OIKOS

Research article

Interspecific competition reduces seed dispersal in an annual plant and slows simulated range expansions

Erin E. McHugh[1,2], **Carla A. Urquhart**[1], **Nicky Lustenhouwer**[3] **and Jennifer L. Williams**[1]

[1]Department of Geography and Biodiversity Research Centre, University of British Columbia, Vancouver, BC, Canada
[2]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada
[3]School of Biological Sciences, University of Aberdeen, Aberdeen, UK

Correspondence: Jennifer L. Williams (jennifer.williams@geog.ubc.ca)

Oikos
2025: e10792
doi: 10.1111/oik.10792

Subject Editor: James Bullock
Editor-in-Chief:
Gerlinde B. De Deyn
Accepted 28 September 2024

Understanding the factors influencing how fast populations can spread across the landscape will be crucial as species ranges shift due to climate change. While the role of abiotic factors in determining expansion speed has been well studied in theory and empirical research, how competition impacts speed has received far less attention. Here, we investigated how seed dispersal distances change in response to competition and how these changes to distributions of dispersed seeds impact expansion speed. We dispersed four genotypes of the annual plant *Arabidopsis thaliana* with variation in life history traits into greenhouse mesocosms of either empty habitat or habitat containing the annual grass competitor, *Lolium multiflorum*. We found that competition decreased both mean and maximum dispersal distance. We then built a simulation model of range expansion with experimental data from this and a prior experiment to explore whether competition slows species expansions primarily through decreasing dispersal or fecundity. We found that competition primarily slows expansion speed through decreases in dispersal, but that when competition impacts both dispersal and fecundity, expansions slow more than with dispersal alone. The genotype with traits associated with longer distance dispersal was the most affected by competition in both experimental dispersal and simulations. This research suggests that not only does competition slow range expansions through decreases in both fecundity and dispersal, but that there may be consequences for evolutionary processes at the leading edge.

Keywords: *Arabidopsis thaliana*, expansion speed, experimental dispersal, interspecific competition, range expansion, seed dispersal

Introduction

Understanding the mechanisms of species range dynamics is critical to biodiversity conservation as species ranges shift due to climate change (Parmesan and Yohe 2003) and invasive species expand their ranges following introduction (Pyšek et al. 2020). Research on range expansions has mainly focused on the role of abiotic factors (Shigesada et al.

© 2024 The Author(s). Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

NORDIC SOCIETY OIKOS
www.oikosjournal.org

1986, Campos et al. 2008, Mustin et al. 2009, Lindström et al. 2011, Pachepsky and Levine 2011, Block and Levine 2021, Usui and Angert 2024) and some biotic interactions such as herbivory and pollination (Fagan and Bishop 2000, Rivest and Vellend 2018, Sullivan and Shaw 2023). However, the role of competition in determining how far and how fast a population can spread is less well understood (Miller et al. 2020). Theory predicts that biotic interactions, and interspecific competition in particular, can constrain species ranges (Connell 1961, Jankowski et al. 2010) and slow expansions (Allen et al. 1996, Kot et al. 1996, Hart and Gardner 1997, Lewis et al. 2002). In experimental range expansions with two species of flour beetles, competition was shown to slow population spread and alter the spatial distribution of expanding populations (Legault et al. 2020). A key next step in connecting theoretical models to populations spreading in nature, where biotic interactions are ubiquitous, is a stronger, mechanistic understanding of how competition alters expansion dynamics.

Interspecific competition is often assumed to impact the expansion speed of a population by reducing survival or fecundity via competition for resources (Okubo et al. 1989, Hart and Gardner 1997). Fecundity is a key trait in determining expansion speed, along with dispersal (Skellam 1991, Hastings 1996, Kot et al. 1996), and mathematical models of range expansions that include interspecific competition assume that competition affects only the population growth rate (Lewis et al. 2002, Weinberger et al. 2002, Holzer and Scheel 2012, Alhasanat and Ou 2020). However, a competitor could also slow an expansion through interfering with its ability to disperse beyond the range edge by acting as a physical barrier to dispersal or by impeding establishment (Bolker et al. 2003). Dispersal can have an even larger effect on expansion speed when evolution of dispersal related traits occurs at the leading edge of an expansion, a process termed spatial sorting, which can result in accelerating expansion speeds over time (Travis and Dytham 2002, Travis et al. 2009, Ochocki and Miller 2017). If competition reduces both fecundity and dispersal (Hosono 1998), it could slow expansions more dramatically than if the effect of competition is on reproduction alone. Further, the effect of competition on expansion speed via its effects on both dispersal and fecundity may not be predictive from the summed effect of competition on each trait on its own.

One way that interspecific competition can influence seed dispersal in plants is through affecting the expression of dispersal-related traits. In wind-dispersed plants, for example, taller individuals with lighter seeds can disperse farther on average (Nathan et al. 2011). With competition, plants may have fewer resources to invest in growth, resulting in shorter individuals (Harper 1977) with more limited dispersal ability. Conversely, it is possible that under competition for light, plants will prioritize vertical growth, increasing their height (Notzold et al. 1997, Cipollini and Bergelson 2002) and thus potential dispersal distances. However, competitors might also weaken the correlation between dispersal and traits such as height (Donohue 1998, Wender et al. 2005, Williams et al. 2016a) and seed weight (Skarpaas et al. 2011, Delefosse et al. 2016). That is, dispersal-related traits may lose their spatial advantage at the leading edge of an expanding population in a competitive environment. Similarly, in passively dispersed plants, the presence of competitors may act as a more efficient barrier to lighter seeds than heavier ones, shifting the direction of the correlation between seed weight and dispersal (Cousens and Rawlinson 2001, Bullock and Moy 2004). For example, in *Arabidopsis thaliana*, height is strongly reduced by neighbour density (Wender et al. 2005), and we might expect that competition would then reduce height more than less plastic traits, such as seed weight (Harper et al. 1970, Paul-Victor and Turnbull 2009). Finally, individuals or species with earlier phenology that separates them in time from their competitors may have a longer period of time during which they can acquire resources, grow, and reproduce (Wolkovich et al. 2013), theoretically leading to increased propagule production and a higher chance of propagules dispersing longer distances.

