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Predicting Pleistocene climate from vegetation

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Predicting Pleistocene climate from vegetation

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Abstract

Climates at the Last Glacial Maximum have been inferred from fossil pollen assemblages, but these inferred climates are colder than those produced by climate simulations. Biogeographic evidence also argues against these inferred cold climates. The recolonization of glaciated zones in eastern North America following the last ice age produced distinct biogeographic patterns. It has been assumed that a wide zone south of the ice was tundra or boreal parkland (Boreal-Parkland Zone or BPZ), which would have been recolonized from southern refugia as the ice melted, but the patterns in this zone differ from those in the glaciated zone, which creates a major biogeographic anomaly. In the glacial zone, there are few endemics but in the BPZ there are many across multiple taxa. In the glacial zone, there are the expected gradients of genetic diversity with distance from the ice-free zone, but no evidence of this is found in the BPZ. Many races and related species exist in the BPZ which would have merged or hybridized if confined to the same refugia. Evidence for distinct southern refugia for most temperate species is lacking. Extinctions of temperate flora were rare. The interpretation of spruce as a boreal climate indicator may be mistaken over much of the region if the spruce was actually an extinct temperate species. All of these anomalies call into question the concept that climates in the zone south of the ice were very cold or that temperate species had to migrate far to the south. Similar anomalies exist in Europe and on tropical mountains. An alternate hypothesis is that low CO₂ levels gave an advantage to pine and spruce, which are the dominant trees in the BPZ, and to herbaceous species over trees, which also fits the observed pattern. Most temperate species could have survived across their current ranges at lower abundance by retreating to moist microsites. These would be microrefugia not easily detected by pollen records, especially if most species became rare. These results mean that climate reconstruction based on terrestrial plant indicators will not be valid for periods with markedly different CO₂ levels.

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1 Introduction

The Pleistocene Last Glacial Maximum (LGM) period of 18 000 years ago has been widely interpreted as a time of bitter cold in eastern North America when tundra and boreal forest extended hundreds of miles south of the ice sheets and the temperate forest of the East retreated to the southern coastal plain, to Florida, and westward into Texas and Mexico (Davis, 1983, 1984; Deevey, 1949; Delcourt and Delcourt, 1984, 1993; Jacobson et al., 1987; Maher et al., 1998; Maxwell and Davis, 1972; Overpeck et al., 1992; Prentice et al., 1991; Ritchie, 1987; Royall et al., 1991; Schoonmaker and Foster, 1991; Tallis, 1991; Watts, 1970, 1971, 1973, 1979, 1980a, b; Watts and Stuvier, 1980; Webb et al., 1988, 1993; Whitehead, 1973; Wilkins et al., 1991). This reconstruction, which may be called the standard model, is commonly presented in textbooks (e.g., Bradley, 1999; Delcourt and Delcourt, 1993; Pielou, 1991; Ritchie, 1987; Tallis, 1991). The standard model is based largely on pollen and macrofossil records. These pollen data have been interpreted qualitatively in some cases, and in other cases transfer functions or response surface models have been used to infer climate from pollen composition, with similar results. By any of these three methods, the inferred LGM climate is much colder than that simulated (Webb et al., 1993, 1997) although it has been unclear whether the climate simulations or the vegetation interpretations are wrong. In addition, the vegetation composition at this time is consistently described as having no analogs in modern periods (Jackson and Williams, 2004).

In this paper it is argued that both of these anomalies arise primarily from a combination of ambiguous pollen interpretation and the effects of low ambient CO₂ at the LGM which would have altered the relative dominance of different taxa in a manner that mimics colder and drier climates. In what follows, several types of evidence are presented that support the contention that LGM climates inferred from pollen data are colder than the likely actual climates. Then these various types of evidence are shown to reconcile with effects of low ambient CO₂. The focus of this study is largely eastern North America for the sake of concreteness, but no-analog vegetation found elsewhere

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at the LGM can be explained by similar mechanisms.

2 Geologic anomalies

By analogy with European mountains, it has been assumed (e.g., Deevey, 1949; Delcourt and Delcourt, 1984) that the southern Appalachians, particularly the Great Smoky Mountains, should have been covered by permanent ice caps and should have generated glaciers. Mountain glaciers produce obvious signs like U-shaped valleys, striations, and moraines. None of these signs has ever been found in the southern Appalachians south of Pennsylvania. More recent treatments assume tundra but not glaciers on the peaks.

