

REPORT

Warming speeds up range expansion in an experimental model system

Kayley Breslin | Tess N. Grainger

Department of Integrative Biology,
 University of Guelph, Guelph, Ontario,
 Canada

Correspondence

Tess N. Grainger
 Email: tess.grainger@uoguelph.ca

Funding information

Natural Sciences and Engineering
 Research Council of Canada (NSERC)
 Discovery Grant; Natural Sciences and
 Engineering Research Council of Canada
 (NSERC) Undergraduate Student
 Research Award

Handling Editor: Christopher P. Catano

Abstract

Dispersal is becoming increasingly critical to understand as climate change forces species to shift their ranges to track changing environments. Although we know that warmer temperatures can prompt species to shift their ranges, we have little understanding of how temperature affects the speed at which they can do so by altering the rate of range expansion. Warmer temperatures could accelerate the rate of range expansion by increasing random, density-independent movement and/or by increasing population growth rates and driving density-dependent movement. To test the effect of temperature on the rate of range expansion, we grew populations of the flour beetle *Tribolium castaneum* in linear connected landscapes at 27.5, 30, or 32.5°C and tracked their expansion for 18 weeks. We then conducted separate assays to isolate the effect of temperature on density-independent dispersal probability and population growth rates. We found that beetles at 32.5°C exhibited the fastest range expansion, and that higher temperatures increased both dispersal probability and population growth rates, suggesting that both mechanisms likely contributed to faster range expansions under warming. Our findings highlight the importance of assessing the effects of temperature on range expansion dynamics in order to fully understand how, and how quickly, ranges will shift under climate change.

KEYWORDS

climate change, dispersal, population dynamics, range expansion, temperature, *Tribolium* flour beetles, warming

INTRODUCTION

Dispersal is a critical ecological process that helps animals locate food, mates, and suitable habitat (Bowler & Benton, 2005; Clobert, 2012; Ronce, 2007). Dispersal also plays a significant role in shaping a species' range by facilitating expansion into new areas (Hastings et al., 2005;

Leroux et al., 2013). As climate change accelerates, dispersal has become increasingly important to understand, as species are shifting their ranges to keep pace with changing temperatures (Chen et al., 2011; Kerr, 2020; Ramalho et al., 2023). Rising temperatures affect not only where organisms can live but could also affect the rate of their range expansions (Barnes et al., 2015;

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.
 © 2026 The Author(s). *Ecology* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

Travis et al., 2013). Indeed, the two principal drivers of range expansion rate, population growth rates and movement rate (Skellam, 1951), both have the potential to be affected by temperature. However, due to the scarcity of research investigating this topic, the effect of temperature on the rate of range expansion, and the mechanisms underlying potential changes, remain unclear.

The first pathway through which temperature could affect the rate of range expansion is simply by influencing an organism's movement rates (Brown et al., 2004; Gibert et al., 2016; Skellam, 1951). Warmer temperatures are known to increase metabolic rates, particularly in ectotherms, because internal enzyme kinetics are temperature-dependent (Brown et al., 2004; Dell et al., 2011; Gibert et al., 2016). Because movement depends on metabolism, warmer temperatures can result in increased movement rates (Dell et al., 2011; Gibert et al., 2016; Hannigan et al., 2023; Lang et al., 2022). These movement rates can be characterized as density-independent, non-directional patterns, akin to random diffusion, which animals display as they navigate their environment (Hannigan et al., 2023). These movement rates can in turn influence dispersal probability, or the likelihood that individuals move from one habitat patch to another (Hannigan et al., 2023; Skellam, 1951). In terms of range expansion, if animals are moving around more, their encounter rate with the range edge or a dispersal corridor should be higher, which could increase the rate of range expansion.

A second pathway through which temperature could influence range expansion is through effects on population growth rate and density (Andow et al., 1990; den Bosch et al., 1990; Hastings et al., 2005; Skellam, 1951). In ectotherms, environmental temperature is a major determinant of population growth rate; at warmer temperatures, ectotherm populations experience accelerated growth rates and faster reproductive output, resulting in higher densities being reached more quickly (Ju et al., 2011; Li et al., 2024; Savage et al., 2004). Faster population growth at warmer temperatures results in more intense competition for resources, which can increase the propensity of animals to leave to find a new habitat (Harrison, 1980; Zhou et al., 2024), and could also increase the rate of range expansion. Although there are two clear ways that temperature could affect range expansion rate in ectotherms—movement rate and population growth rates—to our knowledge, no previous research has attempted to investigate the role of these two mechanisms in driving temperature-induced changes in range expansion.

The goal of this study was to determine the effect of temperature on the rate of range expansion and to explore how movement rates and population growth

rates each contribute to this effect. We used the red flour beetle, *Tribolium castaneum*, in experimental landscapes to answer two key questions: (1) How does temperature affect the rate of range expansion? (2a) Are the effects of temperature on density-independent movement rates a potential mechanism driving this effect? (2b) Are the effects of temperature on population growth rates a potential mechanism driving this effect?

