Dissecting fluctuating selection: A unified population and quantitative genetics framework

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Abstract

One of the longstanding debates in evolutionary biology is the effect of fluctuating selection on genetic changes in populations. However, the extent to which these periodic forces influence organisms at both genomic and phenotypic levels remains unclear. Furthermore, despite the compelling evidence of fluctuating selection from recent studies, there is a disconnect between empirical findings and theoretical models concerning the underlying mechanisms due to the limited evidence regarding the scale and processes that generate stable genome-wide oscillations. This study aims to elucidate the genetic and ecological factors driving fluctuating selection and to identify the parameters that produce consistent oscillatory patterns in allele frequencies. To address these longstanding challenges, we developed a modeling framework integrating quantitative and population genetics to simulate a population under various selection regimes. Using SLiM, a forward evolution simulator, we varied genetic (heritability and genomic architecture) and ecological (selection pressure and season length) parameters. Unlike previous models focusing on selection acting directly on loci, our approach evaluates individual fitness based on the shift in the seasonal optimum relative to the mean phenotype. We also applied spectral analysis to detect periodicity, indicating cyclical selective environments. Our simulations shed light on conditions sustaining oscillations in allele frequencies over time. Spectral analysis successfully identifies the periodic patterns from allele frequency, even under highly complex selection regimes. Not only does our study clarify the conditions that yield persistent oscillatory behaviors, but these parameters are also relatively easy to predict from natural population, providing a possibility of empirically testing these models.

Introduction

Understanding the dynamic nature of evolution in populations is at the core of evolutionary biology. The direction and intensity of selection can vary significantly through time [1–4].Various factors can lead to these fluctuations, perhaps the most notable of these being seasonal variability. In addition, as climate change imposes unprecedented changes in conditions across the globe, fluctuations in selection pressure are predicted to intensify [5] . Thus, the ability to predict how a population will evolve in response to dynamic environmental conditions has implications for the future of biodiversity. However, while there is widespread appreciation for the relevance of fluctuating selection for populations [6–11], we still lack a clear understanding of the potential impact of fluctuating selection on genome-wide allele frequency dynamics.

Many empirical studies have shown that strong selective pressures can produce rapid phenotypic and genomic changes across diverse species, a phenomenon that has been vigorously documented not only in domesticated plants and animals [12, 13] but also in wild populations exposed to well-defined selective pressures [1, 3, 14] and through laboratory experiments [15–17]. Furthermore, the direction and intensity of selection have been shown to fluctuate over time [1–3, 18–21] due to various factors, including seasonal temperature variability, boom and bust cycles of predator populations, and other biotic and abiotic agents [8, 14, 22–25]. In natural populations, a recent observation is very rapid changes in allele frequencies, with some occurring repeatedly in a seasonal cycle, oscillating back and forth each year (e.g., [9, 26–28]), with the explanation for the pattern being fluctuating selection. For example, Behrman et al. suggested that changes in bacterial populations infecting fruit flies, *Drosophila melanogaster*, due to temperature fluctuations between seasons influence the seasonal cycling of immune genes. In addition, Pfenninger & Foucault, studied fluctuating environments using *Chironomus riparius* and confirmed earlier

results from Rudman et al. about the genomic and phenotypic changes brought by the seasonal environment on natural populations [9, 28]. However, population genetic models that include fluctuating selection pressure generally find only a narrow range of parameter space leading to stable oscillations in allele frequencies [23, 29, 30]. This disconnect between theory and empirical results has led to disagreement and uncertainty in whether the observed empirical patterns of oscillating allele frequencies are due to fluctuating selection or some other mechanism [23, 31].

Previous theoretical models of fluctuating selection have typically fallen broadly into two classes: 1) population genetic models that focus on predicting allele frequency trajectories, often focusing on a single or very few loci; and 2) quantitative genetic models that focus on predicting phenotypic trajectories and typically assume a polygenic (often infinitesimal) genetic architecture defined by emergent genetic properties (i.e. heritabilities and genetic correlations) and ignored the dynamics of individual loci. Past computational limitations of tracking loci genome-wide motivated the contrast in these two approaches, but while these limits have been diminishing rapidly over time, most models still fall largely into one framework without fully bridging these approaches, a gap in the field that has been noted by others (e.g., Barghi *et al.* 2020). Many previous quantitative genetic models of fluctuating selection have produced robust predictions for resulting phenotypic evolution [32, 33], the evolution of phenotypic plasticity and bet-hedging [34], and the maintenance of genetic variation [35, 36]**.** While most previous population genetic approaches to fluctuating selection focused on allele frequency dynamics have found only very limited conditions that will lead to stable oscillations in allele frequencies, recently, some models have considered more complex scenarios to define the parameters under which allele frequency oscillations are possible. For example, Wittmann et al. found the maintenance of polymorphism on hundreds of loci under a segregating lift mechanism, which technically involves the change in

77 dominance over seasons[30]. Furthermore, the extension of these models indicates that additional
78 parameters, including genetic and ecological factors, might as well explain the perceived temporal
79 oscillating polymorphisms[23, 31], even though validation is still required. An important detail of
80 most population genetic approaches is that they assign a specific selection coefficient to each locus
81 under consideration. However, in nature, selection acts on the phenotype and dynamics can be
82 quite different when selection is modeled at the phenotypic level with fluctuating optima, rather
83 than with a fluctuating selection coefficient acting directly at specific loci. Thus, there are
84 advantages to integrating quantitative genetic and population genetic approaches in exploring the
85 possible conditions that might lead to stable oscillations in allele frequencies.

86 Here, we develop a general modeling framework integrating population genetic and quantitative
87 genetic approaches, implemented in the powerful and flexible simulation software SLiM [37]. As
88 in other quantitative genetic models, we parameterize the model by assigning a trait heritability
89 and defining specific trait optima and fitness functions based on phenotypic values. Like
90 population genetic models, we specifically consider individual loci genome-wide, tracking
91 frequency changes over time due to the forces of genetic drift and selection. We sought to identify:

92 1) The parameter space in which fluctuating phenotypic optima lead to stable oscillating
93 allele frequencies

94 2) The circumstances in which patterns of fluctuating selection can be inferred from allele
95 frequency and phenotypic data

96 Acquiring knowledge about the above objectives will not only help us understand evolutionary
97 dynamics, but it will also help in implementing accurate predictive models of evolution, enhance
98 conservation efforts, and play a role in both disease and pest control, especially nowadays when
99 species are experiencing various environmental shifts due to climate change.

Methods

Genome size, population setup, and model assumptions

We simulated evolutionary events that use a Wright-Fisher model of a constant population with 10,000 individuals for fluctuating and constant optima and neutral selection. We set a genome size to be approximately 1.2MB for an autosomal chromosome, which varied with a few additional bases (< 1,000 bases) depending on the number of loci affecting the phenotype. Conversely, our study has also considered different genetic architectures: monogenic, oligogenic, and polygenic traits, as shown in the model parameters section. The model assumes known quantitative trait loci (QTL) with a locus effect drawn from exponential distribution. For polygenic and oligogenic models, we assume most loci have minor effects on the phenotype and a few have a large effect size [38]. We did not include a term for genotype by environment interaction in this model, meaning it is not possible for phenotypic plasticity to evolve in our models.

In addition, our simulations assume sexual reproduction with an equal sex ratio, no new mutations, and a recombination rate of 10^{-8}, which is a commonly used value in other SLiM models [37], and it reflects the average recombination rate for many mammals [39]. The initial allele frequency was set to vary among the loci. The probability for an individual to carry a given QTL was drawn from a uniform distribution, and the presence of the allele in individual's genome was determined using a binomial distribution, leading to different initial frequencies across the population. All models were simulated using SLiM V4.2.2 [37], and we tracked each position's frequency and mean population phenotype over generations.

Model parameters.

To better understand the underlying processes governing the changes observed in a population under fluctuating selection, we assessed a range of parameters for genome architecture, heritability, selection strength, and selection length (summarized in Table 1). These parameters are considered essential for affecting the response to selection [40–45]. Our models considered QTLs distributed along the genome (genome size ≈ 1.2MB) with equal neutral regions between loci. In addition, we hypothesize that different values of heritability (check how we defined h^2 in selection models section) might affect the evolvability of a population in different ways, especially when experiencing selection, therefore, we considered its various values in this study. While some previous studies have identified that most fertility-related traits are lowly heritable, in contrast, morphological traits are highly heritable (e.g., fertility vs. height) [44, 46, 47]. Therefore, we predefined the heritability at the initial generation and sought to account for values that encompass a wide range of trait (traits with low to high heritability).