Even without direct competition, resident populations can alter patterns of dispersal in an expanding species by interfering with seed dispersal and establishment. Surrounding vegetation might act as a physical barrier to wind or gravity dispersed seeds (Cousens and Rawlinson 2001, Bullock and Moy 2004, Snell et al. 2019) or alter environmental conditions that contribute to dispersal (Bohrer et al. 2008, Marchetto et al. 2010, Qin et al. 2022). These effects might reduce mean dispersal distances or change the distribution of seeds over space (Cousens and Rawlinson 2001), and in particular may alter the probability of long-distance dispersal (Bohrer et al. 2008, Heydel et al. 2014). It is also possible that the role of some traits in determining how far seeds can disperse is more strongly shaped by the presence of a resident competitor. For example, the ability of surrounding vegetation to interfere with seed dispersal has been shown to depend on seed morphology in a variety of tree species (Pounden et al. 2008). In the context of range expansion, where invading populations might first colonize disturbed patches and later spread into habitat occupied by resident populations, for all of the above reasons, it is possible that plants will experience an impact on dispersal from surrounding vegetation without direct competition per se. Thus, understanding how interspecific competition can influence seed dispersal dynamics with and without direct competition for resources is key to better predicting expansion speed in natural systems.

To better understand how a resident competitor affects dispersal, the role of dispersal-related traits in determining dispersal distances, and the subsequent impact on expansion speed, we first conducted a mesocosm dispersal experiment, where we dispersed individuals growing alone into arrays with and without a resident competitor. We allowed four genotypes of *Arabidopsis thaliana* (Brassicacae) that varied in traits such as height, flowering time, and seed weight, to disperse into greenhouse mesocosms occupied with and without the annual grass *Lolium multiflorum* (Poacaeae) (Campitelli et al. 2016, Lustenhouwer et al. 2019). We then simulated expansions using dispersal distances from this experiment and reductions in fecundity from *A. thaliana* grown with

L. multiflorum that we quantified in a previous experiment in the same study system (Lustenhouwer et al. 2019). We asked:

1) How do competitors alter maximum seed dispersal and variation in the distribution of seed dispersal distances in an annual plant?
2) How does competition alter the strength and direction of the correlation between dispersal distances and related traits such as seed weight, phenology or height, and how does this vary among genotypes?
3) How do changes in dispersal distance stemming from interspecific competition in turn impact expansion speed, relative or in addition to, direct effects of competition on fecundity?

Since *L. multiflorum* acted as a barrier to dispersal and germination in our dispersal experiment, we predicted that the presence of *L. multiflorum* would reduce the average and maximum dispersal distances of *A. thaliana*, but that this effect would be less pronounced in taller genotypes and those with earlier phenology than *L. multiflorum*. As *L. multiflorum* can grow much taller than *A. thaliana* on average, its presence may physically block dispersal. Genotypes of *A. thaliana* that can grow taller or more quickly may not be hindered as drastically as shorter or later-flowering genotypes. In simulations where we included the effects of *L. multiflorum* on reducing fecundity, we expected that including the effects of a competitor on dispersal would slow down expansions more than the effects on fecundity alone. Since dispersal is a key trait in driving expansion speed, even relatively small reductions could have an outsized influence on expansion speed. We also expected that competition would alter which genotypes had the highest expansion speeds in simulated expansions. Depending on the importance of different traits in buffering the effect of a competitor, the strongest dispersers in a competitive environment may vary depending on underlying traits driving dispersal.

Material and methods

Study system

We used the winter annual, *Arabidopsis thaliana* (Brassicaceae), as the focal species for this experiment, leveraging an existing model range expansion system (Williams et al. 2016a, Williams and Levine 2018, Lustenhouwer et al. 2019). For the competitor, we chose *Lolium multiflorum* (Poaceae), also known as annual ryegrass, as *L. multiflorum* has been successfully used as a competitor to reduce the fecundity and height of *A. thaliana* in previous experiments (Campitelli et al. 2016, Lustenhouwer et al. 2019).

Genotype selection

We chose four genotypes of *A. thaliana* using preliminary data on height and phenology (Urquhart and McHugh unpubl.). Genotypes were chosen from the set of recombinant inbred lines (RILs) from the Cvi and L*er* ecotypes, referred to as CVLs (Alonso-Blanco et al. 1998, 1999). These genotypes spanned a variety of traits (Table 1), including phenology, seed size and height (CVL53, CVL58, CVL144, and CVL187).

Dispersal experiment

As we were interested in disentangling the effects of competition on dispersal and fecundity, *A. thaliana* plants were not exposed to competition while they were growing. Instead, we grew individual *A. thaliana* plants in pots, by themselves, before separating them into competition and control dispersal treatments. The individuals in the control treatment dispersed into empty dispersal mesocosms, while individuals in the competition treatment dispersed into dispersal mesocosms occupied by *L. multiflorum* (Fig. 1). Thus, in this experiment, *A. thaliana* was only exposed to competition during dispersal. Each dispersal mesocosm consisted of one row of five pots, filled with only the same sand-soil potting mixture (control treatment) or with pots containing *L. multiflorum* (competitive treatment), extending approximately 40 cm in one direction (Fig. 1). We had five replicates of each genotype (CVL 53, 58, 144, 187) and treatment (competition or no competition) combination, resulting in forty experimental units altogether.

To prepare focal *A. thaliana* individuals for the dispersal mesocosms, we sowed 3–4 seeds into 8.2 × 8.2 × 7.6 cm plastic pots containing a moistened mix of four parts annual plant potting mix to one part silica sand before chilling them at 4°C for cold stratification. Two to three days after germination, seedlings were thinned to one individual per pot. The experiment was split into two blocks commencing on 15 November 2021 and on the 3 and 6 December 2021, respectively. Plants were cold stratified for between 5 and

Table 1. Mean and ranked trait values for each genotype of *A. thaliana*. Mean flowering time, mean silique number, and mean height were measured from plants in the dispersal experiment, whereas seed weight was taken from previous work (Williams et al 2016a). Next to the measurement for each trait, genotypes are given a rank from 1–4, with one being the largest trait value (e.g. the tallest) and four being the smallest trait value (e.g. the shortest).

