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MODERN ANALOGS IN QUATERNARY PALEOECOLOGY: Here Today, Gone Yesterday, Gone Tomorrow?

Stephen T. Jackson[1]
Department of Botany, University of Wyoming, Laramie, Wyoming 82071; email: jackson@uwyo.edu

John W. Williams[1]
Limnological Research Center, Department of Geology and Geophysics, University of Minnesota, Minneapolis, Minnesota 55455; email: willi477@umn.edu

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■ **Abstract** Modern analog analysis, the comparison of Quaternary fossil pollen assemblages with modern assemblages, has long been a mainstay of paleoecological and paleoclimatic inference. The logic of analogical inference involves a comparative element (comparison of modern and fossil assemblages to select matches and assess goodness of fit) and a causal element (assumption that the relationships between modern vegetation and derivative pollen assemblages are matched by those between ancient vegetation and fossil pollen assemblages). An array of numerical and statistical tools have been developed to ensure objective, consistent, and quantitative assessments of similarity between pollen assemblages. Divergent or convergent relationships between vegetation and pollen assemblages can arise from a variety of sources, composing a potential source of error in analog analysis, but such errors can be anticipated and minimized. Pollen assemblages lacking modern analogs are well documented for the late-glacial period (17,000–10,000 years BP) in eastern North America and other regions. Simulated climates for this period also lacked modern analogs owing to increased seasonality of insolation, lowered CO_2, and persistent ice sheets. Most pollen assemblages from the last glacial maximum (23,000–20,000 years BP) in eastern North America have modern analogs, but macrofossil and other evidence suggest that the vegetation may have lacked modern analogs, owing to unique climate realizations and perhaps direct effects of lowered CO_2. Better understanding of the nature of past no-analog vegetation, and the underlying causes, will address important issues in ecology and evolutionary biology and help anticipate biotic responses to the no-analog greenhouse world of the near-future.

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[1] The authors contributed equally to the development of this paper.

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INTRODUCTION

Paleobiologists live in the present but study the past. In order to make sense of what they see in the fossil record, paleobiologists draw extensively from observations of the modern world. Taphonomic and actualistic studies of modern death-assemblages reveal the mechanisms by which fossil assemblages are formed. Form and function in living organisms inspire explanations of functional morphology of extinct organisms. Ecological patterns and processes in the modern world inform understanding of communities and ecosystems of the past. Our knowledge of paleobiology, from the Proterozoic through the Holocene, relies heavily on our experience and knowledge of the present.

Quaternary paleobiologists have a modest advantage over deep-time paleobiologists in that the fossil floras and faunas they study are similar or identical to modern biota. Some species- and genus-level extinctions have occurred during the Quaternary, particularly among vertebrates, and extant lineages underwent evolutionary change, but most Quaternary biota have modern counterparts. Accordingly, knowledge of living organisms and communities can be applied directly toward interpretation of the Quaternary fossil record. This ability has obvious advantages, but it can also be a trap, deceiving us into thinking that we have characterized the rules by which past communities and ecosystems have behaved, when we are actually missing some key elements. For example, knowledge of Quaternary variations in atmospheric CO_2 concentrations emerged only with analysis of ice cores in the early 1980s, and recognition that these variations may have played major roles in structuring plant communities and vegetation has developed only within the past ten years.

Quaternary palynologists work with data that are inherently quantitative, involving large sample sizes. Quaternary pollen assemblages from lakes and bogs integrate vegetation over a broad area (approximately 10^3 km^2), smoothing over local heterogeneities and site-specific biases. These properties have advantages as well as disadvantages. Pollen data lend themselves to formal, numerical approaches to interpretation, including quantitative comparison with modern pollen assemblages. However, what they record is something different from the plant communities or stands studied directly by ecologists. Taxonomic smoothing (owing to inability to discriminate among species and even some genera based on pollen morphology) leads to indeterminacy concerning species composition of vegetation. Differential representation (owing to differential pollen production, dispersal, and preservation among taxa) leads to some taxa being overrepresented and others being underrepresented or absent. Because of widespread pollen dispersal, an individual pollen assemblage represents a distance-weighted integration of vegetation within a radius spanning 10^1–10^2 km, much larger than a "plant community" as conventionally defined. Understanding how pollen assemblages record vegetation composition and pattern has been a major focus of research in Quaternary palynology for several decades, and development of tools to aid interpretation of fossil pollen assemblages has been a major priority for the field.

Among the most powerful tools for interpreting Quaternary pollen and other micropaleontological assemblages has been the analog technique, in which numerical methods (usually multivariate distance metrics) are used to compare individual fossil pollen assemblages with a large array of modern pollen assemblages (Overpeck et al. 1985, 1992; Huntley 1990). In this application, analog refers to a form of inference in which two entities that are alike in some respects are assumed to be similar in other respects as well. Thus, if a fossil pollen assemblage can be matched closely with a modern pollen assemblage, then the vegetation and environment that yielded the fossil assemblage is inferred to be similar to the vegetation and environment associated with the modern assemblage. Application of formal analog techniques has greatly advanced the ability to reconstruct vegetational and environmental changes, particularly since the last glacial maximum 21,500 years BP[2]. The techniques are particularly powerful because they are sensitive to quantitative as well as qualitative differences between assemblages. Widespread application of numerical analog techniques has helped confirm that many fossil pollen assemblages, particularly during the last glacial/interglacial transition, lack modern analogs. The existence of past vegetation lacking modern analogs, proposed by West (1964) based on macrofossil evidence, has important biogeographic, ecological, and paleoclimatic implications.

In this paper we review the logic, development, methodology, and applications of the analog approach in Quaternary paleoecology, emphasizing its successes and breakthroughs as well as its pitfalls and shortcomings. Our emphasis is on reconstructions of past vegetation composition from pollen data in North America and Europe, where the technique has been most thoroughly developed and widely applied. The analog approach has also been applied to paleoclimate reconstruction from fossil pollen data, but vegetation persists in these applications as an implicit intermediary between pollen and climate. Other forms of data (plant macrofossils, diatoms, foraminifera, etc.) have also been analyzed using formal analog methods. The general issues we discuss in this review are relevant to these various applications.

REASONING BY ANALOGY

Analogy is one of the most widespread forms of scientific reasoning in which identification of shared properties between two entities is used to infer that certain other properties are shared (Hesse 1966). In one of the most celebrated applications, Darwin (1859, 1897) observed that domesticated animals and plants possess traits that suit them for particular tasks or functions useful to humans, that breeders select among existing variations within populations for desirable traits (culling out less desirable traits), and that wild animals and plants possess traits that suit them

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[2] All ages reported are in calendar years Before Present (BP) (1950 datum), except where otherwise noted.

for life in their respective environments. He reasoned that the natural environment plays a selective role analogous to that played by breeders of domesticated species, and hence that adaptive traits in natural populations arise from natural selection. Darwin's arguments meet the key criteria identified by Hesse (1966) for successful application of analogy: 1. clear and definable similarities exist between entities (domestic and wild organisms have traits that fit particular functions), 2. positive analogies outweigh negative analogies in some meaningful sense (e.g., the fact that domesticated species are held captive in contrast to wild species is unimportant and even irrelevant in this particular context), and 3. causal relationships within entities are demonstrable (many traits in domesticated species are clearly attributable to artificial selection among natural variants by humans) or plausible (the natural environment varies in space and time, individuals vary within natural populations, "culling" occurs because of overproduction of offspring, and hence natural selection for useful traits can occur).

The logical structure of argument by analogy is portrayed in Figure 1. Two entities, *A* and *B*, have observable properties (*a* and *b*) that are similar. Entity *A* has a second property *a*′ which is also observable, but Entity *B*'s counterpart property

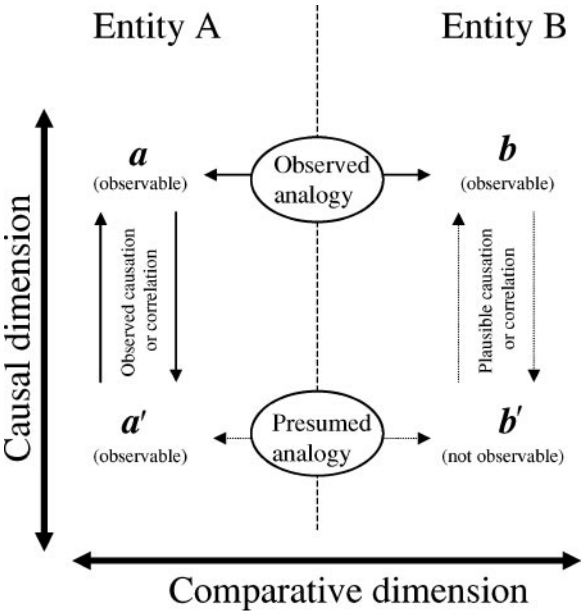

Figure 1 Schematic diagram of the logic of reasoning by analogy, after Hesse (1966). Two different entities (*A* and *B*) are represented. The terms *a*, *a*′, and *b* represent observable properties; *b*′ is a property of Entity *B* that cannot be observed directly. In Entity *A*, the properties *a* and *a*′ are causally linked. The properties *a* and *b* are shared by or similar between the two entities. By analogy, the unobservable property *b*′ of Entity *B* would be considered similar to property *a*′ of Entity *A*.

(b') is not directly observable. By analogy, the shared or similar properties a and b lead to the inference that unknown property b' of Entity B is similar to known property a' of Entity A. In application, these relationships are often treated as proportionalities, where a is to a' as b is to b':

$$a/a' \propto b/b' \qquad (1)$$

Therefore, if a, b, and a' are known, b' can be inferred or estimated. Furthermore, if property b changes, the corresponding change in b' can be assessed based on the change in a' imposed by a similar change in a.

This form of reasoning has weaknesses, however (Hesse 1966), which fall into two categories corresponding to the comparative and causal dimensions of Figure 1. First, some differences will always exist between any two natural entities. Thus, any two entities will have some shared properties and some nonshared properties. Judgment must be imposed to determine the relative importance of positive analogies and negative analogies between entities. Second, relations along the vertical (causal) axis may not be shared between the two entities; correlative relationships between a and a' do not necessarily imply similar relationships between b and b'. Arguments from analogy are strengthened when relationships among properties within each entity (i.e., along the vertical axis) are demonstrably or plausibly causal and when negative analogies between the entities do not involve essential properties or causal relations (Hesse 1966). Confidence in analogy-based inference is further strengthened by additional independent observations, analogies, or arguments that also support the inference. For example, Darwin did not stop with the analogy between selection in domesticated and natural populations, but drew upon observations from natural history and biogeography as well as other analogies to support his theory of evolution by natural selection (Darwin 1859, Gould 2002).

ANALOG ANALYSIS IN QUATERNARY PALEOECOLOGY

The preceding discussion provides a framework for examining the application of modern analogs in Quaternary ecology, where two classes of entities are compared, one fossil and one modern. The first consists of an array of sites (lakes, wetlands, traps, etc.) across the landscape where modern pollen assemblages have been obtained. Composition of these pollen assemblages—the proportions of various plant taxa—represents one property for each entity (a). Each entity also has a second property, vegetation (a'), which consists of the composition and (frequently) spatial array of plant communities surrounding the site within some radius appropriate to pollen dispersal properties and basin size. Vegetation can be defined in various ways, ranging from a generalized characterization of the dominant formation (e.g., tundra, boreal forest, deciduous forest) to a distance-weighted quantitative expression of the abundances of constituent species. A causal relationship exists between the pollen assemblage collected at a site and the surrounding vegetation that contributes the pollen (Prentice 1988, Jackson 1994). However, pollen assemblages are also subject to a variety of taphonomic processes, which can bias and distort the pollen-vegetation relationship.

The second class of entities consists of an array of particular sites at various times in the past. Composition of pollen assemblages from each entity (*b*) is known, based on pollen analysis from a dated sediment horizon or sample. The goal is to infer composition of the vegetation responsible for the fossil pollen assemblage (b'), which is unknown, from the pollen assemblage. The fossil assemblage is compared with an array of modern pollen assemblages to identify the best-matching modern assemblage. The proportionality relationship in Equation 1 is then applied. The numerator terms *a* and *b* represent the modern and fossil pollen assemblages, respectively, and the denominator terms a' and b' represent the modern and ancient vegetation, respectively. Thus, if equivalence is identified between the modern and fossil pollen assemblages ($a \simeq b$), a parallel equivalence is assumed for the denominator terms ($a' \simeq b'$), and the ancient vegetation is inferred to be similar in composition to the corresponding modern vegetation associated with the modern pollen assemblage (Overpeck et al. 1985). (A related application, which we do not discuss in detail, is the use of the degree of difference between fossil pollen assemblages to infer degree of difference or change in vegetation. This logic underlies multivariate analyses of fossil pollen assemblages aimed at estimating rates and magnitudes of temporal change in vegetation (Bennett & Humphry 1995; Grimm & Jacobson 1992; Huntley 1992; Jacobson & Grimm 1986; Overpeck et al. 1991, 1992; Williams et al. 2001).

Pollen analysis has been widely applied in Quaternary ecology since the 1920s, but analog analysis awaited the accumulation of large spatial arrays of modern pollen assemblages, which were first developed in Europe and North America (Aario 1940, Davis 1967, Lichti-Federovich & Ritchie 1968, Wright 1967). Initial applications were informal, involving judgmental matching of modern and fossil assemblages (Davis 1967, 1969; McAndrews 1966; Wright 1967), although some early numerical efforts applied Pearson's product-moment (Davis et al. 1975, Ogden 1977, Ritchie 1977), Spearman's rank correlation coefficients (Ogden 1969, Whitehead & Tan 1969), and Euclidean distance (Whitehead 1979, 1981). The advent of computerized algorithms for multivariate analysis in the 1970s led to formal, numerical matching of fossil and modern pollen assemblages using multivariate distance metrics (Birks & Gordon 1985, Prentice 1980). A watershed was reached with a comprehensive study of some 1618 modern pollen assemblages from eastern North America in which the statistical properties of various distance metrics were compared (Overpeck et al. 1985). Pollen assemblages within and among vegetation formations (e.g., tundra, boreal forest, mixed forest, deciduous forest, etc.) were compared numerically to identify empirical thresholds for evaluating matches and mismatches (Overpeck et al. 1985).

Although the tools have improved with time, the overall logic of analog analysis has remained the same since the early applications in the 1960s. Individual fossil pollen assemblages are compared with a large array of modern assemblages. If the best match between a particular fossil sample and a modern sample meets some minimum criterion (typically an empirically determined numerical threshold), the modern sample is considered a positive analog and the past vegetation at the fossil site is considered to bear some similarity to the vegetation associated with the modern sample. If no samples in the modern array meet the minimum match criterion, the fossil assemblage is determined to have no modern analog, and past vegetation corresponding to that sample is considered to be compositionally unlike any modern vegetation in the universe of modern samples used (Overpeck et al. 1985).

In any particular comparison of a fossil pollen assemblage with a modern assemblage, two kinds of errors can arise: (*a*) false positive, consisting of an erroneous inference of a positive match (i.e., vegetation represented by the fossil assemblage was actually different from that represented by the modern assemblage), and (*b*) false negative, where a mismatch is wrongly inferred (i.e., vegetation represented by the fossil assemblage was actually similar to that associated with the modern pollen assemblage) (Wahl 2004). In comparing a particular fossil assemblage to an array of modern assemblages, the binary decision of whether the fossil assemblage has a modern counterpart (and corresponding vegetation analog) or lacks one (and hence represents vegetation unlike any on the modern landscape), the same classes of errors arise as an aggregate. At that level, a false positive inference would consist of assigning a modern analog to a pollen assemblage that represented vegetation lacking a modern counterpart, and a false negative would occur when a fossil assemblage was wrongly determined to represent unique past vegetation.

These errors can arise either from misapplications along the comparative dimension or from problems in the causal dimension (Figure 1). Errors along the comparative dimension consist of false matches or mismatches between pollen assemblages, whereas those along the causal dimension arise from uncertainties or indeterminacies in the relationships between pollen and vegetation. In the following two sections, we explore the theory, evidence, and tools relevant to the comparative dimension of matching pollen assemblages and the causal dimension of pollen-vegetation relationships, respectively.

THE CAUSAL DIMENSION: RELATING POLLEN ASSEMBLAGES TO VEGETATION COMPOSITION

Of the two dimensions in analogical reasoning, the causal dimension is generally the more problematic as a source of error (Hesse 1966). The general causal relationship between vegetation composition and pollen assemblage composition is not in doubt: Pollen assemblages consist of pollen grains emitted by and dispersed from individual plants on the surrounding landscape. Theoretical and empirical studies illustrate the relationships between vegetation and pollen assemblages, and the processes governing assembly of pollen assemblages are well understood in a general way (Andersen 1970; Davis 1963, 2000; Jackson 1994; Jackson & Lyford 1999; Prentice 1986, 1988; Sugita 1994; Webb 1974; Webb et al. 1978;

Webb & McAndrews 1976). These studies confirm that spatial and temporal variation in pollen assemblages corresponds to spatial and temporal variation in vegetation composition. Although differences among pollen assemblages are not necessarily proportional to vegetational differences, a general correspondence between the two data types is well documented at a variety of spatial scales, from individual forest stands to continents (Bradshaw & Webb 1985, Calcote 1998, Jackson 1990, Jackson & Kearsley 1998, Parshall & Calcote 2001, Solomon & Webb 1985).

