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ORIGINAL ARTICLE

Inferring long-distance dispersal and topographic barriers during post-glacial colonization from the genetic structure of red maple (*Acer rubrum* L.) in New England

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ABSTRACT

Aim This study aims to assess the role of long-distance seed dispersal and topographic barriers in the post-glacial colonization of red maple (*Acer rubrum* L.) using chloroplast DNA (cpDNA) variation, and to understand whether this explains the relatively higher northern diversity found in eastern North American tree species compared with that in Europe.

Location North-eastern United States.

Methods The distribution of intraspecific cpDNA variation in temperate tree populations has been used to identify aspects of post-glacial population spread, including topographic barriers to population expansion and spread by long-distance seed dispersal. We sequenced *c.* 370 cpDNA base pairs from 221 individuals in 100 populations throughout the north-eastern United States, and analysed spatial patterns of diversity and differentiation.

Results Red maple has high genetic diversity near its northern range limit, but this diversity is not partitioned by topographic barriers, suggesting that the northern Appalachian Mountains were not a barrier to the colonization of red maple. We also found no evidence of the patchy genetic structure that has been associated with spread by rare long-distance seed dispersal in previous studies.

Main conclusions Constraints on post-glacial colonization in eastern North America seem to have been less stringent than those in northern Europe, where bottlenecks arising from long-distance colonization and topographic barriers appear to have strongly reduced genetic diversity. In eastern North America, high northern genetic diversity may have been maintained by a combination of frequent long-distance dispersal, minor topographic obstacles and diffuse northern refugia near the ice sheet.

Keywords

AMOVA, chloroplast DNA, genetic bottlenecks, genetic diversity, G_{ST}, north-eastern US, post-glacial spread.

INTRODUCTION

At the end of the last Ice Age, populations of temperate trees spread northwards into deglaciated territory (Delcourt & Delcourt, 1987; Davis & Zabinski, 1992; Petit *et al.*, 2002a). Ecologists interested in how tree populations might respond to contemporary climate warming look to this prehistoric dynamic for insight (Pitelka & Group, 1997; Clark *et al.*, 1998). In recent years, maps of chloroplast DNA (cpDNA) variation across the range of temperate hardwood species have suggested that long-distance seed dispersal (LDD) may have played a role in range expansion at continental scales (Petit *et al.*, 1997, 2002b; McLachlan *et al.*, 2005). Chloroplast DNA is used to understand the spread of genes through seeds because it is usually maternally inherited in angiosperms and does not recombine (Reboud & Zeyl, 1994).

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In Europe, where the largest surveys of genetic variation in forests have been completed, glacial refugia in the south contain diverse, well-differentiated assemblages of cpDNA haplotypes, and some of this diversity was apparently lost during northward colonization (Demesure *et al.*, 1996; Petit *et al.*, 2002b, 2003). This general pattern is apparent even for species that are thought to have maintained cryptic northern refugia close to the ice margin in Europe (Willis *et al.*, 2000; Stewart & Lister, 2001). These studies suggest two reasons for this loss of diversity. First, topographic barriers, such as mountain chains, block the colonization of some cpDNA lineages (Gugerli *et al.*, 2001; Mátyás & Sperisen, 2001; Csaikl *et al.*, 2002; Petit *et al.*, 2002b). Second, infrequent LDD events may have created successive founder events along expanding population fronts, reducing northern genetic diversity and haplotype richness (Ibrahim *et al.*, 1996; Le Corre *et al.*, 1997; Bialozyt *et al.*, 2006). In this process, termed 'embolism' by Bialozyt *et al.* (2006), satellite populations founded by individual LDD events ahead of the main colonization front might be difficult to invade by subsequent dispersers. Spatial clumping of cpDNA haplotypes at scales of 35–45 km in French white oaks could reflect this process of past embolism (Petit *et al.*, 1997).

The severity of topographic barriers to gene flow and of genetic bottlenecks caused by LDD during colonization might depend on the scale and frequency of LDD. Models suggest that the impact of physical barriers on genetic structure is reduced under scenarios of frequent LDD (Davies *et al.*, 2004). Similarly, under some population models, frequent LDD disperses genotypes so efficiently that the 'embolism' effect is not pronounced and genetic diversity is preserved along colonization routes (Bialozyt *et al.*, 2006). Species with strong colonizing ability might maintain genetic diversity along colonization corridors and have weakly subdivided population structure (Petit *et al.*, 2003; Bialozyt *et al.*, 2006).

