Climate of the Past

Predicting Pleistocene climate from vegetation in North America

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Abstract. Climates at the Last Glacial Maximum have been inferred from fossil pollen assemblages, but these inferred climates are colder for eastern North America than those produced by climate simulations. It has been suggested that low CO_2 levels could account for this discrepancy. In this study biogeographic evidence is used to test the CO_2 effect model. 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 extremely cold or that temperate species had to migrate far to the south. An alternate hypothesis is that low CO_2 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. Thus climate reconstruction from pollen data is probably biased and needs to incorporate CO_2 effects. 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 reconstructions based on terrestrial plant indicators will not be valid for periods with markedly different CO_2 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; Davis and Shaw, 2001; 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 (e.g., Farrera et al., 1999; Nakagawa et al., 2002; Peyron et al., 1998; Tarasov et al., 1999; Webb et al., 1993, 1997) 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 (Ganopolski et al., 1998; Huntley et al., 2003; Kageyama et al., 2001; Pinot et al., 1999; Webb et al., 1993, 1997). Determining the correct paleotemperature is important for calibrating general circulation models (e.g., Crowley, 2000; Farrera et al., 1999; Ganopolski et al., 1998; Pinot et al., 1999). In addition, the vegetation composition at this time is consistently described as having no analogs in modern periods. In this paper it is argued that both of these anomalies arise from a combination of ambiguous pollen interpretation and the effects of low ambient CO_2 at the LGM which would have altered the relative dominance of different taxa in a manner that mimics colder and drier climates. Biogeographic and phylogenetic data are cited as independent tests of the CO_2 effect model.

The idea that glacial levels of CO_2 could affect vegetation structure and composition was proposed over a decade

ago (e.g., Beerling, 1996; Beerling and Woodward, 1993; Bennet and Willis, 2000; Cole and Monger, 1994; Cowling, 1999; Cowling and Sykes, 1999; Farquhar, 1997; Harrison and Prentice, 2003; Jolly and Haxeltine, 1997; Polley et al., 1993, 1995; Street-Perrott et al., 1997). Nevertheless, LGM climate as estimated from pollen data generally still does not factor in CO_2 effects (e.g., Elenga et al., 2000; Nakagawa et al., 2002; Peyron et al., 1998; Tarasov et al., 1999) and discussions of simulated LGM climate vs. vegetation (the anomaly problem) either do not mention the role of CO_2 (e.g., Ganopolski et al., 1998; Pinot et al., 1999) or only touch on this effect (e.g., Crowley, 2000; Huntley et al., 2003).

To date, the discussion has featured dueling models. Regression models based on pollen (which seem straightforward) are pitted against simulations of plant communities under low CO_2. It is tempting to be wary of the simulations because they cannot be directly verified. In what follows, several types of independent evidence are presented that imply that LGM climates inferred from pollen data are colder than the likely actual climates. These various types of evidence are shown to reconcile with effects of low ambient CO_2, thereby supporting the models of CO_2 effects. The results of the analysis also bear on questions of glacial refugia. The focus of this study is largely eastern North America for the sake of concreteness, but no-analog vegetation found elsewhere 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 Ushaped 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.

Tundra soils produce distinctive signs, due to processes such as solifluction, cryoturbation, ice wedges, and stone sorting. While such soil disturbances can coexist with trees (as in taiga) the lack of such signs rules out permafrost and therefore contradicts the existence of tundra. 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; Grüger, 1972a, b)

found evidence for temperate 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 (Clayton et al., 2001; 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, 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 in eastern North America as implied by most reconstructions. Wider periglacial zones did of course occur in Europe.

The lack of tundra puts limits on how cold this region could have been.

3 Taxonomic anomalies

A key species in the reconstruction of LGM climates in eastern North America 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 (see, e.g., Davis and Shaw, 2001). 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 (*Carex*). 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 CO_2 atmosphere (Beerling, 1996; Beerling and Woodward, 1993; Jolly and Haxeltine, 1997; Robinson, 1994; Saxe et al., 1998), 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 such as oaks across the "boreal parkland" (e.g., Webb et al., 1988, 1993, 1997), further calls into question their indicator status. When models are created for climate, the climatic tolerance of individual species is used to create a regression model that predicts climate, or a biome is defined from the dominant species, and that biome is used as an indicator of climate. Inclusion of ambiguous genera such as spruce in the model 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 midwestern temperate forest species to the Gulf Coast and Florida (the refugia for deciduous forest in the traditional model), 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 northern temperate species, most of which are either undetectable or diffusely rare across the region (Williams, et. al. 2004). It has been shown (Froyd, 2005; 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. The area in question consists of the geographically unbroken piedmonts and coastal plains of Georgia, South Carolina, Florida and Alabama. Except for fish, there are no real barriers keeping species from moving from east to west across these areas, and they indeed today share a common flora. There is no mechanism to create distinct refuges, as there was in Europe.

