

LONG-DISTANCE SEED DISPERSAL IN PLANT POPULATIONS¹

MICHAEL L. CAIN,^{2,4} BROOK G. MILLIGAN,² AND ALLAN E. STRAND³

²Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003 USA and

³Department of Biology, College of Charleston, Charleston, South Carolina 29424 USA

Long-distance seed dispersal influences many key aspects of the biology of plants, including spread of invasive species, metapopulation dynamics, and diversity and dynamics in plant communities. However, because long-distance seed dispersal is inherently hard to measure, there are few data sets that characterize the tails of seed dispersal curves. This paper is structured around two lines of argument. First, we argue that long-distance seed dispersal is of critical importance and, hence, that we must collect better data from the tails of seed dispersal curves. To make the case for the importance of long-distance seed dispersal, we review existing data and models of long-distance seed dispersal, focusing on situations in which seeds that travel long distances have a critical impact (colonization of islands, Holocene migrations, response to global change, metapopulation biology). Second, we argue that genetic methods provide a broadly applicable way to monitor long-distance seed dispersal; to place this argument in context, we review genetic estimates of plant migration rates. At present, several promising genetic approaches for estimating long-distance seed dispersal are under active development, including assignment methods, likelihood methods, genealogical methods, and genealogical/demographic methods. We close the paper by discussing important but as yet largely unexplored areas for future research.

Key words: assignment tests; genealogy; genetic models; long-distance dispersal; paternity; plant metapopulations; seed dispersal; seed dispersal models.

The checkered landscapes visible from the air vividly demonstrate that the world is a patchy place. The patchy nature of the landscape ensures that the populations of many plant species are spatially isolated from each other, often by hundreds of metres or more. For such species, seed dispersal represents the only way that populations can exchange individuals or colonize empty, but suitable habitat. Because most seeds move short distances (zero to a few tens of metres; see Howe and Smallwood [1982] and citations therein), it follows that unusual events that move seeds long distances are of critical importance. Despite its fundamental role in natural populations, relatively little attention has been paid to long-distance seed dispersal, and, in some instances, its significance has been strongly downplayed (Howe and Smallwood, 1982).

We do not mean to imply that biologists have not been aware of the existence and potential importance of long-distance seed dispersal. For example, with his characteristic ability to identify the essence of a problem, Darwin (1859) argued that both adaptations for seed dispersal and accidental means of long-distance transport were likely to be of importance to plants. His interest in the spread of plant populations led him to make meticulous observations on how seeds could survive immersion in salty water, be transported in mud on the feet of vertebrates, or pass unharmed through the digestive system of birds. He supplemented such observations with logical arguments to show that while seeming to move little, plants possessed the means to establish new colonies at great distances from their birthplace. But, despite the work of Darwin and

others (e.g., Carlquist, 1966, 1967; Sorensen, 1986), long-distance seed dispersal has often been ignored or addressed by studies that are anecdotal in nature.

The lack of information on long-distance seed dispersal is unfortunate since such dispersal events influence many key aspects of plant biology, including population dynamics, evolution of populations, metapopulation dynamics, biological invasions, and the dynamics and diversity of ecological communities (Harper, 1977; Sauer, 1988; Hengeveld, 1989; Hanski and Gilpin, 1997; Hovestadt, Yao, and Linsenmair, 1999). Although there have been recent and dramatic improvements in the estimation of parameters for local seed dispersal curves (Ribbens, Silander, and Pacala, 1994; Clark, Macklin, and Wood, 1998a; Clark et al., 1999; Nathan and Muller-Landau, 2000), the same cannot be said of long-distance dispersal events. Indeed, because long-distance seed dispersal is very difficult to document directly, few even try to do so.

This paper seeks to convey two specific messages. First, we argue that more effort needs to be directed toward quantifying long-distance seed dispersal, the so-called “tail” of the dispersal curve (see also Moody and Mack, 1988; Portnoy and Willson, 1993; Chambers and MacMahon, 1994; Dyer, 1995; Shigesada, Kawasaki, and Takeda, 1995; Collingham, Hill, and Huntly, 1996; Clark et al., 1998b; Higgins and Richardson, 1999). To support this argument, we review the importance of the tail of the dispersal curve in a variety of contexts, placing special emphasis on the impact of long-distance dispersal on plant metapopulation dynamics. Second, we argue that genetic methods provide a broadly applicable way to monitor long-distance seed dispersal in plants. Although the use of genetic data to quantify dispersal is controversial and the methods are in flux (Bossart and Prowell, 1998; Waser and Strobeck, 1998; Whitlock and McCauley, 1999), we think genetic methods provide one of few general approaches by which the tail of the dispersal curve can be estimated.

More generally, our intent in this paper is to urge research-

¹ Manuscript received 31 February 2000; revision accepted 17 March 2000.

The authors thank Hans Damman and Jim Leebens-Mack for stimulating discussion about issues addressed in this paper and Jan van Groenendael, Ran Nathan, and David McCauley for helpful comments on an earlier version of this paper. This research was supported in part by NSF grant DEB-9726502 to D. J. Howard and M. L. Cain.

⁴ Author for correspondence (e-mail: mcain@nmsu.edu; Fax 505-646-5665).

ers not to take a defeatist attitude toward long-distance dispersal. While we emphasize the use of genetics, other strategies also could be used to collect data from the tail of the dispersal curve (see the Discussion). Too often, we have read in print and heard in conversation that long-distance seed dispersal is "too difficult to measure," which suggests that the tail of the dispersal curve cannot be quantified. Our view is that we cannot afford to give up so easily. If we are to make informed predictions on the likely outcome of habitat fragmentation, global warming, and other aspects of global change, we must collect current data on the tail of the seed dispersal curve.

THE IMPORTANCE OF LONG-DISTANCE SEED DISPERSAL

For the purposes of this paper, we consider a seed dispersal event to be of "long distance" if it is over 100 m. This simple operational definition suits our needs, but what constitutes long-distance dispersal may depend on the context at hand. Thus, it can also be useful to define long-distance seed dispersal in a relative fashion, as when a long-distance seed dispersal event is one that occurs in the upper 1% of seed dispersal distances calculated from an empirically estimated dispersal density function or kernel (see Turchin, 1998). We did not use a kernel-based definition in this paper since few existing data sets allow adequate characterization of the tail of the dispersal curve.

In this section, we review several aspects of the importance of long-distance seed dispersal. We begin with a discussion of seed dispersal data and models, and close with a consideration of situations in which the tail of the dispersal curve is central to understanding the phenomenon at hand (colonization of islands, Holocene migrations, global change). We discuss the importance of long-distance seed dispersal to metapopulation dynamics in the following section.

Seed dispersal data—Most plant seeds do not travel far, often only one or a few metres. The limited distances that most seeds travel is well documented for plants of all growth forms (Harper, 1977; Howe and Smallwood, 1982; Willson, 1993; Cain, Damman, and Muir, 1998; Cheplick, 1998).

The restricted dispersal of most seeds leads to the expectation that plants often may be dispersal limited, that is, unable to disperse by seed to suitable habitat. As expected, many studies report evidence of dispersal limitation (Helliwell, 1975; Peterken and Game, 1984; Whitney and Foster, 1988; Primack and Miao, 1992; Fritz and Merriam, 1994; Matlack, 1994; van Dorp, Schippers, and van Groenendael, 1997; Brunet and von Oheimb, 1998; Bossuyt, Hermy, and Deckers, 1999; Corbit, Marks, and Gardescu, 1999). In several of these studies, estimated migration rates (based on the occurrence of the farthest individual from a source population) of forest understory plants ranged from 0.0 to 2.5 m/yr (Matlack, 1994; Brunet and von Oheimb, 1998; Bossuyt, Hermy, and Deckers, 1999). As noted by Cain, Damman, and Muir (1998) and Brunet and von Oheimb (1998), these rates are so low that they cannot possibly account for the recolonization of northern temperate forests following the retreat of the glaciers. The discrepancy between estimated and observed migration rates is not surprising, since dispersal-limitation studies generally provide little infor-

mation on long-distance dispersal events. Thus, while dispersal limitation is common on small spatial scales, results from these studies also (indirectly) highlight the importance of long-distance seed dispersal.