However, the expected correlations between life-history traits and genetic structure have not been clearly supported by empirical studies. Dispersal syndromes do not explain species differences in genetic structure in Europe (Aguinagalde *et al.*, 2005). Furthermore, congeneric North American and European species have similar dispersal modes but different genetic structures (Petit *et al.*, 2003; Magni *et al.*, 2005; McLachlan *et al.*, 2005). With the exception of Petit *et al.* (1997), few studies have examined the impact of post-glacial spread on population genetic structure at the scale at which seeds disperse and bottlenecks occur.

To understand how topographic constraints and LDD might have affected post-glacial spread, we examined the fine-scale cpDNA genetic structure of red maple (*Acer rubrum* L.) in New England, USA. Previous work on cpDNA diversity throughout the range of this species (McLachlan *et al.*, 2005) showed that red maple maintained a surprising amount of genetic diversity in its northern range, whereas similar European species appear to have sustained substantial loss of genetic diversity with latitude, and high genetic differentiation between populations (Petit *et al.*, 2003). This result is partly attributable to the fact that red maple appears to have maintained northern populations near the former ice margin (McLachlan *et al.*, 2005), thus reducing the overall distance of post-glacial colonization and consequently lowering the opportunities for repeated bottlenecks to reduce genetic diversity. However, the expansion of red maple to its current range limit, over 500 km into deglaciated terrain, provides substantial opportunities to examine the roles of LDD and topographic barriers during climate-driven plant colonization.

Data collection for our study targets the scale at which the genetic consequences of LDD are expected to be apparent (Le Corre *et al.*, 1997; Petit *et al.*, 1997; Davies *et al.*, 2004; Bialozyt *et al.*, 2006). If rare long-distance seed dispersal was the primary mode of post-glacial spread, and was therefore important in shaping the distribution of cpDNA haplotypes, we would expect to find spatial clumping in cpDNA haplotypes at the scale of tens of kilometres (Fig. 1a,b), as in Petit *et al.* (1997). Topography is expected to be most important at a scale larger than the scope of this study, but the unique topography of the region permits us to test fine-scale hypotheses that may provide clues to potential larger-scale topographic effects. The Appalachian Mountains are the largest topographical barrier faced by expanding populations in eastern North America. If obstacles like the Appalachian Mountains impeded seed dispersal, we would expect high partitioning of genetic variation among major watersheds when compared with variation within watersheds (Fig. 1b,c). A lack of geographic pattern in genetic diversity would be consistent with several scenarios, including spread by frequent LDD (Davies *et al.*, 2004; Bialozyt *et al.*, 2006).

Study area/study organism

Our 300 km by 300 km study region includes much of New England (Fig. 2). This area consists of mountain highlands cut by two major south-flowing rivers: the Hudson and the Connecticut. To the west of the Hudson River are the Adirondack Mountains of New York. Between the Hudson and Connecticut rivers are the Green Mountains of Vermont. To the east of the Connecticut are the White Mountains of New Hampshire and Maine, and the gradually descending coastal lowlands. The highest peaks in this region are lower than 2000 m. Red maple is currently abundant throughout lower elevations up to 600–850 m.

The topographic breaks that might have affected past colonization, and thus current genetic diversity, correspond to the major watersheds identified in Fig. 2 (Coastal Plain, Connecticut River Valley, and Hudson River Valley). Data collection was designed to determine how such barriers and LDD might have structured diversity by subdividing each watershed into northern, southern and intermediate regions. The nine subgroups are thus: Hudson River valley south (HRS), middle (HRM), and north (HRN); Connecticut River valley south (CRS), middle (CRM), and north (CRN); and Coastal Plain south (CPS), middle (CPM), and north (CPN).