Our study also considered selection strength as a parameter to explore its role in driving genomic and phenotypic diversity within a population. Previous studies show that different selection pressures drive adaptation by influencing evolutionary and population dynamics [48, 49]. Our models used a selection criterion predicated on an individual's fitness derived from the distance between the phenotype and the new optimum (Equation 1). The strength of selection depended on the distance between the population's mean phenotype and the optimum at the current generation, modulated by a constant value that controls the sensitivity of fitness to changes in this distance (Figure 1 & Equation 1). The optima values are defined from the initial generation as the sum or difference of mean phenotype and a standard deviation (referred to as distance to optimum, SD),

depending on which selection model is considered (Equations 2 for constant, 3 for instantaneous, and 4 for gradual selections).

Moreover, we considered different genetic architectures to explore how they interact with other parameters. Various theoretical studies have shown that genetic architecture can significantly affect population evolution while experiencing environmental changes [50]. Remarkably, while single locus and multiple loci models behaved in a similar manner, e.g., driving the population adaptation and extinction, researchers show that models with intermediate loci may contain complex evolutionary behaviors [50–52]. Consequently, our models include a single locus, oligogenic with 10, and polygenic 70, 100, and 300 traits models. The consideration of multiple polygenic models was to assess if there are significant changes in dynamics as the number of loci for a polygenic model increases.

The final set of parameters considered in our models is the number of generations over which the selection event is likely to last (selection length). As described in the next section, this parameter had different ranges depending on the model under consideration (Table 1). All values were chosen arbitrarily to illustrate model behavior, and we employ a four-season framework purely as a complexity system rather than to mimic any specific population. To clarify, in this framework, each season may correspond to a year during which the population undergoes a particular number of generations (which may differ from one season to the next, for four years), and then the cycle repeats.

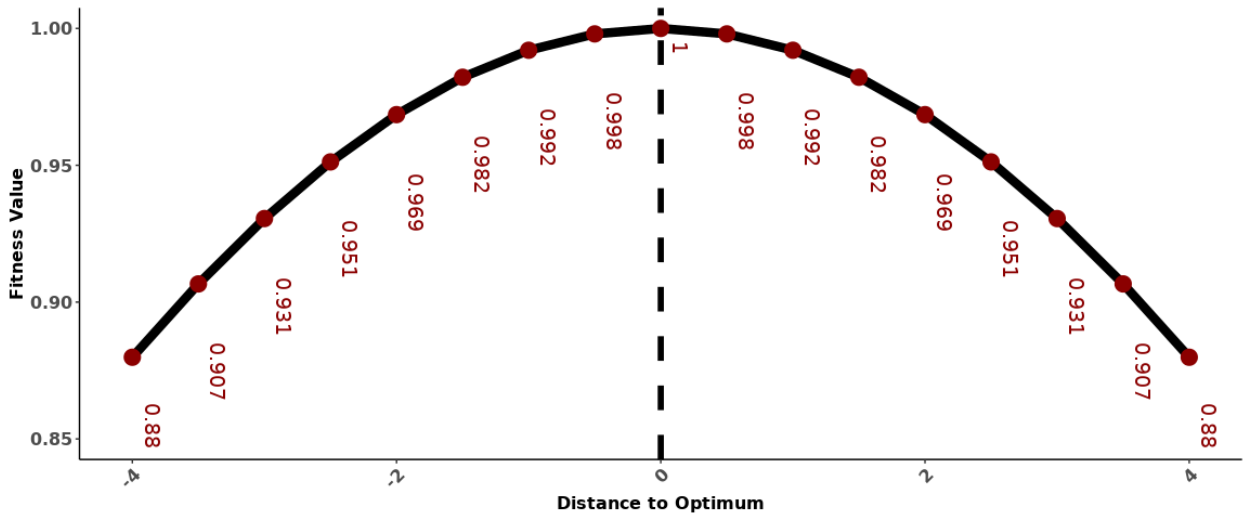


Figure 1. Change in fitness as the optimum moves away from the phenotype (vertical dashed line). The numbers colored numbers are the fitness values at given optimum and each point is at 0.5 interval.

Table 1. Simulation parameters. Note that each parameter value is considered at once except the generation interval in the four unequal seasons model, where all values are used in a single simulation.

Parameters	Size
Population	10,000
Heritability (h^2)	0.1, 0.5, 0.8
Distance to optimum (SD)	1, 2, 3, 4
Selection length (Two equal seasons)	10, 20, 30
Selection length (Four unequal seasons)	12, 22, 10, 16
Number of loci	1, 10, 70, 100, 300

174 **Selection models**

175 The current study primarily focuses on fluctuating selection resulting from instantaneous changes
176 in optima and extends to both simple and complex gradual changes. Additionally, we explored
177 neutral and constant selection (Figure 2.A) to assess the effect of drift and directional selection,
178 respectively, and how these models differ from fluctuating selection models [53, 54] in maintaining
179 polymorphism.

180 We implement the instantaneous model by considering two binary environments with two equal
181 seasons, where the change in optimum phenotype is direct, as illustrated in Figure 2.B. Moreover,
182 it is common to find a natural population experiencing gradual environmental changes [55, 56]; a
183 good example is a temperature change over the seasons. Therefore, we extended our models to
184 consider a gradual shift in optimum over generations. The first gradual model (Figure 2.C) helps
185 to study relatively simple evolutionary scenarios, while the second model (Figure 2.D) helps
186 understand complex evolutionary scenarios in which a population may experience a gradual
187 change in optima with multiple seasons, each resulting in a different number of generations, a
188 typical situation for multivoltine organisms that exhibit different generation numbers over the
189 seasons [57–61]. For instance, when the optimum temperature is very high during a given season,
190 it can hinder an organism's development, and also the reproduction rate. Conversely, at moderate
191 temperatures, the development rate can increase to reduce the time to maturity, which can result in
192 many generations [62–64]. Essentially, a population can experience many generations under
193 favorable environmental conditions subjected to a given selective force. In contrast, fewer
194 generations will experience that selective force in a harsh environment, potentially affecting the
195 observed genetic and phenotypic patterns.

For all models, an individual's fitness determined their contribution to the next generation via sexual reproduction. The fitness (W) for constant and fluctuating selection is a function of the squared distance between the individual's phenotype ($\boldsymbol{Z}$) and the optimum ($\boldsymbol{Z_{opt}}$), the number of standard deviations (distance to optimum) from the initial mean population phenotype (Equation 1).

$$\boldsymbol{W} = \mathbf{exp}\left[-\frac{\mathbf{1}}{\mathbf{125}} * \left(\boldsymbol{Z} - \boldsymbol{Z_{opt}}\right)^{\mathbf{2}}\right] \qquad \text{Eq.1}$$

Where the constant 125 controls the steepness of the fitness function. We did not alter this scaling factor to change the strength of selection, instead altering how far the new optimum was from the population mean to achieve different strengths of selection.

The phenotype ($\boldsymbol{Z}$) is calculated as $\boldsymbol{Z} = \sum_{\boldsymbol{l=1}}^{\boldsymbol{L}}(\boldsymbol{L}) + \boldsymbol{e}$ where L represents the total number of segregating sites affecting trait. Also, **e** is the environmental effect where $\boldsymbol{e} \sim \boldsymbol{N}(\mathbf{0}, \boldsymbol{VE})$ and **VE** is the environmental variance from the heritability equation ($\boldsymbol{h^2} = \boldsymbol{VA}/(\boldsymbol{VA} + \boldsymbol{VE})$; **VA** is the additive variance) [65, 66]. The expected value of VA was calculated using the equation $\boldsymbol{VA} = \frac{\mathbf{2} * \boldsymbol{nloci}}{\mathbf{3}}$, where $\boldsymbol{nloci}$ is the number of loci affecting the trait. This calculation was based on the results from 100 iterative simulations. Therefore, the expected phenotypic standard deviation is $\boldsymbol{sdp} = \boldsymbol{sqrt}(\frac{\boldsymbol{VA}}{\boldsymbol{h^2}})$, and the expected mean phenotype $\boldsymbol{mup} = \boldsymbol{nloci}$. We finally scaled Z to be $\boldsymbol{Z_{(adj)}} = \frac{\boldsymbol{Z - mup}}{\boldsymbol{sdp}}$ so that the population mean reflects the number of loci contributing to the phenotype with an expected mean of 0 and standard deviation of 1 to keep the phenotypes on a similar scale regardless of the number of contributing loci.

