Dispersal Patterns, Dispersal Mechanisms, and Invasion Wave Speeds for Invasive Thistles

Olav Skarpaas* and Katriona Shea†

Department of Biology and Intercollege Graduate Degree Program in Ecology, Pennsylvania State University, University Park, Pennsylvania 16802

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ABSTRACT: Understanding and predicting population spread rates is an important problem in basic and applied ecology. In this article, we link estimates of invasion wave speeds to species traits and environmental conditions. We present detailed field studies of wind dispersal and compare nonparametric (i.e., data-based) and mechanistic (fluid dynamics model–based) dispersal kernel and spread rate estimates for two important invasive weeds, Carduus nutans and Carduus acanthoides. A high-effort trapping design revealed highly leptokurtic dispersal distributions, with seeds caught up to 96 m from the source, far further than mean dispersal distances (approx. 2 m). Nonparametric wave speed estimates are highly sensitive to sampling effort. Mechanistic estimates are insensitive to sampling because they are obtained from independent data and more useful because they are based on the dispersal mechanism. Over a wide range of realistic conditions, mechanistic spread rate estimates were most sensitive to high winds and low seed settling velocities. The combination of integrodifference equations and mechanistic dispersal models is a powerful tool for estimating invasion spread rates and for linking these estimates to characteristics of the species and the environment.

Keywords: wind dispersal, mechanistic dispersal model, integrodifference equations, population spread rate, Carduus nutans, Carduus acanthoides.

Research to understand and predict the spread of invasive species has become increasingly urgent in recent decades, as the widespread and large effects of pest species cause ever more prominent problems. Management planning and implementation require improved information to be effective, especially given the constraints of limited resources. However, studies of propagule dispersal and population spread are relatively difficult to carry out, compared to localized demographic studies. Progress depends on obtaining high-quality dispersal data, describing them in quantitative terms, and incorporating them into tractable spatial formulations that give reliable predictions of population spread.

One of the critical determinants of invasion rates is the probability distribution of dispersal distances, the dispersal kernel (Kot et al. 1996; Neubert and Caswell 2000; Neubert and Parker 2004). Invasion rates are extremely sensitive to the shape of the dispersal kernel, in particular to its tail, that is, rare long-distance dispersal events. Unfortunately, these events are among the most difficult to quantify empirically, and a myriad of sampling methods, of inconsistent usefulness, exist (Turchin 1998; Clobert et al. 2001; Bullock et al. 2002, 2006; Skarpaas et al. 2005). A full bestiary of models for dispersal kernels also exists (Willson 1993; Shaw 1995; Clark et al. 1999; Bullock and Clarke 2000; Greene and Calogeropoulos 2002; Nathan et al. 2002; Paradis et al. 2002; Higgins et al. 2003; Levin et al. 2003). Key issues again pertain to the tail of the dispersal kernel. Normal (Gaussian) and other thin-tailed (i.e., exponentially bounded) dispersal kernels lead to constant invasion rates that are easily estimated using classical models of population spread (Fisher 1937; Skellam 1951; Lewis et al. 2006). However, for many species, the distributions of dispersal distances seem to be best fitted by fat-tailed (i.e., not exponentially bounded) distributions (e.g., Willson 1993; Clark et al. 1999). Such dispersal kernels lead to indefinitely accelerating invasions in models of population spread (Shaw 1995; Kot et al. 1996; Lewis et al. 2006). However, all realized dispersal distributions consist of a finite number of dispersal events and therefore have exponentially bounded tails. Clark et al. (2001; see also Lewis et al. 2006) showed that finite estimates of invasion rates can be obtained for any dispersal kernel using non-
parametric estimation based on empirical distributions of dispersal distances. This approach holds great promise because it can be used to estimate invasion rates directly from raw dispersal data (Clark et al. 2001; Lewis et al. 2006).