Genotype	Seed weight (g)	Seed weight rank	Mean flowering time (days from removal from fridge to first flower)	Flowering time rank	Mean number of siliques	Silique number rank	Mean height (cm)	Mean height rank
CVL 53	3.05×10^{-5}	1	24.2	1	1785	1	39.4	1
CVL 58	2.01×10^{-5}	3	31.0	2	650	4	25.8	2
CVL 144	2.88×10^{-5}	2	47.0	4	662	3	22.6	4
CVL 187	1.80×10^{-5}	4	43.1	3	925	2	23.7	3

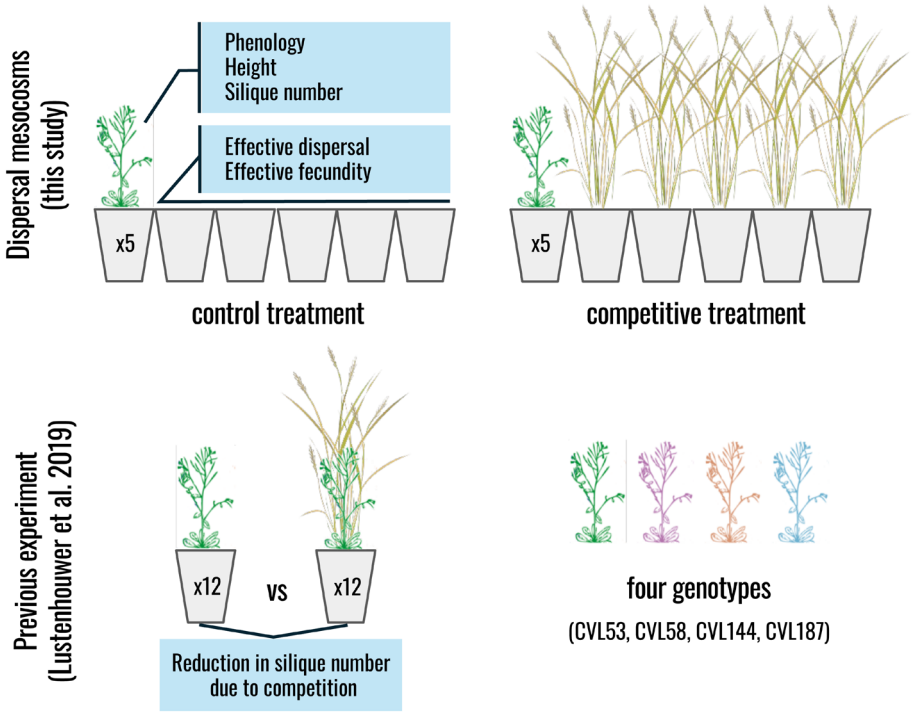


Figure 1. Experimental design and data sources. Numbers inside pots indicate the number of replicates for each of the four genotypes. To separate the effect of competition on dispersal and fecundity, *Arabidopsis thaliana* plants in the dispersal mesocosms (top) were not exposed to competition while growing. Phenology, height and silique number were measured on individuals growing in the dispersal experiment, while effective dispersal and effective fecundity were based on the seedling distribution after dispersal. The reduction in silique number due to competition was estimated from a previous experiment where plants of the same four genotypes were grown individually in the presence or absence of competition with *Lolium multiflorum* (Lustenhouwer et al. 2019).

12 days in order to sync germination dates in the second temporal block, due to initial poor germination. Differing stratification periods did not lead to significantly different plant heights ($F_{1,38}=0.122$, $p=0.728$) or phenologies ($F_{1,38}=0.008$, $p=0.928$), although plants with longer chill times did take longer to flower.

After cold stratification, pots were moved to a growth chamber set for 16 h of daylight, 23°C, and 60% relative humidity for two weeks for germination, then transferred to the University of British Columbia Main Campus Greenhouse (Vancouver, BC, Canada) where they were watered twice a week with a weak solution of water and fertilizer (UBC Plant Services, Vancouver, BC) until they bolted, when watering frequency increased to three times per week. Each *A. thaliana* plant was monitored each weekday for germination date, and dates of bolting (defined as when the budding inflorescence stalk was at least 0.5 cm above the rosette), first flower, and first silique. Plants in each round experienced slightly differing greenhouse environments because of a cold period in the winter of 2021, when the temperature in the greenhouse dropped from ~ 24 to ~15°C over the course of a few weeks. To prepare the dispersal mesocosms for the competition treatment, fifteen seeds each of *Lolium multiflorum* were sown into pots of the same size two weeks following germination of *A. thaliana*. They were watered on the same schedule as *A. thaliana*, albeit with a longer soaking time; pots were thinned to ten *L. multiflorum* plants two weeks after seeds were sown.

When the first few mature siliques began to appear on plants, one pot with *A. thaliana* was moved to each replicate mesocosm for eight weeks (Fig. 1). Mesocosms were separated by wood frames covered with breathable Remay garden cloth (Terralink Horticulture Inc.) with an open top (roughly 50 cm long by 20 cm wide by 60 cm high). Mesocosms prevented seed contamination between replicates while allowing sunlight to reach each plant and maintaining air flow. For the first five weeks, runways were flooded for 10 min with a weak solution of water and fertilizer three days a week, before being cut off to allow the plants to senesce.

We used two different methods to facilitate seed dispersal, with the goal of simulating the motion that *A. thaliana* plants would receive from wind, rain, and animals in a natural environment. Each method was applied once during the dispersal period, when *A. thaliana* seeds were mature and siliques had begun to open (two weeks after cutting off water, or ~ 7 weeks after being moved to the dispersal mesocosms). First, a bamboo stake approximately 1 cm in diameter was dragged through each plant at a height of 12 cm from the soil, about half the average height of *A. thaliana* plants previously grown in the UBC Main Campus Greenhouse. The bamboo stake was dragged through the pot from the back to the front, and then back again. After this, every pot in the mesocosm, as well

as the pot containing the *A. thaliana* plant, was sprayed with water three times from a height of ~55 cm (the height of the mesocosm walls) to simulate a rainstorm. We allowed seeds to disperse for two additional days, and then mesocosms were dismantled. In total, all plants were in dispersal mesocosms for 55–56 days (~8 weeks), with the exception of genotype 58, where eight replicates were moved into the mesocosms 10 days early to accommodate early maturation of siliques.

At the end of the seed dispersal trial, we measured the height of each plant and counted the number of mature siliques. To quantify dispersal distances, we counted the total number of germinated seedlings in each pot and recorded the maximum distance dispersed from the pot containing the focal individual in centimetres (Supporting information). Mesocosm pots were soaked in water before being cold stratified and placed in the growth chamber for 11 days for germination. Thus, our measures of dispersal and fecundity include seedling germination. To reflect this, hereafter we refer to these measurements as effective dispersal and effective fecundity (total number of seeds dispersed from one parent).

