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Community context and dispersal stochasticity drive variation in spatial spread

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1 Community context and dispersal stochasticity
2 drive variation in spatial spread

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11

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14

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23

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25 spread, *Tribolium*

Author

26 Abstract

- 27 1. Dispersal is a key process in shaping species spatial distributions. Species
28 interactions and variation in dispersal probabilities may jointly influence
29 species spatial dynamics.
- 30 2. However, many studies examine dispersal as a neutral process, independent
31 of community context or intraspecific variation in dispersal behavior.
- 32 3. Here, we use controlled, replicated communities of two *Tribolium* species
33 (*T. castaneum* and *T. confusum*) to examine how intraspecific variation in
34 dispersal behavior and community context influence dispersal dynamics in
35 simple experimental landscapes composed of homogeneous habitat patches.
- 36 4. We found considerable individual-level variation in dispersal probability that
37 was unrelated to body size variation. Further, the context of dispersal mat-
38 tered, as *T. castaneum* dispersal was reduced in two-species communities,
39 while *T. confusum* dispersal was unaffected by community composition. In-
40 corporating individual-level variation into a two-species stochastic spatial
41 Ricker model, we provide evidence that individual-level variability in disper-
42 sal behavior results in more variable spatial spread than assuming individ-
43 uals have the same dispersal probability. Further, interspecific competition
44 resulted in more variable spatial spread.
- 45 5. The variability in spatial spread observed in our tightly controlled and repli-
46 cated experimental system and in our stochastic model simulations points to
47 potential fundamental limitations in forecasting species shifting ranges with-
48 out considering potential interspecific interactions and demographic variabil-
49 ity in dispersal behavior.

50 Introduction

51 Dispersal – defined here as individual movement and colonization of habitat
52 patches away from the origin – is a key ecological process that can influence range
53 boundaries (Boyle *et al.*, 2014), metapopulation persistence (Johst, Brandl & Eber,
54 2002), and invasion success (Skarpaas & Shea, 2007). Dispersal maintains genetic
55 diversity between connected populations, and is responsible for both stabilizing
56 and destabilizing (Wang, Haegeman & Loreau, 2015; Abbott, 2011) interconnected
57 populations, depending on the amount of dispersal. An understanding of a species’
58 dispersal kernel shape can allow for mechanistic modeling of population demog-
59 raphy and spatial spread (Morales & Carlo, 2006), which can aid conservation
60 and management efforts, and help forecast potential range shifts. However, quan-
61 tifying dispersal kernels is difficult, because dispersal behavior is determined by
62 environmental conditions (Massot *et al.*, 2002), species interactions (Berg *et al.*,
63 2010), species characteristics (Padial *et al.*, 2014), and individual-level variation
64 (Willson & Whelan, 1993). For instance, species vary in their dispersal ability
65 (e.g., probability or dispersal distance) as a function of body size (Jenkins *et al.*,
66 2007), reproductive fitness (Lavie & Ritte, 1978), and evolutionary history (Ritte
67 & Lavie, 1977; Pellissier, 2015; Bonte & Doherty, 2016), corresponding to a species
68 characteristic which influences dispersal processes. While species-level variation
69 will influence species spread, it is likely to do so in a density-independent man-
70 ner, especially relative to individual-level variation in dispersal probability (Maes,
71 Van Damme & Matthysen, 2013). This intraspecific variation in dispersal behav-
72 ior has been previously associated with individual-level variation in species traits
73 (e.g., body size McCauley & Mabry (2011)), but is potentially a result of animal
74 personalities (Bestion, Clobert & Cote, 2015), stochasticity, or species interactions.

75 While dispersal distance is a continuous quantity, the initiation of dispersal is
76 binary (i.e., did the individual disperse or not?). Scaling to the individual level,
77 this suggests that two identical populations would still vary in their spatial spread
78 as a function of stochasticity in dispersal initiation, assuming all dispersal events
79 resulted in movement of a fixed distance. This would suggest that stochasticity in
80 dispersal decisions could set fundamental limits on our ability to forecast spatial
81 spread, and that these effects are most pronounced for small founder populations.
82 Previous efforts have demonstrated that individual-level variation in dispersal be-
83 havior can enhance variability in species spatial spread dynamics (Giometto *et al.*,
84 2014), especially given relatively small founding populations (Lutz, Diefenbach &
85 Rosenberry, 2015). Recognizing stochasticity in dispersal decisions is important,
86 but there may also be underlying variation in the probability that an individual
87 disperses. This suggests that apart from the stochasticity in dispersal dynam-
88 ics due to dispersal being probabilistic, individual-level variation in this dispersal
89 probability can further influence potential spatial spread. Both of these effects
90 would disproportionately affect small population sizes.

91 If individual dispersal decisions could be replicated, it would be possible to es-
92 timate dispersal probability. This would be the starting point for examining how
93 stochasticity influences potential spatial spread, as intraspecific variation in indi-
94 vidual dispersal probabilities could strongly affect spatial population dynamics.
95 One hypothesis is that dispersal is a neutral process, such that individual varia-
96 tion in dispersal probability is driven by stochasticity, creating an intriguing null
97 expectation that dispersal probability is the same for all individuals. This is dis-
98 cussed, and ultimately rejected as the sole driver of dispersal (Lowe & McPeck,
99 2014), though it seems like stochasticity (a neutral process) is partly driving indi-
100 vidual dispersal behavior (e.g., Mohd *et al.* (2016)). A second hypothesis would be

101 that variation in dispersal probability is related to species trait variation (Stevens,
102 Pavoine & Baguette, 2010). That is, individual dispersal behavior may be deter-
103 mined by the individual's ability to disperse, which may have a trait basis (e.g.,
104 longer legs, larger body size). This does not exclude the existence of stochasticity
105 in dispersal, but would provide some trait structure to individual dispersal prob-
106 abilities. Finally, individual dispersal behavior may also be constrained by the
107 presence or density of a competing species (Svenning *et al.*, 2014). This would
108 suggest that the composition of the local community can influence dispersal of
109 another species, either through modifications to intraspecific density or through
110 direct effects of competitor density on dispersal behavior.

111 Weighing support for these different hypotheses around individual dispersal
112 probability variation requires controlled and replicated multi-patch landscapes,
113 and a well-developed stochastic model in order to provide estimates of spatial
114 spread variability over time. Here, we aimed to address two main questions. First,
115 what are the relative roles of community context and intraspecific trait variation
116 in determining species dispersal propensity? Second, what are the consequences
117 of this individual dispersal variation on subsequent spatial spread? Combining a
118 theoretical spatial spread model with replicated laboratory microcosms of single or
119 multi-species communities of *Tribolium* species, we demonstrate the existence of
120 individual variation in dispersal probability, examine how community composition
121 influences dispersal probability, and explore the consequences of this variation in
122 spatial spread. Together, our replicated experimental trials and model simulations
123 suggest that intraspecific variation in dispersal probability exists even in tightly
124 controlled laboratory populations, and that this variation is unrelated to individual
125 body size, but is related to community composition. Simulating spatial spread of
126 populations embedded in local communities of interacting species, and incorporat-

127 ing realistic variation in individual dispersal propensity, we uncover fundamental
128 limits to the predictability of spatial spread dynamics. This forecast limitation is
129 largely due to individual variation in dispersal propensity, though we also demon-
130 strate how the local community may also influence spatial spread dynamics. It is
131 clear that individual variation in dispersal probability can strongly influence spatial
132 spread, which may become especially important if dispersal propensity is inher-
133 ited, and when founding population sizes are small. Understanding the amount of
134 variation present in intraspecific dispersal propensity may help provide expected
135 lower and upper bounds on spatial spread estimates.

