

# Seed terminal velocity, wind turbulence, and demography drive the spread of an invasive tree in an analytical model

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**Abstract.** Little is known about the relative importance of mechanistic drivers of plant spread, particularly when long-distance dispersal (LDD) events occur. Most methods to date approach LDD phenomenologically, and all mechanistic models, with one exception, have been implemented through simulation. Furthermore, the few recent mechanistically derived spread models have examined the relative role of different dispersal parameters using simulations, and a formal analytical approach has not yet been implemented. Here we incorporate an analytical mechanistic wind dispersal model (WALD) into a demographic matrix model within an analytical integrodifference equation spread model. We carry out analytical perturbation analysis on the combined model to determine the relative effects of dispersal and demographic traits and wind statistics on the spread of an invasive tree. Models are parameterized using data collected in situ and tested using independent data on historical spread. Predicted spread rates and direction match well the two historical phases of observed spread. Seed terminal velocity has the greatest potential influence on spread rate, and three wind properties (turbulence coefficient, mean horizontal wind speed, and standard deviation of vertical wind speed) are also important. Fecundity has marginal importance for spread rate, but juvenile survival and establishment are consistently important. This coupled empirical/theoretical framework enables prediction of plant spread rate and direction using fundamental dispersal and demographic parameters and identifies the traits and environmental conditions that facilitate spread. The development of an analytical perturbation analysis for a mechanistic spread model will enable multispecies comparative studies to be easily implemented in the future.

**Key words:** integrodifference equation; invasion biology; long-distance dispersal; matrix model; mechanistic model; Mount Barker, New Zealand; *Pinus nigra*; plant traits; population biology; seed terminal velocity; Wald analytical long-distance dispersal kernel (WALD).

## INTRODUCTION

Invasive plant species cause major environmental and economic damage worldwide through impacts on local populations and the extensive ranges of some invaders (Drake et al. 1989, Shea and Chesson 2002). A starting point for the prevention and mitigation of invasions is the identification of life-history traits or environmental variables that have a large effect on population growth rate (Ramula et al. 2008) and spread (Fox et al. 2009, Coutts et al. 2011). Modeling approaches have provided tools to analyze the effect of demographic parameters on population growth (May 1974, Caswell 2001, Clark 2007), and recent methods based on integrodifference equations allow for perturbation analysis of spread rate (Neubert and Caswell 2000, Buckley et al. 2005, Miller and Tenhumberg 2010). However, despite these advances, analysis of spread rate is difficult, because it is often

strongly affected by long-distance dispersal (LDD) (Kot et al. 1996, Clark et al. 1998, Trakhtenbrot et al. 2005).

Most seeds typically travel only short distances and LDD events are rare and difficult to predict (Nathan 2006). Early attempts to model population spread were based on models that did not take LDD into account and therefore underestimated spread rates. The recent explosion of interest in LDD has led to new methods for quantifying and understanding dispersal (Nathan et al. 2003, 2008, Bullock et al. 2006). New models of spread have incorporated LDD with demography (Jongejans et al. 2008, Schurr et al. 2008, Soons and Bullock 2008, Thompson and Katul 2008, Nathan et al. 2011). However, the importance of individual mechanistic dispersal parameters on population spread has been mostly assessed by simulation approaches (Jongejans et al. 2008, Thompson and Katul 2008, Coutts et al. 2011, Nathan et al. 2011). Indeed, a limitation in the use of integrodifference equation models for perturbation analysis of spread rate is the need to describe dispersal with a function for which a moment-generating function is known. Functions classically used as dispersal kernels

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that fulfill this requirement are Gaussian or negative exponential (Cousens et al. 2008). Unfortunately, these “thin-tailed” functions do not describe LDD well (Nathan et al. 2008), and more complex, “fat-tailed” dispersal functions are needed (Kot et al. 1996). In addition, for the sake of mathematical tractability, dispersal kernels used in population models are usually phenomenological, with synthetic parameters that do not reflect important features of the underlying dispersal mechanisms. Perturbation analysis is widely used in ecological models (de Kroon et al. 2000) for evaluating the drivers of population dynamics (Ehrlén et al. 2001) and enabling large multispecies comparative studies (Silvertown et al. 1993, Buckley et al. 2010). However, no analytical tools currently exist for determining the relative importance of complex demographic and mechanistic dispersal parameters for spread rate. Here we incorporate a mechanistic dispersal model into an analytical model of population spread and develop an analytical perturbation analysis to determine the key demographic and dispersal parameters that drive spread.

We used the simplified mechanistic Wald Analytical Long-Distance dispersal kernel (WALD; Katul et al. 2005) in combination with a demographic matrix model within Neubert and Caswell's (2000) integrodifference equation approach to model spread speed for an invasive wind-dispersed pine species. WALD has been shown to better predict dispersal distances than previous models (Katul et al. 2005, Skarpaas and Shea 2007, Schurr et al. 2008). It is a simplification of the coupled Eulerian-Lagrangian (CELC) mechanistic model of seed dispersal (Nathan et al. 2002), reducing CELC into an inverse-Gaussian (Wald) function with two parameters representing simple combinations of key physical and biological features of seed dispersal by wind. In this simplified form, WALD has a moment-generating function (Thompson and Katul 2008), allowing us to use Neubert and Caswell's (2000) analytical approach, whereas previous studies incorporating WALD into a spread model have analyzed the relative effects of dispersal parameters only through simulations (Jongejans et al. 2008, Nathan et al. 2011). While simulations enable a large area of parameter space to be explored, the analytical approach has the following advantages: (1) it is computationally efficient, (2) it provides tractable results, based on direct links between parameters and outcomes, (3) unlike simulation approaches it does not require statistical (e.g., regression) analysis of the model outputs (Wisdom et al. 2000), and (4) it allows for a high level of standardization (Caswell 2001) enabling multispecies comparisons.