METHODS

Study species

We used *Tribolium castaneum*, the red flour beetle, as a model system to examine the effect of temperature on the rate of range expansion. *Tribolium* beetles have been used as a model system in ecology and evolutionary biology for over a century (Pointer et al., 2021). They exhibit rapid and temperature-sensitive population growth rates (Park & Frank, 1948), and their population sizes are regulated via density-dependent reproduction, development rates, dispersal, and cannibalism (Pointer et al., 2021). Their life history is marked by recurring dispersal and colonization events between patchy habitats (Dawson, 1977; Pointer et al., 2021), making them an excellent model for studying processes related to movement, including range expansion (Legault et al., 2020; Weiss-Lehman et al., 2017). For our experiment, we used beetles of the “COL-2” strain obtained from the United States Department of Agriculture (USDA) in 2021. This strain has been maintained in controlled laboratory conditions by serial transfer at 30°C and 50%–70% humidity for ~35 years.

Range expansion experiment

We tested the effect of temperature on the rate of range expansion across experimental linear landscapes in three temperature treatments. Each landscape was made up of 12 acrylic boxes (4 cm × 4 cm × 6 cm), with each box representing an individual habitat patch (Appendix S1: Figure S1), following previous range expansion experiments with flour beetles (Legault et al., 2020; Weiss-Lehman et al., 2017). We filled each patch with 30 g of a mix of a high-quality and a low-quality resource for this species (60% whole wheat flour and 40% rice flour). We used this mixed flour medium in order to temper population growth and make tracking population sizes logistically feasible. Patches were arranged in a single row and held together with elastic bands (Appendix S1: Figure S1). Each patch had a 2-mm

diameter hole drilled beneath the flour level on each side to allow for dispersal between patches (Legault et al., 2020; Weiss-Lehman et al., 2017).

We established 10 replicate landscapes at each of three temperatures: 27.5, 30, and 32.5°C. The historic temperature of our laboratory strain was 30°C, and the thermal optimum for this species is 30–31°C (Skourti et al., 2019), and so by selecting moderately cooler and warmer temperatures as our treatments, we aimed to capture conditions that could reveal how realistic deviations from their historic temperature affect movement, growth rates, and ultimately, the rate of range expansion. In particular, our 32.5°C treatment captures the predicted temperature increases (from our strain's historic temperature) due to climate change based on models under current emission trajectories (2.5°C increase by 2100) (IPCC, 2023). Landscapes were maintained in fully dark temperature- and humidity-controlled incubators (50%–70% relative humidity). To control for any variation across incubators, we swapped treatments across chambers each month.

Each landscape was established by introducing 20 adult *T. castaneum* beetles into the first patch. Landscapes were then placed in their respective incubators for a three-week period to allow beetles to create tunnels within the first patch in which to move through the flour (Legault et al., 2020, Appendix S1: Figure S1). During this 3-week-long no-dispersal phase of the study, dispersal holes between patches were blocked with acetate strips (Legault et al., 2020; Weiss-Lehman et al., 2017). After 3 weeks, the acetate strips were removed for 12 h to allow beetles to disperse into neighboring patches. After 12 h, the acetate strips were put back in place to block the holes, and the landscapes were disassembled for population censusing. We selected a dispersal interval of 12 h every 3 weeks in order to constrain movement across our landscapes so that dispersal occurred on a similar timescale to population growth rates, such that both processes had the potential to contribute to range expansion. This type of discrete dispersal is representative of systems in which dispersal is facilitated by periodic events (e.g., organisms whose dispersal is aided by periodic weather events such as wind or flooding).

To census populations, we first inspected each patch in each landscape for signs of beetle activity (i.e., tunnels in the flour). We then sifted the flour out of all patches with any sign of beetle activity as well as the next two seemingly empty patches (to ensure no beetle presence). For any patch that contained adults, pupae, or larvae, we censused all live and dead adult beetles and replaced half of the flour medium with fresh flour. Upon completion of the census, beetles were placed back into their respective patches and landscapes were reassembled in the same

order, placed back in their respective incubators, and the 3-week cycle started again. This was repeated six times, for a total experimental duration of 18 weeks. We used continuous overlapping generations (Agashe et al., 2011; Van Allen & Rudolf, 2013) rather than the discrete generations that are sometimes used in this system (e.g., Hufbauer et al., 2015; Legault et al., 2020) in order to replicate the natural life history of *T. castaneum*, to allow for natural dynamics such as cannibalism across life stages, and to avoid imposing a timing of when the transition from one generation to the next occurs (given that development rate is affected by temperature).

