IMPACTS OF THE APPALACHIAN MOUNTAINS ON SUGAR MAPLE'S POST-GLACIAL MIGRATION

by

MATTHEW MILLER

(Under the Direction of Kathleen Parker)

ABSTRACT

The migration ranges of sugar maple (*Acer saccharum*) since the last ice age, as described by Delcourt and Delcourt (1987), were refined to exclude elevations where sugar maple was unlikely to have existed. The elevations, used as indictors of climate limits, were based on the modern regional elevation limits of sugar maple. The paleo-range maps of the range of sugar maple were combined with a digit elevation model in a geographic information system to remove the climatically unsuitable regions for sugar maple. The Appalachian Mountains were shown to constitute a formidable barrier to gene flow, especially when the elevation limits were lowered to represent the site establishment stress caused by migration. The physical barriers that the Appalachian Mountains presented to the migration of sugar maple provide an explanation for the patterns of genetic diversity observed along sugar maple's northern limit.

INDEX WORDS: *Acer saccharum*, Sugar maple, Genetic diversity, Gene flow, Appalachian Mountains, DEM, Pollen Migration

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MATTHEW MILLER

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MATTHEW MILLER

Major Professor: Kathleen Parker

Committee: Marguerite Madden
Albert Parker

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
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CHAPTER 1

INTRODUCTION

From the beginning of the retreat of the Laurentide ice sheet, approximately 18,000 years ago to today, the geographical ranges of temperate tree species have been migrating northward from their ice-age refugia. Their migrations and range expansions have been documented through the use of pollen analyses performed at various sample sites throughout the eastern United States and Canada. Pollen analysis has proven to be a popular method of reconstructing past species ranges and estimating climatic conditions at various time steps within the temporal resolution of pollen data. The value of pollen analysis is the ability to determine the spatial extent of identifiable species as seen in the context of a temporal framework. By combining a topographic component with the results of pollen analyses in eastern North America, I propose that the geographic distribution of a species through its post-ice age range expansion can be more precisely determined, allowing inferences about the genetic structure of a species to be made.

The location of pollen sampling sites is not random, but is dictated by the availability of collection sites, which include lakes, ponds, and bogs (Faegri 1989). These features are not randomly distributed across landscapes, and too few sites have been studied, or are even available to study, to compensate for this disparity. This results in isopoll maps that do not include topography in the presentation of inferred biome or species ranges (Delcourt et al. 1984; Delcourt and Delcourt 1987). The general ranges of species are depicted with a good measure of confidence, but the complexities introduced by topography need to be accounted for.

Several studies have incorporated pollen analysis data in a genetic study of a species throughout its entire range, particularly in Europe (e.g. European beech [*Fagus sylvatica;* Comps 2001], *Quercus* spp. [Brewer 2002; Petit 2002]); but most studies of postglacial migration or colonization use either pollen data or phylogenetic data, rather than both (MacDonald and Cwynar 1985; Grivet and Petit 2002; Kubisiak and Roberts 2003; Petit 2003). Both palynological and genetic data can provide valuable information about the postglacial genetic structure of species across their geographic ranges (Hewitt 1996; Hewitt 2000). More research is needed to indicate how these two types of data can be used together to gain a better understanding of post-glacial species range expansion. This study explores how historical species ranges estimated from pollen data can be refined by the exclusion of improbable locations of species due to elevation limits through the use of a digital elevation model (DEM) and geographic information system (GIS). Refined post-glacial ranges are used to predict modern-day patterns of genetic variation and structure, which are then compared to existing genetic studies. Indirect measures of genetic structure, which will be used in this study, integrate long-term shifts in species ranges, such as occurred after the Pleistocene.

Background Information

There are only eight species included in the *Acer* genus in North America (Delcourt and Delcourt 1987), which limits ambiguity about identification of pollen grains to the species level. Sugar maple (*Acer sacharrum* Marsh) and red maple (*Acer rubrum*) are by far the two most prevalent maple species in eastern North America.

While the ranges of the two species substantially overlap, red maple is readily found as far south as Florida while the native range of sugar maple does not extend farther south than northern Georgia. Red maple is also able to exist at higher elevations than sugar maple within the same regions (Walters et al. 1990).

A good candidate species for the examination of the effects of topography on range expansion is sugar maple. Genetic studies of sugar maple along geographic transects have been published (Perry and Knowles 1989; Young et al. 1993; Gunter et al. 2000). Furthermore, this deciduous, hardwood tree species exhibits a considerable northward geographic expansion in the pollen record, from a generalized refugium of the southern United States to its modern extent from southern Quebec to Georgia. During the expansion of sugar maple's range, various topographies were encountered, including most notably the Appalachian Mountains. The effects that the Appalachians had on the expansion of sugar maple are not considered in taxon range estimates from pollen data (Delcourt et al. 1984, Delcourt and Delcourt 1987).

Pollen Maps

Many pollen analyses have been made of post-Pleistocene plant migrations. These have been based on individual taxa, as well as larger units (e.g., biomes). The general consensus is that biomes of the past were compositionally dynamic, and thus modern biomes are not representative of the regional biomes that migrated from glacial refugia (Overpeck et al. 1992; Jackson et al. 2000; Williams et al. 2004). Consequently, biome-level data are of little use when examining species-level genetic structure. The paleo-pollen-dominance maps published by P. and H. Delcourt and their colleagues (Delcourt et al. 1984, Delcourt and Delcourt 1987) will be used to define the ranges of sugar maple through time in this study. These isopoll maps are at the genus level, which avoids the problem of having spuriously inferred species boundaries. The genus-level geographic range descriptions can be used as approximate delineations of the range expansion of sugar maple due to the species' substantial contribution to the *Acer* pollen record. Red maple is also a significant contributor to the pollen record, but given that the modern ranges of red maple and sugar maple overlap considerably and that it is often possible to distinguish the two species in the pollen record (Whitehead 1981), the genus-level maps likely represent the ranges of sugar maple well. Because the paleo-range maps used in this study are at the genus-level, only the models that represent the removal of areas where sugar maple was unlikely to exist are described using the species level notation of "sugar maple". Other descriptions use the genus-level descriptor "*Acer*". The varying climatic and other environmental conditions would have stressed migrating species, which would have reduced their ability to colonize stressful environments along the leading edge of their ranges. This increases the confidence in the regional elevation ranges' upper limits for sugar maple.

Species Biology and Previous Genetic Studies

Genetic separation occurs within a species when gene flow through either seed or pollen movement between populations is limited. The seed dispersal of sugar maple has been found to be limited to within 100 meters of the maternal tree (Johnson 1988). The pollen dispersal of sugar maple is much harder to calculate. Gabriel and Garrett (1984) demonstrated that sugar maple is partly wind-pollinated in addition to being pollinated by insects, although the relative importance of the different pollination agents is not known. In all likelihood, the amount of pollen needed to constitute significant gene flow is unlikely to exist in concentrations beyond the resolution of the DEM. This assumption allows predictions about the genetic structure on either side of the Appalachian Mountains to be made because the distance of gene flow from a given tree due to the spread of pollen is not sufficient to mask the physical separations of the range of sugar maple caused by the Appalachian Mountains. This assumption may be supported if the predicted patterns of genetic structure made from this study support the findings of Young et al. (1993).

Three studies of genetic structure in sugar maple have been performed in parts of its range to the west of the Appalachians and along its northern limit (Perry and Knowles 1989; Young et al. 1993; Gunter et al. 2000). Gunter et al. (2000) performed a randomly amplified polymorphic DNA (RAPD) study of three regions along a north-south transect west of the Appalachians. They found that gene flow is not restricted between regions and that genetic diversity is highest in the southern region. Young et al. (1993) found regional differentiation in allozymes in sugar maple along its northern extent, which they attributed to different regional selection pressures or the impact that migration patterns had on gene flow during the post-glacial expansion. Perry and Knowles (1989) discussed the possibility that migration has affected the genetic structure of sugar maple in Ontario; however, they suggested that sugar maple occupied a more northern limit during the Hypsithermal period (9000-2000 yr B.P.) than today. They hypothesized that the allelic heterogeneity observed between their study sites on either side of Lake Superior is a result of a continuous northern limit in Ontario that previously existed at a higher latitude.

Several excellent studies based on a comprehensive network of pollen sites and genetic sampling sites have thoroughly documented post-Pleistocene range expansion of temperate tree taxa in Europe (e.g., Brewer 2000, Petit 2002). Unfortunately, the genetic studies of sugar maple in North America are not as comprehensive, nor are they directly comparable to each other because authors used different markers and loci (Perry and Knowles 1989; Young et al. 1993; Gunter et al. 2000). Therefore more indirect inference is required to understand post-glacial migrations of North American species and the genetic consequences. Unlike Europe where temperate tree species existed in multiple refugia due to the discontinuous southern European regions and peninsulas, the refugia of North American temperate tree species were continuous (Delcourt and Delcourt 1987; Brewer 2002). In the absence of a geographically extensive genetic study of sugar maple, a single ice-age refugium allows for predictions about the effects of post-glacial migration to be made. A continuous refugium results in an extensive period of high gene flow throughout the limited range of sugar maple. The problem of the lack of knowledge about the abundance and density of the species within its refugium remains, but cannot be rectified without more fossil pollen data, which may or may not even be possible to collect. The assumption of high gene flow within a continuous species range for sugar maple's refugium must be made. The expansion of the range of sugar maple would be in the form of long-distance dispersal, which would reduce the genetic diversity along the leading edge of the range. This pattern of migration would be expected to leave a gradient of diversity, with the southern regions having the highest and the northern regions the lowest genetic diversity. The northern regions would also be expected to have fewer alleles and more allelic homozygosity than southern regions (Hewitt 1996).

While Perry and Knowles (1989), Young et al. (1993) and Gunter et al. (2000) provide descriptions of genetic diversity for components of sugar maple's range, their results have not been analyzed together in an attempt to understand in more depth why the observed patterns of genetic diversity exist. Each study examines the genetic diversity of sugar maple within its limited extent of sampling; authors do not discuss how their results compare to the other studies or investigate the historical causes of their results. Young et al. (1993) and Perry and Knowles (1989) used their results to speculate about earlier changes in sugar maple's northern range limits, but their speculation was based on their genetic data and did not consider the Holocene migration of sugar maple. Due to the limited geographic range of Perry and Knowles' (1989) study, I will exclude their paper from the discussion concerning the trends of genetic measures across the range of sugar maple. By combining a digital elevation model (DEM) with previously published isopoll maps (Delcourt et al. 1984, Delcourt and Delcourt 1987), I will examine the effects of the Appalachian Mountains on sugar maple expansion and subsequently evaluate the genetic consequences of the topographic disruption to migration. The models of range expansion and physical connectivity through time from the end of the last ice age for sugar maple provide an integrated approach to explain the observed genetic patterns of Young et al. (1993) and Gunter et al. (2000), and describe more clearly how the topography of the eastern United States affects species migration pathways, specifically of sugar maple. The following questions are the foci of my study.

- From a geographical extent and genetic structure standpoint, how have the Appalachian Mountains affected the migration of sugar maple?
- Do predictions of genetic structure based on my models correspond with the results of Gunter et al. (2000) and Young et al (1993)?
- Do my models support the speculations of Young et al. (1993) about the past range expansion of sugar maple?

- How does the integration of genetic studies, paleo-dominance maps, and a DEM create a better understanding of species migration?

CHAPTER 2

METHODS

The sinusoidal equal-area projected paleo-dominance maps of P. and H. Delcourt and Webb (Delcourt et al. 1984, Delcourt and Delcourt 1987) have three components that will be added to the DEM. The first includes the generalized geographic ranges of sugar maple, and the second is the temporal component of the post-glacial range expansion. The time steps of the maps are at 2,000 year intervals from 18,000 yr B.P. to the present, including a map for 500 yr B.P. These provide the temporal and spatial components of sugar maple's expansion. The third component, the percentage of *Acer* pollen within the sample, provides a measure of abundance of sugar maple in various portions of its range for each time step (Figures 4, 9, 14, 19, 24, 29, 34, 39, 44, 49, 53). To refine the maps, I removed elevations where sugar maples were unlikely to have existed due to climatic conditions outside their tolerance range (Figures 5, 6, 7, 10, 11, 12, 15, 16, 17, 20, 21, 22, 25, 26, 27, 30, 31, 32, 35, 36, 37, 40, 41, 42, 45, 46, 47, 50, 51, 52, 54, 55, 56). The resolution of the maps improves over time due to the increased density of sample sites. Pollen samples that extend back to 18,000 yr B.P. are rare, as they are located in undisturbed anaerobic locations such as ponds or bogs. The isopoll contours are generalized between sample sites, which can be fairly distant from each other. As the time steps become more recent, more sample sites are available and thus the resolution of the maps improves (Figures 3, 8, 13, 18, 23, 28, 33, 38, 43, 48). Given that the intent of this study is to examine the expansion of sugar maple's range and subsequent gene flow on a semi-continental scale, the coarse resolution of both the pollen data and the DEM are not prohibitive to their use.

The DEM is from the USGS, and can be found at http://edcdaac.usgs.gov/gtopo30/gtopo.asp. Two tiles, W100N90 and W100N40, are needed to display the majority of eastern North America (Figure 1). This DEM has 30 arc-second spacing, which is approximately equal to one kilometer. The source data for the land area of the United States are USGS 1-degree DEM's. Canada is largely represented through Digital Terrain Elevation Data (DTED). Both data sources have a vertical accuracy of plus or minus 30 m at the 90 percent confidence level.

Sugar maple's modern elevation limit varies between regions. In the southern Appalachian Mountains sugar maple is found at elevations up to 1,680 m, whereas in the northern part of its range, sugar maple has an upper elevation limit of 760 m (Godman et al. 1990). Three different elevation limits were applied in each time step to account for this geographical variation in sugar maple's elevation limits. The division between regions with different elevation limits is at 40° north latitude. The elevation limits adopted for the northern and southern regions were based on three standards: the modern limits of sugar maple, and both 100 m and 200 m below the modern limits. The model was run with the latter standards because the ability of plant species to colonize the marginal habitats of higher elevations is likely depressed during range expansion. As *Acer* approaches a range comparable to sugar maple's modern extent, the southern elevation limit is increased sequentially until it reaches the highest elevation limit of sugar maple, relative to the imposed restriction. A more representative model of *Acer*'s elevation limits across its range would be constituted by a gradual increase in elevation limits as latitude decreased from the northern edge of its range to its southern limit. Such a model is unnecessary for the purposes of this project. The part of the species' migrating range that determines the establishment of population in areas is the leading edge. The leading edge of *Acer's* range is consistently modeled with the appropriate lowest elevation limits using the two-tiered model based on the natural break in the Appalachian Mountains at 40° north latitude.

Using ArcGIS, the gtopo30 DEM constitutes the base data layer. The two tiles are joined together, and then clipped to include only the eastern half of North America that is displayed in the isopoll maps. The isopoll maps are scanned from maps of Delcourt et al. (1984) and Delcourt and Delcourt (1987) and saved as TIF files. Each time step is georeferenced into a geographic projection in order to digitize the isopoll lines from each time step into shapefiles. The elevations above the modeled limits in each time step are saved as shapefiles and removed from the original ranges. The sample regions of each genetic study are represented by symbols placed at the coordinates of each sample point (Figure 2). These points are present for each time step to determine when sugar maple's range included them and what the abundance of maple pollen was for those times.

The genetic structure of a species is a description of non-random patterns of genetic variation that may be observed within or among populations at different spatial scales. To describe levels of genetic differentiation between populations, the genetic parameters of expected heterozygosity (H_e), proportion of loci heterozygous per individual (H_i), percentage of polymorphic loci (P), and genetic distance (D) (Nei 1972) are used. H_e is the frequency of heterozygotes for a population when the assumption of

Hardy-Weinberg equilibrium is applied, whereas H_i is the mean observed proportion of heterozygous loci per individual. D is a measure of the accumulated allele differences per locus between all possible pairs of individuals in the two different populations, averaged across all individual-pairs. When examined along with geographic distribution, mechanisms of differentiation can be inferred from genetic analyses. These metrics are all indirect measures of genetic structure that tend to integrate historical effects on genetic variation over many generations; therefore, the temporal component of the development of genetic structure is difficult to determine from indirect measures. Also, given the enormous expense of genetic analysis, few complete genetic analyses throughout species ranges have been performed, particularly for North American plant taxa.

In the absence of thorough studies of genetic variation throughout sugar maple's range based on a uniform methodology, this study synthesizes results from two studies based on different genetic markers. Young et al. (1993) used allozymes to determine genetic diversity and Gunter et al. (2000) based their estimates of diversity on RAPDs. RAPD markers are based directly on the genetic coding in an organism whereas allozymes are the protein expressions of genetic coding. The genetic measures used for these different studies are generally comparable, but cannot be combined into a single data set. Comparisons of the DEM-refined sugar maple migration models to the genetic studies were made through qualitative analyses, rather than through a direct comparison of quantitative values for the different genetic structure indices. This is more appropriate in view of the different molecular markers and genetic indices used in the studies, as well as the coarse resolution of the DEM and the isopoll maps.

CHAPTER 3

RESULTS

ACER Migration and Sugar Maple Models

At the end of the last ice age, 18,000 yr B.P., *Acer* ranged from Kentucky to northeastern Mexico (Figure 4). While few sample sites represent this time period for the reconstruction of *Acer's* range (Figure 3), all sites indicate that *Acer* existed at low abundances at this time. Along the Gulf of Mexico, *Acer* did not extend farther east than western Alabama.

In the modeled distributions, when the elevation limit of 760 m is applied to this time period, only a few peaks of the Ouachita Mountains can be excluded from the possible locations of sugar maple occurrence (Figure 5). Lowering the elevation limit to 660 m begins to exclude the higher elevations of the Edwards Plateau in Texas from terrain that *Acer* may have occupied (Figure 6). When the elevation limit is further lowered to 560 m, a number of peaks in the Ouachita Mountains are identified as being above the elevation limits of sugar maple (Figure 7).

The range of *Acer* 16,000 yr B.P. showed a minor regression of maples from eastern Kentucky to western Kentucky, and an expansion from northern Texas to northern Oklahoma (Figure 9). An area of higher *Acer* abundance, between 10-19% of forest composition, developed in northern Louisiana and southern Arkansas during this time period (Figure 9).

In the modeled distributions for 16,000 yr B.P., the Boston Mountains of the Ozark Plateau are within the range of *Acer* and show similar range exclusions to the Ouachita Mountains as the elevation limits are lowered (Figures 10, 11, 12). The regional increase in elevation across the Great Plains also causes range exclusions in Western Oklahoma as the elevation limits of sugar maple in the model are lowered (Figure 12).

By 14,000 yr B.P., *Acer* had expanded northward to central Wisconsin, along the Gulf Coast to southwestern Georgia, and across the Cumberland Plateau and the Blue Ridge Mountains to the Atlantic coastline of North Carolina and southern Virginia (Figure 14). The greatest abundance of maples as a proportion of forest composition was located around the Kansas-Missouri-Nebraska boundary, at a level of 20-29% (Figure 14). This region of greater abundance was surrounded by a larger region of 10-19% abundance that reached up from northern Louisiana. The rest of *Acer's* range is recorded to have existed at low levels of maple abundance: below 10% of forest composition (Figure 14).

When the modern northern elevation limit of 760 m for sugar maple is applied to this time period (Figure 15), a string of peaks in the Cumberland Plateau is excluded from the range. More significantly, the Blue Ridge Mountains separates the maples of the Atlantic Coast from the rest of the maple range, except for one valley connection in western North Carolina that is as thin as five miles wide in multiple locations. The distance that separates the Atlantic maples from the western maple range is as small as a few miles in northern Virginia, but the populations of *Acer* on both sides are completely separated. When the 660 m elevation limit is applied (Figure 16), the North Carolinian maple range bridge remains intact. Once the elevation limit is lowered to 560 m (Figure 17), the Atlantic maples are completely isolated from the rest of the maples, with the shortest distance between the ranges being twenty miles. At this elevation limit, the Cumberland Plateau creates periodic ridgeline range exclusions in eastern Tennessee (Figure 17). Along the western part of maple's range 14,000 yr B.P., the Great Plains prove to be a nearly continuous western limit as the elevation limit of the model is lowered (Figure 17).

The southern margin of the range of *Acer* moved north out of Mexico by 12,000 yr B.P. to occupy the eastern half of Texas and follow the Gulf coastline into the Florida panhandle (Figure 19). Most of Georgia was devoid of maple, but the majority of inland South Carolina, western North Carolina, and western Virginia were occupied with low levels of maple, which increased to an abundance of 10-19% along the eastern edge of the Blue Ridge Mountains (Figure 19). By this time, *Acer* reached southwestern New York along its northeastern range extent. Not only were maples present in this region of the northern Alleghenies, but an area of increased maple abundance, from 10-19% of forest composition, was located around the upland areas (Figure 19). The greatest abundance of *Acer*, 20-29% abundance, was located in the southwestern portion of its range, in eastern Oklahoma, northeastern Texas, and eastern Arkansas (Figure 19). The only other recorded increase in *Acer* abundance above the lowest recordable level is in southern Alabama, where a region of 10-19% abundance exists at this time (Figure 19).

In the modeled ranges, the elevation limit applied to the Blue Ridge Mountains at this time is increased to 990 m to reflect the diminished elevation restriction as the leading edge of *Acer's* range migrated significantly north of 40° N latitude (Figure 20).

At this elevation limit, only a few peaks in the Cumberland Plateau are unsuitable for the presence of sugar maple (Figure 20). Although much larger unsuitable areas exist in the Blue Ridge Mountains with this elevation limit, significant areas of connection exist between the maples on either side of the range, especially in western Virginia (Figure 20). As the elevation limit is lowered, however, the connections between the maples on either side of the Blue Ridge Mountains contract until only a few connections remain when the limit is 790 m (Figures 21, 22).

Only a few peaks of the northern Alleghenies were excluded from *Acer's* range when the modern northern elevation limit of 760 m is applied, but decreasing the elevation limit by only 200 m causes a significant portion of the central arm of northeastern *Acer* range to be unsuitable for the presence of sugar maple (Figure 20). This greater restriction would have forced a split in the northward expansion of *Acer* around the Alleghenies of northern Pennsylvania (Figure 20).

The elevation limit of *Acer* below 40° N latitude was increased to 790 m through 990 m as the model moves from 14,000 yr B.P. to 12,000 yr B.P (Figures 20, 21, 22). With this change, the Great Plains no longer limits sugar maple's western extent as much as in previous time steps (Figure 20, 21, 22). With the increased elevation limit in this southern region, the Ouachita and Boston Mountains no longer limit the range of sugar maple (Figures 20, 21, 22). At this point of range expansion for maple, all three sites where Gunter et al. (2000) studied the genetic relationships among sugar maple populations are included in the range of *Acer* (Figure 19).

The time step of 10,000 yr BP showed an eastward shift not only in *Acer's* range, but also in areas of increased abundance (Figure 24). Although a few areas of increased maple abundance, from 10-19%, existed to the west of Lake Michigan, the main stretch of increased maple presence occurred from southern Alabama, up to the west of the southern Appalachians, into southwestern New York and Pennsylvania (Figure 24). The area of increased abundance in the northern Alleghenies, first evident 12,000 yr B.P. (Figure 19), continued to increase to a presence of 20-29% (Figure 24). As *Acer* migrated into New England, an area of western Maine and New Hampshire also supported maples at a level of 10-19% of forest presence (Figure 24).

During this time period, the higher elevations of the Great Plains only restrict *Acer's* range in the Dakotas; from there, the western range limit runs along the eastern border of Kansas and Oklahoma and down through eastern Texas. For the modeled *Acer* range 10,000 yr B.P., the elevation limits for sugar maple are increased for areas below 40° N latitude to 1020 m through 1220 m (Figure 25, 26, 27). The 1220 m restriction removes patches of the Blue Ridge Mountains from the locations suitable for sugar maple presence, but does not form a continuous barrier which separates the maples on either side of the mountains (Figure 25). Although lowering the elevation limit to 1120 m and then to 1020 m causes significant portions of the Blue Ridge Mountains in West Virginia, western North Carolina, and northern Georgia to be unsuitable for sugar maple, the excluded areas still do not constitute a continuous barrier (Figures 26, 27). The expansion of *Acer's* range to coastal Virginia and through central Georgia and South Carolina causes the Carolinian and Virginian maples, which are isolated from the rest of *Acer's* range by the Appalachian Mountains 12,000 yr B.P., to be re-integrated into the main body of *Acer's* range by 10,000 yr B.P (Figures 25, 26, 27).

Applying the modern northern elevation limit of sugar maple north of 40° N latitude 10,000 yr ago shows that peaks of the Adirondacks, Catskills, Green Mountains, and White Mountains are unsuitable for sugar maple (Figure 25). This effect is magnified as the elevation limit is lowered to 560 m (Figures 26, 27). At this lowest elevation limit, the Adirondack and the Catskill Mountains are plateaus which sugar maple would have had to migrate around (Figure 27). The Green Mountains form a ridge of exclusion that span from southern Quebec into Massachusetts, and similarly, the White Mountains form a barrier to migration that runs from New Hampshire into Maine (Figure 27). Though not as cohesively exclusionary to sugar maple's presence as the Blue Ridge Mountains, the northern Appalachian Mountains are significant barriers to the expansion of sugar maple's range into New England (Figures 25, 26, 27).

By 8,000 yr B.P., *Acer* no longer overlapped or bordered the Great Plains (Figure 29). While *Acer's* presence in Texas remained unchanged from 10,000 yr B.P., the western range boundary of *Acer* ran into Illinois and up into northern Minnesota (Figure 29). The southeastern extent of *Acer's* range remained fairly similar to that of 10,000 yr B.P., with the exception of an isolated population in Florida (Figures 24, 29). In the northeast, *Acer* had extended through New Brunswick and into Nova Scotia, and the northern extent of *Acer* had migrated far enough northward that only two of Young et al.'s (1993) genetic-study sample sites remained north of *Acer's* range (Figure 29). Also, the greatest abundances of *Acer* had become central to *Acer's* range, with two locations of 30-39% of forest composition existing in the western Ohio Valley and around the Alleghenies (Figure 29).

The elevation limits applied to the southern Appalachians for the 8,000 yr B.P. time step range from 1,250 m to 1,450 m (Figures 30, 31, 32). Lowering the elevation limit does increase the number of peaks in the Blue Ridge Mountains that were unlikely to have supported sugar maple, but not enough to cause a significant disruption in the continuity of sugar maple's range (Figures 30, 31, 32). This effect continues from 6,000 yr B.P. through today, when the southern elevation limits applied in the model range from 1,480 m to 1,680 m (Figures 35, 36, 37, 40, 41, 42, 45, 46, 47, 50, 51, 52, 54, 55, 56). The northern Appalachian Mountains do not have any changes in elevation limits from time step to time step during the modeled postglacial migration history of *Acer*; latitudes north of 40° N always have elevation limits that range from 560 m to 760 m (Figures 35, 36, 37, 40, 41, 42, 45, 46, 47, 50, 51, 52, 54, 55, 56). Consequently, the areas removed due to elevation unsuitability remain essentially the same from 10,000 yr B.P. through modern times, with only the Laurentide Mountains adding to the removed areas beginning 8,000 yr B.P (Figures 25, 26, 27, 30, 31, 32, 35, 36, 37, 40, 41, 42, 45, 46, 47, 50, 51, 52, 54, 55, 56).

The center of *Acer* abundance 6,000 yr B.P., with 40-49% of forest composition, extended from the Alleghenies to Georgian Bay in Lake Huron (Figure 34). This center expanded across Michigan to Lake Michigan by 500 yr B.P. (Figures 39, 44, 49). The extent of *Acer's* northern range included all of Young et al.'s (1993) sample sites by 6,000 yr B.P. and reached its modern northern limit at approximately the same time (Figure 34). *Acer's* southern and western boundaries fluctuated slightly between 8,000 yr B.P. and 500 yr B.P (Figures 29, 34, 39, 44, 49). The modern range of the hard maples is similar to *Acer's* range during this time, except that its more southern range boundary barely crosses into northern Georgia and Alabama (Figure 53). The modern time step also shows the greatest abundance of hard maples, 40-49% of forest composition, existing in southern Quebec and New England (Figure 53).

Genetic Measures of Sugar Maple

Young et al. (1993) found appreciable genetic distance between all of their sampled regional populations (Table 1). The sample sites are listed by their latitudinal position from east to west. The percentage of polymorphic loci (P) and mean proportion of loci heterozygous per individual (H_i) showed trends of increasing genetic diversity from the eastern sites to the western sites (Table 1). Gunter et al (2000) also found substantial levels of genetic distance between all pairs of their sample regions. The greatest distance was among the southern and central regions and the shortest distance, or greatest genetic similarity, was among the central and northern regions (Table 2). The regional weighted averages of mean expected heterozygosity (He) values found by Gunter et al. (2000) were appreciably different and ranged from a high of 0.224 in the northern region to a low of 0.209 in the southern region (Table 3).

Table 1. Percentage of polymorphic loci (P), mean proportion of loci heterozygous per individual (H_i), and genetic distance (D_m) from Young et al.'s (1993) sample sites, ordered from east to west. The standard errors of the means are provided in parentheses.

Sites	P	H_i	D_m
CB	0.412	0.088(0.008)	0.006
KJ	0.471	0.108(0.009)	0.007
FN	0.529	0.120(0.008)	0.005
FR	0.471	0.129(0.009)	0.006
MM	0.588	0.131(0.009)	0.007
GA	0.529	0.120(0.012)	0.007
BY	0.529	0.111(0.010)	0.006
PP	0.529	0.094(0.010)	0.011
PK	0.588	0.138(0.010)	0.009

Table 2. Genetic distance (D_m) between regions from Gunter et al. (2000).

Regions	D_m
Northern/Central	0.0137
Northern/South	0.0290
Southern/Central	0.0493

Table 3. Mean expected heterozygosity (H_e) for each region from Gunter et al. (2000).

