RESEARCH PAPER

Environmental fluctuations dampen the effects of clonal reproduction on evolutionary rescue

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Abstract

Evolutionary rescue occurs when genetic change allows a population to persist in response to an environmental change that would otherwise have led to extinction. Most studies of evolutionary rescue assume that species have either fully clonal or fully sexual reproduction; however, many species have partially clonal reproductive strategies in which they reproduce both clonally and sexually. Furthermore, the few evolutionary rescue studies that have evaluated partially clonal reproduction did not consider fluctuations in the environment, which are nearly ubiquitous in nature. Here, we use individual-based simulations to investigate how environmental fluctuations (either uncorrelated or positively autocorrelated) influence the effect of clonality on evolutionary rescue. We show that, for moderate magnitudes of environmental fluctuations, as was found in the absence of fluctuations, increasing the degree of clonality increases the probability of population persistence in response to an abrupt environmental change, but decreases persistence in response to a continuous, directional environmental change. However, with large magnitudes of fluctuations, both the benefits of clonality following a step change and the detrimental effects of clonality following a continuous, directional change are generally reduced; in fact, in the latter scenario, increasing clonality can even become beneficial if environmental fluctuations are autocorrelated. We also show that increased generational overlap dampens the effects of environmental fluctuations. Overall, we demonstrate that understanding the evolutionary rescue of partially clonal organisms requires not only knowledge of the species life history and the type of environmental change, but also an understanding of the magnitude and autocorrelation of environmental fluctuations.

KEYWORDS
environmental change, environmental stochasticity, evolutionary lag, fluctuating selection, partial clonality

1 | INTRODUCTION

Human activities, such as pollution, deforestation and the burning of fossil fuels, are exposing many natural populations to rapid rates of environment change (Lewis & Maslin, 2015). These changes will often make populations locally maladapted. If the change is severe enough that a population's death rate becomes greater than its birth rate at all densities, the population will be destined for local extinction unless it evolves sufficiently to make its growth rate positive (assuming there is no immigration from outside sources).

Understanding which factors determine whether a population will adapt or go locally extinct in response to environmental change is crucial for developing evolutionarily informed conservation policies (Eizaguirre & Baltazar-Soares, 2014; Ferrière et al., 2004; Jørgensen et al., 2019; Sgrò et al., 2011; Smith et al., 2014).

The term "evolutionary rescue" is used to describe the situation in which genetic adaptation allows a population to persist in response to an environmental change that would otherwise have led to extirpation (Bell, 2017; Gomulkiewicz & Holt, 1995; Gonzalez et al., 2013). Evolutionary rescue is less likely to occur with greater magnitudes or rates of environmental change (Bell & Gonzalez, 2009, 2011; Holt & Gomulkiewicz, 2004; Lindsey et al., 2013). Likewise, rescue is less likely if the traits that must evolve in order for the population to persist have low standing genetic variation (Agashe et al., 2011; Lachapelle & Bell, 2012; Ramsayer et al., 2013) or low heritability (Barfield & Holt, 2016). Another determinant of evolutionary rescue is the degree of environmental variation. Increased magnitudes of environmental fluctuations (usually modelled as fluctuations in the optimum phenotype of a trait determining fitness) typically decrease the probability of evolutionary rescue (Bürger & Lynch, 1995; Chevin et al., 2017); however, positively autocorrelated fluctuations can facilitate evolutionary rescue in high-extinction-risk scenarios (Peniston et al., 2020).

While there have been significant advancements in our understanding of the determinants of evolutionary rescue (reviewed by Carlson et al., 2014 and Bell, 2017), most evolutionary rescue studies (both theoretical and empirical) have only considered species with rather simple life histories. In these studies, reproduction is typically completely asexual (e.g., Orr & Unckless, 2008, 2014) or completely sexual (e.g., Bürger & Lynch, 1995; Gomulkiewicz & Holt, 1995; Lynch et al., 1991). However, many species, some of which are of important ecological concern, have partially clonal reproduction such that reproduction occurs both asexually and sexually. For example, stony corals (Order: Scleractinia), which play a foundational role in coral reef communities, reproduce both asexually through fragmentation (Foster et al., 2007) and sexually via the release of eggs and sperm into the water column (Harrison et al., 1984). Partially clonal reproduction is also common among plants. For instance, both the common duckweed (*Spirodela polyrhiza*) and kudzu vine (*Pueraria montana*) reproduce primarily asexually via vegetative propagation, but also reproduce sexually via the pollination of flowers and seed production (Bentley & Mauricio, 2016; Ho et al., 2019). Relying on theory developed primarily assuming either completely asexual or sexual reproduction may lead to errors in predicting how partially clonal organisms will respond to environmental change (Hartfield, 2016; Hartfield & Glémin, 2016). Therefore, it is necessary to develop theory that specifically considers partially clonal reproduction.

Orive et al., (2017) took steps towards understanding the evolutionary rescue of partially clonal organisms, quantifying how both the relative amount of clonal reproduction and the similarity between parents and their clonal offspring affected the probability of rescue. They showed that increasing both these factors promotes evolutionary rescue following an abrupt environmental change (e.g., the introduction of a non-native enemy, point source pollution or habitat loss). Following an abrupt change, pre-existing genetic variation is generally of more importance than novel variation. Therefore, all else being equal at the time of environmental change (e.g., same genetic variation and initial population size), increased degrees of clonality promote evolutionary rescue by allowing well-adapted phenotypes to avoid being dismantled during sexual reproduction (Orive et al., 2017). Conversely, they also showed that increasing clonality decreases the population's ability to withstand continuous linear environmental change (e.g., climate change) because increased clonality reduces the generation of novel genetic variation (via decreased allelic segregation, recombination and mutation) which is necessary to track a continuously changing environment (Orive et al., 2017). This result is partially supported by the empirical work of Lachapelle and Bell (2012), who experimentally showed that obligately sexual populations of the single-celled algae, *Chlamydomonas reinhardtii*, persisted longer than either asexual or facultatively sexual populations when exposed to gradually increasing salt concentrations.

Orive et al., (2017) did not consider stochastic environmental fluctuations and instead assumed either a single abrupt change in the optimal phenotype, after which it remains constant (Figure 1a), or a continuous linear change in the optimal phenotype (Figure 1d). However, in nature, the selection pressures driving maladaptation often vary over time. For example, increasing sea surface temperature is a major threat to coral reef communities because the symbiosis between zooxanthellae and stony corals breaks down when temperatures are anomalously high (Baker et al., 2008; Pandolfi et al., 2011). These anomalously high temperatures occur episodically with the most severe events occurring during El Niño years (Baker et al., 2008). Therefore, with warming sea surface temperatures there is generally selection for increased heat tolerance in stony corals (and/or zooxanthellae), but the selection pressure fluctuates over time (e.g., Figure 1e,f). The near ubiquity of environmental fluctuations in nature brings into question the generality of the conclusions from Orive et al., (2017). For instance, though increased clonality promotes population persistence following a single abrupt change that remains constant afterwards (e.g., Figure 1a), would this still hold given environmental fluctuations after the abrupt change (e.g., Figure 1b,c), in which case increased generation of new genetic variation might help the population track the fluctuations?

