

Reid's Paradox of Rapid Plant Migration

Dispersal theory and interpretation of paleoecological records

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The oak, to gain its present most northerly position in North Britain after being driven out by the cold probably had to travel fully six hundred miles, and this without external aid would take something like a million years. (Reid 1899)

B iologists have long regarded the natural dispersal of large seeds as an impediment to plant range expansion after glacial periods. Global maps predicting biome distributions under future climate change scenarios (e.g., VEMAP 1995) are now prompting ecologists to think about the dispersal problem: If rapid climate change or habitat de-

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A plausible explanation for how rapid migrations were achieved can guide forecasts for tree populations in the twenty-first century

struction remove sizable portions of a plant's range, will seed dispersal allow colonization of distant areas that may become favorable? Dispersal and population spread is a continuing theme of paleoecological research (e.g., Webb 1986, Davis and Zabinski 1992, Melillo et al. 1996), and it has demonstrated empirical migration rates that are three orders of magnitude faster than Clement Reid's estimate.

Tree populations migrated rapidly after the most recent glacial period, which suggests that they might do so again if climate were to change rapidly in the future. However, the leap from late-glacial warming to greenhouse warming of anthropogenic landscapes is broad (King and Herstrom 1996). Estimates of future migration rates cannot be taken directly from paleoecological records, but they might be sharpened by an understanding of how life history and dispersal affected past migrations. A plausible explanation for how rapid migrations were achieved in the past can guide forecasts for tree populations in the twenty-first century.

Although the rapid rates implied by past records bode well for plant populations themselves, the rates are far too high to have been produced by the dispersal mechanisms that are embodied in traditional notions of tree life history and restricted dispersal. We call this dilemma of rapid migration Reid's Paradox, as voiced by him in the opening quotation. Explaining rapid migration has challenged paleoecologists for a century and remains a point of debate (Davis 1987, Johnson and Webb 1989, Prentice 1992, Clark 1993, Huntley 1996).

New insights gained from dispersal theory hold promise not only for understanding some of the intriguing events of the past, but also for anticipating changes to come. A recent workshop held at the National Center for Ecological Analysis and Synthesis in Santa Barbara, California, concluded that elements of a solution to Reid's Paradox can be gleaned from recent advances in the mathematical modeling of dispersal. Model populations disperse seeds according to a broad class of dispersal "kernels," which are functional shapes that describe the scatter of dispersed seed away from the parent tree (van den Bosch et al. 1990, Neubert et al. 1995). Although dispersal theory began with Reid's Paradox (Skellam 1951), only recently has research in paleoecology and dispersal theory begun to converge toward new interpretations of how dispersal can contribute to the rate and variability of an expanding population front. Reid's Paradox serves as an instructive example, not

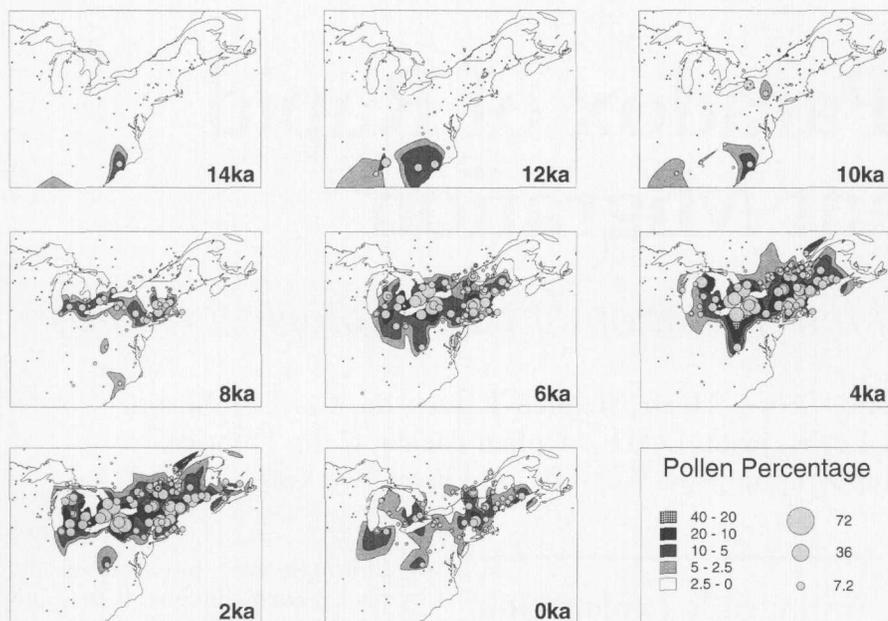


Figure 1. Time-series of beech (*Fagus grandifolia*) pollen percentages from 14 ka to 0 ka (1 ka = 1000 radiocarbon years before present) in eastern North America. Circles indicate locations of paleorecords, and circle size is scaled to the percentage of *F. grandifolia* pollen in sediment samples. Contours interpolated within the spatial grid of pollen samples are shaded to show abundance levels. The general migration pattern is one of northward, then westward, spread. Patterns are irregular, reflecting the scatter of sites with differing soils and topography and also, perhaps, a variable dispersal process.

only of advances beyond traditional views of diffusion, but also of the value of dialogue among disciplines sharing complementary goals.

Reid's Paradox

The dilemma of rapid migration arose early in the interpretation of plant population spread from leaf and seed remains in marsh and bog deposits. Reid's Paradox, laid out in Reid's 1899 book, *The Origin of the British Flora*, points out an apparent conflict between past tree distributions, as indicated by fossil evidence, and distributions predicted from some rather simple life history considerations. Sometime between the end of the last ice age (which, in Reid's day, was estimated to have been 20,000 years ago but is now known to have been approximately 10,000 years ago) and the Roman occupation of Britain, temperate taxa such as oak expanded 1000 km northward to occupy regions that were last populated before the last ice age. The implied rate of spread appeared impossibly great in view of average seed dispersal distances, which were observed to extend not much beyond the edge of the tree. Reid speculated

that relatively rare seed dispersal events by birds must have facilitated population expansion.

Evidence gained over a century of paleoecological research has broadened Reid's Paradox to include many tree taxa in North America and Eurasia. Early efforts to map changing geographic distributions of trees include those of Firbas (1949) in Europe and of Davis (1976, 1981) in North America. The record of past tree distributions now includes a large, cooperatively produced database of fossil pollen collected from thousands of lakes worldwide (Huntley and Birks 1983, NAPD 1990, Wright et al. 1993). These data have been used to produce sequential maps of fossil pollen distribution and abundance, which demonstrate that many tree populations spread rapidly following ice retreat (Figure 1). Several key insights into the abilities of tree species to migrate in response to climate change have emerged through studies of fossil pollen distributions.