Region	H_e
North	0.224
Central	0.218
South	0.209

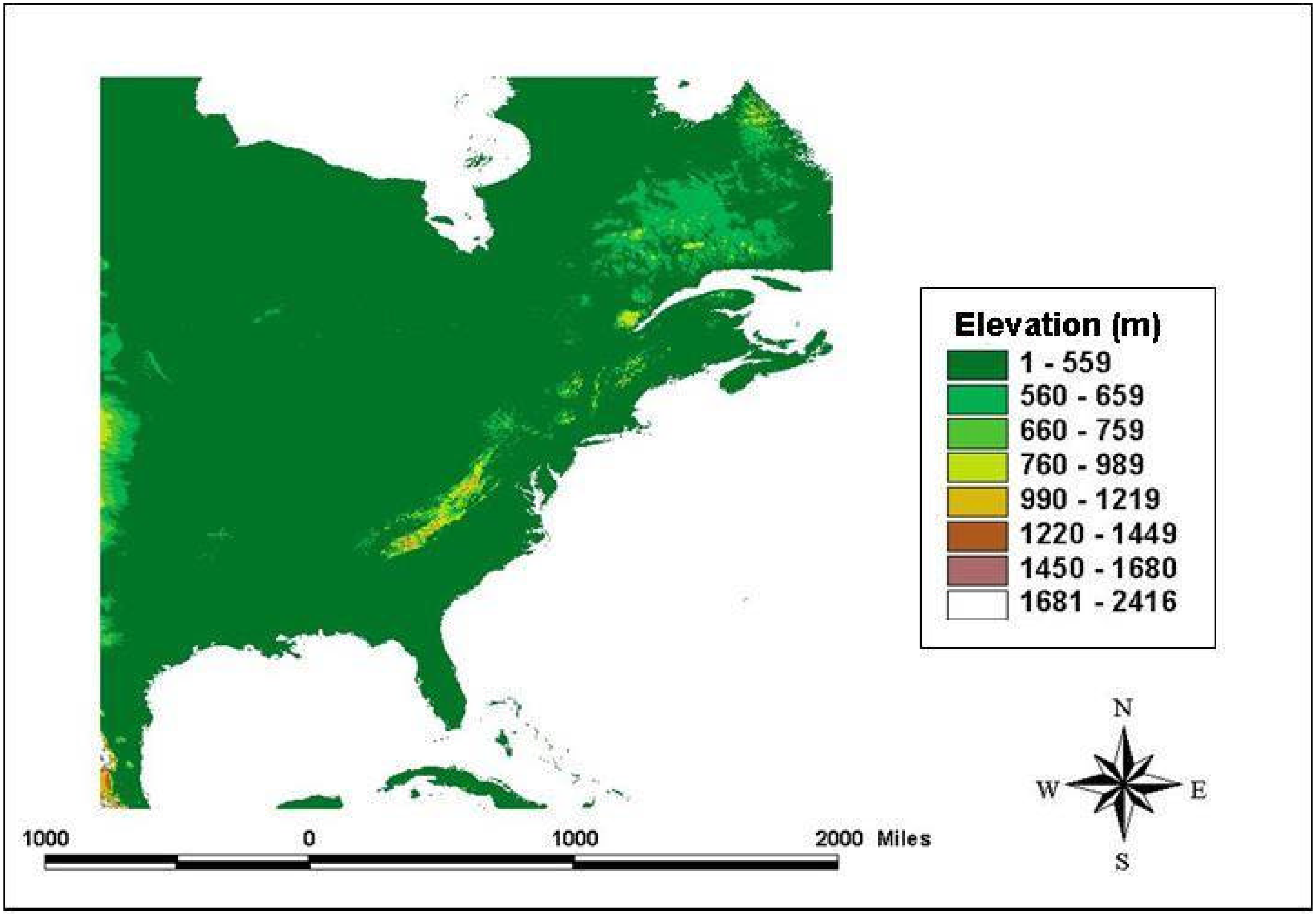

Figure 1. Elevation map of Eastern North America.

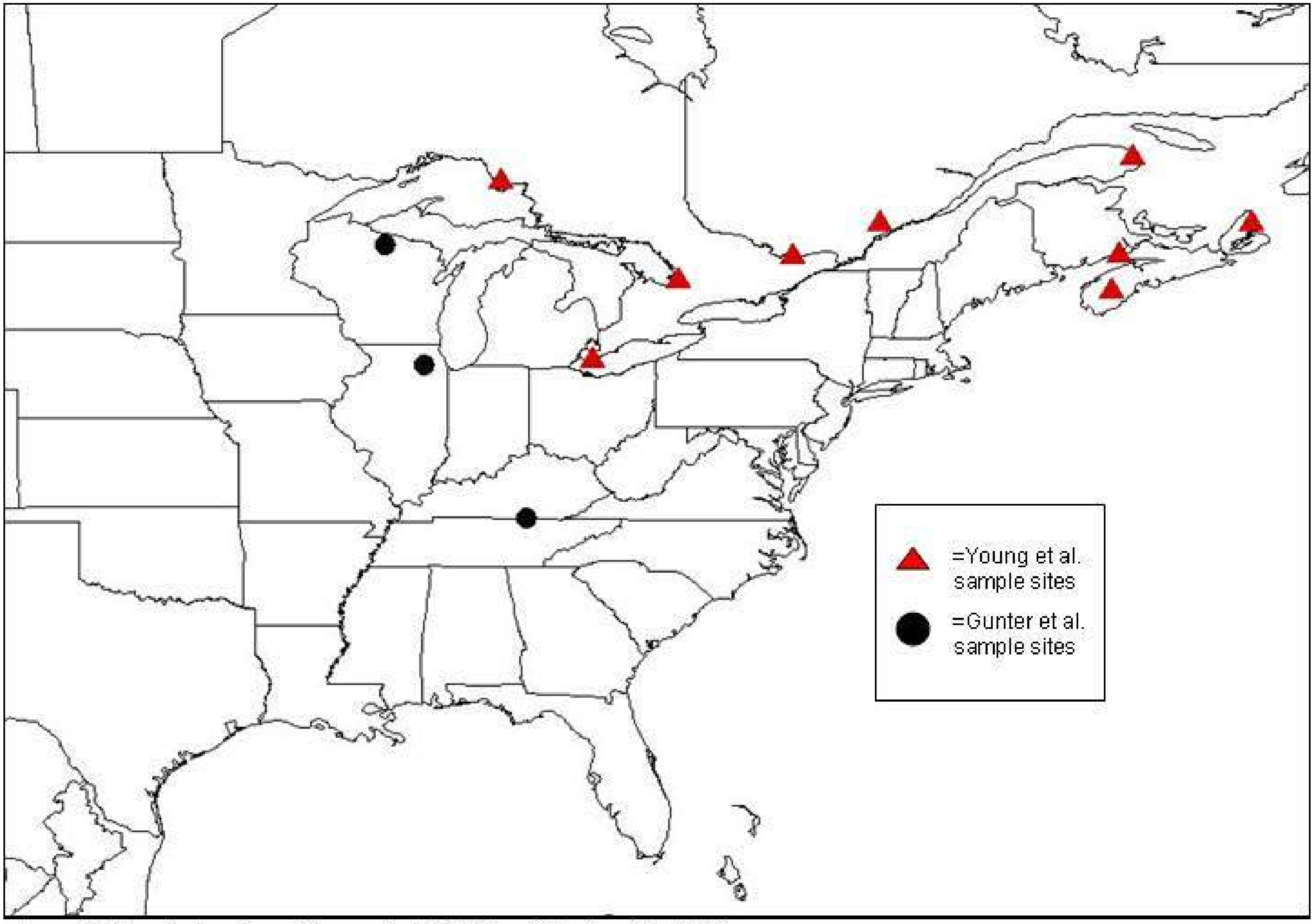

Figure 2. Sample locations of Young et al. (1993) and Gunter et al. (2000).

Figure 3. Paleoecological sites in eastern North America for 18,000 yr B.P. Based on Delcourt and Delcourt (1987).

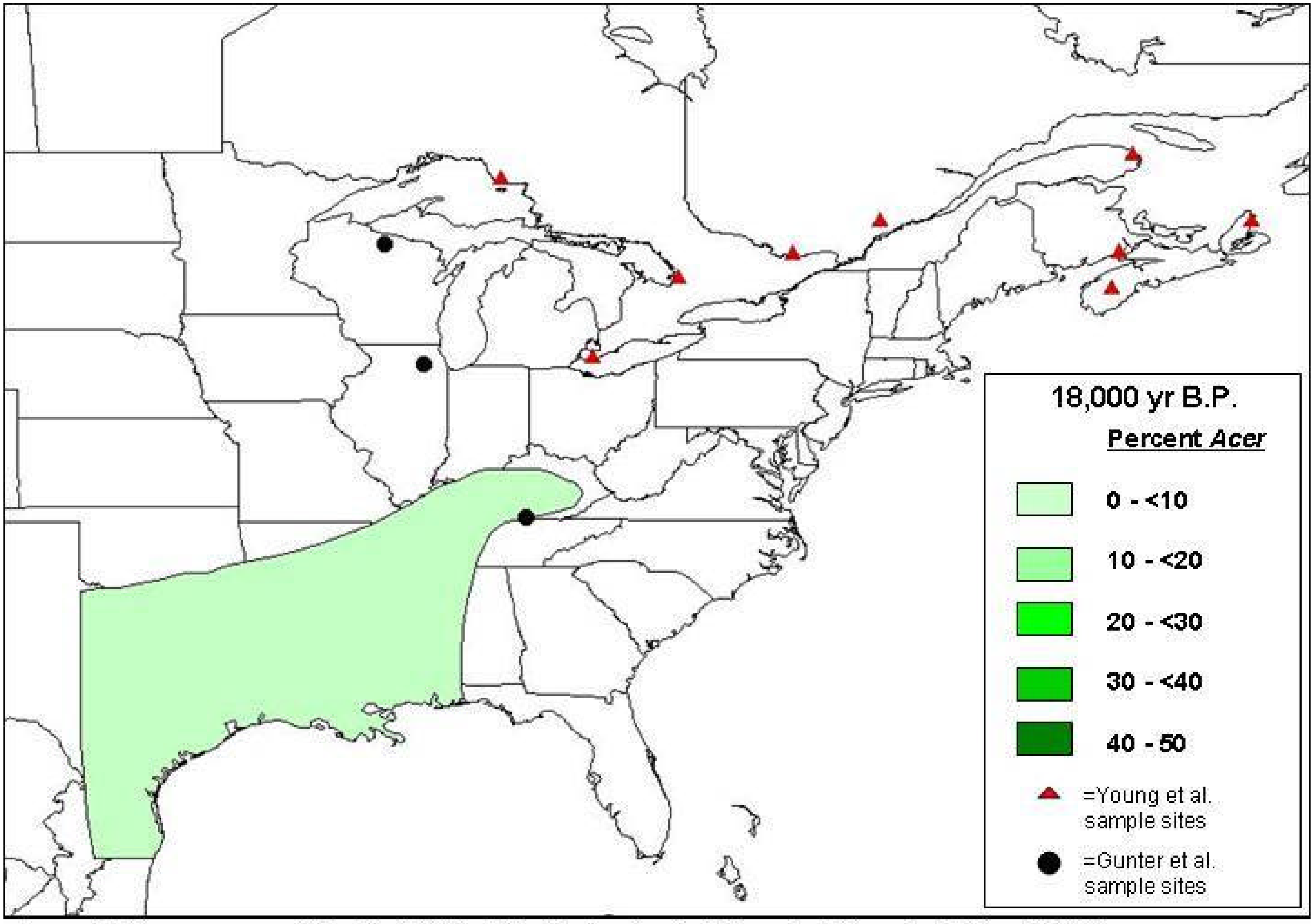

Figure 4. Paleo-range map of *Acer* for 18,000 yr B.P. No elevation limit. Based on Delcourt and Delcourt (1987).

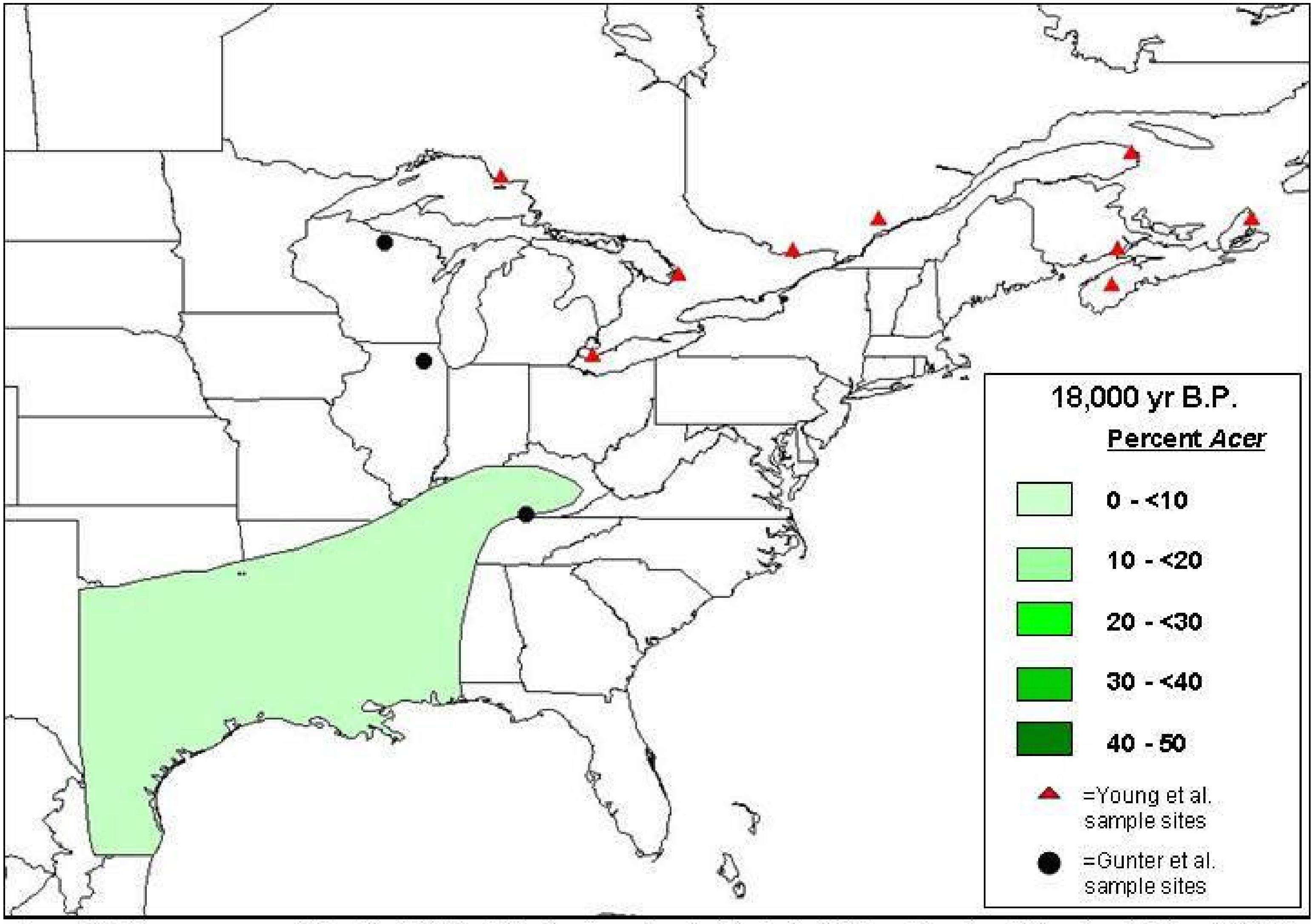

Figure 5. Paleo-range map of *Acer* for 18,000 yr B.P. Southern Appalachian limit = 760 m. Based on Delcourt and Delcourt (1987).

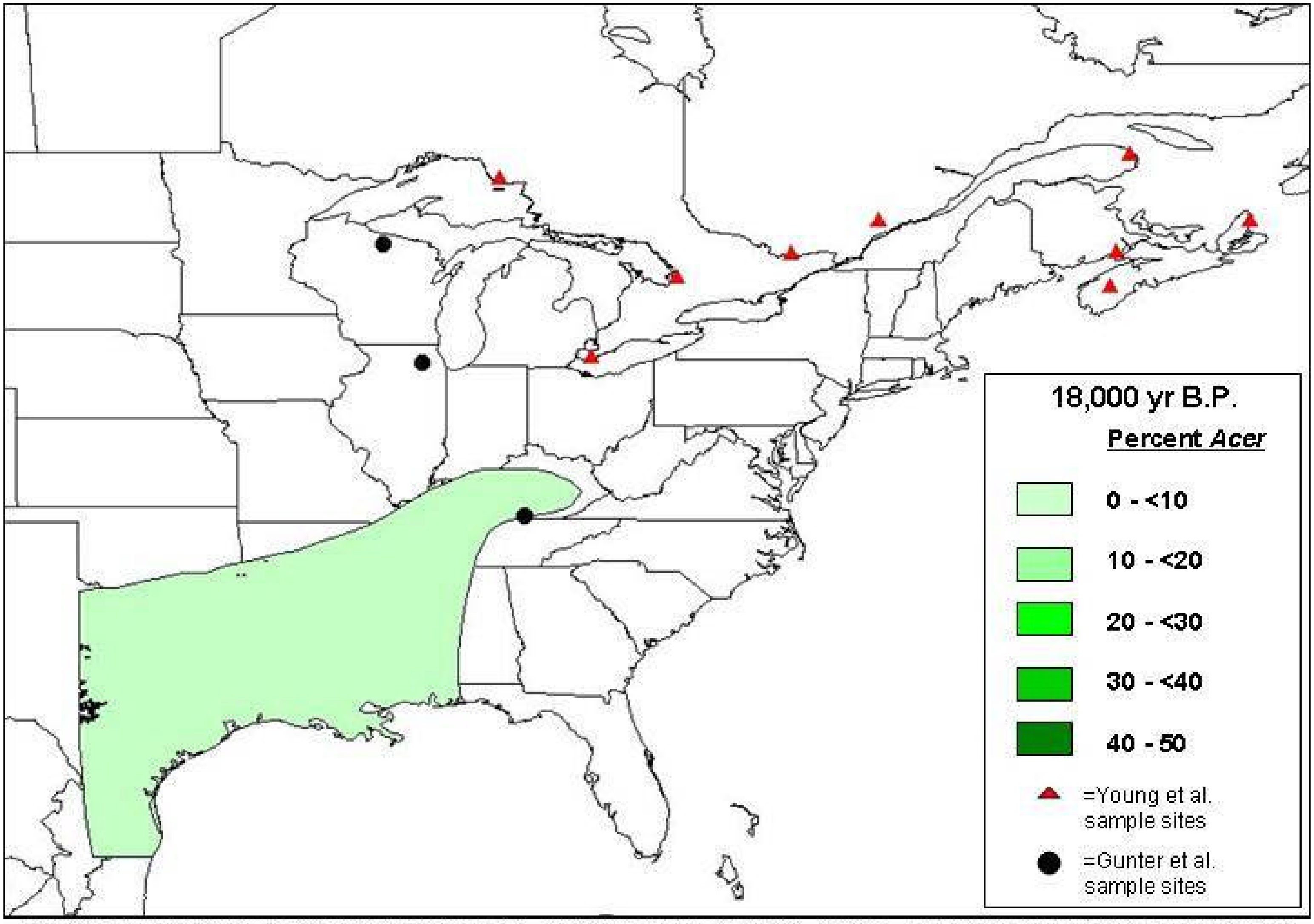

Figure 6. Paleo-range map of *Acer* for 18,000 yr B.P. Southern Appalachian limit = 660 m. Based on Delcourt and Delcourt (1987).

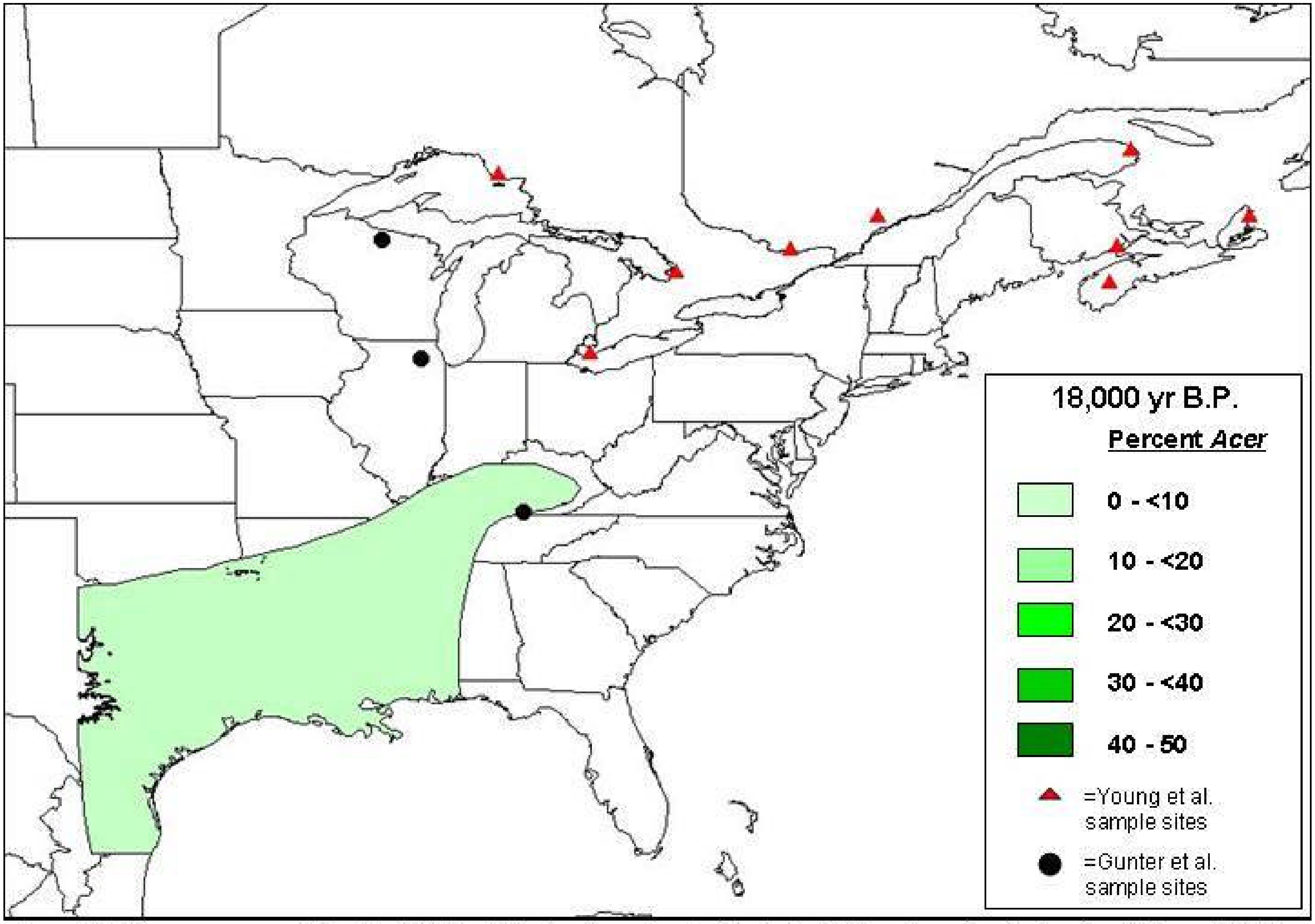

Figure 7. Paleo-range map of *Acer* for 18,000 yr B.P. Southern Appalachian limit = 560 m. Based on Delcourt and Delcourt (1987).

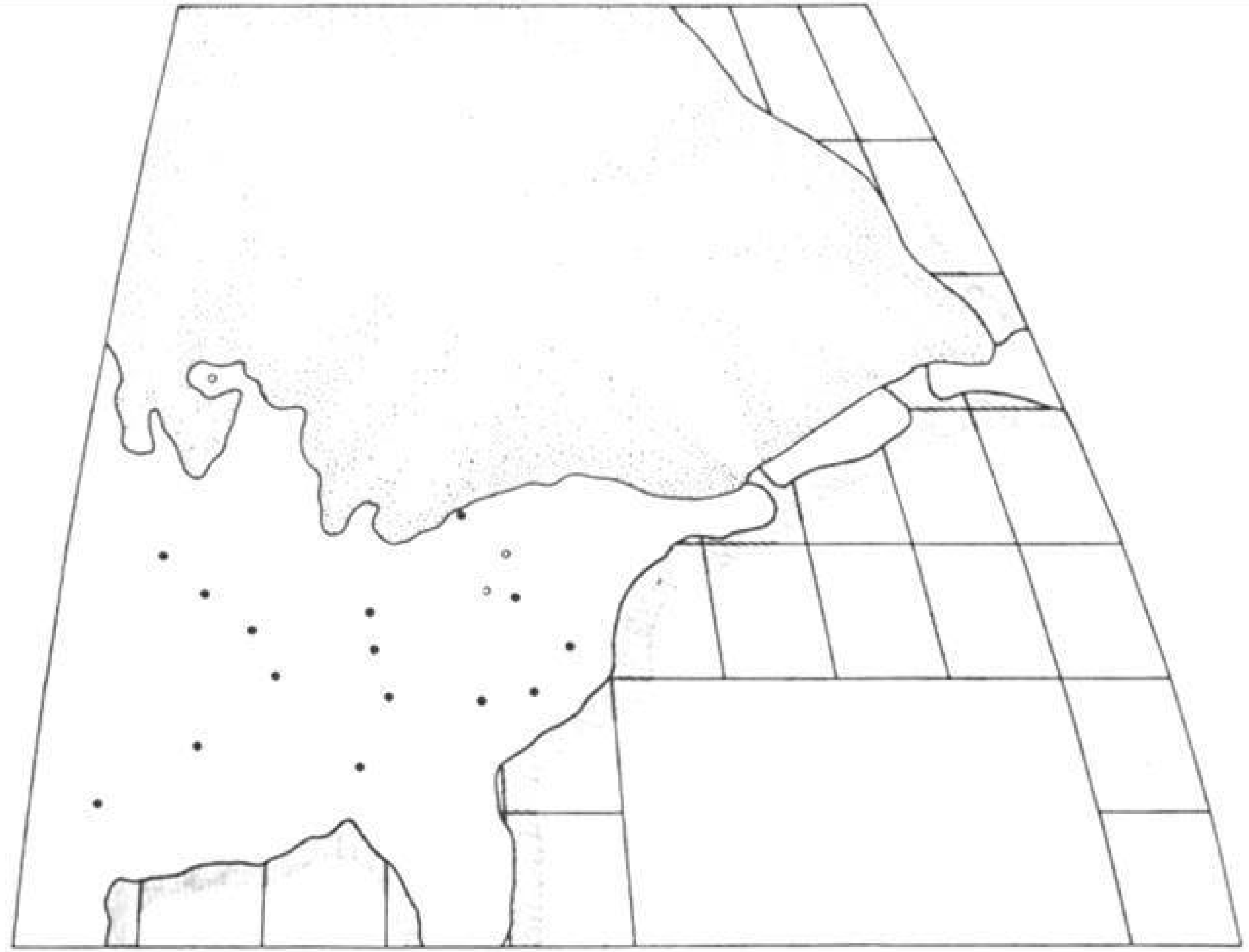

Figure 8. Paleoecological sites in eastern North America for 16,000 yr B.P. Based on Delcourt and Delcourt (1987).

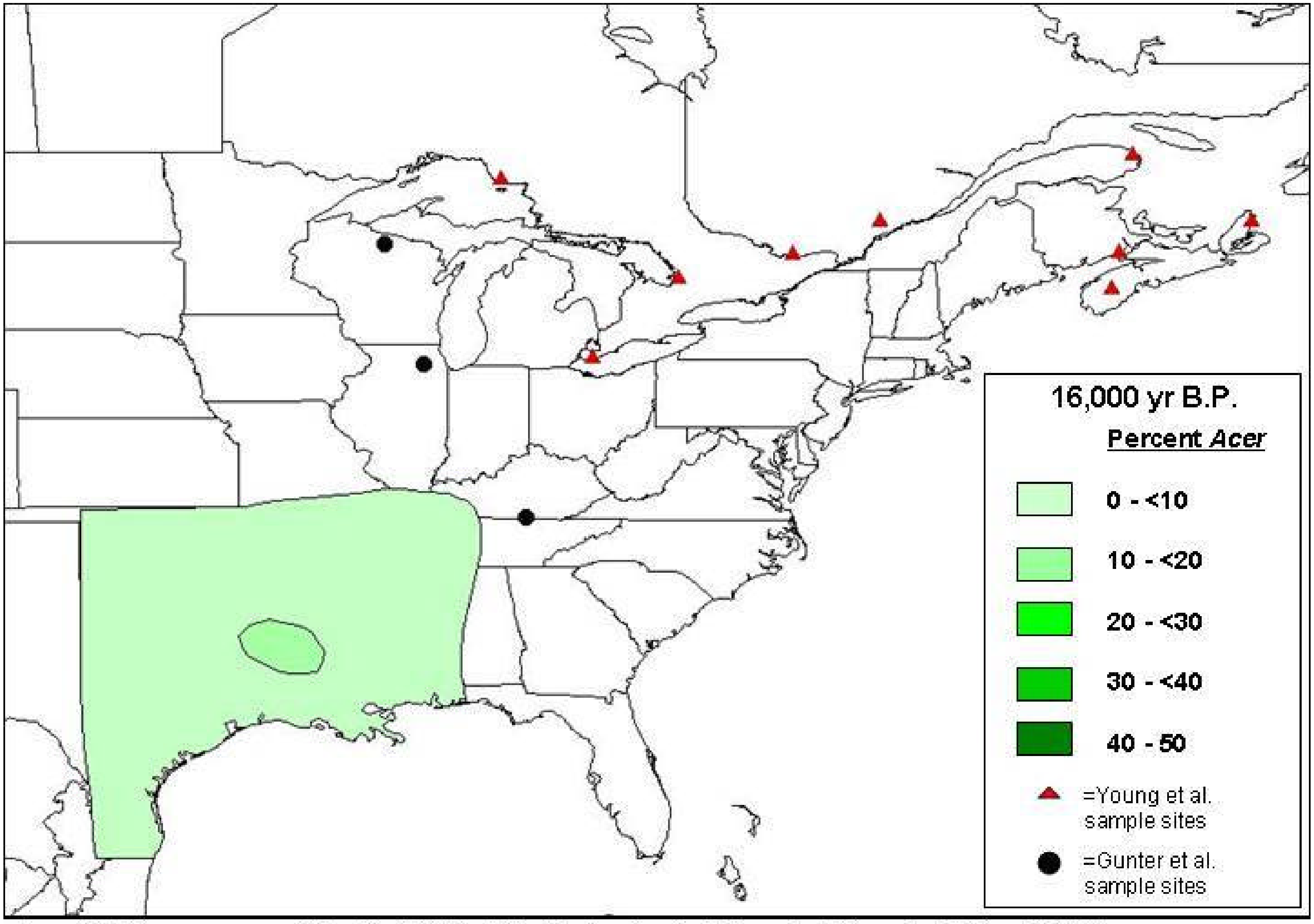

Figure 9. Paleo-range map of *Acer* for 16,000 yr B.P. No elevation limit. Based on Delcourt and Delcourt (1987).

