

Plant Propagation Fronts and Wind Dispersal: An Analytical Model to Upscale from Seconds to Decades Using Superstatistics

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ABSTRACT: Scale separation crossing many orders of magnitude is a consistent challenge in the ecological sciences. Wind dispersal of seed that generates plant propagation fronts is a typical case where timescales range from less than a second for fast turbulent processes to interannual timescales governing plant growth and climatic forcing. We show that the scale separation can be overcome by developing mechanistic and statistical links between processes at the different timescales. A mechanistic model is used to scale up from the turbulent regime to hourly timescales, while a superstatistical approach is used to relate the half-hourly timescales to annual vegetation migration speeds. We derive a semianalytical model to predict vegetation front movement as a function of wind-forcing statistics and characteristics of the species being dispersed. This model achieves better than order-of-magnitude agreement in a case study of tree dispersal from the early Holocene, a marked improvement over diffusion models. Plant migration is shown to depend nonlinearly on the wind environment forcing the movement but linearly on most physiological parameters. Applications of these analytical results to parameterizing models of plant dispersion and the implications of the superstatistical approach for addressing other ecological problems plagued by similar “dimensionality curses” are outlined.

Keywords: analytical modeling, vegetation migration, WALD, wind dispersion.

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Vegetation migration in response to environmental drivers is now receiving significant attention in studies of species invasion and climate change and has been elevated to a fundamental discipline in spatial ecology (Neuhauser 2001; Okubo and Levin 2001; Neilson et al. 2005). The basic challenge confronting models of vegetation movement is the large timescale separation between seed dispersal processes (seconds–hours) and vegetation growth (months–years). For wind-dispersed seeds, the scale separation is exacerbated by the importance of turbulence (which varies over fractions of seconds) governing seed uplifting and subsequent long-distance seed dispersal (Horn et al. 2001; Nathan et al. 2002; Tackenberg 2003; Soons et al. 2004a, 2004b).

The contemporary approach to overcoming this “dimensionality curse” is to represent plant movement by wind as a diffusive process (Klausmeier 1999; HilleRis-Lambers 2001; Lejeune 2002; Rietkerk et al. 2002, 2004). An advantage to this representation is that an explicit relationship between the diffusion coefficient (D), the intrinsic growth rate (r), and the speed of propagation of the biomass front (c) can be derived. For instance, for the prototypical case of the Kolmogorov-Fisher equation with a constant D , the front speed is given by $c = 2(rD)^{1/2}$ (Fisher 1937; Kolmogorov et al. 1937; Murray 2002, pp. 437–482). However, the fact that D cannot be readily inferred from seed attributes (e.g., terminal velocity, release height) and wind conditions prevents prognostic use of such a result. Furthermore, representing plant migration via diffusion remains questionable, and dispersal data suggest a “superdiffusive” aspect to species migration and spread, which requires an alternative treatment. Comparisons between measured vegetation spread rates and those predicted by diffusion models show that diffusion underestimates the propagation speed of vegetation movement (Clark 1998; Clark et al. 1998, 1999, 2001; Nathan et al. 2002; Higgins et al. 2003; Neilson et al. 2005). To match the observed speeds of vegetation movement requires adopting a dispersion kernel with “fat tails” in comparison

to the Gaussian kernel underpinning classical diffusion processes. To circumvent this limitation, several dispersion kernels have been proposed in models of c based on empirical (Clark 1998; Robledo-Arnuncio and Gil 2005; Dauer et al. 2007), phenomenological (Neubert et al. 1995; Kot et al. 1996; Lewis and Pacala 2000), or mechanistic grounds (Neubert et al. 1995; Nathan and Katul 2005; Williams et al. 2006). However, simultaneously preserving mathematical simplicity and prognostic capability remains elusive, and doing so is the subject of this work.

Recent studies have suggested that “upscaling” the effects of turbulent transport processes on seed dispersal kernels from fractions of seconds to half-hourly timescales can be achieved analytically via a mechanistic Wald analytical long-distance dispersion (WALD) model (Katul et al. 2005), the kernel of which resembles an inverse-Gaussian, or Wald, distribution. The primary inputs to the WALD model are mean half-hourly wind speeds (\bar{U}), basic seed attributes (e.g., terminal velocity), and release heights. Furthermore, a number of studies have already shown that the distribution of \bar{U} , sampled over seasonal to annual timescales, can be approximated by a Weibull distribution, and wind atlases document these Weibull wind parameters spatially across continents for wind energy harvest (Troen and Peterson 1989).

Building on these two findings for wind and its effect on seed dispersal, we propose to replace the diffusive term in the Kolmogorov-Fisher equation with the scaled effect of the WALD and Weibull kernels and develop a novel analytical solution for the vegetation front speed. As a case study, order-of-magnitude predictions of c from the analytical solution are then compared to reported vegetation migration rates of the early Holocene period in the United States during the period of postglacial expansion. Finally, the broader implications of the proposed modeling approach for assessing vegetation spread rates are presented in light of recent developments in the field of “superstatistics,” which is now gaining attention in complex-systems science (Beck and Cohen 2003).

