The effects of ploidy and mating system on the evolvability of populations: theoretical and empirical investigations

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Abstract

- Polyploidy has been associated in theoretical works with better adaptive potential, even though it is related to higher selfing rates. Self-fertilization causes an increase in homozygosity and has been related to weaker evolvability. However, there is a lack of empirical studies about the joint effects of polyploidy and selfing on genetic variance.
- We studied genetic variance in *Erysimum incanum*, a Brassicaceae selfing species from the Western Mediterranean basin with three different ploidy levels. We measured a series of phenotypic traits in individuals of each ploidy, obtained by controlled crosses and grown in different climatic conditions. For comparison, we also conducted mathematical simulations to explore how genetic diversity could be affected by the ploidy level and mating system.
- While theoretical approaches showed a positive relationship between ploidy and genetic variance and inbreeding depression, empirical results show lower evolvability and transgressive segregation for polyploids, related also to environmental conditions.
- Genetic variance in *E. incanum* polyploids could be related with recent establishment and adaptation to harsh environments, which explains the apparent contradiction with theory, where more settled and established populations are considered.

Keywords

Erysimum incanum, evolvability, genetic variance, mating system, polyploidy, quantitative genetics.

Introduction

Polyploidy, the condition of having more than two sets of chromosomes, is widespread among plants, and has long been recognized for its significant phenotypic effects, which are thought to play a key role in speciation and adaptation (Masterson, 1994; Soltis and Soltis, 1999; Otto and Whitton, 2000; Barker et al., 2016;). Once viewed as an evolutionary dead end, recent studies suggest that polyploid species may be better equipped to cope with extreme and stressful environments (Bomblies, 2020; Van de Peer et al., 2021). However, polyploids, particularly young autopolyploid lineages, often exhibit higher extinction rates than their diploid counterparts (Mayrose et al., 2011; Arrigo and Barker, 2012; Levin, 2019), raising questions about their long-term adaptive potential. To explain this, Stebbins (1966) hypothesized that gene duplication could dilute the effect of beneficial alleles, thereby limiting adaptation.

Nevertheless, theoretical studies suggest that polyploids may have greater adaptive potential than their diploid relatives, especially over longer evolutionary timescales (Clo, 2022a). Several theoretical arguments support this view. First, because of higher levels of heterozygosity, recessive weakly deleterious mutations are less purged and segregate at higher frequencies compared to diploid populations, increasing genetic diversity (Otto and Whitton, 2000; Clo, 2022a). Second, non-additive genetic effects are expected to contribute more significantly to adaptive potential in polyploids than in diploids (Clo, 2022b). In particular, because two alleles per locus are transmitted through gametes, dominance variance (i.e. digenic interaction variance) becomes a key component of adaptive response (Walsh, 2005). Finally, as polyploidy increases the potential for epistatic interactions, the influence of directional epistasis on adaptation is also predicted to be stronger (Mostafaee & Griswold, 2019; Clo, 2022b).

Empirical support for these theoretical predictions, however, remains limited. For example, Martin and Husband (2012) reported lower evolvability in established tetraploids compared to diploids in *Chamerion angustifolium*, a result that contradicts theoretical expectations. Other estimates of quantitative genetic variation in polyploids are scarce (O'Neil, 1997; Burgess et al., 2007), and generally fall within the range observed in diploid species (Clo et al., 2019). One possible reason for this mismatch is that theoretical models typically assume random mating, whereas polyploidy is frequently associated with shifts in

mating systems, particularly toward increased self-fertilization (Barringer, 2007; Husband et al., 2008), which may influence the patterns of genetic variance.

Self-fertilization has a profound impact on genetic variation by increasing homozygosity and, over time, enabling purging of deleterious mutations, thereby reducing additive genetic variance. Early models predicted contrasting outcomes: Wright (1950) suggested that, under neutrality (i.e., assuming no mutation nor selection on quantitative traits), a fully selfing population should have twice the genetic variance of a fully outcrossing one, which is a highly simplified model compared to the reality of the natural world. Lande (1977), assuming stabilizing selection, found that selfing rates do not affect the genetic variance of traits under stabilizing selection, as increased homozygosity and purging counterbalance each other. Conversely, Charlesworth and Charlesworth (1995) concluded that high selfing rates strongly reduced genetic variance compared with fully outcrossing populations. More recent studies considering a wider range of selfing rates have reconciled these results, showing that the link between a decrease in genetic variance and the mating system is weak for most selfing rates, while for high selfing rates, a sharp decrease in genetic variance is observed (Abu Awad and Roze, 2018; Lande and Porcher, 2015). This reduction in genetic variance is highly sensitive to mutation rate, which leads to differences in the efficiency of purging, and is linked to genetic associations. Indeed, genetic covariance contributes negatively to genetic variance, since fully selfing populations have lower rates of recombination (Abu Awad and Roze, 2018). These covariances can be potentially remobilized during rare outcrossing events leading to transgressive segregation patterns (Clo et al., 2020). However, empirical evidence indicates that the relationship between selfing and reduced evolvability is weaker than theoretical models suggest (Opedal et al., 2017; Clo et al., 2019). This difference between theoretical expectations and empirical results can be explained by the fact that theoretical models mainly consider an additive architecture, neglecting the effects of dominance on quantitative traits. Considering the effect of dominance, Clo and Opedal (2021) have shown that there is little difference in terms of evolvability between selfing, mixed-mating, and outcrossing populations, which is more consistent with empirical findings. Notably, these insights are based solely on diploid systems, with no extension to polyploid contexts, to our knowledge.