Here, we use quantitative genetic individual-based simulations to investigate how environmental fluctuations influence the effect of partial clonality on evolutionary rescue. We simulate both abrupt and continuous environmental changes, with and without environmental fluctuations. We also consider the effect of autocorrelation in environmental fluctuations, which is known to influence evolutionary rescue: increased autocorrelation in environmental fluctuations increases the variance in population trajectories and allows the population mean phenotype to more closely track the optimum (Björklund et al., 2009; Chevin et al., 2017; Peniston et al., 2020). Examples of all six environmental change scenarios considered are shown in Figure 1. Finally, we consider how generational overlap
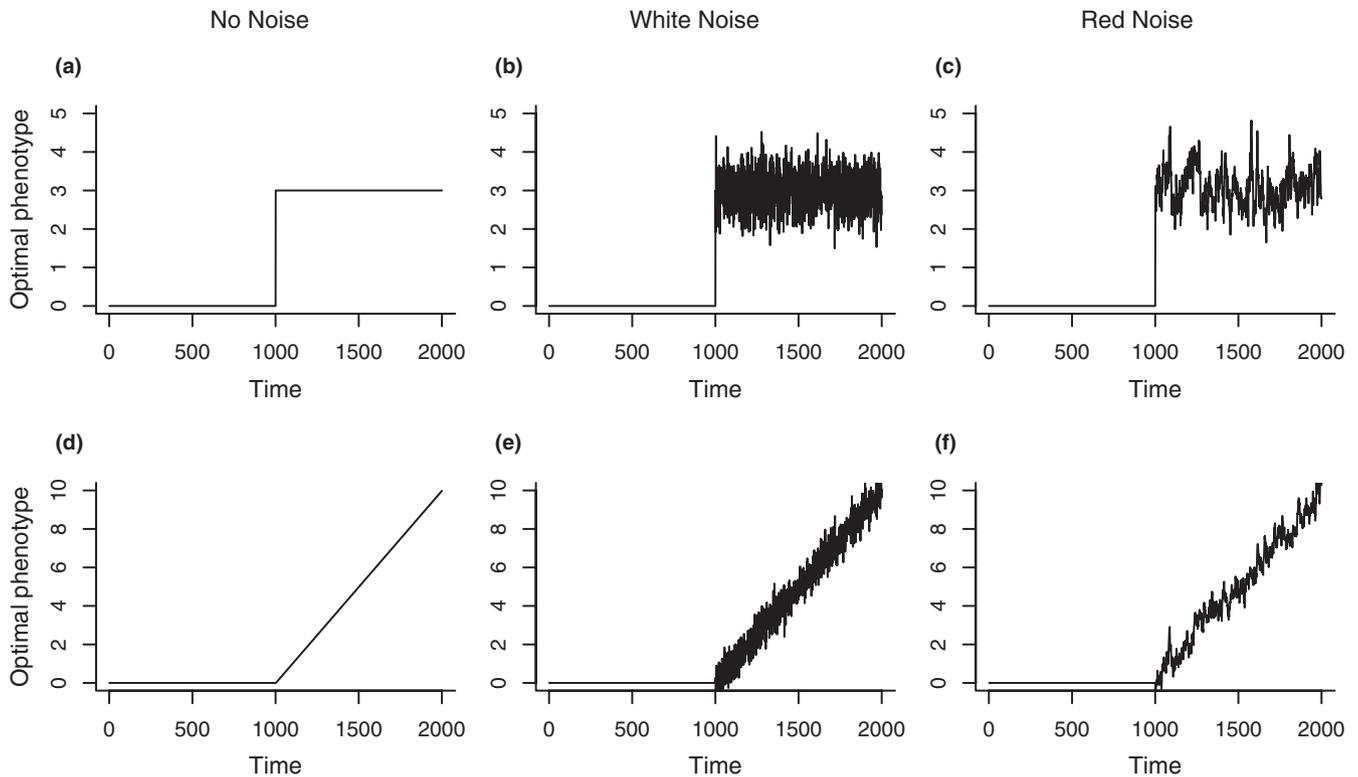
FIGURE 1 Examples of the six different environmental change scenarios evaluated: (a) a single abrupt change with no temporal fluctuations; (b) a single abrupt change with temporally uncorrelated fluctuations afterwards; (c) a single abrupt change with temporally autocorrelated fluctuations afterwards; (d) a continuous environmental change with no temporal fluctuations; (e) a continuous environmental change with temporally uncorrelated fluctuations; and (f) a continuous environmental change with temporally autocorrelated fluctuations. Note that we refer to uncorrelated fluctuations (b,e) as "white noise" and autocorrelated fluctuations (c, f) as "red noise." Parameters were (a) $\bar{\theta} = 3.0$ and $\sigma^2 = 0.0$; (b) $\bar{\theta} = 3.0$, $\sigma^2 = 0.25$, and $\lambda = 0.0$; (c) $\bar{\theta} = 3.0$, $\sigma^2 = 0.25$, and $\lambda = 0.9$; (d) $\delta = 0.01$ and $\sigma^2 = 0.0$; (e)$\delta = 0.01$, $\sigma^2 = 0.25$, and $\lambda = 0.0$; (f) $\delta = 0.01$, $\sigma^2 = 0.25$, and $\lambda = 0.9$; see Table 1 for description of parameters

affects our results by performing simulations allowing each adult to survive with a probability of 0.5 until the next generation (with no age dependence in adult mortality). In general, we show that the main conclusions from Orive et al., (2017) still hold when there are small to moderate magnitudes of environmental fluctuations, but when fluctuations are large, some interesting new patterns can emerge. We also find that overlapping generations typically dampen the effects of environmental variation on evolutionary rescue.

TABLE 1 Key parameters used in simulations

Parameter	Description
r_c	Average fraction of offspring that were produced clonally
ρ	Association between the random components of each parent's and its offspring's phenotypes for clonal reproduction
$\bar{\theta}$	Mean optimal phenotype following abrupt environmental change. Greater values of this parameter represent more severe environmental changes.
δ	Per-time-step mean change in the optimal phenotype for continuous change
σ^2	Variance in the optimal phenotype following environmental change
λ	Correlation coefficient between values of the optimal phenotype in consecutive time steps
K	Number of mating sites available
f	Number of offspring produced by each individual occupying a mating site
μ_g	Meiotic mutation rate
μ_s	Somatic mutation rate
α^2	Variance in mutation effects
ω^2	Inversely related to the strength of stabilizing selection

2 | MATERIALS AND METHODS

Our individual-based simulations were an extension of the simulations in Orive et al., (2017), which themselves were an adaptation of an approach used by Bürger and Lynch (1995). The simulations explicitly tracked individuals and their genotypes, which in turn determine their phenotypes. Our simulation is broken up into discrete time steps. Each time step, individuals underwent viability selection before they reproduced. Unless otherwise specified, generations were discrete, such that no adults survived to the next time step. In some simulations, however, we allowed adults to survive until the next time step with a probability of 0.5 in order to investigate the effect of generational overlap on our results. Definitions of the key parameters in the simulations are provided in Table 1. Parameter values were chosen to closely match those of Orive et al., (2017).

Fitness was determined by a single trait z (phenotype). The genotypic value of each individual was determined by $n = 10$ freely recombining additive diploid loci (previous studies using similar simulations to ours have shown there is little effect of the number of loci on the likelihood of evolutionary rescue for $n > 5$; Holt et al., 2003; Holt & Gomulkiewicz, 2004). Each allelic value could be any real number. An individual's phenotype was the sum of allelic values at all loci plus a random environmental component drawn from a zero-mean, unit-variance Gaussian distribution. The difference between an individual's trait value, z, and the optimal phenotype at time step t, θ_t, determined its probability of surviving to adulthood following the Gaussian function $V = \exp[-(z - \theta_t)^2 / (2\omega^2)]$, where ω^2 is inversely related to the strength of stabilizing selection.