A major phylogeographic study (Soltis et al., 2006) shows that there is a lack of genetic structure concordance across taxa. The genetic structure of a species defines how unique alleles vary over space. Concordance of pattern should occur if species shared a common refuge, as did occur in Europe where concordance is more evident.

While it is evident that some species did retreat to the Gulf Coast (Soltis et al., 2006), there is no evidence for a comprehensive southern refuge for the bulk of the species.

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 high elevation 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.

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 (Pielou, 1991; Tallis, 1991). 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 (Hewitt, 2004). 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 (Soltis et al., 2006), suggesting that species during the Pleistocene were 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, weak or absent genetic gradients, and high genetic richness (Hewitt, 2004; Soltis et al., 2006). 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 (e.g., Baskin and Baskin, 1986, 1989; Estill and Cruzan, 2001; Qian, 1999; Schofield, 2004), 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 other species outcompete 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.

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.

Maps of the distribution of endemic species show that recently glaciated regions lack endemics (Estill and Cruzan, 2001; Qian, 1999; Schofield, 2004). 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 distributions 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 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 congenerics, complete reproductive isolation, and edaphic specialization. A number of endemic plants, for example, have no close relative in the East, and their nearest congener is in China or Europe (e.g., Qian, 1999). 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 sinkhole 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 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 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 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. If they had all been jammed together in a single refuge, they would have merged into a single species. 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 many species could be preserved would seem doubly problematic. This is particularly true due to the geography of eastern North America. The Gulf Coastal Plain lacks significant east-west barriers, so most plant species today occur across most of the plain if they occur there at all. There is no mechanism by which different races or related species of plant could be geographically isolated during the Pleistocene in this region.

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. Beech in formerly glaciated territory appear to originate from populations west of the Appalachian Mountains and just south of the ice sheet (McLachlan et al., 2005). Florida red maple (*Acer rubrum*) is genetically distinct from other red maple populations (McLachlan et al., 2005). Genetic data for red maple further support refugia close to the ice (Soltis et al., 2006). Evidence is also accumulating for southern Appalachian refugia for various animal species (e.g., Austin et al., 2002, 2004; Brant and Ortí, 2003; Church et al., 2003). 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 Gulf Coast, 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 geographically, further multiplying the number of required refuges. Phylogenetic analysis of these species leads to the same conclusion (Soltis et al., 2006).

5 Discussion

The anomalies documented here are not trivial. The biogeographic patterns expected for rapidly migrating species are observed in the glaciated zone, but rarely 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 CO_2 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. Second, a factor that also varied during the glacial period is CO_2, which was so low that it caused CO_2 starvation. CO_2 starvation does not affect all species equally.

At the LGM, about 18 000 years ago, CO_2 levels were very low, less than 200 ppm. This low level of CO_2 constitutes a severe deficiency for growth, and may have shifted competitive dominance between different plant types, as well as affecting overall vegetation biomass (Levis and Foley, 1999). Altered CO_2 levels could also affect pollen production, which would bias biome reconstruction. C_4 grasses have a strong advantage over other plants under low CO_2 (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 CO_2 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 CO_2 levels resulting from stomates being open longer (Drake et al., 1997; Saxe et al., 1998). Where water is not limiting, a cool low CO_2 climate should favor C_3 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 CO_2 climate would favor xeric species such as conifers, which have consistently low stomatal conductance, and herbaceous species, including grasses and sedges. Oaks, as trees with intermediate responsiveness, would have persisted as well on upland sites. 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; Levis and Foley, 1999). This explains the "no-analog" open forest (or parkland) often remarked upon. This discussion shows that species that currently occur together would diverge in their responses under the LGM climate, and that climate predictions based on their occurrence would not be correct. Exact simulations of vegetation would need to be based on more detailed studies of the physiology of each species, few of which have been done.

