Ecology, 86(8), 2005, pp. 2088–2098

MOLECULAR INDICATORS OF TREE MIGRATION CAPACITY UNDER RAPID CLIMATE CHANGE

JASON S. MCLACHLAN,[1,2,3] JAMES S. CLARK,[1,2] AND PAUL S. MANOS[1]

[1]*Department of Biology, Duke University, Durham, North Carolina 27708 USA*
[2]*University Program in Ecology, P.O. Box 90329, Duke University, Durham, North Carolina 27708 USA*

Abstract. Recent models and analyses of paleoecological records suggest that tree populations are capable of rapid migration when climate warms. Fossil pollen is commonly interpreted as suggesting that the range of many temperate tree species expanded at rates of 100–1000 m/yr during the early Holocene. We used chloroplast DNA surveys to show that the geography of postglacial range expansion in two eastern North American tree species differs from that expected from pollen-based reconstructions and from patterns emerging from European molecular studies. Molecular evidence suggests that American beech (*Fagus grandifolia*) and red maple (*Acer rubrum*) persisted during the late glaciation as low-density populations, perhaps within 500 km of the Laurentide Ice Sheet. Because populations were closer to modern range limits than previously thought, postglacial migration rates may have been slower than those inferred from fossil pollen. Our estimated rates of $<$100 m/yr are consistent with model predictions based on life history and dispersal data, and suggest that past migration rates were substantially slower than the rates that will be needed to track 21st-century warming.

Key words: *climate change; molecular markers; paleoecology; range expansion.*

INTRODUCTION

Rapid climate change puts species at risk of extinction by shifting the ''climate envelope'' within which they can persist outside of their current geographic range (Davis and Zabinski 1992, Thomas et al. 2004). The magnitude of this risk depends on the rate at which species are capable of extending their ranges. The ranges of many North American trees will have to expand at rates of 100–1000 m/yr to track the predicted climatic changes of this century (Davis and Zabinski 1992, Iverson and Prasad 2002).

While such rapid rates of spread would seem unlikely for long-lived sedentary organisms like trees, interpretations of fossil pollen data suggest that rapid migration was typical for tree populations responding to postglacial warming (Davis 1981, MacDonald 1993, King and Herstrom 1997). The panels in Fig. 1 are adapted from the most widely cited estimates of North American tree migration rates (Davis 1981, Delcourt and Delcourt 1987). Both reconstructions estimate range expansion rates between 172 and 214 m/yr for maple (*Acer*) and beech (*Fagus*). Migration rates for almost all species examined in these studies exceed 100 m/yr, suggesting that temperate trees generally have the capacity to track future climate change through rapid migration (Clark 1998, Higgins and Richardson 1999). These rapid spread rates are often incorporated in models designed to project ecosystem and community response to contemporary climate change (Malanson and Cairns 1997, Iverson et al. 1999, van Minnen et al. 2000).

Although rapid postglacial migration has become widely accepted, it is difficult to square with estimates of demography and seed dispersal from modern forests. Long-distance dispersal would seem to provide a generic explanation for any rate of spread (Reid 1899, Davis 1986, Clark 1998), but the ability of species to spread rapidly by long-distance dispersal is also constrained by limited seed production and survival. Recent modeling efforts incorporate these life history constraints (Clark et al. 2001, Clark et al. 2003). These models are fitted to empirical seed dispersal and tree life history data, allowing for the ''fat-tailed'' (leptokurtic) shape of seed shadows and stochasticity in population spread. Although these models do not rule out rapid migration through extraordinarily rare long-distance dispersal events, they predict that migration potential may often be limited and that dispersal and life history traits strongly affect the capacity for rapid spread. By contrast, fossil-based studies reconstruct uniformly rapid spread, even for species with dispersal limitation, low fecundity, or long generation times (MacDonald 1993).

The apparent disparities between fossil-based estimates of spread and estimates from modern demographic data prompted us to reconsider migration potential in the face of rapid climate change. Some of the discrepancy may come from long-recognized limitations in our ability to infer late-Quaternary rates of

Manuscript received 29 June 2004; revised 15 October 2004; accepted 2 November 2004; final version received 7 January 2005. Corresponding Editor: L. C. Cwynar.

[3] Present address: Harvard Forest, P.O. Box 68, Petersham, Massachusetts 01366 USA.
E-mail: jsmclach@fas.harvard.edu

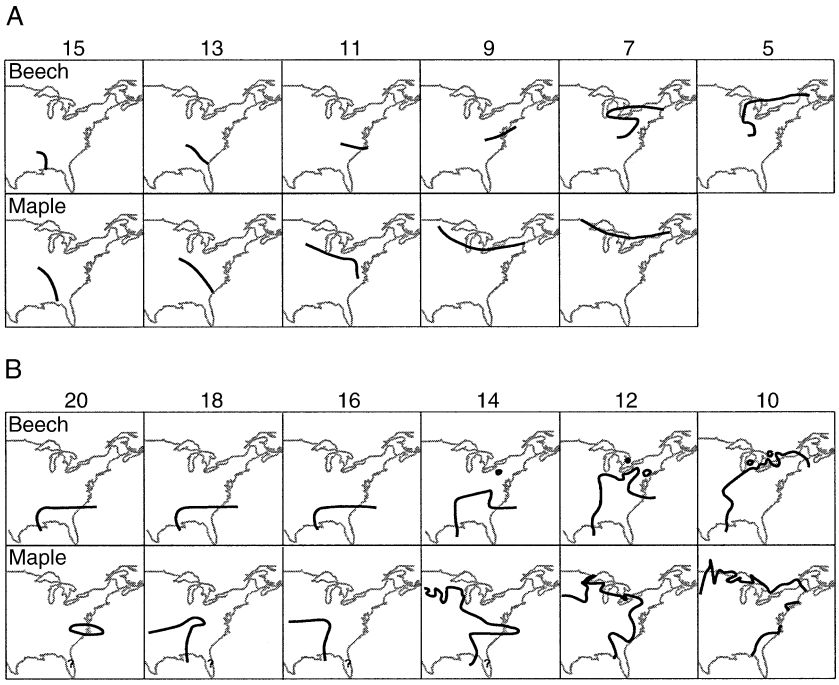

FIG. 1. The advancing northern edge of postglacial migration in beech and maple reconstructed from fossil pollen data. Numbers above pairs of panels are dates in thousands of radiocarbon years before present (yr BP). The figure is adapted from (A) Davis (1981) and (B) Delcourt and Delcourt (1987).

spread from pollen data. These estimates come from interpolated range limits of taxa over successive time intervals (Fig. 1). The range limit is defined by the amount of fossil pollen recovered from sediments. Extensive efforts to estimate the amount of sediment pollen that might mean that a population exists near the sample site have identified sources of uncertainty (Davis et al. 1991, Davis 2000, McLachlan and Clark 2004). Small amounts of pollen may be transported to sediments far outside a species' range. Conversely, the absence of pollen in sediments does not preclude the presence of small outlying populations or extensive low-density populations. During the late glacial, for example, populations of thermophilous trees may have been present in low abundance much farther north than the southern refuges depicted in Fig. 1 (Bennett 1985, Birks 2003).

