

Hello everyone. My name is Trevor Drees and today, I will be presenting to you the results of one of several research projects I've been working on here in the Shea lab. In this presentation, we will examine how increased temperatures shift flower height distributions and seed dispersal patterns in two different species of invasive thistles.

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Let's start with a bit of a roadmap for the presentation here. I'll first open things up with a brief introduction on dispersal and how climate change may affect this process. Then, I'll move into discussing the study system and methods used to quantify dispersal and warming effects, followed by results and then an interpretation of those results.

So, first, some background on dispersal and climate change.

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What is dispersal, exactly? Simply put, it is any movement of organisms that can possibly generate gene flow. Whether it's a pack of wolves moving through the snow to breed in a new area or a seed blowing in the breeze, genes are moving from one location to another.

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Why should we quantify dispersal? Well, there are several good reasons. Not only can we better understand shifts in species distributions or the gene flow between populations, but we can also make better predictions regarding the spread of invasive species. Note that these are only a few of the reasons why quantifying dispersal is important; there are certainly more. But given the study system I work with, quantifying the spread of invasive species is most relevant.

Quantifying the spread of invasive species entails several things, namely: predicting how quickly an invasive species spreads (for example, as a rate in kilometres per year), understanding the life stage(s) that contribute the most to the dispersal process, and understanding the agents that most strongly drive dispersal. The latter two allow for targeting that can be used to curb the spread of invasives (for example, focusing on eliminating individuals at the life stage most responsible for dispersal, or reducing the effectiveness of the most influential dispersal vector).

All in all, we care about quantifying dispersal because a better understanding of dispersal in invasive species can help us make more informed management decisions that save time and money, allowing us to better allocate a limited amount of resources. Quantifying dispersal is not trivial, though, and it's complicated by the fact that...

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... climate change can alter patterns of dispersal. This means that existing estimates of dispersal may not be accurate in future climates. This could be caused by directly affecting dispersal vectors or indirectly by affecting dispersal-related factors, including things such as: temperature, precipitation, wind speeds, and frequency of extreme events such as storms and fires. But not all of these factors affect dispersal in some species, and some will have stronger effects than others, so it is important to consider what species we're examining dispersal in before we even attempt to quantify dispersal and how it is affected by climate change.

For example, consider a wind-dispersed plant like the one shown in the picture here.

Increases in temperature can affect dispersal by increasing the total number of degree days available for growth, leading to taller plants and taller flower heights (i.e. taller seed release heights). More precipitation can also increase height. In both cases, increases in seed release height means that seeds will be suspended in the air for longer and can be blown further by wind.

Increases in wind speed also means that seeds can be blown further by wind.

Increases in the frequency of extreme events can also affect seed dispersal; storms with strong winds can cause seeds to travel extremely long distances, and this may become more common if extreme storms become more frequent.

Land managers worry about how these things, and other shifts related to climate change, will affect invasive species management... so much so that many have incorporated climate change into their management plans, according to a recent survey of land managers across the U.S.

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So, think about all of the factors I previously mentioned. Wouldn't it be nice if we had a single model that could take climatic changes and use them to predict how dispersal patterns, like those for our wind-dispersed invasive plant, could shift? Well, that's ultimately the goal of my work.

But such a model would also be quite complicated, and would require a lot of data. Perhaps it would make sense to start with something simpler, by considering how changes in a single climatic factor affect dispersal? In doing so, we can construct the framework for the model and then later integrate different climatic factor shifts into the model, which would logistically be more feasible than trying to put everything together at the same time.

My plan here is to create such a framework, starting by examining the effects of temperature shifts on dispersal.

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Thus, the goal of the research described here is to use empirical data and mechanistic models to predict how increases in temperature will alter dispersal patterns in invasive plant species, ultimately setting the stage for examining how other climatic shifts affect dispersal.

But, here's an important consideration to think about: not all species will exhibit the same responses to temperature increases. Thus, we need to be specific about which species we're working with, and use them as a case study to inform possible dispersal changes in similar species.