The mainly Iberian–North African plant *Erysimum incanum* (Brassicaceae) offers a valuable system to investigate the joint effects of ploidy and mating system on genetic

variance. This monocarpic, highly selfing species exhibits three ploidy levels (diploid, tetraploid, and hexaploid) across its range in the Iberian Peninsula and Morocco (Nieto-Feliner, 1993; Abdelaziz et al., 2019; Abdelaziz et al., in prep.). It has a selfing mating system with a short and monocarpic life history, which facilitates working with several generations (García-Muñoz et al., 2023). Selfing, as well, is strongly promoted by *Anther rubbing* mechanism which increases the self-pollination chances (Abdelaziz et al., 2019). Cytotypes are distributed across a latitudinal gradient, with diploids and tetraploids in the Iberian Peninsula and all three ploidy levels occurring in Morocco, from the Rif and Middle Atlas (diploids and tetraploids) to the Anti-Atlas (hexaploids), offering a natural context to examine how polyploidy and environment jointly shape genetic diversity.

In this study, we extended our theoretical and applied knowledge of the joint combination of mating system and ploidy level on the amount of heritable variance. To do so, we first generated theoretical expectations of how polyploidy and self-fertilization affect the amount and structure of genetic diversity of quantitative traits under stabilizing selection. In a second time, we estimated the adaptive potential of diploid, tetraploid, and hexaploid populations of *E. incanum*, in controlled and common garden conditions. Regarding theoretical modeling, we found that polyploidy does not qualitatively modify the expectation of the effect of the mating system on the amount and structure of the genetic variance. However, when looking at a fixed selfing rate, the higher the ploidy level, the higher the amount of genetic diversity compared to diploid populations. Empirical data showed, surprisingly, the opposite pattern, with diploids being generally the more evolvable cytotype, while tetraploids and hexaploids have lower genetic diversity.

2 Materials and Methods

2.1 Empirical investigation

2.1.1 Study system

Erysimum incanum is a species of the Brassicaceae family from the Iberian Peninsula and Morocco, part of the INCANUM species complex. We can find populations of three ploidy levels: diploid, tetraploid, and hexaploid (n = 8 chromosomes; Nieto-Feliner, 1993; Abdelaziz

et al.**(ref)**, in prep.). This species complex is predominantly autogamous. Flowers are small, hermaphrodite, and self-compatible, and flowers show the so-called anther rubbing mechanism (Abdelaziz et al., 2019), which strongly promotes selfing. Diploids show a vicariant distribution in the Rif and the Pyrenees Mountains and tetraploids are localized in the south-western Iberian Peninsula and the Middle Atlas Mountains (Nieto-Feliner, 1993; Fennane et al., 1999). Hexaploid populations are situated in the southernmost ranges of Morocco (High Atlas and Anti-Atlas; Abdelaziz et al., in prep.).

2.1.2 Experimental design and phenotypic measurements

To obtain selfing and outcrossing populations, we sowed seeds from wild populations of the three ploidies of *Erysimum incanum* in the common garden at the Faculty of Science of the University of Granada. We chose two populations within each ploidy to collect the seeds. We obtained three generations to standardize maternal effects. We produced two types of controlled crossings: selfing (self-fertilized plants) and outcrossing (crossing two inbred lines). Individuals were tagged according to each crossing, obtaining full-sibling' groups (families). We considered a maximum level of heterozygosity in the outcrossing group after the previous generations of selfing events. We finally obtained 155 diploid individuals (135 selfing in 30 families and 25 outcrossing in 4 families), 189 tetraploid (161 selfing in 52 families and 28 outcrossing in 6 families), and 104 hexaploid maternal lines (66 selfing in 16 families and 38 outcrossing in 8 families). Groups were divided and separately exposed to three environments: greenhouse, common garden in the Faculty of Science of Granada (Spain), and mountain conditions in Hoya de Pedraza Botanic Garden in Sierra Nevada (Granada, Spain).

We measured a series of morphological and floral traits. Morphological traits that we measured were the height of the main stalk, the number and diameter of all stalks, and the total number of flowers. Floral traits were petal length (maximal length from the edge of the petal to the curving point), corolla diameter (distance between edges of two opposite petals), and corolla tube length (distance from sepals' basis to corolla aperture), the length of a long stamen filament and a short filament and the style height (from the basis of the style to the stigma), so that we could calculate herkogamy (i.e. vertical distance difference between long stamen and style).

To obtain information about fitness, we registered the number of fruits per plant, and we estimated the average number of seeds in each plant by counting seeds from four fruits.

We then obtained the fitness value as the product of the total number of fruits and the number of seeds.