The critical problem along the causal dimension in analog analysis is the potential nonsingularity of the relationship between vegetation and pollen assemblages (Figure 2). In a perfect world, the relationship would be singular, with any given plant community yielding one and only one pollen assemblage, and conversely any given pollen assemblage arising from one and only one vegetational array. Unfortunately, the relationship between vegetation and pollen assemblages is more complicated and includes convergences (similar pollen assemblages deriving from different vegetational arrays) and divergences (single vegetational arrays giving rise to different pollen assemblages) (Figure 2). In the context of analog applications,

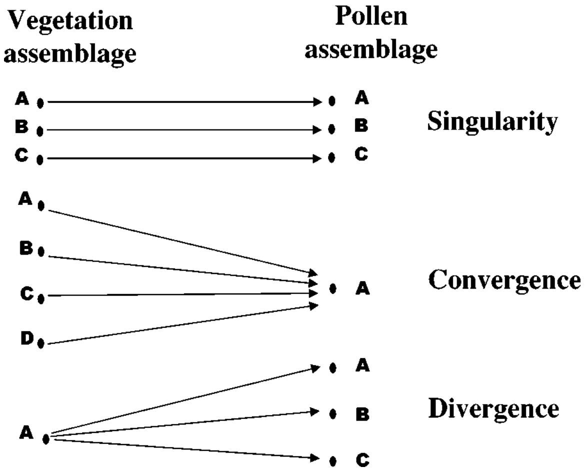

Figure 2 Three conceivable relationships between pollen assemblages and vegetation on the surrounding landscape. Singularity occurs when there is a unique, one-to-one relationship between pollen assemblage and vegetation. Inferring vegetation from pollen data is then straightforward. Convergence occurs when multiple vegetation types or arrays give rise to similar pollen assemblages; this can occur, for instance, owing to taxonomic imprecision in pollen assemblages, dominance of palynologically "silent" taxa, and different combinations of local and distant vegetation patches. Divergence occurs when multiple pollen assemblages are derived from a single vegetation type. This can result from differing pollen source-strengths, composition of vegetation contributing background pollen, differences among basins in pollen-collecting or preservation properties, or other factors.

convergence can lead to false positive analogies (i.e., choosing as the best match a modern pollen assemblage associated with vegetation very different from the target sample). Conversely, divergence can give rise to false negative analogies (i.e., rejecting pollen assemblages that are actually associated with vegetation similar to the target sample).

Convergence can originate from the relatively coarse taxonomic resolution of pollen assemblages. Plant communities differing substantially in genus-level and/or species-level composition (and hence associated with very different environments) can produce similar pollen assemblages (Jackson & Whitehead 1993). For example, modern oak-pine forests might look similar palynologically, regardless of whether the forests were in Massachusetts (*Pinus rigida*, *Quercus alba*, *Q. rubra*) or Mississippi (*P. taeda*, *P. echinata*, *Q. falcata*, *Q. nigra*, *Q. stellata*). Palynologists tend to discount low taxonomic resolution as a source of error in analog studies, and assume that the pollen assemblages will include at least a few taxa with high taxonomic precision (pollen types that are monotypic in the study region (e.g., *Fagus* in eastern North America or Europe) or for which species-level resolution is achievable) or diagnostic features (e.g., restricted geographic distributions and/or climate tolerances). Thus, in the example above, Mississippi assemblages might be distinguished by low percentages of *Liquidambar*, *Celtis*, and/or *Taxodium* pollen, whereas Massachusetts sites might be characterized by modest amounts of *Picea*, *Tsuga*, and/or *Fagus* pollen (Delcourt et al. 1984). There is, however, some danger of circularity in applying this reasoning to fossil pollen assemblages owing to the possibility of unique combinations of species that do not co-occur today.

Convergence and divergence can arise because pollen assemblages are determined not only by source vegetation but by a number of intervening processes and factors, including pollen productivity, pollen dispersal, depositional environment, pollen preservation, and sampling techniques (Webb et al. 1978, Webb & McAndrews 1976). These various factors impart biases and distortions to pollen assemblages. If these biases are relatively small, well characterized, and invariant in space and time, then the singularity of the vegetation-to-pollen relationship should be conserved, and the primary source of error in analog analysis will be convergence resulting from taxonomic imprecision. Unfortunately, this is not always the case: Biases can be substantial, are not always clearly recognized, and can vary spatially and temporally. We explore how pollen productivity, dispersal, and related properties can lead to convergence and/or divergence, and how errors arising from these sources can be recognized and minimized.

Pollen Productivity

Pollen productivity—the number of pollen grains produced per unit plant-abundance—varies widely among plant taxa. For example, *Pinus* trees produce much more pollen per unit biomass than *Fagus* trees, which in turn are more productive than *Larix* trees (Birks & Birks 1980). Variations among species within genera are poorly documented but may be substantial. Interspecific or intergeneric variations in pollen productivity within pollen morphotypes might tend to reinforce the singularity of vegetation/pollen relationships, all else held constant, by imparting a characteristic percentage signature to pollen assemblages from different vegetation types. For example, assemblages from oak-pine forests in one region might have consistently higher oak pollen percentages than in another, despite similar proportions of oak and pine in the forests, simply because the oak species in the first region was more productive. Interspecific or intergeneric variations in productivity might, however, lead to convergence or divergence when several species within the same morphotype co-occur. Changes in relative abundances of species within the same pollen morphotype (e.g., *Quercus* or *Pinus*) within the same general vegetation type (e.g., southeastern oak-pine forest) might lead to disproportionate changes in pollen assemblages. The degree of interspecific variation in pollen productivity and the potential consequences for interpretation of pollen assemblages, respectively, deserve empirical and theoretical study.

Within many species, pollen productivity may be influenced by plant age, growth form, vegetation structure, and environmental factors (Jackson 1994). Systematic variation in one or more of these factors through time may have a strong influence on pollen representation. One of the most troubling is the potential effect of varying CO_2 concentrations, which influences allocation of resources to growth, reproduction, and structure within plants (Field et al. 1992, Mooney 1991). Elevated CO_2 experiments show that plant allocation to reproduction is sensitive to CO_2 concentrations (Farnsworth 1995, He & Bazzaz 2003, LaDeau & Clark 2001, Ward & Strain 1997). *Ambrosia artemisiifolia* plants grown at ambient CO_2 concentrations of 700 ppm produced substantially more pollen than individuals grown at the current ambient concentrations of 350 ppm (Wayne et al. 2002, Ziska & Caulfield 2000). Although some of this increase is attributable to increased net primary production, the number of flowering shoots and the amount of pollen per flowering shoot also increased (Ziska & Caulfield 2000). Direct and indirect influences of lowered glacial-age CO_2 concentrations on pollen productivity are unknown; experimental studies are needed to determine potential effects of lowered CO_2 on pollen productivity, and whether those effects differ systematically among taxa or growth forms.

Sedimentary pollen assemblages are heavily biased toward taxa with high pollen productivity and wind dispersal. Many animal-pollinated taxa and some unproductive and/or poorly dispersed wind-pollinated taxa are poorly represented in pollen assemblages, and in many cases are unreliable as indicators of presence/absence or abundance in vegetation (e.g., *Liriodendron*, *Magnolia*) (Delcourt et al. 1984). Others (e.g., *Populus*, Cupressaceae) are often poorly represented owing to poor preservation. Such underrepresented taxa are particularly problematic. A *Liriodendron*-dominated forest with *Quercus* and *Carya* as subdominants might be indistinguishable palynologically from forest dominated by *Quercus* and *Carya*. The extent of this problem depends on how fine the required vegetational discriminations are. For example, at the coarse level of the formation (a regional vegetation unit defined primarily by physiognomy) both forests will be classified as temperate deciduous forest (e.g., Overpeck et al. 1992), so there is no problem. But the information loss in cases where important taxa are severely underrepresented in pollen assemblages can lead to substantial convergence and erroneous assignment of modern analogs to fossil assemblages under some circumstances.

Pollen Dispersal and its Consequences

Pollen dispersal is dependent on several factors, including the pollination mechanism (i.e., wind versus animal transport), the morphology of the pollen grain, the structure of the pollen-bearing organ, the nature of pollen entrainment into the atmosphere, the stability and other properties of the atmosphere, and the physical structure of the vegetation and the landscape (Jackson & Lyford 1999). Pollen morphotypes vary in size, shape, and density, and hence in dispersal properties. Some interspecific variation in pollen size exists within some genera (e.g., Durham 1946, Eisenhut 1961, Whitehead 1964). Typically, these variations are small compared to the intergeneric variation in pollen morphology and sedimentation velocity [see figure 3 and appendix 2 in Jackson and Lyford (1999)]. These dispersal properties, as well as the functional morphology of the pollen-bearing organs, can be safely assumed to be invariant within taxa at Quaternary timescales. Environmentally induced changes in dispersal (e.g., increased gustiness or wind speed) might have greater effect overall (Jackson & Lyford 1999), but the direction of the effects would be similar among different pollen types. Influence of these variations on analog analyses is probably trivial.

Two critical properties of pollen data derive from atmospheric pollen dispersal. First, pollen assemblages comprise distance-weighted integrations of surrounding vegetation, with the weightings imposed by the pollen-dispersal properties of the respective taxa and the spatial array of vegetation surrounding the depositional site (Jackson 1990, Prentice 1988, Sugita 1994). Second, size of the depositional basin influences the relative contributions of nearby and distant vegetation to pollen assemblages; in general, as basin size decreases, relative pollen contributions from local vegetation will be amplified (Jackson & Lyford 1999, Prentice 1988, Sugita 1994). Consequences of these properties for interpretation of analog analyses have not been assessed formally, although it could be easily done by extending past modeling efforts (Davis & Sugita 1997, Sugita 1994, Sugita et al. 1997).

Interpretational errors deriving from basin-size effects are probably minimal. Basin size exerts its strongest effects on pollen representation at relatively small sizes (Jackson 1994; Jackson & Lyford 1999; Prentice 1985, 1988; Sugita 1993, 1994). Pollen assemblages from basins larger than 1 to 5 hectares (ha) in surface area tend to perceive surrounding vegetation at similar scales, and most fossil and modern sites are $\geq$5 ha in size. Editing of the array of modern pollen assemblages to fit the sampling properties (basin size, site type) of the fossil site can further minimize errors from this and related sources.

The frequency and magnitude of errors arising from the influence of spatial vegetation patterns are probably minimal for most Holocene analog applications. The relatively coarse resolution of vegetation types (typically at the formation level) in most applications to date, and the relatively small amount of major structural and compositional change in vegetation of the past 6000 to 9000 years, render the analog analyses robust. This is confirmed by the general congruence between results of analog analyses and alternative analyses of pollen data (e.g., Jackson et al. 2000; Williams 2003; Williams et al. 2001, 1998), and between analog results and plant-macrofossil records (Jackson et al. 1997).

Greater uncertainty is associated with glacial-age, late-glacial, and early Holocene applications of modern analogs. Pollen assemblages lacking modern analogs are numerous and widespread in the late-glacial and early Holocene, indicating that something was different—either unique vegetational composition or unique spatial arrays of plant communities on the landscape. Although glacial-age pollen assemblages generally have modern analogs, independent evidence from plant macrofossils and phylogeography suggest that vegetation composition and spatial pattern may have been very different then. After reviewing analytical considerations for the comparative dimension of analog analysis, we discuss and evaluate these two case studies in detail, which illustrate both the uncertainties associated with analog analysis and the roles analog analysis can play in informing paleoecological interpretation and provoking further investigations.

THE COMPARATIVE DIMENSION: MATCHING FOSSIL AND MODERN POLLEN ASSEMBLAGES

Quaternary pollen assemblages are conventionally expressed as percent abundance of constituent taxa based on a designated pollen sum (usually consisting of all or most terrestrial pollen types). The primary analytical task in analog analysis consists of identifying modern assemblages most similar to the fossil assemblage of interest. The fossil sample is compared numerically, using a multivariate distance metric, with each member of an array of modern pollen samples (Figure 3). The modern sample or samples nearest the fossil sample (i.e., lowest multivariate distance) are selected as the best matches. The three critical choices involved in analog analysis are (*a*) selecting the distance-metric, (*b*) identifying the universe of modern pollen samples for comparison, and (*c*) assessing whether the fossil sample has one or more suitable modern analogs. An additional series of decisions centers on how best to present and utilize results of the analyses.

Selecting the Distance Metric

A large array of multivariate distance metrics are potentially available for matching pollen assemblages (Legendre & Legendre 1983, Prentice 1980). Prentice (1980) classified distance metrics into three categories based on the relative weights given

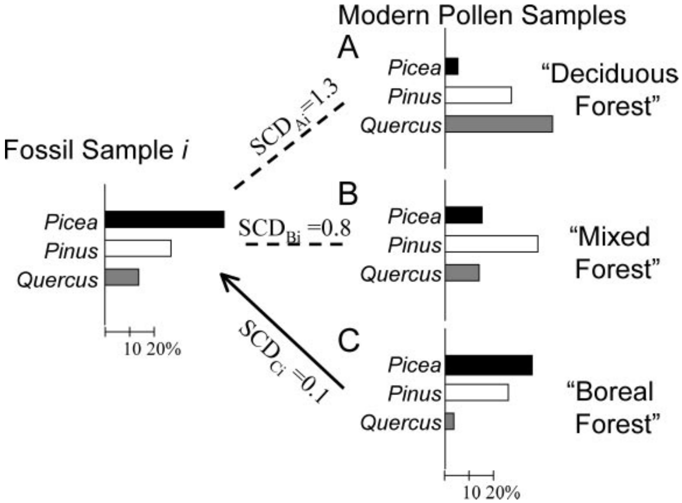

Figure 3 Schematic illustrating the modern analog technique in which the objective is to draw an inference about past vegetation or environment, based upon the similarity between fossil and modern pollen samples and knowledge about modern vegetation and/or environment. Here a fossil pollen sample *i* is compared to three modern pollen samples, collected from a deciduous forest (*A*), cool mixed forest (*B*), and boreal forest (*C*). For simplicity, each pollen spectrum is represented by three pollen types (*Picea*, *Pinus*, and *Quercus*). The dissimilarity between fossil pollen sample *i* and samples *A*, *B*, and *C* is quantified using the squared-chord distance (SCD) metric, where 0 indicates exact similarity and higher values indicate increasing dissimilarity. Because modern pollen *C* is compositionally the most similar (i.e., it has the lowest SCD), fossil pollen sample *i* is inferred to have originated from a boreal forest.

to abundant and rare taxa (Figure 4). Simple distance metrics provide no weightings, and hence are dominated by the most abundant taxa in pollen assemblages, whereas equal-weight distance metrics are highly sensitive to small variations in relatively rare or uncommon taxa. These measures are respectively analogous to (unweighted) covariance or (standardized, and hence equally weighted) correlation in statistical analysis. Because pollen assemblages typically include a mixture of both abundant and rare types, and because we want to make most efficient use of all of the information in the assemblages, the simple and equal-weight metrics are not well suited for most pollen percentage data, in spite of their intuitive simplicity (Prentice 1980).

