Facilitation and competition interact with seed dormancy to affect population dynamics in annual plants

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Abstract
Seed dormancy increases population size via bet-hedging and by limiting negative interactions (e.g., competition) among individuals. On the other hand, individuals also interact positively (e.g., facilitation), and in some systems, facilitation among juveniles precedes competition among adults in the same generation. Nevertheless, studies of the benefits of seed dormancy typically ignore facilitation. Using a population growth model, we ask how the facilitation–competition balance interacts with seed dormancy rate to affect population dynamics in constant and variable environments. Facilitation increases the growth rate and equilibrium size (in both constant and variable environments) and reduces the extinction rate of populations (in a variable environment), and a higher rate of seed dormancy allows populations with facilitation to reach larger sizes. However, the combined benefits of facilitation and a high dormancy rate only occur in large populations. In small populations, weak facilitation does not affect the growth rate, but does induce a weak demographic Allee effect (where population growth decreases with decreasing population size). Our results suggest that facilitation within populations can interact with bet-hedging traits (such as dormancy) or other traits that mediate density to affect population dynamics. Further, by ensuring survival but limiting reproduction, ontogenetic switches from facilitation to competition may enable populations to persist but limit their maximum size in variable environments. Such intrinsic regulation of populations could then contribute to the maintenance of similar species within communities.

KEYWORDS
Allee effect, annual plant, bet-hedging, germination, ontogeny

1 | INTRODUCTION

Seed dormancy, defined as the inability of a viable seed to germinate under current conditions that would otherwise promote germination, is common in plants (Bewley, 1997; Finch-Savage & Leubner-Metzger, 2006) and similar to dormant stages observed in bacteria (Lewis, 2007), plankton (Haitson Jr, 1996) and other organisms. The benefits of seed dormancy arise from the ability of lineages or populations to “store” individuals in a relatively protected state while conditions are unfavorable, for example, during the wrong season or poor years, or when conditions are only ephemerally favorable. When germination is delayed beyond the first year after dispersal, seed dormancy reduces the negative impact of poor years and in turn allows lineages or populations to persist in environments that vary from year to year (Clauss & Venable, 2000; Cohen, 1966; Venable, 2007; Venable & Lawlor, 1980). Thus, seed dormancy can serve as a bet-hedging strategy by limiting the degree to which the population or lineage is exposed to risks that occur aboveground in variable
environments. This strategy is particularly important in annual species that germinate and reproduce in a single year because it prevents the loss of the entire population in years in which no individuals are able to reproduce successfully.

Seed dormancy also reduces competition. Delayed germination allows seeds to wait for less competitive conditions before they attempt to reproduce; thus, the production of a higher fraction of dormant seeds can reduce the effects of crowding on population growth (Ellner, 1985a, 1985b; Ellner, 1987; Gremer & Venable, 2014; Venable & Brown, 1988). Delayed germination via seed dormancy can also reduce sibling competition in systems with limited spatial dispersal by spreading recruitment of an individual's offspring through time (Venable & Lawlor, 1980).

The relationships between competitive dynamics, seed dormancy and environmental variation in annual plants are well resolved, but interactions among plants within populations are not always competitive. Facilitation, a biotic interaction in which an individual benefits from the presence of others, is common in plants and can be attributed to various mechanisms, such as mediation of abiotic stress (e.g., irradiance, wind) and refuge from predation (Bertness & Callaway, 1994; Brooker et al., 2008; Callaway et al., 2002; He, Bertness, & Altieri, 2013). However, to the best of our knowledge, the interactive effects of intraspecific facilitation and the seed dormancy rate on population dynamics have not been explicitly considered (but see Schreiber, Yamamichi, & Strauss, 2019).

Accounting for facilitation is necessary for our understanding of the ways in which seed dormancy affects population dynamics. Facilitation protects individuals from physical stress that may limit population growth or size and in turn increase extinction risk, such as drought and extreme temperature. Therefore, facilitation and seed dormancy may provide alternative solutions to the same problem—reducing the negative impacts of stressful years on population growth. If stressful years favor facilitation, leading to reduced stress experienced by vulnerable stages such as seedlings and juveniles, then the risks that individuals face aboveground will be reduced, and the benefits of seed dormancy in populations will be less pronounced. Furthermore, if facilitation mitigates stress, then it could allow more germination and help populations overcome a major demographic disadvantage of delaying germination: missed opportunities for reproduction.

