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Stochastic Dispersal Processes in Plant Populations

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Abstract

A dispersal model for airborne pollen based on assumptions about wind directionality, gravity, and a wind threshold at which pollen is taken by the wind is developed, using a three dimensional diffusion approximation. The bivariate probability distribution of pollen receipt by flowers at the same height as the pollen source is derived. Gravity, vertical random movements, and vegetation density turn out to have similar effects on this distribution. Maximum likelihood methods for estimating the combined parameters from data with multiple point or continuous pollen sources, and one or more plant varieties, are developed. Using an example data set from the literature, it is shown that our model gives a better fit than more traditional descriptive dispersal models of the form e^{-ar^b}. We also show that estimates of important properties of the dispersal distribution, such as the variances, become considerably smaller using our model than for the more traditional models. Finally, we discuss potential extensions and evolutionary implications of these types of models.

1 Introduction

The amount of gene flow in a geographically structured population strongly influences the opportunity for local differentiation due to either genetic drift or local selection pressures. Of particular interest, in models of continuously distributed populations, is the dispersal variance σ_d^2, which to a good approximation determines the amount of genetic differentiation due to selection (e.g. Slatkin, 1973) and genetic drift (Malécot, 1969). If selection is weak, the dispersal variance also determines the speed of the wave front formed when new advantageous genes are introduced in spatially structured populations (Fisher, 1937; Kolmogorov *et al.*, 1937), provided that the dispersal distribution is not too leptokurtic (Mollison, 1977). More exact solutions of this problem based on the entire distribution are also available (Weinberger, 1982).

Detailed knowledge of dispersal distributions has recently also become important when assessing the risk of spread of genetically modified organisms. Knowing the dispersal variance as well as the exact shape of the distribution may be important e.g. when designing barren zones or trap crops between transgenic cultivars and wild relatives (Morris *et al.*, 1994).

In this paper we focus on dispersal processes in plant populations, particularly dispersal of airborne pollen, but some of the models should also be of general interest. Most dispersal studies in plants only examine the unknown dispersal distribution at a limited number of sampling sites and are not able to follow a randomly chosen set of gametes. Estimates of parameters characterizing the amount of dispersal in a population may therefore, as in all inference problems, be sensitive to the exact assumptions of the model used. Here we first clarify the derivation and implicit assumptions of two widely used models in the literature. Second, we suggest two new models based on a three dimensional diffusion process that incorporates wind directionality, gravity, vegetation density, and a wind velocity threshold, and derive the probability distribution associated with the reproductive events, generated by this process. Third, we develop numerical methods for estimating the parameters of pollen distributions from various kinds of spatial data, including non-point pollen sources, and present an example of such an analysis.

Finally, after having provided the necessary estimation methods, we discuss some evolutionary implications of biased movement. At first this may seem like a narrow technical problem, but directional bias may strongly influence e.g. gene frequency variation in selection-migration clines, and the speed at which the wave front of new mutations or introduced genes will move through spatially structured populations.

2 Dispersal models

2.1 Exponential power function

In the early theoretical studies of population genetics (Wright, 1943; Haldane, 1948), dispersal was assumed to follow the bivariate normal distribution

$$f_{X,Y}(x,y) = \frac{1}{2\pi\sigma_d^2} e^{-\frac{x^2+y^2}{2\sigma_d^2}}, \tag{1}$$

that is, the probability per unit area of dispersal to some point at a distance $r = \sqrt{x^2+y^2}$ from the origin was assumed to be proportional to e^{-ar^2}. However, most studies have concluded that dispersal distributions, in both plant and animal species, are strongly leptokurtic (e.g. Wright, 1968; Levin and Kerster, 1974).

If we include a shape parameter b and let $f_{X,Y}(x,y)$ be proportional to e^{-ar^b} (Bateman, 1947a) and then normalize this density we obtain the bivariate probability distribution

$$f_{X,Y}(x,y) = \frac{a^{2/b} b}{2\pi\Gamma(2/b)} e^{-ar^b}. \tag{2}$$

Some authors (e.g. Wright, 1969, p. 303) have interpreted (2) as if the radial distance $R = \sqrt{X^2 + Y^2}$ in this model follows the exponential distribution

$$f_R(r) = \lambda e^{-\lambda r} \tag{3}$$

in the case of $b = 1$. This distribution is generated if pollen grains move in nearly straight lines and if the probability of deposition in a short length interval $r, r + dr$ is λdr. However, because (2) refers to the *bivariate* distribution of X and Y, this interpretation is incorrect. The distribution for R that follows from (2) is

$$f_R(r) = \frac{a^{2/b} br}{\Gamma(2/b)} e^{-ar^b}, \tag{4}$$

which can be shown using (A.5) in Appendix A. We will include the exponential power function model in the analysis to make comparison with studies based on this model possible.

2.2 Weibull distributed radial distance

The intended purpose of the exponential power model is better achieved if we use the Weibull distribution

$$f_R(r) = abr^{b-1} e^{-ar^b}, \tag{5}$$

for the radial distance R. We see that this distribution includes the exponential distribution (3) in the case of $b = 1$. Using (A.5), it follows from (5) that the corresponding bivariate probability distribution is

$$f_{X,Y}(x, y) = \frac{ab}{2\pi} r^{b-2} e^{-ar^b}. \tag{6}$$

When the shape parameter $b = 2$, we see that (6) is the bivariate normal (1). We can thus interpret this model as some kind of mixture of the normal distribution and the distribution generated by movement in nearly straight lines.

