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Dispersal Evolution in the Presence of Allee Effects Can Speed Up or Slow Down Invasions

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ABSTRACT: Successful invasions by sexually reproducing species depend on the ability of individuals to mate. Finding mates can be particularly challenging at low densities (a mate-finding Allee effect), a factor that is only implicitly accounted for by most invasion models, which typically assume asexual populations. Existing theory on single-sex populations suggests that dispersal evolution in the presence of a mate-finding Allee effect slows invasions. Here we develop a two-sex model to determine how mating system, strength of an Allee effect, and dispersal evolution influence invasion speed. We show that mating system differences can dramatically alter the spread rate. We also find a broader spectrum of outcomes than earlier work suggests. Allowing dispersal to evolve in a spreading context can sometimes alleviate the mate-finding Allee effect and slow the rate of spread. However, we demonstrate the opposite when resource competition among females remains high: evolution then acts to speed up the spread rate, despite simultaneously exacerbating the Allee effect. Our results highlight the importance of the timing of mating relative to dispersal and the strength of resource competition for consideration in future empirical studies.

Keywords: context-dependent dispersal, eco-evolutionary dynamics, invasion speed, mating system, sex-biased dispersal, spatial spread.

Introduction

Population distributions are often dynamic, changing in time and space. Ranges of populations contract as habitat is destroyed or developed (Wilcove et al. 1986), expand as individuals are introduced into new environments (Johnson et al. 2006; Urban et al. 2007) or recolonize old ones (Fagan et al. 2005; Ortiz-Catedral et al. 2009), and change as populations adapt in response to altered climate conditions (Davis and Shaw 2001; Pinsky et al. 2013). A key characteristic of these changes is the rate at which a population is able to grow and spread.

Predicting the rate of population spread has long been of interest in ecology (Elton 1958). A large body of ecological theory has predicted population spread rate to be fairly constant, governed by dynamics near a population's edge (Skellam 1991; Kot et al. 1996; Hastings et al. 2005). More recent theory has shown that evolutionary processes can alter the dispersal behavior of individuals, changing the rate of population spread and, in some cases, leading to an accelerating rate (Travis and Dytham 2002; Phillips et al. 2008; Hargreaves and Eckert 2013; Perkins et al. 2013; but see Phillips 2012 for a mechanism leading to an opposite result).

However, both sets of theoretical studies typically assume an asexual population. This forces a model to ignore sex-specific differences not only in life-history traits, such as body size, survival, and age of maturation (Bradley et al. 1980; Fairbairn 1997; Onyango et al. 2013), but also in movement behaviors, such as tendency to leave the natal area and total distance traveled (Greenwood 1980; Waser and Jones 1983; Clarke et al. 1997; Miller et al. 2011). An added complication of sexually reproducing species is the requirement that individuals find mate(s) before reproducing, which can be increasingly difficult at low densities (Dennis 1989; Wells et al. 1998; Courchamp et al. 2008). Difficulties in finding mates can cause an Allee effect, where population growth decreases at low densities (Stephens et al. 1999). As low densities are typically encountered at the edge of a population's range, Allee effects (due to mate finding and other causes) are likely to be an important factor in determining the rate of spread of sexually reproducing species, with the potential to slow down the rate of spread or even prevent invasions (Lewis and Kareiva 1993; Veit and Lewis 1996; South and Kenward 2001; Taylor and Hastings 2005; Robinet et al. 2008; Contarini et al. 2009;

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Krkošek et al. 2012). Recent models (Miller et al. 2011), together with experimental work (Miller and Inouye 2013), have shown that sex-specific differences in demographic and dispersal parameters alone (ignoring the added complication of demographic Allee effects or dispersal evolution) can drastically influence the spread rate of a population.

While Allee effects have the potential to influence a population's rate of spread, it is also possible that a population may undergo adaptation to minimize the impact of Allee effects. A handful of theoretical studies have recently provided evidence that evolution can indeed help a population mitigate an Allee effect (Kanarek and Webb 2010; Cushing and Hudson 2012; Shaw and Kokko 2014*b*). It may be tempting to predict that any adaptation that allows an individual to overcome an Allee effect should have been selected for, since Allee effects negatively influence an individual's fitness (Taylor and Hastings 2005; Gascoigne et al. 2009). However, this may not be the case if low densities have been rare during the evolutionary history of a species, and current anthropogenically changed conditions have placed populations in a novel selective environment—such as that encountered by any spreading population. Furthermore, allowing dispersal evolution to occur in the context of an Allee effect should generally slow the rate of population spread, as selection acts to alleviate the Allee effect by reducing the distance that individuals travel beyond the current population range (Travis and Dytham 2002).