There are numerous ways that long-distance seed dispersal can occur (Darwin, 1859; van der Pijl, 1982; Janzen, 1984; Sorensen, 1986; Sauer, 1988; Chambers and MacMahon, 1994). These include vertebrate dispersal (by adhesion or ingestion), wind dispersal of seeds (in updrafts and storms, or by secondary dispersal over the substrate), wind dispersal of plants (tumble-plant dispersal), and water dispersal. For several of these categories, long-distance dispersal can occur accidentally, as when seeds stick to the feet of vertebrates (Darwin, 1859), are ingested by foliage-feeding herbivores (Janzen, 1984), or are consumed and later released by a carnivore when it feeds upon an animal that ate fruit or seeds (Nogales, Delgado, and Medina, 1998). Deliberate or accidental transport by people also can be an important mode of long-distance seed dispersal (Fries, 1969; Shigesada, Kawasaki, and Takeda, 1995). See citations in Higgins and Richardson (1999) for further information on unusual forms of long-distance seed dispersal, such as that by resin-collecting, stingless bees.

Overall, what do existing data tell us of long-distance dispersal? In many cases, very little, other than it occurs and, by inference, must be important in some instances (as in Holocene migrations). Maximum seed dispersal distances on the order of 1–20 km have been recorded for a substantial number of plant species (Sauer, 1988; Cheplick, 1998; Nathan, 2000). Examples of even longer seed dispersal distances are cited in the subsection below, *Colonization of islands*.

Although we know plant seeds can travel long distances, few data sets allow accurate characterization of the long-distance component of a seed dispersal curve (Portnoy and Willson, 1993; Higgins and Richardson, 1999). Many attempts to quantify long-distance seed dispersal are hindered by the fact that the model-fitting process may be driven by the large number of short-distance dispersal events; this causes the tail of the dispersal curve to be estimated poorly. In addition, the central tendency (e.g., the mean) and the tail of a dispersal curve can vary independently (Portnoy and Willson, 1993; see Hamrick and Nason [1996] for genetic evidence consistent with this claim), which can cause additional statistical problems. Some of these difficulties are addressed by the "mixture models" discussed in the following section. Still lacking, however, are data sets that were collected under a protocol designed to maximize the chance of observing long-distance seed dispersal events. Thus, the study of long-distance seed dispersal is severely data limited.

Models of long-distance seed dispersal—Long-distance dispersal has caught the attention of modelers. In the past few years, models have been developed that focus on the role of long-distance dispersal in metapopulation dynamics, Holocene migrations, genetic differentiation of populations, biological invasions, global warming, habitat fragmentation, and competitive co-existence (Dyer, 1995; Shigesada, Kawasaki, and Takeda, 1995; Collingham, Hill, and Huntly, 1996; Malanson and Armstrong, 1996; Le Corre et al., 1997; Cain, Damman, and Muir, 1998; Clark, 1998; Clark et al., 1998b; Durrett and Levin, 1998; Holmes and Wilson, 1998; Higgins and Richardson, 1999). The general conclusion to emerge from these mod-

eling efforts is that long-distance dispersal is of critical importance. For example, Shigesada, Kawasaki, and Takeda (1995) and Higgins and Richardson (1999) demonstrate that long-distance dispersal events must be taken into account if we are to make accurate predictions on the rate of biological invasions. Similarly, Dyer (1995) demonstrates the importance of long-distance dispersal in the context of projected climate change, and Malanson and Armstrong (1996) show that long-distance dispersal events increase species richness in a fragmented landscape. As a final example, Le Corre et al. (1997) show that long-distance dispersal events influence the genetic differentiation of populations, leaving a genetic signature that is likely to persist for long periods of time.

Conceptually, many models that incorporate long-distance dispersal describe movement as a stratified process. In a stratified movement model, there are at least two different modes of dispersal, including one that leads to local, short-distance dispersal and one that leads to long-distance dispersal; this is an intuitive approach since seeds often are dispersed by more than one mechanism. Several of the papers cited in the previous paragraph characterize a stratified dispersal process with mixture models, in which different probability distributions are used to model local vs. long-distance dispersal. Mixture models provide a nice analytical framework for modeling long-distance dispersal (Turchin, 1998; Clark et al., 1999; Higgins and Richardson, 1999). The mixture models of Clark and colleagues (Clark, 1998; Clark et al., 1999) and Higgins and Richardson (1999) are of particular interest because, unlike most other studies, the parameters that govern long-distance dispersal in these models were estimated from field data. These papers also illustrate how analytical (Clark, 1998; Clark et al., 1999) and simulation (Higgins and Richardson, 1999) models can be used to examine the importance of long-distance dispersal.

Colonization of islands—Long-distance seed dispersal is obviously essential for the colonization of islands. Indeed, studies of the colonization of islands provide evidence of the most impressive seed dispersal distances known. Ridley (1930) shows that plants with a broad range of dispersal modes, including those with no obvious means of long-distance dispersal, reached Krakatau in ~50 yr. To reach the Krakatau archipelago, the seeds of these species probably traveled 12–40 km from Java, Sumatra, and several smaller islands (Thornton, 1996). Carlquist (1965, 1967) and Sauer (1988) describe numerous other examples of long-distance dispersal to islands. Islands separated by hundreds of kilometres from a source population are usually colonized by water- or animal-dispersed plant species. For example, Sorensen (1986) reviews studies in which plant seeds were dispersed by water or animals for distances that ranged from 650 to 1540 km; no wind-dispersed plants or plants that lacked an obvious dispersal mechanism were found to have dispersed such long distances.

Holocene migrations—Seed dispersal distances of many woodland species are so limited that ordinary means of dispersal are not likely to have enabled them to move the hundreds or thousands of kilometres that they traveled during the Holocene. For example, many temperate forest woodland herbs are ant dispersed (Handel, Fisch, and Schatz, 1981). Ants usually transport the seeds of such species <2 m; the maximum distance known is 35 m for *Asarum canadense* (Cain, Damman, and Muir, 1998). Such limited seed-dispersal

distances could not have led to the Holocene recolonization of northern forests. To illustrate this, we calibrated integrodifference equations (van den Bosch, Metz, and Diekmann, 1990; van den Bosch and Metz, 1996) with seed dispersal (Cain, Damman, and Muir, 1998) and demographic (Damman and Cain, 1998) data for *Asarum canadense*. The models predict that *A. canadense* should have spread 53 km by ant-dispersal over the past 16000 yr. Since this species actually spread 450–1900 km, these results indicate that it did so by other means.

We draw two conclusions from data on seed-dispersal distances of forest understory species. First, long-distance seed dispersal events dominated the Holocene migrations of forest understory species. Second, for many of these species, a stratified movement model is appropriate: local movements occur by one mechanism (e.g., ant dispersal), but other mechanisms (e.g., accidental transport) are required for long-distance dispersal.

Skellam (1951), Birks (1989), Hengeveld (1989), Wilkinson (1997), Clark (1998), Clark et al. (1998b), and many others also have emphasized the importance of long-distance dispersal for the Holocene migration of plants, usually for tree species. The studies of Clark and colleagues (Clark, 1998; Clark et al., 1998b) are particularly interesting in that they indicate that extreme long-distance dispersal values need not be posited for trees to have accomplished the rapid migrations inferred from the paleorecord. Their results are encouraging in that models which are based (in part) on seed dispersal data collected on a small spatial scale can be used to make accurate predictions on large spatial and temporal time scales.