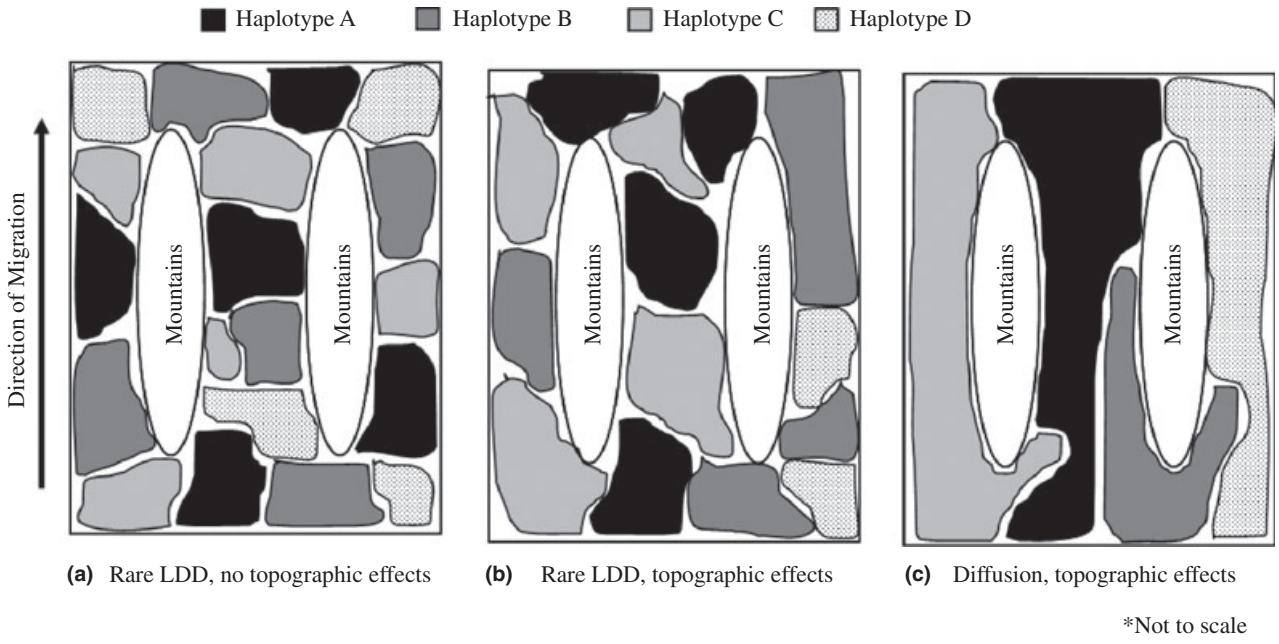

Figure 1 (a) If rare long-distance dispersal structures populations, haplotypes would be distributed in patches. Without topographic barriers, all haplotypes might be found in each watershed. (b) Possible distribution of haplotypes if both long-distance dispersal and topography structure genetic patterns. East-west gene flow is restricted, and thus different assortments of haplotypes are found in each watershed. Furthermore, haplotypes are distributed in patches. (c) Diffusion would cause haplotypes to be distributed in bands along colonization routes. Here, topography prevents east-west diffusion.