Conveniently, genetic structures within species are especially sensitive to the historical dynamics of small populations, due to the importance of founding effects and genetic drift (Hewitt 1996, Petit et al. 2002). Maps of genetic variation across the modern range of species provide an independent record of the location of glacial refuges and the routes of expanding populations (Comes and Kadereit 1998, Taberlet et al. 1998). The chloroplast genome, most commonly used to study population dynamics in trees, is nonrecombining and is maternally inherited in most angiosperms (Reboud and Zeyl 1994). Populations spreading via seed therefore bring their ancestral cpDNA genotype with them, and changes in these lineages only occur through new mutations. Because cpDNA mutation rates are low (Wolfe et al. 1987), modern haplotypes almost certainly predate postglacial colonization, and the modern geographic distribution of cpDNA haplotypes corresponds to the migration routes of expanding populations. Although hundreds of generations have transpired between initial postglacial colonization and the present, postglacial migration routes are still apparent in modern genetic structures because gene flow into established populations is greatly reduced once they reach high population densities (Ibrahim et al. 1996). In Europe and Japan, molecular data are consistent with fossil pollen–based reconstructions of postglacial dynamics (Demesure et al. 1996, Tomaru et al. 1998, Petit et al. 2002). The southern ranges of most haplotypes in these studies coincide with areas identified as glacial refuges by palynological evidence, and a subset of these haplotypes is found farther north, their distribution delineating postglacial migration routes.

Fig. 2 shows the development of a hypothetical genetic structure consistent with southern glacial refuges and rapid Holocene expansion (as in Fig. 1). If glacial refuges are isolated from each other (Fig. 2A), founder effects, genetic drift, and in situ mutation lead to genetic divergence between refuges over time, corresponding to splits in the species' organelle phylogeny. Although population dynamics were undoubtedly complex during the last glaciation (Shuman et al. 2002), cpDNA mutation rates are slow enough that only long-

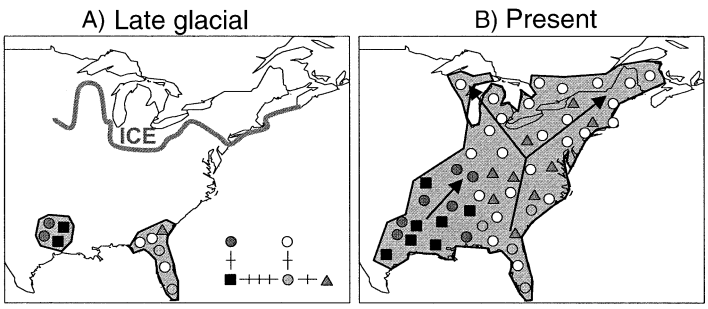

FIG. 2. The development of modern genetic structure in a hypothetical species. Populations expanded along migration routes indicated by arrows from glacial refuges in Florida and Texas. The species' range at each time step is shown in gray. Different symbols indicate different cpDNA haplotypes. Hatch marks along the genetic network in panel (A) indicate mutations. The Texan refuge has diverged from the Floridian refuge in the first panel due to isolation and genetic drift.

term processes, such as the effects of bottlenecks and drift in persistent glacial refuges, are clearly recorded in intraspecific phylogenies (Provan et al. 2001, Brewer et al. 2002). Petit et al. (2002) propose that glacial refuges should be genetically rich, but with variation confined within lineages.

With climate warming, populations expand from these refuges along routes that are genetically identifiable (Fig. 2B). Haplotypes are lost along migration routes, due to sequential bottlenecks during colonization (Hewitt 1996), and new haplotypes do not emerge, due to the low cpDNA mutation rate. The pool of haplotypes in more recently colonized areas is consequently a subset of the haplotype pool in the ancestral range. Rapid expansion by long-distance seed dispersal is thought to increase the rate of haplotype loss along colonization routes due to founder effects (Hewitt 1996, Ibrahim et al. 1996).

We used cpDNA surveys to reconstruct the postglacial expansion of two eastern North American species, red maple (*Acer rubrum*) and American beech (*Fagus grandifolia*). The established paleoecological reconstructions of Holocene range expansion (Fig. 1) comprise one hypothesis about these dynamics. An alternative hypothesis, consistent with limitation to the spread rate imposed by biological constraints and uncertainties in the fossil record, is that temperate species maintained late glacial populations farther north than previously appreciated (Stewart and Lister 2002). Our molecular reconstructions of Holocene dynamics incorporate established assumptions about the origin and maintenance of genetic structure in forests (Demesure et al. 1996, Petit et al. 2002). We assumed that most haplotypes originated before the Holocene and that genetic divergence between regions reflects long-term isolation of populations. We interpreted the distribution of haplotypes in territory formerly occupied by the Laurentide Ice Sheet as corresponding to the postglacial migration routes of those lineages. The southern distribution of those same haplotypes is the farthest south the ancestors of those expanding populations are expected to have been located during the last glaciation.

METHODS

Study organisms: ecology and postglacial spread

Red maple and American beech share broadly similar climatic tolerances and are distributed throughout eastern North America (Fig. 3). Both species are limited by minimum winter temperatures in the north of their ranges and by the dry climates of the prairie states to the west (Burns and Honkala 1990). Red maple has wind-dispersed samaras and is both an early-successional colonist and a persistent understory species. Beech is a late-successional species with nuts dispersed by birds and mammals. With greenhouse warming, both species are expected to expand their ranges northward (Davis and Zabinski 1992). Red maple is projected to maintain much of its southern distribution, though in lower abundance, while beech will probably not survive in most of its southern range (Iverson and Prasad 2002).

The extent to which temperate species were displaced southward during the last ice age has been the subject of persistent debate (Delcourt 2003). Braun (1950) famously identified the Allegheny and Cumberland plateaus of Kentucky and Tennessee as the long-standing refuge of mixed mesophytic flora, including temperate deciduous trees such as beech and maple. In a pioneering synthesis of early paleoecological data, Deevey (1949) argued that Pleistocene climates pushed temperate species much farther south.

