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RESEARCH ARTICLE

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Community context and dispersal stochasticity drive variation in spatial spread

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Abstract

1. Dispersal is a key process in shaping species spatial distributions. Species interactions and variation in dispersal probabilities may jointly influence species spatial dynamics.
2. However, many studies examine dispersal as a neutral process, independent of community context or intraspecific variation in dispersal behaviour.
3. Here, we use controlled, replicated communities of two *Tribolium* species (*T. castaneum* and *T. confusum*) to examine how intraspecific variation in dispersal behaviour and community context influence dispersal dynamics in simple experimental landscapes composed of homogeneous habitat patches.
4. We found considerable individual-level variation in dispersal probability that was unrelated to body size variation. Further, the context of dispersal mattered, as *T. castaneum* dispersal was reduced in two-species communities, while *T. confusum* dispersal was unaffected by community composition. Incorporating individual-level variation into a two-species stochastic spatial Ricker model, we provide evidence that individual-level variability in dispersal behaviour results in more variable spatial spread than assuming individuals have the same dispersal probability. Further, interspecific competition resulted in more variable spatial spread.
5. The variability in spatial spread observed in our tightly controlled and replicated experimental system and in our stochastic model simulations points to potential fundamental limitations in forecasting species shifting ranges without considering potential interspecific interactions and demographic variability in dispersal behaviour.

KEYWORDS

dispersal kernel, intraspecific variation, spatial spread, species interactions, *Tribolium*

1 | INTRODUCTION

Dispersal—defined here as individual movement and colonization of habitat patches away from the origin—is a key ecological process that can influence range boundaries (Boyle et al., 2014), metapopulation persistence (Johst et al., 2002) and invasion success (Skarpaas & Shea, 2007). Dispersal maintains genetic diversity between connected populations, and is responsible for both stabilizing and destabilizing (Abbott, 2011; Wang et al., 2015) interconnected populations, depending on the amount of dispersal. An understanding of a species' dispersal kernel shape can allow for mechanistic modelling of population demography and spatial spread (Morales & Carlo, 2006), which can aid conservation and management efforts, and help forecast potential range shifts. However, quantifying dispersal kernels is difficult, because dispersal behaviour is determined by environmental conditions (Massot et al., 2002), species interactions (Berg et al., 2010), species characteristics (Padial et al., 2014) and individual-level variation (Willson & Whelan, 1993).

For instance, species vary in their dispersal ability (e.g. probability or dispersal distance) as a function of body size (Jenkins et al., 2007), reproductive fitness (Lavie & Ritte, 1978) and evolutionary history (Bonte & Dahirel, 2016; Pellissier, 2015; Ritte & Lavie, 1977), corresponding to a species characteristic which influences dispersal processes. While species-level variation will influence species spread, it is likely to do so in a density-independent manner, especially relative to individual-level variation in dispersal probability (Maes et al., 2013). This intraspecific variation in dispersal behaviour has been previously associated with individual-level variation in species traits (e.g. body size McCauley & Mabry, 2011), but is potentially a result of animal personalities (Bestion et al., 2015), stochasticity or species interactions.

While dispersal distance is a continuous quantity, the initiation of dispersal is binary (i.e. did the individual disperse or not?). Scaling to the individual level, this suggests that two identical populations would still vary in their spatial spread as a function of stochasticity in dispersal initiation, assuming all dispersal events resulted in movement of a fixed distance. This would suggest that stochasticity in dispersal decisions could set fundamental limits on our ability to forecast spatial spread, and that these effects are most pronounced for small founder populations. Previous efforts have demonstrated that individual-level variation in dispersal behaviour can enhance variability in species spatial spread dynamics (Giometto et al., 2014), especially given relatively small founding populations (Lutz et al., 2015). Recognizing stochasticity in dispersal decisions is important, but there may also be underlying variation in the probability that an individual disperses. This suggests that apart from the stochasticity in dispersal dynamics due to dispersal being probabilistic, individual-level variation in this dispersal probability can further influence potential spatial spread. Both of these effects would disproportionately affect small population sizes.

