

Accounting for Variation in Wind Speed Increases Estimated Rate of Spread of an Invasive Thistle

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Abstract

Dispersal is an important factor in how organisms spread across space through time, and variation in the factors that influence dispersal affects the rate at which spread occurs. Here, we use a spatially explicit metapopulation model to examine how the spread rate of the wind-dispersed invasive thistle *Carduus nutans* is affected by variation in wind speeds. Results indicate that when variation in wind speed exists, these thistles are able to invade unoccupied areas faster than when there is no variation in wind speed. Increased variation in wind speed makes extreme wind events more frequent and increases the likelihood of long-distance dispersal, thus making distant habitats accessible when they may not be under less variable wind conditions. This has implications for controlling the spread of invasive species, as better understanding variation within dispersal and the frequency of long-distance dispersal events allows us to better predict how quickly invasives spread.

Introduction

In most terrestrial plant species, the seed or propagule stage is the only part of the life cycle where movement occurs, and dispersal of these propagules is thus crucial to the spatial spread of plant populations. When examining the spatial spread of these populations in the context of invasive plants, being able to understand and quantify dispersal not only allows for natural resource managers to better predict the spread of these invasives, but may also inform management decisions aimed to reduce their abundance on the landscape and/or their ability to spread. Unfortunately, dispersal can be extremely difficult to quantify; not only may an invasive plant have multiple dispersal pathways that occur serially or in parallel, but there is also often significant variation in dispersal distance within each of the different pathways. Lack of knowledge on the number of dispersal pathways, their relation to each other, or variation within each pathway can lead to underestimation of dispersal that adversely affects management decisions.

Variation within dispersal pathways is almost always present, but the extent of that variation can play a role in determining how quickly an invasive plant spreads. An opportunity to better understand how such variation affects the spread of an invasive plant can be found in the thistle *Carduus nutans*. This short-lived perennial thistle of Eurasian origin was first introduced to the United States in 1853 near Harrisburg, PA, and has now been reported in 45 US states and 9 Canadian provinces¹. *C. nutans* is typically found in open fields and disturbed areas, where it exists as a rosette for one or more years before bolting, flowering, and setting seed all over the span of a few months. Individuals can grow up to 1.8 m in height², have winged stems covered in spines, and are capable of forming dense and impenetrable stands. Dispersal via wind is the primary means of movement for these thistles; since their seeds contain lightweight pappi that reduce seed terminal velocity and allow them to travel long distances by wind, these thistles demonstrate very high dispersal potential.

Previous studies have shown that this wind-based dispersal in *C. nutans* is highly leptokurtic, and sensitive to plant characteristics such as seed release height as well as environmental

characteristics such as wind speed³. Furthermore, elasticity analyses on spatial integral projection models of *C. nutans* spread show that, when compared to other plant and/or environmental characteristics, the extent of variation in wind speeds has the strongest effect on how this thistle spreads⁴. This is likely because increased variance in the distribution of wind speeds makes extreme wind events more likely to occur, thus causing long-distance dispersal events to be more frequent and allowing for faster spatial expansion of a given thistle population.

To further build upon the previous analyses that use integral projection models, we address whether the increased spread of this invasive thistle caused by increased variation in wind speed also occurs in a metapopulation framework. While the integral projection models assume a homogenous landscape and are representative of areas such as open pastures and farmland, we instead assume that the thistles can only exist in habitable patches of land and that all other areas are uninhabitable; such an assumption would be suitable for more fragmented areas. In order to examine the effects of wind speed variance in these patchy landscapes, we compare how quickly thistle populations expand using two dispersal kernels: one in which there is no variation in wind speed and another in which wind speeds are sampled from a distribution wind speeds obtained from weather data. We predict that the dispersal model with wind speed variation will allow patches to become occupied faster than the model without wind speed variation since there will be an increased chance of long-distance dispersal.