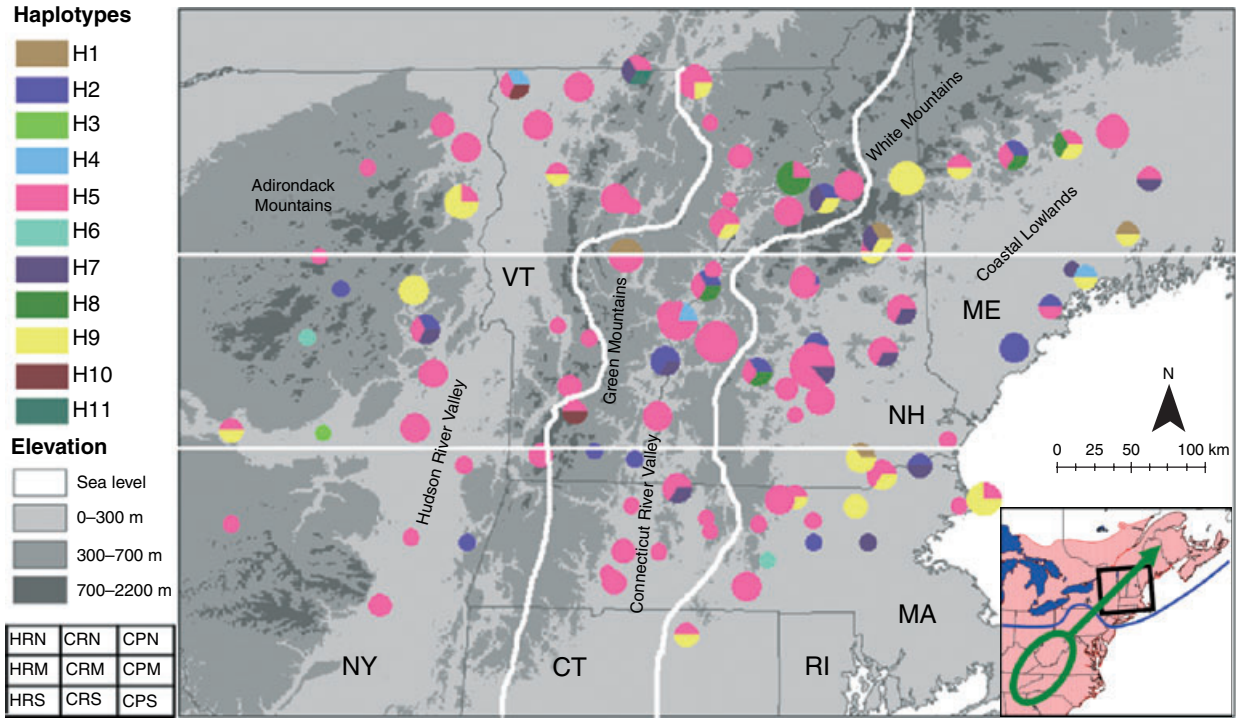

Figure 2 Distribution of haplotypes throughout the study area. Pie charts correspond to individual populations and are scaled according to the sampling intensity per population (one to five individuals) and coloured according to haplotype. Elevations are shaded on a greyscale according to the legend, below which is a schematic representation of the positions of our nine subgroups. On the map, white lines delineate subgroups defined by watershed boundary and latitude. Black lines are state boundaries (states labelled in black). The inset shows the range of red maple (red area), the approximate maximum extent of the Laurentide Ice Sheet (dark blue line), and the location of the putative refugia (green ellipse) that colonized our study area (black box).

Maple pollen (*Acer* spp.) is first found in New England sediments between 11,000 and 9000 yr BP in southern and northern New England, respectively (Davis, 1976; Davis & Jacobson, 1985; Peteet *et al.*, 1994). Pollen data also suggest that tree species were initially restricted to low elevations and thus forced to spread along valley corridors (Spear *et al.*, 1994). Thus, palaeoecological data suggest the Appalachian Mountains may have been a barrier to gene flow in the early stages of post-glacial recolonization.

Previous work (McLachlan *et al.*, 2005) shows the larger phylogeographic context for this regional study. We found that red maples colonized deglaciated terrain from refugia near the margin of the Laurentide Ice Sheet. Red maples in our study area appear to descend from populations north of 35 °N from the Appalachians through eastern Kentucky (Fig. 2 inset).

MATERIALS AND METHODS

Sampling

We sampled between one and five trees (mean = 2.21) from 100 stands (populations) separated from one another by 5–30 km. Because we sampled forested areas near and along roads, our data set is somewhat biased towards valleys and lower-elevation sites. These design considerations do not restrict our capacity to test the hypotheses presented in the Introduction, because these elevations represent the bulk of the red maple range in this landscape. Leaf or bud samples of red maple were collected from throughout the region. Samples were stored on ice for up to 5 days until they were frozen at −80°C in the laboratory.

DNA extraction, polymerase chain reaction and sequencing

We sequenced the cpDNA *trnH* × *psbA* intergenic spacer (Demesure *et al.*, 1995), which has previously been shown to be highly variable in red maple (McLachlan *et al.*, 2005). We extracted DNA from material frozen at −80°C using a Qiagen (Valencia, CA, USA) DNeasy Plant Mini Kit or DNeasy 96 according to the standard protocol. The polymerase chain reaction (PCR) reaction mix consisted of 1 μL of Qiagen *Taq* DNA Polymerase, 1.25 μL of both 10 μM *trnH* and *psbA* primers, 2.5 μL of 10× buffer, 5 μL of buffer Q, 1 μL of 25 mM $MgCl_2$, 1 μL of 10 mM (each) dNTPs, and dH_2O to 25 μL. This mix was run in a PCR Express thermocycler for 3 min at 95°C, followed by 35 cycles of a 94°C denaturation step for 1 min, a 65°C annealing step for 1 min, and a 72°C elongation step for 1 min, and finally one final extension cycle at 72°C for 10 min. We cleaned PCR products with a Qiagen QIAquick PCR Purification Kit according to standard protocol. For sequencing reactions, we used BigDye ver. 3.1 (PE Applied Biosystems, Foster City, CA, USA) and ran out on an ABI Prism 3700 automated sequencer (PE Applied Biosystems). Sequences were aligned and edited in SEQUENCHER ver. 4.1 (Gene Codes, Ann Arbor, MI, USA).