Here we develop an evolutionary individual-based model to determine how mating system, mate-finding Allee effects, and dispersal evolution all interact to determine a population's rate of spread. We find that differences between mating systems can dramatically alter the spread rate by affecting the strength of mate-finding Allee effects. We show that allowing dispersal to evolve in a spreading context slows down population spread if resource competition among females remains relatively low. However, the opposite occurs when competition for resources is high: dispersal evolution speeds up the population spread while paradoxically decreasing the probability of females mating successfully.

Material and Methods

Our basic model structure is similar to the second model developed in Shaw and Kokko (2014*b*), where we considered how mating system and mate-finding Allee effects influence sex-biased dispersal. The main difference is that here we consider both stationary and spreading populations instead of merely considering long-term evolution in stationary worlds. As minor differences, we here assume stronger spatial structure (dispersing individuals move to neighboring patches instead of any other patch) and, for simplicity, fewer mating scenarios. See appendix A (apps. A–C are available online) for model pseudocode and parameters. Full model code is deposited in the Dryad Digital Repository: http://doi.org/10.5061/dryad.t59t0 (Shaw and Kokko 2014*a*).

In our model, individuals (males and females) inhabit a world of discrete patches on a lattice, with the world's boundaries either wrapped or not depending on the question asked (see below). Dispersal behavior is governed by context-dependent settlement rules instead of a fixed dispersal kernel or dispersal rate; individuals choose to settle in a patch on the basis of the current number of males and females present. Individuals disperse, one at a time, by moving randomly to one of the four patches adjacent to their current patch. They repeat this movement until they either choose to settle or reach the maximum number of dispersal steps allowed ($s_{\max}$). Individuals have the possibility of not dispersing at all, as they can choose to settle in their natal patch and not leave. Each individual completes its entire dispersal trajectory before the next individual starts.

The probability that an individual settles in a patch (for steps below the maximum number) is given by

$$p_{\mathrm{F}} = \frac{1}{1 + 0.5e^{-a(R_{\mathrm{FS}} - n_{\mathrm{F}})} + 0.5e^{a(R_{\mathrm{FO}} - n_{\mathrm{M}})}} \quad \text{for females,} \tag{1a}$$

$$p_{\mathrm{M}} = \frac{1}{1 + 0.5e^{a(R_{\mathrm{MO}} - n_{\mathrm{F}})} + 0.5e^{-a(R_{\mathrm{MS}} - n_{\mathrm{M}})}} \quad \text{for males,} \tag{1b}$$

where both are logistic functions of the number of males (n_{M}) and females (n_{F}) in a patch (an example is shown in fig. 1). Under this settlement probability, an individual is more likely to stop dispersing if it encounters a patch with more potential mates and fewer potential competitors. The parameter a does not differ between individuals and describes the steepness of the settlement function. Each individual's strategy consists of two parameters: R_{FS} and R_{FO} for females and R_{MS} and R_{MO} for males. Higher values of R_{FO} and R_{MO} (parameters corresponding to the number of individuals of the opposite sex present) mean a dispersing individual requires a higher number of potential mates in a patch before choosing to settle. Higher values of R_{FS} and R_{MS} (parameters corresponding to the number of individuals of the same sex present) mean that an individual requires a higher number of potential competitors in a patch before choosing not to settle and to continue moving.

To explore the interaction between mating system and dispersal, we considered four scenarios:

Predispersal mating with offspring deposition. Each female mates with one male (if any are present) in her natal patch prior to dispersal, produces and deposits a fraction $(1 + s_{\max})^{-1}$ of her offspring in each patch she visits during