136 **Methods**

137 **Dispersal experiment**

138 Flour beetles (*T. castaneum* and *T. confusum*) were obtained from long-running
139 laboratory populations maintained in $4 \times 4 \times 6$ cm enclosures. Each enclosure
140 consisted of 30 mL of flour and yeast medium (95% wheat flour and 5% brewer's
141 yeast by volume), which serves as both habitat and resource to flour beetles. Stock
142 populations were maintained at 30 °C and $\approx 50\%$ relative humidity. We enforced
143 non-overlapping generations in accordance with previous *Tribolium* experiments
144 (Melbourne & Hastings, 2008, 2009). This results in the removal of age-dependent
145 dispersal effects, as all adult beetles used in the experiment were the same age.

146 To examine the existence and consequences of individual-level variation in dis-
147 persal and community context on spatial spread, we set up landscapes of patches
148 connected by small dispersal channels (3.97 mm diameter) connected to neighbor-
149 ing patches with slightly larger dispersal channels (5.56mm) to facilitate proper
150 patch alignment. Each landscape consisted of four patches joined together in a

151 linear array. A single patch was a 4 cm × 4 cm × 6 cm acrylic container with
152 20g of standard medium (95% flour, 5% brewer's yeast). Populations consisted
153 of either six individuals of either *T. castaneum* or *T. confusum*, or of a mixture
154 of three individuals of both species. We created 20 landscapes for each treatment
155 level, resulting in a total of 60 landscapes (240 patches).

156 Experimental trials were performed by introducing experimental beetle popula-
157 tions to the terminal end of the landscape, and allowing a 24 hour dispersal phase.
158 Beetles of both species were the same age (35 days old) at the start of the exper-
159 iment. To obtain individual-level data on beetle movements, we marked beetles
160 with a small amount of non-toxic paint. We failed to detect an effect of mark-
161 ing beetles on dispersal tendency (see Supplemental Material, Figure S1). After
162 each 24 hour dispersal period, thin acrylic sheeting was inserted between patches
163 to stop dispersal, and the number of patches traveled was recorded. To remove
164 the effect of chemical cues on dispersal behavior, beetles were placed in a fresh
165 landscape for each 24 hour dispersal trial. Experimental trials were replicated 10
166 times, which produces 10 estimates of dispersal distance for each beetle in the
167 experimental landscapes. However, the majority (over 95%) of beetles only trav-
168 eled one patch. Given the rarity of multi-patch dispersal, we simplify our analyses
169 by treating dispersal as binary here (i.e., did the beetle disperse or not?). How-
170 ever, we investigate the number of patches beetles dispersed in the Supplemental
171 Materials. Body length was measured for each beetle at the beginning of the ex-
172 periment. We used a logistic mixed effects model regression (`nlme` in *R* Pinheiro
173 *et al.* (2019)) to investigate dispersal probability as a function of body length and
174 experimental treatment, controlling for landscape-level and individual-level vari-
175 ability by including landscape and individual as random effects. Specifically, we
176 considered a random intercept model, with the individual random effect nested

177 within the random effect of landscape. More information on the random effects
178 model is provided in the Supplemental Material.

179 **Spatial spread model**

180 Local populations of *T. castaneum* (*S*) and *T. confusum* (*F*) were modeled using
181 a discrete time Ricker model. We explored two different models to examine the
182 effect of stochastic local population dynamics relative to the effect of stochasticity
183 in dispersal (and variable dispersal probabilities). The first model only contained
184 demographic stochasticity (Poisson Ricker model). The second model is more com-
185 plex, and incorporates demographic and environmental stochasticity, demographic
186 heterogeneity, and stochastic sex determination. This model – the NBBg model
187 Melbourne & Hastings (2008) – was previously found to provide the best fit to ex-
188 perimental *Tribolium* populations (Melbourne & Hastings, 2008) and communities
189 (Dallas *et al.*, 2019).

190 Demographic stochasticity was incorporated by allowing the number of offspring
191 to be a Poisson random variable and the population size in the next generation
192 modeled as a binomial process with probability of survival proportional to the
193 effect of intraspecific and interspecific competition. Environmental stochasticity
194 and demographic heterogeneity were incorporated by allowing the distribution of
195 birth rates to vary according to a gamma distribution, either dependent on species
196 density (demographic heterogeneity; k_D) or independent of density (environmental
197 stochasticity; k_E). Finally, stochastic sex determination was incorporated by con-
198 sidering the number of females to be binomially distributed with some probability
199 p . Details about model development and parameterization are provided elsewhere
200 (Melbourne & Hastings, 2008; Dallas *et al.*, 2019). Model parameters (Table S1)
201 and further discussion of model structure are provided in the Supplemental Mate-

202 rials. The analogous deterministic model for local populations is:

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

203 After local populations grow according to the stochastic version of Equation
204 1, individuals are allowed to disperse. Dispersal was modeled as a bi-directional
205 process following some probability (d_S or d_F). Dispersing individuals moved one
206 patch per time step, either towards the expanding edge or towards the range center.
207 The number of dispersing individuals was a binomial random variable with some
208 probability of dispersal (d_F or d_S). The fraction of dispersing individuals moving
209 towards expanding edge or range center was controlled by the parameter ζ . We
210 considered ζ to be 0.75 unless otherwise specified, but explored the effect of ζ on
211 spatial spread in the Supplemental Materials.

212 We used our simulation model to examine the role of intraspecific variability
213 and interspecific effects on dispersal probabilities and spatial spread. To do this,
214 we simulated spatial spread of single and multi-species communities for 40 gen-
215 erations. Model simulations were initiated with 40 individuals for single species
216 simulations, or 20 individuals of each species for multi-species simulations. Land-
217 scapes consisted of 100 patches, well beyond the maximum spread observed in any
218 simulation. For each parameter combination, we simulated 5000 landscapes.

219 **Individual-level variation in dispersal probability and spatial spread**

220 Intraspecific variability in individual dispersal rate could have important impli-
221 cations for spatial spread, especially in small founding populations. We incor-
222 porated intraspecific variability in dispersal rates by randomly sampling disper-
223 sal rates from the distribution of dispersal probabilities observed in experimental

224 landscapes. Dispersal probabilities were estimated as the number of times an in-
225 dividual dispersed divided by the number of experimental days. Growth rates and
226 competition coefficients were based on previous estimates using the same exper-
227 imental populations (Dallas *et al.* (2019); Table S1). We examined the effect of
228 individual-level variation in dispersal probability by simulating spatial spread of
229 two interacting species in replicated 100-patch landscapes ($n = 5000$) for 40 gen-
230 erations. Each generation, dispersal was either constant, using the mean dispersal
231 for each species, or was sampled from the distribution of dispersal probabilities for
232 each species.