A third category, signal-noise distance metrics, has intermediate properties, providing modest upweighting of uncommon types, and performs well in practice with pollen percentage data (Bennett & Humphry 1995, Overpeck et al. 1985). Overpeck et al. (1985) demonstrated empirically that signal-noise distance metrics were more effective in analog analysis than simple and equal-weight metrics,

Unweighted

Manhattan metric $d_{ij} = \sum_k \left| p_{ik} - p_{jk} \right|$

Euclidean distance $d_{ij} = \sqrt{\sum_k \left(p_{ik} - p_{jk} \right)^2}$

Squared cosine-t distance $d_{ij} = \sum_k \left(\frac{p_{ik}}{\left(\sum_k p_{ik}^2\right)^{0.5}} - \frac{p_{jk}}{\left(\sum_k p_{jk}^2\right)^{0.5}} \right)^2$

Equal Weight

Standardized Euclidean distance $d_{ij} = \sqrt{\sum_k \left(\frac{p_{ik} - p_{jk}}{s_k} \right)^2}$

Canberra metric $d_{ij} = \sum_k \frac{\left| p_{ik} - p_{jk} \right|}{p_{ik} + p_{jk}}$

Signal to Noise

Squared chord distance $d_{ij} = \sum_k \left(p_{ik}^{0.5} - p_{jk}^{0.5} \right)^2$

Information statistic $d_{ij} = \sum_k \left(p_{ik} \ln \frac{2p_{ik}}{p_{ik} + p_{jk}} + p_{jk} \ln \frac{2p_{jk}}{p_{ik} + p_{jk}} \right)$

Squared X² (X1) $d_{ij} = \sum_k \frac{\left(p_{ik} - p_{jk} \right)^2}{p_{ik} + p_{jk}}$

Squared X² (X2) $d_{ij} = \sum_k \frac{\left(p_{ik} - p_{jk} \right)^2}{\sum_i p_k}$

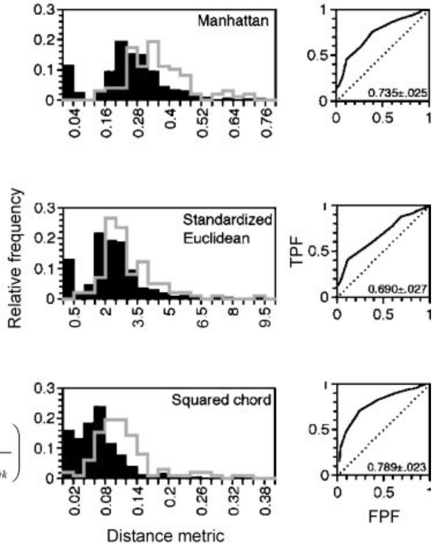

Figure 4 Formulas for common metrics of dissimilarity (Bennett & Humphry 1995, Overpeck 1985, Prentice 1980), aggregated by type (unweighted, equal weight, and signal to noise). Notation: d_{ij} = the dissimilarity between pollen samples *i* and *j*; p_{ik} = the fraction of pollen type *k* in sample *I*; s_k = the standard deviation of proportions for p_k across all pollen samples. The plots at the right show the effectiveness of three representative metrics for discriminating between modern pollen samples collected from the deciduous broadleaf and southern evergreen/mixed forests in eastern North America (Gavin et al. 2003). The histogram plots show (*a*) the minimum distances among pollen samples from the deciduous broadleaf forest (*black bars*) and (*b*) the minimum distances from deciduous forest pollen samples to samples from the southern mixed forest (*gray line*). Low levels of overlap between the histograms indicate that the dissimilarity measure is able to discriminate the two vegetation types. The discriminatory ability of each metric can be evaluated by counting the number of pairs correctly identified as matches (TPF) and number of pairs incorrectly identified as matches (FPF) across all possible threshold values. The total area under the FPF:TPF curve (AUC) provides an overall measure of discriminatory ability for the metric. In this example, the squared-chord measure has the highest discriminatory ability (AUC = 0.789 ± 0.023), followed by the Manhattan and standardized Euclidean metrics. Redrawn from Gavin et al. (2003).

and the three signal-noise metrics [chord distance, information statistic, χ^2(X1)] performed similarly. Chord distance has been applied in nearly all subsequent analog and rate-of-change studies (Anderson et al. 1994, 1989; Baker et al. 1989; Cheddadi et al. 1997; Gajewski et al. 2000; Gavin et al. 2001; Huntley 1990; Jackson et al. 2000; Nakagawa et al. 2002; Overpeck et al. 1992; Sawada et al.

1999; Willard et al. 2003; Williams et al. 2001), although weighted log-transformed Euclidean measures have also been used in paleoclimate reconstructions (Guiot 1987, 1990) and Bennett & Humphry (1995) argue that an alternative χ^2 coefficient [χ^2(X2)] performs better with certain datasets.

The signal-noise metrics have performed well in temperate and boreal regions, where differences among vegetation formations are accompanied by relatively subtle changes in uncommon taxa (e.g., *Acer*, *Juglans*, *Tilia*) as well as larger changes in taxa that are abundant in some formations but not others (e.g., *Pinus*, *Betula*, *Quercus*, Poaceae). However, in some regions, particularly where local pollen productivity is very low (e.g., tundra) and hence assemblages are heavily dominated by a few taxa (often from distant sources), equal-weight distance-metrics may be more effective in accurate analog-matching (Oswald et al. 2003). In these settings, presence/absence of rare pollen types (e.g., *Rubus*, *Thalictrum*, *Selaginella*) contains useful information that is amplified by the equal-weight metrics. Formal analog methods have not been applied widely in the wet tropics. Pollen assemblages in such regions are highly diverse, and presence/absence data appear to be as informative as percentage data in paleoecological applications (Weng et al. 2004). Equal-weight distance-metrics may be especially suitable in much of the tropics, where rare taxa provide most of the vegetational information in pollen assemblages.

Identifying the Universe of Modern Pollen Samples

The success of the analog method, both in determining whether suitable modern analogs exist and, if so, identifying the best matches, depends critically on the size and scope of the modern pollen-assemblage dataset. If the dataset is too limited, errors (both false positive and false negative) can arise because the appropriate modern vegetation was unrepresented in the modern pollen sampling array. This limits application of the analog method to regions where the palynological research community has developed and compiled extensive datasets of modern assemblages. Applications have concentrated primarily on eastern North America, Beringia, and Europe (Anderson et al. 1989, Guiot et al. 1993, Huntley 1990, Overpeck 1985, Overpeck et al. 1992, Williams et al. 2001), where large, geographically extensive datasets are available that include all the major vegetation types. In North America, for example, 4500 modern assemblages are available for comparison (http://www.ngdc.noaa.gov/paleo/gdp.html) (Sawada et al. 2004, Williams 2003). Opportunities exist for analog studies in other regions and continents as pollen datasets expand globally (e.g., Gajewski et al. 2002, Marchant et al. 2002, Prentice et al. 2000). In many cases, geographically restricted sets of modern assemblages are appropriate. For example, the potential sampling universe for a late Holocene pollen assemblage may comprise sites within 100 km of the site (e.g., Calcote 2003), whereas that for a late-glacial site may need to incorporate sites >1000 km away (Williams et al. 2001). Also, because pollen assemblages are influenced by basin size and depositional environment, false positive analogs can arise owing to mismatches between the sampling properties of modern and fossil pollen assemblages. In some cases, arrays of modern samples may need to be stratified for appropriate comparison with fossil assemblages.

Decisions concerning the types and number of modern samples to use as well as the appropriate distance metric to apply will depend on the objectives of the study and the number of modern assemblages available. Investigators working with the 4500-sample North American modern data set can afford the luxury of eliminating some samples based on depositional environment and of using a conservative distance metric (e.g., signal-to-noise metrics). Researchers working with a more restricted set of modern samples may choose (or be forced to choose) to include samples from a broader array of site types and may use less conservative distance-metrics (e.g., equal-weight) or cutoffs for positive matches (see below).

Determining Whether Modern Analogs Exist

Distance metrics formally quantify the degree of similarity among pollen samples, but do not themselves indicate whether two assemblages are similar enough to be considered equivalent or analogous. The most common solution has been to define a critical threshold value for the distance metric, and identify as equivalent any pair of samples with a dissimilarity less than the threshold value (Overpeck et al. 1985). Selection of the appropriate critical value is crucial: Overly strict (low) thresholds increase the occurrence of false negative errors, and overly generous (high) thresholds increase occurrence of false positive errors. The optimum critical value will vary with the choice of distance metric, the characteristics of the modern and fossil pollen datasets, and the ecological scale of analysis. Salient data characteristics include the number of pollen types used to represent each pollen assemblage (Sawada et al. 2004) and the degree of variation among different pollen samples within vegetation types. Optimal thresholds will be higher when the desired ecological resolution is broad (e.g., identifying subcontinental-scale vegetation formations) and lower at finer ecological resolution (e.g., identifying forest stand types within a region). For the squared chord-distance metric, critical values have ranged from 0.05 in local applications (Calcote 1998) to 0.40 for continental-scale paleoclimate reconstructions (Cheddadi et al. 1997, Magny et al. 2001), with values of 0.12 to 0.20 most commonly used in vegetational and paleoclimatic inference at intermediate scales (Brugam et al. 1997; Davis et al. 2000; Jackson et al. 2000; Markgraf et al. 2002; Mensing 2001; Overpeck et al. 1992, 1985; Teed 2000; Willard et al. 2001). Several authors have used multiple critical values to indicate varying degrees of confidence in analog determination or to draw paleoenvironmental inferences at multiple ecological scales (Anderson et al. 1989, Ewing 2002, Grigg et al. 2001).

Recent advances in method have focused on formalizing the selection of critical values. Initial applications of modern analog methods relied upon visual inspection of scatter plots to select critical values (Anderson et al. 1989, Overpeck et al. 1985). Implicit in this approach is the need to select a threshold that jointly minimizes the number of false negative and false positive matches (Wahl 2004). A second solution, termed the jump approach, is to order all modern samples by degree of dissimilarity to a fossil pollen sample, search for large breaks (jumps) in dissimilarity within the sorted list, and retain as analogs all modern samples preceding the break in dissimilarity (Waelbroeck et al. 1998, Williams 2003, Sawada et al. 2004). The jump approach thereby does not require a fixed critical value, but instead introduces a different parameter, α, the increase in dissimilarity required to identify a jump.

A third solution has been to formalize the selection of an optimal threshold through the application of receiver-operating characteristic (ROC) curves (Gavin et al. 2003, Oswald et al. 2003, Wahl 2004). ROC analysis also provides a formal framework for evaluating the information content of dissimilarity metrics (Gavin et al. 2003). In ROC analysis, which is widely used in medical research (Henderson 1993, Zweig & Campbell 1993), the training observations are separated into two populations: those that are known to have a "positive" result and those that are known to have a "negative" result. A frequency histogram for each population is arrayed along an axis of test-statistic values (Figure 4). In the paleoecological application of ROC analysis, each observation consists of a pair of modern pollen samples. Results are designated positive if the two pollen samples were obtained from the same vegetation type and negative otherwise. The dissimilarity metric corresponds to the test statistic on the x-axis (Figure 4). Superior test statistics will produce a greater spread between the positive and negative distributions, and each test statistic will have an optimum threshold value that minimizes the number of false positives and false negatives. The discriminatory ability of each distance metric can be evaluated by first measuring the fraction of matching pairs correctly identified as positive matches (TPF) and the fraction of nonmatching pairs incorrectly identified as matches (FPF) and then plotting these fractions across all possible threshold values (Figure 4). The total area under the FPF:TPF curve (AUC) provides an overall measure of discriminatory ability for the metric. ROC analyses of surface pollen samples from the deciduous broadleaf and southern evergreen mixed forests in eastern North America have confirmed that signal-noise metrics are significantly better than equal-weight and most unweighted distance metrics (Gavin et al. 2003). The discriminatory value of any distance metric may vary depending on spatial scale, vegetation types, and size of the modern data set. The optimal critical value may also vary. For example, Gavin et al. (2003) reported optimal critical values between 0.06 and 0.15 for squared-chord distance in distinguishing among vegetation formations in eastern North America, whereas Wahl (2004), using the same distance-metric for a smaller data set in a more restricted area in southern California, identified optimal critical values ranging from 0.19 to 0.285.

Typically, a fossil pollen sample will have positive matches with multiple modern samples, each of which represents a different vegetational setting and associated climate. A final analytical decision, therefore, is to determine how to assign properties to the fossil pollen sample given a number of possible modern analogs.

The simplest solution is to assign the properties associated with the single modern sample that most closely matches the modern sample (e.g., Delcourt & Delcourt 1985; Gajewski et al. 2000; Huntley 1990; Overpeck et al. 1992, 1985). At the other extreme, the mean, median, or modal value associated with all matching modern pollen samples may be assigned to the fossil pollen sample (e.g., Jackson et al. 2000). Intermediate solutions are to average a preset number of the closest modern analogs, usually from 5 to 15 (e.g., Allen et al. 2000, Cheddadi et al. 1997, Field et al. 1994, Guiot et al. 1993, Nakagawa et al. 2002, Sawada et al. 1999) or to calculate a weighted average using the dissimilarity scores as the basis for weighting (e.g., Allen et al. 2000, Calcote 2003, Cheddadi et al. 1998, Nakagawa et al. 2002). Choice of approach depends on the nature of the questions being investigated. However, using the single most similar modern pollen sample is not recommended because of uncertainties in the pollen percentage estimations for both the fossil and modern samples; the single most similar pollen assemblage may not necessarily represent the most similar vegetation type or environment.

Visualization and Application of Analog Analyses

Numerous approaches have been used to visualize results of analog analyses. Initial applications of the modern analog technique in palynological research focused on interpreting the vegetation history of individual sites (Overpeck 1985, Overpeck et al. 1985). Overpeck et al. (1985) demonstrated the ability of dissimilarity metrics to identify analogous pollen samples by building reconstructed pollen "stratigraphies" that are stacked composites of the most similar modern pollen samples (Figure 5). The reconstructed sequences closely resemble the originals, except where high dissimilarity values indicate that the fossil pollen samples have no close modern counterparts. Baker et al. (1989) plotted frequency diagrams of the vegetation types associated with the top ten analogs. Information about the temporal changes at a site can be deduced by mapping changes in the location of the most similar modern pollen samples (Baker et al. 1989, Clark et al. 1996, Gajewski et al. 2000, Overpeck 1985, Teed 2000) or the dissimilarity values associated with all modern analogs (Anderson et al. 1994, 1989; Whitlock et al. 1993). For example, at Elk Lake, Minnesota (Figure 6), pollen assemblages dating to the beginning of the Holocene are most similar to modern pollen assemblages collected from taiga forests in eastern Canada, indicating colder-than-present conditions, but by 9600 years BP, climates and vegetation were apparently similar to those found in the region at present. Increasing aridity by 7900 years BP is indicated by a westward shift in the distribution of modern analogs, with a return again to near-modern conditions by 3000 years BP (Bartlein & Whitlock 1993). Such visualizations help ground quantitative inferences of temperature and precipitation based upon analog measures.

The inference of climatic history from individual pollen records is one of the most common applications of analog methods (e.g., Cheddadi et al. 1998, Davis et al. 2000, Davis & Shafer 1992, Digerfeldt et al. 1997, Grigg et al. 2001, Huang

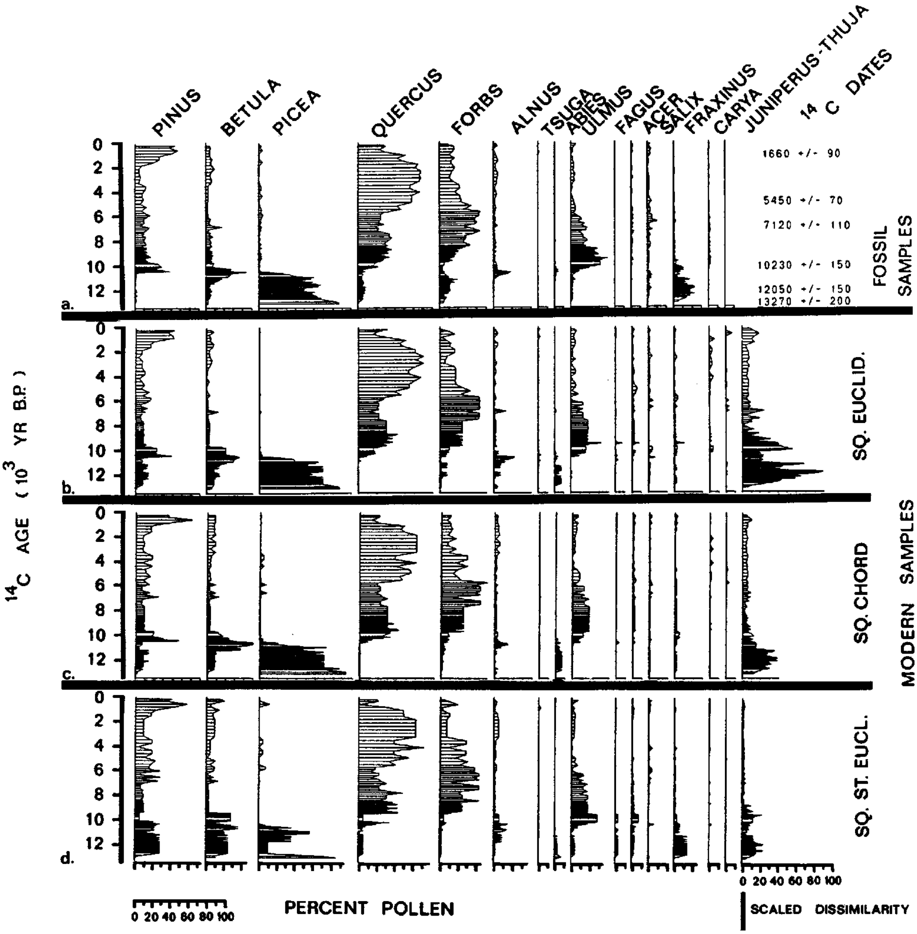

Figure 5 (*a*) Fossil pollen record from Kirchner Marsh (Wright et al. 1963) and reconstructed records generated from the closest modern analogs identified by the squared-Euclidean (*b*), squared-chord (*c*), and squared-standardized-Euclidean metrics (*d*). The rightmost graph in (*b*)–(*d*) indicates the dissimilarity values associated with each modern pollen spectra. For most of the record, the modern pollen samples selected by the various dissimilarity measures are compositionally closely similar to each other and the original fossil pollen samples. However, high dissimilarities near the bottom of the core indicate that those fossil pollen samples have no close counterparts in the modern pollen samples, and the various metrics select divergent modern analogs. For this interval, the squared-chord and squared-Euclidean metrics select modern pollen samples with high *Picea* abundances, whereas the squared-standardized-Euclidean metric (an equal-weight metric) favors modern pollen samples with high *Fraxinus* abundances. Redrawn from Overpeck et al. (1985).