Modelling Approach

Population Model

The population dynamics of this system were modelled using a spatially explicit metapopulation approach for ten different habitable patches. Unstructured logistic growth in each patch was simulated using the Ricker model such that

$$N_{i,t+1} = N_{i,t} \exp \left(r - \frac{rN_{i,t}}{K} \right) + R_{i,t} \quad (1)$$

where $N_{i,t}$ is the number of individuals in a given patch i at time t . Added to this quantity is $R_{i,t}$, or the number of incoming propagules that establish, and is expressed as

$$R_{i,t} = c \sum_{\substack{j=1 \\ j \neq i}}^{10} N_{j,t} P_{i,j} \left(1 - \frac{N_{i,t}}{K} \right) \quad (2)$$

or the sum of propagules that establish in patch i and are sourced from all other patches j that each have some population $N_{j,t}$. Here, the constant c represents the product of the number of seeds produced by one individual and the per-seed probability of establishment in an unoccupied patch; this was set to 1 for all simulations and means each plant produces

one seed that, if landing in an unoccupied patch, will establish. The term $P_{i,j}$ represents the proportion of dispersed seeds whose dispersal distance is greater than or equal to the distance between patches i and j ; that is, the proportion of seeds that successfully disperse to another patch. $P_{i,j}$ will typically be higher for adjacent patches that are close together, but patches i and j need not be adjacent in order for dispersal to occur. $N_{j,t}P_{i,j}$ is multiplied by the logistic term inside of the summation to account for the fact that seeds arriving in already-populated patches are less likely to establish.

All ten habitable patches are assumed to be the same size and quality, and thus have the same carrying capacity and baseline population growth rates; for all analyses here, the carrying capacity K was set at 5000 and the baseline growth rate λ was 1.7 such that $r = 0.531$. We also assume no environmental stochasticity, and that these finite patches are the only habitable areas surrounded by an uninhabitable matrix. Given the patches are finite, we also make the reasonable assumption that both growth rate and the probability of establishment display linear and negative per-capita density dependence. The models were tested for three different patch configurations: one configuration where patches gradually became spaced further apart as their distance from the initial patch increased, a second configuration where two clusters of patches were separated by an approximately 100-m gap, and a third configuration where most patches were all clustered together while the remaining ones were more distant. For all three patch configurations, nine patches started empty and the other was a “founder patch” of 10 individuals. 100 different simulations were realised for each of the three patch configurations, with each simulation consisting of 30 1-year timesteps.

Dispersal Model

All dispersal events were simulated from a dispersal kernel derived from the WALD, or Wald analytical long-distance dispersal, model. This mechanistic model is based in fluid dynamics and simplifies a Lagrangian stochastic model to create a dispersal kernel that estimates the likelihood a wind-dispersed propagule will travel a given distance⁵. The kernel is the inverse Gaussian distribution

$$p(r) = \left(\frac{\lambda'}{2\pi r^3} \right)^{\frac{1}{2}} \exp \left[-\frac{\lambda'(r - \mu')^2}{2\mu'^2 r} \right] \quad (3)$$

and is a slight adaptation from the original equation⁵, using r to denote dispersal distance. Here, λ' is the location parameter and μ' is the scale parameter, which depend on environmental and plant-specific properties of the study system. The location and scale parameters are defined as $\lambda' = (H/\sigma)^2$ and $\mu' = HU/F$; these are functions of the height H of seed release, wind speed U at seed release height, seed terminal velocity F , and the turbulent flow parameter σ that depends on both wind speed and local vegetation roughness.

Two types of wind dispersal were modelled in our analyses. The first wind dispersal model is based on a mean wind speed with dispersal events being sampled from $p(r)$ using previous *C. nutans* measurements³ such that the mean seed release height \bar{H} was 1.41 m and the mean seed terminal velocity \bar{F} was 0.35 m/s; the mean wind speed \bar{U} was 2.15 m/s and was taken

as the average of all non-zero wind speeds measured at the site (seed release was assumed not to occur for wind speeds of zero). The second wind dispersal model incorporates additional variation by accounting for the different wind speeds detected at the site such that dispersal events are sampled over the kernel

$$k(r) = \int p(U)p(r) dU \quad (4)$$

where $p(U)$ is the probability density function for wind speed. Note that this second model still uses the same values of \bar{H} and \bar{F} as the first one, but the values of λ' and μ' used to create the distribution $p(r)$ are different because the wind speeds differ.

