*Ecology: ECY22-1180 (Drees, Trevor H; Shea, Katriona)*

**Elevated temperatures shift flower head height distributions and seed dispersal patterns in two invasive thistle species**

**Dear Dr. Taylor,**

**Many thanks for the thoughtful comments and reviews on our manuscript “Elevated temperatures shift flower head height distributions and seed dispersal patterns in two invasive thistle species” (*ECY22-1180*). We appreciate the invitation to revise and resubmit our work to *Ecology*, and have addressed your comments and the reviewers’ helpful feedback/concerns in the updated manuscript as described below. Before providing point-by-point responses, we briefly describe the larger changes made to the manuscript and provide an overview of the more minor revisions.**

**First and foremost, we have projected population spread rates for *C. nutans* using demographic information from previous work on our study species. While an overview of the methods is given in the main text, a more detailed exposition can be found in our new Appendix S1. Our results indicate an approximately 42.2% increase in spread rate with warmed maternal plants, and up to approximately 28.5% overestimation of spread rates when using the maximum flower head height as a point source rather than the distribution of flower head heights. These results also take into account other warming-induced demographic shifts observed in previous studies. Note that we focus our efforts on modeling *C. nutans* spread since there is ample demographic data from previous studies, including data on warming-induced demographic shifts in key vital rates such as survival and seed production. We did not model spread for *C. acanthoides* due to a lack of suitable demographic data (and discarded the possibility of using *C. nutans* demographic data for *C. acanthoides* as too speculative).**

**Second, we fine-tuned some inputs and parameters on our dispersal models, with the main goal of providing fairer comparisons to previous work. In particular, we changed to how we calculate maximum flower head height in dispersal simulations in the manuscript; rather than sampling from maximum heights, we now use the mean of all maximum heights, which better matches how previous studies calculated maximum height in dispersal analyses. Numerical estimates are thus slightly different than in the previous version of the manuscript, but the qualitative results are the same (i.e., there are still large increases in dispersal distances under warming, and overestimation when using maximum height). We moved our prior results (sampling from maximum heights) to the Appendix S2 for completeness. Figures have been updated to reflect this as well, though the differences between the old and new figures are minimal.**

**Third, we cut the length of the discussion per the guidance of Reviewer 1. However, we also necessarily included discussion of spread results and some of suggested additions from Reviewer 2. Thus, our manuscript is the same number of pages (29) as before, with approximately the same word count. We also updated the references and made other minor copy edits throughout.**

**Once again, we appreciate the feedback and opportunity for resubmission, and hope that you will find the revisions satisfactory.**

**Sincerely,**

**Trevor Drees and Katriona Shea**

**Response to REVIEWER 1**

*This is a sound study exploring a very simple question. It establishes the potential importance of the interaction between plant morphology, dispersal and temperature – and by implication to climate change. There have been very few studies of the interaction between plant morphology, growing conditions and dispersal. That makes the paper relatively original. However, I must also say that the conclusion is hardly unexpected. The paper confirms what is intuitively obvious and is therefore hardly a breakthrough in scientific understanding.*

**Thank you for your comment on our work’s originality, and for the helpful suggestion to model spread (from your final comment). As you will see in our revised manuscript, and counter to your expectation, we demonstrate the potential for fairly large impacts on spread rate.**

*The experimental design is extremely simple. The only measurement was inflorescence height. The modelling method is suitable, although it relies on the assumption that the WALD model is appropriate. The results are straightforward. The only criticism I have is of the failure to adequately consider some basic assumptions, which may or may not have implications for the results. The recognition of assumptions is fundamental to sound science.*

**The experimental design was intended to isolate a single factor and its potential to alter inference; its simplicity is intentional. Nevertheless, measuring individual head height on plants with tens or hundreds of heads is time-consuming and laborious, which is likely why such effort has not been attempted in other studies. Our intent was in part to address the degree to which such effort is warranted. As stated in the manuscript, the WALD model has been previously shown to be entirely appropriate for *Carduus* species (e.g., Skarpaas and Shea 2007). We agree entirely that the recognition of assumptions is fundamental, and have now added further clarification on such assumptions to the manuscript, as detailed in the responses below.**

*Since flower height/seed release height is the only morphological parameter included, implicit assumptions are that seed size (and hence falling velocity) and seed number do not vary with inflorescence height. Is this reasonable? Looking at photographs of both species, it would appear that terminal inflorescences tend to be larger. And the effect on morphology is likely to be highly density-dependent. Do higher inflorescences have more seeds; and are those seeds larger? I would like to have seen data showing that the assumptions are appropriate, or failing that discussion of the fact that it could represent a limitation of the study. It would not be difficult to use the model itself to explore the sensitivity of the conclusions to this assumption.*

**As described above, our study was intended to isolate a single factor and explore its potential to alter inference. We did not measure capitulum size and whether it varies by height, and thus assume that all capitula contain the same number of seeds, with the same individual seed dispersal characteristics. If, for example, terminal capitula are larger, this will increase the influence of the taller inflorescences and moderate the magnitude of the difference in dispersal and spread estimates. We now briefly address this in the discussion as a limitation of the study.**

*Four plants growing in 2m by 2m would presumably be typical of a low density weed infestation. So the difference between dispersal at maximum height and dispersal summed throughout the plant may be greater than might be found under high density where most of the inflorescences are high up. Worth mentioning?*

**This is an excellent point, and we have added some text about this to the discussion. Flower heads that do not rise above the rest of the thistle vegetation would likely not disperse far since they would be shielded from the wind (per the cited study by Marchetto *et al*. 2010); as such, the difference in dispersal and spread estimates from between maximum height and height distribution would be greater at high densities.**

