

Review

Not peer-reviewed version

Impacts of Evolutionary Forces on Allele and Genotype Frequency of Organisms

[Zelege Ashango](#) * and [Wosene Gebreselassie Abteu](#)

Posted Date: 6 June 2025

doi: 10.20944/preprints202506.0510.v1

Keywords: evolutionary forces; allele frequency; genetic diversity; adaptation



Preprints.org is a free multidisciplinary platform providing preprint service that is dedicated to making early versions of research outputs permanently available and citable. Preprints posted at Preprints.org appear in Web of Science, Crossref, Google Scholar, Scilit, Europe PMC.

Copyright: This open access article is published under a Creative Commons CC BY 4.0 license, which permit the free download, distribution, and reuse, provided that the author and preprint are cited in any reuse.

Review

Impacts of Evolutionary Forces on Allele and Genotype Frequency of Organisms

Zelege Ashango ^{1,*} and Wosene Gebresilassie ²

¹ Plant science department, Dawro Tarcha campus, Wolaita Sodo University; PhD Student at horticulture and plant science department, College of Agriculture and Veterinary Medicine, Jimma University, Ethiopia

² Horticulture and Plant science department, College of Agriculture and Veterinary medicine, Jimma University, Ethiopia

* Correspondence: zelekemarc2014@gmail.com

Abstract: Evolutionary forces—selection, genetic drift, gene flow, and mutation—exert profound influences on allele and genotype frequencies within populations, thereby shaping genetic diversity and adaptive capacity. This review synthesizes contemporary findings regarding the interplay of these forces in driving evolutionary change, with an emphasis on population genetics, molecular evolution, and the variation of quantitative traits. The discourse delves into selection dynamics, illuminating the significance of positive selection in the emergence of adaptive traits, purifying selection in the preservation of genomic integrity, and balancing selection in the maintenance of genetic diversity. Furthermore, the phenomenon of genetic drift is scrutinized within the context of small populations, where stochastic fluctuations can dramatically alter allele frequencies, frequently culminating in the fixation or loss of alleles. Gene flow and migration are explored as pivotal mechanisms that introduce genetic variation, effectively counteracting the influences of drift and selection pressures. The review also assesses mutation rates and their contributions to genetic innovation, underscoring their pivotal role in fostering evolutionary novelty. Recent investigations that integrate genomic time-series data alongside AI-driven evolutionary modeling yield valuable insights into temporal changes in allele frequencies. Case studies of both plant and animal populations vividly illustrate how evolutionary forces sculpt genetic architecture, influencing phenotypic traits, adaptation to environmental stressors, and the divergence of species. Prospective research avenues underscore the necessity for the integration of multi-omics approaches, encompassing genomics, transcriptomics, and epigenetics, to refine evolutionary models. The review concludes by asserting that a comprehensive understanding of evolutionary forces is indispensable for forecasting genetic trends, conserving biodiversity, and enhancing breeding strategies.

Keywords: evolutionary forces; allele frequency; genetic diversity; adaptation

1. Introduction

Evolutionary forces are mechanisms that propel alterations in allele and genotype frequencies within populations across generations. These forces encompass mutation, genetic drift, gene flow, and natural selection, each playing a pivotal role in fostering genetic variation and adaptation. Mutation serves as the primary conduit for introducing novel alleles into a population, thereby acting as the fundamental source of genetic diversity (Peischl and Kirkpatrick, 2012). Genetic drift entails stochastic fluctuations in allele frequencies attributed to fortuitous events, particularly exerting substantial influence in diminutive populations (Bajay, 2025). Gene flow, or migration, denotes the transference of alleles between populations, augmenting genetic diversity and thwarting divergence (de Moraes et al., 2025). Natural selection encapsulates the differential survival and reproduction of individuals predicated upon advantageous traits, culminating in adaptive modifications in allele frequencies (Wiley, 2021; Allendorf et al., 2022). Collectively, these forces sculpt genetic diversity, shape population structure, and propel evolutionary processes.

Population genetics is integral to genomic selection and breeding as it offers profound insights into genetic variation, inheritance patterns, and the evolutionary forces that shape allele frequencies. Its contributions to breeding encompass, but are not limited to, the optimization of training populations in genomic selection, the management of genetic diversity, the enhancement of selection efficiency, the prediction of trait heritability, the integration of multi-omics approaches, and the provision of evolutionary insights. Population genetics aids in the selection of diverse and representative training populations for genomic prediction, thus ensuring heightened accuracy in breeding programs (Edwards et al., 2019; Stadler et al., 2025). Through the analysis of allele frequencies and genetic drift, breeders can sustain genetic variability, thereby averting inbreeding depression and bolstering adaptability (Bruce and Lynch, 2018). A nuanced understanding of population structure and linkage disequilibrium enhances marker-based selection, empowering breeders to identify superior genotypes with greater precision (Würschum et al., 2013; Novo et al., 2022). Furthermore, population genetics equips breeders to estimate the heritability of traits, thereby informing decisions regarding which traits can be effectively enhanced through selection (Wray and Visscher, 2008; Lohmueller, 2014). The amalgamation of population genetics with transcriptomics, proteomics, and metabolomics facilitates trait discovery and accelerates breeding for stress tolerance and nutrient efficiency (Pott et al., 2021). An understanding of evolutionary forces such as mutation, migration, and selection empowers breeders to devise adaptive breeding strategies aimed at climate resilience and sustainable agriculture (Allan et al., 2024).

2. Genetic Population

Population genetics represents the intricate study of genetic variation within populations and the manner in which evolutionary forces sculpt allele frequencies over time. It furnishes a comprehensive framework for comprehending genetic diversity, adaptation, and the processes underlying evolution. Within the realm of population genetics, the term “gene pool” denotes the entirety of genetic material present within a breeding population. This encompasses all alleles located at various loci across the individuals comprising that population. The composition of the gene pool fundamentally influences the potential for evolutionary change and adaptive capacity. Populations exhibiting high genetic diversity possess an enhanced ability to acclimatize to environmental fluctuations, whereas those with limited genetic diversity are more vulnerable to genetic drift and inbreeding depression. The concept of the gene pool is pivotal to evolutionary biology, as it determines the genetic potential of a population to respond to selection pressures (Miller and Khoury, 2018; Yali and Mitiku, 2024).

Genetic variability denotes the distinctions in genetic composition among individuals within a given population. It is paramount for the process of evolution, as it furnishes the essential substrate for natural selection. The origins of genetic variability encompass mutation, recombination, gene flow, genetic drift, and selection. Mutation introduces novel alleles into the gene pool, thereby enhancing genetic diversity. Recombination intricately reshuffles genetic material during meiosis, engendering new allele combinations. The translocation of alleles between populations mitigates genetic divergence. Random fluctuations in allele frequencies exert a pronounced influence in smaller populations. Natural selection entails differential survival and reproduction predicated on advantageous traits. Genetic variability is indispensable for population resilience, enabling organisms to adapt to environmental pressures and avert extinction (Gupta, 2022).

The Hardy-Weinberg principle offers a mathematical framework to elucidate allele frequencies within a population under idealized conditions (absence of mutation, selection, migration, genetic drift, or nonrandom mating). Should a population maintain Hardy-Weinberg equilibrium, allele frequencies remain stable across generations. Conversely, deviations from this equilibrium signify that evolutionary forces are exerting influence on the population, resulting in genetic alterations (Davinack, 2024).

Numerous factors modulate genetic variability and allele frequencies within genetic populations. The mutation rate dictates the introduction of new alleles. Selection pressure shapes

allele frequencies predicated on fitness advantages. Smaller populations are subjected to more pronounced effects of genetic drift. Environmental fluctuations impact selection dynamics and genetic adaptation. Comprehending these forces empowers breeders and geneticists to refine genomic selection strategies, thereby enhancing trait prediction and breeding efficacy (Star et al., 2007; Emily et al., 2020; Abraham et al., 2020).

Population structure profoundly influences the distribution of allele frequencies by shaping genetic diversity, evolutionary dynamics, and adaptive potential. Structured populations exhibit non-random mating patterns, geographical barriers, and subpopulation differentiation, all of which contribute to genetic variation. Population structure pertains to the existence of subpopulations within a species that experience limited genetic interchange. Genetic differentiation arises when allele frequencies diverge between subpopulations due to restricted gene flow. Fixation index (ϕ_{ST}) quantifies genetic differentiation between populations, with elevated ϕ_{ST} values signifying pronounced genetic divergence (Wang, 2012; Willing et al., 2012). Populations characterized by low ϕ_{ST} values maintain genetic homogeneity, whereas those with high ϕ_{ST} values display distinct allele frequency distributions attributable to constrained gene flow (Porrás-Hurtado et al., 2023). Gene flow introduces novel alleles into a population, thereby diminishing genetic differentiation. Conversely, limited gene flow can lead to allele fixation, wherein certain alleles become predominant in isolated populations. High gene flow sustains genetic diversity and mitigates local adaptation (Star et al., 2007). For instance, in spatially heterogeneous environments, populations subjected to low gene flow may develop locally adapted alleles, while those with robust gene flow exhibit more uniform allele distributions. Small populations are susceptible to stronger genetic drift, resulting in random fluctuations in allele frequencies. Founder effects manifest when a new population is initiated by a diminutive number of individuals, culminating in a reduction of genetic diversity. Bottleneck events drastically curtail population size, amplifying the likelihood of allele fixation. Research indicates that minor allele frequency thresholds substantially influence population structure inference, thereby affecting genomic analyses (Porrás-Hurtado et al., 2023). Natural selection favors alleles that enhance survival and reproductive success within specific environments. Spatially heterogeneous selection engenders allele frequency divergence among populations (Star et al., 2007). Balancing selection preserves genetic variation by favoring heterozygotes or rare alleles (Charlesworth, 2006; Chapman et al., 2019). For example, populations subjected to disparate environmental pressures may exhibit distinct allele frequency distributions, reflecting adaptation to localized conditions. The Hardy-Weinberg equilibrium presupposes random mating and the absence of evolutionary forces. Structured populations frequently deviate from equilibrium due to nonrandom mating, selection, and genetic drift (Karlin, 1968; Sánchez and Woolliams, 2004). Assortative mating augments homozygosity, while disassortative mating promotes heterozygosity. Comprehending these deviations aids researchers in forecasting evolutionary trends and formulating effective breeding strategies. In summary, population structure directly impacts allele frequency distributions by shaping genetic diversity, influencing selection dynamics, and determining evolutionary trajectories. Recognizing these effects is imperative for advancements in plant breeding, conservation genetics, and evolutionary biology.

3. Genes in Populations

Allele and genotype frequency calculations are fundamental in population genetics, helping researchers understand genetic variation, evolutionary dynamics, and breeding strategies. These calculations are often based on the Hardy-Weinberg equilibrium, which provides a mathematical framework for predicting allele distributions in a population.

3.1. Allele Frequency Calculation

Allele frequency refers to the proportion of a specific allele in a population. It is calculated using the formula:

$$p = \frac{2N_{AA} + N_{Aa}}{2N}$$

$$p = \frac{N_{Aa} + 2N_{aa}}{2N}$$

Where:

- p = frequency of the dominant allele (A)
- q = frequency of the recessive allele (a)
- N_{AA} = number of homozygous dominant individuals
- N_{Aa} = number of heterozygous individuals
- N_{aa} = number of homozygous recessive individuals
- N = total number of individuals in the population

Since allele frequencies must sum to 1, the relationship is $p + q = 1$. This equation helps estimate allele frequencies in populations under random mating conditions and absence of evolutionary forces (Nakhleh, 2010).