Note that the bivariate probability density (6) decreases faster than exponentially with the distance from the origin (when $b = 1$) due to the fact that dispersal is in two dimensions (Fig. 1). Also note that, for $b < 2$, the probability density tends to ∞ as r tends to zero, in contrast to the exponential power model. Also note that X and Y are not independent unless $b = 2$ even though this distribution is symmetrical around the origin.

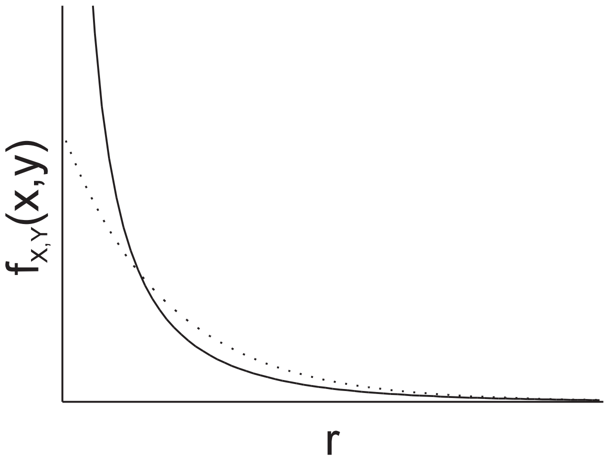

FIG. 1: The Weibull model (solid line) leads to a bivariate probability distribution $f_{X,Y}(x,y)$ that decreases faster than exponentially with the distance from origo, in contrast to the exponential power model (dotted line).

The evolutionarily important variances of X and Y can be calculated from the second moment about the origin of the Weibull distribution (5) which is

$$E(R^2) = a^{-2/b}\Gamma(\frac{2}{b}+1) \tag{7}$$

(Kendall *et al.*, 1983, p. 182). From (A.1) it then follows that

$$Var(X) = Var(Y) = \frac{1}{2}a^{-2/b}\Gamma(\frac{2}{b}+1). \tag{8}$$

2.3 Brownian motion in three dimensions

The Weibull model in the previous subsection is still rather descriptive and does not give much insight into how underlying biologically important mechanisms may influence the amount of dispersal. In this and the next subsection we propose two models specific to dispersal of airborne pollen that incorporate such mechanisms.

In contrast to for example insect-vectored pollen, it is clear that airborne pollen freely disperses in all three dimensions. Various factors such as wind directionality and gravity influence the movement path of each pollen grain. The movement also has stochastic components due to turbulence. At some point in time, each pollen grain is either deposited on the vegetation or it falls to the ground. Only a small proportion is deposited on reproductive parts of the vegetation, resulting in pollination. Below we derive the spatial distribution of these events. We start by first considering the movement path.

A diffusion process is a stochastic continuous-time, continuous-space Markov process and is characterized by its infinitesimal drift and variance parameters defined by

$$\begin{aligned} \mu_x(x) &= \lim_{\Delta t \to 0} \frac{1}{\Delta t} E(\Delta X | X(t) = x) \\ \sigma_x^2(x) &= \lim_{\Delta t \to 0} \frac{1}{\Delta t} E(\Delta X^2 | X(t) = x), \end{aligned} \tag{9}$$

(Karlin and Taylor, 1981, ch. 15). We will consider a diffusion process with three components $\{X(t), Y(t), Z(t)\}$ starting at the origin with infinitesimal variances σ^2 for both the components $X(t)$ and $Y(t)$, σ_z^2 for $Z(t)$, infinitesimal drift parameters μ_x, μ_y representing wind direction and velocity, and μ_z representing the average speed at which pollen grains fall to the ground. If these parameters are independent of x, y, z and t the movement path is a Brownian motion with drift. These assumptions are reasonable, at least for the horizontal movement components, if the vegetation is nearly homogeneous on the characteristic spatial scale of the movement path.

It now follows that the vertical component $Z(t)$ of the process at a given time $T = t$ has the conditional normal distribution

$$f_{Z|T=t}(z) = \frac{1}{\sqrt{2\pi}\sigma_z\sqrt{t}} e^{-\frac{(z-\mu_z t)^2}{2\sigma_z^2 t}}, \tag{10}$$

(Karlin and Taylor, 1981, p. 217).

If we assume that the each pollen grain is equally likely, at any point in time, to be deposited on reproductive or non-reproductive parts of the vegatation, that is, if the probability of deposition in a small time interval $t, t + dt$ is independent of x, y, z and t and equal to λdt, it follows that the time T to deposition is exponentially distributed with

$$f_T(t) = \lambda e^{-\lambda t}. \tag{11}$$

It is clear that, in most cases, the density of the vegetation represented by λ will depend strongly on z. However, to keep the model numerically tractable, it seems necessary to ignore this dependency.