[~ 6:00]

So now, let's take a look at the study system we are using, as well as the methods used to quantify dispersal and how temperature increases affect it.

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The two species we will use for our study system are *Carduus nutans* and *Carduus acanthoides*. I will refer to these species from here on out by just the species epithet, so *nutans* and *acanthoides*. Both of these are invasive thistles often found in highly disturbed areas such as roadsides and pastures. *Nutans* tends to have large flowers that droop from a long peduncle, while *acanthoides* tends to have a greater number of flowers that are smaller and don't have a pronounced peduncle. *Nutans* is often called "nodding thistle" due to the way the flower head droops, while *acanthoides* is often called plumeless thistle due to its, well, lack of a plume.

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These two thistles are invasive in many places across the world. While they both are originally from Europe and Central Asia, they can be found outside of their native range in countries such as South Africa, Australia, New Zealand, Canada, and the U.S., among others. In North America, *nutans* seems to have a much wider distribution than *acanthoides*, and can be found in the vast majority of U.S. states and Canadian provinces as can be seen on these maps. Note that these maps show only where they have been reported: they may be present in some of the states and provinces shown in white, just not yet reported.

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Seeds are the propagules through which these two thistle species are dispersed. Both seeds have a very similar structure, with a smooth elongated achene and a small elaiosome at the end. The elaiosome is particularly attractive to ants and plays a role in ant-mediated seed dispersal. Notice that despite the similar structure, *nutans* seeds are significantly larger than *acanthoides* seeds. So, if these are the propagules, how are they dispersed?

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Well, wind is the primary dispersal vector for these thistle seeds. They are often blown out of the flower head after a gust of wind, as can be seen in the photo here on the left. The seeds are small and are carried in the wind due to their lightweight pappus, the small feathery structure on top of the seed. This pappus allows seeds to stay suspended in the air for significantly longer, increasing the time that they are exposed to wind and thus the distance they travel. Note that wind is not the only mode of dispersal, though. As I mentioned earlier, these seeds can be moved by ants after they land on the ground, as their elaiosome attracts ants and offers a "reward" for dispersing the seeds. These elaiosomes also offer an easy way for the ants to move the seeds around, acting as a sort of handle for the ants to drag around seeds that are larger and exceed their body mass. Also, these seeds can be transported by humans too as a contaminant of agricultural products, for example by accidentally being rolled into hay bales.

So, we know that wind is the primary dispersal mode, but how can we model it? How can we quantify it? It's important to understand that as species move across the landscape, there are two extremely important factors among others: how many propagules are produced (the

reproductive aspect) and how far they go (the movement aspect). The latter is less studied because it's more challenging to measure, and is the focus of this presentation. We have already quantified the reproductive aspect of dispersal in this species, and seek to know more about the less-studied movement aspect.

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We can actually simulate wind dispersal using an inverse Gaussian distribution based on a fluid dynamics model, and obtain the probability of a seed travelling a given distance.

This  $p(r)$  is a dispersal kernel, or probability distribution, for a seed travelling some distance  $r$  from release. This is an inverse gaussian distribution whose shape is influenced by two parameters.

First, a scale parameter  $\lambda$  that is calculated from the mean wind speed, height at which the wind speed is measured, height of the surrounding vegetation, and the seed release height.

Then, a mean/location parameter  $\mu$  that is calculated from the mean wind speed, seed release height, and mean seed terminal velocity. The quantities that go into calculating  $\lambda$  and  $\mu$  should give you an idea of the factors that are essential for estimating wind dispersal, namely: wind speed, seed terminal velocity, and seed release height.

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This based dispersal model yields a kernel that looks something like this, with a peak close to zero and a fat tail indicative of a highly leptokurtic distribution. The vast majority of seeds don't travel far from the parent plant, but a small few do. It is those small few that often highly influence how quickly a population spreads across a landscape.

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This model of wind dispersal has actually been tested in several systems for various wind-dispersed plant species, including *nutans* and *acanthoides*.