We parameterized the model with high-frequency wind statistics and demographic data collected for the invasive tree *Pinus nigra* subsp. *laricio* (Corsican pine) in 2008 and 2009 at two locations at a New Zealand site where Corsican pine was planted around 1910 and has since spread to the southeast over several kilometers (Buckley et al. 2005). One location is at the origin of the

unidirectional invasion, with the second location ~2 km from the origin on the other side of a dominant landscape feature (Mount Barker). We used parameterized models from both locations to compare with historical spread rates obtained through analysis of aerial photographs at two time points (Buckley et al. 2005). This is the first time, to our knowledge, that the WALD model has been tested using historical spread data. We decomposed the two WALD parameters into their mechanistic component parameters to carry out a full perturbation analysis of spread rate to demographic and dispersal traits as well as wind properties. Here we show how this allowed us to accurately reconstruct the spatially explicit spread patterns and to test (1) the effect of location and wind direction on the spread of Corsican pine and (2) the relative importance of demographic and dispersal parameters for spread rate. We discuss our results in the context of management of this invasive tree species.

## MATERIAL AND METHODS

### *Study species and site*

Corsican pine (*Pinus nigra* Arn. subsp. *laricio*) is one of six recognized subspecies of black pine (*P. nigra*; Quézel and Médail 2003). Corsican pine occurs throughout the mountain zone of Mediterranean Europe and is reported as invasive in Australia and New Zealand (Richardson and Rejmanek 2004). Corsican pine (hereafter “pine”) is well adapted to a wide range of soil and climatic conditions, with the exception of calcareous substrate, and is a typical wind-dispersed species, producing large numbers of winged seeds (Kerr et al. 2008). These features make it an ideal biological model to study wind-driven invasions.

We studied a pine invasion front at 620 m elevation on a flat terrace beneath Mount Barker in the Rakaia Catchment, Canterbury, New Zealand (171°35'15" E, 43°21'30" S). Soils are derived from a thick layer of loess over graywacke moraine till (Dehlin et al. 2008). Annual precipitation at Lake Coleridge (1.5 km distant) is 907 mm, and mean temperature at the site is 8.3°C (D. A. Peltzer, unpublished data). Pines were planted in a shelter-belt north of Mount Barker around 1910 and have since spread to the southeast. Aerial photographs from the area (Buckley et al. 2005) revealed two phases in the invasion: a first relatively slow progression between 1910 and 1965 and a rapid spread following 1965. As pines establish in grasslands, understory is limited to short grass, and we therefore consider only the pine canopy for our wind calculations.

### *Spread model development*

We built a stage-structured matrix model of pine population dynamics and dispersal using Neubert and Caswell's (2000) integrodifference equation approach (see also Buckley et al. 2005). The code was developed in R (R Development Core Team 2008). Model structure is a simplified version of the matrix presented in Buckley et

TABLE 1. Parameter values for the life history matrix **A** and for the dispersal matrix **K**.

Symbol	Unit	Point estimate	Range	Description
Demographic parameters				
$s_a$	yr <sup>-1</sup>	0.983	0.971–0.988	adult survival‡
$f_1$	yr <sup>-1</sup>	806	31–7719	subadult fecundity†
$f_2$	yr <sup>-1</sup>	10 671	837–28473	adult fecundity†
$a_m$	yr	15	11–17	age of first reproduction†
$r_j$	yr <sup>-1</sup>	0.78	0.68–0.88	retention in juvenile class†
$e_s$	yr <sup>-1</sup>	0.188	SD = 0.043	establishment rate‡
$s_j$	yr <sup>-1</sup>	0.96	0.89–0.99	juvenile survival†
Dispersal parameters				
$h_c$	m	11.2	11–11.5	canopy height†
$h_{r1}$	m	4.8	3.8–8.5	seed release height, subadults†
$h_{r2}$	m	8.2	4.8–11.5	seed release height, adults†
$\kappa$	–	0.4	0.3–1	turbulence coefficient§
$v_t$	m/s	0.85	SD = 0.07	seed terminal velocity†
$\bar{U}$	m/s	1.87	0.61–7.74	mean horizontal wind speed†
$\sigma_w$	m/s	0.60	0.17–2.09	SD of the vertical wind speed†

† Parameter values based on field data from 2008–2009.

‡ Parameter values from Buckley et al. (2005).

§ Parameter values from Thompson and Katul (2008) and Poggi et al. (2008).

al. (2005). The stage-structured population projection matrix **A** is

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & f_1 e_s & f_2 e_s \\ s_j & s_j r_j & 0 & 0 \\ 0 & s_j(1 - r_j) & 0 & 0 \\ 0 & 0 & s_a & s_a \end{bmatrix}. \quad (1)$$

The matrix **A** describes life stage transitions with a yearly time step (see also the life-history diagram shown in Appendix A), from seedlings to juveniles, subadults (reproducing for the first time), and fully reproducing adults.