In the 1980s, two influential paleoecological studies estimated the rates of species migration by explicitly reconstructing the ranges of trees over the course of the Holocene (Fig. 1). Past distributions of maple are shown at the genus level because not all palynologists identify red maple pollen to species. Disjunct distributions of maple, mapped at 20×10^3 and 18×10^3 yr BP in Fig. 1B, ''illustrate that although maple species were probably widespread throughout the region between 25° N and 38° N, they occurred in low numbers that were close to the lower limit of resolution for paleoecological resolution'' (Delcourt and Delcourt 1987). Nevertheless, rates of Holocene migration in that study are based on the expansion of maple from a late glacial refuge south of 37° N and west of 87° W, similar to that reconstructed by Davis (1981) in Fig. 1A. Both studies identify the Gulf Coastal Plain as the refuge of beech during the last glacial maximum (LGM), though Davis places it farther west than Delcourt and Delcourt (Fig. 1). Delcourt and Delcourt describe a northward postglacial migration through middle Tennessee and the central Appalachians, then into

central Pennsylvania, Ohio, Indiana, and Illinois, finally spreading into New England and southern Quebec by 10×10^3 yr BP. By contrast, Davis identifies the migration route of beech as east of the Appalachians into New England, followed by a western expansion across southern Ontario, then south into Indiana and Ohio.

The maps shown in Fig. 1 continue to be the most cited source for rates of postglacial migration in North America (e.g., Malcolm et al. 2002, Iverson et al. 2004, Powell and Zimmerman 2004). More recent paleoecological syntheses often delineate the detectable range of a pollen type as the smoothed contour enclosing relative abundances of that type exceeding a small threshold. For beech and maple, this limit is often set between 0.5 and 1% (e.g., Webb et al. 1993, Williams et al. 2004), but these studies do not equate this ''isopoll'' boundary with the taxon's range limit due to concerns about the over- or underrepresentation of pollen in sediments. Maps of changing isopoll boundaries for beech and maple by J. W. Williams et al. (*available online*)[4] occasionally indicate isolated northern populations for both species during the early Holocene, in contrast to the reconstructions of Davis (1981) and Delcourt and Delcourt (1987). However, Williams et al. do not assume that their isopoll boundaries correspond to range limits, and they consequently do not calculate postglacial migration rates for these taxa.

Field and laboratory procedures

We sequenced ~1500 base pairs from several noncoding cpDNA regions in 130 red maple individuals from 117 populations, and in 122 American beech trees from 100 populations, distributed evenly from throughout their modern ranges. Sample locations and GenBank accession numbers are listed in the Supplement. Leaf and bud samples were collected from adult trees away from human settlement and frozen at −80°C. We extracted genomic DNA from frozen material using a standard protocol (DNeasy Plant Mini Kit, Qiagen, Venlo, The Netherlands). In American beech we sequenced an intergenic spacer between the *trnL* (UAA) 3′ exon and *trnF* (GAA) (Taberlet et al. 1991), the intron between *trnK* and *matK* genes (Manos and Steele 1997), and the spacer region between the coding genes *atpB* and *rbcL* (Hodges and Arnold 1994). In red maple we sequenced *trnK* and *matK, rbcL* by *atpB*, and the noncoding *trnH* by *trnK* region (Demesure et al. 1995). PCR products were produced using Qiagen *Taq* DNA Polymerase and cleaned with a commercial column (QIAquick PCR Purification Kit, Qiagen). Sequencing reactions followed standard protocols (BigDye, PE Applied Biosystems, Foster City, California, USA), and final products were run out on an ABI Prism 3700 automated sequencer (PE Applied Biosystems). Sequences were examined and edited using the program Sequencher (Gene Codes Corporation, Ann Arbor, Michigan, USA).

Molecular variation

We inferred haplotype networks using unweighted characters and the branch and bound search option in PAUP* (Swofford 2002). Although insertion/deletions (indels) do not occur randomly in the cpDNA genome, and may therefore be subject to homoplasy, this phenomenon does not appear to strongly affect interpretation in intraspecific studies such as this one (Hamilton et al. 2003). We consequently coded indels as presence/absence characters and added as binary data to the sequence matrix. However, single base pair–length mutations detected in highly repetitive sequence motifs were excluded from the analysis, because they are labile and appear to be prone to higher levels of homoplasy (van Oppen et al. 2002).

We evaluated the effects of genetic bottlenecks on our species during postglacial spread by calculating the ratio of the total number of haplotypes found in each species to the number found in the top five degrees of latitude that we sampled (the northern 556 km). We compared this ratio to similar values estimated from other studies of cpDNA variation in temperate woody species. Sampling effort differed between studies, so we standardized across studies using the rarefaction approach (Hurlbert 1971, Simberloff 1972). Our common sample size was 100 individuals across the species' range and 20 individuals in the northern five degrees sampled.

Potential rates of spread

We combined our cpDNA surveys with established fossil-based range reconstructions to calculate postglacial migration rates under alternative sets of assumptions. Because beech pollen is only distinguishable to genus, and maple pollen is often not distinguished beyond the genus level in practice, we were compelled to compare species-level genetic data to pollen data at the genus level. This presents no difficulties for *Fagus*, which is monospecific in eastern North America, but maps of *Acer* pollen represent at least six common species of maple.

An upper estimate of spread rate is based on the established assumption that pollen data accurately reflect the range limits of our species. We mapped the range reconstructions of Davis (1981, Fig. 1A) and Delcourt and Delcourt (1987) (Fig. 1B) onto our haplotype maps (Fig. 3). For each time step, we calculated the maximum distance that each haplotype could have moved within the range boundaries reconstructed in these studies. We also considered the possibility that a threshold of 0.5% of arboreal pollen is a better indicator of the presence of beech trees near a pollen site (Webb 1986, Woods and Davis 1989, Davis et al. 1991, King and Herstrom 1997, Williams et al. 2004). In the ab-

[4] ⟨http://www.ngdc.noaa.gov/paleo/pubs/williams2004/williams2004.html⟩

sence of empirical data, we assumed the same 0.5% threshold for maple pollen. We overlayed contours containing >0.5% beech and maple pollen (Williams et al. 2004; J. W. Williams, *unpublished data*) onto our haplotype maps at thousand-year intervals from 21×10^3 to 8×10^3 yr BP and calculated rates of spread in the same manner.

A lower estimate of spread is based on the assumption that small populations existed outside of the range limits inferred from pollen data (Bennett 1985, McLachlan and Clark 2004, Williams et al. 2004), an assumption supported by our molecular evidence. We estimated the rates at which haplotypes in deglaciated territory spread from the margin of the former ice sheet to their northern range limits. We calculated the postglacial range expansion of each haplotype whose range spans the ice margin as the distance from the glacial margin to the northernmost sample of that haplotype. We divided this distance by the amount of time (in millennia) between 21×10^3 yr BP (the maximum ice sheet extent) and the time when the pollen range limits reached this northern sample. This approach assumes that the range limits reconstructed by Davis (1981), Delcourt and Delcourt (1987), and the 0.5% isopoll line are conservative measures of the local presence of our taxa. It is the minimum rate of spread allowed by the available data.