3.2. Genotype Frequency Calculation

Genotype frequency refers to the proportion of individuals with a specific genotype in a population. It is calculated using:

$$f_{(AA)} = N_{AA}/N$$

$$f_{(Aa)} = N_{Aa}/N$$

$$f_{(aa)} = N_{aa}/N$$

Where:

- $f_{(AA)}$ = frequency of homozygous dominant individuals
- $f_{(Aa)}$ = frequency of heterozygous individuals
- $f_{(aa)}$ = frequency of homozygous recessive individuals

Under Hardy-Weinberg equilibrium, genotype frequencies can be predicted using allele frequencies:

$$f_{(AA)} = p^2$$

$$f_{(Aa)} = 2pq$$

$$f_{(aa)} = q^2$$

These formulas allow researchers to assess whether a population is evolving or maintaining genetic stability (Wang, 2012). Allele frequency determination allows breeders to estimate the likelihood of desirable traits appearing in offspring. It is used in genetic diversity management to prevent inbreeding depression and maintain adaptive potential. In evolutionary studies it is used to track allele frequency shifts due to selection, mutation, migration, and genetic drift.

Population genetics hinges upon comprehending how evolutionary forces sculpt allele frequencies across temporal scales. Three fundamental mechanisms, gene flow, genetic drift, and fixation indices, exert significant influence over genetic diversity and population architecture. Gene flow denotes the translocation of alleles among populations, instigated by migration or gamete transfer. It introduces genetic variability and mitigates the tendency of populations to diverge genetically. By incorporating novel alleles, gene flow enhances genetic diversity and diminishes genetic differentiation between populations, thereby fostering homogeneity. Nonetheless, it can counterbalance genetic drift by sustaining allele frequencies. For instance, in structured populations, restricted gene flow culminates in allele fixation, whereas elevated gene flow preserves genetic diversity (Nakhleh, 2010).

Genetic drift represents the stochastic fluctuation of allele frequencies attributable to random events, particularly pronounced in diminutive populations. In contrast to natural selection, genetic drift is non-directional and may precipitate allele loss or fixation. The potency of genetic drift

escalates in smaller populations, leading to swift alterations in allele frequencies. This phenomenon can culminate in a reduction of genetic diversity, thereby diminishing adaptability. Founder effects manifest when a nascent population is established by a limited number of individuals, resulting in diminished genetic variation. Bottleneck events dramatically curtail population size, heightening the probability of allele fixation (Wein and Dagan, 2019; Olazcuaga et al., 2023). For example, island populations frequently encounter pronounced genetic drift, yielding distinctive allele distributions. Allele fixation indices are employed to gauge genetic differentiation among subpopulations, with the most prevalent index being ϕ_{ST} , which quantifies the proportion of genetic variance attributable to population structure.

$$\phi_{ST} = \frac{H_T - H_S}{H_T}$$

Where:

- H_T = Total genetic diversity in the species.
- H_S = Average genetic diversity within subpopulations.

The fixation index (ϕ_{ST}) value approaching zero signifies a lack of genetic differentiation or extensive gene flow, whereas a value nearing one indicates complete genetic differentiation or an absence of gene flow. Intermediate values reflect varying degrees of population structure (Wang, 2012). Gene flow, genetic drift, and fixation indices collaboratively influence population genetics by affecting allele frequencies, genetic diversity, and evolutionary trajectories. A comprehensive understanding of these mechanisms is imperative for genomic selection, conservation genetics, and evolutionary biology.

4. Hardy-Weinberg Equation and Equilibrium

The Hardy-Weinberg principle is a pivotal concept in the realm of population genetics that furnishes a mathematical framework for comprehending allele stability within a population under optimal conditions. It functions as a null model, enabling researchers to discern the evolutionary forces at play within a population by juxtaposing observed genetic data with anticipated frequencies. The Hardy-Weinberg principle posits that allele and genotype frequencies remain invariant across generations in a population that is not subjected to evolutionary pressures such as mutation, selection, genetic drift, migration, or nonrandom mating. This equilibrium is elegantly articulated through the following mathematical expression:

$$p^2 + 2pq + q^2 = 1$$

Where:

- p = frequency of the dominant allele
- q = frequency of the recessive allele
- p^2 = frequency of homozygous dominant genotype (AA)
- $2pq$ = frequency of heterozygous genotype (Aa)
- q^2 = frequency of homozygous recessive genotype (aa)

This equation allows researchers to predict genotype distributions based on allele frequencies, assuming **random mating and absence of evolutionary forces** (Andrews, 2010).

4.1. Assumptions of Hardy-Weinberg Equilibrium (HWE)

The Hardy-Weinberg equilibrium (HWE) represents a cornerstone principle in the field of population genetics, elucidating the anticipated stability of allele and genotype frequencies within a population under idealized conditions. Nevertheless, actual populations frequently diverge from these assumptions due to the influence of evolutionary forces. For a population to sustain Hardy-Weinberg equilibrium, the following conditions must be satisfied:

- **Large population size:** A substantial population minimizes genetic drift and mitigates random fluctuations in allele frequencies.

- **No mutation:** Allele frequencies remain constant in the absence of mutations that introduce novel genetic variations.
- **No migration:** In the absence of allelic introduction or removal resulting from migration between populations, allele frequencies remain unaltered.
- **Random mating:** When individuals engage in mating without preferential selection, ensuring an equitable distribution of alleles, allele frequencies do not fluctuate.
- **No natural selection:** When all genotypes within the population experience equivalent reproductive success and survival, this precludes shifts in allele frequencies.

These assumptions establish a null model for discerning the evolutionary forces at play within a population. Should any of these assumptions be contravened, alterations in allele frequencies will manifest, signifying the influence of evolutionary forces on the population.

4.2. Deviations from Hardy-Weinberg Equilibrium

When any of the assumptions of Hardy-Weinberg Equilibrium (HWE) are contravened, allele and genotype frequencies undergo alterations, signifying that evolutionary processes are exerting influence over the population. Factors precipitating deviations encompass mutation, genetic drift, gene flow, selection, and nonrandom mating. Mutation introduces novel alleles, thereby modifying the genetic composition. Genetic drift characterized by stochastic fluctuations in allele frequencies, particularly pronounced in smaller populations, can result in either allele loss or fixation. Gene flow, the translocation of alleles between populations, disrupts the established equilibrium. Differential survival and reproductive success preferentially favor specific alleles. Furthermore, assortative or disassortative mating affects genotype frequencies. Empirical studies have demonstrated that deviations from HWE can significantly impact genetic association analyses, yielding biased estimates of allele-based risk effects ([Thomas et al., 2006](#)).

4.3. Hardy-Weinberg Principle and Allele Stability

The Hardy-Weinberg principle serves as a pivotal benchmark for identifying genetic alterations within populations. Deviations from anticipated allele frequencies signify processes such as selection, mutation, genetic drift, or migration. This principle bears significant implications for genetic association studies, population structure analyses, and breeding programs. Violations of Hardy-Weinberg Equilibrium (HWE) can compromise the reliability of genotype-trait associations ([Thomas et al., 2006](#)). Moreover, deviations from HWE elucidate genetic differentiation and the influence of evolutionary pressures ([Masuda et al., 2022](#)).

In the realms of plant and animal breeding, comprehending deviations from Hardy-Weinberg equilibrium is instrumental in refining breeding strategies; it facilitates the prediction of genotype distributions, aids in monitoring genetic diversity to avert inbreeding depression, and evaluates the efficacy of selection within genomic prediction models. In medical genetics, this principle is employed to forecast the prevalence of recessive genetic disorders.

The Hardy-Weinberg principle functions as a foundational reference for allele stability, enabling researchers to detect evolutionary forces, estimate genetic variation, and enhance breeding strategies. While actual populations seldom conform entirely to all Hardy-Weinberg assumptions, the observed deviations yield invaluable insights into genetic dynamics and evolutionary processes.

5. Factors Affecting Allele and Genotype Frequencies

5.1. Mutation

Mutation represents a fundamental evolutionary force that introduces novel genetic variation into plant populations. The rate and nature of mutations significantly influence allele and genotype frequencies, thereby shaping genetic diversity, adaptation, and breeding outcomes. Mutation rates in plants exhibit variability contingent upon species, genomic regions, and environmental conditions. The frequency of mutations dictates the rapidity with which new alleles emerge within a population.

Elevated mutation rates foster enhanced genetic diversity but may also precipitate the introduction of deleterious alleles. Conversely, diminished mutation rates preserve genetic stability while concurrently impairing adaptability. Variation in mutation rates markedly influences allele frequency distributions, thereby affecting population structure. Empirical studies suggest that mutation rates in plants are modulated by environmental stressors, such as radiation, chemical mutagens, and oxidative damage (Elena and de Visser, 2003; Alday, 2023).

Mutations arise through a plethora of mechanisms, each exerting distinct effects on genotype frequencies. Point mutations, characterized by single nucleotide alterations, possess the potential to modify allele frequencies. Insertions or deletions (Indels) can disrupt gene functionality and subsequently influence genotype distributions. Gene duplication elevates allele copy number, thereby affecting genetic variation. Chromosomal rearrangements, as large-scale mutations, fundamentally reshape population genetics. Collectively, these mechanisms contribute to genetic drift, selection, and adaptation, thereby influencing genotype frequencies across generations (Star and Spencer, 2013; Lynch et al., 2016).

Several models are employed to elucidate the influence of mutations on population genetics. Three pivotal models utilized to quantify mutation rates and their ramifications on allele frequencies are the infinite sites model (ISM), the mutation-drift equilibrium model (MDEM), and the mutation-selection balance model (MSBM). The ISM posits that each mutation transpires at a distinct site within the genome, thereby precluding recurrent mutations at the same locus. This model serves to estimate mutation rates and allele frequency distributions. Research indicates that repeat mutations lead to deviations from the ISM (Harpak et al., 2016; Wikipedia, 2025). This model proves advantageous for estimating mutation rates in extensive populations characterized by minimal genetic drift. Its equation is:

$$\theta = 4N_e\mu$$

Where:

- θ = mutation rate per site
- N_e = effective population size
- μ = mutation rate per generation

A lower θ value (< 0.001) signifies minimal genetic variation, commonly observed in small populations or those characterized by low mutation rates. This suggests a limited evolutionary potential, rendering the population vulnerable to the challenges of environmental changes. A moderate θ value ($0.001 - 0.01$) indicates a balanced mutation rate, thereby facilitating gradual adaptation. Conversely, a high θ value (> 0.01) denotes accelerated genetic diversification, thereby augmenting evolutionary flexibility. The ISM model serves as a vital tool for estimating genetic diversity within populations. It is instrumental in phylogenetic studies that trace evolutionary divergence and supports the discovery of genetic markers in genomic selection by identifying rare alleles.