The Model

The Basic Equations

The one-dimensional Fisher-Kolmogorov equation, which describes the local increase and spread in space of a logistically growing population, is given by

$$\frac{\partial P(x, t)}{\partial t} = rP(x, t) \left[1 - \frac{P(x, t)}{K} \right] + D \frac{\partial^2 P(x, t)}{\partial x^2},$$

where the total biomass of the species per unit area ($P(x, t)$, [ML^{-2}]) grows logistically at rate r ($ML^{-2} T^{-1}$) before

growth saturates at a carrying capacity K (ML^{-2}), x is distance (L), and t is time (T). To consider the spread of a plant species due to seed dispersal, the equation can be generalized to

$$\frac{\partial P(x, t)}{\partial t} = r \left[1 - \frac{P(x, t)}{K} \right] \left[P(x, t) + \alpha \int_{\Omega} W(x') P(x', t) dx' \right]. \quad (1)$$

Here, x' is a dummy variable denoting distance (L). At each time step (dt), a proportion (α [T^{-1}]) of the biomass is spatially distributed according to a dispersal kernel $W(x)$, applied over a spatial domain Ω . All parameters (r , K , and α) are assumed to be constant in space and time. The r and K parameters follow their standard interpretations from logistic growth models. The “spread-and-survival” parameter α is related to fecundity. For each time step and each point in space, it defines the biomass that is spread as seed from that point and subsequently germinates and grows, that is, the spreading and surviving biomass. In this formulation, α is defined as a proportion of $P(x, t)$, and it is assumed that $\alpha \ll 1$. This treatment of movement contrasts with the original Fisher-Kolmogorov equation, in which biomass spread rates depend on the local spatial variation in biomass $\partial^2 P / \partial x^2$ and a diffusion coefficient D ($L^2 T^{-1}$). Equation (1) recovers the steady state solution of the traditional Fisher-Kolmogorov equation if $W(x)$ is a Gaussian kernel (see “The Classical Fisher Equation and Gaussian Dispersal Kernels” in app. A of the online edition of the *American Naturalist*).

In the case of wind-dispersed biomass, fast turbulent processes must be resolved. For integrating across these processes to arrive at hourly timescales, the WALD model kernel is used; it is given by

$$W(x) = \sqrt{\frac{\lambda}{2\pi x^3}} \exp \left[-\frac{\lambda(x - \mu)^2}{2\mu^2 x} \right], \quad (2)$$

where

$$\lambda^{1/2} \approx \frac{z_r}{\sqrt{\kappa h(2\theta)}}$$

and

$$\mu = \frac{z_r \bar{U}}{V_t}.$$

The parameters relate to the characteristics of the applied half-hourly mean wind speed field (\bar{U}) and θ (defined

below), the seed release height of the plants (z), and the height of the surrounding canopy (h), and other than \bar{U} , they are assumed to be constant in space and time. The parameter θ is defined as σ_w/\bar{U} , where σ_w is the standard deviation of the wind velocity in the vertical direction. The parameter θ represents the importance of turbulence in lifting the seed from the canopy versus the action of the mean wind speed in moving the seed horizontally; V_t is the terminal velocity of the seeds, that is, the steady velocity at which they fall; and κ is a proportionality constant relating the size of turbulent eddies within the canopy to the canopy height (Katul et al. 2005), where κ is of order 1, taken as 0.6 for the purposes of this study. In a standard boundary layer, where eddies scale with the height from the ground, $\kappa = 0.4$ and is Von Karman's constant; for within-canopy flow conditions, however, κ is expected to be >0.4 because of wake generation and the fact that the seed-carrying eddies no longer scale with height from the ground. The parameters σ_w and \bar{U} are strongly correlated, and θ can be approximated as a constant at near-neutral atmospheric conditions just above the canopy (when heating or cooling of the air does not affect turbulent generation). The μ parameter defines the mean dispersal distance, while λ defines a scaling parameter.

As evidenced from equation (2), the WALD kernel yields a multiplicative combination of a power-law term describing the dispersal kernel tails and "censoring" by an exponential distribution that accounts for gravity. For high terminal velocities, the WALD kernel approaches a simple ballistic model. If seed terminal velocities are much less than the mean wind speed, then the kernel tails decay according to a power law ($\sim x^{-3/2}$) and at a slower rate than in many comparable dispersal kernels, such as the bivariate Student's t distribution (Clark et al. 1999). For finite terminal velocities and mean wind speeds, the WALD kernel is bounded, ensuring that asymptotic approaches to constant propagation speeds exist (Mollison 1991; Kot et al. 1996).

The Wave Speed

The motion described by the generalized Fisher-Kolmogorov equation generates a traveling wave front of expanding biomass. To recover the velocity of plant movement, the velocity of the nonlinear wave front is needed. To derive this velocity, the approach outlined by Kot et al. (1996) is used, beginning with the "linear conjecture" that the velocity of the nonlinear wave front is equivalent to that of its linearization. This conjecture is valid for populations that do not exhibit an Allee effect; that is, the net growth rate is independent of population density (Mollison 1991). The differential equation is linearized by assuming that at the leading edge of the wave, $P/K \ll 1$ (i.e.,

the population is very much less than the carrying capacity), resulting in

$$\frac{dP}{dt} = r \left[P + \alpha \int_{-\infty}^{\infty} P(x')W(x - x') dx' \right], \quad (3)$$

and in discrete form, this equation becomes

$$P_{t+1} = rdt \left[P_t + \alpha \int_{-\infty}^{\infty} P(x')W(x - x') dx' \right] + P_t, \quad (4)$$

where dt is the time step. With appropriate choice of units in the rate terms r and α , dt can be set to unity and canceled. If a traveling-wave solution exists, then

$$P_{t+1}(x) = P_t(x - c), \quad (5)$$

where c is the front speed to be determined next.