Spatial patterns of genetic variation

Topographic effects

We tested the hypothesis that mountain ranges in the Northern Appalachians obstructed seed flow during post-glacial colonization by examining whether genetic variation was partitioned among the major watersheds in our study region. Because mountain barriers are more apparent in the northern part of our study area, we limited this analysis to these northern two tiers of subgroups (Fig. 2). We separated the 37 populations in this area containing three or more individuals into Coastal Plain, Connecticut River Valley, and Hudson River Valley groups. Using the software ARLEQUIN ver. 3.01 (Excoffier *et al.*, 2005), we tested the proportion of genetic variance explained by these groups in a hierarchical analysis of molecular variance (AMOVA; Weir & Cockerman, 1984; Excoffier *et al.*, 1992; Weir, 1996).

Genetic diversity and differentiation

Patterns of haplotype richness, genetic diversity, and genetic differentiation between populations are all expected to reflect the influence on gene flow of topographic barriers and LDD. If the embolism effect shaped genetic variation in our study area, founder effects by long-distance dispersers of different genotypes are hypothesized to differentiate populations, and bottlenecks at colonization are hypothesized to result in reduced genetic diversity and haplotype richness (Fig. 1; Bialozyt *et al.*, 2006). Topographic barriers might also result in a loss of diversity with latitude. We calculated genetic differentiation within subgroups among populations (G_{ST_SUB}) with three or more individuals using PermutCpSSR ver. 2.0 (Pons & Petit, 1996). We then used CONTRIB ver. 1.01 (Petit *et al.*, 1998) to calculate haplotype richness and the subgroup diversity (h_K) after pooling all individuals in each subgroup and standardizing to a common sample size (El Mousadik & Petit, 1996; Petit *et al.*, 1998).

We also calculated the diversity (h_T) and genetic differentiation (G_{ST}) of the entire study area in two ways. The first considers only populations with three or more individuals, which is the standard calculation and thus directly comparable to other published studies (e.g. Petit *et al.*, 2003). We call these 'overall' h_T and G_{ST}, respectively. The second pools all samples within each subgroup, regardless of population size, and considers each of the nine subgroups as a population. Low 'among-subgroup' G_{ST} would indicate that watersheds and latitudinal groups are not highly differentiated, and thus topography was not an important barrier at this scale.

Long-distance dispersal effects

Petit *et al.* (1997) argue that patchiness at the scale of tens of kilometres would indicate a strong effect of rare LDD on regional genetic structure. We tested for patchiness in the most

common haplotypes by calculating Moran's index (I) of spatial autocorrelation at distance classes of 10 km using ECODIST software (S. Goslee and D. Urban, http://cran.r-project.org/doc/packages/ecodist.pdf).

RESULTS

We obtained sequence data for 221 individuals from 100 populations within the study area (Fig. 2, see Table S1 in Supplementary Material). Of those, 43 populations contained three or more individuals (139 total). We identified nine polymorphic sites within a segment of 370 base pairs. Five were base substitutions and four were insertion-deletions. One single-nucleotide repeat was ignored because of concerns about hypervariability that might reflect post-glacial mutations (van Oppen *et al.*, 2000). We detected 11 haplotypes in the study area, with haplotype H5 being the most common, followed distantly by haplotypes H9, H2 and H7. Haplotypes H1, H3, H4, H6, H8, H10 and H11 were rare, occurring in between one and seven individuals. Of these, haplotypes H10 and H11 have not previously been identified outside the study area (McLachlan *et al.*, 2005). Both are one mutation away from the nearest haplotype (H5) and are found in Vermont twice and once, respectively.