Data analysis

We fit negative exponential dispersal kernels to effective dispersal estimates from each mesocosm replicate using maximum likelihood (Bolker 2022); negative exponential distributions were found to fit better than lognormal and log-hyperbolic secant functions (Bullock et al. 2017) in exploratory analysis (Urquhart unpubl.). The effective fecundity of *A. thaliana* was quantified by summing the number of seedlings across the dispersal mesocosm for each replicate. To determine how traits predicted maximum dispersal distance (i.e. the raw distance of the furthest dispersed seed from the parent), we fit four different models, each testing one trait (height, silique number, genotype and phenology) as a fixed effect, in addition to competition treatment. Separate models were fit for each trait to consider the effects of each trait on dispersal independently. Additionally, we constructed a model that looked at the interactive effects of habitat and height. We included a fixed block effect in all models to account for the differences in temperature across two temporal blocks corresponding to the dates plants were dispersing. For models that did not involve silique number, we used all forty replicates; for tests that used silique number, one replicate for which silique number was not recorded was omitted. Coefficient of variation was calculated for maximum dispersal distance in empty versus competitive habitats. Data analyses were conducted in R ver. 4.3.2 (www.r-project.org).

Simulations

To investigate the impacts of competition on expansion speed, we parameterized a spread simulation with our experimental data. The simulation was based on an integrodifference equation used to describe the spread of species with discrete life-stages (Kot et al. 1996, Pachepsky and Levine 2011), used in previous expansion speed simulation research (Williams et al. 2016b, Urquhart and Williams 2021):

$$N_{t+1}(x) = \int k|x-y| \cdot g\left(N_t(y)\right) dy$$

Here, $N_{t+1}(x)$ is the population at location x at time $t+1$, $k|(x-y)|$ is the dispersal kernel from point y to point x, and $g(N_t(y))$ is population growth in the previous time step. The equation for population growth is a Beverton–Holt equation that models the population growth of annual plants (Watkinson 1980, Levine and Rees 2002, Williams et al. 2016b, Urquhart and Williams 2021):

$$g\left(N_t(y)\right) = \frac{\lambda \cdot N_t(y)}{1+\alpha \cdot N_t(y)}$$

Where $g(N_t(y))$ represents seed production in a generation, λ is the low-density reproductive rate, $N_t(y)$ is the population at time t and at location y, and α is the sensitivity to intraspecific competition.

Dispersal was modelled on a negative exponential dispersal kernel (Kot et al. 1996, Williams et al. 2016b, Urquhart and Williams 2021):

$$k(x-y) = \frac{m}{2} e^{-m|x-y|}$$

In this equation, m represents the rate of decay of the probability of a seed moving from the patch containing the parent, y, to the new patch, x.

To investigate how fecundity and dispersal impact expansion speed, we ran simulations using four different combinations of parameters (fecundity (λ) and dispersal (m), each with and without competition) for each RIL. Fecundity (λ) was calculated by using the effective fecundity, or the sum of germinated seedlings in all pots of each runway. To examine how competition reduced fecundity in simulations, we calculated how many fewer seeds would have dispersed if focal individuals had been grown with *L. multiflorum* using data from our previous experiment (Fig. 1, Lustenhouwer et al. 2019). To do this, we reduced effective fecundity (this experiment) proportionally using the ratio of silique number for *A. thaliana* grown with and without competition from *L. multiflorum* (previous experiment; Lustenhouwer et al. 2019). Thus, in simulations where competition reduced λ, the effective fecundity of genotype 53 was reduced by ~90.5%, 58 by 95.6%, 144 by 94.2%, and 187 by 93.6%. For dispersal, we used the m values from fitted dispersal kernels for each treatment and genotype. We set α to 0.1 for all simulations, close to the mean observed value of 0.078 in L*er*, one of the parental ecotypes (Williams et al. 2016b, Williams and Levine 2018, Urquhart and Williams 2021). Previous research suggests that α plays a small role in determining expansion speed in homogeneous landscapes (Williams et al. 2016a). Simulations were run for each RIL and each combination of λ and m, for a total of four sets of four scenarios, or 16 scenarios total. Simulations were run for 30 generations, starting with 3 individuals, and we replicated each scenario 500 times. Expansion speed was calculated as the number of patches invaded divided by the

number of generations of spread. Simulation results were analysed in R ver. 4.3.1 (www.r-project.org).

Results

Competition reduced the mean dispersal distance of seeds, as calculated from the fitted dispersal kernels ($1/m$, where m is the rate parameter of the negative exponential distribution), from 4.4 cm to 2.2 cm, a 50% reduction in mean dispersal distance ($F_{1,38} = 8.96$, $p = 0.005$, Fig. 2), and reduced m by ~ 64% across treatments. Maximum dispersal distance differed significantly between empty and *L. multiflorum* treatments ($F_{1,38} = 11.956$, $p = 0.001$, Fig. 3), with seeds dispersing a greater maximum distance in empty mesocosms. Dispersal into a competitive habitat was also more variable: *L. multiflorum* mesocosms had a coefficient of variation of 0.551 in maximum dispersal distance compared to 0.319 in empty mesocosms. The number of germinated seeds was lower with increased distance from the parent plant (Supporting information); additionally, competition reduced the number of total germinated seeds in dispersal mesocosms by about 30% (Supporting information).

Only height and silique number had a significant impact on maximum dispersal distance (Fig. 3), with increased height and increased silique number correlating to increased maximum dispersal distance (Table 2A–B). Other traits (shown in Table 1) did not affect dispersal (Supporting information), although seed weight was not included in analyses, as data were only at the genotype level and thus redundant in linear models. We found no significant interaction between height and competition treatment ($p = 0.291$, Table 2B). Time to reproductive maturity in *A. thaliana* did not significantly affect the total number of seeds dispersed; instead, total number of seeds dispersed depended on which temporal block the plant was in ($F_{1,37} = 7.764$, $p = 0.008$), with plants in the second temporal block (warmer conditions) dispersing more

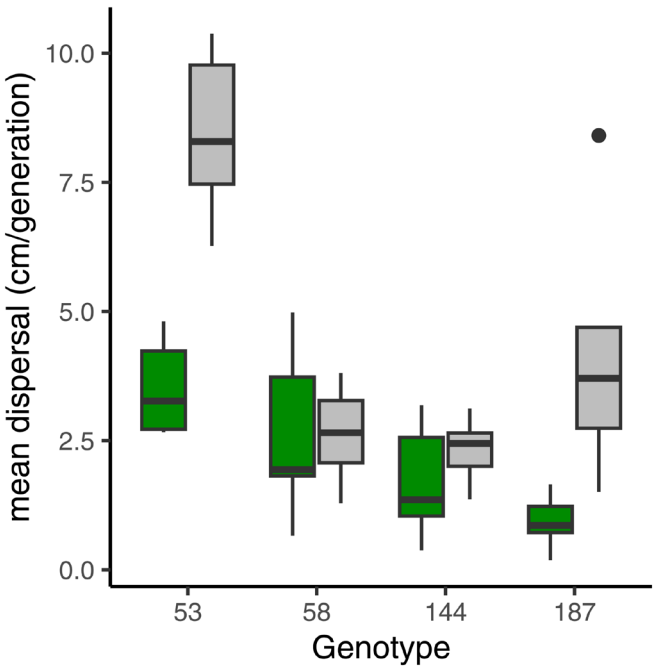


Figure 2. Mean dispersal distance for each *A. thaliana* genotype in empty mesocosms and those containing *L. multiflorum* (calculated from fitted dispersal kernels). Each boxplot shows the 75th, 50th (black line), and 25th percentiles; whiskers show outliers no more than 1.5 times the interquartile range, and dots show outlying points. Competition treatment is shown in green, empty (no competition) treatment in grey.