Assuming a solution of the form $P \propto e^{-sx}$ for the linearized equation and substituting equation (4) into equation (5) gives

$$e^{s(c-x)} = r \left[e^{-sx} + \alpha \int_{-\infty}^{\infty} e^{-sx'}W(x - x') dx' \right] + e^{-sx}, \quad (6)$$

$$e^{sc} = r \left[1 + \alpha \int_{-\infty}^{\infty} e^{s(x-x')}W(x - x') dx' \right] + 1. \quad (7)$$

Let $u = x - x'$. Then,

$$e^{sc} = r \left[1 + \alpha \int_{-\infty}^{\infty} e^{su}W(u) du \right] + 1. \quad (8)$$

This expression gives the characteristic equation for the wave front speed c . The component $\int_{-\infty}^{\infty} e^{su}W(u) du$ is the moment-generating function of the Wald distribution, hereafter referred to as "MG(s)," which, for a finitely bounded WALD kernel, is differentiable and defined as

$$MG(s) = \exp \left\{ \frac{\lambda}{\mu} \left[1 - \left(1 - \frac{2\mu^2 s}{\lambda} \right)^{1/2} \right] \right\}, \quad (9)$$

$$\begin{aligned} \frac{\partial MG(s)}{\partial s} &= \frac{\mu \exp \left((\lambda/\mu) \left[1 - \left[1 - (2\mu^2 s/\lambda) \right]^{1/2} \right] \right)}{\left[1 - (2\mu^2 s/\lambda) \right]^{1/2}} \\ &= \frac{\mu MG(s)}{\left[1 - (2\mu^2 s/\lambda) \right]^{1/2}}. \end{aligned} \quad (10)$$

The solution for the wave front must be real and positive and therefore exists at the double root of the characteristic equation, given by its derivative,

$$ce^{sc} = r\alpha MG'(s). \quad (11)$$

Equation (11), combined with equation (8), provides a parametric description of c and r :

$$c = \frac{r\alpha MG'(s)}{r[1 + \alpha MG(s)] + 1}, \quad (12)$$

$$r = \frac{e^{s(r\alpha MG'(s)/(r[1 + \alpha MG(s)] + 1))} - 1}{1 + \alpha MG(s)}. \quad (13)$$

Using a known value of r to solve equation (13) for s allows the direct determination of c .

The solution is primarily dictated by the values of r , α , λ , and μ . Because of the implicit nature of the equation, a numerical root-finding method is required (see app. B in the online edition of the *American Naturalist* for the algorithm). The linear conjecture implies that a number of more complicated models also have an asymptotic wave speed represented by equations (12) and (13). For instance, incorporating a time delay to maturity in the plants does not necessarily affect the asymptotic wave speed, although the time to reach the asymptote increases. The results in equations (12) and (13) were derived by including the most basic processes of growth and dispersion but neglecting retarding factors such as predation, interspecific competition, and landscape heterogeneity. Thus, the propagation rate predicted by such analysis can be taken as an upper bound on realistic values.

Upscaling Using Superstatistics

Up to this point, the model has assumed that all parameters are fixed in space and time. However, there are many sources of variability that affect these parameters over timescales commensurate with biomass growth and the spatial scales of migration. In the time domain, the most pervasive is the variation in mean half-hourly ambient wind speed, which changes on hourly timescales over a

typical range of 0–12 m s⁻¹, that is, several orders of magnitude, in the eastern United States (Van der Hoven 1957). This exceeds variability in mean growth rate or spread-and-survival rate, both of which vary by at most a single order of magnitude on seasonal to interannual scales. Resolving the effect of the rapid variation in half-hourly mean wind speed is necessary before attempting to understand variability in the slower processes, and doing so is the focus of the analytical upscaling attempts in this article. Despite the focus on the mean wind speed temporal variability, variability in other parameters can be considered via numerical simulations. The detailed consideration of variation in multiple parameters, however, confounds analytic tractability. Instead, a sensitivity analysis is presented to show the effect of variability in ecological and forcing parameters on c .

The distribution of hourly (or half-hourly) mean wind speeds, \bar{U} , has been well studied and is often represented as a Weibull distribution with scale parameter b and shape parameter k , that is,

$$p(\bar{U} = y) = \frac{ky^{k-1}}{b^k} \exp \left[-\left(\frac{y}{b} \right)^k \right], \quad (14)$$

typically expressed as $p(\bar{U}) = \text{Weib}(b, k)$ (Takle and Brown 1978; Conradsen et al. 1984; Garcia et al. 1998). Hence, variations in mean half-hourly wind speed over long timescales (seasonal to interannual) are accounted for by drawing \bar{U} from a Weibull distribution. This approach is known as “superstatistics” and is currently gaining considerable interest in complex-systems science, whereby the statistics governing variability in distributional parameters are used to evaluate variation that is extensively spread in space or time. The resulting distributions are analogous to using “mixture models,” analytical composites of the distributions describing long- and short-timescale processes (Beck and Cohen 2003; Porporato et al. 2006). The significance of turbulent transport is clearly seen in the superstatistical framework by constructing the dispersal kernels, at an annual timescale, for a purely ballistic scenario (i.e., in the absence of turbulence, using the Weibull distribution but not the Wald) and for a turbulent-transport scenario, using the Weibull distribution as a superstatistical input to the WALD kernel. Turbulence causes seed transport to be extended by up to two orders of magnitude over purely ballistic cases. The resulting dispersal kernels are shown in figure 1.