Simulations of the effect of low CO_2 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 CO_2 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 CO_2 levels. They would thus not correspond to snowline depressions (e.g., Greene et al., 2002) or other indicators of temperature.

If lowered CO_2 affected vegetation in eastern North America, what changes would 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. Significantly, mesic microsites such as coves, north slopes, and stream valleys would provide refuges for mesic species across their entire original range, especially in the highly dissected Appalachian region, because the effect of CO_2 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 CO_2 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. This analysis provides independent biogeographic support for model-based projections of the effects of CO_2 on LGM vegetation. Other factors such as altered fire regimes and herbivores could also impact the details of reconstructions.

The above discussion has implications for the locations of refugia in Europe. The traditional reconstruction of LGM Western Europe has been a treeless steppe-tundra as far south as southern France (Stewart and Lister, 2001), with presumed refugia in the Mediterranean areas such as the Iberian and Italian peninsulas (Stewart and Lister, 2001). 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; Willis and van Andel, 2004). 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 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 CO_2 effect. These mesic plant communities would provide a home for the animals found there. Just such steep valley and stream-margin 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 CO_2 effect model. To an even greater extent than in North America, the reduction of tree cover due to the CO_2 effect may have given a false impression of extreme dryness in Europe. It is not asserted that all aspects of the situation are analogous.

There are a number of implications of these results for

the practice of climate reconstruction and for testing climate models against historical proxy data. Regression or response surface approaches (e.g., Farrera et al., 1999; Nakagawa et al., 2002; Peyron et al., 1998; Tarasov et al., 1999; Web et al., 1993, 1997) implicitly assume that species' climate responses are stable over time, but the CO_2 effect model suggests that this assumption is violated. The use of plant functional types to reconstruct either biomes (e.g., Elenga et al., 2000) or climate (e.g., Peyron et al., 1998; Tarasov et al., 1999) has the same issues as response surface models and also assumes that similar species will respond to a changing climate as a group. It was shown above that normally co-occurring species will show divergent responses to CO_2 change. Very few studies can be found that take explicit account of CO_2 effects when reconstructing vegetation and climate (e.g., Guiot et al., 2000; Levis et al., 1999; Jolly and Haxeltine, 1997). Regression and response surface models, including models of plant functional types, also are unable to account for other changes in the conditions at the LGM. For instance, seasonal distributions of temperature were not strictly analogous to latitudinal shifts. That is, the colder temperatures at the LGM did not produce seasonal shifts that correspond to a simple northward movement of place. This throws off calibration of models of plant response to climate. Annual variability may have been altered, fire regimes may have been different, and in North America the presence of large herbivores that later went extinct really should not be ignored. All of these factors could have shifted the community composition in ways that would give the impression of some climate effect.

Testing of general circulation models is likewise affected by the CO_2 response of vegetation. While there is some recognition that CO_2 could affect pollen interpretations, the range of weight given to this issue ranges from none (Nakagawa et al., 2002; Pinot et al., 1999) to a consideration of only the C_3 vs. C_4 effect (Crowley, 2000; Farrera et al., 1999). Few climate model comparisons to paleotemperature proxies have fully factored in the CO_2 effects on leaf area, plant types, and water use efficiency in the temperature reconstruction. The treatment of vegetative cover and transpiration rate within climate simulation models is probably also deficient in this regard, though published descriptions of this model component are not usually adequate to determine exactly how vegetation is modeled.

In summary, the entire interpretation of LGM vegetation and climate in eastern North America may have been biased by the CO_2 effect. It was neither as cold nor as dry as has been assumed. Lower treelines were probably caused by the CO_2 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 CO_2 level was appreciably different from today may lead to incorrect conclusions unless the effect of CO_2 on relative growth rates is accounted for.

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References

Austin, J. D., Lougheed, S. C., Neidrauer, L., Chek, A. A., and Boag, P. T.: Cryptic lineages in a small frog: The post-glacial history of the spring peeper, *Pseudacris crucifer* (Anura: Hylidae), Molecular Phylogenetics and Evolution, 25, 316–329, 2002.

Austin, J. D., Lougheed, S. C., and Boag, P. T.: Discordant temporal and geographic patterns in maternal lineages of eastern North American frogs, *Rana castebeiana* (Ranidae) and *Pseudacris crucifer* (Hylidae), Molecular Phylogenetics and Evolution, 32, 799–816, 2004.