233 **The local community and spatial spread**

234 The community context of dispersal is important, as interspecific interactions may
235 influence dispersal behavior through competition or chemical signaling. We exam-
236 ined this in a general sense by simulating 100-patch landscapes of the two *Tribolium*
237 species, with all demographic rates parameterized from previous experiments. We
238 controlled the interspecific effects on dispersal through the introduction of two
239 parameters (d_{SF} and d_{FS}), which function as density-dependent dispersal reduc-
240 tion terms. Dispersal rates were sampled from the empirical distributions for each
241 species, and spatial spread was simulated for 40 generations. We further examined
242 the effect of interspecific interactions on reduced dispersal in the Supplemental
243 Materials.

244 **Results**

245 **Variation in dispersal probability in experimental landscapes**

246 Individual dispersal varied considerably, with many individuals never dispersing,
247 and some individuals dispersing repeatedly throughout the course of the experi-

248 ment (Figure 1). Based on our logistic mixed effects model, there was a positive
249 relationship between dispersal probability and experimental day, suggesting that
250 individuals tended to disperse more often in the later days of the experiment,
251 which potentially relates to age-dependent dispersal (Table 1). We failed to detect
252 a relationship between individual trait variation (i.e., body length) and dispersal
253 probability (see Supplemental Materials), but did find that *T. castaneum* dispersal
254 was reduced in the presence of *T. confusum*, owing to either interspecific interac-
255 tions or to intraspecific density effects (Figure 2).

256 **Individual-level variation in dispersal probability and spatial spread**

257 We simulated our two-species Ricker model – incorporating the four sources of
258 stochasticity discussed above – for populations embedded in a landscape of 100
259 habitat patches, as well as for a simplified Ricker model only incorporating demo-
260 graphic stochasticity. Spatial model simulations revealed that the distance traveled
261 by the dispersing species was more variable when dispersal probability was drawn
262 from the set of individual dispersal probabilities obtained from experimental tri-
263 als compared to the neutral assumption treating species dispersal probability as
264 constant (Figure 3). Further, incorporating multiple forms of stochasticity did not
265 influence spatial spread nearly as much as individual-scale variation in dispersal
266 behavior, suggesting that demographic and environmental stochasticity may in-
267 fluence local population dynamics strongly, but treating dispersal as a stochastic
268 process with variable intraspecific dispersal probabilities yielded far more variable
269 spatial spread relative to assuming constant dispersal probabilities among individ-
270 uals.

271 **The community context of spatial spread**

272 Interspecific interactions can potentially influence spatial spread variability through
273 the direct impacts of competition on species population growth rates, or by al-
274 tering dispersal behavior. In our experimental landscapes, the reduction in *T.*
275 *castaneum* dispersal in the presence of *T. confusum* could be due to interspecific
276 interactions, or through intraspecific density-dependence of *T. castaneum*. That is,
277 while overall density was held constant, if beetles are not functionally equivalent,
278 *T. castaneum* may "experience" a reduced density in the presence of *T. confusum*,
279 and density-dependent dispersal in this system would result in the observed reduc-
280 tion in dispersal. However, through model simulations, we found that variability,
281 but not average distance traveled, in spatial spread was influenced by interspecific
282 reductions in dispersal (Figure 4), with increasing competitor dispersal inhibition
283 resulting in more variable spatial spread for both species. Dispersal inhibition was
284 modeled as a reduction on the dispersal probability of each individual in a popula-
285 tion of one species, dependent on the density of the competing species. Increasing
286 interspecific competitive effects (α_{SF} and α_{FS}) did not strongly influence spatial
287 spread dynamics (Figure S3).

288 **Discussion**

289 Understanding the variability and speed of spatial spread is a pressing need in
290 both basic and applied ecology, as dispersal variability limits our intrinsic ability
291 to predict spatial spread, with obvious applied consequences to the management
292 of endangered or invasive species. Here, we examined how spatial spread is influ-
293 enced by community composition and intraspecific variation in dispersal probabili-
294 ties, finding that *Tribolium* species varied in their dispersal rates at the individual
295 level, and that dispersal was reduced for one species when allowed to interact with

296 a competitor. This builds on existing work in the *Tribolium* system suggesting
297 that stochasticity can set clear limits to the predictability of spatial spread in sin-
298 gle species systems (Melbourne & Hastings, 2009). In simulations of a stochastic
299 multi-patch Ricker model, we found that intraspecific variation in dispersal proba-
300 bility strongly influenced variability in spatial spread, and that this variation was
301 highest when founding population size was small (Figure S4). Density-dependent
302 dispersal inhibition resulted in more variable spatial spread, likely as a direct result
303 of the stochasticity in population dynamics leading to variable density-dependent
304 effects of species on one another. That is, a sudden increase in population size
305 would strongly decrease spatial spread of the competing species through density-
306 dependent effects, which can be seen in the reduced slope of *T. confusum* under
307 increased dispersal inhibition of the faster growing *T. castaneum*. Together, our
308 findings suggest that both intraspecific variation and community effects can influ-
309 ence variability and speed of spatial spread. Given the increasing importance of
310 prediction in ecology, we must account for uncertainty in spread rates as a result
311 of the influence of species interactions and intraspecific variation in dispersal.

312 Intraspecific variability in individual dispersal probability has the ability to al-
313 ter spatial spread (Kautz *et al.*, 2016) at the population level, especially when
314 founding populations are small (Hastings *et al.*, 2005). Previously, Melbourne &
315 Hastings (2009) found that variability in spatial spread of *Tribolium* beetles was
316 a result of stochasticity in demographic processes. Here, we present evidence that
317 intraspecific variability in dispersal behavior could result in the same degree of
318 variation in spatial spread, independent of local population demographics. Un-
319 derstanding the basis for this variability in dispersal behavior can provide insight
320 into when founding populations would be expected to spread and has implications
321 for species invasion success. Further, if there was a genetic basis for dispersal

322 propensity, independent of individual morphology, the spatial landscape of genetic
323 diversity of a spreading population would favor certain genotypes at the leading
324 edge of the expansion creating more variability in spatial spread than what we
325 observed (Weiss-Lehman *et al.*, 2019).

326 We failed to detect a relationship between dispersal probability and individual
327 body size, a relationship that has been previously observed in bird species (Steyn,
328 Mitchell & Terblanche, 2016). In the *Tribolium* model system, leg length was found
329 to be related to individual movement in a maze-like environment (Arnold, Cassey
330 & White, 2017), suggesting that perhaps other morphological measures could ex-
331 plain dispersal behavior or propensity. Regardless of the potential morphological
332 basis, the observed variation in dispersal probability suggests that certain indi-
333 viduals are more prone to disperse than others, suggesting that dispersal is not a
334 result of neutral dynamics – discussed in detail in Lowe & McPeck (2014) – and
335 that dispersal probability may have a basis in phenotypic traits or physiological
336 tolerances (Bestion, Clobert & Cote, 2015). A final consideration is that animal
337 personality drives variation in dispersal propensity, leading to intraspecific varia-
338 tion important for spatial spread (Sih *et al.*, 2015). This is difficult to quantify and
339 disentangle from stochasticity and species traits, but is also an important source
340 of intraspecific variation in dispersal behavior.