2.1.3 Evolvability for selfing individuals

To measure the evolutionary potential of different ploidy groups, we calculated the environmental and genetic variances for the different phenotypic traits of each selfing group at every ploidy level (diploid, tetraploid, and hexaploid; Table 2; see Table S1 for detailed results). Total genetic variance is expected to be a better proxy of the evolutionary potential than additive variance for predominantly selfing species (Sztepanacz et al., 2023), because some forms of dominance variances become heritable with inbreeding (Kelly, 1999). It has been shown theoretically (Clo and Opedal, 2021), and empirically (Sztepanacz et al., 2023) that these new components can contribute substantially to the genetic diversity of quantitative traits. We calculated evolvability as the ratio of the genetic variance VG for a given trait and its squared mean (x^2) using the following formula from Houle (1992):

$$e = V_G/x^2 \quad (1)$$

To extract genetic variance, we performed a general linear model test on the data to assess family-level effects using R 4.1.3 (Table 3). Genetic variance was considered as the between-group variance, while environmental variance was represented by the within-group variance. With these two data points, we could also calculate the broad-sense heritability for each trait. Evolvability is a more accurate way to approach the adaptive potential of populations because the additive variance of a trait is correlated with 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 exhibits substantial additive variance. We checked if ploidy had any effect on evolvability and heritability with Kruskal-Wallis tests as well as a t-test for both measurements.

2.1.4 Transgressive segregation

To assess how these populations could evolve in terms of diversity relative to their heterozygosity, we looked at transgressive segregation patterns. We first looked at the

minimum and maximum phenotypic values within the selfing and outcrossing groups for each ploidy level to apply the following classical transgressive segregation formula from Rieseberg et al. (2003, 1999):

$$TS1 = (N(OC < min_S) + N(OC < max_S))/N(OC) \quad (2)$$

Where TS= Transgressive segregation; N=number, OC=outcrossing, S=selfing, max=maximum value for a trait measurement; min=minimum number for a trait measurement. We assessed transgressive segregation using the index proposed by Koibe et al. (2019) as well, where we calculated the proportion of outcrossing individuals out of the range defined by the phenotype distribution on selfing group:

$$TS2 = \frac{max_{OC} - min_{OC}}{max_S - min_S} \quad (3)$$

We then calculated segregation variance of outcrossing offspring for each ploidy compared with the selfing group as the proportion of phenotypic variance from outcrossing offspring (V^P_{OC}) compared to selfing ones (V^P_S) as follows:

$$VR = \frac{V^P_{OC}}{V^P_S} \quad (4)$$

This ratio gives information about the novel phenotypes available in a group regarding the previous one, so that is the capacity of a group to generate these new phenotypes, an indirect way of evaluating mid-term evolutionary potential. We also performed a Kruskal-Wallis test to explore ploidy effects on transgressive segregation.

2.2 Theoretical model

2.2.1 General assumptions

A simulation model is developed to observe the evolution of a phenotypic trait Z in a population of size N_{pop}. The model is an extension of Clo (2022a) in which we are now

considering the mating systems of populations, and higher ploidy levels (hexaploids). The selfing rate and the ploidy level are both parameters of the model. The considered populations can be diploids, tetraploids or hexaploids, and each chromosome contains L loci. The selfing rate is a real number that can be set from 0 (fully outcrossing) to 1 (fully selfing). The phenotypic trait value z of an individual is given by the following equation:

$$z = g + e \quad (5)$$

where e is a random environmental component drawn from a normal distribution with parameters 0 and V_e, and g is the genotype of an individual computed as follows:

$$g_{px} = d \sum_{i=0}^{L-1} \sum_{j=0}^{p-1} (g_i^{M_j} + g_i^{P_j}) \quad (6)$$

where p is the ploidy level, $g_i^{M_j}$ (resp. $g_i^{P_j}$) is the value stored in the locus i of the maternal (resp. paternal) chromosome j, and d is the dosage used to manage the effect of ploidy on genotypic values, set to 1 for diploid populations. In other words, the genotype of an individual is the sum of all values stored in its genome, with a dosage factor for polyploid populations. The fitness of an individual with phenotype z is given by the following equation:

$$W_Z = e^{-\delta^2/(2\omega^2)} \quad (7)$$

where δ is the difference between the phenotypic trait value z and an optimal trait value set to 0, and ω^2 denotes the width of the fitness function, i.e., the strength of selection. All the notations and values used in the model and simulations are detailed in Table 1.

2.2.2 Individual-based simulations

At the beginning of the simulation, N_{pop} identical genomes are created with p chromosomes per individual, where p = 2, 4 or 6. The value initially stored in each locus is the optimum value 0. The simulation stops when an equilibrium for fitness is reached, more precisely when

the quotient between two values of the mean fitness of the population, calculated 1000 generations apart, is greater than 99%.

The life cycle consists of three phases: selection, recombination, and mutation. A parent for the next generation is selected if the ratio between the fitness of the parent and the maximum fitness is greater than a randomly generated number between 0 and 1, drawn from a uniform distribution. If the selfing rate is higher than a new randomly generated number between 0 and 1, the same parent is selected again. Otherwise, a different parent is selected in the same way as described above. Each parent then passes on a gamete to the next generation, i.e. half of their chromosomes after recombination. Crossovers are modeled here as a random permutation between the alleles present at the same locus on homologous chromosomes. After gamete production, each haplotype can be subject to mutations. The number of mutations per haplotype is drawn from a Poisson distribution with parameter U, and their positions in the genome are randomly sampled from the L possible loci. The additive value of this mutation is then drawn from a normal distribution with parameters 0 and a^2.