However, the problem of extrapolating beyond the data remains. It is not clear how sensitive wave speed estimates using the nonparametric approach are to sampling effort at the tail (in particular, how smaller-scale studies may restrict estimates of wave speed). To circumvent this problem, Clark et al. (2001) suggested fitting a parametric kernel to the data and then estimating wave speeds using discrete data generated from the kernel. In principle, the estimates converge to the “true” wave speed for high numbers of dispersal observations. Still, this requires a qualified choice among the available models for dispersal. Models have often been chosen on the basis of their goodness of fit to dispersal distance data, regardless of the interpretability of the model parameters. Ideally, however, one would want a model in which the parameters are directly related to the dispersal mechanism. This facilitates independent estimation of the parameters and decreases the risks of extrapolation beyond the measured conditions (Nathan and Muller-Landau 2000). Such a model, the Wald analytical long-distance dispersal (WALD) model, was recently proposed for wind dispersal (Katul et al. 2005). This model is derived from Lagrangian theory for turbulent wind transport and makes better predictions about dispersal distances, particularly long-distance dispersal, than previous analytical mechanistic models (Okubo and Levin 1989; Katul et al. 2005).

In this article, we use both mechanistic and nonparametric methods to estimate rates of population spread. We show that, in contrast to the mechanistic estimates, the nonparametric estimates are highly sensitive to restricted sampling. We apply the two approaches to data from replicated high-effort empirical dispersal studies for two economically important invasive weeds: Carduus nutans L. and Carduus acanthoides L. (musk and plumeless thistle, respectively; Asteraceae). These Eurasian-origin thistles rank high among the most commonly listed weeds on state noxious-weed lists in the United States (Skinner et al. 2000), and one or both are also invasive in Australia, New Zealand, South America, and, recently, South Africa. The demography and management of local populations of the two invasive thistle species have been fairly well studied (Desrochers et al. 1988; Shea and Kelly 1998; Shea et al. 2005, 2006; Jongejans et al. 2007), but a better understanding of their spatial dynamics will be vital to their management as they spread into new areas. Here, we demonstrate the utility of the mechanistic approach for understanding and predicting dispersal and population spread.

Linking Dispersal and Population Spread

To estimate invasion rates, we need a framework for linking dispersal and local population dynamics. We first present this framework, which motivates the following section on dispersal measurement and dispersal model parameterization. We then describe the estimation of population wave speeds using the different kinds of dispersal models.

To link dispersal and population spread, we used the framework of integrodifference equations (Neubert and Caswell 2000; Neubert and Parker 2004; Lewis et al. 2006). Lewis et al. (2006) show that under the assumption of isotropic dispersal in a two-dimensional landscape, the directional rate of spread $c_d$ from the initial entry point is

$$c_d = \min_{s \geq 0} \left[ \frac{1}{s} \ln \left[ \lambda M_d(s) \right] \right],$$

where $\lambda$ is the population growth rate; $M_d(s)$ is the “directional” moment-generating function (MGF), the MGF of a two-dimensional dispersal kernel marginalized in the direction of interest; and $s$ is an auxiliary variable. The function $M_d(s)$ can be evaluated in several ways, depending on the available dispersal data and kernel estimates (Lewis et al. 2006, eqq. [16]–[24]). For a dispersal kernel $k(r)$ giving the density of propagules per unit length arriving at distance $r$ from the source, $M_d(s)$ is given by (Lewis et al. 2006, eq. [20])

$$M_d(s) = \int_0^s k(r) I_0(sr) \, dr,$$

where $I_0$ is the modified Bessel function of the first kind and zeroth order (Abramowitz and Stegun 1970). This integral may be intractable for many dispersal kernels, but it can always be easily approximated by an empirical MGF using raw dispersal data or a large number of simulated dispersal distances based on $k(r)$ (Clark et al. 2001). For $N$ radial dispersal distances $r$, the directional empirical MGF $M^N_d(s)$ is (Lewis et al. 2006, eq. [21])

$$M^N_d(s) = \frac{1}{N} \sum_{i=1}^N I_0(s r_i).$$

For large $N$, $M^N_d(s)$ converges to $M_d(s)$. Thus, equation (3) is a convenient way to estimate the directional MGF, and hence the directional rate of spread (eq. [1]), for any dispersal kernel.

Weinberger’s original asymptotic result for spread in one dimension (Weinberger 1982) and the expression for directional spread (eq. [1]) both hold for any population
with a per capita growth rate $\lambda > 1$. Thus, while the spread rate is insensitive to the shape of the population growth curve at higher densities, it is very sensitive to the dispersal kernel. To assess spread rates, we therefore need to establish the shape of the dispersal kernel.