The construction of the dispersal kernel as a mixture of the Weibull distribution and the Wald distribution also bears close analogy to existing phenomenological treatments of vegetation dispersion. For instance, the widely

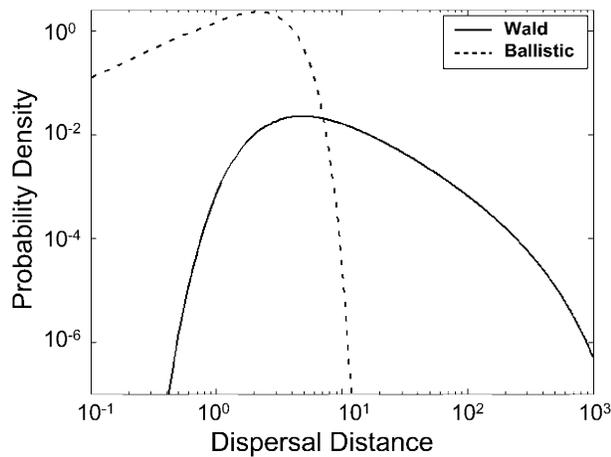


Figure 1: Comparison of WALD and ballistic kernels on log-log plot. Kernels are shown for annual timescales and *Fraxinus pennsylvanica* parameters. The ballistic kernel considers only advection of a seed falling with terminal velocity V_t and being advected by the mean wind speed, whose distribution is taken from the Weibull parameters. The WALD kernel accounts for turbulence in addition to advection and results in finite probabilities of dispersion at length scales two orders of magnitude greater than those of the ballistic kernel.

used 2Dt kernel is a mixture of a normal and an exponential distribution (Clark et al. 1999), although in the current case, the mixture is based on the statistics of mechanically derived processes. In summary, the model achieves an upscaling from turbulent timescales to half-hourly timescales via the WALD kernel and from half-hourly timescales to annual timescales via the Weibull distribution of wind speeds, and it can be further upscaled by consideration of interannual variability of Weibull parameters (fig. 2).

To use the analytical result in equations (12) and (13), a parameterization that accounts for the Weibull variations in \bar{U} and their interaction with the turbulent transport described by the WALD kernel is needed. What we seek is the appropriate (or effective) wind speed with which to parameterize a WALD dispersal kernel for wind-transported seeds over annual timescales. Numerical simulations indicate that simple moments of the Weibull distribution (mean, mode, etc.) grossly underestimate this wind speed. This is because the interaction of the Wald and Weibull distributions amplifies the effect of the tails of the distribution. There is no simple way to parameterize this effect, because the marginal distribution arising from a Wald distribution forced by the Weibull distribution cannot be obtained analytically. Given a realization of the plant front velocity c , however, it is possible to work backward (by using eqq. [12] and [13] in an inverse sense) to infer a single value for \bar{U} that would reproduce this c value

from the numerical simulation. If this value is determined for an ensemble of realizations of c , as generated by Monte Carlo analysis, a distribution of such “effective wind speeds” (U_{eff}) can be computed. The mean of U_{eff} (\bar{U}_{eff}) reproduces the mean of the plant front velocities when applied to the numerical model. To proceed by defining \bar{U}_{eff} preserves the flexibility of the model, which can be parameterized with \bar{U}_{eff} (the determination of which is addressed in the next section) and appropriate WALD parameters for any combination of forest type and wind climate. A realization of U_{eff} can be obtained from an empirically measured seed dispersal kernel over annual timescales by fitting the WALD parameterization to this kernel. The difficulties associated with measuring the tails of the dispersal kernel, however, would likely cause this sample of U_{eff} to be underestimated, while reconstructing the distribution of U_{eff} would be highly labor intensive (Bullock et al. 2006). The disparity between the applied Weibull distribution and the distribution of U_{eff} resulting from its application to the logistic-WALD model is shown in figure 3.

Having defined U_{eff} , we proceed by constructing a relationship between the Weibull parameters and the effective velocity to allow prognostic usage. A wide range of wind distributions and their effect on c were explored by varying the parameters of the Weibull distribution in a range of $b \in [1, 3]$, $k \in [1, 4]$ (covering the range of plausible values for winds). Distributions of c were obtained from a Monte Carlo simulation with 500 realizations for each combination of Weibull parameters (see “Numerical Simulations” in app. A of the online edition of the *American Naturalist* for details of numerical simulations), and distributions of U_{eff} were computed from these using equations (12) and (13) in an inverse sense. Weibull, gamma, and normal distributions were fitted to the resulting U_{eff} distribution, and goodness of fit was assessed using the Akaike Information Criterion (AIC; Akaike 1974). A relation between the distribution of U_{eff} and the distribution of mean applied wind speeds was empirically derived, using a curve-fitting algorithm that tested multiple functional forms of the fitting functions and returned those with the least square error (Phillips 2007). Tenth- and ninetieth-percentile bounds on the parameters were derived numerically from the fitted distribution and used to provide bounds on the estimate of U_{eff} . The combination of the analytical results and these regression equations provided a closed-form semianalytical model combining information about the wind climate and the vegetation properties to predict a likely range of wave speeds for vegetation dispersal.