There was "ceiling" density dependence, such that population size was regulated by the number of mating sites, K. If more than K individuals survived to adulthood, K adults were randomly selected to fill mating sites. Otherwise, all adults occupied a mating site. Each time step, for each adult occupying a mating site, a mate was randomly selected from all surviving adults in the population (individuals were hermaphroditic/monoecious, and selfing was possible).

Each mating pair then produced offspring. The individual occupying a mating site had a fixed reproductive effort f, which was the number of offspring produced (we assumed that there was an equal cost to producing clonal and sexual offspring). A fraction of this reproduction effort r_c was devoted to clonal reproduction, and the rest was allocated to sexual reproduction. For instance, if $r_c = 0.2$, for each offspring produced, there was a 20% chance it would be the result of clonal reproduction and an 80% chance it would be the result of sexual reproduction. This was a stochastic process, so r_c is the expected fractional investment in clonal reproduction, but any individual or population could have invested more or less by chance.

For sexual reproduction, the genotype of each offspring was determined by randomly (and independently) selecting one allele at each locus from each parent. This process simulates free recombination. For clonal reproduction, both haplotypes of the parent occupying the mating site were passed on to the offspring, such that there was complete linkage. For sexual reproduction, a mutation occurred on each haplotype (alleles from the same parent) with a probability

μ_g (the effective per-locus mutation rate is therefore $\mu_g/10$). If a mutation occurred, a random value drawn from a zero-mean Gaussian distribution with variance α^2 was added to the value of a randomly selected locus on that haplotype. For clonal reproduction, we used the same procedure for mutation, but with lower mutation rate μ_s, which simulated somatic mutations.

Another feature of clonal reproduction is that clonal offspring may inherit some proportion of the random component of their parent's phenotype, which includes nonadditive genetic values of the trait, as well as any random environmental effects (e.g., developmental noise). To incorporate this phenomenon into our simulations, the random component of each clonal offspring's phenotype was determined by the equation

$$e_k = \rho e_k^* + \sqrt{1 - \rho^2}\,\zeta,$$

where e_k and e_k^* are, respectively, the random components of the offspring's and parent's phenotype, ζ is a zero-mean, unit-variance Gaussian deviate and ρ (which ranges from 0 to 1) is the association between the random components of the parent's and offspring's phenotype (e.g., nonadditive genetic value plus the random environmental deviation). In nature, we would expect low values of ρ for gametic modes of clonal reproduction such as reproduction via apomictic seeds (Verhoeven & Preite, 2014). By contrast, we would expect larger values of ρ when clonal reproduction involves large proportions of somatic tissue (e.g., fragmentation or fission).

Each simulation was initiated with Kf juveniles, whose genotypes were randomly assigned from a Gaussian distribution with mean 0 and a variance determined by the stochastic house-of-cards approximation given in Bürger and Lynch (1995). For the first 1,000 time steps, the optimal phenotype was 0. During this period, the population was well adapted because the initial mean phenotype of the population closely matched the optimal phenotype. This protocol simulated time before environmental change, during which the population could reach a selection-mutation-drift balance. During this period, reproduction was completely sexual, and the environment did not fluctuate. We made these assumptions in order to ensure that each population had comparable genetic variation at the time of environmental change. Following the equilibration period, environmental change (change in the optimal phenotype) began. We analysed six different environmental change scenarios (Figure 1): (1) a single abrupt change with no temporal fluctuations, (2) a single abrupt change with uncorrelated fluctuations, (3) a single abrupt change with autocorrelated fluctuations, (4) a continuous, directional (linear) environmental change with no temporal fluctuations, (5) a continuous, directional environmental change with uncorrelated fluctuations and (6) a continuous, directional environmental change with autocorrelated fluctuations. Throughout, we will refer to temporally uncorrelated fluctuations as "white noise" and temporally autocorrelated fluctuations as "red noise."

For the scenarios with an abrupt change in the optimum phenotype (scenarios 1–3), the mean optimal phenotype immediately changed from 0 to $\bar{\theta}$ at time step 1,000. Because the initial mean

phenotype was 0, the greater the magnitude of $\overline{\theta}$ the more mal-adapted the population was just after the step change. Note that we made the initial degree of environmental change always be $\overline{\theta}$ instead of a random value with mean $\overline{\theta}$ because the effect of the initial degree of environmental change on rescue is well known, and we were interested in the effect of temporal variation afterwards (Peniston et al., 2020 made this same assumption). Following the step change, the simulation continued for another 1,000 time steps during which the optimal phenotype could temporally vary around its mean $\overline{\theta}$. The optimal phenotype each time step after the environmental change was determined by the recursion

$$\theta_{t+1} = \overline{\theta} + \lambda \left[\theta_t - \overline{\theta}\right] + \sigma \left[\sqrt{1 - \lambda^2}\right] \zeta \tag{1}$$

where θ_t is the optimal phenotype in time step t, σ is the standard deviation of the optimal phenotype, ζ is a zero-mean, unit-variance Gaussian random deviate, and λ is the correlation coefficient between optimal phenotypes in consecutive time steps ($0 \leq \lambda \leq 1$). Greater positive values of λ indicate more positive autocorrelation among values of the optimal phenotype. Our assumption that the initial degree of environmental change was always $\overline{\theta}$ instead of a random value with mean $\overline{\theta}$ results in the statistical properties of the environmental fluctuations in our simulations initially not matching those indicated by our parameter values because the initial variance of the environmental sequence is 0. Over time, the variance approaches an equilibrium value of σ^2; at generation t, the variance is $\sigma^2 (1 - \lambda^{2t})$, and the correlation coefficient simultaneously approaches λ. Peniston et al. (2020) showed that this assumption does not qualitatively alter the influence of environmental variation on evolutionary rescue. Our simulations ended with an assay period of 100 time steps, during which the mean optimal phenotype was fixed at $\overline{\theta}$.

For scenarios with a continuous environmental change (scenarios 4–6), we first generated a zero-mean autocorrelated random Gaussian sequence using Equation 1 and then added $\delta(t - 1000)$ to the value at each time step t for $t > 1,000$. Therefore, the optimal phenotype increased with a mean rate of δ and without fluctuations ($\sigma^2 = 0$) this change was linear (e.g., Figure 1d). The environmental change lasted for 1,000 generations and the simulation ended with an assay period of 100 time steps, during which the mean optimal phenotype was fixed at 1000δ, the expected value at the end of the environmental change period.

For each of the six scenarios, we measured the probability of persistence for a range of values of r_c and ρ (when one value was varied, the other was fixed). For scenarios with environmental variation (scenarios 2, 3, 5 and 6), we ran simulations for a range of variances in the optimal phenotype σ^2 with autocorrelation values of either $\lambda = 0$ ("white noise") or $\lambda = 0.9$ ("red noise"). The probability of persistence was calculated as the proportion of simulations in which the population persisted until the end of the assay period. We ran 800 replicates of the simulation for each parameter set. The full C++ source code and accompanying documentation are available online in the Dryad Digital Repository: https://doi.org/10.5061/dryad.dv41ns1xm.

2.1 | Results: Abrupt change in optimal phenotype

2.1.1 | Relative investment in clonal reproduction (r_c)

Our simulations confirm the results of Orive et al., (2017)—evolutionary rescue following a step change in the environment is more likely in populations with a greater relative investment in clonal reproduction (Figure 2a,b, solid lines). Recall that this occurs because pre-existing genetic variation (which was kept the same for all degrees of clonality) is generally more important than new genetic variation following an abrupt environmental change (Orive et al., 2017). Our simulations expand these results to show that this general pattern persists even with temporal fluctuations in the optimal phenotype (Figure 2a,b, dashed lines). In agreement with previous studies (Chevin et al., 2017; Peniston et al., 2020), we also found that environmental variation generally decreased the probability of evolutionary rescue, but that positively autocorrelated fluctuations (red noise) can facilitate the rescue of populations exposed to a severe environmental change (compare solid and dashed lines in Figure 2a,b). However, the advantage with variation was generally quite small and occurred for a limited range of mean environmental change. For simplicity, we will not focus on these severe degrees of environmental change and instead focus on low to moderate degrees of change in the mean optimal phenotype, where there was often a substantial reduction in persistence.