**Dispersal Studies**

In order to measure dispersal and estimate dispersal kernels, four dispersal studies were carried out in central Pennsylvania for the invasive thistles *Carduus nutans* and *Carduus acanthoides* (Asteraceae). These species are similar in appearance and life history but exhibit ecological and physical differences (Desrochers et al. 1988) that may affect dispersal and spread. Both species are found primarily in pastures and disturbed areas. They are short-lived perennials that reproduce only once (i.e., they are monocarpic) and colonize exclusively by seed. *Carduus nutans* has slightly larger seeds (3.0–4.0 mm long) and pappi (25–35 mm in diameter) than *C. acanthoides* (seeds 2.5–3.5 mm, pappi 20–30 mm). *Carduus acanthoides* also often grows taller than *C. acanthoides* and produces more seeds per individual. In central Pennsylvania, flowering of *C. nutans* is usually completed by late June, and the peak dispersal season is in July; for *C. acanthoides* the peak dispersal season is July–August.

**Study Design**

The objective of our dispersal studies was to give a complete characterization of the seasonal dispersal kernel (i.e., the full seasonal probability distribution of dispersal distances), with particular emphasis on estimating the tail of the distribution. There are several options for dispersal measurement, including indirect methods such as off-spring counts or molecular markers (Turchin 1998; Ouborg et al. 1999; Clobert et al. 2001; Bullock et al. 2002; Nathan et al. 2003). However, to be able to separate propagule dispersal from postdispersal processes (mortality, germination, etc., which are included in the growth function of eq. [1]), we need to measure dispersal directly, for example, by trapping or tracking propagules (Bullock et al. 2006). We chose to use traps to monitor dispersal over the main dispersal season (Skarpaas et al. 2005).

The two thistles do not co-occur in most of central Pennsylvania (Allen and Shea 2006). To avoid accidental introduction to new areas, the studies were carried out at different sites within the existing ranges of the two species (*C. nutans*: Garman farm, Elliotsburg, PA; *C. acanthoides*: Haller farm, Pennsylvania State University, State College, PA). Both sites were in pastures (the species’ primary habitat) in regular use, but cattle were excluded during the 4 weeks of the studies. The studies were carried out in large, relatively flat fields, with a gentle slope to the south on the Garman farm and to the north at the Haller farm. The Haller farm field was in the middle of a large open area with several adjacent fields; the Garman farm field was partly surrounded by scattered trees but at a sufficient distance that they were unlikely to interfere with wind patterns. The studies were carried out during the peak dispersal season (July for *C. nutans*, mid-July to mid-August for *C. acanthoides*). Replicate studies (same site, same duration during peak dispersal season, and same trapping design) were carried out in 2003 and 2004.

Point seed sources were created by transplanting 30–40 existing rosettes of the thistles into a circular patch with a small radius (0.8 m) to approximate a point source. All other conspecifics were removed. Rough estimates of seed production based on fecundity in field populations (K. Shea, unpublished data) suggested that the seed sources would produce on the order of 100,000–400,000 seeds. Creating as large a seed source as possible dramatically improves kernel estimates (Skarpaas et al. 2005). Seed release heights were quantified by measuring the heights of all flower heads on the source plants that ripened during the experiments in the first year. Detailed measurements were not obtained in the second year, but the ranges of source plant and flower head heights were similar. Vegetation heights were measured both years at 20 randomly selected points in the experimental fields.