Movement rate assay

To determine the direct effect of temperature on movement rates (independent of the effect of temperature on population growth rates), we conducted a separate experiment. The set-up was similar to that of the main experiment (same three temperatures and same flour medium); however, landscapes consisted of only 2 individual habitat patches (acrylic boxes), and there were 5 replicate landscapes for each temperature treatment (for a total of fifteen 2-patch landscapes). To initiate this assay, we introduced 10 adults into the first patch in each landscape, where they were allowed 3 weeks to acclimate and form tunnels. Acetate strips were then removed for 12 h to permit dispersal into patch 2. Upon completion of the 12 h dispersal period, adult beetles were censused in each patch. Only one 3-week (21 day) cycle was completed to prevent population growth, as it takes between 35 and 62 days for *T. castaneum* to complete its life cycle on this flour medium and across our three experimental temperatures (Weiss et al., 2025). This assay thus removed the possibility of population growth, allowing us to isolate the direct effect of temperature on dispersal rate.

Population growth rate assay

To determine the direct effect of temperature on population growth rates, we conducted a separate experiment in isolated populations (i.e., no movement across habitat patches). For this experiment, we used the same three temperatures and the same flour medium as described above, and had three replicate populations per temperature. To initiate the experiment, we added 15 adult *T. castaneum* to 10 g in a 68-mL lidded plastic container. We then allowed populations to grow and expand and censused all live and dead adult beetles in each population every 2 weeks for 22 weeks (Appendix S1: Figure S2). After each census, we added an additional 5 g

of the appropriate flour type in order to provide a continuous supply of fresh resources.

Statistical analyses

To analyze the effect of temperature on range expansion rate, we constructed a linear mixed-effects model with distance spread as the response variable (Weiss-Lehman et al., 2017). We defined distance spread as the furthest patch to be reached by at least one adult beetle (Weiss-Lehman et al., 2017). In this model, the fixed effects were time (“census number” modeled as a continuous variable to allow for slope estimation), temperature (a categorical variable with three levels: 27.5, 30, or 32.5°C), and the interaction between temperature and time (i.e., the slope). We used the interaction (slope of distance spread per unit time) as our estimate of range expansion rate (Sunde et al., 2023; Usui & Angert, 2024; Weiss-Lehman et al., 2017). We also included replicate landscape number as a random effect to account for the non-independence of repeated measurements from the same experimental units. One replicate was lost in an experimental mishap and was excluded from the analysis. We then conducted a one-way ANOVA to test for the effect of temperature on range expansion rate, and a post hoc Tukey test to determine which temperatures’ slopes differed from one another (using the “emmeans” package with the Tukey adjustment).

To determine the direct effect of temperature on movement rates from our movement rate assay, we used a generalized linear model with a binomial distribution, with temperature as the predictor variable and the number of adult beetles that moved (successes) or did not move (failures) as the response variable. We tested the effect of temperature on the likelihood of moving using an ANOVA (analysis of deviance for a binomial model) and a post hoc Tukey test to determine which temperatures’ movement rates differed from one another. We also tested for (and found no evidence of) overdispersion. For visual clarity, we plotted movement as the proportion of individuals that dispersed.

To analyze the effects of temperature on population growth rates, we fit a Gompertz population growth model to our growth rate data for each population. On a log scale, the Gompertz model is a simple linear difference equation $x_t = a + bx_{t-1}$, where x_t is the natural log of population size at time t , a is the population’s intrinsic growth rate, and b is the strength of intraspecific competition (Ives et al., 2003) (see Appendix S1 for full description of model). The parameter of interest from this model was a , the intrinsic growth rate, and parameter estimates were extracted using the broom package in R. To test the

effect of temperature on population intrinsic growth rate, we fit a linear model with a as the response variable and temperature as a categorical predictor. We used an ANOVA to test for an overall temperature effect, and a post hoc Tukey honestly significant difference (HSD) test to determine which temperatures’ growth rate differed from one another. All statistical analyses were conducted in R (v 4.4.1), and all figures were made using the “ggplot2” package. All data used in this paper are available in Dryad in Grainger and Breslin (2025).

RESULTS

In our main experiment, by the end of 18 weeks the beetle populations in all experimental landscapes had expanded their ranges at least into the second patch, and the furthest range expansion we observed was to the 9th patch (Figure 1, Appendix S1: Figure S2). There was a significant effect of time (census number) ($F_{1,188} = 337$, $p < 0.001$), but no significant direct effect of temperature on the total distance spread ($F_{2,189} = 0.45$, $p = 0.64$). However, there was a significant interaction between temperature and time ($F_{2,188} = 6.72$, $p = 0.0015$), indicating that the slope of distance over time (i.e., the rate of range expansion) was significantly different across our three temperatures. The post hoc pairwise slope comparison revealed that the rate of range expansion at 32.5°C was significantly higher than at both 27.5 and 30°C, while there was no significant difference between 27.5 and 30°C (Appendix S1: Table S1).

In our analysis of our movement rate assay, we found a significant positive effect of temperature on dispersal probability ($\chi^2 = 8.75$, $df = 2$, $p = 0.013$, Figure 2a). Post hoc pairwise comparisons revealed that there was only a significant difference between the 27.5°C and the 32.5°C treatments, with a higher dispersal probability occurring at 32.5°C (Figure 2a, Appendix S1: Table S2).