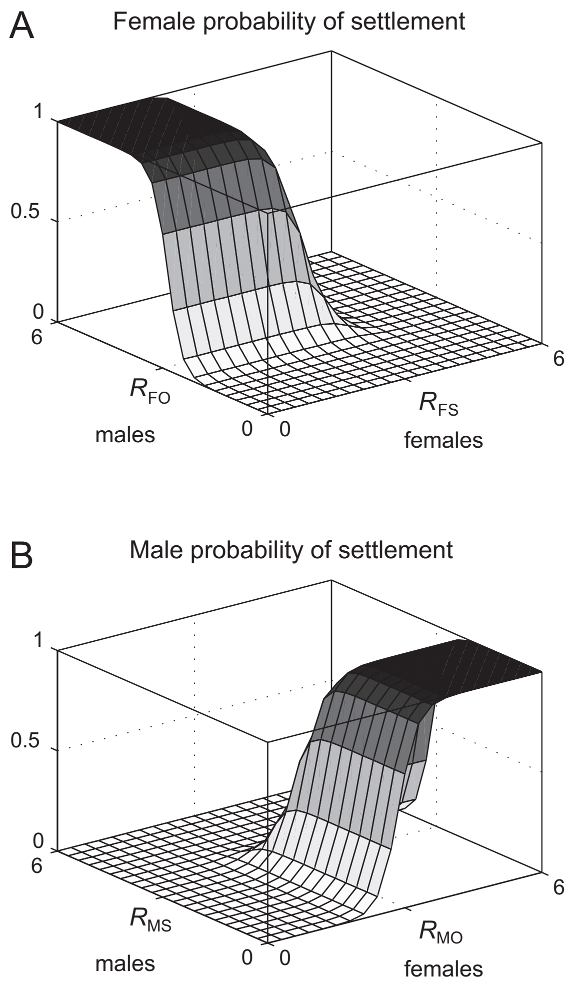

Figure 1: Sex-specific dispersal settlement functions. The probability that an individual settles in a given patch (eqq. [1]) is a function of the local number of males and females, where females are more likely to settle for more males and fewer females (*A*) and males are more likely to settle for fewer males and more females (*B*). An individual's strategy is defined by two parameters (R_{FS} and R_{FO} for females and R_{MO} and R_{MS} for males) that determine the location of the midpoint of this probability function with respect to females and males, respectively. In both panels, the shape parameter is $a = 5$.

dispersal, and produces/deposits the remaining offspring in the patch where she settles.

Mating en route. Each individual (male or female) mates during dispersal with one mate (if present) in each patch visited, and offspring are produced in the patch where the female finally settles. A female's first mate sires all her offspring (first male sperm precedence).

Postdispersal monogamous mating. Mating and reproduction occur after settlement in monogamous pairs that form at random within the settlement patch. In patches with an unequal sex ratio, some individuals of the more common sex will not reproduce.

Postdispersal polygynandrous mating. Mating and reproduction occur after settlement polygynandrously; every offspring produced in a patch has a mother and a father randomly drawn from the individuals present. There is no reproduction in any patch that ended up with individuals of only one sex.

During each generation of a simulation, individuals are born and then disperse and mate according to one of these scenarios. Dispersal incurs a mortality cost: we assume the probability of surviving dispersal decreases with the number of steps taken according to an exponential distribution with mean s. The parameter s then describes the expected "safe" number of steps that an individual can disperse and still survive. Each mated female has the potential to produce Poisson(b) offspring, where b is a fecundity parameter. Each offspring produced develops randomly as a female or a male (even sex ratio). All parents and all but n of the offspring produced in each patch die (competition occurs at the patch level). This concludes a generation. Simulations were run for hundreds to thousands of generations (see below).

To simplify inheritance, we use haploid genetics where offspring inherit each of the four settlement alleles (R_{FS}, R_{FO}, R_{MS}, and R_{MO}) from a parent at random (no linkage) with a small mutation in parameter value (a Gaussian random number with mean 0 and standard deviation μ).

We ran simulations under a variety of parameter values: $b = \{1, 2, 3, \ldots, 14\}$, $n = \{1, 2, 3, \ldots, 10\}$, and $s = \{20, 50, 100\}$. In particular, we focused on two extreme sets of conditions. In the first case ($b = 4$, $n = 10$, $s = 20$), each patch supports more offspring than any single female produces (on average), and mortality rate during dispersal is high (approximately a 22% risk of dying for individuals dispersing the maximum number of dispersal steps, $s_{\max}$); therefore, the density of available mates is low. As a result, resource competition among females should remain low. In the second case ($b = 10$, $n = 5$, $s = 100$), each patch supports fewer offspring than a single mated female produces, and there is a low mortality rate during dispersal (approximately a 5% risk of dying for individuals dispersing the maximum number of dispersal steps, $s_{\max}$). As a result, resource competition among females should be high.

For each combination of mating scenario and parameter values, we first ran a set of simulations to determine the dispersal settlement strategies favored in a stationary population (at carrying capacity) and then ran a set of simulations to determine the outcome of introducing a few individuals into an empty environment.

Stationary Simulations

For the stationary simulations, individuals inhabited a lattice of 21-by-21 patches with wrapping boundaries (individuals could disperse off the left side of the environment and reappear at the right; same for top and bottom). The population was started at carrying capacity (*n* individuals in each patch). We evolved both male and female strategies simultaneously for 2,000 generations (enough to typically ensure convergence) with mutation parameter μ set to 0.01. We ran one simulation for each combination of mating scenario and parameter values for the two focal sets of parameter values described above (eight simulations) plus one simulation for the postdispersal monogamous mating for all values of *n*, *b*, and *s* (for a total of 428 stationary simulations).