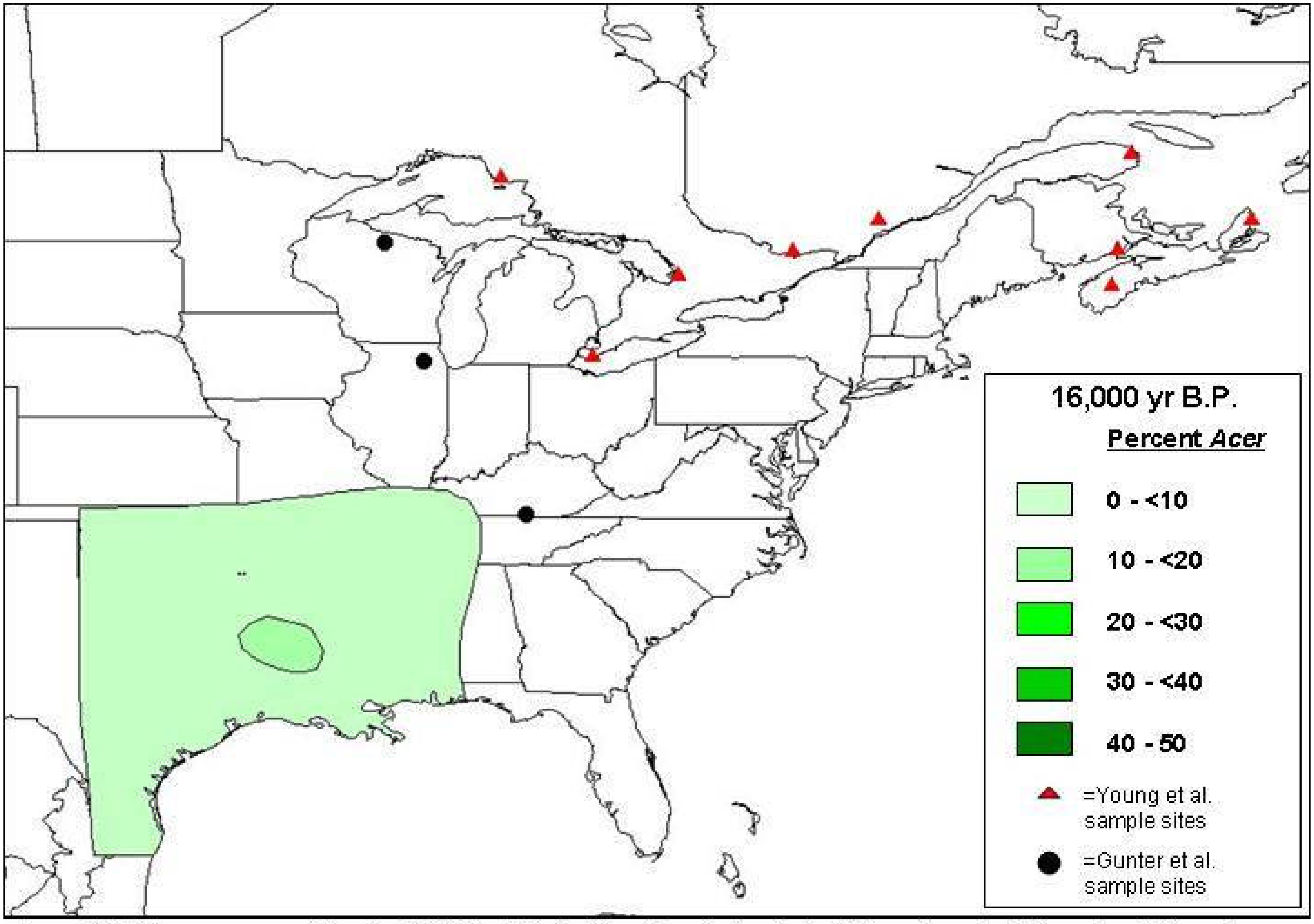

Figure 10. Paleo-range map of *Acer* for 16,000 yr B.P. Southern Appalachian limit = 760 m. Based on Delcourt and Delcourt (1987).

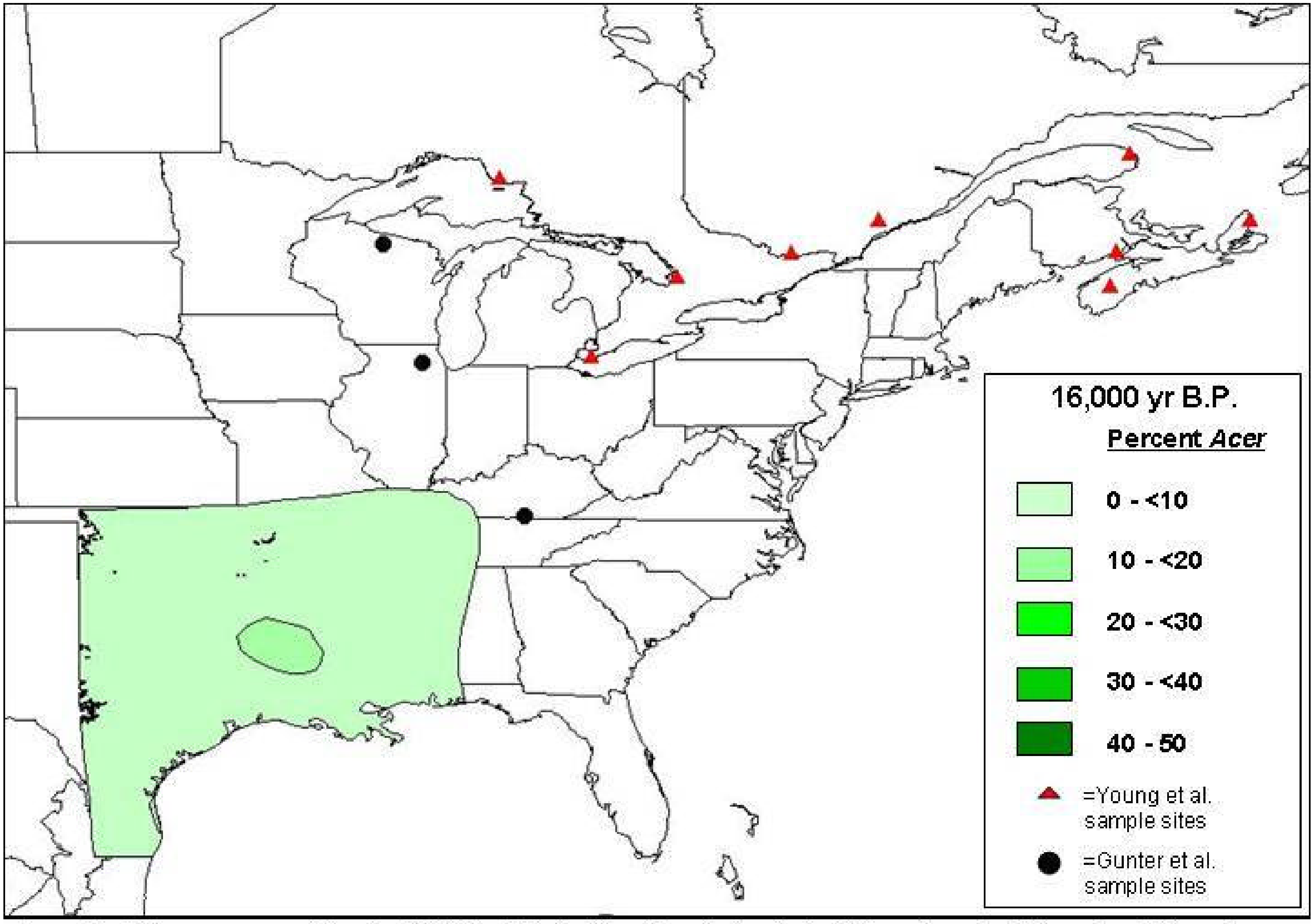

Figure 11. Paleo-range map of *Acer* for 16,000 yr B.P. Southern Appalachian limit = 660 m. Based on Delcourt and Delcourt (1987).

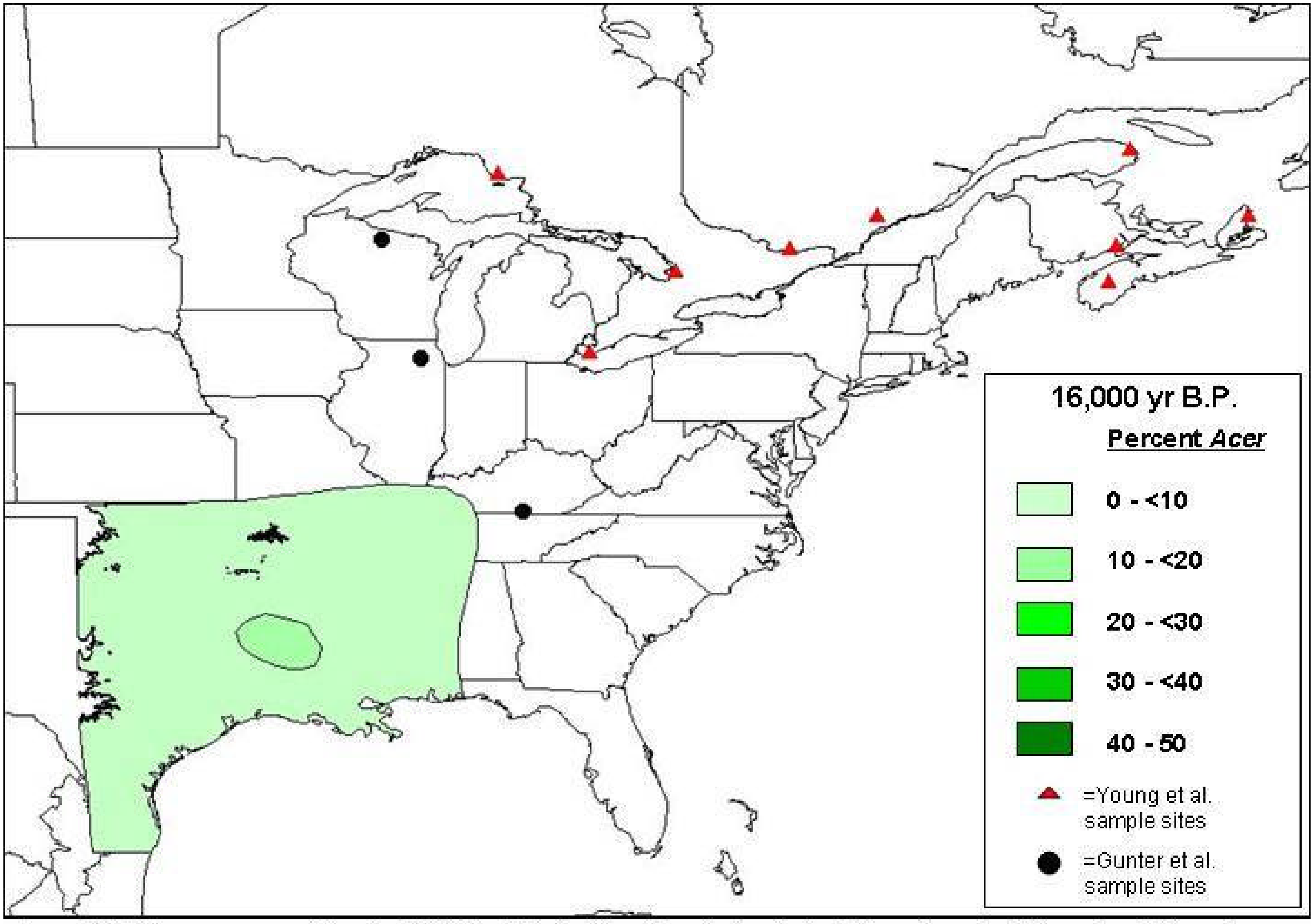

Figure 12. Paleo-range map of *Acer* for 16,000 yr B.P. Southern Appalachian limit = 560 m. Based on Delcourt and Delcourt (1987).

Figure 13. Paleoecological sites in eastern North America for 14,000 yr B.P. Based on Delcourt and Delcourt (1987).

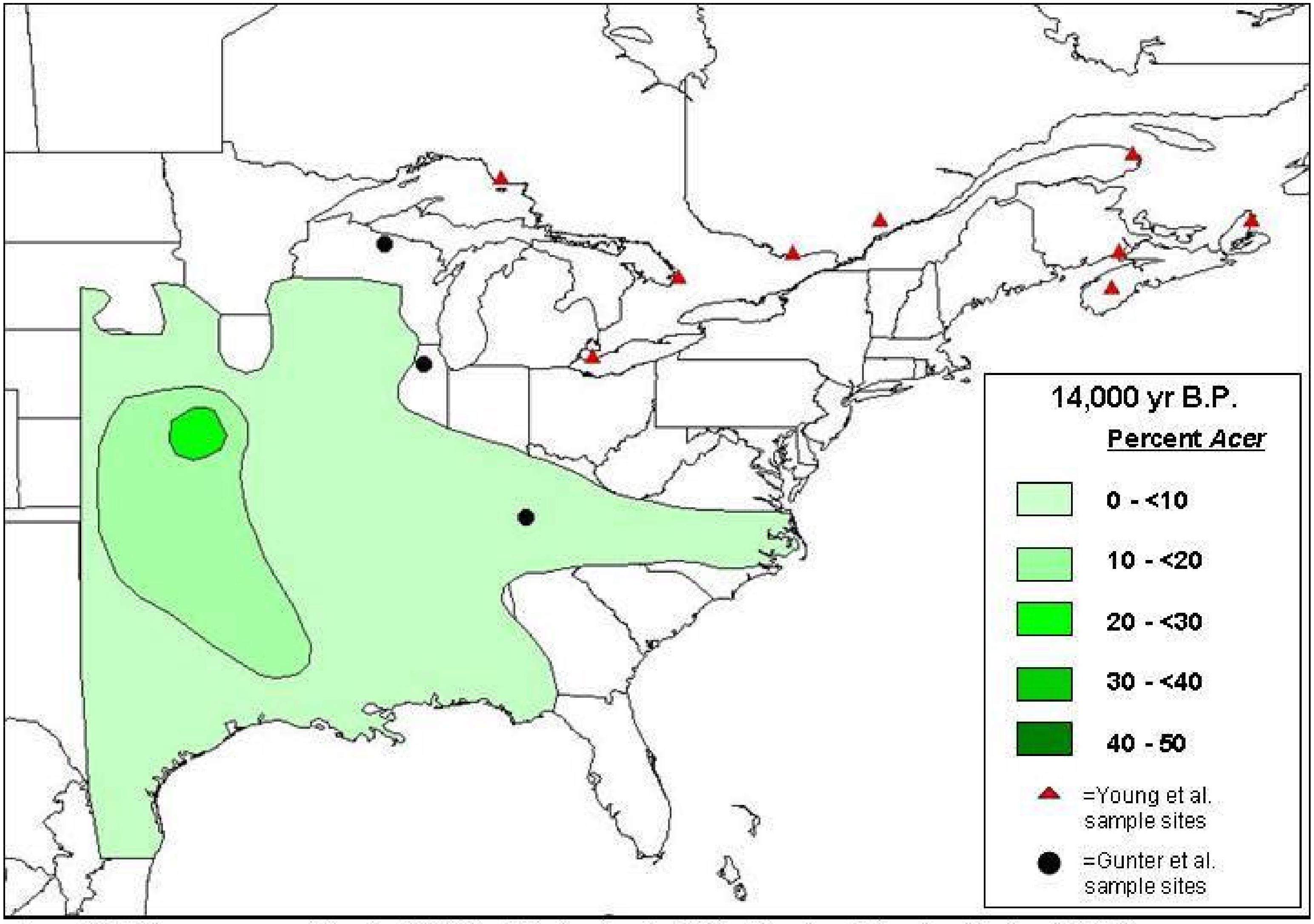

Figure 14. Paleo-range map of *Acer* for 14,000 yr B.P. No elevation limits. Based on Delcourt and Delcourt (1987).

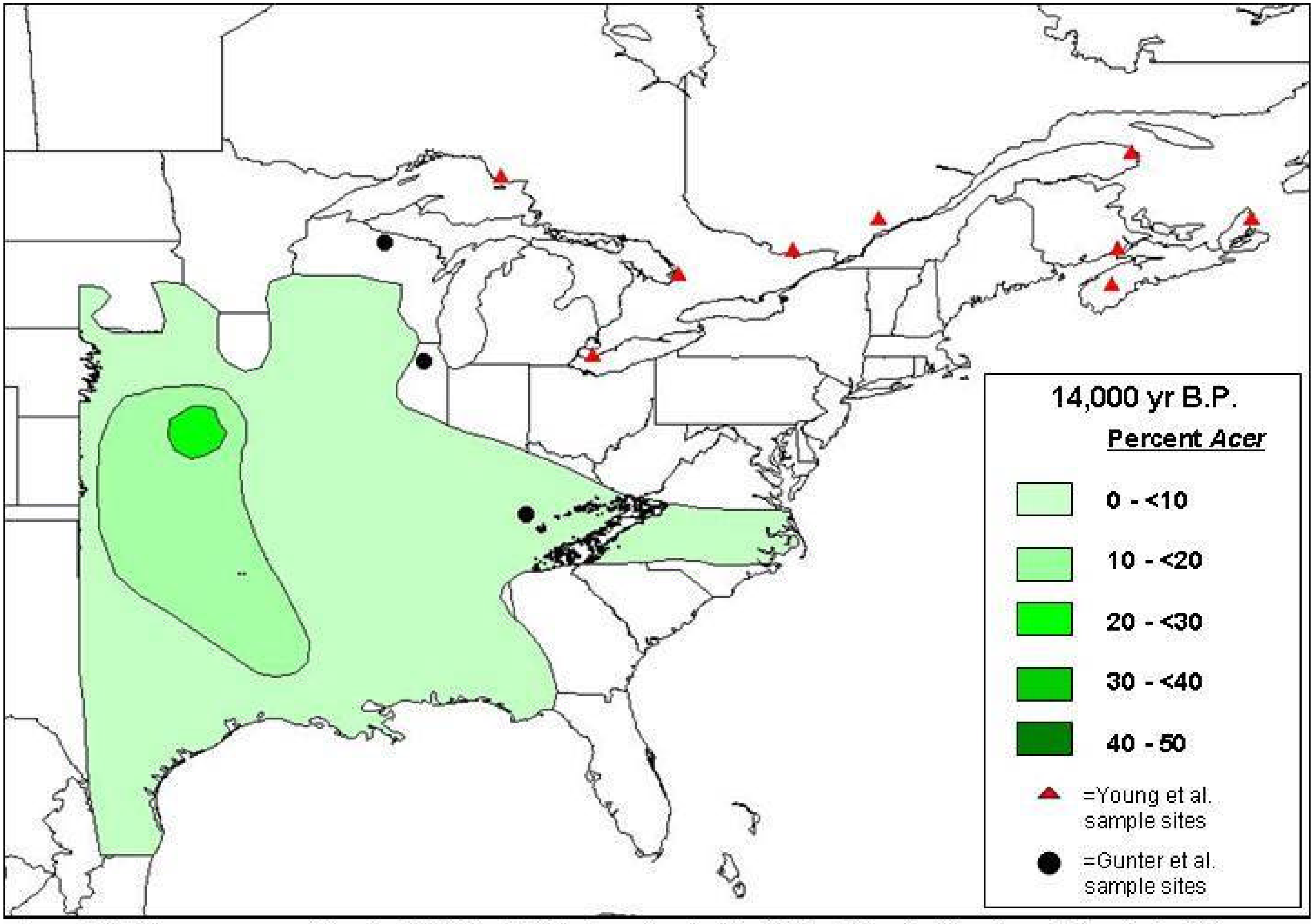

Figure 15. Paleo-range map of *Acer* for 14,000 yr B.P. Northern Appalachian limit = 760 m. Southern Appalachian limit = 760 m. Based on Delcourt and Delcourt (1987).

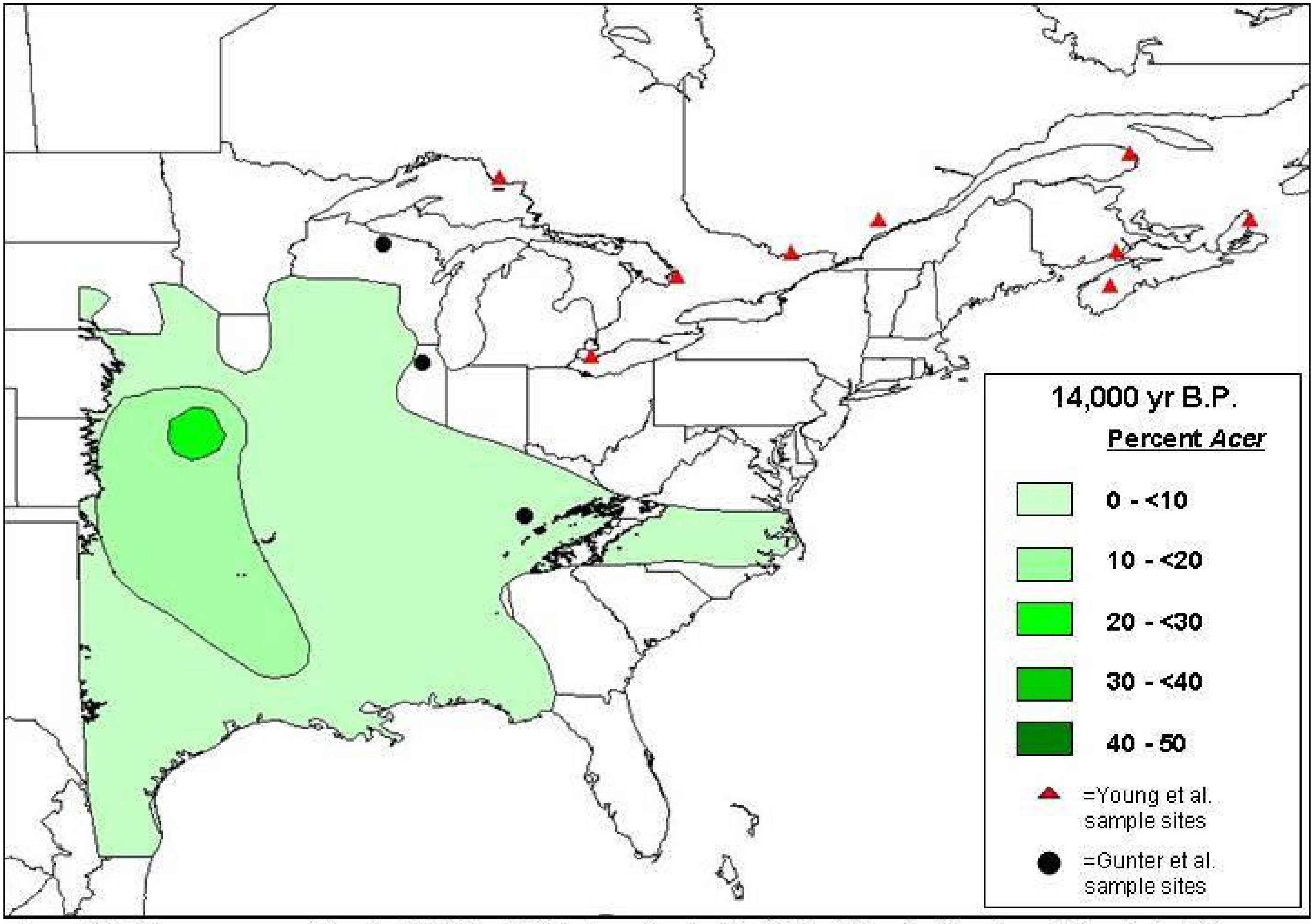

Figure 16. Paleo-range map of *Acer* for 14,000 yr B.P. Northern Appalachian limit = 660 m. Southern Appalachian limit = 660 m. Based on Delcourt and Delcourt (1987).

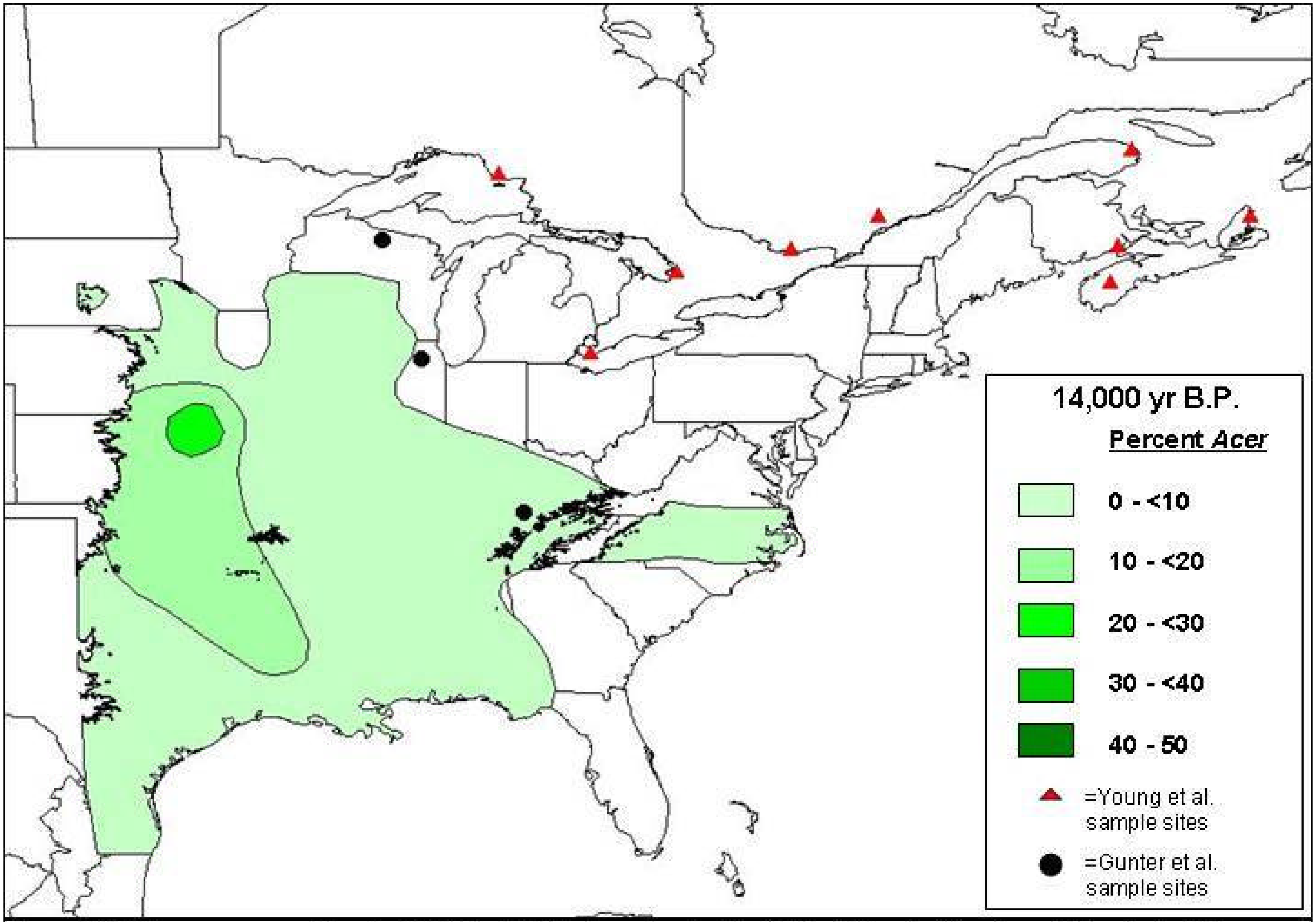

Figure 17. Paleo-range map of *Acer* for 14,000 yr B.P. Northern Appalachian limit = 560 m. Southern Appalachian limit = 560 m. Based on Delcourt and Delcourt (1987).

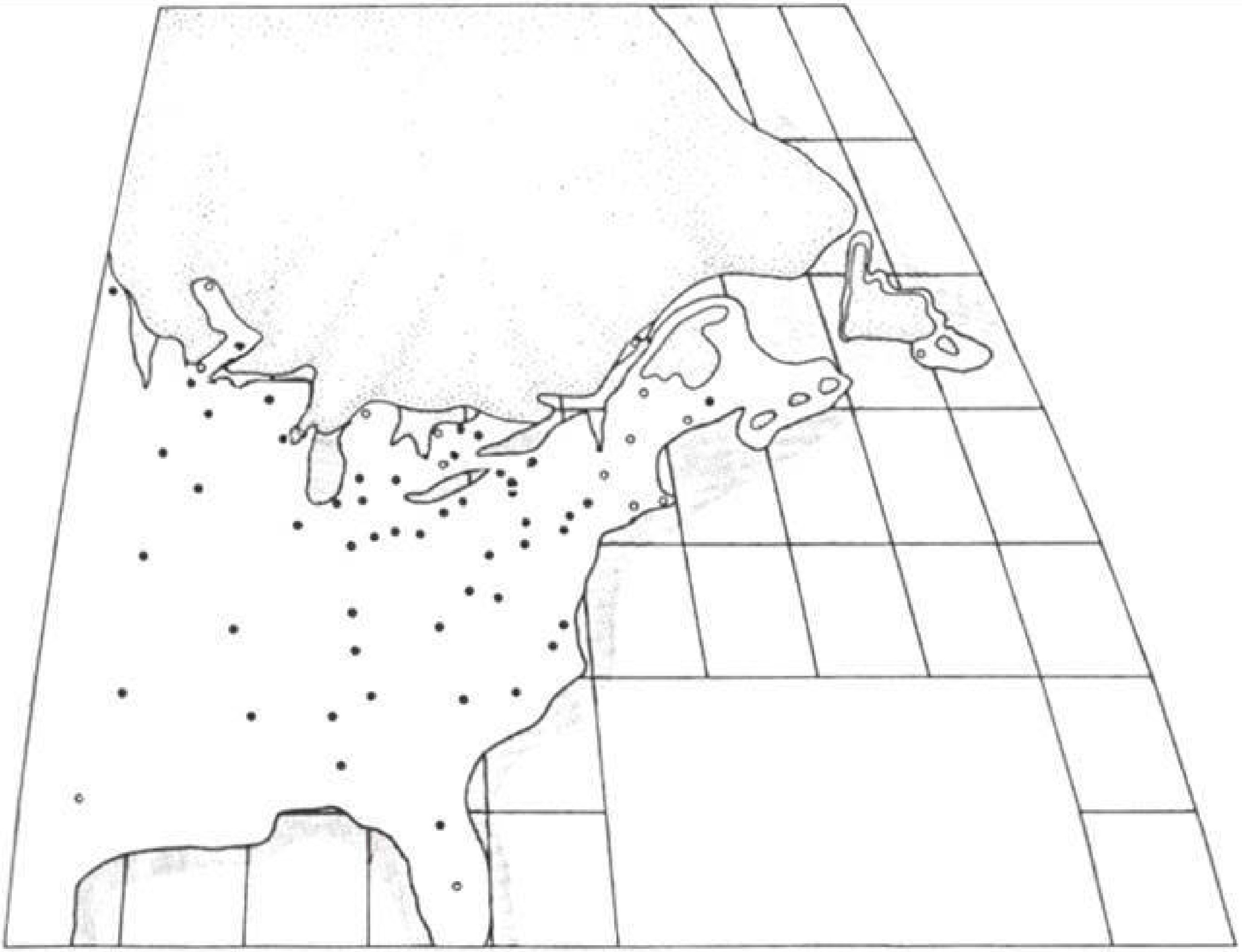

Figure 18. Paleoecological sites in eastern North America for 12,000 yr B.P. Based on Delcourt and Delcourt (1987).