The parameters are described in Table 1. Parameters are assumed to be typical of low-density populations and both classes of adults are assumed to have the similar dispersal kernels, varying only in the height of release. The dispersal kernels are contained in a matrix **K** of the same dimensions as **A** (Neubert and Caswell 2000).

We modeled dispersal using WALD (Katul et al. 2005, Thompson and Katul 2008), an analytical model with mechanistic properties. WALD reduces complex mechanisms of uplift and transport of seeds into the following one-dimensional kernel to describe the probability of a seed landing at a distance  $x$  from the source:

$$P_{\text{wald}}(x) = \sqrt{\frac{\gamma}{2\pi x^3}} \exp\left[-\frac{\gamma(x - \mu)^2}{2x\mu^2}\right] \quad (2)$$

where  $\mu$  and  $\gamma$  are the scale and shape parameters of the kernel, respectively, defined as

$$\mu = \frac{\bar{U} h_{ri}}{v_t} \quad (3)$$

and

$$\gamma = \frac{\bar{U} h_{ri}^2}{2\kappa h_c \sigma_w} \quad (4)$$

where  $\bar{U}$  is the mean horizontal wind speed,  $\sigma_w$  is the standard deviation of the vertical wind speed,  $h_{ri}$  is the height of seed release (subscript  $i$  referring to two adult classes),  $h_c$  is the canopy height,  $v_t$  is the seed terminal velocity, and  $\kappa$  is a turbulence coefficient. We used wind data collected at the site to quantify  $\bar{U}$ ,  $\sigma_w$ , and  $\kappa$  within a canopy (see *Parameter estimation*).

#### Parameter estimation

Parameter estimates for the model were obtained from data collected in 2008 and 2009 at the Mount Barker study site and from the literature (see Table 1). Wind data were collected in two different sites: at the base of the northern slope of Mount Barker close to the origin of the invasion (hereafter “north tower”; 171°35′40″ E, 43°20′57″ S), and on a flat area south of Mount Barker (“south tower”; 171°37′03″ E, 43°21′24″ S). Demography was assumed not to vary between these sites and was sampled 1 km from the south tower (Fig. 1).

*Demographic and dispersal parameters.*—In July 2008 and July and August 2009 we identified and tagged all Corsican pines present in six plots (30 × 30 m) with density ranging from 122 to 400 trees/ha. Age was determined by counting the internodes, as Corsican pine produces a new node every year. Survival between 2008 and 2009 gave an estimate of survival for juveniles. We estimated age of first maturity from trees that did not bear cones in 2008 but did in 2009. In 2009 we counted the number of cones carried by all adult trees present, splitting the trees into subadults (first time bearing cones) and adults. Corsican pine cones can be clearly seen on the tree and at the time of the study the previous year’s cones had fallen, allowing us to count only cones produced in 2009. Cones were double counted by the same two observers throughout the study and their counts were averaged. To estimate the number of viable seeds per cone we sampled 20 cones on an additional 10 trees outside the plots at regular intervals during the