The optimum $\boldsymbol{Z_{opt}}$ for each mode of selection was obtained as:

$$\boldsymbol{Z_{opt(constant)}} = \overline{\boldsymbol{Z}} + \boldsymbol{n\sigma_Z} \qquad \text{Eq.2}$$

$$Z_{opt(instantaneous)} = \bar{Z} \pm n\sigma_Z \quad \text{Eq.3}$$

$$Z_{opt\,(gradual)} = \frac{\left[\bar{Z} \pm n\sigma_Z * sin\left(2\pi * \frac{T}{i}\right)\right]}{S} \quad \text{Eq.4}$$

$\bar{Z}$ is the mean phenotype, n is an integer number (0 < n < 5), σ_Z is the phenotype's standard deviation for a given generation, T is the current generation, i is the number of generations the current season (environmental condition) takes, S is scaling factor equals 1 for gradual two equal seasons and 4 for gradual four unequal seasons (Figure 2).

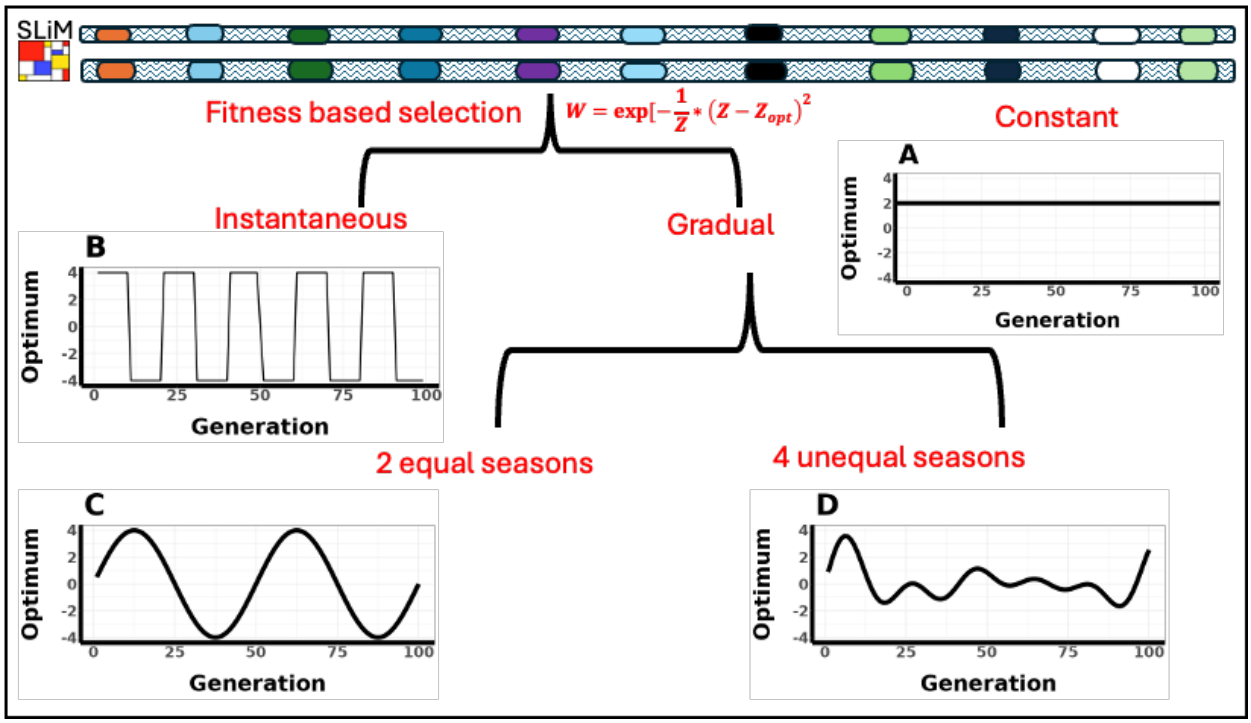


Figure 2. Illustration of simulation in SLiM featuring positions with known effect and how optimum changes for each selection model: A reflects the constant model, B shows the instant change in optimum, C shows the sinusoidal change for two equal seasons, and D is for sinusoidal change for four unequal seasons. The lines show the change in optimum over generations.

Identifying signals of fluctuating selection from allele frequency and mean phenotype

We used ggplot2 [67] to visualize changes in allele frequency and the population mean phenotype over time. Furthermore, spectral analysis as a mathematical tool that decomposes a time-domain

signal into its frequency-domain representation, it reveals how variance in a time series is distributed across different frequencies [68]. Consequently, we used spectral analysis to decompose the allele frequency signal and identify seasonality (the selection period), which enabled us to detect fluctuating selection in our dataset. Specifically, we first averaged the allele frequencies across all loci to obtain a single mean frequency per generation. We then organized these mean values into time-series, with each generation corresponding to a time point, to illustrate changes in allele frequency over time. Finally, we estimated the spectral density of each time series using the spectrum function from base R [69] and applied a smoothing span of 2 to reduce noise and reveal the dominant periodic components. This approach enabled us to detect and characterize cyclical patterns in allele frequencies across generations.

Results

In our models, the key parameters were (1) selection strength, (2) heritability, (3) the number of generations per selection season (season length), and (4) genetic architecture. We considered these parameters for several different selection models, including instantaneous selection (Supplemental 1), gradual two equal seasons (Supplemental 2), gradual with four unequal seasons (Supplemental 3), neutral selection (Supplemental 4), and constant selection (Supplemental 5), with subsections for parameters' interactions.

Instantaneous selection for polygenic traits

The instantaneous selection model focuses on sudden shifts in selection pressure after a time; therefore, it provides a direct way to analyze evolutionary dynamics while accounting for multiple genetic and ecological parameters. We first only consider the model with 100 loci and explore the effects of the other parameters. Following these results based on a 100 loci model, we vary the genetic architecture and discuss its effects in the next section. By applying the instantaneous

section model to various combinations of parameters under polygenic traits, we observed meaningful effects on dynamics of allele frequency and population mean phenotype (Figure 3). Higher parameter values (SD, h^2, and Gen) often produced more apparent amplitude oscillations (Figure 3.A), especially in mean phenotypes (Figure 3.B). Also, spectral analysis confirmed these findings by showing more pronounced peaks under high heritability and strong selection pressure (Figure 3.C), while it reveals broader peaks when the selection period increased (Supplemental Figure 1.2.3 - 1.2.4).

Among these parameters, heritability (h^2) had a particularly notable influence on the magnitude of oscillations ($h^2 = 0.8 > 0.5 > 0.1$). Highly heritable traits amplified selection effects with pronounced fluctuations in allele frequencies and phenotypes. Conversely, low heritability masked changes in allele frequencies and reduced shifts in mean phenotypes, making ongoing selection less obvious. Despite the allele frequency and phenotypic observations on the effect of heritability, the spectral analysis showed a more prominent, distinct peak at all heritability levels (Supplemental Figures 1.2. Heritability increases from top to bottom).

Besides heritability, selection pressure - defined by the distance between the phenotype and the new optimum - also shaped how allele frequencies and phenotypes evolved over time. More substantial selection (for example, SD = 4 vs. 1) led to greater fluctuation and variability in allele frequencies (Figure 3.A), alongside more pronounced oscillations in phenotypes. The spectral analysis supported these observations, indicating that strong selection reduced variation in spectral density among replicates, and each unit of selection intensity still produced a clear peak (Figure 3.C).

In addition to heritability and selection pressure, the selection season (number of generations per season, Gen) further influenced how much fluctuating selection could affect dynamics in the

population. Longer periods (e.g., 30 generations) allowed more time for selection to act, producing more visible oscillations in allele frequencies and mean phenotypes than shorter periods (e.g., 10 generations). Although these differences sometimes appeared subtle in raw allele frequency data, spectral analysis detected seasonal patterns under shorter selection periods, albeit with narrower peaks (Supplemental Figure 1.2.4: from short (SI 1.2.4.1) to long (SI 1.2.4.3) period).

As these parameters interact, different combinations affect the persistence and intensity of oscillations across generations. For instance, low selection pressure (SD = 1), low heritability, (h^2 = 0.1), and a short season (10 generations) yielded relatively stable frequencies with minimal fluctuations. Increasing any of these factors, particularly selection pressure or heritability, intensified oscillation amplitude. Notably, combining high selection pressure (SD = 4), high heritability, (h^2= 0.8), and a long season (30 generations) produced persistent oscillations across multiple loci (Figure 3.A, lower right). However, higher fluctuations tend to be intensified for loci at intermediate initial frequencies (between 0.25 and 0.75). Additionally, phenotypic trends paralleled these allele frequency changes and became more evident under stronger selection or higher heritability. Unlike allele frequency, phenotypic change is very apparent when there is an increase in either one of the parameters (heritability, selection period, and intensity), a condition that is hard to quickly notice for heritability and selection season by simply visualizing allele frequencies.