Fluctuations in the optimal phenotype alter the relationship between relative investment in clonal reproduction (r_c) and the probability of rescue. We evaluated the benefit of increasing the relative investment in clonal reproduction by calculating (via linear interpolation between the two closest points) the degree of environmental change at which 50% of the populations went extinct (hereafter the "50% extinction value") and evaluating how this value changed with different values of r_c (Figure 2c,d). In an environment without fluctuations ($\sigma^2 = 0.0$), increasing r_c almost linearly increased the 50% extinction value (Figure 2c,d; black lines), meaning that populations with a greater relative investment in clonal reproduction could withstand greater degrees of environmental change. With fluctuations in the optimal phenotype, increasing r_c still increased the 50% extinction value, but the slope of the relationship was less steep and tapered off slightly at higher values of r_c (Figure 2c,d; coloured lines). This reduction in the benefits of increased investment in clonal reproduction was more dramatic with greater degrees of fluctuation in the optimal phenotype and higher values of autocorrelation.

These effects of environmental variation can be explained by recalling that Orive et al., (2017) found that increased investment in clonal reproduction was beneficial following a step change in the environment, but detrimental when the environment was continuously changing. Fluctuations in the optimal phenotype are essentially small, continuous changes in the environment. Therefore, while an increased investment in clonal reproduction can be beneficial following an abrupt environmental change, it can decrease the ability of the population to track more minor environmental fluctuations afterwards. This makes biological sense, as
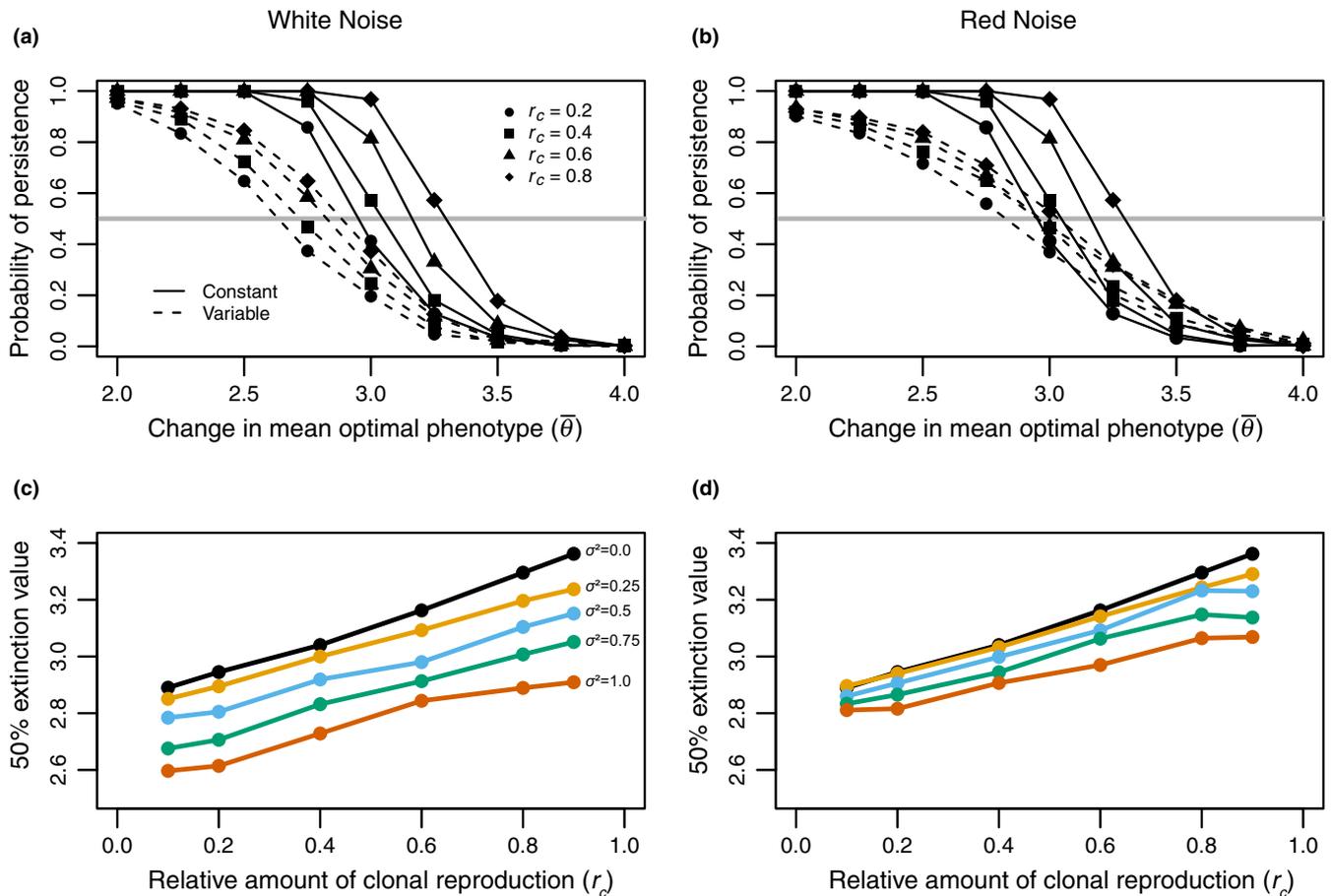
FIGURE 2 The effect of environmental variation on the relationship between the relative amount of clonal reproduction (r_c) and the probability of evolutionary rescue following an abrupt environmental change. (a) and (b) show the probability of the population persisting for 1,000 time steps (plus the assay period) for different degrees of change in the optimal phenotype. Solid lines show results for an unfluctuating optimal phenotype ($\sigma^2 = 0.0$), and dashed lines show results for fluctuating optimal phenotype ($\sigma^2 = 1.0$). (c) and (d) show the degree of change in the optimal phenotype at which the probability of persisting until the end of the simulation was 50% (the "50% extinction value") for different relative amounts of clonal reproduction. The 50% extinction value is indicated by the horizontal grey line in (a) and (b). Different colours denote different amounts of variation in the optimal phenotype (σ^2). In the left column (a,c) fluctuations in the optimal phenotype are uncorrelated ($\lambda = 0.0$, white noise) and in the right column (b,d) fluctuations in the optimal phenotype are positively autocorrelated ($\lambda = 0.9$, red noise). Parameters for all panels were $K = 256$, $f = 4$, $\omega^2 = 1$, $\mu_g = 0.01$, $\mu_s = 0.0001$, $\rho = 0.5$, $\alpha^2 = 0.05$