If individual dispersal decisions could be replicated, it would be possible to estimate dispersal probability. This would be the starting point for examining how stochasticity influences potential spatial spread, as intraspecific variation in individual dispersal probabilities could strongly affect spatial population dynamics. One hypothesis is that dispersal is a neutral process, such that individual variation in dispersal probability is driven by stochasticity, creating an intriguing null expectation that dispersal probability is the same for all individuals. This is discussed, and ultimately rejected as the sole driver of dispersal (Lowe & McPeek, 2014), though it seems like stochasticity (a neutral process) is partly driving individual dispersal behaviour (e.g. Mohd et al., 2016). The second hypothesis would be that variation in dispersal probability is related to species trait (Stevens et al., 2010). That is, individual dispersal behaviour may be determined by the individual's ability to disperse, which may have a trait basis (e.g. longer legs, larger body size). This does not exclude the existence of stochasticity in dispersal, but would provide some trait structure to individual dispersal probabilities. Finally, individual dispersal behaviour may also be constrained by the presence or density of a competing species (Svenning et al., 2014). This would suggest that the composition of the local community can influence dispersal of another species, either through modifications to intraspecific density or through direct effects of competitor density on dispersal behaviour.

Weighing support for these different hypotheses around individual dispersal probability variation requires controlled and replicated multi-patch landscapes, and a well-developed stochastic model in order to provide estimates of spatial spread variability over time. Here, we aimed to address two main questions. First, what are the relative roles of community context and intraspecific trait variation in determining species dispersal propensity? Second, what are the consequences of this individual dispersal variation on subsequent spatial spread? Combining a theoretical spatial spread model with replicated laboratory microcosms of single or multi-species communities of *Tribolium* species, we demonstrate the existence of individual variation in dispersal probability, examine how community composition influences dispersal probability and explore the consequences of this variation in spatial spread. Together, our replicated experimental trials and model simulations suggest that intraspecific variation in dispersal probability exists even in tightly controlled laboratory populations, and that this variation is unrelated to individual body size, but is related to community composition. Simulating spatial spread of populations embedded in local communities of interacting species, and incorporating realistic variation in individual dispersal propensity, we uncover fundamental limits to the predictability of spatial spread dynamics. This forecast limitation is largely due to individual variation in dispersal propensity, though we also demonstrate how the local community may also influence spatial spread dynamics. It is clear that individual variation in dispersal probability can strongly influence spatial spread, which may become especially important if dispersal propensity is inherited, and when founding population sizes are small. Understanding the amount of variation present in intraspecific dispersal propensity may help provide expected lower and upper bounds on spatial spread estimates.

2 | MATERIALS AND METHODS

2.1 | Dispersal experiment

Flour beetles (*Tribolium castaneum* and *Tribolium confusum*) were obtained from long-running laboratory populations maintained in 4 × 4 × 6 cm enclosures. Each enclosure consisted of 30 ml of flour and yeast medium (95% wheat flour and 5% brewer's yeast by volume), which serves as both habitat and resource to flour beetles. Stock populations were maintained at 30°C and ≈50% relative humidity. We enforced non-overlapping generations in accordance with previous *Tribolium* experiments (Melbourne & Hastings, 2008, 2009). This results in the removal of age-dependent dispersal effects, as all adult beetles used in the experiment were the same age.

To examine the existence and consequences of individual-level variation in dispersal and community context on spatial spread, we set up landscapes of patches connected by small dispersal channels (3.97 mm diameter) connected to neighbouring patches with slightly larger dispersal channels (5.56 mm) to facilitate proper patch alignment. Each landscape consisted of four patches joined together in a linear array. A single patch was a 4 cm × 4 cm × 6 cm acrylic container with 20 g of standard medium (95% flour, 5% brewer's yeast). Populations consisted of either six individuals of either *T. castaneum* or *T. confusum*, or of a mixture of three individuals of both species. We created 20 landscapes for each treatment level, resulting in a total of 60 landscapes (240 patches).