RESULTS

Molecular variation

A total of 25 polymorphisms were detected in the three noncoding regions we examined in red maple. In our analysis, we included seven insertion/deletions and 15 base pair substitutions. We excluded three microsatellite regions with single base pair repeats from our analysis. In beech, we scored 27 base pair substitutions and four insertion/deletions and excluded two microsatellite regions. Together these mutations allow the identification of 20 red maple haplotypes and 17 beech haplotypes. The most parsimonious haplotype networks consistent with the results of Neighbor-Joining analysis are shown in Fig. 3. Three red maple clades and four beech clades, grouped by colored ellipses in the haplotype networks, are supported in both methods of phylogenetic reconstruction.

Centers of diversity within the southern distribution of these clades indicate the location of the glacial refuges, where lineages diversified through mutation (Demesure et al. 1995, Hewitt 1996, Petit et al. 2002, cf. Fig. 2). In red maple, several haplotypes in both clade A and clade C are found in the southern Appalachians, and no member of either of these clades is found farther south than 34° N (Fig. 3). Most individuals north of the former ice margin descend from these lineages. The center of diversity in the red maple clade B occurs along the coastal plain between Georgia and Louisiana, suggesting a second, more southern, glacial refuge for red maple. Haplotype 9 in this clade extends along the Atlantic coast to New Jersey, but we found no northern populations of red maple that descend from this southern group. The remaining red maple haplotypes (10–13) do not comprise a phylogenetic clade, so the inference of diversification in a long-standing refuge does not apply to them. Clearly, Floridian red maples (haplotype 12) have a separate history from other southern populations. The cluster of haplotype 11 in Arkansas may indicate the location of yet another isolated population in what appears to have been an extensive, but possibly fragmented, late glacial range. Disjunct populations of haplotype 11 in New Brunswick are distinguished from these Arkansan populations by a single base-length mutation and are assumed to be of independent origin. Haplotypes 10 and 13 are broadly distributed from southern populations to north of the former ice margin. Without supporting phylogenetic detail, it is impossible to determine whether these variants were distributed widely during the last glaciation, or whether they expanded from smaller refuges somewhere between Louisiana and the former ice margin.

In beech, members of clade A are only found above 35° N and are restricted to west of the Appalachian Mountains (Fig. 3). Haplotypes in clade D are also distributed in and to the west of the Appalachians, but haplotypes 15 and 11 are distributed farther south than haplotypes of clade A. The center of origin of beech clade C is enigmatic. Most members of this clade were only found north of the former ice margin and may represent postglacial mutations. More likely, given the slow mutation rate of cpDNA (Wolfe et al. 1987), they represent rare haplotypes that were not sampled south of the ice margin by chance. The only wide-ranging member of clade C (haplotype 10) is found throughout the modern range of beech, providing little information about its late glacial distribution. The remaining haplotypes, including members of clade B, are rare. The array of rare haplotypes found only in North Carolina suggests the possibility of a long-standing population in this region.

Reduction in genetic diversity with latitude is expected to result from bottlenecks along long migration routes (Hewitt 1996, Petit et al. 2003). Both species investigated here retained almost half their genetic diversity in their northernmost range, higher than found in most other woody temperate species (Table 1). Taxa maintaining comparably high allelic richness in their northern distributions (after standardization) have either been extensively spread by humans (*Prunus avium* [Mohanty et al. 2001]) or are species with boreal distributions that probably had northern glacial refuges (*Calluna vulgaris* [Rendell and Ennos 2002] and *Salix* spp. [Palme et al. 2003]). Other species of maple and beech do not share the high northern cpDNA richness found in red maple and American beech. *Acer pseudoplatanus* and *Fagus sylvatica* retained relatively few haplotypes at high latitudes. *A. campestre* and *F. cren-*