The trapping design for each site was optimized within practical constraints defined by plant characteristics, estimated seed production, literature on previous measurements of dispersal by wind (Smith and Kok 1984; Kelly et al. 1988; McCallum 1989; Feldman and Lewis 1990), basic knowledge about wind patterns, size of available study areas, and economy (cost of traps and available field help). We have previously demonstrated that the optimal trap layout may depend on the dispersal pattern (Skarpaas et al. 2005). We showed that under perfectly isotropic dispersal, sampling along transects or sectors radiating from the source was optimal. When there was a directional bias, and this bias was unknown to the researcher, annuli of traps were better. However, when the bias was known and therefore could be corrected for in the model fitting, the best designs were transects and sectors laid out in the prevailing directions. On the basis of these results, we designed a hybrid strategy of annuli close to the seed source (out to 8 m) to detect isotropy and sectors in the prevailing wind directions to detect long-distance dispersal (out to 120 m). The directions of long-distance sectors were determined on the basis of information from a local farmer (W. Garman, personal communication), in the case of *C. nutans*, and a nearby weather station, in the case of *C. acanthoides* (H. Skinner, unpublished data). The same trap layouts were used in 2003 and 2004 (fig. 1), except for a...
Figure 1: Trap layout (dashed gray lines) and the number of trapped seeds (indicated by circle size and shading) in each trap at the end of each study. The inset plots show traps at 1–4 m from the source enlarged for clarity; these are omitted from the main plots. Each trap consisted of a strip of sticky trap (25 cm wide and \( \pi r/16 \) m long) at radial distances (\( r \)) 1, 2, 4, 8, 16, and 32 m from the source; two, three, and four strips were placed in parallel at 64, 96, and 120 m, respectively, in each long-distance sector. The total area of traps was 120 m\(^2\) (94 m\(^2\) for C. acanthoides in 2004).

Dispersal Patterns

The seed-trapping design gave excellent data for dispersal modeling and spread rate estimation. For both species, seeds were trapped in most traps within 4 m of the source, and a few seeds were caught in traps at larger distances, up to 96 m for C. nutans and 16 m for C. acanthoides (fig. 1). In both years, more seeds were trapped for C. nutans (3,168 and 1,893 seeds in 2003 and 2004, respectively) than for C. acanthoides (1,354 and 720 seeds, respectively).

Dispersal direction was unimodal in all four studies (Rayleigh test of uniformity, general unimodal alternative, \( P < .001 \)). The main direction of dispersal was easterly for C. nutans in both years; for C. acanthoides, it was northerly in 2003 and southeasterly in 2004. Although more seeds were dispersed in some directions than in others, mean dispersal distance in the trap sectors was not significantly correlated with sector angle (centered on main dispersal direction and cosine transformed) in any of the four studies (two-sided Pearson correlation tests, \( P > .19 \)).

Dispersal Modeling

The dispersal patterns observed in the trapping studies are samples of the total seed shadow \( S \) (Clark et al. 1999; Skarpaas et al. 2005),
where \( Q \) is the seed source strength (number of seeds dispersed), \( r \) is the distance (m) from the source, and \( \theta \) is the angle (radians). The distance kernel \( k(r) \) is the probability density function (PDF) for dispersal distances, and \( g(\theta) \) is the PDF for dispersal directions, assuming independence between distance and direction. This assumption was supported by our empirical results (see “Dispersal Patterns”). For prediction of spread rates (eq. [1]), we are interested in estimating \( k(r) \). We have previously shown that when dispersal is anisotropic, in the sense that \( g(\theta) \) is not uniform, the parameter estimation for the isotropic kernel \( k(r) \) may be improved substantially by considering the distribution of directions explicitly (Skarpaas et al. 2005). Because the distribution of dispersal directions was unimodal and significantly different from uniform in all four studies ("Dispersal Patterns"), we modeled \( g(\theta) \) using a wrapped normal, or von Mises, distribution (see appendix in the online edition of the American Naturalist; Evans et al. 2000; Jammalamadaka and SenGupta 2001).

### Dispersal Kernels

For the distribution of dispersal distances \( k(r) \), we used two models: (1) the Wald analytical long-distance dispersal (WALD) model (Katul et al. 2005), integrated over the dispersal season, and (2) the empirical distribution of the raw dispersal distance data (Clark et al. 2001) for the entire dispersal season. In contrast to empirical (or phenomenological) models of dispersal, WALD has the desirable property that its parameters are directly linked to characteristics of the species and the environment that can be obtained independently of dispersal distance data. This model is derived from well-established models in fluid mechanics and predicts an inverse Gaussian (Wald) distribution of dispersal distances \( r \) (Katul et al. 2005, their eq. [5b]):

\[
p(r) = \frac{1}{2\pi r} \exp \left[ -\frac{r^2}{2\mu'^2r} \right],
\]

where \( \mu' \) is the mean (the location parameter) and \( \chi' \) is the scale parameter. These parameters are related to species and environment characteristics as follows:

\[
\mu' = \frac{HU}{F}, \quad \chi' = \left( \frac{H^2}{\sigma} \right),
\]

where \( H \) is the seed release height, \( F \) is seed settling velocity, \( U \) is the hourly mean horizontal wind velocity between \( H \) and the ground, and \( \sigma \) is a turbulent flow parameter that reflects wind variation due to vegetation structure and weather conditions (Katul et al. 2005). To account for variability in terminal velocity and seasonal wind conditions, the WALD model was integrated over these variables to obtain the seasonal dispersal kernel

\[
k(r) = \int \int p(F)p(U)p(r) \, dF \, dU,
\]

where \( p(F) \) and \( p(U) \) are the PDFs of \( F \) and \( U \), respectively, and \( p(r) \) is the WALD model (eq. [5]). Distributions of \( F \) were obtained from lab measurements of seed settling velocity (see appendix), \( H \) and \( U \) were obtained from onsite measurements of flower head heights and wind velocities (see “Dispersal Studies”), and \( \sigma \) was estimated from the wind velocity measurements (Hsieh and Katul 1997; Katul et al. 2005; for further details on parameter estimation, see appendix). To evaluate the predictions of the integrated WALD model, we compared it to a range of commonly used empirical dispersal models fitted to the dispersal distance data (exponential, lognormal, and half-Cauchy; see table A1 in the online edition of the American Naturalist).

For both Carduus nutans and Carduus acanthoides, the distributions of dispersal distances were highly right skewed (fig. 2). Of the empirical models, lognormal performed best overall. WALD performed just as well as alternative empirical models (table A2 in the online edition of the American Naturalist). The estimated mean dispersal distances for this model (\( \mu' \)) were slightly larger than the observed means (corrected for sampling effort at different distances; table 1), implying that dispersal data at even greater distances might be necessary for reliable parameterization of the empirical models.

### Invasion Wave Speeds

We modeled spread rates for Carduus nutans and Carduus acanthoides using equation (1) and the dispersal kernels estimated from the dispersal data. Our purpose here was to provide preliminary estimates of spread rates independent of local population growth. We therefore used a constant population growth rate \( \lambda = 2.2 \), an empirical estimate for C. nutans in New Zealand (Shea and Kelly 1998; Shea et al. 2005). We estimated the directional spread rates \( c_s \) in two ways: (1) using the parameterized integrated WALD model for each species (eq. [8]; table 1) as the dispersal kernel \( k(r) \), and (2) using the empirical dispersal data directly, with the dispersal distance of each trapped seed set to the midpoint of the trap. We refer to these as the mechanistic approach and the nonparametric approach, respectively. In both cases, we calculated \( M^d(s) \)
using equation (3). For each mechanistic estimate of \( c_d \), we used 1,000 realizations of the integrated WALD model (eq. [8]), sampling from lognormal distributions of terminal velocities and empirical distributions of wind speeds (see appendix). We then repeated this procedure for 1,000 bootstrap replicates, to obtain a distribution of estimates for \( c_d \). We similarly bootstrapped the empirical data 1,000 times to obtain a distribution of nonparametric estimates for \( c_d \). The effect of long-distance sampling effort on spread rates was explored by comparing spread rate estimates based only on short-distance traps to estimates obtained by including traps at longer distances. Thus, for each subset of traps (1–2, 1–4, ..., 1–120 m), we estimated the moment-generating functions (eq. [3]) and calculated the wave speed by numerically minimizing equation (1), using the nonlinear minimization function “nlm” in R (R Development Core Team 2005).