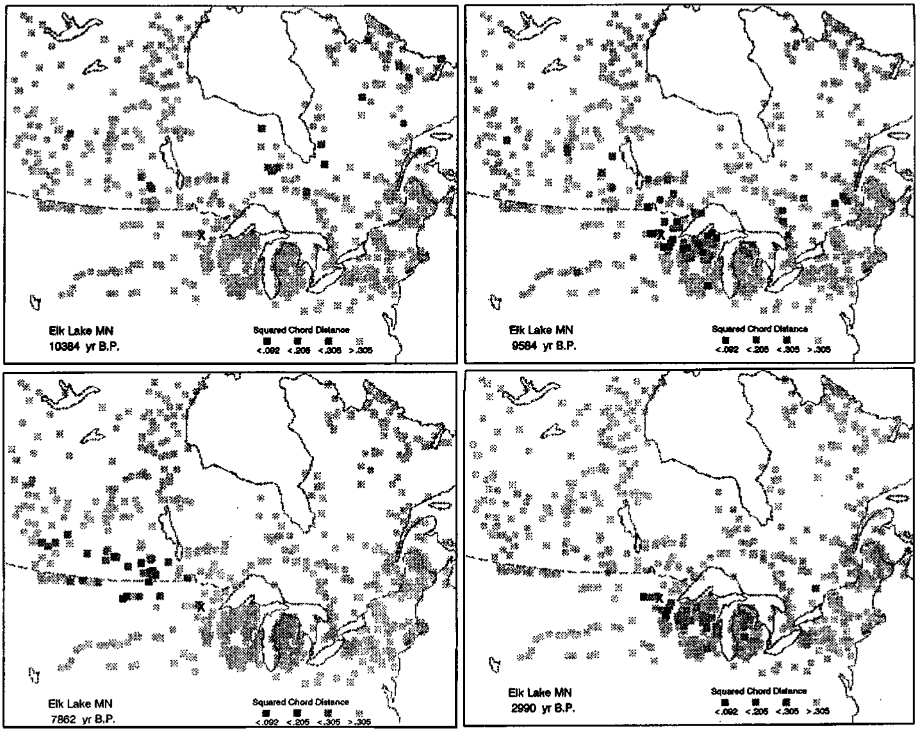

Figure 6 Map of surface pollen samples in eastern North America, classified according to their squared-chord distances to fossil pollen samples at Elk Lake, MN, for four time periods. The changing spatial distribution of close modern analogs results from the temporal changes in vegetation and climate at Elk Lake. At 10,384 years BP climates were colder than present and the regional vegetation resembled modern boreal forests. At 9584 years BP climates and vegetation were apparently similar to those found in the region at present. Increasing aridity by 7862 years BP is indicated by a westward shift in the distribution of modern analogs, with a return again to near-modern conditions by 2990 years BP. Redrawn from Whitlock et al. (1993).

et al. 2002, Magny et al. 2001, Mensing 2001, Nakagawa et al. 2002). Analog analyses of networks of pollen records have produced paleovegetational and paleoclimatic reconstructions at regional to continental scales (Calcote 2003, Cheddadi et al. 1997, Davis et al. 2000, Gajewski et al. 2000, Guiot et al. 1993, Overpeck et al. 1992, Williams 2003, Williams et al. 2000a).

Although distance metrics have been used most commonly as an intermediate step in paleoclimatic and paleoecological analyses, they can also provide useful information about rates of change and the extent of plant associations with no modern analog. Rates of palynological change, assumed to track rates of vegetational change, are calculated by measuring the dissimilarity between temporally adjacent pollen samples from the same site (Field et al. 1994, Jacobson et al. 1987, Lindbladh et al. 2000, Lotter et al. 1992). Rate-of-change measurements are sensitive to the accuracy of the age model (Bennett & Humphry 1995) and the uneven temporal distribution of pollen samples. For this reason, pollen abundances are usually interpolated to regular intervals prior to rate-of-change calculations (Grimm & Jacobson 1992, Huntley 1992, Lotter et al. 1992, Williams et al. 2001). Contour maps or time series that display the minimum multivariate distance between fossil assemblages from a particular time interval and modern assemblages are particularly effective as a diagnostic tool for assessing goodness of fit in analog assignments and as a means for revealing spatiotemporal patterns of assemblages lacking modern analogs (Allen et al. 2000, Bartlein 1997, Brugam et al. 1997, Gavin et al. 2001, Huntley 1990, Jackson et al. 2000, Overpeck et al. 1985).

LATE-GLACIAL VEGETATION IN EASTERN NORTH AMERICA: ABSENCE OF ANALOGS OR FALSE-NEGATIVES?

Paleoecologists have long noted that late-glacial and early Holocene pollen assemblages from extensive areas in eastern North America were unusual in their combination of pollen types from boreal trees (*Picea*, *Larix*, *Abies*), semi-arid herbs (*Artemisia*), sedges (Cyperaceae), and temperate trees (*Quercus*, *Fraxinus*, *Ostrya/Carpinus*, *Ulmus*, *Acer*), as well as low abundances or absences of pollen from taxa that today are widespread in eastern North America and are well represented in modern pollen samples (*Pinus*, *Alnus*, *Betula*) (Amundson & Wright 1979, Davis 1967, Wright et al. 1963). Isopoll maps for individual (Webb et al. 1983, Webb 1987b) and multiple pollen taxa (Figure 7) (Jacobson et al. 1987) show that these assemblages were widespread in interior regions (Midwestern United States and adjacent Canada), and were most extensive between 17,000 and 12,000 years BP. Mapped vegetation reconstructions based upon modern analog methods formally confirmed the existence of no-analog fossil pollen assemblages in the late-glacial of eastern North America (Overpeck et al. 1985, 1992).

Direct mapping of dissimilarity scores between fossil and modern pollen assemblages at selected time intervals provide a more detailed picture of spatial and temporal patterns in the no-analog assemblages (Figure 7) (Williams et al. 2001). Between 21,000 and 18,000 years BP, high dissimilarities were restricted to the Mississippi Valley region. The region of high dissimilarities expanded northward and eastward between 17,000 and 15,000 years BP to the Great Lakes region, peaking in areal extent between 15,000 and 14,000 years BP (Figure 7). The areal extent of high dissimilarities declined between 14,000 and 11,000 years BP, and most early Holocene pollen assemblages match moderately well to some modern pollen assemblages.

Most of the anomalous pollen assemblages between 17,000 and 12,000 years BP are characterized by high abundances of *Picea* and Cyperaceae pollen (Figure 7), but the abundances of other pollen types vary along spatial and temporal gradients.

Between 15,000 and 12,000 years BP, for example, *Fraxinus* percentages are higher in the upper Midwest and *Ostrya-Carpinus* percentages are higher to the east, with a broad area of overlap in the center (Figure 7). High *Artemisia* percentages are confined to the western portion of the no-analog associations. Both Larix and *Abies* are underrepresented in pollen records, but *Larix* appears to have been more common in western regions and *Abie*s more common in the east.

Composition of the no-analog pollen associations changed markedly between 13,000 and 12,000 years BP, when *Ulmus*, *Quercus*, and *Pinus* abundances increased while *Picea* and Cyperaceae abundances declined. The anomalous pollen assemblages at 12,000 years BP coincide with the Younger Dryas Chronozone and have no counterparts in either Holocene or late-glacial pollen assemblages (Shuman et al. 2002).

The absence of modern analogs for the late-glacial pollen assemblages makes their interpretation particularly challenging. Three explanations for the anomalous assemblages have been proposed (Davis 1967, Wright 1971): (*a*) they are artifacts of mixing of pollen of different ages in sediments, (*b*) the hardwood pollen types were not produced locally but instead were blown in from distant forests, and (*c*) the pollen assemblages in fact represent plant associations or landscape patterns with no modern counterpart. Careful analyses of sediment stratigraphies and radiocarbon dates have ruled out the mixing of assemblages (Cushing 1965), and long-distance pollen transport has been viewed in most recent summaries as minor given the broad areal extent of the no-analog assemblages. However, in a recent review Birks (2003) has argued that the late-glacial no-analogs represent long-distance transport of hardwood pollen into unproductive tundra and woodland vegetation. Pollen influxes in modern tundra and forest-tundra environments are low, and modern pollen samples collected from such regions can include substantial percentages of pollen from distant sources (e.g., Lichti-Federovich & Ritchie 1968). Birks (2003) argues that the widespread occurrence of macrofossils of boreal and tundra plants in late-glacial assemblages from Minnesota indicates that the no-analog pollen assemblages in the late-glacial are artifacts of steepened latitudinal vegetation gradients. We examine and critique this argument, drawing attention to evidence that temperate hardwoods were indeed constituents of the regional vegetation during the no-analog period in the Upper Midwest.

Macrofossil assemblages from lakes and wetlands in the region during the no-analog period are dominated by boreal taxa, particularly *Picea*, and macrofossils of temperate hardwood taxa are absent (Birks 2003, Jackson et al. 1997). Macrofossil assemblages from such depositional settings primarily represent plants growing within a few meters or tens of meters of the basin edge (Dunwiddie 1987, Glaser 1981), and hence populations of plants that do not inhabit edges of small lakes and wetlands are undetected. Furthermore, plant macrofossil assemblages are heavily biased toward taxa that produce large numbers of small, readily dispersed and easily preserved organs (leaves, seeds, fruits, etc.) (Birks 1973). None of the hardwood taxa represented in the no-analog pollen assemblages are well represented in macrofossil assemblages from lakes and wetlands today, even when they are locally abundant in vegetation; seeds and fruits are large, few in number, and poorly dispersed, and hardwood leaves decompose more readily than conifer needles.

Plant macrofossils from hardwood taxa are most often found in fluvial depositional settings, where rapid, episodic burial and sorting of debris by size and density can concentrate large seeds and fruits or leaf layers. In fact, the only glacial-age macrofossil records of hardwood taxa from eastern North America are from fluvial sediments (Delcourt et al. 1980, Givens & Givens 1987, Jackson & Givens 1994). Recent studies of late Quaternary macrofossil and pollen assemblages from fluvial sediments in the Upper Midwest have added extraordinary detail to our understanding of vegetational and floristic change in the region (Baker 2000; Baker et al. 1996, 2002). Late-glacial fluvial assemblages from northeastern Iowa and adjacent Minnesota all have abundant *Picea* macrofossils, and other boreal taxa (*Larix*, *Betula glandulosa*, *Selaginella selaginoides*) also occur in some assemblages (Baker et al. 1996, 2002). However, *Acer* macrofossils occur in one assemblage from northeast Iowa dating to 13,400 years BP (Baker et al. 1996), and *Tilia americana* macrofossils occur at a site in southeast Minnesota 13,200 years BP (Baker et al. 2002). Macrofossils of *Quercus rubra* and *Corylus cornuta* occurred with *Picea glauca*, *P. mariana*, and *Larix laricina* in a fluvial deposit dated 14,350 years BP in southwestern Iowa, and *Acer negundo* occurred with *Picea* and *Larix* macrofossils in organic silts dated 13,800 years BP in southeastern Iowa (Baker et al. 1980). These occurrences clearly indicate that temperate hardwoods grew together with *Picea* and other boreal taxa in the late-glacial Upper Midwest.

Fraxinus nigra and *Ulmus americana* macrofossils co-occur with *Picea*, *Larix*, and *Abies* in northeastern Iowa at 10,450 years BP (Baker et al. 1996). Another fluvial site in southeastern Nebraska lacks late-glacial macrofossils, but macrofossils of temperate hardwoods (including *Carya cordiformis*, *Fraxinus americana*, *Juglans nigra*, *Ostrya virginiana*, *Quercus* sp., *Ulmus americana*, *U. rubra*, and *Morus rubra*) are abundant in sediments dating to 10,050 years BP (Baker 2000). Most of these species are near their current northwestern range boundaries at this site, and their early occurrences in Iowa and Nebraska suggest either extremely rapid migration following the late-glacial/Holocene transition, or local occurrence in the Upper Midwest during the late-glacial period. More studies of fluvial and other depositional environments should clarify the late-glacial geographic distributions of temperate hardwoods and other species.

Another argument against long-distance pollen transport as an explanation for the no-analog assemblages comes from the fact that, except for *Quercus*, none of the hardwood taxa so well represented in the late-glacial pollen assemblages are overrepresented in pollen assemblages today. In fact, late-glacial pollen percentages for several of these taxa often exceed those recorded anywhere in eastern North America today. For example, *Fraxinus* pollen exceeds 20% at multiple late-glacial sites in Ohio (Shane 1991), Illinois (King 1981), and Minnesota (Cushing 1967), whereas in modern assemblages *Fraxinus* percentages greater than 10% are extremely rare (Delcourt et al. 1984). *Ostrya/Carpinus* and *Ulmus* show similar patterns.

Another peculiar feature of the no-analog assemblages is the low abundance of *Pinus*, *Betula*, and *Alnus*, which are today associated with most *Picea*-dominated assemblages. All three of these taxa are very well represented in pollen assemblages, and macrofossils document local occurrence of *Betula papyrifera* and *Alnus* sp. over much of the no-analog region (Jackson et al. 1997). The low abundance of *Betula* and *Alnus* pollen despite widespread local populations is difficult to square with simultaneous high abundance of temperate hardwoods dispersed from distant sources.

Anomalous biotas during the late-glacial period are not limited to eastern North American pollen assemblages. Late Pleistocene mammal assemblages in North America contain species that today have disjoint ranges (Graham & Grimm 1990, Graham et al. 1996, Graham & Mead 1987, Stafford et al. 1999). Late-glacial pollen assemblages from Beringia (Anderson et al. 1989) and Europe (Huntley 1990) are also characterized by high dissimilarity relative to modern assemblages. Finally, late-glacial macrofossil assemblages from woodrat middens in the southwestern desert regions show many cases in which species co-occurred at a local scale that do not grow together or even in the same regions today (Betancourt 1990, Spaulding 1990, Van Devender 1990).

Although we believe that the evidence points strongly toward late-glacial vegetation that differed from modern vegetation in fundamental ways, Birks' (2003) critique helps in reframing the issues in terms of the spatial and ecological scales at which analogs may be lacking. We propose three alternative scenarios that might underlie the no-analog pollen assemblages (Figure 8). First, under a "deep no-analog" scenario, the pollen assemblages represent groups of plant species growing in close proximity in the same habitats (e.g., *Picea*, *Ostrya*, and *Ulmus*). Second, under a "shallow no-analog" scenario, the pollen assemblages represent anomalous landscapes in which individual communities resembled modern communities in species composition, but with a landscape arrangement of communities (density, size, spatial array) unlike any today. Finally, under a "no no-analog" hypothesis, the fossil assemblages were produced by anomalously steep gradients in regional vegetation (and climate), where the proximity of different vegetation types led to long-distance dispersal and hence high representation of temperate hardwood types in *Picea*-dominated assemblages to the north. An important goal for paleoecologists should be to devise studies capable of discriminating among these three hypotheses.

EASTERN NORTH AMERICA DURING THE LAST GLACIAL MAXIMUM: BOREAL/MIXED FORESTS OR FALSE-POSITIVE ANALOGS?

Vegetation and climate of unglaciated eastern North America during the last glacial maximum (23,000–20,000 years BP) has long been a source of controversy (Jackson et al. 2000). Pollen assemblages from extensive areas in the unglaciated southeastern United States have been interpreted as representing taiga, boreal forest, and mixed conifer/deciduous forest based on both conventional, judgmental interpretation of fossil pollen data (Delcourt & Delcourt 1981; Delcourt & Delcourt 1987; Watts 1980; Whitehead 1967, 1973, 1981) and on formal classification analyses using modern-analog and fuzzy-logic approaches (Jackson et al. 2000; Overpeck et al. 1992; Williams et al. 2001, 2000b). Jackson et al. (2000) identified some assemblages that lacked modern analogs, but these were primarily in peripheral areas (east Texas, peninsular Florida). However, for many of the fossil assemblages in the rest of the region, only one or two modern assemblages (of 1744 used in the analyses) provided positive matches (Jackson et al. 2000).

Pollen assemblages from most of eastern North America during the last glacial maximum were dominated by *Pinus*, *Picea*, and *Quercus*, with significant representation of herbaceous taxa (Asteraceae, Cyperaceae, Poaceae) and low amounts of *Carya* and other hardwoods (Jackson et al. 2000). Jackson & Whitehead (1993), in discussing similar assemblages from the interstadial that preceded the last glacial maximum, pointed out the inability to discriminate among the 12 extant species of *Pinus* Subg. *Pinus*, 21 (or more) species of *Quercus*, 10 species of *Carya*, or 3 species of *Picea* extant in eastern North America, and noted that the low taxonomic precision of the pollen data might lead to false positive matches with modern assemblages.