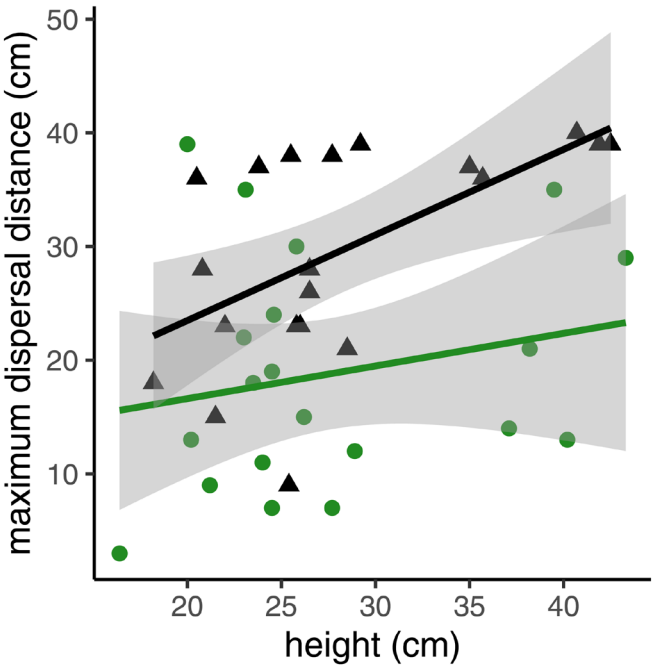


Figure 3. Maximum dispersal distance as a function of plant height. Each point is one replicate; green triangles represent the dispersal of *A. thaliana* into habitat with *L. multiflorum* (competition treatment), while black dots represent the dispersal of *A. thaliana* into empty habitat (control). Slope of regression line for control = 0.753; slope for competition treatment = 0.287. Grey polygons represent SE.

Table 2. (A) Results of linear model examining the effects of silique number and treatment (empty runways or runways containing *L. multiflorum*) on maximum dispersal distance. (B) Results of linear model examining the effects of height and treatment (empty runways or runways containing *L. multiflorum*) on maximum dispersal distance.

Source of variation	df	F-value	p-value
(A)			
Competition treatment	1	7.410	0.010
Silique number	1	5.233	0.028
Temporal block	1	1.973	0.169
Residuals	35		
(B)			
Competition treatment	1	11.555	0.002
Height	1	8.798	0.005
Temporal block	1	2.020	0.164
Competition treatment × height	1	1.150	0.291
Residuals	35		

seeds. Phenology did not significantly affect maximum dispersal distance ($F_{1,38} = 3.004$, $p = 0.091$), although maximum dispersal distance decreased slightly as time to first flower increased.

Competition reduced expansion speed across all genotypes (Fig. 4). Without competition, CVL 53 (tallest, earliest flowering, and most fecund genotype) had the highest expansion speed, and CVL 58 (least fecund genotype) the lowest. With competition affecting both fecundity and dispersal, CVL 53 showed the greatest decrease in expansion speed and CVL 58 showed the smallest (Fig. 4). The simulation results show that for CVLs 53, 144 and 187, reductions in dispersal associated with competition decreased expansion speed more than reductions in fecundity (Fig. 4). However, for CVL 58, the opposite trend was found: reductions in dispersal did not decrease expansion speed as much as reductions in fecundity. It is worth noting that overall, this genotype was the least sensitive to competition.

Discussion

We aimed to understand the mechanisms for how competition reduces expansion speed, via dispersal and fecundity, using experimental dispersal in *A. thaliana* and simulated range expansions. We found that dispersal distance significantly decreased with the presence of a competitor in our experiment. In simulations, this reduction in dispersal distance from competition slowed expansions. With a combined impact of competition on dispersal and fecundity, expansions were slower than with reductions to either trait alone for most genotypes. There is a growing understanding that interspecific competition can modify dispersal (Fronhofer et al. 2015, Snell et al. 2019). Here, we show that this is an important mechanism in the reduction of expansion speed due to interspecific competition.

Competition significantly decreased dispersal distance in our experiments, with variation among genotypes (Fig. 2). As we expected, the grass acted as a physical barrier to dispersal, and its presence may have impeded germination in *A. thaliana* seeds that did manage to disperse. The degree to which maximum dispersal distance was reduced in each genotype depended on height; other measured traits were not significant in predicting dispersal distance, but unmeasured traits such as branchiness may have impacted dispersal. The tallest, quickest-flowering genotype (CVL 53) had the greatest maximum dispersal distance without competition, as we expected based on prior research (Williams et al. 2016a, Lustenhouwer et al. 2019). With competition, dispersal distance in CVL 53 was reduced more significantly than other genotypes, lowering the overall variability in mean dispersal distance across genotypes. Thus, the spatial advantage that CVL 53 may have had in the absence of a competitor was greatly reduced with competition.