It is important to acknowledge that the WALD model itself assumes that wind turbulence is low, wind flow is vertically homogenous, and terminal velocity is achieved immediately upon seed release, all of which are not always accurate regarding wind dispersal events. Also, because we are using an unstructured population model, we are not accounting for heterogeneity within populations and assume that all plants are the same height, meaning that seeds are released from the same height above the ground. We further assume that dispersal occurs via wind only and there is no secondary dispersal which, as is discussed later, may not be the case for this system and can underestimate the rate at which this invasive species spreads.

Results

As we might expect, an increase in the distance between a given patch and the founder patch corresponded to an increase in the time elapsed before that given patch became occupied, with more distant patches colonised later than closer patches; that is, colonisation time was positively correlated with distance from the founder patch. For example, across all simulations and patch configurations, patches that were less than 20 m from the founder patch were on average colonised in a year and ones 50 m from the founder patch in 4 years or less. However, this distance-dependent increase in colonisation time was significantly less pronounced when variation in wind speeds was present, suggesting that there is likely an interaction between patch distance and wind speed variation.

In the first patch configuration (Figure 1), as we would expect, we observe that patches further from the founder patch take longer to colonise; initial colonisation times for the patches close to the founder patch were on the order of only a few years and were relatively unaffected by variation in wind speed. As distance from the founder patch increased, the mean initial colonisation time increased as well, but the difference in said time became more pronounced when comparing simulations with and without wind speed variation. For example, for a patch 100 m from the founder patch, it took approximately 9 years for colonisation to occur in the absence of wind speed variation, but only 4 years if such variation was accounted for; for a patch 200 m away, this difference becomes larger, with a colonisation time of 27 years for no wind variation and 6 years with variation. Trends similar to those discussed here were also observed in the third patch configuration (Figure 3).