Consideration of other data sources suggests that vegetation of the last glacial maximum may have lacked modern analogs, despite the positive pollen analogs. First, plant macrofossil data from several sites indicate that several tree taxa were at least locally present in vegetation despite very poor representation in the pollen assemblages. *Pinus strobus* and *Betula papyrifera* occurred near Bob Black Pond in northeast Georgia during the last glacial maximum, for example, whereas pollen of *P. strobus* and *Betula* sp. were each $<1\%$ of the pollen sum (Jackson et al. 2000; S.T. Jackson, unpublished). In the Tunica Hills of Louisiana/Mississippi, *Quercus* spp., *Juglans nigra*, *Carpinus caroliniana*, *Carya* spp., and *Ulmus americana* occurred in macrofossil assemblages dating to the last glacial maximum (Givens & Givens 1987, Jackson & Givens 1994). All of these taxa occurred in pollen assemblages only in trace amounts ($\ll 1\%$), except for *Quercus*, which never exceeded 10% in the *Picea*-dominated assemblages (Jackson & Givens 1994). Similarly, *Carya*, *Juglans nigra*, and *Fagus grandifolia* were represented by macrofossils at the Nonconnah Creek site in western Tennessee and were absent or in trace amounts in the pollen assemblages (Delcourt et al. 1980). Of these taxa, *Quercus, Betula,* and *Pinus strobus* are highly productive of pollen and are very well represented in pollen assemblages throughout their geographic ranges (Davis & Webb 1975, Delcourt et al. 1984, Webb & McAndrews 1976). *Fagus*, *Carya*, *Carpinus*, *Juglans*, and *Ulmus* are moderately represented in pollen assemblages today; none are among the problematic palynologically “silent” taxa.

A second suggestion that vegetation may have lacked modern analogs comes from evidence that temperate hardwoods may have been more widespread in the southeastern United States during the last glacial maximum than indicated by the pollen data (Jackson et al. 2000). Delcourt et al. (1980) documented macrofossils of several temperate hardwoods as far north as 35°N, a latitude at which all glacial-age pollen assemblages are dominated by *Pinus* and *Picea* (Jackson et al. 2000). Geographic studies of genetic markers in extant populations of *Acer rubrum* and *Fagus grandifolia* suggest that these species may have been widely distributed during the last glacial maximum, with populations possibly as far north as the Ohio River valley (J.S. McLachlan, personal communication).

Finally, the co-occurrence of temperate hardwoods and *Picea* in the Tunica Hills (Givens & Givens 1987, Jackson & Givens 1994) and at Nonconnah Creek (Delcourt et al. 1980) is itself unusual. The geographic ranges of the hardwood taxa and the three extant *Picea* species overlap in the Great Lakes and St. Lawrence regions and in New England (Little 1971), but they generally occur in different habitats. Plant communities with all of these taxa, as indicated by the macrofossil data, occur today only on a very restricted spatial scale. The *Picea* species associated with hardwoods in the Tunica Hills was *P. critchfieldii*, a now-extinct species (Jackson & Weng 1999). Thus, from a compositional standpoint, the Tunica Hills vegetation had no modern analog. *P. critchfieldii* occurred as far east as Georgia (Jackson & Weng 1999), and descriptions of *Picea* cones from the Nonconnah Creek site (Delcourt et al. 1980) match its gross morphology. However, some cones from the Nonconnah Creek site (in collections at the Memphis Pink Palace Museum) are probably assignable to *P. glauca*, an extant boreal species (S.T. Jackson, personal observation, October 2000).

The reasons for the apparent discrepancy between the pollen and macrofossil data are not clear. At Bob Black Pond, macrofossils of *Pinus banksiana* and *Picea* spp. were much more abundant than those of *P. strobus* and *Betula papyrifera*, paralleling the pollen percentages (S.T. Jackson, unpublished). Similarly, *Picea* macrofossils were much more abundant than the hardwoods macrofossils in the Tunica Hills and Nonconnah Creek sediments, similar to the pollen data. Thus, the hardwoods and *P. strobus* may have been in very low local abundance relative to the dominant pines and spruces (deep no-analog in which boreal and temperate species co-occurred in communities). Alternatively, the hardwoods and *P. strobus* may have represented local populations near the sites (small ponds, stream valleys), with pines and spruces dominating the uplands at a regional scale (shallow no-analog in which landscape patterns differed from today). These hypotheses are not mutually exclusive. It may be significant that no glacial-age pollen assemblages have yet been documented anywhere in the region that are dominated by *Pinus strobus* or hardwoods. However, site coverage remains sparse (Jackson et al. 2000).

Alternatively, the apparent underrepresentation of temperate hardwoods relative to *Pinus* and *Picea* in pollen assemblages during the last glacial maximum may not be due to sparse populations or unusual landscape patterns, but instead may derive from environmentally driven changes in pollen productivity. In particular, lowered CO_2 concentrations at the last glacial maximum (180 to 200 ppm) (Petit et al. 1999) may have imposed a severe limitation upon the carbon budgets of individual plants, forcing shifts in resource allocation and reproduction strategies. Allocation and reproductive responses to CO_2 variations likely vary among species, with the greatest differences expected between plants using the C_3 and C_4 photosynthetic pathways (Dippery et al. 1995, Ehleringer et al. 1997, Ward et al. 1999). A plausible, although untested, hypothesis for the underrepresentation of temperate hardwood taxa in pollen records from the last glacial maximum is that these taxa were more sensitive to variations in CO_2 and experienced greater depressions in pollen productivities relative to *Picea*, *Pinus*, and other coniferous taxa. This effect would be in addition to any shifts in plant-climate relationships or vegetation structure caused by low CO_2 concentrations (Cowling 1999, Cowling & Sykes 1999). Macroscopic charcoal evidence from Europe indicates that temperate hardwoods in central Europe were also extensive during the last glacial maximum yet poorly represented in pollen assemblages (Willis et al. 2000). The impact of full-glacial CO_2 concentrations on pollen productivity is still unknown, but its potential importance is massive insofar as it may alter the fundamental sensitivity of the pollen sensor.

Vegetation of the last glacial maximum remains enigmatic. Most pollen assemblages dating to that period in eastern North America have at least some modern analogs, but whether these represent true analogs in terms of vegetation composition, structure, or pattern is open to question. Integration of paleoecological data, experimental studies, modeling, and genetic studies is required to clarify the issue. Additional paleoecological studies, including macrofossil studies capable of high taxonomic and spatial precision, will provide a sounder empirical basis for evaluating distributions of species and local composition of plant communities. Modeling and/or experimental studies to assess potential CO_2 effects on pollen representation will help assess fossil pollen assemblages. Genetic studies provide important clues concerning the whereabouts of species and populations during the last glacial maximum (Hewitt 2000, Petit et al. 2003) and can help fill knowledge gaps in the fossil record and direct paleoecologists to regions and taxa for which further studies are needed.

HOW CAN COMMUNITIES LACKING MODERN ANALOGS ARISE?

Important questions remain concerning the nature of past communities and the extent to which they are comparable to modern communities at local and regional scales. However, it is clear that pollen assemblages with few or no modern analogs were widespread during the late-glacial period, and that both late-glacial and last-glacial-maximum vegetation differed in important respects from extant vegetation. These phenomena require explanation.

No-analog communities have been ascribed to ecological and biogeographic factors, including migration lag, geographic barriers, soil development, and differing centers of distribution during the last glacial maximum (Birks 1989; Davis 1976, 1981; Delcourt & Delcourt 1985, 1987; West 1964, 1980). Species migrated at different rates and in different directions as climate warmed and ice sheets retreated, leading to ephemeral assemblages consisting of whichever species happened to be in the vicinity and were capable of tolerating the prevailing environment. These communities, at disequilibrium with prevailing climate, were subsequently invaded by species better adapted to postglacial climate, resulting ultimately in communities that were in equilibrium with climate and that resembled modern communities.

The importance of migration lag, geographic barriers, and refugium locations in governing composition of late Quaternary vegetation, however, is under increasing question. Phylogeographic studies suggest that some, perhaps many, species were widely dispersed during the last glacial maximum, rather than being restricted to one or a few refugia far south of the ice sheet (McLachlan et al. 2003). Paleoecological studies and seed-dispersal theory indicate that migrations can be very rapid (Clark et al. 1998), and instances of long-distance dispersal events spanning 100 or more kilometers across large lakes, mountain ranges, and desert basins are well documented (Betancourt et al. 1991, Lyford et al. 2003, Webb 1987a). Plant macrofossils indicate that *Betula papyrifera* and *Alnus* spp. were widely distributed in eastern North America south of the ice sheet during the late-glacial period, indicating that the low abundance of these taxa in no-analog pollen assemblages did not stem from migration lag (Jackson et al. 1997). Unique communities can certainly develop when potential dominants are absent from the species pool. But such cases have yet to be adequately documented from the late Quaternary fossil record.

An alternative hypothesis for the development of unique communities and vegetation arrays is the existence of unique environmental conditions and gradients. The multiple environmental factors influencing individuals, populations, and communities comprise a multivariate environmental space that is capable of changing shape, position, and orientation (Figure 9) (Jackson & Overpeck 2000). Individual species have unique ecological responses to the multivariate environment, depending on morphology, physiological tolerances, phenotypic plasticity, and other features. Species can co-occur only where their fundamental niches overlap, and this zone of overlap may or may not overlap with the realized environmental space at a particular time (Figure 9). Thus, a particular species assemblage may occur at one time under a particular environmental realization, but may disappear later as the environment changes (Figure 9). By this mechanism, past assemblages with modern analogs would occur in regions and time periods where environmental conditions approximately matched those prevailing somewhere today. Conversely, past assemblages lacking modern analogs would occur in regions and time periods where the environmental array had no modern counterpart.

A test of this hypothesis for the late-glacial pollen assemblages of eastern North America was provided by a comparison of spatial and temporal patterns between the pollen data (Figure 7) and climate simulated from general circulation models (GCMs) (Figure 10) (Williams et al. 2001). Dissimilarity values between modern and fossil pollen assemblages were mapped for selected time windows, and dissimilarities between simulated paleoclimates and modern climates were mapped

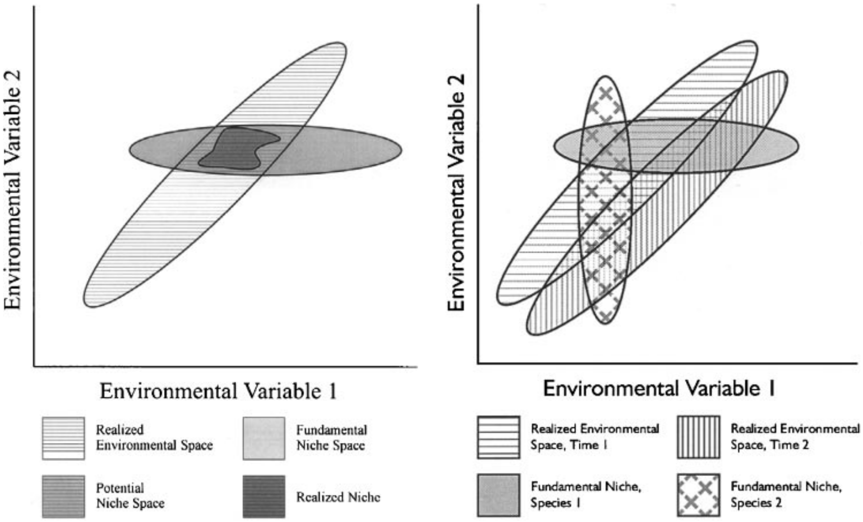

Figure 9 (*a*) Model of the niche structure of a species or population in response to two environmental variables (Jackson & Overpeck 2000). The realized environmental space represents the particular realization of combinations of the two variables at a particular time. The fundamental niche represents the area of environmental space as defined by the two variables within which individuals of the species can survive and reproduce. The potential niche represents the intersection between the fundamental niche and the realized environmental space. Populations of the species can potentially occupy any site falling within the potential niche space, barring barriers to dispersal or other factors (e.g., biotic interactions). The realized niche is the actual environmental space occupied by populations of the species at a given time, and is by definition a subset of the potential niche. (*b*) Implications of environmental change for species assemblages. Two species can co-occur only when their potential niches intersect (i.e., when the intersection of their fundamental niches overlaps with a portion of realized environmental space). At Time 1 in the figure, Species 1 and 2 can co-occur. However, at Time 2, these species cannot co-occur and will have disjoint ranges because the area where their potential niches intersect falls outside the realized environmental space for Time 2. By this mechanism, species assemblages can arise and vanish as the environment changes, providing a plausible mechanism for no-analog communities of the past (and future). Compare with the realized-climate scatterplots in Figure 10.

for the same time periods. The map series show parallel patterns, with extensive no-analog pollen assemblages and climates in interior eastern North America from 16,000 to at least 11,000 years BP, with both pollen data and climate simulations in the Holocene finding close matches to modern data (Figures 7 and 10) (Williams et al. 2001). Overlaid scatterplots of the modern and late-glacial climate simulations show that late-glacial climates were characterized by colder-than-present winters

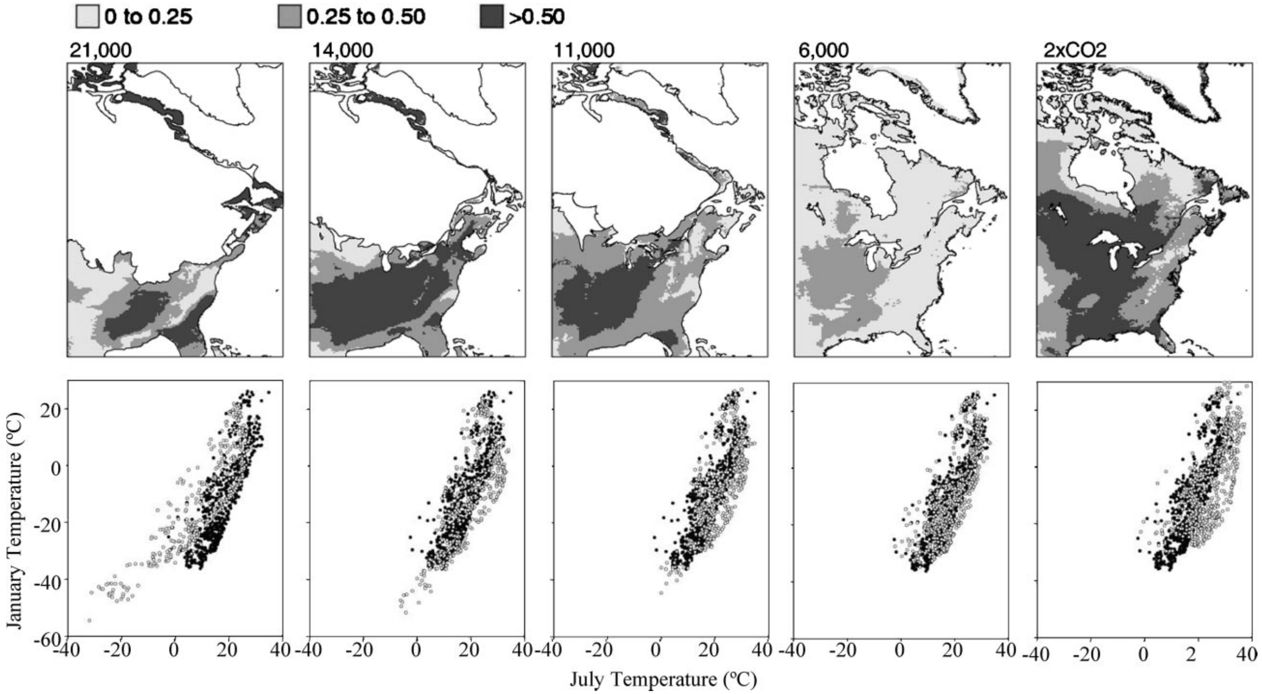

Figure 10 Top row: Maps of the minimum dissimilarity between present climates and CCM1 climate simulations for 21 ka, 14 ka, 11 ka, 6 ka (all redrawn from Williams et al. 2001), and a doubled-CO_2 climate scenario. The dissimilarity between each gridpoint and all modern gridpoints was measured and the minimum dissimilarity was retained for mapping. Compare these mapped climatic dissimilarities to the palynological dissimilarities mapped in Figure 7. Bottom row: Changes in the realized climate space. Filled circles represent a subset of gridpoints randomly drawn from a 25-km equal-area gridded North American climate dataset (Thompson et al. 1999), and are the same among all plots. Open circles represent a random draw of gridpoints from the North American CCM1 climate simulations corresponding to the above maps (Bartlein et al. 1998).

and warmer-than-present summers, indicating increased seasonality relative to present (Figure 10). For both the pollen data and simulated climates, dissimilarities peak between 16,000 and 14,000 years BP, a time when three of the major forcers of late Quaternary climates (e.g., orbitally driven variations in insolation, ice sheet extent, and CO_2 concentrations) differed from their present state (Figures 10 and 11). Pollen records from Beringia also peaked in dissimilarity during the late-glacial period (Anderson et al. 1989), but the timing of this peak lags maximal dissimilarities in eastern North America by a few thousand years, and is nearly contemporaneous with the maximal peak in insolation (Figure 11). The timing of the Beringian dissimilarities is consistent with evidence that vegetation and climate dynamics in high latitudes may be closely linked to orbitally forced variations in insolation (Ritchie et al. 1983).