- Species were capable of changing geographic distributions in response to 1000-year climate changes (Kutzbach and Guetter 1986). These climate changes affected large regions

that were quickly occupied as population ranges shifted at rates exceeding 100 m/yr (Davis 1981, Ritchie and MacDonald 1986, Huntley and Webb 1989). For example, recent estimates of the tree population expansion rate across Europe and North America range from 150 to 500 m/yr, with rates being highest in the early Holocene and then diminishing (Huntley and Birks 1983, Delcourt and Delcourt 1987, Birks 1989).

- Rapid migrations occurred in response to superimposed short-term (10–100 yr) climate changes (Gear and Huntley 1991, Chapellaz et al. 1993, Lamb et al. 1995).

- Tree species moved at different rates and in different directions as a result of climate change. These differences may have arisen from species-specific tolerances to different climate variables (Johnson and Webb 1989, Prentice et al. 1991).

- Large potential "barriers" to seed dispersal, such as the North Sea, Baltic Sea, and Lake Michigan, appear to have posed few obstacles to migration (Reid 1899, Webb 1986, Huntley and Webb 1989, Woods and Davis 1989, Kullman 1996), but larger barriers, such as the Atlantic Ocean, did block seed dispersal.

The rapid shifts in the ranges of many tree taxa at the time of ice retreat, between 16,000 and 10,000 years ago, suggest the possibility that haphazard, long-distance establishment events might explain these shifts. Reid's rough calculations of population spread expected from life history considerations, by contrast, assume that a diffusion process involving relatively uniform, incremental, step-by-step advance would underlie tree migration. The rate of such an advance would be determined by two basic elements: the size of the steps (dispersal distance) and the rate of population growth. Reid understood the importance of dispersal, and his use of generation time demonstrated a partial recognition of the importance of population growth. The average dispersal distance implied by his calculations clearly does not support a diffusion view of tree spread, and neither does the fact that populations apparently leaped across large bodies of water. When Reid invoked birds to explain

the movements of seed well beyond the main population, he was denying diffusion in a strict sense and appealing to a far more uneven (and qualitatively different) process. Such uneven processes are also a feature of recent developments in dispersal theory.

Dispersal theory embraces the "fat tails"

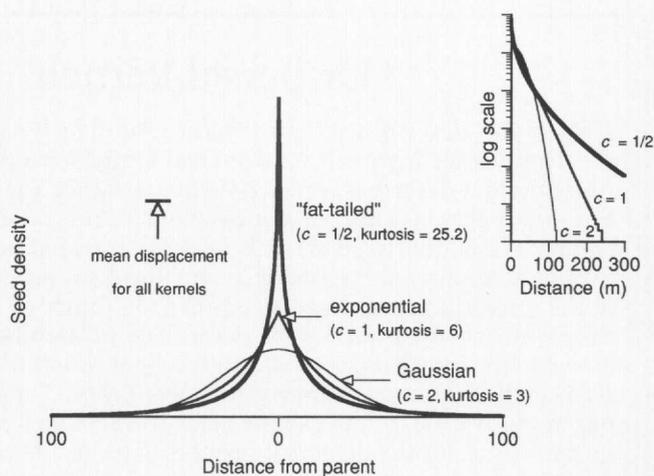
The benchmark article inaugurating current interest in dispersal theory (Skellam 1951) was also the first to formalize the problem that diffusion could not explain the migration of tree populations. Skellam (1951) was sufficiently inspired by Reid's Paradox to open his broad treatment of population movement with this example. Skellam showed that Reid had defined a problem containing the elements of a diffusion equation. A diffusing population initially spreads as a Gaussian distribution. The distribution tends to grow at the edges, due to reproduction, and to flatten in the center, due to interactions that limit population growth at high density; eventually, the population frontier expands as a wave traveling at constant velocity. Analysis of the leading edge of the wave is straightforward because its rate of spread does not depend on the complex, nonlinear interactions that control growth rates in the population interior (e.g., competition).

The dispersal distances that would have been necessary to explain wave velocity—that is, the distance the front had moved—can be calculated given elapsed time since retreat of the Pleistocene ice, an estimate of tree generation time, and an estimate of seed production. Skellam stated the problem in this way: Suppose a population of oaks contains individuals that produce an average of $R_0 = 10^7$ seeds in a lifetime. What dispersal distance, D , is needed to explain a movement of $X(n) = 10^3$ km in $n = 300$ generations since ice retreat? Simple diffusion predicts that after n generations, the population front moves:

$$X(n) = Dn \sqrt{\ln R_0}$$

Consistent with Reid's conclusion, the mean dispersal distance of seeds implied by the model is impossibly

Figure 2. Three dispersal kernels that have the same average dispersal distance but differ in kurtosis. (left) The high kurtosis of the fat-tailed kernel means that it is more peaked at the source (i.e., where distance from parent = 0) than the lower-kurtosis curves. Differences in the tails (i.e., far from the parent) of the three dispersal kernels appear minor, but a log scale (inset at right) illustrates how a fat-tailed distribution allows for rare long-distance dispersal. The values of the parameter c and kurtosis values are described in the box on page 16.



large, approaching 1 km. Thus, the classic article that sparked interest in diffusion models of population spread begins with an application demonstrating its failure. Skellam's analysis of Reid's Paradox ends by concurring with Reid's speculations that seed dispersal must have been assisted by birds.

Skellam's early demonstration that diffusive spread could not account for Holocene tree migration may explain why theoretical treatment of Holocene tree migrations ceased as soon as it began. The failure of dispersal theory to explain Holocene tree spread appeared to spell an early doom for its application to paleoecological records, and the disciplines of paleoecology and dispersal theory embarked on divergent paths. Over the last few decades, paleoecological research has rarely included application of migration models (but see Dexter et al. 1987). Dispersal theory was used to explore problems in diffusion, a logical application. Diffusion models successfully describe diverse problems in population biology (Okubo 1980, Hengeveld 1994), and they yield a rich spectrum of dynamic behaviors for simple communities of interacting populations.

Although diffusion models have proven useful in many contexts, examples of population spread have continued to arise that cannot be well described by simple step-by-step movement. For example, whereas most dispersing seeds remain near the parent plant, some fraction dis-

perses great distances. This small minority of long-distance dispersal events might disproportionately influence some aspects of population dynamics, especially rates of geographic spread. Models that relaxed some of the strict assumptions of diffusion (see below) were, therefore, clearly needed.