In our analysis of our population growth rate assay, we found a significant positive effect of temperature on population growth rate ($F_{2,6} = 7.187$, $p = 0.025$, Figure 2b). The post hoc comparison revealed that there was only a significant difference between the 27.5°C and the 32.5°C treatments, with the fastest population growth rates occurring at 32.5°C (Figure 2b, Appendix S1: Table S3).

DISCUSSION

In this study, we tested the effect of temperature on the rate of range expansion in flour beetles and investigated the potential for two underlying mechanisms to contribute to this process. We found that range expansion rate

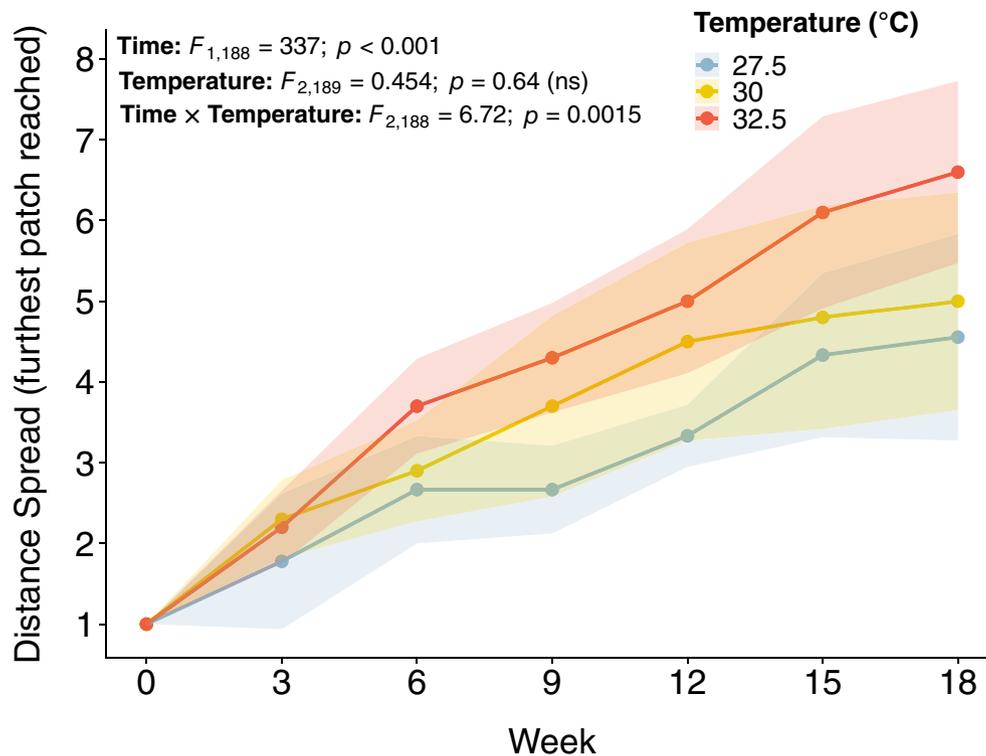


FIGURE 1 The effect of temperature on distance spread by *Tribolium castaneum* flour beetles in 12-patch experimental landscapes (main experiment). Solid points represent the mean distance spread (furthest patch reached) for each temperature ($N = 9$ for 27.5°C, $N = 10$ for 30°C, and $N = 10$ for 32.5°C). Shaded regions show 95% CIs. See Appendix S1: Table S1 for full results of post hoc pairwise comparisons.

increased with temperature, with the fastest expansion rate at our highest temperature (Figure 1). We also determined that temperature significantly increased beetles' density-independent movement rates, resulting in a probability of dispersing between patches several times higher at 32.5°C than at 27.5°C (Figure 2a). Finally, we found a positive effect of temperature on population growth rates, again with our highest temperature having significantly faster growth rates than our lowest temperature (Figure 2b). Overall, our results demonstrate that higher temperatures can speed up range expansions, and suggest that this could be mediated by both increased movement rates and faster population growth rates.

Although temperature-driven changes in insect population growth are well documented (Ju et al., 2011; Li et al., 2024; Savage et al., 2004), and temperature-driven changes in density-independent movement have been studied in some species (Barnes et al., 2015; Hannigan et al., 2023), to our knowledge, no previous study has investigated the role that these two processes play in mediating the effect of temperature on range expansion rate. We found that both growth rate and movement rate increased with warming (Figure 2), highlighting the sensitivity of each of these two individual processes to temperature. Further research is needed to determine how general these effects are across taxa, and we would expect

that they are most likely to apply in ectotherms, whose metabolism is directly linked to temperature (Brown et al., 2004). These results, if general, suggest that a full understanding of range expansion rate under global change requires that the effects of temperature on both of these mechanisms be considered (Skellam, 1951).