increasing clonal reproduction decreases the rate of generation of new genetic variation (assuming a low somatic mutation rate), which is necessary for evolutionarily tracking environmental fluctuations. Our focus is on partially clonal organisms, but this point is emphasized by looking at fully clonal populations ($r_c = 1$), which in fluctuating environments had a lower 50% extinction value than many partially clonal populations and thus were more prone to extinction (Figure S1).
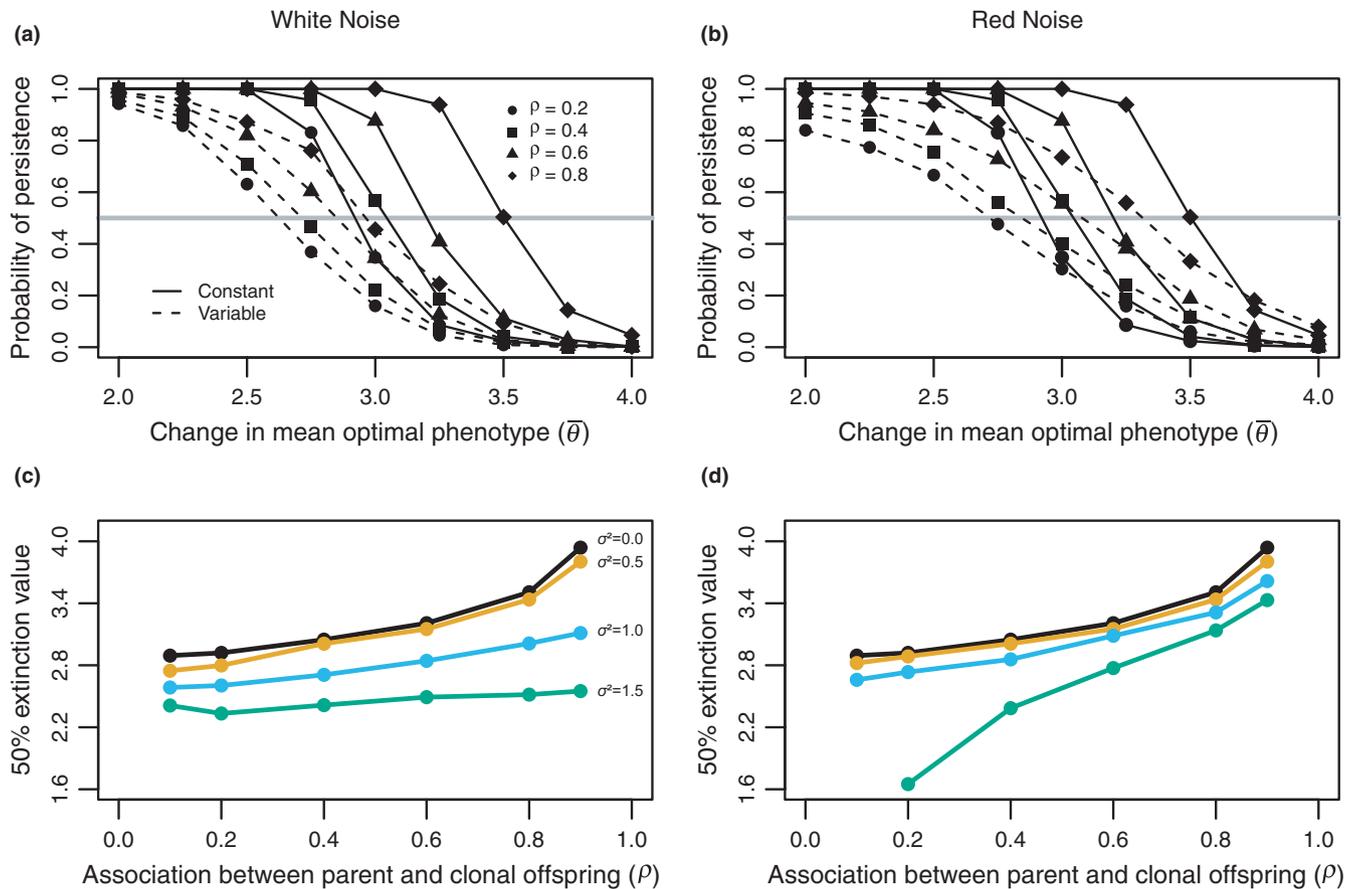
2.1.2 | Association between parent and clonal offspring phenotypes (ρ)

Our simulations also confirm the results of Orive et al., (2017), in showing that evolutionary rescue following a step change in the environment is more likely in populations with a greater association between parent and offspring phenotypes (Figure 3a,b, solid lines). Our simulations show that this general pattern persists in temporally

fluctuating environments. Temporal variation typically decreases the probability of evolutionary rescue, except for very high values of $\overline{\theta}$ (Figure 3a,b, dashed lines). However, fluctuations in the optimal phenotype do change the relationship between the association between parent and offspring phenotypes (ρ) and the probability of rescue.

In unfluctuating environments, increasing ρ increased the 50% extinction value at an accelerating rate (Figure 3c,d; black lines). When there were uncorrelated fluctuations in the environment (white noise), this relationship between ρ and the 50% extinction value became more linear and less steep (Figure 3c). Conversely, when there were positively autocorrelated fluctuations in the environment (red noise), the relationship between ρ and the 50% extinction value steepened (Figure 3d). Both of these patterns were more dramatic with increased magnitudes of fluctuations.

The decreased benefits of increasing ρ with white noise (Figure 3c) can be explained as follows: with random uncorrelated fluctuations in the optimal phenotype, the phenotype that was beneficial in the

FIGURE 3 The effect of the association between the random component of the phenotypes of parent and clonal offspring (ρ) and the probability of evolutionary rescue following an abrupt environmental change followed by environmental variation. (a and b) show the probability of the population persisting for 1,000 time steps (plus the assay period) for different degrees of change in the optimal phenotype. Solid lines show results for an unfluctuating optimal phenotype ($\sigma^2 = 0.0$) and dashed lines show results for fluctuating optimal phenotype ($\sigma^2 = 1.0$). (c and d) show the degree of change in the optimal phenotype at which the probability of persisting until the end of the simulation was 50% (the "50% extinction value") for different ρ. The 50% extinction value is indicated by the horizontal grey line in (a and b). Different colours denote different amounts of variation in the optimal phenotype (σ^2). In the left column (a, c) fluctuations in the optimal phenotype are uncorrelated ($\lambda = 0.0$, white noise) and in the right column (b, d) fluctuations in the optimal phenotype are positively autocorrelated ($\lambda = 0.9$, red noise). Parameters for all panels were $K = 256$, $f = 4$, $\omega^2 = 1$, $\mu_g = 0.01$, $\mu_s = 0.0001$, $r_c = 0.5$, $\alpha^2 = 0.05$

parents' generation might not be beneficial in the offspring's generation. In contrast, in a red noise environment, a beneficial phenotype in the parents' generation is likely to be beneficial in the offspring's generation as well, and thus an increased value of ρ is even more beneficial in an environment with autocorrelated fluctuations than it is in an environment with only a single abrupt change. Unlike increasing r_c, increasing ρ does not decrease the new genetic variation in the population, although it does decrease the phenotypic variation.

2.2 | Results: Linear change in expected optimal phenotype

2.2.1 | Relative investment in clonal reproduction (r_c)

These simulations also confirmed the results of Orive et al., (2017), in that greater relative investment in clonal reproduction (r_c) decreases the probability of a population persisting in a linearly changing

environment (Figure S2, solid lines). Furthermore, this general pattern persists even if there are temporal fluctuations in the optimal phenotype (Figure S2, dashed lines). In agreement with Bürger and Lynch (1995), we also found that increased degrees of variation decrease the probability of a population persisting to the end of the simulation.

