High juvenile mortality overwhelms benefits of mating potential for reproductive fitness

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ABSTRACT

An individual's access to mates, i.e., its 'mating potential,' can constrain its reproduction but may also influence its fitness through effects on offspring survival. For instance, mate proximity may correspond with relatedness and lead to inbreeding depression in offspring. While offspring production and survival might respond differently to mating potential, previous studies have not considered the simultaneous effects of mating potential on these fitness components. We investigated the relationship of mating potential with both production and survival of offspring in populations of a long-lived herbaceous perennial, *Echinacea angustifolia*. Across seven years and 14 sites, we quantified the mating potential of maternal plants in 1278 mating bouts and followed the offspring from these bouts over eight years. We used aster models to evaluate the relationship of mating potential with the number of offspring that emerged and that were alive after eight years. Seedling emergence increased with mating potential. Despite this, the number of offspring surviving after eight years showed no relationship to mating potential. Our results support the broader conclusion that the effect of mating potential on fitness erodes over time due to demographic stochasticity at the maternal level.

INTRODUCTION

Mating potential, defined by the abundance and proximity of potential mates, constrains the reproductive success of sexually reproducing plants, especially those that are self-incompatible and live in small populations (e.g., Wagenius et al. 2020; reviewed in Gascoigne et al. 2009). However, mating potential may also affect offspring viability. For example, relatedness between individuals often increases with their proximity (Wright 1943). A plant with many closely related potential mates nearby might produce more inbred offspring, which may have lower fitness due to reduced heterozygosity and inbreeding depression, compared with a more isolated plant (Nason and Ellstrand 1995). Alternatively, an abundance of potential mates in close proximity could correspond with a diverse mating pool, which could contribute to the production of robust offspring (Paschke et al. 2002). While many studies have assessed the effects of mating potential on seed production (e.g., Wagenius 2007), few track the fate of seeds to emergence, and fewer still beyond that, particularly in long-lived species or natural environments (Aguilar et al. 2019).

Studies that investigate the fitness consequences of mating potential commonly focus on early measures of reproductive success, such as pollination rates or fecundity, as fitness proxies (Harder and Johnson 2009). Fitness comprises multiple components that link an individual's mating success and fecundity to the production of viable offspring, but complete fitness accounts are notoriously difficult to obtain, particularly for long-lived plants (Campbell et al. 2017). Later measurements of reproductive success, such as the number of offspring that survive to adulthood, undoubtedly yield more precise fitness estimates than earlier measures (Reid et al. 2019). However, whether early fitness proxies provide a coarse yet reliable representation of the association between mating potential and fitness or a misleading representation remains unclear. Early measures of reproductive success may not reliably indicate the fitness consequences of mating potential if, for instance, high juvenile mortality equalizes differences between maternal plants with variable reproductive output (Price et al. 2008; Campbell et al. 2017) or trade-offs between the number of offspring and parental investment in each favor intermediate fecundity (Smith and Fretwell 1974). Thus, early proxies for reproductive success, such as seed production and seedling emergence, may inaccurately reflect mating potential's fitness effects.

Mating potential could affect separate fitness components differently in both direction and magnitude due to multiple, potentially simultaneous mechanisms. These mechanisms include positive effects of mate abundance on seed production, negative effects of mate proximity associated with inbreeding on juvenile survival, and other density-dependent processes. For example, mating potential may have opposing consequences for offspring production and survival if high mating potential increases offspring production, but the resulting high competition among offspring reduces survival (Waser et al. 2010). In contrast, distinct effects of mating potential on separate fitness components in the same direction could compound. For example, high mating potential may increase mating among relatives and inbreeding depression in offspring, which could reduce fitness at multiple life history stages; inbred plants might initially grow to a smaller size or more slowly than non-inbred neighbors and then suffer further disadvantages from reduced access to light (Schmitt and Ehrhardt 1990). Finally, mating potential may influence one fitness component but have no effect on another. For instance, mating potential might increase the number of seedlings that emerge following a mating bout, but have no relationship with the survival of these offspring as juveniles. In this case, the initial fitness advantage (i.e., in offspring abundance) that a maternal plant with high mating potential has over one with low mating potential after a mating bout could persist or erode over time, depending on rates of juvenile mortality and demographic stochasticity at the level of maternal plants' offspring cohorts. This outcome would be consistent with evidence that luck, especially related to early life-history stages, can decide fitness differences more than differences in fitness-related traits among individuals (Snyder and Ellner 2018; Snyder et al. 2020). If parental mating potential does affect juvenile survival, this would produce structured variation among maternal plants that demographic theory suggests can reduce demographic stochasticity and extinction risk at the population level (Kendall and Fox 2003, Fox 2005).

The goal of this study was to investigate the separate and joint relationships of mating potential with an early and a later measure of fitness: offspring emergence and offspring persistence following eight years, respectively. Our primary questions were these: Do fitness components beyond seed production relate to mating potential? Does mating potential's relationship with early and late fitness components differ, leading to amplification, dampening, or negation of its overall effect? In addition, we ask whether seed production offers a reliable proxy for later fitness differences, comparing differences among cohorts and sites.

To investigate these questions, we studied natural populations of *Echinacea angustifolia* in western Minnesota, focusing on components of maternal fitness, i.e., the number of offspring produced via seed, rather than via pollen export. Previous studies in this system found that pollination success and seed production increase with mating potential (Wagenius 2006; Ison and Wagenius 2014; Richardson et al. 2021). However, *E. angustifolia* populations in this system also are subject to severe inbreeding depression that compromises survival and reproduction in progeny of sibling matings (Wagenius et al. 2010). We expected that seedling emergence might increase with mating potential through positive effects of mate abundance on mating success, but that juvenile survival would decrease, reflecting the association between mate proximity, relatedness, and inbreeding depression.

In each summer 2006-2012, we mapped locations of all individual flowering plants at 14 sites. In each spring 2007-2013, we searched for seedlings around plants in each site that had flowered the previous season, totaling 1278 observations of maternal plant mating bouts. We then tracked the survival of each year's offspring cohort for the next eight years. We used aster models (Shaw et al. 2008) to partition the effects of mating potential on maternal fitness into its independent relationships with progeny emergence and survival. We developed a simple model to predict when demographic stochasticity at the maternal plant level will overwhelm initial fitness differences, such as those due to mating potential.

MATERIALS AND METHODS

Study Area and Organism

Echinacea angustifolia is a hermaphroditic perennial forb native to the North American tallgrass prairie. We studied natural *E. angustifolia* populations in Grant and Douglas Counties, Minnesota, USA, where remnants of tallgrass prairie habitat persist in a largely agricultural landscape matrix. Of the sites in this study, six are located within roadside rights-of-way, three are on land managed by the U.S. Fish and Wildlife Service, four are on private property, and one is within a preserve managed by The Nature Conservancy. *E. angustifolia* is long-lived and slow growing, with an estimated generation time of 21 years in our study area (Dykstra 2013). Under natural conditions, plants rarely flower before their seventh year (Wagenius et al. 2012), after which they may not flower every year. Individuals typically produce one composite flowering head (capitulum), but we have observed individuals with over 20 heads (Wagenius et al. 2020). Flowering rates vary among populations and years, resulting in variation in plants' access to mates (Waananen et al. 2018; Wagenius et al. 2020; Nordstrom et al. 2021). Because *E. angustifolia* is tap-rooted and does not spread clonally, its reproduction depends upon seed production (Wagenius 2004; Wagenius et al. 2007). Previous work in our study area has found that seed set is limited by the abundance and proximity of suitable mates, rather than by visits from pollinators, which are primarily generalist bees (Wagenius 2006; Wagenius and Lyon 2010; Ison and Wagenius 2014; Richardson et al. 2021). Flowering stems of *E. angustifolia* are typically 30-60 cm tall; its fruits (achenes) are gravity-dispersed and do not form a persistent seed bank (Wagenius et al. 2012).

Mate suitability is restricted by *E. angustifolia*'s sporophytic self-incompatible (SI) mating system, which prevents self-fertilization and fertilization by pollen grains from other plants that share an allele at a self-recognition locus, or "S-locus" (Wagenius 2004). In large populations, SI mating systems reduce inbreeding by precluding selfing and limiting mating between relatives; for example, under Mendelian inheritance full-siblings are expected to share an allele at the S-locus 25% of the time. By this mechanism, deleterious recessive alleles at all non-S-loci are expressed—and selected against—less frequently in SI species, especially in large populations; as a result, populations of self-incompatible species often harbor substantial genetic load. Indeed, in *E. angustifolia*, a previous study estimated biparental inbreeding depression at 68% in the offspring of sibling-mating (Wagenius et al. 2010). Habitat fragmentation is expected to increase the frequency of mating between relatives; studies of fine-scale genetic structure in *E. angustifolia* support this idea by showing that, in small populations, for plants separated by up to 20 m the observed sharing of alleles is similar to that expected between half-siblings or full cousins (Wagenius 2000). As a result, having many potential mates nearby may also result in allele sharing and the production of low-fitness offspring due to inbreeding depression.