The model fits the data pretty well, too, for our study system, as can be seen in the plots here. In these experiments, dispersal distances were collected out in the field using sticky trap to capture dispersed seeds and create empirically-derived distributions of dispersal distances. The models were then compared to those empirically-derived distributions. Note that the kernel shape here is different than what was in the previous slide because of the logarithmic graph axes.

When tested against a variety of other dispersal models, this model outperformed all of the others and was most representative of the dispersal distances observed out in the field.

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So, we have our dispersal model now. For seeds released from some height, it uses a mean wind speed and mean terminal velocity to estimate the probability of travelling a given distance. But those wind speeds and terminal velocities can vary! The wind is not blowing at the same speed all day, and seeds vary in mass and pappus size so there will be variation in terminal velocity too.

Thus, to capture that variation in wind speed  $p(U)$  and terminal velocity  $p(F)$ , we integrate our dispersal model across the observed distributions of these two factors. For this, we use wind speeds from a weather station near our field site, and seed terminal velocities measured from seed drop experiments in the lab. Incorporating variation in wind speed and seed terminal velocity gives us a more realistic model of dispersal.

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We've now covered how to model dispersal. But what about the temperature increases? After all, we're trying to figure out how temperature increases affect dispersal patterns.

To do this, we used an experiment to assess how warming affects seed release height, which strongly affects dispersal distances. For each species, we randomly assigned half of the plants translucent open-top fibreglass chambers, which increase the ambient temperature by approximately 0.6 degrees Celsius without affecting soil moisture or snow depth. These open-top chambers, or OTCs, are the same ones used in arctic tundra warming experiments, so they come from tried and tested methods. Chambers were placed around the thistles in the autumn shortly after planting, and remained until seeds dispersed in the summer, thus being present over pretty much the entire thistle life cycle.

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Previous studies have actually shown, at least in *nutans*, that warming increases mean height and shifts dispersal kernels to the right, leading to longer dispersal distances being more common. This is evident in the kernels shown here: for warmed plants, the peak moves down and short dispersal distances become less common, while the tail shifts up and to the right.

However...

We don't know if the same thing happens for *acanthoides*, as previous studies have not examined that. Also, previous studies have only considered seed release as a single point source at the maximum flower height; what about all of the other release heights? These thistles have more than one flower. The heights of the other flowers also influence dispersal distances, as seeds are still released from all of these other flowers in addition to the tallest one. Using the maximum seed release height instead of the entire distribution may overestimate dispersal; land managers that overestimate dispersal distances might be looking for these thistles in areas where it isn't necessary, wasting time and money.

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If we use the maximum height like previous studies did, we're only considering a single point of seed release on a given plant.

But that's not the case, as seeds are released from other flowers on the same plant too. So the question here is how does the dispersal kernel change when we account for those other seed release heights?

If you recall, this is what our kernel looks like after accounting for variation in wind speeds  $p(U)$  and seed terminal velocity  $p(F)$ .

Now, we can integrate across the distribution of flower heights,  $p(H)$ , to account for dispersal across the entire plant rather than just from the maximum height.

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So, thinking about how warming affects seed release height (which in turn affects dispersal distances) as well as how our estimates of dispersal distances can change if we look at all of the flower heights rather than just the tallest one, we seek to address three questions with this research. First, how does increased temperature affect the distribution of flower heights (and thus seed release heights)? Second, how does increased temperature affect dispersal distances over the distribution of flower heights? And third, are there differences in dispersal when using the distribution of seed release heights rather than the maximum height?

[~18:00]

Let's take a look at the results.

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First, how does increased temperature affect the distribution of flower heights (and thus seed release heights)?

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Our results indicate that, on average, flowers from warmed thistles are taller compared to flowers from unwarmed thistles. As can be seen in the left pair of bars in the chart, warmed *nutans* flowers are approximately 14 centimetres taller than their unwarmed counterparts; *acanthoides*, represented by the right pair of bars, are approximately 20.5 centimetres taller when warmed. Each of these differences are statistically significant.