MDEM model elucidates the equilibrium between the mutation that introduces novel alleles and the genetic drift that erodes alleles due to stochastic sampling effects. MDEM adeptly reconciles the influx of mutations with the ramifications of genetic drift. It forecasts alterations in allele frequencies within diminutive populations.

$$H = \frac{4N_e\mu}{1 + 4N_e\mu}$$

Where:

- H = expected heterozygosity
- N_e = effective population size
- μ = mutation rate

Low genetic diversity ($H < 0.1$) signifies a population that is acutely vulnerable to genetic drift, rendering it less capable of adapting to environmental fluctuations. A moderate level of genetic diversity ($0.1 - 0.5$) indicates a balanced variation, which facilitates some degree of adaptability while remaining susceptible to the effects of drift. Conversely, high genetic diversity ($H > 0.5$) denotes a

robust evolutionary potential, endowing the population with considerable resilience. MDEM serves as a critical tool in evaluating the erosion of genetic diversity in endangered species. It informs breeding initiatives aimed at preserving genetic variation and forecasts allele fixation probabilities within small populations.

The MSBM model elucidates the persistence of deleterious mutations within populations, notwithstanding the opposing force of natural selection. This model articulates the introduction of novel alleles through mutation, while selection concurrently eliminates harmful variants, culminating in an equilibrium allele frequency (q). It is extensively employed in genomic selection to refine breeding strategies (Bruce and Lynch, 2018; Qu et al., 2020). The NSBM equation is:

$$q = \sqrt{\frac{\mu}{s}}$$

Where:

- q = equilibrium frequency of deleterious allele
- μ = mutation rate
- s = selection coefficient against the allele

Low q (< 0.01) signifies that the deleterious allele is infrequent, indicative of robust purifying selection. A moderate q ($0.01 - 0.1$) suggests a balance between mutation and selection, permitting the allele's persistence. A high q (> 0.1) implies that the allele is prevalent, indicating either weak selection pressures or elevated mutation rates. The MSBM framework aids in forecasting mutation load within breeding populations. It informs selection strategies aimed at eradicating harmful alleles while elucidating the maintenance of genetic variation in the face of selection pressures. Mutation rates and mechanisms are pivotal in shaping allele and genotype frequencies in plant populations. A comprehensive understanding of these processes is crucial for advancements in genomic selection, evolutionary biology, and conservation genetics.

5.2. Genetic Drift and Founder Effects

Genetic drift and founder effects are pivotal evolutionary forces that shape allele and genotype frequencies within plant populations. These mechanisms exert considerable influence, particularly in small or isolated populations, where stochastic events can profoundly alter genetic diversity. Genetic drift pertains to random fluctuations in allele frequencies attributable to chance occurrences rather than natural selection. This phenomenon is particularly pronounced in diminutive populations, where allele frequencies can shift unpredictably. Drift may culminate in the loss of rare alleles across generations and can precipitate allele fixation; for instance, certain alleles may become predominant solely by coincidence. Furthermore, drift amplifies homozygosity and diminishes adaptability, potentially leading to inbreeding depression. Empirical studies on endangered plant species indicate that genetic drift can result in diminished genetic variation, rendering populations increasingly susceptible to environmental perturbations (Edwards et al., 2021; Ashley et al., 2023).

The founder effect transpires when a small cohort of individuals establishes a new population, thereby carrying only a fraction of the original genetic diversity. This scenario engenders distinct allele frequencies in comparison to the source population, thereby constraining genetic variation and limiting the adaptability of crops to environmental stressors. Additionally, it heightens the risk of inbreeding and increases homozygosity, which can adversely affect plant fitness. Furthermore, it fosters rapid evolutionary changes that give rise to unique allele distributions in isolated populations. For instance, plant populations on islands frequently display pronounced founder effects, culminating in genetic differentiation from their mainland counterparts.

Several models facilitate the estimation of the impacts of genetic drift and founder effects. The most widely utilized models include the Wright-Fisher model, Kimura's neutral theory model, and coalescent theory model. The Wright-Fisher model serves as a foundational framework in population genetics, elucidating random allele frequency alterations attributable to genetic drift in finite

populations. It demonstrates how allele frequencies fluctuate randomly across generations due to sampling effects and predicts the probability of allele fixation over successive generations. This model operates under several assumptions, including non-overlapping generations, constant population size, and random mating. Its equation for genetic drift estimation is

$$P(X_{t+1} = k) = \binom{2N}{k} p^k (1 - p)^{2N-k}$$

Where:

- $P(X_{t+1} = k)$ = probability of allele frequency in the next generation
- N = population size
- p = allele frequency in the current generation

Low effective population size ($N < 100$) signifies pronounced genetic drift, leading to rapid fixation or loss of alleles. A moderate effective population size (N between 100 and 1000) reflects a balance between the influences of genetic drift and natural selection. Conversely, a high effective population size ($N > 1000$) indicates diminished drift, with selection predominating the alterations in allele frequencies. This metric is instrumental in predicting allele fixation probabilities within breeding populations and is valuable in evaluating the erosion of genetic diversity attributable to drift. Furthermore, it is employed in marker-assisted selection to refine breeding strategies (Ferrer-Admetlla et al., 2016).

Kimura’s neutral theory of molecular evolution posits that the majority of mutations are neutral, propagating through genetic drift rather than through selective pressures. This theoretical framework is essential for estimating mutation rates and elucidating changes in allele frequencies. Its equation is

$$\theta = 4N_e\mu$$

Where:

- θ = mutation rate per site
- N_e = effective population size
- μ = mutation rate per generation

A low θ (< 0.001) signifies diminished genetic diversity, wherein genetic drift prevails and adaptive processes are sluggish. A moderate θ (0.001 - 0.01) indicates a delicate equilibrium between mutation and drift, facilitating the gradual accumulation of neutral mutations. Conversely, a high θ (> 0.01) denotes substantial genetic diversity, characterized by the rapid accumulation of mutations, thereby enhancing evolutionary potential. Kimura’s neutral theory elucidates the maintenance of genetic variation within populations (Kimura, 1983; Bürger, 1986). This theory aids in forecasting the accumulation of mutations in small populations and serves as a guiding framework for breeding programs aimed at preserving genetic diversity.

Coalescent theory delineates the trajectory of gene ancestry as it recedes through time, elucidating the ramifications of genetic drift and founder events. It conceptualizes the process by which alleles converge into a common ancestor, thereby offering profound insights into the historical dynamics of populations (Nordberg, 2000; Kuhner, 2008). The mathematical formulation for estimating coalescent time is

$$T_{MRCA} = \frac{2N_e}{k(k-1)}$$

Where:

- T_{MRCA} = time to most recent common ancestor
- N_e = effective population size

- k = number of sampled alleles

A low T_{MRCA} (< 100 generations) signifies recent common ancestry, implying rapid allele fixation attributable to robust selection or genetic drift. A moderate T_{MRCA} (100 - 10,000 generations) indicates a balance between mutation and drift, facilitating the gradual accumulation of genetic diversity. Conversely, a high T_{MRCA} (> 10,000 generations) denotes a profound evolutionary history, suggesting that the population has preserved genetic variation over extensive timescales. The coalescent theory model serves to reconstruct population history utilizing genetic data. It is employed in genomic prediction models to evaluate the ramifications of genetic drift. Additionally, it underpins phylogenetic studies by estimating divergence times.

5.3. Gene Flow

Gene flow represents a pivotal evolutionary force that shapes allele and genotype frequencies within plant populations. It introduces novel genetic material, augments genetic diversity, and curtails population divergence. Gene flow transpires when alleles are transferred between populations through mechanisms such as pollen dispersal, seed movement, or vegetative propagation. Within the context of gene flow, new alleles infiltrate a population, thereby enhancing its adaptability. Populations engaged in gene exchange tend to exhibit increased genetic similarity. Gene flow acts as a bulwark against allele fixation and sustains genetic variation by counteracting the effects of genetic drift. Furthermore, it exerts an influence on local adaptation; high levels of gene flow may dilute locally adapted alleles, while restricted gene flow can foster specialization. For instance, research on crop breeding populations has demonstrated that pollen-mediated gene flow sustains genetic diversity across fragmented landscapes. Gene flow modifies genotype frequencies by introducing heterozygous combinations and reshuffling genetic material, thereby elevating heterozygosity and bolstering genetic resilience. It facilitates hybridization events that can result in innovative trait combinations. However, excessive gene flow, often referred to as genetic swamping, may undermine local adaptation. Investigations into maize populations have illustrated that gene flow from transgenic varieties can significantly alter genotype distributions (Dyer et al., 2009; Wang and Huang, 2024). Migration and gene flow intricately shape genetic diversity within plant populations, influencing allele frequencies, genotype distributions, and potential for adaptation. A comprehensive understanding of these processes is crucial for genomic selection, conservation genetics, and the formulation of effective plant breeding strategies.

Gene flow profoundly impacts allele frequencies, genetic diversity, and population structure. Three principal models are employed to estimate the ramifications of gene flow on allele frequencies: the island model (IM), the stepping-stone model (SSM), and the migration-selection balance model (MSBM). The IM delineates gene flow among subpopulations, positing that populations are partitioned into discrete units (islands) with uniform migration rates between them. This model facilitates the quantification of gene flow and genetic differentiation. The equation utilized for estimating the rate of gene flow is:

$$IM = \frac{1}{1 + 4Nm}$$

Where:

- IM = genetic differentiation between subpopulations
- N = effective population size
- m = migration rate

Low IM (< 0.05) indicates high gene flow, minimal differentiation between populations. Moderate IM (0.05-0.15) implies balanced drift and migration, indicating moderate differentiation. High (> 0.15) suggests strong genetic drift, significant population divergence due to limited migration. IM is used to predict genetic homogenization across populations. It helps assess gene flow impact on breeding populations. It is used in conservation genetics to maintain genetic diversity. The

stepping-stone model describes gradual gene flow between neighboring populations rather than unrestricted migration across all populations. It is particularly useful for studying pollen dispersal in plants. Its equation for gene flow estimation is:

$$SSM = \frac{1}{1 + 2Nm}$$

Where:

- SSM = genetic differentiation between subpopulations
- N = effective population size
- m = migration rate

A low SSM (< 0.05) indicates substantial gene flow and negligible genetic differentiation among neighboring populations. A moderate SSM (0.05-0.15) signifies a balance between genetic drift and migration, reflecting a moderate level of differentiation. Conversely, a high SSM (> 0.15) denotes pronounced genetic drift and significant population divergence stemming from restricted migration. Spatial structure modeling (SSM) is instrumental in elucidating spatial genetic structure within fragmented landscapes. This methodology is employed in crop breeding to investigate gene flow dynamics. Additionally, it bolsters phylogenetic research by estimating genetic connectivity among populations. The migration-selection balance model (MSBM) elucidates how gene flow mitigates selection pressures, thereby preserving genetic diversity while facilitating adaptation. This model is extensively utilized in crop breeding to harmonize the retention of advantageous alleles with genetic interchange. Equation for migration-selection balance model is:

$$q = \frac{\mu}{s + m}$$

Where:

- q = equilibrium allele frequency
- μ = mutation rate
- s = selection coefficient
- m = migration rate

The migration-selection balance model (MSBM) serves to elucidate the equilibrium between gene flow (migration) and natural selection within a population. It is particularly instrumental in comprehending how local adaptation is preserved in the face of incoming alleles from external populations. The model forecasts the frequency of locally adapted alleles contingent upon the intensity of selection and the rate of migration. When migration is pronounced relative to selection, locally adapted alleles may become inundated. Genetic swamping transpires when gene flow from a more prevalent species overwhelms the genetic integrity of a rarer species, resulting in the substitution of local genotypes with hybrids (Rutherford et al., 2019). MSBM can quantify the genetic burden imposed by incoming alleles, enabling researchers to evaluate whether migration yields beneficial or detrimental outcomes. If the selection pressure is sufficiently robust to counteract migration, local adaptation occurs. Otherwise, genetic homogenization could occur. If $m/s < 1$, selection prevails, facilitating the persistence of local adaptation and on the other hand, if $m/s > 1$, migration eclipses selection, culminating in genetic swamping. In multi-locus scenarios, the threshold may fluctuate based on recombination rates and genetic architecture (Yeaman et al., 2011). Empirical studies indicate that strong selection coupled with low migration favors the retention of locally adapted alleles (Yanchukov et al., 2014). These models provide potent instruments for appraising the effects of migration and gene flow, thereby aiding researchers in optimizing genomic selection, conservation genetics, and evolutionary inquiries. A profound understanding of their applications enhances breeding strategies and assessments of genetic diversity.