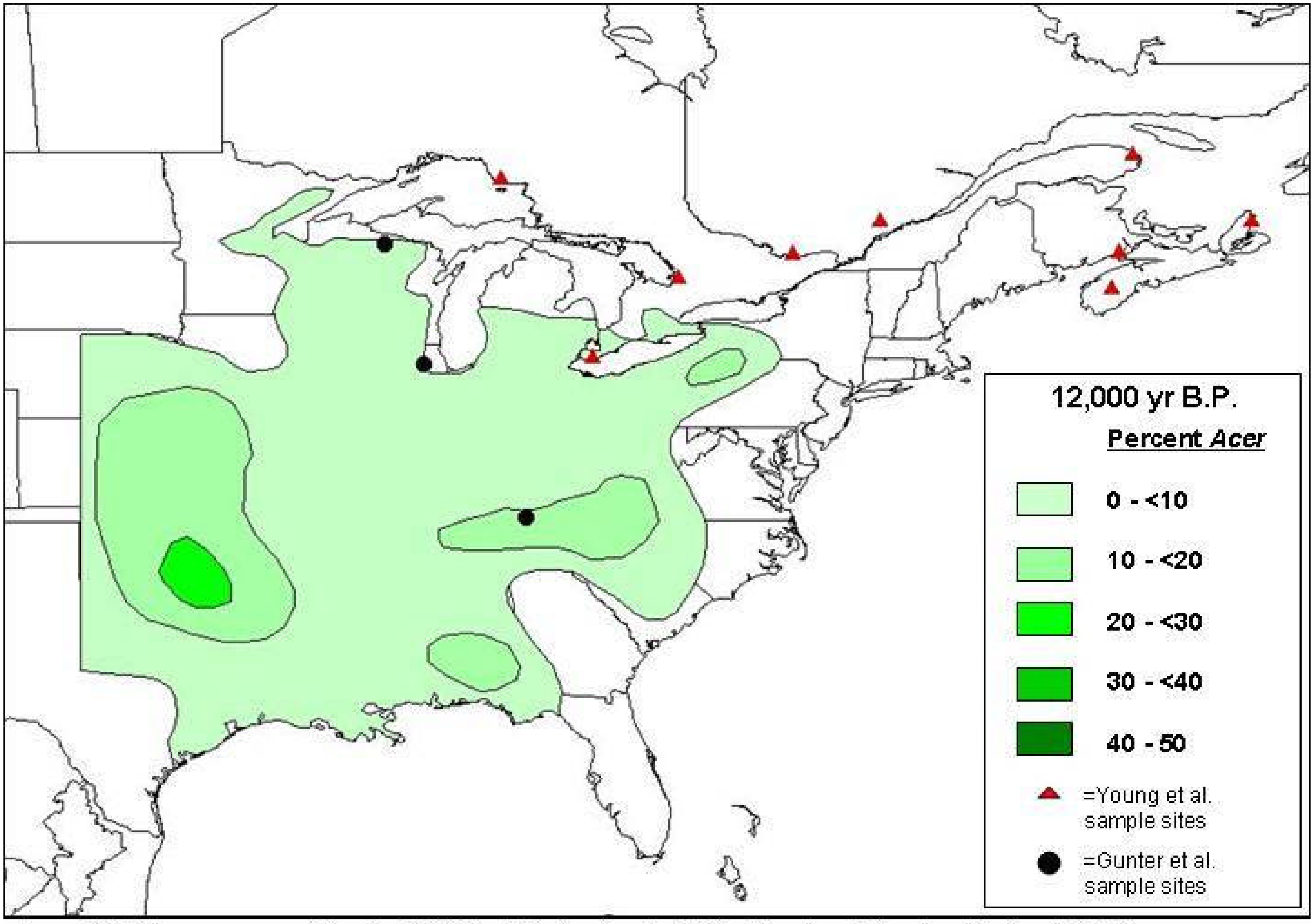

Figure 19. Paleo-range map of *Acer* for 12,000 yr B.P. No elevation limits. Based on Delcourt and Delcourt (1987).

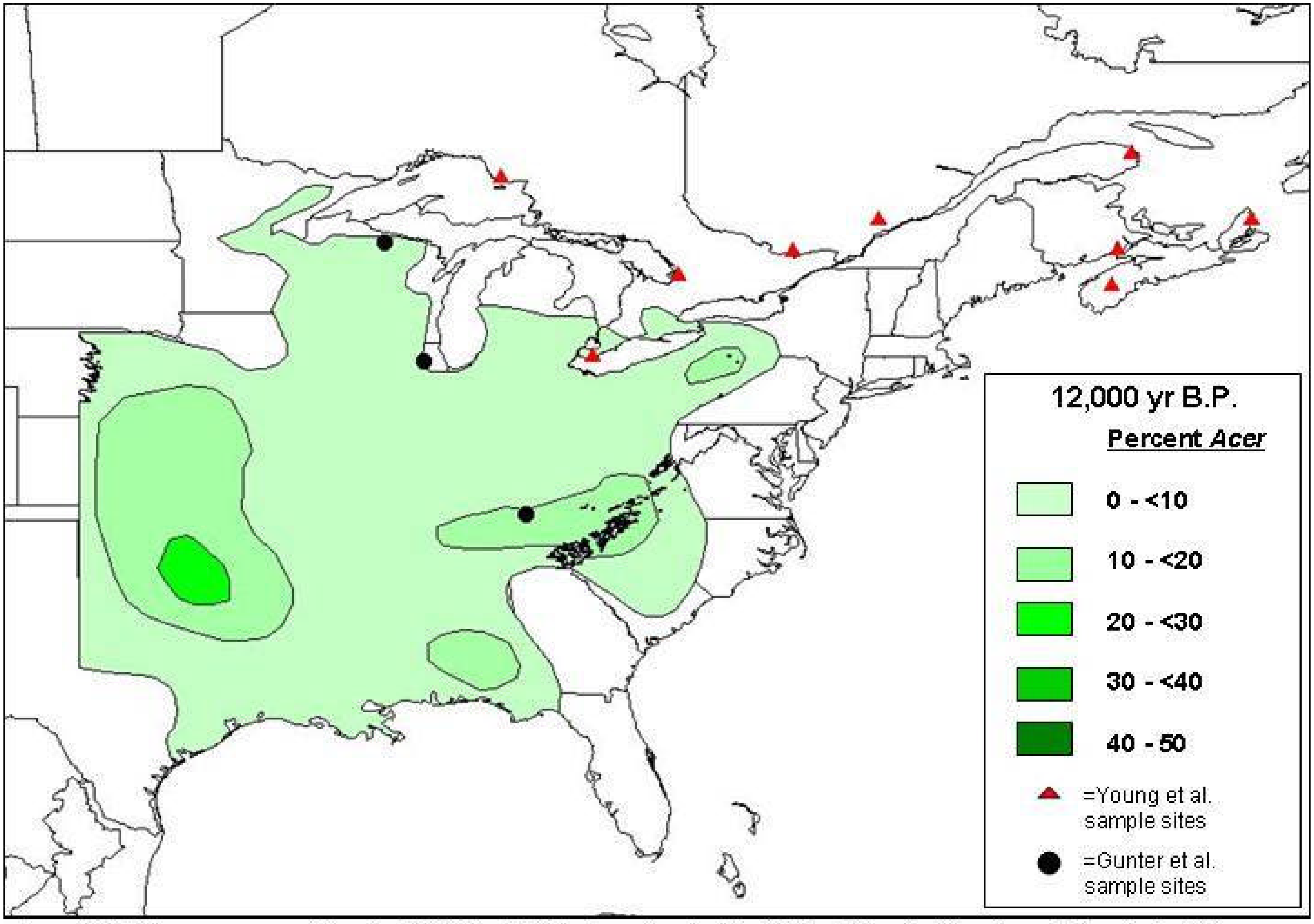

Figure 20. Paleo-range map of *Acer* for 12,000 yr B.P. Northern Appalachian limit = 760 m. Southern Appalachian limit = 990 m. Based on Delcourt and Delcourt (1987).

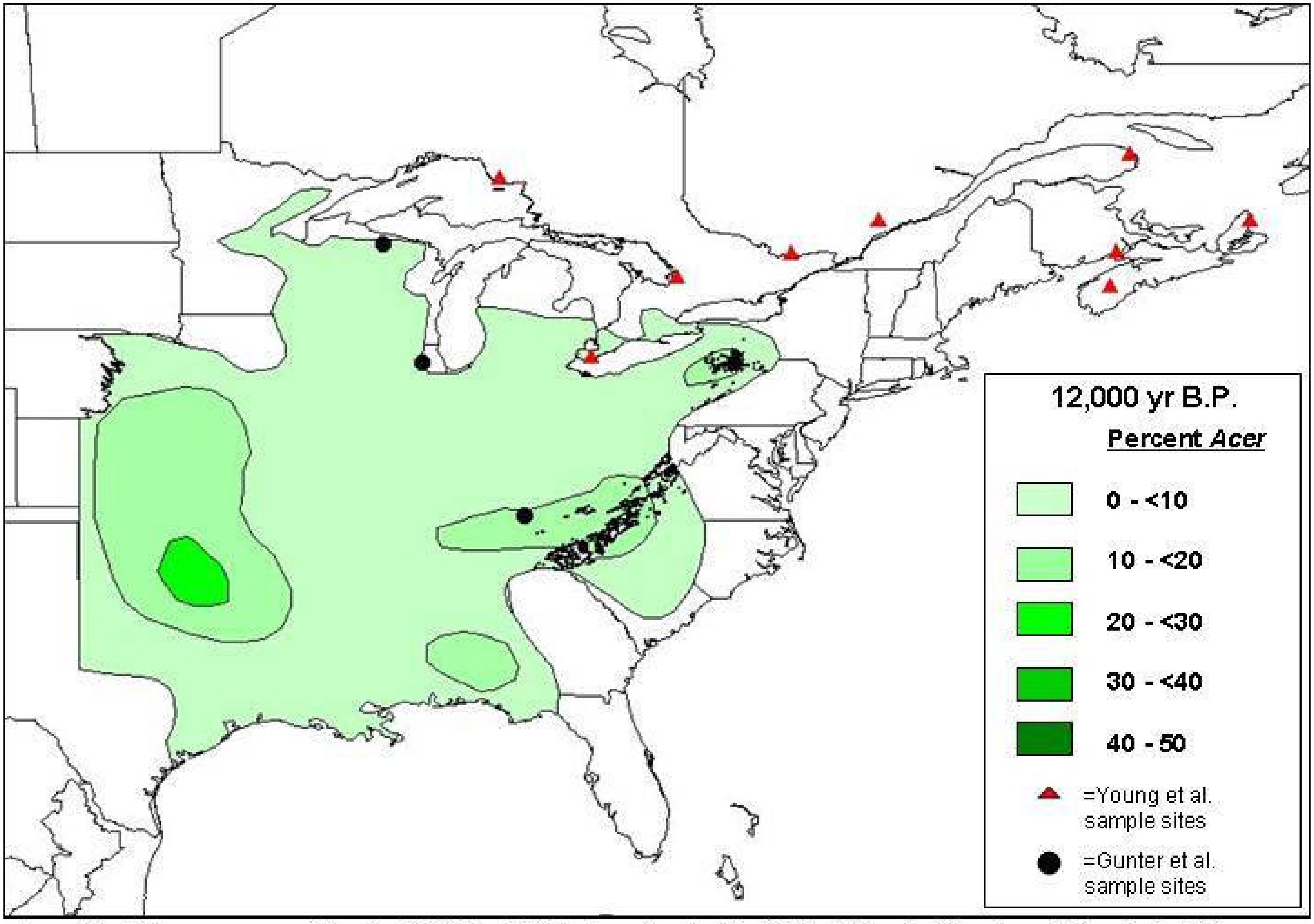

Figure 21. Paleo-range map of *Acer* for 12,000 yr B.P. Northern Appalachian limit = 660 m. Southern Appalachian limit = 890 m. Based on Delcourt and Delcourt (1987).

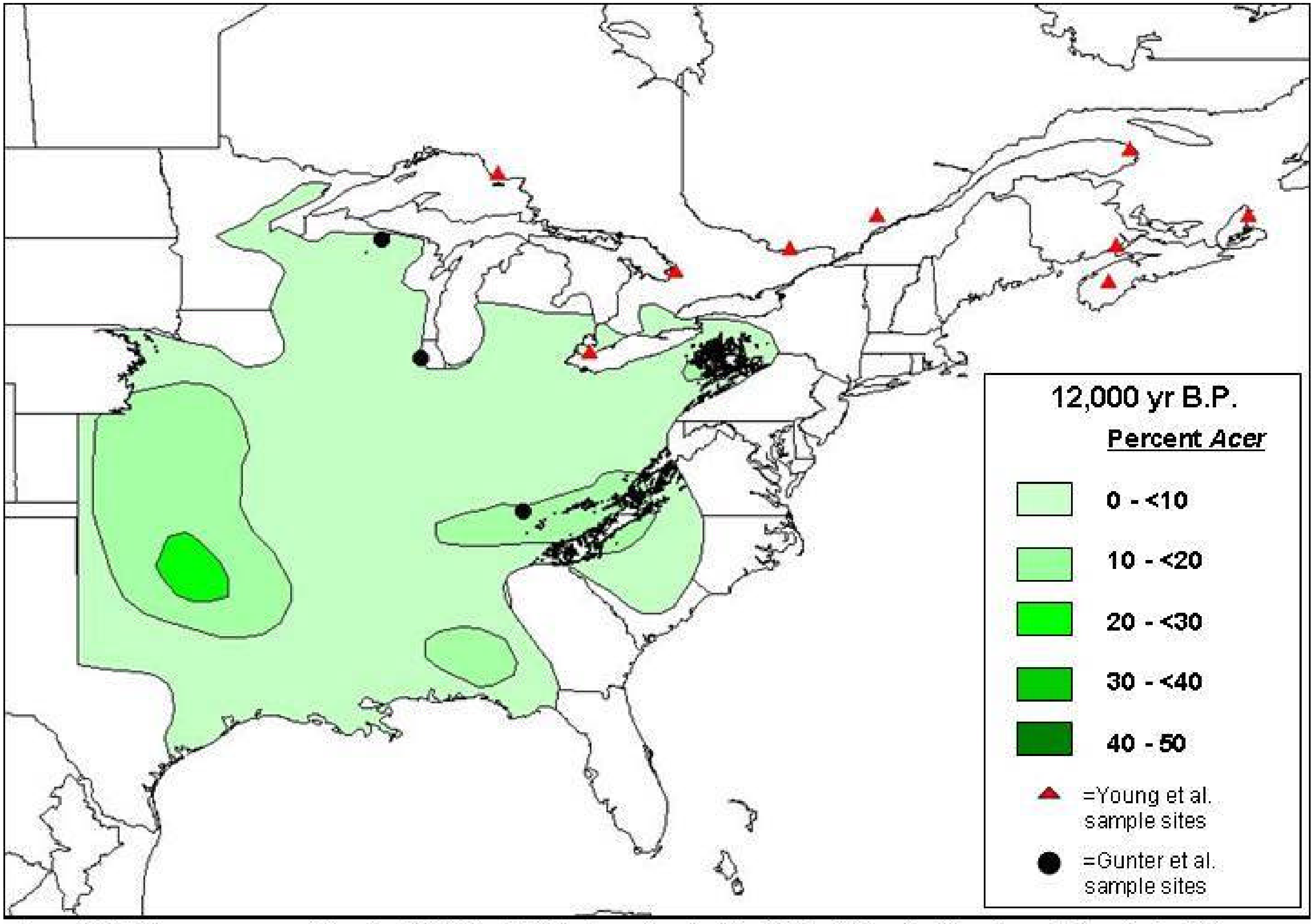

Figure 22. Paleo-range map of *Acer* for 12,000 yr B.P. Northern Appalachian limit = 560 m. Southern Appalachian limit = 790 m. Based on Delcourt and Delcourt (1987).

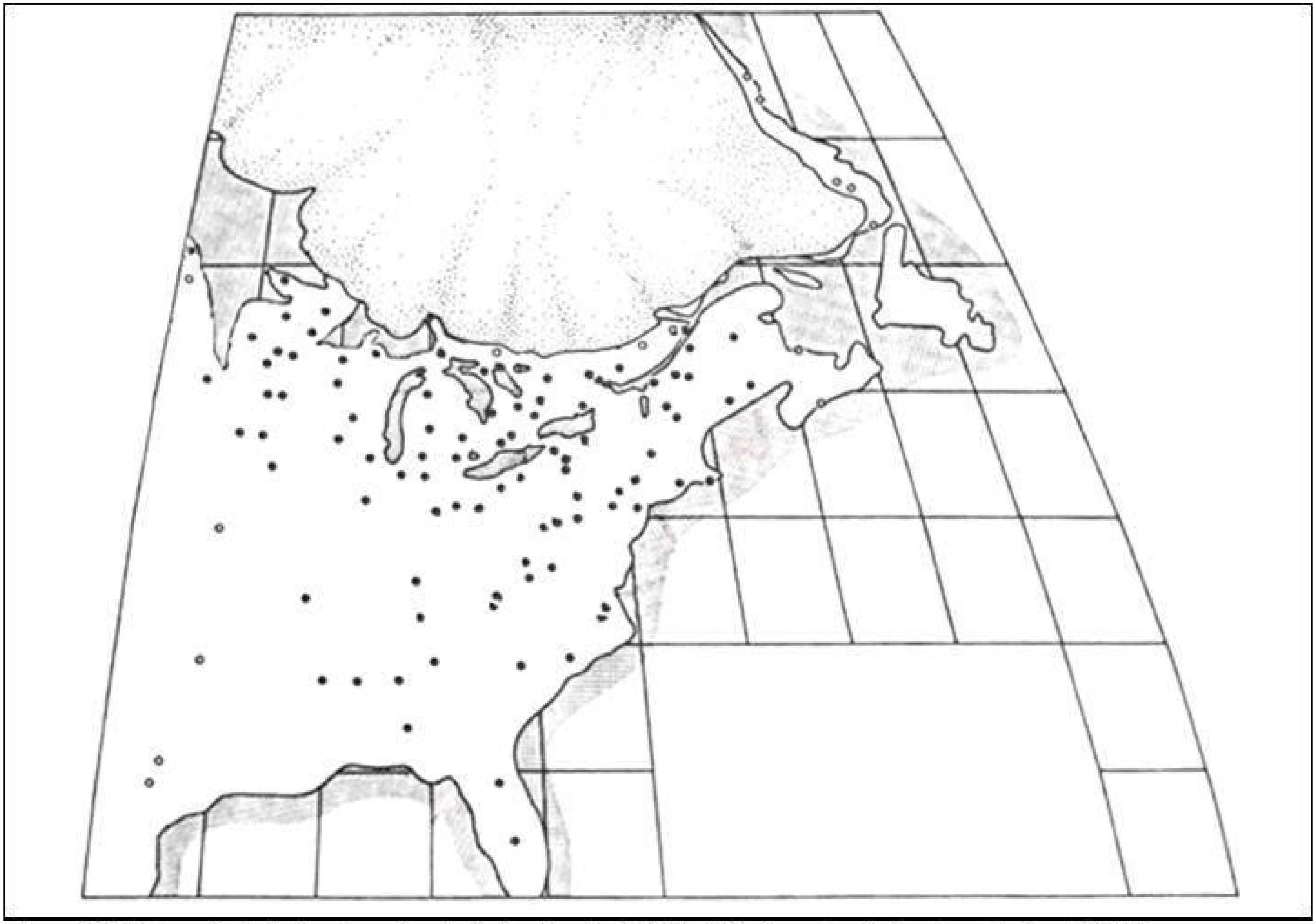

Figure 23. Paleoecological sites in eastern North America for 10,000 yr B.P. Based on Delcourt and Delcourt (1987).

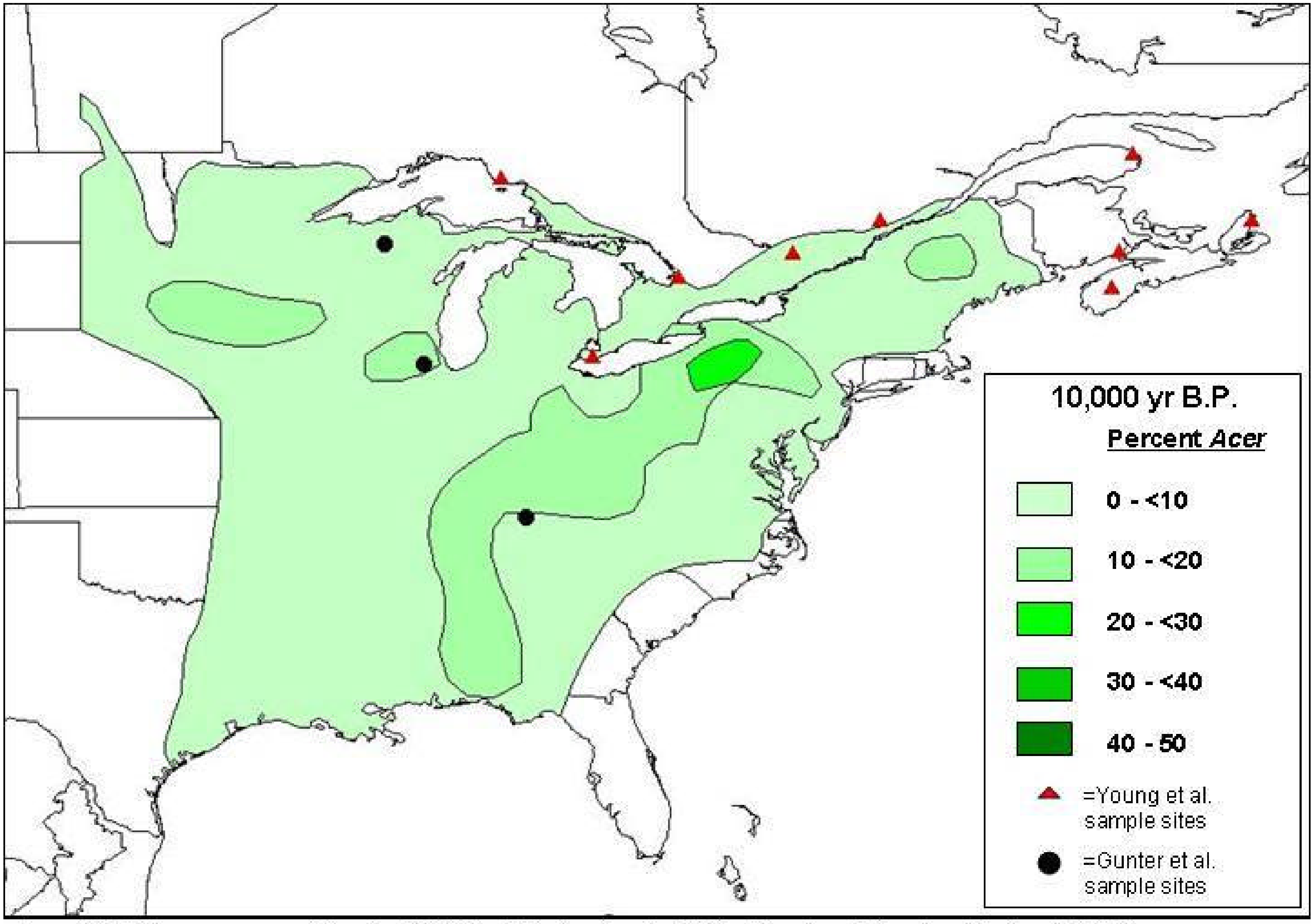

Figure 24. Paleo-range map of *Acer* for 10,000 yr B.P. No elevation limits. Based on Delcourt and Delcourt (1987).

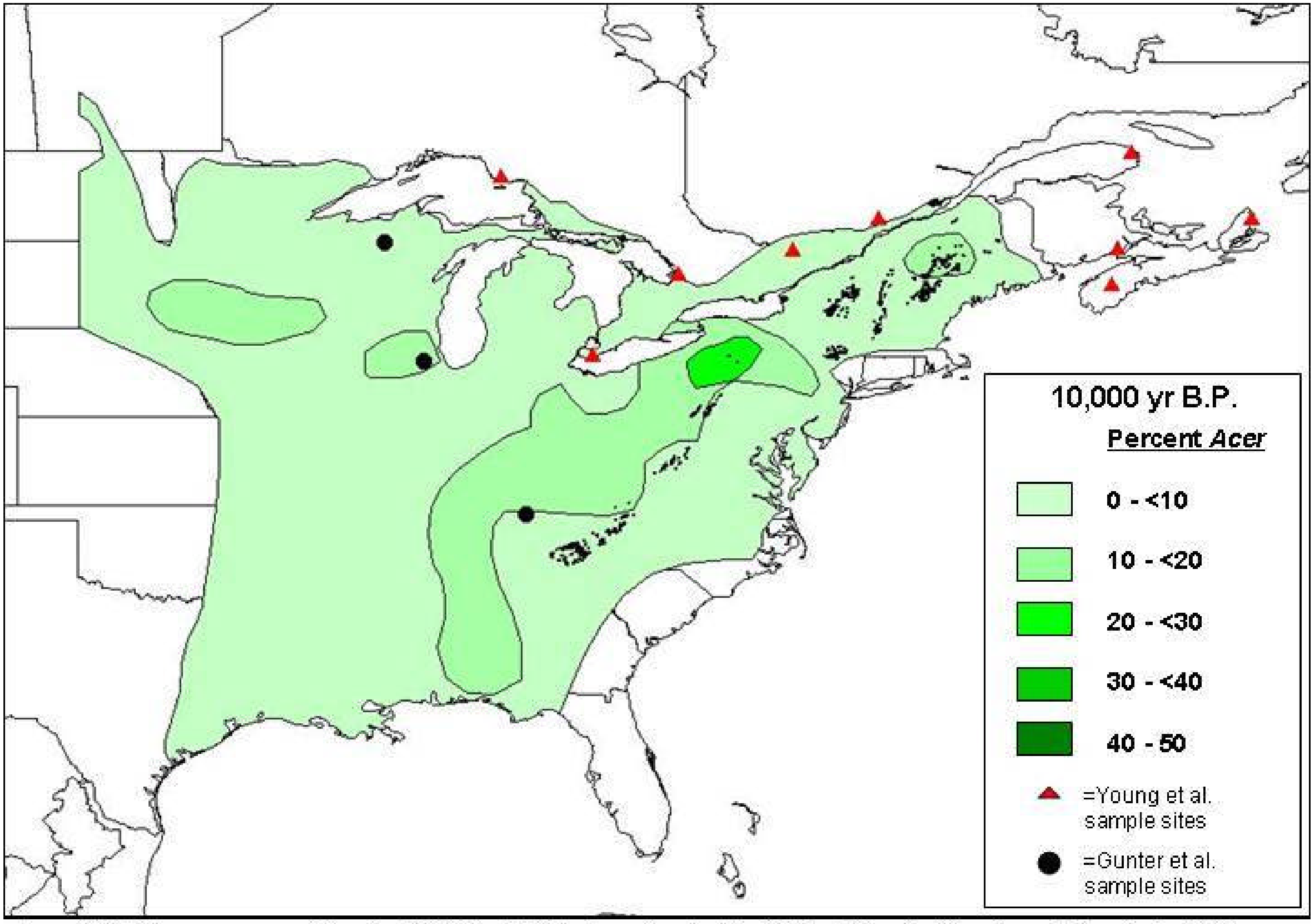

Figure 25. Paleo-range map of *Acer* for 10,000 yr B.P. Northern Appalachian limit = 760 m. Southern Appalachian limit = 1220 m. Based on Delcourt and Delcourt (1987).

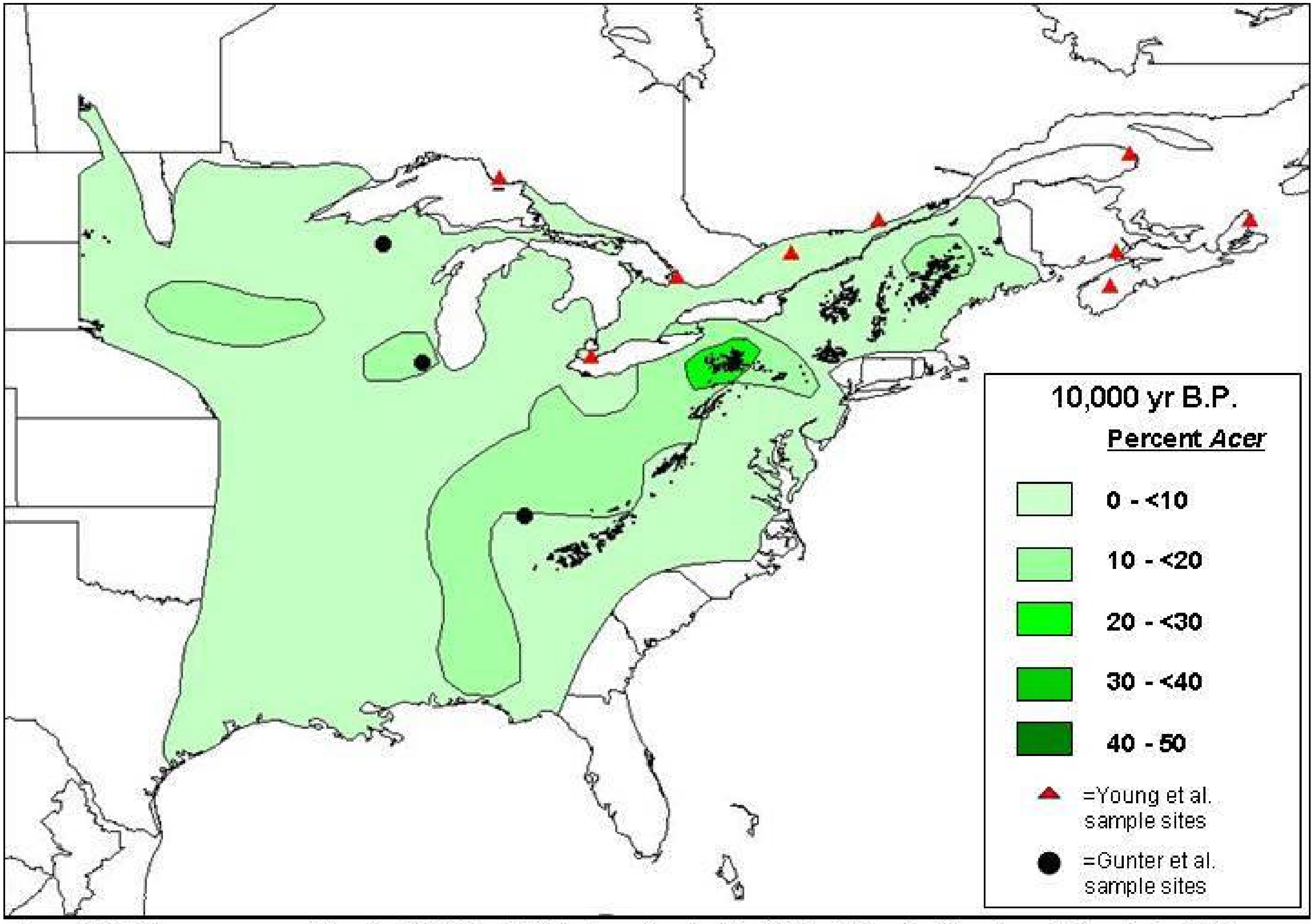

Figure 26. Paleo-range map of *Acer* for 10,000 yr B.P. Northern Appalachian limit = 660 m. Southern Appalachian limit = 1120 m. Based on Delcourt and Delcourt (1987).