The empirical (nonparametric) spread rate estimates were highly sensitive to the spatial scale of the sampling effort: the estimates increased as traps at greater distances

Table 1: Dispersal parameters for Carduus nutans and Carduus acanthoides

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<td>( F ) (m s(^{-1}))</td>
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<td>.39</td>
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<td>( H ) (m)</td>
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<tr>
<td>( U ) (m s(^{-1}))</td>
<td>.54</td>
<td>.64</td>
<td>.80</td>
<td>.82</td>
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<tr>
<td>( U_{\text{max}} ) (m s(^{-1}))</td>
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<td>( \sigma_{\text{g}} ) (m s(^{-1}))</td>
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<td>( \sigma ) (m s(^{-1}))</td>
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<td>( \lambda ) (m)</td>
<td>6.63</td>
<td>8.80</td>
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<td>( \mu' ) (m)</td>
<td>2.14</td>
<td>2.54</td>
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<td>( \mu ) (m)</td>
<td>2.13</td>
<td>1.79</td>
<td>1.60</td>
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Note: \( F \) = mean terminal seed settling velocity; \( H \) = mean seed release height; \( U \) = mean hourly horizontal wind speed between \( H \) and the ground; \( U_{\text{max}} \) = maximum hourly wind speed; \( \sigma_{\text{g}} \) = standard deviation of hourly wind speeds; \( \sigma \) = turbulent flow parameter; \( \lambda \) = scale parameter; \( \mu' \) = estimated mean dispersal distance; \( \mu \) = observed mean dispersal distance. For definitions and details on parameter estimation, see “Dispersal Modeling” and the appendix.
were included. For *C. acanthoides*, the estimates asymptoted at about 3 m year$^{-1}$ for traps out to 16 m (fig. 3), the farthest traps that caught seeds (fig. 1). For *C. nutans*, the estimates climbed to about 10 m year$^{-1}$ when the long-distance traps that caught seeds were included (96 m in 2003, 64 m in 2004; fig. 1). For both species, the estimates of wave speeds using the mechanistic approach were the same as or higher than the highest nonparametric estimates using the full data set (fig. 3). The mechanistic estimates were fairly similar among the studies but had wide confidence intervals, suggesting that variability in species traits and dispersal conditions may strongly affect invasion speeds. In addition to the short-term variability included in the parameters of the WALD model (eq. [5]), the seasonal and between-year variability of wind speeds is clearly important for wave speed estimates with the seasonally integrated model (eq. [8]). The highest estimates were obtained for *C. nutans* in 2004 and for *C. acanthoides* in 2003, the studies with the highest seasonal variability and highest maximum wind speeds (table 1). For realistic ranges of environmental variables and species traits for the thistles, the predicted spread rate, $c_d$, varies by more than an order of magnitude (fig. 4). The spread rate increases exponentially with lower settling velocities ($F$) and linearly with higher release heights ($H$). Horizontal wind speeds ($U$) and instability ($j$), which tend to co-vary, both have a strong positive and approximately linear effect on spread rates.

**Discussion**

A crucial step in the estimation of invasion wave speeds is the measurement and modeling of dispersal. Using a large sampling effort and an efficient trap layout for detecting anisotropy and long-distance dispersal, we were able to accurately measure wind dispersal and to estimate spread rates for two invasive thistles. We measured seed dispersal at larger distances than most previous studies of herbs and shrubs (see, e.g., Bullock and Clarke 2000; Jongejans and Telenius 2001). The observed dispersal kernels were generally highly leptokurtic, as for most wind-dispersed herbs (e.g., Willson 1993; Jongejans and Telenius 2001; Skarpaas et al. 2004; Soons et al. 2004). The mean dispersal distances of the two species were similar, approximately 2 m, despite differences in seed release height, seed settling velocity, and wind patterns. This corresponds well to previous measurements of dispersal for these species (Smith and Kok 1984; Kelly et al. 1988; McCallum 1989; Feldman and Lewis 1990). Our studies provide additional detailed information on the shape of the dispersal distribution of settled seeds near and far in primary habitats. For both species, the observed distributions of dispersal distances, corrected for directional bias, were highly right skewed and best fitted by leptokurtic dispersal kernels (appendix). The WALD model (Katul et al. 2005) represents a major step forward in modeling such distributions. Not only does it fit our data just as well as widely used empirical models, it also provides a mechanistic analytical link between species traits, environmental conditions, and dispersal distances, is logistically easier to parameterize (being estimated independently of dispersal data), and can be extrapolated to other environmental conditions.