Measuring Mating Potential

Each summer from 2006 to 2012, we surveyed sites for flowering *E. angustifolia* as part of an ongoing annual demographic study in these populations. We obtained coordinates for each flowering plant using a survey station in 2006-2011 and a TopCon GRS-1 Device in 2012, both of which offer <1 cm precision. We counted the number of flowering heads (defined as heads that successfully produced pollen) that each individual produced, which we refer to as the 'head count.' We quantified mating potential as the weighted sum of the distances between a focal plant and its seven nearest potential mates.

Specifically, we calculated a weighted sum of the distances between a focal maternal plant and its k = 1-7th nearest flowering conspecific neighbors (i.e., its likely pollen sources) (Appendix A). The relationship between 1-kth nearest neighbors and reproductive success (seed set) for *E. angustifolia* at these sites varies little between $k = 2$ and $k = 18$ (Wagenius 2006), suggesting that the results of this analysis should not be sensitive to the value of k. We were limited to k = 7 because at our largest site, where the population size is several thousand individuals and it was not feasible to survey each one, we monitored individuals within a transect. Thus, we could not assess distance to every neighbor within the site. We did, however, endeavor to map at least the seven nearest neighbors of plants within the transect. We weighted each distance by an exponential decay parameter γ that determines the strength of the relationship between distance and a neighbor's contribution to mating potential. Previous research at these sites found that $\gamma = 1/13.3\ m^{-1}$ best described patterns of mating success in *E. angustifolia* (Wagenius et al. 2007); 13.3 m corresponds to the average pollen movement distance between individuals. For focal maternal plants at sites with fewer than seven other conspecifics, we quantified mating potential with as many individuals as flowered in the site. In our calculation, neighbors with different numbers of flowering heads contribute to mating potential equally. Whether multi-headed neighbors have a competitive or facilitative effect on a focal plant's mating success can be highly context dependent (Rathcke 1983). Furthermore, the vast majority of flowering plants (~87%) produced only a single flowering head, so the consequences of this assumption are likely small. A one-unit difference in mating potential could represent various differences in distances between maternal plants and their seven nearest neighbors. For example, in our data, a maternal plant with relatively low mating potential of two was isolated from its nearest seven neighbors by 4 - 60 m while a maternal plant with mating potential of three was within 7 - 14 m of its nearest seven neighbors. A maternal plant with a relatively high mating potential of five was 1- 8 m away from its 1 - 7^{th} nearest neighbors; for more details about mating potential calculations, see Appendix A.

Seedling Surveys

Between 2007 and 2013, we surveyed *E. angustifolia* seedlings at each of the 14 sites. The initial goal of this effort was to quantify seedling recruitment rates across sites and years. We describe our seedling survey methods in detail elsewhere (Dykstra 2013; Nordstrom et al. 2021) and briefly here. To select our sampling locations at each site, we randomly selected 18 plants that had flowered in the previous year. We then searched for seedlings within a specified radius of each selected plant; we refer to this area as a 'focal circle,' the selected plant as the 'maternal plant,' and the radius as the 'search radius.' Typically, we searched for seedlings within a 41 cm search radius. Dispersal beyond the radii of our search areas is possible, though likely infrequent based on *E. angustifolia*'s heavy seeds (>2 mg) and lack of specialized seed dispersal traits. If fewer than 18 plants had flowered at the site in the previous year, we searched for seedlings at all possible maternal plants and increased the search radius of each focal circle, usually to 50 cm (30 site-years, 160 focal circles). This happened most often in four sites (ngc, rndt, sgc, eth) with smaller *E. angustifolia* populations. In one instance, only one plant had flowered at a site in the previous year, and we searched for seedlings within an 80 cm radius. In 2007, at two sites where flowering density was high in the previous year, we searched for seedlings within 32 cm of the focal circle.

A modest proportion (204 of 1278) of our focal maternal plants were within 41 cm of another plant that had also flowered in the previous year. In these cases, we assigned the seedling to the focal maternal plant, acknowledging that this decision is uncertain. The consequences of misassignment for our analysis, however, are low, because two plants within 41 cm will have nearly equal mating potential. To assess capacity for dispersal of seeds beyond our search radii, we also conducted searches for seedlings in 163 additional circles (~2 per site in each year) centered at random points within 4 meters but beyond 1.5 meters from any plant that had flowered in the previous year. Altogether, these searches yielded two seedlings, indicating that dispersal beyond the range of the focal circles is rare. This suggests that (1) seedling counts per focal circle are an accurate measure of emergence per maternal plant and (2) the focal plant, not a neighbor, likely produced the seedlings within a circle. We searched for seedlings in May or early June, when seedling cotyledons remained evident. To facilitate finding the individual progeny in later years, we mapped the location of each seedling relative to other seedlings, the focal plant, and other established *E. angustifolia* within or near the search radius. In total, we searched for seedlings in 1278 focal circles, not including the 163 circles centered at randomly selected locations and tracked cohorts that emerged across seven years and at 14 sites.

For each annual seedling cohort, 2007-2013, we tracked offspring survival for eight subsequent years. We searched each circle in the late summer (August-September) following emergence to assess survival over the first growing season. Thereafter, we visited focal circles once annually during late summer to assess the survival of the progeny identified in the seedling search. When we did not find one of the progeny in a given year, we noted this and searched for it again for at least two more years. If we found the individual in one of these years, we revised its demographic status in previous years to “alive.” If we did not find the juvenile in the subsequent two years, we no longer searched for it in following years and revised our records to "dead" in all years that we did not find it.

Statistical Analysis

We used fixed-effect aster analyses (Geyer et al. 2007; Shaw et al. 2008) to evaluate the dependence of maternal fitness on mating potential. Aster analyses model the joint distribution of life-history components based on graphical models that represent the dependence of later observed components on those expressed earlier and statistical distributions suitable for each component. Each component corresponds to a distinct 'node' in the graph (Figure 1). In this case, the number surviving at the end of eight years depended on the initial number of progeny emerging and their survival in each successive year. We implemented these models using the aster package (Geyer 2021) in R software version 4.3.1 (R Core Team 2023). Such a modeling approach is necessary because fitness, as a multi-component measure, generally does not conform to any standard statistical distribution. Appropriate specification of distributions for each fitness component is required to obtain valid estimates of sampling variance, and thus valid inference. We initially included fitness components for the number of seedlings emerging after a mating bout (Poisson distributed), the number of seedlings surviving at the end of the first growing season after emergence (binomially distributed), and the number of progeny surviving in each of eight subsequent years (each binomially distributed). However, we observed an excess of zeros in the seedling counts at emergence, which may result from a variety of processes including those unrelated to mating potential's effects on emergence, such as herbivory or disturbance. To account for this overdispersion, we also included an additional node indicating whether any seedlings emerged (Bernoulli distributed). We then revised the distribution of the number of seedlings emerging after a mating bout to be zero-truncated Poisson.

Do fitness components beyond seed production depend on mating potential?

To assess relationships between mating potential and maternal plant fitness via progeny emergence and survival, we constructed four models for dependence of different life history stages: “Null,” “Null + Emergence,” “Null + Survival,” and “Null + Emergence + Survival.” on mating potential. Each aster model consisted of a joint analysis of all fitness components. The “Null” model included one predictor affecting the number of seedlings at emergence, search radius, and three predictors affecting both seedling count at emergence and survival in subsequent years: cohort year, site, and maternal head count. We included all predictors, including site and year, as fixed factors because of our interest in reporting estimates for each site and year. The “Null + Emergence” model included all the predictors in the “Null,” as well as a parameter to estimate the effects of mating potential specifically on seedling emergence. Similarly, the “Null + Survival” model included all the predictors in the “Null” model and a parameter for the effects of mating potential specifically on progeny count in year eight. Finally, the “Null + Emergence + Survival” model included the “Null” model predictors and mating potential as predictors of both seedling emergence and final progeny count in year eight.

To identify the best performing model, we used likelihood ratio tests, which compare the goodness-of-fit of nested models and assess whether the added complexity of the larger model yields a significant improvement in fit over the smaller one. We compared the “Null + Emergence” and “Null + Survival” models to both the minimal “Null” model and to the most complex “Null + Emergence + Survival” model.

To gain insight to the effects of mating potential relative to cohort year, site, and head count on maternal plants’ number of progeny eight years following a mating bout, we visualized the effect sizes of the model coefficients in the best performing model. We note, however, that, as with other generalized linear models, interpretation of the parameter estimates is not entirely straightforward, due to the non-linear relationship between the underlying 'canonical' scale of the analysis and the scale of biological measurement. In addition, we constructed a set of models that included all combinations of cohort year, site, and head count in the best performing model. To compare the adequacy of these non-nested models, we calculated the Akaike Information Criterion (AIC), which assesses the extent to which the models captured information about the underlying processes influencing fitness (Akaike 1974), for each model. We calculated the difference in AIC values between models (ΔAIC) and normalized these values to calculate Akaike weights, which reflect the probability that the model is the best of the set (Wagenmakers and Farrell 2004).