Experimental trials were performed by introducing experimental beetle populations to the terminal end of the landscape, and allowing a 24-hr dispersal phase. Beetles of both species were the same age (35 days old) at the start of the experiment. To obtain individual-level data on beetle movements, we marked beetles with a small amount of non-toxic paint. We failed to detect an effect of marking beetles on dispersal tendency (see Supporting Information; Figure S1). After each 24-hr dispersal period, thin acrylic sheeting was inserted between patches to stop dispersal, and the number of patches travelled was recorded. To remove the effect of chemical cues on dispersal behaviour, beetles were placed in a fresh landscape for each 24-hr dispersal trial. Experimental trials were replicated 10 times, which produces 10 estimates of dispersal distance for each beetle in the experimental landscapes. However, the majority (over 95%) of beetles only travelled one patch. Given the rarity of multi-patch dispersal, we simplify our analyses by treating dispersal as binary here (i.e. did the beetle disperse or not?). However, we investigate the number of patches beetles dispersed in the Supporting Information. Body length was measured for each beetle at the beginning of the experiment. We used a logistic mixed effects model regression (`nlme` in R Pinheiro et al., 2019) to investigate dispersal probability as a function of body length and experimental treatment, controlling for landscape-level and individual-level variability by including landscape and individual as random effects. Specifically, we considered a random intercept model, with the individual random effect nested within the random effect of landscape. More information on the random effects model is provided in the Supporting Information.

2.2 | Spatial spread model

Local populations of *T. castaneum* (*S*) and *T. confusum* (*F*) were modeled using a discrete time Ricker model. We explored two different models to examine the effect of stochastic local population dynamics relative to the effect of stochasticity in dispersal (and variable dispersal probabilities). The first model only contained demographic stochasticity (Poisson Ricker model). The second model is more complex, and incorporates demographic and environmental stochasticity, demographic heterogeneity and stochastic sex determination. This model—the `NBBg` model Melbourne and Hastings (2008)—was previously found to provide the best fit to experimental *Tribolium* populations (Melbourne & Hastings, 2008) and communities (Dallas et al., 2020).

Demographic stochasticity was incorporated by allowing the number of offspring to be a Poisson random variable and the population size in the next generation modelled as a binomial process with probability of survival proportional to the effect of intraspecific and interspecific competition. Environmental stochasticity and demographic heterogeneity were incorporated by allowing the distribution of birth rates to vary according to a gamma distribution, either dependent on species density (demographic heterogeneity; k_D) or independent of density (environmental stochasticity; k_E). Finally, stochastic sex determination was incorporated by considering the number of females to be binomially distributed with some probability *p*. Details about model development and parameterization are provided elsewhere (Dallas et al., 2020; Melbourne & Hastings, 2008). Model parameters (Table S1) and further discussion of model structure are provided in the Supporting Information. The analogous deterministic model for local populations is:

$$\begin{aligned} S_{t+1} &= S_t \, R_S \, e^{-(\alpha_{SS} S_t + \alpha_{SF} F_t)} \\ F_{t+1} &= F_t \, R_F \, e^{-(\alpha_{FF} F_t + \alpha_{FS} S_t)}. \end{aligned} \tag{1}$$

After local populations grow according to the stochastic version of Equation 1, individuals are allowed to disperse. Dispersal was modelled as a bi-directional process following some probability (d_S or d_F). Dispersing individuals moved one patch per time step, either towards the expanding edge or towards the range centre. The number of dispersing individuals was a binomial random variable with some probability of dispersal (d_F or d_S). The fraction of dispersing individuals moving towards expanding edge or range centre was controlled by the parameter ζ. We considered ζ to be 0.75 unless otherwise specified, but explored the effect of ζ on spatial spread in the Supporting Information.