5.4. Natural Selection

Natural selection plays a quintessential role in shaping gene and genotype frequencies within a population by favoring alleles that enhance survival and reproductive success. Directional selection elevates the prevalence of advantageous alleles while diminishing the frequency of deleterious ones. For instance, the propagation of drought-resistant alleles in agricultural crops exemplifies adaptive selection in response to arid conditions. Stabilizing selection preserves intermediate phenotypes by purging extreme variations. Conversely, disruptive selection promotes extreme traits at the expense of intermediate phenotypes, potentially catalyzing speciation. Should a particular homozygous genotype exhibit superior fitness, its prevalence will increase over successive generations. Certain heterozygous genotypes confer survival advantages, thereby sustaining genetic diversity. Intense selection pressure can diminish genetic diversity, rendering populations more susceptible to environmental fluctuations. Mutation serves as a conduit for introducing novel alleles upon which selection may act. Gene flow can counterbalance selection by infusing fresh genetic material. Genetic drift, characterized by stochastic fluctuations in allele frequency, may eclipse selection in diminutive populations.

5.4.1. Directional Selection

Directional selection constitutes a mechanism of natural or artificial selection that preferentially favors one extreme phenotype over its counterparts, resulting in a shift in allele frequencies toward the advantageous trait. Within the realm of botany, this phenomenon plays a pivotal role in the adaptation to environmental pressures, such as drought resistance, pest tolerance, and nutrient utilization efficiency. Alleles associated with advantageous traits become increasingly prevalent within the population, while less beneficial alleles may be gradually lost across generations. In the context of directional selection, populations exhibit rapid adaptation to environmental fluctuations. For instance, investigations into wheat's resistance to fungal pathogens illustrate that directional selection enhances the frequency of resistance alleles (Mourad et al., 2024). As selection elevates a specific allele, homozygous individuals possessing that allele become more prevalent. Directional selection propels the average trait value toward the selected extreme. However, if directional selection is excessively vigorous, genetic variation may diminish, thereby undermining adaptability. Research on maize drought tolerance exemplifies that directional selection augments the prevalence of genotypes exhibiting improved water-use efficiency (Sheoran et al., 2022).

Commonly employed models to elucidate the effects of directional selection on gene and allele frequencies include the quantitative genetic model and Fisher's fundamental theorem of natural selection. The quantitative genetic model delineates how selection modifies allele frequencies in accordance with the heritability of traits.

$$R = h^2S$$

Where:

- R = response to selection
- h^2 = heritability of the trait
- S = selection differential

Quantitative genetic model helps predict trait evolution in breeding programs. It guides selection strategies for improving crop resilience and used in adaptive trait modeling for conservation genetics. Quantitative genetic models analyze the inheritance of complex traits influenced by multiple genes and environmental factors. The interpretation of results typically involves variance components, heritability estimates, genetic correlations, and genomic estimated breeding values (GEBVs). Partitioning phenotypic variance into genetic (additive, dominance, epistatic) and environmental components help understand proportion of genetic control on traits. Determining the proportion of trait variation due to genetic factors guides selection strategies. Assessing relationships between traits help optimize breeding decisions. Predicting an individual's genetic potential for a trait using marker effects is used to identify high potential genotypes. Threshold values for

quantitative genetic models outputs depend on the trait and selection objectives. Common thresholds include heritability, LOD score, and genomic prediction accuracy. Heritability ($h^2 > 0.3-0.5$) indicates strong genetic control, supporting selection. LOD score (>3.0) suggests significant quantitative trait loci (QTL) effects (Sharma et al., 2022). Genomic prediction accuracy (>0.6) ensures reliable selection decisions (Rabier et al., 2016; Dekkers et al., 2021).

Quantitative genetic models are instrumental in forecasting trait evolution within breeding programs. They inform selection strategies aimed at enhancing crop resilience and are employed in adaptive trait modeling for conservation genetics. These models scrutinize the inheritance of intricate traits that are influenced by a multitude of genes and environmental factors. The interpretation of outcomes typically encompasses variance components, heritability estimates, genetic correlations, and genomic estimated breeding values (GEBVs).

Dissecting phenotypic variance into genetic (additive, dominance, epistatic) and environmental components elucidates the extent of genetic control over traits. Ascertaining the proportion of trait variation attributable to genetic factors is pivotal in guiding selection strategies. Evaluating interrelationships between traits facilitates the optimization of breeding decisions. The prediction of an individual's genetic potential for a trait through marker effects serves to identify genotypes with high potential. The threshold values for the outputs of quantitative genetic models are contingent upon the specific trait and selection objectives. Common thresholds include heritability, LOD score, and genomic prediction accuracy. A heritability estimate ($h^2 > 0.3-0.5$) signifies robust genetic control, thereby bolstering the case for selection. A LOD score exceeding 3.0 indicates substantial effects of quantitative trait loci (QTL) (Sharma et al., 2022). Additionally, genomic prediction accuracy of greater than 0.6 ensures dependable selection decisions (Rabier et al., 2016; Dekkers et al., 2021).

Fisher's fundamental theorem of natural selection elucidates how selection augments mean fitness by favoring advantageous alleles. It posits that the rate of increase in mean fitness attributable to natural selection is equivalent to the genetic variance in fitness at that moment. It explains how selection increases population fitness and helps quantify genetic variance in breeding populations. Crop breeding, it is used in to optimize trait selection. The equation for fitness increase is:

$$\frac{dW}{dt} = V_G$$

Where:

- W = mean fitness of the population
- V_G = genetic variance in fitness

Fisher's fundamental theorem of natural selection posits that the rate of increase in a population's fitness is commensurate with its genetic variance in fitness at any given moment. This implies that populations exhibiting elevated genetic variance in fitness will undergo more rapid adaptation through the mechanism of natural selection. The theorem intimates that populations endowed with greater genetic diversity possess a heightened capacity for evolutionary transformation. Conversely, when genetic variance is minimal, the pace of adaptation diminishes. Only the genetic components of fitness play a pivotal role in facilitating evolutionary change, as environmental factors do not exert a direct influence on the selection process. Although the theorem does not delineate a strict threshold value, practical applications suggest that higher genetic variance (exceeding 0.2–0.5) fosters more robust selection responses, while low variance (below 0.1) indicates constrained evolutionary potential. The efficiency of selection is contingent upon the equilibrium between genetic variance and environmental influences.

The directional selection model in population genetics meticulously monitors the fluctuations in allele frequencies across generations as a consequence of directional selection. It prognosticates the fixation probabilities of advantageous alleles. The equation delineating the alterations in allele frequency is as follows:

$$p' = p + sp(1 - p)$$

Where:

- p' = *allele frequency in the next generation*
- p = *current allele frequency*
- s = *selection coefficient*

Directional selection models in population genetics serve to elucidate the fixation of alleles within plant populations. They also inform strategies for selecting traits associated with stress tolerance and facilitate assessments of genetic diversity in conservation initiatives. Directional selection is characterized by the phenomenon wherein individuals exhibiting extreme phenotypic traits possess superior fitness, resulting in a progressive shift in allele frequencies across generations. The interpretation of results typically encompasses changes in allele frequencies, the selection coefficient, the reduction of genetic variance, and the anticipated response to selection. Beneficial alleles experience an increase in frequency, whereas deleterious alleles diminish. The selection coefficient (s) quantifies the intensity of selection exerted on a trait, with elevated values signifying stronger selective pressure. Over extended periods, directional selection may lead to a diminution of genetic diversity as advantageous alleles become fixed within the population. The response to selection forecasts the expected alteration in the mean trait value. A selection coefficient ($s > 0.1$ – 0.2) denotes a robust selective pressure. Furthermore, heritability ($h^2 > 0.3$ – 0.5) corroborates an effective response to selection, while genomic prediction accuracy (>0.6) ensures the reliability of selection decisions. Various models of directional selection are employed to monitor changes in allele frequencies across generations and to predict the fixation probability of advantageous alleles. These models constitute powerful instruments for estimating the ramifications of directional selection, thereby aiding researchers in optimizing genomic selection, conservation genetics, and evolutionary studies. A comprehensive understanding of their applications enhances breeding strategies and assessments of genetic diversity.

5.4.2. Stabilizing Selection

Stabilizing selection is a process that preferentially favors intermediate phenotypes over extreme variations, thereby preserving genetic stability within plant populations. This mode of selection diminishes genetic diversity while safeguarding advantageous traits that enhance survival and reproductive success. Stabilizing selection fortifies genetic stability, curtails extreme variants, and augments population adaptability. Within this framework, intermediate alleles remain predominant, precluding drastic fluctuations in allele frequencies. Alleles linked to extreme phenotypes diminish across generations, ensuring that plants retain traits finely tuned to their environmental conditions. For instance, research on seed size in crop species illustrates that stabilizing selection sustains an optimal range of seed sizes, preventing the predominance of excessively large or small seeds (Wellmann et al., 2023; Ambika et al., 2014). Stabilizing selection elevates the frequency of heterozygous genotypes, diminishes the prevalence of extreme homozygous genotypes, and conserves adaptive traits. This selection mechanism balances genetic variation while thwarting extreme phenotypic shifts. It restricts the dominance of traits that may compromise fitness and ensures that populations preserve beneficial genetic combinations. Investigations into flowering time in wheat reveal that stabilizing selection maintains an optimal flowering period, effectively preventing early or late bloomers from becoming predominant (Rhoné et al., 2010; Kamran et al., 2014; Flohr et al., 2018).

The frequently employed models to elucidate the effects of stabilizing selection are the quantitative genetic model and the Bulmer effect model. The quantitative genetic model elucidates how selection perpetuates trait stability across generations. It predicts genetic variance reduction using the breeder's equation:

$$R = h^2 S$$

Where:

- R = response to selection
- h^2 = heritability of the trait
- S = selection differential

The Bulmer effect model elucidates the phenomenon whereby selective pressures diminish genetic variance across generations, attributable to selection-induced linkage disequilibrium. This effect manifests as a consequence of selection favoring individuals with elevated breeding values, culminating in a reduction of additive genetic variance in ensuing generations. The quantification of the Bulmer effect is instrumental in forecasting genetic gain within breeding programs. It serves as a guide for the optimization of selection intensity, thereby preserving genetic diversity. Furthermore, it is employed in marker-assisted selection to enhance genomic predictions. The Bulmer effect quantifies how selection alters genetic variance using the following equation:

$$V'_A = V_A(1 - i^2h^2)$$

Where:

- V'_A = reduced additive genetic variance after selection
- i = selection intensity
- h^2 = heritability
- V_A = Initial additive genetic variance before selection

This equation elucidates that intensified selection engenders more pronounced reductions in genetic variance, thereby influencing the long-term response to selection. Elevated selection intensity (i) precipitates a more significant diminishment of genetic variance. Traits characterized by high heritability (h^2) undergo more pronounced Bulmer effects, as selection adeptly harnesses genetic variance. Across successive generations, genetic variance attains a state of stabilization, culminating in an asymptotic response to selection. In general, stabilizing selection safeguards genetic integrity within plant populations by favoring intermediate traits, thereby sculpting allele and genotype frequencies. Comprehending these dynamics is imperative for advancements in genomic selection, evolutionary biology, and conservation genetics.