Does mating potential's relationship with early and late fitness components differ, leading to amplification, dampening, or negation of its overall effect?

To visualize the relationship between mating potential and maternal fitness and how it changed over time from seedling emergence through eight years post-emergence, we obtained model predictions of seedling emergence and progeny count at emergence (year zero in the spring), year zero in the fall, and each subsequent year through year eight for hypothetical plants from the site and cohort that had median emergence and survival using the "Null + Survival + Emergence" model.

We also used Kendall's Tau-b correlation coefficient to describe the strength of the association between maternal plants' number of offspring at emergence and after eight years in the observed data. Kendall's Tau-b is a rank-based measure of association that does not rely upon the data conforming to a bivariate normal distribution; its values range between -1 and 1. The strength and direction of the association offers suggestive evidence about whether the separate relationships between mating potential and early and late fitness components lead to amplification (strong positive association between early and late components), negation (negative association), or attenuation (weak positive association) in their cumulative effects.

Does seedling emergence offer a reliable proxy for later fitness differences by site and cohort?

Finally, to assess how other model predictors related to early and late fitness components, we visualized the effects of site and cohort on seedling emergence and progeny count at year eight by obtaining model predictions for hypothetical plants with average mating potential at each site and in each year of emergence, using the best-performing model.

RESULTS

Seedling and Mating Potential Surveys

On average, each maternal plant had few offspring emerge (0.71 seedlings per maternal plant) and survive. In total, we found 914 seedlings. Of these, only 98 survived to eight years. The distribution of seedling emergence was highly skewed; we found no seedlings in 76% of our initial searches (973 of 1278). Half of the remaining searches (155 of 305) produced just one seedling. In one focal circle, we found 45 seedlings, which exceeded the circle with the second most by 19 seedlings. After eight years, however, no maternal plant had more than seven surviving progeny; the maternal plant that produced 45 seedlings had three. Maternal plants' mating potential, dependent upon the proximity of conspecific neighbors (Figure S1), also varied widely. For example, the maternal plant with the highest mating potential had seven neighbors within 40 centimeters, while the maternal plant with the lowest mating potential had only one conspecific neighbor flowering within the same site, and that plant was 130 m away. In contrast, maternal plant head count varied little: 996 of 1278 (78%) of maternal plants had one flowering head in the year before our search for its seedlings.

Do fitness components beyond seed production depend on mating potential?

The number of seedlings that emerged increased with mating potential. Likelihood ratio tests indicated that the “Null + Emergence” model, which included the effect of mating potential on the number of seedlings emerging, but no direct effect of mating potential on the number surviving to eight years (see Table 1 for model summary), outperformed all others (Table 2). Specifically, likelihood ratio tests indicated that the “Null + Emergence” model had significantly higher likelihood than the “Null” model (“Null” vs. “Null + Emergence,” Table 2) and was statistically indistinguishable from the more complex model that included effects of mating potential on both seedling emergence and offspring survival through eight years (“Null” vs. “Null + Emergence + Survival,” Table 2). In contrast, the model including only the effect of mating potential on offspring survival performed no better than the “Null” model (“Null” vs. “Null + Survival,” Table 2) and far worse than the model that included the effect of mating potential on emergence as well (“Null + Survival” vs. “Null + Emergence + Survival,” Table 2). Under the “Null + Emergence” model, the effect of mating potential on seedling emergence was positive and significantly different from zero (Emergence:Mating Potential, $\beta = 0.10$, $p < 0.0001$, Figure S2).

Based on a set of models created by dropping terms from the best-performing model (“Null + Emergence”), our model predictor analysis indicated that head count, cohort, site, and mating potential all influenced the number of seedlings that emerged. The full model (including predictors for head count, cohort, site, and mating potential) outperformed all other models (AIC = 4750.3, w(AIC) = 1) (Table S1). The second-best model in this analysis included all predictors except mating potential (head count, cohort, site), but the Akaike weight analysis indicated no support for it compared to the full model (ΔAIC = 20.5; w(AIC) = 0; Table S1).

Does mating potential's relationship with early and late fitness components differ, leading to amplification, dampening, or negation of its overall effect?

Maternal plants' number of offspring at emergence was positively correlated with their number of offspring surviving to age eight (Kendall's Tau-b, $\tau = 0.40$, $p < 0.0001$, Figure S3). Our model comparisons indicated, however, that after accounting for the relationship between mating potential and seedling emergence, there was no evidence of a direct relationship between mating potential and seedlings' survival to eight years (Table 2). Visualizing the predicted offspring counts at each time point (seedling emergence to year 8) with respect to mating potential revealed steady erosion in the strength of the relationship between mating potential and maternal fitness, as measured by offspring count (Figure 2).

Does seedling emergence offer a reliable proxy for later fitness differences by site and cohort?

Final offspring count varied among offspring cohorts (Figure 3A) and sites (Figure 3B), but as with mating potential, initial differences in offspring count by cohort and site were far larger than final differences (effect sizes shown in Figure S2). Maternal plants producing offspring in certain years (e.g., 2011) saw larger numbers of offspring emerge and maintained their advantage over maternal plants in lower-emergence years through eight years (Figure 3A, Figure S4). However, the difference in the number of surviving offspring by year eight among cohort years was small; the predicted offspring count at year eight for all but two cohorts (2011 and 2007) were indistinguishable. Similarly, certain sites had detectably high (e.g., site 'eelr') or low offspring (e.g., site 'ngc') emergence and survival through eight years (Figure 3B, Figure S5). Again, however, variation in the number of offspring among all sites was small, with predicted values for all less than 0.4 seedlings.

DISCUSSION

The number of offspring that emerged following a reproductive bout increased with the mating potential of the maternal plant (Table 2). These results support the hypothesis that the benefits of mating potential, e.g., increased access to pollen donors and reduced pollen limitation, outweigh its potentially simultaneous costs, e.g., inbreeding depression, at least for offspring emergence. That mating potential enhances early fitness components is consistent with previous findings that mate availability promotes seed set in these populations (Wagenius et al. 2020). It is important to note that mating potential may be associated with environmental factors (e.g., light availability) that could vary with the density of flowering plants and offspring emergence or survival; distinguishing effects of mating potential from those of associated factors would require an experimental approach. However, regardless of the potentially amplifying effect of environmental confounding, we found no evidence that mating potential related directly to offspring survival, or the number of offspring eight years after a reproductive bout (Table 2).

Notably, we observed far fewer offspring per maternal plant than the number of seeds a typical individual with adequate pollination could produce. Based on the average number of fruits per individual in our study area (mean = 164 achenes, unpublished data) and average seed set (mean = 0.38 seeds/achene, unpublished data), a typical individual might produce approximately 60 seeds in a mating bout. In contrast, we found a mean of 0.71 seedlings around maternal plants in the spring following a mating bout, and zero seedlings around 973 (76%) of the maternal plants; low emergence in *E. angustifolia* is likely due to several causes, including seed predation, competition with existing vegetation, and germination under unfavorable annual conditions. For instance, in an experimental study, prescribed burns in spring prior to seed dispersal enhanced seedling establishment (Wagenius et al. 2012), but few spring burns occurred in our study populations during the years that we surveyed emergence (4 of 91 site-years; Nordstrom et al. 2021, Wagenius et al. 2021). Furthermore, only 11% of offspring were still alive after eight years (98 of 914 found initially). Only two offspring reached reproductive maturity by age 8 and more will likely die before flowering. Thus, at least in considering the outcomes of single mating bouts, factors that reduce seedling emergence and juvenile survival, rather than those governing seed fertilization, limit maternal plants' fitness.

A maternal plant's maintenance of an initial fitness advantage over others depends on the size of its initial advantage—in our case, how many more seedlings a maternal plant with high mating potential produces than do others with low mating potential—and juvenile survival (Figure 4). Consider the analogy of a lottery, in which a ticket represents a seedling, e.g., a ticket holder with two tickets represents a maternal plant that produces two seedlings. How much of a difference does it make to buy two tickets, rather than one, when the odds of winning are very low? We might expect the same result: no winning tickets. Similarly, given that we observed a small range of seedling counts (95% of mating bouts produced four or fewer seedlings) and low juvenile survival (11% survived to age eight), it is unsurprising that high mortality obscured initial differences: most offspring died, including those that formed the small margin between high- and low-emergence (and high- or low-mating potential) maternal plants.