In the absence of environmental fluctuations, increasing the relative investment in clonal reproduction almost linearly decreased the 50% extinction value (here defined as the rate of environmental change, δ, at which 50% of the simulated populations did not persist until the end of the simulation) (Figure S3; black lines). Overall, temporal variation increases extinction risk (Figure S2), for both white and red noise. With increased degrees of both uncorrelated and autocorrelated variation in the optimal phenotype (σ^2), the relationship between the relative investment in clonal reproduction and the 50% extinction value became less steep (Figure S3), meaning that increased relative amounts of clonal reproduction were relatively less detrimental to population persistence in more variable

environments. For a continuous change, persistence depends on the generation of new genetic variation, the vast majority of which is contributed by sexual reproduction. Therefore, it is not surprising that the 50% extinction value appears to be almost proportional to the amount of sexual reproduction $(1-r_c)$. Also, the largest effect of variation is at the smallest r_c. One possible explanation for this is that the variation causes a significant decrease in the 50% extinction value even in a fully sexual population. Together, these two factors would account for the decreasing magnitude of the slopes with an increasing magnitude of environmental variation.
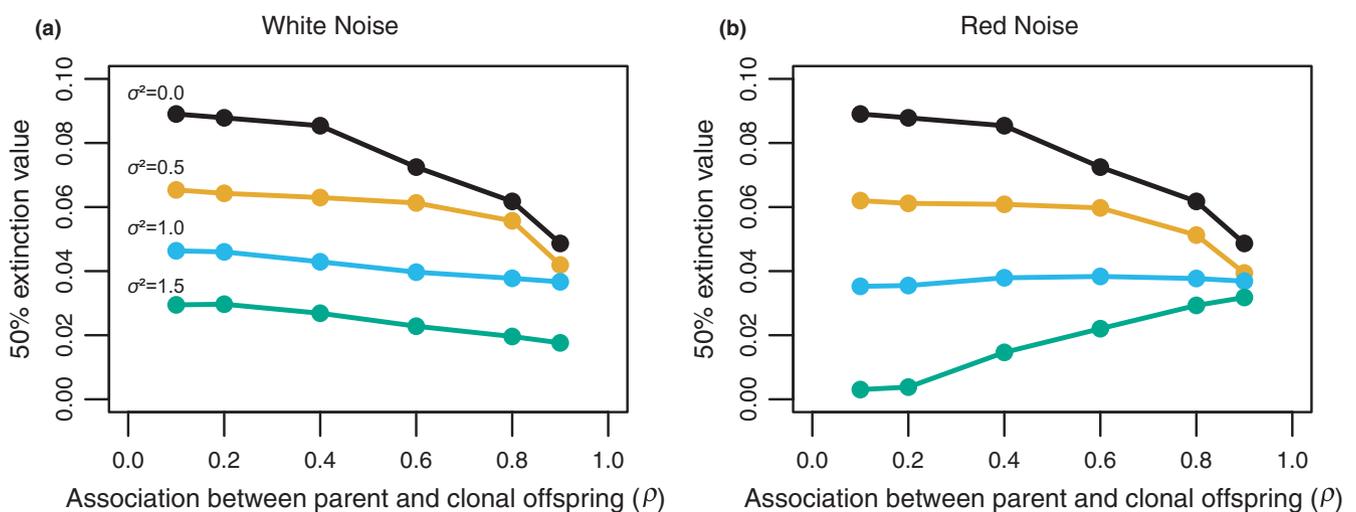
2.2.2 | Association between parent and clonal offspring phenotypes (ρ)

These simulations also confirmed the results of Orive et al., (2017) showing that a greater association between parent and offspring phenotypes (ρ) decreases the probability of a population persisting in an unfluctuating, linearly changing environment (Figure S4, solid lines). However, while this general pattern persisted for most situations including fluctuations in the optimal phenotype (e.g., Figure S4, dashed lines), there are some areas of parameter space in which it did not (described below).
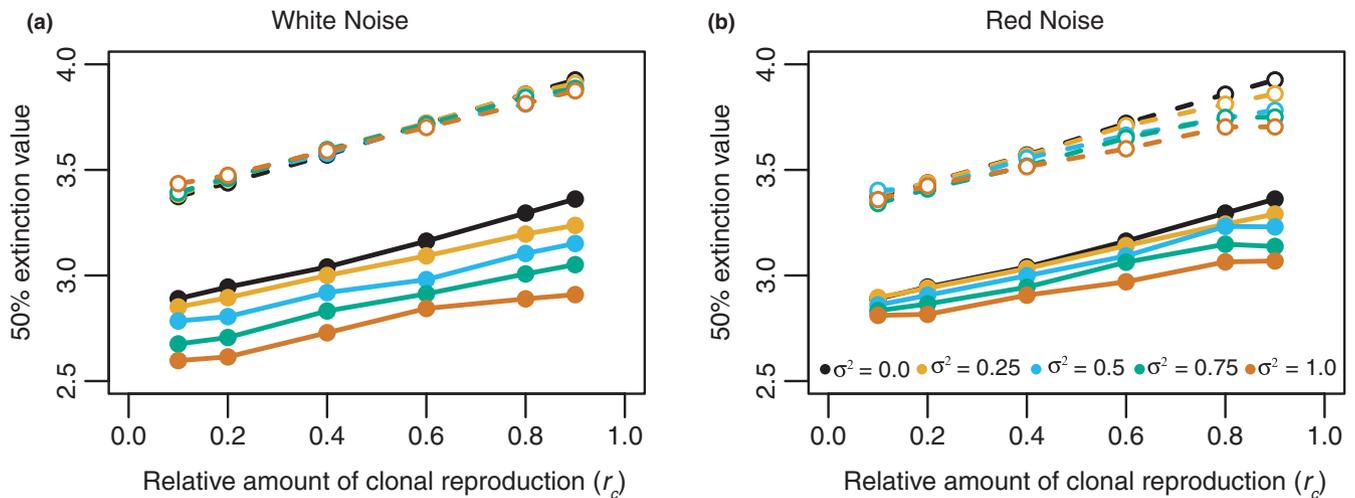
In the absence of environmental fluctuations, increasing the degree of phenotypic association between parent and clonal offspring decreases the probability of a population persisting at an accelerating rate (Figure 4; black lines). With uncorrelated fluctuations in the optimal phenotype, the probability of persistence overall likewise declines, and this relationship becomes less steep with increasing degrees of variation in the optimal phenotype (Figure 4a). When the fluctuations in the optimal phenotype are positively autocorrelated, the relationship between the degree of association between parent

and clonal offspring and the 50% extinction value becomes less steep with increasing levels of variation until it reaches a threshold value at which point the slope of the relationship switches directions (Figure 4b). In other words, when fluctuations in the optimal phenotype are large enough and positively autocorrelated, increasing the degree of association between parents and clonal offspring *increases* the probability of a population persisting in a continuously changing environment (Figure 4b; green and blue lines).

These patterns emerge because environmental fluctuations decrease the negative effects of increasing ρ and can even make them positive. In an unfluctuating, continuously changing environment, it is detrimental for parents and offspring to be more similar because the offspring's environment will always differ from their parents'. With environmental fluctuations, this may not be the case, as there can be stochastic runs of similar environments, thus decreasing the negative effects of offspring being similar to parents. If the degree of environment variation is sufficiently large, environmental fluctuations can have a greater influence on the optimal phenotype (and thus selection) than the underlying relentless but slow directional change. In these scenarios, if fluctuations are highly autocorrelated, parents and offspring are likely to experience similar selection regimes and thus it can be beneficial for parents and offspring to be more similar even if there is an overall trend for continuous, directional environmental change (Figure 4b; blue and green lines), which in the absence of fluctuations makes clonality less advantageous. Also note that the continuous change is always in the same direction and therefore requires that new variation (alleles with higher values) be continually produced. In contrast, the fluctuations go in both directions, so generating new variation is less important, especially if alleles that tend to produce maladaptation in one environment are not eliminated too quickly, so they are available when the environment changes in their direction.