From (10) and (11), and from the definition of conditional probability, it follows that the joint density of Z and T is

$$\begin{aligned} f_{Z,T}(z,t) &= f_{Z|T=t}(z) f_T(t) \\ &= \frac{\lambda}{\sqrt{2\pi}\sigma_z\sqrt{t}} e^{-\lambda t - \frac{(z-\mu_z t)^2}{2\sigma_z^2 t}}. \end{aligned} \tag{12}$$

Because pollination occurs at approximately the same height as the starting point of each pollen grain, it is of interest to find the distribution of T under the condition of deposition at $Z = 0$. Setting $z = 0$ and normalizing (12) yields

$$f_{T|Z=0}(t) = \sqrt{\frac{\lambda + \mu_z^2/(2\sigma_z^2)}{\pi t}} e^{-(\lambda + \frac{\mu_z^2}{2\sigma_z^2})t}. \tag{13}$$

We see that the parameters λ, μ_z and σ_z^2 are confounded in this model, that is, it is impossible to find separate estimates of any of them. Combining them into a single parameter $\lambda_z = \lambda + \mu_z^2/(2\sigma_z^2)$, we recognize (13) as a Gamma distribution of order $1/2$ with scale parameter λ_z.

We now consider the horizontal components of the movement path. The bivariate distribution of the Brownian motion $X(t), Y(t)$ at a given time $T = t$ is

$$f_{X,Y|T=t}(x, y) = \frac{1}{2\pi\sigma^2 t} e^{-\frac{(x-\mu_x t)^2 + (y-\mu_y t)^2}{2\sigma^2 t}}. \tag{14}$$

Combining (13) and (14), we find (see appendix B), using the law of total probability, that

$$\begin{aligned} f_{X,Y|Z=0}(x, y) &= \int_0^\infty f_{X,Y|T=t}(x, y) f_{T|Z=0}(t) dt \\ &= \frac{1}{2\pi r\sqrt{\gamma}} e^{\frac{1}{\gamma}(\tau_x x + \tau_y y) - \sqrt{1/\gamma + \tau_x^2/\gamma^2 + \tau_y^2/\gamma^2}\, r}, \end{aligned} \tag{15}$$

where

$$\tau_x = \frac{\mu_x}{2\lambda_z}, \qquad \tau_y = \frac{\mu_y}{2\lambda_z}, \qquad \gamma = \frac{\sigma^2}{2\lambda_z}. \tag{16}$$

The expectations $(EX, EY) = (\tau_x, \tau_y)$ and, in the case of no wind directionality $\gamma = Var(X) = Var(Y)$. Furthermore, the variance, skewness and kurtosis of the distribution increase, not surprisingly, with the wind velocity. Also note that the density function tends to ∞ in origo.

2.4 Wind threshold model

In the previous section we assumed that the parameters describing wind velocity and direction (μ_x and μ_y) were constants. This may be true over a short time interval, such as the movement of a single pollen grain, but on a longer time scale it is clear that these parameters themselves vary considerably. To investigate the effects of this variation we make some simplifying assumptions.

First, assume that μ_x and μ_y are much larger than σ^2 and nearly constant during the movement of single pollen grains, so that the horizontal components of the movement path are nearly straight lines. Note that the assumptions made about $Z(t)$ in the previous subsection remain unchanged, that is, there is still random fluctuations in the vertical component of the movement path.

Second, assume that there is some threshold wind velocity μ_0 at which pollen grains are released from the anthers and taken by the wind. Such a threshold wind velocity has been demonstrated in many species (Gregory, 1973, chapter IV). The distance moved by each pollen grain is now $R = \mu_0 T$ where T has the conditional distribution (13). The conditional distribution of R given deposition at flower height $Z = 0$ is then

$$f_{R|Z=0}(r) = \sqrt{\frac{\lambda_0}{\pi r}} e^{-\lambda_0 r}, \tag{17}$$

where $\lambda_0 = \lambda_z/\mu_0$ is the scale parameter.

Third, assume that each component of the wind velocity vector $\{\mu_x(t), \mu_y(t)\}$ changes independently over time according to an Ornstein-Uhlenbeck diffusion process. This is a diffusion process having constant infinitesimal variance, and a infinitesimal drift with a central tendency proportional to $\mu_x(t) - \mu_{x0}$ that keeps the process around its equilibrium μ_{x0} (Karlin and Taylor, 1981, p. 170). From the properties of this diffusion process we know that the stationary distribution of the wind velocity vector is the bivariate normal (Karlin and Taylor, 1981, p. 221).

It is now of interest to find the distribution of the the wind direction Θ at the points in time when the wind speed reach the threshold wind velocity μ_0, that is, we are interested in the stationary distribution of the wind velocity vector, under the condition $|\mu_x(t), \mu_y(t)| = \mu_0$. This distribution is known to be, expressed in terms of Θ, the von Mises distribution

$$f_\Theta(\theta) = \frac{1}{2\pi I_0(\kappa)} e^{\kappa \cos(\theta - \theta_0)}, \tag{18}$$

(Batschelet, 1981). This distribution is in many respects the circular analogue of the Normal distribution. The parameter θ_0 is the "mean" direction and $1/\kappa$ is the "variance". The function I_0 in the normalizing constant is a modified Bessel function of first kind.