The mechanistic model suggests that differences in dispersal distances are due to a combination of species traits (seed release height and terminal velocity) and environ-

**Figure 3**: Estimates of invasion speed with 95% bootstrap confidence intervals (error bars) for *Carduus nutans* (filled symbols) and *Carduus acanthoides* (open symbols) in 2003 (circles) and 2004 (triangles) using the nonparametric (raw dispersal data) and mechanistic (integrated Wald analytical long-distance dispersal) approaches. For the nonparametric approach, each point gives the wave speed estimated using all the data up to the given trap distance.
Figure 4: Predicted directional spread rates, $c_d$, using the mechanistic approach (median of 1,000 bootstrap replicates at each grid point). Spread rates are plotted for a range of (A) species traits (seed release height $H$ and settling velocity $F$) and (B) wind conditions (horizontal wind speed $U$ and turbulence parameter $\sigma$), corresponding to realistic values for the Carduus thistles. In A, we used the empirical distributions of wind speed measurements for all experiments; in B, we used values of $H$ and $F$ for Carduus nutans (table 1; appendix); and in both cases, $\lambda = 2.2$.

mental conditions (wind conditions, which are partly a function of vegetation structure). There is some unexplained variance in dispersal distances that may be due to several factors, including variability of vertical wind speeds, seed source geometry, seed release thresholds, phenology, and air humidity (Cousens and Rawlinson 2001; Greene and Calogeropoulos 2002; Katul et al. 2005; Schippers and Jongejans 2005; Skarpaas et al. 2006). However, despite this unexplained variance, the WALD model gives predictions of dispersal distances that are comparable to those of alternative empirical models. This is valuable for modeling seed dispersal and invasion wave speeds.

Our results clearly show that the nonparametric approach to wave speed estimation (Clark et al. 2001) is highly sensitive to sampling effort at the tail; failure to place traps at long enough distances from the source may lead to serious underprediction of spread rates. This suggests that the tails of the distributions may remain elusive in many dispersal studies and that the nonparametric approach should be used with caution. For example, empirical spread rate estimates of $<1$ m yr$^{-1}$ for Carduus acanthoides (Jongejans et al. 2007) are most likely too low because dispersal was measured only to 4 m in that experiment. However, even with exceptionally high sampling effort, as in this study, we may not be able to estimate realistic wave speeds based directly on dispersal data. For our trapping design, the detection threshold is about 100 seeds m$^{-1}$ (fig. 2). At the tail of the distribution, seed densities may be much lower but may still contribute significantly to the spread of the population.

Another weakness of estimates based directly on data, or empirical models fitted to such data, is that they will be valid only for the specific conditions under which dispersal was measured. Mechanistic models, such as WALD, are useful for estimating dispersal in other locations or under different environmental conditions because the parameters, which are based on the dispersal mechanism, can easily be measured for each location and set of environmental conditions.

In the United States, both thistles were first recorded in the northeast: Carduus nutans near Harrisburg, Pennsylvania, in about 1853 and C. acanthoides in New Jersey in 1879 (Desrochers et al. 1888). In the time since these first records, both have spread widely across the United States and Canada (Allen and Shea 2006); even using high-end estimates of population growth, the maximal spread rates estimated for wind dispersal in this study (fig. 3) clearly do not account for this rapid continental-scale spread. Carduus nutans reached New Zealand and thence Australia as a contaminant of agricultural seed (Popay and Medd 1995); similar human-mediated mechanisms are likely culprits in the United States also. However, such mechanisms account for only the gross pattern seen, with presence-absence noted on the scale of a state. Closer inspection shows that the current distribution of these species at the spatial scale of a county or even smaller is, in
fact, very heterogeneous (Allen and Shea 2006). Our data on spread via wind dispersal will be critical to estimates of rates of infilling within the broader invaded range. Applied benefits will also arise from coupling these dispersal kernels with increasingly detailed demographic models (Neubert and Caswell 2000). Management strategies that most strongly affect local population growth rates are not necessarily those that will best curb spatial spread (Shea 2004). Our estimates will thus allow the development of optimal management strategies designed specifically to slow the infilling process.

To conclude, the present study has provided valuable insights into the mechanisms of wind dispersal and spread of these invasive thistles. The mechanistic approach is highly useful for understanding and predicting dispersal on the basis of characteristics of the species and their environment, and it can be applied to other wind-dispersed species. Mechanistic models of dispersal, linked with models of local demography, will become powerful tools for addressing fundamental issues in invasion biology.

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