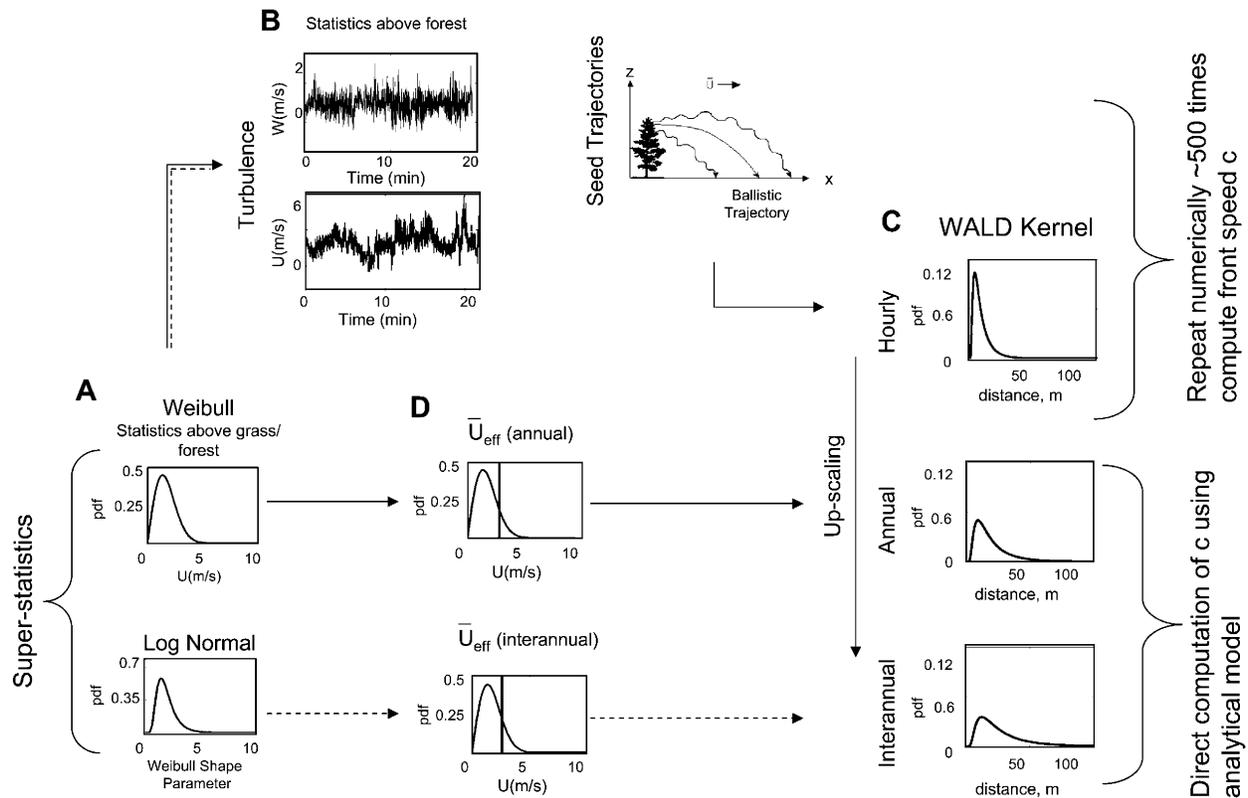


Figure 2: Conceptual model for scaling of biomass growth and dispersal. *A*, The Weibull and (conceptually) a lognormal distribution generate U values that force the WALD kernels at different timescales. *B*, The WALD kernel (showing the probability density function of seed dispersal distances) results from a distribution of seed trajectories and provides the scaling between turbulent and half-hourly timescales. *C*, At longer timescales, the increasing variability results in “fatter” tails in the WALD kernel. Computation of the vegetation front speed may proceed numerically via Monte Carlo simulation, where a mean wind speed is repeatedly sampled from the Weibull distribution, the hourly WALD kernel is computed, and the process is repeated until the asymptotic front speed is reached. This is repeated ~ 500 times to predict the front speed. *D*, More expediently, the \bar{U}_{eff} parameter can be computed and used to directly describe the annual (or, conceptually, the interannual) WALD kernels, which are then solved analytically for the vegetation front speed.

Case Study: North American Postglacial Expansion

The palynological record from the early Holocene epoch provides an ideal case study of vegetation migration because trees expanded their range in the wake of retreating glaciers (Delcourt and Delcourt 1987; MacDonald 1993). This record is useful because it extends over a sufficient temporal and spatial area to allow spread rates to be clearly determined, and, unlike contemporary records, it is not confounded by anthropically enhanced dispersion. We used the analytical version of the logistic-WALD model to examine the migration of eight wind-dispersed species (four *Acer* [maple], two *Fraxinus* [ash], one *Pinus* [pine], and one *Betula* [birch] species). Our intent was not to obtain a one-to-one comparison but rather to demonstrate that the order of magnitude of spread rates could be independently derived from what is currently known about these species and assumed wind conditions. Seed terminal-velocity data were

obtained from the literature (Green 1980; Matlack 1987, 1992; Nathan et al. 2002; Williams et al. 2006); however, biomass growth rates were not available. We estimated the biomass at maturity using allometric equations (Jenkins et al. 2003), in conjunction with diameter at breast height and stand age at maturity (USDA 1990), and used these as first-order estimates of growth rate. For the smaller tree *Acer negundo* (box elder), which was outside the range of species considered by Jenkins et al. we adopted species-specific allometric equations (Schlaegel 1982). The constants used are shown in table 1.

The vegetation expansion consisted of two phases: an initial replacement of low tundra by boreal forests followed by replacement of boreal forest with deciduous forests (Delcourt and Delcourt 1987). Selection of wind data therefore must consider both the expansion into open tundra, most applicable to *Betula* and *Pinus* species, and the

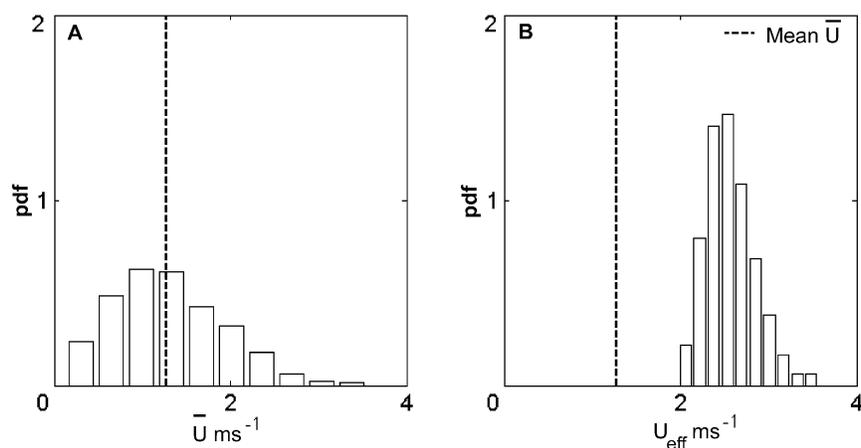


Figure 3: A, Distribution of mean half-hourly wind speeds (\bar{U}), with the mean of the distribution shown. B, Distribution of effective wind speeds (U_{eff}), derived from numerical simulations of the logistic-WALD model, for the forcing shown in A. Note that the mean of the forcing wind speed (dashed line) underpredicts the distribution of effective wind speeds. pdf = probability density function.