Using (A.4) it now follows that

$$f_{X,Y}(x, y) = \frac{\sqrt{\lambda_0}}{\sqrt{2}(\pi r)^{3/2} I_0(\kappa)} e^{-\lambda_0 r + \kappa \cos(\theta - \theta_0)}. \tag{19}$$

As expected, because this distribution can be regarded as a mixture of distributions in the form of (15), it is more leptokurtic than that distribution, at least when there is no wind directionality. The variances can be calculated by simulating (19) using standard methods.

3 Model fitting

3.1 Spatial considerations

Let $g_j(x, y)$ be the density of pollen of type j deposited at a point (x,y) in space. In the case of a single point source in origo $g_j(x, y) = f_{X,Y}(x, y)$. However, if the pollen source is e.g. a crop field, the variable contribution from all plants has to be taken into account. In this case, and in general

$$g_j(x, y) = \iint\limits_{\Re^2} f_{X,Y}(x - \xi, y - \varsigma) h_j(\xi, \varsigma) d\xi d\varsigma, \tag{20}$$

where $h_j(\xi, \varsigma)$ is the density of plant variety j at (ξ, ς). Of course, often, the dimension of the pollen source is negligible compared to the distance to the sampling site, and the pollen source can be treated as a point. In the case of several point sources or detailed knowledge of the position of all individual plants, (20) can be written as

$$g_j(x, y) = \sum_k f_{X,Y}(x - x_{jk}, y - y_{jk}), \tag{21}$$

where (x_{jk}, y_{jk}) is the position of plant number k of variety j.

In the next two sections we derive the appropriate likelihood functions for two types of data, both involving n different sampling sites $i = 1, 2, \ldots, n$ of size A_i at different positions (x_i, y_i).

3.2 Poisson data

This method only involves one plant variety. At each site, the number of pollen grains M_i that are deposited (on e.g. small slides coated with gelatine) is recorded. During a single experiment a large number of pollen grains m will be emitted from the pollen source. In most cases m is unknown and should consequently be treated as a parameter. Since the expected number of pollen grains deposited at each site will be small relative to m, it is reasonable to assume that M_i is Poisson distributed with parameter

$$\lambda_i = E(M_i) = mg(x_i, y_i)A_i. \tag{22}$$

The likelihood function is then

$$L(\beta, m|\mathbf{M}) = \prod_{i=1}^{n} \frac{\lambda_i^{M_i} e^{-\lambda_i}}{M_i!}, \tag{23}$$

where β are the parameters of the dispersal model (2), (6), (15), or (19).

3.3 Binomial data

Another sampling method is to use two plant varieties $j = 1$ and $j = 2$ that are easy to distinguish at an early stage of development and to let the two populations interbreed. After pollination has occurred, N_i seeds are collected from each site i, grown under controlled conditions, and M_i of the progeny plants are recorded as being pollinated by type $j = 1$.

By the same argument as in the previous subsection it is clear that the number of pollen grains of each variety deposited at site i is Poisson distributed with expectations $mg_1(x_i, y_i)A_i$ and $mg_2(x_i, y_i)A_i$. The probability that a single progeny is of type $j = 1$ is thus

$$p_i = \frac{g_1(x_i, y_i)}{g_1(x_i, y_i) + g_2(x_i, y_i)}, \tag{24}$$

and M_i is binomially distributed with parameters p_i, N_i. (In the case of more than two plant varieties the multinomial distribution can be used.) The likelihood function is

$$L(\beta|\mathbf{M}) = \prod_{i=1}^{n} \binom{N_i}{M_i} p_i^{M_i} (1 - p_i)^{N_i - M_i}. \tag{25}$$

As before β are the parameters of one of the dispersal models.

Numerical methods for finding maximum likelihood estimates of the parameters from Poisson and binomial data are given in Appendix C.

4 Results

The different dispersal models were tested on data from the third experiment in Bateman (1947b). This experiment was done by setting up a total of 25 equally spaced small slides coated with gelatine along 3 perpendicular transects extending in northern, eastern and southern directions relative to a maize plot (see Fig. 2). Some of the sampling sites were inside or close to the maize plot. We assumed that maize plants within this plot were

TABLE I: The pollen counts M_i recorded at each sampling site i summed over all exposures, at different distances and directions from the center of the maize plot. Data from Bateman (1947b)

Distance	North	East	South
0	2495		
1		2133	3396
2	78	327	668
3	9	86	246
4	6	56	91
5	3	46	72
6	1	22	33
7	0	14	16
8		6	
9	0	1	

uniformly continuously distributed. All slides were located at a height of 0.91m above the ground. Five sets of slides were exposed under different weather conditions, and each exposure lasted 24 hours except the second one which lasted for 48 hours, and the number of pollen grains deposited at each slide during each exposure was counted. Because it is the distribution of deposited pollen averaged over time which is of ecological and evolutionary interest, it is most relevant to fit the dispersal models to the pollen counts summed over all exposures at each sampling site. The data is given in Table I. The maximum likelihood estimates of the parameters of each of the four models are given in Table II.

First note that the standard deviations estimated using the Brownian motion and wind threshold model are about half the estimate obtained using the traditional model (Table II). These estimates are of course, as in all statistical inference, conditional on the model used.