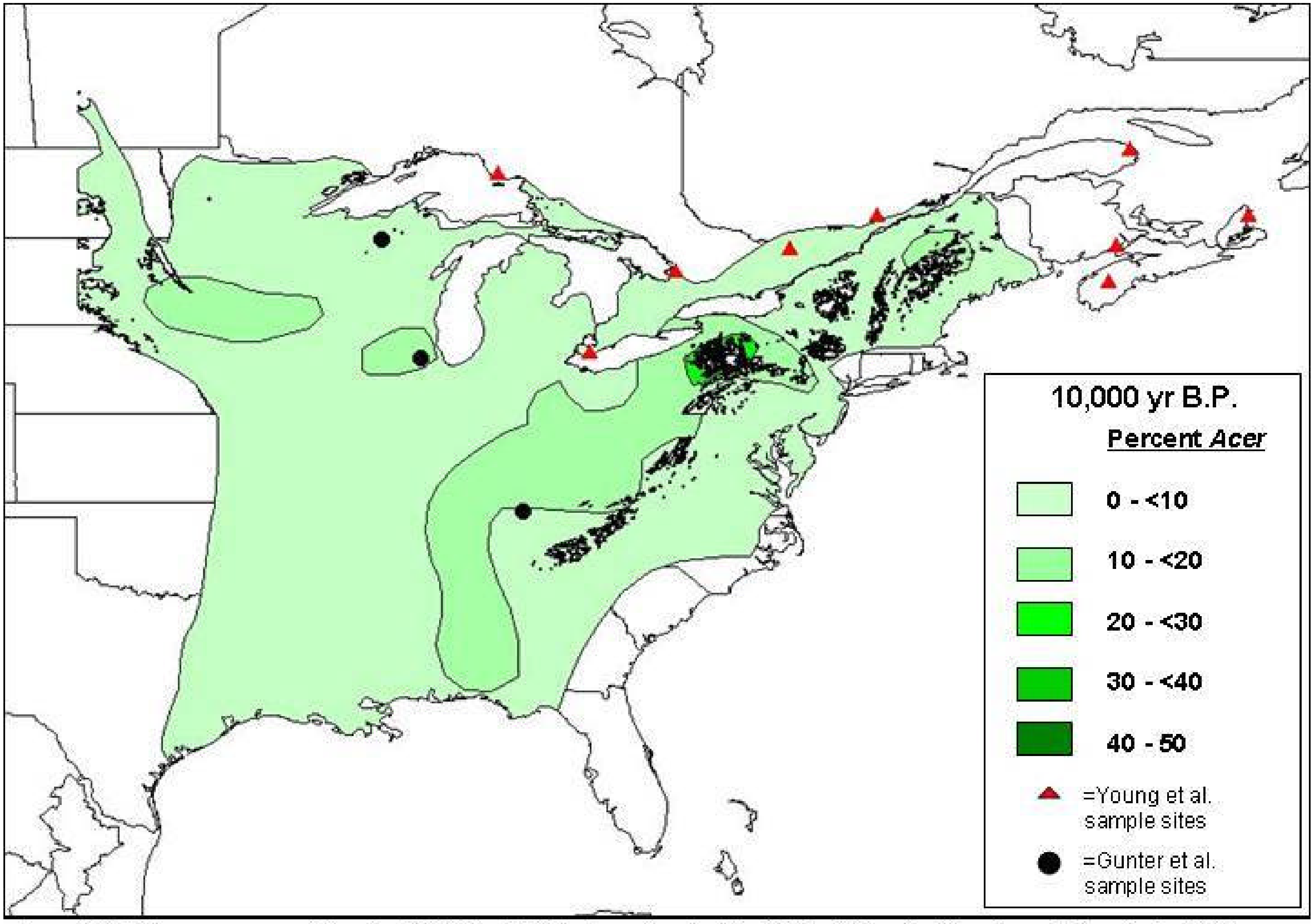

Figure 27. Paleo-range map of *Acer* for 10,000 yr B.P. Northern Appalachian limit = 560 m. Southern Appalachian limit = 1020 m. Based on Delcourt and Delcourt (1987).

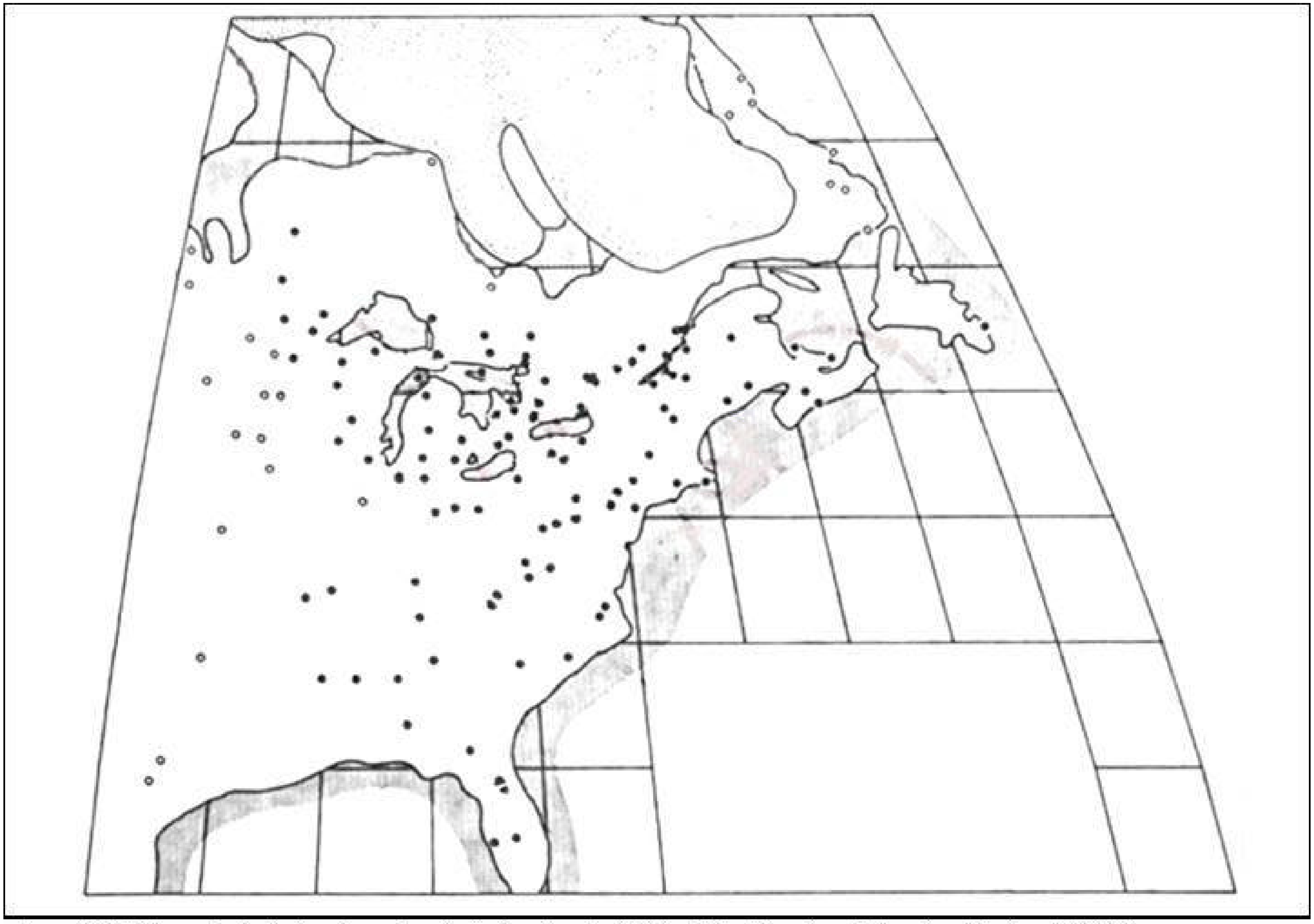

Figure 28. Paleoecological sites in eastern North America for 8,000 yr B.P. Based on Delcourt and Delcourt (1987).

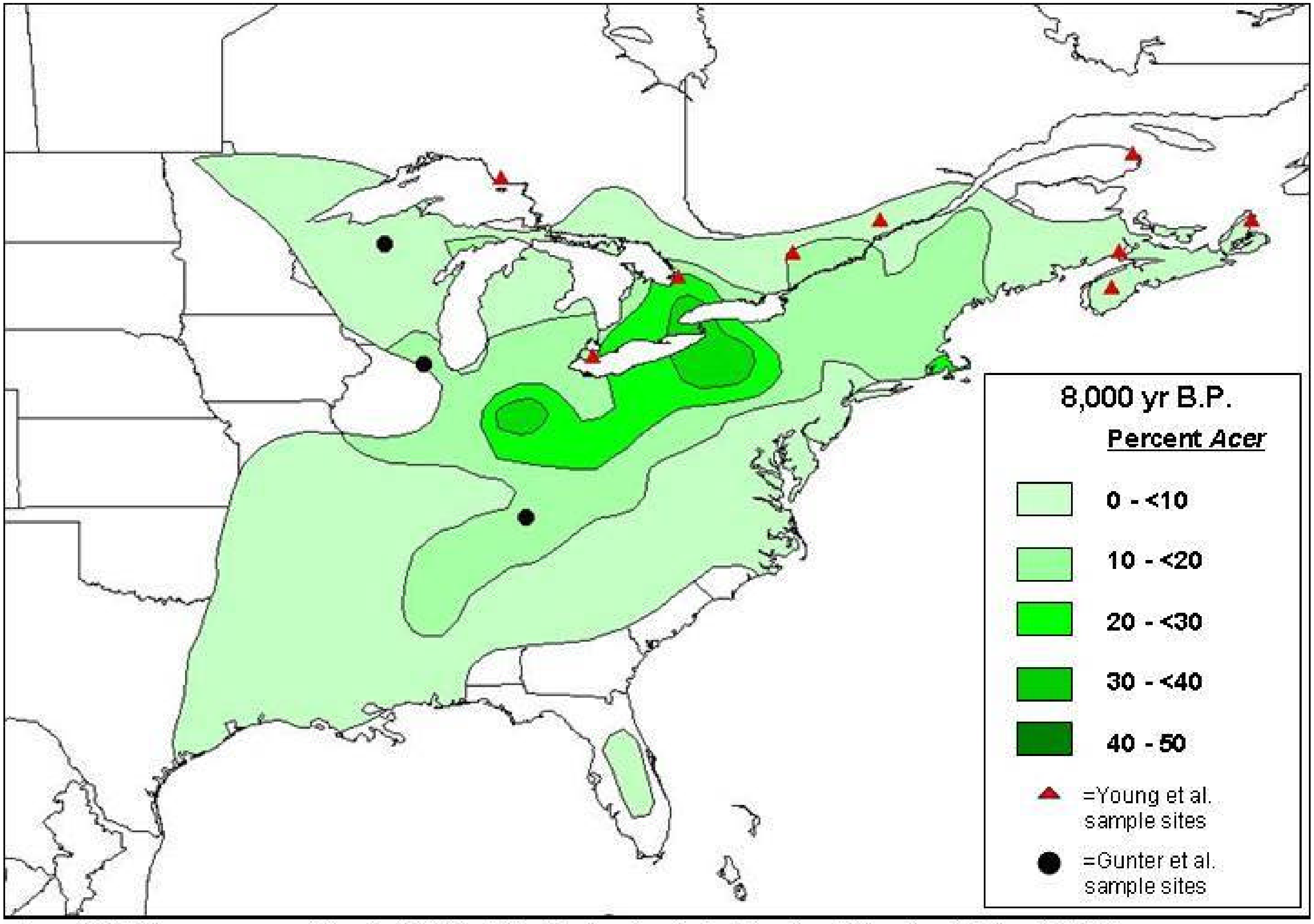

Figure 29. Paleo-range map of *Acer* for 8,000 yr B.P. No elevation limits. Based on Delcourt and Delcourt (1987).

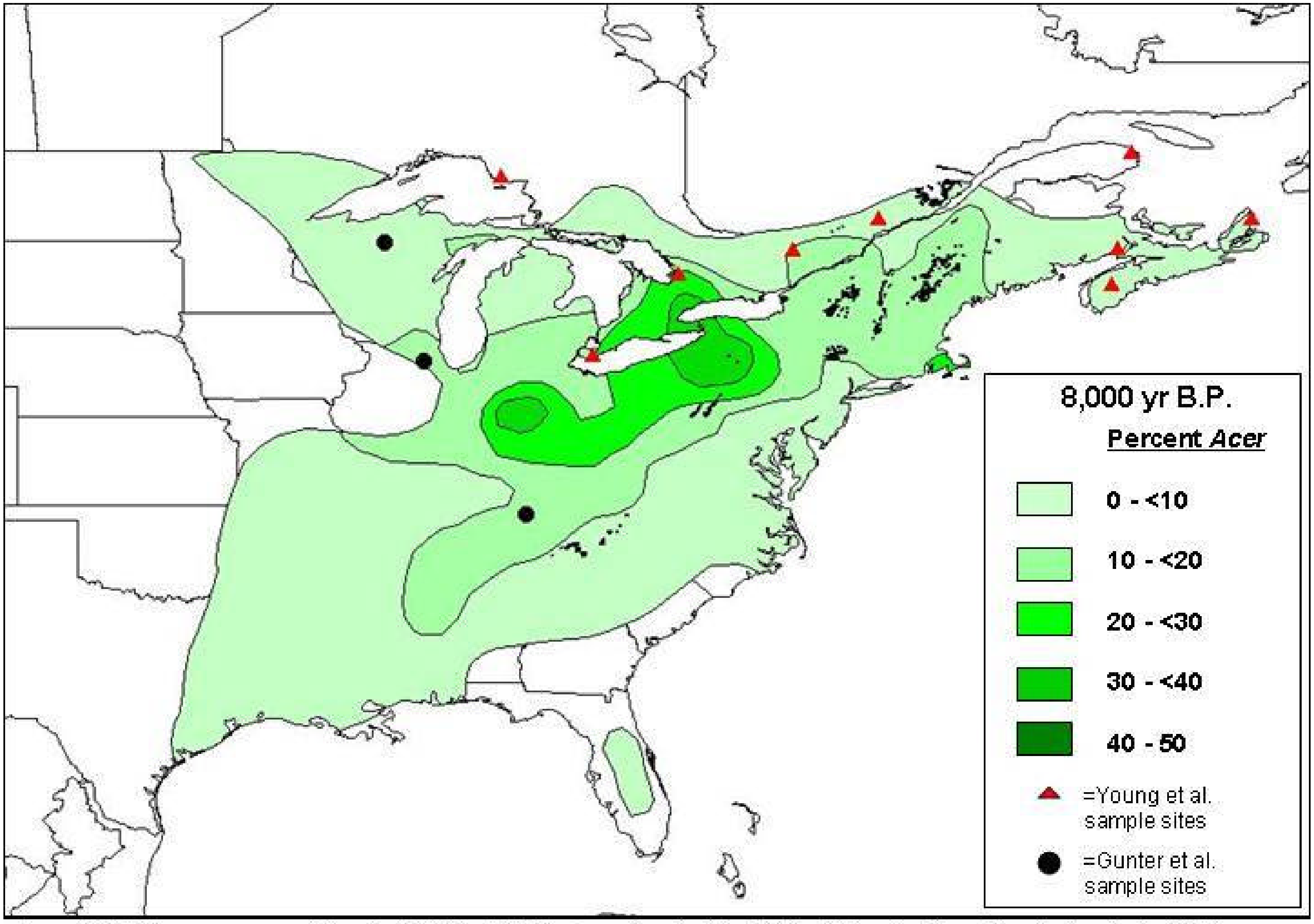

Figure 30. Paleo-range map of *Acer* for 8,000 yr B.P. Northern Appalachian limit = 760 m. Southern Appalachian limit = 1450 m. Based on Delcourt and Delcourt (1987).

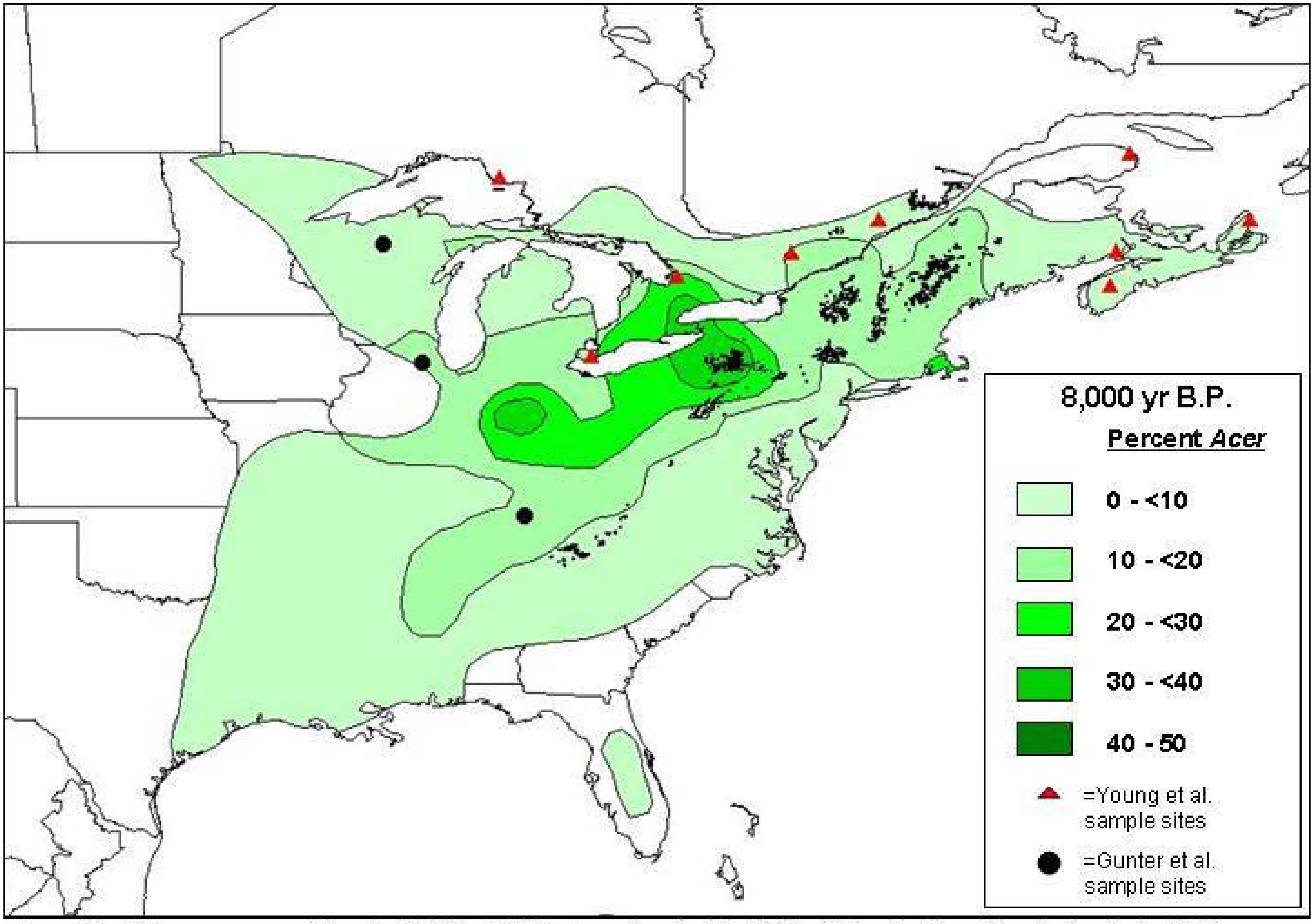

Figure 31. Paleo-range map of *Acer* for 8,000 yr B.P. Northern Appalachian limit = 660 m. Southern Appalachian limit = 1350 m. Based on Delcourt and Delcourt (1987).

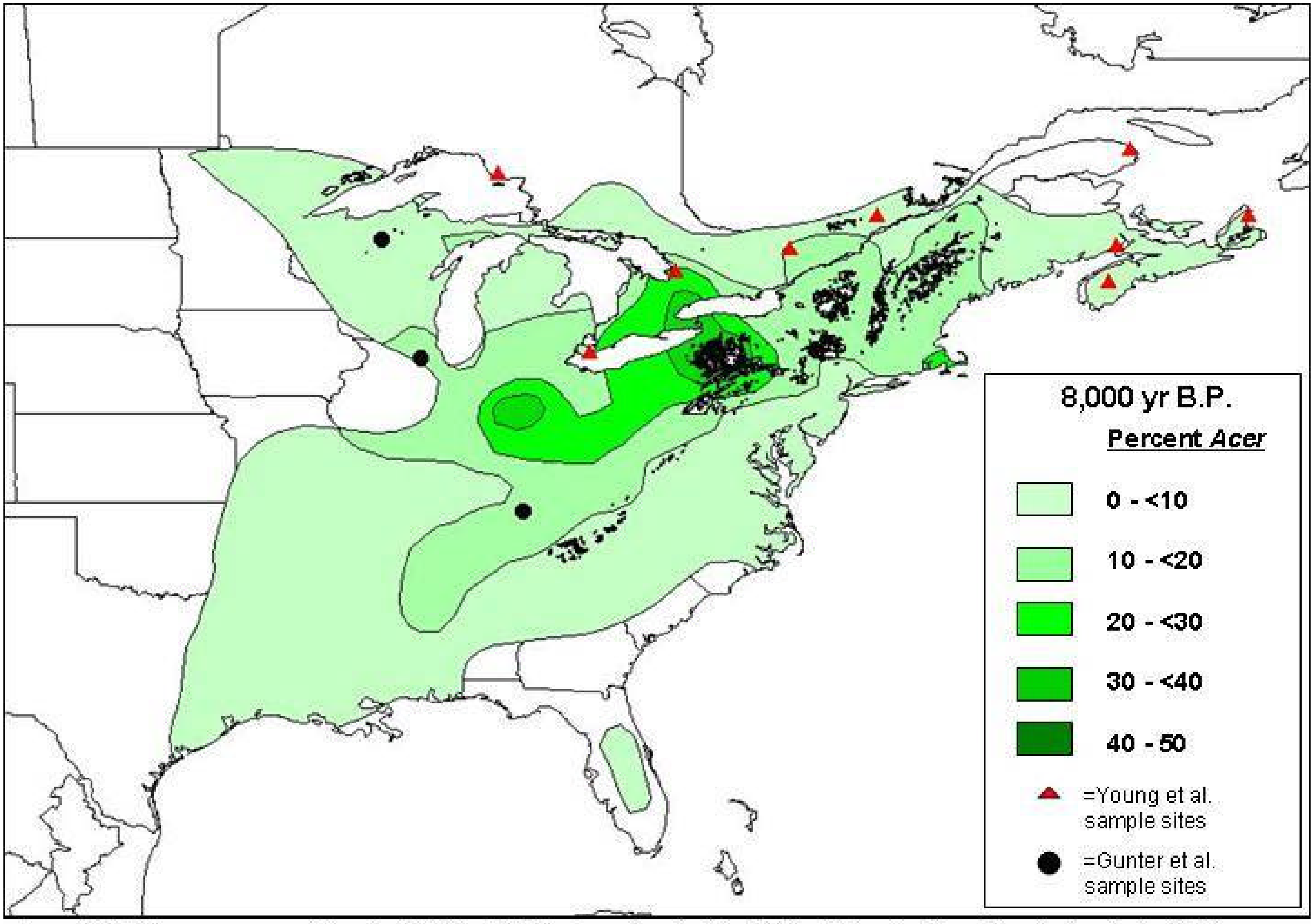

Figure 32. Paleo-range map of *Acer* for 8,000 yr B.P. Northern Appalachian limit = 560 m. Southern Appalachian limit = 1250 m. Based on Delcourt and Delcourt (1987).

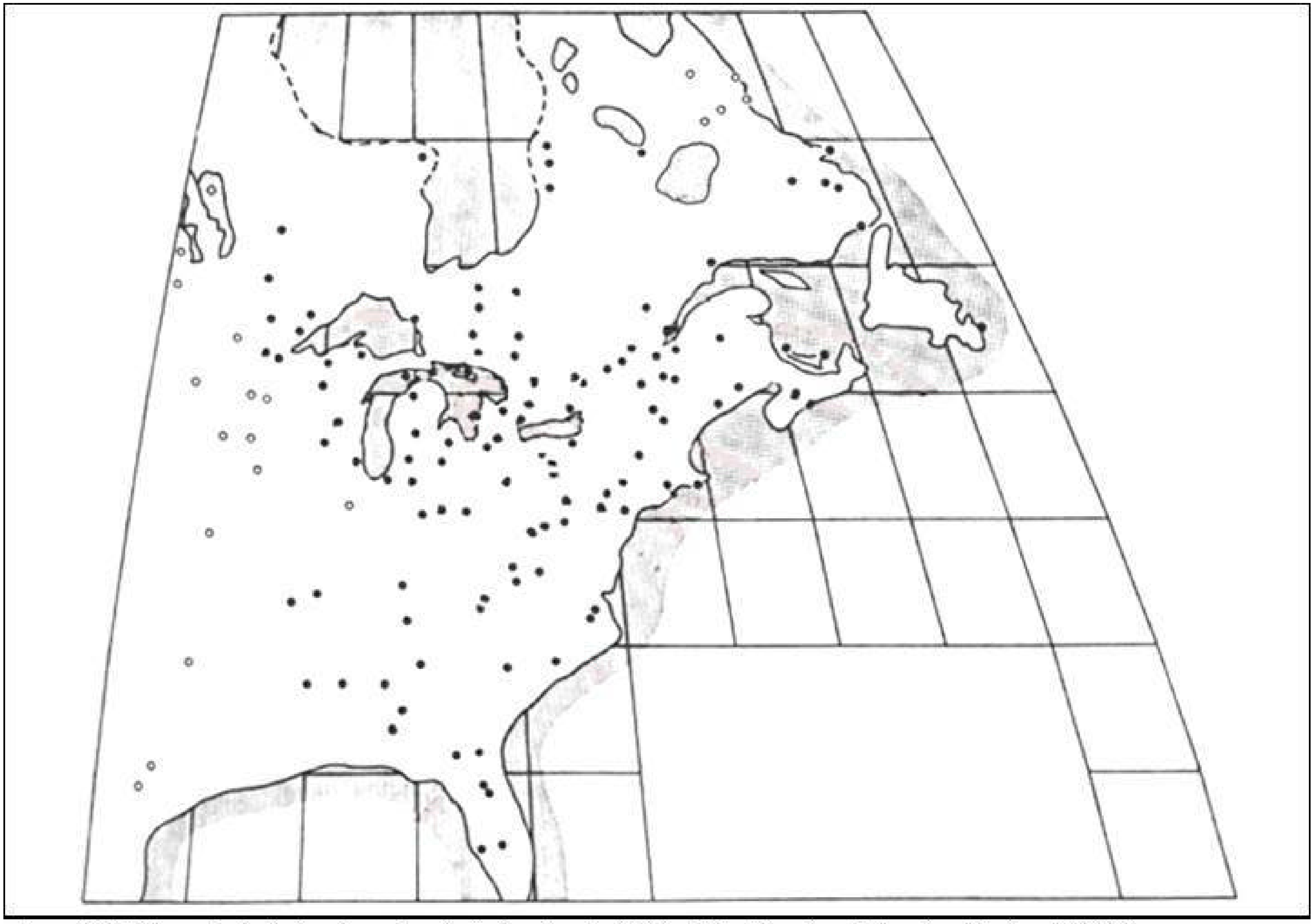

Figure 33. Paleoecological sites in eastern North America for 6,000 yr B.P. Based on Delcourt and Delcourt (1987).

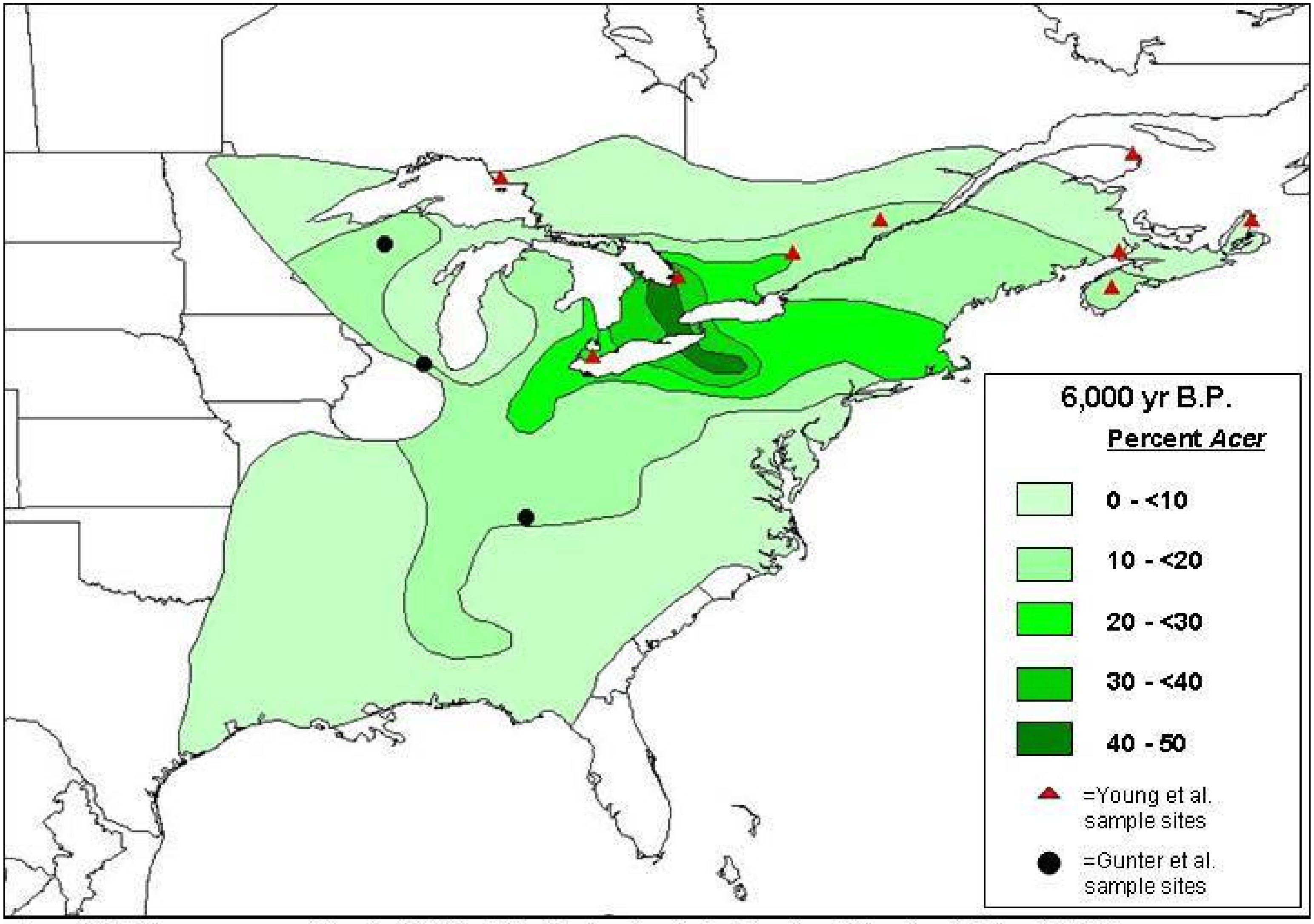

Figure 34. Paleo-range map of *Acer* for 6,000 yr B.P. No elevation limits. Based on Delcourt and Delcourt (1987).