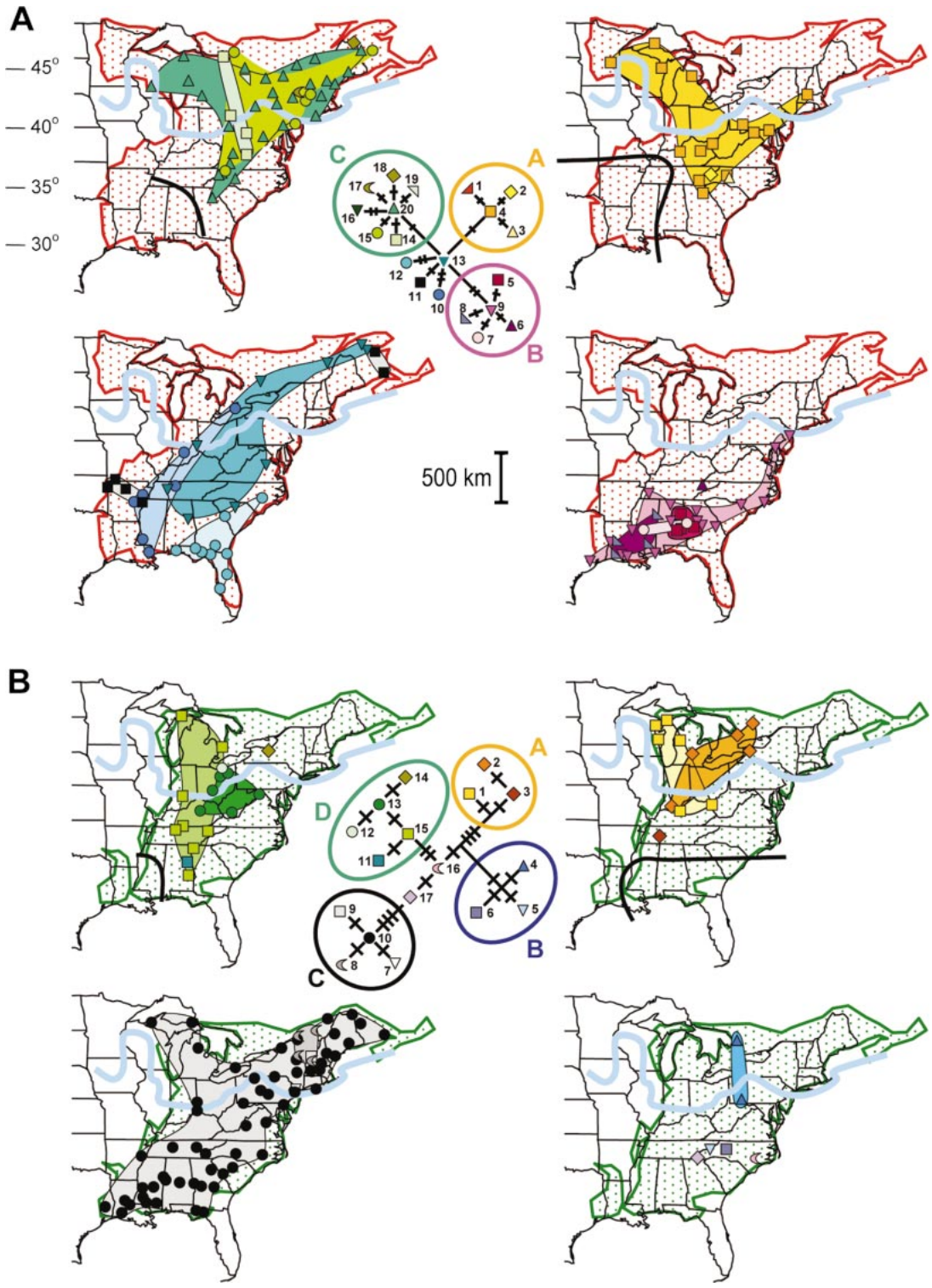

FIG. 3. The modern range of (A) red maple and (B) American beech and the distribution of their cpDNA haplotypes. The most parsimonious haplotype networks are shown for each species, with major clades grouped by colored ellipses. Character changes along internodes are indicated with hatch marks. The blue line illustrates the southern extent of the Laurentide Ice Sheet at the last glacial maximum. Thick black lines delineate the range of each species reconstructed by pollen at 15×10^3 yr BP (Davis 1981; upper left map) and at 16×10^3 yr BP (Delcourt and Delcourt 1987; upper right map).

TABLE 1. Haplotype richness at the northern range limits of temperate woody species.

Species, by location	Latitude (°) of northernmost sample	No. haplotypes (no. after rarefaction in parentheses) From northern 5°†	From total range‡	From northern 5°/from total range§	Source
North America					
Fagus grandifolia	47.3	8 (6.6)	17 (15.2)	0.47 (0.44)	1
Acer rubrum	48.41	9 (7.6)	20 (18.1)	0.45 (0.42)	1
Europe					
Calluna vulgaris	68.45	5 (4.8)	12 (10.1)	0.42 (0.47)	2
Salix spp.	57.87	15 (8.9)	29 (19.6)	0.52 (0.45)	3
Prunus avium	57.53	5 (4.4)	16 (11.0)	0.31 (0.40)	4
Quercus spp.	57.87	4 (3.3)	10 (9.2)	0.40 (0.36)	3
Acer campestre	54.27	5 (3.9)	14 (10.8)	0.36 (0.36)	3
Populus tremula	57.87	10 (6.6)	30 (20.0)	0.33 (0.33)	3
Tilia cordata	57.87	5 (4.0)	16 (13.6)	0.36 (0.30)	3
Fraxinus spp.	57.87	2 (2.0)	7 (5.8)	0.35 (0.29)	3
Betula pendula	67.01	3 (2.9)	13 (9.9)	0.23 (0.29)	5
Alnus glutinosa	64.22	3 (3.0)	13 (10.9)	0.23 (0.28)	6
Ulmus spp.	57.87	11 (6.6)	41 (25.5)	0.27 (0.27)	3
Corylus avellana	57.87	1 (1.0)	5 (3.9)	0.20 (0.26)	3
Carpinus betulus	56.75	1 (1.0)	4 (4.0)	0.25 (0.25)	3
Fagus sylvatica	57.87	1 (1.0)	6 (4.6)	0.17 (0.22)	3
Acer pseudoplatanus	57.32	3 (3.0)	22 (17.8)	0.14 (0.17)	3
Prunus spinosa	57.87	4 (3.6)	40 (27.6)	0.13 (0.13)	3
Japan					
Fagus crenata	42.37	3‖	9‖	0.33‖	7

Notes: Sources are: 1, this study; 2, Rendell and Ennos (2002); 3, Petit et al. (2003); 4 Mohanty et al. (2001); 5, Palme et al. (2003); 6, King and Ferris (1998); and 7, Okaura and Harada (2002).

† The first value is before rarefaction; the second value (in parentheses) has been standardized for rarefaction, to a common sampling effort of 20 individuals.

‡ The first value is before rarefaction; the second value (in parentheses) has been standardized for rarefaction, to a common sampling effort of 100 individuals.

§ The first value is before rarefaction; the second value (in parentheses) is after rarefaction.

‖ Okaura and Harada (2002) sequenced a total of 24 individuals, so we could not standardize their results to $N = 100$ using rarefaction.

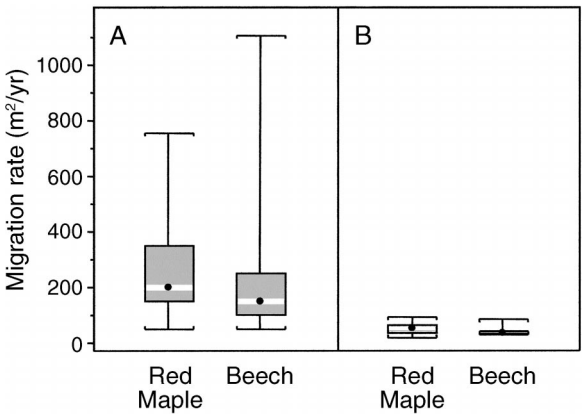

FIG. 4. The range of postglacial migration rates of red maple and American beech assuming that (A) fossil pollen reconstructions (Davis 1981, Delcourt and Delcourt 1987) accurately identify late glacial refuges, and that (B) molecular data accurately identify late glacial refuges (see *Methods*). The solid black dot is the median value. The box indicates the interquartile range. Whiskers indicate the limits of the data.

ata maintained intermediate levels of cpDNA richness, although differences in sampling design between studies do not permit us to standardize levels of *F. crenata* diversity via rarefaction (Table 1).

Rates of spread

Our upper estimate of spread rate is based on the straightforward assumption that published pollen-based reconstructions accurately reflect changing species distributions and that molecular data can resolve the migration routes of populations within species ranges (see *Methods*). Under this assumption, we obtain estimates of spread rate even greater than those based on pollen alone (Fig. 4A). These high estimates result from the presumed long distance traveled from the Deep South in combination with the most likely migration pathways, which are identified with molecular evidence.

However, the disjunction between the spatial patterns of spread suggested by pollen data (Fig. 1) and molecular data (Fig. 3) suggests that fossil pollen data do not accurately identify the routes of population spread. If we assume that pollen reconstructions primarily identify well-established populations, we find that

these species may have spread as slowly as 80–90 m/yr (Fig. 4B), less than half the rate estimated by pollen alone (Davis 1981, Delcourt and Delcourt 1987, King and Herstrom 1997). Rates calculated using 0.5% isopoll boundaries for maple and beech in Williams et al. (*data available online*; see footnote 4) did not differ substantially from those shown in Fig. 4 (results not shown).