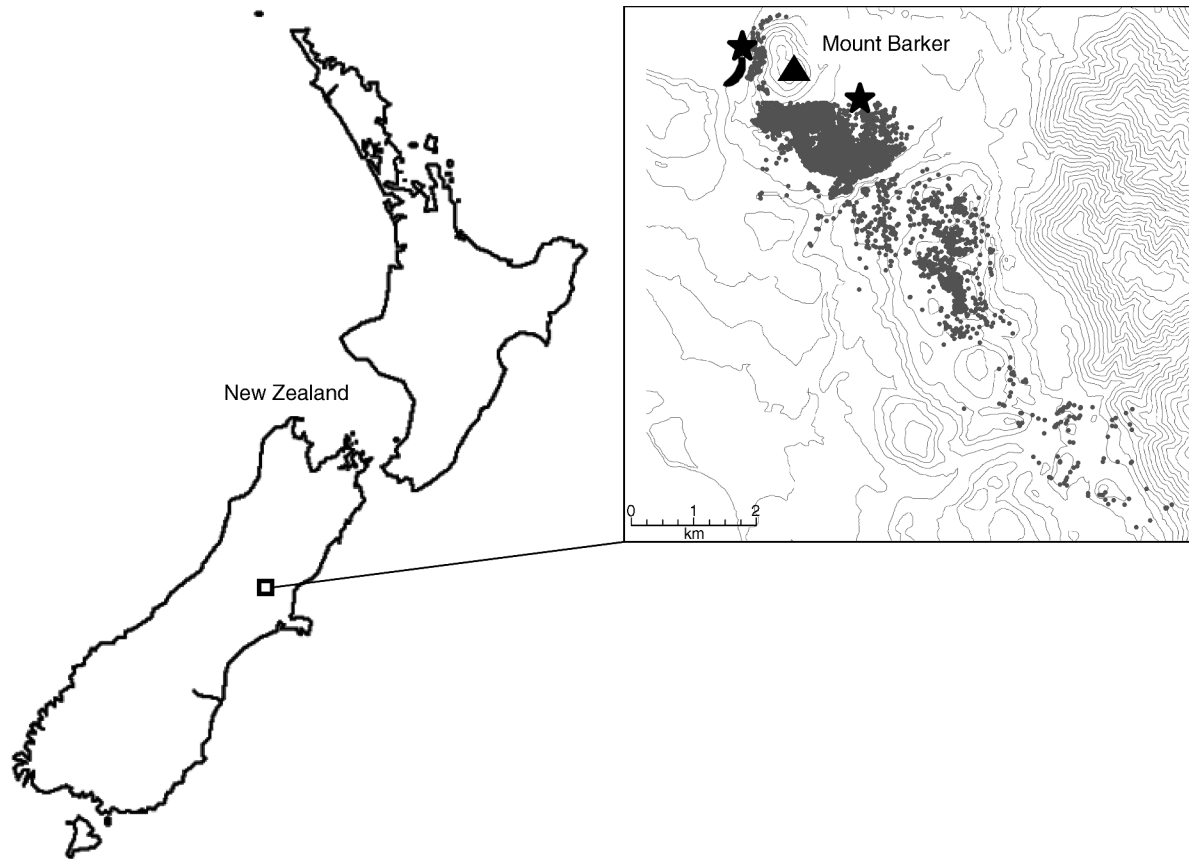


FIG. 1. Map of New Zealand with the Mount Barker study site (triangle). The black region beneath the top left star represents the 1910 shelterbelt from which pine spread started. Pine spread as observed on a 1980 aerial photo is shown with gray dots. Wind data were collected at the north and south towers, which are indicated by stars.

dispersal season. The proportion of filled (viable) seed was determined by crushing the seeds. Seed terminal velocity was measured in a closed chamber (Wright et al. 2008) from 104 seeds collected on 10 trees in July 2008. Retention in the juvenile class ( $r_j$ ) was calculated such that after  $(a_m - 1)$  time steps of surviving trees remained nonreproductive at  $a_m$ , the age of first reproduction: with  $r_j = 0.02^{1/(a_m - 1)}/s_j$  where  $s_j$  is the juvenile survival rate. This ensures that  $r_j$  was calculated conditional on survival and the values of  $a_m$  and  $s_j$  used ensured that  $r_j$  was always between 0 and 1 (Table 1). Height of seed release ( $h_r$ ) was sampled from a truncated normal distribution with mean and variance calculated from tree height and cone distribution data for adults and subadults (Nathan et al. 2001). A point estimate of canopy height  $h_c$  was calculated as the 85th percentile of tree heights with a range of values between the 80th and 90th percentiles used (Duncanson et al. 2010). Other vital rates (establishment rate and adult survival) were based on Buckley et al. (2005).

*Wind data.*—We used CSAT3 sonic anemometers (Campbell Scientific, Logan, Utah, USA) placed at three different heights (3.7, 8.3, and 13.1 m) and Campbell

Scientific loggers to collect wind data (20-minute average, variance, and covariance of wind vectors) throughout the dispersal season (24 June 2009–24 September 2009). For 10 random points in a 30-m radius around each tower we assessed the leaf area distribution (LAD) required for wind computations by measuring leaf area index (LAI) at ground level and every 2 m to canopy height with an AccuPar (Decagon Devices, Pullman, Washington, USA) light meter with a 10-m probe. LAD for every vertical section is the difference in LAI between the top and the bottom of that section.

For the data collected from both towers we followed the same procedure. We used data from the anemometer closest to canopy height (8.3 m) to obtain orthogonal wind vectors. We calculated normalized standard deviation of wind vectors for points with  $u^*$  (friction velocity) between 0.15 and 3 (Nathan and Katul 2005). In order to estimate the values of  $\bar{U}$  and  $\sigma_w$ , we ran the Massman-Weil (MW) simplified analytical model (Massman and Weil 1999, Katul et al. 2005) to produce the within-canopy vertical profile of mean horizontal wind velocity and variance of the vertical velocity over

time. Averaging these profiles from ground to canopy height along the LAD profile results in the parameters  $\bar{U}$  and  $\sigma_w$  required for WALD (Katul et al. 2005).

To estimate the nondimensional turbulence coefficient  $\kappa$  we used values from the literature to fit a moderately dense canopy (the detailed estimation can be found in Appendix B).

#### Perturbation analysis

Following Neubert and Caswell's (2000) approach, we used the moment-generating function (mgf) of the dispersal kernel that exists for some small interval around  $s = 0$  and is given for  $P_{\text{wald}}(x)$  by

$$\text{mgf}_i(s) = \exp \left[ \frac{\gamma}{\mu} \left( 1 - \sqrt{1 - \frac{2\mu^2 s}{\gamma}} \right) \right] \quad (5)$$

where the subscript  $i = 1$  or  $2$  and indicates that the function varies between the two adult classes.