Facilitation may also modify competition, which is known to interact with seed dormancy rates to affect population dynamics. Facilitation and competition can both occur in a single system in response to spatial or temporal variation in stress (García-Cervigón, Iriondo, Linares, & Olano, 2016; Goldberg, Turkington, Olsvig-Whittaker, & Dyer, 2001; Maestre, Callaway, Valladares, & Lortie, 2009; Malkinson & Tielbörger, 2010; Pugnaire & Luque, 2001; Wright, Schnitzer, & Reich, 2014, 2015). Specifically, as environmental stress increases, facilitation becomes more likely, whereas competition becomes less likely. One particularly striking example of this covariance is a transition from facilitation to competition over the course of a single individual’s lifetime (Armas & Pugnaire, 2009; Leverett, Schieder IV, & Donohue, 2018; Lortie & Turkington, 2008; Miriti, 2006). This transition occurs over a stress gradient generated by a change in organisms' sensitivities to the environment as they age: young (e.g., seedlings and juveniles) are more susceptible to the effects of physical stress, whereas adults, having already become established, are primarily limited by resources that determine their growth and fecundity (Miriti, 2006; Parrish & Bazzaz, 1985).

This pattern in which facilitation precedes competition over the life cycle may result in even more detrimental effects of density than would be observed if only competition occurred. For example, by reducing the stress to which individuals are exposed in earlier stages, intraspecific facilitation can promote growth and an increase in competition in later stages (Zhang, Jia, & Wang, 2017). In the case of annual plant populations, increasing density could be beneficial early in the life cycle as individuals struggle to cope with stress but then be detrimental later in the life cycle as individuals grow and reproduce, especially if individuals are clumped in space. This may in turn lead to an ontogenetic switch from positive density dependence in survival to negative density dependence in reproduction that ensures high survival rates but limits reproduction (Miriti, 2006). As a consequence, if both facilitation and competition are strong, then heightened survival may magnify competition in adults and in turn limit population size and persistence.

How might the seed dormancy rate interact with the balance of facilitation and competition that individuals experience over ontogeny to affect populations? There are at least two possibilities. First, facilitation could reduce the negative effects of the environment and in turn increase survival, buffering populations against stressful years and reducing extinction probabilities in variable environments. If so, we predict that facilitation will lower the seed dormancy rate needed to minimize extinction risk. Second, facilitation among juveniles could lead to increased competition among adults, suppressing population growth at high densities and in turn limiting population size. If so, we predict that populations experiencing facilitation will have greater equilibrium sizes if the seed dormancy rate is higher (which would reduce the fraction of the population available to participate in facilitation and subsequent competition).

Here, we use an optimization model and simulations of population growth to examine how the balance of facilitation and competition in populations of annual plants interacts with seed dormancy rates to affect population growth, size and extinction. We first examine how the facilitation–competition balance and seed dormancy affect population dynamics in a constant environment in which the bet-hedging benefits of seed dormancy do not occur. We then ask how facilitation, competition and seed dormancy affect population size and extinction
rates in variable environments. Although facilitation and competition may act simultaneously in some species and just vary in their relative strengths for juvenile and adult stages, here for simplicity we consider the case where juveniles only experience facilitation and adults only experience competition. We show that facilitation preceding competition can either increase or have no effect on the annual plant population growth rate, depending on the size of the population. We demonstrate that the rate of seed dormancy that is best for increasing the growth rate in small or large populations depends on the facilitation–competition balance those populations experience.

2 | METHODS & RESULTS

2.1 | The model

We first develop a model that describes the population growth of a single species of summer annual plant in discrete time. The model is similar to those used in previous studies to examine how the seed dormancy rate affects growth in annual plant populations (Cohen, 1966; Gremer & Venable, 2014), except that in our case, the components of per capita reproduction are modeled separately to accommodate distinct processes of survival and reproduction. Here we imagine a summer annual with the growing season over the summer and the non-growing season over the winter; our model could easily be applied to other seasonal patterns (e.g., a winter annual). We start by considering a number of seeds before winter \([N_t]\), of which a fraction \((S_w)\) survive the winter. A fraction of those surviving seeds then germinate \((G)\) the following spring, yielding

\[ J(N_t) = N_t S_w G, \]  