Recent analyses of population spread have begun to include models in which the underlying dispersal kernel (seed distribution) is leptokurtic (see box page 16). Leptokurtic kernels describe distributions of offspring that are clustered near the source and "fat" in the tails (Figure 2). The fat-tailed kernel in Figure 2 has large kurtosis, meaning that the curve density is high near zero and at large distances (Figure 2 inset). The incorporation of rare long-distance wanderers in population models makes the tail of the kernel fat and its analysis somewhat complex. The random walk that underlies diffusion, by contrast, simplifies to local, step-wise motion of individuals. This local motion, in turn, greatly simplifies analysis of migration to an asymptotically constant rate of spread, as demonstrated in Skellam's calculation for Reid's Paradox. However, leptokurtic kernels describe a situation in which step size is highly variable, with a few individuals taking great strides. The longer strides are rare events and, thus, infrequently observed and hard to measure.

Recent models that accommodate leptokurtic seed dispersal (Mollison

Dispersal kernels

Dispersal is described in mathematical models by a kernel indicating the distance seeds travel. A "dispersal kernel" is a probability density function that describes seed arrival at a distance x from a parent plant. For simplicity, assume that movement occurs along one dimension (right or left), that seed arrivals are concentrated near the parent and decline with distance x , and that the dispersal process is "unbiased," in the sense that seeds have an equal probability of being dispersed to the right or left of the parent plant. The probability that a seed will arrive in the interval $(x, x + dx)$ to the right or left of the parent, where dx a small increment, is approximately $k(x)dx$. The kernel $k(x)$ always has mode at $x = 0$, but the shape of k can vary considerably, depending on the nature of the dispersal process (e.g., Neubert et al. 1995). The concept of a "fat-tailed" kernel can best be demonstrated by a density function that is expressed in terms of two parameters, a "distance parameter," α , and a "shape parameter," c , that determines higher moments (including kurtosis):

$$k(x) = \frac{c}{2\alpha\Gamma(1/c)} \exp\left[-\frac{|x|^c}{\alpha}\right]$$

where $\Gamma()$ is the gamma function with argument $1/c$. From the moments of $k(x)$, we find the mean displacement of a seed moving to the right or left to be

$$\mu_1 = \frac{\alpha\Gamma(2/c)}{\Gamma(1/c)}$$

and kurtosis to be

$$\frac{\Gamma(5/c)\Gamma(1/c)}{\Gamma^2(3/c)}$$

This density is quite general and includes several familiar density functions, including the exponential ($c = 1$) and Gaussian ($c = 2$). Fat-tailed distributions are ones with kurtosis larger than the exponential distribution or c parameters less than 1 (Figure 2). These fat-tailed distributions are characterized by accelerating spread (Kot et al. 1996).

1972, 1977, van den Bosch et al. 1990, Kot et al. 1996) have begun to yield results that are relevant to the Holocene spread of trees. Surprisingly, the rarest (and, thus, least often observed) long strides turn out to have overwhelming effects on migration, making dispersal highly variable. Colonists that become detached from the main population accelerate spread well beyond that expected from the average dispersal distance (Figure 3), an average that is controlled largely by the small-stepping majority. They also make the rate of spread highly variable. The conse-

quence is an ill-defined population front that is difficult to describe and, hence, to analyze. Spatially and temporally variable densities include satellite populations that become established by rare, distant colonists and subsequently grow and coalesce with the expanding main population (Figure 4).

One of the non-intuitive results emerging from analyses of fat-tailed (i.e., highly leptokurtic) kernel shapes is the possibility for accelerating spread of the population (Figure 3a). Unlike diffusion, which yields a traveling wave of constant velocity, a

kernel that is sufficiently fat in the tail (i.e., fatter than an exponential density) can spread by "great leaps forward that get increasingly out of hand" (Mollison 1977). Depending on the "fatness" of the kernel tail, population spread can be a polynomial or exponential function of time (Kot et al. 1996). Because an observed migration (e.g., the Holocene spread of a given taxon) is but one realization of a stochastic process that spans finite time, there may be no way to determine asymptotic rates of spread or even to guess at their existence. That is, not only can the asymptotic rate of spread be great, but a maximum rate may not exist.

Elements of a solution: theory and paleoecology converge

Results from model analyses of seed dispersal can aid interpretation of the paleoecological record. Some elements of an explanation for rapid Holocene tree migrations have arisen directly from paleoecology, but others can be sharpened by theoretical analysis. The first and most fundamental element revealed by models is the inescapable role of local population growth rate. This point was made by Skellam (1951), but interpretations of Holocene tree spread, with the exception of Dexter et al. (1987) have largely ignored it. Paleoecologists since Reid's day have recognized that generation time paces the leaps forward of a population frontier; new recruits at a population boundary must achieve seed-bearing age before they can disperse their seed beyond the advancing front (Webb 1986, Birks 1989, Johnson and Webb 1989). In difference equation models, such as used by Skellam (1951) and Kot et al. (1996), generation time sets the time step of the model. But the rate of spread also depends on seed number—the more seed, the higher the population growth rate, and the more rapid the migration. The odds of great strides forward are enhanced simply by increasing seed amount, which raises the odds of seed arrival at long as well as short distances. All reproduction and dispersal models (diffusion and others) incorporate reproductive capacity when determining spread (van den Bosch et al. 1990, Kot

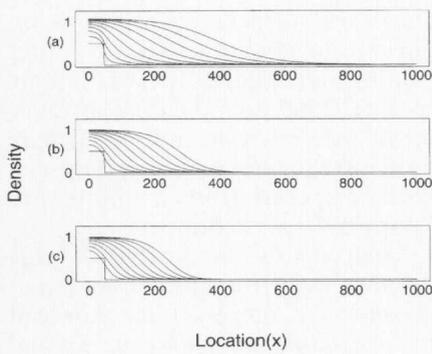


Figure 3. Population spread resulting from a fat-tailed kernel (top) compared with traveling waves of constant velocity (middle and bottom). In each case, average seed dispersal distance is the same but the kernel shape is different. Each panel shows the front at successive time steps. Each dispersal kernel corresponds to one of the kernels in Figure 2: in the top panel, $c = 1/2$; in the middle panel, $c = 1$; and in the lower panel, $c = 2$. The fat-tailed kernel ($c = 1/2$) generates accelerating spread over time.

et al. 1996). Reproduction is an element of population spread that can be overlooked in the absence of models.