The minimum value of the wave speed defines the asymptotic spread rate and is calculated as  $c^* = \min_{0 < s < \delta} [1/s \ln \rho_1(s)]$ , where  $\rho_1$  is the dominant eigenvalue of the matrix  $\mathbf{H}(s)$ , which includes both the stage-structured demography and dispersal parameters.  $\mathbf{H}(s) = \mathbf{A} \circ \mathbf{M}(s)$ , where  $\mathbf{M}(s)$  is a matrix of the same dimension as  $\mathbf{A}$  with the moment-generating function of the kernel in the dispersing elements and  $\circ$  is the element-by-element or Hadamard product (for details see Neubert and Caswell [2000] and Appendix C). Sensitivity of wave speed to model parameters measures how a small additive change in the parameter affects wave speed, whereas elasticity measures how a proportional change in the parameter affects wave speed. We therefore used the following formula to decompose sensitivity of  $c^*$ , wave speed, to particular stage transitions ( $a_{k,l}$ ) into sensitivity of  $c^*$  to the underlying demographic parameters ( $x$ ), using methods in Caswell (2001):

$$\frac{\partial c^*}{\partial x} = \sum_{k,l} \frac{\partial c^*}{\partial a_{k,l}} \frac{\partial a_{k,l}}{\partial x} \quad (6)$$

where  $k, l$  give the subscripts of each transition  $a$ . Similarly elasticities of  $c^*$  to the underlying demographic parameters are given by

$$\left( \frac{x}{c^*} \right) \frac{\partial c^*}{\partial x} = \left( \frac{x}{c^*} \right) \sum_{k,l} \left( \frac{\partial c^*}{\partial a_{k,l}} \right) \frac{\partial a_{k,l}}{\partial x}. \quad (7)$$

We calculated sensitivities and elasticities of  $c^*$  to demographic transitions according to Neubert and Caswell (2000) (see also Buckley et al. [2005] and Appendix C). To calculate sensitivities and elasticities of  $c^*$  to underlying dispersal parameters, we substituted in the moment-generating function (Eq. 5) the mechanistic equivalents of the parameters  $\mu$  and  $\gamma$  (Eqs. 3 and 4) and calculated the derivatives (Eq. 6) using the full set of parameters described in Table 1. We thus obtained a set of six partial derivatives that

describe the effect of underlying mechanistic dispersal parameters on spread rate (see Appendix C for the detail of calculations).

This method allows us to present which parameters, if altered, lead to the greatest additive (sensitivities) or proportional (elasticities) changes in spread speed,  $c^*$ . We ran this perturbation analysis using the whole estimated range of parameter values (Table 1) resampled 10 000 times to produce robust estimation of  $c^*$  and sensitivity/elasticity values and to obtain maximum and minimum values for  $c^*$  (Wisdom et al. 2000).

Sensitivity analysis shows the effect of a small perturbation of a parameter on spread rate. We checked the validity of the sensitivity decomposition and investigated the effects of larger perturbations by running the model with fixed point values for all parameters but one and plotted the resulting spread rate  $c^*$  against a wider range of the values of that parameter.

As the pine invasion is largely unidirectional, spreading in a southeasterly direction, we tested for the contribution of different wind directions to pine spread and ran the model for four wind directions (northeast, southeast, southwest, northwest).

## RESULTS

### Parameter estimation

Table 1 summarizes the results of parameter estimation. We found and sampled 272 juveniles (individuals shorter than 2 m) and 43 trees taller than 2 m. In 2009, 93 trees were carrying cones, including 15 that were carrying cones for the first time, allowing us to define a different fecundity value  $f$  for adults and subadults (Table 1). Age of first reproduction  $a_m$  varied between 11 and 17 yr, with a median of 15 yr.

Horizontal wind speed varied strongly between sites, being on average twice as high (2.2 m/s) at the south tower as at the north tower (1.1 m/s); however, the standard deviation of vertical wind speed was similar (median values of 0.6 and 0.5 m/s, respectively) between towers. A graphical validation of the wind profiles can be found in Appendix B: Fig. B1.

### Effect of location and wind direction on the spread of Corsican pine

Both maximum and mean spread rate  $c^*$  (Fig. 2) varied strongly across sets of parameters, being much higher for winds blowing from the northwest and at the south tower. Corsican pines have expanded at the Mount Barker site at an average rate of 80 m/yr since the introduction of the species in 1910 (as directly observed from aerial photos of the area from 1965 and 1980) (Buckley et al. 2005). This value is close to the mean spread rate predicted by our model, completely independently of the observed spread data, for northwesterly winds (mean value of 69 m/yr across both towers). There is also a striking correspondence between

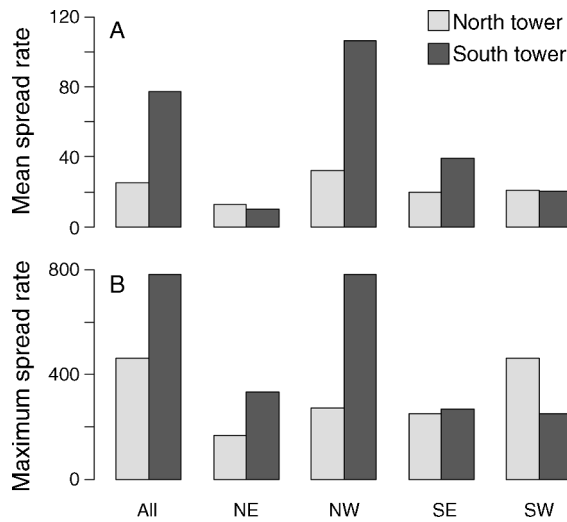


FIG. 2. (A) Mean and (B) maximum spread rate produced by the model using data from the south and north towers and along wind directions (All, all wind directions).

the predicted fastest spread direction, resulting from the northwesterly winds, and the observed southeasterly pattern of spread. Observation of aerial photos also revealed a slower spread before 1965, then mostly located on the north side of Mount Barker, than later when the invasion reached the southern side of the site. The observed values of spread (23 m/yr before 1965 and 173 m/yr between 1965 and 1980) are relatively well matched by our model predictions for northwesterly winds at the north and south towers (32 m/yr and 106 m/yr, respectively; Fig. 2).