5.4.3. Disruptive Selection

Disruptive selection favors extreme phenotypes over intermediate traits, thereby fostering increased genetic diversity and facilitating potential speciation. Within plant populations, this form of selection plays a pivotal role in adaptive divergence, particularly in heterogeneous environments. Disruptive selection elevates the frequency of extreme alleles (Xu, 2022), signifying that alleles associated with pronounced traits become more prevalent. Consequently, there is a concomitant reduction in the prevalence of intermediate alleles, resulting in a decline in the number of alleles that encode for average phenotypes. The genetic divergence instigated by disruptive selection may culminate in the emergence of distinct subpopulations, paving the way for speciation. For instance, investigations into flower color polymorphism in wildflowers reveal that disruptive selection sustains distinct color morphs, thereby averting the dominance of a singular phenotype. This selection process engenders a heightened frequency of homozygous extreme genotypes, leading to an increased representation of individuals exhibiting extreme traits within the population. This dynamics results in a diminished frequency of heterozygous genotypes, as intermediate phenotypes wane under selection pressure. Such processes give rise to subpopulations that may evolve unique genetic compositions. Research on seed size variation in plants illustrates that disruptive selection favors both large and small seeds, thereby preserving genetic diversity. The models frequently employed to elucidate the effects of disruptive selection include the quantitative genetic model and the adaptive landscape model. As previously discussed, the quantitative genetic model delineates

how selection modifies genetic variance across generations, predicting trait divergence through the breeder's equation.

$$R = h^2 S$$

Where:

- R = response to selection
- h^2 = heritability of the trait
- S = selection differential

The adaptive landscape model, pioneered by Sewall Wright, provides a compelling visualization of how selection influences genetic variation by delineating fitness peaks and troughs (Hansen, 2013). It elucidates the trajectory of populations as they advance toward adaptive peaks, wherein fitness is optimized. This model finds application in crop breeding, facilitating the preservation of diverse phenotypic traits. The disruptive selection model in population genetics serves as a crucial tool for monitoring shifts in allele frequencies resulting from selection pressures, and it is instrumental in forecasting long-term genetic divergence within plant populations. Disruptive selection amplifies genetic diversity by favoring extreme phenotypic traits, thereby shaping allele and genotype frequencies. Comprehending these dynamics is vital for genomic selection, evolutionary biology, and conservation genetics. Equation for adaptive landscape dynamics:

$$W = f(x)$$

Where:

- W = represents the fitness of an organism or genotype.
- x = is a vector of genetic or phenotypic traits influencing fitness.
- f = is the function describing the relationship between traits and fitness

Disruptive selection models in population genetics elucidate the dynamics of allele frequency fluctuations attributable to disruptive selection, forecasting the prevalence of extreme traits while concomitantly diminishing the frequency of intermediate traits. This framework is instrumental in modeling genetic divergence within plant populations. Moreover, it informs selection strategies aimed at preserving genetic diversity and bolsters studies on speciation by anticipating allele fixation.

$$p' = p + sp(1 - p)(1 - 2p)$$

Where:

- p' = allele frequency in the next generation
- p = current allele frequency
- s = selection coefficient

5.4.4. Balancing Selection

Balancing selection sustains genetic diversity within plant populations by favoring a multitude of alleles rather than permitting a singular allele to become fixed. Two principal mechanisms of balancing selection are heterozygote advantage and negative frequency-dependent selection. These mechanisms play a crucial role in preserving genetic variation and influencing allele and genotype frequencies. Heterozygote advantage, often referred to as overdominance, arises when individuals possessing heterozygous genotypes exhibit greater fitness compared to their homozygous counterparts. This mechanism ensures the retention of both alleles within the population, thereby preventing the elimination of one allele through selective pressures. Heterozygote advantage bolsters genetic diversity by permitting both alleles to coexist within the population. It enhances heterozygosity by conferring a selective advantage to heterozygous individuals and obstructs allele fixation by preventing either allele from attaining complete dominance. For instance, investigations into self-incompatibility genes in plants illustrate how heterozygote advantage mitigates inbreeding and upholds genetic diversity. Mathematical model for heterozygote advantage is:

$$p = \frac{p^2 w_{AA} + pq w_{Aa}}{p^2 w_{AA} + 2pq w_{Aa} + q^2 w_{aa}}$$

Where:

- p' = allele frequency in the next generation
- w_{AA}, w_{Aa}, w_{aa} = fitness values of different genotypes
- p and q are initial frequencies

Negative frequency-dependent selection transpires when infrequent alleles possess a fitness advantage, thereby thwarting the ascendance of any singular allele (Brisson et al., 2018). This mechanism is pivotal in preserving genetic diversity over time. Negative frequency-dependent selection amplifies the prevalence of rare alleles. As an allele becomes increasingly scarce, its relative fitness advantage escalates. This process inhibits genetic homogeneity and fosters the coexistence of multiple alleles. It sustains population stability and mitigates the risk of genetic bottlenecks. For instance, investigations into flower color polymorphism in wildflowers reveal that uncommon color variants are preferentially selected by pollinators, thereby safeguarding genetic diversity. Mathematical model for negative frequency-dependent selection is:

$$w_i = w_o - s f_i$$

Where:

- w_i = fitness of allele ii
- w_o = baseline fitness
- s = selection coefficient
- f_i = frequency of allele ii

Balancing selection serves a pivotal function in sustaining genetic diversity within plant populations. The advantage of heterozygosity guarantees the persistence of both alleles, while negative frequency-dependent selection inhibits allele fixation by preferentially favoring rare variants. These mechanisms are indispensable for the realms of genomic selection, evolutionary biology, and conservation genetics.

5.5. Recombination Effects

Recombination is a quintessential process in plant genetics that reshuffles alleles during meiosis, engendering genetic diversity and influencing allele and genotype frequencies. It assumes a pivotal role in genomic selection, evolutionary biology, and conservation genetics by facilitating adaptation and trait enhancement. Recombination amplifies genetic diversity, forming novel allele combinations and augmenting adaptability. It disrupts linkage disequilibrium and diminishes associations between linked alleles, thereby permitting independent inheritance. Furthermore, it forestalls allele fixation and preserves genetic variation by counteracting the effects of genetic drift. Empirical studies illustrate that recombination rates exhibit variability across plant genomes, with elevated recombination frequencies observed at chromosome termini and diminished rates within centromeric regions (Zou et al., 2024; Brazier and Glémin, 2024). Recombination enhances heterozygosity and promotes genetic variation by increasing the prevalence of heterozygous genotypes. It fosters hybridization and facilitates the emergence of novel trait combinations in breeding programs. Additionally, it influences selection efficiency and augments the accuracy of genomic selection by reshuffling advantageous alleles. Investigations into recombination hotspots within plant genomes reveal that gene regulatory sequences, particularly promoters, are enriched in recombination sites (Brazier and Glémin, 2024).

Recombination plays an indispensable role in shaping genetic diversity, influencing allele frequencies, and facilitating adaptation within plant populations. Three principal models—the recombination rate model (RRM), the linkage disequilibrium decay model (LDDM), and the gene conversion model (GCM)—serve to quantify the effects of recombination and provide profound insights into genomic selection, evolutionary biology, and conservation genetics. The recombination rate model estimates the frequency of recombination events across genomic regions, aiding researchers in comprehending crossover dynamics and the maintenance of genetic diversity. The identification of recombination hotspots in plant genomes is facilitated by the recombination rate,

which also informs marker-assisted selection by optimizing crossover rates and supports trait mapping in breeding programs (Li and Stephens, 2003; Cutter et al., 2019). Equation for recombination rate estimation is:

$$r = \frac{c}{L}$$

Where:

- r = recombination rate per generation
- c = number of crossover events
- L = length of the genomic region

LDDM elucidates the manner in which recombination diminishes allele associations across generations, thereby influencing genetic diversity and adaptation. It serves as a predictive tool for the sustenance of genetic diversity within plant populations. Furthermore, it informs selection strategies aimed at optimizing the ramifications of recombination. Additionally, it bolsters phylogenetic research by facilitating the estimation of genetic connectivity. Equation for linkage disequilibrium decay:

$$D_t = D_0(1 - r)^t$$

Where:

- D_t = linkage disequilibrium at time t
- D_0 = initial linkage disequilibrium
- r = recombination rate

The GCM meticulously monitors non-reciprocal recombination events, wherein genetic material is transposed from one allele to another without the occurrence of crossover. It facilitates the modeling of allele frequency fluctuations attributable to gene conversion. Furthermore, it informs selection strategies aimed at preserving genetic diversity. Additionally, it underpins genetic mapping endeavors within plant breeding programs. Equation for gene conversion rate:

$$G = \frac{\mu}{1 + 4N_e r}$$

Where:

- G = gene conversion rate
- μ = mutation rate
- N_e = effective population size
- r = recombination rate

Recombination effects models serve as formidable instruments for estimating the ramifications of recombination, empowering researchers to refine genomic selection, conservation genetics, and evolutionary investigations. A profound comprehension of their applications augments breeding methodologies and enhances assessments of genetic diversity.

5.6. Nonrandom Mating

Nonrandom mating exerts a significant influence on allele and genotype frequencies by modifying the genetic architecture within plant populations. Two primary forms, assortative mating, where like mates with like and disassortative mating, where opposites attract, are commonly observed. Assortative mating transpires when individuals with analogous phenotypes preferentially engage in copulation, culminating in heightened homozygosity, diminished genetic variation, and an increased risk of inbreeding depression. In this scenario, a greater number of individuals inherit identical alleles, which further constricts genetic diversity (Merrill et al., 2019; Massey et al., 2025).