Spreading Simulations

Next we determined what happened if a subset of individuals that had evolved in a stationary population (as above) were introduced into a new empty environment with the opportunity to spread. For these simulations, a total of 9*n* individuals from the last generation of the stationary simulations were chosen at random. These individuals were introduced to the nine centermost patches of a long, thin lattice of 5-by-2,001 patches, where individuals could wrap across the shorter dimension boundaries only. We then let the simulation proceed as above but stopped it once the population had grown and spread to a threshold distance: when the median distance of individuals in the population reached 200 length units from the center (to set the spatial scale, one patch is considered a 1-by-1 unit square). We recorded the time it took the population to reach this stage as our measure of spread speed; a shorter time obviously indicates faster spread.

To examine general model behavior, we ran 10 replicate simulations (each with a random set of starting individuals) for all combinations of mating scenario, the two focal sets of parameter values, and the presence or absence of evolution during spread ($\mu = 0$ and 0.05), plus two replicate simulations for the postdispersal monogamous mating case for all combinations parameter values (*b*, *n*, *s*) and the presence or absence of evolution during spread, for a total of 1,840 spreading simulations. For each run, we also recorded the dispersal strategies (R_{FS}, R_{FO}, R_{MS}, and R_{MO}) that evolved and the fraction of females that mated.

To quantify the impact of mate-finding Allee effects, we contrasted our results with one simulation per mating scenario where females otherwise followed the same life history as above, but (i) females were able to reproduce parthenogenetically regardless of whether they had mated with a male, (ii) offspring inherited parameter values from their mother alone, and (iii) we set the mutation parameter μ to 0. These changes avoid adaptation to these new parthenogenetic conditions and remove all mate limitation.

Results

Settlement Strategies

For stationary simulations, when mating occurred after dispersal males and females generally evolved similar settlement strategies (figs. B1*A*–B1*D*, B2*A*–B2*D*; figs. B1–B8, C1 are available online). In contrast, when mating occurred during dispersal, males had an overall lower probability of settling than did females (figs. B1*E*, B1*F*, B2*E*, B2*F*). When mating occurred before dispersal, females had a lower probability of settling than males but only when resource competition was high. When resource competition was low, females and males were about equally likely to settle (figs. B1*G*, B1*H*, B2*G*, B2*H*). Without evolution during spread, there was little spatial variation across the population in both the settlement strategies used (not surprisingly) and the number of steps taken during dispersal (figs. 2*A*, B3, B4). In contrast, with evolution during spread there was high spatial variation in dispersal steps taken but intriguingly little spatial variation in settlement strategies (figs. 2*B*, B5, B6). This shows that the phenotype (observed dispersal behavior) can evolve to show much more spatial variation than the genotype. Note that individuals in our spreading simulations can move either toward or away from the core. Settlement strategies anywhere along the range are consequently impacted by their performance at a variety of densities once densities have become variable (the scenarios involving spread). Phenotypically plastic movement decisions can then lead to spatial variation in behavior even if spatial sorting of genotypes remains negligible.

Mating Scenario Influenced Spread

The amount of time it took a population of individuals to grow and spread in a new environment depended strongly on the mating scenario considered. Populations spread fastest when mating occurred before or during dispersal (fig. 3*A*, 3*B*). When mating occurred after dispersal, populations that mated polygynandrously spread faster than those mating in monogamous pairs. The difference was especially pronounced with high resource competition: the population spread almost an order of magnitude faster with predispersal mating (~250 generations) than with postdispersal monogamous mating (~2,050 generations).

Mate-finding Allee effects slowed the spread rate: populations spread generally faster in simulations where all females were able to reproduce regardless of whether they had mated with a male (fig. 3*A*, 3*B*, gray vs. black). However, the magnitude of this difference varied across scenarios. Allee effects caused a severalfold slowing down in simulations where mating occurred after dispersal, but the difference in speed was minor when mating occurred be-