(1)

juvenile plants. Survival of juveniles is density dependent (with a positive relationship between the number and survival of juveniles) and given by

\[ l(N_t) = \frac{a + FJ(N_t)}{1 + FJ(N_t)}, \]  

(2)

where \(a\) is the minimum survival rate, equal to 0.01; and \(F\) is the strength of facilitation. As the number of juveniles increases, more juveniles survive due to facilitation. When facilitation does not occur \((F = 0.0)\), the survival rate is equal to \(a\) regardless of juvenile number. Surviving juveniles become adults, where

\[ A(N_t) = N_t S_w G(N_t) \]  

(3)

is the number of adult plants at the end of the summer. Competition occurs among adults as a negative relationship between the number and fecundity of individual adults,

\[ b(N_t) = \frac{b_{\text{max}}}{1 + CA(N_t)}, \]  

(4)

where \(b_{\text{max}}\) is the maximum fecundity of each adult, equal to 2,000; and \(C\) is the strength of competition. As the number of adults increases, each adult produces fewer seeds due to resource limitation. The functional form that we use for competition does not lead to over-compensatory dynamics, which are known to interact with seed dormancy rates to affect population growth (Ellner, 1987). Finally, seeds that did not germinate \((1 - G)\) survive the summer with probability \(S_s\). Thus, the total number of seeds the following year is given by

\[ N_{t+1} = N_t [S_w G(N_t) b(N_t) + S_w (1 - G) S_s], \]  

(5)

the sum of newly produced seeds that year plus the number of surviving dormant seeds from preceding years (Figure 1a). Note that while we measure population size as the number of seeds, the number of juveniles or adults can be easily tracked by using Equations (1) and (3) above.

We varied the balance of facilitation and competition that individuals in the population experienced over ontogeny by implementing relationships between survival and the number of juveniles and between reproduction and the number of adults (Figure 1b,c). For more information on model parameters, please see Table S1 (Supporting Information 1).

2.2 | Effects of seed dormancy and the facilitation–competition balance on population dynamics in constant environments

We first investigated how the rate of seed dormancy and the balance of facilitation and competition over ontogeny interact to affect population dynamics in constant environments. We examined the effects of these factors both on the growth rate \((\lambda = N_{t+1}/N_t)\) at small population size \((N_t = 2)\), which determines how rapidly a population can recover from a small size, and on the population's stable equilibrium size \((N^*)\), which determines the expected long-term population size in the absence of environmental variation. We derived analytic expressions for both the population growth rate and population equilibrium size (Supporting Information 1). For simplicity, we considered six facilitation–competition balance scenarios in which facilitation was absent \((F = 0.0)\), weak \((F = 0.001)\) or strong \((F = 1.0)\), and competition was either weak \((C = 0.1)\) or strong \((C = 1.0)\).

In any plant population, the seed survival rate will affect the number of individuals that are available to germinate, survive and reproduce each year. For a given rate of seed dormancy, increasing seed survival increases the growth rate of a small population as well as the stable equilibrium size of the population (Supporting Information 2, Figure S1). In
our model, the growth rate of small populations is more sensitive to seed survival in the winter ($S_w$) than to seed survival in summer ($S_s$) (Supporting Information 2, Figure S1a) because winter seed survival affects all seeds, whereas summer seed survival only affects seeds that did not germinate in a given year. In contrast, equilibrium size is affected equally by seed survival rates in both summer and winter (Supporting Information 2, Figure S1c). When seed survival rates are higher, facilitation among juveniles has a stronger positive effect on both population growth and equilibrium size because more individuals are available to germinate and participate in facilitation and then reproduce. Because seed survival rates have a straightforward, positive effect on population growth and equilibrium size, for simplicity we limit our subsequent analyses to populations in which summer and winter seed survival are each 0.6 ($S_s = S_w = 0.6$), which is approximately equal to the average seed survival rate measured across 12 species of annual plants (Gremer & Venable, 2014).

In a constant environment, population growth (in the short-term) is intuitively always maximized when there is no seed dormancy because more individuals contribute to reproduction (Figure 2a,b; Supporting Information 2, Table S2). This is true as long as the growth rate of small populations with full germination ($G = 1$) is greater than that of populations with no germination ($G = 0$), that is, that reproduction by each germinating seed ($a \cdot b_{max}$) is greater than the survival probability of each dormant seed during the same season ($S_s$). Furthermore, because resource limitation is weak when the population is small, the strength of competition among adults has little
effect on growth in populations that do not experience facilitation (compare solid lines in Figure 2a,b, and note that \( \lambda(N_t = 0) \) does not depend on the strength of competition, \( C \), in Equation (A3)).