Global change—Information on long-distance dispersal is needed to understand how global change is likely to influence life on Earth. For example, invasive species pose a threat to biodiversity in many regions of the world (Drake et al., 1989; Vitousek et al., 1997). To predict the likely course of a given invasion, attention must be paid to the ability of the invasive species to disperse long distances (Shigesada, Kawasaki, and Takeda, 1995; Higgins, Richardson, and Cowling, 1996; Higgins and Richardson, 1999). Similarly, modeling efforts have demonstrated that the predicted impact of various forms of environmental change depends greatly on whether long-distance dispersal events are included in the model (Dyer, 1995; Collingham, Hill, and Huntly, 1996; Malanson and Armstrong, 1996; Higgins and Richardson, 1999).

Results from such studies suggest that predictions about global change will not be accurate if we do not have good estimates of the dispersal curve, including its long-distance component. Consider global warming models. As discussed in Pitelka and the Plant Migration Workshop Group (1997), most models of global warming either take a “climate envelope” approach, in which plant species are assumed to reach all areas of suitable habitat (e.g., Iverson and Prasad, 1998), or they assume that no dispersal occurs. The latter is clearly wrong, but so is the former. To improve models of global warming and other aspects of global change, we must use realistic dispersal curves. In particular, it is important to collect data on current rates of long-distance seed dispersal. If we do not do this, and instead calibrate the tail of the dispersal curve with data from previous plant migrations (e.g., those for the spread of trees during the Holocene), we ignore the impact that recent, human-caused changes to the landscape may have had on the ability of plants to disperse long distances.

SEED DISPERSAL AND PLANT METAPOPOPULATIONS

The metapopulation concept has emerged as a dominant paradigm for the description of natural populations (Hanski and Gilpin, 1997). Following current usage (e.g., Hanski and Simberloff, 1997), we define metapopulations broadly as a set of spatially disjunct populations linked by dispersal. Spatially disjunct populations of plants are often separated from each other by many hundreds of metres, while most plant seeds disperse far less than 100 m. Thus, the extent to which plant populations in a metapopulation are linked by dispersal will depend entirely on the extent to which long-distance seed dispersal occurs. A priori, then, we know that long-distance dispersal is important in plant metapopulations. Examples where long-distance seed dispersal is not only important, but essential, include species that lack dormancy and whose habitat either degrades in a predictable fashion (Valverde and Silvertown, 1997) or is subject to catastrophic forms of disturbance (Menges, 1990). For such species, long-distance seed dispersal is the mechanism by which suitable habitat is colonized, thereby enabling the metapopulation to persist despite the fact that individual populations are doomed.

The central importance of long-distance seed dispersal to plant metapopulations brings us immediately to a troubling issue: as discussed above, we know very little about long-distance dispersal in plants. Often, we also lack information on seed bank dynamics. Thus, it is common to know little about either of the two ways that plants can come to occupy empty but suitable habitat: dispersal through space (long-distance seed dispersal) and dispersal through time (dormancy). In addition, it can be difficult to document the extinction rate of local plant populations, due to the large spatial scale required for such studies. Thus, it is hard to measure parameters related to population extinction, seed dormancy, and seed dispersal in plants (but see van Groenendael, Ouborg, and Hendriks [1999] for a useful framework within which to estimate the relevant parameters). These difficulties help to explain why relatively few studies have analyzed the dynamics of plant populations within a metapopulation framework (Eriksson, 1996; Husband and Barrett, 1996).

Husband and Barrett (1996) argued that such challenges also represent a source of opportunity. We share this view. We find the metapopulation framework extremely useful for plants because it encourages us to face such difficult issues as long-distance seed dispersal, environmental heterogeneity over space and time, the role of seed dormancy, and the interplay between gene flow and local selection. For empiricists, facing such issues will require obtaining good estimates of the hard-to-measure parameters mentioned in the previous paragraph; we discuss how this can be done for long-distance dispersal in the following section (*The use of genetics to quantify long-distance seed dispersal*) and in the Discussion. For theoreticians, facing the challenging issues raised by a metapopulation perspective will require examining how long-distance seed dispersal, seed dormancy, and other features of the biology of plants influence the results of metapopulation models. We elaborate on this point below, emphasizing the role of long-distance dispersal in spatially explicit models of metapopulation dynamics.

Spatially explicit models of metapopulation dynamics—Metapopulation models are increasingly used to examine both single species and community dynamics (Hanski and Gilpin,

1997). To some degree, all metapopulation models are spatial, in that they are concerned with the dynamics of populations (patches) assumed to be spatially isolated from one another. But space is an implicit variable in many metapopulation models in that no attention is paid to the spatial arrangement of populations (Hanski and Simberloff, 1997). Such models assume that dispersal is equally likely among all populations. In some instances, this assumption may be realistic at intermediate spatial scales (e.g., 200 m to 20 km; see Cain, Damman, and Muir, 1998), but in general it is not realistic at either small or large spatial scales.

The urge to incorporate a more realistic portrayal of dispersal has led to the development of spatially explicit models that account for the spatial arrangement of populations within a metapopulation. Here too, there is a wide range in how much “realism” a given model incorporates. For example, Hanski and coworkers have constructed spatial models in which the probability of colonization decreases with the distance between populations (Hanski, 1994; Hanski et al., 1995; Wahlberg, Moilanen, and Hanski, 1996). While spatially explicit, these models ignore features of the landscape that may have a critical impact on dispersal between populations and, hence, on colonization probabilities (Wiens, 1997). Thus, Wiens and others have called for the development of metapopulation models that are embedded in the full complexity of the natural landscape; examples of this approach are described in Hanski and Simberloff (1997) and Wiens (1997).

However constructed, spatially explicit models of metapopulation dynamics typically suffer from poor information on dispersal. This lack of information can limit the utility of highly detailed, spatially explicit models (Moilanen and Hanski, 1998). Overall, results from metapopulation models, as well as the central importance of long-distance dispersal in actual plant metapopulations, indicate that predictive models of plant metapopulation dynamics must be calibrated with better information on long-distance dispersal.

THE USE OF GENETICS TO QUANTIFY LONG-DISTANCE SEED DISPERSAL

The thrust of our paper thus far is that good data on long-distance dispersal are essential but very scarce. Long-distance seed dispersal is inherently hard to measure directly, and there are at present no broadly applicable methods to collect the data that are needed to calibrate the tail of the dispersal curve. We think this problem can be solved by using genetic methods to document the extent to which plant populations are linked by long-distance seed dispersal.

Genetic estimates of dispersal usually are based on seedlings or later stages of development. When samples are taken in this manner, genetic estimates of dispersal reflect both the movement (dispersal per se) and establishment of seeds. As such, genetic estimates of seed dispersal curves usually provide a measure of “effective seed dispersal,” that is, dispersal plus establishment, not actual seed dispersal.

In many cases, what matters most is the joint dispersal and establishment of seeds, not the movement of seeds to locations in which they cannot establish. In other cases, however, it is clearly important to understand dispersal per se, as well as any factors that might cause an effective dispersal curve to differ from the actual dispersal curve. In cases where primary interest is on actual seed dispersal curves, seeds can be collected (e.g., in seed traps) and used to form either genetic or ecolog-

ical estimates of dispersal. Genetic or ecological estimates of dispersal based on seedlings or later stages could also be constructed to determine whether effective dispersal curves differ from actual dispersal curves.

Marker data—A variety of genetic markers can be used to quantify the dispersal curve. As discussed by Hoelzel (1998), Parker et al. (1998), Ouborg, Piquot, and van Groenendael (1999) and others, such markers include allozymes, DNA sequences, microsatellites, restriction fragment length polymorphisms (RFLPs), and DNA randomly amplified from the genome (e.g., RAPDs and AFLPs).

Flowering plants exchange genes among populations by the movement of pollen and seed. Only dispersal via seed directly affects colonization of new populations. Movement of both pollen or seed, however, leaves a genetic signature within and among populations. Therefore, estimating migration among plant populations from nuclear DNA, which is transferred via pollen and seed, may tend to overestimate seed dispersal. Because of this effect, estimation of the tail of a seed dispersal curve requires at least some use of markers inherited only through seeds.