A simple binomial model illustrates how our results are consistent with demographic stochasticity at the maternal plant level resulting from low survival and offspring counts. If the final difference in offspring count between two maternal plants (X) is a binomially distributed random variable that depends on the difference in offspring count at emergence ('trials'), E, and probability of survival of each of these offspring, S, then the expected final difference in offspring count is ES (Figure 4A). When $ES \geq 1$, or alternatively when $E \geq 1/S$, we expect the individual with the fitness advantage at emergence would also have at least one more offspring after survival. Based on a survival rate of 11% ($S = 0.11$) as we observed, after eight years, a maternal plant that had nine seedlings initially emerge would maintain, in expectation, a fitness advantage over a maternal plant that produced none. Maternal plants produced nine or more seedlings following only 1.5% of mating bouts (20 of 1278) in our study; thus, based on this reasoning, our observation of erosion of the initial fitness advantages was consistent with realized emergence and mortality.

We note that the probability of X being greater than or equal to 1, i.e., that any seedlings making up the fitness advantage at emergence survive, is $1 - (1\text{-}S)^E$. For $S = 0.11$ and $E = 9$, there is still only a 65% chance of at least one of these emerging seedlings surviving to age eight. This underscores that, with low seedling and juvenile survival, even large increases in fecundity through maternal mating advantage will not guarantee a maintained fitness advantage. At the same time, the stochastic nature of survival means that the range of possible outcomes is wide. We developed a simulation based on our binomial model (code and details provided in Appendix B) demonstrating that even at low rates of juvenile survival, individuals may maintain their emergence advantages by chance (e.g., points above the dashed line in Figure 4B). In our study, the highest fitness maternal plants at year eight were indeed plants that had high fitness assessed at emergence.

The binomial model of survival we describe assumes that the probability of survival is the same for all seedlings; deviation from the expected survival rate arises due to sampling. We have found no evidence that variation in survival depends on maternal mating potential. This result suggests demographic consequences of genetic drift in small populations, as demonstrated experimentally by Newman and Pilson (1997), was either not related to mating potential or had little influence on maternal fitness relative to demographic stochasticity. However, we did find limited evidence for variation in offspring survival structured by cohort, independent of mating potential, which theory predicts could reduce the effects of demographic stochasticity at the population level (Kendall and Fox 2002). Reduced demographic stochasticity may reduce risks of extinction of small populations. We also note that we focus here on the outcome of single reproductive bouts; iteroparous plants could "enter the lottery" multiple times through repeated reproductive episodes. Additionally, unexplained heterogeneity in maternal fitness in our data could result from other sources that we did not measure or adequately specify in our models. For instance, maternal seedheads differ in size, which may contribute to variation in the number of emerging seedlings through variation in fruit count and duration of flowering, which influences a plant's opportunities to mate. However, the erosion of mating potential effects that we observed was consistent with stochastic variation in maternal fitness (i.e., offspring counts) given low seedling emergence and juvenile survival probabilities.

Do initial fitness proxies accurately represent relative fitness differences in relation to mating potential or other factors? Our results showed that mating potential-based differences in offspring count at emergence largely eroded before offspring reached reproductive maturity

(Figure 2, Figure 3). Thus, early fitness proxies offered an unreliable representation of the relative fitness differences we ultimately observed. This conclusion is consistent with previous studies of long-lived plants, which find that population growth is often disproportionately sensitive to survival rates (Franco and Silvertown 2004). For instance, using a subset of the data presented in this study, Dykstra (2013) found that population growth rate was sensitive to both seedling emergence and juvenile survival, and Nordstrom et al. (2021) found that differences among populations' demographic responses to burning hinged on whether juvenile survival was high or low. Our results here demonstrate a similar dynamic at the level of reproductive individuals: individuals having more offspring in the year after flowering, due to high mating potential, may not have correspondingly high fitness if juvenile survival is low. Altogether, these findings caution against deriving inferences, for instance, of relative fitness or population growth rate, from early fitness proxies (e.g., seed set) without investigating their correspondence with later reproductive outcomes.

Population persistence and ongoing evolutionary change depend on recruitment of successive generations of reproductively mature plants from seeds. To put our results into a lifetime context for *E. angustifolia*, an iteroparous and hermaphroditic species, we must consider multiple bouts of mating and fitness components. Our findings suggest that, per mating bout, many *E. angustifolia* in our study area fail to produce any offspring that survive to adulthood. The same may be true for individuals across their lifetimes. As offspring survival decreases, a maternal plant's production of at least one successful offspring depends on an increasing number of reproductive episodes over its lifetime. With an average of one seedling per year and 11% offspring survival to reproductive maturity, maternal plants would have to undergo approximately nine reproductive bouts to produce (on average) a single offspring that survives to age eight. Many *E. angustifolia* individuals fail to reach this threshold of reproductive bouts (Waananen et al. 2018), implying that these populations may be in decline. This would be consistent with our previous studies, which have found that the growth rates of certain populations, especially smaller ones, fall below replacement (Dykstra 2013). As for evolutionary change, we acknowledge that a complete accounting of an individual's genetic contribution to the next generation would also include the success of its offspring generated through pollen export (e.g., male fitness; Morgan and Conner 2001; Kulbaba and Shaw 2021), which, at the individual level, may respond differently to mating potential. Thus, the extent to which the outcome of one reproductive bout reflects lifetime fitness, both demographically and genetically, depends on the relationship between mating potential, frequency of reproduction, and fitness components across an individual's lifespan. Taking these relationships and their variability into account would improve estimates of properties often derived from fitness proxies, such as mean population fitness or population growth rates.

CONCLUSIONS

Initial measures of fecundity, or proxies for the quantity of offspring produced, often represent the terminal component in estimates of individual fitness. By "bridging the generation gap" between parental reproduction and offspring survival (Price et al. 2008), we revealed that the apparent fitness disparities in offspring emergence related to mating potential were transitory. This finding is consistent with findings of Snyder and Ellner (2018) that luck can obscure the relationship between fitness and individual differences, especially in plants, and that luck in early life history stages can be decisive for fitness outcomes (Snyder et al. 2020). We suspect similar dynamics may be common in other long-lived plant species and other taxa subject to low reproductive output and high juvenile mortality. However, mating potential may more likely affect later fitness components in systems with smaller population sizes or greater spatial genetic structure, and thus more vulnerable to effects of inbreeding on juvenile survival. The insights of our study help to clarify the interpretation of analyses using initial measures of reproductive success as the basis for derived measures such as mean population fitness and population growth rates. Future studies that quantify how iteroparity reinforces or diminishes the patterns we observed here would further advance accounting of lifetime fitness and understanding of the fitness consequences of mating potential.

ACKNOWLEDGMENTS

We thank many members of Team Echinacea 2006-2021, without whom this work would not have been possible. Comments from Mary Price, Jared Beck, three anonymous peer reviewers, the editor, and the associate editor greatly improved this manuscript. This work was funded by NSF awards 2051562, 2050455, 1557075, 1555997, 1052165, 1051791, 0545072, and 0544970 and the Dayton Bell Museum Fund.

DATA AND CODE ACCESSIBILITY

The data and code for our analysis are publicly available from the Data Repository for the University of Minnesota (Waananen et al. 2022; DOI: 10.13020/b74k-7f48). We have not provided coordinates for plants here because we have observed poaching (plants being dug up from the roots) at these sites in the past. However, we will make these data available to researchers upon request, provided that exact locations are not made public in future studies.

STATEMENT OF AUTHORSHIP

ABD, SW, RGS, and GK conceptualized the study design and developed survey methods. SW and RGS acquired funding. All authors collected data. All authors, especially EGE and RDT, helped compile the data. AW performed data analysis and coded the simulation with support from LKR, SN, and RGS. AW wrote the original draft, which all authors reviewed and edited.

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TABLES

Table 1

DESCRIPTION OF ASTER MODELS

Name	Formula	Df	Deviance
Null	Graph Nodes + Emergence : Search Radius + Layer : (Cohort + Site + Head Count)	52	-4590.4
Null + Emergence	Null Formula + Emergence : Mating Potential	53	-4567.8
Null + Survival	Null Formula + Yr8Survival : Mating Potential	53	-4588.7
Null + Emergence + Survival	Null Formula + Emergence : Mating Potential + Yr8Survival : Mating Potential	54	-4567.3

Note. — "Graph nodes" refer to the fitness components within the aster model (see Figure 1). "Layer" is a variable indicating the correspondence of observations to nodes representing either seedling emergence or subsequent progeny counts. "Emergence" and "Yr8Survival" refer to an indicator variable for nodes corresponding to the initial or final counts of progeny, respectively. Terms separated by colons indicate a predictor influencing a node or set of nodes.

