Differences between the costs and establishment rates of clonal and sexual offspring
affect the probability of evolutionary rescue in plant populations

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Abstract

Evolutionary rescue can facilitate population persistence following an environmental change, but the success of this process depends on a large number of factors. To date, only a small number of theoretical studies have considered the impact of reproductive mode, specifically facultative sex, on evolutionary rescue despite the prevalence of organisms that implement this reproductive strategy. These initial studies concluded that greater investment in clonal reproduction generally increases the probability of evolutionary rescue following an abrupt environmental change and reduces the probability of rescue following a directional environmental change. However, one key assumption of the underlying models is that clonal offspring are equivalent to sexual offspring with respect to production costs and juvenile survivorship. Previous work instead suggests that clonal offspring tend to be more costly to produce and have higher juvenile survivorship compared to sexual offspring; the contribution of sexual offspring to the maintenance of established populations is also known to be highly variable across clonal plant species. This study evaluated how these differences between clonal and sexual offspring impact the relationship between clonal allocation and the probability of evolutionary rescue by increasing the relative cost of clonal offspring and varying the relative establishment rate of sexual offspring in simulated clonal plant populations. Following an abrupt environmental change, greater clonal reproduction increased the probability of evolutionary rescue only when the establishment rate of sexual offspring was low. The sexual establishment rate did not affect the outcome following a directional environmental change: greater clonal reproduction always reduced the probability of evolutionary rescue. Across all simulations, the probability of evolutionary rescue fell as the establishment rate of sexual offspring declined. Incorporating known differences between clonal and sexual offspring into models of clonal plant populations is thus critical for understanding the persistence of natural populations in the face of environment change.

Introduction

All organisms must cope with environmental change, and investigations of how populations respond to these changes have become more prevalent with rising concern over global climate change and other human-mediated disturbances. One way that populations adjust to new conditions is through evolutionary rescue (coined by Gomulkiewicz & Holt 1995), in which adaptive evolution prevents the population from declining to extinction and promotes population growth to minimize the risk of extinction from stochastic processes. Theoretical, experimental, and observational studies from the past several decades have identified a number of factors that contribute to a population's probability of successful evolutionary rescue (reviewed in Carlson *et al.* 2014 and Bell 2017). However, the majority of these studies focus entirely on obligately sexual or asexual organisms. Of equal importance is considering how facultatively sexual organisms may persist in a changing environment. The combination of sexual and asexual reproduction exerts substantial influence over genetic processes within a population (as discussed in Otto 2009, Lively & Moran 2014, Hartfield 2016, and Otto 2020), and in turn may affect its capacity to adapt in response to different types of environmental change.

Facultative sexual reproduction is found in a diverse array of species, including many angiosperms, reef-building corals, and a variety of invertebrates such as *Daphnia*, aphids, and monogonont rotifers. Nonetheless, there have been only a handful of studies to date that investigate how the relative amount of sexual and asexual (clonal) reproduction influences the likelihood of a population persisting through an environmental change. Using an individual-based model, researchers observed that greater clonal reproduction tended to increase the probability of evolutionary rescue following a stepwise environmental change, but reduced the probability of rescue in a directionally changing environment (Orive *et al.* 2017). A subsequent investigation found that these general results hold when environmental fluctuations are incorporated into the model, though very large fluctuations can reduce the effects of clonality under either type of environmental change (Peniston *et al.* 2021). These previous studies provide valuable insights into how partial clonality affects evolutionary rescue, but some of the simplifying assumptions made in these models could limit the degree to which they capture the behavior of real populations.

In these previous studies, one key assumption has been that the offspring of clonal and sexual reproduction are equivalent in their costs and behaviors. The production of a clonal offspring required the

same resource investment as a sexual offspring, and juvenile survivorship due to ecological factors was only implicitly considered as part of the relative cost parameter. Indeed, only a relatively small subset of the simulations assumed clonal offspring were 1.5 times as costly as sexual offspring. Prior knowledge of facultatively sexual species, however, introduces considerable doubt that the true resource demands and juvenile survivorship of offspring produced through clonal and sexual reproduction are equal. Clonal reproduction is said to have a two-fold advantage over sexual reproduction because sexual lineages must produce both male and female offspring while asexual lineages need only produce females (Maynard Smith 1971). Despite this apparent advantage, some studies have noted higher mortality or reduced fecundity within asexual lineages that would alter the relative cost of reproduction (Wetherington *et al.* 1987; Corely & Moore 1999; Kramer & Templeton 2001; Kearney & Shine 2005). Differences between sexual and asexual reproduction can also be found within a single lineage, as in facultatively sexual species. For cyclical parthenogens such as *Daphnia*, the switch to sexual reproduction typically incurs a direct opportunity cost, as clutch sizes from sexual reproduction tend to be smaller and total reproductive output is reduced. The resource demands of each type of offspring are less clear: not only is accurate measurement difficult, but it has also been argued that comparing the production of sexual and clonal offspring is inappropriate due to their different ecological roles (Cook 1985). Failure to address both the cost and behavioral differences between clonal and sexual offspring introduces a potential disconnect between the proportion of resources allocated towards each reproductive mode and the number of viable offspring that result from each process. An investigation that incorporates these differences between clonal and sexual offspring would thus provide a more accurate assessment of how clonal allocation affects evolutionary rescue in populations that employ facultative sex.

Facultatively sexual organisms also show a diversity of life histories, and it is unclear whether the general results found in the previous studies apply only to a specific type of life history. Many angiosperms are capable of clonal reproduction through vegetative propagation, for example, and the cost of generating a single clonal propagule requires more resources than the production of a single seed (Cook 1985; Jurik 1985). Additionally, juvenile survivorship of clonal propagules due to ecological factors is often several times higher than that of seedlings, likely on account of the greater maternal investment and, in some instances, persistent connections to the parent plant (Cook 1985). Modeling clonal and sexual offspring as equivalent, as was done in these recent studies, effectively assumes that the greater juvenile survivorship of clonal propagules exactly compensates for their higher cost of production. However, the degree to which seedlings contribute to maintaining clonal plant populations varies across species: some established populations experience recurrent seedling recruitment and others persist almost entirely via vegetative propagation (Cook 1985; Eriksson 1989). It is therefore highly unlikely that the differences between clonal and sexual offspring with respect to their relative costs and contributions to population dynamics would be exactly balanced in all cases. Offspring production and juvenile survivorship should instead be evaluated as separate processes to more accurately represent the differences between clonal and sexual offspring, and to facilitate an exploration of how the typical role of seedlings in population maintenance affects the probability of evolutionary rescue in different clonal plant populations.

