Stochastic simulations decipher the role of site-specific selection and seed migration in the maintenance of genetic variation in self-fertilizing annual weeds species

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Abstract

High rates of self-fertilization have long been associated with weediness in plants. Complete self-fertilization prevents effective genetic recombination, reducing effective population sizes by one half, theoretically reducing genetic variation present in populations. However, predominantly self-fertilizing plants such as downy brome (*Bromus tectorum*) have been successful in adapting to and subsequently invading many environments or adapting to management inputs. They often have adaptively relevant levels of multi-locus standing genetic variation manifests as phenotypic variation within a single locale of the invaded range. How populations of predominantly self-fertilizing species maintain genetic variation within locales remains unclear. A single locus, self-fertilizing, two-island Fisher-Wright forward genetic simulation with migration was used to explore fundamental questions about the implications of self-fertilization, selection, and migration on the maintenance of genetic/phenotypic variation in populations of annual self-fertilizing weeds species. The Fisher-Wright simulation demonstrated that with migration between locales and differential selection on the allelic state within locales, genetic variation could be maintained indefinitely within locales. Our study corroborates the use of best management practices for minimizing or preventing seed spread that are recommended for the management of herbicide resistance, such as cleaning vehicles or equipment that is transported between sites.

INTRODUCTION

The mechanisms of genetic adaptation, other than herbicide resistance, that allow the continued success of weeds have largely been neglected (Neve et al. 2009). Understanding these mechanisms is not only crucial to understanding the genetic phenomena we currently observe in weeds, but also allows us to predict how populations of weeds will adapt and respond to changes in their environments (Ward et al. 2008) as well as management systems. Understanding how weeds will respond genetically to management practices will allow for weed scientist to intentionally manipulate cropping/management systems for achieving a desired outcome (Neve et al. 2009). Less emphasis has been placed upon genetic mechanisms underlying success in weeds in the agroecosystem to management inputs other than herbicide selection, as there was less emphasis on invasive plant biology in general, and even less research conducted in an evolutionary context (Neve et al. 2009). Indeed, the widespread failure of herbicides, and glyphosate in particular, due to herbicide resistance (Heap & Duke 2017) has prompted weed scientists to explore the mechanisms of resistance to glyphosate (Baek et al. 2021). However, discovering the mechanisms of herbicide resistance will never lead to the discovery of a herbicide that weeds, with enough selection, will not overcome (Gaines et al. 2020).

Population genetics and evolutionary biology have been used by weed scientists to understand the genetic mechanisms contributing to the success of weeds (Clements and DiTommaso 2011; Leon et al. 2020; Neve et al. 2009). However, we have not as a discipline utilized stochastic simulations. Although stochastic simulations are used differently across many domains, including finance (Judge et al. 2019), engineering (Sabetta et al. 2021), operations management (Thevenin et al. 2020), genetics (Gaynor et al. 2021) and ecology (Wang et al. 2019), they are all similar in the need to evaluate systems when

uncertainty is present (Henderson & Nelson 2006). In weed science, stochastic simulations have been sparsely used for modeling weed management when using different strategies in a variable climate (Jones & Medd 2005), or assessing the risk of developing herbicide resistance (Liu et al. 2016; Neve et al. 2011). Although using simulations to examine genetic variation itself in weeds has been proposed (Neve et al. 2009), only one simulation has been used to implicitly simulate the effects of management explicitly on genetic variation, finding that the seed bank can maintain variation in a perennial species (Lauenroth and Gokhale 2023). Thus, here we are proposing the use of a simple stochastic simulation to explain the observed phenomena (Hossieni et al. 2022, Revolinski 2022, Revolinski et al. 2023) of genetic variation existing within a population of a self-fertilizing species located within a single location.

Although herbicide resistance is an important trait for adaptation of weeds to cropping systems, other traits also play a role in the adaptation of weeds to cropping systems. Barrett (Barrett 1983) discussed the formation of “races”, whereas we will refer to as “genotypes”, within agroecosystems that often adapt by mimicking how the crop grows in a particular agroecosystem. However, for the formation of adapted genotypes, regardless of the adaptive strategy, there must be standing genetic variation with-in locales to facilitate the adaptation of a weed population to the locally practiced agroecosystem. For example, a single population of teosinte (*Zea mexicana* Schrad.), was found to have mimicked the corn grown in Mazatlán, Mexico by developing seed dormancy so that seeds would only germinate the years corn was planted in the fields (Wilkes 1977). Gene flow from the corn as a cause can be ruled out because none of the corn has seed dormancy (Wilkes 1977), leaving only the possibility that dormancy variation in the teosinte came from standing variation, migrants to the population or a new mutation. As teosinte was a small isolated population (Wilkes 1977) there was unlikely to be migration or new mutations contributing to the variation in dormancy that could be selected upon, the variation in seed dormancy was likely already present. Grass species, including teosinte and *B. tectorum*, often vary within the species in their levels of seeds dormancy with high seed dormancy being associated with dry or hot environments and low dormancy associated with cooler/wetter environments (Lopez et al. 2011; Allen and Meyer 2002). While standing genetic variation and diversity can be explained within sites of teosinte because of its outcrossing and diecious nature (Muyle et al. 2020; Zajitschek and Connallon 2018), similar observations of dormancy variation found in *B. tectorum* cannot be explained by the heterozygote advantage (Fisher 1923) or negative frequency dependent selection of self-incompatibility loci (Brisson 2018; Wright 1964) due to the extremely high-frequency of self-fertilization in *B. tectorum* (Morrow and Stahlman 1984). Although little variation in seed dormancy in *B. tectorum* was identified in the most extreme of sites, the environmentally moderate sites from the invasive range of *B. tectorum* exhibited great variation in seed dormancy status between full-sib families (Allen and Meyer 2002).