Difficulties due to the different taxonomic resolution between maple pollen and red maple genetic data affect these calculations to an unknown degree. We do not know, for instance, whether red maple is represented in the leading edge of the migrating pollen front. However, our more general point—that pollen reconstructions do not capture key dynamics of postglacial spread—is not affected by this problem because maps of spreading pollen (Fig. 1) and spreading genes (Fig. 3) are completely disjunct. LGM populations of red maples in clades A and C are not identified by fossil pollen reconstructions, so our upper estimate of spread, as well as estimates of spread based on pollen alone, are not correct. Our lower spread rates are reliable to the extent that red maple existed in areas within the reconstructed pollen contours.

Discussion

In the mid-20th century, E. Lucy Braun and Edward S. Deevey characterized opposite sides of a debate about the extent to which temperate forest species in eastern North America were displaced southward during the last glaciation (Delcourt 2003). In subsequent decades, the development of one of the world's densest networks of paleoecological sites has helped to narrow the debate; we now know that plant communities, such as the mixed mesophytic forest, did not coevolve in place over many glacial cycles, as put forward by Braun (Davis 1981, Williams et al. 2004). It also appears that most temperate eastern taxa maintained populations farther north during cold phases than hypothesized by Deevey (Jackson et al. 2000, Delcourt 2003). However, our understanding of the actual location of glacial refuges for most eastern North American species has remained vague. A recent review of eastern forests during the LGM states that, for common temperate taxa including beech and maple, ''We cannot yet determine whether the hardwood taxa were restricted to the Lower Mississippi Valley region or occurred more widely in scattered small populations.'' (Jackson et al. 2000).

The regions identified by pollen reconstructions as source areas for postglacial migration (Fig. 1) correspond to some of the glacial refuges identified in this study, but not to all of them. Both Davis (1981) and Delcourt and Delcourt (1987) show maple populations expanding from populations in the southwest of our study area. The distribution of red maple clade B and possibly haplotypes 10–13 are consistent with this scenario (Fig. 3). However, these haplotypes made only a small contribution to the spread of red maple into northern regions. Most trees in formerly glaciated terrain descend from populations in the Appalachian Mountains or interior plateaus, northeast of the late glacial ranges estimated in pollen studies.

Similarly, beech may have existed along the Gulf Coastal Plain during the late glaciation as hypothesized in Fig. 1 (a beech macrofossil dating to the LGM has been identified near Memphis, Tennessee [Delcourt et al. 1980]). However, our data indicate that divergent lineages of beech also persisted in interior refuges near the former ice margin. No members of clade A, the source of most populations in the Upper Midwest and southern Ontario, were found in refuges reconstructed by pollen data (Fig. 3). Furthermore, our data do not rule out the possibility that broadly distributed haplotypes like 10 and 15 may also have occurred farther north during the late glaciation. Allozyme data support our finding that beech along the southern Coastal Plain are genetically distinct from northern populations (Kitamura and Kawano 2001). After deglaciation, haplotypes from beech clades A and D spread directly northward into the Midwest, a pattern inconsistent with reconstructions showing a westward colonization of the region (Davis 1981, Williams et al. 2004). The geographic origin of beech populations east of the Appalachians is not definitive, but our results are consistent with a separate coastal migration route.

Conflicts between patterns in pollen and molecular data can be reconciled by recognizing that they record different aspects of population expansion. The dynamics of small populations in glacial refuges and at the initial stages of colonization provide the strongest signal in the genetic structure of populations. Pollen data can fail to identify small or diffuse populations, but they reliably record the distribution of populations once they reach higher densities (Davis et al. 1991, McLachlan and Clark 2004). Increases in beech pollen in the Upper Midwest, for instance, may correspond to the expansion of existing small populations rather than the initial arrival of the species (Bennett 1985).

Spread from previously undetected northern refuges would also account for the maintenance of high levels of genetic diversity at the northern range limit of our species (Table 1). The reduction in genetic diversity with latitude proposed by Hewitt (1996, 2000) results from sequential bottlenecks along long migration routes. There is evidence from both fossil and molecular data that some species listed in Table 1 may have had more northern distributions than previously thought (Willis et al. 2000, Stewart and Lister 2002, Petit et al. 2003). However, many species, including most taxa listed in Table 1, appear to have emerged from distant LGM refuges along the Mediterranean and in the Caucasus (Demesure et al. 1996, Petit et al. 2002, Petit et al. 2003).

The presence of small populations of thermophilous trees in northern late glacial forests in North America does not change the interpretation of postglacial veg-

etation change at the biome level (Williams et al. 2004). However, northern populations of these species, even at low densities, may help constrain our understanding of late-glacial climate. Beech and red maple are currently limited by cold winter temperatures at their northern range limits (Burns and Honkala 1990). Average January temperatures at the northern limit of both species are between −15°C and −20°C (Thompson et al. 1999), but both species tolerate temperatures as low as −40°C (Burns and Honkala 1990). A recent pollen-based LGM climate reconstruction suggests that the Appalachians and interior plateaus, where we propose small populations of these species existed, had average winter temperatures colder than those currently found within the ranges of beech and red maple (Jackson et al. 2000). However, a different pollen-based climate reconstruction and results from general circulation models suggest that average January temperatures during the LGM were within the modern climate range of beech and red maple in these areas (Webb et al. 1998).

Our results also call into question some entrenched notions concerning the population dynamics of invasion. Migration rates determined by pollen data are uniformly high, even for species with poor seed dispersal or long generation times (MacDonald 1993). Because these estimates are so much greater than would be expected based on observations of species' life history and seed dispersal (Clark et al. 1998), ecologists have proposed mechanisms for rapid spread outside of observed data, such as infrequent long-distance seed dispersal (Webb 1986, Clark 1998), or reduced interspecific competition during postglacial colonization (Davis 1976). The presence of cryptic northern populations reduces the need for such explanations by allowing slower migration rates (Fig. 4).

Our low estimates of migration rate are more consistent with models based on modern life history. Approximate rates of spread (C) are based on estimated dispersal kernels, expected offspring (R_0), and generation time (T). High variability in seed dispersal and stochastic establishment violate assumptions of standard diffusion models, but approximate solutions are available from stochastic models that admit fat-tailed dispersal kernels:

$$C \approx \frac{1}{T}\sqrt{\frac{\pi u R_0}{2}}$$

where u is a dispersal parameter that is proportional to the mean squared dispersal distance (Clark et al. 2001, 2003). For red maple, using a generation time of 10 yr (Burns and Honkala 1990) and fitted dispersal parameter of 101 ± 1.8 m^2 (Clark et al. 2004), we obtain rates of spread consistent with molecular evidence for net reproductive rates on the order of 10^3 offspring/adult tree. This value may be high, even for a period of rapid population growth (Clark et al. 2003), but it is more realistic than R_0 values on the order of 10^5 offspring/adult that would be necessary to accommodate the high migration rates interpreted from fossil pollen. We do not have dispersal estimates for American beech, but estimates for species with similar dispersal vectors, long generation times, and low fecundity result in predicted rates of spread much lower than paleoecological estimates and even lower than those from molecular data. Thus modern life history data and molecular evidence agree that estimates derived from fossil pollen may be unrealistically high, they provide compatible estimates for red maple, and they suggest that beech would have required substantial long-distance dispersal (Webb 1986) just to achieve the rates estimated from molecular data.