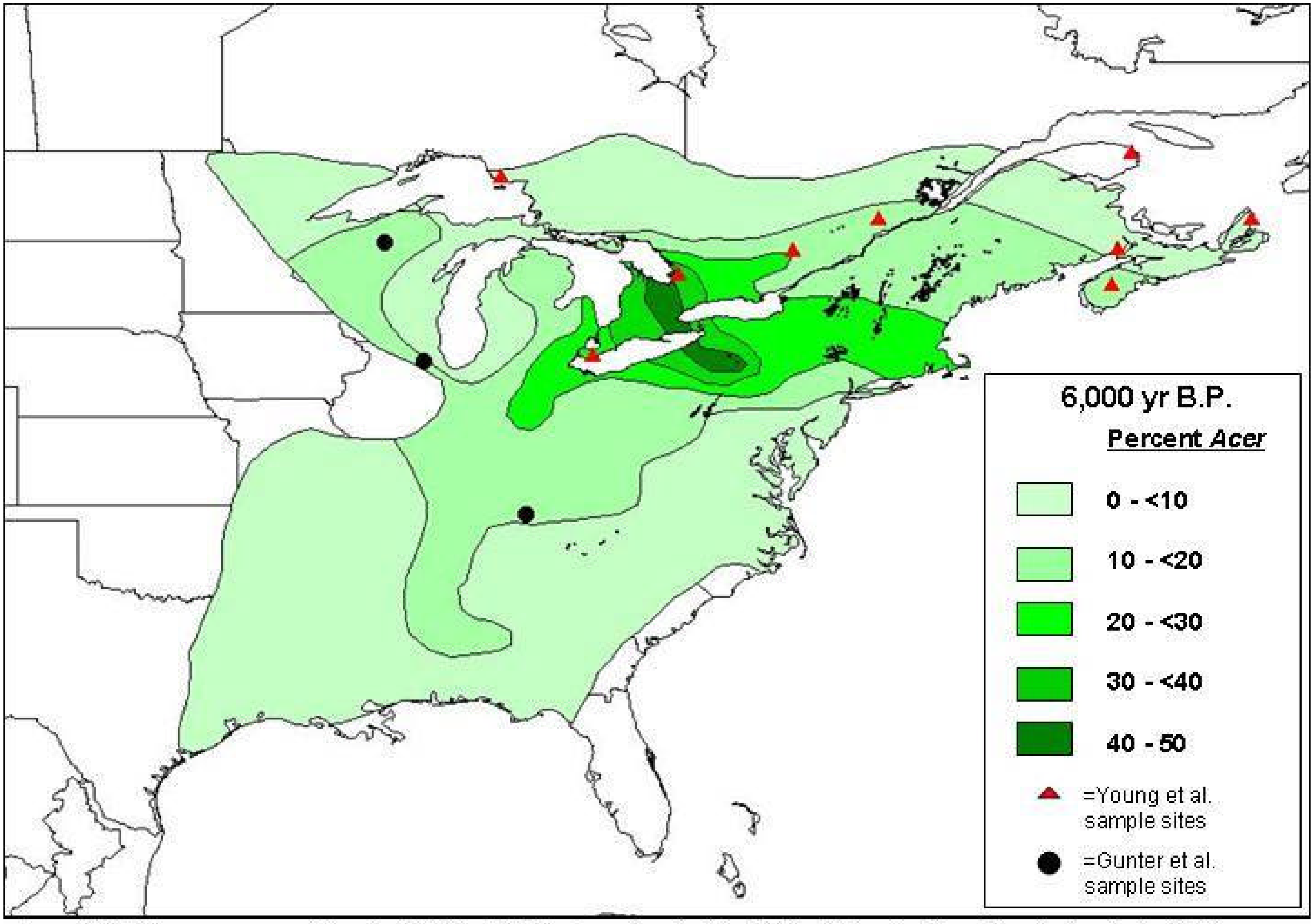

Figure 35. Paleo-range map of *Acer* for 6,000 yr B.P. Northern Appalachian limit = 760 m. Southern Appalachian limit = 1680 m. Based on Delcourt and Delcourt (1987).

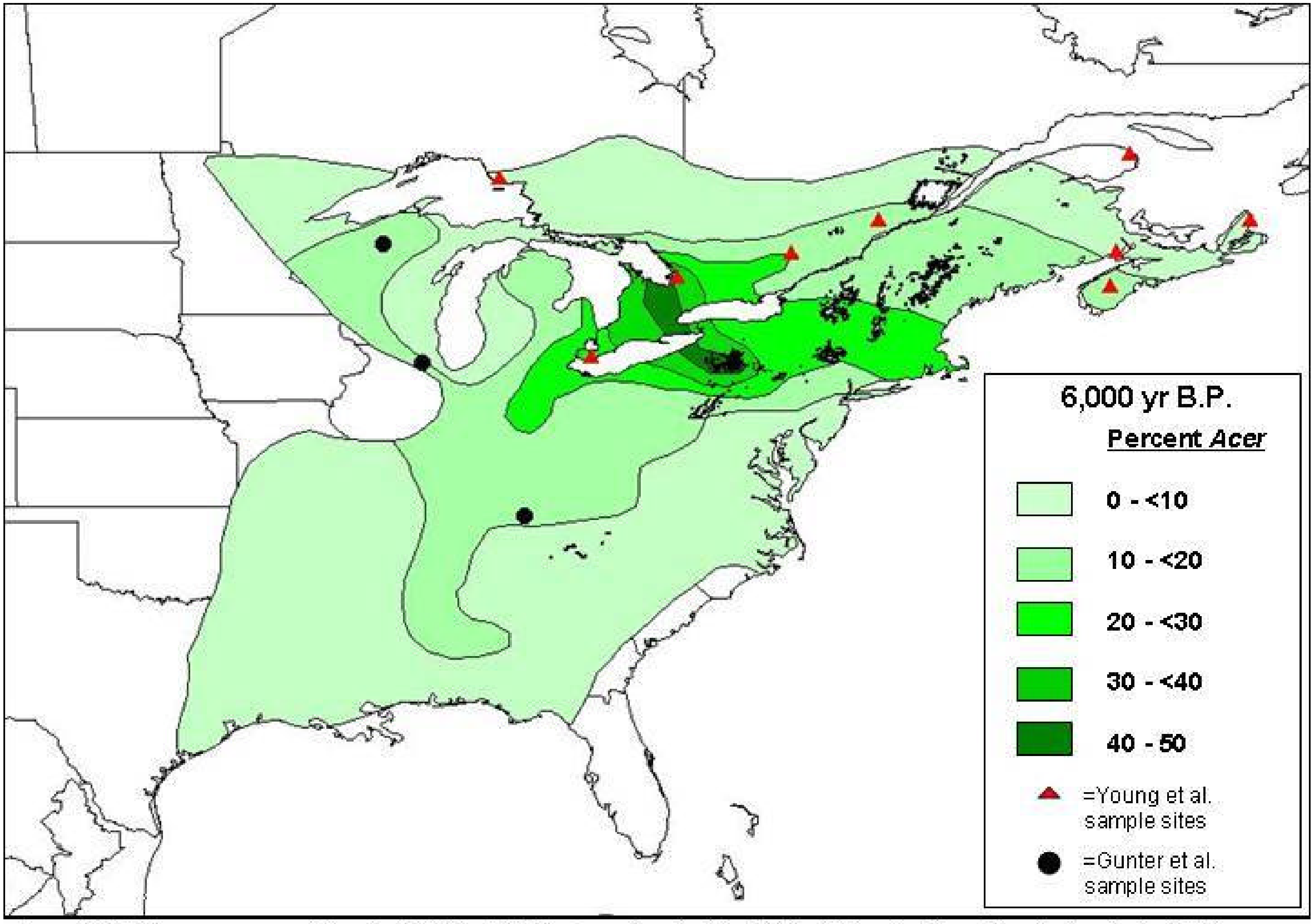

Figure 36. Paleo-range map of *Acer* for 6,000 yr B.P. Northern Appalachian limit = 660 m. Southern Appalachian limit = 1580 m. Based on Delcourt and Delcourt (1987).

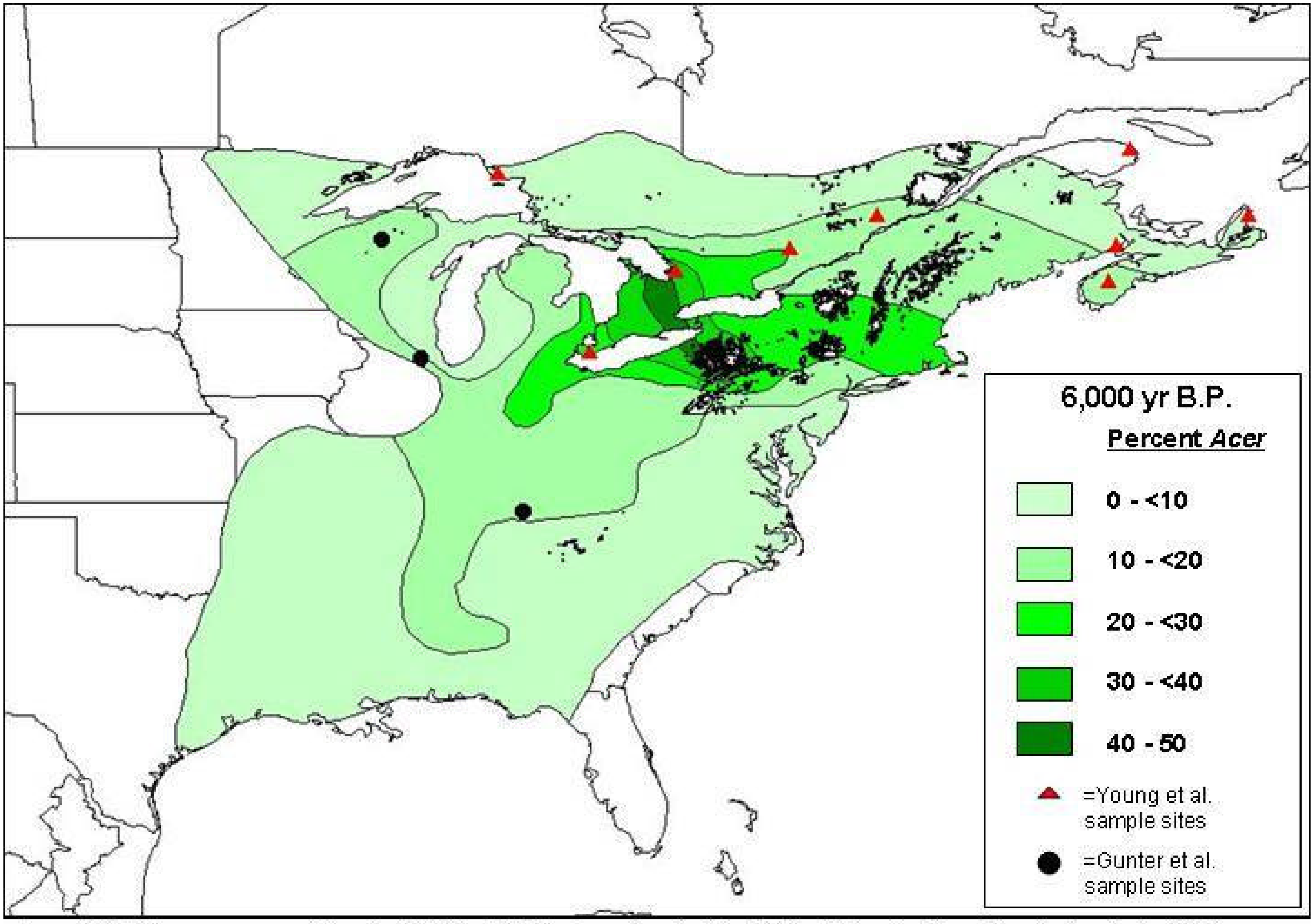

Figure 37. Paleo-range map of *Acer* for 6,000 yr B.P. Northern Appalachian limit = 560 m. Southern Appalachian limit = 1480 m. Based on Delcourt and Delcourt (1987).

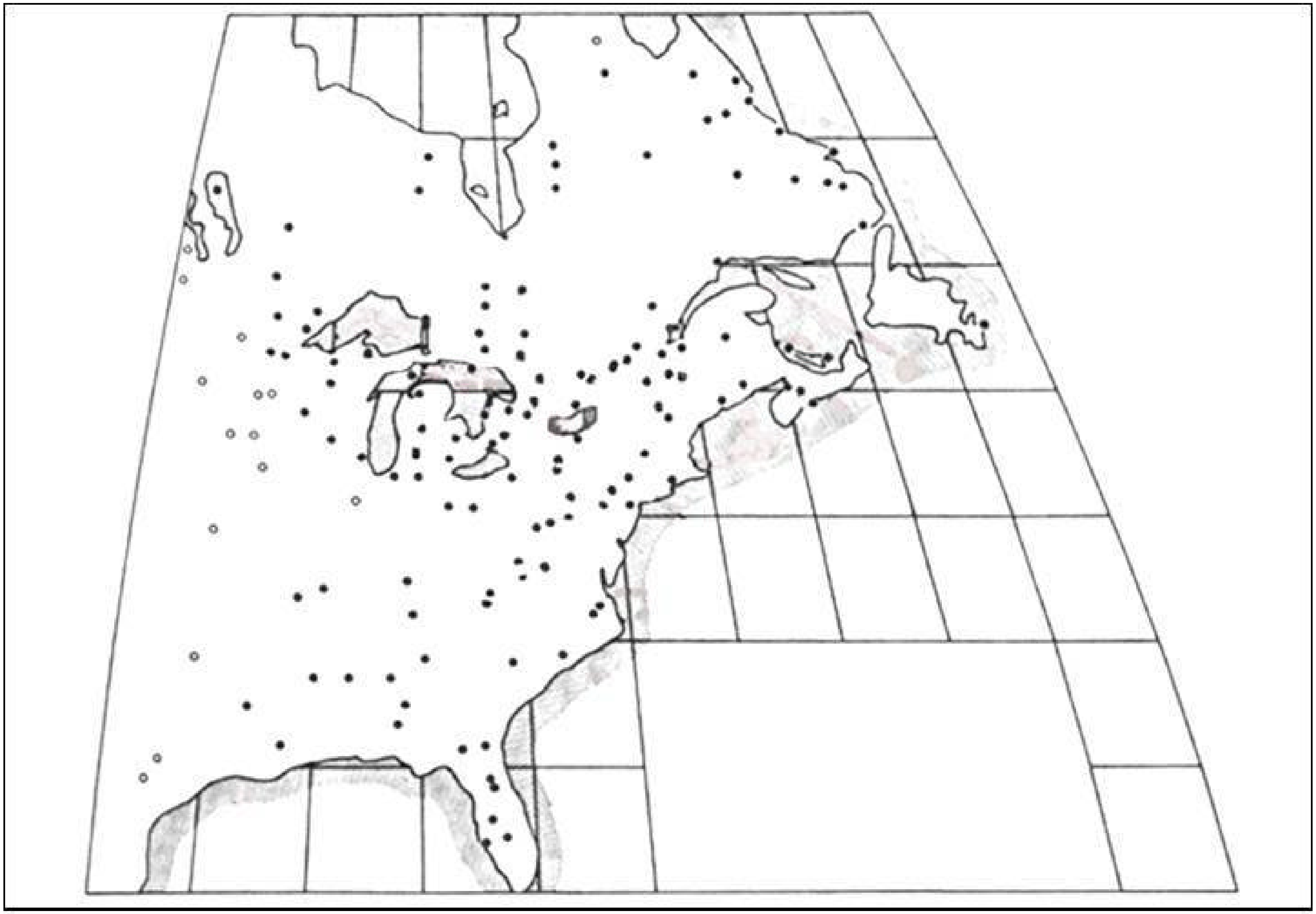

Figure 38. Paleoecological sites in eastern North America for 4,000 yr B.P. Based on Delcourt and Delcourt (1987).

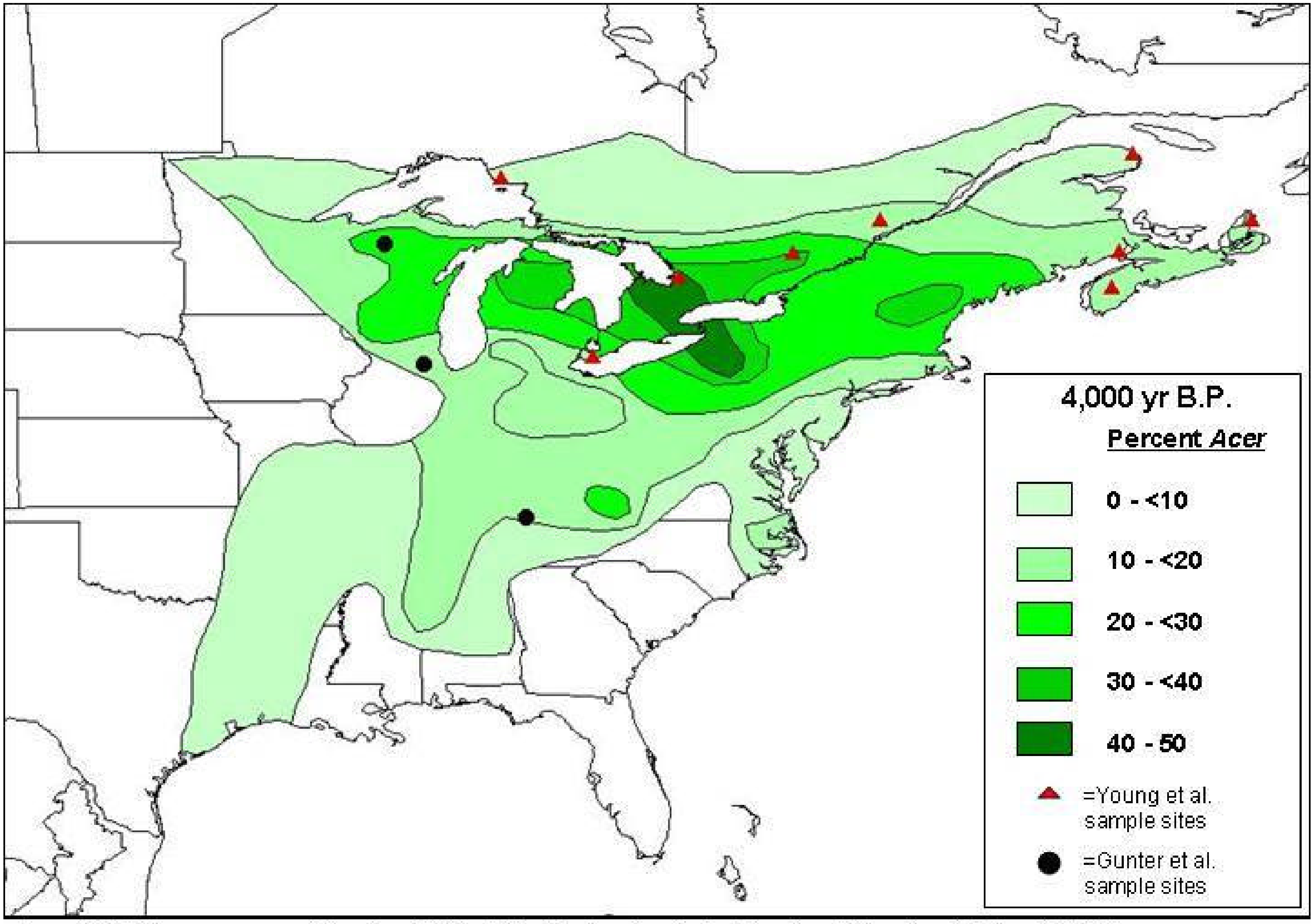

Figure 39. Paleo-range map of *Acer* for 4,000 yr B.P. No elevation limits. Based on Delcourt and Delcourt (1987).

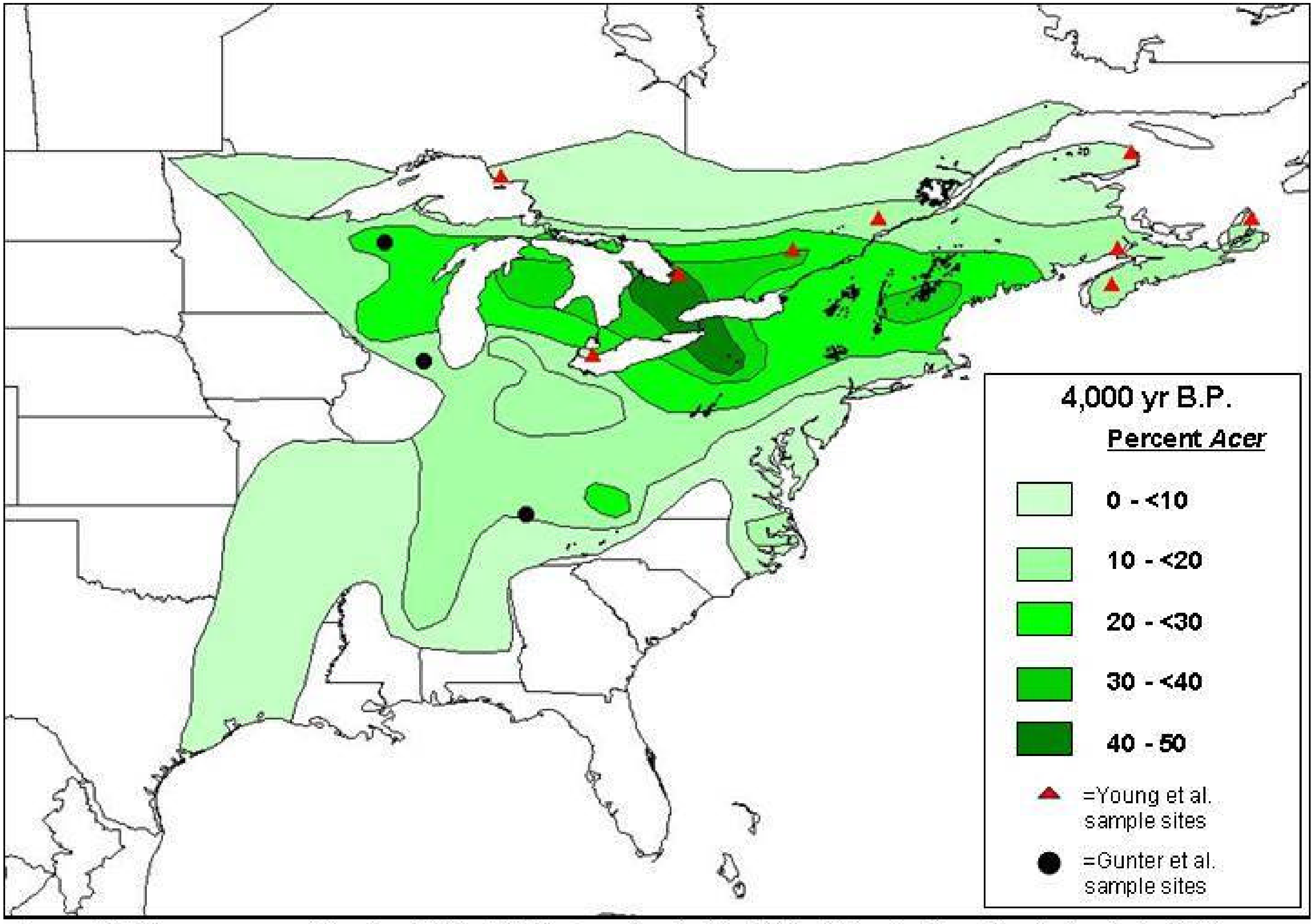

Figure 40. Paleo-range map of *Acer* for 4,000 yr B.P. Northern Appalachian limit = 760 m. Southern Appalachian limit = 1680 m. Based on Delcourt and Delcourt (1987).

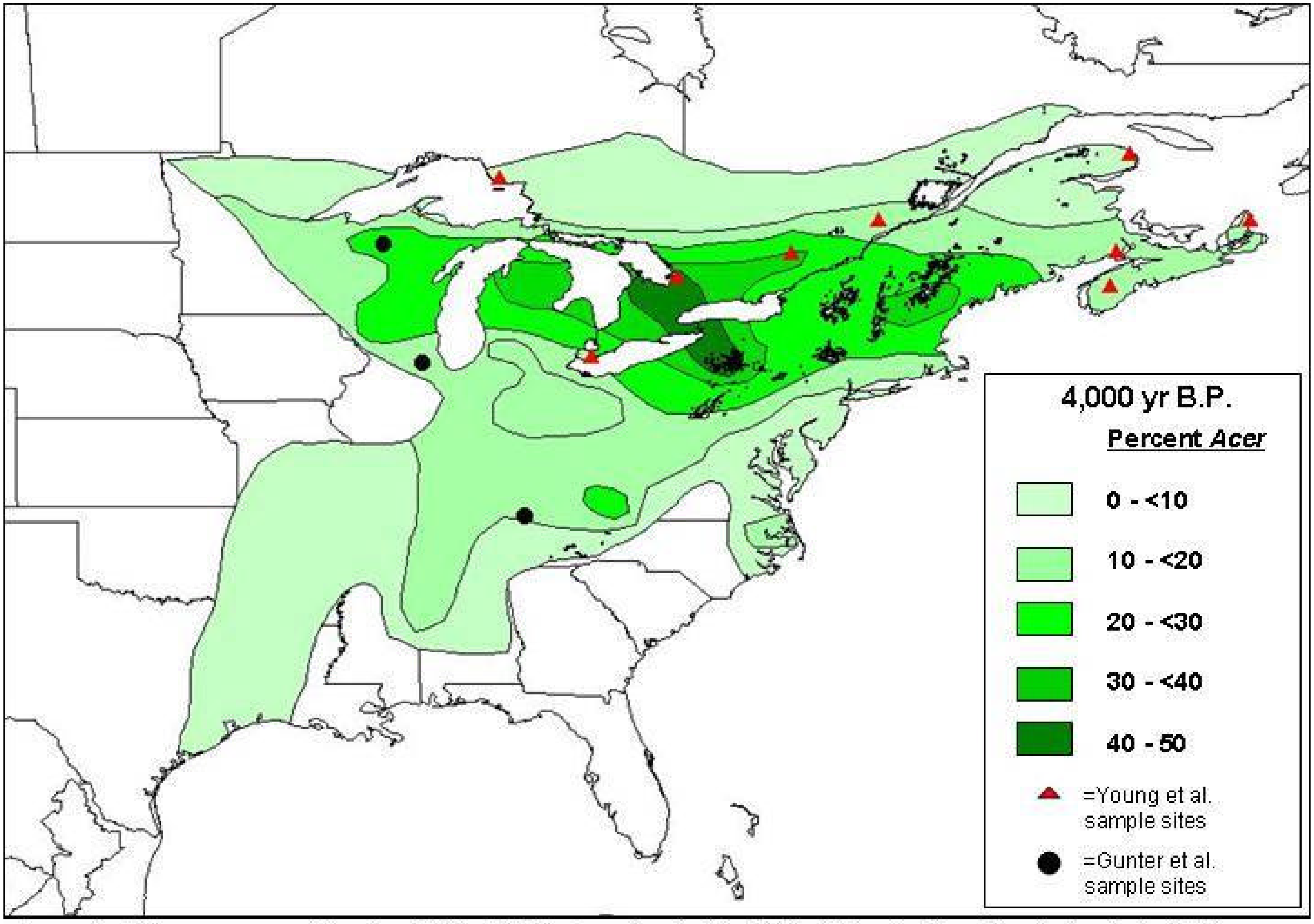

Figure 41. Paleo-range map of *Acer* for 4,000 yr B.P. Northern Appalachian limit = 660 m. Southern Appalachian limit = 1580 m. Based on Delcourt and Delcourt (1987).

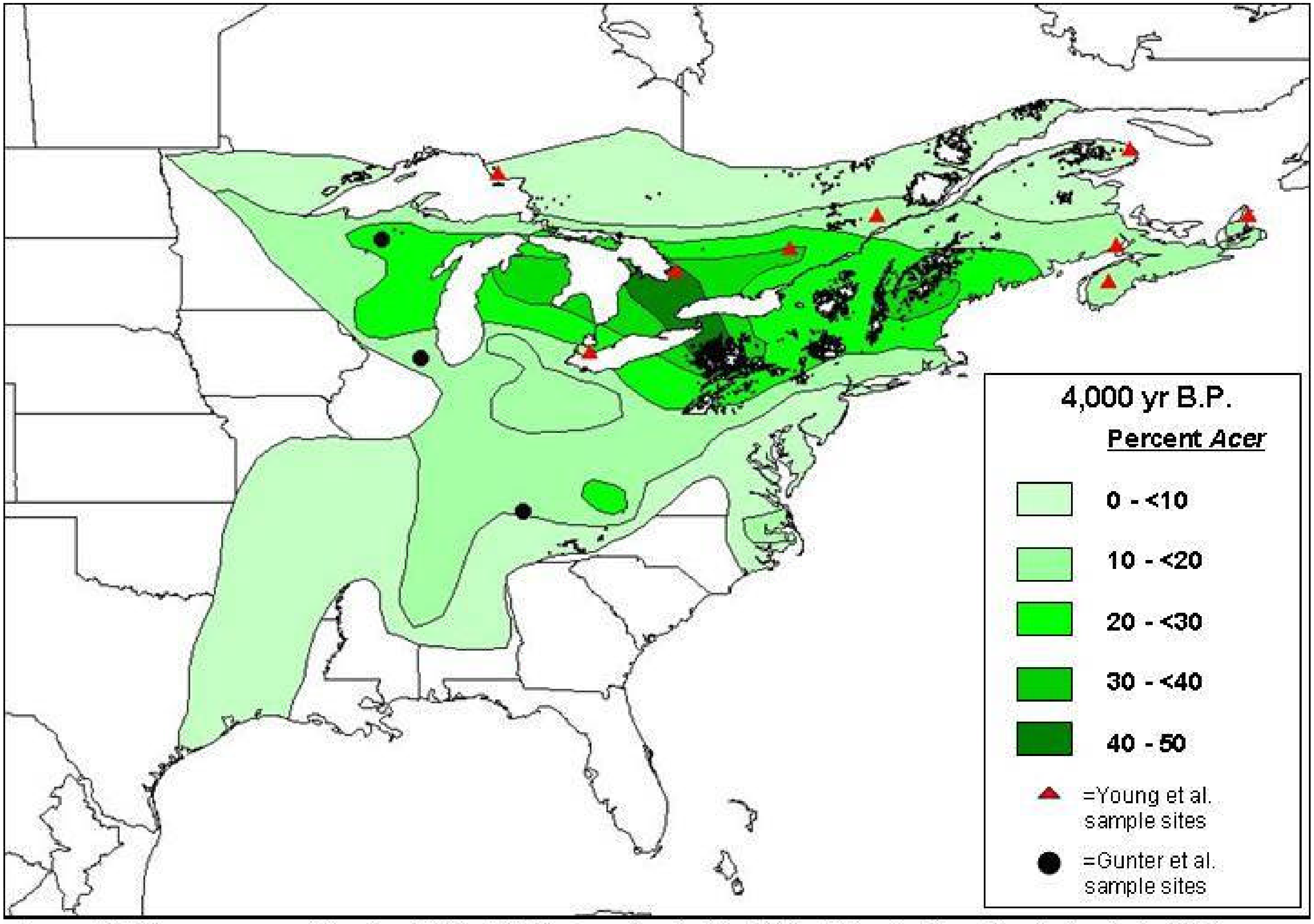

Figure 42. Paleo-range map of *Acer* for 4,000 yr B.P. Northern Appalachian limit = 560 m. Southern Appalachian limit = 1480 m. Based on Delcourt and Delcourt (1987).