At the end of the simulation, the genetic variance V_g, the genic variance V_a and the genetic covariance COV_g at equilibrium are computed. The genetic variance corresponds to the variance between the complete genotypes, and the genic variance is the sum of the variances calculated at each locus separately. The three variables are linked by the following equation:

$$V_g = (1 + f)V_a + COV_g \quad (8)$$

where f is the inbreeding coefficient of the studied population.

Inbreeding depression is also computed using the following formula:

$$ID = 1 - W_s/W_{OC} \quad (9)$$

where W_s is the fitness of selfed individuals, and W_{oc} the fitness of outcrossed individuals in the population. These fitnesses are computed by generating 100 selfed and 100 outcrossed individuals from parents sampled at the mutation-selection-drift equilibrium.

To validate the results, the genetic variance obtained with the simulation considering a diploid and fully outcrossing population is compared with the stochastic house-of-cards

approximation (formula 21.a) from Bürger et al. (1989). Using the notations from Table 1, this approximation can be rewritten as:

$$V_g = \frac{4U(1+\omega^2)}{1+\frac{1+\omega^2}{N_{pop}a^2}} \quad (10)$$

The value obtained with the simulation is close enough to the one obtained with the stochastic house-of-cards approximation to confirm the smooth running of the simulation.

2.2.3 Choice of parameters

Simulations were run for different parameters. The haploid genomic mutation rate U is set to either 0.005 or 0.1, according to the range found in the literature (Keightley and Bataillon, 2000; Shaw et al., 2002; Halligan and Keightley, 2009). The parameters used for the number of loci L, the variance of mutational effects a^2, the variance of environmental effects V_e and the strength of selection ω^2 are similar to those used in Bürger et al. (1989); Ronce et al. (2009), and are the following: L = 50, a^2 = 0.05, V_e = 1 and ω^2 = 1 or 9 (see also Clo and Opedal (2021)). The dosage effect d is set to 0.67 (Porturas et al., 2019; Clo and Kol´aˇr, 2021). In each simulation, the population contains N_{pop} = 250 individuals. The parameter values are summarized in Table 1.

3 Results

3.1 Empirical data

3.1.1 Evolvability for selfing individuals

We estimate evolvability for each phenotypic trait within selfing individuals to assess the evolutionary potential across ploidy levels and environments. In both common garden and mountain settings, diploid level consistently exhibited the highest evolvability levels (Tables 2 & 3). In contrast, tetraploid and hexaploid individuals showed significantly reduced evolvability under mountain conditions, but not under common garden conditions (Tables 2 & 3). Across all the ploidy levels, mountain conditions tended to increase evolvability (Tables 2 & 3). However, ploidy itself did not exert a statistically significant main effect on evolvability when considered independently (Tables 2 & 3).

3.1.2 Transgressive segregation

We assessed transgressive segregation using three complementary indices (Table 4 for greenhouse and Table 5 for common garden): the classical index (TS1) by Rieseberg et al. (2003), the range-based index (TS2) from Koibe et al. (2019), and the variance ratio (VR). TS2 index and the variance ratio proved more sensitive to detecting transgressive phenotypes, whereas the classical Rieseberg index was more conservative.

General linear model analyses revealed that polyploidy levels have a negative effect on transgressive segregation, while mountain conditions had a positive effect, particularly for the Koibe index and the variance ratio. In contrast, the Rieseberg index (TS1) showed no significant effects of ploidy, environment, or their interaction.

3.2 Theoretical expectations

Figure 1 and Figures S1-S3 present trends in genetic variance, the genic variance, and the genetic covariance as functions of the selfing rate, under varying combinations of mutation rate (U) and (ω^2), as defined in Table 1. Across all parameter sets, both genetic variance and the genetic covariance decrease with increasing selfing rate, regardless of the parameters (Figures 1, S1-S3). Polyploid populations consistently exhibited higher genetic variance, higher genic variance, and higher genetic covariance in absolute value (as the covariance is

mostly negative; Figure 1). The ratios between the genetic, the genic variance, and the covariance between diploid and polyploid populations tend to decrease overall as the selfing rate increases (Figures 1, S1-S3).

On the other hand, the variations of the genic variance as a function of the selfing rate depend on the haploid mutation rate U. Figures 1 and S2 indicate that for a mutation rate U of 0.1, the genic variance increases with the selfing rate. Figures S1 and S3 show that the genic variance is a decreasing function of the selfing rate when U = 0.005. Moreover, a higher mutation rate U leads to higher values of the genetic variance, the genic variance, and the genetic covariance in absolute value, for all ploidy levels and all selfing rates. Finally, the stronger the selection (smaller ω^2), the lower the amount of genetic diversity in populations (see, for example, Figure 1 compared to Figure S2).

Regarding inbreeding depression, results from Figure 2 indicate a general decline in inbreeding depression with increasing selfing rate across all parameter combinations. Moreover, inbreeding depression was consistently more pronounced in polyploid populations compared to diploids (Figure 2).

4. Discussion

In this study, we found that polyploidy is associated with reduced genetic diversity and a lower potential for transgressive segregation. These findings stand in contrast with our theoretical predictions, which suggest that, all else being equal, polyploidy should enhance evolvability and increase the likelihood of generating transgressive phenotypes due to greater genetic covariance following recombination.