The zone south of the ice that is assumed to be tundra in the traditional model should have retained some physical signs of tundra soils, such as solifluction, cryoturbation, ice wedges, and stone sorting, evident today in New England. No such signs have been found more than a few miles south of the edge of the ice between Wisconsin and Pennsylvania. For example, Braun (1951) noted that at a site only 15 miles south of the ice margin in Ohio, evidence of congeliturbation, although present, did not indicate severe frost action, an observation also supported by Wolfe (1951). Black (1976) concluded that there is no evidence for permafrost in Illinois, Indiana, and Ohio south of the ice margin. A number of sources (Burns, 1958; Gooding, 1963; Gröger, 1972a, b) found evidence for forest vegetation right up to the ice margin throughout the period of the last glacial advance in Illinois, Indiana, and Ohio. Farther north and west, in Minnesota, Montana, and the Dakotas, the southern glacial margins were frozen to their beds and signs of permafrost are present (Mickelson et al., 1983). Péwé (1983) compiled abundant evidence for permafrost from the driftless area of Wisconsin and from across Pennsylvania, but none from central Illinois east to the edge of Pennsylvania. Péwé (1983) shows some evidence for patterned ground on the high peaks of the Appalachians, but only as far south as the southern Virginia-West Virginia border. Periglacial forms south of this either are undated or are not reliably identified (Péwé,

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1983). Denny (1951) documented frost action in Pennsylvania that diminishes with distance from the ice margin. There is thus evidence for a band of permafrost and periglacial climate in Pennsylvania and Wisconsin but none in between. This reconstruction makes sense because the area of western Pennsylvania is higher in elevation than are southern Ohio, Indiana, and Illinois. Thus, permafrost (and tundra) was not a universal feature of the ice front region as implied by most reconstructions.

3 Taxonomic anomalies

A key species in the reconstruction of LGM climates is spruce (*Picea*). The pollen of various species of spruce are very difficult to distinguish. Since all existing spruce species in eastern North America require a cold climate, they have generally been considered together. In this context, pollen profiles dominated by spruce and herbaceous species have been classified as boreal parkland.

It is now apparent, however, that a major portion of the southern range of spruce may have been occupied by a now-extinct species (Jackson and Weng, 1999) which was common in the lower Mississippi valley and east at least to western Georgia. Given that fossil stumps of this species can be found growing with oaks and with strictly southern species, this was likely a temperate spruce. This spruce pollen is thus not necessarily indicative of cold climates. This may have biased climate reconstructions at the LGM to a considerable degree.

A similar problem occurs with sedges (Cyperaceae). This taxonomic group has been interpreted as diagnostic of boreal or tundra habitats. However, sedges are also common in grasslands and forests and would have been favored under a low CO₂ atmosphere, as will be discussed below.

In both cases, the species have been considered key indicators or diagnostic species of boreal forest but lumping species is known to produce misleading indicators of climate (Finkelstein et al., 2006). The fact that their pollen is found mixed with that of temperate species further calls into question their indicator status. Inclusion of these

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species/groups in a model that predicts climate from vegetation will create a cold bias. This analysis also helps explain part of the no-analog vegetation situation.

4 Biogeographic anomalies

The geographic distributions of plants can reveal a great deal about the history of a region. This is true of evidence for refugia, genetic gradients, distributions of endemics, and the existence of races and subspecies.

4.1 Glacial refuge anomalies

The traditional model assumes that temperate forest was forced to retreat to the far south (Gulf Coast region) by the cold (e.g., Bennett, 1985; Cain et al., 1998; Delcourt and Delcourt, 1984, 1993; Watts and Stuvier, 1980). Hewitt (2004) posits an Appalachian refuge, but without citing any data. When we look for fossil evidence for the migration of temperate forest species to the Gulf Coast and Florida and/or Mexico (the refugia for deciduous forest in the traditional model, with Mexico being mentioned mainly in older literature), we encounter a striking lack of evidence. Lakes in the Gulf Coast area, Texas, and Florida either do not date back far enough (i.e., not as far as the LGM) or show a continuous presence of oak-pine associations (including such shrubs as wax myrtle at Sheelar Lake) similar to those present today (Bryant, 1977; Bryant and Holloway, 1985; Delcourt and Delcourt, 1993; Givens and Givens, 1987; Jackson and Givens, 1994; Watts, 1973; Watts and Stuvier, 1980). The most recent pollen maps do not show any distinct refugia for temperate species, most of which are either undetectable or diffusely rare across the region (Williams et al., 2004). It has been shown (Froyd, 2005; Jackson and Williams, 2004; McLachlan and Clark, 2004) that rare species can be hard to detect in pollen samples. Thus, data do not support the existence of a Florida or Gulf Coast refuge or a Gulf Coast migration route to Mexico. In fact, evidence exists for the presence of many temperate tree species across the