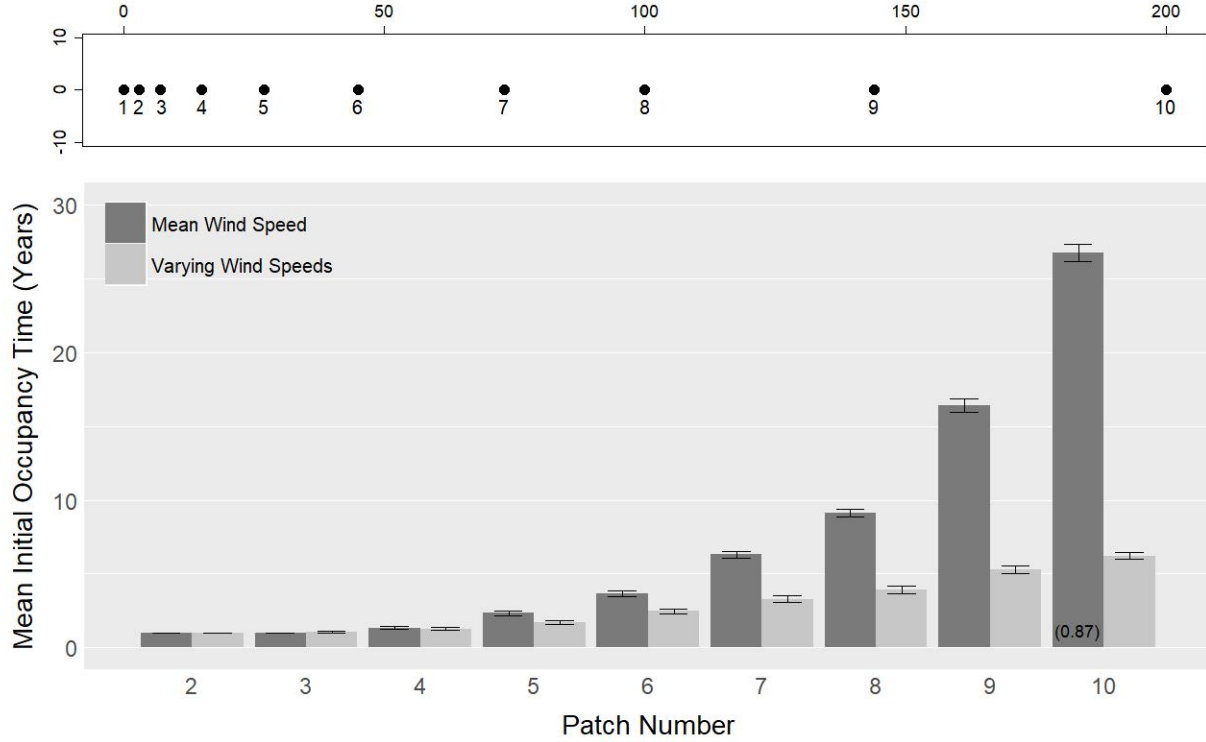


Figure 1: Patch configuration 1 (upper) and mean colonisation time for all patches in the presence/absence of wind speed variation (lower). Distances in the patch arrangement are given in metres, and patch 1 is the founder patch. Error bars indicate a 95% confidence interval for the estimate of mean colonisation time, and numbers in parentheses indicate the proportion of simulations in which colonisation was achieved in instances where this proportion was less than 1.

In the second patch configuration (Figure 2), we observe similar patterns as those seen in the other two configurations: patches further away take longer to colonise, but the amount of time it takes for that to occur is greatly reduced when wind speed variation is present. However, because there is an approximately 100-m gap between the two clusters of patches, the fact that propagules may have difficulty crossing the gap leads to slightly different outcomes in simulations without wind speed variation; here, these extremely isolated patches were colonised only 16% of the time or less, and the few colonisation events that did occur took on average more than 20 years. This extreme distance between the two patch clusters was not as problematic for dispersal when wind speed variation was present, as the distant patches were colonised 100% of the time and only after an average of 6 years.

Discussion

Our results support the idea that variation in wind speeds plays an important role in influencing the speed at which the invasive thistle *C. nutans* spreads across the landscape. Increased variation in wind speeds allows for higher wind speeds to be more frequent, meaning that extreme dispersal events will occur more frequently and increase the likelihood that