Because they have hitherto provided the only indication of plant population migration rates in response to global warming, fossil pollen estimates of rapid spread have become widely cited. Our molecular data provide a strong indication that the reconstructions of past range limits that are the basis of these estimates are inaccurate. Molecular and fossil data together are compatible with much slower rates of postglacial spread than previously interpreted, and thus may not justify assumptions of rapid spread in the future. If models that capture the key features of population spread predict slow spread, and we can no longer appeal to apparent rapid migration in the past, then the evidence points to potential losses of our dominant tree species over much or all of their ranges.

Acknowledgments

We thank J. W. Williams for providing pollen contour maps; S. Oh, K. Hancock, and N. Hamilton for laboratory assistance; and the many leaf collectors who helped us sample individuals from across eastern North America. This work was funded through grants from the National Science Foundation (DEB-0089769) and the Forest History Society.

Literature Cited

Bennett, K. D. 1985. The spread of *Fagus grandifolia* across eastern North America during the last 18000 years. Journal of Biogeography **12**:147–164.

Birks, H. H. 2003. The importance of plant macrofossils in the reconstruction of late glacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. Quaternary Science Reviews **22**:453–473.

Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Press, New York, New York, USA.

Brewer, S., R. Cheddadi, J. L. de Beaulieu, M. Reille, and data contributors. 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. Forest Ecology and Management **156**:27–48.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Agricultural Handbook 654, Volume 2. USDA Forest Service, Washington, D.C., USA.

Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleo record. American Naturalist **152**:204–224.

Clark, J. S., et al. 1998. Reid's Paradox of rapid plant migration. BioScience **48**:13–24.

Clark, J. S., S. LaDeau, and I. Ibanez. 2004. Fecundity of trees and the colonization-competition hypothesis. Ecological Monographs **74**:415–442.

Clark, J. S., M. Lewis, and L. Horvath. 2001. Dispersal and population spread. American Naturalist **157**:537–554.
Clark, J. S., M. Lewis, J. S. McLachlan, and J. Hille Ris Lambers. 2003. Estimating population spread: what can we forecast and how well? Ecology **84**:1979–1988.
Comes, H. P., and J. W. Kadereit. 1998. The effect of Quaternary climatic changes on plant distribution and evolution. Trends in Plant Science **3**:432–438.
Davis, M. B. 1976. Pleistocene biogeography of temperate deciduous forests. Geoscience and Man **13**:13–26.
Davis, M. B. 1981. Quaternary history and the stability of forest communities. Pages 132–153 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession: concepts and application. Springer-Verlag, New York, New York, USA.
Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pages 269–284 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.
Davis, M. B. 2000. Palynology after Y2K: understanding the source area of pollen in sediments. Annual Review of Earth and Planetary Science **28**:1–18.
Davis, M. B., M. W. Schwartz, and K. Woods. 1991. Detecting a species limit from pollen in sediments. Journal of Biogeography **18**:653–668.
Davis, M. B., and C. Zabinski. 1992. Changes in geographic range resulting from greenhouse warming: effects on biodiversity in forests. Pages 297–308 *in* R. L. Peters and T. E. Lovejoy, editors. Global warming and biodiversity. Yale University Press, New Haven, Connecticut, USA.
Deevey, E. S., Jr. 1949. Biogeography of the Pleistocene, Part I: Europe and North America. Bulletin of the Geological Society of America **60**:1315–1416.
Delcourt, H. R. 2003. Forests in peril: tracking deciduous trees from ice-age refuges into the greenhouse world. McDonald and Woodward, Blacksburg, Virginia, USA.
Delcourt, P. A., and H. R. Delcourt. 1987. Long term forest dynamics of the temperate zone: a case study of late-Quaternary forests in eastern North America. Springer-Verlag, New York, New York, USA.
Delcourt, P. A., H. R. Delcourt, R. C. Brister, and L. E. Lackey. 1980. Quaternary vegetation history of the Mississippi embayment. Quaternary Research **13**:111–132.
Demesure, B., B. Comps, and R. J. Petit. 1996. Chloroplast DNA phylogeography of the common beech (*Fagus sylvatica* L.) in Europe. Evolution **50**:2515–2520.
Demesure, B., N. Sodzi, and R. J. Petit. 1995. A set of universal primers for amplification of polymorphic noncoding regions of mitochondrial and chloroplast DNA in plants. Molecular Ecology **4**:129–131.
Hamilton, M. B., J. M. Braverman, and D. F. Soria-Hernanz. 2003. Patterns and relative rates of nucleotide and insertion/deletion evolution at six chloroplast intergenic regions in New World species of Lecythidaceae. Molecular Biology and Evolution **20**:1710–1721.
Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnaean Society **58**:247–276.
Hewitt, G. M. 2000. The genetic legacy of Quaternary ice ages. Nature **405**:907–913.
Higgins, S. I., and D. M. Richardson. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. American Naturalist **153**:464–475.
Hodges, S. A., and M. L. Arnold. 1994. Columbines: a geographically widespread species flock. Proceedings of the National Academy of Sciences (USA) **91**:5129–5132.
Hurlbert, S. H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology **52**:577–586.
Ibrahim, K. M., R. A. Nichols, and G. M. Hewitt. 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. Heredity **77**: 282–291.
Iverson, L. R., and A. M. Prasad. 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. Forest Ecology and Management **155**:205–222.
Iverson, L. R., A. M. Prasad, and M. W. Schwartz. 1999. Modeling potential future individual tree-species distributions in the eastern United States under a climate change scenario: a case study with *Pinus virginiana*. Ecological Modelling **115**:77–93.
Iverson, L. R., M. W. Schwartz, and A. M. Prasad. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? Global Ecology and Biogeography **13**:209–219.
Jackson, S. T., R. S. Webb, K. H. Anderson, J. T. Overpeck, T. Webb, III, J. W. Williams, and B. C. S. Hansen. 2000. Vegetation and environment in eastern North America during the last glacial maximum. Quaternary Science Reviews **19**:489–508.
King, R. A., and C. Ferris. 1998. Chloroplast DNA phylogeography of *Alnus glutinosa* (L.) Gaertn. Molecular Ecology **7**:1151–1161.
King, G. A., and A. A. Herstrom. 1997. Holocene migration rates objectively determined from fossil pollen data. Pages 91–102 *in* B. Huntley, W. Cramer, A. V. Marsa, I. C. Prentice, and J. R. M. Allen, editors. Past and future environmental changes: the spatial and evolutionary responses of terrestrial biota. Springer-Verlag, New York, New York, USA.
Kitamura, K., and S. Kawano. 2001. Regional differentiation in genetic components for the American beech, *Fagus grandifolia* Ehrh., in relation to geological history and mode of reproduction. Journal of Plant Research **114**:353–368.
MacDonald, G. M. 1993. Fossil pollen analysis and the reconstruction of plant invasions. Advances in Ecological Research **24**:67–110.
Malanson, G. P., and D. M. Cairns. 1997. Effects of dispersal, population delays, and forest fragmentation on tree migration rates. Plant Ecology **131**:67–79.
Malcolm, J. R., A. Markham, R. P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography **29**:835–849.
Manos, P. S., and K. P. Steele. 1997. Phylogenetic analyses of ''higher'' Hamamelididae based on plastid sequence data. American Journal of Botany **84**:1407–1419.
McLachlan, J. S., and J. S. Clark. 2004. Reconstructing historical ranges with fossil data. Forest Ecology and Management **197**:139–147.
Mohanty, A., J. P. Martin, and I. Aguinagalde. 2001. A population genetic analysis of chloroplast DNA in wild populations of *Prunus avium* L. in Europe. Heredity **87**:421–427.
Okaura, T., and K. Harada. 2002. Phylogeographical structure revealed by chloroplast DNA variation in Japanese beech (*Fagus crenata* Blume). Heredity **88**:322–329.
Palme, A. E., Q. Su, A. Rautenberg, F. Manni, and M. Lascoux. 2003. Postglacial recolonization and cpDNA variation of silver birch, *Betula pendula*. Molecular Ecology **12**: 201–212.
Petit, R. J., et al. 2002. Identification of refugia and postglacial colonization routes of European white oaks based on chloroplast DNA and fossil pollen evidence. Forest Ecology and Management **156**:49–74.
Petit, R. J., et al. 2003. Glacial refugia: hotspots but not melting pots of genetic diversity. Science **300**:1563–1565.
Powell, J. A., and N. E. Zimmerman. 2004. Multiscale analysis of active seed dispersal contributes to resolving Reid's paradox. Ecology **85**:490–506.