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region at the LGM, even if they do not show up readily in the pollen record (Jackson and Williams, 2004).

A related fact is that the high elevation rock outcrop flora of the southern Appalachians would be expected to be derived from boreal/alpine elements that would have moved in during the LGM. Instead, Wiser (1998) found very little overlap between the flora in the southern Appalachians and high elevation flora in the Presidential Range mountains of New Hampshire and the White Mountains, while the latter do show the expected affinities to alpine/tundra floras.

There is thus no documentation for even one southern refuge for northern or Appalachian species except a plausibility argument. That is, while these species *could* have survived in the Gulf Coast region or Florida, there is no pollen or other evidence that they did so. These species are mostly not found north of the Great Lakes and are thus not compatible with the assumed boreal climates in the zone south of the ice in the region east of the Mississippi.

4.2 Genetic gradients

After the last glacial advance 18 000 years ago, and the beginning of the Holocene, the North American ice cap began a rapid retreat. Plants colonizing the previously glaciated lands could potentially spread rapidly over a very large newly deglaciated area. Such rapid spread causes particular effects on population genetic structure. If a species was confined to a very small refuge with a small population, a genetic bottleneck combined with homogenization will produce a population with very little genetic differentiation. As this population spreads across the deglaciated zone, the genetic uniformity will be maintained for a long time. For trees, only a few hundred generations have passed since the LGM, too little for either random mutation or local adaptation to have had much effect. An example of this phenomenon is red pine (*Pinus resinosa*), which occurs largely in previously glaciated terrain and which has very low heterozygosity (Burns and Honkala, 1990). Almost no species can be found matching this pattern south of the ice sheets, suggesting that species during the Pleistocene were

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not confined to small refugia.

If, on the other hand, a species invades the deglaciated zone from a wide front with a large initial population and high heterozygosity, the rapid migration will cause a gradual loss of rare alleles as the distance from the refugial population increases (Hewitt, 2004). This pattern is seen in lodgepole pine (*Pinus contorta*), which has high heterozygosity in the unglaciated refugia and progressive decrease in heterozygosity with distance north (Burns and Honkala, 1990). The same genetic structure is seen in black spruce (*Picea mariana*) in the formerly glaciated zone, in which northernmost populations have low mitochondrial DNA diversity (Gamache et al., 2003).

In contrast to these expectations for rapidly migrating populations, species in the unglaciated (but supposedly Pleistocene-era tundra or boreal zone) East show deep DNA divergence (which means long isolation) between separate sub-populations, no genetic gradients, and high genetic richness (Hewitt, 2004). If these species had been excluded by cold from the area south of the Great Lakes (southern Appalachians) and migrated back into this region, genetic diversity gradients should exist but they do not.

4.3 Distribution of endemics

If tundra and boreal forest/parkland formed zones south of the ice margin in the East, then temperate vegetation would have had to retreat to the far south to refuges, as is commonly assumed. The data on endemism seriously constrain theories proposing large-scale migrations of vegetation at the LGM. Many endemics occur just south of the ice margin; almost none are found within the glaciated area, and those that do generally are either hybrids or are recently derived. The only possible explanation for this observation is that the unglaciated East had climates that these endemic species could tolerate throughout the glacial period.

Local endemics are species or discrete races with a restricted geographic distribution (Brown and Gibson, 1983; Cain, 1944). Endemics may arise in a number of ways. In some cases, a species that is originally widespread may become progressively restricted to a unique habitat as climate changes, physiography changes, or

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other species out-compete it. It thereby becomes a relict species. For example, a swamp-dwelling species might progressively lose habitat during periods of uplift when swamps are drained.