A second contribution of model analysis has been to clarify how long-distance dispersal affects spread. Notions of rapid spread and large leaps represent a convergence of theoretical results and speculation from the paleoecological record. Reid appealed to this possibility as a way around the strict confines of diffusion. Animal dispersal and rare establishment events that might result from storms have been invoked to explain rapid migrations of many temperate tree taxa (Davis 1981, Davis et al. 1986, Webb 1986). Davis (1986), Prentice (1992), and Clark (1993) noted specifically that episodic, long-distance colonization events violate a diffusion model. Predictions from models containing leptokurtic dispersal may not conflict with fossil pollen evidence.

Models showing that a large average dispersal distance is not required for rapid spread should influence the interpretation of paleoecological records. Although it is not possible to establish the details of the dispersal kernel that might have governed any particular realization of a stochastic migration, the conclusion that rates of spread were too fast for simple diffusion appears inescapable.

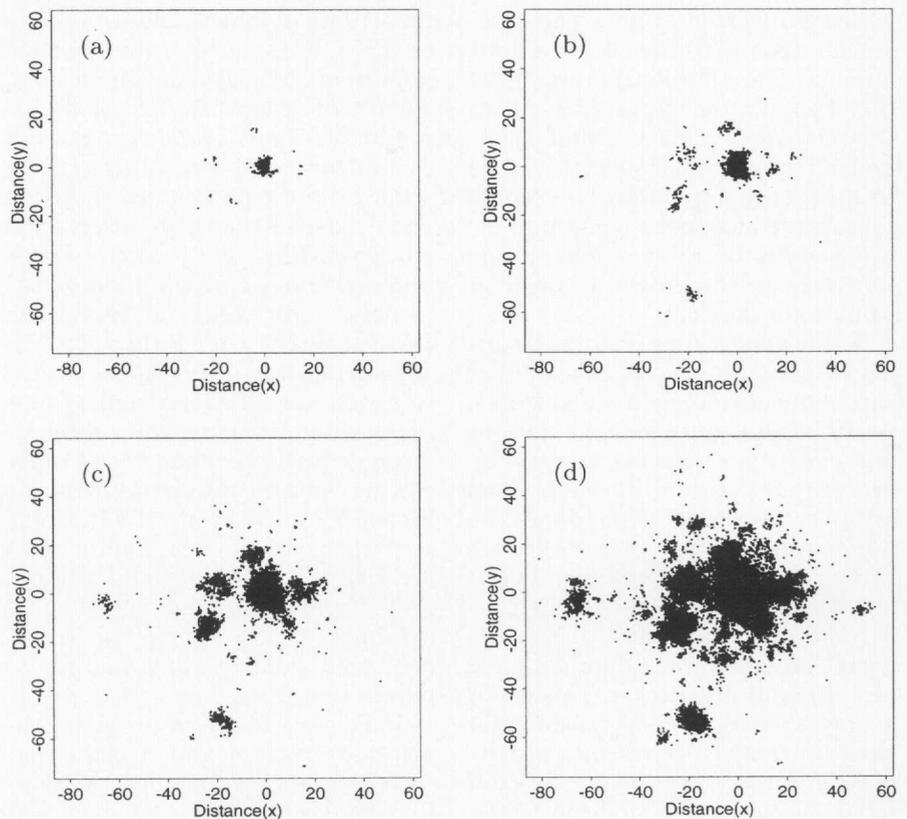


Figure 4. Monte Carlo simulation of patchy population spread using a mixed dispersal kernel (see box page 20) with $c = 1$, $p = 0.99$, $\alpha_1 = 0.5$, and $\alpha_2 = 10$. Twenty individuals were established from coordinate (0, 0) at time zero. At each generation, each individual produces a Poisson number of offspring, with a mean of 1.2. Dots indicate offspring locations after 20 generations (a), 30 generations (b), 40 generations (c), and 50 generations (d). Note the presence of new outlying populations, which spread and eventually coalesce.

If fat-tailed dispersal kernels are needed to explain rapid spread, but rates of spread decrease over time (rather than accelerate; Birks 1989), then there may be reason to suspect that Holocene spread was actually limited by a comparatively slow rate of climate change.

Beyond the focus on rapid spread is an additional parallel between theory and paleoecology: the evolving concept of an expanding front. As applied mathematicians were discovering that leptokurtic dispersal makes for temporally variable (Mollison 1977) and patchy (Lewis in press) population spread, paleoecologists began to view migration as a process whereby outlying populations might colonize well ahead of an advancing front (Davis 1986, Prentice 1992). This changing concept of fronts has immediate implications for interpretation of the paleoecological record.

Much attention and debate on patterns of Holocene tree spread has relied on "finding the front" (e.g., Bennett 1985, Davis et al. 1991, MacDonald 1993). In the past, estimates of population spread rates involved drawing lines on a map around the inferred distribution of a taxon based on a low, "threshold" pollen abundance. Paleoecologists attempted to average over much of the poor geographic coherency in these low values to calculate how the range limit changed from one time increment to the next. There are many sources of variability in these low values that recommend this type of averaging. For instance, if 2.5% beech pollen were used as a threshold to mean that beech trees grew near a study site in Figure 1, then how would the front be drawn in areas where adjacent sites vary between 0% and 5%? If a few beech

pollen grains appear in the paleoecological record followed by a long absence, does this observation mean that a population appeared and then went locally extinct? Could a few pollen grains have, instead, blown in from distant populations, or could the sample have been contaminated in the laboratory? Averaging can tend to overcome the potential for error or noise in the data.

Models containing leptokurtic dispersal actually predict this type of variability, including irregular fronts, possibly with outlying populations initiated by rare dispersal events (Figure 4) that eventually coalesce and are overrun by an expanding core population. Model analysis makes such "outliers" a requirement of fat-tailed dispersal kernels—that is, they become the expectation of the dispersal process rather than a source of noise that obscures it. This is not to say that every errant pollen grain must necessarily represent a nearby population of trees (e.g., Jackson 1990, Jackson and Whitehead 1991). But theory alters the interpretation of outliers and, therefore, the assignment of the "front."

Candidates for dispersal

Theory shows that rapid tree migration is plausible given the proper dispersal kernel, but it does not identify what factors determine the kernel. Theory further identifies the fat tail, which cannot be characterized directly, as the most important part of the kernel. Fortunately, lessons from mathematical models do not depend on a precise characterization of the tail. Different kernel forms and broad ranges of parameter values predict that migration can be fast and variable. Rather than exact descriptions of the tail, therefore, only a sense of the existence of long-distance arrivals and what might cause them are required. As more is learned about the agents of dispersal, the better will be our ability to predict migration potential in the face of alternative scenarios of environmental change.