Spectral analysis under the instantaneous selection model further clarifies how those fluctuations persist across parameter combinations. It consistently shows a peak for seasonal selection, regardless of parameter size and combinations. However, it is possible to deduce the effect of each parameter through comparisons, especially with multiple replicates. Smaller parameters cause significant variability in spectral density, while increases in parameters like heritability and

selection strength reduce this variability (see Figure 3.C). Overall, high selection intensity, a longer selection period, and substantial additive genetic variance maintain genome-wide variation over generations, allowing observed allele frequency oscillations to persist for many generations.

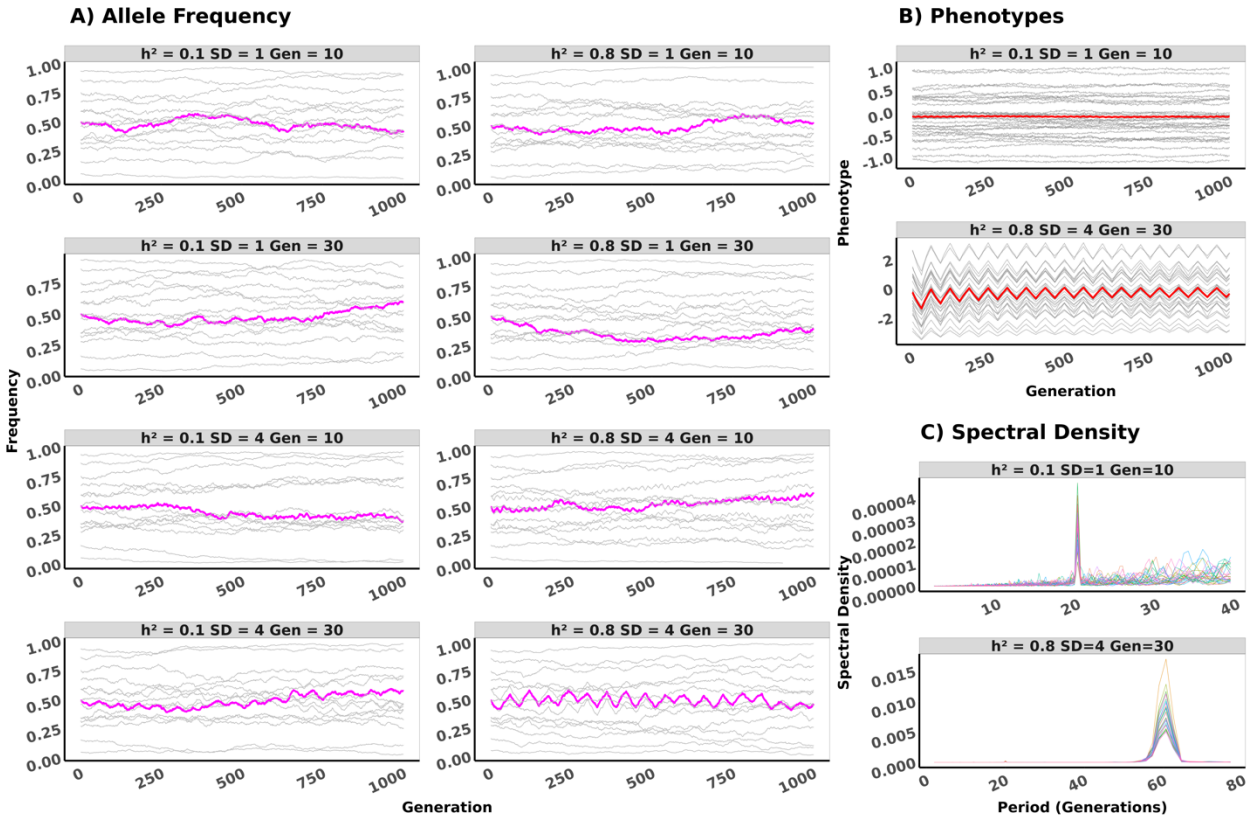


Figure 3. *Evolutionary dynamics for a population with polygenic trait (loci = 100) experiencing an instantaneous fluctuating selection.* ***A****. represents allele frequency dynamics and shows parameter combinations from a single replicate for 1000 generations. Each line in the plot represents the frequency trajectory of a locus among 15 loci randomly sampled from 100 loci, and the magenta line highlights dynamics of single locus.* ***B.*** *Distribution of population mean phenotype dynamics representing 30 replicates over 1000 generations with red line representing the mean across all replicates.* ***C.*** *The spectral density from allele frequency for all 2000 generations; each colored line represents a single replicate. The large peak in the spectral plots marks a complete cycle of selection season. The variables are heritability (h^2), selection strength (SD: number of standard deviations also known as distance to optimum), and the selection length in terms of number of generations (Gen).*

316 **Genetic architecture: Polygenic, Monogenic, and Oligogenic Traits**

317 In addition to evaluating the parameters that influence an instantaneous selection on polygenic
318 trait, we also examined how genetic architecture affects observed evolutionary dynamics. We
319 hypothesized that the number of loci influencing the trait could interact with other parameters,
320 heritability, selection strength, and selection duration. Overall, the patterns identified in our
321 polygenic model extend to monogenic and oligogenic traits, although fewer positions affecting the
322 trait tend to produce more pronounced oscillations in allele frequencies and phenotypes. That
323 makes it easier to distinguish the influence of each parameter, mainly heritability and selection
324 duration, which exert more subtle effects in polygenic contexts.

325 Overall, monogenic traits display the most conspicuous cyclic fluctuations in allele frequencies
326 and allow seasonality detection (Supplemental figure 1.1.1). Oligogenic traits also exhibit clear,
327 though somewhat weaker, oscillations than monogenic traits (Figure 4) due to some loci
328 demonstrating no great changes in frequency. In monogenic and oligogenic models, higher
329 heritability and intense selection accelerate and amplify allele-frequency shifts, whereas lower
330 parameter values yield weaker oscillations (Supplemental Figures 1.1.1 and 1.1.2). Although
331 polygenic traits seem to distribute selection effects across many loci, there are fewer dramatic
332 changes per single locus as seen from figure 4. Subsequently, analyzing all loci collectively can
333 reliably reveal cyclical patterns in such a complex genomic architecture while using allele
334 frequency and phenotypic trajectories. These differences are driven by the fact that the heritability
335 of the trait is held constant in each case. Thus, for a given heritability, having fewer causative loci
336 means that each of those loci will contribute a larger share to the percentage of genetic variation
337 for the trait and thus have a larger genetic effect. Thus, the observation that individual loci show

338 greater fluctuations when there are fewer loci is driven by this effect, rather than it being a feature
339 of the genetic architecture itself.
340 Moreover, spectral analysis effectively identifies seasonality/oscillations under all genetic
341 architectures but is less effective at distinguishing differences among these architectures for a
342 single replicate (Although not shown). Monogenic and oligogenic models often show distinct
343 peaks with high spectral densities, while polygenic traits typically have lower spectral densities
344 (Figure 4.C). Nevertheless, the greater variation in spectral peaks across replicates in monogenic
345 traits may demonstrate the susceptibility to genetic drift. Oligogenic traits occupy an intermediate
346 position with more remarkable changes in a few key loci, particularly under high heritability and
347 intense selection. Polygenic traits, however, require higher heritability and selection strength to
348 display cyclical changes visibly across many loci, but the spectral analysis clearly shows that it
349 more reliably detects fluctuations in the polygenic model. As a result, even though the shifts are
350 more subtle when there are more loci sharing the effect, the analysis across all of them gives a
351 well-defined signal. Ultimately, despite the differences, spectral analysis reliably detects
352 seasonality across all genetic architectures, particularly when considering aggregate behavior
353 across loci.

354 Finally, in addition to the described means of differentiating behaviors per genomic architecture,
355 we calculated the percentage of fixed loci, as they may as well reflect the variability in spectral
356 peak across replicates. The results show that when relatively few loci (monogenic and oligogenic)
357 affect the trait, the proportion of fixed alleles is substantially higher than in polygenic systems
358 (Figure 5). In polygenic traits, increasing the number of causative loci does not notably alter
359 fixation rates, and other parameters (e.g., heritability or selection duration) have little impact on
360 this outcome (Figure 5). The fixation rates are percentages that were calculated as the ratio of the

total number of loci fixed at one and lost to the total number of loci from all replicates, multiplied by 100.