For many flowering plants, the cytoplasmic organellar genomes (that is, mitochondrial and chloroplast DNA) are inherited only through seeds (Corriveau and Coleman, 1988); ideally, this form of inheritance should be confirmed through genetic analyses (Milligan, 1992). In studies that have compared nuclear and cytoplasmic markers at the population level, nuclear markers moved more frequently than cytoplasmic markers (McCauley, 1994; Strand, 1997). Use of a cytoplasmic genome raises several caveats. First, cytoplasmic genomes are haploid, thus analytical techniques that depend upon diploid genotypes cannot be used. Second, although cytoplasmic DNA contains many genes, these genes are inherited as a single locus. The variance around estimates of population structure and inferred migration rates typically increases as the number of loci employed decreases. As a result, dispersal estimates derived from cytoplasmic genetic markers may not be very precise. Nevertheless, because they are often dispersed only by seed, cytoplasmic markers are essential for genetic estimates of seed dispersal in plants.

In the remainder of this section, we review genetic estimates of plant dispersal rates; all the methods reviewed here assume selectively neutral markers. We evaluate the utility of these methods for quantifying the tail of the seed dispersal curve in the Discussion.

Contemporary estimates of dispersal—In this section we describe genetic methods that provide contemporary or short-term estimates of dispersal among populations. A general advantage of this approach is that it provides data on current rates of dispersal, thus serving as the genetic analogue of an ecological mark-recapture study. A potential disadvantage of contemporary measures of dispersal is that they may fail to capture the rare events that form the tail of a dispersal curve.

Parentage analysis—Parentage analysis seeks to assign parents to members of a population or group of populations. These approaches either exclude possible parents based upon multilocus genotypes (Broyles, Schnabel, and Wyatt, 1994), or they use a maximum-likelihood estimation procedure that assigns parentage probabilistically based upon multilocus genotypes (Roeder, Devlin, and Lindsay, 1989; Milligan and

McMurry, 1993). Methods based on parentage analysis can be extremely powerful and have been used to estimate immigration rate of pollen in plant populations (Ellstrand and Marshall, 1985), seed migration (Meagher and Thompson, 1987; Schnabel, Nason, and Hamrick, 1998), and patterns of local movement in animal populations (Prodohl et al., 1998).

An advantage of parentage analysis is that it uses genetic markers to document particular dispersal events, thus providing a relatively direct measure of dispersal. A disadvantage of parentage analysis is that the populations of interest must be sampled exhaustively so that all potential parents have equal chance of identification. As the number and size of populations under consideration increase, this requirement can become overwhelming in terms of the resources available to the researcher. In addition, parentage analysis is based on assumptions that may not hold in nature, such as (a) source populations are discrete (enabling one to have a nonarbitrary way to determine the allele frequencies of each source population) and (b) there is no linkage disequilibrium among the loci sampled.

Assignment methods—Assignment tests use allele frequencies in each potential source population to calculate the likelihood that a particular individual's genotype originated from each of the source populations (including the population in which the individual was initially sampled). The population in which the likelihood is highest is considered to be the population that produced the individual (Paetkau et al., 1995; Nielsen, 1997; Shriver et al., 1997; Waser and Strobeck, 1998; Roques, Duchense, and Bernatchez, 1999).

A major advantage of assignment methods is that populations do not have to be sampled exhaustively. However, assignment methods are based on assumptions that may be violated in natural populations, namely that source populations are discrete, that there is no linkage disequilibrium among the loci sampled, and that these loci are each in Hardy-Weinberg equilibrium.

Long-term estimates of dispersal—In this section we describe genetic methods that integrate the results of many dispersal events over long periods of time. An advantage shared by all long-term estimates of dispersal is that they may be more likely than contemporary estimates of dispersal to capture the rare events that constitute the tail of the dispersal curve. A disadvantage common to long-term estimates of dispersal is that historical rates of dispersal may differ from current rates of dispersal. For example, increasing habitat fragmentation might reduce the ability of a species to disperse long distances, thus causing historical estimates of dispersal to overestimate the current tail of a dispersal curve.

F_{ST} -based methods—Wright (1951) established the following relationship between population genetic structure and the apparent number of migrants exchanged per generation: $N_m = 1/4(1/F_{ST} - 1)$. In this equation, F_{ST} , a measure of among-population genetic variance relative to the total variance, is inversely related to N_m , the effective number of migrants exchanged per generation. When using this approach to estimate migration, F_{ST} (or one of its analogues) is calculated from patterns of marker genetic diversity and N_m is then determined from Wright's (1951) equation. F_{ST} -based methods are often used to estimate migration (see reviews by Neigel, 1997, and Bohonak, 1999).

F_{ST} -based approaches for estimating dispersal among pop-

ulations require relatively few samples per population and can use sequence, microsatellite, or allozyme data. However, F_{ST} -based estimates of migration suffer from several disadvantages (Bossart and Prowell, 1998; Whitlock and McCauley, 1999), including: (1) the derivation of Wright's formula depends on assumptions that are false or that may not hold in many natural populations, such as (a) all populations have an equal and constant population size, (b) propagules are exchanged among all populations with equal probability, and (c) an equilibrium has been reached between gene flow and genetic drift; (2) $N_e m$ has poor statistical properties; and (3) in most instances, the effective population size (N_e) used in Wright's formula is much smaller than the census size, N , potentially resulting in an underestimate of actual propagule movement.

With information in addition to genetic marker diversity data, it may be possible to compensate for some of the disadvantages mentioned above. For example, it is possible to model the decay of a population system towards equilibrium using information on the history of the population system and the effective population size of the system (Strand, Milligan, and Pruitt, 1996; Strand, 1997). Knowledge of the effective population sizes also may allow a simple conversion from "effective" to "real" migrants based upon the ratio of census to effective sizes within each population.

Likelihood methods—At least two likelihood-based approaches that estimate the amount of migration among populations from distributions of allele frequencies have been recently developed (Rannala and Hartigan, 1996; Tufto, Engen, and Hindar, 1996). The main substantive difference between these two methods is that Tufto, Engen, and Hindar (1996) allow for arbitrary patterns of migration, whereas Rannala and Hartigan (1996) assume an island structure. Migration estimates derived from likelihood methods may provide less bias and reduced variance relative to estimates based on F_{ST} (Rannala and Hartigan, 1996). The likelihood methods developed to date do not assume that the system of populations are in migration-drift equilibrium, but they do assume that effective population sizes are equal or at least known through independent information.

Genealogical methods—Genealogical or coalescent approaches in population biology can be used to estimate many population-level characteristics including effective population size (Strobeck, 1983; Kuhner, Yamato, and Felsenstein, 1995), population growth rate (Kuhner, Yamato, and Felsenstein, 1998), and migration rate (Slatkin and Maddison, 1989; Beerli and Felsenstein, 1999). For example, the method of Beerli and Felsenstein (1999) jointly estimates the effective size (N_e) of individual populations and the rate at which these populations exchanged migrants (m) in the past. The Beerli and Felsenstein estimator takes advantage of the genealogical relationships among alleles both within and among populations to estimate N_e and m using a maximum-likelihood approach.

Genealogical approaches are very promising and offer several key advantages. Like the approaches based upon F_{ST} or its analogs, genealogical approaches can use many different types of molecular data. Furthermore, in principle genealogical approaches can allow any model of population structure to be used in the estimation procedure. For example, the estimator developed by Beerli and Felsenstein allows for unequal population sizes and asymmetric migration rates. Relatively little is known about how robust genealogical estimators are to de-

viations from the assumptions used to derive the estimators; such assumptions include constant population size, constant mutation rate, constant migration rate, and a drift-migration balance.

Genealogical/demographic methods—A final means of estimating dispersal distributions involves joint analysis of demographic and genetic data. This method relies on the fact that the time to coalescence for a pair of alleles, and hence the degree of DNA sequence differentiation, depends on the demography of a population. Even for populations with complex demographic features, the expected coalescence times for alleles can be determined directly from life-table data (Orive, 1993). Assumptions of the genealogical/demographic approach include constant population size, constant mutation rate, and constant migration rate.