The simulated climates for the last glacial maximum (21,000 years BP) also show extensive regions of high dissimilarity to modern climates, in contrast to the pollen assemblages (Figures 7 and 10). In contrast to late-glacial climates, climate gridpoints at 21,000 years BP that are outside the modern climate envelope tend to be colder and less seasonal than modern climates. This supports the interpretation that the composition or spatial structure of full-glacial vegetation was novel compared to both late-glacial and modern vegetation, and that such features are not captured by the positive analogs between last glacial maximum and modern pollen assemblages. Overall, the comparative analog study of pollen and simulated paleoclimate in eastern North America (Williams et al. 2001) provides strong support for the hypothesis that no-analog pollen assemblages arose from no-analog climates, although it does not incorporate the effects of lowered CO_2.

CAN NO-ANALOG ASSEMBLAGES BE PREDICTED FOR PAST OR FUTURE CLIMATES?

A critical challenge for paleoecology is to determine whether we can develop models capable of predicting the composition of no-analog pollen assemblages for the past. Can we, for example, explain why late-glacial vegetation in interior eastern North America was dominated by *Picea*; why hardwood taxa were also widespread and abundant; and why boreal trees and shrubs (*Betula papyrifera*, *Abies balsamea*, *Pinus banksiana*, *Alnus* spp.), although widespread, occurred only sparsely in contrast to modern boreal forests? What particular combination of seasonal temperature and precipitation regimes might have led to this kind of vegetation? Why was vegetation structure sufficiently open to permit significant representation of *Artemisia* and other herbs? Was landscape-scale texture of vegetation fine-grained or coarse-grained?

This is an immense challenge, requiring integration of paleoclimate modeling and inference, vegetation-climate and pollen-climate modeling, paleoecological data, and ecological theory and experimentation. Paleoclimate simulations capture key features of past climates (Bartlein et al. 1998, Webb et al. 1998), but also have substantial uncertainties about the precise spatial distribution of climate variables. Response-surface models linking climate with pollen

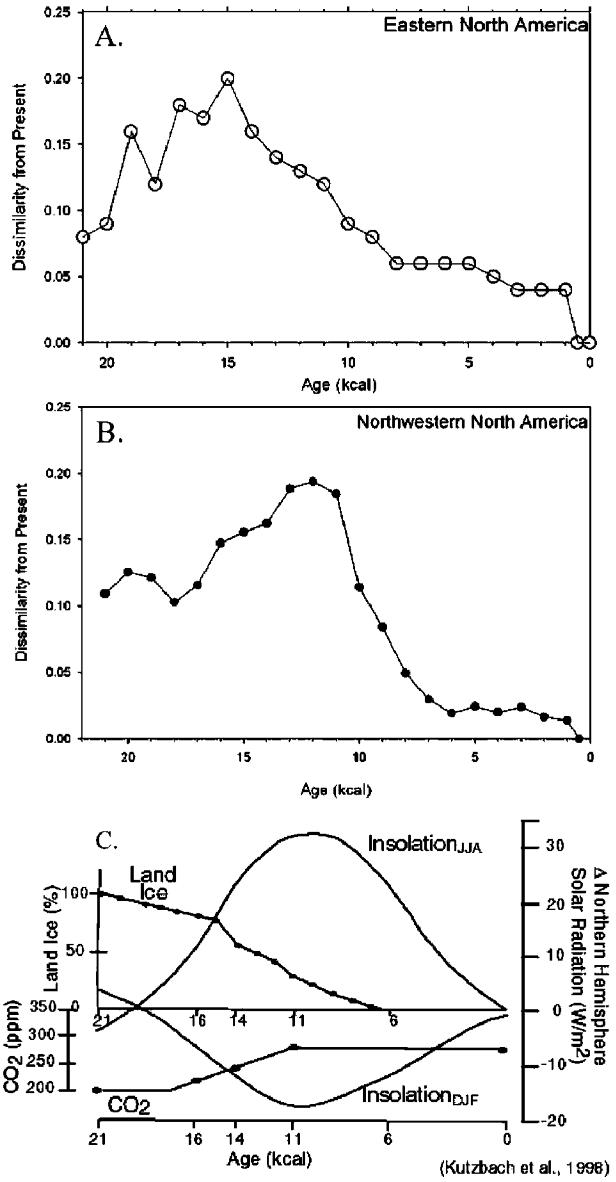

Figure 11 Time series plots of the median dissimilarity from present (squared-chord distance) for fossil pollen samples in (*a*) eastern North America and (*b*) the North American portion of Beringia. (*c*) Secular variations in the boundary conditions used to drive the CCM1 climate simulations: Northern Hemisphere summer (JJA) and winter (DJF) insolation (W/m^2), land ice extent, and atmospheric CO_2 concentrations. Figures (*a*) and (*c*) are redrawn from Williams et al. (2001).

(Bartlein et al. 1986, Webb et al. 1993) and plant species distributions (Lenihan & Neilson 1995, Shafer et al. 2001) use a relatively small suite of climatic variables, which are founded upon our best understanding of the bioclimatic limits constraining species establishment and survival, but our understanding is imperfect and other variables may be more important for determining vegetation and pollen distributions. Application of these models is based on the assumption that the particular variables most relevant to vegetation composition covary with the variables used in the models. Although such covariation is reasonable along spatial gradients, the covariation may not be sustained in time (Jackson 2000, Jackson & Overpeck 2000). For example, the no-analog climates of the late-glacial period had a stronger seasonal temperature contrast than today (Williams et al. 2001); this reflects the fact that summer and winter temperatures, which covary positively along longitudinal and elevational gradients, may show no covariation or (in this case) negative covariation in time. Furthermore, these empirically based models do not cover combinations of climatic variables that do not occur today (i.e., no-analog climates) (Figure 9) (Jackson & Overpeck 2000). The extent to which these models can be extrapolated outside the modern realized climate space is not yet clear. Finally, the extent to which composition and landscape pattern of past no-analog vegetation was mediated by interspecific competition, disturbance regimes, or edaphic factors (e.g., widespread deposition of calcareous loess from river valleys draining active glaciers) is unknown. Targeted application of existing paleoclimate simulations and response-surface models toward reconstructing no-analog pollen assemblages and communities will indicate what elements might be lacking in our current understanding of climatic change and vegetational response. Additional research should focus on building and testing first-principle vegetation models aimed at accurate prediction of vegetation dynamics in no-analog environments. This is no small challenge: Dynamic vegetation models scaled to represent regional to global processes are usually limited to a few plant functional types to reduce complexity (e.g., Kucharik et al. 2000, Moorcroft et al. 2001).

Understanding the nature of no-analog vegetation, including spatial and ecological scale, represented by the late-glacial pollen assemblages is important, for it bears upon the broader question of whether species associations persist over time or are ephemeral, which has fundamental implications for ecology, evolution, and conservation (Ackerly 2003, Bennett 1997, Davis & Zabinski 1992, Hunter et al. 1988, Jackson & Overpeck 2000). Much of the debate over the no-analog assemblages has relied upon data originally collected for other purposes. Further advance will require the collection of new records, with both pollen and macrofossil records, carefully sited to encompass a broad range of environments at a sub-landscape scale.

The kaleidoscopic nature of environmental change, where multiple environmental variables form new combinations and gradients through time (Figure 10), is at the heart of the no-analog problem (Jackson 2000, Jackson & Overpeck 2000). Changing realizations of the environment induce changing combinations of species populations in communities and on landscapes. Complex, multivariate environmental changes at millennial timescales are characteristic of the entire

Quaternary (Jackson & Overpeck 2000, Webb & Bartlein 1992), and perhaps for all or most of geologic time.

Future climates will certainly consist of unique combinations of climate variables that do not exist in the modern world. In the absence of other factors, these new climatic realizations would become manifest over centuries to millennia. However, climate forcing by greenhouse gases is rapidly taking us toward climatic realizations that may be as different from the twentieth century as the twentieth century was from late-glacial times (Figure 10). Climates of the mid to late twentyfirst Century may have few analogs in the modern world or anywhere else in the Quaternary (Figure 10) (Crowley 1990, Intergov. Panel Clim. Change 1995). If history is any guide, we may be on the verge of biotic reorganization into new communities and landscape mosaics that have no analogs anywhere in the Quaternary. These reorganizations will be mediated not only by climate, but also by effects of elevated CO_2 concentrations (unprecedented in the Quaternary), by intercontinental biotic exchanges (i.e., exotic invasions), and by widespread effects of human activities. Our ability to predict the nature and course of these reorganizations will be limited unless we can develop models capable of explaining biotic responses to complex environmental changes of the past. A robust explanatory theory that explains how no-analog assemblages have arisen in the past is vital for identification of regions, biotic communities, and ecosystems that are particularly vulnerable to disruption and reorganization as we enter a new greenhouse world.

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LITERATURE CITED

Aario L. 1940. Waldgrenzen und subrezenten Pollenspektren in Petsamo Lappland. *Ann. Acad. Sci. Fenn.* A54:1–120

Ackerly DD. 2003. Community assembly, niche conservatism and adaptive evolution in changing environments. *Int. J. Plant Sci.* 164(3 Suppl.):S165–84

Allen JRM, Watts WA, Huntley B. 2000. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment; the record from Lago Grande di Monticchio, southern Italy. *Quat. Int.* 73/74:91–110

Amundson DC, Wright HE Jr. 1979. Forest changes in Minnesota at the end of the Pleistocene. *Ecol. Monogr.* 49:1–16

Andersen ST. 1970. The relative pollen productivity and pollen representation of north European trees, and correction factors for tree pollen spectra determined by surface pollen analyses from forests. *Dan. Geol. Und. R_kke II* 96:1–199

Anderson PM, Bartlein PJ, Brubaker LB. 1994. Late Quaternary history of tundra vegetation in northwestern Alaska. *Quat. Res.* 41:306–15

Anderson PM, Bartlein PJ, Brubaker LB, Gajewski K, Ritchie JC. 1989. Modern analogs of late-Quaternary pollen spectra from the western interior of North America. *J. Biogeogr.* 16:573–96

Baker RG. 2000. Holocene environments reconstructed from plant macrofossils in stream deposits from southeastern Nebraska, USA. *Holocene* 10:357–65

Baker RG, Bettis EA III, Denniston RF, Gonzalez LA, Strickland LE, Krieg JR. 2002. Holocene paleoenvironments in southeastern Minnesota—chasing the prairie-forest ecotone. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 177:103–22

Baker RG, Bettis EA III, Schwert DP, Horton DG, Chumbley CA, et al. 1996. Holocene paleoenvironments of northeast Iowa. *Ecol. Monogr.* 66:203–34

Baker RG, Van Nest J, Woodworth G. 1989. Dissimilarity coefficients for fossil pollen spectra from Iowa and western Illinois during the last 30,000 years. *Palynology* 13:63–77

Baker RG, Van Zant KL, Dulian JJ. 1980. Three late-glacial pollen and macrofossil assemblages from Iowa. *Palynology* 4:197–203

Bartlein PJ. 1997. Past environmental changes: characteristic features of Quaternary climate variations. See Huntley et al. 1997, pp. 11–29

Bartlein PJ, Anderson KH, Anderson PM, Edwards ME, Mock CJ, et al. 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. *Quat. Sci. Rev.* 17:549–86

Bartlein PJ, Prentice IC, Webb T III. 1986. Climatic response surfaces from pollen data for some eastern North American taxa. *J. Biogeogr.* 13:35–57

Bartlein PJ, Whitlock C. 1993. Paleoclimatic interpretation of the Elk Lake pollen record. See Bradbury & Dean 1993, pp. 275–93

Bennett KD. 1997. *Evolution and Ecology: The Pace of Life*. Cambridge: Cambridge Univ. Press. 241 pp.

Bennett KD, Humphry RW. 1995. Analysis of late-glacial and Holocene rates of vegetational change at two sites in the British Isles. *Rev. Palaeobot. Palynol.* 85:263–87

Betancourt JL. 1990. Late Quaternary biogeography of the Colorado Plateau. See Betancourt et al. 1990, pp. 259–92

Betancourt JL, Schuster WS, Mitton JB, Anderson RS. 1991. Fossil and genetic history of a pinyon pine (*Pinus edulis*) isolate. *Ecology* 72:1685–97

Betancourt JL, Van Devender TR, Martin PS, eds. 1990. *Packrat Middens: The Last 40,000 Years of Biotic Change*. Tucson: Univ. Ariz. Press

Birks HH. 1973. Modern macrofossil assemblages in lake sediments in Minnesota. In *Quaternary Plant Ecology,* ed. HJB Birks, RG West, pp. 173–89. Oxford: Blackwell

Birks HH. 2003. The importance of plant macrofossils in the reconstruction of Lateglacial and vegetation climate: examples from Scotland, western Norway, and Minnesota, USA. *Quat. Sci. Rev.* 22:453–73

Birks HJB. 1989. Holocene isochrone maps and patterns of tree-spreading in the British Isles. *J. Biogeogr.* 16:503–40

Birks HJB, Birks HH. 1980. *Quaternary Palaeoecology*. London: Edward Arnold. 289 pp.

Birks HJB, Gordon AD. 1985. *Numerical Methods in Quaternary Pollen Analysis*. London: Academic. 317 pp.

Bradbury JP, Dean WE, eds. 1993. *Elk Lake, Minnesota: Evidence for Rapid Climate Change in the North-Central United States*. Boulder, CO: Geol. Soc. Am.

Bradshaw RHW, Webb T III. 1985. Relationships between contemporary pollen and vegetation data from Wisconsin and Michigan, USA. *Ecology* 66:721–37

Brugam RB, Giorgi M, Sesvold C, Johnson SM, Almos R. 1997. Holocene vegetation history in the Sylvania Wilderness Area of the western Upper Peninsula of Michigan. *Am. Midl. Nat.* 137:62–71

Calcote R. 1998. Identifying forest stand types using pollen from forest hollows. *Holocene* 8:423–32

Calcote R. 2003. Mid-Holocene climate and the hemlock decline: the range limit of *Tsuga canadensis* in the western Great Lakes region, USA. *Holocene* 13:215–24

Cheddadi R, Lamb HF, Guiot J, van der Kaars S. 1998. Holocene climatic change in Morocco: a quantitative reconstruction from pollen data. *Clim. Dyn.* 14:883–90

Cheddadi R, Yu G, Guiot J, Harrison SP, Prentice IC. 1997. The climate of Europe 6000 years ago. *Clim. Dyn.* 13:1–9

Clark JS, Fastie C, Hurtt G, Jackson ST, Johnson C, et al. 1998. Reid's paradox of plant migration. *BioScience* 48:13–24

Clark JS, Royall PD, Chumbley C. 1996. The role of fire during climate change in an eastern deciduous forest at Devil's Bathtub, New York. *Ecology* 77:2148–66

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

Cowling SA, Sykes MT. 1999. Physiological significance of low atmospheric CO_2 for plant-climate interactions. *Quat. Res.* 52:237–42

Crowley TJ. 1990. Are there any satisfactory geologic analogs for a future greenhouse warming? *J. Clim.* 3:1282–92

Cushing EJ. 1965. Problems in the Quaternary phytogeography of the Great Lakes region. In *The Quaternary of the United States*, ed. HE Wright Jr, DG Frey, pp. 922. Princeton, NJ: Princeton Univ. Press

Cushing EJ. 1967. Late-Wisconsin pollen stratigraphy and the glacial sequence in Minnesota. See Cushing & Wright 1967, pp. 59–88

Cushing EJ, Wright HE Jr, eds. 1967. *Quaternary Paleoecology*. New Haven, CT: Yale Univ. Press

Darwin C. 1859. *On the Origin of Species*. Cambridge, MA: Harvard Univ. Press. 513 pp. 1964 Facsimile Ed.

Darwin C. 1897. *The Variation of Animals and Plants Under Domestication*. New York: D. Appleton. 968 pp.

