Mathematical Models for Plant Dispersal

M. A. Lewis (Alberta),
J. Bullock (NERC Centre for Ecology and Hydrology, UK)

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1 Scientific Background

The ability of plants to move into new environments and adapt to global change depends crucially upon the dispersal of the plant seeds [2]. The probability density function describing the spatial redistribution of seeds about a parent plant ('dispersal kernel') has been the subject of intensive mathematical and biological study. Classical mathematical theory of traveling waves, nonlinear PDEs and related integral models as well as detailed biological studies have shown that it is this dispersal kernel that determines the rate at which plants can spread spatially when introduced into new environments [26], or when responding to changing environmental conditions [5].

The importance of dispersal applies equally to invasive pest plants (many of which are extremely costly to agriculture), to persistence of threatened plants and species, and to the movement of indigenous plants, such as hemlock and spruce, in response to climate change. Thus plant dispersal plays a key role in today's most pressing ecological concerns: invasive species and adaption of vegetation to global climate change and conservation biology.

While invasive species in North America extract an immense ecological and economic toll (with estimated costs exceeding \$130 billion US per year), the impact of costs and changes incurred by vegetation response to climate change is unclear. However, one thing is certain: in northern Canada and Fennoscandinavia the best estimates to date indicate vegetation will have to move at rates exceeding 1000 meters per year to keep up with changing temperature isoclines [17].

Mathematicians and quantitative biologists have addressed the problems of plant spread using a variety of different models, including reaction-diffusion, integrodifference, random-walk and simulation models. This has lead to a very rich and broad theory for calculating rates of spread. The theory goes back to the work of Fisher [7], Kolmogorov [11] and others in the 1930's using traveling wave analysis of parabolic PDE models, and extends to modern day with recent results on spread rates in populations with long-distance (non-diffusive) dispersal [12, 6], stage structure [19], spread in fluctuating environments [23, 18], stochastic spread [16, 5], and spread in the presence of secondary ecological interactions [14].

However, the mathematical models underlying the theory assume that the dispersal kernel, describing the possible dispersal distances, is known with arbitrary accuracy. The primary stumbling block in applying the theory to real plant spread has turned out to be uncertainty in the shape of the dispersal kernel, particularly over long distances. It can be shown that small changes in the "tails" of the dispersal kernel can result in order-of-magnitude changes in predicted spread rates—the rare, long-distance dispersal events described by the tails of the kernel are the dominant factor in the determining rate of spread [13, 10].

While plant seeds can be redistributed by wide variety of mechanisms (animals, birds, water, ballistic dispersal and so forth), a primary mechanism for plant seed dispersal is movement by wind flow. The quest to accurately determine the tail of dispersal kernels for wind-dispersed seeds has proceeded in at least three different ways: (1) Theoretically derive kernels, based on underlying assumptions about the dispersal process. These analytically derived kernels arise as solutions, or approximate solutions to mechanistic PDE sub-models [23, 10]. (2) Computationally derive kernels, based on models for turbulent wind flow, ranging from Large Eddy Simulation of Navier Stokes wind flow to simulation of the related Fokker-Planck approximation for 3D turbulent and wind-based dispersal in the the atmospheric boundary layer [24, 25, 23]. (3) Empirically derive kernels, using accurate measurement of highly detailed seed trap data over long distances [2, 1, 9, 21].

Each of the above approaches has strengths and weaknesses. Theoretically derived kernels are of great use in models of plant spread because they are relatively tractable by analysis. The weakness of this approach is that its relative simplicity means it may not adequately describe important long-distance dispersal events. Computational models, based on approximations for Navier-Stokes flow have a solid mechanistic basis for the long-distance dispersal, but are computationally intensive, and difficult to simplify. Empirical models have the benefit that they are based on real dispersal data but it is often logistically infeasible to measure extremely long-distance dispersal of seed.

2 Focused Research Group Results

The meeting brought together mathematicians and quantitative biologists. This cross-disciplinary research environment led to specific advances in the modeling of plant dispersal. The focused research group comprised of James Bullock (NERC, Dorset), David Greene (Concordia), Steve Higgins (UFZ, Leipzig), Mark Lewis (Alberta), Annemarie Pielaat (Alberta), Tom Robbins (Utah), Merel Soons (Utrecht), Oliver Tackenberg (Regensburg). Prior to the FRG, each group member had made significant contributions to the study of long-distance dispersal and biological invasions (see References). The composition was divided evenly between senior (Bullock, Greene, Higgins and Lewis) and junior (Pielaat, Robbins, Soons, Tackenberg) researchers.

The group tackled three major problems: (1) How to accurately estimate population spread rates using empirical dispersal data, fitted to to nonlinear integrodifference models [15], (2) The formulation of a generalized dispersal function that precisely predicts long-distance wind-mediated seed dispersal, based on physics of the atmospheric boundary layer [22] (3) Comparison of computational models for wind-mediated seed dispersal [3]. Each of these group efforts is being written up in a paper (given above).