Despite variation across genotypes (Table 1), most of the traits we measured were not correlated with maximum dispersal distance in our experiment. Only height, which is a well-known predictor of dispersal distances more generally in wind- and passively-dispersed plants (Nathan et al. 2011), including *A. thaliana* (Wender et al. 2005), was a significant predictor (Fig. 3). Unlike other traits, plant height has a direct effect on dispersal; that is, not mediated via seed number. We expected other traits such as time to flowering to have an indirect effect on dispersal via altering the number of seeds dispersed (Wolkovich et al. 2013). If plants that flowered earlier produced more seeds, they would be more likely to have rare, longer distance dispersal events. We did see that plants that made more siliques, and thus seeds, dispersed slightly

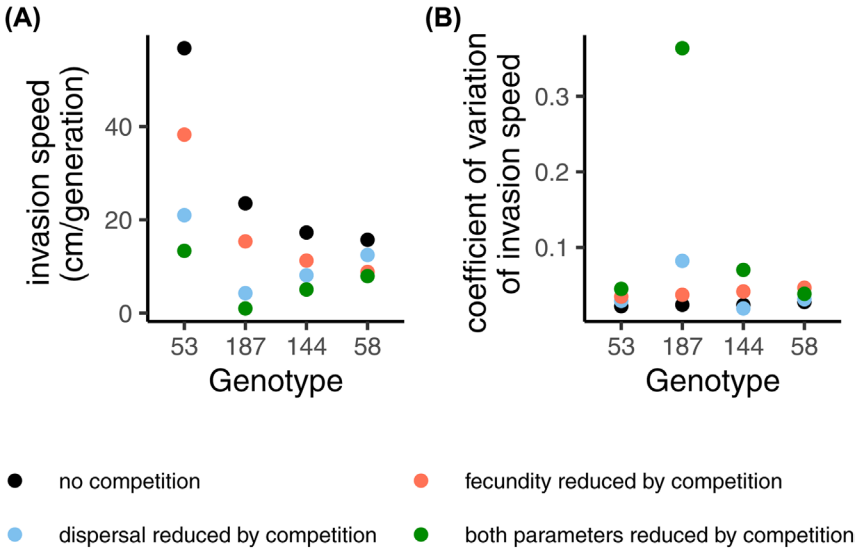


Figure 4. Results of spread simulations for each genotype for four scenarios where competition affects fecundity (λ) or dispersal (*m*), both or neither. (A) Mean expansion speed across 500 replicate simulations in centimetres dispersed per generation. (B) Coefficient of variation for expansion speed.

further; however, early-flowering plants did not. Anecdotally, we noticed that those genotypes that experienced more cold weather grew the most, perhaps because they were delaying reproduction. While these results were not statistically significant, they imply that correlations between multiple traits and dispersal may be difficult to predict, and traits that influence dispersal directly are likely more important.

By allowing plants to grow uninhibited by competition and then disperse seeds into an experimental landscape with a resident competitor, our experiment was designed to disentangle the effects of competition on fecundity and dispersal. We used previous data on silique number of the same four genotypes grown in the presence and absence of *Lolium multiflorum* to estimate the direct effect of competition on fecundity (Fig. 1, Lustenhouwer et al. 2019); however, it is possible that direct competition would also change plant height and/or phenology. Further research is needed to determine if genotypes experience different reductions in height, and by extension dispersal, under competition. For the four genotypes included in this study, competition with *Lolium multiflorum* did not affect plant phenology (Lustenhouwer unpubl.).

Competition reduced expansion speed in spread simulations of all four genotypes (Fig. 4). However, there was variation in the degree of reduction depending on whether competition affected fecundity, dispersal or both traits. While most theory that incorporates interspecific competition only considers its effect on population growth rate (Lewis et al. 2002, Weinberger et al. 2002, Holzer and Scheel 2012, Alhasanat and Ou 2020), we found that expansions are slowed more considerably when interspecific competition reduces dispersal in three of four genotypes (CVLs 53, 144 and 187). Thus, it is likely that models that do not account for decreases in mean dispersal distance from competition overestimate expansion speed in competitive systems. As in our experimental results for dispersal, the genotype with the highest expansion speed when spreading into empty habitat (CVL 53) experienced the greatest reduction in expansion speed when a competitor was present. The genotype with the smallest reduction in mean dispersal due to competition (CVL 58) was the only one where reductions in fecundity had a larger impact on expansion speed.

While we did not include evolution in the simulations, and considered expansions with just one genotype within each simulation, the variation in speed we found among genotypes can provide insights into how likely each genotype is to be present at the leading edge of an expansion when multiple genotypes are present. That is, with intraspecific competition only, we might expect that the fastest genotype (CVL 53) would become dominant at the leading edge over time, due to its higher maximum dispersal distance and seed production (Burton et al. 2010, Ochocki and Miller 2017). However, with interspecific competition, all four genotypes spread at similar speeds, increasing the likelihood of any one of them being found at the leading edge. This may effectively increase the strength of founder effects at the leading edge of range expansions, which may have implications for the genetic diversity of spreading populations (Peter and Slatkin 2015, Miller et al. 2020). This may also shift traits under selection at the leading edge away from those related to dispersal. Instead, selection may favour traits conferring greater competitive ability at the leading edge, as has been shown in models (Williams et al. 2016b, Urquhart and Williams 2021, Poloni and Lutscher 2023) and experiments (Williams et al. 2016a, Usui and Angert 2024) investigating selection imposed from environmental stresses. Although models of expanding populations are becoming better able to represent natural populations by incorporating evolution (Deshpande and Fronhofer 2022, Lutscher et al. 2022, Poloni and Lutscher 2023), most models of expanding populations assume that they spread into empty habitat (Miller et al. 2020), which is almost never true in nature. Our results demonstrate that evolutionary dynamics may be altered when interspecific competition is present, and thus we might miss key insights by assuming populations spread into empty space.

Conclusion

In this experiment, we demonstrated that competition can impact the expansion speed of an annual plant through hindering seed dispersal in addition to reductions in fecundity. We found that different genotypes, which differed in dispersal-related traits, were impacted by competition to varying extents, with what was initially the fastest genotype experiencing the strongest decline in expansion speed under competition. Our dispersal experiment only looked at how competition limits dispersal for one generation of spread; a logical next step is investigating how competition affects dispersal over several generations, including through effects on fecundity, and the resulting evolutionary consequences. Considering our results show that advantages conferred to an early-flowering, fecund genotype were blocked by the grass competitor, looking at the shape of expanding waves when a competitor is present and the spatial distribution of genotypes in the expanding wave would improve our ability to predict natural range expansions. This work demonstrates the importance of considering the impact of competition on more than just fitness and fecundity. As we have shown, competition can reduce dispersal per se, and thus slow range expansions even without corresponding reductions in fecundity.

Acknowledgements – We thank Melina Biron and the UBC Plant Services team for maintaining the greenhouses and setting up irrigation, and Noelle Beckman, Megan Frederickson, Tom Miller, Lauren Sullivan and Takuji Uusi for providing valuable comments on earlier versions of this manuscript. We would also like to thank the other members of the Williams lab for their support and their feedback on the initial results of this project.
Funding – This research was supported by the Natural Sciences and Engineering Research Council of Canada, through a Discovery Grant to JLW, a Canada Graduate Scholarships-Master's Award and Canada Graduate Scholarships-Doctoral to CAU, and an Undergraduate Student Research Award to EEM.