This phenomenon constrains adaptability to environmental fluctuations and fosters the accumulation of deleterious alleles that may compromise fitness. For instance, investigations into flower color inheritance in snapdragons illustrate that assortative mating fortifies specific color morphs, thereby diminishing genetic diversity. A mathematical model for assortative mating:

$$f(AA) = p^2 + sp(1 - p)$$

Where:

- $f(AA)$ = frequency of homozygous dominant genotype
- p = allele frequency
- s = assortative mating coefficient

Disassortative mating transpires when individuals with disparate phenotypes preferentially engage in reproductive partnerships, culminating in heightened heterozygosity, the preservation of rare alleles, and enhanced resistance to diseases. This phenomenon augments genetic diversity and adaptability, mitigating allele loss attributable to genetic drift; furthermore, heterozygous individuals frequently demonstrate superior resilience. Investigations into self-incompatibility genes in flora elucidate that disassortative mating forestalls inbreeding and sustains genetic diversity ([Greenspoon and Gonigle, 2014](#)). Additionally, disassortative mating aids in optimizing breeding strategies by regulating genetic diversity. In the realm of evolutionary biology, it serves to elucidate how mating preferences influence allele distributions. In conservation genetics, it provides a framework for population management, thereby averting genetic bottlenecks. Mathematical model for disassortative mating effect is:

$$f(Aa) = 2pq + dp(1 - p)$$

Where:

- $f(Aa)$ = frequency of heterozygous genotype
- p = allele frequency
- d = disassortative mating coefficient

5.7. Population Size and Environmental Pressures

Population size and environmental pressures profoundly influence allele and genotype frequencies within plant populations through mechanisms such as genetic drift, selection, and migration. Genetic bottlenecks manifest when a population experiences a significant reduction in size due to events such as droughts, habitat destruction, or disease outbreaks. This phenomenon leads to a diminishment of genetic diversity and the fixation of particular alleles as a result of random sampling effects. For instance, a rare drought-resistant allele may become predominant if only a limited number of surviving plants possess it. Founder effects emerge when a small subset of a population establishes itself in a new environment, carrying merely a fraction of the genetic diversity found in the original population. This can precipitate rapid divergence in allele frequencies relative to the source population. For example, a small group of plants migrating to a novel habitat may lack alleles conferring disease resistance, thereby rendering them susceptible. Climate-driven alterations, such as shifts in temperature, precipitation, and soil conditions, impose selective pressures that favor certain alleles. For instance, in regions experiencing prolonged drought, alleles associated with deep root systems and efficient water utilization may proliferate in frequency ([Beavis et al., 2023](#)).

Various models are employed to elucidate the effects of population size and environmental pressures. These models include the Hardy-Weinberg equilibrium (HWE) model, the Wright-Fisher model, Kimura's neutral theory, and coalescent theory models. The Hardy-Weinberg equilibrium (HWE) model establishes a baseline for allele frequencies in an ideal population devoid of evolutionary forces. Deviations from HWE signify the influence of selection, drift, or migration ([Biology Insights Team, 2025](#)). The Wright-Fisher model delineates genetic drift in finite populations, illustrating how allele frequencies fluctuate randomly across generations. It is

particularly pertinent for small populations impacted by bottlenecks or founder effects (Beavis et al., 2023). Kimura's neutral theory posits that the majority of genetic variation arises from neutral mutations rather than selection, thereby elucidating allele frequency changes in populations where selection pressures are minimal (Beavis et al., 2023). Coalescent theory traces the lineage of alleles across generations to infer historical population dynamics, proving invaluable for comprehending how past bottlenecks and founder events have shaped contemporary genetic diversity.

6. Factors Affecting Evolutionary Forces

6.1. Mutation Rate

Mutation rate variability significantly influences evolutionary dynamics, encompassing mutation, migration, and natural selection, by modulating genetic diversity, adaptive potential, and population dynamics. Mutations introduce novel genetic variations, serving as the foundational substrate for evolution. Elevated mutation rates can expedite genetic diversity, whereas diminished rates may constrain adaptive capacity. For instance, in environments undergoing rapid transformation, increased mutation rates may bolster survival by fostering advantageous traits.

Furthermore, mutation rate variability impacts the genetic architecture of migrating populations. Populations characterized by heightened mutation rates may introduce unprecedented alleles into novel environments, thereby shaping local adaptation. For example, a plant species dispersing to a drought-prone habitat may possess mutations that enhance water-use efficiency.

Selection processes operate on mutations, privileging beneficial variants while purging deleterious ones. Elevated mutation rates can precipitate an augmented load of harmful mutations, potentially compromising fitness. Conversely, in stable environments, lower mutation rates may be favored to preserve well-adapted genotypes.

6.2. Selective Pressure

Selective pressures in both artificial and natural environments sculpt evolutionary dynamics such as mutation, migration, and natural selection by influencing genetic diversity, adaptation, and allele frequencies. In natural ecosystems, mutations occur randomly and are subject to environmental constraints, including climatic fluctuations and pathogenic pressures. Conversely, in artificial settings, human-mediated selection—exemplified by breeding programs—may preferentially amplify specific mutations, thereby hastening trait fixation. For instance, in agricultural breeding, mutations that confer herbicide resistance are deliberately selected, while in wild flora, mutations that enhance drought resilience emerge as a result of natural selection. In natural environments, migration introduces genetic variability, enabling populations to adapt to novel conditions. In contrast, migration in artificial contexts is frequently regulated; for instance, selective breeding restricts gene flow, thereby diminishing genetic diversity. Wild plant populations, for example, exchange alleles through pollen dispersal, whereas controlled breeding programs limit gene flow to preserve desired phenotypic traits (Jenczewski et al., 2003; Johnson and Galloway, 2008). In natural environments, selection favors traits that bolster survival and reproductive success amidst environmental challenges. In artificial environments, however, selection is steered by human preferences, often prioritizing yield, aesthetic appeal, or disease resistance. For example, wild maize has evolved traits conducive to drought resistance through the mechanisms of natural selection, whereas contemporary maize varieties are cultivated for optimal yield under regulated conditions (Sheoran et al., 2022; Liu and Qin, 2021).

6.3. Gene flow

Gene flow assumes a pivotal role in shaping evolutionary dynamics, encompassing mutation, migration, and natural selection, by influencing genetic diversity, adaptation, and population structure. It serves to introduce novel mutations into a population, thereby augmenting genetic variation. In instances where populations exhibit low mutation rates, gene flow can serve as a

compensatory mechanism by introducing new alleles. For instance, a drought-resistant allele disseminated through pollen dispersal may significantly enhance survival prospects in arid environments.

Gene flow facilitates the transference of alleles between populations, thereby diminishing genetic differentiation. Elevated levels of gene flow can result in the homogenization of populations, whereas restricted gene flow may foster local adaptation. In fragmented habitats, for example, limited gene flow can precipitate genetic drift and the erosion of advantageous alleles. The impact of gene flow on local adaptations can be dual-faceted, either bolstering or undermining these adaptations depending on prevailing selective pressures. Beneficial alleles can disseminate rapidly via gene flow, thereby enhancing fitness in novel environments. For example, in coastal flora, salt-tolerance alleles may propagate inland through gene flow, thereby facilitating adaptation.

7. Impacts of Factors Affecting Allele Frequency

The factors influencing allele frequency—mutation, natural selection, genetic drift, and gene flow—play a pivotal role in sculpting genetic diversity and shaping evolutionary trajectories. Mutations serve to introduce novel alleles, thereby providing the essential raw material for evolutionary processes. Beneficial mutations may become fixed within populations, whereas neutral or deleterious mutations are likely to be lost over time. Natural selection favors alleles that confer advantages in survival and reproductive success, leading to directional, stabilizing, or disruptive selection that profoundly influences population genetics. In smaller populations, allele frequencies may fluctuate due to stochastic events, potentially culminating in the fixation or loss of alleles and accelerating reproductive isolation. Migration facilitates the introduction of new genetic material, counteracting the tendency toward divergence. Conversely, diminished gene flow can promote genetic differentiation, which is a fundamental driver of speciation. These evolutionary forces interact in a dynamic manner, significantly affecting genetic diversity, adaptation, speciation, and the resilience of populations.

7.1. Genetic Diversity

Factors influencing allele frequency, such as mutation, genetic drift, natural selection, and gene flow, plays an indispensable role in shaping genetic diversity within populations. Mutation serves as a source of novel alleles, thereby augmenting genetic variation. Beneficial mutations can facilitate adaptation, while deleterious mutations may be eliminated through selective pressures. For instance, mutations that confer drought resistance in plants can proliferate in arid environments. Genetic drift, characterized by random fluctuations in allele frequencies, particularly in small populations, can result in the erosion of genetic diversity and the fixation of certain alleles. A case in point is the potential disappearance of a rare allele due to stochastic events such as habitat destruction. Natural selection preferentially favors alleles that enhance survival and reproductive success. It can also enhance genetic diversity when multiple traits confer advantages in varying environments. For example, plant species inhabiting high-altitude regions may evolve alleles that confer cold tolerance. Moreover, the movement of alleles between populations is vital for maintaining genetic diversity. Migration can introduce advantageous alleles or disrupt local adaptations. An illustrative example is the dispersal of pollen between plant populations, which can facilitate the spread of beneficial traits.

7.2. Adaptation

Factors influencing allele frequency, such as mutation, genetic drift, natural selection, and gene flow, play an indispensable role in shaping adaptation by affecting genetic diversity and population resilience. Mutation serves as a catalyst for introducing novel genetic variations, some of which may significantly enhance adaptability to environmental fluctuations. Beneficial mutations can proliferate within populations, thereby augmenting survival and reproductive success. For instance, mutations that confer drought resistance in plants may experience increased frequency in arid ecosystems.

Random fluctuations in allele frequencies, particularly in small populations, can result in the loss of adaptive alleles. Genetic drift can diminish genetic diversity, thereby constraining a population's capacity to respond to environmental changes. For example, a rare allele associated with pest resistance may be eradicated due to stochastic events. Natural selection preferentially favors alleles that enhance survival and reproductive efficacy, thereby steering adaptation across generations. This process can culminate in specialization within distinct environments, thereby enhancing overall fitness. For example, flora inhabiting high-altitude regions may evolve alleles that confer cold tolerance. Gene flow facilitates the introduction of new alleles into populations, thereby preserving genetic diversity and promoting adaptation. It can disseminate advantageous traits across populations, thereby bolstering resilience. For instance, pollen dispersal between plant populations may introduce beneficial traits.

7.3. Speciation

Several factors exert a profound influence on allele frequency within populations, each significantly impacting the processes of speciation. The principal determinants encompass mutation, natural selection, genetic drift, and gene flow, with each factor playing a unique role in sculpting genetic diversity and shaping evolutionary trajectories. Mutations serve as the catalyst for introducing novel genetic variations, which may culminate in the emergence of distinctive traits. When advantageous, these mutations can become established within a population, thereby contributing to divergence among populations and the eventual emergence of new species. Natural selection preferentially favors alleles that enhance survival and reproductive success, instigating adaptive transformations. Over time, populations subjected to disparate selective pressures may diverge, culminating in the formation of distinct species. In smaller populations, stochastic fluctuations in allele frequencies can lead to either fixation or the loss of alleles. Genetic drift can expedite reproductive isolation, particularly in populations that are geographically isolated. Conversely, migration facilitates the introduction of new alleles into populations, counterbalancing divergence. A reduction in gene flow between populations permits the accumulation of genetic differences, thereby facilitating the process of speciation. These evolutionary forces interact in a dynamic manner, intricately shaping genetic diversity and propelling speciation events.

7.4. Population Resilience

Factors influencing allele frequency, including mutation, genetic drift, natural selection, and gene flow, plays a pivotal role in shaping population resilience by affecting genetic diversity, adaptability, and potential for survival. Mutation introduces novel genetic variations, some of which may enhance resilience to environmental fluctuations. Beneficial mutations can augment survival, whereas deleterious mutations may diminish fitness. For instance, mutations that confer disease resistance in crops can significantly bolster population resilience.

Random fluctuations in allele frequencies, particularly in small populations, can precipitate the loss of adaptive alleles. Genetic drift can diminish genetic diversity, thereby constraining a population's capacity to respond to environmental shifts. For example, a rare allele associated with pest resistance may be inadvertently lost due to stochastic events, thereby undermining resilience.