Despite the exponential power and Weibull models' ability to incorporate different degrees of kurtosis, we see from Fig. 2 that they still give a very poor fit due to their inability to model wind directionality. Both the Brownian motion and especially the wind threshold model give a much better fit to the data. From Fig. 2 we see that the Brownian motion model slightly overestimates the deposition distribution at intermediate distances, that is, this model does not explain all the leptokurtosis in the data. The reason for this discrepancy may be that the parameters vary between exposures.

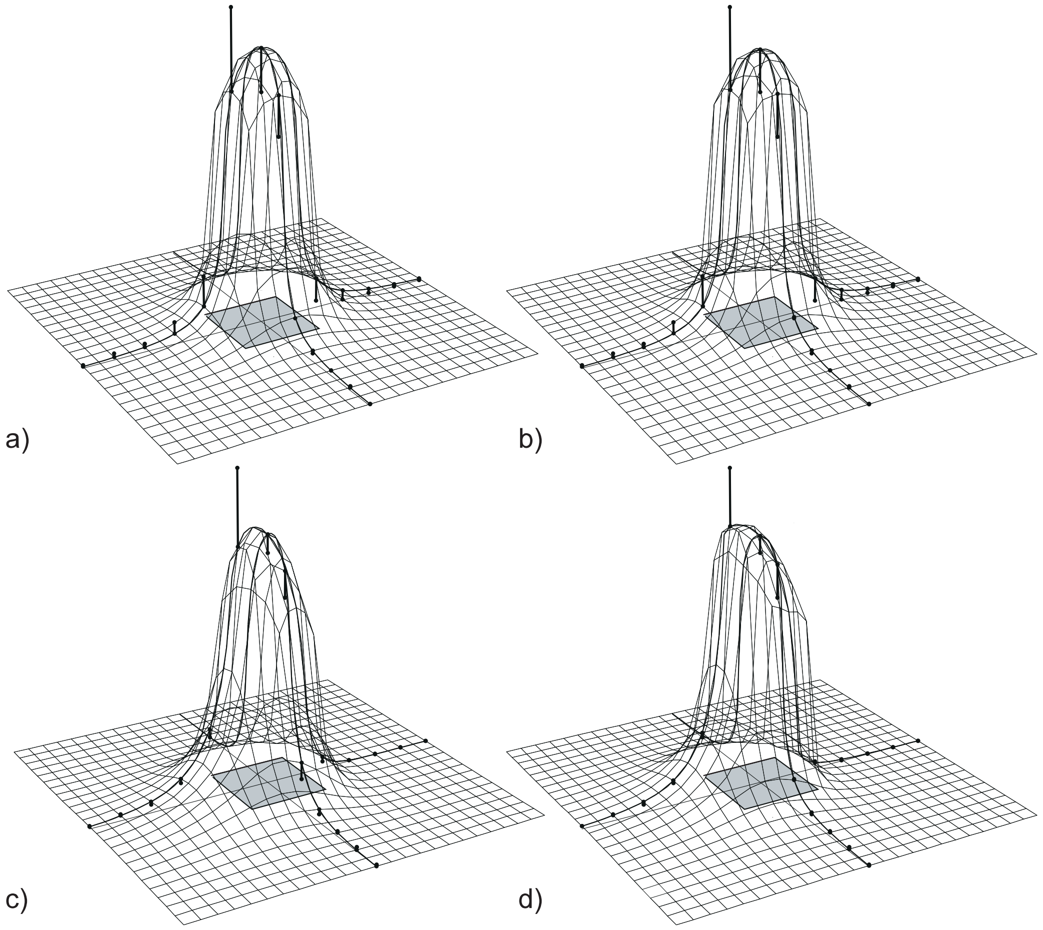

FIG. 2: Plots of the deposition density $g(x, y)$ calculated for the dispersal models fitted to the data in Table I. The vertical lines represent the difference between the observed data and the model predictions at each sampling site. The pollen source (a maize field) is shown as a square around origo. a) Exponential power model. b) Weibull model. c) Brownian motion in three dimensions. d) Wind threshold model.

TABLE II: The dispersal models fitted to the data in Table I. The maximum likelihood estimates ± standard errors calculated using bootstrapping are given. The standard deviation of the X and Y components of the fitted distributions is given in the two last rows.

	Exponential power function (2)	Weibull model (6)	Brownian motion in three dimensions (15)	Wind threshold model (19)
	$a = 14 \pm 2$	$a = 0.84 \pm 0.02$	$\tau_x = 0.8 \pm 0.6$	$\lambda = 0.67 \pm 0.03$
	$b = 0.14 \pm 0.02$	$b = 0.60 \pm 0.03$	$\tau_y = -1.5 \pm 0.6$	$\kappa = 1.36 \pm 0.07$
			$\gamma = 2.2 \pm 0.3$	$\theta_0 = -78 \pm 3$
m	4854 ± 140	4618 ± 91	5593 ± 318	12197 ± 884
$\ln L$	-808	-801	-361	-188
$SD(X)$	3.37	2.90	1.86	1.73
$SD(Y)$			2.58	1.98

To investigate this we also fitted the Brownian motion model to single exposures. This model is meant to represent the distribution generated in short time periods during which the diffusion parameters may be approximately constant. Not surprisingly, all the diffusion parameters τ_x, τ_y and γ vary considerably among exposures (Table III). Although a formal likelihood ratio test of this result (perhaps based on simulations) would be desirable to do, the small standard errors of the estimates for each single exposure suggest that the differences are significant.