This study explores how differences in the resource demands and juvenile survivorship of clonal and sexual offspring influence the relationship between clonal reproduction and evolutionary rescue. As in previous studies, populations with different levels of clonal allocation are subjected to simulations of abrupt and directional environmental change scenarios. Through these simulations, this study considers (1) how incorporating known differences between offspring of clonal and sexual reproduction alters the effect of greater clonal allocation on the probability of evolutionary rescue, and (2) how the variable role of seedlings in the maintenance of clonal plant population affects the probability of evolutionary rescue, independent of the allocation towards clonal reproduction. Specifically, the model assumes that clonal offspring are more costly to produce than sexual offspring and varies the relative rate of juvenile survivorship for sexual offspring. Extending the previous models of facultatively sexual populations in this way provides a more complete understanding of how the two modes of reproduction, and particularly the differences between them, affect how clonal plant populations may respond to environmental change.

Methods

Model Description:

The model used in this research is an extension of that used by Peniston *et al.* (2021), which is in turn an extension of the individual-based model used by Orive *et al.* (2017) that was adapted from Bürger and Lynch (1995)'s approach to studying evolutionary rescue.

These models simulate a population experiencing an environmental change to which it must adapt or else face extinction. The population is composed of hermaphroditic, self-compatible individuals that possess a single phenotypic trait *z*, which is determined by 10 diploid loci and an environmental component. Simulation of an environmental change is accomplished by altering the optimal trait value: abrupt environmental changes are an instantaneous change in the optimal phenotype from the initial value to the final value, and gradual environmental changes are an annual increase in the optimal phenotype by a pre-specified increment value. The population is subjected to selection based on trait *z* such that the success of evolutionary rescue is dictated by whether the population can adapt as the optimal phenotype changes.

Simulation Overview

Simulations begin with model initialization, in which all model parameters are defined based on user input. A list of these parameters and their values can be found in Table 1.

Many of these parameters and their values are grounded in those used in the previously published versions of this model (Orive *et al.* 2017; Peniston *et al.* 2021). However, these previous iterations assumed that the cost of generating a clonal offspring is equivalent to the cost of generating a sexual offspring ($d = 1.0$) and did not model offspring establishment as separate from offspring production. Some have argued that the production of clonal offspring requires more resources (Jurik 1985; Orive et al. 2017), and it has been shown that clonal offspring exhibit substantially higher establishment rates compared to sexual offspring (Cook 1985). Thus, several modifications were made to the model, including increasing the relative cost of clonal offspring and adding two parameters to facilitate the explicit simulation of offspring establishment: the establishment rate of clonal offspring (`ec`) and the ratio of clonal to sexual establishment rates (`ratio`). The birth rate was also increased to ensure that the average number of total offspring per reproductive event remains similar to the value used in previous studies, despite these modifications.

The initialization process defines the sequence of values describing environmental conditions over the course of the entire simulation based on the provided value for `theta` or `delta` (according to the type of environmental change being simulated), `rho`, and `var`. The optimal trait phenotype is initially set to 0 and changes according to this sequence during the simulation. An initial population is also created, consisting of `K*B` individuals with trait values normally distributed around the initial optimum.

Model initialization is followed by a 1000 year burn-in period, during which time the population is subject to selection but the environment is held constant. Individuals reproduce exclusively through sexual reproduction during this phase of the simulation. This burn-in yields variable population sizes but ensures that the genetic diversity of the populations is unaffected by the clonal allocation value until the environment changes. Populations from different simulations are therefore reasonably comparable at the time of the environmental change, and the investigation can concentrate on the impact of clonal allocation during the rescue process (the impact of standing genetic diversity on evolutionary rescue outcomes has already been thoroughly investigated; Lande & Shannon 1996; Barrett & Schluter 2008; Bell 2013).

The period of environmental change begins immediately after the burn-in period. Individuals reproduce through both clonal and sexual reproduction, and the environmental change also includes fluctuations. Each year of the simulation sees the existing population subjected to selection followed by a round of reproduction; both of these processes are described in greater detail below. This phase of the simulation lasts for 1000 years, at which point the environment is once again held static.

Simulations continue for another 200-year period during which time selection and both modes of reproduction occur in the new (constant) environment. At the end of this phase, one full run of the simulation is complete.

Selection

In this model, selection is on juvenile survival to reproduction according to an individual's phenotypic value of trait *z* relative to the optimal trait value. An individual's probability of survival follows a Gaussian function, $\exp[-(z - \theta_t)^2 / (2w^2)]$, in which θ_t is the optimal trait value at time step *t*, *z* is the individual's trait value, and w^2 is inversely related to the strength of stabilizing selection (defined at model initialization; Peniston *et al.* 2021).

Reproduction

Reproduction is limited by the number of mating sites in the population, K, defined during model initialization. Specifically, a maximum of K individuals in the population will reproduce as female at each time step; these individuals are selected at random when the population exceeds K. For sexual reproduction, the male parent in each mating event is chosen at random from the entire population, including those individuals that will not mate as female that time step and the individual functioning as the female parent in the mating (the modeled organisms are self-compatible).

Each mating yields a predetermined number of offspring from clonal and sexual reproduction that are determined by the equations [B (rc /d)] and [B (1 − rc)], respectively. Each value is rounded to the nearest whole number. Although there are pre-defined expectations for the number of clonal and sexual offspring per mating, the establishment rates for clonal and sexual offspring determine the probability with which those offspring are successfully added to the population.

The establishment rate of clonal offspring (ec) is 0.75, which falls within the range of observed ramet recruitments rates of herbaceous perennials such as *Viola blanda* (sweet white violet, 0.82) and *Ranunculus repens* (creeping buttercup, 0.71; Cook 1985). All clonal offspring receive the maternal parent's genotype, with the possibility of a somatic mutation on each haplotype; the somatic mutation rate is specified by us in model initialization. The environmental component of the offspring's phenotype is sampled from a normal distribution (mean = 0, sd = 1), but may be influenced by the environmental component of the maternal parent's phenotype according to the parameter p.

Sexual offspring are added to the simulated population at a rate that is relative to the clonal establishment rate (ec) according to the equation [ec/ratio], in which ratio is the ratio of the clonal establishment rate to the sexual establishment rate. The sexual establishment rate therefore declines as ratio increases, following the curve of a reciprocal function. Sexual offspring receive one haplotype from each parent: the alleles are selected independently, and both haplotypes are subject to potential meiotic mutations at rate ug (set during model initialization). The environmental component of the offspring's phenotype is sampled from a normal distribution (mean = 0, sd = 1), with no influence from either parent.

Following reproduction, adults in the population survive to the next time step with some probability specified by the parameter surv.