In a special issue of *Weed Science* from 2012 (Norsworthy et al. 2012), the authors recommend reducing migration between and within fields to reduce the risk of herbicide resistance developing in weeds. The rationale behind the recommendation is that migration can increase the genetic variation present in a cropping system for selection to act upon, facilitating the genetic adaptation of weeds to herbicides. However, reducing migration between and within fields is a multi-faceted issue. Long distance seed dispersal often transports genetic information a much longer distance than pollen flow (Bacles et al.

2006) and there are several mechanisms present to facilitate the transport of seeds short and long distances. Mammalian wild-life such as deer can transport seeds several miles between farm fields (Myers et al. 2004), while avian wild-life can transport seeds thousands of miles (Proctor 1968, Farmer et al. 2017). Additionally, tumble weeds driven by the wind can distribute gene information across landscapes (Spring et al. 2022). However, the prevalence of farming equipment, automotive vehicles, and international shipping of agronomic commodities have enabled human-mediated transport of weeds seeds on the intra-national and inter-international scales (Taylor et al. 2012, Shimono and Konuma 2008, Adhikari et al. 2023). The distribution of *B. tectorum* in newly invaded ranges has been found to be highly correlated with the proximity to roads, indicating that *B. tectorum* - a self-fertilizing annual weed - is spreading by vehicles along the roadways (Speziale 2018). During the original spread of *B. tectorum* across the intermountain Pacific Northwest, *Bromus* species were spread along the railroads in contaminated grain and discarded hay that was used for animal bedding or packed goods (Henderson 1898, Mack 1981).

Best management practices (BMPs) for managing herbicide resistance (Norsworthy et al. 2012) theoretically reduce the genetic variation that underlies reproductive phenology and other adaptive traits in weeds. The BMPs for herbicide resistance aim to lower weed densities present within cropping systems and thus increasing the relative effect of genetic drift, resulting in a reduction in genetic/phenotypic variation present within the weeds populations (Lauenroth and Gokhale 2023). The BMPs for managing herbicide resistance that call for reduced migration of weeds propagules (i.e., seeds, tubers, corms, and pieces of shoots), and clearing non-crop areas bordering the crop fields of weeds reduce immigration of weeds seeds into the cropping systems consequently reducing the genetic/phenotypic variation present by limiting migration and population sizes (Willi et al. 2006). The reductions in genetic/phenotypic variation caused by the BMPs for herbicide resistance could, theoretically, continuously erode the genetic variation (Kimura 1969) required for weeds populations to adapt to environmental conditions and management strategies. Indeed, maintaining large population sizes and migration between populations is fundamental to preserving the adaptive ability of species in modern conservation settings (Hoffman et al. 2017).

Empirical data from *Lobelia inflata* (L.), a self-fertilizing species, indicated that differential selection on phenotypes between sites maintains genetic variation within the range occupied by the species (Cote and Simons 2020; Hughes and Simons 2015), corroborating a previous theory (Hedricks 1998) indicating spatial selection maintained genetic variation in species independent of self-fertilization rate. Additionally, as demonstrated in a clonal species, multiple introduction sources and high levels of local migration can maintain standing genetic variation within locales, when no outcrossing is present (Barbosa et al. 2019). However, for self-fertilizing species, the mechanism for maintaining variation within locales remains uncharacterized. Interestingly, Stebbins (Stebbins 1957) observed many of the most notorious plants with high self-fertilization rates also had specialized structures for seed dispersal and annual life cycles. Species like *B. tectorum* and marestail (*Erigeron canadensis* L.), common self-fertilizing weeds, have specialized structures for seed dispersal by either being dispersed by attachment

to animals and equipment or floating in the wind, respectively. The question then, is what role does migration play in the genetic adaptability of weeds?