*Relative importance of demographic and dispersal variables for spread rate*

The quantitative effects of the different parameters on spread rate as measured at the south tower are shown in Fig. 3 (note that for the sake of simplicity, we aggregated parameters  $f_1$  and  $f_2$ , which had similar effects on  $c^*$ , into a single parameter  $f$ , and similarly  $h_{r1}$  and  $h_{r2}$  into  $h_r$ ). We show the median value of sensitivity and elasticity along with the confidence interval for the median based on the full replication set. Results show strong sensitivity of asymptotic spread rate  $c^*$  to seed terminal velocity  $v_t$  and to all three wind parameters, especially the standard deviation of vertical wind speed  $\sigma_w$  and the turbulence coefficient  $\kappa$ . Two demographic parameters also exhibited a strong additive effect on  $c^*$ , the establishment probability  $e_s$  and the yearly juvenile survival  $s_j$ . Maturity delay  $r_j$  had a consistent negative effect on  $c^*$ , across treatments and in both sensitivity and elasticity analyses. Elasticities (Fig. 3B) also show the importance of dispersal parameters, particularly the effect of mean horizontal wind speed  $\bar{U}$ , and a strong effect of canopy height  $h_c$  that was not detected in sensitivity analysis. It is worth noting that fecundity parameters had a minimal effect on  $c^*$ .

The ranking of the importance of different parameters showed remarkable consistency across different subsets of wind data. Apart from some variation in the relative effect of  $\kappa$  and  $\sigma_w$ , the perturbation analysis using the wind data measured at the north tower (Fig. 3C) and for different wind directions (Appendix D) did not show any notable difference from the analysis run on the whole data set obtained at the south tower.

The analytical method was validated by the point estimate simulations. The slopes of  $c^*$  response to

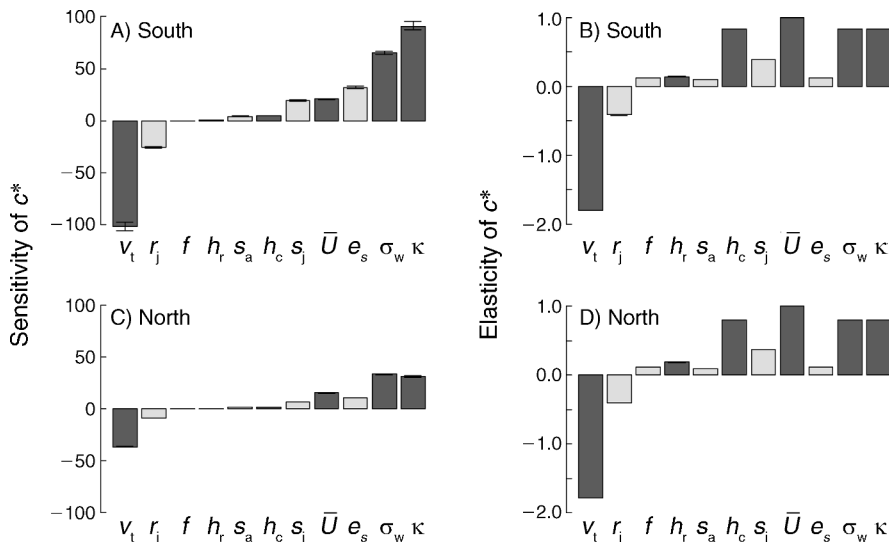


FIG. 3. Sensitivity and elasticity of  $c^*$  to dispersal (black bars) and demographic (light gray bars) parameters, using wind data from the (A, B) south tower and (C, D) north tower. Column height is the median of values from all replicates, with error bars where visible indicating 95% empirical confidence intervals for the medians. See Table 1 for explanations of parameter abbreviations.