Although the phylogenetic distance between haplotypes arriving along a common colonization route into our study area provides little information for the purposes of this study, we provide an updated haplotype network as supplementary material (Fig. S1) to facilitate comparisons between this study and that of McLachlan *et al.* (2005). The network shows that the haplotypes in the study area belong to two closely related clades that were previously shown to originate in the Appalachians south of the ice (Fig. 2 inset; McLachlan *et al.*, 2005). In this study, we sequenced fewer cpDNA base pairs than did McLachlan *et al.* (2005), so haplotypes shown here do not correspond directly to those in the previous study. A table matching old and new haplotype designations and GenBank accessions is also included (Table S2).

Topographic effects

Hierarchical AMOVA of populations grouped by watershed shows that haplotypic structure is independent of topography in New England (Table 1). The covariance components of genetic variance (Excoffier, 2000) in our data were 77% within populations ($P = 0.0001$), 25% within watersheds ($P = 0.0002$), and < 0% between watersheds ($P = 0.8407$), showing that groups separated by mountain chains were not distinct. Statistically, watersheds do not differ, and haplotypes are distributed nearly evenly throughout the study area; however, the relative frequency of H9 (and perhaps of H1

Table 1 Hierarchical analysis of molecular variance using populations with three or more individuals grouped according to watershed (Hudson, Connecticut, or coastal) for the northern two tiers of subgroups.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	*P*-value
Among watersheds	2	0.854	−0.00898	−1.82	0.8407
Among populations within watersheds	34	26.429	0.12266	24.84	0.0002
Within populations	83	31.55	0.38012	76.98	0.0001
Total	119	58.833	0.49381	100	

Table 2 Diversity and differentiation indices for subgroups.

Subgroup	*N*	NH	NH_R	h_K	N_{POP}	Mean	NH_{POP}	G_{ST_SUB}
CPS	31	6	3.4	0.67 (0.06)	5	3.2	3	0.39 (0.19)
CPM	37	6	3.1	0.58 (0.08)	8	3.13	4	0.21 (0.26)
CPN	26	6	3.8	0.74 (0.06)	5	3.4	6	0.28 (0.30)
CRS	14	3	2.4	0.39 (0.15)	1	3	2	NC
CRM	29	7	3.2	0.52 (0.11)	7	3.43	6	0.32 (0.09)
CRN	24	5	3.1	0.54 (0.11)	6	3.33	5	0.30 (0.08)
HRS	8	2	2	0.25 (0.18)	0	0	0	NC
HRM	24	6	3.4	0.59 (0.11)	4	3	5	0.65 (0.33)
HRN	28	6	2.9	0.48 (0.11)	7	3.14	6	0.32 (0.09)

The left half shows the pooled number of individuals in a subgroup (N), the number of haplotypes (NH), the number of haplotypes after rarefaction (NH_R), and the diversity within each subgroup (h_K; standard errors in parentheses) of nine subgroups. Diversity (h_K) does not differ among the nine subgroups, suggesting that mountains did not channel diversity. The right half shows the number of populations with three or more samples (N_{POP}), the mean number of individuals per population (Mean), the total number of haplotypes in populations with three or more samples (NH_{POP}), and the relative differentiation among populations within subgroups (G_{ST_SUB}; NC = not calculated).

and H7) is higher in the coastal region than in areas to the west.

Genetic diversity and differentiation

For the entire region, overall $h_T = 0.61$ and $G_{ST} = 0.31$; thus, the study area has a relatively high total diversity but that diversity is not strongly partitioned among populations.

The nine latitudinal/watershed subgroups within the study area generally increase or maintain haplotype richness (NH_R) and diversity (h_K) with increasing latitude, and show no watershed effect (Table 2). A linear regression shows no relationship between haplotype richness after rarefaction and latitude for the nine subgroups ($P = 0.259$; regression of individual population-level richness against latitude is also not significant, $P = 0.1971$). Moreover, within-subgroup diversities are statistically similar for all subgroups. Again, the total diversity in the region is high ($h_T = 0.56$), but most of this diversity is found within subgroups rather than distributed among subgroups ($G_{ST} = 0.05$). Low among-subgroup G_{ST} indicates a lack of genetic differentiation between subgroups within watersheds and between watersheds, further suggesting that mountains did not play an important role in sorting populations and preventing east-west gene flow at this scale.

Long-distance dispersal effects

Tests of spatial autocorrelation using Moran's *I* for the four most common haplotypes (H2, H5, H7, H9) show little spatial clustering (Fig. 3). Spatial clustering of haplotypes at fine scales has been interpreted to be the consequence of LDD and founder effects (Petit *et al.*, 1997). We saw no fine-scale clustering and only marginally significant autocorrelation in haplotypes H2, H5 and H9 at some large distance classes over 30 km (Fig. 3). Moreover, in many populations each sample was a different haplotype (Fig. 2).