Table 2

LIKELIHOOD RATIO TEST COMPARISONS OF NESTED MODELS

Model Comparison	Test Df	Test deviance	Test *P*-value
Null *vs.* Null + Emergence	1	22.65	<0.0001
Null + Emergence *vs.* Null + Emergence + Survival	1	0.54	0.47
Null *vs.* Null + Survival	1	1.75	0.18
Null + Survival *vs.* Null + Emergence + Survival	1	21.44	<0.0001

Note. — Comparisons test the null hypothesis that a reduced model (listed first) performs as well as a more complex one by comparing the difference in deviance (a goodness-of-fit measure) between the nested models ('Test Deviance') to a χ^2 distribution with degrees of freedom equal to the difference in degrees of freedom between the models ('Test Df'). 'Test *P*-value' indicates the probability of a value from χ^2_{Df} greater than the difference in deviance. These tests evaluate hypotheses that mating potential affects progeny emergence, survival, or both. The specific terms in each model are detailed in Table 1. We consider P-values < 0.05 statistically significant.

FIGURE LEGENDS

Figure 1. Graphical model for aster analysis of offspring emergence and survival. Arrows point from prior to later nodes. Labels above the arrows indicate the distribution we used to represent that transition: Ber = Bernoulli, Poi = Zero-Truncated Poisson, Bin = binomial. "Number of Seedlings" indicates the count of seedlings found in the initial search (Year 0 Spring), while "Number of Surviving Offspring" nodes represent the progeny count in the fall after emergence and subsequent annual surveys.

Figure 2. Predicted offspring count per mating bout at emergence (shown in purple) and in year eight (shown in green) based on the full model ('Null + Emergence + Survival'). Predictions here represent hypothetical individuals with one head that had seedlings emerge in 2012 in the site 'sap', a small remnant with intermediate seedling emergence and survival (Figure 3). Shaded bands indicate one standard error on each side of the mean. Mating potential is a weighted sum of distance between a maternal plant and its 1^{st} - 7^{th} nearest conspecific neighbors at time of flowering (Appendix A).

Figure 3. Predicted offspring count per mating bout at emergence and after eight years by (A) cohort and (B) site. Predictions here are derived from the 'Null + Emergence' model for hypothetical individuals with one head; in (A) the hypothetical individuals are from site 'sap' and in (B) the cohort is 2012. The shaded areas indicate one standard error on each side of the mean.

Figure 4. (A) Output from simulation model investigating final offspring count as a function of a maternal plant's emergence advantage and the chance of juvenile survival. The solid curve represents $E = 1/S$; below this, we expect an initial advantage to be obviated by low survival. Dashed lines indicate the observed juvenile survival rate (S =11%) and the corresponding emergence advantage required for a higher final offspring count. (B) Simulations investigating final offspring advantage given different emergence advantages and S = 11%. Points above the dashed line indicate simulations in which the emergence advantage was maintained. Points are jittered to avoid overplotting; the line is lowered below one to account for vertical jitter.

Figure 1

Maternal Plant Flowers $\xrightarrow{Ber}$ Any Seedlings Emerge $\xrightarrow{Poi}$ Number of Seedlings (Year 0 Spring) $\xrightarrow{Bin}$ Number of Surviving Offspring (Year 0 Fall) $\xrightarrow{Bin}$ … $\xrightarrow{Bin}$ Number of Surviving Offspring (Year 0 Fall)

