Polyploidization: Consequences of genome doubling on the evolutionary potential of populations

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AJB SYNTHESIS ARTICLE

Short Title: Multifarious consequences of polyploidy on adaptive potential

Polyploidization: Consequences of genome doubling on the evolutionary potential of populations

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Abstract

Whole-genome duplication is common in plants and is considered to have a broad range of effects on individuals' phenotypes and genomes and to be an important driver of plant adaptation and speciation. Despite their increased capacity to cope with challenging environments, polyploid lineages are generally as prone to extinction, and sometimes more prone, than their diploid progenitors. Although several explanations have been proposed to explain the short- and long-term disadvantages of polyploidy on the survival probability of populations, the consequences of whole-genome doubling on the heritable variance remain poorly studied. Whole-genome doubling can have major effects not only on the genetics, but also on the ecology and life history of the populations. Modifications of other properties of populations can reverse the effects of polyploidization per se on heritable variance. In this synthesis, I summarize the empirical and theoretical knowledge about the multifarious consequences of genome doubling on the heritable variance of quantitative traits and on the evolutionary potential of polyploid populations compared to their diploid progenitors. I propose several ways to decipher the consequences of whole-genome doubling on survival probability and to study the further consequences of shifting the ecological niche and life-history traits of a population. I also highlight some practical considerations for comparing the heritable variance of a trait among different cytotypes. Such investigations appear to be timely and necessary to understand more about the paradoxical aspects of polyploidization and to understand the evolutionary potential of polyploid lineages in a global warming context.

KEYWORDS

evolvability, extinction, genetic variation, mating system, whole-genome duplication

Whole-genome duplication has occurred repeatedly throughout the evolution of eukaryotes (Gregory and Mable, 2005; Leebens-Mack et al., 2019) and is considered to have a broad range of effects on individuals' phenotypes and genomes and to be an important driver of plant adaptation and speciation (Van de Peer et al., 2017). It is widely documented that polyploidization can enhance the populations' ecological flexibility (Dubcovsky and Dvorak, 2007; Fawcett et al., 2009), potentially explaining the persistence and expansion of polyploid lineages during geological mass extinction periods (Vanneste et al., 2014a, b), and their

contemporary distribution, where polyploids are frequently found in disturbed and extreme environments (Pandit et al., 2011; Te Beest et al., 2012; Levin and Soltis, 2018).

Despite their increased capacity to cope with more challenging environments (Van de Peer et al., 2021), polyploid lineages are generally as, and sometimes more, prone to extinction as their diploid progenitors (Mayrose et al., 2011, 2015; Arrigo and Barker, 2012; Soltis et al., 2014a, b, c). Polyploidization arises with several costs in new polyploid individuals, like genomic instability, mitotic and meiotic abnormalities, reduction of fitness, and minority cytotype exclusion (Levin, 1975; Comai, 2005; Otto, 2007; Doyle and Coate, 2019; Clo and Kolář, 2021; Gemble et al., 2022). Nevertheless, these immediate consequences of genome doubling cannot explain the phylogenetic extinction patterns, because although they can lead to the extinction of young individuals, it occurs so quickly after polyploidization (a few generations) that it is likely phylogenetically undetectable (Levin, 2019). In the short and long term, polyploidy can be associated with higher genetic load (due to recessive deleterious mutations or transposable elements), slower selection on recessive beneficial mutations, and sometimes slower growth rates (Otto and Whitton, 2000; Otto, 2007; Baduel et al., 2018), all of which potentially explain the higher extinction rates found in some phylogenetic analyses.