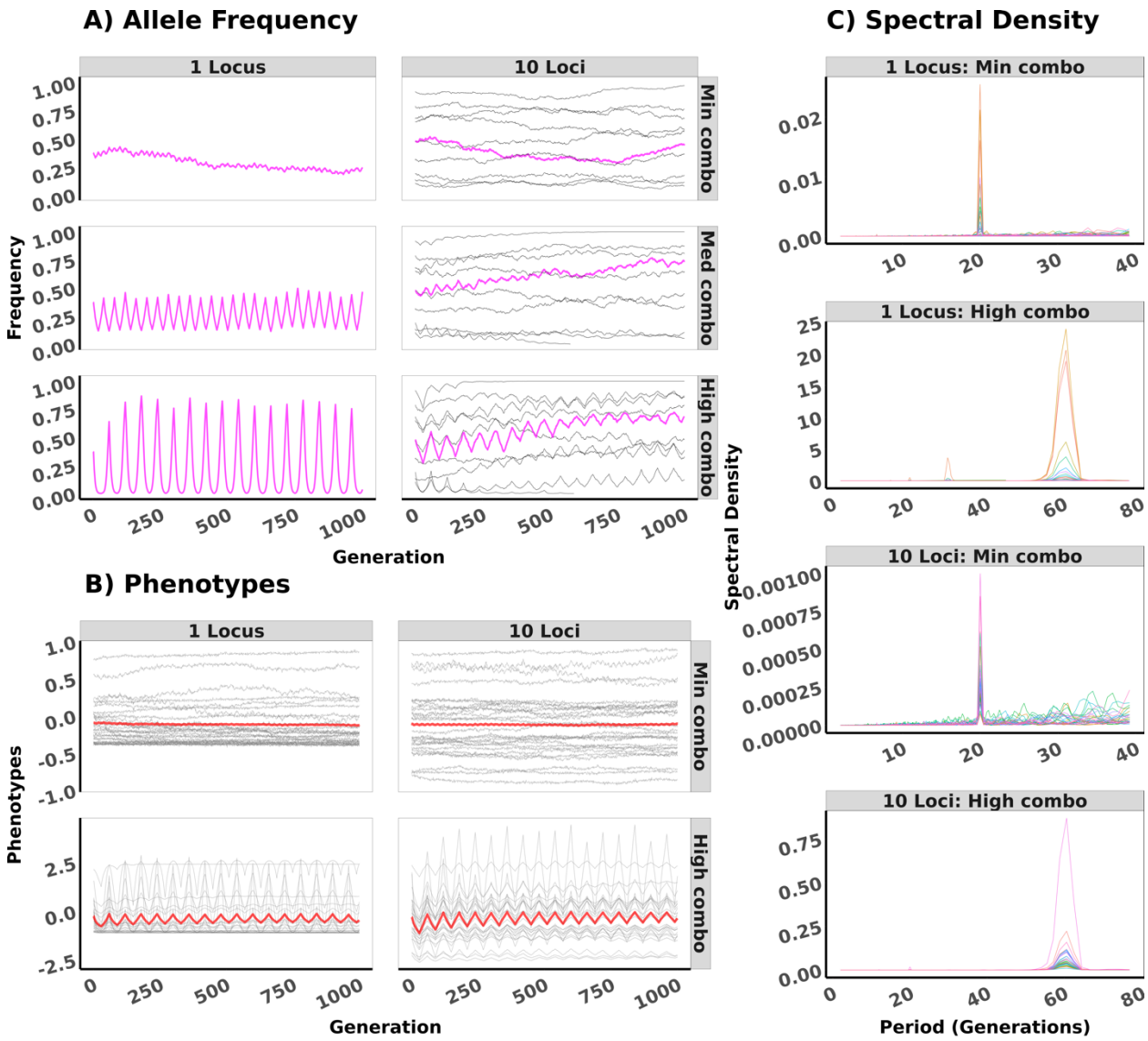


Figure 4. *Comparison of genetic architectures (monogenic and oligogenic traits) under instantaneous fluctuating selection.* ***A.*** *represents allele frequency dynamics for a single replicate for small (Min combo: h^2 = 0.1, SD = 1, Gen = 10), medium (Med combo: h^2 = 0.5, SD = 2, Gen = 20), and large (High combo: h^2 = 0.8, SD = 4, Gen = 30) parameter combinations over 1000 generations. Each line represents the frequency trajectory of a locus, with the magenta line highlighting the dynamics of a single locus.* ***B.*** *Shows distribution of population mean phenotype dynamics for 30 replicates over 1000 generations, with the red line representing the overall mean for both small and high parameter combinations in each architecture.* ***C.*** *displays spectral density of allele frequency over 2000 generations, where each colored line represents a single replicate*

for both small and large parameter combinations for each architecture. The large peak in the spectral plot marks a complete cycle of the selection season.

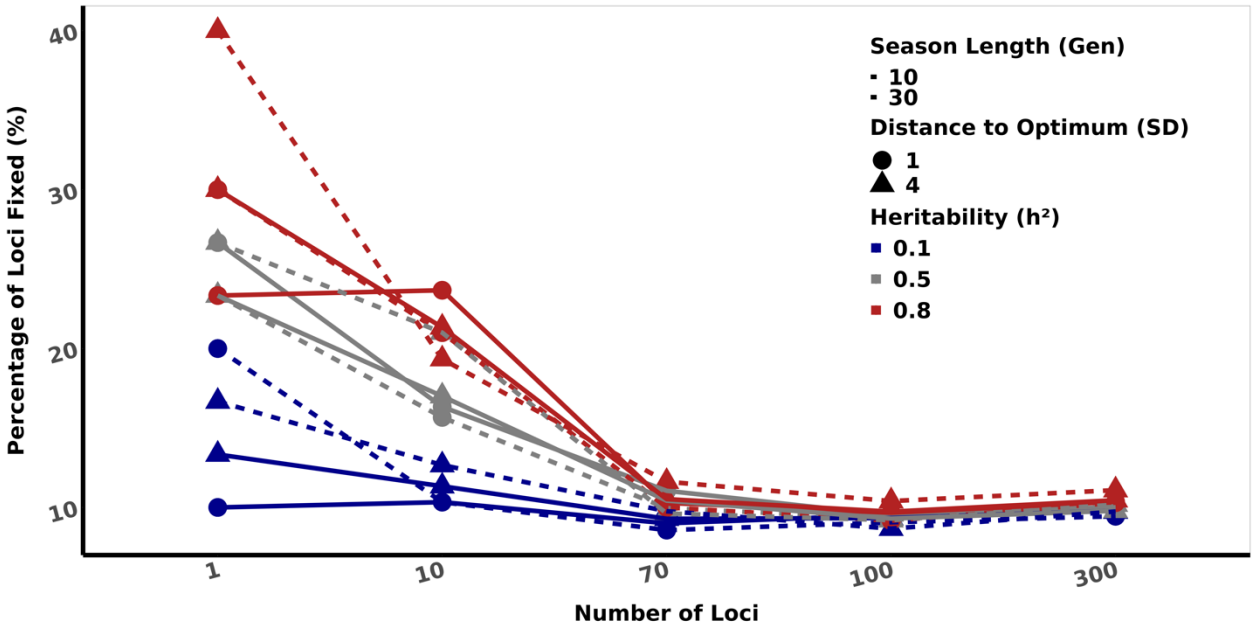


Figure 5. *Percentage of fixed loci across different genetic architectures based on parameter interactions. The monogenic trait exhibits the highest percentage of fixed loci among the 30 replicates, followed by the oligogenic model, while the polygenic model shows a consistent fixation rate.*

Beyond instantaneous selection: gradual selection models

Apart from the instantaneous model, we explored two gradual optima-change models, one with two equal seasons and another with four unequal seasons, to capture more complex scenarios of fluctuating selection [70]. These gradual-change models introduce selection more slowly, with smooth transitions between seasonal optima; hence, they reflect natural environments where conditions do not shift abruptly.

Unlike the instantaneous model, the gradual two-season model tends to obscure clear seasonal selection events, particularly in polygenic traits (Figures 6 & 7). Although gradual two-season behaves similarly to the instantaneous model, its fluctuations are less pronounced as the slower transition reduces the overall selection impact. When selection strength is relatively low,

increasing heritability or extending the selection season does not produce the same prominent allele frequency shifts seen under instantaneous selection (Figure 5, see Supplemental 2.1). Observing cyclical allele frequency changes requires high selection intensity, especially in polygenic traits. Monogenic and oligogenic traits (Supplemental Figure 2.1.1 and 2.1.2), although fluctuations are weaker than in the instantaneous model, remain detectable. Likewise, spectral analysis can identify periodicity effectively in these data, showing no major differences between the gradual two-season and instantaneous models (Supplemental Figures 2.2).