Plausible candidates exist for rare, long-distance transport of seed. Birds can transport fleshy fruits 1 km or more. Frugivorous mammals, such as foxes and bears, can travel more

than 10 km/d (Storm and Montgomery 1975, Willson 1993), making them important, albeit underappreciated, agents of long-distance seed dispersal. Blue jays (*Cyanocitta cristata*) cache acorns and beech nuts as far as 4 km from the parent tree (Johnson and Adkisson 1985), an observation anticipated by Reid (1899). Clark's nutcrackers (*Nucifraga columbiana*) disperse pine seeds up to 22 km (Vanderwall and Balda 1977). Whereas animal dispersal is confined to taxonomically restricted groups of trees, abiotic factors are, of course, more general. Tornadoes and other storms can transport seeds many kilometers (Snow et al. 1995). Some seeds (e.g., of birches; *Betula* spp.) are released in winter and secondarily dispersed by wind across snow (Matlack 1989). Water can transport seeds long distances along riparian corridors.

It is easy to point to potential dispersal vectors and declare that their existence reconciles the conflict between theory and data, but the process of seed dispersal is complex and often ineffective (Schupp 1993). The behavior of animal dispersers may be conducive to neither long-distance directional movement of seeds nor successful establishment. Although migrating passenger pigeons (*Ectopistes migratorius*, now extinct) are thought to have moved fagaceous nuts long distances, it is often overlooked that the nuts mature when flocks would have been migrating south, in the opposite direction of Holocene tree spread in the northern hemisphere (e.g., Birks 1989). Moreover, passenger pigeons would have killed most of the seed with their muscular gizzards, and they did not cache nuts in the ground (Johnson and Webb 1989). Large flocks might still have enhanced spread by increasing the overall rate of seed dispersal (Webb 1986), but bird migrations were not a simple pipeline for poleward spread of tree populations at the end of the last ice age. The same situation applies to autumn-ripening fleshy-fruited species dispersed by autumn migrants moving south. Summer-ripening species whose fruits mature before birds begin their autumn migrations face the potential of limited seed movement. Moreover, much animal-in-

duced seed dispersal is not random, but rather directed toward other fruiting individuals, often of the same species. Consequently, long-distance movement from an individual may only infrequently result in long-distance dispersal from a population (Hoppes 1987, Schupp 1993).

Even when a seed is carried a large distance away from the current population range, dispersal may not lead to successful establishment. Animal species differ in the probability that a seed that they disperse will produce a new adult (Schupp 1993). Compared with birds, temperate terrestrial mammals often damage more seeds in gut transit, deposit seeds in larger clumps that may be more susceptible to density-dependent mortality, and deposit seeds in microhabitats that are poorly suited for recruitment or survival (Johnson and Webb 1989, Schupp 1993, Willson 1993). Moreover, deep burial of seed in burrows by small mammals often precludes successful germination (Vanderwall 1990). However, mammals are more likely than most birds to disperse seeds the requisite long distances. Therefore, both mammals and birds may contribute to rapid migrations of fleshy-fruited species, with mammals providing the occasional successful long-distance dispersal necessary for large leaps and birds providing the effective local dispersal necessary for rapid population growth. A similar "division of labor" may exist for nut-bearing trees, with blue jays providing the leap forward and rodents providing effective local dispersal.

Our incomplete identification of plausible long-distance dispersers makes the link between dispersal theory and Holocene tree migrations tentative. Hickory (*Carya* spp.), whose nuts cannot be opened by most jays, has no obvious long-distance disperser, yet it appears to have spread northward almost as fast as some species with plausible long-dispersers (e.g., oaks; *Quercus* spp.). Were hickory dispersers present in the past that are not recognized today? Or has some other explanation for Holocene distributions of hickory (e.g., the presence of pre-existing isolated populations close to the ice front) been overlooked? It is also possible that extinct Pleistocene ani-

mals and humans that exploited nuts as a food source contributed to tree population spread. Although modern studies of dispersal and migrations cannot tell us which animals transported the seeds of which tree species, they can shed light on past and future seed movements and on their potential contributions to population spread.

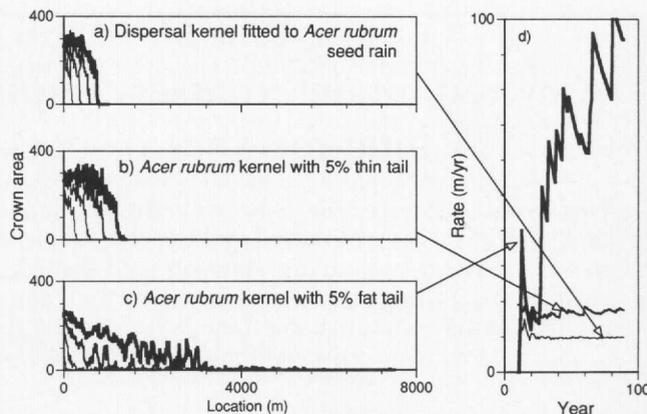
Long-term implications of short-term analysis

Because tree populations migrated rapidly in the past, will they be able to repeat this performance in the face of future climate changes? Whether rapid spread is a basic potential of tree populations or, instead, the outcome of special circumstances following glaciations can be determined only by analyzing the factors that control migration. Because past migrations cannot be observed directly, it is necessary to rely on indirect methods, combining observational data and mathematical models, to assess the efficacy of postulated dispersal mechanisms to produce rapid migration.

Two types of modeling efforts are now being used to analyze how life history and dispersal control population spread. The “forward” approach starts with assumptions about life history and dispersal and then uses these to predict how populations will migrate. The assumptions consist of functions (e.g., a diffusion equation) that are parameterized with data (e.g., average dispersal distance). This analysis might yield such quantities as rates and patterns of spread. These predictions are then judged against the paleoecological evidence (e.g., Figure 1). The “inverse” approach, by contrast, starts with an observed pattern of spread and then asks whether the life histories and dispersal kernels required by a model of that pattern are compatible with observation. It was inverse reasoning that allowed Reid (1899) and Skellam (1951) to conclude that average seed dispersal distances were not compatible with a diffusion model of the high migration rates of the early Holocene. Obviously, forward and inverse methods complement one another; Reid’s comparison compelled him to ponder

Figure 5. Comparison of spread rates simulated with a tree population model (James S. Clark, unpublished data) using three different dispersal kernels showing the front 20-year intervals. (a) Slow spread predicted from the dispersal kernel fitted to seed data for *Acer rubrum* in the southern Appalachians (Clark et al. 1997). (b) Mixed model, described in box page 20, with a

fraction $p = 0.95$ in the kernel $k_1(x)$ fitted to *A. rubrum* data and $(1 - p) = 0.05$ in a thin-tailed ($c = 2$) kernel $k_2(x)$ having a large dispersion parameter $\alpha_2 = 100$. (c) Mixed model similar to the middle panel, but the tail $k_2(x)$ is fat ($c = 1/2$). The fitted data produce the slow, constant spread of diffusion, whereas allocating 5% of seed production to the fat-tailed kernel results in rates of spread comparable to those observed in the early Holocene (d). The thin tail (b) produces constant spread at a higher rate than a kernel with no tail (a), but spread does not accelerate (d).



the feasibility of rare, long-distance dispersal events by birds and water.