Genealogical/demographic methods can be extended to estimate dispersal rates (Milligan, unpublished data). As an illustration, consider a pair of populations interconnected by dispersal. A demographic projection matrix may be used to describe the demography of each population singly (Caswell, 1989). Dispersal between the populations represents a demographic transition from a life-history stage in one population into a life-history stage of the other population. The pair of populations may therefore be described by a demographic projection matrix of greater rank (Caswell, 1989), some elements of which reflect intrapopulation demographic rates (growth, survival, reproduction) and some elements of which reflect interpopulation dispersal. Given demographic information on each population, the former elements are known while the latter elements must be estimated.

DNA sequence data from alleles in each population can be used to estimate the projection matrix elements that represent interpopulation dispersal. Because coalescence time, and hence sequence divergence, depends on the demographic rates (Orive, 1993), one can determine dispersal rates that maximize the fit between the observed sequence divergence and that expected from the demographic model.

A joint genealogical/demographic approach offers several advantages. First, it is applicable to any set of populations that can be described by projection matrices. Second, unlike current implementations of other indirect genetic measures of dispersal rates, the fit between the estimation model and the observations can be tested. Although dispersal estimates are derived from the mean coalescence time, the demographic model provides a complete distribution of coalescence times, which can be compared for goodness of fit to the observed distribution of sequence divergence. The joint genealogical/demographic approach also allows one to perform a sensitivity analysis of the impact of dispersal parameters on the intrinsic rate of increase of both the metapopulation and each individual population. A disadvantage of the genealogical/demographic approach is the time and expense required to collect demographic data. Finally, like the Beerli and Felsenstein estimators described in the previous subsection, the robustness of joint genealogical/demographic estimators of dispersal rates is largely unknown.

DISCUSSION

As discussed throughout this paper, information about long-distance seed dispersal is crucial to understanding many aspects of the biology of plants, such as the dynamics of plant

metapopulations, the spread of invasive species, and the response of plants to global change. Unfortunately, very little quantitative information about long-distance seed dispersal exists. A further complicating factor is that the ability of plants to disperse long distances can be expected to change over time. Seed dispersal events take place within complex natural landscapes. As those landscapes are fragmented over time, the ability of seeds to move long distances may be reduced. Thus, especially in the context of predicting how plants are likely to respond to global change, it is important to obtain current and ongoing measures of long-distance seed dispersal.

Seeds that travel long distances are inherently difficult to observe. We have argued in this paper that genetic methods can be used to provide data on the tail of the dispersal curve (see also Silvertown, 1991; Waser and Strobeck, 1998; Bohonak, 1999; Ouborg, Piquot, and van Groenendael, 1999). However, genetics do not provide a simple, magic bullet with which to study long-distance seed dispersal. For example, it is necessary to use cytoplasmic DNA markers to separate gene flow by pollen from gene flow by seed, yet such markers may provide low resolution because they are inherited as a single genetic locus. In addition, what constitutes the best genetic approach will depend on the species under study and the research questions of interest. Finally, genetic methods for estimating the tail of the dispersal curve are still under development; while these methods are promising, much remains to be done. Thus, we cannot provide a simple recipe for how to apply genetics to the study of long-distance seed dispersal. Instead, in the following section we discuss how several promising approaches can be used to estimate the frequency with which seeds travel long distances. More generally, we urge a multifaceted approach: to quantify the tail of the dispersal curve researchers should use whatever combination of genetic and ecological methods allows them to collect the data they need for the species they are interested in.

Using genetics to estimate long-distance seed dispersal—Genetic methods used to study dispersal can be subdivided into those that document current dispersal events only (contemporary estimates of dispersal) and those that document dispersal events over long periods of time (long-term estimates of dispersal). In the section *The use of genetics to quantify long-distance seed dispersal*, we discussed two contemporary estimates of dispersal, parentage analysis and assignment methods, and four long-term estimates of dispersal, F_{ST} -based methods, likelihood methods, genealogical methods, and genealogical/demographic methods. Here we evaluate how useful current implementations of each of these approaches is for calibrating the tail of the dispersal curve; often it may be helpful to compare results from contemporary and long-term estimates of dispersal.

Parentage analysis can be used to construct frequency distributions of the distance that seeds or seedlings are located from their mother plants—including movements among populations—as illustrated by Schnabel, Nason, and Hamrick (1998). However, parentage analysis requires that all potential parents be sampled, a requirement that quickly becomes overwhelming when studying many or large populations. Thus, at present we recommend this approach only for the study of few or small populations. As more rapid methods to process large numbers of samples are developed, parentage analysis will be useful in a broader range of applications.

Assignment methods show considerable promise for the

study of long-distance seed dispersal. Based on a seedling's genotype, assignment methods determine the most likely population from which the seedling originated; this approach is similar to parentage analysis but is preferable in that it does not require the study populations to be sampled exhaustively. When used in conjunction with data on the number of seeds produced in different populations, assignment methods can be used to construct curves that plot the frequency with which seeds disperse (and establish) vs. distance. Current drawbacks of assignment methods include (a) only a single locus, the cytoplasmic DNA, provides a direct measure of seed dispersal among populations, and (b) little is known of how well assignment methods recover the dispersal curve (Waser, Strobeck, and Paetkau, 2000). Despite these drawbacks, it is encouraging that in a study in which the population of origin of migrating individuals was known, assignment methods provided up to 90% accuracy when only a single genetic locus was used (Roques, Duchense, and Bernatchez, 1999). In addition, nuclear DNA markers can be used in conjunction with cytoplasmic markers to help discern the population of origin of a given seedling. For example, if an assignment test based on nuclear markers strongly supports a single population as the most likely population of origin, then both the seed and pollen may have originated from that population. In contrast, if two populations are indicated as the most likely populations of origin, then one may be the population from which the pollen originated, the other from which the seed originated.

Of the four long-term estimates of dispersal, at present F_{ST} -based methods show relatively little promise for quantifying the tail of dispersal curves. Currently, F_{ST} -based methods are hampered by unrealistic assumptions about the structure of populations, as well as by statistical problems in the estimation of migration rates (see the section entitled *The use of genetics to quantify long-distance seed dispersal*); in principle, many of these difficulties could be overcome by developing non-equilibrium estimates of migration from F_{ST} .

The remaining three estimates of long-distance seed dispersal, likelihood methods, genealogical methods, and genealogical/demographic methods, hold considerable promise for estimating the tail of the dispersal curve. For each of these approaches, dispersal parameters can be estimated for broad classes of dispersal curves and different dispersal functions can be "competed" against each other to determine which provides a better fit to the data. Strictly genealogical methods estimate both dispersal parameters and N_e from genetic data. In contrast, genealogical/demographic methods and likelihood methods estimate only dispersal parameters from genetic data. Thus, genealogical/demographic and likelihood approaches may provide more precise estimates of dispersal parameters than strictly genealogical methods, but any such increase in precision comes at the additional cost of collecting demographic data.

Alternatives to genetics—We have emphasized how genetics can be used to glean data on long-distance dispersal in plants. However, genetic data often do not allow direct characterization of a seed dispersal curve since it is usually seedlings (or later stages) that are sampled, not seeds. When seeds are not sampled genetically, genetic estimates of seed dispersal reflect both the movement (dispersal per se) and establishment of seeds. In such cases, genetic approaches provide an "effective" seed dispersal curve, not the actual seed dispersal curve. Hence, depending on the questions of interest, it may be help-

ful to use other methods alone or in conjunction with genetic analyses. We describe several alternatives to genetics here; see Turchin (1998), Higgins and Richardson (1999), and Nathan and Muller-Landau (2000) for more information.