Author contributions

Erin E. McHugh: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (supporting); Investigation (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Carla A. Urquhart**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (supporting); Writing – review and editing (equal). **Nicky Lustenhouwer**: Conceptualization (supporting); Data curation (supporting); Investigation (supporting); Visualization (supporting); Writing – review and editing (supporting). **Jennifer L. Williams**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Supervision (lead); Visualization (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.r4xgxd2pt (McHugh et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Alhasanat, A. and Ou, C. 2020. On the conjecture for the pushed wavefront to the diffusive Lotka–Volterra competition model. – J. Math. Biol. 80: 1413–1422.

Allen, E. J., Allen, L. J. S. and Gilliam, X. 1996. Dispersal and competition models for plants. – J. Math. Biol. 34: 455–481.

Alonso-Blanco, C., Peeters, A. J. M., Koornneef, M., Lister, C., Dean, C., van den Bosch, N., Pot, J. and Kuiper, M. T. R. 1998. Development of an AFLP based linkage map of L*er* , Col and Cvi *Arabidopsis thaliana* ecotypes and construction of a L*er* /Cvi recombinant inbred line population. – Plant J. 14: 259–271.

Alonso-Blanco, C., Blankestijn-de Vries, H., Hanhart, C. J. and Koornneef, M. 1999. Natural allelic variation at seed size loci in relation to other life history traits of *Arabidopsis thaliana*. – Proc. Natl Acad. Sci. USA 96: 4710–4717.

Block, S. and Levine, J. M. 2021. How dispersal evolution and local adaptation affect the range dynamics of species lagging behind climate change. – Am. Nat. 197: E173–E187.

Bohrer, G., Katul, G. G., Nathan, R., Walko, R. L. and Avissar, R. 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. – J. Ecol. 96: 569–580.

Bolker, B. 2022. bbmle: tools for general maximum likelihood estimation. – https://cran.r-<project.org/web/packages/bbmle/index.html.

Bolker, B. M., Pacala, S. W., Neuhauser, C. and Lundberg, A. E. P. 2003. Spatial dynamics in model plant communities: what do we really know? – Am. Nat. 162: 135–148.

Bullock, J. M. and Moy, I. L. 2004. Plants as seed traps: interspecific interference with dispersal. – Acta Oecol. 25: 35–41.

Bullock, J. M., Mallada González, L., Tamme, R., Götzenberger, L., White, S. M., Pärtel, M. and Hooftman, D. A. P. 2017. A synthesis of empirical plant dispersal kernels. – J. Ecol. 105: 6–19.

Burton, O. J., Phillips, B. L. and Travis, J. M. J. 2010. Tradeoffs and the evolution of life-histories during range expansion. – Ecol. Lett. 13: 1210–1220.

Campitelli, B. E., Des Marais, D. L. and Juenger, T. E. 2016. Ecological interactions and the fitness effect of water-use efficiency: competition and drought alter the impact of natural *MPK12* alleles in *Arabidopsis*. – Ecol. Lett. 19: 424–434.

Campos, D., Méndez, V. and Ortega-Cejas, V. 2008. Lattice models for invasions through patchy environments. – Bull. Math. Biol. 70: 1937–1956.

Cipollini, D. F. and Bergelson, J. 2002. Interspecific competition affects growth and herbivore damage of *Brassica napus* in the field. – Plant Ecol. 162: 227–231.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. – Ecology 42: 710–723.

Cousens, R. D. and Rawlinson, A. A. 2001. When will plant morphology affect the shape of a seed dispersal "kernel"? – J. Theor. Biol. 211: 229–238.

Delefosse, M., Povidisa, K., Poncet, D., Kristensen, E. and Olesen, B. 2016. Variation in size and chemical composition of seeds from the seagrass *Zostera marina* – ecological implications. – Aquat. Bot. 131: 7–14.

Deshpande, J. N. and Fronhofer, E. A. 2022. Genetic architecture of dispersal and local adaptation drives accelerating range expansions. – Proc. Natl. Acad. Sci. USA 119: e2121858119.

Donohue, K. 1998. Maternal determinants of seed dispersal in *Cakile edentula*: fruit, plant and site traits. – Ecology 79: 2771–2788.

Fagan, W. F. and Bishop, J. G. 2000. Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens. – Am. Nat. 155: 238–251.

Fronhofer, E. A., Poethke, H. J. and Dieckmann, U. 2015. Evolution of dispersal distance: maternal investment leads to bimodal dispersal kernels. – J. Theor. Biol. 365: 270–279.

Harper, J. L. 1977. Population biology of plants. – Academic Press.

Harper, J. L., Lovell, P. H. and Moore, K. G. 1970. The shapes and sizes of seeds. – Annu. Rev. Ecol. Syst. 1: 327–356.

Hart, D. R. and Gardner, R. H. 1997. A spatial model for the spread of invading organisms subject to competition. – J. Math. Biol. 35: 935–948.

Hastings, A. 1996. Models of spatial spread: a synthesis. – Biol. Conserv. 78: 143–148.

Heydel, F., Cunze, S., Bernhardt-Römermann, M. and Tackenberg, O. 2014. Long-distance seed dispersal by wind: disentangling the effects of species traits, vegetation types, vertical turbulence and wind speed. – Ecol. Res. 29: 641–651.

Holzer, M. and Scheel, A. 2012. A slow pushed front in a Lotka–Volterra competition model. – Nonlinearity 25: 2151–2179.

Hosono, Y. 1998. The minimal speed of traveling fronts for a diffusive Lotka–Volterra competition model. – Bull. Math. Biol. 60: 435–448.

Jankowski, J. E., Robinson, S. K. and Levey, D. J. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. – Ecology 91: 1877–1884.

Kot, M., Lewis, M. A. and Van Den Driessche, P. 1996. Dispersal data and the spread of invading organisms. – Ecology 77: 2027–2042.