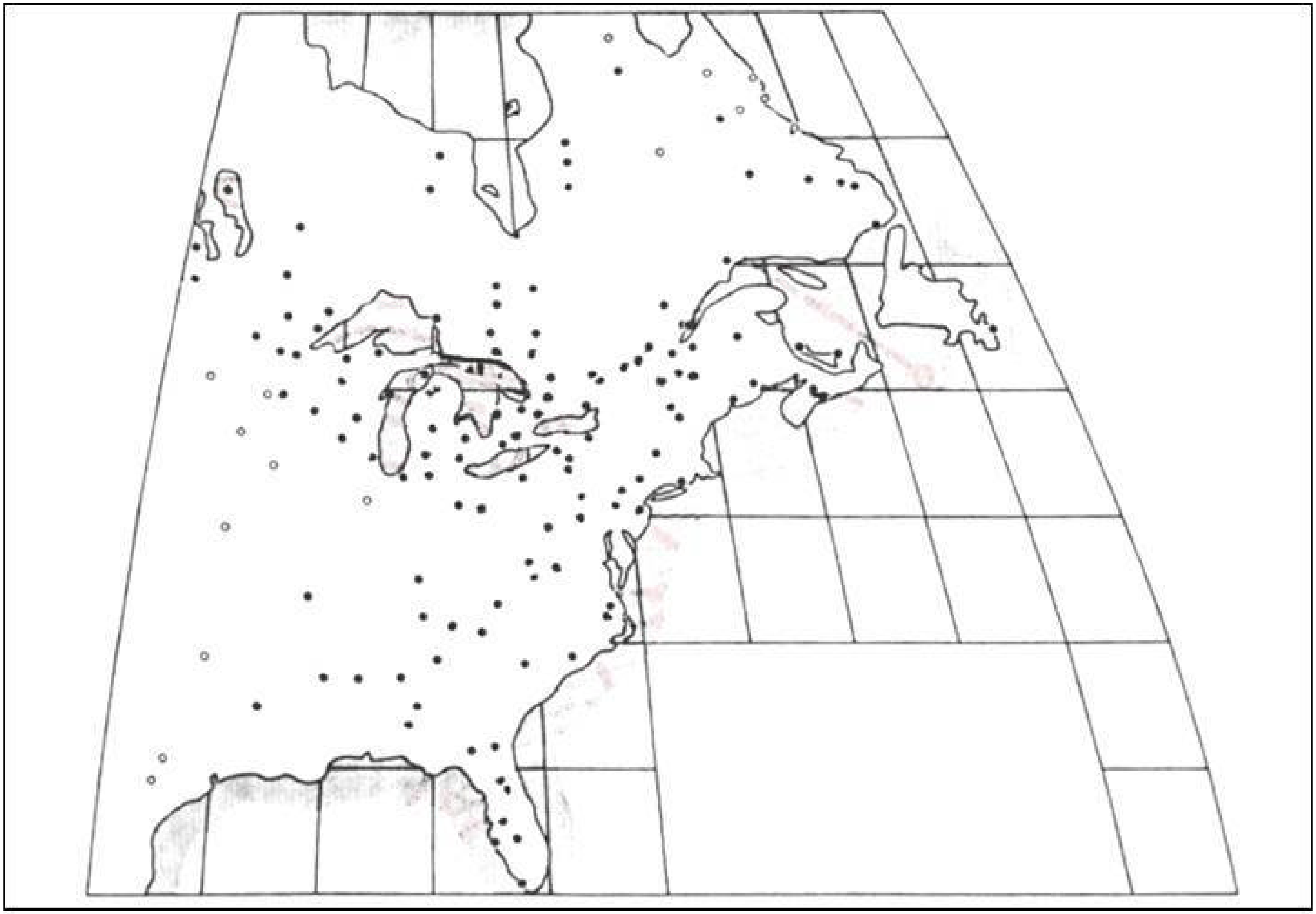

Figure 43. Paleoecological sites in eastern North America for 2,000 yr B.P. Based on Delcourt and Delcourt (1987).

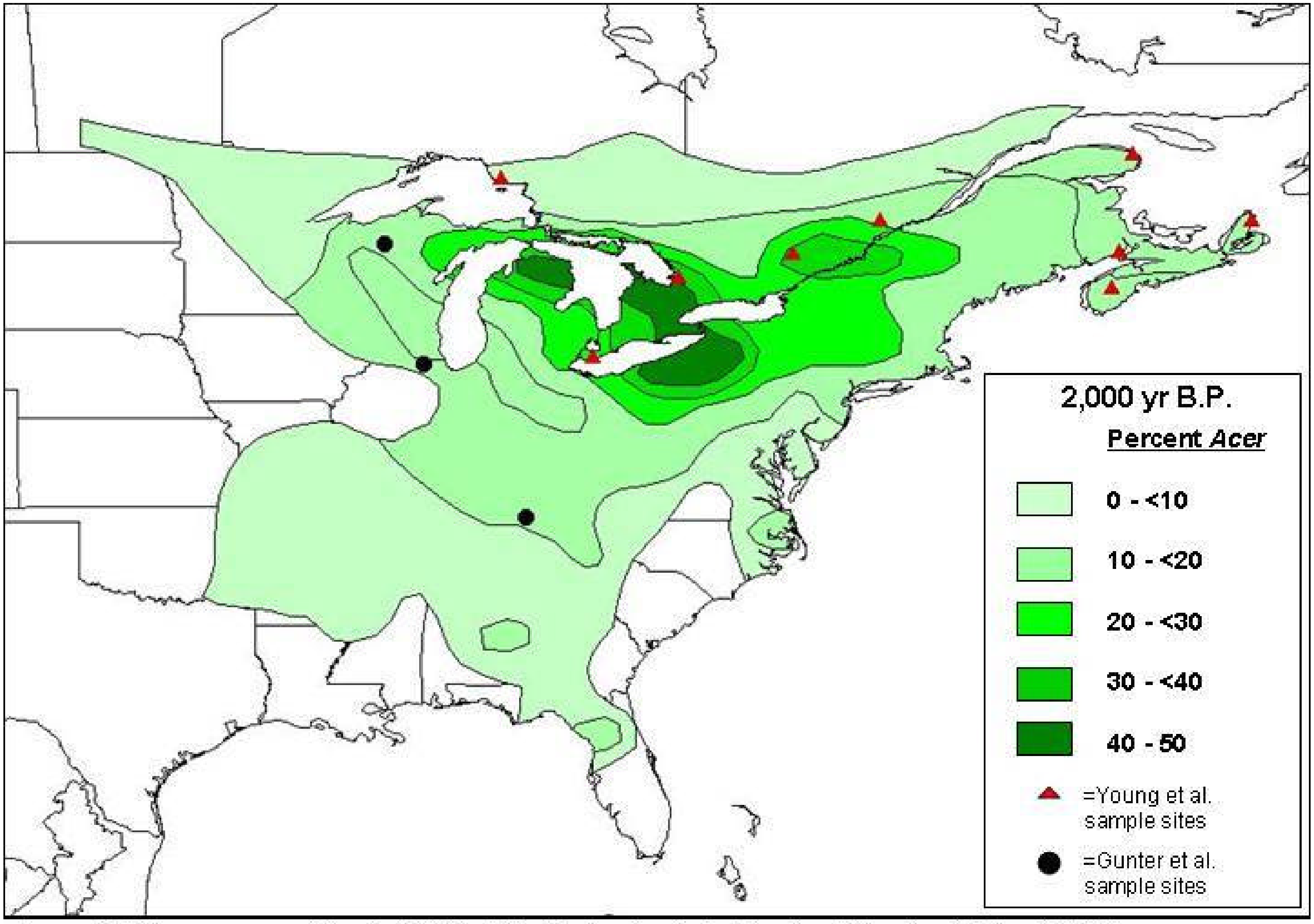

Figure 44. Paleo-range map of *Acer* for 2,000 yr B.P. No elevation limits. Based on Delcourt and Delcourt (1987).

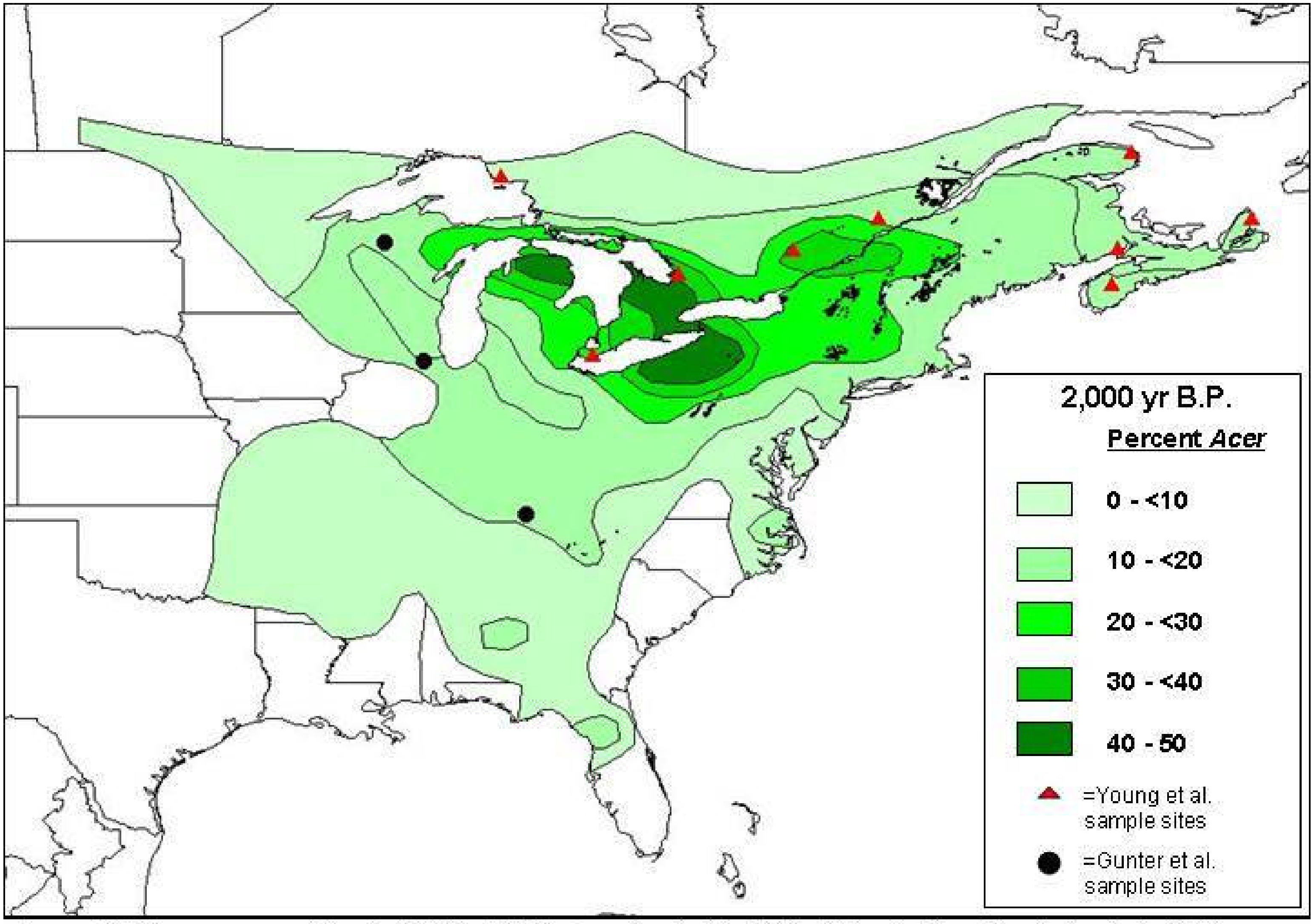

Figure 45. Paleo-range map of *Acer* for 2,000 yr B.P. Northern Appalachian limit = 760 m. Southern Appalachian limit = 1680 m. Based on Delcourt and Delcourt (1987).

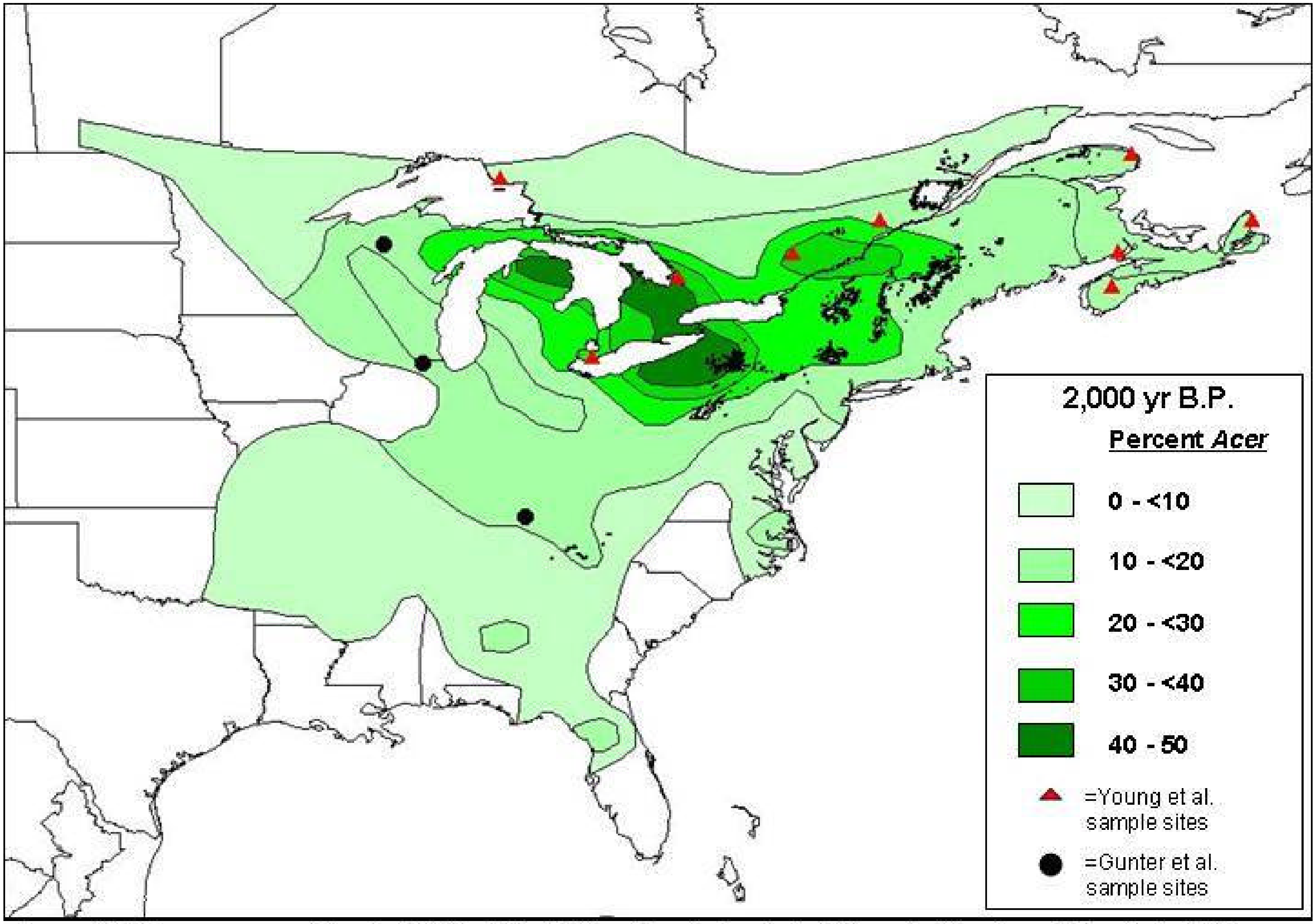

Figure 46. Paleo-range map of *Acer* for 2,000 yr B.P. Northern Appalachian limit = 660 m. Southern Appalachian limit = 1580 m. Based on Delcourt and Delcourt (1987).

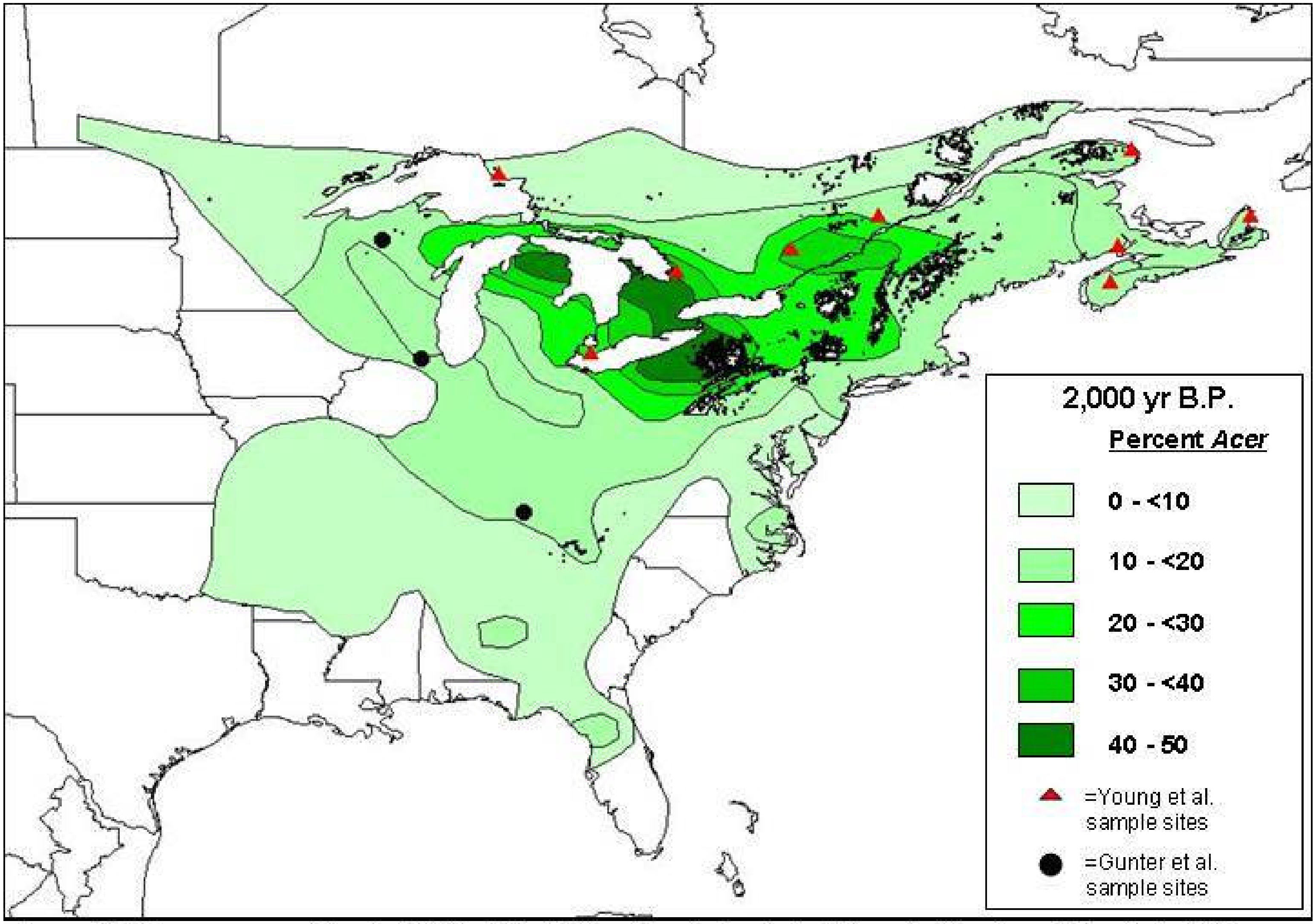

Figure 47. Paleo-range map of *Acer* for 2,000 yr B.P. Northern Appalachian limit = 560 m. Southern Appalachian limit = 1480 m. Based on Delcourt and Delcourt (1987).

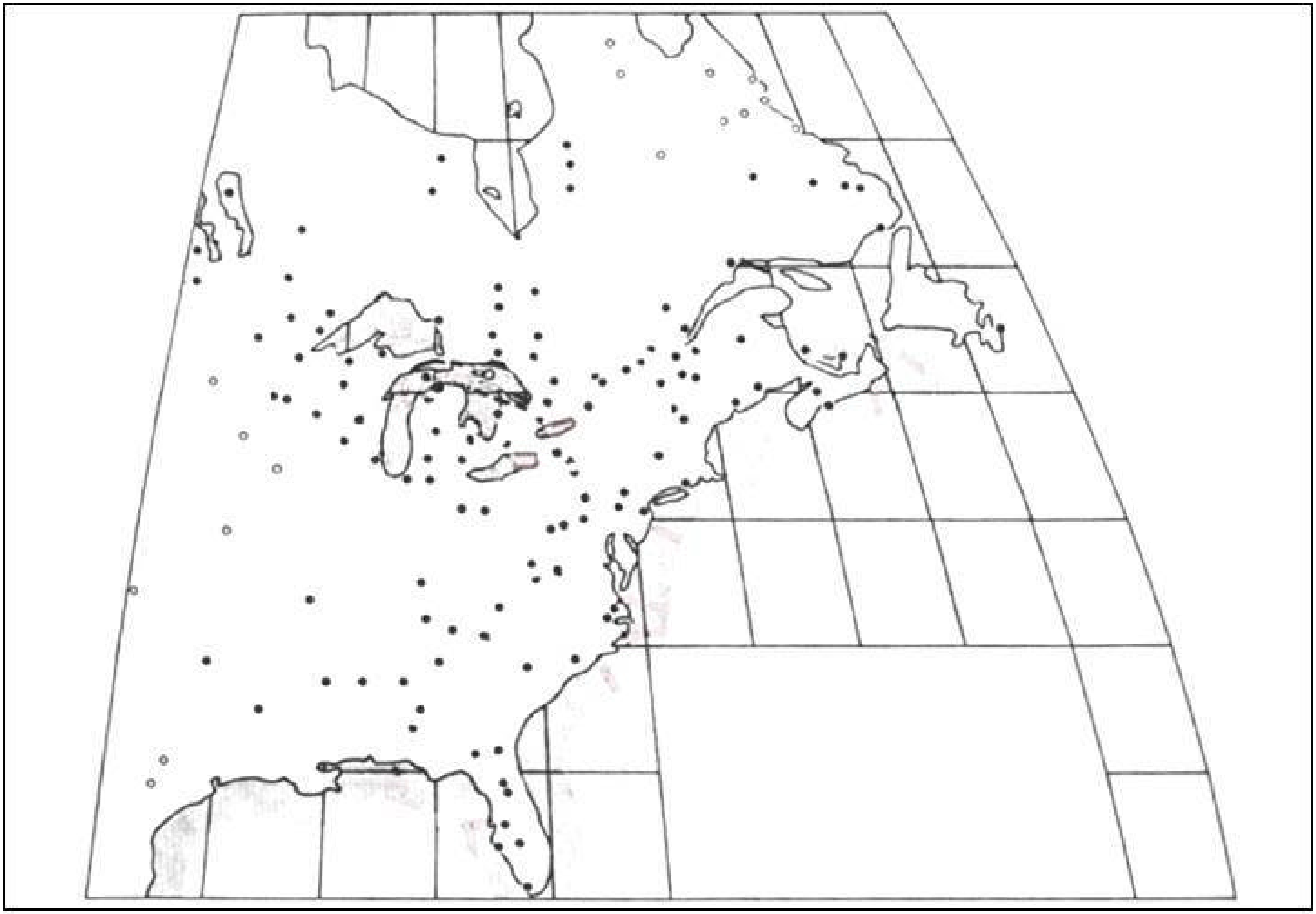

Figure 48. Paleoecological sites in eastern North America for 500 yr B.P. Based on Delcourt and Delcourt (1987).

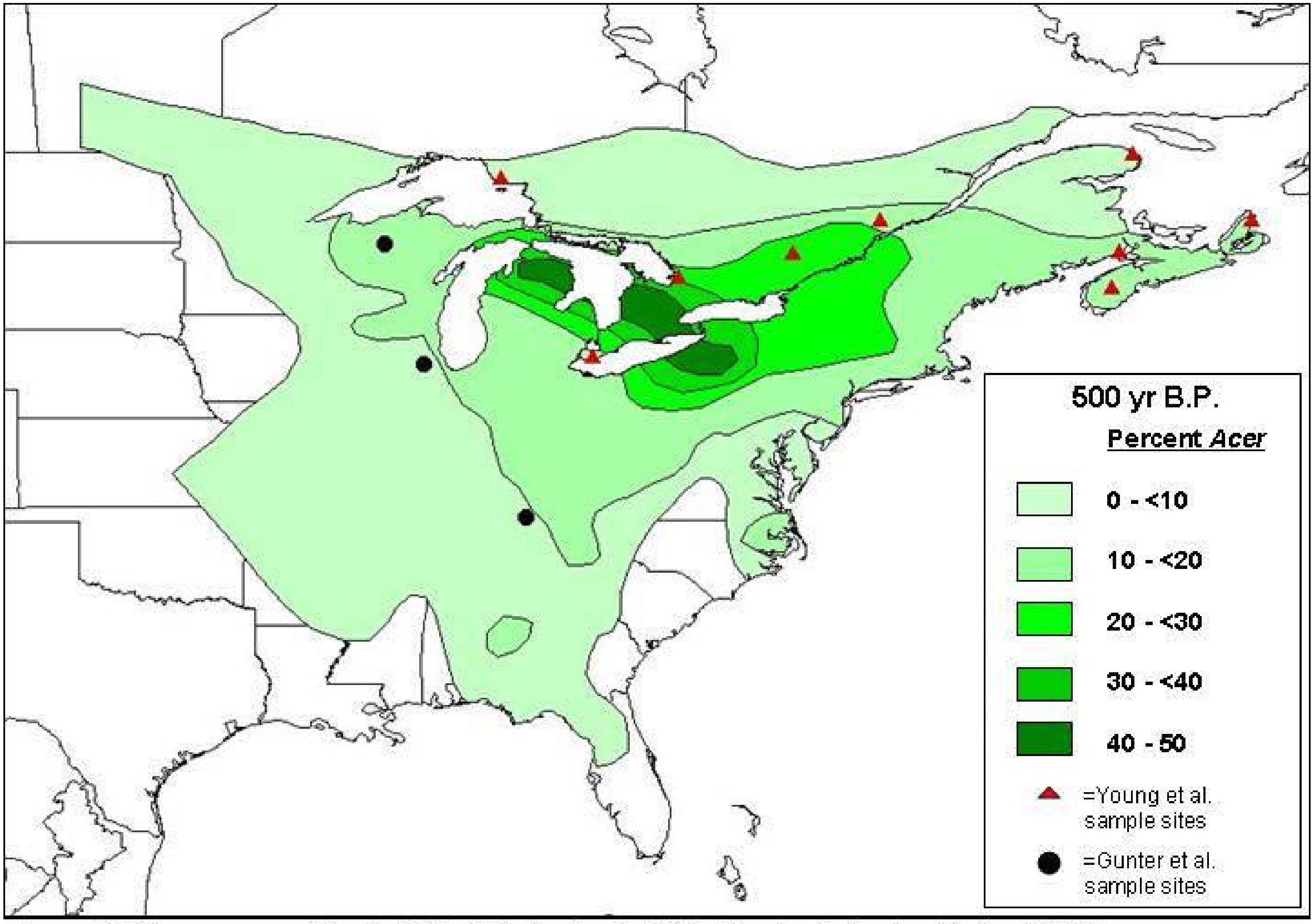

Figure 49. Paleo-range map of *Acer* for 500 yr B.P. No elevation limits. Based on Delcourt and Delcourt (1987).

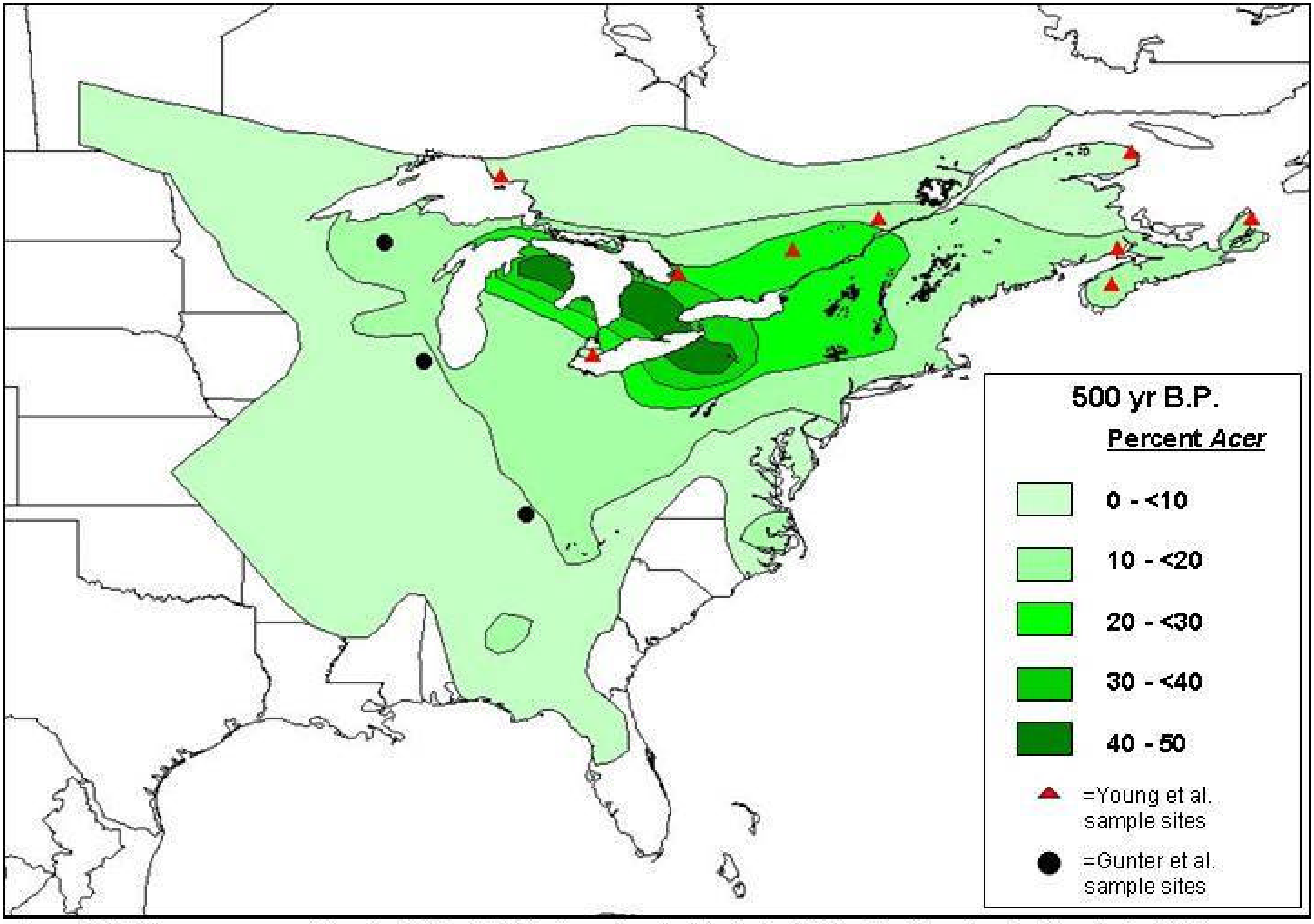

Figure 50. Paleo-range map of *Acer* for 500 yr B.P. Northern Appalachian limit = 760 m. Southern Appalachian limit = 1680 m. Based on Delcourt and Delcourt (1987).