Local seed dispersal events can be followed by using a variety of physical marking techniques to label individual seeds. These methods may not work well when attempting to track seeds that travel long distances, because of the rarity of such events and because it may be difficult to determine where the seeds land. However, marked or individually-released seeds can be used to estimate the parameters of mechanistic models, which in turn can be used to estimate the tail of a dispersal curve (Nathan and Muller-Landau, 2000). Data on long-distance dispersal can be gathered by marking individual fruits. For example, Mack (1995) inserted tags into 700 fruits, 30 of which were recovered to document dispersal events of up to 1000 m. In some instances, alleles that have an easy-to-observe phenotypic effect and that are unique to plants from a known location can be used to tag individuals in much the same way that dyes or paints are used in standard ecological studies. Similarly, seeds produced by plants grown in an unusual chemical environment may carry a unique chemical signal. Chemical tagging methods that can be surveyed rapidly in the field have the potential to provide a broadly applicable way to mark and directly follow the movement of plant seeds from known release points. However, we are not aware of any published studies that have used chemical tagging to document long-distance seed dispersal.

With sufficient time and resources, seed-trap methods can be extended to provide information on long-distance seed dispersal events; these data could then be used to estimate the tail of the dispersal distribution (see Turchin [1998] for estimation procedures). In addition, data obtained from seed traps that cover an extensive area could be used in conjunction with statistical analyses that sought to test how large a tail was consistent with the seed-trap data (see Clark, 1998).

Finally, it is often of interest to determine whether plants are dispersal limited, recruitment limited, or both. The general issue of dispersal vs. recruitment limitation can be addressed in a variety of ways, one of which is to compare actual and effective dispersal curves. Such a comparison could be done with genetic data alone, ecological data alone, or, perhaps most fruitfully, a combination of genetic and ecological data. For example, seeds collected in seed traps could be analyzed genetically and used to form genetic estimates of actual seed dispersal curves; of course, ecological estimates of actual seed dispersal curves can also be obtained from the same seed trap data. Effective seed dispersal curves could be estimated from genetic analyses on seedlings or later stages of development, or from seedling dispersion data (e.g., using the inverse method of Ribbens, Silander, and Pacala, 1994). If substantial differences between the actual and effective seed dispersal curves are found, ecological experiments could be performed to uncover causes of these differences.

Directions for future work—The single most pressing need for future work is to collect better data on long-distance seed dispersal. If, as is likely, data from the tail of the dispersal curve remain sparse, curve-fitting can be difficult. However, there is a well-developed statistical literature on fitting the tails of distributions; see Portnoy and Willson (1993), Turchin (1998), and references therein.

We close by highlighting five other promising areas for future research.

Improve genetic estimates of long-distance seed dispersal—At present, we have selected assignment methods, likelihood methods, genealogical methods, and genealogical/demographic methods as promising genetic approaches from which to estimate the tail of the dispersal curve. However, for these and other genetic approaches, much work remains to be done. Most of the methods discussed in this paper are in early stages of development; all could be extended to include more realistic situations. Overall, analytical techniques have lagged behind the development of marker technology. Thus, there is a strong need to refine existing methods and to develop new ways to use genetics to collect data from the tail of the dispersal curve.

Apply long-distance dispersal data to real-life problems—There is a great need for better dispersal data in many areas of applied ecology. For example, spatially realistic metapopulation models can be used to predict consequences of habitat fragmentation for the persistence of species. Predictions of spatially realistic models depend critically on how dispersal is modeled; thus it is imperative to collect data on the tail of dispersal curves and use them to examine metapopulation persistence. Similarly, an urgent question is whether plant species can migrate rapidly enough to keep up with projected global climate change. Data on long-distance seed dispersal can be used to answer this question on a species-by-species basis.

Develop new models of long-distance seed dispersal—In the past few years, a series of models has been developed to explore the consequences of long-distance seed dispersal (see *The importance of long-distance seed dispersal: models of long-distance seed dispersal*). However, much remains to be done. For example, little work has examined the impact of long-distance seed dispersal on plant metapopulation dynamics, either at the species or community level. In an evolutionary context, little is known about how long-distance dispersal influences evolutionary dynamics, such as the interplay between local adaptation and gene flow, or the formation and maintenance of different types of hybrid zones (but see Nicholls and Hewitt, 1994). In addition, much insight could be gained from models (and field work) that explore the underlying mechanisms of long-distance seed dispersal (see Nathan and Muller-Landau, 2000). Finally, it is essential to analyze the effects of error on model predictions. Although estimates of parameters that describe the tail of dispersal curves will always contain significant error, little is known about to degree to which such error influences results from models (but see Higgins and Richardson, 1999; Mooij and DeAngelis, 1999).

Compare how well different genetic methods recover long-distance dispersal events—If genetic methods are to be used to collect data on long-distance seed dispersal events, we will need a much better understanding of how robust the methods are to violations of the assumptions used to derive them. In addition, we need to understand how well the different methods perform under different sets of conditions. For example, assignment methods might work best when there is a high degree of genetic differentiation among populations (thus allowing maternal populations to be readily identified), yet when there is high genetic differentiation the rate of gene flow may be so low that the method fails to document the rare events

that form the tail of the dispersal curve. To learn how such aspects of population structure affect the utility of genetic approaches for documenting long-distance dispersal, comparative studies on the performance of different genetic methods under a wide range of assumptions about the structure of populations and the nature of long-distance dispersal could be implemented with computer simulations.

Document current rates of seed-dispersal evolution—Little is known about current rates of evolution of traits that affect seed dispersal. However, Cody and McC. Overton (1996) provide evidence that plants that colonized islands off the coast of British Columbia evolved reduced seed dispersal distances within 10 yr, presumably because selection favored individuals whose seeds were not lost in the surrounding ocean waters (see also Olivieri and Gouyon, 1997). Results from this study should be viewed as preliminary since the heritabilities of the measured seed dispersal traits are not known and since some of the traits may have been under selection for features other than dispersal (e.g., observed increases in seed size might be due at least in part to selection for seedling establishment). Nevertheless, the implications of this study are potentially far-reaching: if rapid evolution of reduced seed dispersal distances in fragmented landscapes is common, such evolutionary changes would make it less likely that plant species can persist as their habitat is fragmented or that they can migrate rapidly enough to keep up with global climate change.