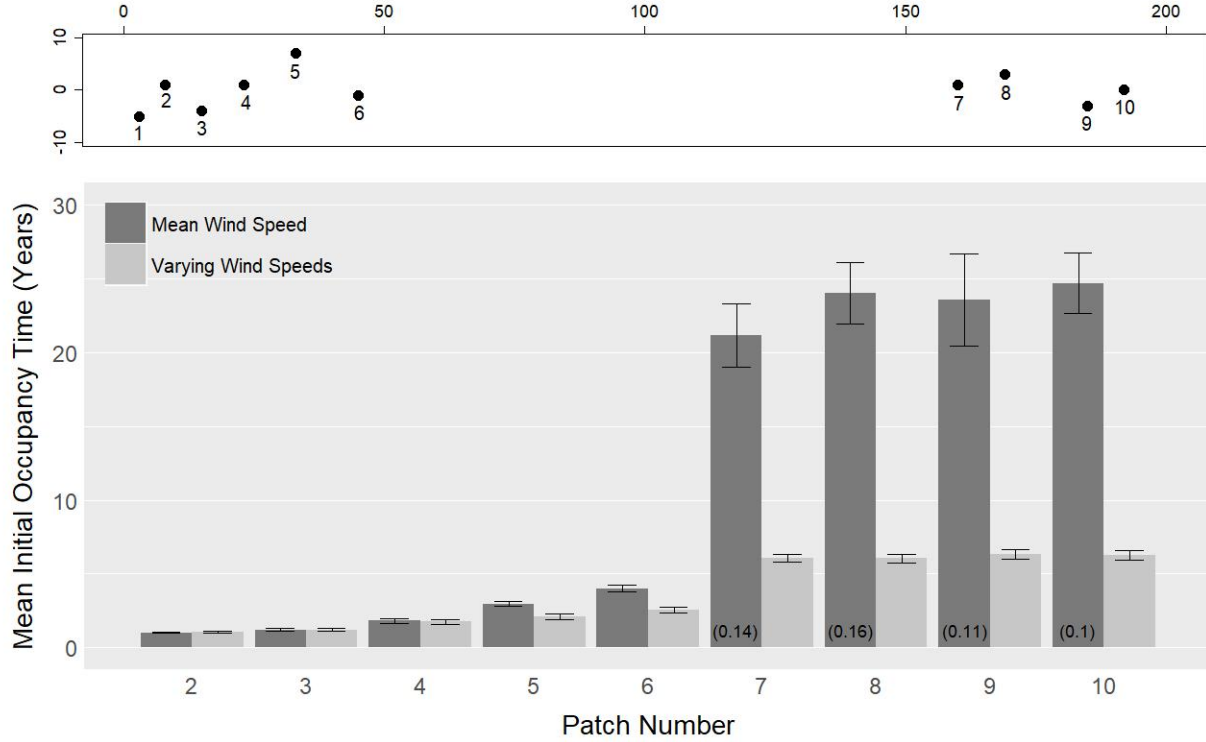


Figure 2: Patch configuration 2 (upper) and mean colonisation time for all patches in the presence/absence of wind speed variation (lower). Distances in the patch arrangement are given in metres, and patch 1 is the founder patch. Error bars indicate a 95% confidence interval for the estimate of mean colonisation time, and numbers in parentheses indicate the proportion of simulations in which colonisation was achieved in instances where this proportion was less than 1.

a propagule will establish in an unoccupied area. This is especially evident for habitable areas/patches that are more remote, as was clear in simulations for the second patch configuration; while these remote areas may be inaccessible under normal conditions, extreme dispersal events are far more likely to result in colonisation and can allow these remote areas to serve as a new source of propagules for adjacent areas.

It is also important to note that, when looking at *C. nutans* invasions, wind speed variance is only one source of variation in dispersal distances; there are several other dispersal pathways in this thistle that each have their own variation in their respective dispersal distances. For example, there is evidence that *C. nutans* seeds experience secondary dispersal by insects such as crickets, grasshoppers, and ants after primary dispersal by wind⁶; not only does dispersal by each of these three insects have its own variation, but this variation exists on top of the variation in wind dispersal. Such combinations of variation from serial dispersal pathways could possibly lead to instances where an extreme wind dispersal event is followed by an extreme insect dispersal event, yielding large dispersal distances that would be less likely under only wind dispersal. Given that much of the work on *C. nutans* dispersal (including this report) has not accounted for secondary dispersal, extreme serial dispersal events are not well understood, and current estimations of invasion speeds may actually underrepresent the true rate of invasion.