341 Whereas intraspecific variation in dispersal propensity influences spatial spread
342 largely for smaller populations, the effect of interspecific interactions on spatial
343 spread may be relatively insensitive to species density. This adds an interesting
344 aspect to current examinations of the influence of biotic interactions on determin-
345 ing species range boundaries (Svenning *et al.*, 2014; Urban, Zarnetske & Skelly,
346 2013), as it suggests that interspecific interactions at the intersecting range mar-
347 gins of two competing species may contribute to setting geographic range bound-

348 aries, and interspecific interactions in co-occurring species may influence species
349 dispersal and range expansion or contraction. This suggests the intriguing possi-
350 bility that the ability of a population to track favorable abiotic conditions could
351 be influenced by the existing community. In the case of *dispersal antagonism* –
352 where the presence or density of a competing species slows or prevents dispersal
353 of another species – as observed in our experiment, a species may be slowed at
354 its trailing edge by interactions with novel competitors (leading to populations
355 which potentially fail to track climate), or pushed back against as species spread
356 into new geographic areas with a different set of competing species. Further, if
357 two species with similar environmental tolerances were tracking the environment
358 together, dispersal antagonism might link dispersal dynamics across species, such
359 that a rates of spatial spread become correlated between species (Svenning *et al.*,
360 2014; Thomas, 2010). In an extreme case, populations released from species in-
361 teractions may spread faster, resulting in disjunct populations and a potentially
362 measurable difference in spatial spread rates as a function of competitor presence
363 or density. Experiments aimed at disentangling the effects of intraspecific variation
364 in density and interspecific interactions leading to altered spatial spread will con-
365 tribute important information on the functional equivalence of competing species
366 in interactive communities.

367 Inference obtained from our examination of *Tribolium* spatial population dynam-
368 ics may not be directly applicable to conservation or management applications in
369 natural systems. However, our simplified landscapes offered a means to explore the
370 potential range of effects on spatial spread due to species interactions and dispersal
371 variation, hopefully motivating future explorations in natural systems. Environ-
372 mental effects on dispersal probability or distance are well-recognized (Parmesan,
373 2006; Thomas, 2010), but the relative importance of environmental conditions

374 and intraspecific variation in dispersal probability is presently unknown. That
375 is, variation in individual dispersal behavior could be far more important than
376 environmental constraints on dispersal, especially in the case of small population
377 sizes. Understanding the role of population size on dispersal variation is an area
378 of study deserving further attention. Second, our experiment did not attempt to
379 determine if interspecific changes in dispersal probability were contingent upon
380 the density of the competitor, or whether dispersal itself was dependent on species
381 abundance. Tunnel building by *Tribolium* species creates dispersal corridors, sug-
382 gesting that dispersal inhibition could be a result of either the failure to construct
383 these tunnels due to species interactions, or the active destruction of tunnels by
384 the competing species. While the mechanism by which dispersal inhibition occurs
385 is currently unknown—and potentially specific to the *Tribolium* system—there are
386 numerous ways in which species interactions could either facilitate or reduce dis-
387 persal probability and resulting spatial spread dynamics (Svenning *et al.*, 2014;
388 Thomas, 2010; De Meester *et al.*, 2015). Finally, there is a clear separation be-
389 tween our experiment, which was run with beetles all from a single generation,
390 and the theoretical exploration of spatial spread variability, which was simulated
391 for many generations. This approach does not allow for the direct comparison
392 of models fitted to spatial spread data from the experimental system, but does
393 instead provide a clear demonstration of the existence of intraspecific dispersal
394 variability and the potential effects of this on spatial spread dynamics.

395 Together, our findings suggest that even under ideal conditions – in which patch
396 quality, environmental conditions, and species abundance are controlled in repli-
397 cated landscapes – individual differences in dispersal probabilities and community
398 context can strongly influence variability in spatial spread. Understanding the
399 mechanistic basis for dispersal facilitation or antagonism is a pressing research

400 need, as species track a changing climate (Chen *et al.*, 2011) and as communi-
401 ties change as a result of species invasions and range shifts (Williams & Jackson,
402 2007; Lurgi, López & Montoya, 2012). Acknowledging intraspecific variability in
403 dispersal probability and distance, as well as recognizing the influence of com-
404 munity composition on dispersal and spatial spread dynamics are two pressing
405 needs, creating a clear knowledge gap. Addressing this gap will likely require the
406 development of modeling approaches capable of capturing spatial dynamics of en-
407 tire communities, and long term monitoring efforts of communities in directionally
408 shifting or variable environments.

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Tables

Table 1: Logistic mixed effects model of dispersal as a function of experimental treatment (*T. castaneum* and *T. 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.

Treatment	Estimate	SE	<i>t</i>	<i>p</i>
<i>T. castaneum</i>	0.039	0.017	2.35	0.021
<i>T. confusum</i> (mixed)	0.006	0.018	0.35	0.73
<i>T. castaneum</i> (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

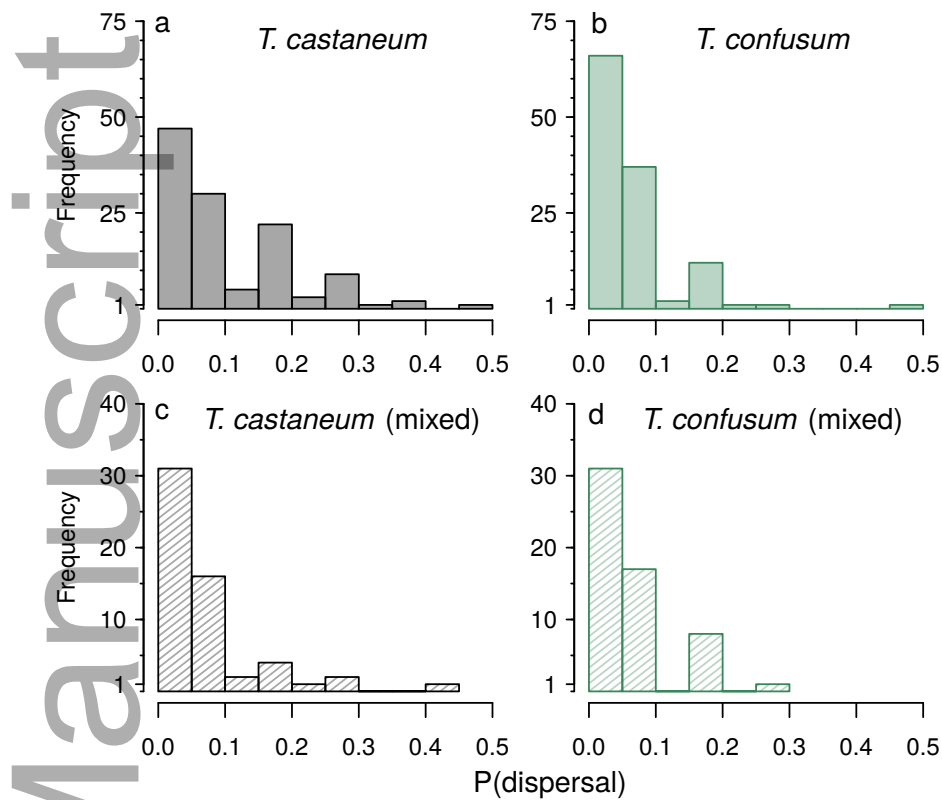


Figure 1: Dispersal probabilities were highly variable, with most individuals never dispersing throughout the experimental period, and some individuals dispersing multiple times. The community context was important, as *T. confusum* reduced *T. castaneum* dispersal probability, either as a function of 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).