The four-season gradual model is more complex than others because it involves different selection season lengths (12, 22, 10, and 16 generations) in a single cycle. Thus, we do not isolate the effect of season length but instead focus on heritability and selection intensity. This setup reflects environments with uneven selection pressures throughout the year or across life stages, complicating evolutionary dynamics and blurring distinctions between selection and neutral drift (see later section). Even under high parameter combinations, observing periodic shifts in allele frequencies for polygenic traits is challenging (Figure 7.A) under this type of selection model. In contrast, monogenic and oligogenic traits can still exhibit noticeable oscillations at certain loci under strong selection or high heritability (Thus, additional scenarios are needed to explore the effect of specific season lengths).

Moreover, phenotypic changes generally follow the same trends as allele frequencies and can sometimes reveal more distinct oscillations (7.A and 7.B). However, these oscillations are still less prominent than in two-season or instantaneous models. Hence, as the selection model becomes more complex, higher selection intensity is required for parameters such as heritability and season length to effectively uncover seasonality in allele frequencies or phenotypes, as both gradual models demonstrate. While the gradual two-season model can display phenotypic fluctuations at

lower heritability and shorter selection periods, the more complex four-season model struggles to produce visible allele oscillations under low parameters. Both gradual models still reveal distinctive phenotypic changes in monogenic and oligogenic traits, but polygenic traits under four-season fluctuations show the least pronounced patterns, indicating that as patterns of fluctuation in selection become more complex, it may be more challenging to detect fluctuating selection in the genome.

Although clear spectral peaks are often difficult to detect in the four-seasons model, spectral analysis remains more effective than direct inspection of allele frequency trajectories for identifying periodic signals (Figure 7.C, Supplemental Figures 3.2.1 and 3.2.2). Under low selection intensity, the spectral density peak among replicates is not well-defined, regardless of heritability; however, highly heritable traits present less noise, thus increasing the chance of recognizing the periodic patterns more readily. The results emphasize that genetic architecture and selection model complexity significantly influence how populations respond to fluctuating environments. Also, spectral analysis remains a powerful tool for confirming periodic selection signals across various evolutionary scenarios while visualizing allele frequencies and phenotypes can help deduce initial conclusions.

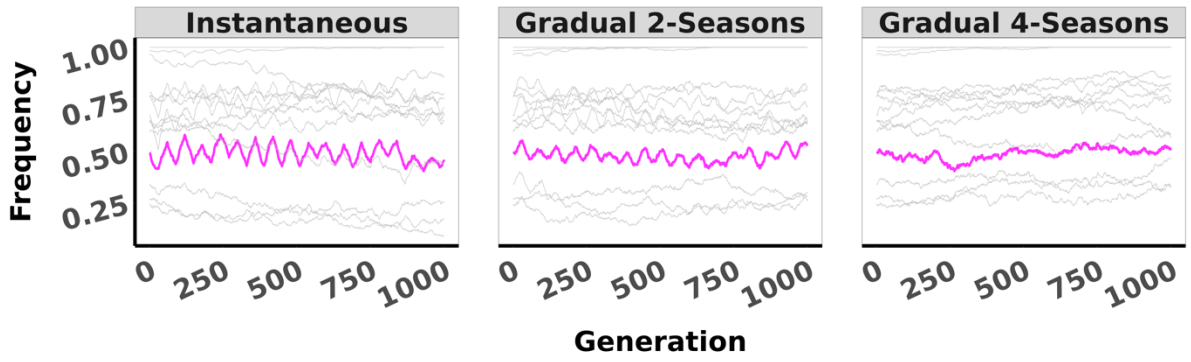
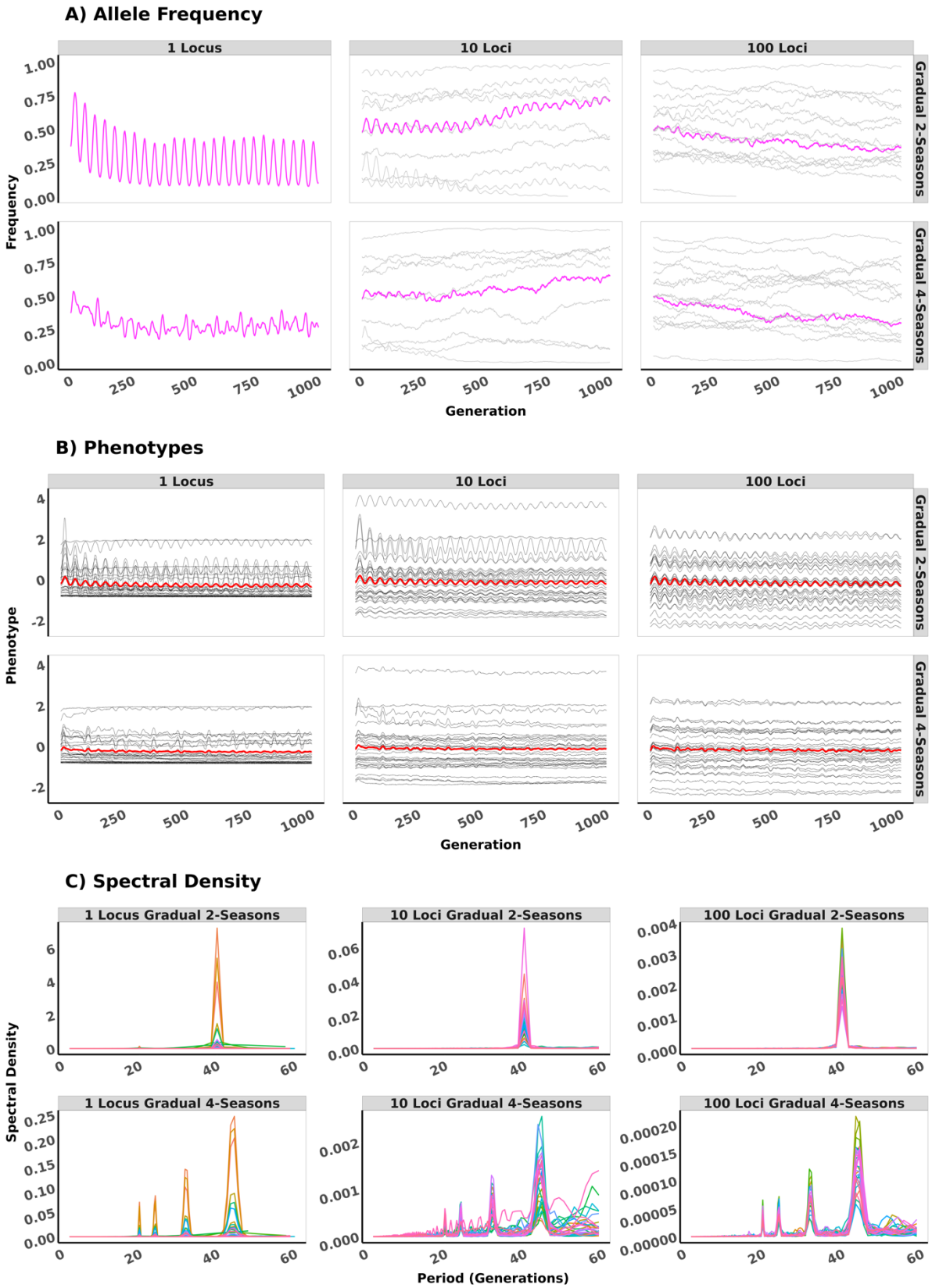


Figure 6: *Allele frequencies from 15 sampled loci out 100 to compare all fluctuating selections models with instantaneous selection showing clearer seasonal oscillations, the gradual two-season, and finally gradual four unequal-season model with a* $h^2 = 0.5$, *SD =2, and Gen (for two season models) = 20.*


A) Allele Frequency
1 Locus
10 Loci
100 Loci
Gradual 2-Seasons
Gradual 4-Seasons
Frequency
Generation
B) Phenotypes
Phenotype
C) Spectral Density
1 Locus Gradual 2-Seasons
10 Loci Gradual 2-Seasons
100 Loci Gradual 2-Seasons
1 Locus Gradual 4-Seasons
10 Loci Gradual 4-Seasons
100 Loci Gradual 4-Seasons
Spectral Density
Period (Generations)

436

Figure 7: *Comparison of gradual selection models.* ***A.*** *Allele frequency trajectories for a single replicate of monogenic, oligogenic, and polygenic traits are shown. In the polygenic model, only 15 of 100 loci are displayed. The highlighted loci illustrate that the dynamics are compared within the same genetic architecture (i.e., the highlighted positions are not identical across different architectures).* ***B.*** *Phenotypic dynamics for 30 replicates are presented, with the overall mean per generation highlighted.* ***C.*** *Spectral analysis for 30 replicates is displayed, with each color representing a different replicate. For all models, the parameters are* $h^2 = 0.5$, *SD = 0.2, and Gen = 20. Thus, the spectral peaks in both the instantaneous and gradual two-season models occur at 40, representing a full seasonal cycle. The four-season models exhibit four peaks, corresponding to the four-generation intervals, with a complete cycle occurring at twice the generation interval per season.*

Difference between fluctuating selection models to neutral and constant selection models

Comparing fluctuating optima models with neutral and constant selection models is indispensable to fully understanding how fluctuating selection affects allele frequencies and phenotypes. Under both neutral and constant selection scenarios, neither allele frequencies nor phenotype trajectories display clear seasonal oscillations, as confirmed by spectral density analyses (see supplemental file for more details: Sections 4 and 5 for neutral and constant selections, respectively).