We used our simulation model to examine the role of intraspecific variability and interspecific effects on dispersal probabilities and spatial spread. To do this, we simulated spatial spread of single and multi-species communities for 40 generations. Model simulations were initiated with 40 individuals for single species simulations, or 20 individuals of each species for multi-species simulations. Landscapes consisted of 100 patches, well beyond the maximum spread observed in any simulation. For each parameter combination, we simulated 5,000 landscapes.

2.3 | Individual-level variation in dispersal probability and spatial spread

Intraspecific variability in individual dispersal rate could have important implications for spatial spread, especially in small founding populations. We incorporated intraspecific variability in dispersal rates by randomly sampling dispersal rates from the distribution of dispersal probabilities observed in experimental landscapes. Dispersal probabilities were estimated as the number of times an individual dispersed divided by the number of experimental days. Growth rates and competition coefficients were based on previous estimates using the same experimental populations (Dallas et al., 2020; Table S1). We examined the effect of individual-level variation in dispersal probability by simulating spatial spread of two interacting species in replicated 100-patch landscapes (n = 5,000) for 40 generations. Each generation, dispersal was either constant, using the mean dispersal for each species, or was sampled from the distribution of dispersal probabilities for each species.

2.4 | The local community and spatial spread

The community context of dispersal is important, as interspecific interactions may influence dispersal behaviour through competition or chemical signalling. We examined this in a general sense by simulating 100-patch landscapes of the two *Tribolium* species, with all demographic rates parameterized from previous experiments. We controlled the interspecific effects on dispersal through the introduction of two parameters (d_{SF} and d_{FS}), which function as density-dependent dispersal reduction terms. Dispersal rates were sampled from the empirical distributions for each species, and spatial spread was simulated for 40 generations. We further examined the effect of interspecific interactions on reduced dispersal in the Supporting Information.

3 | RESULTS

3.1 | Variation in dispersal probability in experimental landscapes

Individual dispersal varied considerably, with many individuals never dispersing, and some individuals dispersing repeatedly throughout the course of the experiment (Figure 1). Based on our logistic mixed effects model, there was a positive relationship between dispersal probability and experimental day, suggesting that individuals tended to disperse more often in the later days of the experiment, which potentially relates to age-dependent dispersal (Table 1). We failed to detect a relationship between individual trait variation (i.e. body length) and dispersal probability (see Supporting Information), but did find that *T. castaneum* dispersal was reduced in the presence of *T. confusum*, owing to either interspecific interactions or to intraspecific density effects (Figure 2).

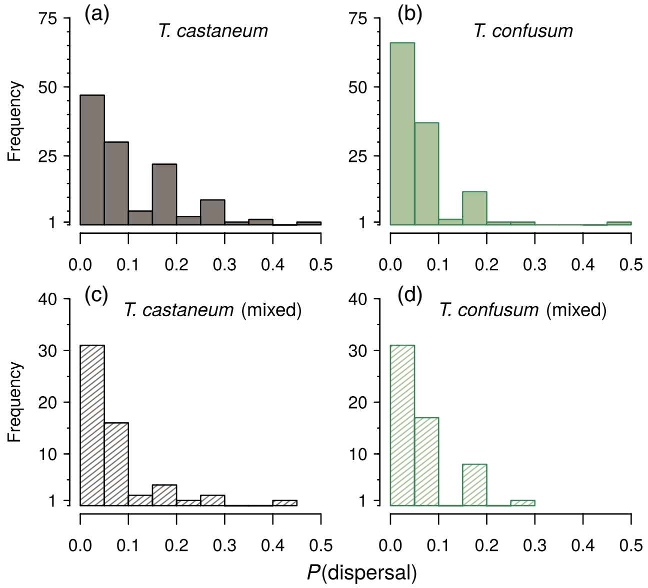

FIGURE 1 Dispersal probabilities were highly variable, with most individuals never dispersing throughout the experimental period, and some individuals dispersing multiple times. The community context was important (panels c and d), as Tribolium confusum reduced Tribolium castaneum dispersal probability, either as a function of interspecific effects (e.g. competition) or because of intraspecific density dependence (assuming T. castaneum cued more to its own density than the overall density of competing individuals)