The n-island model, describing the effects of migration and differential selection between discrete islands in non-overlapping generations, was one of the first methods to model migration and selection (Wright 1931). The n-island model, in its simplest form, is the continent-island model, which defines the allelic frequency of the island at the next generation in terms of the proportion of the fixed size population, recurrently receiving migrants from the massive continent:

$$\varvec{P}(A_{t+1}) = (1 - m)\, A_t + m\, \bar{A} \quad [1]$$

where genotype A is the mutant genotype and a is the wild type, $\varvec{P}(A_{t+1})$ refers to the frequency of the mutant genotype on the island in the next generation, m refers to the proportion of the island population consisting of migrants, A_t refers to the frequency of the mutant genotype on the island in the current generation, and $\bar{A}$ refers to the frequency of the mutant genotype on the continent. Although simple, the continent island model has been used successfully to optimize migration levels in conservation management (Bodine and Martinez 2014; Luikart et al. 1998).

We hypothesize that if differential selection and migration of genotypes between the sites occurs then genetic variation can be indefinitely maintained within and between sites. Our objective is to use stochastic simulations to determine if differential selection among environments coupled with migration can sustain genetic variation within sites for an obligate self-fertilizing plant species.

MATERIALS AND METHODS

Fisher-Wright Two-island Model with Migration. A single locus, two-allele haploid stochastic Fisher-Wright simulation was performed with two islands, a constant population size of 200 individuals at each island, and an initial genotype frequency of 0.5, running for 2000 generations. At the beginning of each generation the probability of sampling the mutant genotype on each island was calculated based on a Fisher-Wright model accounting for differential selection.

$$P\left(A_{t+1}\right) = \frac{(A_t N)(1+s)}{(A_t N)s+N} \quad [2]$$

Where genotype A is the mutant genotype and a is the wild type, $\varvec{P}\left(A_{t+1}\right)$ refers to the probability of sampling individuals with the mutant genotype A on the island in the next generation, A_t refers to the frequency of the mutant genotype on the island in the current generation, s refers to the selection coefficient, and N refers to the total population size on the island. For both islands, the next generation was drawn from a binomial distribution with the respective $\varvec{P}\left(A_{t+1}\right)$ for each island calculated using equation [2] as the probability of success and 200 trials. Simulations differed by the presence of migration and differential selection between the islands. In simulations with pairwise

migration, the number of migrants was set to two migrants per generation. Migration was the last step in a generation, occurring as the reciprocal exchange of individuals between islands after the new populations were drawn. In simulations with differential selection, s the effect of the mutant genotype on survival was set to 0.05 one island and − 0.05 at the other island. Thus, the mutant will have a 55% chance of being passed on at one island and a 45% chance to be passed on to the next generation at the other island, the wildtype genotype will behave the same as the mutant but the probabilities at each island will be flipped in respect to the mutant. All of the simulations presented here assume a mutation that has already occurred with recombination not present due to the obligatory self-fertilization. The differential effect of the mutant versus the wild-type are assumed to be from the different environments at the two farms stemming from climactic, environmental, or management factors differing between the two farms (islands). The mutation is assumed to have occurred previously, where both the wildtype and mutant are assumed to be introduced from separate introduction events. Four simulations were performed to explore the effects of migration and differential selection on maintaining genetic variation. In the first simulation there was no migration or differential selection, the second had migration but no differential selection, the third had differential selection but no migration, and the fourth had migration and differential selection between islands. These simulations were chosen to show the effects migration and selection in a factorial manner. Fifty replications of each simulation were performed and plotted. The simulation was implemented in the JULIA programming language (Bezanson et al. 2017). The simulation is visualized (Fig. 1.) in context to a hypothetical farming situation where one farmer owns two fields that are some miles apart but in the same region, so the farmer uses the same planting equipment each year to plant both fields, reciprocally spreading weeds seeds between the two fields. The code for the simulation is available on figshare at 10.6084/m9.figshare.24977712.

The parameters of the simulation were chosen to demonstrate how genetic variation can be maintained indefinitely by migration and selection, while being easy to understand and computationally feasible. Stochastic population genetics simulations often will simulate thousands of generations to show how trends will hold over time (Barfield et al. 2011; Nuismer et al. 1999). To develop and demonstrate theoretical population genetic principles, population geneticists historically have simplified concepts to a point that natural phenomena can be explained (Peng et al. 2012). A realistic population genetics simulation for weeds would involve thousands of populations with millions of individuals, making the computation of such simulation impractical. However, an extremely complex simulation is not needed to demonstrate a theoretical concept concerning the maintenance of genetic variation after multiple founder events. Rather, simple concepts should be tested by similarly simple simulations, although the implications may be more complex.

Selection coefficient required to maintain genetic variation at various population sizes.