In neutral models, there are random fluctuations with no discernible pattern mainly because allele frequencies change solely via genetic drift. That is, all the genetic architectures show similar allele frequency dynamics, and loci with terminal initial frequency fix (Supplemental figure SI 4.1). By contrast, constant selection models exert steady selective pressures, leading to predictable shifts in allele frequencies and phenotypes until they plateau, either when certain alleles fix, are lost, or when the population reaches its optimum. The plateauing behavior is particularly pronounced in polygenic models (Supplemental Figures, sections 5.1 and 5.2 for allele frequencies and phenotypes, respectively, under constant selection). Monogenic traits under strong selection often go to fixation more quickly, while polygenic and oligogenic traits tend to remain within specific

464 frequency ranges over many generations. Such behavior does not appear under neutrality, where
465 frequencies drift randomly.

466 Despite these distinctions, spectral analyses of neutral and constant selection models reveal no
467 evident periodicity in either regime (see Supplemental file, section 4.3 and 5.3 for neutral and
468 constant selections, respectively). Consequently, it is difficult to pinpoint out the effects of
469 individual parameters via spectral analysis in these two models.

470 In contrast, fluctuating selection models, both instantaneous and gradual, introduce seasonally or
471 temporally varying selective pressures that can drive noticeable oscillations in allele frequencies
472 and phenotypes. These oscillations are especially marked in monogenic and oligogenic traits, as
473 well as in polygenic traits with high heritability under strong selection. However, when selection
474 intensities or heritability are low, the behavior of polygenic traits under fluctuating selection may
475 appear similar to that under neutral or constant selection (Figure 8). Insufficient selection pressure
476 or limited heritability prevents large frequency shifts and cause some alleles to remain in stable
477 ranges (mimicking constant selection) or to drift randomly (mimicking neutrality). As selection
478 intensity and heritability increase, however, the oscillatory patterns become more pronounced,
479 clearly setting fluctuating selection apart from either purely directional (constant) or random
480 (neutral) processes.

481 The gradual two-season model often exhibits easily detectable seasonal oscillations in allele
482 frequencies, much like the instantaneous model. In more complex scenarios, such as the four
483 unequal season model, these oscillations may be harder to distinguish from neutrality, particularly
484 for polygenic traits (Figure 8.A and 8.B). At lower parameter values, the peaks in spectral analyses
485 may be weak, resembling neutral drift. Nonetheless, increasing certain parameters can amplify the

oscillatory signal, making it possible to differentiate fluctuating selection from neutrality in some cases.

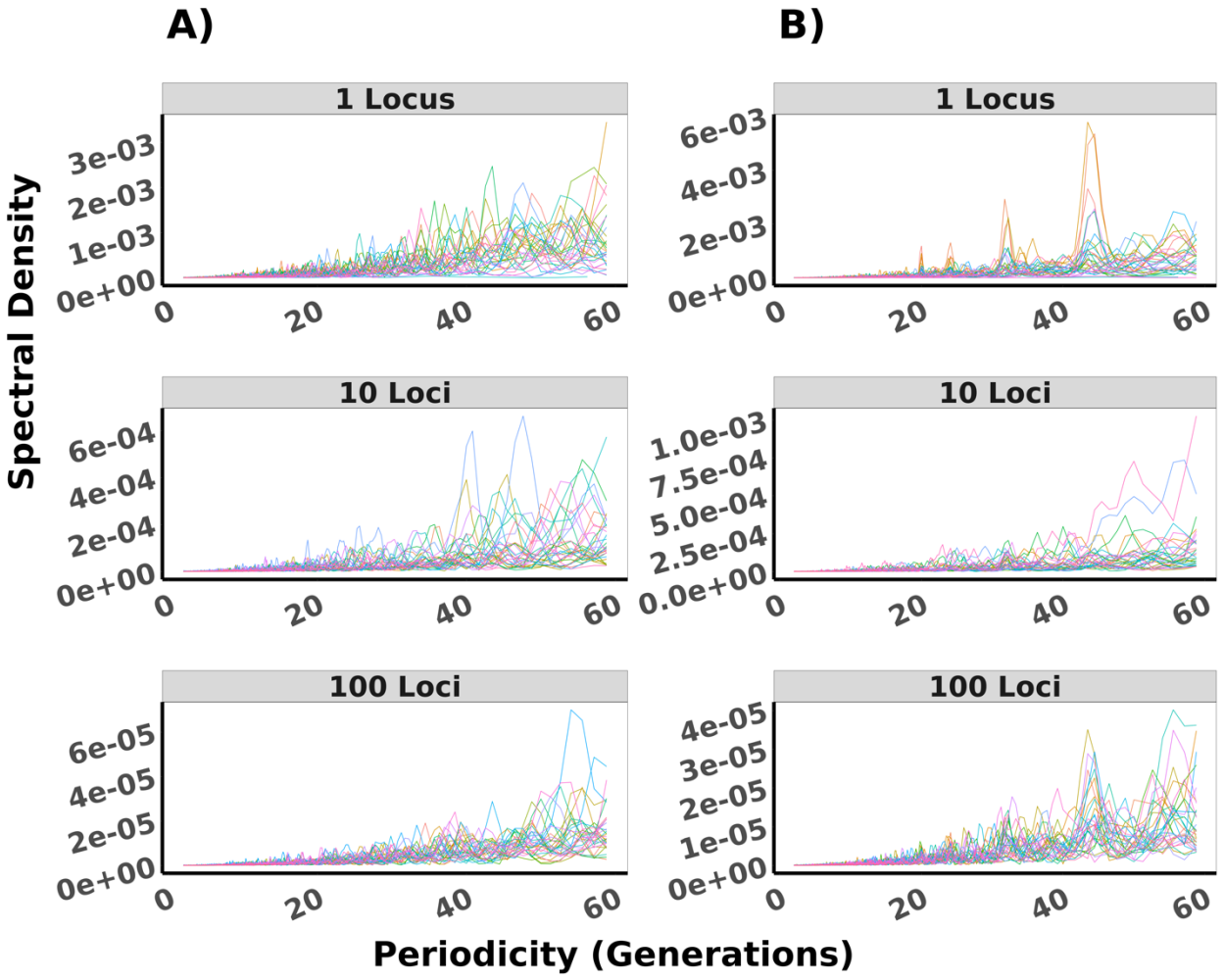


Figure 8*: A represents a neutral model and B representing the four unequal-season model for each genomic structure with low parameter combinations. The oligogenic and polygenic trait models for both selection regimes are very similar although the gradual model represents less variation among replicates, and the monogenic trait shows the spectral peak representing the involved seasons for gradual model.*

Discussion

Parameters leading to persistent allele frequency oscillations

A topic of recent debate has been the conditions under which fluctuating selection will lead to stable oscillations that persist across time and whether the recently observed empirical results [6] are genuinely due to fluctuating environmental conditions. Previous models have produced mixed results, with some showing restrictive parameter spaces leading to stable oscillations [31, 36] and others suggest numerous loci may remain polymorphic under certain seasonal dominance assumptions [30] and protection from selection [23]. However, it remains challenging to empirically verify those conditions, partly because dominance relationships and other relevant parameters, for instance, degree of protection, are often difficult to quantify in natural populations, as noted by the authors. In contrast, our study examines relatively easy-to-measure parameters in natural populations and demonstrates that cyclic allele frequencies can persist at many positions even under low selective pressure, particularly when selection acts instantaneously. However, the magnitude of these oscillations scales directly with selection strength; thus, it is the primary determinant of how pronounced the cyclical patterns are, and the combination of selection strength with other parameters leads to numerous positions with stable oscillations.