Baskin, J. M. and Baskin, C. C.: Distribution and geographical/evolutionary relationships of cedar glade endemics in southeastern United States, ASB Bulletin, 33, 138–154, 1986.

Baskin, J. M. and Baskin, C. C.: Cedar glade endemics in Tennessee, and a review of their autecology, J. Tennessee Academy Sci., 64, 63–74, 1989.

Beerling, D. J.: Ecophysiological responses of woody plants to past CO_2 concentrations, Tree Physiology, 16, 389–396, 1996.

Beerling, D. J. and Woodward, F. I..: Ecophysiological responses of plants to global environmental change since the Last Glacial Maximum, New Phytologist, 125, 641–648, 1993.

Bennett, K. D.: The spread of *Fagus grandifolia* across eastern North America during the last 18 000 years, J. Biogeogr., 12, 147–164, 1985.

Bennett, K. D. and Willis, K. J.: Effect of global atmospheric carbon dioxide on glacial-interglacial vegetation change, Global Ecol. Biogeogr., 9, 355–361, 2000.

Black, R. F.: Periglacial features indicative of permafrost: Ice and soil wedges, Quaternary Res., 6, 3–26, 1976.

Bradley, R. S.: Paleoclimatology: Reconstructing climates of the Quaternary, Second edition, Elsevier Academic Press, Amsterdam, 1999.

Brant, S. V. and Ortí, G.: Phylogeography of the northern short-tailed shrew, *Blarina brevicauda* (Insectivora: Soricidae): Past

fragmentation and postglacial recolonization, Molecular Ecol., 12, 1435–1449, 2003.

Braun, E. L.: *Deciduous forests of eastern North America*, Hafner Press, London, 1950.

Braun, E. L.: Plant distribution in relation to the glacial boundary, Ohio J. Sci., 51, 139–146, 1951.

Brown, J. H. and Gibson, A. C.: Biogeography, C. V. Mosby Co., St. Louis, MO, 1983.

Bryant, V.M., Jr.: A 16,000 year pollen record of vegetation change in central Texas, Palynology, 1, 143-156, 1977.

Bryant, V. M. and Holloway, R. G.: A late Quaternary paleoenvironmental record of Texas: An overview of the pollen evidence, 39-70 in V.M. Bryant and R.G. Holloway (eds.), Pollen records of late Quaternary North American sediments, American Association of Stratigraphic Palynologists Foundation, Dallas, 1985.

Burns, G. W.: Wisconsin age forests in western Ohio: II, Vegetation and burial conditions, Ohio J. Sci., 58, 220–230, 1958.

Burns, R. M. and Honkala, B. H.: Silvics of North America, Vol. 1, Conifers, USDA Handbook 654, 1990.

Cain, S. A.: Foundations of plant geography, Harper & Row, New York, 1944.

Cain, M. L., Damman, H., and Muir, A.: Seed dispersal and the Holocene migration of woodland herbs, Ecol. Monogr., 68, 325–347, 1998.

Camp, W. H.: A biogeographic and paragenetic analysis of the American beech (*Fagus*), 166–169 in Yearbook of the American Philosophical Society, 1950.

Church, S. A., Kraus, J. M., Mitchell, J. C., Church, D. R., and Taylor, D. R.: Evidence for multiple Pleistocene refugia in the postglacial expansion of the eastern tiger salamander, *Ambystoma tigrinum tigrinum*, Evolution, 57, 372–383, 2003.

Clayton, L., Attig, J. W., and Mickelson, D. M.: Effects of late Pleistocene permafrost on the landscape of Wisconsin, USA, Boreas, 30, 173–188, 2001.

Cole, D. R. and Monger, H. C.: Influence of atmospheric CO_2 on the decline of C_4 plants during the last deglaciation, Nature, 368, 533–536, 1994.

Cooper, A. W. and Mercer, E. P.: Morphological variation in *Fagus grandifolia* Ehrh. in North Carolina, Journal of Elisha Mitchell Scientific Society, 93, 136–149, 1977.

Cowling, S. A.: Simulated effects of low atmospheric CO_2 on structure and composition of North American vegetation at the Last Glacial Maximum, Global Ecol. Biogeogr., 8, 81–93, 1999.

Cowling, S. A. and Sykes, M. T.: Physiological significance of low atmospheric CO_2 for plant-climate interactions, Quaternary Res., 52, 237–242, 1999.