Theoretical evolution of genetic diversity after polyploidization

Our simulations showed that the evolution in genetic diversity in polyploids qualitatively mirrors that in diploids. For all ploidy levels, both genetic variance and (mostly negative) genetic covariance declined with increasing selfing rates. Inbreeding depression also decreased with increasing selfing rates. However, at any given selfing rate, polyploids maintained higher genetic variance and inbreeding depression than diploids. These findings are consistent with theoretical expectations (Otto & Whitton, 2000; Clo, 2022a).

Notably, polyploids under full selfing exhibited lower genetic variance than fully outcrossing diploids under full outcrossing, emphasizing the importance of mating strategies in shaping adaptive potential, a pattern also observed empirically (Martin and Husband, 2012). While selfing consistently reduced genetic variance, this decline was gradual in diploids and became more pronounced only at high selfing rates, particularly when mutation rates were elevated—again aligning with prior studies (Abu Awad and Roze, 2018; Lande and Porcher, 2015). In this work, these results have been extended to polyploid populations. For polyploids, simulations showed that the decrease in genetic variance and covariance as functions of the selfing rate is faster than for diploids.

Interestingly, our simulations also highlight that inbreeding depression increased with the ploidy level, but decreased with higher selfing rates, regardless of ploidy. The latter reflects the increased homozygosity in selfing individuals, which facilitates purging of deleterious alleles (Ronfort, 1999). However, the greater inbreeding depression observed in polyploids compared to diploids likely results from higher heterozygosity of deleterious mutations (Ronfort, 1999), a finding that contradicts some empirical studies suggesting that polyploids should exhibit equal or lower inbreeding depression than diploids (Clo & Kolář, 2022).

How polyploidy affects evolvability in practice:

Our empirical results revealed that evolvability differs across ploidy levels and environments (Table 2). Diploid populations consistently exhibited the highest evolvability under both common garden and mountain conditions. This aligns with previous work showing higher evolvability in diploids compared to established tetraploids (Martin & Husband, 2012). On the contrary, other studies report similar or lower heritable diversity in polyploids (O'Neil, 1997; Burgess et al., 2007; Ebadi et al., 2023), partly supporting our findings and challenging broad generalizations derived from theory (Clo, 2022a).

Several factors may explain this discrepancy. Newly formed polyploids may experience reduced genetic diversity due to allelic dilution and post-polyploidization bottlenecks (Clo, 2022b; Mortier et al., 2024). Additionally, while selfing facilitates establishment in novel environments, it does not enhance genetic diversity as outcrossing does (Wright et al., 2008). Therefore, discrepancies between theoretical predictions and empirical patterns may stem from subsequent evolutionary changes in life history traits and responses to local environmental conditions.

Bridging theory and empirical results:

Two scenarios could potentially reconcile our theoretical predictions with observed data. First, one might hypothesize that sampled diploid populations are predominantly outcrossing while polyploid populations are predominantly selfing, an arrangement that would naturally produce lower evolvability in polyploids. However, this scenario contradicts previous studies on *E, incanum*, which rather show that polyploidy is associated with a shift toward more outcrossing phenotypes. For example, changes in *Erysimum incanum* in flower size and spatial position of sexual organs related to genome duplication tend to be more fitted to outcrossing strategies (García-Muñoz et al., 2023).

A more plausible explanation is that polyploidy alters the selective landscape (the ω^2 parameter in our simulations), by modifying the ecology of populations. Polyploidy is associated with periods of environmental turmoil and contemporary stressful conditions (see Van de peer et al. 2021 for a review), and harsher conditions are known to decrease the evolvability of populations (Pujol and Pannell, 2008; Martinez-Padilla et al., 2017; Pennington et al., 2021). Our data support this interpretation: while mountain environments generally enhanced evolvability, likely due to increased ecological heterogeneity, the interaction between polyploidy and environments was negative, especially for hexaploids. These populations, located in more arid southern regions, appear to experience harsher environmental constraints. Polyploid lineages can undergo rapid niche differentiation (Baniaga et al., 2020; Padilla-García et al., 2023), and adaptation to narrow, extreme environments may reduce within-population genetic variance. In contrast, diploid and tetraploid populations inhabit more variable habitats, potentially retaining broader evolutionary potential. A summary of the study's results and the current literal is available in Table 6.

Transgressive segregation and polyploidy

Our results also challenge the assumption that polyploidy promotes transgressive segregation. Polyploidy levels were negatively associated with transgressive segregation, while mountain conditions had a positive effect (as shown by TS2 and the variance ratio; Table 3). In contrast, TS1 revealed no significant effects. This suggests that polyploidy does not necessarily increase the likelihood of generating novel phenotypes beyond the parental range, despite theoretical predictions of enhanced genetic covariance in polyploids (Clo, 2022b), and empirical evidences of previous studies suggesting that increased heterozygosity

in polyploids leads to novel allele combinations and diversity (Sattler et al., 2015; De los Reyes, 2019).

Interestingly, common garden conditions were associated with reduced transgressive segregation, while greenhouse conditions appeared to enhance it. This highlights the role of environmental complexity in shaping the emergence of novel trait combinations. Although polyploids often display broader phenotypic ranges (Čertner et al., 2019), their adaptive potential may still be greater in more variable environments, despite the observed reduction in transgressive segregation under certain conditions.