Provan, J., W. Powell, and P. M. Hollingsworth. 2001. Chloroplast microsatellites: new tools for studies in plant ecology and evolution. Trends in Ecology and Evolution **16**: 142–147.

Reboud, X., and C. Zeyl. 1994. Organelle inheritance in plants. Heredity **72**:132–140.

Reid, C. 1899. The origin of the British Flora. Dulau, London, UK.

Rendell, S., and R. A. Ennos. 2002. Chloroplast DNA diversity in *Calluna vulgaris* (heather) populations in Europe. Molecular Ecology **11**:69–78.

Shuman, B. N., T. Webb, P. J. Bartlein, and J. W. Williams. 2002. The anatomy of a climatic oscillation: vegetation change in eastern North America during the Younger Dryas chronozone. Quaternary Science Reviews **21**:1777–1791.

Simberloff, D. S. 1972. Properties of the rarefaction diversity measurement. American Naturalist **106**:414–418.

Stewart, J. R., and A. M. Lister. 2002. Cryptic northern refugia and the origins of the modern biota. Trends in Ecology and Evolution **16**:608–613.

Swofford, D. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0b10. Sinauer Associates, Sunderland, Massachusetts, USA.

Taberlet, P., L. Funagalli, A.-G. Wust-Saucy, and J.-F. Cosson. 1998. Comparative phylogeography and postglacial colonization routes in Europe. Molecular Ecology **7**:453–464.

Taberlet, P., G. Ludovic, G. Pautou, and J. Bouvet. 1991. Universal primers for amplification of 3 noncoding regions of chloroplast DNA. Plant Molecular Biology **17**:1105–1109.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature **427**:145–148.

Thompson, R. S., K. H. Anderson, P. J. Bartlein, and S. A. Smith. 1999. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America. USGS Professional Paper 1650-A, USGS Information Services, Federal Center, Denver, Colorado, USA.

Tomaru, N., M. Takahashi, Y. Tsumura, M. Takahashi, and K. Ohba. 1998. Intraspecific variation and phylogeographic patterns of *Fagus crenata* (Fagaceae) mitochondrial DNA. American Journal of Botany **85**:629–636.

van Minnen, J. G., R. Leemans, and F. Ile. 2000. Defining the importance of including transient ecosystem responses to simulate C-cycle dynamics in a global change model. Global Change Biology **6**:595–611.

van Oppen, M. J. H., C. Rico, G. F. Turner, and G. M. Hewitt. 2002. Extensive homoplasy, nonstepwise mutations, and shared ancestral polymorphism at a complex microsatellite locus in Lake Malawi cichlids. Molecular Biology Evolution **17**:489–498.

Webb, S. L. 1986. Potential role of passenger pigeons and other vertebrates in the rapid Holocene migrations of nut trees. Quaternary Research **26**:367–375.

Webb, T., K. H. Anderson, P. J. Bartlein, and R. S. Webb. 1998. Late Quaternary climate change in eastern North America: a comparison of pollen-derived estimates with climate model results. Quaternary Science Reviews **17**: 587–606.

Webb, T., P. J. Bartlein, S. P. Harrison, and K. H. Anderson. 1993. Vegetation, lake levels and climate in eastern North America for the past 18,000 years. Pages 415–467 *in* P. J. Bartlein, editor. Global climates since the last glacial maximum. University of Minnesota Press, Minneapolis, Minnesota, USA.

Williams, J. W., B. N. Shuman, T. Webb, III, P. J. Bartlein, and P. Leduc. 2004. Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. Ecological Monographs **74**:309–334.

Willis, K. J., E. Rudner, and P. Sumegi. 2000. The full glacial forests of Central and southeastern Europe. Quaternary Research **53**:203–213.

Wolfe, K. H., W-H. Li, and P. M. Sharp. 1987. Rates of nucleotide substitutions vary greatly among mitochondrial, chloroplast, and nuclear DNAs. Proceedings of the National Academy of Sciences (USA) **84**:9054–9058.

Woods, K. D., and M. B. Davis. 1989. Paleoecology of range limits: beech in the Upper Peninsula of Michigan. Ecology **70**:681–696.

SUPPLEMENT

Data files of sample locations, and GenBank accession numbers for red maples and beech used in the study, are available in ESA's Electronic Data Archive: *Ecological Archives* E086-110-S1.