Final Assay

At the end of the 1000-year environmental change period, the model enters a 200-year survey period during which the environment is static. Simulation output includes the population size at the start and end of this final phase, along with the average population-level lag in the trait value compared to the optimum during this phase (directional environmental change only).

Simulation Experiments:

The impact of differences in juvenile survivorship of clonal and sexual offspring due to ecological factors (and thus the relative contribution of seedlings) on the probability of successful evolutionary rescue in clonal plant populations was evaluated through a series of simulation experiments that varied the ratio between clonal and sexual establishment rates (ratio). Low values of ratio correspond to high sexual establishment rates, and the sexual establishment rate declines as ratio increases to become more representative of a species that persists largely through clonal propagation. The experiments conducted for this study evaluated 11 different ratios, from 1.0 to 6.0 in increments of 0.5, which span values previously

observed in natural populations of clonal plants (Cook 1985). No experiments in which `ratio` > 5.0 had a single simulation in which the population survived, therefore only 9 of the 11 values evaluated will be discussed.

A variety of environmental change scenarios were evaluated in the study; these scenarios are defined by the type and size/pace of the change, as well as the variance of environmental fluctuations. Environmental changes could be abrupt, as in a sudden disturbance, or directional as in a shifting climate. Simulations of an abrupt environmental change included small (`theta` = 2.0), moderate (`theta` = 2.5), and large (`theta` = 3.0) changes in the optimal phenotype, and simulations of directional change included slow (`delta` = 0.025), moderate (`delta` = 0.05), and fast (`delta` = 0.075) rates of change. Simulations with an even larger abrupt change (`theta` = 4.0) were also run, but so few yielded instances of successful evolutionary rescue that the results are not presented. All environmental change scenarios included autocorrelated fluctuations in the optimal trait value, described as "red noise" by Peniston *et al.* (2021). The variances of these fluctuations were one of six values (0.25 to 1.5, in increments of 0.25) based on those evaluated by Peniston *et al.* (2021). In total, the experiments in this study included 42 unique environmental change scenarios.

Investigations that used previous versions of this model explored how clonal allocation affects the probability of successful evolutionary rescue (Orive *et al.* 2017; Peniston *et al.* 2021). Three clonal allocation values were therefore incorporated into the study: 25% clonal, 50% clonal, and 75% clonal.

Simulation experiments in this study were used to investigate how increasing the establishment rate ratio affects the relationship between clonal allocation and the probability of evolutionary rescue. For every unique combination of environmental change scenario and clonal allocation value, the eleven `ratio` values were evaluated in 500 replicate simulations each; one experiment is defined as this set of 5500 simulations.

Analysis:

A simulation results in successful evolutionary rescue when the population size at the end of the final assay period exceeds 100 individuals, which is consistent with the standard used in previous studies (Peniston *et al*. 2021). As a population size of 100 is approximately 39% of the maximum number of mating sites used in all simulations (`K` = 256), this represents a reasonable minimum population size at which a population may be considered at low risk of extinction. The probability of evolutionary rescue was calculated as the proportion of the 500 replicate simulations that resulted in evolutionary rescue. All research questions were evaluated by plotting the probability of evolutionary rescue with respect to the establishment rate ratio.

Results

Abrupt Environmental Change

These simulation experiments confirm the results of previous studies and show that the probability of evolutionary rescue following an abrupt environmental change declines as the magnitude of the change increases (Fig 1A). Similarly, increasing the magnitude of environmental fluctuations also reduces the probability of evolutionary rescue (Fig 1B). These results hold true for all clonal allocation values included in this study, as well as across all establishment rate ratios.

The ratio between the clonal and sexual establishment rates alters the relationship between clonal allocation and the probability of evolutionary rescue following an abrupt environmental change. Simulations from this investigation reveal that increasing clonal allocation confers a higher probability of evolutionary rescue only when the establishment rate ratio is high (Fig. 2). The difference in the probability of rescue with increasing clonal allocation values can be subtle for a given `ratio`. Indeed, the advantage of greater allocation towards clonal reproduction becomes much less pronounced under more extreme environmental changes and larger environmental fluctuations (Fig 2).

Figures 1 and 2 also show that a higher ratio between the clonal and sexual establishment rates lowers the probability of evolutionary rescue. The slope of this decline varies with the environmental change scenario and clonal allocation value, but the overall trend is consistent.

Populations that survived the period of environmental change typically exceeded the minimum population size that defined instances of successful evolutionary rescue at the end of the 200-year assay period. Indeed, there was little variation in the final population size: simulations in which evolutionary rescue was successful yielded similar population sizes, and there were no simulations in which the population persisted through the assay period but failed to meet the minimum size threshold. Some simulations yielded populations that survived the environmental change only to go extinct during the final 200 years of the simulation. However, this outcome was so infrequent that further analysis was not possible due to low sample size.

Directional Environmental Change

As with an abrupt environmental change, increasing the magnitude of environmental fluctuations under a directional environmental change reduces the probability of evolutionary rescue (Fig 3B). A faster pace of environmental change similarly reduces the probability of evolutionary rescue (Fig 3A).

Simulations of directional environmental change show that a higher allocation to clonal reproduction reduces the probability of evolutionary rescue when the environment changes gradually (Fig 4). This relationship holds true regardless of the ratio between clonal and sexual establishment rates and under all environmental change scenarios investigated during the study. Furthermore, increasing the ratio between clonal and sexual establishment rates always reduces the probability of rescue, though the shape of this relationship varies (Fig 3, 4).

An examination of population sizes at the end of the environmental change period and at the end of the 200-year assay period yielded similar observations to what was seen in simulations of an abrupt environmental change. In instances of successful evolutionary rescue, there was little variation in the final population size, with all populations far exceeding the minimum size threshold. Greater variability was seen in the population size immediately following the period of environmental change, particularly for environmental change scenarios with greater environmental variance. As above, only a few simulations yielded populations that survived the environmental change only to go extinct during the final 200 years of the simulation.

Discussion

This study investigated how the differences between clonal and sexual offspring in clonal plant populations impact the relationship between clonal allocation and the probability of evolutionary rescue under a variety of environmental change scenarios. Specifically, clonal offspring were considered more costly to produce, and the relative contribution of seedlings to the population was manipulated by altering the ratio between the clonal and sexual establishment rates. Increasing this establishment rate ratio was shown to reduce the probability of evolutionary rescue, regardless of clonal allocation or environmental change scenario. The impact of greater clonal allocation on the probability of evolutionary rescue, however, depended on both the type of environmental change experienced and the establishment rate ratio. Following an abrupt environmental change, greater allocation towards clonal reproduction increased the probability of evolutionary rescue only when the establishment rate ratio was relatively high. At lower establishment rate ratios, the probability of evolutionary rescue tended to be similar across the different levels of clonal allocation, with low clonal allocation yielding a slightly higher probability of rescue in some cases. After a directional environmental change, greater allocation towards clonal reproduction reduced the probability of evolutionary rescue for all establishment rate ratios.