later expansion into forested areas, applicable to *Acer* and *Fraxinus* species. *Acer* species also expanded their range significantly into prairies in the Midwest, and thus the open conditions may apply to this genus as well. Accordingly, the mean, tenth- and ninetieth-percentile bounds on U_{eff} were estimated from a long-term half-hourly mean wind speed records collected at the Duke Forest (near Durham, NC) in a grass-covered forest clearing and above a hardwood canopy, and front propagation data are presented for both these conditions for all species (“Wind Data and Wind Statistics from Duke Forest” in app. A of the online edition of the *American Naturalist*). The value of θ was determined by assuming that the wind statistics should be derived from above the forest canopy. An estimate of $\theta = 0.36$ was obtained from typical wind statistics above a dense canopy. These estimates were then used in the semianalytical model to calculate the vegetation wave front propagation speed. Calculated wave speeds were divided by 2π to convert between the one-dimensional analytical result and the two-dimensional spread rates given by the pollen data, assuming random wind direction.

A sensitivity analysis on the endogenous variables in the logistic-WALD model was undertaken (“Sensitivity Analysis of the Semianalytical Model” in app. A of the online edition of the *American Naturalist*). The major findings of this sensitivity analysis (discussed further in “Results”), were that the front speed is linear in \bar{U}_{eff} and that for small values of the spread-and-survival parameter α (<0.01), the choice of α does not significantly alter c but alters only the time taken to reach the asymptote. Accordingly, α was set to 5×10^{-6} , an order-of-magnitude estimate at half-hourly timescales. To assess the suitability of using the

Duke Forest wind data as a surrogate for data across the range of the postglacial expansion, a further sensitivity analysis was undertaken on the Weibull parameters. This analysis indicated that the likely variability in \bar{U}_{eff} across a sample of forested sites in North Carolina, Indiana, Massachusetts, and Maine was of the order of 8% and that this was directly comparable to the likely variation associated with changes in land cover type (9%). Given the linearity of the front speed in \bar{U}_{eff} , the geographic variability in the Weibull statistics is expressed as uncertainty of less than 10% in the biomass front speed.

Results

Generation of U_{eff} from Weibull Wind Parameters

Based on the AIC, a gamma distribution was the best fit to the U_{eff} distribution arising from the Monte Carlo simulations. Hence, in a first-order estimate of U_{eff} , a gamma distribution was used, with the distribution gamma (ω, ν) described as

$$p(x|\omega, \nu) = \frac{1}{\nu^\omega \Gamma(\omega)} x^{\omega-1} e^{-x/\nu}, \quad (15)$$

where Γ is the gamma function. The nonlinear regression between the Weibull (b, k) parameters for \bar{U} and the effective wind speed U_{eff} generated functions to predict the mean of U_{eff} (denoted \bar{U}_{eff}), given the wind statistics. The gamma parameters ω and ν , which are required to specify the distribution of U_{eff} , were also determined. High coefficients of determination (r^2) were achieved for all regressions (table 2; fig. 4).

Table 1: Data used to parameterize the logistic-WALD model, front speed results from the pollen record, and the predicted speeds from the logistic-WALD model

Species	DBH ^a (cm)	Mature biomass ^b (kg)	Est. growth			Canopy height (m)	Pollen record wave speed (m year ⁻¹)	Predicted wave speed: forest–open (m year ⁻¹)		Predicted wave speed: forest–forest (m year ⁻¹)	
			rate (kg year ⁻¹)	V_t^c (m s ⁻¹)	z_r^d (m)			Mean	Err. bounds ^e	Mean	Err. bounds ^e
<i>Acer rubrum</i>	8.9	21	2.6	.67	10	17.2	126–200	218	134–334	262	238–384
<i>Acer saccharum</i>	19	143	3.6	1.0	10	17.2	126–200	131	81–201	158	143–231
<i>Acer negundo</i>	60	114	1.9	.92	9.5	19	126–200	94	58–144	113	102–165
<i>Acer saccharinum</i>	29.7	341	7.9	.87	12.5	25	126–200	581	359–888	696	634–1,021
<i>Betula lenta</i>	20.1	137	3.4	1.6	15	20	212	59	37–90	71	65–105
<i>Fraxinus americana</i>	15.8	91	2.5	1.4	13.1	18.7	123	52	31–78	62	56–91
<i>Fraxinus pennsylvanica</i>	20	162	7.7	1.6	11.9	17	123	111	69–170	133	121–195
<i>Pinus taeda</i>	23	164	8.2	.7	11.7	14.6	81–400	542	335–829	650	591–953
Mean							169	224		268	

Note: The error bounds shown incorporate the tenth- and ninetieth-percentile estimates of U_{eff} and an 8% error associated with geographic variation in wind properties; κ was set to 0.6 for the simulations.

^a Diameter at breast height.

^b Mature biomass of a single tree.

^c Terminal velocity.

^d Seed release height.

^e Error bounds due to geographic variation.