To determine the selection coefficient required to maintain genetic variation at various population sizes, the same two-island Fisher-Wright simulations with 200 rather than 2000 generations were conducted with population sizes at each island varying from 10 to 100, increasing in increments of 10. At each population size the selection coefficient, starting at zero, was increased by increments of 0.01 stopping

when at least 50 out of 100 singular simulations did not result in fixation of one genotype after 200 generations. The stopping point was considered the selection coefficient required to maintain genetic variation. For each population size, the entire process was repeated 30 times to determine variation of the simulations (30 x 100 = 3000 simulations). After the simulations were completed, the 3-parameter exponential decay function from the drc package (Ritz et al. 2015) in the R programming language (R Core Team 2021) was used to determine the decay function for the selection coefficient required to maintain genetic variation as population sizes increased. The ggplot2 (Wickham 2016) R-package was used to plot the exponential decay function from the simulations.

Determining the impacts of population size and strong selection in the absence of migration on time until genotype fixation.

To determine the effect of selection and population size on the number of generations for genetic variation to be lost (one genotype becomes fixed in the population) a series of simulations were performed with and without strong selection (S = 0.25) on population sizes varying from 10 to 320 incremented by doubling (N = 10, 20, 40, 80, 160, 320). Simulations followed the two-island Fisher-Wright simulation described earlier with a few changes. Migration was removed to determine time for genetic variation to become eliminated in the hypothetical situation that migration was not present. For each population size and selection level (S = 0.00 or 0.25) the simulation was repeated 3000 times with 30 runs of 100 simulations so that multi-threading could be used to distribute the 30 runs. Each simulation was run with 2000 generations so that the point that fixation was reached could be recorded. The simulations were intended identify impacts of selection on a wide range of population sizes, thus the results plotted by the asymptotic model (for the with selection simulations) in the drc R-package and regular linear regression using the lm function in base R (for the drift only simulations) were plotted in the $\log_2$ scale of both the response and dependent variable using the ggplot2 R-package.

RESULTS AND DISCUSSION

The only simulation able to maintain genetic variation within sites indefinitely included both migration and differential selection (Fig. 2d), potentially explaining the genetic and phenotypic variation found within populations of *B. tectorum* and other predominantly self-fertilizing species sampled from a single site. The simulation with no migration or differential selection led to independent genetic drift at islands where loci would become fixed for either allelic state (Fig. 2a). Differential selection with no migration resulted in the fixation of alleles quickly to the advantageous state, at both islands (Fig. 2c). When migration occurred without differential selection, both islands eventually drifted toward fixation of the same allele (Fig. 2b). However, migration did slow the drift even when no selection was present (Fig. 2a and Fig. 2b). When differential selection and migration were applied together, both islands maintained a reservoir of the advantageous allele to the island with a variation of the other allele maintained from inter-island migration (Fig. 2d). The variation maintained within-site by migration and selection is maintained indefinitely (Fig. 2d).

As population sizes increased, the necessary selection coefficient required to maintain the genetic variation decreased following an exponential decay function (Fig. 3). Based on the exponential decay function, when population sizes are very large a small selection coefficient is sufficient to maintain genetic variation indefinitely when migration is present. Farm fields are connected through traffic, tillage equipment, planters, sprayers, and combines. If selection pressure differs between fields connected by traffic, genetic variation can be maintained indefinitely. However, because selection imposed by herbicides is strong, if there was no migration between sites, then fixation of a single, most fit, genotype would occur quickly in the presence of herbicides (Fig. 4). When selection is imposed, the number of generations to fixation follows an asymptotic trend, rather than a linear trend, in respect to number of generations (Fig. 4). Without migration, imposing selection on weeds populations with management strategies such as herbicide applications will greatly accelerate the fixation of a single genotype (i.e. an allele in the simulation) in producers' production systems.

Like conservation scientists, weed scientist should consider the role of management programs on genetic variation, albeit for the opposite reason. A species conservationist who strives to maintain genetic variation in endangered species (Storfer 1999; Laikre et al. 2020), to prevent inbreeding depression and thus subsequent extinction, must grapple with the fact that the evolutionary forces of natural selection, genetic drift, and gene flow do not act in isolation (Andrews 2010; Star and Spencer, 2013), so too should weed scientists. Lewontin (1974) contended that neither neutral models (Kimura 1968) nor selective models (Fisher 1930) fully explained genetic variation present in populations when considering the effects of stochastic loss of alleles in finite populations (Wright 1948). Recently, stochastic modeling has allowed evolutionary biologists to understand that gene flow, selection and drift all work together to maintain genetic variation in cross-fertilizing species (Star and Spencer 2013).

Our results corroborated that the forces of selection, drift and geneflow worked together to either maintain or purge genetic variation, even though in our simulation cross-fertilization (heterozygosity) was not considered. In our simulations here, the genetic drift or selection would quickly erode genetic variation within sites unless there was migration present (Fig. 4). Weed scientists, agricultural/rangeland managers, and ecologists want to reduce pressure from invasive weed species; thus, one of their goals should be to reduce the genetic variation that allows invasive species to adapt. Because professionals working to manage weeds populations are often unable to reduce population sizes of the weed greatly drift, or eliminate differential selection applied on weeds by various cropping systems, reducing migration through cleaning of equipment or vehicles involved with farming and rangelands management is an imperative first step to reducing the adaptive capacity present in self-fertilizing annual weeds.