Understanding how, and through which mechanisms, temperature influences range expansion is critical for predicting shifts in species distributions under climate change. Currently, most models used to predict species distributions across landscapes incorporate dispersal using fixed kernels that do not respond to environmental variation, and few studies incorporate temperature-dependent dispersal into these models (Amarasekare, 2024; Leroux et al., 2013). Our finding that range expansion rate increases with warming indicates that this simplification could be failing to capture environmental effects on expansion rates and limiting the realism of range shift projections under climate change. However, while our results have important implications for understanding range shifts under climate change, studies in more natural systems are needed to confirm our findings, for two reasons. First, our study examined range expansion dynamics in a controlled microcosm at a small scale, when in reality range expansion is a landscape-scale process that often includes rare

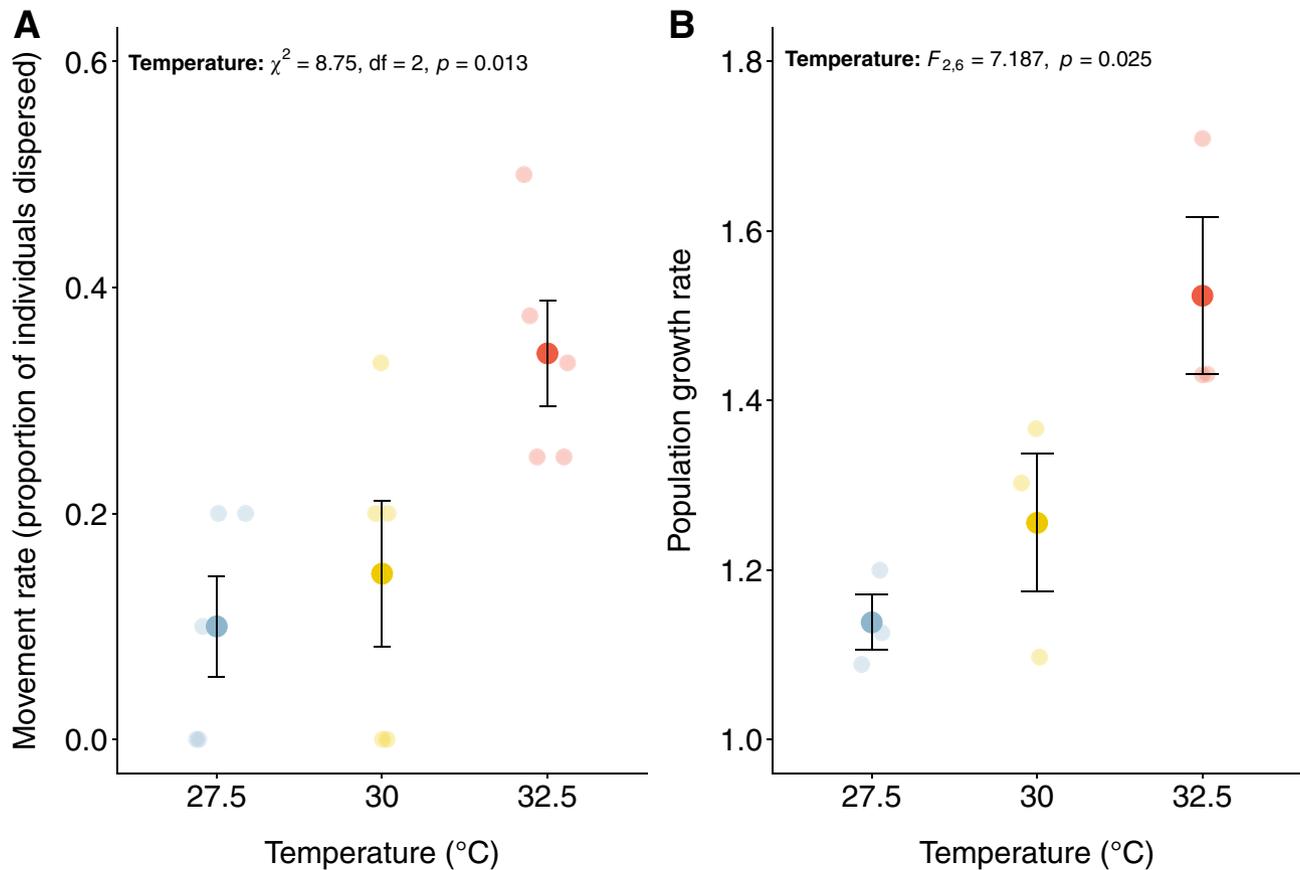


FIGURE 2 The effect of temperature on two potential mechanisms underlying range expansion in *Tribolium castaneum* flour beetles: movement rate and population growth. Panel (A) shows the effect of temperature on the proportion of beetles (out of a total of 10 beetles) that dispersed over the course of 12 h in a two-patch dispersal assay. Panel (B) shows the effect of temperature on population growth rates in a 22-week growth rate assay. For both panels, darker, opaque points indicate treatment means, while lighter, faded points show values from each experimental replicate, and error bars represent the SE of the mean. For both panels, see Appendix S1: Table S2 for full results of post hoc pairwise comparisons.