Previous studies have explored the relationship between clonal allocation and the probability of evolutionary rescue following an environmental change using simulation experiments (Orive *et al.* 2017; Peniston *et al.* 2021). These studies were among the first to consider the impact of clonal versus sexual reproduction in the context of evolutionary rescue (Yamamichi 2022). However, these models assume that the offspring of clonal and sexual reproduction may be considered equal with respect to the costs of

production and juvenile survivorship due to ecological factors. As noted by both Orive *et al.* (2017) and Peniston *et al.* (2021), however, the cost of producing a single clonal offspring is rarely equivalent to the cost of producing a single sexual offspring. Indeed, one clonal propagule is thought to require more resources than a single seed (explored briefly in Orive *et al.* 2017) but have high juvenile survivorship (Cook 1985; Jurik 1985). Combining these differences between clonal and sexual offspring into a single, fixed cost parameter assumes that the two balance in the same way for all species and fails to account for the diversity among clonal plants with respect to the role of seedlings in population dynamics (Eriksson 1993).

To address these limitations, this study explicitly modeled both the production and establishment of clonal and sexual offspring, and explored whether altering the ratio between the clonal and sexual establishment rates affects the findings of previous studies. The results from this investigation indicate that the establishment rate ratio does not alter the relationship between clonal allocation and the probability of evolutionary rescue following a directional environmental change: greater allocation towards clonal reproduction always reduced the probability of rescue. This is in agreement with the conclusions of Orive *et al.* (2017) and Peniston *et al*. (2021). However, the previous studies' conclusions that greater clonal allocation enhances the probability of rescue following an abrupt change is only partially supported by the results presented here: this relationship only held true when the establishment rate ratio was high. In other words, a greater allocation to clonal reproduction was advantageous after an abrupt environmental change only when the sexual establishment rate (or juvenile survivorship due to ecological factors) of the population was relatively low.

Clonal plant populations exhibit a wide range of sexual establishment rates, though seedling establishment is typically regarded as a rare occurrence (Cook 1985; Eriksson 1989). One survey of demographic studies and published observations of seedlings in clonal plant populations found evidence of repeated seedling recruitment into adult populations for only 40% of species considered (Eriksson 1989). These species, which include white clover (*Trifolium repens*) exhibit a strategy termed "repeated seedling recruitment" (RSR) and represent one end of a spectrum (Eriksson 1993). At the other end of this spectrum are species with the "initial seedling recruitment" (ISR) strategy, in which populations experience no seedling recruitment beyond their initial founding and are instead maintained entirely through clonal reproduction; Canada goldenrod (*Solidago canadensis*) is one such species (Eriksson 1993). By varying the establishment rate ratio, this study was able to explore how the relationship between clonal allocation and the probability of evolutionary rescue is affected by the species' position on the RSR/ISR spectrum.

The shift from an RSR to ISR strategy was accomplished by increasing the ratio between the clonal and sexual establishment rates across simulations. A low establishment rate ratio corresponds to a high seedling establishment rate (RSR), and the sexual establishment rate declines as the ratio increases (ISR). All simulation experiments show that this shift reduced the probability of evolutionary rescue. This was somewhat expected: as a consequence of the model's construction, movement from RSR to ISR strategies is accompanied by a reduction in the average total number of offspring per reproductive event within a given level of clonal allocation, as well as an increase in the average proportion of offspring that are clonal (Tables S1-S3). Larger population size is known to confer a greater probability of rescue (Gomulkiewicz & Holt 1995; Bell 2013; see also review by Carlson *et al.* 2014). Nonetheless, this result indicates that species exhibiting an RSR strategy are more likely to experience rescue than those exhibiting an ISR strategy, regardless of the environmental change scenario or relative allocation towards clonal reproduction.

For any given position on the RSR/ISR spectrum, the probability of evolutionary rescue was affected by the clonal allocation value. Simulations showed that increasing the allocation towards clonal reproduction reduced the probability of rescue for species of any strategy after a directional environmental change, and, in some cases, for RSR species following an abrupt environmental change. Although greater allocation to clonal reproduction increases the average total number of offspring per reproductive event, it also increases the average proportion of those offspring that were clonal (Tables S1-S3). Clonal reproduction, rather than contributing to variation within the population, instead propagates "old" genotypes that were successful under prior environmental conditions. In a changing environment, however, the population's ability to adapt to new conditions depends upon this variation (Lande & Shannon 1996;

see also review by Carlson *et al*. 2014). Thus, increasing clonality reduces the probability of evolutionary rescue following a directional environmental change.

In contrast, greater allocation towards clonal reproduction enhanced the probability of evolutionary rescue for ISR species in simulations of an abrupt environmental change. Because the environment changes in a single step, "old" genotypes that survive and successfully reproduce are also likely to be successful in the next time step. Clonal reproduction may therefore contribute to the maintenance of population size by preventing segregational or recombination load (Orive *et al*. 2017). As the establishment rate ratio increases, representing a shift from an RSR to ISR strategy, the average total number of offspring declines and the proportion of those offspring that are clonal increases (Tables S1-S3). This may be why the advantages of higher clonal allocation following an abrupt environmental change reported in previous studies are only apparent for ISR species in this investigation: the higher proportion of clonal offspring could become more important when fewer offspring are produced. The impact of increasing clonality on a population's potential to persist through environmental change thus depends not only on the type of environmental change, but also on the relative contribution of seedlings to the population.

Given the general rarity of observed seedling establishment, it is worth noting that clonal plant populations may all possess an ISR strategy, as it is defined in this study. In simulations where the establishment rate ratio is 5.0, for example, the sexual establishment rate is 0.15. This the highest ratio evaluated that yielded instances of successful evolutionary rescue, and yet the sexual establishment rate may be high relative to what has been seen in natural populations (the sexual establishment rate of *Ranunculus repens*, for example, was recorded as 0.12; Sarukhan & Harper 1973). It was not possible to evaluate lower sexual establishment rates in this study, however, as no simulations with an establishment rate ratio greater than 5.0 produced instances of successful evolutionary rescue. Nonetheless, clonal plant populations with substantially higher establishment rate ratios have been observed. Indeed, *Ranunculus repens* (creeping buttercup) exhibited a ratio of 5.9 (Sarukhan & Harper 1973, cited in Cook 1985), *Narcissus pseudonarcissus* (wild daffodil) had an observed ratio of 9.0 (Barkham 1980, cited in Cook 1985), and a ratio of 34 was seen in *Pilosella floribunda* (synonym *Hieracium floribundum*, pale hawkweed; Thomas & Dale 1975, as cited in Cook 1985), though the recorded clonal and sexual establishment rates of the latter two species were orders of magnitude lower than the values used in this study (Cook 1985). Future simulations with different absolute establishment rates may be required to evaluate ISR species with extreme establishment rate ratios.