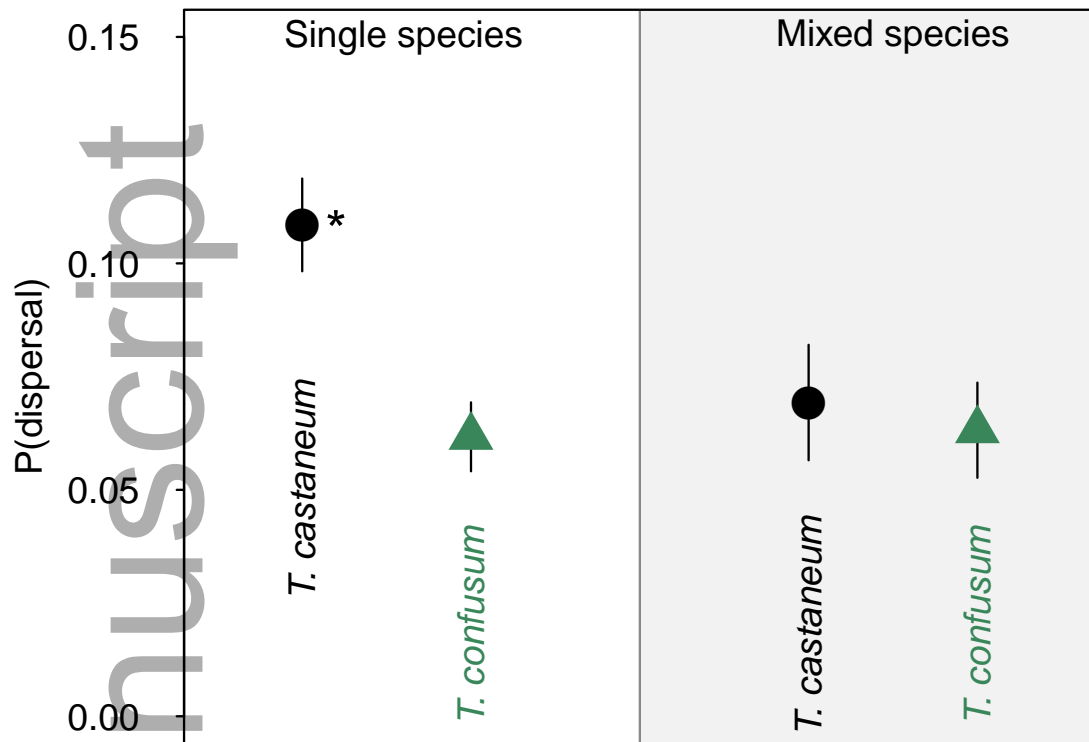


Figure 2: The probability of dispersal was strongly reduced when *T. castaneum* was allowed to interact with *T. confusum*, while *T. confusum* dispersal was unaffected.

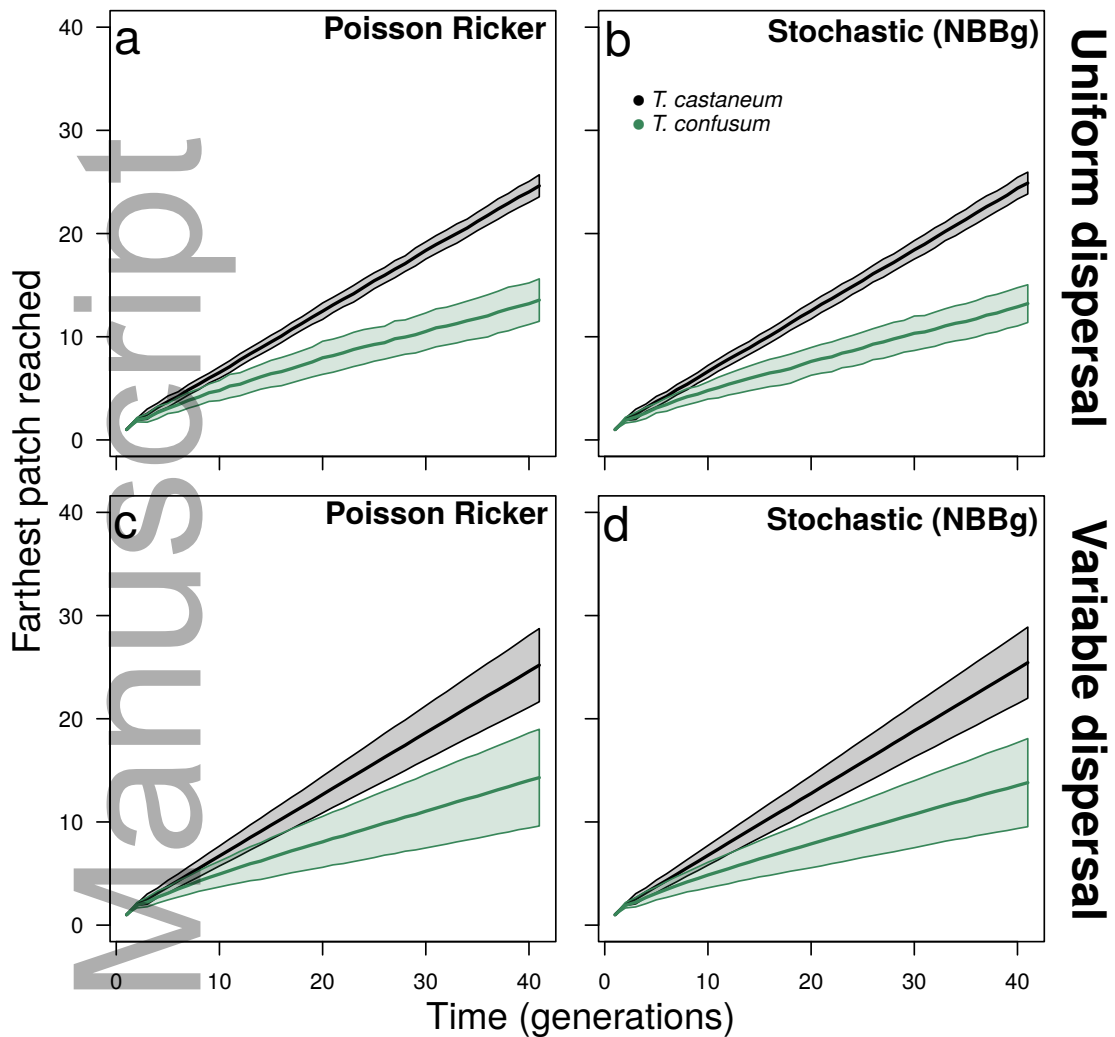


Figure 3: Incorporating individual-level variability in dispersal probabilities (*c* and *d*) lead to more variation in the most distant patch reached (*y*-axis) over the course of 40 generations (*x*-axis) relative to assuming each individual had the same dispersal probability (*a* and *b*). Individual 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*).