Crowley, T. J.: CLIMAP SSTs re-visited, Clim. Dyn., 16, 241–255, 2000.

Davis, M. B.: Quaternary history of deciduous forests of eastern North America and Europe, Annals of the Missouri Botanical Garden, 70, 550–563, 1983.

Davis, M. B.: Holocene vegetational history of the eastern United States, 166–181, in: Late-Quaternary environments of the United States, edited by: Wright Jr., H. E., Vol. 2, The Holocene, Longman, London, 1984.

Davis, M. B. and Shaw, R. G.: Range shifts and adaptive responses to quaternary climate change, Science, 292, 673–679, 2001.

Deevey Jr., E. S.: Biogeography of the Pleistocene, Geological Soc. Am. Bull., 60, 1315–1416, 1949.

Delcourt, H. R. and Delcourt, P. A.: Ice age haven for hardwoods, Natural History, 84, 22–28, 1984.

Delcourt, P. A. and Delcourt, H. R.: Paleoclimates, paleovegetation, and paleofloras during the late Quaternary, 71–94 in Flora of North America Editorial Committee (ed.), Flora of North America, Oxford University Press, New York, 1993.

Denny, C. S.: Pleistocene frost action near the border of the Wisconsin drift in Pennsylvania, Ohio J. Sci., 51, 116–125, 1951.

Drake, B. G., Gonzàlez-Meler, M. A., and Long, S. P.: More efficient plants: A consequence of rising atmospheric CO_2?, Ann. Rev. Plant Physiol. Plant Molecular Biol., 48, 609–639, 1997.

Elenga, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V., Bottema, S., Buchet, G., de Beaulieu, J.-L., Hamilton, A.C., Maley, J., Marchant, R., Perez-Obiol, R., Reille, M., Riollet, G., Scott, L., Straka, H., Taylor, D., Van Campo, E., Vincens, A., Laarif, F., and Jonson, H.: Pollen-based biome reconstruction for southern Europe and Africa 18 000 yr bp, J. Biogeogr., 27, 621–634, 2000.

Estill, J. C. and Cruzan, M. B.: Phytogeography of rare plant species endemic to the southeastern United States, Castanea, 66, 3–23, 2001.

Farquhar, G. D.: Carbon dioxide and vegetation, Science, 278, 1411, 1997.

Farrera, I., Harrison, S. P., Prentice, I. C., Ramstein, G., Guiot, J., Bartlein, P. J., Bonnefille, R., Bush, M., Cramer, W., von Grafenstein, U., Holmgren K., Hooghiemstra, H., Hope, G., Jolly, D., Lauritzen, S.-E., Ono, Y., Pinot, S., Stute, M., and Yu, G.: Tropical climates at the Last Glacial Maximum: A new synthesis of terrestrial palaeoclimate data. I. Vegetation, lake-levels and geochemistry, Clim. Dyn., 15, 823–856, 1999.

Finkelstein, S. A., Gajewski, K., and Viau, A. E.: Improved resolution of pollen taxonomy allows better biogeographical interpretation of post-glacial forest development: Analyses from the North American Pollen Database, J. Ecol., 94, 415–430, 2006.

Froyd, C. A.: Fossil stomata reveal early pine presence in Scotland: Implications for postglacial colonization analyses, Ecology, 86, 579–586, 2005.

Gamache, I., Jaramillo-Correa, J. P., Payette, S., and Bousquet, J.: Diverging patterns of mitochondrial and nuclear DNA diversity in subarctic black spruce: Imprint of a founder effect associated with postglacial colonization, Molecular Ecol., 12, 891–901, 2003.

Ganopolski, A., Rahmstorf, S., Petoukhov, V., and Claussen, M.: Simulation of modern and glacial climates with a coupled global model of intermediate complexity, Nature, 391, 351–356, 1998.

Gilbert, C. R.: Zoogeography of the freshwater fish fauna of southern Georgia and peninsular Florida, Brimleyana, 13, 25–54, 1987.

Givens, C. R., and Givens, F. M.: Age and significance of fossil white spruce (*Picea glauca*), Tunica Hills, Louisiana-Mississippi, Quaternary Res., 27, 283–296, 1987.

Gooding, A. M.: Illinoian and Wisconsin glaciations in the Whitewater basin, southeastern Indiana, and adjacent areas, J. Geol., 71, 665–682, 1963.