Davis MB. 1963. On the theory of pollen analysis. *Am. J. Sci.* 261:897–912

Davis MB. 1967. Late-glacial climate in northern United States: a comparison of New England and the Great Lakes region. See Cushing & Wright 1967, pp. 11–43

Davis MB. 1969. Climatic changes in southern Connecticut recorded by pollen deposition at Rogers Lake. *Ecology* 50:409–22

Davis MB. 1976. Pleistocene biogeography of temperate deciduous forests. *Geosci. Man* XIII:13–26

Davis MB. 1981. Quaternary history and the stability of forest communities. In *Forest Succession*, ed. DC West, HH Shugart, DB Botkin, pp. 132–77. New York: Springer-Verlag

Davis MB. 2000. Palynology after Y2K—understanding the source area of pollen in sediments. *Annu. Rev. Earth Planet. Sci.* 28:1–18

Davis MB, Douglas C, Calcote RR, Cole KL, Winkler MG, Flakne R. 2000. Holocene climate in the western Great Lake National Parks and Lakeshores: implications for future climate change. *Cons. Biol.* 14:1–16

Davis MB, Sugita S. 1997. Reinterpreting the fossil pollen record of Holocene tree migration. See Huntley et al. 1997, pp. 181–93

Davis MB, Zabinski C. 1992. Changes in geographical range resulting from greenhouse warming: Effects on biodiversity in forests. In *Global Warming and Biological Diversity*, ed. RL Peters, TE Lovejoy, pp. 121–42. New Haven, CT: Yale Univ. Press

Davis OK, Shafer DS. 1992. A Holocene climatic record for the Sonoran Desert from pollen analysis of Montezuma Well, Arizona, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 92:107–19

Davis RB, Bradstreet TE, Stuckenrath R Jr, Borns HW Jr. 1975. Vegetation and associated environments during the past 14,000 years near Moulton Pond, Maine. *Quat. Res.* 5:436–65

Davis RB, Webb T III. 1975. The contemporary distribution of pollen in eastern North America: a comparison with the vegetation. *Quat. Res.* 5:395–434

Delcourt HR, Delcourt PA. 1985. Comparison of taxon calibrations, modern analogue techniques, and forest-stand simulation models for the quantitative reconstruction of past vegetation. *Earth Surf. Process. Landf.* 10:293–304

Delcourt PA, Delcourt HR. 1981. Vegetation maps for eastern North America: 40,000 yr B.P. to the present. In *Geobotany II*, ed. RC Romans. New York: Plenum

Delcourt PA, Delcourt HR. 1987. *Long-Term Forest Dynamics of the Temperate Zone: A Case Study of Late-Quaternary Forests in Eastern North America*. New York: Springer-Verlag. 439 pp.

Delcourt PA, Delcourt HR, Brister RC, Lackey LE. 1980. Quaternary vegetation history of the Mississippi embayment. *Quat. Res.* 13:111–32

Delcourt PA, Delcourt HR, Webb T III. 1984. *Atlas of Mapped Distributions of Dominance andModern Pollen Percentages for Important Tree Taxa of Eastern North America*. Dallas, TX: Am. Assoc. Stratigraphic Palynol. Found. 131 pp.

Digerfeldt G, deBeaulieu JL, Guiot J, Mouthon J. 1997. Reconstruction and paleoclimatic interpretation of Holocene lake-level changes in Lac de Saint-Leger, Haute-Provence, southeast France. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 136:231–58

Dippery JK, Tissue DT, Thomas RB, Strain BR. 1995. Effects of low and elevated CO_2 on C_3 and C_4 annuals. *Oecologia* 101:13–20

Dunwiddie PW. 1987. Macrofossil and pollen representation of coniferous trees in modern sediments from Washington. *Ecology* 68:1–11

Durham OC. 1946. The volumetric incidence of atmospheric allergens. III. Rate of fall of pollen grains in still air. *J. Allergy* 17:70–78

Ehleringer JR, Cerling TE, Helliker BR. 1997. C_4 photosynthesis, atmospheric CO_2, and climate. *Oecologia* 112:285–99

Eisenhut G. 1961. Untersuchungen über die Morphologie und Ökologie der Pollenkörner heimischer und fremdländischer Waldbäume. *Forstwiss. Forsch.* 15:1–68

Ewing HA. 2002. The influence of substrate on vegetation history and ecosystem development. *Ecology* 83:2766–81

Farnsworth EJ, Bazzaz FA. 1995. Inter- and intra-generic differences in growth, reproduction, and fitness of nine herbaceous annual species grown in elevated CO_2 environments. *Oecologia* 104:454–66

Field C, Chapin FS III, Matson PA, Mooney HA. 1992. Responses of terrestrial ecosystems to the changing atmosphere: A resource-based approach. *Annu. Rev. Ecol. Syst.* 23:201–35

Field MH, Huntley B, Müller H. 1994. Eemian climate fluctuations observed in a European pollen record. *Nature* 371:779–83

Gajewski K, Lézine A-M, Vincens A, Delestan A, Sawada M, Afr. Pollen Database. 2002. Modern climate-vegetation-pollen relations in Africa and adjacent areas. *Quat. Sci. Rev.* 21:1611–31

Gajewski K, Vance R, Sawada M, Fung I, Gignac LD, et al. 2000. The climate of North America and adjacent ocean waters ca. 6ka. *Can. J. Earth. Sci.* 37:661–81

Gavin DG, McLachlan JS, Brubaker LB, Young KA. 2001. Postglacial history of subalpine forests, Olympic Peninsula, Washington, USA. *Holocene* 11:177–88

Gavin DG, Oswald WW, Wahl E, Williams JW. 2003. A statistical approach for evaluating distance metrics and analog assignments for pollen records. *Quat. Res.* 60:356–67

Givens CR, Givens FM. 1987. Age and significance of fossil white spruce (Picea glauca), Tunica Hills, Louisiana-Mississippi. *Quat. Res.* 27:283–96

Glaser PH. 1981. Transport and deposition of leaves and seeds on tundra: a late-glacial analog. *Arc. Alp. Res.* 13:173–82

Gould SJ. 2002. *The Structure of Evolutionary Theory*. Cambridge: Harvard Univ. Press. 1433 pp.

Graham RW, Grimm EC. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *Trends Ecol. Evol.* 9:289–92

Graham RW, Lundelius EL Jr, Graham MA, Schroeder EK, Toomey RS III, et al. 1996. Spatial response of mammals to Late Quaternary environmental fluctuations. *Science* 272:1601–6

Graham RW, Mead JI. 1987. Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America. See Ruddiman & Wright 1987, pp. 371–402

Grigg LD, Whitlock C, Dean WE. 2001. Evidence for millennial-scale climate change during marine isotope stages 2 and 3 at Little Lake, western Oregon, U.S.A. *Quat. Res.* 56:10–22

Grimm EC, Jacobson GL Jr. 1992. Fossil-pollen evidence for abrupt climate changes during the past 18000 years in eastern North America. *Clim. Dyn.* 6:179–84

Guiot J. 1987. Late Quaternary climatic-change in France estimated from multivariate pollen time-series. *Quat. Res.* 28:100–18

Guiot J. 1990. Methodology of the last climatic cycle reconstruction in France from pollen data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 80:49–69

Guiot J, Harrison SP, Prentice IC. 1993. Reconstruction of Holocene precipitation patterns in Europe using pollen and lake-level data. *Quat. Res.* 40:139–49

He JS, Bazzaz FA. 2003. Density-dependent responses of reproductive allocation to elevated atmospheric CO_2 in *Phytolacca americana*. *New Phytol.* 157:229–39

Henderson AR. 1993. Assessing test accuracy and its clinical consequences: a primer for receiver operating characteristic curve analysis. *Ann. Clin. Biochem.* 30:521–39

Hesse MB. 1966. *Models and Analogies in Science*. Notre Dame, IN: Univ. Notre Dame Press. 184 pp.

Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405:907–13

Huang Y, Shuman BN, Wang Y, Webb T III. 2002. Hydrogen isotope ratios of palmitic acid in lacustrine sediments record late Quaternary climate variations. *Geology* 30:1103–6

Hunter ML Jr, Jacobson GL Jr, Webb T III. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conserv. Biol.* 2:375–85

Huntley B. 1990. Dissimilarity mapping between fossil and contemporary pollen spectra in Europe for the past 13,000 years. *Quat. Res.* 33:360–76

Huntley B. 1992. Rates of change in the European palynological record of the last 13 000 years and their climatic interpretation. *Clim. Dyn.* 6:185–91

Huntley B, Cramer W, Morgan AV, Prentice HC, Allen JRM, eds. 1997. *Past andFuture Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota*. Berlin: Springer

Intergov. Panel Clim. Change. 1995. *Climate Change 1995—The Science of Climate Change: Contribution of Working Group I to the Second Assessment Report of the IPCC.* Cambridge, UK: Cambridge Univ. Press

Jackson ST. 1990. Pollen source area and representation in small lakes of the northeastern United States. *Rev. Palaeobot. Palynol.* 63:53–76

Jackson ST. 1994. Pollen and spores in Quaternary lake sediments as sensors of vegetation composition: theoretical models and empirical evidence. In *Sedimentation of Organic Particles*, ed. A Traverse, pp. 253–86. Cambridge, UK: Cambridge Univ. Press

Jackson ST. 2000. Out of the garden and into the cooler? A Quaternary perspective on deep-time paleoecology. *Paleontol. Soc. Pap.* 6:287–308

Jackson ST, Givens CR. 1994. Late Wisconsinan vegetation and environment of the Tunica Hills region, Louisiana/Mississippi. *Quat. Res.* 41:316–25

Jackson ST, Kearsley JB. 1998. Quantitative representation of local forest composition in forest-floor pollen assemblages. *J. Ecol.* 86:474–90

Jackson ST, Lyford ME. 1999. Pollen dispersal models in Quaternary plant ecology: assumptions, parameters, and prescriptions. *Bot. Rev.* 65:39–75

Jackson ST, Overpeck JT. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26(Suppl.):194–220

Jackson ST, Overpeck JT, Webb T III, Keattch SE, Anderson KH. 1997. Mapped plant-macrofossil and pollen records of late Quaternary vegetation change in eastern North America. *Quat. Sci. Rev.* 16:1–70

Jackson ST, Webb RS, Anderson KH, Overpeck JT, Webb T III, et al. 2000. Vegetation and environment in eastern North America during the last glacial maximum. *Quat. Sci. Rev.* 19:489–508

Jackson ST, Weng C. 1999. Late Quaternary extinction of a tree species in eastern North America. *Proc. Natl. Acad. Sci.USA* 96:13847–52

Jackson ST, Whitehead DR. 1993. Pollen and macrofossils from Wisconsinan interstadial sediments in northeastern Georgia. *Quat. Res.* 39:99–106

Jacobson GL Jr, Grimm EC. 1986. A numerical analysis of Holocene forest and prairie vegetation in central Minnesota. *Ecology* 67:958–66

Jacobson GL Jr, Webb T III, Grimm EC. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. See Ruddiman & Wright 1987, pp. 277–88

King JE. 1981. Late Quaternary vegetational history of Illinois. *Ecol. Monogr.* 51:43–62

Kucharik CJ, Foley JA, Delire C, Fisher VA, Coe MT, et al. 2000. Testing the performance of a dynamic global ecosystem model: water balance, carbon balance, and vegetation structure. *Global Biogeochem. Cycles* 14:795–825

LaDeau SL, Clark JS. 2001. Rising CO_2 levels and the fecundity of forest trees. *Science* 292:95–98

Legendre L, Legendre P. 1983. *Numerical Ecology*. Amsterdam: Elsevier Sci. 419 pp.

Lenihan JM, Neilson RP. 1995. Canadian vegetation sensitivity to projected climatic change at three organizational levels. *Clim. Chang.* 30:27–56

Lichti-Federovich S, Ritchie JC. 1968. Recent pollen assemblages from the Western Interior of Canada. *Rev. Palaeobot. Palynol.* 7:297–344

Lindbladh M, Bradshaw R, Holmqvist B. 2000. Pattern and process in south Swedish forests during the last 3000 years, sensed at stand and regional scales. *J. Ecol.* 88:113–28

Little EL Jr. 1971. *Atlas of United States Trees. Rep. 1146*, For. Serv., U.S. Dep. Agric., Washington, DC

Lotter AF, Ammann B, Sturm M. 1992. Rates of change and chronological problems during the late-glacial period. *Clim. Dyn.* 6:233–39

Lyford ME, Jackson ST, Betancourt JL, Gray ST. 2003. Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecol. Monogr.* 73:567–83

Magny M, Guiot J, Schoellammer P. 2001. Quantitative reconstruction of Younger Dryas to mid-Holocene paleoclimates at Le Locle, Swiss Jura, using pollen and lake-level data. *Quat. Res.* 56:170–80

Marchant R, Almeida L, Behling H, Berrio JC, Bush M, et al. 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. *Rev. Palaeobot. Palynol.* 121:1–75

Markgraf V, Webb RS, Anderson KH, Anderson L. 2002. Modern pollen/climate calibration for southern South America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 181:375–97

McAndrews JH. 1966. Postglacial History of Prairie, Savanna and Forest in Northwestern

Minnesota. *Torrey Bot. Club Mem.* 22:1–72

McLachlan JS, Clark JS, Manos PS. 2003. Conservation lessons from the Last Glacial Maximum. *Ecol. Soc. Am. Annu. Meet. Abstr.* 230

Mensing SA. 2001. Late-Glacial Early Holocene vegetation and climate change near Owens Lake, eastern California. *Quat. Res.* 55:57–65

Mooney HA, Drake BG, Luxmoore RJ, Oechel WC, Pitelka LF. 1991. Predicting ecosystem responses to elevated CO_2 concentrations. *BioScience* 41:96–104

Moorcroft PR, Hurtt GC, Pacala SW. 2001. A method for scaling vegetation dynamics: the ecosystem demography model. *Ecol. Monogr.* 71:557–86

Nakagawa T, Tarasov PE, Nishida K, Gotanda K, Yasuda Y. 2002. Quantitative pollen-based climate reconstruction in central Japan: application to surface and Late Quaternary spectra. *Quat. Sci. Rev.* 21:2099–113

Ogden JG. 1969. Correlation of contemporary and Late Pleistocene pollen records in the reconstruction of postglacial environments in northeastern North America. *Mitt. Int. Ver. Limnol.* 17:64–77

Ogden JG. 1977. Pollen analysis: state of the art. *Géograph. Phys. Quat.* 37:151–59

Oswald WW, Brubaker LB, Hu FS, Gavin DG. 2003. Pollen-vegetation calibration for tundra communities in the Arctic Foothills, northern Alaska. *J. Ecol.* 91:1022–33

Overpeck JT. 1985. A pollen study of a late Quaternary peat bog, south-central Adirondack Mountains, New York. *Geol. Soc. Am. Bull.* 96:145–54

Overpeck JT, Bartlein PJ, Webb T III. 1991. Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science* 254:692–95

Overpeck JT, Webb RS, Webb T III. 1992. Mapping eastern North American vegetation change of the past 18 ka: no-analogs and the future. *Geology* 20:1071–74

Overpeck JT, Webb T III, Prentice IC. 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quat. Res.* 23:87–108

Parshall T, Calcote R. 2001. Effect of pollen from regional vegetation on stand-scale forest reconstruction. *Holocene* 11:81–87

Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola J-M, et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–36

Petit RJ, Aguinagalde I, de Beaulieu JL, Bittkau C, Brewer S, et al. 2003. Glacial refugia: hotspots but not melting pots of genetic diversity. *Science* 300:1563–65

Prentice IC. 1980. Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. *Rev. Palaeobot. Palynol.* 31:71–104

Prentice IC. 1985. Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. *Quat. Res.* 23:76–86

Prentice IC. 1986. Long-term processes, response times and equilibrium in vegetation. *Vegetatio* 67:131–42

Prentice IC. 1988. Records of vegetation in time and space: the principles of pollen analysis. In *Vegetation History*, ed. B Huntley, T Webb III, pp. 17–42. Dordrecht: Kluwer

Prentice IC, Jolly D, BIOME 6000 Participants. 2000. Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa. *J. Biogeogr.* 27:507–19

Ritchie JC. 1977. The modern and late Quaternary vegetation of the Campbell-Dolomite Uplands, near Inuvik, NWT, Canada. *Ecol. Monogr.* 47:401–23

Ritchie JC, Cwynar LC, Spear RW. 1983. Evidence from north-west Canada for an early Holocene Milankovitch thermal maximum. *Nature* 305:126–28

Ruddiman WF, Wright HE Jr, eds. 1987. *North America and Adjacent Oceans During the Last Deglaciation*. Boulder: Geol. Soc. Am.

Sawada M, Gajewski K, de Vernal A, Richard P. 1999. Comparison of marine and terrestrial Holocene climatic reconstructions from northeastern North America. *Holocene* 9:267–77

Sawada M, Viau AE, Vettoretti G, Peltier WR, Gajewski K. 2004. Comparison of North-American pollen-based temperature and global lake-status with CCCma AGCM output at 6ka. *Quat. Sci. Rev.* In press

Shafer SL, Bartlein PJ, Thompson RS. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. *Ecosystems* 4:200–15

Shane LCK. 1991. *Vegetation History of Western Ohio*. Minneapolis, MN: Limnol. Res. Cent., Univ. Minn.