Facilitation allows faster growth of small populations, especially when dormancy is low (dashed and dotted lines vs. solid lines in Figure 2a,b). However, if competition among adults is strong (Figure 2b), then facilitation among juveniles can lead to large population sizes and resource limitation. For this reason, the growth rates of populations with strong facilitation and low dormancy are not as high if competition is stronger. In sum, the growth of small populations is maximized when the seed dormancy rate is low, and facilitation increases the rate of initial population growth as long as competition is not so strong that resources become limited at small population sizes.

Although lower dormancy (i.e., more germination) promotes population growth, it will ultimately limit population size. A lower rate of seed dormancy forces more individuals to compete for resources when the population is large and resource-limited. Accordingly, in populations without facilitation, an intermediate rate of seed dormancy maximizes the size of the population at equilibrium (solid lines in Figure 2c,d). An intermediate rate of seed dormancy is favorable because it is high enough to help prevent strong competition among adults when the population is large (Figure 3a,b) but low enough to allow a sufficient amount of reproduction to enable population growth (Figure 4a,b). The rate of seed dormancy that allows the largest equilibrium size is the same regardless of the strength of competition that individuals experience, although...
FIGURE 4 Population growth in a constant environment. Effects of seed dormancy and the facilitation-competition balance over ontogeny on population growth (λ) as a function of density in a constant environment. Each panel indicates the effect of population size on population growth for a given combination of facilitation among juveniles (rows) and competition among adults (columns). Within each panel, lines represent populations with different rates of seed dormancy: Dotted lines indicate low dormancy (1 − G = 0.1), dashed lines indicate intermediate dormancy (1 − G = 0.5), and solid lines indicate high dormancy (1 − G = 0.9). The horizontal gray lines indicate no change in population size; values above this line indicate that the population is growing, and values below indicate that the population is shrinking.

Facilitation causes a higher rate of seed dormancy to maximize equilibrium size (dashed and dotted lines in Figure 2c,d). When populations are large, less dormancy leads to more germination; more germination increases the juveniles around for facilitation, in turn leading to stronger competition at the adult stage and thus decreased reproduction (Figure 3c–f). A high rate of seed dormancy mitigates the resource limitation that occurs among adults when the survival rate of juveniles is high and allows adults to maintain high reproductive rates, which promotes a greater equilibrium size.

The actual seed dormancy rate that maximizes the equilibrium size of populations depends on the relative strengths of facilitation and competition (Figure 2c,d). When competition is weak, the seed dormancy rate that maximizes equilibrium size with weak facilitation (0.94) is about the same as that with strong facilitation (0.97). In contrast, when competition is strong, the seed dormancy rate that maximizes equilibrium size is much lower with weak facilitation (0.88) than with strong facilitation (0.97). This result is due to the dual effect of facilitation: facilitation always increases survival but exacerbates resource limitation when populations are large. As long as competition is weak, facilitation leads to more reproductive adults and offsets the death of ungerminated seeds, thereby allowing a high dormancy rate and not exacerbating resource limitation. As a result, a high dormancy rate maximizes equilibrium size, regardless of the strength of facilitation. However, when competition is strong and fecundity is severely limited in large populations (i.e., those near equilibrium), weak facilitation is not sufficient unless more seeds germinate, participate in facilitation and ultimately contribute to reproduction; thus, a lower dormancy rate maximizes equilibrium size under such conditions.

Although a high rate of dormancy may increase the population’s stable equilibrium size in populations that experience facilitation, it also increases extinction risk when the population is small. Populations with weak facilitation exhibit a weak demographic Allee effect, in which population growth increases with size (solid lines in Figure 4c,d) (Allee, 1931; Courchamp, Clutton-Brock, & Grenfell, 1999; Stephens, Sutherland, & Freckleton, 1999). The Allee effect is exacerbated with high dormancy rates, which reduce population growth at small population sizes. This occurs because a high rate of dormancy limits the number of juveniles participating in facilitation for increasing survival and eventually adults participating in reproduction and thereby precludes rapid population growth. Stronger facilitation allows more germinating individuals to survive, which increases growth rates of small populations and mitigates the Allee effect (solid lines in Figure 4e,f vs. Figure 4c,d). Thus, the rate of seed dormancy that maximizes the growth rate in a population with facilitation will depend on whether the population is small or large.