FIGURE 4 The rate of environmental change (δ) at which 50% of the simulated populations did not persist until the end of the simulation (the "50% extinction value") for different degrees of association between parent and clonal offspring (ρ). Different colours denote different amounts of variation in the optimal phenotype (σ^2). (a) Depicts uncorrelated fluctuations in the optimal phenotype ($\lambda = 0.0$, white noise) and (b) depicts positively autocorrelated fluctuations in the optimal phenotype ($\lambda = 0.9$, red noise). Parameters for both panels were: $K = 256$, $f = 4$, $\omega^2 = 1$, $\mu_g = 0.01$, $\mu_s = 0.0001$, $r_c = 0.5$, $\alpha^2 = 0.05$

(a) White Noise **(b)** Red Noise

FIGURE 5 The degree of abrupt change in the mean optimal phenotype ($\bar{\theta}$) at which 50% of the simulated populations did not persist until the end of the simulation (the "50% extinction value") for different relative amounts of clonal reproduction (r_c). Solid lines are results without any adult survival (no generational overlap), and dashed lines are results with 50% adult survival to the next time step. Different colours denote different amounts of variation in the optimal phenotype (σ^2). (a) Depicts uncorrelated fluctuations in the optimal phenotype ($\lambda = 0.0$, white noise) and (b) depicts positively autocorrelated fluctuations in the optimal phenotype ($\lambda = 0.9$, red noise). Parameters for both panels were $K = 256$, $f = 4$, $\omega^2 = 1$, $\mu_g = 0.01$, $\mu_s = 0.0001$, $\rho = 0.5$, $\alpha^2 = 0.05$

2.3 | Results: Generational Overlap

2.3.1 | Abrupt environmental change

We implemented generational overlap by allowing adults to survive until the next time step with a probability of 0.5. Recall that, for all results presented above, all adults died at the end of each time step. In our simulations, we observed that populations with 50% adult survivorship could withstand a greater degree of abrupt environmental change (Figure 5 and Figure S5). This occurs because allowing adults to survive (with no selection on adults) increases the population growth rate and, all else being equal, results in a less rapid rate of initial decline, facilitating evolutionary rescue in altered environments (Gomulkiewicz & Holt, 1995; Orive et al., 2017). That is, increasing adult survivorship, and thus generational overlap, increased the probability of evolutionary rescue following an abrupt environmental change both with and without environmental fluctuations. The addition of generational overlap did not change the effects of increasing either the relative investment in clonal reproduction (r_c; Figure 5) or association between parent and clonal offspring phenotypes (ρ; Figure S5); increasing either still increased the probability of evolutionary rescue following an abrupt environmental change.

The addition of generational overlap did, however, alter the effect of environmental variation on evolutionary rescue. With 50% adult survival, the negative effects of increasing environmental variation were much smaller than when there was no adult survival (Figure 5 and Figure S5). Environmental variation is less detrimental with adult survivorship because with survivorship, the adults in the population are a sample of individuals that, as juveniles, were well adapted over a range of previous time steps, as opposed to only individuals who were adapted to the previous time step, as would be true without generational overlap. This increases the genotypic and

phenotypic variation in the population and thus makes the population better able to withstand short-term fluctuations in the optimal phenotype.

2.3.2 | Linear change in expected optimal phenotype

With a continuous, directional change in the optimal phenotype, the effects of generational overlap had opposite effects on population persistence, depending on the degree of environmental variation. With low magnitudes of environmental variation, the addition of 50% adult survival decreases the rate of environmental change that a population can withstand (Figure 6 and Figure S6; dashed black and orange lines are below the corresponding solid lines). There are two major causes for this pattern. First, increased adult survival (without other changes in life history) increases generation time and thus the per-generational degree of environmental change is greater, leading to more evolutionary lag (Orive et al., 2017). Second, adults that survive several time steps might have been well adapted to the past environment but maladapted at the current time step. This results in "gene flow through time" which can hamper adaptation (Orive et al., 2017; Yamamichi et al., 2019). Our results suggest that this outweighs the growth rate advantage of adult survivorship.

Conversely, with greater magnitudes of environmental variation, the addition of 50% adult survival increases the rate of environmental change that a population can withstand (Figure 6, the dashed blue and green lines are above the corresponding solid lines; Figure S6 dashed red lines above solid red lines). Yamamichi et al. (2019) saw a similar result for a model that incorporated generational overlap via dormancy. This pattern arises because with environmental fluctuations, genetic variation increases with generational overlap (because
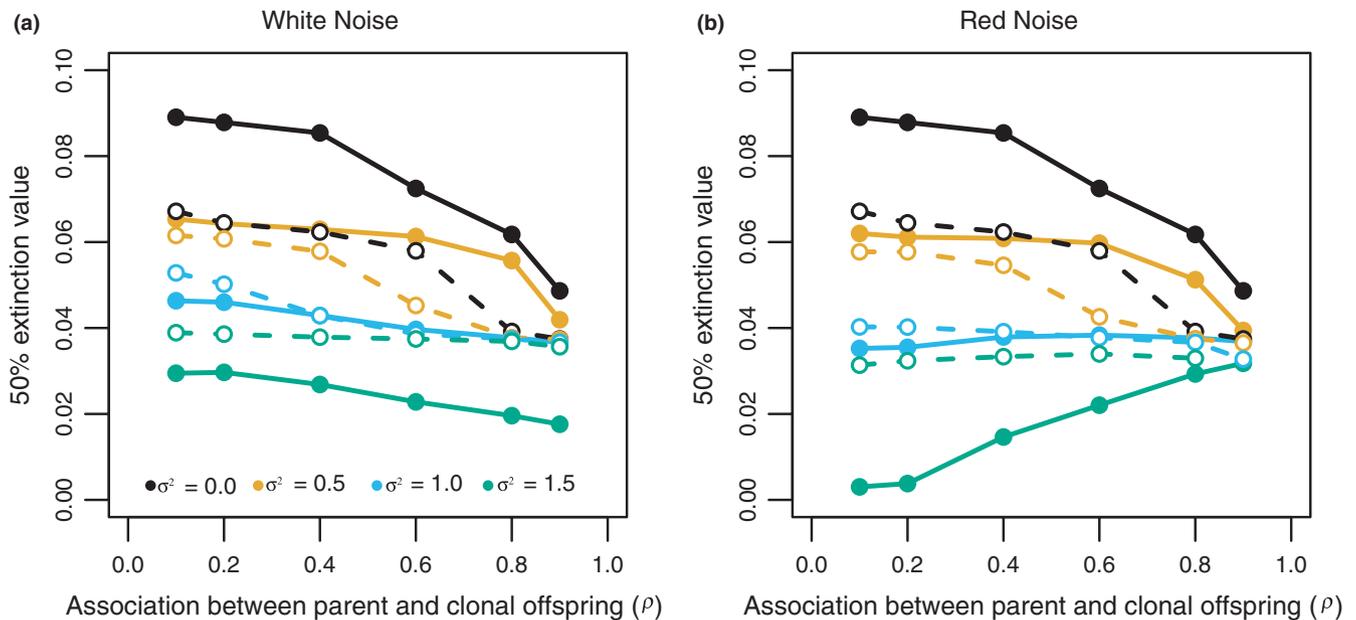
FIGURE 6 The rate of environmental change (δ) at which 50% of the simulated populations did not persist until the end of the simulation (the "50% extinction value") for different degrees of association between parent and clonal offspring (ρ). Solid lines are results of simulations without any adult survival (no generational overlap), and dashed lines are results of simulations in which adults survived to the next time step with a probability of 0.5. Different colours denote different amounts of variation in the optimal phenotype (σ^2). (a) Depicts uncorrelated fluctuations in the optimal phenotype ($\lambda = 0.0$, white noise) and (b) depicts positively autocorrelated fluctuations in the optimal phenotype ($\lambda = 0.9$, red noise). Parameters for both panels were $K = 256$, $f = 4$, $\omega^2 = 1$, $\mu_g = 0.01$, $\mu_s = 0.0001$, $r_c = 0.5$, $\alpha^2 = 0.05$

the population at each time step is a sample of individuals arising at different time points in the past), which can counteract the negative effects of increased generation times (Yamamichi et al., 2019). We have extended the results of Yamamichi et al., (2019) to show that generational overlap can promote adaptation for a large range of degrees of clonality (r_c and ρ) as long as there is sufficient environmental variation (Figure 6 and Figure S6).