but influential long-distance dispersal events (Hastings et al., 2005; Nathan et al., 2008; Trakhtenbrot et al., 2005). While it has been shown that small-scale experiments can provide critical insight into the factors that drive range expansions (e.g., Lustenhouwer et al., 2023; Melbourne & Hastings, 2009; Usui & Angert, 2024; Williams et al., 2016), and that local-scale movement, behavior, and population dynamics can meaningfully alter range expansion rate (Bartón et al., 2012; Hastings et al., 2005), an important future direction will be to determine if and how longer distance dispersal events are affected by a warming climate, and whether this alters the conclusions reported here. And second, dispersal in natural systems is a highly complex and context-dependent process influenced by multiple interacting factors, including resource availability, competition, and an individual's condition (Bowler & Benton, 2009; Grainger et al., 2018; Hastings et al., 2005; Pellissier, 2015). Our experiment, by necessity, removed many important factors that could affect dispersal and

range expansion in order to examine the effect of a single factor (temperature) in the absence of potentially confounding processes. As such, studies in more natural field conditions that include more of this complexity are needed to confirm our findings and to determine how important a driver temperature is relative to other factors (Lustenhouwer et al., 2023).

While our study revealed that both random movement rates and population growth rates each have the potential to contribute to faster range expansions under warmer temperatures in flour beetles, species-specific biology and life history traits will determine the importance of these two factors in driving range expansion in other systems. The impact of these factors on range expansion rates is likely to vary among species with differing generation times, dispersal patterns, responses to crowding, and other life history traits. In systems for which metabolic rates have clear links to movement rates, including many insects and aquatic organisms (Dell et al., 2011; Gibert et al., 2016; Lang et al., 2022), or

those that undergo density-dependent dispersal, such as aphids (Harrison, 1980) and tephritid flies (Albrechtsen & Nachman, 2001), the mechanism we explored here will be particularly relevant. In contrast, for species with more passive dispersal such as scale insects (Wright et al., 2024) or plankton (O'Connor et al., 2007), temperature-induced changes in movement rates and population density may not be as important drivers of range expansion rates. This underscores the need for further research to disentangle the mechanisms underlying range expansion rates across diverse taxa, particularly for those species whose current ranges are threatened by global change.

Species are undergoing range shifts at an unprecedented rate due to climate change (Chen et al., 2011; Kerr, 2020; Ramalho et al., 2023), making it vital to understand how temperature may influence range expansion rates. If predictive models fail to incorporate key factors, such as temperature-driven changes in movement and population density, they risk missing critical processes shaping these range shifts. Despite this, the effects of temperature on the rate of range expansion remain largely unexplored, with most studies focusing on broader climate and range shift patterns. By addressing this gap, our study provides new insights into the mechanisms driving range expansion and highlights the importance of integrating temperature effects on both movement rates and population growth rates into future predictions.

AUTHOR CONTRIBUTIONS

Kayley Breslin and Tess N. Grainger conceived the idea for the paper. Kayley Breslin conducted the experiment and the data analyses with input from Tess N. Grainger. Kayley Breslin wrote the manuscript and Tess N. Grainger contributed substantially to revisions.

ACKNOWLEDGMENTS

We thank K. Robinson, A. Chhoker, E. Gruntz, S. Chong-King, and M. Mucci for help with the experiment. We thank L. Weiss for collecting the growth rate data and M. Barbour for helping with the analysis of these data. We also thank the Grainger Lab, G. Legault, T. Usui, K. Stark, and two anonymous reviewers for valuable feedback on the project and the manuscript. Funding was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to Tess N. Grainger and a Natural Sciences and Engineering Research Council of Canada (NSERC) Undergraduate Student Research Award to Kayley Breslin.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Grainger & Breslin, 2025) are available in Dryad at <https://doi.org/10.5061/dryad.gf1vhhn0v>.