To summarize, facilitation among juveniles increases both the growth rate of small populations and the equilibrium size of the population. When the population is small, a low rate of seed dormancy allows more individuals to reproduce, and the occurrence of facilitation among juveniles increases this benefit. Furthermore, a low rate of seed dormancy can reduce extinction rates in small populations experiencing facilitation by mitigating a weak demographic Allee effect. In contrast, when a population experiencing facilitation is large (i.e., near its equilibrium), a high rate of seed dormancy prevents the strong resource limitation.
among adults that suppresses the equilibrium size of the population.

2.3 Effects of seed dormancy and the facilitation–competition balance on population size and extinction rates in variable environments

Because seed dormancy and changes in density dependence over ontogeny interact to affect population growth and equilibrium size in a constant environment, we can expect that they also affect extinction rates in variable environments. We introduced environmental variation in population growth by including good years, in which survival, fecundity and the strengths of facilitation and competition were allowed to vary, and bad years, in which no reproduction occurred (Figure 1d,e; Supporting Information 1). We examined scenarios in which the probability of reproductive failure (\( p \)) was either 0.05 (occasional) or 0.25 (frequent). However, because the value of \( p \) had little effect on the relationships between the seed dormancy rate, the facilitation–competition balance and population dynamics, we only present results for environments in which \( p = 0.05 \). In order to capture the covariance of competition and facilitation that typically occurs along gradients of environmental stress, we adjusted the strength of facilitation based on survival, such that facilitation among juveniles was strongest in the years when survival otherwise would have been low (i.e., in more stressful years, which promote facilitation), and we adjusted the strength of competition based on fecundity, such that competition among adults was strongest in the years when reproduction otherwise would have been high (i.e., in more permissive years).

Because we could not derive an analytic expression for equilibrium population size in variable environments, we simulated the growth of 1,000 populations for 100 generations to examine how seed dormancy rate affects population size. We performed these simulations for populations founded by two individuals (seeds). We defined extinct populations as those where the final population size \( (N) \) fell below an extinction threshold equal to 1 seed, and defined extant populations as those above this threshold. We examined how the seed dormancy rate affected the mean final population size after 100 generations of growth (including both extinct and extant populations), and we asked whether this relationship changed depending on the balance of facilitation and competition over ontogeny. We also examined how the seed dormancy rate is related to extinction rates in variable environments by calculating the proportion of populations that went extinct.

To confirm that facilitation increases population growth rates in variable environments (as it does in constant environments), we calculated the average population growth rate \( (N_{t+1} / N_t) \) of 100 replicate populations experiencing each combination of facilitation and competition over 1 generation (with \( N_i = 2 \), assuming \( G = 0.5 \). Strong facilitation indeed dramatically increases the population growth rate, regardless of whether competition is weak \( (5.21 \pm 0.492 \text{ [mean } \pm \text{ SE]} \) and \( 218.03 \pm 13.686 \) for \( F = 0.0 \) and 1.0, respectively) or strong \( (5.17 \pm 0.486 \) and \( 172.32 \pm 9.84 \) for \( F = 0.0 \) and 1.0, respectively). The growth rate of populations experiencing weak facilitation, on the other hand, is similar to that of populations experiencing no facilitation (when \( F = 0.001 \), the growth rate is \( 5.57 \pm 0.504 \) and \( 5.52 \pm 0.497 \) for \( C = 0.1 \) and 1.0, respectively).

Consistent with the results in a constant environment, an intermediate rate of seed dormancy allows populations to reach larger sizes in the absence of facilitation (solid lines in Figure 5a,b; Supporting Information 2, Table S3). Stronger competition also reduces the growth and size of populations when the environment varies, and a slightly higher (but still intermediate) rate of seed dormancy is needed to maximize population size by protecting populations from fluctuations in size caused by bad years.