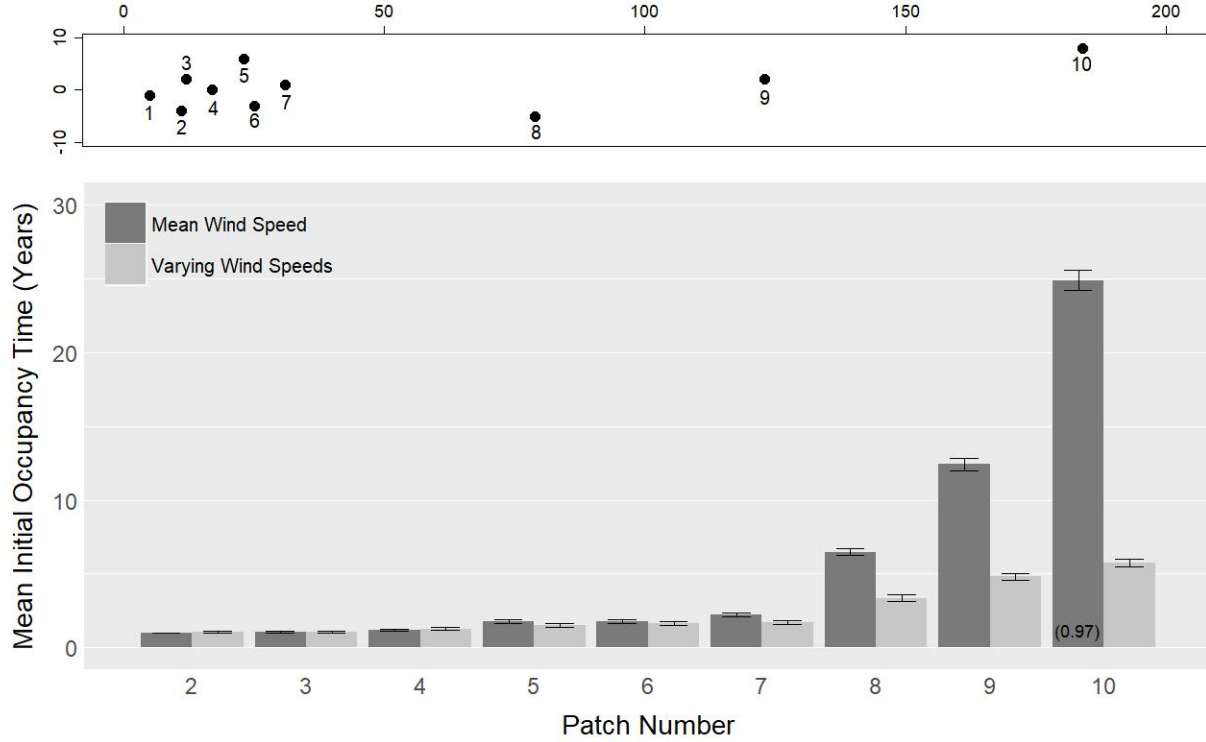


Figure 3: Patch configuration 3 (upper) and mean colonisation time for all patches in the presence/absence of wind speed variation (lower). Distances in the patch arrangement are given in metres, and patch 1 is the founder patch. Error bars indicate a 95% confidence interval for the estimate of mean colonisation time, and numbers in parentheses indicate the proportion of simulations in which colonisation was achieved in instances where this proportion was less than 1.

Another important note to make is that the patterns of variation within primary and secondary dispersal are themselves subject to change and are not necessarily fixed in time. One driver of change that has been a concern for invasive species such as this thistle management is climate change⁷, which could drastically alter dispersal patterns in this species. For example, areas predicted to experience an increase in the frequency or severity of extreme storm events may also experience an increased likelihood for extreme winds that give rise to long distance dispersal, increasing the speed at which these thistles spread; additionally, changes in climate could also affect presence or activity of secondary dispersal vectors such as insects, which would affect how seeds are moved after dispersal by wind. The issue of climate change essentially makes an already challenging problem even more difficult: not only are we still figuring out how to quantify all of the dispersal pathways in this thistle and trying to understand how they are integrated, but now we must also quantify how these different dispersal pathways are going to change over time. Future work should address these challenges by first better understanding the basics: that is, quantifying the other dispersal pathways besides wind. Such work should focus on quantifying local dispersal by insects and long-range dispersal by humans, and should also seek to identify other possible dispersal vectors with significant contributions to dispersal as well as assess the relative importance of the different dispersal pathways. By developing a better understanding the different disper-

sal pathways and how they interact, we can attempt to quantify how climate change might change variation within those pathways and their relative importance within the dispersal process.

In summary, we conclude that increased variation in wind speeds increases the rate of long-distance *C. nutans* dispersal events and the speed at which they spread. These findings are significant because they imply that understanding variation in a dispersal pathway is important for obtaining accurate estimates of dispersal, and failing to include this variation could underestimate the potential for invasive species to spread across a given area. We also acknowledge that though wind dispersal is the focus of this study, it is only one dispersal pathway in a larger dispersal framework; other dispersal pathways must be better understood to obtain a better knowledge of how this species spreads, and climate change will provide a challenge to predicting the how populations of this invader shift and expand over space and time.

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