Greene, A. M., Seager, R. and Broecker, W. S.: Tropical snowline depression at the Last Glacial Maximum: Comparison with proxy records using a single-cell tropical climate model, J. Geophys. Res., 107(D8), doi:10.1029/2001JD000670, 2002.

Grüger, E.: Late Quaternary vegetational development in south-

central Illinois, Quaternary Res., 2, 217–231, 1972a.

Grüger, E.: Pollen and seed studies of Wisconsinan vegetation in Illinois, USA, Geological Soc. Am. Bull., 83, 2715–2734, 1972b.

Guiot, J., Torre, F., Jolly, D., Peyron, O., Boreux, J. J., and Cheddadi, R.: Inverse vegetation modeling by Monte Carlo sampling to reconstruct palaeoclimates under changed precipitation seasonality and CO_2 conditions: application to glacial climate in Mediterranean region. Ecol. Modell., 127, 119–140, 2000.

Harrison, S. P. and Prentice, C. I.: Climate and CO_2 controls on global vegetation distribution at the last glacial maximum: Analysis based on palaeovegetation data, biome modeling and palaeoclimate simulations, Global Change Biol., 9, 983–1004, 2003.

Harvill Jr., A.M.: Phytogeography of the Virginias and the equilibrium concept of landscape, Castanea, 38, 266–268, 1973.

Hewitt, G. M.: Genetic consequences of climatic oscillations in the Quaternary, Philosophical Transactions of the Royal Society of London B, 359, 183–195, 2004.

Hultén, E.: Outline of the history of Arctic and boreal biota during the Quaternary Period, Bokforlags Aktiebolager Thule, Stockholm, 1937.

Huntley, B., Alfano, M. J., Allen, J. R. M., Pollard, D., Tzedakis, P. C., de Beaulieu, J.-L., Grüger, E., and Watts, B.: European vegetation during Marine Oxygen Isotope Stage-3, Quaternary Res., 59, 195–212, 2003.

Jackson, S. T. and Givens, C. R.: Late Wisconsinan vegetation and environment of the Tunica Hills regions, Louisiana and Mississippi, Quaternary Res., 41, 316–325, 1994.

Jackson, S. T. and Weng, C.: Late Quaternary extinction of a tree species in eastern North America, PNAS, 96, 13 847–13 852, 1999.

Jacobson Jr., G. L., Webb III, T., and Grimm, E. C.: Patterns and rates of vegetation change during the deglaciation of eastern North America, 277–288, in: The geology of North America, Ruddiman, W. F. and Wright Jr., H. E., Vol. K-3, North America and adjacent oceans during the last deglaciation, Geological Soc. Am., 1987.

Jolly, D. and Haxeltine, A.: Effect of low glacial atmosphere CO_2 on tropical African montane vegetation, Science, 276, 786–788, 1997.

Kageyama, M., Peyron, O., Pinot, S., Tarasov, P., Guiot, J., Joussaume, S., and Ramstein, G.: The Last Glacial Maximum climate over Europe and western Siberia: a PMIP comparison between models and data, Clim. Dyn., 17, 23–43, 2001.

Levin, D. A. and Wilson, A. C.: Rates of evolution in seed plants: Net increase in diversity of chromosome numbers and species numbers through time, Proceedings of the National Academy of Sciences, 73, 2086–2090, 1976.

Levis, S. and Foley, J. A.: CO_2, climate, and vegetation feedbacks at the Last Glacial Maximum, J. Geophys. Res., 104, 31 191–31 198, 1999.

Maher Jr., L.J., Miller, N. G., Baker, R. G., Curry, B. B., and Mickelson, D. M.: Paleobiology of the sand beneath the Valders diamicton at Valders, Wisconsin, Quaternary Res., 49, 208–221, 1998.

Maxwell, J. A. and Davis, M. B.: Pollen evidence of Pleistocene and Holocene vegetation on the Allegheny Plateau, Maryland, Quaternary Res., 2, 506–530, 1972.

McLachlan, J. S. and Clark, J. S.: Reconstructing historical ranges with fossil data at continental scales, Forest Ecol. Manage., 197,

139–147, 2004.

McLachlan, J. S., Clark, J. S., and Manos, P. S.: Molecular indicators of tree migration capacity under rapid climate change, Ecology, 86, 2088–2098, 2005.