Legault, G., Bitters, M. E., Hastings, A. and Melbourne, B. A. 2020. Interspecific competition slows range expansion and shapes range boundaries. – Proc. Natl Acad. Sci. USA 117: 26854–26860.
Levine, J. M. and Rees, M. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. – Am. Nat. 160: 452–467.
Lewis, M. A., Li, B. and Weinberger, H. F. 2002. Spreading speed and linear determinacy for two-species competition models. – J. Math. Biol. 45: 219–233.
Lindström, T., Håkansson, N. and Wennergren, U. 2011. The shape of the spatial kernel and its implications for biological invasions in patchy environments. – Proc. R. Soc. B 278: 1564–1571.
Lustenhouwer, N., Williams, J. L. and Levine, J. M. 2019. Evolution during population spread affects plant performance in stressful environments. – J. Ecol. 107: 396–406.
Lutscher, F., Popovic, L. and Shaw, A. K. 2022. How mutation shapes the rate of population spread in the presence of a mate-finding Allee effect. – Theor. Ecol. 16: 255–269.
Marchetto, K. M., Jongejans, E., Shea, K. and Isard, S. A. 2010. Plant spatial arrangement affects projected invasion speeds of two invasive thistles. – Oikos 119: 1462–1468.
McHugh, E. E., Urquhart, C. A., Lustenhouwer, N. and Williams, J. L. 2024. Data from: Interspecific competition reduces seed dispersal in an annual plant and slows simulated range expansions. – Dryad Digital Repository, https://doi.org/10.5061/dryad.r4xgxd2pt.
Miller, T. E. X., Angert, A. L., Brown, C. D., Lee-Yaw, J. A., Lewis, M., Lutscher, F., Marculis, N. G., Melbourne, B. A., Shaw, A. K., Szűcs, M., Tabares, O., Usui, T., Weiss-Lehman, C. and Williams, J. L. 2020. Eco-evolutionary dynamics of range expansion. – Ecology 101: e03139.
Mustin, K., Benton, T. G., Dytham, C. and Travis, J. M. J. 2009. The dynamics of climate-induced range shifting; perspectives from simulation modelling. – Oikos 118: 131–137.
Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F. M. and Katul, G. G. 2011. Spread of North American wind-dispersed trees in future environments: spread of wind-dispersed trees. – Ecol. Lett. 14: 211–219.
Notzold, R., Blossey, B. and Newton, E. 1997. The influence of below ground herbivory and plant competition on growth and biomass accumulation of purple loosestrife. – Oecologia 113: 82–93.
Ochocki, B. M. and Miller, T. E. X. 2017. Rapid evolution of dispersal ability makes biological invasions faster and more variable. – Nat. Commun. 8: 14315.
Okubo, A., Maini, P. K., Williamson, M. H. and Murray, J. 1989. On the spatial spread of the grey squirrel in Britain. – Proc. R. Soc. B 238: 113–125.
Pachepsky, E. and Levine, J. M. 2011. Density dependence slows invader spread in fragmented landscapes. – Am. Nat. 177: 18–28.
Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.
Paul-Victor, C. and Turnbull, L. A. 2009. The effect of growth conditions on the seed size/number tradeoff. – PLoS One 4: e6917.
Peter, B. M. and Slatkin, M. 2015. The effective founder effect in a spatially expanding population. – Evolution 69: 721–734.
Poloni, S. and Lutscher, F. 2023. Integrodifference models for evolutionary processes in biological invasions. – J. Math. Biol. 87: 10.
Pounden, E., Greene, D. F., Quesada, M. and Contreras Sánchez, J. M. 2008. The effect of collisions with vegetation elements on the dispersal of winged and plumed seeds. – J. Ecol. 96: 591–598.
Pyšek, P. et al. 2020. Scientists' warning on invasive alien species. – Biol. Rev. 95: 1511–1534.
Qin, X., Liang, W., Liu, Z., Liu, M., Baskin, C. C., Baskin, J. M., Xin, Z., Wang, Z. and Zhou, Q. 2022. Plant canopy may promote seed dispersal by wind. – Sci. Rep. 12: 63.
Rivest, S. and Vellend, M. 2018. Herbivory and pollen limitation at the upper elevational range limit of two forest understory plants of eastern North America. – Ecol. Evol. 8: 892–903.
Shigesada, N., Kawasaki, K. and Teramoto, E. 1986. Traveling periodic waves in heterogeneous environments. – Theor. Popul. Biol. 30: 143–160.
Skarpaas, O., Silverman, E. J., Jongejans, E. and Shea, K. 2011. Are the best dispersers the best colonizers? Seed mass, dispersal and establishment in *Carduus* thistles. – Evol. Ecol. 25: 155–169.
Skellam, J. 1991. Random dispersal in theoretical populations. – Bull. Math. Biol. 53: 135–165.
Snell, R. S. et al. 2019. Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. – AoB Plants 11: plz016.
Sullivan, L. L. and Shaw, A. K. 2023. Take me for a ride: herbivores can facilitate plant reinvasions. – Ecology 104: e4132.
Travis, J. M. J. and Dytham, C. 2002. Dispersal evolution during invasions. – Evol. Ecol. Res. 4: 1119–1129.
Travis, J. M. J., Mustin, K., Benton, T. G. and Dytham, C. 2009. Accelerating invasion rates result from the evolution of density-dependent dispersal. – J. Theor. Biol. 259: 151–158.
Urquhart, C. A. and Williams, J. L. 2021. Trait correlations and landscape fragmentation jointly alter expansion speed via evolution at the leading edge in simulated range expansions. – Theor. Ecol. 14: 381–394.
Usui, T. and Angert, A. L. 2024. Range expansion is both slower and more variable with rapid evolution across a spatial gradient in temperature. – Ecol. Lett. 27: e14406.
Watkinson, A. R. 1980. Density-dependence in single-species populations of plants. – J. Theor. Biol. 83: 345–357.
Weinberger, H. F., Lewis, M. A. and Li, B. 2002. Analysis of linear determinacy for spread in cooperative models. – J. Math. Biol. 45: 183–218.
Wender, N. J., Polisetty, C. R. and Donohue, K. 2005. Density-dependent processes influencing the evolutionary dynamics of dispersal: a functional analysis of seed dispersal in *Arabidopsis thaliana* (Brassicaceae). – Am. J. Bot. 92: 960–971.
Williams, J. L. and Levine, J. M. 2018. Experimental evidence that density dependence strongly influences plant invasions through fragmented landscapes. – Ecology 99: 876–884.
Williams, J. L., Kendall, B. E. and Levine, J. M. 2016a. Rapid evolution accelerates plant population spread in fragmented experimental landscapes. – Science 353: 482–485.
Williams, J. L., Snyder, R. E. and Levine, J. M. 2016b. The influence of evolution on population spread through patchy landscapes. – Am. Nat. 188: 15–26.
Wolkovich, E. M., Davies, T. J., Schaefer, H., Cleland, E. E., Cook, B. I., Travers, S. E., Willis, C. G. and Davis, C. C. 2013. Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. – Am. J. Bot. 100: 1407–1421.