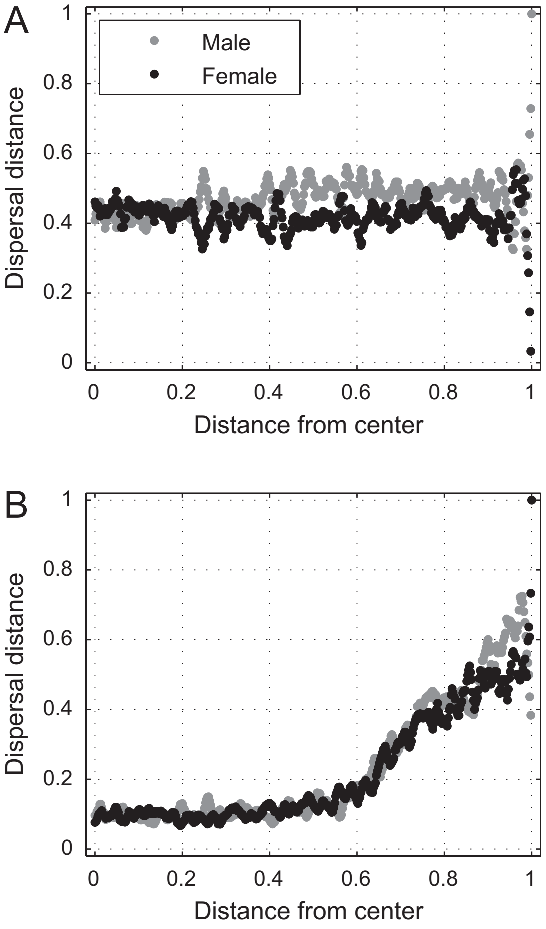

Figure 2: Evolution leads to spatial patterns in dispersal behavior. Shown is an average cross section of the normalized dispersal distance for males and females (averaged across individuals and 10 replicates) in spreading environments as a function of normalized distance from introduction site with no evolution during spread ($\mu = 0$; *A*) and continued evolution during spread ($\mu = 0.05$; *B*). Parameters: postdispersal polygynandrous mating, $b = 4$ (average offspring per female), $n = 10$ (individuals per patch), $s = 20$ (dispersal survival parameter).

fore or during dispersal. These strong differences are particularly intriguing given that the probability of mating was never very low (above 0.8 in all simulations).

Dispersal Evolution Can Speed Up or Slow Down Population Spread

We ran simulations in the presence and absence of evolution of dispersal parameters during spread. In the scenario of postdispersal monogamy with low resource competition, continuing evolution led to R_{FO} and R_{MO} evolving downward and R_{FS} and R_{MS} evolving upward (fig. B7). All four changes led individuals to be more likely to settle quickly for a given number of mates and/or competitors. As a result, females had an overall higher probability of mating (fig. 4*A*), but individuals tended not to disperse far and the population took longer to reach the threshold distance (fig. 4*C*).

In contrast, for postdispersal monogamy with high resource competition, continuing evolution led to lower values for all parameters. As above, it led to stronger tendency to settle in the presence of potential mates (higher R_{FO} and R_{MO}) but now coupled with evolving (slightly) lower values for R_{FS} and R_{MS} (fig. B7). Individuals therefore evolved a stronger tendency to settle in patches with potential mates as well as a reduced tendency to settle in patches with potential competitors. The latter factor appears to be the overriding one: most individuals dispersed far and had a relatively low probability of mating (fig. 4*B*). Mating failures did not greatly harm population spread, however, because those individuals that did find mates tended to be in relatively distant patches with no competitors present. Their offspring experienced little competition, which made the risky strategy of long-distance dispersal profitable. The resulting tendency for individuals to disperse far means that the population took much less time to spread than in other scenarios (fig. 4*D*). These patterns generally held across parameter space: whether resource competition was low ($n \gg b$) or high determined whether evolution during spread tended to increase or decrease the invasion speed (fig. B8).

For postdispersal polygynandry, results under high resource competition were similar to results from monogamy simulations (allowing evolution led to slower spread than without evolution; figs. 4, B7). However, under low resource competition allowing evolution led to individuals having a higher probability of mating and slightly faster spread than not allowing evolution (fig. 4*C*). This is likely because individuals mating polygynandrously experienced fewer mating failures than those mating monogamously; therefore, selection to maximize the chances of landing in a patch with a favorable sex ratio was weaker. Finally, in cases where mating occurred before or during dispersal, whether we allowed dispersal rules to evolve to be different from the end point of stationary simulations generally had little effect on population spread and mating probabilities (fig. 4) because even if evolution was allowed, the evolutionary response in dispersal rules remained minor (fig. B7). Simulation data underlying all figures are deposited in the Dryad Digital Repository: http://doi.org/10.5061/dryad.t59t0 (Shaw and Kokko 2014*a*).