Conclusion and perspectives

In summary, our empirical findings suggest that diploids are more evolvable than polyploids and that ploidy level has limited influence on transgressive segregation. These results contrast with theoretical expectations that posit increased genetic variance with higher ploidy. One likely explanation lies in differences in selective pressures, as hexaploids tend to live in more arid and extreme environments and have adapted to more restricted conditions than their diploid and tetraploid counterparts.

Our current model does not incorporate non-additive genetic effects, such as dominance or epistatic interactions. While dominance reduces the difference in adaptive potential among mating strategies in diploids, its role in polyploids has not yet been explored. Similarly, epistasis may enhance the adaptive potential in tetraploids, and even more in hexaploids, suggesting a direction for future investigation.

Refining the model to distinguish between neo- and established polyploids, and to incorporate events such as bottlenecks, would also provide a better understanding of the adaptive potential of polyploids and selfing populations.

Future models should distinguish between neo- and established polyploids and include demographic processes such as founder effects or bottlenecks to better reflect real-world scenarios. Although theoretical models provide valuable general frameworks, they cannot fully account for the complexities of natural populations. Empirical data are therefore essential to refine and improve these models.

Our results reinforce the importance of combining theoretical and empirical approaches to better understand how mating systems and ploidy jointly influence the adaptive potential of

plant populations. This integration is crucial for predicting evolutionary trajectories under environmental change, especially in diverse and dynamic systems such as *Erysimum incanum*.

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Data availability: The simulation model is available at: https://github.com/DianeDouet/ploidy_mating_QG. The experimental dataset generated during the current study is available from the corresponding author on reasonable request.

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Symbol	Meaning	Values
N_{pop}	Population size	250
L	Number of loci	50
U	Mutation rate per haplotype	0.1 or 0.005
a^2	Variance of mutational effects	0.05
d	Dosage effect	0.67
V_e	Variance of environmental effects	1
ω^2	Strength of selection	1 or 9

Table 1. Summary of notations and values.

Greenhouse	**Diploid**	1.063±0.504
	Tetraploid	3.432±1.764
	Hexaploid	2.104±1.766
Common garden	**Diploid**	2.418±1.089
	Tetraploid	0.949±0.806
	Hexaploid	1.303±1.006
Mountain	**Diploid**	77.747±148.852
	Tetraploid	3.563±3.758
	Hexaploid	0.609±0.473

Table 2. Evolvability means and standard deviations for each ploidy and environmental levels in individual and flower traits of *Erysimum incanum*.

	Estimate	SD	Error	t value
(Intercept)	1.063	16.548	0.064	0.94896
Tetraploid	2.369	23.402	0.101	0.91961
Hexaploid	1.042	23.402	0.045	0.96460
CG	1.355	23.402	0.058	0.95396
MT	76.684	23.402	3.277	0.00155**
Tetraploid:CG	-3.838	33.096	-0.116	0.90796
Hexaploid:CG	-2.157	33.096	-0.065	0.94820
Tetraploid:MT	-76.553	33.096	-2.313	0.02326*
Hexaploid:MT	-78.180	33.096	-2.362	0.02057*

Table 3. Statistics of general linear model of evolvability on ploidy and environment effects on individual and flower traits of *Erysimum incanum*. Greenhouse and diploid levels are used as default conditions. CG: Common garden; MT: Mountain.

	Diploid			Tetraploid			Hexaploid		
	TS2	TS1	Variance ratio	TS2	TS1	Variance ratio	TS2	TS1	Variance ratio
Plant height	0	0,512	0,584	0,021	1,234	1,034	0,016	0,922	0,9
Number of stalks	0	0,947	1,894	0	0,727	0,777	0	0,769	0,656
Stalk diameter	0,02	0,943	1,196	0,021	0,933	1,369	0,016	1,049	1,031
Number of flowers	0,061	0,538	0,93	0	0,713	0,748	0	0,947	0,791
Petal length	0,02	1,426	1,383	0,042	1,107	0,946	0	0,564	0,934
Flower diameter	0,061	0,927	0,782	0,021	0,973	0,841	0	0,882	0,998
Corolla tube length	0,041	1,013	1,454	0,083	1,06	1,503	0	0,931	1,286
Long filament length	0,082	1,168	1,338	0,021	0,727	0,855	0	0,872	0,875
Short filament length	0,041	1,093	1,149	0,021	0,85	0,879	0	0,699	0,799
Style length	0,02	0,854	1,048	0,021	0,801	0,879	0,016	0,909	1,341
Herkogamy	0,02	0,939	0,799	0	0,83	1,177	0,048	0,954	1,42

Table 4. Transgressive segregation indexes for individual and phenotypic traits in *Erysimum incanum* in the greenhouse. We considered TS1 as the classical index proposed by Rieseberg et al. (1999, 2003) TS2 as the proposed index by Koibe et al., (2019) and variance ratio between outcrossing and selfing groups.