Surprisingly, although a lack of genetic diversity is often proposed and was the first argument used by Stebbins to explain why polyploidization should promote extinction (Stebbins, 1971), the interaction between polyploidization and adaptive potential remains poorly studied, at least empirically. In this synthesis, the adaptive potential of a population refers to the heritable variance of populations, which is the fraction of phenotypic variance determined by the genes transmitted from parents to offspring (Falconer and Mackay, 1996). A large number of theoretical studies have shown that polyploidization can have both positive and negative effects on short- and long-term adaptive potential (Haldane, 1927; Wright, 1938; Rowe, 1982; Rowe and Hill, 1984; Ronfort, 1999; Otto and Whitton, 2000; Griswold and Williamson, 2017; Mostafaee and Griswold, 2019). When the focus has been on autotetraploid species to avoid the confounding effects of hybridization, there have been empirical estimates of adaptive potential for agronomic species such as potato (Ortiz and Golmirzaie, 2003; Slater et al., 2014; Amoros et al., 2020) or strawberry (Xue et al., 2015) and a few estimates for natural populations (O'Neil, 1997; Burgess et al., 2007; Martin and Husband, 2012). Most of the estimates are for tetraploid populations only, without direct comparison to their diploid progenitors, giving limited insights into how polyploidization affects the short-term adaptive potential of a population.

We are currently lacking a more general view of how genome duplication modifies the adaptive potential and the capacity for survival of lineages on both short- and long-time scales. This lack is especially notable considering that, in addition to the genetic consequences of polyploidization, whole-genome doubling is often associated with the modification of the ecology and life-history traits of populations (Glennon et al., 2014; Rice et al., 2019; Van Drunen and Husband, 2019), which are also expected to modify the adaptive potential of populations. In this synthesis, I summarize the different genetic, ecological, and life-history modifications associated with whole-genome doubling. By linking these different aspects of polyploidization, I show that the different modifications can lead to very different effects on the populations' adaptive potential, over short and long times. In the second part, I highlight the practical challenges associated with estimating the adaptive potential of each cytotype and how to decipher the multiple consequences of polyploidization on the evolution of genetic diversity in polyploid lineages.

<h1>EFFECT OF POLYPLOIDIZATION PER SE ON THE ADAPTIVE POTENTIAL OF POPULATIONS

<h2>Polyploidization and its consequences on heritable variance

In the following section, I assume tetrasomic inheritance and only refer to autopolyploid species.

The primary consequence of polyploidy is to modify the distribution of genotypic values (defined as the average phenotype of individuals with a given genotype). Let's consider a bi-allelic locus, with the two alleles with frequency p and q. For similar allelic frequencies, the proportion of extreme homozygous genotypic values are, respectively, p^2 and q^2 in diploids and p^4 and q^4 in tetraploids at random mating equilibrium (Kempthorne, 1955). As a consequence, the distribution of genotypic values is much narrower around the mean of the population in tetraploids compared to diploids, reducing the phenotypic and heritable variance. For example, if we consider the population just after the polyploidization event, with allelic frequencies and mean population values similar in diploids and tetraploids, the heritable variance of a trait should be divided by two after polyploidization under additivity (Wright, 1938; Table 1). Nevertheless, polyploidization is often associated with bigger phenotypic values (Porturas et al., 2019; Clo and Kolář, 2021), which in turn, is expected to increase the heritable variance of the trait. Following the same assumptions as before (similar allelic frequencies, and an additive genetic architecture), if the mean population value of the tetraploids is t times larger than the one of diploids, the

heritable variance of the tetraploid population will be $\frac{t^2}{2}$ times larger than in the diploid progenitors (Clo, 2022). Based on empirical data, *t* is expected to be around 1.2 and 1.3 for morphological traits (Porturas et al., 2019; Clo and Kolář, 2021), which would lead to an immediate decrease of 15% to 28% in the heritable variance in tetraploid populations compared to the diploid.

This decrease in heritable variance is temporary because the allelic frequencies will rapidly change in the tetraploid populations, notably in presence of non-additive gene actions (i.e., dominance and epistasis). Due to the higher level of heterozygosity found in polyploids compared to diploids, recessive mutations are expected to reach higher frequencies in polyploid populations (Otto and Whitton, 2000), quickly allowing the heritable variance of the polyploids to reach and overcome the variance of diploid populations (generally in less than 100 generations (Clo, 2022). In addition, with dominance, the production of gametes with two alleles results in the inheritance of both additive and dominant genetic effects. As a consequence, the dominance variance also contributes partially and transiently to the adaptive potential of an autotetraploid population (Walsh, 2005).