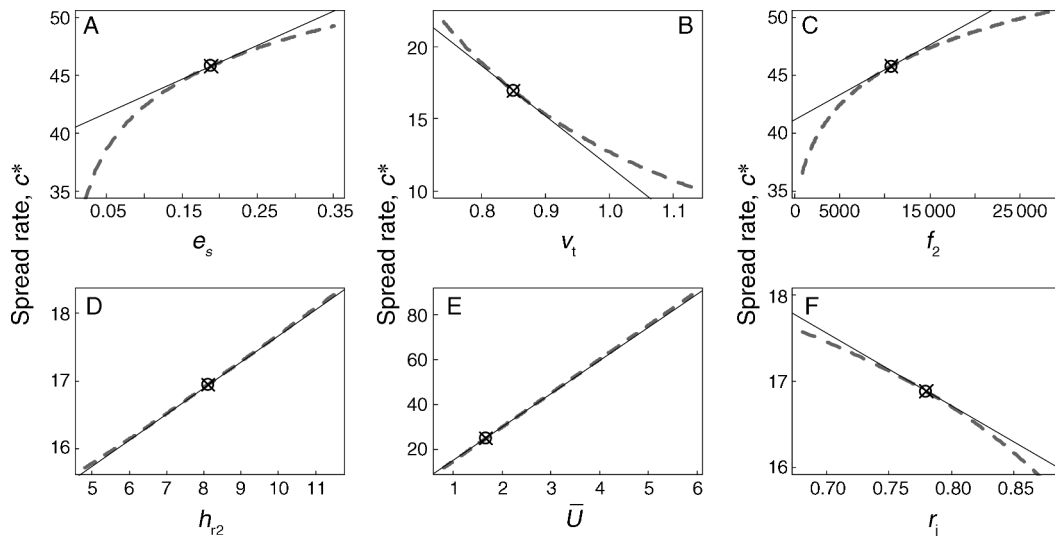


FIG. 4. Graphical check of the analytical sensitivity analysis showing the numerical response of spread rate (dashed lines) to changes in six model parameters over a wide range, all other parameters being set to their point estimate value for each experiment. The analytical point estimate sensitivity of spread rate to each parameter is shown on the graph as a tangent (solid line) at the corresponding spread value (crossed circle). Parameters are (A) establishment, (B) seed terminal velocity, (C) adult fecundity, (D) adult seed release height, (E) mean horizontal wind speed, and (F) retention in the juvenile stage.

individual parameters (Fig. 4) equaled the value of the sensitivity calculated in the perturbation analysis, confirming the adequacy of the decomposition of the sensitivities of the dispersal parameters.

#### DISCUSSION

By incorporating a mechanistic dispersal model (WALD) with an integrodifference equation spread model we analyzed the relative effect of dispersal and demographic parameters on the spread rate of an invasive population. WALD has been increasingly used in dispersal modeling studies (Katul et al. 2005, Skarpaas and Shea 2007, Schurr et al. 2008, Nathan et al. 2011), but this is the first time that an analytical sensitivity and elasticity analysis has been developed and that WALD predictions were tested against historical spread data. This approach, combined with an extensive empirical data set, gave clear and, for the most part, accurate predictions of spread rate and highly interpretable results. Our approach is specific to wind-dispersed species due to its mechanistic component, although it is conceivable that a similar approach could be applied to other systems in which mechanistic functions have been developed. As such it constitutes a standardized way of quantifying the importance of different drivers of spread. While several studies have shown that dispersal and LDD in particular determine spread rate (Clark et al. 1998, Buckley et al. 2005, Jongejans et al. 2008), we have shown here the relative influence of different components of the dispersal process to spread rate. In particular we found that seed terminal velocity has the largest influence on spread rate for this wind-dispersed species. This result held for two contrasting locations with different wind profiles.

#### *Effect of location and wind direction on the spread of Corsican pine*

We found that both the speed and direction of spread are extremely well predicted from northwesterly winds (observed 80 m/yr, predicted 69 m/yr). This is a considerable improvement on Buckley et al.'s (2005) spread estimates (1500 m/yr) for the same study system using a phenomenological dispersal kernel parameterized from observed spread rates (whereas WALD is parameterized independently of observed spread rates). We used a slightly different demographic matrix from that used by Buckley et al. (2005), with a higher population growth rate that would have tended to increase spread rate; therefore, it was the improvement in the dispersal component that led to the more accurate spread estimate.

The variability in our spread estimates (ranging from 3 to 702 m/yr) is mostly due to spatial and temporal variability in wind statistics and corresponds with the spatiotemporal variability in the pine invasion at our study site. The invasion started in the northern part of Mount Barker, where winds are weaker ( $1.27 \pm 0.56$  m/s [mean  $\pm$  SD] at the north tower vs.  $2.48 \pm 1.49$  m/s at the south tower), and accordingly spread rates were predicted to be much lower (mean of 32 m/yr for northwesterly winds) than at the southern part (south tower mean spread rate of 106 m/yr for northwesterly winds). Observed southeast spread rates were 23 m/yr until 1965, when most of the population was confined to the northern part of the site. From 1965 to 1980 observed spread rates increased markedly to 173 m/yr when the invasive population expanded into the southern part of the site. Our predicted spread rates

from the south tower, while much higher than from the north tower, may therefore be an underestimate of spread likely due to interannual variation in wind statistics.

We used data from just one dispersal season, and, given the high levels of variability in wind statistics observed within that season, we would expect spread rates to vary strongly between years. WALD assumes a planar-homogenous flow in a flat landscape and some modeled wind statistics did not fit data from the northern site. This could be due to forest edge effects, as mentioned previously, or topography (e.g., Poggi et al. 2008, Patton and Katul 2009). However, comparison of observed and predicted spread rates indicate that WALD still performs very well for the northern site, suggesting it is robust to deviations from these simplifying assumptions.

By using samples of wind data from two sites, over time, and across different directions, we showed how variable spread can be in a single and not particularly large landscape. We recommend that further studies account for within-dispersal-season variability and also investigate interannual variation.