The model used in this study also demonstrated how differences in the environmental change scenario affect the probability of evolutionary rescue. Regardless of whether the population experienced an abrupt or directional environmental change, a more drastic change in environmental conditions (simulated as a larger step-wise change or a faster pace of environmental change) reduced the probability of evolutionary rescue, as did greater variance in environmental fluctuations. Both observations are well-documented in the evolutionary rescue literature from theoretical and experimental studies (Gomulkiewicz & Holt 1995; Bell 2013; Carlson *et al*. 2014). That these observations emerged from the model used in this study demonstrates that it simulates reasonable population responses to a variety of environmental change scenarios and provides some validation of the model's quality.

As with all models, it is important to consider the impact of underlying model assumptions and how future investigations might address these assumptions. This study specifically addressed previous models' assumption that clonal and sexual offspring are equivalent with respect to their costs of production and juvenile survivorship due to ecological factors by modifying the relevant parameters. Reproduction during the burn-in period was entirely sexual in order to ensure the genetic diversity of populations from different simulations was comparable at the time of the environmental change. Individuals in this model are also assumed to be hermaphroditic and self-compatible, but this applies only to some species of clonal plants (other species may be dioecious or otherwise self-incompatible). An evaluation of selfing rates during simulations could reveal the degree to which the latter assumption influences model outcomes. Further modifications to the model could also facilitate an investigation of clonal allocation and evolutionary rescue in dioecious species. Finally, clonal allocation was treated as a fixed parameter in this study. Future

investigations could introduce variation in clonal allocation within the simulated population and explore how clonal allocation may evolve in response to environmental change.

Another facet of the model that remains relatively unexplored is the lag between the mean population trait value and the optimal trait value, both during the environmental change and in the final assay period. Model output includes the average lag over the course of the final assay period for simulations of a directional environmental change, but this singular value provides only limited insights. The average lag values observed in this study tended to be quite small, and increasing the allocation towards clonal reproduction significantly altered the distribution of the average population lag under most combinations of establishment rate ratio and environmental change scenario evaluated (Tables S4-S6); when there was a significant difference, higher clonal allocation resulted in greater average population lag. However, as this summary metric does not capture how the population lag changes through time, there is little that can be said about how increasing clonal allocation affects the evolutionary trajectory of a population during evolutionary rescue. Future work should expand the model output to include more detailed monitoring of population lag through time.

Conclusion

As environments change, the ability of a population to persist is dependent upon how well it can adjust to the new conditions, either through phenotypic plasticity or genetically via evolutionary rescue. Theoretical, experimental, and observational studies have identified a number of factors that contribute to the probability of successful evolutionary rescue, including the amount of standing genetic variation in the population and the magnitude and pattern of environmental change (reviewed in Carlson *et al.* 2014 and Bell 2017). However, these studies have almost exclusively considered organisms that employ obligately sexual or asexual reproduction. Facultative sex is employed by a number of species, such as clonal plants, and affects the spread of adaptive traits in the population. To date, there have been a few studies that have explored how the amount of clonal reproduction in these populations affects the probability of evolutionary rescue (Orive *et al.* 2017; Peniston *et al.* 2021). It is also important to consider the differences between offspring produced via clonal versus sexual reproduction and the diversity among clonal plant species to develop an understanding of evolutionary rescue in natural populations. This study assumed that clonal offspring are more costly to produce than sexual offspring and found that the effect of increasing clonal allocation on the probability of evolutionary rescue depends upon both the type of environmental change and the relative establishment rate of sexual offspring. When predicting how facultative sex affects the likelihood of evolutionary rescue after an environmental change, one must take into account not only the species' relative investment in clonal reproduction, but also the typical role of seedlings in the maintenance of an established population.

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Figures:

Table 1: Descriptions of all model parameters and their values.

| Parameter	Description	Value(s)	References
K	Number of mating sites in the population	256	Peniston et al. (2021)
B	Birth rate; maximum number of sexual offspring generated per reproductive event	10	
rc	Relative investment in clonal reproduction	[0.25, 0.5, 0.75]	
d	Relative cost of a clonal offspring compared to a sexual offspring	1.5	Orive et al. (2017)
ec	Establishment rate of clonal offspring	0.75	Cook (1985)
p	Strength of association between the environmental component of parent and clonal offspring phenotypes	0	Peniston et al. (2021)
w	Inversely related to strength of selection	1.0	Peniston et al. (2021)
ug	Meiotic mutation rate	0.01	Peniston et al. (2021)
us	Somatic mutation rate	0.0001	Peniston et al. (2021)
rho	Autocorrelation in fluctuations of the optimal phenotype	0.9	Peniston et al. (2021); "red noise"
var	Variance in fluctuations of the optimal phenotype	[0.25. 0.5, 0.75, 1.0, 1.25, 1.5]	Peniston et al. (2021)
surv	Probability of adult survival across successive years	0	Peniston et al. (2021)
theta/ delta	Magnitude/Pace of environmental change (abrupt/directional)	[2.0, 2.5, 3.0, 4.0] [0.025, 0.05, 0.075]	Peniston et al. (2021)
min	Lowest ratio of clonal to sexual establishment rates (ratio) evaluated	1.0	Cook (1985)
max	Highest ratio of clonal to sexual establishment rates (ratio) evaluated	6.0	
step	Step size of ratio values	0.5	
reps	Number of replicate simulations per parameter set	500	
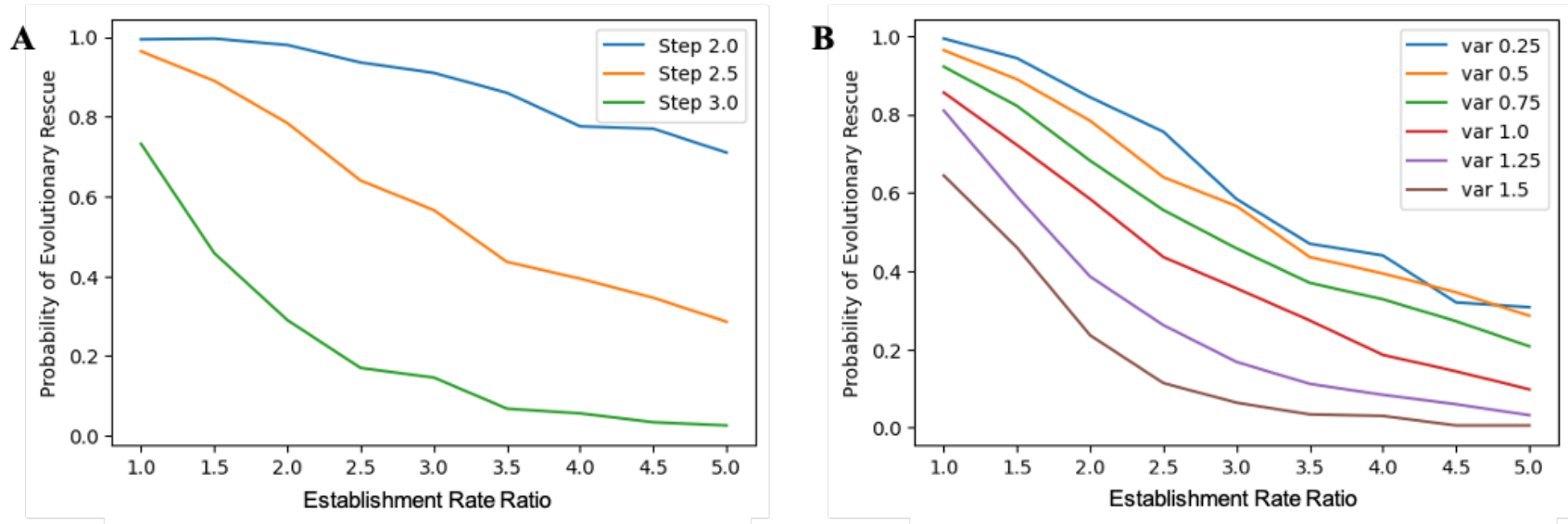
Figure 1: Larger step environmental changes (A) and greater variance in environmental fluctuations (B) both reduce the probability of evolutionary rescue. Both graphs depict the results of simulations with 50% clonal allocation. In panel A variance is held constant at 0.5, and in panel B the step size is fixed at 2.5.