LITERATURE CITED

- BEERLI, P., AND J. FELSENSTEIN. 1999. Maximum likelihood estimation of migration rates and population numbers of two populations using a coalescent approach. *Genetics* 152: 763–773.
- BIRKS, H. J. B. 1989. Holocene isochrone maps and patterns of tree-spreading in the British Isles. *Journal of Biogeography* 16: 503–540.
- BOHONAK, A. J. 1999. Dispersal, gene flow, and population structure. *Quarterly Review of Biology* 74: 21–45.
- BOSSART, J. L., AND D. P. PROWELL. 1998. Genetic estimates of population structure and gene flow: limitations, lessons, and new directions. *Trends in Ecology and Evolution* 13: 202–206.
- BOSSUYT, B., M. HERMY, AND J. DECKERS. 1999. Migration of herbaceous plants across ancient-recent forest ecotones in central Belgium. *Journal of Ecology* 87: 628–638.
- BOYLES, S., A. SCHNABEL, AND R. WYATT. 1994. Evidence for long-distance pollen dispersal in milkweeds (*Asclepias exaltata*). *Evolution* 48: 1032–1040.
- BRUNET, J., AND G. VON OHEIMB. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology* 86: 429–438.
- CAIN, M. L., H. DAMMAN, AND A. MUIR. 1998. Seed dispersal and the Holocene migration of woodland herbs. *Ecological Monographs* 68: 325–347.
- CARLQUIST, S. 1965. Island life. Natural History Press, Garden City, New York, New York, USA.
- . 1966. The biota of long-distance dispersal. I. Principles of dispersal and evolution. *Quarterly Review of Biology* 41: 247–270.
- . 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific islands. *Bulletin of the Torrey Botanical Club* 94: 129–162.
- CASWELL, H. 1989. Matrix population models: construction, analysis, and interpretation. Sinauer, Sunderland, Massachusetts, USA.
- CHAMBERS, J. C., AND J. A. MACMAHON. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* 25: 263–292.
- CHEPLICK, G. P. 1998. Seed dispersal and seedling establishment in grass populations. In G. P. Cheplick [ed.], *Population biology of grasses*, 84–105. Cambridge University Press, Cambridge, UK.
- CLARK, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152: 204–224.
- , C. FASTIE, G. HURTT, S. T. JACKSON, C. JOHNSON, G. A. KING, M. LEWIS, J. LYNCH, S. PACALA, C. PRENTICE, E. W. SCHUPP, T. WEBB III, AND P. WYCKOFF. 1998b. Reid's paradox of rapid plant migration. *BioScience* 48: 13–24.
- , E. MACKLIN, AND L. WOOD. 1998a. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* 68: 213–235.
- , M. SILMAN, R. KERN, E. MACKLIN, AND J. H. RISLAMBERS. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80: 1475–1494.
- CODY, M. L., AND J. MCC. OVERTON. 1996. Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* 84: 53–61.
- COLLINGHAM, Y. C., M. O. HILL, AND B. HUNTLY. 1996. The migration of sessile organisms: a simulation model with measurable parameters. *Journal of Vegetation Science* 7: 831–846.
- CORBET, M., P. L. MARKS, AND S. GARDESCU. 1999. Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* 87: 220–232.
- CORRIVEAU, J. L., AND A. W. COLEMAN. 1988. Rapid screening method to detect potential biparental inheritance of plastid DNA and the results for over 200 angiosperm species. *American Journal of Botany* 75: 1443–1458.
- DAMMAN, H., AND M. L. CAIN. 1998. Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. *Journal of Ecology* 86: 13–26.
- DARWIN, C. 1859. The origin of species. John Murray, London, UK.
- DRAKE, J. A., H. A. MOONEY, F. DI CASTRI, R. H. GROVES, F. J. KRUGER, M. REJMANEK, AND M. WILLAMSON, [EDS.] 1989. Biological invasions: a global perspective. John Wiley & Sons, Chichester, UK.
- DURRETT, R., AND S. LEVIN. 1998. Spatial aspects of interspecific competition. *Theoretical Population Biology* 53: 30–43.
- DYER, J. M. 1995. Assessment of climate warming using a model of forest species migration. *Ecological Modelling* 79: 199–219.
- ELLSTRAND, N. C., AND D. L. MARSHALL. 1985. Interpopulation gene flow by pollen in wild radish, *Raphanus sativus*. *American Naturalist* 126: 606–612.
- ERIKSSON, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* 77: 248–258.
- FRIES, M. 1969. Aspects of floristic changes in connection with the development of the cultural landscape. *Oikos* (Supplement) 12: 29–34.
- FRITZ, R., AND G. MERRIAM. 1994. Fencerow and forest edge vegetation structure in eastern Ontario farmland. *Ecoscience* 1: 160–172.
- HAMRICK, J. L., AND J. D. NASON. 1996. Consequences of dispersal in plants. In O. E. Rhodes, R. K. Chesser, and M. H. Smith [eds.], *Population dynamics in ecological space and time*, 203–236. University of Chicago Press, Chicago, Illinois, USA.
- HANDEL, S. M., S. B. FISCH, AND G. E. SCHATZ. 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bulletin of the Torrey Botanical Club* 108: 430–437.
- HANSKI, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63: 151–162.
- , AND M. E. GILPIN [EDS.] 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- , J. PÖYRY, T. PAKKALA, AND M. KUUSAAARI. 1995. Multiple equilibria in metapopulation dynamics. *Nature* 377: 618–621.
- , AND D. SIMBERLOFF. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In I. A. Hanski and M. E. Gilpin [eds.], *Metapopulation biology: ecology, genetics, and evolution*, 5–26. Academic Press, San Diego, California, USA.
- HARPER, J. L. 1977. *Population biology of plants*. Academic Press, London, UK.
- HELLIWELL, D. R. 1975. The distribution of woodland plant species in some Shropshire hedgerows. *Biological Conservation* 7: 61–72.
- HENGVELD, R. 1989. *Dynamics of biological invasions*. Chapman and Hall, London, UK.
- HIGGINS, S. I., AND D. M. RICHARDSON. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist* 153: 464–475.
- , AND R. M. COWLING. 1996. Modeling invasive plant spread: the role of plant-environment interactions and model structure. *Ecology* 77: 2043–2054.
- HOELZEL, A. R. [ED.] 1998. *Molecular genetic analysis of populations*. IRL Press, Oxford, UK.
- HOLMES, E. E., AND H. B. WILSON. 1998. Running from trouble: long-dis-

