



The infinitesimal model for autopolyploids and mixed-ploidy populations

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Abstract

We define the infinitesimal model of quantitative genetics (*sensu* Barton et al. [2017]) for the inheritance of an additive quantitative trait in a mixed-ploidy population consisting of diploid, triploid and autotetraploid individuals producing haploid and diploid gametes. We implement efficient simulation methods and use these to study the quantitative genetics of mixed-ploidy populations and the establishment of tetraploids after an environmental challenge and in a new habitat.

Key words: Polyploidy, quantitative genetics, infinitesimal model

Introduction

Model & Methods

We first develop the infinitesimal model (in the sense of Barton et al. [2017], i.e. the ‘Gaussian descendants’ approximation [Turelli, 2017]) for an autotetraploid population. We then consider mixed-ploidy populations in which diploids, triploids and tetraploids coexist and interbreed through the production of haploid and diploid gametes that combine freely.

The infinitesimal model

Consider a population which expresses a quantitative trait determined by a large number of additive loci of small effect. The infinitesimal model approximates the inheritance of such a trait by assuming that the trait value Z_{ij} of a random offspring from parents with trait values z_i and z_j follows a Gaussian distribution with mean equal to the midparent value and variance which is independent of the mean:

$$Z_{ij} \sim \mathcal{N}\left(\frac{z_i + z_j}{2}, V_{ij}\right) \quad (1)$$

Here, V_{ij} is referred to as the *segregation variance* in family (i, j) . This is the variation generated among offspring from the same parental pair due to random Mendelian segregation in meiosis. This approximation can be justified as arising from the limit where the number of loci determining the trait tends to infinity [Barton et al., 2017].

An equivalent, and for our purposes useful, way to characterize the model in diploids and polyploids is to write $Z_{ij} = Y_i + Y_j$, where Y_i and Y_j are independent Gaussian random variables $Y_i \sim \mathcal{N}\left(\frac{z_i}{2}, V_i\right)$ (and similarly for Y_j). We refer to Y_i as the (random) gametic value of individual i , and to V_i as the *gametic segregation*

variance of individual i (clearly $V_{ij} = V_i + V_j$). This formulation is helpful in that it highlights that Mendelian segregation occurs independently in both parents when gametes are produced, which then combine additively to determine the offspring trait value.

If we assume a population consisting of infinitely many unrelated individuals, expressing a trait with genetic variance V_z and segregation variance V_0 , we find that under random mating the variance in the offspring generation is

$$\begin{aligned} V'_z &= \mathbb{E}[\text{Var}[Z_{ij}|Z_i, Z_j]] + \text{Var}[\mathbb{E}[Z_{ij}|Z_i, Z_j]] \\ &= \mathbb{E}[V_{ij}] + \text{Var}\left(\frac{Z_i + Z_j}{2}\right) \\ &= V_0 + \frac{V_z}{2}. \end{aligned} \quad (2)$$

So that at equilibrium ($V'_z = V_z$), we have $V_z = 2V_0$ [Barton et al., 2017].

Denoting by X the contribution to the trait value associated with a randomly sampled haploid genome from the population, we also have that, at equilibrium, $V_z = 2V_0 = mV$, where $V = \text{Var}[X]$ and m is the ploidy level. Note that no assumptions regarding m have been made in the definition of the model. Indeed, as long as all individuals are of the same *even* ploidy level, eq. (1) and eq. (2) apply equally well to the inheritance of an additive trait in polyploids as in diploids. Two factors however do lead to differences with the standard diploid model due to their effect on V_i : (1) the potential occurrence of double reduction in polyploids affects the relationship between V and the segregation variance and (2) the evolution of the segregation variance over time in finite populations is affected by the ploidy level.

Perhaps we should organize the text around the table below. First outline mixed-ploidy population, then indicate that we need the variances associated with the

cytotype	haploid gamete variance	diploid gamete variance
diploid	$\frac{1}{2}(1 - F)V$	$2\alpha_2(1 - F)V$
triploid	$\frac{2}{3}(1 - F)V$	$\frac{2}{3}(1 + \alpha_3)(1 - F)V$
tetraploid	–	$(1 + 2\alpha_4)(1 - F)V$

different gametes that are produced. Gamete formation occurs independently, so that is all we need. So start with the infinitesimal model framed in terms of uniting gametes, and highlight that this works for any ploidy level, and mixed-ploidy populations as long as we can work out the segregation variances.

Results

Discussion

Competing interests

No competing interest is declared.

Author contributions statement

Not applicable.

Data availability statement

The authors affirm that all data necessary for confirming the conclusions of the article are present within the article, figures, and supplementary material. Software implementing the numerical methods and individual-based simulations is available at <https://github.com/arzwa/InfGenetics>.

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Supplementary figures

Supplementary Information

Double reduction in autotetraploids

When an autopolyploid forms multivalents during prophase I, a form of ‘internal inbreeding’ may occur as a result of the phenomenon called *double reduction* [Huang et al., 2019]. Double reduction happens when, as a result of recombination, replicated gene copies on sister chromatids move to the same pole during anaphase I (see Stift et al. [2010] or Huang et al. [2019] for helpful illustrations). The frequency of double reduction at a locus in the presence of multivalent formation is determined by the frequency at which that locus is involved in a cross-over (which depends on the distance to the centromere), and, in tetraploids, has an upper bound at 1/6 [Mather, 1935, Stift et al., 2010].

Consider a locus with genotype $ABCD$ in an autotetraploid. In the absence of double reduction, six distinct gametes are produced with equal frequencies. When double reduction happens, four additional types of gametes carrying replicated gene copies (AA, BB, CC or DD gametes) will be produced with equal frequencies. The segregation variance will hence be increased in the presence of double reduction, as more distinct types of gametes are produced compared to disomic inheritance. For a random genotype $X_1X_2X_3X_4$, we can find the gametic segregation variance contributed by a locus when double reduction happens as

$$\begin{aligned}\mathbb{E}[\text{Var}[Y|X_1, X_2, X_3, X_4]] &= \text{Var}[Y] - \text{Var}[\mathbb{E}[Y|X_1, X_2, X_3, X_4]] \\ &= \text{Var}[2X] - \text{Var}\left[\frac{1}{4}(2X_1 + 2X_2 + 2X_3 + 2X_4)\right] \\ &= 4v - \frac{1}{4}4v = 3v\end{aligned}$$

where X denotes the additive effect of a random allele at the locus drawn from the reference population and $v = \text{Var}[X]$. In the absence of double reduction we have

$$\begin{aligned}\mathbb{E}[\text{Var}[Y|X_1, X_2, X_3, X_4]] \\ &= 2\text{Var}[X] - \text{Var}\left[\frac{1}{6}\sum_{i=1}^3\sum_{j=i+1}^4(X_i + X_j)\right] = v\end{aligned}$$

Assuming that the probability of double reduction at any locus is α (also α_4 below), and summing over independent loci, we find that the gametic segregation variance in the presence of double reduction should be

$$\frac{V_0}{2} = (1 - \alpha)V + 3\alpha V = V(1 + 2\alpha). \quad (1)$$