The maintenance of genetic variation within sites through differential selection and migration mechanisms has profound implications for observed genetic and phenotypic variation in self-fertilizing invasive species. *Bromus tectorum*, a self-fertilizing annual species, in the invaded range has substantial phenotypic variation within site (Revolinski et al. 2023, Rice et al. 1997). Within-site phenotypic variation, generated by the maintenance of genetic variation, impacts the efficacy of management of invasive species. For example, genotypes of *B. tectorum* vary in the number of growing degrees required to reach

maturity (Lawrence 2015, Revolinski et al. 2023). In low external input farming systems typical of eastern Washington, where a farmer would apply control inputs in single application, inherent phenotypic variation for maturity facilitates *B. tectorum* avoidance of management inputs – early cohorts *B. tectorum* are not impacted, or there is germination and seed set after the input.

Although our simulation of Wright's two-island model is not complex in the assumptions made by the model and the interpretation of results, the outcome of evolutionary forces that the simulation reveals extends far beyond a two-island system. In the inland PNW where *B. tectorum* plagues cropping systems, many distinct multi-locus genetic groups of *B. tectorum* are present (Revolinski 2022) within a highly heterogenous environment where specific genetic groups (or lineages) likely have a biological fitness advantage at specific sites (Holt 2009). If migration of weeds seed between sites occurs on a regular basis than lineages of *B. tectorum* adapted to specific sites will colonize those sites, but standing genetic variation will be maintained within the sites by the influx of individuals migrating between sites. With many farmers farming multiple fields, renting or sharing equipment in the inland PNW, there is likely a complex web of human-mediated migration networks of weeds seeds in the region. The complex migration web is likely maintaining the genetic variation observed in *B. tectorum*.

As indicated by the results of the study, migration facilitates the maintenance of genetic variation within site for self-fertilizing annual species. The management implication is that cleaning equipment transported between sites (Fig. 1) will reduce variation present within sites – or fields (Fig. 2). Best management practices for preventing herbicide resistance already include preventing migration of propagules between sites (Norsworthy et al. 2012). Weeds adapt to niches to exist within agricultural systems (Prentis et al. 2008), using best management practices, such as cleaning farm equipment to reduce migration, to reduce the genetic variation will inhibit the ability of weeds to adapt to those niches that facilitate success. Our results corroborate reducing seed propagule spread on equipment will slow adaptation of self-fertilizing weeds to the cropping system by reducing the available genetic variation for adaptation to management systems or inputs.

Based on our findings, we predict that self-fertilizing annual invasive species such as *B. tectorum* will continue to thrive where migration and differential selection maintains adaptive variation. Cleaning farming equipment between uses in different fields could break-up the human-mediated migration complexes driving the maintenance of genetic variation in self-fertilizing annual weeds. Therefore, we would recommend that cleaning farm equipment and other actions to reduce human-mediated transport are implemented at regional levels to reduce the genetic variation available for weeds to adapt in those systems. Additionally, the simulations presented here demonstrate the value of forward stochastic genetic simulations in explaining observable phenomena in weeds. We hope that our manuscript will inspire other scholars working with weeds to utilize population genetic models more general than those models considering only herbicide resistance as a trait.

DECLARATIONS

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Conflicts of interest

The authors have no conflicts of interest to disclose.