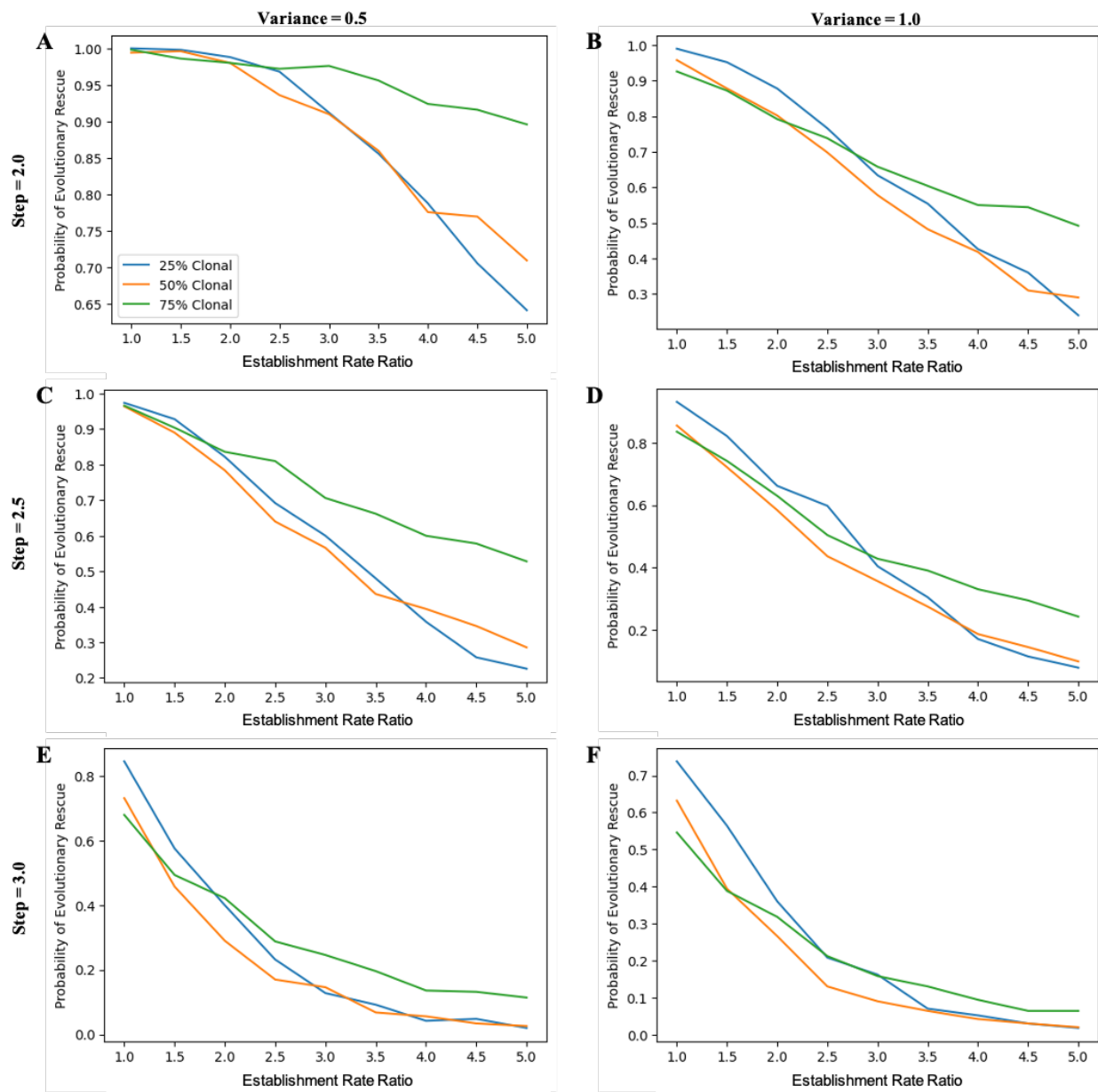**Figure 2:** Increasing allocation to clonal reproduction increases the probability of evolutionary rescue only when `ratio` is high. This pattern holds across different step sizes of environmental change and magnitudes of environmental variance.

Figure 3: Faster pace of environmental change (A) and greater variance in environmental fluctuations (B) both reduce the probability of evolutionary rescue. Both graphs depict the results of simulations with 50% clonal allocation. In panel A variance is held constant at 0.5, and in panel B the pace of environmental change is fixed at 0.05.