By allowing populations to grow more quickly when they are small (Figure 2a,b) and reach larger sizes with time (Figure 5a,b), an intermediate rate of seed dormancy also minimizes the probability of extinction in variable environments when populations only experience competition (solid lines and black circles in Figure 5c,d). By decreasing population size, stronger competition slightly increases extinction risk, especially when the population has a lower dormancy rate and thus a smaller hedge against bad years (solid lines in Figure 5c,d). Thus, a slightly higher (but still intermediate) rate of seed dormancy minimizes extinction risk in variable environments with strong competition.

Facilitation increases the sizes of populations and reduces their probabilities of extinction in variable environments (dashed lines in Figure 5). Consistent with the results in a constant environment, populations reach the largest size at a higher rate of seed dormancy when facilitation occurs compared to when only competition occurs (dashed lines in Figure 5a,b). Weak facilitation reduces extinction risk compared to no facilitation, for all rates of seed dormancy. Although a high rate of dormancy would maximize population size, the increased growth rate from weak facilitation is only felt at large population sizes, which requires higher germination rates, and so a lower rate of dormancy (lower equilibrium population size, but higher growth rate) minimizes extinction risk. Strong facilitation further reduces extinction risk compared to weak facilitation, for all rates of seed dormancy. As above, a high rate of dormancy would maximize population size. However, in contrast here, the increased growth rate from strong facilitation is felt at all population
sizes, so a lower rate of dormancy is no longer needed to minimize extinction; rather a much higher rate of dormancy minimizes extinction risk. Thus, strong facilitation, by mitigating the Allee effect, allows a very high rate of dormancy to both promote large population sizes and minimize the risk of extinction.

To summarize, when the environment varies across years, an intermediate dormancy rate allows populations that only experience competition to recover quickly from small sizes without the need for low dormancy; therefore, a higher rate of dormancy is favorable in populations with facilitation than in those that only experience competition. However, if facilitation is not sufficiently strong, populations are subject to a weak Allee effect (exacerbated by high dormancy rates) that prevents them from reaching large sizes. This leads to extinction rates similar to those in populations that do not experience facilitation.

3 | DISCUSSION

We suggested two possible ways in which facilitation among juveniles may interact with a classic bet-hedging trait—seed dormancy in annual plants—to affect population dynamics: (a) by reducing extinction risk, facilitation could reduce the optimal dormancy rate in variable environments and (b) by increasing competition among adults, facilitation could increase the optimal dormancy rate in order to prevent resource limitation in large populations. Consistent with the second prediction, we found that because juvenile facilitation increases adult competition and leads to low reproduction in large populations, a higher rate of seed dormancy allows populations to reach greater equilibrium sizes. Higher seed dormancy rates allow populations to reach larger sizes by reducing the fraction of the population participating in facilitation and competition when the population is large. If the dormant fraction is sufficiently high, then it can work synergistically with facilitation to benefit populations by reducing extinction risk. However, these benefits may only be realized in larger populations, as the combination of weak facilitation among juveniles and a high rate of seed dormancy causes a demographic Allee effect that prevents growth and in turn leads to extinction in small populations. Overall, our results indicate that positive density dependence in populations can modify the rate of seed dormancy and potentially other traits that allow populations to persist in variable environments.

3.1 | Seed dormancy and the interactive effects of intrinsic and extrinsic drivers of population dynamics

Vital rates that determine population growth are sensitive to physical conditions in the underlying environment (extrinsic factors) as well as interactions among individuals in the population (intrinsic factors). Thus, environmental variation and density dependence can both affect the values of traits linked with vital rates that maximize the success of populations, such as seed dormancy. Based on theoretical models, higher seed dormancy is favorable in the absence of any density dependence if the environment varies across years (Cohen, 1966), and it can be favored in the absence of environmental variation if competition is sufficiently strong (Ellner, 1987). However, the seed dormancy rate that actually occurs in
annual plant populations in the wild is best explained by the combined effects of competition and environmental variation (Gremer & Venable, 2014).

Importantly, the effects of density on population vital rates do not occur independently of the underlying environment. Instead, interactions among individuals that lead to density-dependent survival and reproduction, including facilitation and competition, are modified by underlying physical conditions that change over time and space (Lok, Overdijk, Tinbergen, & Piersma, 2013; Maestre et al., 2009; Pugnaire & Luque, 2001; Wright et al., 2014, 2015). For this reason, the effect of seed dormancy rates on the growth and success of populations may depend on the interaction between the underlying environment and the effects of density. As shown here, positive density dependence in populations via facilitation (an intrinsic factor) can offset the negative effects of annual variation in stress (an extrinsic factor), reducing the probability of extinction in variable environments. If facilitation occurred alone (i.e., if the population was never resource limited), then one would predict that a lower rate of seed dormancy would be needed in populations experiencing facilitation to offset the effect of environmental variation. However, in populations with limited resources and therefore stronger competition, a high rate of seed dormancy is required before facilitation increases the growth rate. Otherwise, too much germination increases juvenile survival, which leads to high adult density, strong competition, and a lower equilibrium density.