Polysomic segregation creates the opportunity for more epistatic interactions because of the multiple allele copies per locus (Mostafaee and Griswold, 2019), and epistasis has been shown to contribute to population differentiation in tetraploid populations of *Campanulastrum americanum* (Etterson et al., 2007) and to inbreeding depression in tetraploid populations *Medicago sativa* (Bingham et al., 1994). Epistasis is expected to have an impact on the evolutionary potential of populations only if interactions are directional on average (i.e., if epistasis interactions tend to increase or decrease the trait value). Because the directionality of epistasis is hard to estimate, very few investigations have been done (Le Rouzic, 2014). When detected, epistatic interactions tend to enhance fitness and to increase the size of floral traits (Johansen-Morris and Latta, 2006; Monnahan and Kelly, 2015; Oakley et al., 2015; Clo et al., 2021). In the short term, directional positive epistasis tends to increase the amount of additive variance of a quantitative trait (Carter et al., 2005; Monnahan and Kelly, 2015).

<h2>Polyploidization and modification of gene-flow landscapes

In addition to modifying the distribution of the existing variability within populations, polyploidy also opens the door to new sources of variations. There is accumulating evidence that

whole-genome duplication can break down reproductive barriers, allowing gene flow between previously isolated species (Schmickl and Yant, 2021). Gene flow has been documented between tetraploid frog lineages of the genus *Neobatrachus*, resulting in higher neutral genetic diversity of the tetraploids compared to the diploids in the studied populations (Novikova et al., 2020). Similar results have been found in plants, with gene flow between tetraploid populations of *Arabidopsis arenosa* and *A. lyrata* (Arnold et al., 2016; Marburger et al., 2019), which helped *A. arenosa* to establish in serpentine localities, for example (Arnold et al., 2016). Although more studies are needed to quantify the frequency of these hybridization events between polyploid lineages, the breakdown of reproductive barriers associated with whole-genome doubling offers a new source of genetic diversity, increasing the potential of polyploid populations to respond to environmental changes.

<h2>Theoretically advantageous, empirically deleterious?

Little is known, empirically, about the consequences of polyploidization on a population's adaptive potential. Martin and Husband (2012) found that the realized heritability for flowering time is 0.31 in established autotetraploids of *Chamerion angustifolium*, while diploid populations of the same species exhibited a significantly higher realized heritability of 0.40. No other direct comparisons among tetraploids and diploids of the same species in controlled environments are available in the literature, but the few estimates of heritability found in natural autotetraploid populations (O'Neil, 1997; Burgess et al., 2007), or in agronomic polyploid species (Ortiz and Golmirzaie, 2003; Slater et al., 2014; Xue et al., 2015; Amoros et al., 2020) are in the range of what is found in diploids (Geber and Griffen, 2003; Clo et al., 2019). With this very limited set of studies, it appears that autotetraploids don't have higher adaptive potential than diploids. The discrepancy between the theory and data can come from the fact that polyploidy also modifies the ecology and life history of populations (Glennon et al., 2014; Rice et al., 2019; Van Drunen and Husband, 2019), and these modifications are expected to modify the adaptive potential of populations.

<h1>EVOLUTION OF POLYPLOIDY AND ITS IMPACT ON THE ECOLOGY AND LIFE HISTORY OF POPULATIONS

<h2> The evolution of polyploidy and how it can impact populations' adaptive potential

The formation of a new polyploid population often involves a significant population bottleneck associated with few founding individuals (Ramsey and Schemske, 1998; Otto and Whitton, 2000), which is expected to initially decrease the evolutionary potential of a neopolyploid population (Layman and Busch, 2018). Polyploidization has been theoretically suggested to be more likely in diploid populations with a low effective population size, because drift allows unreduced gametes (Clo et al., 2022) and tetraploid individuals (Rausch and Morgan, 2005) to reach high frequency in a diploid population. These results suggest that polyploidization is more likely to occur in diploid populations with small effective population sizes, which is theoretically expected to decrease the heritable variance (Bürger et al., 1989), although no empirical support has been found (Wood et al., 2016). If polyploid populations come more often from diploid populations with reduced genetic diversity, it is more likely that polyploidization comes with an initially low adaptive potential. Nevertheless, these effects are only transient and will only increase the short period of time in which polyploids are more prone to extinction than diploids.