An unfortunate side effect of not having data in all four directions is that the maximum likelihood estimates of τ_x, for exposures 1 and 4, when the

TABLE III: Brownian motion model fitted to each of the five exposures.

Exposure	τ_x	τ_y	γ
1	-77.83 ± 0.03	-42.35 ± 0.05	53.77 ± 2.75
2	14.62 ± 0.24	-14.61 ± 0.16	12.12 ± 0.64
3	2.22 ± 0.33	-2.21 ± 0.37	2.20 ± 0.29
4	-301.03 ± 0.03	-376.59 ± 0.03	304.63 ± 22.45
5	1.19 ± 0.20	0.26 ± 0.16	1.40 ± 0.29

wind blew in the unsampled direction, became very large and negative. We believe that these estimates are severely biased due to lack of sampling sites in the dominant wind direction.

5 Discussion

5.1 Comparison with other studies

The estimate of the shape parameter b is at first sight surprisingly small, and for the exponential power model it is as small as 0.14. Using the same model on dispersal data in *Drosophila pseudoobscura*, Wright (1968) obtained much larger estimates of b in the range from 0.8 to 1.3. These estimates are, however, difficult to interpret. The Weibull model, which corresponds to an exponentially distributed radial distance in the case of $b = 1$, fitted to Bateman's (1947) data, gives an estimate of b closer to but still less than 1.

Morris *et al.* (1994) and Kareiva *et al.* (1994), working with data along transects orthogonal to a straight boundary between transgenic and non-transgenic varieties of crop plants, obtained estimates of b equal to 0.21 and 0.30. The b of their model is not directly comparable to our estimate, however, because they were considering only the movement component perpendicular to the boundary. The marginal distribution of this movement component would be what is called double exponential (or Laplace)(Kendall *et al.*, 1983, p. 191), if one assumes that the movement path is a two-dimensional Brownian motion, and if one assumes that there is "constant probability" of deposition so that the time to deposition becomes exponential. Extending this model to include a shape parameter b is one way of arriving at Kareiva *et al.*'s (1994) model. The underlying mechanism of our model (6) is however different, and our b is not directly comparable to the shape parameter of Kareiva *et al.*'s (1994) model.

5.2 Validity of assumptions

The new models (15) and (19) based on diffusion in three dimensions, slow changes in wind conditions over time, and a threshold wind velocity at which pollen grains are taken by the wind, give a better fit to the data.

We assumed that the diffusion parameters as well as λ, representing the density of the vegetation, are independent of the location in space. Even though it is well known that many of the parameters in our model depend on the height above the ground, e.g. σ_z^2 representing vertical random movements (Zannetti, 1990, p. 123), μ_x and μ_y representing the wind velocity (Luna and

Church, 1974), and obviously λ, we still believe that our model is a realistic approximation to the diffusion processes occurring close to flower height. Modeling the dependency of the diffusion parameters on z may be more important in dispersal models of seeds that, in contrast to pollen, is deposited on the ground (Okubo and Levin, 1989; Greene and Johnson, 1989).

The male pollen-producing flowers of many plants are, perhaps as part of the reproductive strategy, higher above the ground than female flowers. In our model we assumed that both male and female flowers occur only at a single height $Z = 0$ above the ground, which should not be a bad assumptions as long as the layer containing male and female flowers is thin compared to the distance between neighboring plants. Alternatively, if the height z_i of each sampling site is recorded, and if the extent and density of the pollen source in all three dimensions is known, one could integrate the contribution of the pollen source over the three dimensional space. It should then be possible to obtain separate estimates of more parameters, but this would also require data of better quality.

There appears to be more variance at each sampling site than expected from our simple Poisson model, especially at the sampling sites inside the maize plot (see Fig. 2c and d). There are several explanations for this:

First, it is obvious that pollen grains did not arrive independently of each other at each sampling site as assumed in our simple Poisson model. The dependency in the real data leads to more variance.

Second, the assumptions of deposition in $Z = 0$ has the consequence that $f_{T|Z=0}(t)$ tends to infinity as t tends to zero (13). This means that the pollen count expectations at each sampling site are very sensitive to the exact position of neighboring plants. Precise data on these positions were not available in Bateman (1947b).

A third explanation of the high variance at each sampling is that the flowering periods of the plants may have been asynchronous, so that just a few plants from the total population contributed to the deposition distribution. That is, the variance at each sampling site is not only due to the fact that each pollen grain moved in a random manner, but also that the initial positions of the contributing plants with which the sampling site happened to be in synchrony were random.

5.3 Further directions

The models presented hear are only meant to describe the movement of air-borne pollen. It would however be easy to build models for other movement mechanisms, for example for seeds or for insect-vectored pollen. Some pollinators such as bumble bees do for example tend to move into the wind

(Woodell, 1978). This movement may be may be adequately described as a two-dimensional diffusion process with directional bias, but could otherwise be modeled using assumptions similar to the ones used here.