When both heritability and selection intensity were high, the population exhibited pronounced oscillations, a finding consistent with classical quantitative genetic theory [44, 71, 72]. Moreover, with intermediate to high selection pressure and heritability, we can visually see those fluctuations at high amplitude, contradicting the claim that not all positions will experience strong selection [73]. Under these conditions, we observed marked fluctuations and, at times, near-fixation of alleles, consistent with other reports suggesting that increased selection intensity may lead to allele fixation [41, 53, 74–77]. However, complete fixation is often prevented because the environment

522 fluctuates, thereby maintaining numerous alleles at intermediate frequencies. Furthermore, longer
523 seasons grant sufficient time for selection to shift allele frequencies, as seen in the evolutionary
524 experiment study by [15] and [78], and mean phenotypes toward the new optimum, accentuating
525 oscillations. Conversely, shorter selection periods can diminish these effects because the
526 environment changes again before the population fully adapts, as seen in classic field studies such
527 as Grant and Grant's finch research [1] and theoretical predictions [79]. Also, the fact that we
528 cannot observe the oscillation directly from allele frequencies does not mean that the fluctuating
529 selection is not happening and is involved in maintaining polymorphism [80]. Our results illustrate
530 that extending the selection season amplifies the visible shifts in allele frequencies, especially
531 under high selection pressure, thereby producing more pronounced cyclical patterns. Oscillations
532 are very challenging to observe for individual loci in polygenic traits with small parameter
533 combinations, however, spectral analysis readily recovers the spectral peak, especially in the
534 instantaneous model and the two gradual season models. Therefore, the identification of oscillatory
535 behavior will be predicated on the parameter combination and the complexity of the selection
536 regimes. That is, trait's heritability, length of selection season and its strength will determine the
537 level of oscillation among alleles.

538 **Genomic architecture effect on oscillation and fixation**

539 Previous theoretical models investigating the effects of fluctuating selection on genome dynamics
540 often used the approach of selection acting directly on the causative loci, generally demonstrating
541 that polymorphism could be maintained under specific conditions, notably if heterozygote fitness
542 exceeded that of homozygotes [81, 82]. They also indicated that single-locus models could lead to
543 fixation over extended periods of fluctuating selection, thus limiting long-term polymorphism [32,
544 35, 82, 83]. In contrast to those models that focused on a single locus selection coefficient, our

study employs a phenotype-based selection approach [84, 85], where changes in environmental conditions shift the optimal phenotype and shifts in selection on the causative loci are emergent. The results support temporary genetic diversity by showing that monogenic models exhibit larger fluctuations, mainly because a single genetic locus drives the entire phenotypic shift for a given heritability. In some cases, these fluctuations persist until fixation occurs, while in others they endure for an extended period. Although monogenic models tend to show a high rate of fixation, alleles do not always fix, and the degree of fixation depends on the specific parameter combination.

Extending our analysis from single-locus models to oligogenic and polygenic frameworks reveals that selection acts simultaneously across multiple loci, leading to oscillations in allele frequencies and phenotypes under appropriate conditions. In contrast to single-locus models, where parameter changes strongly influence allele fixation, polygenic models tend to mask selection effects at individual loci, with the cumulative impact spreading across a large genomic architecture [86–89]. Therefore, that diffused selection effect can explain the need for intense selection on highly heritable polygenic traits to sustain observable oscillations in allele frequencies across many loci. In addition, our current results indicate that alleles with intermediate initial frequencies fluctuate more than others. This pattern could reflect heterozygote advantage [32] or an antagonistic pleiotropy, where one allele is favored in one season and disfavored in the next [30, 90]. If this interpretation holds, then the parameters in our study would more effectively explain the observed oscillations, and they might be easier to predict than the reversal dominance model proposed in previous research. Therefore, further investigation into potential overdominance effects, including elevated genetic load, is warranted, as discussed by Wittmann et al. (2017).

568 **Fluctuations in complex selection regimes**

569 Our study contrasts two principal types of fluctuating selection models: (1) instantaneous (where
570 the environment switches sharply between two states) and (2) gradual (where the environment
571 transitions more smoothly through two equal or four unequal seasons). The observed similarities
572 in instantaneous and gradual two equal season models likely arise from having constant season
573 lengths and selection peaks. In contrast, when there are four unequal seasons with different peaks
574 strength (highest optimum for each season), the population struggles to adapt to each peak; thus,
575 the complex oscillatory dynamics. Nevertheless, gradual models better represent complex natural
576 environments where multiple selection regimes occur over time. These more complex scenarios,
577 especially those with four unequal seasons, create subtle patterns that can resemble neutral or
578 constant selection when parameters (e.g., selection strength, heritability) are low [30, 91, 92].
579 Indeed, a particularly long or short season under these gradual models can either strengthen or
580 weaken selection signals, respectively, making detection more difficult [19, 93, 94] for the latter.

581 We employed spectral analysis to tackle the challenge of identifying subtle oscillatory signals.
582 This approach successfully discerned cyclical patterns in allele frequency across most parameter
583 combinations, particularly in simpler models (i.e., the instantaneous and two equal seasons
584 models). However, spectral analysis struggled to detect periodicity when parameter values were
585 low (e.g., low heritability or weak selection) or when the model included multiple complex
586 environments (as in the four-unequal-season model). These difficulties mirror empirical findings
587 [11] and may be explained by the short duration of each season, which hinders the population's
588 ability to adapt to new conditions. A similar challenge in identifying seasonality was observed in
589 the statistical analysis of experimental data from Bergland et al. (2014), who reported seasonal
590 allele-frequency oscillations in thousands of SNPs. However, a subsequent reanalysis [95] failed

591 to replicate this result, likely due to the complex selection pressures experienced by the population
592 or the timing of sample collection (i.e., the generation intervals used by Bergland et al. in their
593 2014 data set). These results highlight and define the limits for detecting fluctuating selection from
594 allele frequency data under complex scenarios.

595 Ideally, sequencing multiple sequential generations for a long time would help identify seasonality
596 from genomic data using the currently developed statistical tools. However, its feasibility is almost
597 impossible due to the associated cost and labor. Although Phillips et al. 2020 [96] did not examine
598 fluctuating selection, they argued that taking more samples over time can dramatically improve
599 our ability to understand the complexity into evolutionary dynamics. Therefore, researchers
600 studying populations under complex fluctuating conditions should also aim to estimate the optimal
601 sampling points required to capture such dynamics. Furthermore, new computational methods,
602 including machine learning and generative models, may reduce empirical demands or detect
603 cyclical selection signals even in sparser datasets [97].

604 **Limitations and Future Directions**

605 Our simulations assume non-overlapping generations, constant population sizes, no new
606 mutations, and fixed recombination rates, all of which may limit the extent to which these results
607 can generalize. In addition, our models did not allow for any genotype by environment interaction
608 at any loci. Previous quantitative genetic models of fluctuating selection have frequently identified
609 the conditions under which fluctuating selection is expected to lead to the evolution of phenotypic
610 plasticity driven by genotype by environment interactions [98–100]. Our models did not allow for
611 the evolution of plasticity in this way, removing a major potential way for populations to adapt to
612 fluctuating selection pressures. Thus, our results shed light on whether it is ever possible for
613 fluctuating selection to drive recurrent, stable, allele frequency oscillations in a population, given

these simplifying assumptions. Future models incorporating additional factors, including allowing for mutation, genotype by environment interactions, and incorporating dynamic population sizes are necessary to capture the complexity of natural populations [45, 101–103]. Future research should also test these observations through evolve-and-resequence experiments and refine methods for parameter estimation from time-series genomic data. This work offers a foundation for understanding how traits evolve and persist under dynamic natural conditions by revealing how seasonal and environmental changes modulate selective pressures over time.

Concluding remarks

This study highlights the intricate interplay among heritability, genomic architecture, selection intensity, and season length in shaping oscillatory allele-frequency dynamics under fluctuating environments. High heritability and strong selection produce pronounced and persistent frequency oscillations, and these effects become more evident when selection acts over longer seasons. Meanwhile, the broad genomic architecture of polygenic traits can mask individual locus fluctuations, yet substantial oscillations still emerge when selection is sufficiently strong. Spectral analysis is valuable for detecting cyclical patterns, but its effectiveness diminishes in highly complex or weakly selective environments. Therefore, improved methods are needed to identify seasonality from very complex models.

Overall, our results underscore the importance of the discussed ecological and genetic parameters in understanding the evolutionary fate of populations under fluctuating selection. Accurately modeling additional parameters and empirically testing these dynamics will be key to predicting evolutionary outcomes and identifying conditions that promote sustained genetic diversity as environmental variability increases.

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