REFERENCES

- Agashe, D., J. J. Falk, and D. I. Bolnick. 2011. "Effects of Founding Genetic Variation on Adaptation to a Novel Resource." *Evolution* 65: 2481–91.
- Albrechtsen, B., and G. Nachman. 2001. "Female-Biased Density-Dependent Dispersal of a Tephritid Fly in a Fragmented Habitat and its Implications for Population Regulation." *Oikos* 94: 263–272.
- Amarasekare, P. 2024. "Temperature-Dependent Dispersal and Ectotherm Species' Distributions in a Warming World." *The Journal of Animal Ecology* 93: 428–446.
- Andow, D., P. Kareiva, S. A. Levin, and A. Okubo. 1990. "Spread of Invading Organisms." *Landscape Ecology* 4: 177–188.
- Barnes, A. D., I. K. Spey, L. Rohde, U. Brose, and A. I. Dell. 2015. "Individual Behaviour Mediates Effects of Warming on Movement across a Fragmented Landscape." *Functional Ecology* 29: 1543–52.
- Bartoń, K., T. Hovestadt, B. Phillips, and J. Travis. 2012. "Risky Movement Increases the Rate of Range Expansion." *Proceedings of the Royal Society of London, Series B: Biological Sciences* 279: 1194–1202.
- Bowler, D. E., and T. G. Benton. 2005. "Causes and Consequences of Animal Dispersal Strategies: Relating Individual Behaviour to Spatial Dynamics." *Biological Reviews* 80: 205–225.
- Bowler, D. E., and T. G. Benton. 2009. "Variation in Dispersal Mortality and Dispersal Propensity among Individuals: The Effects of Age, Sex and Resource Availability." *The Journal of Animal Ecology* 78: 1234–41.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85: 1771–89.
- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. "Rapid Range Shifts of Species Associated with High Levels of Climate Warming." *Science* 333: 1024–26.
- Clobert, J. 2012. *Dispersal Ecology and Evolution*. Oxford: Oxford University Press.
- Dawson, P. S. 1977. "Life History Strategy and Evolutionary History of Tribolium Flour Beetles." *Evolution* 31: 226–29.
- Dell, A. I., S. Pawar, and V. M. Savage. 2011. "Systematic Variation in the Temperature Dependence of Physiological and Ecological Traits." *Proceedings of the National Academy of Sciences* 108: 10591–96.
- den Van Bosch, F., J. A. Metz, and O. Diekmann. 1990. "The Velocity of Spatial Population Expansion." *Journal of Mathematical Biology* 28: 529–565.
- Gibert, J. P., M. C. Chelini, M. F. Rosenthal, and J. P. DeLong. 2016. "Crossing Regimes of Temperature Dependence in Animal Movement." *Global Change Biology* 22: 1722–36.
- Grainger, T., and K. Breslin. 2025. "Data for: Warming Speeds Up Range Expansion in an Experimental Model System." Dryad. [Dataset]. <http://doi.org/10.5061/dryad.gf1vhhn0v>.
- Grainger, T. N., A. I. Rego, and B. Gilbert. 2018. "Temperature-Dependent Species Interactions Shape Priority Effects and the Persistence of Unequal Competitors." *The American Naturalist* 191: 197–209.