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We can see that the entire distributions of flower heights are different after warming. It seems that warming shifts the distributions to the right, resulting in taller flowers all across the plant. This can be seen in both *nutans* (the top graph) and *acanthoides* (the bottom graph).

The dotted lines here represent the mean flower height for warmed and unwarmed thistles, corresponding to the bars shown on the last slide.

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So, we see that warming shifts the distribution of flower heights across the entire plant to the right, leading to taller flowers. How does this change in the distribution of flower heights affect dispersal, though?

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Well, it turns out that warming-induced increases in flower height also change the shape of the dispersal kernels. For both *nutans* (the top graph) and *acanthoides* (the bottom graph), differences between the warmed and unwarmed dispersal kernels are statistically significant; they are indeed two different distributions. For the warmed flower height distribution in each species, peaks of the distributions decrease and the rest of the distribution shifts to the right; that is, shorter dispersal distances become less common, while longer dispersal distances become more common.

Here, we've just taken the same plots on the previous slides and zoomed in on the tails of the dispersal kernels. The tails of the warmed distributions are slightly higher than those of the unwarmed distributions, indicating that longer dispersal distances are more common in warmed thistles. While the tails of the distributions don't seem too different, minor differences here can actually have significant impacts on dispersal at longer distances.

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And we can see that here. This graph displays the minimum dispersal distance for a given percentile of dispersal distances; that is, if we took the outcome of all dispersal events and put

them in order by distance, what would the minimum distance be for the top 10% (or 5%, or 1%, or 0.1%) of events. It appears that as we look at increasingly rare dispersal events, the distances we observe are greater for warmed than unwarmed *nutans*. This makes sense; the graphs in the last slide show that the tails of the warmed distributions are slightly higher than those of the unwarmed distributions, so we would expect to see more long distance dispersal events and increases in the distances involved in said events.

We also see the same trend for *acanthoides* as well.

Note that the bootstrap intervals in our figures grow larger for increasingly rare dispersal events. Part of this is because we're incorporating variability in wind speed and seed terminal velocity into our analyses, so we're bound to see more variability in long-distance dispersal in the first place. If we used only the mean wind speed and mean seed terminal velocity, the error bars would not be as large.

Here, I've just taken the previous two graphs and put them side-by-side for easier comparison. This is mostly just to show that long-distance dispersal events tend to cover a greater distance in *nutans* than in *acanthoides* since *nutans* flowers tend to be taller, and thus seeds are released higher and spend more time in the air.

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So, we see that warmed thistles yield taller flowers when considering the entire height distributions, and that dispersal distances over the distribution of flower heights tend to be greater for warmed thistles. But when looking at dispersal distances, does it really make a difference if we use the distribution of flower heights instead of just using the maximum height like the previous studies did?

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Here, you can see what happens when we compare kernels using maximum height to those using the distribution of flower heights, for each species warmed or unwarmed. The top two graphs are for *nutans*, and the bottom two are for *acanthoides*. Keeping the same colour scheme we've used for all of the previous graphs, red represents warmed plants, while grey represents unwarmed plants. This time, dotted lines represent kernels using only the maximum height, while solid lines represent using the entire distribution of flower heights. Mind that up until now, our dispersal kernels have used the entire distribution of flower heights. The kernel pairs may not look too different, but statistically speaking, most of them are. For *nutans*, we see that in both the warmed and unwarmed treatments, dispersal kernels using maximum flower height have lower peaks and shift to the right, meaning that longer dispersal distances become more common. Note that we saw the same trend earlier when comparing warmed thistles to unwarmed ones. And this makes sense too: if we're using the maximum possible height, of course dispersal distances will be greater than if we're using the distribution of flowers on a plant, since all but one of the flowers are below the maximum and will thus release seeds from a lower height.

We see the same pattern for *acanthoides*: dispersal kernels using maximum flower height again have lower peaks and shift to the right, meaning that longer dispersal distances become more



common. Note that the maximum height and height distribution dispersal kernels for the unwarmed treatment (in the third graph) are not different at the  $\alpha = 0.05$  level.