Accurate prediction of spread rates. The mathematical description of population growth and spread we considered is the integrodifference equation. Here, a discrete-time model is coupled with the dispersal and non-overlapping generations are assumed. This model is written as

$$n_t(x) = \int_\Omega f(n_t(y))\, K(x,y)\, dy, \tag{1}$$

where Ω is the region over which the population is spreading, $n_t(x)$ is the population density at point x and time $t = 0, 1, \ldots$, f describes nonlinear population dynamics, and $K(x,y)$ is the dispersal kernel describing movement from y to x. More complex versions of the model include x in higher space dimensions, and n_t a vector of interacting species or stages within a population. Population spread rate describes the asymptotic speed at which a locally introduced population $n_0(x)$ asymptotically travels in space and time. Calculation of the spread rate in this model was pioneered by Weinberger [26]. As described in the "Scientific Background" section, such spread rates are crucial in the context of invading populations and environmental change.

Despite the Weinberger's elegant theory, the process of using fitted dispersal kernels to estimate population spread rates has been problematic. Parametric kernels with different shaped 'tails' produce drastically different estimates for spread rate, despite providing similar fits to the measured dispersal.

We proposed and tested a new method for weighting the fit of parametric dispersal kernels to data on dispersal distance so as to reduce bias in the predicted spread rate. This is a brand new approach, that came out of a "break-out" discussion subgroup. The weighting is based on a calculation that involves the steepness of the leading edge of the invading population $n_t(x)$, which can be calculated using a new "empirical estimator" method [4]. Our tests showed that it can produce accurate and reliable estimates for population spread rates where none were possible previously. The paper, outlining the new method, its application and its testing, has been 70 % written up during the meeting [15] and will be soon submitted for publication.

A generalized dispersal kernel To date there is no widely accepted dispersal function for describing wind-mediated seed dispersal in terms of atmospheric boundary layer parameters (such as wind speed, turbulent mixing parameters and so forth). A group member, Robbins [23], recently derived the existing "Okubo-Levin" [20] dispersal kernel from first principles. This involved deriving a stochastic differential equation (SDE) model for individual individual seeds, and analyzing it using a Fokker-Planck expansion to yield an Eulerian description of particle movement in the form of a partial differential equation (PDE). Subsequent analysis of the PDE model using similarity methods yields an explicit formula for the Okubo-Levin kernel for the deposition rate of particles on the ground [20] in the limit where the seeds have no inertia.

While the Okubo-Levin model is analytically tractable, it misses some important details. We determined three major factors that are left out: (1) variation in the mean wind speed (2) unstable boundary layer dynamics at low wind speeds and (3) temporal autocorrelation in the turbulent wind dynamics. These factors can be included in the computational simulations (below), and it was the critical comparison the computational models and data (below) that made it clear the importance of these three features. Our goal was to incorporate each of these factors into the explicit formulation of the kernel, and to compare predictions, based on the atmospheric measurements against dispersal data in the Bullock and Clarke [1] and Tackenberg [25] data sets.

We found analytical methods to incorporate the wind speed variation and unstable boundary layer dynamics into the explicit formula, yielding a "modified Okubo-Levin" model. We have not yet found a way of incorporating the autocorrelation, but have devised a general approach to do this which we believe will be successful after further work. We tested the model predictions against data sets when possible. Our goal is to write up this work as a paper [22].

Critical comparison of computational models for deriving kernels. Three approaches for computational derivation of dispersal kernels have been proposed recently. They are all individual-based and are linked in their fundamental form, but differ in complexity.

A SDE model was developed by Robbins [23]. This assumes that vertical wind fluctuations are uncorrelated and the wind profile is neutrally stable, but allows for inertial forces acting on the seed. The "STG" model of Soons [24] is a trajectory model that takes into account autocorrelation in wind fluctuations and simulates a realistic wind flow pattern. However, it does not allow for the effect of boundary layer instability (thermals). "PAPPUS", developed by Tackenberg [25] is a highly realistic model which uses measured data on horizontal and vertical wind profiles, and thus will represent the effects of boundary layer instability on long distance seed dispersal.

Our approach was to compare these models by using them to derive kernels in relation to particular measured seed dispersal data. Targeted data sets were from Bullock and Clarke [1] and Tackenberg [25], which represented a range of meteorological and ecological conditions. Models were parameterized using relevant meteorological measures from these field sites. We included a fourth model in this analysis; the "modified Okubo and Levin" model, referred to above, to represent a much simplified, but theoretically attractive analytical solution to kernel estimation.

Model accuracy was assessed simply by determining the relationship with dispersal data, but models were also compared in terms of differences in spread rate estimates (determined using the Weinberger [26] moment generating function method). Long distance dispersal (i.e. longer tails to the dispersal kernel) was facilitated by the incorporation of autocorrelated wind fluctuations and thermals. Both lift seeds into higher wind profiles, which have stronger horizontal wind velocities. However, simpler models are accurate in some cases, and the group identified possible extensions to the simpler models to incorporate varying conditions. Extensions to the modified Okubo and Levin model are detailed above. The SDE model of Robbins [23] was also developed to represent autocorrelation accurately. A paper is in preparation [3].

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