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Figures

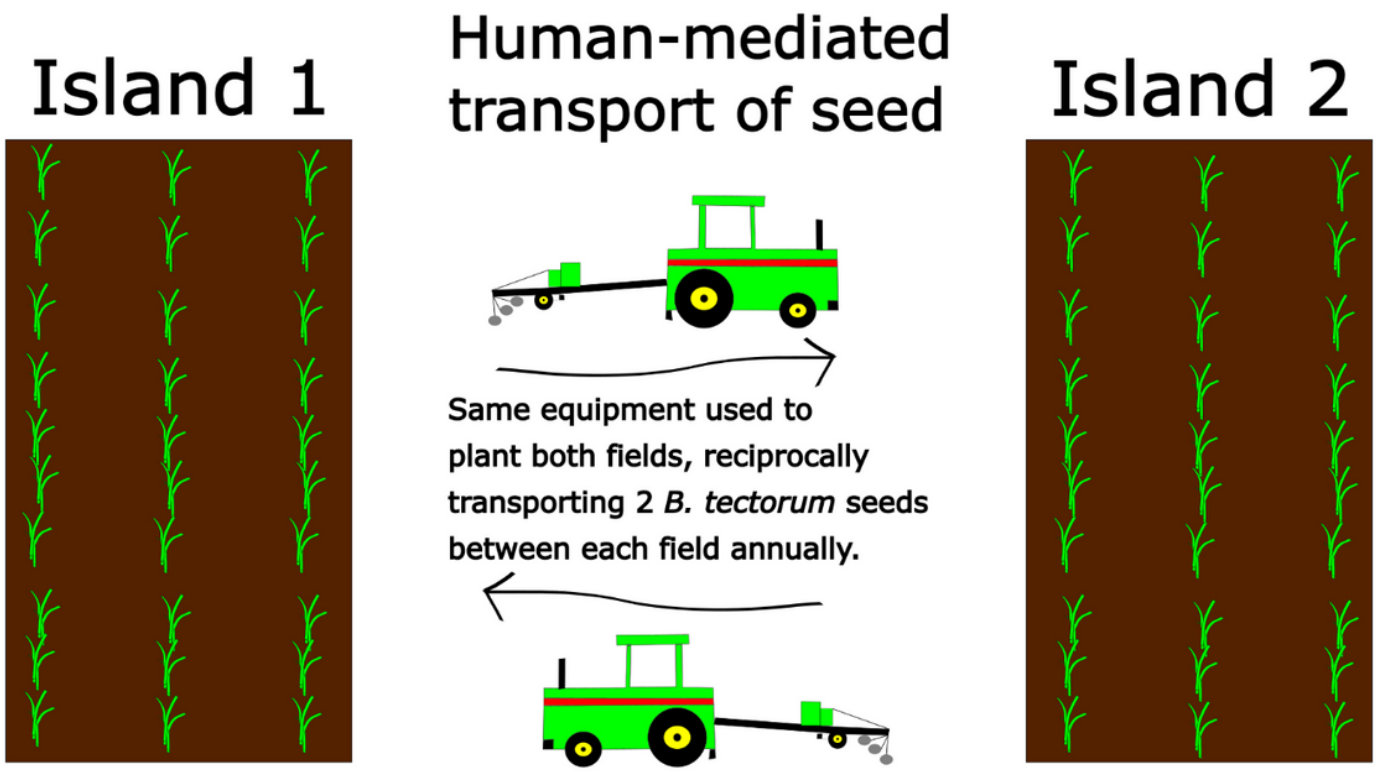

Figure 1

Depiction of a hypothetical farming scenario for two-island Fisher-Wright model where a farmer is using the same planting equipment to plant both farm fields, spreading weed seed between the two fields reciprocally on an annual basis.