	Diploid			Tetraploid			Hexaploid		
	TS1	**TS2**	**Variance ratio**	**TS1**	**TS2**	**Variance ratio**	**TS1**	**TS2**	**Variance ratio**
Plant height	0	0,012	0	0,048	1,088	1,14	0,041	1,018	1,346
Number of stalks	0	0,333	0,201	0,048	2,167	4,999	0,02	1,667	1,849
Stalk diameter	0	0,674	0,541	0	0,598	0,715	0,02	1,296	1,177
Number of flowers	0,25	0,209	0,057	0	0,574	0,941	0,082	1,521	1,402
Petal length	0	0,204	0,105	0	0,466	0,543	0	0,621	0,801
Flower diameter	0	0,461	0,504	0,048	0,914	1,52	0	0,912	1,017
Corolla tube length	0	0,236	0,125	0	0,556	0,557	0,061	1,003	0,714
Long filament length	0	0,222	0,175	0	0,494	0,619	0	0,65	0,613
Short filament length	0	0,408	0,523	0	0,831	1,022	0	0,726	0,969
Style length	0	0,132	0,083	0	0,4	0,738	0	0,684	0,64
Herkogamy	0	0,077	0,023	0	0,663	1,112	0	0,637	0,838

Table 5. Transgressive segregation indexes for individual and phenotypic traits in *Erysimum incanum* in the common garden. We considered TS1 as the classical index proposed by Rieseberg et al. (1999, 2003) TS2 as the proposed index by Koibe et al., (2019) and variance ratio between outcrossing and selfing groups.

	Previous theory	Study model	Empirical results
Ploidy	Higher genetic variance due to heterozygosity and epistatic effects. But loss of positive effects in the short term (Stebbins, 1966).	Higher genetic variance at higher ploidies but higher reduction in selfing scenarios.	Lower evolvability in higher ploidy levels compared with diploids, especially in harsh environments (mountains).
Selfing rate	Lower genetic variance (Charlesworth & Charlesworth, 1995; Abu Awad & Roze, 2018). It can be kept in low and medium levels.	Lower genetic variance in every ploidy level.	Not clear isolated effects as evolvability is only evaluated in selfing populations.
Ploidy × selfing rate	Lack of joint studies.	The advantage of polyploids in terms of genetic variance is reduced in higher selfing levels.	Not higher variance in polyploids, possible influence of environmental factors and population size changes.
Global conclusions	Expected higher genetic variance in polyploids.	With the same selfing rates, higher genetic variance for polyploids.	Higher evolvability in diploids and a higher influence of environmental conditions than on ploidy level.

Table 6. Comparative summary of effects of ploidy and mating system in genetic variance according to previous knowledge, the here developed mathematical model, and empirical results of our study.