With an increased understanding of the underlying processes and the various parameters that affect dispersal of pollen it should also be possible to give rough estimates of the dispersal variances based on direct measurements of the underlying parameters themselves. This approach has been used by Morris (1993) to predict the spatial distribution generated by movement of pollen carried by honey bees (*Apis melifera* L.). In the case of airborne pollen, parameters such as vertical velocities can be calculated directly from the size and weight of each pollen grain (Levin and Kerster, 1974). Local climatic parameters such as wind velocities are also easily measured. It would however be more difficult to measure the parameter λ, representing the density and "stickyness" of the vegetation.

Another interesting direction to further develop the models presented here would be to incorporate various forms of selection associated with the dispersal process, for example to what extent various genotypes are compatible, as well as the fertility of different genotypes. Knowledge about such fitness components is much needed in risk assessment of transgenic plant cultivars. One of the major concerns is that escaped genes might give a selective advantage to its possessor in the wild. This might occur if foreign genes previously unavailable to natural selection are inserted. Once just a few such gene copies escape and become established, fixation in wild populations is nearly inevitable. However, according to general life history theory we should expect most modifications to be disadvantageous (Regal, 1988; Lenski, 1991), but invading genes can still become fixed in such situations if the immigration rate or the dispersal variance is large compared to the spatial and effective size of the invaded populations (Nagylaki and Lucier, 1979; Gliddon, 1994) and if selection against invading genes is weak.

5.4 Evolutionary implications

This study has demonstrated that the dispersal distribution, not very surprisingly, is biased in the direction of the wind. The expected displacement $E(X)$ was estimated to be of the same order of magnitude as the standard deviation of the distribution $\sigma_d = SD(X)$.

Most theoretical population genetic models have been based on the assumption of symmetric dispersal distributions. For example, such models predict that the wave front formed by genes with a selective advantage equal to s when introduced in spatially structured populations, will move with a speed of $v = \sqrt{2s}\sigma_d$ (Fisher, 1937; Kolmogorov *et al.*, 1937). If directional bias is included in this model the amount of dispersal is, to a good approximation, characterized by the first and second moments of the distribution, $\mu_d = E(X)$ and $\sigma_d^2 = Var(X)$. Relying on the diffusion approximation, the wave front must now move with the increased speed of $v = \sqrt{2s}\sigma_d + \mu_d$, as the only effect of directional bias is that the complete genetic structure of the population gets "carried away" with the wind. Note that the prediction of this more realistic model, for small values of s, is very different from the prediction of the simplified model based on the assumption of symmetry, even if μ_d is not much larger than σ_d.

Directional bias potentially has similar large effects on selection-migration gene frequency clines. This has been demonstrated empirically in Scots pine (*Pinus sylvestris* L.) populations in Sweden and Finland, where pollen dispersal is not restrained by high mountain ranges. In these areas, local populations of Scots pine are not optimal for use in reforestation, and an increased survival of 7-10% can be obtained by a southward transfer of one degree of latitude (e.g. Persson and Ståhl, 1990), indicating a large effect of directional bias in the gene flow from south to north. Nagylaki (1978), using a diffusion approximation of the gene frequency dynamics, showed that the effect of asymmetric dispersal is a displacement in the gene frequency cline downwind, and that the condition for maintaining a locally favored allele becomes less stringent when dispersal is asymmetric.

A Some properties of bivariate probability distributions

For any bivariate distribution, $R^2 = X^2 + Y^2$ and it thus follows that $E(R^2) = E(X^2) + E(Y^2)$. If the distribution is symmetrical about the origin we have $\mathrm{Var}(X) = \mathrm{Var}(Y)$ and $EX = EY = 0$. Because $\mathrm{Var}(X) = E(X^2) - (EX)^2$ it then follows that

$$\mathrm{Var}(X) = E(X^2) = \frac{1}{2}E(R^2), \tag{A.1}$$

that is, the variance in X can be found by evaluating the second moment about the origin of the distribution of R.

Another useful relationship exists between the univariate distributions of R and Θ and the bivariate distribution of X and Y. Assume that $f_\Theta(\theta)$ is independent of R. Consider a small area

$$dA = dxdy = rd\theta dr. \tag{A.2}$$

The probability that a pollen grain ends up in dA is then

$$\begin{aligned} & f_{X,Y}(x,y)dxdy = P(X,Y \in dA) \\ & = P(R \in r, r+dr)P(\Theta \in \theta, \theta + d\theta) \\ & = f_\Theta(\theta)d\theta f_R(r)dr. \end{aligned} \tag{A.3}$$

Combining (A.2) with (A.3) we find that

$$f_{X,Y}(x,y) = f_R(r) f_\Theta(\theta)/r. \tag{A.4}$$

If Θ is uniformly distributed in the interval $(0, 2\pi)$ with $f_\Theta(\theta) = 1/(2\pi)$ then

$$f_{X,Y}(x,y) = \frac{f_R(r)}{2\pi r}. \tag{A.5}$$

B Brownian motion in three dimensions

We first derive expectations, variances, skewness and kurtosis of the generated distribution, using moment generating functions (Kendall *et al.*, 1983). The moment generating function of the conditional bivariate normal density (14) is

$$M_{X,Y|T=t}(u,v) = e^{\mu_x tu + \mu_y tv + \frac{1}{2}(u^2+v^2)\sigma^2 t}. \tag{B.1}$$