Figure 4: Increasing allocation to clonal reproduction reduces the probability of evolutionary rescue for all values of `ratio`. This pattern hold across different paces of environmental change and magnitudes of environmental variance.
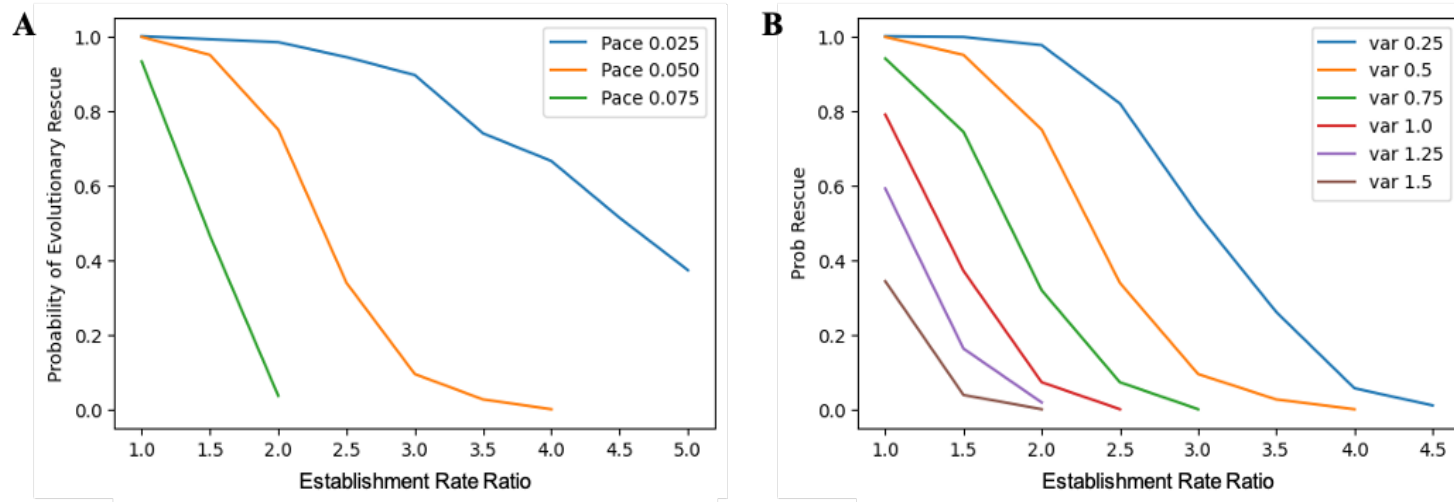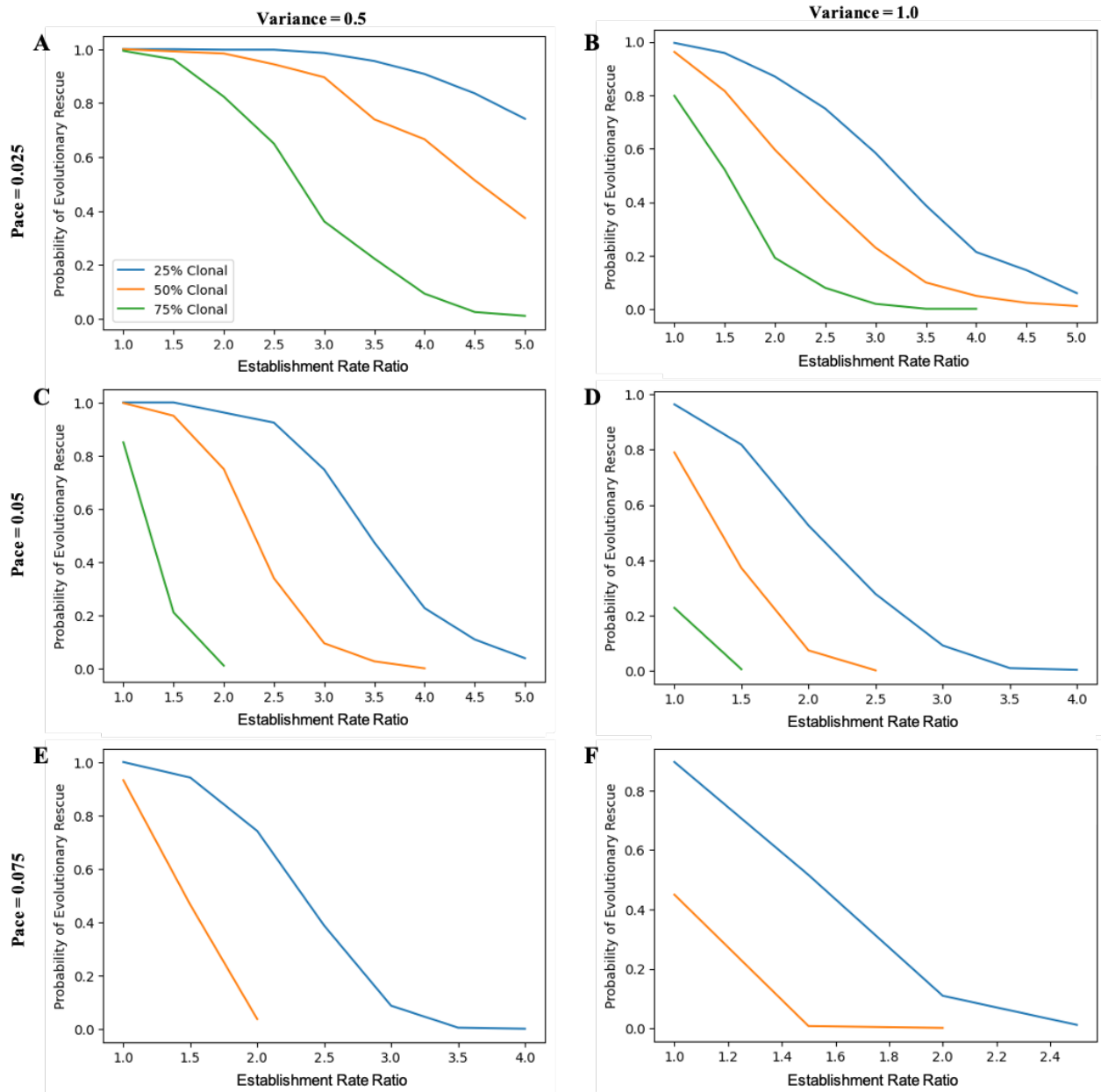
Supplemental Figures

Table S1: The average number of offspring added to the population per reproductive event and the average proportion of those offspring that are the product of clonal reproduction when clonal allocation is 25%.