We have also demonstrated that two intrinsic factors (facilitation and competition) can interact with each other to affect population dynamics. The phenomenon in which facilitation limits individual performance by increasing competition, which we demonstrate here, has also been noted in other studies. For example, in a study of the desert perennial Ambrosia dumosa, Miriti (2006) found that adults increased the survival of juveniles that emerged near them, but those juveniles eventually competed with the adults that originally facilitated them. Similarly, in theoretical models of self-thinning dynamics, Zhang et al. (2017) demonstrated that intraspecific facilitation relaxes stress and in turn increases intraspecific competition that occurs later. Stable populations may result from such dynamics if intraspecific facilitation promotes successful establishment and persistence but intraspecific competition among established individuals limits the size of the population. Such intrinsic regulation of population size could promote diversity in communities of similar species (Antonovics & Levin, 1980; Chesson, 2000). However, as we have shown, the effect of an ontogenetic switch from facilitation to competition on population stability in annual plants will depend on seed dormancy—too much can lead to extinction via Allee effects if facilitation is not sufficiently strong, while too little magnifies competition and suppresses the maximum size of the population.

3.2 The optimal rate of seed dormancy in populations

We have examined the combined effects of the facilitation—competition balance and seed dormancy on population growth, size and extinction. Our model quantifies the seed dormancy rates that maximize either growth rate or population size. We find that there is a tension between these two with low dormancy maximizing the growth rate (effective “r-seletion”; MacArthur & Wilson, 1967) and high dormancy maximizing population size (K-selection). However, traits such as seed dormancy that affect both individual and population performance may not necessarily evolve to values that are predicted based on the success of populations (Shaw, Jalasvuori, & Kokko, 2014). In order to examine the evolution of seed dormancy in populations with different patterns of density dependence, an evolutionarily stable strategy-type approach in which lineages with different trait values compete against each other would need be to be employed. Nevertheless, although our model does not include evolution, our results do provide insight into the seed dormancy values that would be optimal under specific sets of conditions. In doing so, this study identifies the relative values of seed dormancy that enable populations to persist in variable environments, and these seed dormancy rates may reflect the direction in which seed dormancy would evolve in different contexts.

Whether a high seed dormancy rate maximizes the growth rate in populations experiencing facilitation will depend on the size of the population and the intensity of competition. We found that a high rate of seed dormancy and facilitation among juveniles can increase the equilibrium density of a population, thus potentially reducing the impact of poor years on that population’s size in variable environments. However, facilitation leads to a positive relationship between population growth and size, with too-small populations risking extinction in variable environments. Thus, facilitation and a lower rate of seed dormancy may enhance successful colonization of novel environments, but as populations become larger and established, stronger seed dormancy will need to evolve to prevent extinction. Furthermore, in systems with strong facilitation, demographic Allee effects may not be prevalent, in which case a very high rate of seed dormancy will allow populations to reach large sizes and persist. Consistent with the idea that stronger dormancy is more likely to be beneficial in established populations, a lack of dormancy does not persist in seed plant lineages over long periods of evolutionary time (Willis et al., 2014). Instead, as Willis et al. (2014) discuss, a lack of seed dormancy may be beneficial during colonization by promoting the persistence of populations, but it is likely to be a short-lived
state that quickly evolves to a dormant state or goes extinct. Thus, while an intermediate or low rate of seed dormancy may enable lineages to colonize and become established in novel environments, it is not necessarily beneficial in the long term.