Fastie’s (1995) investigation of colonization around Glacier Bay, Alaska, following rapid retreat of glaciers there between 1750 and 1840 provides basic elements for a forward analysis of tree spread. Recruitment, measured up to 4 km away from refugial populations, yields rough estimates of reproductive rates and dispersal. Detailed tree-ring analyses of establishment within these stands provide the demographic data needed to calculate population growth. The broad dispersal observed at Glacier Bay resulted in migration rates across 50 km of deglaciated terrain of 300–400 m/yr, rates that are comparable to early Holocene migration rates for many tree taxa, including spruce (*Picea* spp.) in western North America (Ritchie and MacDonald 1986, Cwynar 1990). The observed pattern of seedling recruitment is consistent with a highly leptokurtic dispersal kernel. Thus, reproduction and dispersal evidence from existing seedlings are elements of a forward analysis that can be used to predict migration rates that are consistent with tree-ring evidence at Glacier Bay and fossil pollen data for the early to mid-Holocene.

The complementarity of forward and inverse modeling is especially valuable when evidence is incomplete. For example, a combined for-

ward and inverse approach is being used to ask whether seed dispersal kernels of temperate hardwood species are compatible with rapid spread (James S. Clark, unpublished data). The approach involves data modeling methods that make it possible to estimate local dispersal patterns under closed canopies with overlapping conspecific crowns (Ribbens et al. 1994, Clark et al. in press). Spatial distributions of parent trees and of seed accumulation in the understory uniquely define dispersal kernels for “locally” dispersed seed at scales of 1–100 m. When these fitted dispersal kernels are embedded within tree population models, they predict rates of spread (1–30 m/yr) that are substantially slower than maximum rates in the pollen record (Figure 5a). The inability to measure the noisy tails of dispersal kernels directly frustrates further progress with a forward model. Additional headway requires an inverse approach.

Inverting the problem, therefore, one must search for a dispersal kernel that satisfies two criteria: it is capable of producing rapid spread, (i.e., it has a fat tail), and it agrees with seed production rates and dispersal distances that can be observed in nature. Rates of spread depend largely on the shape of this tail (“how far”) and on the fraction of seed allocated to the tail (“how much”). The tail cannot be fitted directly to

A mixed model to assess implications of long-distance dispersal

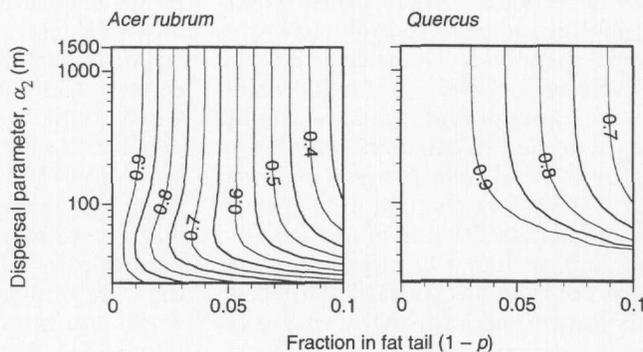
How would the tail of the dispersal kernel have to look to explain the high migration rates observed in the early Holocene, but constrained to be consistent with actual data on seed dispersal? One modeling strategy uses a mixed dispersal kernel, which consists of two probability density function components: $k_1(x)$ and $k_2(x)$, with a fraction p allocated to one component and $(1 - p)$ to the other:

$$k(x) = pk_1(x) + (1 - p)k_2(x)$$

The two components, $k_1(x)$ and $k_2(x)$, have shapes determined by different parameter values α_1, c_1 and α_2, c_2 , respectively.

The mixed model $k(x)$ can be used to append a long, adjustable tail without changing the general shape of a kernel $k_1(x)$ that has been fitted to locally dispersed seed in the forest understory. This mixed model thus allows large changes in the shape (c_2) or length (α_2) of the tail, described by $k_2(x)$, and to adjust how much seed is allocated to the tail—that is, $(1 - p)$. Simulations of tree population dynamics provide estimates of the values of p and α_2 needed to produce high migration rates. A likelihood ratio test comparing the mixed model with that fitted to data shows whether the ranges of p and α_2 extend to those required to produce rapid migration. Figure 5d compares the spread obtained by a mixed kernel having 5% of the seed allocated to a tail with mean dispersal of 200 m with the spread obtained by a kernel without this tail.

Figure 6. Probability surfaces from likelihood ratio tests of seed data under the assumption that a fraction $(1 - p)$ of seed comes from long-distance dispersal described by a fat-tailed kernel $k_2(x)$ with dispersal parameter α_2 (see box this page). The parameters represent the amount of dispersion (i.e., the “length” of the tail, α_2) and fraction in the tail $(1 - p)$.



The contours express the probability that a model with a long, fat tail differs from purely local seed dispersal. High probabilities (those approaching unity), in the lower left of contour plots, mean that a mixed model that includes a small tail (both $(1 - p)$ and α_2 are small) explains the data as well as purely local dispersal. Low probabilities, in the upper right of each plot, mean tails that are too long or contain too much seed to be compatible with the data. Plots show that observed seed dispersal for *Quercus* are compatible with long (more than 200 m) dispersion parameters in the tails, because the probability surface shows values well above those that might cause us to reject the hypothesis of local seed rain (e.g., probabilities less than 0.05). *A. rubrum* probabilities for similar parameter values are lower, indicating that data are less likely to be consistent with long-distance dispersal.

seed data because long-distance dispersal is sporadic. One can, however, ask how much tail a dispersal kernel can have and still be consistent

with observed patterns of seed rain. Perhaps a dispersal kernel with a long, fat tail will fit the data as well as one without such a tail (Kot et al.

1996). Rather than demonstrate the existence of the tail, one can ask: How much tail will the data admit? If the data admit a tail that is sufficiently fat to produce rapid migration in a population model, then the Paradox evaporates.