3.2 | Individual-level variation in dispersal probability and spatial spread

We simulated our two-species Ricker model—incorporating the four sources of stochasticity discussed above—for populations embedded in a landscape of 100 habitat patches, as well as for a simplified Ricker model only incorporating demographic stochasticity. Spatial model simulations revealed that the distance travelled by

TABLE 1 Logistic mixed effects model of dispersal as a function of experimental treatment (*Tribolium castaneum* and *Tribolium confusum* either in isolation or two-species communities), experimental day and individual body length. Dispersal increased over time, and *T. castaneum* dispersed more often than *T. confusum*, though this effect disappears in the two-species (mixed) treatment. Landscape and individual are included as random effects. Bolded *p*-values indicate significance assessed at α = 0.05

Treatment	Estimate	*SE*	*t*	*p*
T. castaneum	0.039	0.017	2.35	**0.021**
T. confusum (mixed)	0.006	0.018	0.35	0.73
T. castaneum (mixed)	0.0130	0.018	0.70	0.48
Body length	−0.005	0.018	−0.30	0.77
Experimental day	0.004	0.002	2.66	**0.008**

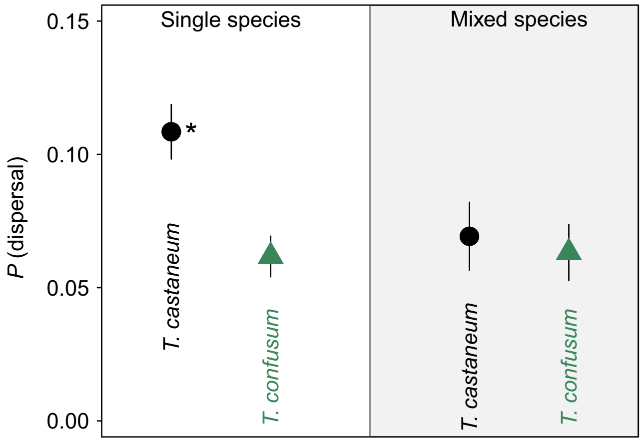

FIGURE 2 The probability of dispersal was strongly reduced when *Tribolium castaneum* was allowed to interact with *Tribolium confusum*, while *T. confusum* dispersal was unaffected. The star symbol (*) corresponds to significant differences at α = 0.05

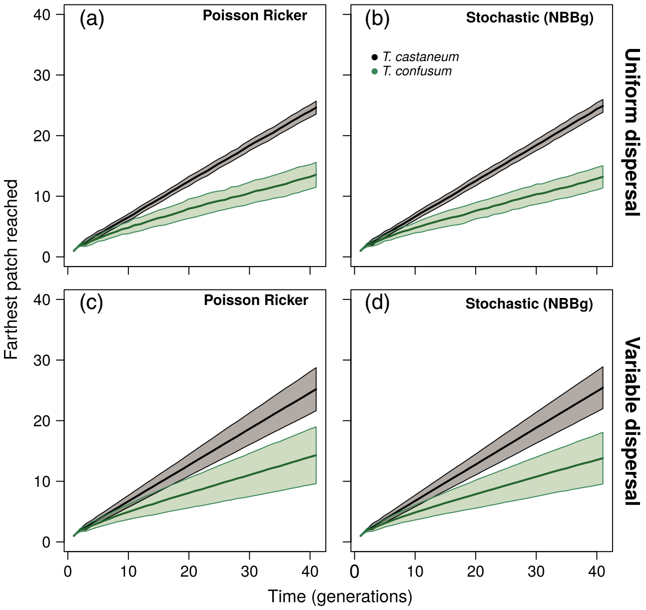

FIGURE 3 Incorporating individual-level variability in dispersal probabilities (c and d) lead to more variation in the most distant patch reached (*y*-axis) over the course of 40 generations (*x*-axis) relative to assuming each individual had the same dispersal probability (a and b). Individual dispersal variation was far more important than the incorporation of environmental stochasticity, environmental heterogeneity and stochastic sex determination in the *Stochastic* (*NBBg*) model (panels b and d) relative to a model only incorporating demographic stochasticity (*Poisson Ricker*)