<h2>Polyploidization and its impact on the ecology of a species

In addition to the genetic modifications, polyploid lineages are also more tolerant of stressful conditions compared to diploid populations (see Doyle and Coate, 2019; Bomblies, 2020; Van de Peer et al., 2021 for reviews). For example, polyploidy has been associated with higher tolerance to salt (Chao et al., 2013) and drought stress (Ruiz et al., 2016), and higher resistance to pathogens and herbivory (Hannweg et al., 2016; Hias et al., 2018; Wang et al., 2018). As a consequence, polyploid lineages sometimes increase their ecological and geographical distributions (Glennon et al., 2014; Rice et al., 2019), with polyploids being frequently found at range margins (Levin, 1975; Fowler and Levin, 1984; Rojas-Andrés et al., 2020), or in extreme environments (Brochmann et al., 2004) and extreme latitudes (Rice et al., 2019), in which habitat suitability decreases (Sexton et al., 2009; Pironon et al., 2017), with increases in temperature extremes and seasonality, and less biotic diversity (Mittelbach et al., 2007; Hardie and Hutchings, 2010). Harsher environments (Martínez-Padilla et al., 2017), range margins (Pennington et al., 2021), and range expansion (Pujol and Pannell, 2008) are known to decrease the adaptive potential of populations, due to stronger selection and recurrent population bottlenecks that decrease genetic diversity. It is possible that the better ability of polyploids to colonize range margins and harsher environments lead, in the long term, to a decrease in the

adaptive potential of populations due to the decrease in suitability of the newly colonized environments.

<h2>Polyploidy and modification of life-history traits

Polyploidization is generally associated with specific life-history traits. Polyploid species are expected to be more frequently perennial (Van Drunen and Husband, 2019), asexual (Van Drunen and Husband, 2019), and self-fertilizing (Barringer, 2007; Husband et al., 2008). There are several hypotheses explaining these patterns. First, these life-history traits reduce the strength of the minority cytotype exclusion (Levin, 1975) by increasing the probability of generating tetraploids within and across generations. Second, polyploidy can favor the evolution of these traits multiple times. In the *Solanaceae* family, the gametophytic self-incompatibility system is immediately broken after whole-genome duplication (de Nettancourt, 1977; Robertson et al., 2011), easing the transition toward selfing. Empirically, there is no evidence that perennials suffer from a decrease in adaptive potential compared to annuals (Geber and Griffen, 2003). Asexual (Lande, 1976; Lynch and Gabriel, 1983) and predominantly selfing species (Charlesworth and Charlesworth, 1995; Lande and Porcher, 2015; Abu Awad and Roze, 2018) have been theoretically thought to decrease the adaptive potential of populations when the genetic variance of traits is mainly additive. The contribution of non-additive gene effects and associated variances (i.e., dominance and epistasis) are expected to compensate for the decrease in additive variance in both asexuals (Neiman and Linksvayer, 2006) and selfers (Clo and Opedal, 2021), which is supported empirically (see Neiman and Linksvayer, 2006 for a review on asexuals, and Opedal et al., 2017 and Clo et al., 2019 for selfers). The modification of these key life-history traits apparently should not drastically affect the adaptive potential of polyploid species, but more empirical data are necessary to confirm the recent theoretical advances in these fields.

<h1>EMPIRICAL CONSIDERATIONS

<h2>How to decipher the consequences of polyploidization on adaptive potential

To decipher the different consequences of polyploidization, one has to carefully select the populations for comparing the evolutionary potential among cytotypes. For example, for studying the consequences of polyploidization per se on the adaptive potential of populations, it is necessary to compare diploids and polyploids in similar ecological conditions and not differing

in key life-history traits. Mixed-ploidy populations or those in zones of contact between diploid and polyploid populations within a mixed-ploidy species seem to be perfect candidates (Kolář et al., 2017). Using synthetic tetraploid populations generated from the same diploid population will allow studying the temporal variation of adaptive potential after polyploidization (Comai, 2005; Tate et al., 2009; Hegarty et al., 2013). Then to investigate the additional consequences of shifting the ecological niche, the habitat suitability, or the mating system of populations, we need to add polyploid populations that have the aforementioned modifications.