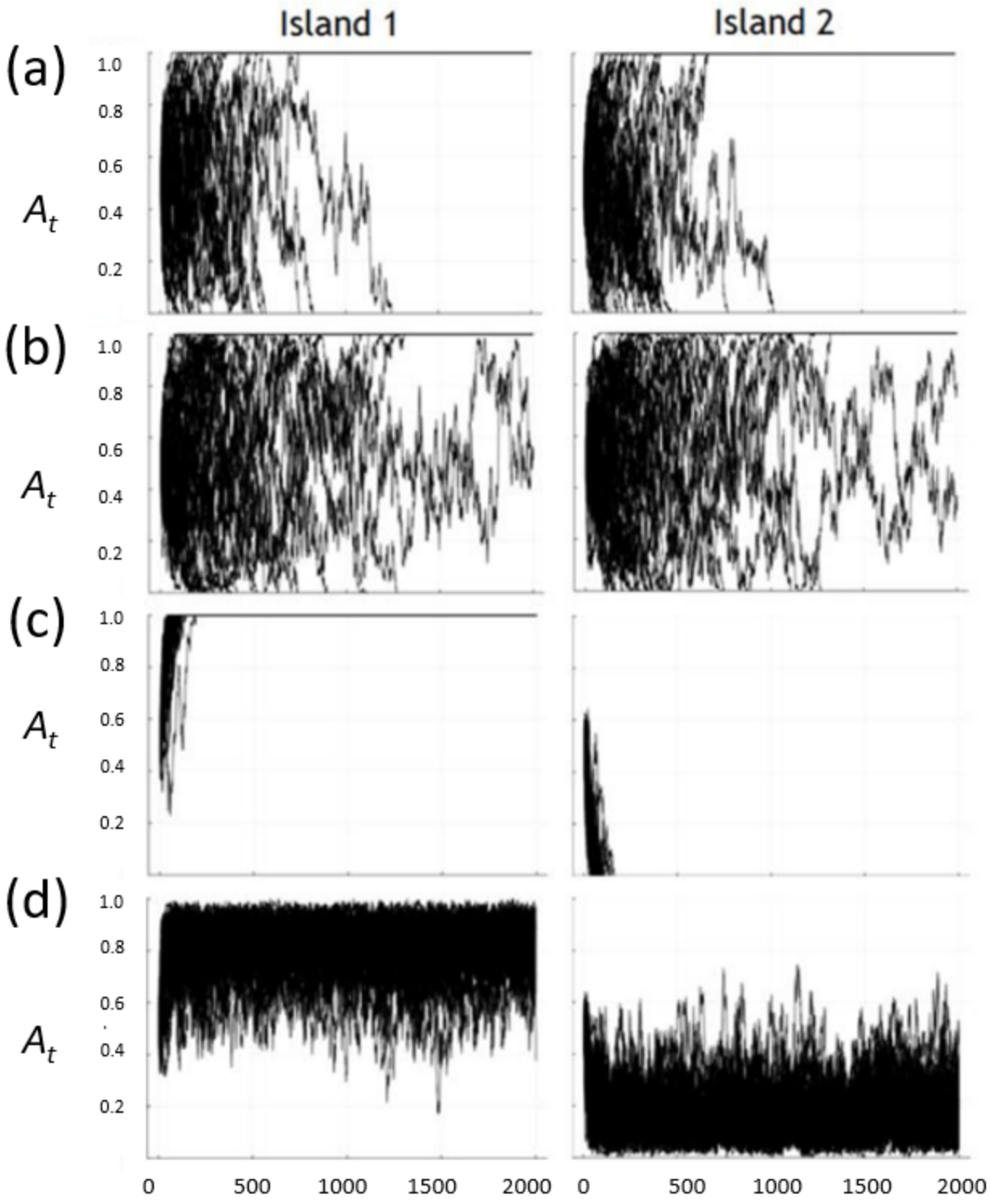

Figure 2

Frequency of genotype *A* on two potentially inter-connected islands at time *t*. (A) is no migration or differential selection, (B) is with migration (pairwise, two individuals per generation) but no differential selection, (C) is selection but no migration, and (D) is migration (pairwise, two individuals per generation) and differential selection.

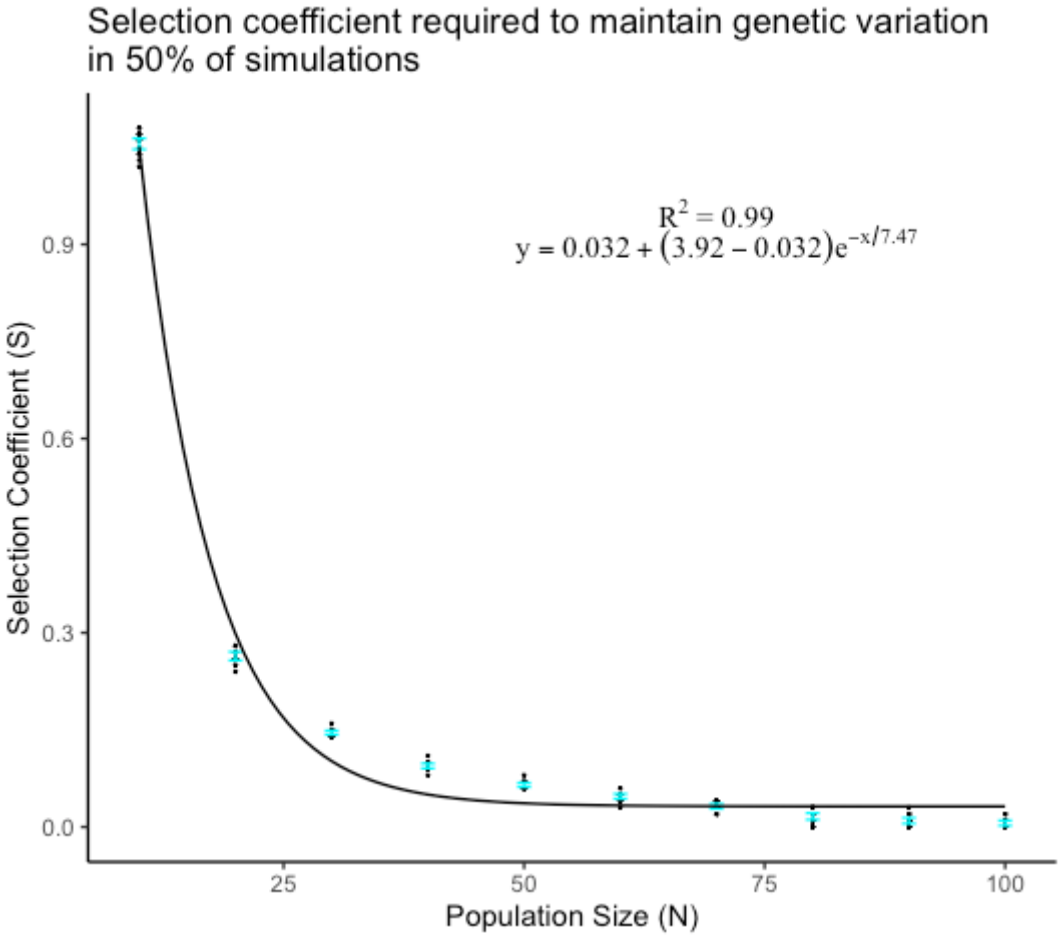

Figure 3

Selection coefficient to maintain genetic variation in the Fisher-Wright two-island model 50% of the time for 200 generations as population sizes increase, ranging from 10 to 100 increasing by 10. Confidence intervals represent 99% confidence intervals for the selection coefficient required to maintain genetic variation in at least 50% of the simulations.