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Again, we have our graph that displays the dispersal distance for a given percentile of dispersal distances; so, if we took the outcome of all dispersal events and put them in order by distance, what would the minimum distance be for the top 10% (or 5%, or 1%, or 0.1%) of events. Only this time, we're examining differences between using maximum height or the entire height distribution rather than examining differences between warmed and unwarmed. It appears that as we look at increasingly rare dispersal events, the distances we observe are greater when using maximum height instead of the entire height distribution for unwarmed *nutans*. This makes sense, given what was discussed in the previous few slides: seeds are released higher when using the max height and will thus travel further.

We see the same pattern with warmed *nutans*...

And with unwarmed *acanthoides*...

And with warmed *acanthoides*...

Again, the bootstrap intervals in our figures increase in size for increasingly rare dispersal events. Note that in all of the graphs, the differences when using the max height compared to the entire distribution of heights are there, but they're not very large.

Here, I've just taken the last four graphs and put them all on the same slide so it's a little easier to compare them. We see when comparing *nutans* to *acanthoides*, seeds in those long-distance dispersal events tend to travel a little bit further, with the difference a bit more pronounced in the unwarmed plants. Within each species, warming increases distances in those long-distance dispersal events. And in general, using the maximum flower height yields higher distances for long-distance dispersal events when compared to using the entire height distribution.

[~28:00]

So, what did we learn from our experiment and analyses?

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Our study is the first to examine the distributions of seed release heights over the entire plant for *Carduus nutans* and *Carduus acanthoides*, and how warming affects those distributions.

We learned that warming increases the mean flower heights for both *nutans* and *acanthoides*, and shifts the distribution mean rightward. Previous studies have demonstrated this shift with maximum flower height; we demonstrate this shift with the entire flower height distribution.

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We also learned that warming changes the shape of the dispersal kernel.

Our results show that even when using the entire height distribution instead of the max height, warming shifts the dispersal kernel to the right and makes the tail “fatter”; dispersal at shorter distances becomes less common, while dispersal at longer distances becomes more common.

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And we learned that even though the tails of the dispersal kernels may not look that different, even minor differences in these tails can affect dispersal distances. Warming increases the magnitude of long-distance dispersal events, and this increase becomes more pronounced when looking at more rare dispersal events, like that 1 in 1000 seed that gets carried by a strong gust of wind and is blown 60 metres away.

The variation in the magnitude of those more rare events also increases.

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It's these long-distance dispersal events at the tails of the distribution that are highly influential in how a population moves across the landscape; models of population spread are often sensitive to these rare events. Sometimes, all it takes is one seed to start a new colony several hundred metres away from the main population.

Thus, warming-induced increases in the magnitude of long-distance dispersal events could very well increase spread rates. While we have not yet done this with using the entire flower height distribution, increased spread rates have been observed when using the maximum height.

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And these results have implications for weed management. As warming leads to greater dispersal distances, the spread of weeds will be more challenging to contain. Knowing how invasive plants respond to warming can help us continue effective management in future climates, and be better equipped to handle effects of warming-induced phenological changes in invasives we manage.

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For now, we've created a model examining effects of temperature increase on dispersal. But make no mistake, this achievement is not as small as it might seem because in creating this

dispersal model, we have actually set up all of the framework necessary to move forward and incorporate other elements of climate change to examine how they affect dispersal too. These other elements can be incorporated with ease.

For example, we can incorporate projected shifts in wind speed. This wouldn't be difficult at all since our model already uses wind speeds to estimate dispersal; all we would have to do is use projected wind speeds instead of the ones measured at our field site. I've actually already been working on modelling how changes in wind speeds affect dispersal.

We could even incorporate shifts in other climatic variables as well.

We will continue to consider additional variables one at a time. Rather than a small step in the right direction, we've really made more of a leap, but there are still more steps before we cross the finish line.

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That concludes my presentation. If you have any questions, please ask them in-call, post them in the chat, or email me. Finally, I would like give a big thanks to all the members of the Shea lab for their assistance in this research and the valuable feedback they have provided.

**[~35:00]**