Discussion

Otherwise comprehensive reviews of invasion ecology surprisingly often neglect the effects of sexual reproduction

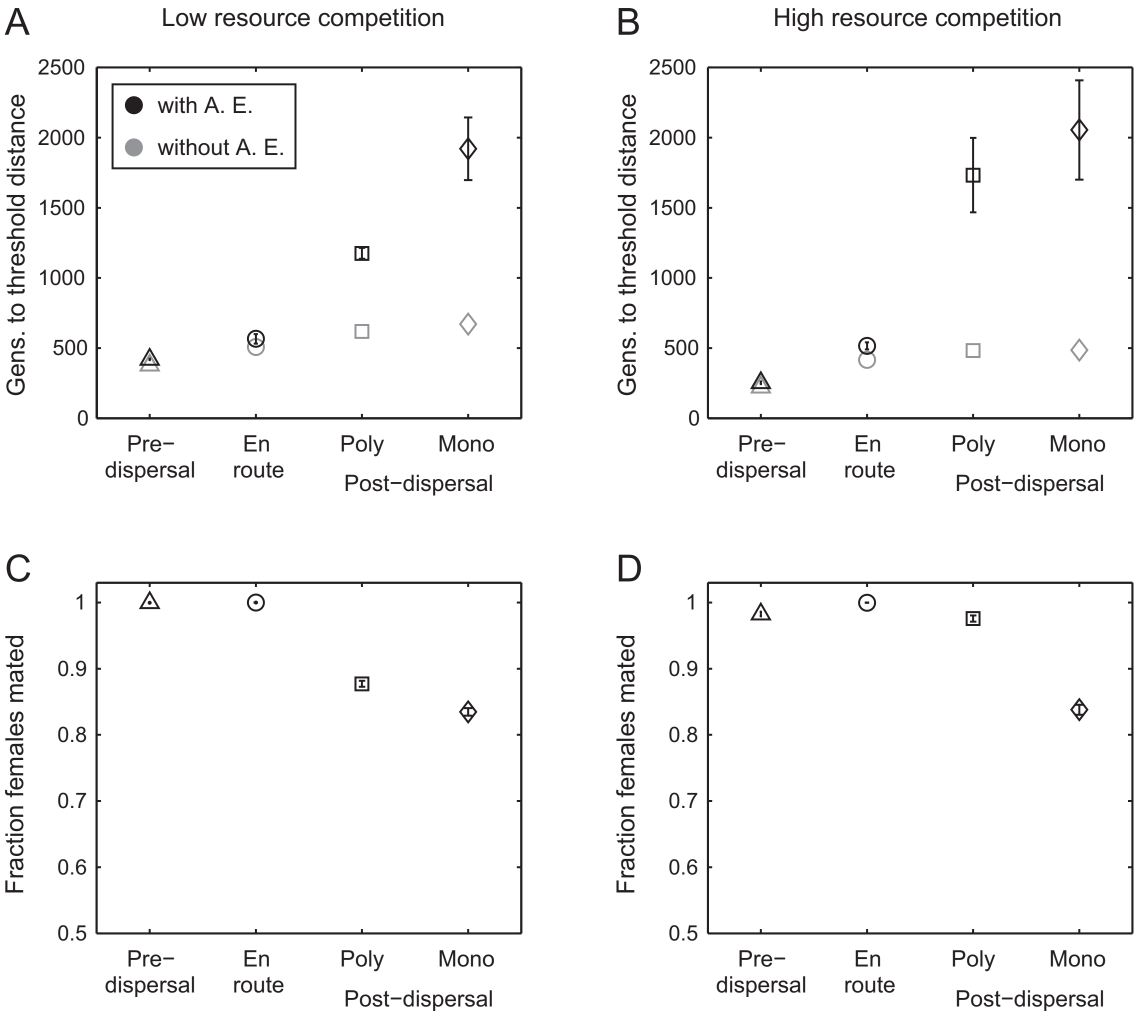

Figure 3: Influence of mating scenario and mate-finding Allee effect. Shown are the number of generations it took the spreading population to reach the threshold distance (*A*, *B*) and the fraction of females that mated under different mating scenarios: predispersal, en route, or postdispersal with polygynandry or monogamy (*C*, *D*). Data are the average across 10 replicates with standard deviation bars. Parameters: $\mu = 0$ (mutation standard deviation); $b = 4$, $n = 10$, $s = 20$ (*A*, *C*); and $b = 10$, $n = 5$, $s = 100$ (*B*, *D*). Gray symbols in *A* and *B* show the time to reach the threshold distance when females reproduced regardless of whether they mated with a male (no mate-finding Allee effect). A. E. = Allee effect.