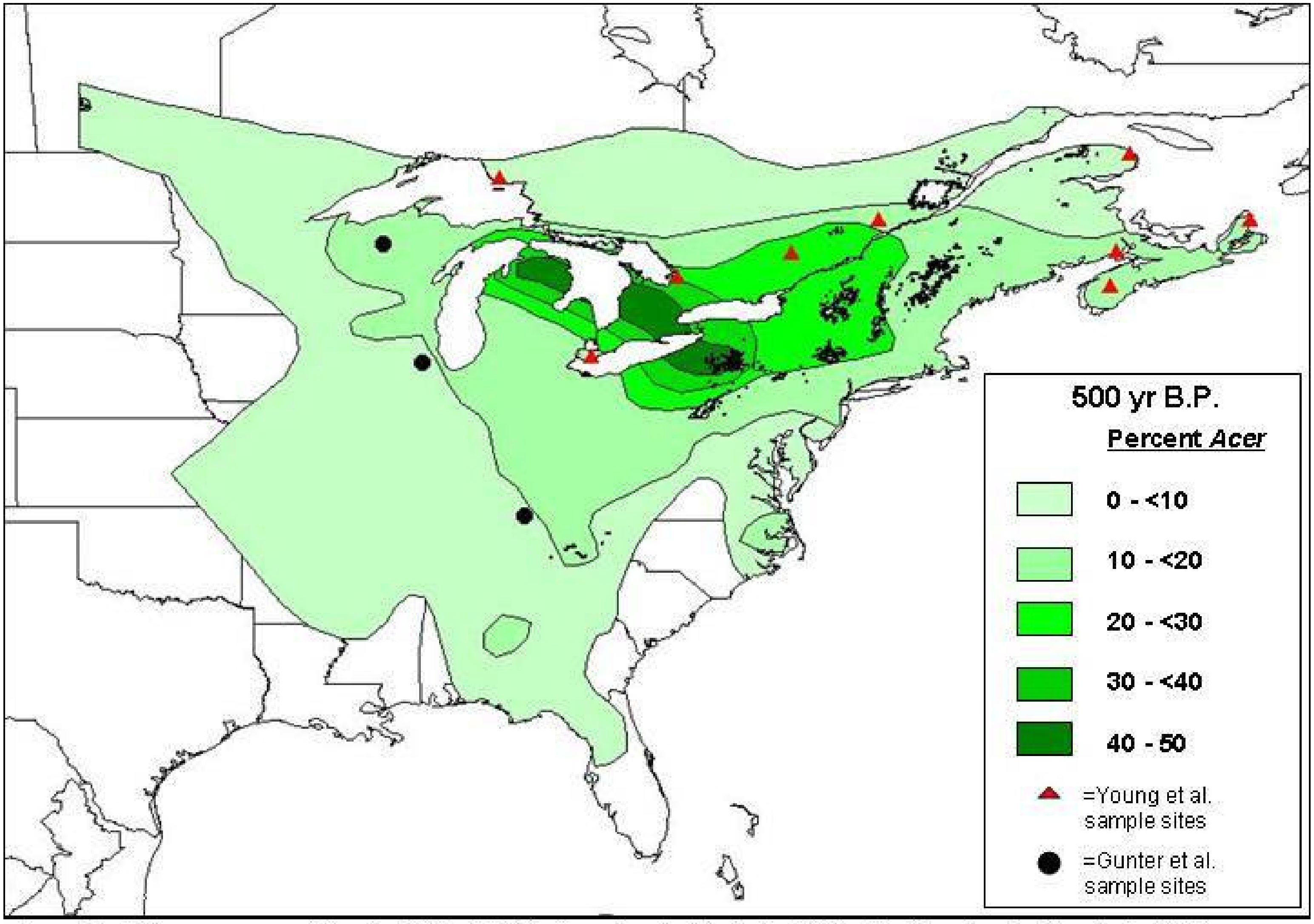

Figure 51. Paleo-range map of *Acer* for 500 yr B.P. Northern Appalachian limit = 660 m. Southern Appalachian limit = 1580 m. Based on Delcourt and Delcourt (1987).

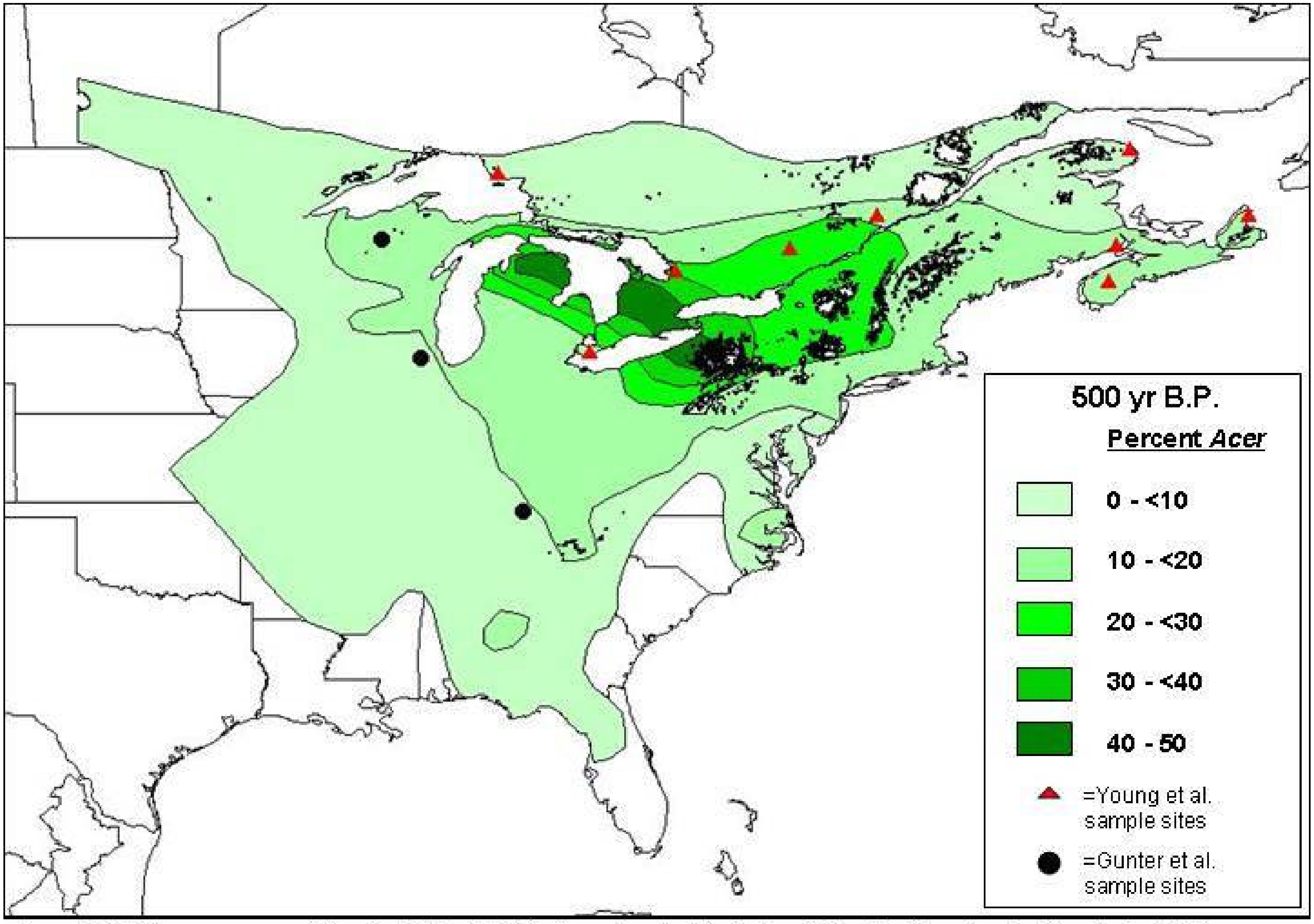

Figure 52. Paleo-range map of *Acer* for 500 yr B.P. Northern Appalachian limit = 560 m. Southern Appalachian limit = 1480 m. Based on Delcourt and Delcourt (1987).

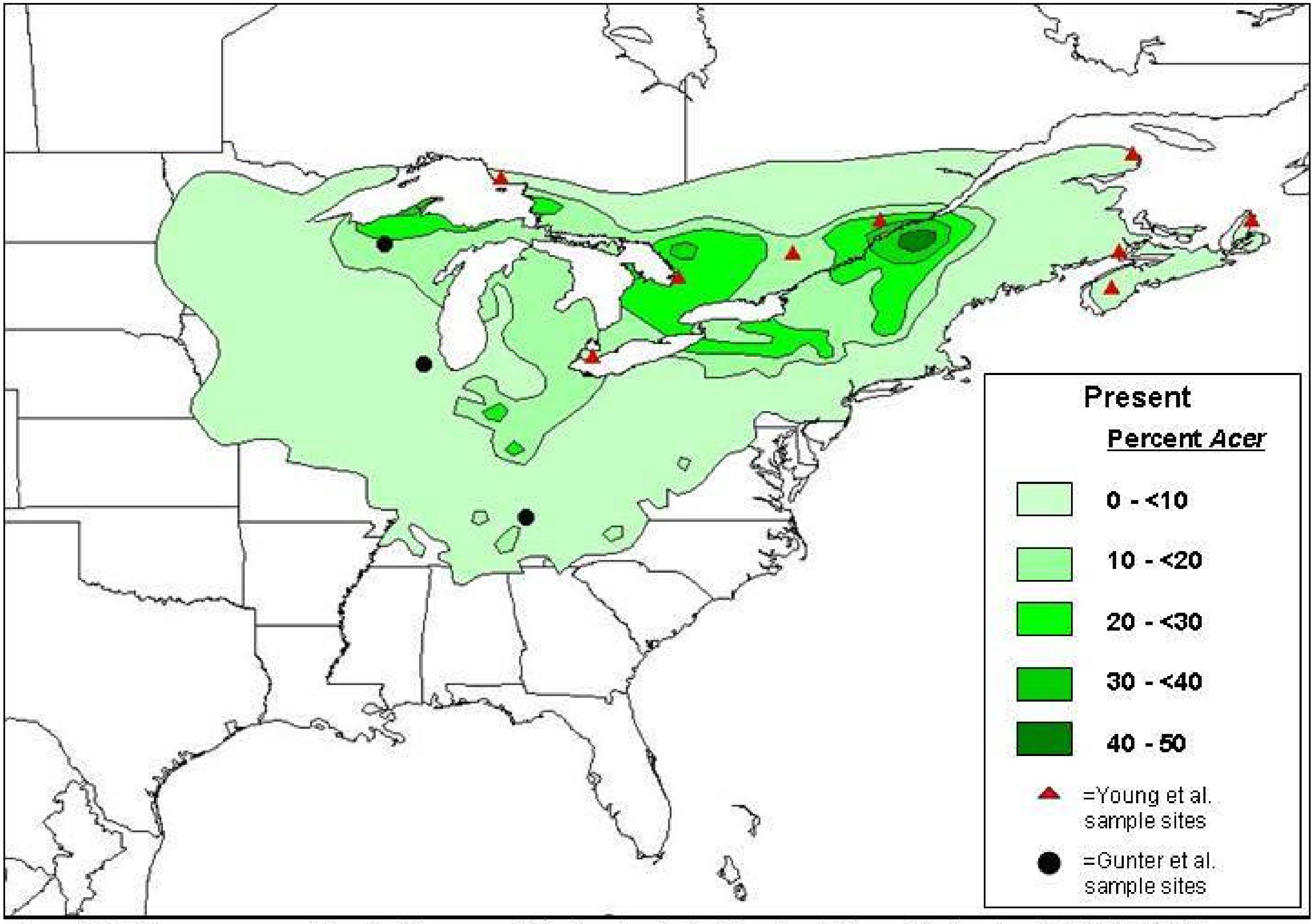

Figure 53. Paleo-range map of *Acer* for the present. No elevation limits. Based on Delcourt, Delcourt, and Webb III (1984).

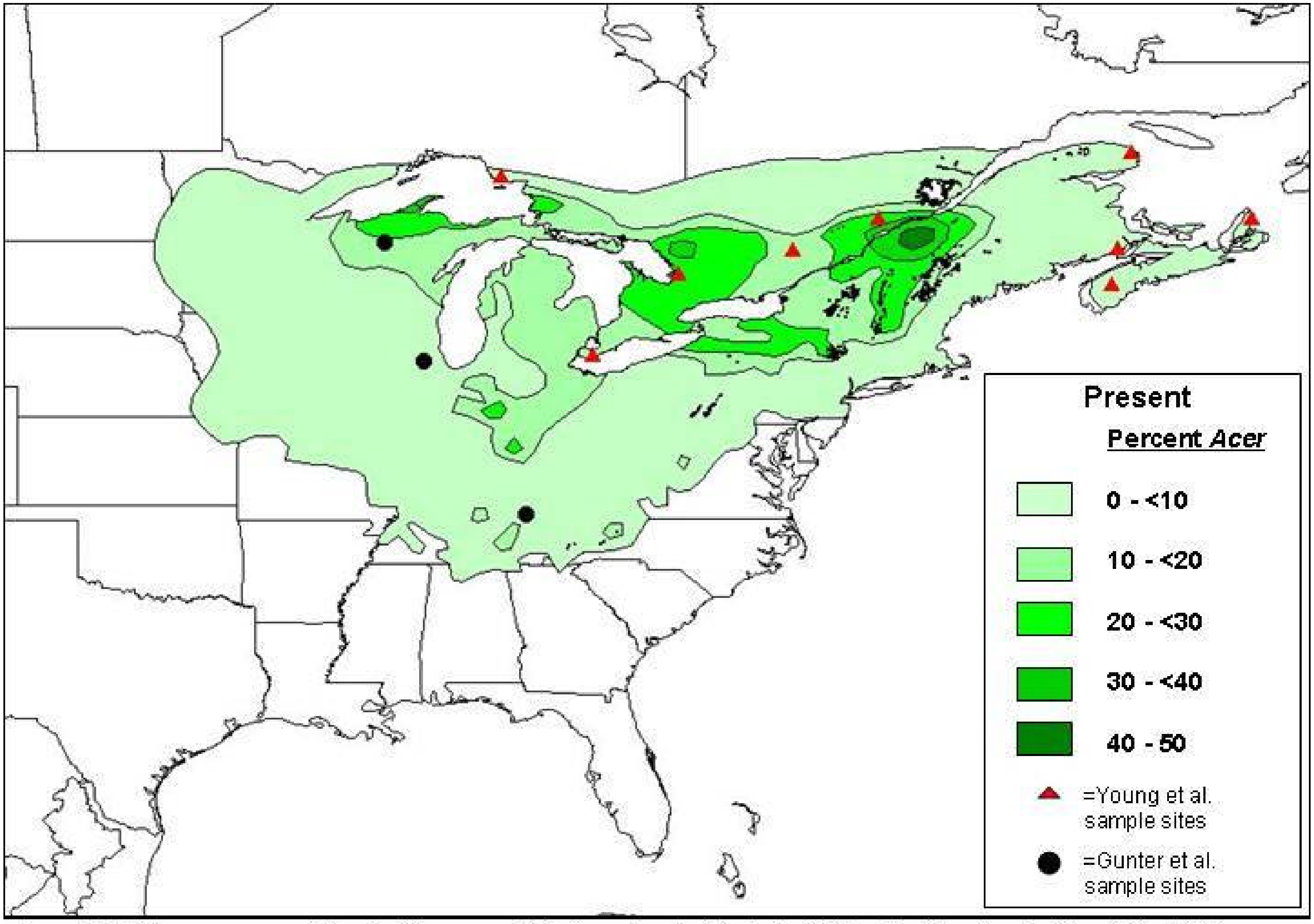

Figure 54. Paleo-range map of *Acer* for the present. Northern Appalachian limit = 760 m. Southern Appalachian limit = 1680 m. Based on Delcourt, Delcourt, and Webb III (1984).

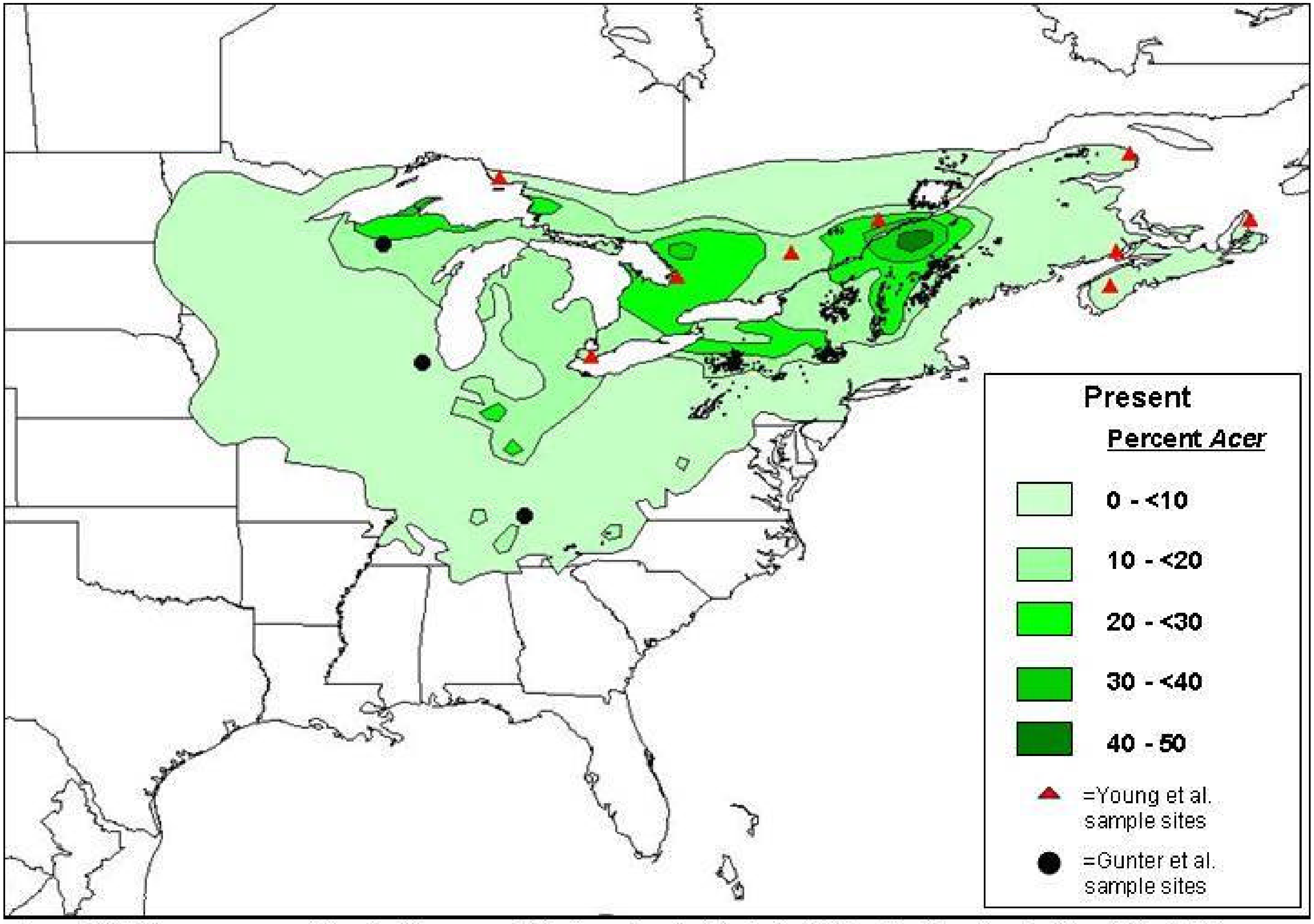

Figure 55. Paleo-range map of *Acer* for the present. Northern Appalachian limit = 660 m. Southern Appalachian limit = 1580 m. Based on Delcourt, Delcourt, and Webb III (1984).

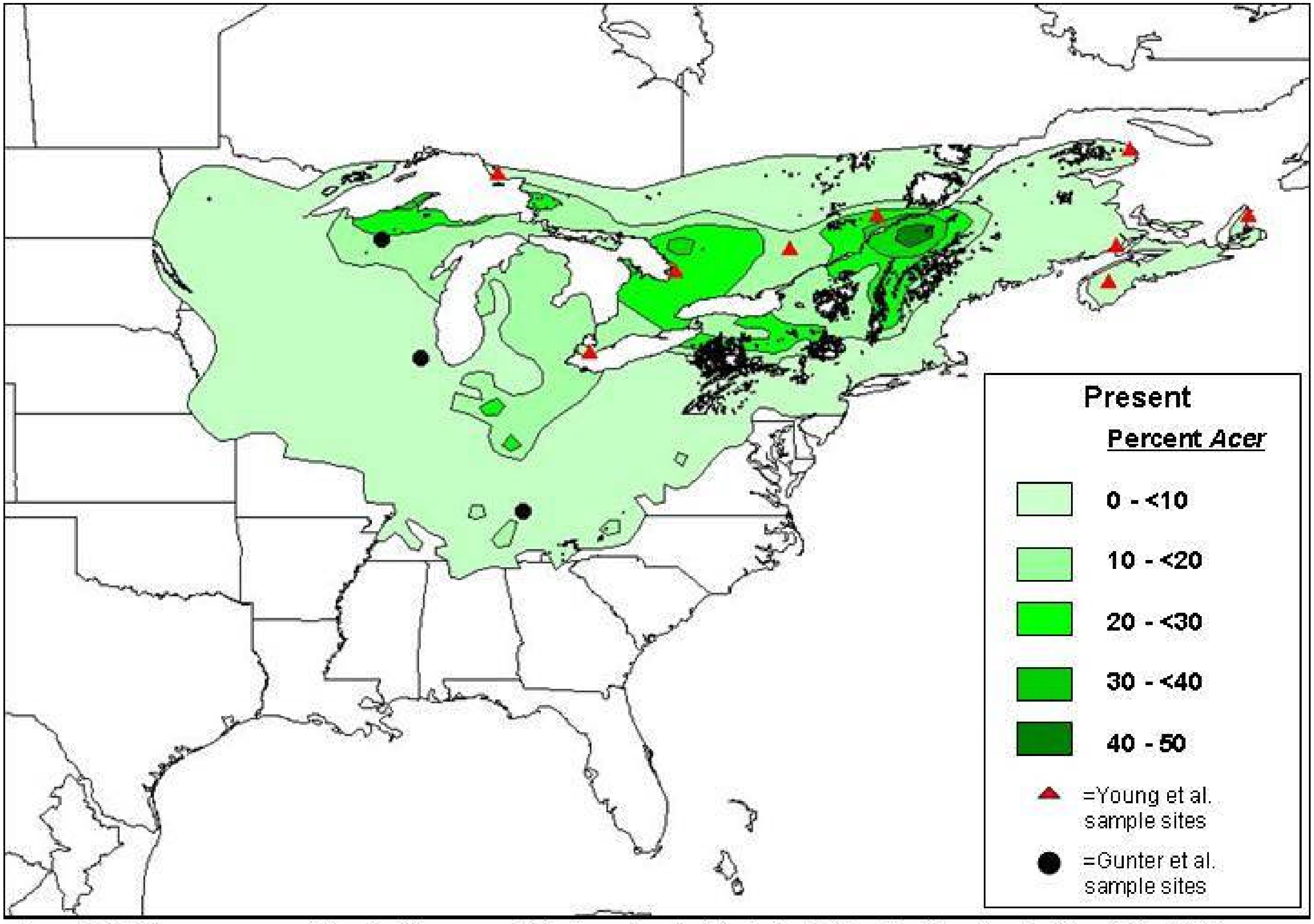

Figure 56. Paleo-range map of *Acer* for the present. Northern Appalachian limit = 560 m. Southern Appalachian limit = 1480 m. Based on Delcourt, Delcourt, and Webb III (1984).

CHAPTER 4

DISCUSSION

The postglacial range expansion of North American temperate tree species resulted in sugar maple migrating from a glacial refuge in the southern U.S. and Mexico to its modern range in the central and northeastern U.S. From an existence at a marginal percentage of forest composition 18,000 yr B.P., as determined through the pollen record, sugar maple abundance has increased so that several regions in the northern U.S. and Canada are dominated by the species. The genetic distribution of sugar maple can be directly observed through various methods of genetic study, but development of a scenario to explain the observed genetic patterns requires an integration of paleo-data, computer modeling, and species site condition tolerances. Through the combination of these elements, a better picture of the migration of sugar maple and the factors that limited its migration pathways is developed.

The modeled distributions show that between 14,000 yr B.P. to 10,000 yr B.P., the Appalachian Mountains acted as a physical barrier to the migration pathways and gene flow of sugar maple (Figures 15, 16, 17, 20, 21, 22, 25, 26, 27). The Cumberland and Blue Ridge Mountains constituted a barrier between sugar maple in North Carolina and Virginia and in the rest of the species' range. By lowering the elevation limit of sugar maple tolerance 200 m below the modern elevation limit in the northern part of its range, a complete separation of populations in the two parts of sugar maple's range results. Only long distance dispersal events would have been able to effect a genetic bridge between the two parts of its distribution. This separation of sugar maple's range disappeared by 10,000 yr B.P (Figures 25, 26, 27). Although it is likely that the genetic impacts of the separation remain to this day, no genetic studies of sugar maple have sampled along either side of the Blue Ridge Mountains to determine the genetic impact.

The expansion of sugar maple to the northeastern U.S. and Canada was an extension of sugar maple's northern range in 14,000 yr B.P. that existed to the west of the Appalachian Mountains (Figures 14, 19). Sugar maple populations to the east of the Blue Ridge Mountains did not likely contribute to the gene pool of the sugar maples that colonized the northeastern U.S. and Canada. The sugar maples that did expand into northern Pennsylvania and New York 12,000 yr B.P. encountered a series of mountain systems of the northern Appalachians that presented physical barriers to the range expansion of the species. From 12,000 yr B.P. to 10,000 yr B.P., the Alleghenies, the Adirondacks, the Catskills, the Green Mountains, and the White Mountains all limited the migration pathways available to sugar maple (Figures 20, 21, 22, 25, 26, 27). As the elevation limit is lowered from 760 m to 560 m in these time steps, the modeled migration distribution barriers become increasingly formidable, though not to the extent of completely isolating one area of sugar maple from every other area (Figures 20, 21, 22, 25, 26, 27).

The genetic patterns of sugar maple along its northern extent, as published by Young et al. (1993), show a general trend of increasing genetic diversity from the east to the west. Both the percentage of polymorphic loci (P) and mean individual heterozygosity (H_i) have lower values in the eastern sample sites. Every sample site is genetically isolated from each other as shown by the genetic distance values (D_m).

Young et al. (1993) propose two scenarios that could explain the observed genetic patterns. The first scenario is that site specific selection is occurring. Site specific selection occurs when certain traits are favored at a local scale because they confer a greater fitness in a particular environmental setting. The actions of site specific selection would result in genetic patterns that are defined by the local selective pressures, possibly masking genetic patterns produced through other mechanisms. The second scenario is that the genetic patterns are the result of gene flow during the migration of sugar maple. Although the models constructed in this study cannot conclusively support or refute the hypothesis of site specific selection, they demonstrate how gene flow may have been limited by the northern Appalachian Mountains, which supports Young et al.'s (1993) second scenario.

Gunter et al.'s (2000) study of the genetics of sugar maple in the western part of its range also shows some genetic evidence of sugar maple's modeled range expansion, although the results are less consistent. They examined several aspects of genetic variation in the northern, central, and southern subregions within the western part of sugar maple's range. The genetic distance values between subregions show that each region is genetically distinct from each other, but not in the linear pattern that would be expected. The northern region in Gunter et al's (2000) study is less distinct from the southern region than from the central region (Table 2). Typically as geographic distance increases, so does genetic distinctness, or distance. Mean expected heterozygosity also shows a somewhat ambiguous pattern. The leading edge of a migration is the result of successive founding events, which results in a gradient of genetic diversity with the more recently colonized areas having less genetic diversity than the older, established sites

(McDonald and Cwynar 1985). The opposite pattern is seen by Gunter et al. (2000). The southern region, which has been colonized by sugar maple longer than the central or northern regions, has the lowest mean expected heterozygosity (Table 3). It may be that selection is acting on the southern region, lowering the mean expected heterozygosity. Even though genetic distance and mean expected heterozygosity do not clearly reflect the patterns expected from the migration of sugar maple, the number of unique alleles in each region does. Gunter et al. (2000) observed that the northern region contained one unique allele, while the southern region contained seven unique alleles. This observation matches the expectation that the southern region should contain more genetic diversity than the northern region.

The impact of genetic drift on genetic diversity cannot be ruled out as an influencing factor of the genetic patterns observed by Young et al. (1993) or Gunter et al. (2000). If the sugar maple populations at their sample sites experienced significant reductions in population size, random genetic drift could have reduced the observed genetic diversity. Reducing the size of a population increases the potential for rare alleles to go locally extinct, thus reducing the genetic diversity of the population. Without detailed sample site histories, the influence of genetic drift needs to be recognized as a potential factor that shaped the genetics of the sampled sugar maple populations.

Integrating paleo-data, computer modeling, and species site condition tolerances builds the scenario through which the genetic distributions seen in Young et al. (1993) and Gunter et al. (2000) can be explained. It is clear that an integrative approach towards species range development since the last ice age is an important step towards understanding how species migration proceeded. The question as to whether site specific selection or gene flow during migration is the dominant factor in structuring the genetics of sugar maple across its range remains open. Further studies of how different selection pressures affect the allozyme and RAPD alleles will help determine the degree to which sugar maple's genetics are the result of selection. Examining the genetics of sugar maple around restrictive mountain ranges would also provide valuable clues about how the genetics of sugar maple have developed since the end of the last ice age. One region of particular interest is the Blue Ridge Mountains, due to its splitting the range of sugar maple 14,000 yr B.P. (Figures 15, 16, 17). Continued study of sugar maple genetics will help clarify the species history.

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