- Hannigan, S., C. Nendel, and M. Krull. 2023. "Effects of Temperature on the Movement and Feeding Behaviour of the Large Lupine Beetle, *Sitona gressorius*." *Journal of Pest Science* 96: 389–402.
- Harrison, R. G. 1980. "Dispersal Polymorphisms in Insects." *Annual Review of Ecology and Systematics* 11: 95–118.
- Hastings, A., K. Cuddington, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. Freestone, S. Harrison, et al. 2005. "The Spatial Spread of Invasions: New Developments in Theory and Evidence." *Ecology Letters* 8: 91–101.
- Hufbauer, R. A., M. Szűcs, E. Kasyon, C. Youngberg, M. J. Koontz, C. Richards, T. Tuff, and B. A. Melbourne. 2015. "Three Types of Rescue Can Avert Extinction in a Changing Environment." *Proceedings of the National Academy of Sciences* 112: 10557–62.
- IPCC. 2023. *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by Core Writing Team, H. Lee and J. Romero, 35–115. Geneva: IPCC. <https://doi.org/10.59327/IPCC/AR6-9789291691647>.
- Ives, A. R., B. Dennis, K. L. Cottingham, and S. R. Carpenter. 2003. "Estimating Community Stability and Ecological Interactions from Time-Series Data." *Ecological Monographs* 73: 301–330.
- Ju, R.-T., F. Wang, and B. Li. 2011. "Effects of Temperature on the Development and Population Growth of the Sycamore Lace Bug, *Corythucha ciliata*." *Journal of Insect Science* 11: 16.
- Kerr, J. T. 2020. "Racing against Change: Understanding Dispersal and Persistence to Improve Species' Conservation Prospects." *Proceedings of the Royal Society of London. Series B, Biological Sciences* 287: 20202061.
- Lang, B. J., J. M. Donelson, C. F. Caballes, S. Uthicke, P. C. Doll, and M. S. Pratchett. 2022. "Effects of Elevated Temperature on the Performance and Survival of Pacific Crown-of-Thorns Starfish (*Acanthaster cf. solaris*)." *Marine Biology* 169: 43.
- Legault, G., M. E. Bitters, A. Hastings, and B. A. Melbourne. 2020. "Interspecific Competition Slows Range Expansion and Shapes Range Boundaries." *Proceedings of the National Academy of Sciences* 117: 26854–60.
- Leroux, S. J., M. Larrivé, V. Boucher-Lalonde, A. Hurford, J. Zuloaga, J. T. Kerr, and F. Lutscher. 2013. "Mechanistic Models for the Spatial Spread of Species under Climate Change." *Ecological Applications* 23: 815–828.
- Li, W., N. H. Bashir, M. Naeem, R. Tian, X. Tian, and H. Chen. 2024. "Age-Stage, Two-Sex Life Table of *Atractomorpha lata* (Orthoptera: Pyrgomorphidae) at Different Temperatures." *Insects* 15: 493.
- Lustenhouwer, N., F. Moerman, F. Altermatt, R. D. Bassar, G. Bocedi, D. Bonte, S. Dey, et al. 2023. "Experimental Evolution of Dispersal: Unifying Theory, Experiments and Natural Systems." *The Journal of Animal Ecology* 92: 1113–23.
- Melbourne, B. A., and A. Hastings. 2009. "Highly Variable Spread Rates in Replicated Biological Invasions: Fundamental Limits to Predictability." *Science* 325: 1536–39.
- Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar. 2008. "Mechanisms of Long-Distance Seed Dispersal." *Trends in Ecology & Evolution* 23: 638–647.
- O'Connor, M. I., J. F. Bruno, S. D. Gaines, B. S. Halpern, S. E. Lester, B. P. Kinlan, and J. M. Weiss. 2007. "Temperature Control of Larval Dispersal and the Implications for Marine Ecology, Evolution, and Conservation." *Proceedings of the National Academy of Sciences* 104: 1266–71.
- Park, T., and M. B. Frank. 1948. "The Fecundity and Development of the Flour Beetles, *Tribolium confusum* and *Tribolium castaneum*, at Three Constant Temperatures." *Ecology* 29: 368–374.
- Pellissier, L. 2015. "Stability and the Competition-Dispersal Trade-off as Drivers of Speciation and Biodiversity Gradients." *Frontiers in Ecology and Evolution* 3: 52.
- Pointer, M. D., M. J. Gage, and L. G. Spurgin. 2021. "Tribolium Beetles as a Model System in Evolution and Ecology." *Heredity* 126: 869–883.
- Ramalho, Q., M. M. Vale, S. Manes, P. Diniz, A. Malecha, and J. A. Prevedello. 2023. "Evidence of Stronger Range Shift Response to Ongoing Climate Change by Ectotherms and High-Latitude Species." *Biological Conservation* 279: 109911.
- Ronce, O. 2007. "How Does it Feel to be like a Rolling Stone? Ten Questions about Dispersal Evolution." *Annual Review of Ecology, Evolution, and Systematics* 38: 231–253.
- Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. "Effects of Body Size and Temperature on Population Growth." *American Naturalist* 163: 429–441.
- Skellam, J. G. 1951. "Random Dispersal in Theoretical Populations." *Biometrika* 38: 196–218.
- Skourti, A., N. G. Kavallieratos, and N. E. Papanikolaou. 2019. "Laboratory Evaluation of Development and Survival of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) under Constant Temperatures." *Journal of Stored Products Research* 83: 305–310.
- Sunde, J., M. Franzén, P.-E. Betzholtz, Y. Francioli, L. B. Pettersson, J. Pöyry, N. Ryrholm, and A. Forsman. 2023. "Century-Long Butterfly Range Expansions in Northern Europe Depend on Climate, Land Use and Species Traits." *Communications Biology* 6: 601.
- Trakhtenbrot, A., R. Nathan, G. Perry, and D. M. Richardson. 2005. "The Importance of Long-Distance Dispersal in Biodiversity Conservation." *Diversity and Distributions* 11: 173–181.
- Travis, J. M., M. Delgado, G. Bocedi, M. Bague, K. Bartoń, D. Bonte, J. M. J. Travis, et al. 2013. "Dispersal and Species' Responses to Climate Change." *Oikos* 122: 1532–40.
- Usui, T., and A. L. Angert. 2024. "Range Expansion Is both Slower and more Variable with Rapid Evolution across a Spatial Gradient in Temperature." *Ecology Letters* 27: e14406.
- Van Allen, B. G., and V. H. Rudolf. 2013. "Ghosts of Habitats Past: Environmental Carry-over Effects Drive Population Dynamics in Novel Habitat." *American Naturalist* 181: 596–608.
- Weiss, L., M. Barbour, and T. N. Grainger. 2025. "An Experimental Test of the Effects of Temperature and Resource Quality on Carrying Capacity." *Biology Letters* 21: 20250380.
- Weiss-Lehman, C., R. A. Hufbauer, and B. A. Melbourne. 2017. "Rapid Trait Evolution Drives Increased Speed and Variance in Experimental Range Expansions." *Nature Communications* 8: 14303.
- Williams, J. L., B. E. Kendall, and J. M. Levine. 2016. "Rapid Evolution Accelerates Plant Population Spread in Fragmented Experimental Landscapes." *Science* 353: 482–85.
- Wright, E. R., K. D. Chase, and S. F. Ward. 2024. "Quantifying the Potential for Wind and Phoresy to Drive off-Plant Movement of Crapemyrtle Bark Scale, *Acanthococcus lagerstroemiae* (Kuwana) (Hemiptera: Eriococcidae): Implications for Spread in Urban Landscapes." *Agricultural and Forest Entomology* 26: 210–17.

Zhou, P., X. Z. He, C. Chen, and Q. Wang. 2024. "Age and Density of Mated Females Affect Dispersal Strategies in Spider Mite *Tetranychus ludeni* Zacher." *Insects* 15: 387.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Breslin, Kayley, and Tess N. Grainger. 2026. "Warming Speeds up Range Expansion in an Experimental Model System." *Ecology* 107(2): e70313. <https://doi.org/10.1002/ecy.70313>