The addition of generational overlap did not seem to significantly change the interactive effect of environmental variation and r_c on evolutionary rescue (Figure S6). However, with a large magnitude of autocorrelated environmental variation we did not see the positive effects of increasing ρ that we saw in the absence of generational overlap (Figure 6b).

3 | DISCUSSION

We have evaluated how environmental fluctuations influence the effect of clonality on evolutionary rescue. We show that for small to moderate magnitudes of fluctuations increasing either the relative investment in clonal reproduction, or the similarity between parent and clonal offspring phenotypes, increases the probability of population persistence in response to an abrupt environmental change, but decreases persistence in response to a continuously changing environment. These results confirm that the conclusions from models that ignore environmental variation (Orive et al., 2017) hold for moderate magnitudes of variation. However, we do find that with

large magnitudes of variation, both the benefits of clonality following a step change and the detrimental effects of clonality following a continuous, directional change are typically reduced. In fact, in the latter case, with positively autocorrelated environmental change (red noise), an increased similarity between parents and clonal offspring can increase the probability of persistence.

In addition, our results confirmed that the conclusions regarding the effects of environmental variation on evolutionary rescue developed from models which assumed either fully clonal (Peniston et al., 2020) or fully sexual reproduction (Bürger & Lynch, 1995; Chevin et al., 2017; Peniston et al., 2020) hold for partially clonal organisms. Regardless of the degree of clonality, following an abrupt environmental change, increased magnitudes of environmental variation typically decrease the probability of evolutionary rescue, but they can promote evolutionary rescue if the degree of environmental change is large and fluctuations are positively autocorrelated (Figures 2 and 3). In response to a continuous, directional environmental change, increased degrees of environmental variation decrease the probability of population persistence. In addition, we show that the effects of environmental variation on evolutionary rescue are generally dampened with increased generational overlap.

We have also extended recent work regarding the effects of generational overlap on rapid evolution in the context of evolutionary rescue. Although increased generational overlap is typically thought to hinder adaptation to directional environmental change (Orive et al., 2017), Yamamichi et al., (2019) showed that intermediate levels of generational overlap can actually be optimal for adaptation

to directional environmental change if environmental variation scaled by the strength of selection is intermediate and the rate of mean environmental change is slow. This occurs because increased generational overlap increases genetic variation in fluctuating environments (via a temporal storage effect) but also increases the per-generation rate of environmental change (Yamamichi et al., 2019). Similar to Yamamichi et al., (2019), we found that sometimes increased generational overlap can actually facilitate adaptation to directional change. Because of computational limitations, we explored a more limited set of parameter space than did Yamamichi et al., (2019), but we have broadened their results to show that, given the proper conditions, increased generational overlap can promote adaptation for a large range of degrees of clonality. Furthermore, Yamamichi et al., (2019) modelled generational overlap via dormancy while we did so via adult survival. The similarity of our results supports the conclusion that these patterns are a result of generational overlap and not specific to either dormancy or adult survival (similar relationships between dormancy and adult survival have been well documented in studies of temporal storage effects promoting coexistence; Chesson, 2000).

We have made many simplifying assumptions in our simulations that should be considered when interpreting our results. For instance, we only considered forms of asexual reproduction that are purely clonal (asexual reproduction that results in genetically identical offspring). Results might differ for other forms of asexual reproduction that involve recombination (see Orive & Krueger-Hadfield, 2021, for a discussion of clonal versus aclonal forms of asexual reproduction). We assumed that all individuals were hermaphroditic and that there was no cost of sex. Furthermore, our models assume that species have fixed life history strategies that do not change with environmental conditions. Many species, however, have condition-dependent life histories in which environmental conditions can influence the relative frequencies of asexual and sexual reproduction (Ram & Hadany, 2016). For example, the freshwater crustacean *Daphnia magna* reproduces primarily asexually, but individuals reproduce sexually when exposed to environmental stressors (Kleiven et al., 1992; Mitchell et al., 2004). Our results and those of Orive et al., (2017) suggest that increasing the frequency of sexual reproduction in response to environmental change would typically decrease the probability of rescue following an abrupt change and increase the probability of rescue in response to a continuous change. However, additional realistic biological traits should be considered that were not incorporated in our models. For instance, environmental fluctuations may cause individuals to plastically alter their life history strategies in concert with changes in their environments. Future studies should explicitly model evolutionary rescue in species with condition-dependent life histories.

We have simulated environmental change and fluctuations in a particular way. We assumed that before the environmental change there were no environmental fluctuations and that all reproduction was fully sexual. This assumption was made in order to keep initial genetic variation similar among simulations because we were interested in the effects of clonal reproduction and environmental fluctuations during the rescue process, not beforehand. Incorporating

clonal reproduction and environmental fluctuations before the environmental change would likely have changed initial conditions (there would likely be more genetic variation in populations with higher degrees of sexual reproduction and environmental variation). Environmental fluctuations before an environmental change could also have caused the populations to go extinct before the environmental change even occurred. Greater magnitudes of environmental variation typically increase the probability of a (well-adapted) population going extinct because it lowers the long-run population growth rate (Lande, 1993) and increased autocorrelation in environmental fluctuations can either increase or decrease the probability of extinction depending on the magnitude of variation, the form of density dependence and the spatial structure of the population (Petchey et al., 1997; Ripa & Lundberg, 1996; Schwager et al., 2006).

It is also important to recognize that our results were all obtained from stochastic individual-based simulations and not analytical or deterministic models. Stochastic individual-based simulations allow for more realism and complexity than other modelling techniques, but they do not allow the same level of mechanistic understanding that often comes with analytical or deterministic models. In particular, we only looked at a limited set of parameter values, which could in theory have biased our results. In an effort to avoid these biases, we chose parameter values similar to those used the individual-based simulations of previous studies (Orive et al., 2017; Peniston et al., 2020). However, it is still possible that patterns different from those we observed in our simulations could emerge with different sets of parameters.

The simplified original models of evolutionary rescue provided valuable insights into understanding how populations respond to environmental change (e.g., Gomulkiewicz & Holt, 1995; Orr & Unckless, 2014), but they did not examine realistic biological and environmental complexities such as partially clonal reproduction and environmental variation. Partially clonal reproductive strategies can be found throughout the tree of life, ranging from bacteria (Thomas & Nielsen, 2005) to bryophytes (During, 1979), to corals (Foster et al., 2007), to even potentially some squamate reptiles (Groot et al., 2003; Neaves & Baumann, 2011), and all organisms live in environments that are temporally variable to some degree. If we hope to develop effective conservation policies that will promote evolutionary rescue in these organisms, we must develop models that consider these richly complicated life histories, as well as the temporal texture of the environment in which organisms live. Our models are a step in this direction by assaying the implications of the interplay between the degree of clonality and environmental variation during evolutionary rescue, elements which must enter into more detailed, system-specific models to inform conservation policies.

PEER REVIEW

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.