Applications to the Case Study

The mean speed of vegetation movement predicted in the case study was within a factor of 5 or better of that in the palynological record for all species considered (table 1). The sensitivity analysis of the wind statistics indicated that there is a linear correlation between the Weibull parameters, when compared across multiple sites, and that this correlation damps the effect of changes in the wind statistics. Over the area of interest, this resulted in a near-linear sensitivity of U_{eff} to the Weibull parameters and constrained the error associated with geographic variation to the order of 10% (see “Wind Data and Wind Statistics across Multiple Regions,” fig. A2, and table A3 in app. A for details). This uncertainty did not greatly alter the quality of the predictions by comparison to the mean cases. The sensitivity analysis of endogenous parameters indicated that the dependence of the predicted wave speeds was approximately linear in the growth rate (r) and the wind speed applied (\bar{U}_{eff}), nearly linear in the canopy height (h) and the vertical velocity standard deviation (σ_w), and nonlinear in terminal velocity (V_t), release height (z_r), and the spread-and-survival parameter (α). In particular,

for values of α less than 0.01, the propagation speed was almost insensitive to further decreases in α over several orders of magnitude (see “Sensitivity Analysis of the Semi-analytical Model” in app. A for details).

Discussion

By linking the Weibull mean wind statistics to the description of the WALD parameters through \bar{U}_{eff} , the half-hourly timescale of wind variability is scaled up to the timescales of biomass growth. In analyzing the numerical results to achieve this scaling, our goal was to ensure that direct analytical implementation was achievable. This motivated the approximation of the distribution of U_{eff} as gamma (ω, ν). In reality, the distribution of U_{eff} is a transformation of the Weibull distribution via the WALD kernel and the logistic equation with no known analytical representation and cannot be fully represented via a two-parameter approximation such as the gamma distribution. Accordingly, the quality of the gamma distribution in describing U_{eff} varies with the parameters of the Weibull function, resulting in some inevitable error. However, the

Table 2: Regression equations and r^2 (coefficient of determination) values for \bar{U}_{eff} , ω , and ν as functions of the Weibull parameters b and k

Parameter	Regression equation	Regression coefficients	r^2
\bar{U}_{eff}	$s_0 \tanh(k) + s_1(b/k^{1.5}) + s_2$	$s_0 = .8187, s_1 = 3.4233, s_2 = .0963$.99
ω_{gamma}	$\gamma_0[\tan^{-1}(b)k^2] + \gamma_1(k^2/b) + \gamma_2$	$\gamma_0 = 8.3426, \gamma_1 = 6.3476, \gamma_2 = 10.9000$.99
ν_{gamma}	$\varphi_0(\tan b/k^2) + (\varphi_1 \tanh b)/k^2 + \varphi_2$	$\pi_0 = -.0086, \pi_1 = .4172, \pi_2 = -.0184$.88

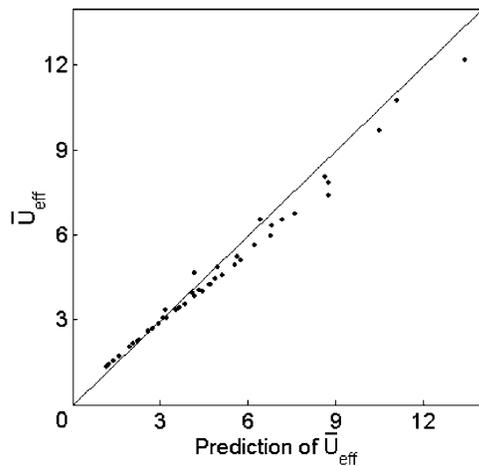


Figure 4: Pairwise plot of \bar{U}_{eff} predicted via regression and \bar{U}_{eff} .

linear dependence of the wave speed on U_{eff} ensures that the effect of these errors is first-order only, meaning that the achieved fit is acceptable, given the aims of the model to provide a tractable approach to estimating spread rates. If greater accuracy is needed, U_{eff} should be calculated more precisely via numerical simulations.

The logistic-WALD model reproduced vegetation propagation speeds to a good approximation without invoking isolated extreme events (e.g., hurricanes) as the mechanism promoting long-distance dispersal. Rather than relying on such phenomena, the logistic-WALD model implies that long-distance dispersal is an expected outcome of the interaction between seed movement and the complex wind statistics across a range of timescales. Mathematically, this is the result of the interaction between the tails of the Weibull (whose genesis is mesoscale- and weather-related variation about \bar{U}) and WALD (whose genesis is turbulent dispersion) distributions, as outlined in figure 2.

Several limitations to the data used in the postglacial-expansion case study prevented a one-on-one comparison between predicted and recorded biomass propagation speeds. While terminal-velocity data were measured for all species, other parameters, particularly the growth rate, were estimated through generic allometric equations and basic assumptions such as a constant growth rate throughout the plant's life span.

Results presented for wind data collected both from a forest clearing, most applicable to early-colonizing species, and from a forest canopy, as applicable to later-succession species, were within the order-of-magnitude limits sought. The linear effect on c of changing land cover type or geographic location was small, at $\sim 10\%$, and by comparison to the uncertainties associated with approximating the pa-

leoclimatological record with contemporary wind statistics, this variation can be considered negligible. For contemporary applications of the model, results could be improved through appropriate spatial averaging of wind statistics. However, it should be noted that errors remain in approximating the postglacial-expansion wind statistics by current wind distributional properties of the Weibull distribution.