5 A second type of origin of endemics involves evolution in a unique habitat, leading to the generation of a race, a subspecies, and ultimately a new species. For example, in the tropics the species on isolated volcanic peaks are often derived from tropical lowland elements and are unrelated to those on other mountains. Striking examples occur in cave populations of animals, with the cave population diverging drastically in morphology from the normal population. How many specialized species could have evolved since the LGM is unknown, but data on speciation rates from the fossil record (Levin and Wilson, 1976) suggest that very few species could have originated in such a short time. This is especially true for trees, which have only experienced a few hundred generations since the LGM. Telltale signs of recent origin for endemics are the proximity of the parent species, incomplete genetic isolation, and limited morphologic divergence. These signs of recent origin do not apply to most endemics in the unglaciated regions but do apply to those found in the recently glaciated regions.

10 Maps of the distribution of endemic species show that recently glaciated regions lack endemics. The high frequency of endemics in central Alaska led Hultén (1937) to propose that a large portion of Beringia remained unglaciated and served as a refuge, a view since substantiated by geological studies. As Braun (1950, 1951) noted, the southern Appalachians, particularly the region of the Cumberland Plateau and the Blue Ridge escarpment, is a center of both species richness and endemism for the eastern United States. Both occur because this region has an ancient floristic history (since at least middle Tertiary time) as the only area of large mountains in the East. The mountains have a wide variety of soils, climates (often moist and equable), and topographies that both provide habitat for many species and encourage endemism by imposing barriers that isolate populations. Many endemics can be found in this region across life forms including trees (*Abies fraseri*), ferns, shrubs, herbaceous plants, fish (Gilbert, 1987), salamanders, crayfish, and centipedes. The extremely limited distri-

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5 butions of many endemics in the southern Appalachians pose a real difficulty for any theory of local extinctions, distant refuges, and subsequent reimmigration, as does evidence concerning the time of their origin. Given the large number of endemics, such a major forced migration should have caused many extinctions, but very few Pleistocene
10 extinctions of land plants in eastern North America have been documented (Potts and Behrensmeyer, 1992; Roy et al., 1996). As a group, these endemics exhibit many signs of ancient origin, including high morphologic divergence from related species, geographic isolation from congeners, complete reproductive isolation, and edaphic specialization. A number of endemic plants, for example, have no close relative in the
15 East, and their nearest congener is in China or Europe. The very few endemics in glaciated regions do not exhibit these signs.

A telling example of the significance of endemics is a community centered on sink-hole ponds in the Blue Ridge Mountain region of Virginia (Church et al., 2003). In this small 1350 ha area are found disjunct and endemic populations of 70 plants and
20 animals. The adaptation of these species to this unique habitat would prohibit these species from migrating under a changing climate.

We are led to the conclusion that the endemics in the unglaciated region have origins that predate the LGM and therefore that they survived the glacial climate in the locations where they are found, whereas endemics in glaciated regions have a recent
25 origin.

4.4 Distribution of races and subspecies

The geographic distribution of races and subspecies provides invaluable information for interpreting past climatic changes. Even though most race and subspecies distinctions cannot be made using pollen data, such distinctions cannot be ignored. If multiple
25 distinct races of a species can be identified, then (1) each must have had a separate glacial refuge to prevent introgression; or (2) they all evolved since the LGM; or (3) the bulk of the range of the species was not disturbed during the glacial period. Because, as noted, finding even a single glacial refuge in the far south has proven problematic,

finding multiple refugia within which each of the distinct races of these species could be preserved would seem doubly problematic.

Fagus grandifolia has three distinct races, the gray, red, and white beeches (Bennett, 1985; Camp, 1950; Cooper and Mercer, 1977), which differ on multiple traits. These three races readily hybridize where their ranges overlap. The genetics data for *Liriodendron* point to a number of distinct races. Virginia pine has two distinct races, as defined by genetics data (Parker et al., 1997); one to the northwest and one to the southeast of the main Appalachian axis. Although Parker et al. (1997) attribute the origin of the northwestern population to a postglacial migration from the southeast, based on its lower genetic diversity (often found in colonizing populations), the substantial number of unique alleles found in various northwestern populations suggest that it is not merely a genetic subset of the southeastern population. Rather, this gives a suggestion of prolonged isolation, possibly throughout the Pleistocene, in which case it had to remain to the northwest of the mountains during the LGM to remain separate from the southeastern race. Fraser fir, found in the southern Appalachians, will hybridize with balsam fir, but the only hybrids at present are near West Virginia. In all of these cases the distinct races would have required the existence of multiple refuges in order to persist.