Ratio	Clonal Establishment Rate	Sexual Establishment Rate	Average Clonal Offspring	Average Sexual Offspring	Average Total Offspring	Average Proportion Clonal
1.0	0.75	0.75	1.25	5.625	6.875	0.181818
1.5	0.75	0.5	1.25	3.75	5.0	0.25
2.0	0.75	0.375	1.25	2.8125	4.0625	0.307692
2.5	0.75	0.3	1.25	2.25	3.5	0.357143
3.0	0.75	0.25	1.25	1.875	3.125	0.4
3.5	0.75	0.214286	1.25	1.607143	2.857143	0.4375
4.0	0.75	0.1875	1.25	1.40625	2.65625	0.470588
4.5	0.75	0.16667	1.25	1.25	2.5	0.5
5.0	0.75	0.15	1.25	1.125	2.375	0.526316
5.5	0.75	0.136364	1.25	1.022727	2.272727	0.55
6.0	0.75	0.125	1.25	0.9375	2.1875	0.571429

Table S2: The average number of offspring added to the population per reproductive event and the average proportion of those offspring that are the product of clonal reproduction when clonal allocation is 50%

Ratio	Clonal Establishment Rate	Sexual Establishment Rate	Average Clonal Offspring	Average Sexual Offspring	Average Total Offspring	Average Proportion Clonal
1.0	0.75	0.75	2.5	3.75	6.25	0.4
1.5	0.75	0.5	2.5	2.5	5.0	0.5
2.0	0.75	0.375	2.5	1.875	4.375	0.571429
2.5	0.75	0.3	2.5	1.5	4.0	0.625
3.0	0.75	0.25	2.5	1.25	3.75	0.6667
3.5	0.75	0.214286	2.5	1.07	3.571429	0.7
4.0	0.75	0.1875	2.5	0.9375	3.4375	0.727273
4.5	0.75	0.16667	2.5	0.8333	3.3333	0.75
5.0	0.75	0.15	2.5	0.75	3.25	0.769231
5.5	0.75	0.136364	2.5	0.681818	3.181818	0.785714
6.0	0.75	0.125	2.5	0.625	3.125	0.8

Table S3: The average number of offspring added to the population per reproductive event and the average proportion of those offspring that are the product of clonal reproduction when clonal allocation is 75%

Ratio	Clonal Establishment Rate	Sexual Establishment Rate	Average Clonal Offspring	Average Sexual Offspring	Average Total Offspring	Average Proportion Clonal
1.0	0.75	0.75	3.75	1.875	5.625	0.6667
1.5	0.75	0.5	3.75	1.25	5.0	0.75
2.0	0.75	0.375	3.75	0.9375	4.6875	0.8
2.5	0.75	0.3	3.75	0.75	4.5	0.8333
3.0	0.75	0.25	3.75	0.625	4.375	0.857143
3.5	0.75	0.214286	3.75	0.535714	4.285714	0.875
4.0	0.75	0.1875	3.75	0.46875	4.21875	0.88889
4.5	0.75	0.16667	3.75	0.416667	4.166667	0.0
5.0	0.75	0.15	3.75	0.375	4.125	0.909091
5.5	0.75	0.136364	3.75	0.340909	4.090909	0.916667
6.0	0.75	0.125	3.75	0.3125	4.0625	0.923077

Table S4: Testing for differences in average population lag during the 200-year assay period across clonal allocation values when the pace of directional change is 0.025/year.

Variance	Ratio	Test	p-value	Notes
0.05	1.0	Kruskal-Wallis	1.34e-7	
	1.5	Kruskal-Wallis	2.65e-17	
	2.0	Kruskal-Wallis	3.70e-26	
	2.5	Kruskal-Wallis	2.58e-31	
	3.0	Kruskal-Wallis	1.25e-40	
	3.5	Kruskal-Wallis	1.065e-29	
	4.0	Kruskal-Wallis	1.802e-17	*n*=47 for 75% clonal allocation
	4.5	Kruskal-Wallis	3.64e-16	*n*=13 for 75% clonal allocation
		Mann-Whitney U	2.936e-13	25% and 50% clonal allocation
	5.0	Kruskal-Wallis	3.18e-8	*n*=6 for 75% clonal allocation
		Mann-Whitney U	4.06e-7	25% and 50% clonal allocation
1.0	1.0	Kruskal-Wallis	1.84e-5	
	1.5	Kruskal-Wallis	9.28e-7	
	2.0	Kruskal-Wallis	2.72e-7	
	2.5	Kruskal-Wallis	6.22e-5	*n*=40 for 75% clonal allocation
	3.0	Kruskal-Wallis	0.00276	*n*=10 for 75% clonal allocation
		Mann-Whitney U	0.02402	25% and 50% clonal allocation
	3.5	Mann-Whitney U	0.1325	*n*=1 for 75% clonal allocation; 25% and 50% clonal allocation
	4.0	Mann-Whitney U	0.2014	*n*=25 for 50% clonal allocation
	4.5	Mann-Whitney U	0.4836	*n*=12 for 50% clonal allocation
	5.0	Mann-Whitney U	0.3487	*n*=6 for 50% clonal allocation; *n*=30 for 25% clonal allocation

Table S5: Testing for differences in average population lag during the 200-year assay period across clonal allocation values when the pace of directional change is 0.05/year.

Variance	Ratio	Test	p-value	Notes
0.05	1.0	Kruskal-Wallis	4.66e-15	
	1.5	Kruskal-Wallis	2.55e-19	
	2.0	Kruskal-Wallis	6.87e-11	$n=6$ for 75% clonal allocation
		Mann-Whitney U	3.28e-8	25% and 50% clonal allocation
	2.5	Mann-Whitney U	2.16e-5	
	3.0	Mann-Whitney U	0.000697	
	3.5	Mann-Whitney U	0.1037	$n=14$ for 50% clonal allocation
	4.0			$n=1$ for 50% clonal allocation
1.0	1.0	Kruskal-Wallis	1.50e-10	
	1.5	Kruskal-Wallis	0.0109	$n=3$ for 75% clonal allocation
		Mann-Whitney U	0.00275	25% and 50% clonal allocation
	2.0	Kruskal-Wallis	0.00644	$n=37$ for 50% clonal allocation
	2.5			$n=1$ for 50% clonal allocation

Table S6: Testing for differences in average population lag during the 200-year assay period across clonal allocation values when the pace of directional change is 0.075/year.

Variance	Ratio	Test	p-value	Notes
0.05	1.0	Kruskal-Wallis	1.27e-12	
	1.5	Mann-Whitney U	6.57e-8	
	2.0	Mann-Whitney U	0.55345	n=19 for 50% clonal allocation
	2.5			n=0 for 50%, 75% clonal allocation
1.0	1.0	Mann-Whitney U	0.000375	n=1 for 75% clonal allocation
	1.5			n=4 for 50% clonal allocation