Natural selection favors alleles that enhance survival and reproductive success, driving adaptation across generations. This process can lead to specialization in distinct environments, thereby augmenting resilience. For instance, flora in saline soils may evolve alleles conferring salt tolerance, thereby improving their viability.

Gene flow facilitates the introduction of new alleles into populations, preserving genetic diversity and promoting adaptation. It can disseminate advantageous traits across populations, thereby enhancing resilience. For example, pollen dispersal among plant populations can introduce beneficial traits, reinforcing overall population robustness.

8. Conclusion and Recommendations

Mutations introduce novel alleles, significantly influencing the adaptability of populations. While the majority of mutations are either neutral or deleterious, beneficial mutations can catalyze evolutionary transformation. Selection pressures favor alleles that augment fitness, resulting in patterns of directional, stabilizing, or disruptive selection. This mechanism underlies the optimization of traits in breeding programs. Random fluctuations in allele frequencies, particularly within small populations, can precipitate the fixation or loss of alleles, thereby accelerating reproductive isolation and speciation. Migration serves to introduce genetic variation, counteracting the effects of divergence. Conversely, diminished gene flow engenders genetic differentiation, a pivotal factor in speciation events. To enhance the efficacy of contemporary breeding methodologies such as genomic selection, it is imperative to integrate evolutionary principles into breeding strategies. Consequently, the following applications in breeding strategies are proposed:

- **Optimizing training populations:** Leveraging models of genetic drift and selection to refine training populations through strategies such as CDmean and Avg_GRM_self.
- **Harnessing adaptive alleles:** Identifying advantageous mutations via Genome-Wide Association Studies (GWAS) and incorporating these into breeding pipelines to enhance stress tolerance and nutrient efficiency.
- **Enhancing genetic diversity:** Strategically managing gene flow to sustain diversity while mitigating excessive homogenization within breeding populations.
- **Phenomics-driven selection:** Employing Unmanned Aerial Vehicles (UAVs), RGB (Red, Green, Blue) imaging, and Light Detection and Ranging (LiDAR) technology to evaluate phenotypic responses to selection pressures, thereby improving the precision of trait predictions.

9. Future Prospects

This review highlights the following emerging directions for integrating evolutionary genetics with multi-omics technologies to advance predictive models for population adaptation.

- **Genomic-transcriptomic synergy:** Combining GWAS with transcriptomic data to uncover regulatory networks influencing allele frequency shifts.
- **Epigenetic modifications in selection:** Investigating how DNA methylation and histone modifications impact allele retention and trait heritability.
- **AI-driven predictive models:** Developing machine learning frameworks to simulate evolutionary trajectories and optimize breeding strategies.
- **Climate-responsive genomic selection:** Incorporating environmental variables into genomic prediction models to enhance adaptation strategies for climate resilience.

References

- Abraham, A., LaBella, A. L., Capra, J.A., Rokas, A. 2022. Mosaic patterns of selection in genomic regions associated with diverse human traits. *PLoS Genet* 18(11): e1010494. <https://doi.org/10.1371/journal.pgen.1010494>
- Alday, J. 2023. Environmental stressors and cellular mutations: Unveiling responses and adaptations. *J Cell Sci Mut.* 7(5):166
- Allendorf, F. W., and others. 2022. *Natural Selection, Conservation and the Genomics of Populations*, 3rd ED; Oxford Academic. <https://doi.org/10.1093/oso/9780198856566.003.0008>
- Ambika, S., Manonmani, V., Somasundaram, G. 2014. Review on Effect of Seed Size on Seedling Vigour and Seed Yield. *Research Journal of Seed Science*, 7: 31-38. <https://scialert.net/abstract/?doi=rjss.2014.31.38>
- Andrews, C. 2010. The Hardy-Weinberg Principle. *Nature Education Knowledge* 3(10):65

- Bajay, M.M. 2025. What Is the Meaning of Genetic Drift? In: Bohrer Monteiro Siqueira, M.V., Konzen, E.R., Galetti Junior, P.M. (eds) Population Genetics in the Neotropics. Springer, Cham. https://doi.org/10.1007/978-3-031-83685-5_4
- Beavis, W., K. Lamkey, and A. A. Mahama. 2023. Gene Frequencies. In W. P. Suza, & K. R. Lamkey (Eds.), Quantitative Genetics for Plant Breeding. Iowa State University Digital Press.
- Beavis, W., L. Merrick, K. Meade, A. Campbell, D. Muenchrath, and S. Fei. 2023. Population Genetics. In W. P. Suza, & K. R. Lamkey (Eds.), Crop Genetics. Iowa State University Digital Press. DOI: 10.31274/isudp.2023.130
- Biology Insights Team, 2025. Factors Affecting Allele Frequency in Populations. Accessed on 7 May 2025, Available at: <https://biologyinsights.com/factors-affecting-allele-frequency-in-populations/>
- Brazier, T., Glémin, S. 2022. Diversity and determinants of recombination landscapes in flowering plants. PLoS Genet 18(8): e1010141. <https://doi.org/10.1371/journal.pgen.1010141>
- Brazier, T., Glémin, S. 2024. Diversity in Recombination Hotspot Characteristics and Gene Structure Shape Fine-Scale Recombination Patterns in Plant Genomes, Molecular Biology and Evolution, 41 (9), msae183, <https://doi.org/10.1093/molbev/msae183>
- Brisson, D. 2018. Negative Frequency-Dependent Selection Is Frequently Confounding. Front. Ecol. Evol. 6:10. doi: 10.3389/fevo.2018.00010
- Bruce, W., Lynch, M. 2018. Interaction of Selection, Mutation, and Drift', Evolution and Selection of Quantitative Traits; Oxford Academic, <https://doi.org/10.1093/oso/9780198830870.003.0007>
- Bürger, R. 1986. On the maintenance of genetic variation: global analysis of Kimura's continuum-of-alleles model. J. Math. Biol. 24, 341–351. <https://doi.org/10.1007/BF00275642>
- Chapman, R.J., Hill, T., Unckless, L.U. 2019. Balancing Selection Drives the Maintenance of Genetic Variation in Drosophila Antimicrobial Peptides, Genome Biology and Evolution, 11(9): 2691–2701, <https://doi.org/10.1093/gbe/evz191>
- Charlesworth, D. 2006. Balancing Selection and Its Effects on Sequences in Nearby Genome Regions. PLoS Genet 2(4): e64. <https://doi.org/10.1371/journal.pgen.0020064>
- Cutter, A. D. 2019. Recombination and linkage disequilibrium in evolutionary signatures', A Primer of Molecular Population Genetic, Oxford Academic. <https://doi.org/10.1093/oso/9780198838944.003.0006>, accessed 6 May 2025.
- Davinack, A. 2024. Molecular Ecology & Evolution: An Introduction. Accessed on May 6 2025, Available at: <https://openpress.wheatoncollege.edu/molecular ecologyv1/part/population-genetics/>
- de Moraes, M.L.T., Silvestre, de M. M.A., Rossini, B.C., Marino, C.L. 2025. How Do Gene Flow and Migration Affect Populations? In: Bohrer Monteiro Siqueira, M.V., Konzen, E.R., Galetti Junior, P.M. (eds) Population Genetics in the Neotropics. Springer, Cham. https://doi.org/10.1007/978-3-031-83685-5_6
- Dekkers, J.C.M., Su, H. & Cheng, J. 2021. Predicting the accuracy of genomic predictions. Genet Sel Evol 53(55). <https://doi.org/10.1186/s12711-021-00647-w>
- Dyer, G.A., Serratos-Hernández, J.A., Perales, H.R., Gepts, P., Piñeyro-Nelson, A., Chávez A, et al. 2009. Dispersal of Transgenes through Maize Seed Systems in Mexico. PLoS ONE 4(5): e5734. <https://doi.org/10.1371/journal.pone.0005734>
- Edwards, C. E., Tessier, B.C., Swift, J.F., Bassüner, B., Linan, A.G., Albrecht, M.A, et al. 2021. Conservation genetics of the threatened plant species Physaria filiformis (Missouri bladderpod) reveals strong genetic structure and a possible cryptic species. PLoS ONE 16(3): e0247586. <https://doi.org/10.1371/journal.pone.0247586>
- Edwards, S.M., Buntjer, J.B., Jackson, R. et al. 2019. The effects of training population design on genomic prediction accuracy in wheat. Theor Appl Genet 132, 1943–1952. <https://doi.org/10.1007/s00122-019-03327-y>
- Elena, S.F., de Visser, J.A.G. 2003. Environmental stress and the effects of mutation. J Biol 2, 12. <https://doi.org/10.1186/1475-4924-2-12>
- Emily, B. J., Young, W. L., Corlett, W. W., Daniel, J. S., Stephen, I. W., John, R. S., 2020. The Evolutionary Forces Shaping Cis- and Trans-Regulation of Gene Expression within a Population of Outcrossing Plants, Molecular Biology and Evolution, 37(8): 2386–2393, <https://doi.org/10.1093/molbev/msaa102>