<h2>Accurately compare the evolutionary potential between cytotypes

Although estimating the additive variance of a quantitative trait is generally not a difficult task, some characteristics of polyploid species make that some precautions have to be taken. First, polyploidy is frequently associated with bigger trait values (Vamosi et al., 2007; Porturas et al., 2019; Clo and Kolář, 2021). In such a case, to accurately compare the evolutionary potential among cytotypes, one needs to standardize the heritable variance (Falconer and Mackay, 1996). There are two predominant metrics to standardize the heritable variance: by (1) the phenotypic variance (heritability, or h^2), or (2) by the mean square of the trait (evolvability, e) (Hansen et al., 2011). Both standardizations have pros and cons, but evolvability is thought to be a better proxy of the adaptive potential of species, because the additive variance of a trait is correlated to both the environmental and epistatic variances (Carter et al., 2005; Hansen et al., 2011), such that the heritability of a trait can be close to zero while the trait exhibit substantial additive variance. However, for some kinds of traits, evolvability can be a meaningless metric (see Pélabon et al., 2020 for details), for example, for any scale where the mean can be equal to 0.

A second consideration is that the dominance variance(s) contributes to the adaptive potential of polyploid species (Walsh, 2005). Decomposing the genetic variance of a population from sibling or pedigree analyses and then inferring the evolvability could lead to biased estimates, notably due to the limited statistical power to infer correctly the dominance variance in such experiments (Wolak and Keller, 2014; Walsh and Lynch, 2018). Artificial selection experiments seem the most straightforward way to accurately estimate the evolvability of a population because those experiments allow one to catch the realized heritability/evolvability of a population (containing both additive and dominance contributions) (Lynch and Walsh, 1998).

<h1>CONCLUSIONS AND PERSPECTIVES

Whole-genome doubling was originally thought to decrease the genetic diversity of populations. Recent theoretical studies showed that this negative effect is only temporary, and polyploidization is theoretically expected to quickly increase the adaptive potential of populations. However, the few empirical data available do not confirm this theoretical prediction. The contradiction between theory and data could come from the fact that genome doubling modifies other properties of populations, potentially reversing the effects of polyploidization per se on adaptive potential (see Figure 1 for an overview). Although I tried to link different research areas to speculate on the consequences of polyploidization on the adaptive potential of populations, all the predictions remain hypothetical. Quantitative genetics studies that quantify the heritable variance of natural and agronomic polyploid populations are too rare and do not allow us to understand the different aspects of polyploidization on the adaptive potential of a species. Future studies comparing the adaptive potential among cytotypes and controlling for the multiple consequences of whole-genome doubling are now necessary, to understand how and when polyploidization increases the extinction probability of populations. Such investigations appear to be timely and necessary to understand more about the paradoxical aspects of polyploidization and the evolutionary potential of polyploid lineages in a global change context.

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<h1>DATA AVAILABILITY STATEMENT

No data were used in this manuscript.

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Table 1. Genotypic frequencies and values at random mating equilibrium, for diploid and tetraploid populations, for a bi-allelic model (Kempthorne, 1955), p and q are respectively the frequency of the alleles A_1 and A_2. For the numerical example, $p_1 = p_2 = 0.5$.

Diploid population			
Genotype	A_1A_1	A_1A_2	A_2A_2
Frequency	p^2	$2pq$	q^2

Value	–2		0		2
Variance	$0.25\cdot(-2)^2 + 0.5\cdot0^2 + 0.25\cdot2^2 = 2$				
Tetraploid population					
Genotype	$A_1A_1A_1A_1$	$A_1A_1A_1A_2$	$A_1A_1A_2A_2$	$A_1A_2A_2A_2$	$A_2A_2A_2A_2$
Frequency	p^4	$4\,p^3q$	$6\,p^2q^2$	$4\,pq^3$	q^4
Value	–2	–1	0	1	2
Variance	$0.0625\cdot(-2)^2 + 0.\ 25\cdot(-1)^2 + 0.375\cdot0^2 + 0.0625\cdot1^2 + 0.0625\cdot2^2 =$ 1				

Figure 1. Summary of the consequences of polyploidization on the adaptive potential of populations. The investigated effects refer to mechanisms that have been investigated theoretically or empirically.