Mickelson, D. M., Clayton, L., Fullerton, D. S., and Borns Jr., H. W.: The late Wisconsin glacial record of the Laurentide ice sheet in the United States, 3-37 in: Late-Quaternary environments of the United States, edited by: Wright Jr., H. E., Vol. 1, The late Pleistocene, S.C. Porter (Ed.), University of Minnesota Press, Minneapolis, 1983.

Nakagawa, T., Tarasov, P. E., Nishida, K., Gotanda, K., and Yasuda, Y.: Quantitative pollen-based climate reconstruction in central Japan: application to surface and Late Quaternary spectra, Quaternary Sci. Rev., 21, 2099–2113, 2002.

Overpeck, J. T., Webb, R. S., and Webb III, T.: Mapping eastern North American vegetation change of the past 18 ka: No-analogs and the future, Geology, 20, 1071–1074, 1992.

Parker, K. C., Hamrick, J. L., Parkers, A. J., and Stacy, E. A.: Allozyme diversity in *Pinus virginiana* (Pinaceae): Intraspecific and interspecific comparisons, Am. J. Botany, 84, 1372–1382, 1997.

Péwé, T. L.: The periglacial environment in North America during Wisconsin time, 157–189 in: Late-Quaternary environments of the United States, edited by: Wright Jr., H. E., Vol. 1, The late Pleistocene, S.C. Porter (Ed.), University of Minnesota Press, Minneapolis, 1983.

Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., de Beaulieu, Bottema, S., and Andrieu, V.: Climatic reconstruction in Europe for 18 000 yr B.P. from pollen data, Quaternary Res., 49, 183–196, 1998.

Pielou, E. C.: After the Ice Age, University of Chicago Press, Chicago, 1991.

Pinot, S., Ramstein, G., Harrison, S. P., Prentice, I. C., Guiot, J., Stute, M., and Joussaume, S.: Tropical paleoclimates at the Last Glacial Maximum: Comparison of Paleoclimate Modeling Intercomparison Project (PMIP) simulations and paleodata, Clim. Dyn., 15, 857–874, 1999.

Polley, H. W., Johnson, H. B., Marino, B. D., and Mayeux, H. S.: Increase in C_3 plant water-use efficiency and biomass over glacial to present CO_2 concentrations, Nature, 361, 61–64, 1993.

Polley, H. W., Johnson, H. B., and Mayeux, H. S.: Nitrogen and water requirements of C_3 plants grown at glacial to present carbon dioxide concentrations, Functional Ecol., 9, 86–96, 1995.

Potts, R. and Behrensmeyer, A. K.: Late Cenozoic terrestrial ecosystems, 419–436, in: Terrestrial ecosystems through time, edited by: Behrensmeyer, A. K., Damuth, J. D., DiMichele, W. A., Potts, R., Sues, H.-D., and Wing, S. L., University of Chicago Press, Chicago, 1992.

Prentice, I. C., Bartlein, P. J., and Webb III, T.: Vegetation and climate change in eastern North America since the last glacial maximum, Ecology, 72, 2038–2056, 1991.

Qian, H.: Spatial pattern of vascular plant diversity in North America north of Mexico and its floristic relationship with Eurasia, Ann. Botany, 83, 271–283, 1999.

Ritchie, J. C.: Postglacial vegetation of Canada, Cambridge University Press, Cambridge, 1987.

Robinson, J. M.: Speculations on carbon dioxide starvation, late Tertiary evolution of stomatal regulation and floristic modernization, Plant, Cell Environment, 17, 345–354, 1994.

Roy, K., Valentine, J. W., Jablonski, D., and Kidwell, S. M.: Scales of climatic variability and time averaging in Pleistocene biotas: Implications for ecology and evolution, Trends in Ecology and Evolution, 11, 458–463, 1996.

Royall, P. D., Delcourt, P. A., and Delcourt, H. R.: Late Quaternary paleoecology and paleoenvironments of the central Mississippi alluvial valley, Geol. Soc. Am. Bull., 103, 157–170, 1991.

Saxe, H., Ellsworth, D. S., and Heath, J.: Tree and forest functioning in an enriched CO_2 atmosphere, New Phytologist, 139, 395–436, 1998.

Schofield, W. B.: Endemic genera of bryophytes of North America (north of Mexico), Preslia Praha, 76, 255–277, 2004.

Schoonmaker, P. K. and Foster, D. R.: Some implications of paleoecology for contemporary ecology, Botanical Rev., 57, 204–245, 1991.