the dispersing species was more variable when dispersal probability was drawn from the set of individual dispersal probabilities obtained from experimental trials compared to the neutral assumption treating species dispersal probability as constant (Figure 3). Further, incorporating multiple forms of stochasticity did not influence spatial spread nearly as much as individual-scale variation in dispersal behaviour, suggesting that demographic and environmental stochasticity may influence local population dynamics strongly, but treating dispersal as a stochastic process with variable intraspecific dispersal probabilities yielded far more variable spatial spread relative to assuming constant dispersal probabilities among individuals.

3.3 | The community context of spatial spread

Interspecific interactions can potentially influence spatial spread variability through the direct impacts of competition on species population growth rates, or by altering dispersal behaviour. In our experimental landscapes, the reduction in *T. castaneum* dispersal in the presence of *T. confusum* could be due to interspecific interactions, or through intraspecific density dependence of *T. castaneum*. That is, while overall density was held constant, if beetles are not functionally equivalent, *T. castaneum* may 'experience' a reduced density in the presence of *T. confusum*, and density-dependent dispersal in this system would result in the observed reduction in dispersal. However, through model simulations, we found that variability, but not average distance travelled, in spatial spread was influenced by interspecific reductions in dispersal (Figure 4), with increasing competitor dispersal inhibition resulting in more variable spatial spread for both species. Dispersal inhibition was modelled as a reduction on the dispersal probability of each individual in a population of one species, dependent on the density of the competing species. Increasing interspecific competitive effects (α_{SF} and α_{FS}) did not strongly influence spatial spread dynamics (Figure S3).

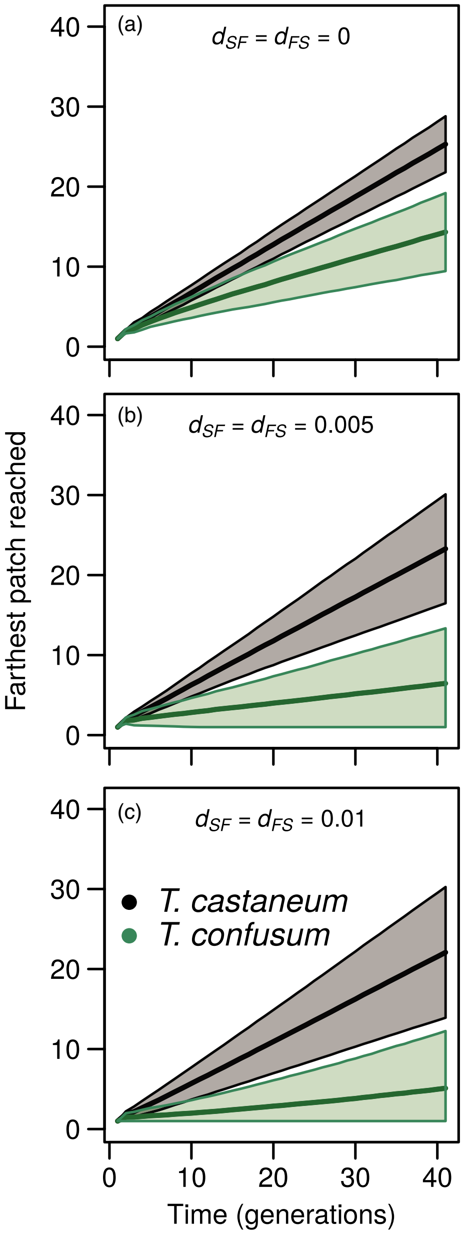

FIGURE 4 Species interactions may influence dispersal behaviour of a competing species, incorporated into our model using interspecific dispersal inhibition terms d_{SF} and d_{FS}. Relative to a case where dispersal was unaffected by interspecific competition (panel a), small changes to dispersal inhibition through interspecific competition resulted in much more variation in the spatial spread of both species (panels b and c)