#### *Demographic and dispersal variables as drivers of spread*

The ranking of sensitivities and elasticities was strongly consistent across locations and wind directions. The parameter with the largest effect (additive and proportional, as shown by sensitivity and elasticity analyses) was seed terminal velocity  $v_t$ . Seed terminal velocity tends to vary greatly among plant species (Tackenberg et al. 2003), and it has recently been shown that interspecific variation in  $v_t$  among North American wind-dispersed trees is an important determinant of variation in spread rate (Nathan et al. 2011). Yet  $v_t$  is relatively consistent within a species (see Greene and Johnson 1992) and can thus be a useful indicator of potential invasiveness (Higgins et al. 1996). Indeed, species with small seed mass (directly related to low  $v_t$ ) tend to be more successful invaders (Richardson and Rejmanek 2004, Richardson and Pysek 2006). Previous studies (Greene and Johnson 1996, Nathan et al. 2001, Nathan and Katul 2005) showed that intraspecific variation in  $v_t$  is less important in determining dispersal distance than the natural variation in wind speed, in contrast to the trend revealed in our analysis. This is likely explained by the much stronger winds ( $5.43 \pm 6.12$  m/s) measured by Nathan et al. (2001) compared to those measured in this study ( $1.87 \pm 1.28$  m/s). However, in agreement with Nathan et al. (2001) we found wind statistics to be important determinants of spread. Standard deviation of vertical winds,  $\sigma_w$ , and horizontal wind speed  $\bar{U}$  ranked consistently high in the perturbation analysis, confirming the importance of both vertical (uplift caused by turbulence) and horizontal movement in LDD (Nathan et al. 2002, Nathan and Katul 2005, Wright et al. 2008).

Spread rate was strongly increased by the turbulence coefficient  $\kappa$ , as higher  $\kappa$  values imply larger eddies that can lift up seeds and enhance LDD (Nathan and Katul 2005). For simplicity,  $\kappa$  has previously been considered a constant equal to the Von Kármán constant ( $\kappa = 0.4$ ; e.g., Skarpaas and Shea 2007, Jongejans et al. 2008, Nathan et al. 2011). Yet,  $\kappa$  actually varies as a function of canopy density. Our finding that spread rate is very sensitive to variation of  $\kappa$  implies that future applications of WALD should determine whether the default  $\kappa = 0.4$ , which corresponds to a forested landscape of intermediate canopy density, is appropriate to the studied system.

While we find a strong effect of maturity delay  $r_j$ , juvenile survival  $s_j$ , and establishment probability  $e_s$  on spread rate (following other studies, e.g., Higgins et al. 1996, Buckley et al. 2005, Nathan et al. 2011), fecundity parameters ( $f_1$  and  $f_2$ ) have the weakest effects. The relatively high establishment rate (0.188) and survival rate (0.96) in our model likely explain the weak effect of fecundity compared, for instance, to Nathan et al. (2011). Indeed, we find that at low fecundity the elasticity of spread speed to fecundity increases (Fig. 4). This confirms the importance of establishment in the net propagule pressure: only surviving propagules matter for population growth. Our results suggest that Corsican pine is generally not seed limited, reinforcing the importance of other factors influencing its spread dynamics.

#### *Management implications*

Perturbation analysis assesses which parameters contribute the most to spread rate and as such is useful for identifying effective management targets for controlling invasions (Neubert and Parker 2004, Buckley et al. 2005; also see Ramula et al. 2008 for demographic guidelines). We were able to analytically identify the mechanisms that drive the rate of spread for Corsican pine, differentiating between dispersal (seed terminal velocity, mean wind velocity, and turbulence) and demographic processes (probability of establishment and retention and survival in the juvenile stage). The precise ranking of the parameters' effects is site- and species-specific (Wisdom et al. 2000), but most of our results are in agreement with other studies, and large simulated perturbations demonstrate that the sensitivity rankings are relatively robust (Fig. 4). It seems clear from our results and those of Nathan et al. (2011) that seed terminal velocity is a key determinant of the wind dispersal process and that more data on that particular trait are needed. Comparison of terminal velocities between species may contribute to risk profiling of potential invaders.

Control actions can be designed to directly target the demographic parameters, e.g., juvenile survival can be reduced using livestock grazing (Buckley et al. 2005). While seed attributes are unlikely to be affected by management, anthropogenic changes in landscape struc-



ture can drastically affect wind statistics (Trakhtenbrot 2011). A mechanistic understanding of how seed attributes and wind statistics determine spread could help with prioritizing sites within a region for control (Buckley et al. 2005). Selection of high-priority eradication or containment sites could be facilitated by mapping wind dynamics (wind direction, speed, turbulences). Although detailed wind profiles such as those used here are not straightforward to obtain, good estimators of wind statistics can be generated from mesoscale models (see for instance Bohrer et al. 2008), enabling the applicability of our approach on a broader scale. One remaining challenge is the inclusion of spatial heterogeneity in such models (Trakhtenbrot 2011), which requires important inputs from physics and mathematics, a worthwhile effort when one considers the implications of dispersal processes for plant species distributions in a changing world (Nathan 2006).

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## SUPPLEMENTAL MATERIAL

### Appendix A

Life-history diagram and transition parameters for Corsican pine (*Ecological Archives* E093-035-A1).

### Appendix B

Calculation and analysis of wind profiles (*Ecological Archives* E093-035-A2).

### Appendix C

Calculations for the perturbation analysis (*Ecological Archives* E093-035-A3).

### Appendix D

Sensitivity and elasticity of spread rate for four wind directions (*Ecological Archives* E093-035-A4).