Figure 2

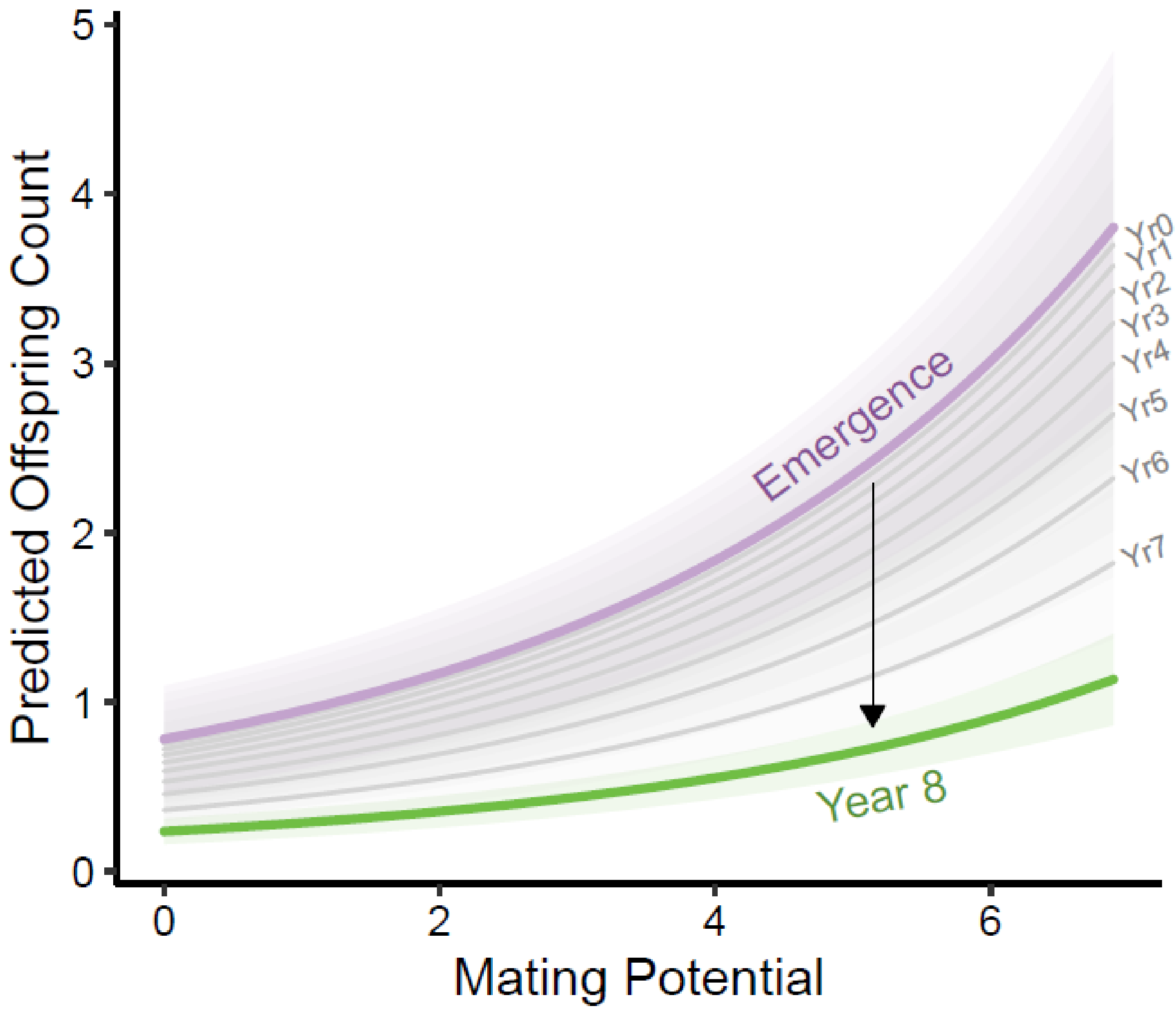


Figure 3

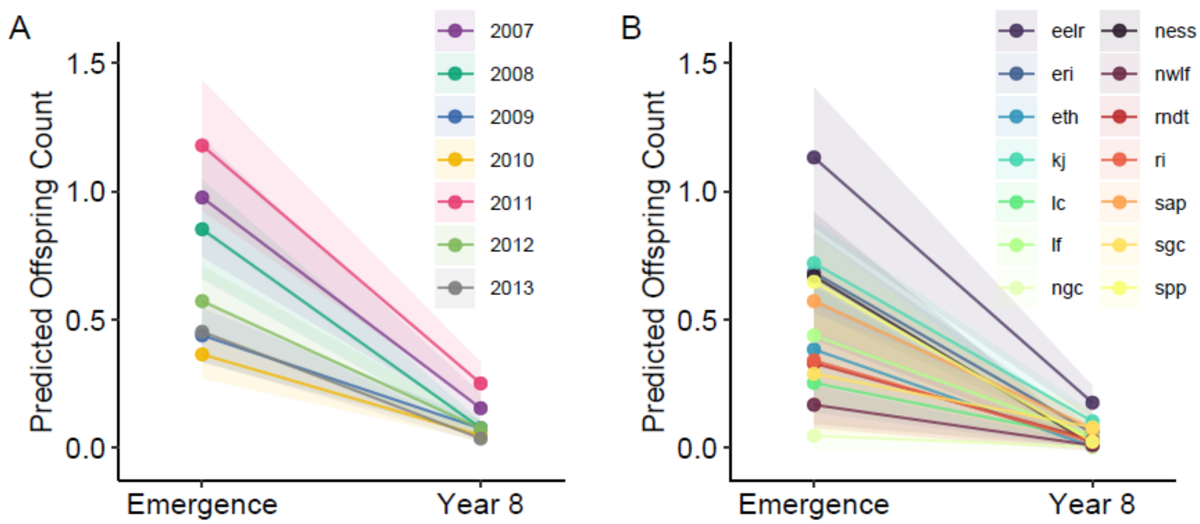
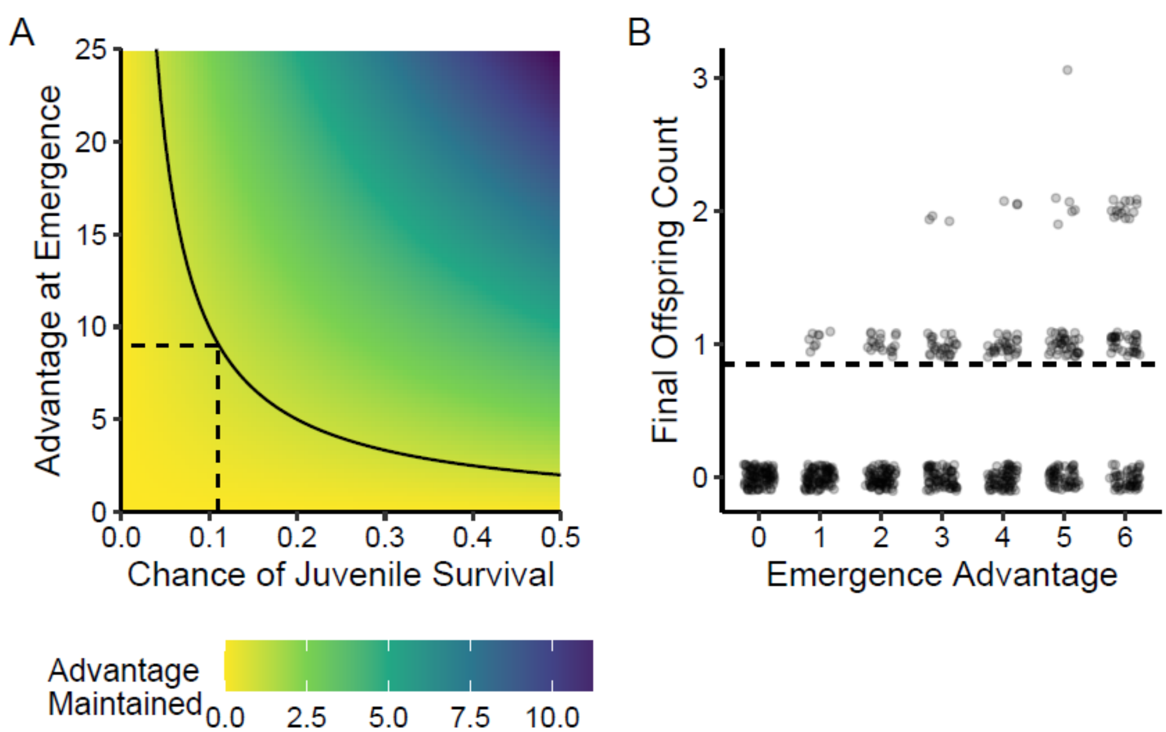


Figure 4



Supplementary Material to "High juvenile mortality overwhelms benefits of mating potential for reproductive fitness"

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Contents: Supplemental Tables and Figures, Appendix A: Details of Mating Potential Calculations, Appendix B: Demographic Stochasticity Simulation Details

Supporting Tables and Figures

Supplemental Table 1

RESULTS OF AIC ANALYSIS USING AKAIKE WEIGHTS

Covariates Included in Model	Par	AIC	ΔAIC	w(AIC)
M + H + C + S	33	4750.3	0	1
M + C + S	32	4787.7	37.4	0
M + H + S	27	4783.7	33.4	0
M + H + C	20	4790.5	40.2	0
H + C + S	32	4770.8	20.5	0
M + S	26	4823.4	73.1	0
M + C	19	4843.1	92.8	0
C + S	31	4805.7	55.4	0
M + H	14	4826.6	76.4	0
H + S	26	4810.4	60.1	0
H + C	19	4832.3	82.1	0
M	13	4887.1	136.9	0
S	25	4850.2	99.9	0
H	13	4874.1	123.9	0
C	18	4879.3	129.0	0
None	12	4929.0	178.7	0

Note.—Par indicates the number of estimated parameters in the model; AIC is the Akaike Information Criterion; ΔAIC is the difference between AIC and the minimum AIC in the set of competing models; w(AIC) is the Akaike weight for the model. All models also contained all graph nodes and the effect of search radius on initial emergence. That is, we generated the set of models by iteratively dropping all combinations of head count (H), cohort (C), site (S), and mating potential (M) from the Null + Emergence model.

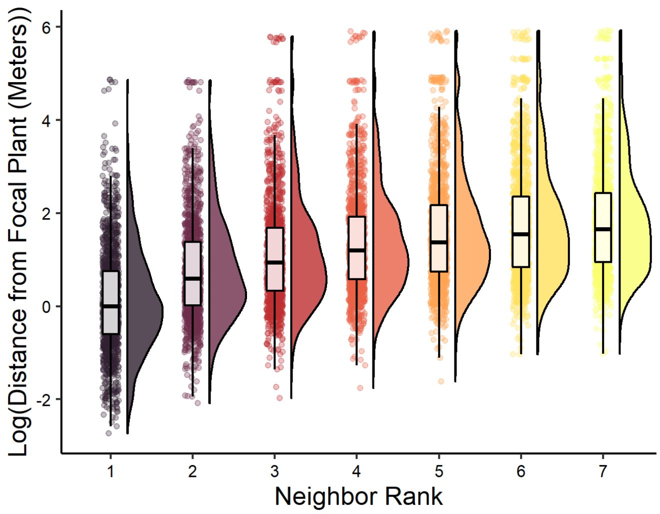

Figure S1. Log_{10} of distances (m) between a maternal plant and its 1st through 7th nearest neighbors across all sites and years in the study.

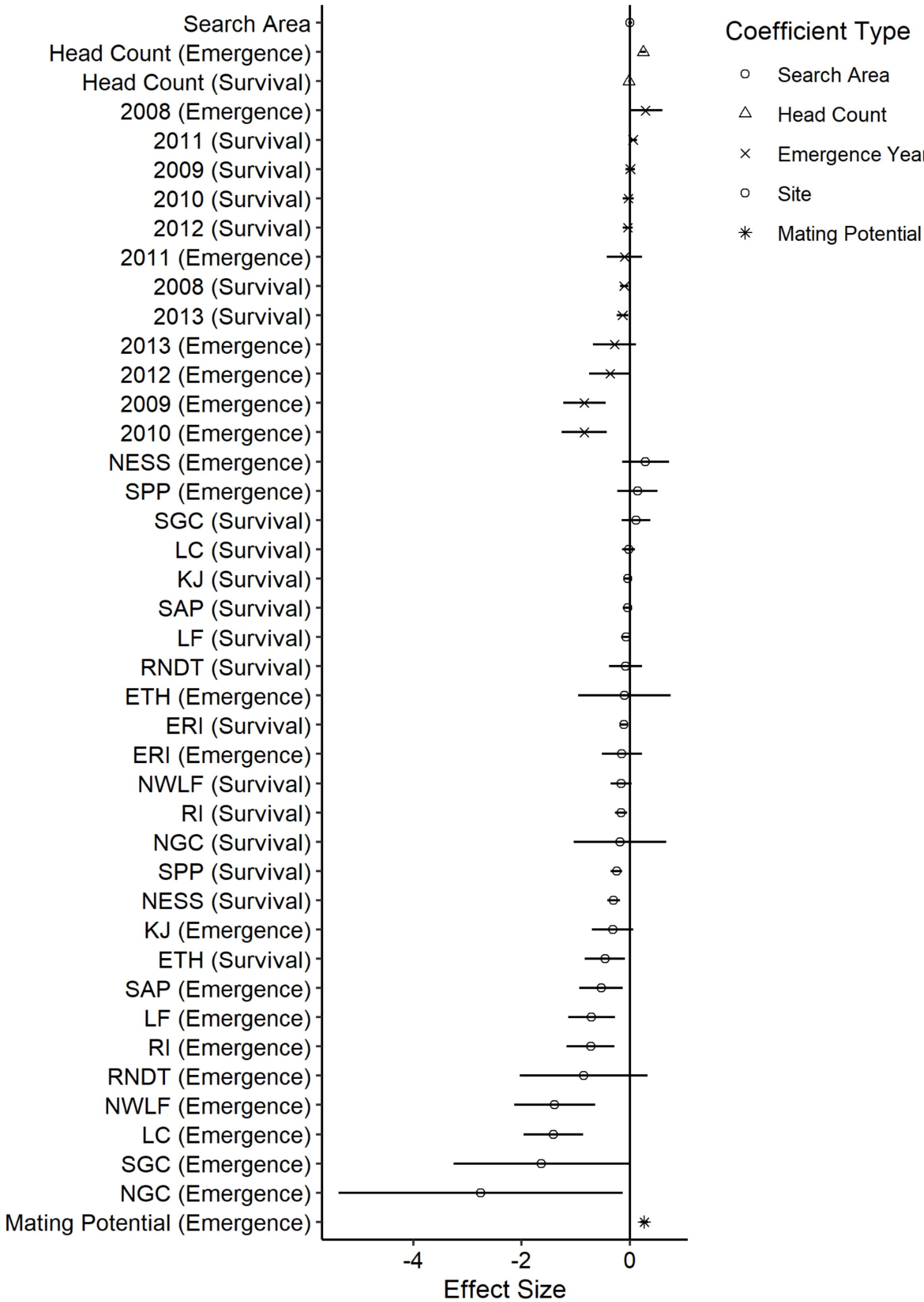
Search Area
Head Count (Emergence)
Head Count (Survival)
2008 (Emergence)
2011 (Survival)
2009 (Survival)
2010 (Survival)
2012 (Survival)
2011 (Emergence)
2008 (Survival)
2013 (Survival)
2013 (Emergence)
2012 (Emergence)
2009 (Emergence)
2010 (Emergence)
NESS (Emergence)
SPP (Emergence)
SGC (Survival)
LC (Survival)
KJ (Survival)
SAP (Survival)
LF (Survival)
RNDT (Survival)
ETH (Emergence)
ERI (Survival)
ERI (Emergence)
NWLF (Survival)
RI (Survival)
NGC (Survival)
SPP (Survival)
NESS (Survival)
KJ (Emergence)
ETH (Survival)
SAP (Emergence)
LF (Emergence)
RI (Emergence)
RNDT (Emergence)
NWLF (Emergence)
LC (Emergence)
SGC (Emergence)
NGC (Emergence)
Mating Potential (Emergence)
-4
-2
0
Effect Size
Coefficient Type
Search Area
Head Count
Emergence Year
Site
Mating Potential