4 | DISCUSSION

Understanding the variability and speed of spatial spread is a pressing need in both basic and applied ecology, as dispersal variability limits our intrinsic ability to predict spatial spread, with obvious applied consequences to the management of endangered or invasive species. Here, we examined how spatial spread is influenced by community composition and intraspecific variation in dispersal probabilities, finding that *Tribolium* species varied in their dispersal rates at the individual level, and that dispersal was reduced for one species when allowed to interact with a competitor. This builds on existing work in the *Tribolium* system suggesting that stochasticity can set clear limits to the predictability of spatial spread in single species systems (Melbourne & Hastings, 2009). In simulations of a stochastic multi-patch Ricker model, we found that intraspecific variation in dispersal probability strongly influenced variability in spatial spread, and that this variation was highest when founding population size was small (Figure S4). Density-dependent dispersal inhibition resulted in more variable spatial spread, likely as a direct result of the stochasticity in population dynamics leading to variable density-dependent effects of species on one another. That is, a sudden increase in population size would strongly decrease spatial spread of the competing species through density-dependent effects, which can be seen in the reduced slope of *T. confusum* under increased dispersal inhibition of the faster growing *T. castaneum*. Together, our findings suggest that both intraspecific variation and community effects can influence variability and speed of spatial spread. Given the increasing importance of prediction in ecology, we must account for uncertainty in spread rates as a result of the influence of species interactions and intraspecific variation in dispersal.

Intraspecific variability in individual dispersal probability has the ability to alter spatial spread (Kautz et al., 2016) at the population level, especially when founding populations are small (Hastings et al., 2005). Previously, Melbourne and Hastings (2009) found that variability in spatial spread of *Tribolium* beetles was a result of stochasticity in demographic processes. Here, we present evidence that intraspecific variability in dispersal behaviour could result in the same degree of variation in spatial spread, independent of local population demographics. Understanding the basis for this variability in dispersal behaviour can provide insight into when founding populations would be expected to spread and has implications for species invasion success. Further, if there was a genetic basis for dispersal propensity, independent of individual morphology, the spatial landscape of genetic diversity of a spreading population would favour certain genotypes at the leading edge of the expansion creating more variability in spatial spread than what we observed (Weiss-Lehman et al., 2019).

We failed to detect a relationship between dispersal probability and individual body size, a relationship that has been previously observed in bird species (Steyn et al., 2016). In the *Tribolium* model system, leg length was found to be related to individual movement in a maze-like environment (Arnold et al., 2017), suggesting that perhaps other morphological measures could explain dispersal behaviour or propensity. Regardless of the potential morphological basis, the observed variation in dispersal probability suggests that certain individuals are more prone to disperse than others, suggesting that dispersal is not a result of neutral dynamics—discussed in detail in Lowe and McPeek (2014)—and that dispersal probability may have a basis in phenotypic traits or physiological tolerances (Bestion et al., 2015). A final consideration is that animal personality drives variation in dispersal propensity, leading to intraspecific variation important for spatial spread (Sih et al., 2015). This is difficult to quantify and disentangle from stochasticity and species traits, but is also an important source of intraspecific variation in dispersal behaviour.