- Ferrer-Admetlla, A., Leuenberger, C., Jensen, D.J., Wegmann, D. 2016. An Approximate Markov Model for the Wright–Fisher Diffusion and Its Application to Time Series Data, *Genetics*, 203(1): 831–846, <https://doi.org/10.1534/genetics.115.184598>
- Flohr, M.B., Hunt, R.J., Kirkegaard, A.J., Evans, R.J., Lilley, M.J. 2018. Genotype × management strategies to stabilise the flowering time of wheat in the south-eastern Australian wheatbelt,” *Crop and Pasture Science* 69(6), 547-560. <https://doi.org/10.1071/CP18014>
- Greenspoon, P.B., Gonigle, L.K. 2014. Host-parasite interactions and the evolution of nonrandom mating. *Evolution*. 2014 Dec;68(12):3570-80. doi: 10.1111/evo.12538. Epub 2014 Nov 20. PMID: 25314225; PMCID: PMC4258116.
- Gupta, P. 2022. Population Genetics. In: Kar, D., Sarkar, S. (eds) *Genetics Fundamentals Notes*. Springer, Singapore. https://doi.org/10.1007/978-981-16-7041-1_21
- Hansen, T. F. 2013. Adaptive Landscapes and Macroevolutionary Dynamics’, in Erik Svensson, and Ryan Calsbeek (eds), *The Adaptive Landscape in Evolutionary Biology*; Oxford Academic, , <https://doi.org/10.1093/acprof:oso/9780199595372.003.0013>, accessed 6 May 2025.
- Harpak, A., Bhaskar, A., Pritchard, J.K. 2016. Mutation Rate Variation is a Primary Determinant of the Distribution of Allele Frequencies in Humans. *PLoS Genet* 12(12): e1006489. doi:10.1371/journal.pgen.1006489
- Jenczewski, E., RONFORT, J., Anne-Marie CHÈVRE, A.2003. Crop-to-wild gene flow, introgression and possible fitness effects of transgenes. *Environ. Biosafety Res.* 2: 9–24. <https://doi.org/10.1051/ebr:2003001>
- Johnson, L.M., Galloway, L.F. 2008. From horticultural plantings into wild populations: movement of pollen and genes in *Lobelia cardinalis* . *Plant Ecol* 197, 55–67. <https://doi.org/10.1007/s11258-007-9359-9>
- Kamran, A., Iqbal, M., Spaner, D. 2014. Flowering time in wheat (*Triticum aestivum* L.): a key factor for global adaptability. *Euphytica* 197, 1–26. <https://doi.org/10.1007/s10681-014-1075-7>
- Karlin, S. 1968. Equilibrium behavior of population genetic models with non-random mating. Part I: Preliminaries and special mating systems. *Journal of Applied Probability*. 5(2):231-313. doi:10.2307/3212254
- Kimura, M. 1983. Maintenance of genetic variability at the molecular level. In: *The Neutral Theory of Molecular Evolution*. Cambridge University Press; 253-304.
- Kuhner, K.M. 2008. Coalescent genealogy samplers: windows into population history. *Trends in Ecology and Evolution* 24 (2). <https://doi.org/10.1016/j.tree.2008.09.007>
- Li, N., Stephens, M. 2003. Modeling Linkage Disequilibrium and Identifying Recombination Hotspots Using Single-Nucleotide Polymorphism Data, *Genetics*, 165 (4): 2213–2233, <https://doi.org/10.1093/genetics/165.4.2213>
- Liu, S., Qin, F. 2021. Genetic dissection of maize drought tolerance for trait improvement. *Mol Breeding* 41, 8. <https://doi.org/10.1007/s11032-020-01194-w>
- Lohmueller, K. E. 2014. The Impact of Population Demography and Selection on the Genetic Architecture of Complex Traits. *PLoS Genet* 10(5): e1004379. <https://doi.org/10.1371/journal.pgen.1004379>
- Lynch, M., Ackerman, S.M., Gout, J., Long, H., Sung, W., Thomas, K.W., . Foster, L.P., 2016. Genetic drift, selection and the evolution of the mutation rate. *NATURE REVIEWS | GENETICS*. 17(705): 704-714.
- Massey, J. D., Szpiech, A.Z., Goldberg, A. 2025. Differentiating mechanism from outcome for ancestry-assortative mating in admixed human populations, *Genetics*, 229 (4), iyaf022, <https://doi.org/10.1093/genetics/iyaf022>
- Masuda, M., Thrower, F., Nichols, M.K., 2009. The Effects of Violating Hardy–Weinberg Equilibrium Assumptions on a Cluster-based Population Mixture Analysis of Steelhead Populations in Southeast Alaska, *North American Journal of Fisheries Management*, 29 1): 140–150, <https://doi.org/10.1577/M08-032.1>
- Merrick, L., Campbell, A., Muenchrath, D., Fei, S. 2016. Mutations and Variation. In W. P. Suza, & K. R. Lamkey (Eds.), *Crop Genetics*. Iowa State University Digital Press. DOI: 10.31274/isudp.2023.130
- Merrill, R.M., Rastas, P., Martin, S.H., Melo, M.C., Barker, S., Davey, J., et al. 2019. Genetic dissection of assortative mating behavior. *PLoS Biol* 17(2): e2005902. <https://doi.org/10.1371/journal.pbio.2005902>
- Miller, R. E., Khoury, C. K. 2018. The Gene Pool Concept Applied to Crop Wild Relatives: An Evolutionary Perspective”. In: Greene SL, Williams KA, Khoury CK, Kantar MB, and Marek LF, eds., *North American*

- Crop Wild Relatives, Volume 1: Conservation Strategies. Springer, https://dx.doi.org/10.1007/978-3-319-95101-0_6
- Mourad, A.M.I., Ahmed, A.A.M., Baenziger, P.S., Börner, A., Sallam, A. 2024. Broad spectrum resistance to fungal foliar diseases in wheat: recent efforts and achievements. *Front. Plant Sci.* 15:1516317 <https://doi.org/10.3389/fpls.2024.1516317>
- Nakhleh, L. 2010. Population Structure and Gene Flow. <https://www.cs.rice.edu/~nakhleh/COMP571/Slides-Fall2010/PopulationStructure.pdf>
- Novo, I., Santiago, E., Caballero, A. 2022. The estimates of effective population size based on linkage disequilibrium are virtually unaffected by natural selection. *PLoS Genet* 18(1): e1009764. <https://doi.org/10.1371/journal.pgen.1009764>
- Olazcuaga, L., Lincke, B., DeLacey, S., Durkee, L. F., Melbourne, B. A., Hufbauer, R. A. 2023. Population demographic history and evolutionary rescue: Influence of a bottleneck event. *Evolutionary Applications*, 16, 1483–1495. <https://doi.org/10.1111/eva.13581>
- Peischl, S., Kirkpatrick, M. 2012. Establishment of New Mutations in Changing Environments, *Genetics*, 191(3), 895–906. <https://doi.org/10.1534/genetics.112.140756>
- Porras-Hurtado, L., Ruiz, Y., Santos, C., Phillips, C., Carracedo, A., Lareu, V.M. 2023. An overview of STRUCTURE: applications, parameter settings, and supporting software. *Frontiers in Genetics*. 4(98): <https://doi.org/10.3389/fgene.2013.00098>
- Pott, D.M., Durán-Soria, S., Osorio, S. et al. 2021. Combining metabolomic and transcriptomic approaches to assess and improve crop quality traits. *CABI Agric Biosci* 2, 1 (2021). <https://doi.org/10.1186/s43170-020-00021-8>
- Qu, J., Kachman, S.D., Garrick, D., Fernando, R.L., Cheng, H. 2020. Exact Distribution of Linkage Disequilibrium in the Presence of Mutation, Selection, or Minor Allele Frequency Filtering. *Front. Genet.* 11:362. doi: 10.3389/fgene.2020.00362
- Rabier, C.-E., Barre, P., Asp, T., Charmet, G., Mangin, B. 2016. On the Accuracy of Genomic Selection. *PLoS ONE* 11(6): e0156086. <https://doi.org/10.1371/journal.pone.0156086>
- Rhoné, B., Vitalis, R., Goldringer, I., Bonnin, I. 2010. Evolution of Flowering Time in Experimental Wheat Populations: A Comprehensive Approach to Detect Genetic Signatures of Natural Selection, *Evolution*, 64(7): 2110–2125. <https://doi.org/10.1111/j.1558-5646.2010.00970.x>
- Rutherford, S., van der Merwe, M., Wilson, P.G. et al. 2019. Managing the risk of genetic swamping of a rare and restricted tree. *Conserv Genet* 20, 1113–1131. <https://doi.org/10.1007/s10592-019-01201-4>
- Sánchez, L., Woolliams, A.J., 2004. Impact of Nonrandom Mating on Genetic Variance and Gene Flow in Populations with Mass Selection, *Genetics*, 166(1): 527–535, <https://doi.org/10.1534/genetics.166.1.527>
- Sharma, A., Szymczak, S., Rühlemann, M., Freitag-Wolf, S., Knecht, C., Enderle, J., ... Dempfle, A. 2022. Linkage analysis identifies novel genetic modifiers of microbiome traits in families with inflammatory bowel disease. *Gut Microbes*, 14(1). <https://doi.org/10.1080/19490976.2021.2024415>
- Sheoran, S., Kaur, Y., Kumar, S., Shukla, S., Rakshit, S., Kumar, R. 2022. Recent Advances for Drought Stress Tolerance in Maize (*Zea mays* L.): Present Status and Future Prospects. *Front. Plant Sci.* 13:872566. <https://doi.org/10.3389/fpls.2022.872566>
- Stadler, A., Müller, W.G., Futschik, A. 2025. A comparison of design algorithms for choosing the training population in genomic models. *Front. Genet.* 15:1462855. doi: 10.3389/fgene.2024.1462855
- Star, B., Spencer, G.H. 2013. Effects of Genetic Drift and Gene Flow on the Selective Maintenance of Genetic Variation, *Genetics*, 194(1): 235–244, <https://doi.org/10.1534/genetics.113.149781>
- Star, B., Stoffels, J.R., Spencer, G.H. 2007. Evolution of Fitnesses and Allele Frequencies in a Population with Spatially Heterogeneous Selection Pressures, *Genetics*, 177(3): 1743–1751, <https://doi.org/10.1534/genetics.107.079558>
- Wang, J. 2012. On the measurements of genetic differentiation among populations. *Genet Res (Camb)*. 94(5):275–89. <https://dx.doi.org/10.1017/S0016672312000481>
- Wang, D.L., Huang, Y.C. 2024, Evolutionary dynamics of maize: implications from gene flow studies, *Maize Genomics and Genetics*, 15(4): 182-190 (doi: 10.5376/mgg.2024.15.0018)

- Wein, T., Dagan, T., 2019. The Effect of Population Bottleneck Size and Selective Regime on Genetic Diversity and Evolvability in Bacteria, *Genome Biology and Evolution*, 11(11): 3283–3290, <https://doi.org/10.1093/gbe/evz243>
- Wellmann, R. 2023. Selection index theory for populations under directional and stabilizing selection. *Genet Sel Evol* 55, 10. <https://doi.org/10.1186/s12711-023-00776-4>
- Wikipedia, 2025. Fisher's fundamental theorem of natural selection. Accessed on May 6 2025. Available at: https://en.wikipedia.org/wiki/Fisher%27s_fundamental_theorem_of_natural_selection
- Wikipedia: 2025. Infinite sites model. Accessed May on 20 2025, available at https://en.wikipedia.org/wiki/Infinite_sites_model.
- Wiley, R. H. 2021. Natural Selection. In: Shackelford, T.K., Weekes-Shackelford, V.A. (eds) *Encyclopedia of Evolutionary Psychological Science*. Springer, Cham. https://doi.org/10.1007/978-3-319-19650-3_2095
- Willing, E.M., Dreyer, C., van Oosterhout, C. 2012. Estimates of Genetic Differentiation Measured by F_{ST} Do Not Necessarily Require Large Sample Sizes When Using Many SNP Markers. *PLoS ONE* 7(8): e42649. <https://doi.org/10.1371/journal.pone.0042649>
- Wray, N., Visscher, P. 2008. Estimating trait heritability. *Nature Education* 1(1):29
- Würschum, T., Langer, S.M., Longin, C.F.H. et al. 2013. Population structure, genetic diversity and linkage disequilibrium in elite winter wheat assessed with SNP and SSR markers. *Theor Appl Genet* 126, 1477–1486. <https://doi.org/10.1007/s00122-013-2065-1>
- Xu, S. 2022. Concept and Theory of Selection. In: *Quantitative Genetics*. Springer, Cham. https://doi.org/10.1007/978-3-030-83940-6_14
- Yali, W, Mitiku, T. 2024. Gene pool, classification and its importance in modern crop improvement program. *Int J Agric Sc Food Technol* 10(2): 068-073. DOI: <https://dx.doi.org/10.17352/2455-815X.000209>
- Yanchukov, A., Proulx, S.R. 2014. Migration-Selection Balance at Multiple Loci and Selection on Dominance and Recombination. *PLoS ONE* 9(2): e88651. <https://doi.org/10.1371/journal.pone.0088651>
- Yeaman, S., Whitlock, C.M., 2011. The Genetic Architecture of Adaptation under Migration–Selection Balance, *Evolution*, 65 (7): 1897–1911, <https://doi.org/10.1111/j.1558-5646.2011.01269.x>
- Zou, M., Shabala, S., Zhao, C. et al. 2024. Molecular mechanisms and regulation of recombination frequency and distribution in plants. *Theor Appl Genet* 137, 86. <https://doi.org/10.1007/s00122-024-04590-4>

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.