(Hastings et al. 2005; Blackburn et al. 2011). Yet invasions by sexually reproducing species require successful mating. Here we have developed an individual-based simulation model with sex-specific dispersal strategies to determine how mating scenario, strength of mate-finding Allee effect, and dispersal evolution determine the invasion speed of a spreading population. We find that dispersal evolution in the presence of a mate-finding Allee effect can either speed up or slow down the rate of population spread and simultaneously either exacerbate or alleviate the Allee effect, depending on the strength of resource competition. Altering the mating system or, alternatively, artificially removing the mate-finding Allee effect by introducing parthenogenesis can increase the rate of population spread by almost an order of magnitude.

Previous work has shown that Allee effects can change the effect of dispersal evolution on the rate of population spread from positive to negative, that is, evolution in the absence (presence) of an Allee effect increases (decreases) spread rates (Travis and Dytham 2002). In their model, Travis and Dytham (2002) assume an asexual population and incorporate an Allee effect by not allowing individuals to reproduce if they are alone in a patch. Our results demonstrate that, in the presence of mate-finding Allee effects, dispersal evolution can either slow down or speed up the rate of spread depending on the strength of resource

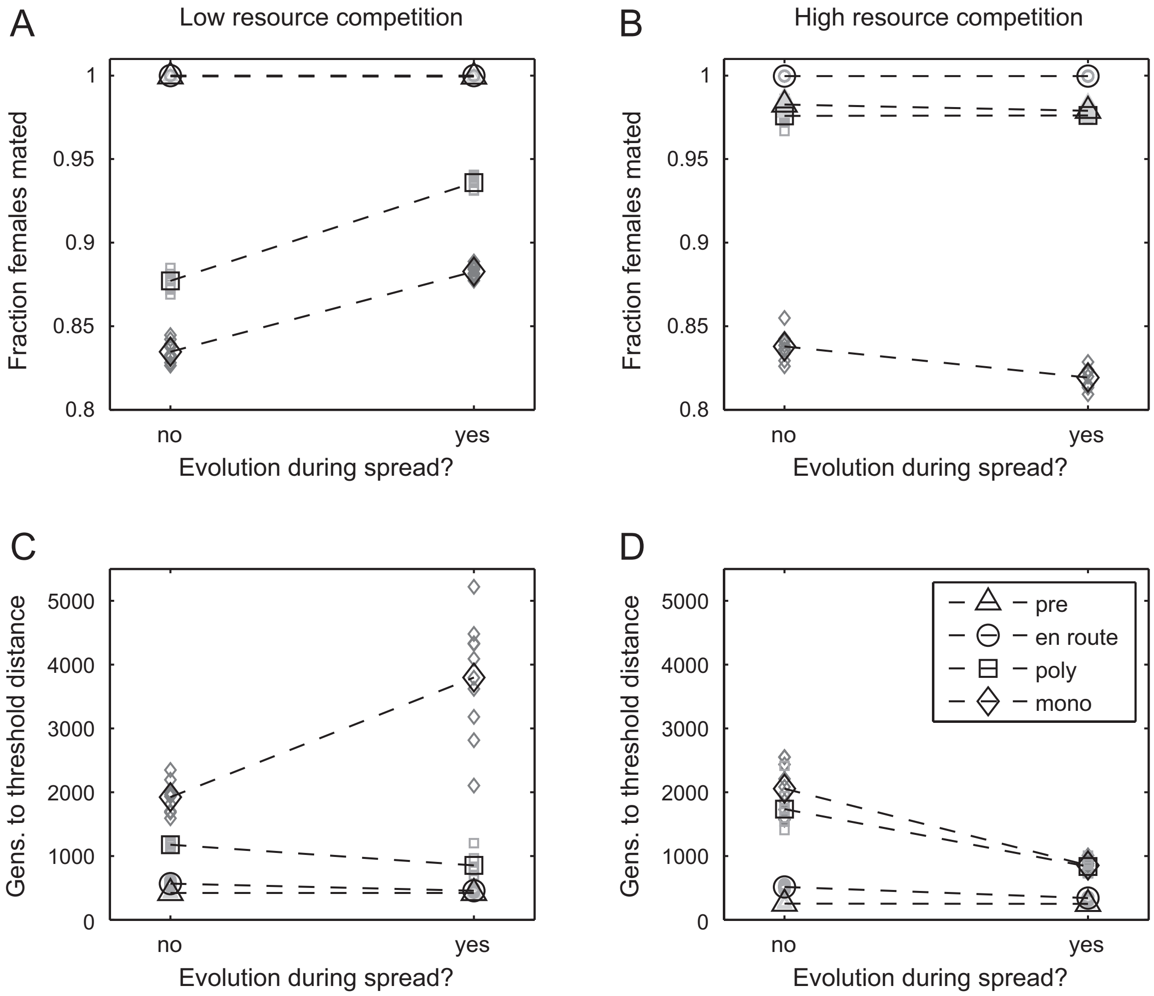

Figure 4: Influence of dispersal evolution on mating success and spread rate. Shown are the fraction of females that mated with at least one male (*A*, *B*) and the number of generations it took the spreading population to reach the threshold distance (*C*, *D*), with and without evolution during spread (*X*-axis) when mating occurs after dispersal in monogamous pairs (diamonds) or polygynandrously (squares), en route (circles), or before dispersal (triangles). Each gray symbol is the outcome of one simulation, and black symbols show the average across 10 replicates. Parameters: $b = 4$ (average offspring per female), $n = 10$ (individuals per patch), $s = 20$ (dispersal survival parameter; *A*, *C*); $b = 10$, $n = 5$, $s = 100$ (*B*, *D*).

competition among females. We outline the basic intuition for this below (see app. C for more mathematical details).

When resource competition remains low, a female has little to lose by settling in a patch with other females present; it may thus prove a greater mistake to try to avoid competition (including kin competition; see Kubisch et al. 2013) if this carries a risk of mating failure in regions of low individual abundance. Therefore, it is adaptive for females to err on the side of ensuring they land in a patch with some males even if there are females already present. Clearly, this results in little movement in the population as a whole.

In contrast, when resource competition is high, a female settling in a patch with other females (whose offspring will compete with her own) risks having few or no surviving offspring as well as creating kin competition (implicitly included in our model due to inheritance of strategies). Therefore, females now adaptively err on the side of ensuring they land in a patch with few or no other females despite the increased risk of mating failures; the occasional lucky strike of a successful mating in a competitor-free patch more than compensates. As a result, females (and males) travel long distances. Our study thus adds an evolutionary angle to the findings of Dwyer and Morris (2005), who similarly found (although in a one-sex model) that resource-dependent dispersal could strongly affect invasion dynamics.