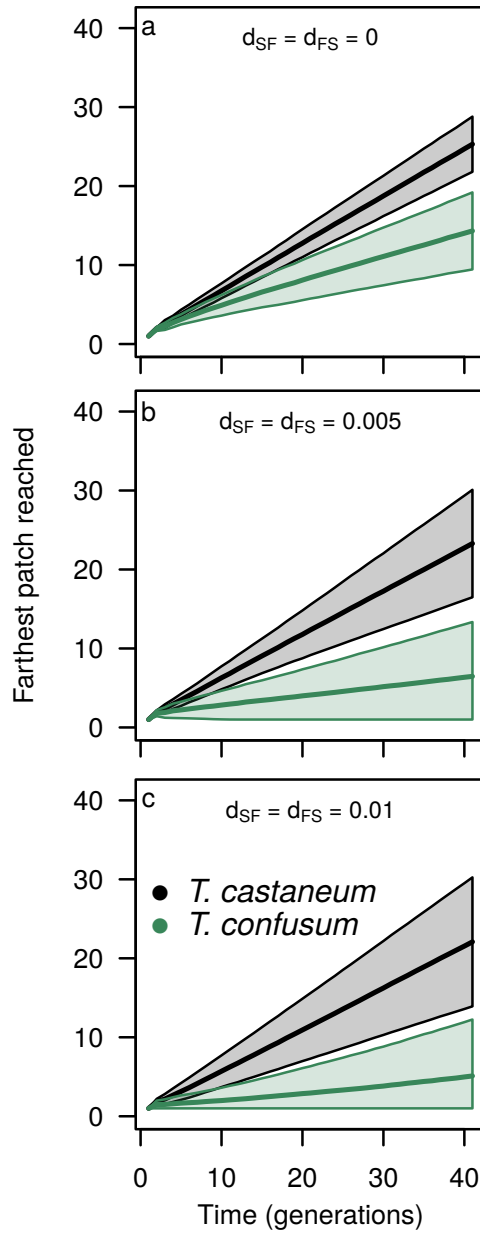


Figure 4: Species interactions may influence dispersal behavior of a competing species, incorporated into our model using interspecific dispersal inhibition terms d_{SF} and d_{FS} . Relative to a case where dispersal was unaffected by interspecific competition (panel *a*), small changes to dispersal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

528 Supplemental materials

529 Model parameterization

530 Here, we provide details about simulation model parameters. Demographic param-
531 eters were obtained from a previous experiment (Dallas *et al.*, 2019), and dispersal
532 probabilities were estimated from the experimental landscapes in this experiment.

Table S1: Parameters used in the model simulations, based on parameter estimates from previous experiments (Dallas *et al.*, 2019), but with the distribution of dispersal probabilities (d_S and d_F) estimated from experimental landscapes.

Parameter	Definition	Value
R_S	number day ⁻¹	4.82
R_F	number day ⁻¹	2.77
α_{SS}	Effect of S on S	0.011
α_{FF}	Effect of F on F	0.002
α_{SF}	Effect of F on S	0.006
α_{FS}	Effect of S on F	0.002
d_S	Dispersal probability of S	0.236
d_F	Dispersal probability of F	0.129
d_{SF} and d_{FS}	Interspecific dispersal reduction	0 - 0.01
k_D	Demographic heterogeneity	3255.8
k_E	Environmental stochasticity	4.84

533 **The effect of marking beetles on dispersal**

534 Marking beetles with non-toxic paint could have potentially reduced dispersal
535 probability through decreased mobility. However, we failed to detect this effect in
536 our experimental beetles (Table S2 and Figure S1).

Table S2: Paint color did not influence dispersal behavior of *T. castaneum* or
T. confusum, suggesting that marking individuals with paint did not strongly
influence dispersal behavior.

Species	Treatment	df	Sum Sq	Mean Sq	<i>F</i>	<i>p</i>
<i>T. castaneum</i>	Paint color	5	0.02	0.00	0.31	0.9088
	Residuals	114	1.48	0.01		
<i>T. confusum</i>	Paint color	5	0.02	0.00	0.54	0.7490
	Residuals	114	0.81	0.01		

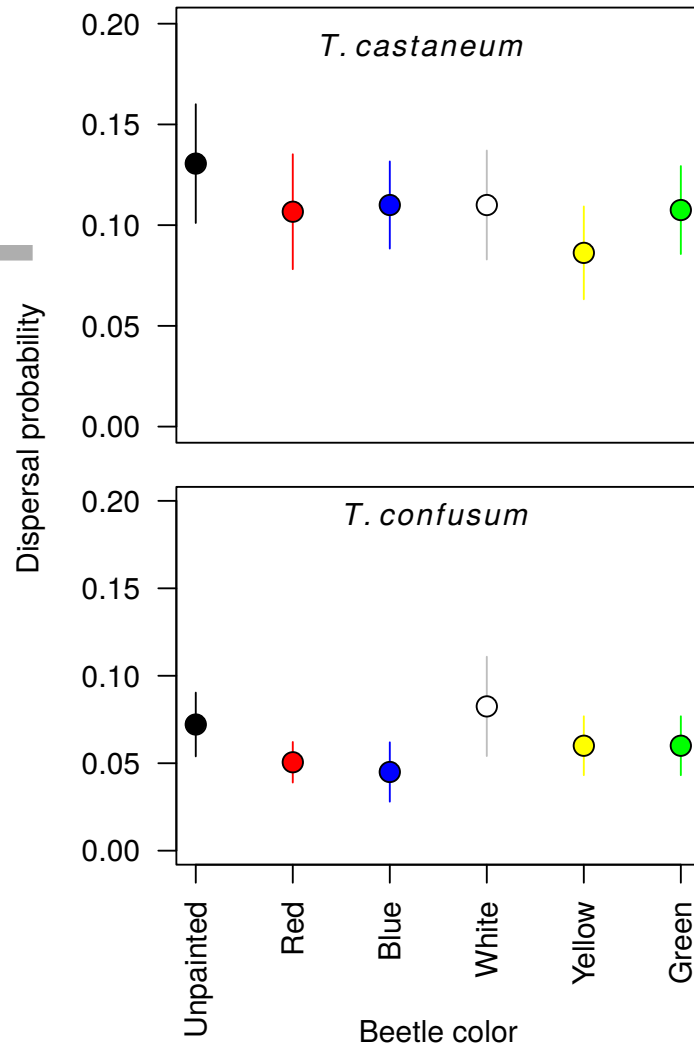


Figure S1: Unmarked beetle individuals (black points) did not disperse more often than marked beetles.