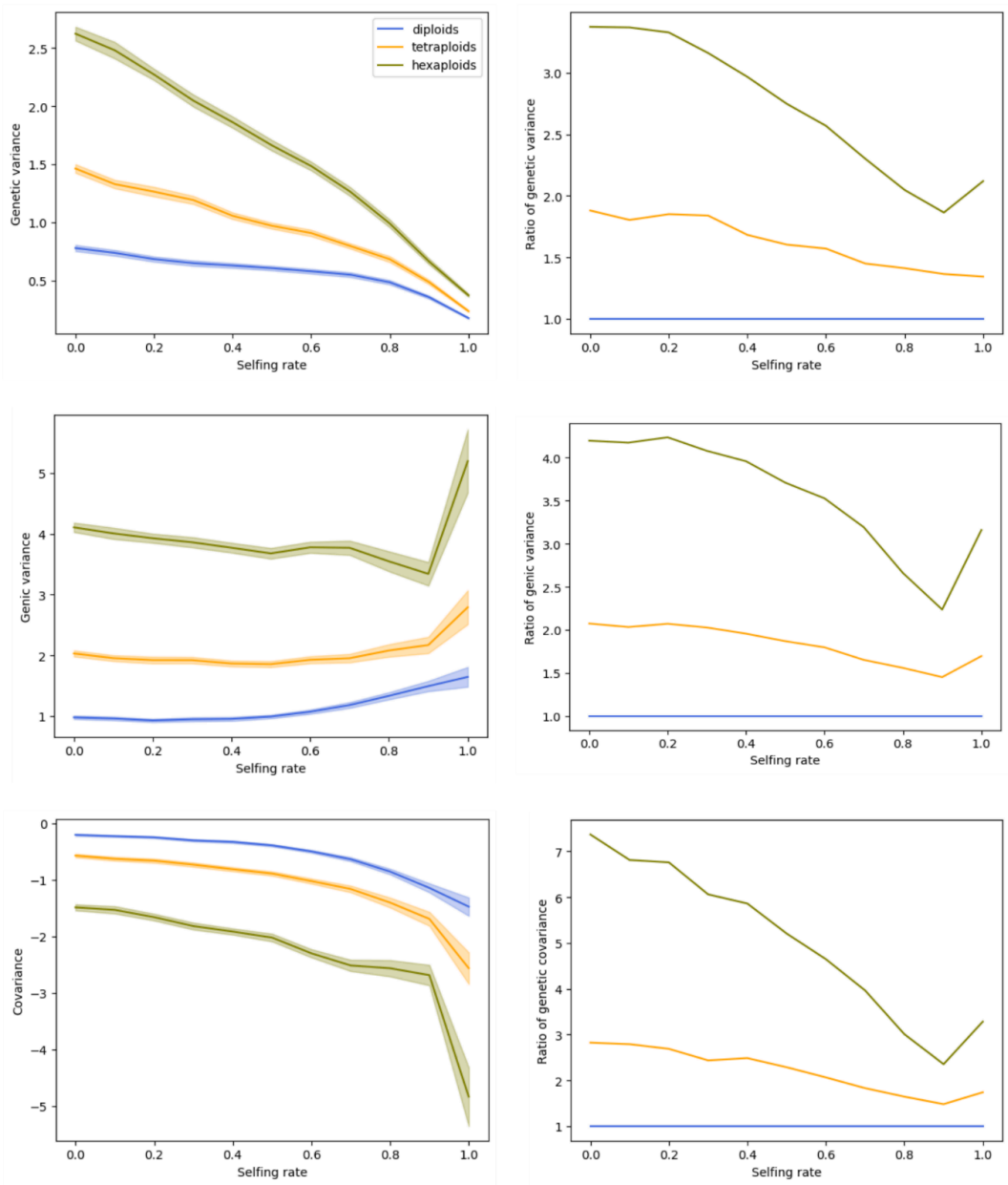

Figure 1. Genetic variance, genic variance and covariance and their 95% confidence intervals (left) and their ratios between diploid and polyploid populations (right) as functions of the selfing rate for different levels of ploidy, when $U = 0.1$ and $\omega^2 = 1$.

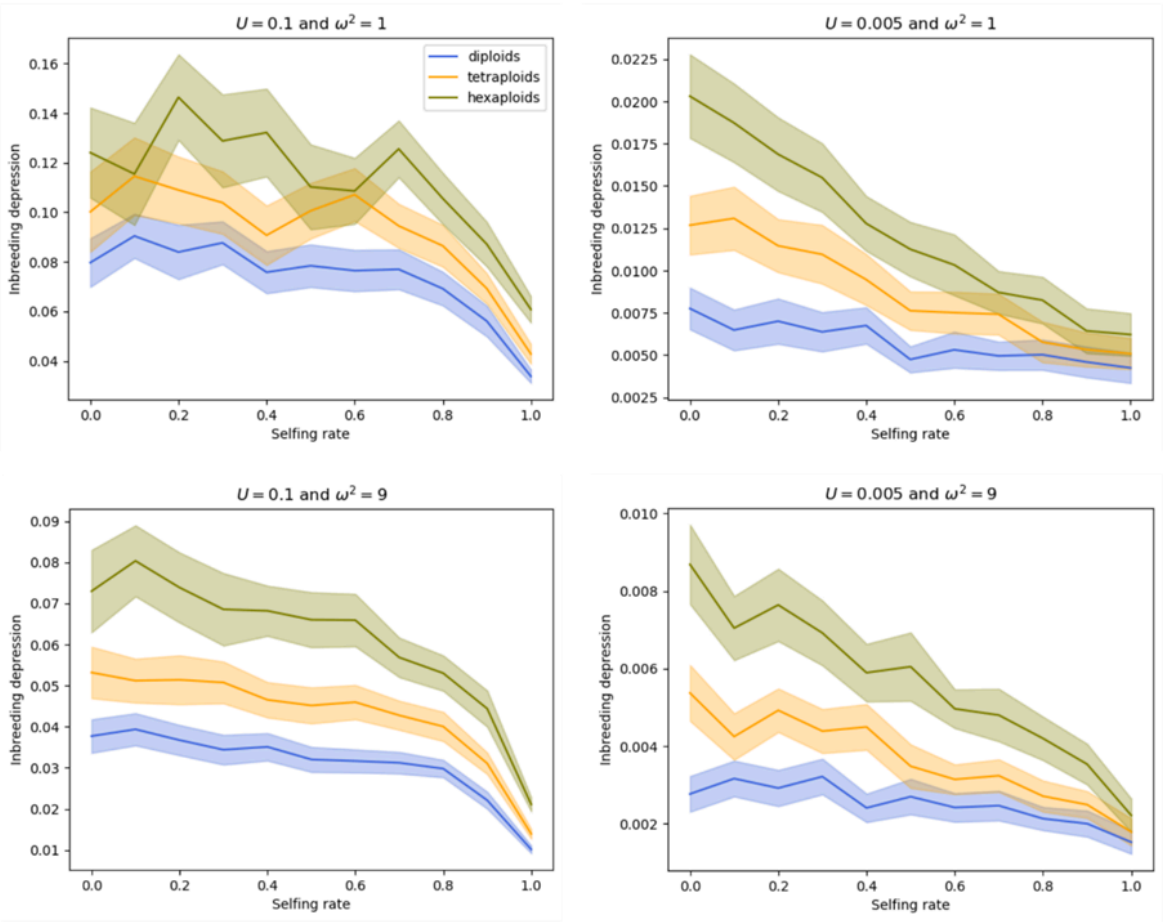

Figure 2. Inbreeding depression and associated 95% confidence intervals as a function of the selfing rate for different values of the parameters U and ω^2, and for different levels of ploidy.

Supporting information:

Table S1. Evolvabilities of individual and floral traits in *Erysimum incanum* for each ploidy and environment level

Figure S1. Genetic variance, genic variance, and covariance and their ratios between diploid and polyploid populations as functions of the selfing rate for different levels of ploidy, when $U = 0.005$ and $\omega^2 = 1$.

Figure S2. Genetic variance, genic variance, and covariance and their ratios between diploid and polyploid populations as functions of the selfing rate for different levels of ploidy, when $U = 0.1$ and $\omega^2 = 9$.

Figure S3. Genetic variance, genic variance, and covariance and their ratios between diploid and polyploid populations as functions of the selfing rate for different levels of ploidy, when $U = 0.005$ and $\omega^2 = 9$.