We may similarly look at closely related species for evidence of LGM distributions. Sugar maple and Florida maple are not well separated morphologically. Where their ranges overlap, they hybridize readily. If sugar maple had migrated to the far south it would have occupied the same range as Florida maple, in which case the two species would have merged. A similar problem exists with Virginia pine. This pine is only kept from crossing with *Pinus clausa* (a Gulf Coast species) by their considerable geographic separation (Parker et al., 1997). If Virginia pine had moved down into Florida at the LGM, it would have merged with this closely related species. These examples are just a sample of the many cases where closely related species are today prevented from crossing by geographic separation but would have merged if crowded together in a single coastal plain refuge. The races of these several species do not coincide

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geographically, further multiplying the number of required refuges.

The standard model postulates a far south refuge, in which multiple races would be hard to keep separated, both during the LGM and while they migrated north, but evidence for this is lacking.

5 Discussion

The anomalies documented here are not trivial. The biogeographic patterns expected for rapidly migrating species are observed in the glaciated zone, but not at all in the unglaciated zone. Boreal zone species exhibit low genetic variation or diversity gradients, but species in the unglaciated zone show high genetic richness, no gradients, and deep (ancient) DNA divergence between populations. Endemics are very rare in the glaciated zone, and endemics in this zone appear to be mostly recent (due to hybridization, for example). Sister species, subspecies, and races are common across the unglaciated East but not in the glaciated zone. To keep all of these groups separate during the Pleistocene so that they did not hybridize/homogenize out of existence would require multiple LGM refuges, but no such refuges have been found in the far South. If the pollen data say one thing and the biogeographic data flatly contradict this inference, what can we conclude?

There is a possible resolution to this paradox based on climate and CO₂ factors. First, glacial climates are not simply a general cooling of the climate. Glacial epoch climates were cooler, but more so in summer (Pielou, 1991). Thus, the existence of “boreal” species farther south than today does not mean that climates were bitterly cold, because summer temperatures are the most limiting to boreal tree seedlings. Second, a factor that also varied during the glacial period is CO₂, which was so low that it caused CO₂ starvation. CO₂ starvation does not affect all species equally.

At the LGM, about 18 000 years ago, CO₂ levels were very low, less than 200 ppm. This low level of CO₂ constitutes a severe deficiency for growth, and would have shifted competitive dominance between different plant types, as well as affecting overall vege-

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tation biomass. C₄ grasses have a strong advantage over other plants under low CO₂ (Cole and Monger, 1994; Farquhar, 1997; Polley et al., 1993, 1995), though not under low temperatures. Robinson (1994) shows that the extent of stomatal regulation plants exhibit in response to CO₂ level varies by taxa in a manner that suggests that this trait is a modern adaptation. Ancient taxa such as conifers exhibit little stomatal responsiveness compared to angiosperms. The benefit of stomatal responsiveness trades off against greater water loss at low CO₂ levels resulting from stomates being open longer (Drake et al., 1997; Saxe et al., 1998). Where water is not limiting, a low CO₂ climate should favor grasses, forbs and angiosperm trees over conifers (Beerling, 1996; Beerling and Woodward, 1993; Jolly and Haxeltine, 1997; Robinson, 1994; Saxe et al., 1998). This suggests that mesic broadleaf trees should have remained competitive in mesic microsites during the Pleistocene. On most upland sites, however, a low CO₂ climate would favor xeric species such as conifers, which have consistently low stomatal conductance, and drought-tolerant herbaceous species, including grasses and sedges. Oaks, as trees with intermediate responsiveness, would have persisted as well. We in fact observe extensive open conifer forest replacement of broadleaf forest at the LGM in eastern North America, with a persistent oak component. Simulation studies also show that the reduced water use efficiency expected at the LGM would produce a xeric, open forest (with low leaf area index) south of the ice dominated by conifers (Cowling, 1999; Harrison and Prentice, 2003; Jolly and Haxeltine, 1997). This explains the “no-analog” open forest (or parkland) often remarked upon.

