We suggest that these data provide independent tests of the hypothesis that historical versus ecological factors—such as patterning of appropriate habitat—underlie the distribution of diversity. In each case, the most diverse populations lie near plausible Pleistocene refugia based on geological or floristic data.

We are left with the working hypothesis that the set of observed patterns is historically determined.

However, for at least one case for a member of the New England flora—the yellow lady-slipper—genetic diversity may reflect recent genetic drift and not the location of a refugium. Wallace and Case (2000) compared both 1) northern and southern populations of *Cypripedium parviflorum* var. *pubescens*, and 2) the north-south variety pair var. *makasin* and var. *parviflorum*. They demonstrated that allozyme diversity in both pairs is higher in northern, previously glaciated areas. Restriction of allozymes does not present the clear patterns seen in other genera, such as in *Lathyrus*. Wallace and Case pointed out that (in contrast to *Asclepias*) the southern populations of the yellow lady-slippers are the more fragmented and suggested that genetic drift has led to loss of diversity in the south. They speculated that open, disturbed habitats were common to the north during the retreat of the glacier, while closed forests and more narrowly defined habitat to the south were disadvantageous for the species there. Thus, although historical determination of current genetic diversity is common in New England species, experimental inquiries must assess recent, ecological contributions to the distribution of genetic diversity as well.

What of palynological data—do they in fact witness past distribution changes? Clark et al. (1998) as well as Cain et al. (1998) addressed the problem of incremental range expansion being too slow to allow return of the northern flora to its present distribution in the time since the retreat of the glaciers. They rejected simple incremental expansion for a model that includes both episodic long-distance colonization and local diffusion-like dispersal. Rejecting their own earlier conclusions, Clark et al. (2001) presented model results predicting that migration rates should be slow. They posited northern, undocumented refugia as the source of propagules for present-day northern populations. This idea is hard to accept in the light of the multiple cases in which Holocene palynological data have strong geographic patterns of northern expansion over time, and refugia are witnessed by both genetic and palynological data.

The alternative, that estimates for rates of range expansion are too low, seems more likely. It may be that migration into habitat exposed by glacial retreat is more like the migration of invasive species at present (Hewitt 2000). For instance, Williamson et al. (2005) demonstrated that initial migration of invasives into new

regions is rapid and patchy, but increase in geographic coverage over time shows orderly expansion and is either geometric or logarithmic. They presented evidence of rates of geographic spread decreasing over time, which they suggested is because the species runs out of habitat in the region. The opening of new terrain with glacial retreat created conditions much like those explored in the work of Williamson et al.—similar if less dramatic changes in climate may have led to rapid advance of forest species into tundra.

People think of the whole of the New England flora retreating southward to Pleistocene refugia in the southern Appalachians and the southeast coastal plain, as was evidently the case for forest tree species and forest-floor herb species. However, the plants in our flora have apparently arrived from more or less remote refugia in every direction: some (like *Dryas*) have already come and gone since the end of glaciation. Among the sources of our flora, as judged from this review, are the High Arctic, the mountains of the American West, and the unglaciated and now largely submerged North Atlantic Coastal Plain as well as the better-known refugia to the south, both along the coastal plain and to the west in the lower Mississippi valley. In general, New England populations of widespread species are far from their species' center of genetic diversity, presumably because Pleistocene refugia were remote from glaciated New England. The single local refugium inferred from high local genetic diversity (the sunken terrain east of Cape Code as far as the region of Sable Island) is in the sole unglaciated region of New England as inferred from the fossil record (e.g., Whitmore et al. 1967). In contrast, the most depauperate species in our flora appear to be north-woods species that have expanded rapidly into habitats established after the retreat of the continental glacier in the Holocene from already peripheral populations. Given the wide array of geographic sources for the members of our flora, our present-day plant communities (as delineated in such works as Thompson and Sorenson 2000) are most likely transient, constantly changing assemblages of species.

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