Figure S2. Effect sizes of model coefficients from the best performing aster model, which included effects of mating potential on maternal plant's number of seedlings emerging, but not on the number of offspring persisting at year eight. Points indicate model estimates while line ranges denote +/- one standard error. In parentheses, "Emergence" and "Survival" indicate which layer of the graph the covariates affected: the emergence layer consisted of the "Seedling Emergence" node, while the "Survival" layer consisted of all nodes following emergence. The effect sizes for categorical variables (site and cohort) are presented in reference to site EELR and the 2007 cohort. Aster models also estimate coefficients for each node of the graph; for simplicity, we have omitted these estimates here.

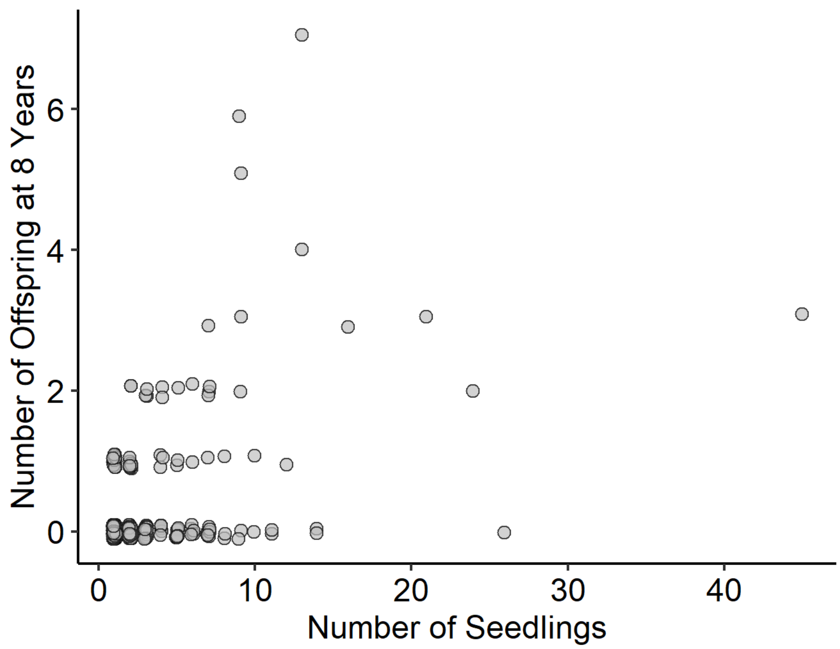

Figure S3. Relationship between a maternal plant's number of seedlings and its number of offspring at eight years. Points are slightly transparent and jittered to reduce overplotting.

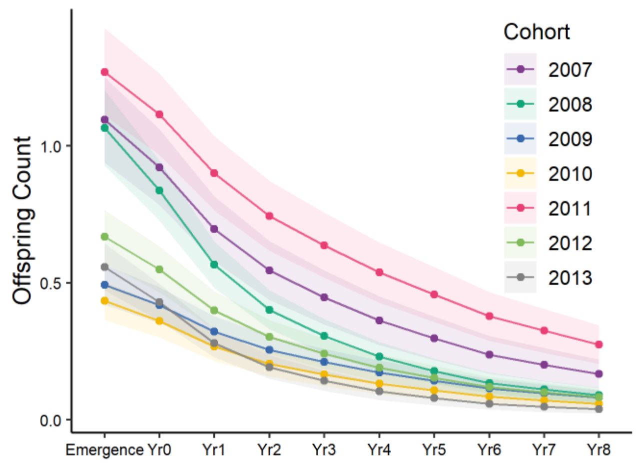

Figure S4. Predicted offspring count by year of emergence. Predictions here are for a one-headed hypothetical individual at the site ‘sap’, a small remnant with intermediate seedling emergence and survival. Shaded bands indicate one standard error on each side of the mean.

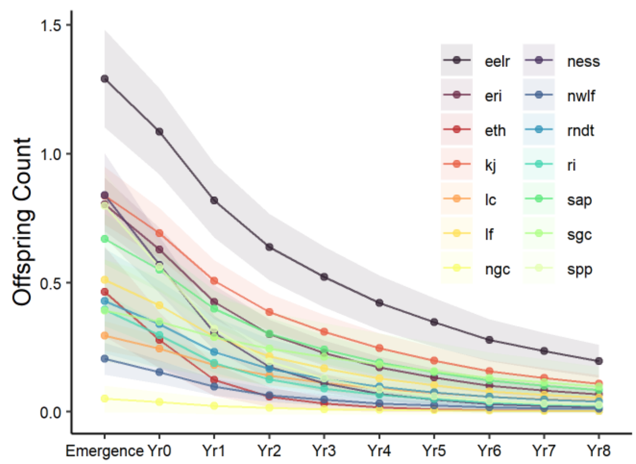

Figure S5. Predicted offspring count by site. Predictions here are for a one-headed hypothetical individual with an offspring cohort emerging in 2012, a year that had intermediate emergence. Shaded bands indicate one standard error on each side of the mean.

Appendix A. Details of Mating Potential Calculations

As described in the main text, we calculated mating potential (MP) as an inverse-weighted sum of the distances (*d*) between a focal plant *i* and its 1-*k*th nearest conspecific neighbors, *j* (Wagenius et al. 2007):

$$MP_i = \sum_{1}^{k} e^{d_{ij}*-\gamma}$$

Specifically, we calculated mating potential with *k* = 7 and γ = 1/13.3. For plants at sites with fewer than seven other conspecifics, we quantified mating potential with as many individuals as flowered in the site. The value of the exponential decay parameter γ determines how quickly a neighbor's contribution to a focal plant's mating potential decays with distance. The relationship between distance and contribution to mating potential is $e^{d*-\gamma*d}$ and is displayed for γ = 1/13.3 in Figure A1. Given the form of this function, the difference in contribution to mating potential of highly proximate neighbors and intermediately proximate neighbors is much greater than the difference between intermediately proximate neighbors and distant neighbors. We did not have phenology data to include a within-season temporal component to our mating potential metric, as we have done in previous studies (Wagenius et al. 2020). However, our previous analyses have found that mating potential depends more on annual flowering rates than within-season timing (Waananen et al. 2018). Below we provide example calculations illustrating how the proximity of neighbors influences mating potential. Note that, given k = 7, the maximum of this function is 7, which would occur if all seven of the nearest neighbors were 0 m away from the focal plant.