Whereas intraspecific variation in dispersal propensity influences spatial spread largely for smaller populations, the effect of interspecific interactions on spatial spread may be relatively insensitive to species density. This adds an interesting aspect to current examinations of the influence of biotic interactions on determining species range boundaries (Svenning et al., 2014; Urban et al., 2013), as it suggests that interspecific interactions at the intersecting range margins of two competing species may contribute to setting geographic range boundaries, and interspecific interactions in co-occurring species may influence species dispersal and range expansion or contraction. This suggests the intriguing possibility that the ability of a population to track favourable abiotic conditions could be influenced by the existing community. In the case of *dispersal antagonism*—where the presence or density of a competing species slows or prevents dispersal of another species—as observed in our experiment, a species may be slowed at its trailing edge by interactions with novel competitors (leading to populations which potentially fail to track climate), or pushed back against as species spread into new geographic areas with a different set of competing species. Further, if two species with similar environmental tolerances were tracking the environment together, dispersal antagonism might link dispersal dynamics across species, such that the rates of spatial spread become correlated between species (Svenning et al., 2014; Thomas, 2010). In an extreme case, populations released from species interactions may spread faster, resulting in disjunct populations and a potentially measurable difference in spatial spread rates as a function of competitor presence or density. Experiments aimed at disentangling the effects of intraspecific variation in density and interspecific interactions leading to altered spatial spread will contribute important information on the functional equivalence of competing species in interactive communities.

Inference obtained from our examination of *Tribolium* spatial population dynamics may not be directly applicable to conservation or management applications in natural systems. However, our simplified landscapes offered a means to explore the potential range of effects on spatial spread due to species interactions and dispersal variation, hopefully motivating future explorations in natural systems. Environmental effects on dispersal probability or distance are well-recognized (Parmesan, 2006; Thomas, 2010), but the relative importance of environmental conditions and intraspecific variation in dispersal probability is presently unknown. That is, variation in individual dispersal behaviour could be far more important than environmental constraints on dispersal, especially in the case of small population sizes. Understanding the role of population size on dispersal variation is an area of study deserving further attention. Second, our experiment did not attempt to determine if interspecific changes in dispersal probability were contingent upon the density of the competitor, or whether dispersal itself was dependent on species abundance. Tunnel building by *Tribolium* species creates dispersal corridors, suggesting that dispersal inhibition could be a result of either the failure to construct these tunnels due to species interactions, or the active destruction of tunnels by the competing species. While the mechanism by which dispersal inhibition occurs is currently unknown—and potentially specific to the *Tribolium* system—there are numerous ways in which species interactions could either facilitate or reduce dispersal probability and resulting spatial spread dynamics (De Meester et al., 2015; Svenning et al., 2014; Thomas, 2010). Finally, there is a clear separation between our experiment, which was run with beetles all from a single generation, and the theoretical exploration of spatial spread variability, which was simulated for many generations. This approach does not allow for the direct comparison of models fitted to spatial spread data from the experimental system, but does instead provide a clear demonstration of the existence of intraspecific dispersal variability and the potential effects of this on spatial spread dynamics.

Together, our findings suggest that even under ideal conditions—in which patch quality, environmental conditions and species abundance are controlled in replicated landscapes—individual differences in dispersal probabilities and community context can strongly influence variability in spatial spread. Understanding the mechanistic basis for dispersal facilitation or antagonism is a pressing research need, as species track a changing climate (Chen et al., 2011) and as communities change as a result of species invasions and range shifts (Lurgi et al., 2012; Williams & Jackson, 2007). Acknowledging intraspecific variability in dispersal probability and distance, as well as recognizing the influence of community composition on dispersal and spatial spread dynamics are two pressing needs, creating a clear knowledge gap. Addressing this gap will likely require the development of modelling approaches capable of capturing spatial dynamics of entire communities, and long-term monitoring efforts of communities in directionally shifting or variable environments.

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AUTHORS' CONTRIBUTIONS

T.D. designed the study. T.D., B.M. and A.H. contributed to analyses and manuscript writing.

DATA AVAILABILITY STATEMENT

Data and analytical code are available on figshare at https://doi.org/10.6084/m9.figshare.7035731.v1 (Dallas et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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