- tance dispersal and the competitive coexistence of inferior species. *American Naturalist* 151: 578–586.
- HOVESTADT, T., P. YAO, AND K. E. LINSEMAIR. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1–25.
- HOWE, H. F., AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.
- HUSBAND, B. C., AND S. C. H. BARRETT. 1996. A metapopulation perspective in plant population biology. *Journal of Ecology* 84: 461–469.
- IVERSON, L. R., AND A. M. PRASAD. 1998. Predicting abundances of 80 tree species following climate change in the eastern United States. *Ecological Monographs* 68: 465–485.
- JANZEN, D. H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *American Naturalist* 123: 338–353.
- KUHNER, M. K., J. YAMATO, AND J. FELSENSTEIN. 1995. Estimating effective population size and mutation rate from sequence data using Metropolis-Hastings sampling. *Genetics* 140: 1421–1430.
- , AND ———. 1998. Maximum likelihood estimation of population growth rates based on the coalescent. *Genetics* 149: 429–434.
- LE CORRE, V., N. MACHON, R. J. PETIT, AND A. KREMER. 1997. Colonization with long-distance seed dispersal of maternally inherited genes in forest trees: a simulation study. *Genetical Research* 69: 117–125.
- MACK, A. L. 1995. Distance and non-randomness of seed dispersal by the dwarf cassowary *Casuarius bennetti*. *Ecography* 18: 286–295.
- MALANSON, G. P., AND M. P. ARMSTRONG. 1996. Dispersal probability and forest diversity in a fragmented landscape. *Ecological Modelling* 87: 91–102.
- MATLACK, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75: 1491–1502.
- MCCAULEY, D. E. 1994. Contrasting the distribution of chloroplast DNA and allozyme polymorphism among local populations of *Silene alba*: implications for studies of gene flow in plants. *Proceedings of the National Academy of Sciences, USA* 91: 8127–8131.
- MEAGHER, T. R., AND E. A. THOMPSON. 1987. Analysis of parentage for naturally established seedlings within a population of *Chamaelirium luteum* (Liliaceae). *Ecology* 68: 803–812.
- MENGES, E. S. 1990. Population viability analysis for an endangered plant. *Conservation Biology* 4: 52–62.
- MILLIGAN, B. G. 1992. Is organelle DNA strictly maternally inherited? Power analysis of a binomial distribution. *American Journal of Botany* 79: 1325–1328.
- , AND C. K. MCMURRY. 1993. Dominant vs. codominant genetic markers in the estimation of male mating success. *Molecular Ecology* 2: 275–283.
- MOOIJ, W. M., AND D. L. DEANGELIS. 1999. Error propagation in spatially explicit population models: a reassessment. *Conservation Biology* 13: 930–933.
- MOILANEN, A., AND I. HANSKI. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79: 2503–2515.
- MOODY, M. E., AND R. N. MACK. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* 25: 1009–1021.
- NATHAN, R. 2000. Dispersal biogeography. In S. A. Levin, [ed.], *Encyclopedia of biodiversity*, Academic Press, New York, New York, USA.
- , AND H. C. MULLER-LANDAU. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285.
- NEIGEL, J. E. 1997. A comparison of alternative strategies for estimating gene flow from genetic markers. *Annual Review of Ecology and Systematics* 28: 105–128.
- NICHOLS, R. A., AND G. M. HEWITT. 1994. The genetic consequences of long distance dispersal during colonization. *Heredity* 72: 312–317.
- NIELSEN, R. 1997. A likelihood approach to populations samples of microsatellite alleles. *Genetics* 146: 711–716.
- NOGALES, M., J. D. DELGADO, AND F. M. MEDINA. 1998. Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). *Journal of Ecology* 86: 866–871.
- OLIVIERI, I., AND P.-H. GOUYON. 1997. Evolution of migration rate and other traits: the metapopulation effect. In I. A. Hanski and M. E. Gilpin [eds.], *Metapopulation biology: ecology, genetics, and evolution*, 293–323. Academic Press, San Diego, California, USA.
- ORIVE, M. E. 1993. Effective population size in organisms with complex life-histories. *Theoretical Population Biology* 44: 316–340.
- OUBORG, N. J., Y. PIQUOT, AND J. M. VAN GROENENDAEL. 1999. Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology* 87: 551–568.
- PARKER, P. G., A. A. SNOW, M. D. SCHUG, G. C. BOOTON, AND P. A. FUERST. 1998. What molecules can tell us about populations: choosing and using a molecular marker. *Ecology* 79: 361–382.
- PETERKEN, G. F., AND M. GAME. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology* 72: 155–182.
- PITELKA, L. F., AND THE PLANT MIGRATION WORKSHOP GROUP. 1997. Plant migration and climate change. *American Scientist* 85: 464–473.
- PAETKAU, D., W. CALVERT, I. STIRLING, AND C. STROBECK. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4: 347–354.
- PORTNOY, S., AND M. F. WILLSON. 1993. Seed dispersal curves: behavior of the tail of the distribution. *Evolutionary Ecology* 7: 25–44.
- PRIMACK, R. B., AND S. L. MIAO. 1992. Dispersal can limit local plant distribution. *Conservation Biology* 6: 513–519.
- PRODOHL, P. A., W. J. LOUGHRY, C. M. McDONOUGH, W. S. NELSON, E. A. THOMPSON, AND J. C. AVISE. 1998. Genetic maternity and paternity in a local population of armadillos assessed by microsatellite DNA markers and field data. *American Naturalist* 151: 7–19.
- RANNALA, B., AND J. HARTIGAN. 1996. Estimating gene flow in island populations. *Genetical Research* 67: 147–158.
- RIBBENS, E., J. A. SILANDER, AND S. W. PACALA. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75: 1794–1806.
- RIDLEY, H. N. 1930. *The dispersal of plants throughout the world*. Reeve, London, UK.
- ROEDER, K., B. DEVLIN, AND B. G. LINDSAY. 1989. Application of maximum likelihood methods to population genetic data for the estimation of individual fertilities. *Biometrics* 45: 363–379.
- ROQUES, S., P. DUCHENSE, AND L. BERNATCHEZ. 1999. Potential of microsatellites for individual assignment: the North Atlantic redfish (genus *Sebastes*) species complex as a case study. *Molecular Ecology* 8: 1703–1717.
- SAUER, J. D. 1988. *Plant migration: the dynamics of geographic patterning in seed plant species*. University of California Press, Berkeley, California, USA.
- SCHNABEL, A., J. D. NASON, AND J. L. HAMRICK. 1998. Understanding the population genetic structure of *Gleditsia triacanthos* L.: seed dispersal and variation in female reproductive success. *Molecular Ecology* 7: 819–832.
- SHIGESADA, N., K. KAWASAKI, AND Y. TAKEDA. 1995. Modeling stratified diffusion in biological invasions. *American Naturalist* 146: 229–251.
- SHRIVER, M. O., M. W. SMITH, L. JIN, A. MARCINI, J. M. AKEY, R. DEKA, AND R. E. FERRELL. 1997. Ethnic-affiliation estimation by use of population-specific DNA markers. *American Journal of Human Genetics* 60: 957–964.
- SILVERTOWN, J. 1991. Dorothy's dilemma and the unification of plant population biology. *Trends in Ecology and Evolution* 6: 346–348.
- SKELLAM, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38: 196–218.
- SLATKIN, M., AND W. P. MADDISON. 1989. A cladistic measure of gene flow inferred from the phylogenies of alleles. *Genetics* 123: 603–613.
- SORENSEN, A. E. 1986. Seed dispersal by adhesion. *Annual Review of Ecology and Systematics* 17: 443–463.
- STRAND, A. E. 1997. Integrating demography and genetics in *Aquilegia*. Ph. D. dissertation, New Mexico State University, Las Cruces, New Mexico, USA.
- , B. G. MILLIGAN, AND C. M. PRUITT. 1996. Are populations islands? Analysis of chloroplast DNA variation in *Aquilegia*. *Evolution* 50: 1822–1829.
- STROBECK, C. 1983. Estimation of the neutral mutation rate in a finite population from DNA sequence data. *Theoretical Population Biology* 24: 160–172.
- THORNTON, I. 1996. *Krakatau: the destruction and reassembly of an island ecosystem*. Harvard University Press, Cambridge, Massachusetts, USA.
- TUFTO, J., S. ENGEN, AND K. HINDAR. 1996. Inferring patterns of migration from gene frequencies under equilibrium conditions. *Genetics* 144: 1911–1921.

- TURCHIN, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, Massachusetts, USA.
- VALVERDE, T., AND J. SILVERTOWN. 1997. A metapopulation model for *Primula vulgaris*, a temperate forest understorey herb. *Journal of Ecology* 85: 193–210.
- VAN DEN BOSCH, F., AND J. A. J. METZ. 1996. The velocity of spatial expansion: an overview of the individual based approach. *Aspects in Applied Biology* 46: 231–238.
- , ———, AND O. DIEKMANN. 1990. The velocity of spatial expansion. *Journal of Mathematical Biology* 28: 529–565.
- VAN DER PILL, L. 1982. Principles of dispersal in higher plants. Springer-Verlag, Berlin, Germany.
- VAN DORP, D., P. SCHIPPERS, AND J. M. VAN GROENENDAEL. 1997. Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automation model. *Landscape Ecology* 12: 39–50.
- VAN GROENENDAEL, J. M., N. J. OUBORG, AND R. J. J. HENDRIKS. 1998. Criteria for the introduction of plant species. *Acta Botanica Neerlandica* 47: 3–13.
- VITOUSEK, P. M., H. A. MOONEY, J. LUBCHENCO, AND M. M. MELILLO. 1997. Human domination of Earth's ecosystems. *Science* 277: 494–499.
- WAHLBERG, N., A. MOILANEN, AND I. HANSKI. 1996. Predicting the occurrence of endangered species in fragmented landscapes. *Science* 273: 1536–1538.
- WASER, P. M., AND C. STROBECK. 1998. Genetic signatures of interpopulational dispersal. *Trends in Ecology and Evolution* 13: 43–44.
- , ———, AND D. PAETKAU. 2000. Estimating interpopulation dispersal rates. In J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne [eds.], *Carnivore conservation*. Cambridge University Press, Cambridge, UK, in press.
- WHITLOCK, M. C., AND D. E. MCCAULEY. 1999. Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. *Heredity* 82: 117–125.
- WHITNEY, G. G., AND D. R. FOSTER. 1988. Overstorey composition and age as determinants of the understorey flora of woods of central New England. *Journal of Ecology* 76: 867–878.
- WIENS, J. A. 1997. Metapopulation dynamics and landscape ecology. In I. A. Hanski and M. E. Gilpin [eds.], *Metapopulation biology: ecology, genetics, and evolution*, 43–62. Academic Press, San Diego, California, USA.
- WILKINSON, D. M. 1997. Plant colonization: are wind dispersed seeds really dispersed by birds at larger spatial and temporal scales? *Journal of Biogeography* 24: 61–65.
- WILLSON, M. F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108: 261–280.
- WRIGHT, S. 1951. The genetical structure of populations. *Annals of Eugenics* 15: 323–354.