537 **Mixed effect models of dispersal**

538 We used mixed effect models in the main text to examine the relationship between
539 dispersal decision (a binary variable) as a function of experimental treatment (sin-
540 gle or double species community), individual body length, and the day of the ex-
541 periment (used as a proxy for individual age, as all individuals were approximately
542 the same age at the start of the experiment). The random effects we needed to
543 consider were the effect of the experimental unit in which the beetles were housed,
544 and the effect of the individual itself. To do this, we treated landscape and in-
545 dividual both as random effects (specifically random intercept), with individual
546 nested within landscape. This accounts for variation at the individual beetle level,
547 as 348 beetles were monitored over the course of 10 days. It also accounts for the
548 effect of the landscape, of which there were a total of 60 constructed landscapes.

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549 **Dispersal probability and distance traveled unrelated to body**
550 **size**

551 Dispersal probability has previously been related to species body size, where larger
552 individuals either disperse more often, or disperse longer distances. Here, we ex-
553 amined the relationship between *Tribolium* body length and both dispersal prob-
554 ability and distance. We failed to detect an effect of body length of either species
555 on dispersal probability or distance (Table S3). There are numerous potential rea-
556 sons for the lack of importance of body size on dispersal probability and distance.
557 First, given that individuals were all the same age at the time of the experiment,
558 there was only a small amount of variation in body length estimates. Second,
559 previous studies may conflate age and size, such that size-biased dispersal ability
560 is actually a function of age instead of body size. Lastly, our linear experimental
561 landscapes may not capture dispersal dynamics of natural *Tribolium* populations,
562 as dispersal was possible when tunneling beetles discovered small holes near the
563 bottom of each habitat patch.

Table S3: Pearson's correlations between measures of dispersal–dispersal probability and dispersal distance– and *Tribolium* species body length (mm). We failed to detect relationships between individual body length and dispersal ability or distance.

Variable	Species	ρ	t	p
Dispersal probability	<i>T. castaneum</i>	0.13	1.40	0.16
	<i>T. confusum</i>	-0.17	-1.91	0.06
	<i>T. castaneum</i> (mixed)	0.23	1.73	0.09
	<i>T. confusum</i> (mixed)	0.21	1.56	0.13
Dispersal distance	<i>T. castaneum</i>	0.12	1.27	0.21
	<i>T. confusum</i>	-0.17	-1.84	0.07
	<i>T. castaneum</i> (mixed)	0.22	1.62	0.11
	<i>T. confusum</i> (mixed)	0.17	1.28	0.21

564 **Variability in dispersal distance among treatments**

565 In the main text, we examined variation in dispersal probability as a function of
566 community context, experimental day, and body size. Here, we examine dispersal
567 distance, finding that *T. castaneum* tended to disperse farther than *T. confusum*,
568 but this effect disappeared in multi-species communities, echoing our main text
569 findings with respect to *T. castaneum* dispersal probability in single and multi-
570 species assemblages.

Table S4: Linear mixed effect model of mean dispersal distance as a function of species treatment (*T. castaneum* and *T. confusum* either in isolation or two-species communities). Landscape was treated as a random effect. Mean dispersal distance was greater in single species populations of *T. castaneum*, suggesting the importance of community context, or the non-equivalence of species contributions to overall density (i.e., *T. confusum* do not contribute to density-dependent processes of *T. castaneum*).

Treatment	Estimate	SE	df	<i>t</i>	<i>p</i>
<i>T. castaneum</i>	0.040	0.02	72	2.24	0.028
<i>T. confusum</i> (mixed)	0.012	0.02	72	0.62	0.538
<i>T. castaneum</i> (mixed)	0.012	0.02	72	0.62	0.537
Body length	-0.009	0.019	3403	-0.486	0.627

571 **Effect of directional dispersal**

572 Individuals in the model were allowed to disperse towards the leading edge or back
573 towards the range center, a behavior controlled by the ζ parameter, which is the
574 fraction of individuals dispersing towards the leading edge. Here, we vary the
575 fraction of dispersers moving towards the expanding population edge (ζ) to see
576 how directional dispersal influences spatial spread. We find that lower values of ζ
577 result in a smaller farthest habitat patch reached, and less variable spatial spread
578 dynamics (Figure S2).

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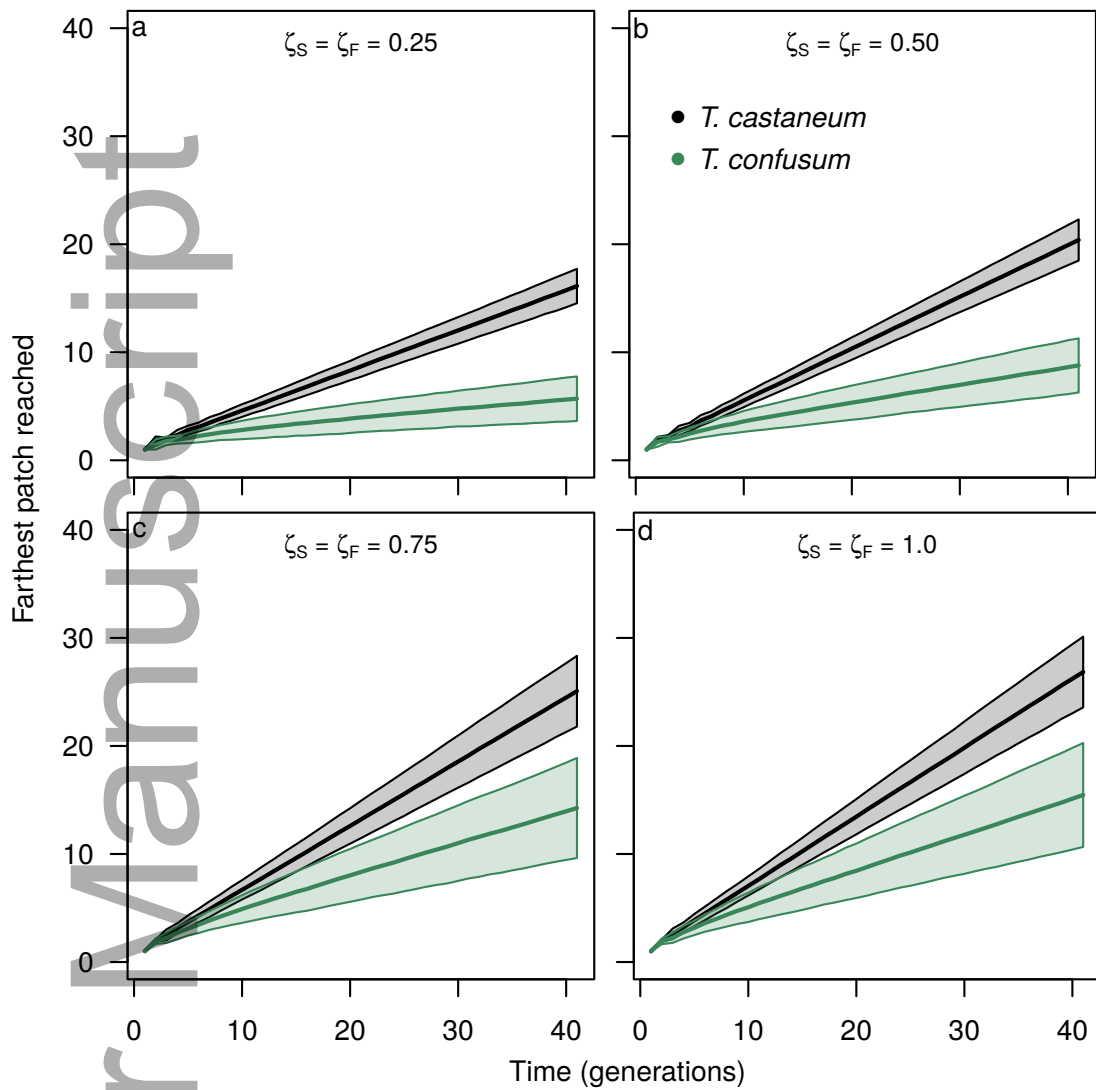