*Another assumption is that the OTCs in themselves do not affect plant morphology, only via temperature. How tall were the chambers? It is well known that the application of repeated physical force (simulated wind) to plants in glasshouses can reduce their stature (see literature on brushing of vegetable crops e.g. by Joyce Latimer): so, protection from waving around in the wind could explain why they grew taller in chambers. It might not have been temperature per se. Can this be discounted? I suggest that it should be mentioned as a possibility rather than ignored. The only comment in the paper seems to be that the OTCs follow the tundra experiment manual, which is no guarantee in itself that chambers have no effect other than temperature.*

**We have added information on OTC dimensions to the manuscript, and apologize for the omission. Our OTCs are 0.4 m in height. The thistles grow as rosettes for most of their life, and rosettes are flush with the ground and shielded from wind by surrounding vegetation during that time; as such, wind would have minimal to no effect here. They then grow to substantial heights relatively rapidly, where the vast majority of biomass in both warmed and unwarmed plants is above the OTC top and subject to wind exposure.**

*I found the Discussion very long, considering the simplicity of the results. In my opinion, it over-stretches the significance of the results. Temperature, by changing plant morphology, can potentially alter dispersal distances and hence rate of spread. And models using maximum inflorescence height are likely to over-estimate dispersal distance. It really does not justify implications beyond that. In fact, a very important point is overwhelmed by most of the very generic statements about climate and spread rate: that even though the tail is fatter, very few of the millions of simulated seeds are actually projected to disperse very long distances. Most still do not travel very far even though the kernel is fatter. So, how much will the rate of spread of the species increase under elevated temperatures? Not much, presumably? It would be nice to see that modelled.*

**We have cut the length of the discussion, removing parts that are not as relevant to our investigation. However, we disagree that the discussion does not justify any additional implications beyond what is stated above, and this position is echoed by Reviewer 2. For example, there are relevant management implications that come with over/under-estimating dispersal and population spread, and they should at least briefly be discussed, given that understanding movement of an invasive species is a theme underlying our article.**

**We have also added in estimations of spread rates for *C. nutans* (see appendix S1 for methods and tabled results), with important findings highlighted in the Results, and implications of these findings in the Discussion. Our results indicate an approximately 42.2% increase in spread rate under warming, and up to approximately 28.5% overestimation of spread rates when using the maximum flower head height as a point source rather than the distribution of flower head heights. These results also take into account other warming-induced demographic shifts observed in previous studies. Note that we focus our efforts to model spread on *C. nutans* since there is ample demographic data from previous studies, including warming-induced demographic shifts in key vital rates such as survival and seed production; we did not model spread for *C. acanthoides* due to a dearth of the demographic data necessary to do so. While we could model *C. acanthoides* spread by simply using *C. nutans* demographic data, we prefer not to do so for the sake of accuracy and thoroughness.**

**Response to REVIEWER 2**

*This paper combines assessment of climate change effects on growth form with assessment of modeling accuracy when predicting wind-mediated dispersal of invasive thistles. While the paper places significant focus on its contributions to dispersal model performance by integrating the distribution of dispersal heights rather than simplifying dispersal to stem from a single point at the top of the plant, the very substantial impact of a relatively small amount of warming on thistle growth and height (and thus the taller dispersal point for some seeds) seems to me to be the more universally interesting result – the effect was much greater than I would have expected. This seems to have implications for seed dispersal across the board – do such effects emerge for most invasive species, regardless of dispersal mode? Such a finding has broad implications for invasion biology and movement ecology across systems.*

**Thank you, we agree the results are important, and have added more on the implications to the discussion, as described below.**

*I recommend that the authors consider adding a broader treatment of the implications of such faster and higher growth into the discussion, by talking about the impact of such changes on invasive species and systems more broadly, beyond just the wind-dispersed, modeled system examined here. It seems there are implications for vertebrate-dispersed species, too, for example, since species that grow faster and produce taller or more abundant fruits/seeds might be more attractive for dispersers. In the section where the authors refer to manager needs, it might make sense to expand this to talk about the implications of their findings for the combination of factors managers should consider when considering the likely effects of climate change on their systems, including increased growth rates/reproduction/spread among invasive species. A discussion of the circumstances/contexts/plant characteristics that may facilitate such a growth increase under climate change could also be useful here.*

**We have added additional text to the discussion addressing implications for management regarding** **combination of factors managers should consider when considering the likely effects of climate change on their systems; when looking at the spread rates, we want to consider the changes in dispersal due to height, but also the changes in other demographic factors such as survival and reproduction. Using warming-induced shifts in single demographic factors may not fully capture the potential increase in spread rate.**

**While we would like to add additional text on implications for species beyond those that are just wind-dispersed, as well as a deeper discussion of the circumstances/contexts/plant characteristics that may facilitate such a growth increase under climate change, Reviewer 1 wants us to cut the length of the discussion substantially; this additional content would likely be outside of the scope of discussion that Reviewer 1 seeks. Thus, we have balanced the requests of the two reviewers by retaining the focus on wind-dispersed plants.**

*That said, the portions of this paper examining the performance of the models under various assumptions and scenarios were clear, straightforward, and well-written, and the work is likely to facilitate appropriate adaptation in other modeling efforts by other researchers.*

**Thank you so much for the kind words, and we also hope our work will have impact in the fields of invasion and movement ecology.**

*Lines 86-88: “need for” and “necessary” are redundant; this sentence should be simplified.*

*Line 256: change “is” to “are”*

**We have made the grammatical revisions highlighted above, thank you.**

*Line 357: I agree that the extra data collection need may not be worth it, but it’s also true that if a model over-estimates spread and then that spread doesn’t manifest, it’s possible that people could become complacent about a particular invasion, so that is a risk of overestimates.*

**We have included additional remarks on when the extra data collection for the full distribution of flower head heights may or may not be worth pursuing.**