The inverse method involves comparing likelihoods of observing a pattern of seed rain in a forest under alternative assumptions of different kernel shapes. A kernel that assumes only local dispersal (i.e., a kernel without a long tail) includes a parameter α (see box page 16) that is estimated by maximum likelihood analysis of seed trap data (Clark et al. in press). The likelihood of the data is then computed under the alternative hypothesis that the kernel includes a small amount of seed that is dispersed longer distances, described by a fat tail. This alternative kernel introduces two new parameters, a second dispersal parameter α_2 describing “how far” the tail extends, and a fraction $(1 - p)$, describing “how much” goes into the tail (see box this page). We cannot estimate these parameters from data, but we can search for parameter values that are compatible with the data, as judged by likelihood ratio tests. If we place “too much” seed in a tail that extends “too far,” then the fit becomes unacceptable. But there is a range of parameter values (not too much or not too far) that the models fit equally well (Figure 6). If this parameter range includes values that can predict rapid migration, we have at least one candidate for a solution to Reid’s Paradox, one that is based on real data. Current research (James S. Clark, unpublished data) analyzes how alternative kernels that fit seed rain data affect spread in population models (Figure 5).

Combined approaches that integrate analysis and theory can improve our understanding of how dispersal affects population spread. For instance, George Hurtt and Stephen Pacala (unpublished data) are using inverse methods to calibrate the dispersal kernels in forward models to spatial and temporal pattern in fossil pollen data on the subcontinental scale, that is, the “long-distance” component of dispersal. Dispersal parameters estimated at this scale can be compared with parameter es-

timates from local studies, such as that by Clark et al. (in press). Consistency between estimates obtained by different methods and covering different scales builds confidence in the interpretation of range movement by dispersal patterns that are observed today. Inconsistent estimates can support alternative hypotheses to rapid spread from distant, full-glacial distributions, such as expansion from local refugia (Reid 1899, McGlone 1988).

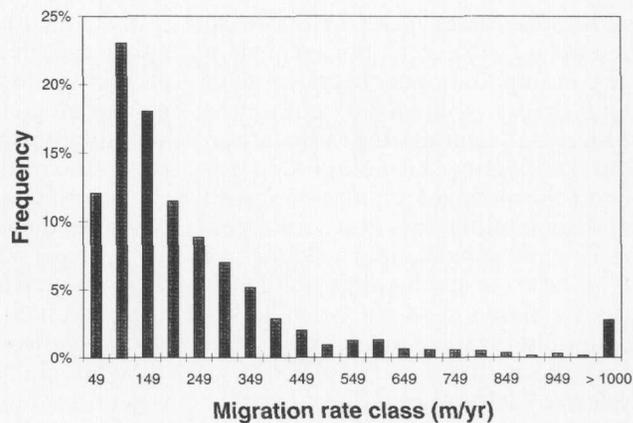
New ways to analyze and model a population front from pollen data can also broaden our view of migration pattern. King and Herstrom (1996) abandoned the traditional calculation of migration rates based on changes in the perceived locations of an expanding front. They estimated rates of spread from a hexagonal grid of "arrival dates" interpolated from nearest fossil pollen sites in the northeastern United States and adjacent Canada, sidestepping entirely the problem of defining a front location. Histograms of migration rates estimated by this method (Figure 7) indicate that a few episodes of high migration rates could account for the "rapid" range expansion of tree populations after deglaciation; median rates are substantially less than mean rates.

Complementary to this analysis is a spatially explicit model of tree population dynamics (including seed dispersal) applied to the modern landscape of Michigan (George A. King and Alan Solomon, manuscript in preparation). This more mechanistic forward approach illustrates both an uneven migration "front" caused by episodic dispersal events and the potential for rapid migration, even when such events are rare (Figure 8). Together, the range of forward and inverse modeling studies shed light on the pattern and rates of spread that may aid in interpreting past rapid migrations and in evaluating the potential for spread in the face of future climate and land-use changes.

Sharpening the data

Whereas models help paleoecologists to explore the efficacy of postulated mechanisms that produce rapid spread of tree populations, future progress will rely on improved paleoecological records. Analysis of mi-

Figure 7. Histogram of calculated *Picea* migration rates in eastern North America during the Holocene. Rates were calculated from a 50-km grid of interpolated arrival dates. Vectors were drawn between the grid point in which pollen first appears and the nearest grid point where pollen was already present (King and Herstrom 1996). The range of each rate class is 50 m/yr. The mean and median rates are 220 m/yr and 140 m/yr, respectively.



gration requires accurate dating and spatially dense data. Interpreting paleoecological records depends on knowing how pollen data record tree populations and how physical factors influence seedling establishment. Characterizing population patterns such as those in Figure 1 requires spatial and temporal detail. The underpinning of migration analysis is radiocarbon dating, which is subject to counting errors and to contamination from "dead" carbon in ancient bedrock, from vertical movement of soluble carbon, and from uncertain stratigraphy (Webb and Webb 1988, MacDonald et al. 1991, Pilcher 1993, Webb 1993). Many fossil pollen sites were dated before these uncertainties were fully appreciated, so dating is often imprecise or inaccurate.

Spatial gaps in continental data networks (Huntley and Prentice 1993, Webb et al. 1993, Jackson et al. 1997) also remain obstacles to characterization of pollen distribution. Densities of fossil pollen sites are low (approximately one site per 40,000 km²) in all but a few regions (Webb 1993), so dispersal events or population patterns cannot usually be resolved at scales of below 10–100 km. An exception is in the northern Great Lakes region, where a high density of fossil sites provides fine-resolution mapping of immigrations (Davis et al. 1986, 1991, Davis 1987, Woods and Davis 1989).

Analysis of population spread also requires improved methods for data interpretation. Migration studies rely on fossil pollen as a proxy of tree populations. However, interpreting

populations from pollen grains is not straightforward, because pollen grains of some taxa (e.g., pines and oaks) can move great distances (Prentice 1988, Jackson 1994). Plant macrofossils constitute an alternative source of data to test inferences from pollen and to provide spatial and taxonomic precision that is not attainable from pollen data (Figure 9; Dunwiddie 1987, Jackson and Whitehead 1991, Jackson et al. 1997). Pollen and plant macrofossil data together can provide a basis for robust inference of past plant distributions and population sizes at a range of spatial scales.

Interpreting past migrations requires not only high-quality paleo-records, but also knowledge of climate trends and of fine-grained pattern in environmental factors that affect tree establishment. Although past migrations were rapid at times, movement at many population frontiers was constrained by climate. Because much of past climate change is interpreted from fossil pollen data, there is a danger of circular reasoning when attempting to interpret how past climate change affected past migrations (Prentice et al. 1991). Paleoecologists will have to rely on evidence for past climate that is independent of fossil pollen data if they are to interpret how climate constrained population spread. Fine-grained environmental heterogeneity, which actually controls the establishment of seedlings in new locations, is determined, in part, by disturbances such as fire and wind throw. The evidence for past disturbance is still rudimentary.