DISCUSSION

Our analysis is an explicit response to an expanding body of published work claiming that long-distance seed dispersal and topographic barriers are the primary factors influencing the spread of populations (and therefore genes) during post-glacial range expansion. Our comparable data set contains greater or equal amounts of polymorphism (6–11 haplotypes; Petit *et al.*, 1997; Gugerli *et al.*, 2001; Mátyás & Sperisen, 2001; Csaikl *et al.*, 2002), and our finding of one common haplotype is typical of such data sets. However, these other studies all identified geographic structure in the distribution of genetic polymorphism. Furthermore, the theoretical models underpinning these studies, simulations of spread highlighting the effect of LDD and geographic barriers to spread, also employ few haplotypes (mostly three to four; Le Corre *et al.*, 1997; Davies *et al.*, 2004; Bialozyt *et al.*, 2006). This suggests that higher levels of polymorphism are not needed to detect these processes if they exist.

If rare LDD played a large role in the post-glacial spread of red maple, populations might be genetically differentiated as a result of the strong founder effects of individual dispersal events (Le Corre *et al.*, 1997; Petit *et al.*, 1997; Bialozyt *et al.*, 2006). Such clumping might result in reduced genetic diversity with latitude through the 'embolism' effect (Ibrahim *et al.*, 1996; Le Corre *et al.*, 1997; Bialozyt *et al.*, 2006). Our data did not show genetic clumping (Fig. 3), differentiation between populations (overall G_{ST}; Table 2, right), or loss of diversity with latitude (Table 2, left).

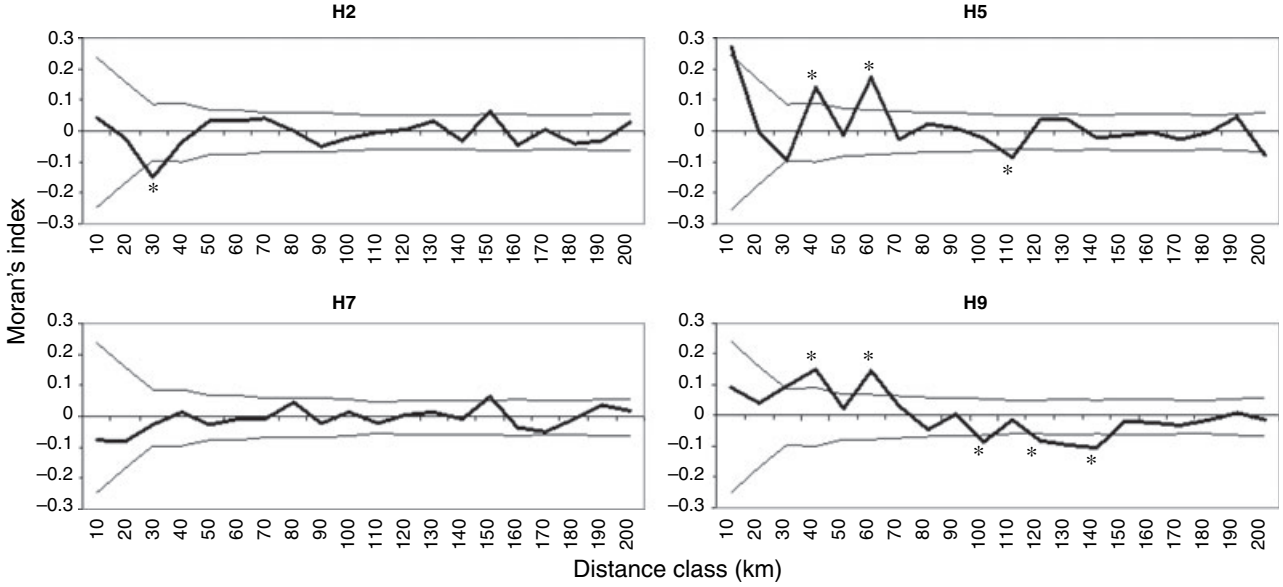

Figure 3 Spatial autocorrelation of the four most common haplotypes (H2, H5, H7, H9) measured by Moran's index. Thin lines are 95% confidence intervals. Significant values are marked with an asterisk (*).