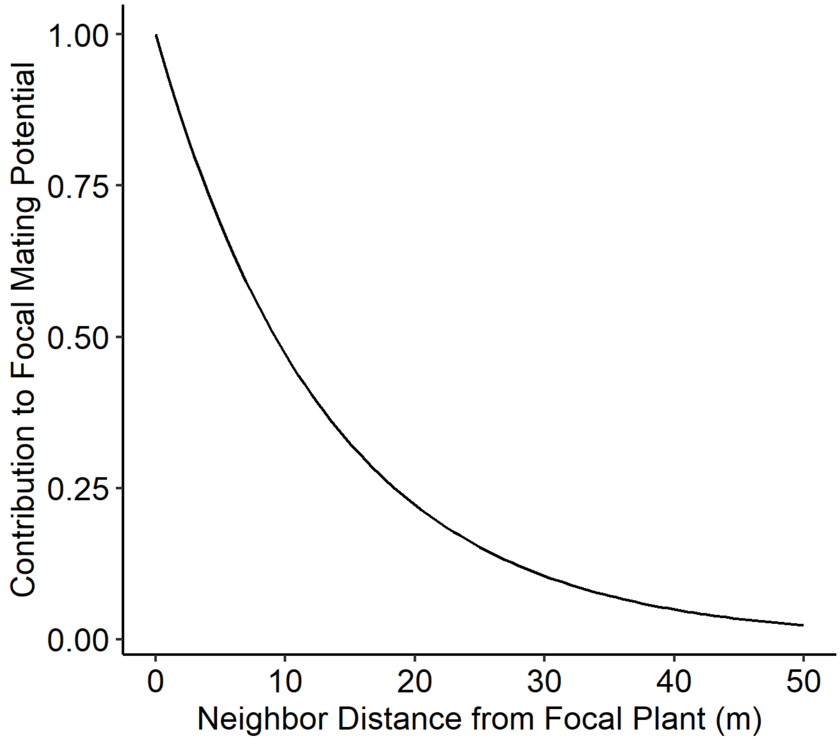

Figure A1. Relationship between a neighbor's distance to a focal plant and its contribution to the focal plant's mating potential for γ = 1/13.3.

These values are summed across *k* neighbors. To illustrate, calculations for several examples with k = 7 and γ = 1/13 for focal plants in our dataset are below.

Example 1

Focal plant with 1-7th neighbors 4.75, 6.64, 13.97, 19.97, 31.68, 44.65, and 60.61 m away.

$$MP = e^{4.75*-\frac{1}{13.3}} + e^{6.64*-\frac{1}{13.3}} + e^{13.97*-\frac{1}{13.3}} + e^{19.97*-\frac{1}{13.3}} + e^{31.68*-\frac{1}{13.3}} + e^{44.65*-\frac{1}{13.3}} + e^{60.61*-\frac{1}{13.3}} = 0.70 + 0.61 + 0.35 + 0.22 + 0.09 + 0.03 + 0.01 = 2.01$$

R Code:

```
# Distances from 1-7th neighbors to focal plant
distances <- c(4.75, 6.64, 13.97, 19.97, 31.68, 44.65, 60.61)

# Contribution of each neighbor to focal plant mating potential
sapply(distances, FUN = function(x) exp(x*(-1/13.3)))

# Sum individual neighbor contributions for focal plant mating potential
sum(sapply(distances, FUN = function(x) exp(x*(-1/13.3))))
```

Example 2

Focal plant with 1-7th neighbors 7.55, 10.31, 11.05, 11.66, 11.94, 12.95, and 14.94 m away.

$$MP = e^{7.55*-\frac{1}{13.3}} + e^{10.31*-\frac{1}{13.3}} + e^{11.05*-\frac{1}{13.3}} + e^{11.66*-\frac{1}{13.3}} + e^{11.94*-\frac{1}{13.3}} + e^{12.95*-\frac{1}{13.3}} + e^{14.94*-\frac{1}{13.3}} = 0.57 + 0.46 + 0.44 + 0.42 + 0.41 + 0.38 + 0.33 = 2.99$$

R Code:

```
# Distances from 1-7th neighbors to focal plant
distances <- c(7.55, 10.31, 11.05, 11.66, 11.94, 12.95, 14.94)

# Contribution of each neighbor to focal plant mating potential
sapply(distances, FUN = function(x) exp(x*(-1/13.3)))

# Sum individual neighbor contributions for focal plant mating potential
sum(sapply(distances, FUN = function(x) exp(x*(-1/13.3))))
```

Example 3

Focal plant with 1-7th neighbors 1.39, 2.18, 4.41, 4.91, 5.16, 6.33, and 7.71 m away.

$$MP = e^{1.39*-\frac{1}{13.3}} + e^{2.18*-\frac{1}{13.3}} + e^{4.41*-\frac{1}{13.3}} + e^{4.91*-\frac{1}{13.3}} + e^{5.16*-\frac{1}{13.3}} + e^{6.33*-\frac{1}{13.3}} + e^{7.71*-\frac{1}{13.3}} = 0.90 + 0.85 + 0.72 + 0.69 + 0.68 + 0.62 + 0.56 = 5.02$$

R Code:

```
# Distances from 1-7th neighbors to focal plant
distances <- c(1.39, 2.18, 4.41, 4.91, 5.16, 6.33, 7.71)

# Contribution of each neighbor to focal plant mating potential
sapply(distances, FUN = function(x) exp(x*(-1/13.3)))

# Sum individual neighbor contributions for focal plant mating potential
sum(sapply(distances, FUN = function(x) exp(x*(-1/13.3))))
```

References

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Wagenius, S., E. Lonsdorf, and C. Neuhauser. 2007. Patch aging and the S-Allee effect: breeding system effects on the demographic response of plants to habitat fragmentation. Am. Nat. 169:383–397.

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Appendix B. Demographic Stochasticity Simulation Details

We developed a simulation model to explore when differences between maternal plants' fitness due to seedling emergence would persist if no relationship exists between mating potential and survival. This corresponds to the hypothesis that mating potential influences the quantity of offspring that emerge, as is supported by evidence about how mating potential influences seed set, but has no relationship with mating quality, which would be the case when there is not a strong association between mate abundance and offspring fitness, e.g., a population without strong spatial genetic structure. For each simulation, we represented fitness differences as one plant's advantage over another in its number of offspring at emergence. We simulated emergence advantages (E) at each integer between 1 and 50 seedlings and juvenile survival rates (S) between 0 and 1 in twenty evenly spaced increments. For each seedling comprising the advantage in 1 to E, we drew at random whether or not it survived where chance of survival was equal to S. Then, we tallied how many offspring were still alive, i.e., how much of the advantage observed at emergence persisted. We repeated the simulation for each combination of E and S 100 times and calculated the average number of surviving offspring across all replicates of each combination. To gain insight specific to the survival rate and range of number of seedlings per maternal plant we observed in our system, we repeated the simulation with the survival rate observed from emergence to age 8 in our data and E at each integer between 1 and 10.

Results

Our simulations illustrated that when survival rates were lower, maternal plants needed a greater advantage in number of offspring at emergence (i.e., a greater emergence advantage) to maintain a fitness advantage after eight years (Figure 4A; Figure B1). When the survival rate was high, emergence advantages were persistent and even a small advantage in offspring count at emergence translated to more offspring at a later life stage. In contrast, at low survival rates, even an emergence advantage of 50 seedlings (the maternal plant with the largest number of seedlings that we observed had 45) did not reliably secure an advantage following survival. When we considered this model with a survival rate of 0.11 we found similar patterns; across the range of emergence advantages we most commonly observed, between 0 and 6 offspring difference between high- and low-emergence maternal plants, the final advantage of a high-emergence maternal plant was still typically 0 (Figure 4B). However, our simulation also illustrated exceptions to this expectation; even at low emergence advantages (e.g., $E = 1$), our simulation showed instances where the advantage was maintained.

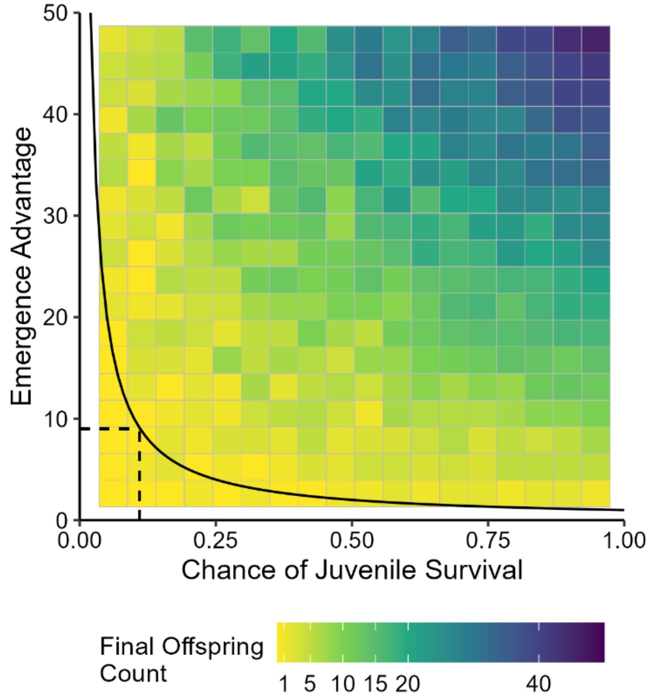

Figure B1. Simulation results of binomial model of maternal fitness advantages at offspring emergence (E) given the chance of juvenile survival (S). The solid line shows $E = 1/S$, above which an initial advantage would be expected to persist following juvenile survival. Dashed lines indicate the observed chance of survival and corresponding E required to maintain an advantage.