Another factor that may modify the optimal rate of seed dormancy for populations is the ability of seeds to respond to environmental cues. In our model, seeds cannot detect and respond to the quality of a given year. Germination cueing occurs when seeds germinate (or not) in response to cues that indicate conditions are favorable (or not) for establishment (reviewed in Baskin & Baskin, 2014). Species may use a combination of seed dormancy, which aligns the period during which seeds can germinate with an appropriate season or year, and germination cueing, which provides seeds with finer control of the conditions under which they germinate (Auge et al., 2015; Baskin & Baskin, 2014; Burghardt, Edwards, & Donohue, 2016; Donohue, Rubio de Casas, Burghardt, Kovach, & Willis, 2010; Footitt, Clay, Dent, & Finch-Savage, 2014; Venable & Lawlor, 1980). If seeds in our model were also able to employ cueing, then the benefits of a high rate of seed dormancy (e.g., a hedge against poor years) may be diminished, in which case a high rate of dormancy would not be as beneficial when the environment varies across years. Furthermore, if facilitation only alters vital rates under unfavorable conditions, then it may be less influential when cueing is occurring. Alternatively, since cueing behaviors can lead to increased density and thus intensify the interactions among individuals (Metcalf, Burghardt, & Koons, 2015), the rate of seed dormancy may need to be higher to reduce the occurrence of competition in large populations that employ germination cueing. Models that account for both seed dormancy and germination responses to environmental cues could be combined with population models in order to examine how facilitation, competition and environmental variation jointly affect population growth and extinction rates.

3.3 | Future directions

We have examined how facilitation and competition over ontogeny interact with seed dormancy to affect the growth, size and extinction of annual plant populations, but we have focused on a subset of the possible values of these parameters. Expanding the values of the investigated parameters would provide a more complete picture of the relationships between seed dormancy, environmental quality and the balance of facilitation and competition that occurs within populations. First, one could expand the scenarios of ontogenetic switches in facilitation and competition beyond what we have included. This could include using a wider range of values, allowing facilitation and competition to occur simultaneously, or examining cases where competition precedes facilitation. For example, facilitation among adults via pollinator attraction occurs in some systems (Laverty, 1992; Moeller, 2004). Theoretical studies have shown that when interspecific facilitation occurs after interspecific competition in a two-species system, it can affect both equilibrium population size and the extinction rate (Feldman, Morris, & Wilson, 2004). For cases in which competition occurs before facilitation in the life cycle in a single population, the rate of seed dormancy that maximizes population success may be similar to that for cases in which only competition occurs.

Second, it would be worth examining how the magnitudes of the correlations between environmental quality and facilitation or competition affect the dynamics evaluated here. The relationship between facilitation and environmental stress may be stronger in some environments than in others, for example along elevational gradients or even among patches in a small geographic area. Examining the relationship between seed dormancy and interactions between the physical environment and density dependence within populations may provide insight to the drivers of variation in seed dormancy along spatial environmental gradients (Debieu et al., 2013; Montesinos-Navarro, Picó, & Tonsor, 2012; Wagmann et al., 2012).

Third, it would be interesting to examine additional functional forms of the relationships between environmental quality and the magnitudes of positive and negative density dependence. For example, the tendency for facilitation to increase with stress can break down in extremely stressful environments (Koyama & Tsuyuzaki, 2013; Malkinson & Tielbörger, 2010). In such cases, the relationship between environmental quality and facilitation may not be monotonic and linear, as we have assumed here.

Finally, one could consider a broader range of forms of stochasticity. Intriguingly, in our model stochasticity did not affect equilibrium population size much (Figure 2c,d vs. Figure 5a,b). The fact that we do not see an effect of stochasticity on equilibrium population size even using our complex version of stochasticity suggests to us that we would see the same result even with a more simplified version of stochasticity. Future work could explore a more simplified version of stochasticity to see if this indeed holds.

4 | CONCLUSION

Studies of the conditions under which seed dormancy is beneficial, such as in variable environments and under competition for resources within lineages, populations and communities, have largely ignored the potential for facilitative interactions to modify those conditions. We have shown that the rate of seed dormancy that maximizes facilitative interactions is higher than that in populations without facilitation. This occurs because facilitation both reduces the impact of
environmental variation and exacerbates competition that occurs later in the life cycle. Accounting for the effects of temporal variation in plant–plant interactions generated by annual environmental variation and ontogenetic changes in susceptibility to stress will improve our understanding of the population dynamics of annual plants, the evolution of traits that contribute to those dynamics, and the coexistence of similar species in variable environments. Finally, our results may be applicable to non-plant species that exhibit dormancy and facilitation, such as biofilm-forming bacteria.

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