Because deficiencies in the fossil record are subject to improvement, a continuing dialogue between data and theory will ensure continued progress. Accumulating radiocarbon dates will refine chronologies, sharpening the record of population spread and expanding the range of questions that paleoecological data can be used to test. The high site densities available near the Great Lakes cannot be attained in all regions, but hypothesis-driven data collection in selected regions can refine migration estimates and be used to test assumptions and predictions of models. Webb (1993) advocates constructing data sets that allow resolution and coverage at several spatial and temporal scales. Such hierarchically nested data sets will help to surmount the limitation of not being able to obtain high-resolution data everywhere. Subcontinental-scale networks of plant macrofossil data are still in development, but they have already added detail to population spread (Jackson et al. 1997). Improved ways to identify climate changes (Wright et al. 1993) and disturbance (Bradshaw and Zackrisson 1990, Clark et al. 1996) during invasions of new populations will lead to better understanding of the factors that control migrations at broad spatial scales.

Anticipating spread

Past conditions do not tell us what to expect in the future. Future rates of climate change could exceed those of the late Quaternary, and future rates of spread cannot be inferred from Holocene rates, particularly because Holocene rates were far from constant. Migrations in coming decades may result in changing community structure, as spreading populations outrun their slower-migrating competitors, pollinators, seed dispersers, or natural enemies and as they encounter new ones as the population frontier extends to new areas. To anticipate the responses of tree populations to climate change, models must cope with the specific conditions of today, including the fact that spread must occur through a landscape whose spatial structure and potential for plant establishment have been modified substantially

(Pitelka et al. 1997). The role of paleoecological data in developing predictive models may be subtle. The paleoecological data reveal certain key, qualitative features of the process—above all, that migration rates can be rapid and are governed by the tail of the dispersal kernel, not by the mean dispersal distance. In addition, these data may provide a test for more mechanistic models of the migration process.

So far, global, grid-based dynamic vegetation models have treated migration implicitly as an all-or-nothing phenomenon—that is, dispersal is assumed either to be not a barrier (so that abundant propagules of “appropriate” plant functional types are always assumed to be present) or to be confined to locations (model grid cells) where a given plant type already exists. A full description of the transient response of vegetation to climate change, however, will also require spatially explicit treatment of propagule spread between locations as a process modifying vegetation dynamics, as well as some way to represent the effects of landscape fragmentation on the effectiveness of spread. Possible approaches to this problem were developed at a workshop on climate change and plant migrations in Bateman’s Bay, Australia. The workshop participants agreed to represent vegetation dynamics in large-scale models based on insights derived from finer-scale, species-specific models of spread, with contemporary invasions and Holocene migrations serving to constrain model parameters that may be difficult to estimate directly from modern observations (Pitelka et al. 1997). Such a combination of model- and observation-based studies is likely to provide a dual benefit: advancing the development of models that can assess the range of outcomes of present and future global change, and illuminating the natural processes by which plant species have survived the vagaries of natural environmental change.

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Figure 8. Output from a migration model for tree taxa with wind-dispersed seeds (George A. King and Alan Solomon, manuscript in preparation). The map displays the range of a hypothetical tree species in the state of Michigan at the twenty-fifth generation of the simulation. The simulation was initialized with the species occupying only the southern edge of the region, with favorable climatic and ecological conditions to the north. The uneven migration front is caused by seed dispersal during high wind events. The colored areas indicate the extent of seed dispersal after the corresponding number of generations. The white area represents that part of the simulation region to which seeds have not yet dispersed.



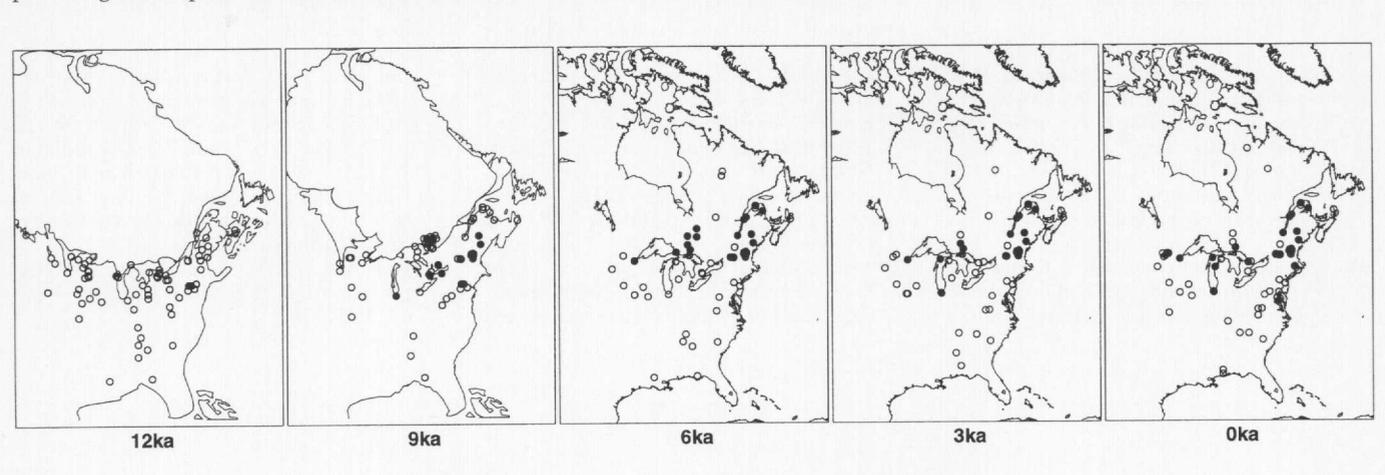
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Figure 9. Time series of *Pinus strobus* macrofossil occurrences from 12 to 0 ka (1 ka = 1000 years before present, based on the radiocarbon time scale) obtained from published sources. Shaded circles in macrofossil maps indicate sites where *P. strobus* macrofossils are present; open circles indicate sites where *P. strobus* macrofossils are absent. Between 12 and 9 ka, spread eastward, westward, and northward was relatively rapid; between 9 and 6 ka, movement northward and westward continued. The northern range shifted southward in the central Great Lakes between 6 and 3 ka. These patterns are not clearly indicated in maps of pollen percentages, which pool all 13 eastern North American *Pinus* species (Webb et al. 1993, Jackson et al. 1997). The macrofossil data provide greater spatial and taxonomic resolution. Modified from Jackson et al. 1997.



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