The conditional Gamma distribution of $T|Z = 0$ (13) has moment generating function

$$\begin{aligned} M_T(s) = E(e^{sT}) &= \int_0^\infty \sqrt{\frac{\lambda_z}{\pi t}} e^{-(\lambda_z - s)t} dt \\ &= \sqrt{\frac{\lambda_z}{\lambda_z - s}} = \frac{1}{\sqrt{1 - s/\lambda_z}}. \end{aligned} \tag{B.2}$$

and the unconditional moment generating function of X, Y is then

$$\begin{aligned} & M_{X,Y}(u,v) = E_T(M_{X,Y|T}(u,v)) \\ & = E_T(e^{u\mu_x T + v\mu_y T + \frac{1}{2}(u^2+v^2)\sigma^2 T}) \\ & = M_T(\mu_x u + \mu_y v + \frac{1}{2}(u^2+v^2)\sigma^2) \\ & = \frac{1}{\sqrt{1 - (\mu_x u - \mu_y v - \frac{1}{2}(u^2+v^2)\sigma^2)/\lambda_z}} \\ & = \frac{1}{\sqrt{1 - 2\tau_x u - 2\tau_y v - \gamma(u^2+v^2)}}. \end{aligned} \tag{B.3}$$

where the parameter substitutions are given by (16). After evaluating the first four cumulants defined by

$$\kappa_r = \frac{\partial^r}{\partial u^r} \ln M_{X,Y}(u,v)|_{u=v=0}, \tag{B.4}$$

we find that

$$EX = \kappa_1 = \tau_x \tag{B.5}$$

$$\mathrm{Var}(X) = \kappa_2 = 2\tau_x^2 + \gamma \tag{B.6}$$

$$\mathrm{Skewness}(X) = \frac{\kappa_3}{\kappa_2^{3/2}} = \frac{8\tau_x^3 + 6\tau_x\gamma}{(2\tau_x^2+\gamma)^{3/2}} \tag{B.7}$$

$$\mathrm{Kurtosis}(X) = \frac{\kappa_4}{\kappa_2^2} = \frac{48\tau_x^4 + 48\tau_x^2\gamma + 6\gamma^2}{(2\tau_x^2+\gamma)^2}. \tag{B.8}$$

with similar formulas for Y. Note that the expected distance traveled by each pollen grain, not surprisingly, is equal to the wind velocity μ_x multiplied by the expected deposition time $1/(2\lambda_z)$. Also note that both the variance and the skewness of the distribution increase with the wind velocity μ_x. Furthermore, the distribution is always strongly leptokurtic with kurtosis between 6 and 12. Its maximum skewness is equal to $4/\sqrt{2}$.

Combining (13) and (14), the unconditional distribution becomes

$$\begin{aligned} f_{X,Y|Z=0}(x,y) &= \int_0^\infty f_{X,Y|T=t}(x,y) f_{T|Z=0}(t)dt \\ &= \int_0^\infty \frac{1}{2\pi\sigma^2 t} e^{-\frac{(x-\mu_x t)^2+(y-\mu_y t)^2}{2\sigma^2 t}} \sqrt{\frac{\lambda_z}{\pi t}} e^{-\lambda_z t} dt \\ &= \frac{\lambda_z^{1/2}}{2(\pi)^{3/2}\sigma^2} e^{\frac{1}{\sigma^2}(x\mu_x + y\mu_y)} \int_0^\infty \frac{1}{t^{3/2}} e^{-(\frac{x^2+y^2}{2\sigma^2})\frac{1}{t} - (\frac{\mu_x^2+\mu_y^2}{2\sigma^2}+\lambda_z)t} dt \\ &= \frac{1}{2\pi r\sqrt{\gamma}} e^{\frac{1}{\gamma}(\tau_x x + \tau_y y) - \sqrt{1/\gamma + \tau_x^2/\gamma^2 + \tau_y^2/\gamma^2}\, r}. \end{aligned} \tag{B.9}$$

The integral involved in the third step of the above equation was solved using the symbolic mathematical program Maple (Char, 1988).

Interestingly, if $\tau_x = \tau_y = 0$, that is, if there is no wind directionality, it follows from (B.9) and (A.5), that the radial distance $R|Z=0$ will be exponentially distributed with parameter $1/\sqrt{\gamma}$, that is, although the underlying process is different, the generated distribution is equal to that in section 2.2.

C Numerical methods

To maximize the likelihood of one of the dispersal models we start with some initial values for the parameters. The expected number of pollen grains of each plant variety j deposited at each sampling site can then be calculated numerically by standard methods, using (20), and the likelihood is then given by (23) or (25) in the case of more than one plant variety. Adjusting the parameters repeatedly, using some numerical algorithm for maximization of functions of several variables, e.g. the AMOEBA routine (Press *et al.*, 1986), we obtain maximum likelihood estimates of the parameters. It is advisable to transform the parameters onto the whole real line, using for example the usual log transformation for parameters that are constrained to be positive.

The standard errors of the estimates can be found by parametric bootstrapping (Efron and Tibshirani, 1993), by simulating say, 100 bootstrap samples from the fitted model, and then calculating the variance of the bootstrap estimates obtained by fitting the model to each bootstrap sample.

A Pascal program for doing the calculations is available from the first author.

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