Shuman B, Thompson W, Bartlein P, Williams JW. 2002. The anatomy of a climatic oscillation: vegetation change in eastern North America during the Younger Dryas chronozone. *Quat. Sci. Rev.* 21:1777–91

Solomon A, Webb T III. 1985. Computer-aided reconstruction of late-Quaternary landscape dynamics. *Annu. Rev. Ecol. Syst.* 16:63–84

Spaulding WG. 1990. Vegetational and climatic development of the Mojave Desert: the last glacial maximum to the present. See Betancourt et al. 1990, pp. 166–99

Stafford TW Jr, Semken HA Jr, Graham RW, Klippel WF, Markova A, et al. 1999. First accelerator mass spectrometry ^{14}C dates documenting contemporaneity of nonanalog species in late Pleistocene mammal communities. *Geology* 27:903–6

Sugita S. 1993. A model of pollen source area for an entire lake surface. *Quat. Res.* 39:239–44

Sugita S. 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *J. Ecol.* 82:881–97

Sugita S, MacDonald GM, Larsen CPS. 1997. Reconstruction of fire disturbance and forest succession from fossil pollen in lake sediments: potential and limitations. In *Sediment Records of Biomass Burning and Global Change*, ed. JS Clark, H Cashier, JG Goldammer, BJ Stocks, pp. 387–412. Berlin: Springer-Verlag

Teed R. 2000. A >130,000-year-long pollen record from Pittsburg Basin, Illinois. *Quat. Res.* 54:264–74

Thompson RS, Anderson KH, Bartlein PJ. 1999. *Atlas of relations betweencClimatic parameters and distributions of important trees and shrubs in North America—introduction and conifers. Rep. 1650-A*, U.S. Dep. Inter., U.S. Geol. Surv., Denver

Van Devender TR. 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. See Betancourt et al. 1990, pp. 134–63

Wahl E. 2004. Optimal cutoff values for selecting pollen/vegetation analogs with dissimilarity metrics in the modern analog technique. *Rev. Palaeobot. Palynol.* In press,doi:10.1016/S0034-6667(03)00137-4

Waelbroeck C, Labeyrie L, Duplessy J-C, Guiot J, Labracherie M, et al. 1998. Improving past sea surface temperature estimates based on planktonic fossil faunas. *Paleoceanography* 13:272–83

Ward JK, Strain BR. 1997. Effects of low and elevated CO_2 partial pressure on growth and reproduction of *Arabidopsis thaliana* from different elevations. *Plant Cell Environ.* 20:254–60

Ward JK, Tissue DT, Thomas RB, Strain BR. 1999. Comparative responses of model C3 and C4 plants to drought in low and elevated CO_2. *Global Change Biol.* 5:857–67

Watts WA. 1980. Late-Quaternary vegetation history at White Pond on the inner coastal plain of South Carolina. *Quat. Res.* 13:187–99

Wayne P, Foster S, Connolly J, Bazzaz F, Epstein P. 2002. Production of allergenic pollen by ragweed (Ambrosia artemisiifolia L.) is increased in CO_2-enriched atmospheres. *Ann. Allergy Asthma Immunol.* 88:279–82

Webb RS, Anderson KH, Webb T III. 1993. Pollen response-surface estimates of late-Quaternary changes in the moisture balance of the northeastern United States. *Quat. Res.* 40:213–27

Webb SL. 1987a. Beech range extension and vegetation history—pollen stratigraphy of two Wisconsin lakes. *Ecology* 68:1993–2005

Webb T III. 1974. A vegetational history from northern Wisconsin: evidence from modern and fossil pollen. *Am. Midland Nat.* 92:12–34

Webb T III. 1987b. The appearance and disappearance of major vegetational assemblages: long-term vegetational dynamics in eastern North America. *Vegetatio* 69:177–87

Webb T III, Anderson KH, Bartlein PJ, Webb RS. 1998. Late Quaternary climate change in eastern North America: a comparison of pollen-derived estimates with climate model results. *Quat. Sci. Rev.* 17:587–606

Webb T III, Bartlein PJ. 1992. Global changes during the last 3 million years: climatic controls biotic responses. *Annu. Rev. Ecol. Syst.* 23:141–73

Webb T III, Cushing EJ, Wright HE Jr. 1983. Holocene changes in vegetation of the Midwest. In *Late Quaternary Environments of the United States. Volume 2. The Holocene*, ed. HE Wright Jr, pp. 142–65. Minneapolis, MN: Univ. Minnesota Press

Webb T III, Laseski RA, Bernabo JC. 1978. Sensing vegetational patterns with pollen data: choosing the data. *Ecology* 59:1151–63

Webb T III, McAndrews JH. 1976. Corresponding patterns of contemporary pollen and vegetation in central North America. *Geol. Soc. Am. Mem.* 145:267–99

Weng C, Bush MB, Silman MR. 2004. Elevational characteristics of modern pollen rain recorded in moss-polsters and surface sediments in the Rio Manu watershed, Peru. *J. Trop. Ecol.* 20:1–12

West RG. 1964. Inter-relations of ecology and Quaternary paleobotany. *J. Ecol.* 52:47–57

West RG. 1980. Pleistocene forest history in East Anglia. *New Phytol.* 85:571–622

Whitehead DR. 1964. Fossil pine pollen and full-glacial vegetation in southeastern North Carolina. *Ecology* 45:767–77

Whitehead DR. 1967. Studies of full-glacial vegetation and climate in southeastern United States. See Cushing & Wright 1967, pp. 237–48

Whitehead DR. 1973. Late-Wisconsin vegetational changes in unglaciated eastern North America. *Quat. Res.* 3:613–21

Whitehead DR. 1979. Late-glacial and post-glacial vegetational history of the Berkshires, western Massachusetts. *Quat. Res.* 12:333–57

Whitehead DR. 1981. Late-Pleistocene vegetational changes in northeastern North Carolina. *Ecol. Monogr.* 51:451–71

Whitehead DR, Tan KW. 1969. Modern vegetation and pollen rain in Bladen County, North Carolina. *Ecology* 50:235–48

Whitlock C, Bartlein PJ, Watts WA. 1993. Vegetation history of Elk Lake. See Bradbury & Dean 1993, pp. 251–274

Willard DA, Cronin TM, Verardo S. 2003. Late-Holocene climate and ecosystem history from Chesapeake Bay sediment cores, USA. *Holocene* 13:201–14

Willard DA, Weimer LM, Riegel WL. 2001. Pollen assemblages as paleoenvironmental proxies in the Florida Everglades. *Rev. Palaeobot. Palynol.* 113:213–35

Williams JW. 2003. Variations in tree cover in North America since the Last Glacial Maximum. *Global Planet. Change* 35:1–23

Williams JW, Bartlein PJ, Webb T III. 2000a. *Data-model comparisons for eastern North America—inferred biomes and climate values from pollen data*. Presented at Proc. Third Palaeoclim. Model. Intercomp. Proj. Workshop, Montreal, Canada

Williams JW, Shuman BN, Webb T III. 2001. Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology* 82:3346–62

Williams JW, Summers RL, Webb T III. 1998. Applying plant functional types to construct biome maps from eastern North American pollen data: comparisons with model results. *Quat. Sci. Rev.* 17:607–28

Williams JW, Webb T III, Richard PJH, Newby P. 2000b. Late Quaternary biomes of Canada and the Eastern United States. *J. Biogeogr.* 27:585–607

Willis KJ, Rudner E, Sümegi P. 2000. The full-glacial forests of central and southeastern Europe. *Quat. Res.* 53:203–13

Wright HE Jr. 1967. The use of surface samples in Quaternary pollen analysis. *Rev. Palaeobot. Palynol.* 2:321–330

Wright HE Jr. 1971. Late Quaternary vegetational history of North America. In *The Late Cenozoic Glacial Ages*, ed. KK Turekian, pp. 426–64. New Haven, CT: Yale Univ. Press

Wright HE Jr, Winter TC, Patton HL. 1963. Two pollen diagrams from southeastern Minnesota: problems in the regional late-glacial and postglacial vegetational history. *Geol. Soc. Am. Bull.* 74:1371–96

Ziska LH, Caulfield FA. 2000. Rising CO_2 and pollen production of common ragweed (Ambrosia artemisiifolia), a known allergy-inducing species: implications for public health. *Aust. J. Plant Physiol.* 27:893–98

Zweig MH, Campbell G. 1993. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clin. Chem.* 39:561–77

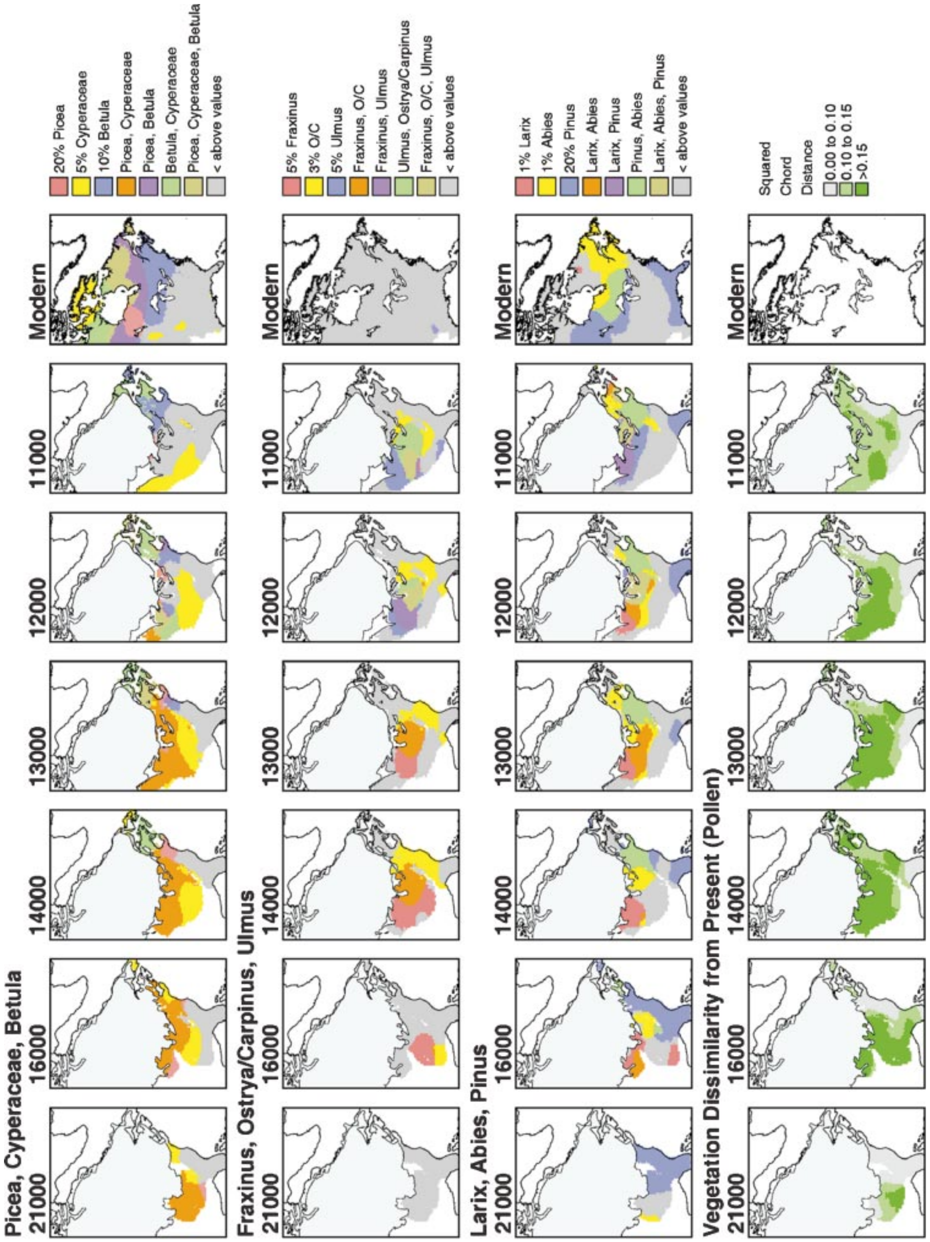
Picea, Cyperaceae, Betula
Fraxinus, Ostrya/Carpinus, Ulmus
Larix, Abies, Pinus
Vegetation Dissimilarity from Present (Pollen)
21000
16000
14000
13000
12000
11000
Modern
20% Picea
5% Cyperaceae
10% Betula
Picea, Cyperaceae
Picea, Betula
Betula, Cyperaceae
Picea, Cyperaceae, Betula
< above values
5% Fraxinus
3% O/C
5% Ulmus
Fraxinus, O/C
Fraxinus, Ulmus
Ulmus, Ostrya/Carpinus
Fraxinus, O/C, Ulmus
< above values
1% Larix
1% Abies
20% Pinus
Larix, Abies
Larix, Pinus
Pinus, Abies
Larix, Abies, Pinus
< above values
Squared Chord Distance
0.00 to 0.10
0.10 to 0.15
>0.15

Figure 7 Mapped changes in plant associations (*rows 1–3*) and palynological dissimilarity from present (*row 4*) for the past 21,000 years in eastern North America. The top three rows are multitaxon isopoll maps in which each taxon is represented by a single contour and each combination of taxa is represented by a unique color. Late-glacial pollen assemblages in the Great Lakes region are characterized by high abundances of spruce, sedge, ash, hornbeam/hophornbeam, larch, and fir pollen and low abundances of pine, birch, and alder pollen. This combination of pollen types is rare in modern pollen assemblages, resulting in high dissimilarity values for the late-glacial pollen spectra. Modified from Williams et al. (2001).

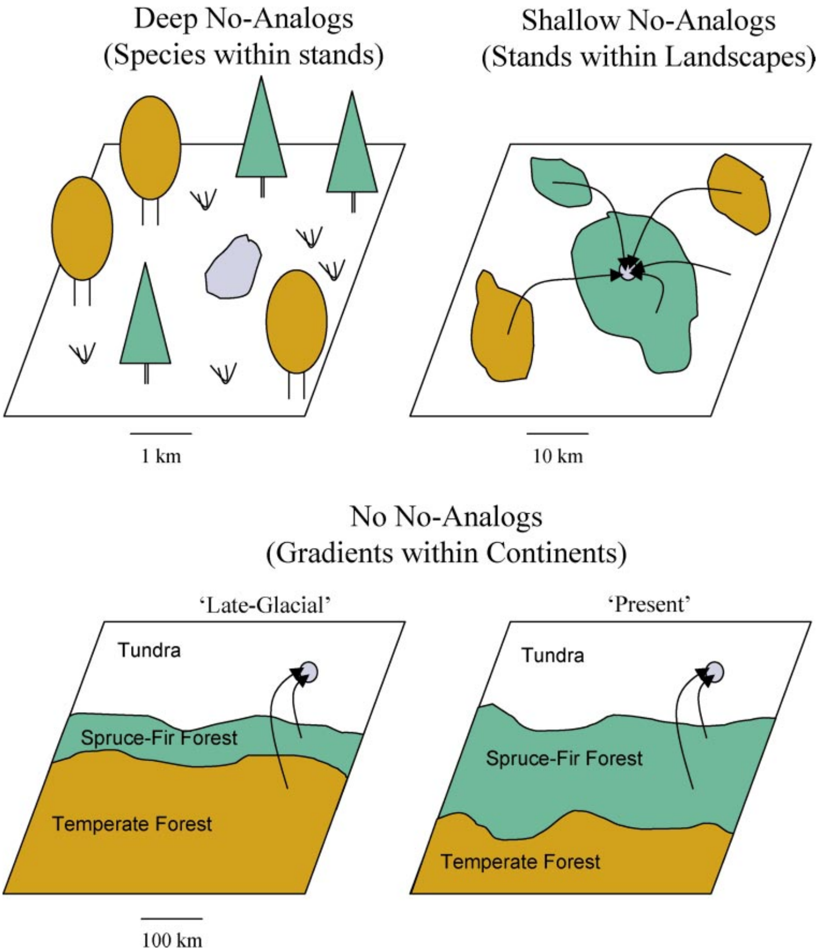

Figure 8 Cartoon illustrating three levels of ecological no-analogs that could be represented by the anomalous mixtures of pollen types found in late-glacial pollen assemblages: (*a*) "Deep no-analogs" in which individuals from species that today are not associated were growing in close proximity; (*b*) "Shallow no-analogs" in which individual stands are similar in composition to modern stands, but the array of stands across the landscape differs from present; (*c*) "No no-analogs" in which late-glacial vegetation formations are essentially alike to modern vegetation formations, but steepened climatic and vegetational gradients in the past allow the influx of pollen from distant formations. Brown indicates, respectively, individuals, stands, or formations of temperate deciduous trees such as ash and hornbeam/hophornbeam. Green indicates, respectively, individuals, stands, or formations of cold-tolerant conifers such as spruce, fir, or larch. White indicates, respectively, individuals, populations, or formations of sedges, grasses, and other herbaceous taxa. A basin from which a pollen record might be collected is represented as a light blue circle or polygon; the size of the lake is not to scale. Arrows represent the transport of pollen from distant vegetation bodies to the collecting basin.

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