Under many dispersal scenarios, we would expect that barriers such as the Appalachian Mountains might play a role in differentiating genetic diversity at regional scales. Such topographic barriers did not differentiate the distribution of red maple genotypes within our study region (Tables 1 and 2).

Together, our data suggest that the two most widely cited ecological explanations for bottlenecks during Holocene colonization, rare LDD and topographic barriers, were not important during the post-glacial spread of red maple in North America. Our data might reflect expansion through frequent LDD, with genetic diversity being preserved across large areas by mixing from many sources – Bialozyt *et al.*'s (2006) 'reshuffling' effect. Topographic barriers would potentially be less of an obstacle to genetic mixing in the face of effective LDD (Davies *et al.*, 2004).

However, the distinction between 'abundant' and 'rare' LDD depends on assumptions about the distribution of seed dispersal distances and demographic parameters. Projections of contemporary seed dispersal in red maple allow *c.* 0.001% of seeds to disperse beyond 5 km, but this estimate is extremely uncertain (Clark *et al.*, 2003). In general, the amount of very long-distance seed dispersal required to allow the maintenance of genetic diversity through 'reshuffling' appears difficult to square with our understanding of seed dispersal in red maple.

Whatever role such reshuffling of diversity through LDD played in the post-glacial colonization of red maple, it does not seem to provide a general explanation for the distribution of genetic diversity across maple species. As is the case in oaks (Petit *et al.*, 2002b; Magni *et al.*, 2005), populations of European maples are more strongly differentiated than those of North American species [compare G_{ST} values of 0.66 and 0.71 for *Acer campestre* and *A. pseudoplatanus* (Petit *et al.*, 2003) with *A. rubrum* values in Table 2 and an overall G_{ST} of 0.31], and there is a greater loss of diversity with latitude in European maples than has been observed in North America (McLachlan *et al.*, 2005). These species have similar dispersal modes and life histories, so the differences in their genetic structure suggests that something other than dispersal bottlenecks during initial post-glacial colonization is responsible for patterns of genetic diversity on the modern landscape.

One possible explanation for the lack of genetic structure in our data is that subsequent population dynamics might have altered the genetic structure of founding populations. Although models suggest that spatial genetic structure is relatively stable after recolonization (Ibrahim *et al.*, 1996; Le Corre *et al.*, 1997), natural disturbance over thousands of years or even human disturbance in the last few centuries may have altered the distribution of haplotypes across the landscape. In a previous paper (McLachlan *et al.*, 2005), we proposed that red maple colonized deglaciated territory with populations too small to be detected by standard fossil pollen analysis. A slow colonization with a long period of seed exchange between scattered diffuse populations might allow the same degree of haplotype mixing as in Bialozyt *et al.*'s (2006) scenario of haplotype reshuffling through colonization by frequent LDD. We note that a diverse array of eastern North American trees lack fine-scale genetic structure and maintain northern diversity (Magni *et al.*, 2005; McLachlan *et al.*, 2005). Our proposal predicts such a common pattern among species with divergent dispersal syndromes and demographics.

Over the course of the Quaternary, North American woody taxa experienced fewer extinctions than did their European counterparts (Svenning, 2003). Fossil pollen and genetic data show that the last glaciation restricted populations of temperate European trees so severely that their range-wide population structure is still marked by Last Glacial Maximum bottlenecks and that they lack genetic diversity in their northern ranges. Similar taxa in eastern North America may have had broad diffuse distributions and survived post-glacial population expansion without the major genetic bottlenecks caused by topographic barriers or rapid population expansion by means of LDD. Such generalizations may be useful to consider in view of the fact that forests currently face the largest and most rapid climate change since the end of the last Ice Age.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Coordinates of sampling sites, watershed and subgroup groupings, and the frequency of each haplotype at each sampling site within the study area.

Table S2 Comparison of haplotypes from this study with those of the previous range-wide study of McLachlan *et al.* (2005) and GenBank accession numbers.

Figure S1 Haplotype network of all known red maple *trnH-psbA* haplotypes, including those found only outside our study area (Ha-Hg; McLachlan *et al.*, 2005).

This material is available as part of the online article from: http://www.blackwell-synergy.com/10.1111/j.1365-2699.2008.01915.x (this link will take you to the article abstract).

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