Soltis, D. E., Morris, A. B., McLachlan, J. S., Manos, P. S., and Soltis, P. S.: Comparative phylogeography of unglaciated eastern North America, Molecular Ecol., 15, 4261–4293, 2006.

Stewart, J. R. and Lister, A. M.: Cryptic northern refugia and the origins of the modern biota, Trends Ecol. Evolution, 16, 608–613, 2001.

Street-Perrott, F. A., Huang, Y., Perrott, R. A., Eglinton, G., Barker, P., Khelifa, L. B., Harkness, D. D., and Olago, D. O.: Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems, Science, 278, 1422–1426, 1997.

Svenning, J.-C.: Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora, Ecol. Lett., 6, 646–653, 2003.

Tallis, J. H.: Plant community history, Chapman and Hall, New York, 1991.

Tarasov, P. E., Peyron, O., Guiot, J., Brewer, S., Volkova, V. S., Bezusko, L. G., Dorofeyuk, N. I., Kvavadze, E. V., Osipova, I. M., and Panova, N. K.: Last Glacial Maximum climate of the former Soviet Union and Mongolia reconstructed from pollen and plant macrofossil data, Clim. Dyn., 15, 227–240, 1999.

Watts, W. A.: The full-glacial vegetation of northwestern Georgia, Ecology, 51, 17–33, 1970.

Watts, W. A.: Postglacial and interglacial vegetation history of southern Georgia and central Florida, Ecology, 52, 676–689, 1971.

Watts, W. A.: The vegetation record of a mid-Wisconsin interstadial in northwest Georgia, Quaternary Res., 3, 257–268, 1973.

Watts, W. A.: Late Quaternary vegetation of central Appalachia and the New Jersey coastal plain, Ecol. Monogr., 49, 427–469, 1979.

Watts, W. A.: The late Quaternary vegetation history of the southeastern United States, Ann. Rev. Ecol. Syst., 11, 387–409, 1980a.

Watts, W. A.: Late Quaternary vegetation history at White Pond on the inner coastal plain of South Carolina, Quaternary Res., 13, 187–199, 1980b.

Watts, W. A. and Stuvier, M.: Late Wisconsin climate of northern Florida and the origin of species-rich deciduous forest, Science, 210, 325–327, 1980.

Webb III, T., Anderson, K. H., Bartlein, P. J., and Webb, R. S.: Late Quaternary climate change in eastern North America: A comparison of pollen-derived estimates with climate model results, Quat. Sci. Rev., 17, 587–606, 1997.

Webb III, T., Bartlein, P. J., Harrison, S. P., and Anderson, K. H.: Vegetation, lake levels, and climate in eastern North America for the past 18 000 years, 415–467, in: Global climates Since the Last Glacial Maximum, edited by: Wright Jr., H. E., Kutzbach, J. E., Webb III, T., Ruddiman, W. F., Street-Perrott, F. A., and Bartlein, P. J., University of Minnesota Press, Minneapolis, 1993.

Webb III, T., Bartlein, P. J., and Kutzbach, J. E.: Climatic change in eastern North America during the past 18 000 years: Comparisons of pollen data with model results, 447–462, in: The geology of North America, edited by: Ruddiman, W. F. and Wright Jr., H. E., , Vol. K-3, North American and adjacent oceans during the last deglaciation, Geological Society of America, 1988.

Whitehead, D. R.: Late Wisconsin vegetational changes in unglaciated eastern North America, Quaternary Res., 3, 621–631, 1973.

Wilkins, G. R., Delcourt, P. A., Delcourt, H. R., Harrison, F. W., and Turner, M. R.: Paleoecology of central Kentucky since the Last Glacial Maximum, Quaternary Res., 36, 224–239, 1991.

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

Willis, K. J. and van Andel, T. H.: Trees or no trees? The environments of central and eastern Europe during the Last Glaciation, Quaternary Sci. Rev., 23, 2369–2387, 2004.

Willis, K. J. and Whittaker, R. J.: The refugial debate, Science, 287, 1406–1407, 2000.

Wiser, S. K.: Comparison of southern Appalachian high-elevation outcrop plant communities with their northern Appalachian counterparts, J. Biogeogr., 25, 501–513, 1998.

Wolfe, J. N.: The possible role of microclimate, Ohio J. Sci., 51, 134–138, 1951.