Figure S2: Variability in spatial spread as a function of directional dispersal (ζ), where $\zeta = 0.5$ corresponds to individuals equiprobably dispersing towards range center and towards expanding population edge, and $\zeta = 1$ corresponds to all individuals dispersing towards population edge.

579 **The effect of competition on spatial spread**

580 Interspecific competition did not have a strong effect on the spatial spread of
581 species, except when the competitive effect of *T. castaneum* on *T. confusum* was
582 high, which lead to very little spatial spread of *T. confusum*. In some cases, the
583 effect resulted in exclusion of *T. confusum*, identified by the black squares in Figure
584 S3.

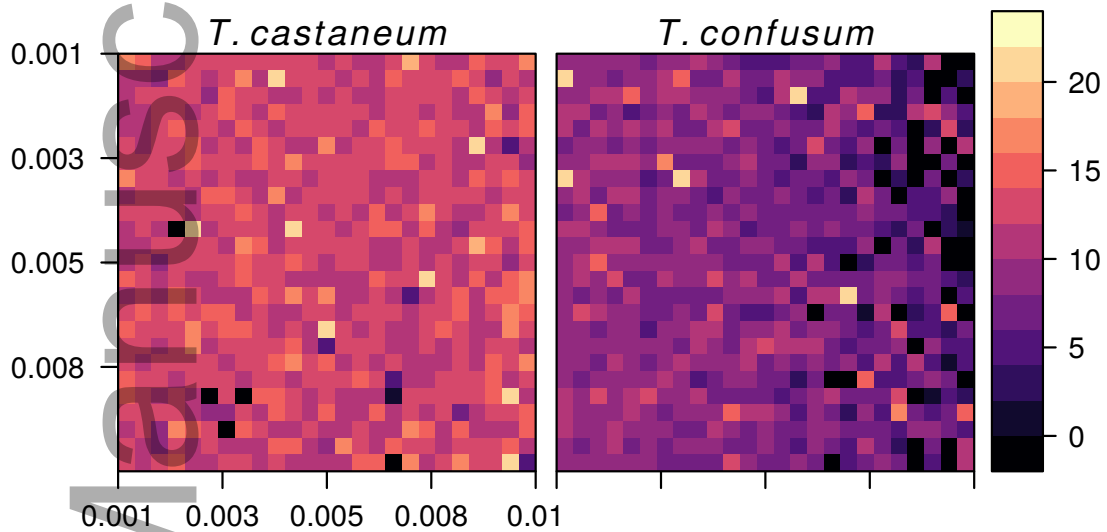


Figure S3: Interspecific competition influenced the furthest patch traveled in model simulations when the effect of *T. castaneum* on *T. confusum* was strong, resulting in *T. confusum* moving very little across the landscape.

585 **Initial population size and variability in spatial spread**

586 Initial population size influenced the variability in spatial spread dynamics, as
587 smaller populations are more sensitive to individual-scale variation in dispersal
588 probability. This supports the idea that founder effects can strongly influence
589 spatial spread dynamics (Peter & Slatkin, 2015; Slatkin & Excoffier, 2012), a well-
590 accepted concept with limited empirical support due to the difficulty of observing
591 replicated spatial spread along a gradient of founding population sizes.

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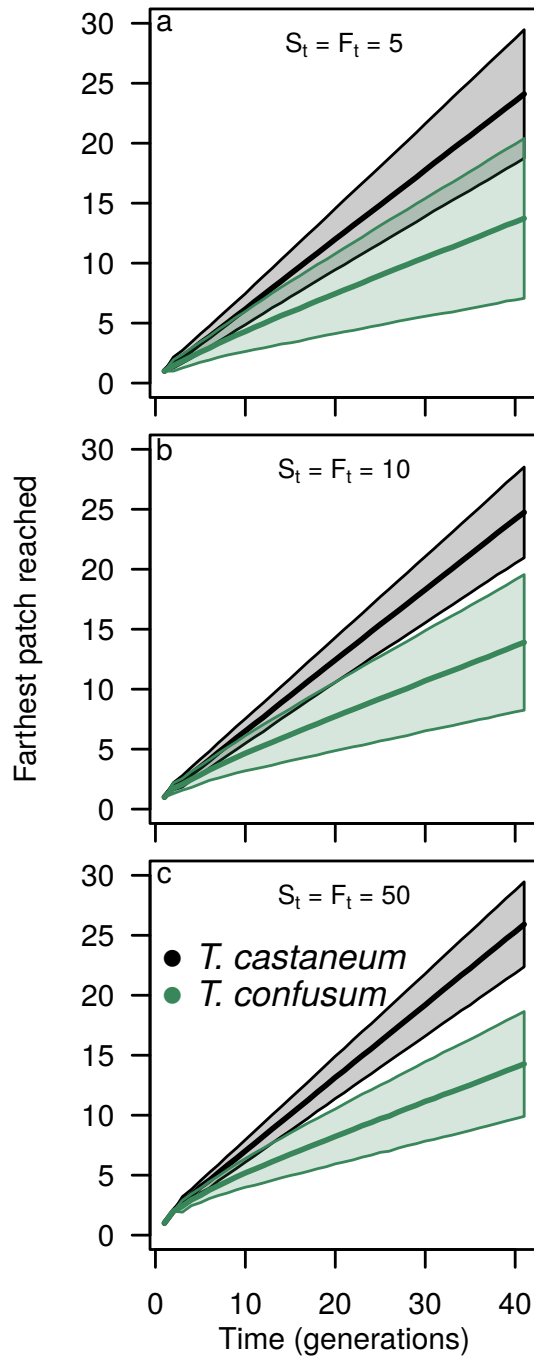


Figure S4: Variability in spatial spread as a function of initial population sizes of both species, suggesting that smaller founder populations result in more variable spatial spread.