The logistic-WALD model is a simplified representation of some of the complex processes that govern species migration and currently constitute an active topic of research (Lewis and Pacala 2000; Moorcroft et al. 2006). Despite the simplicity of the model, it contains an appropriate treatment of the multiscale processes involved, and its results hold clear analogies to more complex representations. As outlined in the introduction to this article, the omission of retarding processes, such as competition, from the process description allows us to consider the derived speed to be a maximum, obtained under ideal conditions for invasion. As such, it is analogous to the concept of "invasion by extremes," in which the most rapidly transported seeds become responsible for invasion and population establishment (Clark et al. 2001). Using fat-tailed dispersal kernels, Clark et al. were unable to reproduce the Holocene invasion speeds for a range of species without artificially increasing seed survival rates (the α parameter in our formulation). Our finding that c loses sensitivity to α as α becomes arbitrarily small allows the logistic-WALD model to recover the appropriate order of magnitude of the spread rates without such artificial increases in survival. Provided that dispersal occurs over a sufficiently long period to allow the asymptotic speed to be reached, low seed viability does not necessarily restrict the vegetation front movement but restricts just the timing at which the maximum front speed occurs. Note that the α parameter addresses the distribution and establishment of seed biomass only; increasing seedling mortality effectively reduces the growth rate parameter r in the logistic-WALD model, with resulting linear reductions in the wave speed.

Stochastic studies of plant movement via long-range dispersal events have highlighted the importance of the "outlier-expansion" effect, in which outlier populations establish remotely from the main population, remain effectively stationary for some period of time, and then expand to close the gaps between the populations, often with remarkable speed (Shigesada et al. 1995; Clark 1998; Clark et al. 1998, 2001; Neilson et al. 2005; Kawasaki et al. 2006). In continuous terms, the logistic-WALD model accomplishes this expansion by a very similar mechanism. Small quantities of biomass are distributed at long distances from the established population, and the biomass associated with these populations remains small (in comparison to the carrying capacity) for a considerable period of time.

These small quantities can be conceptualized as representing a distribution of potential outlier populations away from the starting point. As the wave front passes these points, a large and rapid increase in biomass occurs, analogous to the expansion phase of the outlier-expansion model.

Within the many diffusion models of biomass movement, parameterization of the diffusion coefficient remains a challenge and a source of uncertainty (Okubo and Kareiva 2001; Murray 2002, pp. 437–482). Exemplified by “Reid’s paradox” (Clark et al. 1998), the effective diffusion coefficients needed to reproduce typical biomass migration rates exceed those derived from experimental observations relying on spread distance and timescale arguments (i.e., approximations of diffusion coefficients D as L^2/T) by orders of magnitude. For wind-dispersed plants, the logistic-WALD model offers a way to improve the parameterization of such “effective” diffusion coefficients. The WALD kernel can be parameterized using local wind statistics and the characteristics of the dominant plant species under consideration. The semianalytical solution can then be used to give the asymptotic wave speed c . An effective diffusion coefficient, should it be needed, can then be determined using the relationship $D = c^2/4r$. The use of the logistic-WALD model to derive an effective diffusion coefficient in these cases provides a new and defensible approach to parameterization of existing diffusion-based models. For algorithmic implementation of this scheme to determine c and effective diffusion coefficients, see appendix B.

Conclusion

Our aim in formulating a biomass dispersal model based on the WALD kernel was to mimic the simplicity of diffusion as a description of biomass movement, that is, an expression approaching the simplicity of $c = 2(rD)^{1/2}$, while avoiding the anomalous results produced by diffusion and improving spread rate parameterization. This approach required that, with the exception of the mean wind speed, parameters be treated as constant in space and time. The logistic-WALD model achieves the improvements for wind-dispersed biomass in three ways. First, the upscaling from turbulent-transport timescales to biomass growth timescales is now explicit and mechanistic rather than assumed or empirically fitted to one particular site. Second, the logistic-WALD model can be completely parameterized from independent data: knowing sufficient information about the species’ growth rate, the wind climate in which it grows, and its seed attributes allows upper bounds on the speed of the biomass front to be estimated. Third, the logistic-WALD model is shown to provide reasonable estimates of known biomass dispersal rates for the early Holocene expansion, circumstances in which diffusion-

based estimates are known to grossly underestimate such data.

The superstatistical approach adopted here, in which processes are related across scales through deriving relationships between their statistical descriptors, is now showing promise in many applications, including the prediction of rainfall on interannual timescales (Porporato et al. 2006) and improved descriptions of turbulent motion (Beck and Cohen 2003). Future application of such approaches could allow a similarly simple model to account for variability at the interannual scale. Long-time series data of wind measurements that capture several decades of variability at multiple spatial scales are starting to become available (Kalnay et al. 1996), providing appropriate data sets for examination of interannual variability in a “normal” setting and thus baselines against which to evaluate future trends in the wind climate. Studies of potential changes to the wind climate show an emerging trend of change in the extremes of wind climate, ranging from fewer extreme events associated with weakening of the Asian monsoon to expectation of increasing severity of hurricane activity associated with warmer sea surface temperatures (Emanuel 1987; Knutson and Tuleya 1999; Lun and Lam 2000; Walsh 2004; Webster et al. 2005; Pryor et al. 2006; Xu et al. 2006; Yan et al. 2006). The sensitivity of wind dispersal to extremes of the wind regime means that these changes have important implications for plant migration, which can now be accounted for within a proposed framework of “hierarchical superstatistics.” Here the superstatistics of the Weibull distribution would be evaluated from time series data and scaling relationships developed to predict \bar{U}_{eff} over longer timescales, as depicted conceptually in figure 2. Such hierarchical superstatistical models are expected to find broad applicability in a wide range of ecological modeling problems in which the “dimensionality curse” impairs predictive capacity and important processes span a range of timescales from fractions of seconds to multiple years.

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