Our findings generate several predictive patterns of potential invasiveness and invasion speed across species. At a broad scale, we anticipate that the relative timing of mating and movement should be a key factor, as it influences overall mating success and strength of the mate-finding Allee effect. In particular, species where individuals mate before or during dispersal should have the fastest invasion speeds. Past studies have suggested similar patterns (Awad et al. 2013; Miller and Inouye 2013) and demonstrated the importance of dispersal timing in invasions (Strecker and Arnott 2010). Future experimental or comparative studies should consider the relative timing of mating and dispersal to see whether these factors affect invasion speed as we predict.

We also found fast spread in simulations where females could reproduce regardless of whether they had mated. This is a clear demonstration of Baker's law, the idea that selfing should be more common in colonizing populations (Baker 1955). Although originally described by Baker as equally applicable to both animal and plant populations, most references to Baker's law come from the plant literature. Given that pest species are often well studied (and have in some cases been clearly shown to suffer from mate-finding Allee effects; Contarini et al. 2009; Yamanaka and Liebhold 2009), it is intriguing how few studies contrast different eradication techniques depending on the mating system (see Yamanaka and Liebhold 2009 for a rare example), and we are unaware of such contrasts that have also included dispersal behavior.

Comparing within species that are constrained to mate after dispersal, we expect (perhaps counterintuitively) that resource competition will be more important than mate finding as a determinant of individual fitness. In the extreme, selection to avoid competition may lead to individuals evolving movement behaviors that decrease overall mating probability. Here, the key factor is strength of local resource competition between females, which has long been identified as an important factor in the evolution of dispersal (Hamilton and May 1977; Duputié and Massol 2013).

Future studies could use our framework to explore a number of other questions about mating system, life history, and population spread. What is the impact of evolving other traits associated with mating and life-history characteristics (e.g., offspring sex ratio)? Would allowing individuals to reproduce more than once during their life influence the rate of spread, as suggested by a recent empirical study (Sol et al. 2012)? How does the distance over which mates are detected (which will impact the strength of the mate-finding Allee effect; South and Kenward 2001) influence spread? Would using a different (e.g., Mendelian) genetic system alter our results? What happens if colonists into the novel environment are nonrandom colonists (e.g., those that tend to travel the farthest) instead of a random sample from the source population, as we assume? Finally, how do mating system and sex-specific dispersal influence the rate and dynamics of range shifts, particular under changing environmental conditions (e.g., Henry et al. 2013)?

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