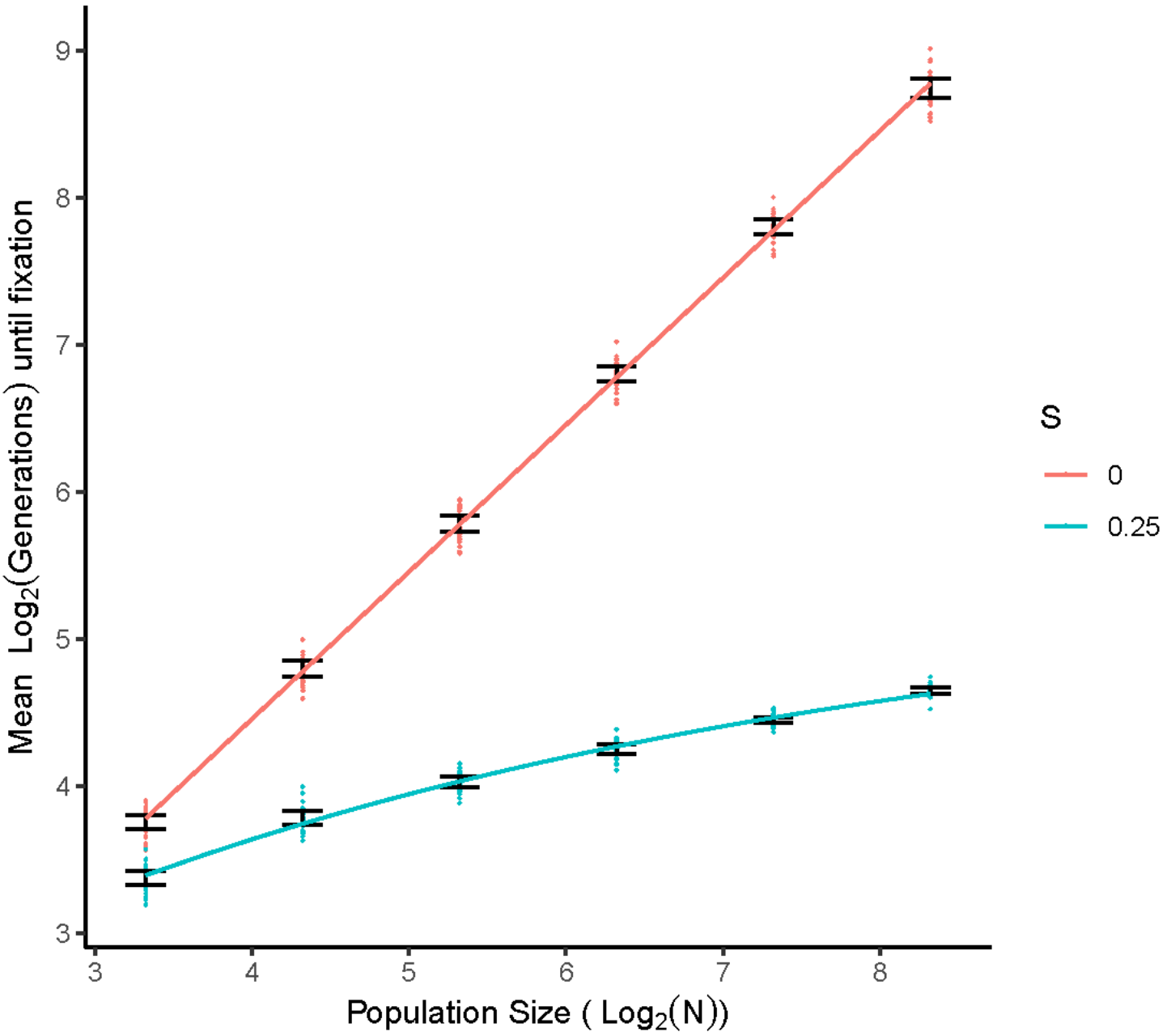

Figure 4

Average number of generations until fixation as populations sizes increases, when migration is removed from simulations. Both generations and population size are in $\log_2$ scale because population sizes ranged from 10 to 320 being doubled between each simulation series. Confidence intervals represent 99% confidence intervals for the means of the 30 replications of the 100 simulations.