Simulations of the effect of low CO₂ levels show that it could cause a major lowering of alpine treelines (Bennett and Willis, 2000; Cowling and Sykes, 1999; Street-Perrott et al., 1997). Jolly and Haxeltine (1997) simulated the montane ecotone for African mountains and showed that the entire LGM lowering of treeline at their study site is consistent with the effect of low CO₂ without assuming any drop in temperature. Lower treelines at the LGM have typically been taken as evidence for colder temperatures, but could really be the result of changes in CO₂ levels.

If lowered CO₂ affected vegetation in eastern North America, what changes would

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be expected? Grasses and other grassland species would be expected to expand their range into forest, perhaps creating parkland. Forest communities would shift to drought tolerant species such as pines and oaks, with spruce being particularly able to invade, as it is the most drought tolerant boreal tree. Significantly, mesic microsites such as coves, north slopes, and stream valleys would provide refuges for mesic site species across their entire original range, especially in the highly dissected Appalachian region, because the effect would be similar to an overall drying. High precipitation, midelevation regions such as the Cumberland Plateau and the Southern Blue Ridge Escarpment would provide prominent refuges. In contrast, topography provides much less protection against extreme cold. An LGM African montane site (Jolly and Haxeltine, 1997) shows this pattern, with low levels of tropical montane forest pollen persisting in LGM profiles dominated by ericaceous shrubs. While drought-tolerant boreal elements such as white spruce (or the extinct temperate *Picea crutchfieldii*) could have moved south under a cooler, low CO₂ climate, most eastern boreal trees are not drought tolerant and would not have been able to move far south. We observe exactly this pattern of change in the pollen record, with most boreal trees being absent from the supposed boreal parkland south of the ice. Several authors have proposed that the southern Appalachians were a refuge (e.g., Braun, 1950; 1951; Church et al., 2003; Harvill, 1973; Hewitt, 2004). This view now has increased plausibility.

We can compare these results to the situation in Europe. The traditional reconstruction of LGM Western Europe has been a treeless steppe-tundra as far south as southern France, with presumed refugia in the Mediterranean areas such as the Iberian and Italian peninsulas. However, fossils of thermophilous trees and mammals have been dated to the LGM in Belgium, England, Hungary, Slovakia, and Germany, among other places (Stewart and Lister, 2001). In addition, populations of numerous trees and animals such as Scots pine in Scotland (Stewart and Lister, 2001) and hedgehog in Germany (Willis and Whittaker, 2000) are either genetically distinct from Mediterranean populations (Scots pine) or have no southern relatives (hedgehog). For these species, it appears that they persisted throughout the LGM in refugia scattered across

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Europe in what is assumed to be a climate too cold for them to persist. Stewart and Lister (2001) interpret these refugia, most of those known being fossils from cave sites in steep valleys, as thermal refuges from the ice age cold. However, steep valleys are not particularly known for providing thermal refuges in present-day northern habitats. In fact, in hilly terrain, it is south and west facing midslopes and ridges that are warmest, not valleys, which receive less sun and are subject to cold air drainage. It is more likely that these valleys provided mesic refuges from the combined effects of a drier climate and the reduced water use efficiency caused by the CO₂ effect. The mesic plant communities would provide a home for the animals found there. Just such steep valley and stream-margin mesic refuges are found today in dry regions across the world. It is noteworthy that tree species that went extinct in Europe were less drought tolerant than surviving species (Svenning, 2004), as predicted by the CO₂ effect model. To an even greater extent than in North America, the reduction of tree cover due to the CO₂ effect may have given a false impression of extreme cold in Europe.

In summary, the entire interpretation of LGM vegetation and climate in eastern North America may have been biased by the CO₂ effect. It was neither as cold nor as dry as has been assumed. Lower treelines were probably caused by the CO₂ effect. The “no-analog” conifer woodlands are the direct result of changes in water use efficiency between taxa and the lumping of spruce species and sedge species into generic-level categories. The presence of spruce in eastern North America was *not* an indicator of a boreal climate. Massive vegetation dislocations and migrations did not occur prior to ice melt, and the entire LGM unglaciated region acted as a refuge for species of the eastern deciduous forest. This explains the almost complete lack of tree species extinctions in this region. It also suggests that the use of plant remains to predict climate for any period of the past in which CO₂ level was appreciably different from today may lead to incorrect conclusions unless the differential effect of CO₂ on growth rates of different species is accounted for.

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