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Inbreeding depression in polyploid species: a meta-analysis

Josselin Clo[‡], Filip Kolář^{‡,‡}

[‡] Department of Botany, Faculty of Science, Charles University in Prague, Benátská 2, CZ-128 01 Prague, Czech Republic

[‡] Institute of Botany of the Czech Academy of Sciences, Zámek 1, CZ-252 43 Průhonice, Czech Republic

21 **Abstract:**

22

23 Whole-genome duplication is a common mutation in eukaryotes with far-reaching phenotypic
24 effects, the resulting morphological and fitness consequences and how they affect the survival
25 of polyploid lineages are intensively studied. Another important factor may also determine the
26 probability of establishment and success of polyploid lineages: inbreeding depression.
27 Inbreeding depression is expected to play an important role in the establishment of neopolyploid
28 lineages, their capacity to colonize new environments, and in the simultaneous evolution of
29 ploidy and other life-history traits such as self-fertilization. Both theoretically and empirically,
30 there is no consensus on the consequences of polyploidy on inbreeding depression. In this meta-
31 analysis, we investigated the effect of polyploidy on the evolution of inbreeding depression, by
32 performing a meta-analysis within angiosperm species. The main results of our study are that
33 the consequences of polyploidy on inbreeding depression are complex and depend on the time
34 since polyploidization. We found that young polyploid lineages have a much lower amount of
35 inbreeding depression than their diploid relatives and their established counterparts. Natural
36 polyploid lineages are intermediate, and have a higher amount of inbreeding depression than
37 synthetic neopolyploids, and a smaller amount than diploids, suggesting that the negative effect
38 of polyploidy on inbreeding depression decrease with time since polyploidization.

39

40 **Keywords:** polyploidy, genome doubling, fitness, inbreeding depression, polyploid
41 establishment.

42

43

44 **Introduction:**

45

46 Polyplodization has occurred numerous times during the evolution of eukaryotes [1,2]
47 and has been shown to have a broad range of phenotypic and genomic effects and to be an
48 important mechanism for plant adaptation and speciation [3]. Nevertheless, polyplodization
49 initially arises with several disadvantages in neopolyploids, like mitotic and meiotic
50 dysfunction, genomic instability, decrease in fitness, and negative frequency-dependent
51 selection [4–9].

52 Another important factor may also determine the probability of survival and success of
53 polyploid lineages: inbreeding depression (ID hereafter) [10,11]. ID can be defined as the
54 reduction of fitness found in selfed progenies compared to outcrossed progenies [12], and is
55 predominantly due to the expression of recessive deleterious alleles at their homozygous state
56 [13]. ID theoretically plays an important role in polyploids establishment. The initially low
57 frequency of polyploid lineages within a diploid population may lead to strong bi-parental
58 inbreeding [14]. In such conditions, it has been shown theoretically that a decrease in ID in
59 polyploids compared to diploids is necessary for them to establish [10,11].

60 Polyploidy is theoretically expected to have both positive and negative effects on the
61 amount of ID (see [15] for review). In the short term, it has been shown theoretically that in
62 autopolyploid species, the strong bottleneck associated with polyplodization can strongly
63 decrease the amount of ID due to the loss and/or the fixation of recessive deleterious mutations
64 [16]. Even if not tested, we can expect similar consequences in allopolyploid species. In
65 autopolyploid species with polysomic inheritance, even without a loss of genetic diversity, if
66 frequencies of deleterious mutations remain similar in different cytotypes, as homozygosity
67 increases at slower rates in autopolyploids compared to diploids [17], the expression of ID

68 should be less severe in neoautopolyploids. In the long-term, the better masking of recessive
69 deleterious mutations in autopolyploids should make them segregate at higher frequencies than
70 in diploid populations [18]. Depending on the dominance coefficients of the mutations in the
71 autopolyploid heterozygous genotypes, this increase in frequency can make ID to be smaller
72 [19] or higher [20] in autopolyploids compared to diploids. Empirically, both a decrease [21,22]
73 or an increase [23,24] of ID in synthetic and natural autopolyploids compared to diploids have
74 been observed, and no strong consensus can be made. Allopolyploidy received much less
75 attention, and there are consequently fewer expectations than in autopolyploid species. Hedrick
76 [25] nevertheless showed that in homosporous, allopolyploid ferns, because offspring will be
77 strongly homozygous due to intragametophytic selfing, ID should be lower in allopolyploids
78 compared to diploids.

79 In this study, we investigated the effect of polyploidy on the evolution of ID. To do so,
80 we performed a meta-analysis within angiosperm species. The main results of our study are that
81 the effect of polyploidy on ID is complex and depends on the time since polyploidization. We
82 found that synthetic polyploid lineages have a lower amount of ID than their diploid progenitors
83 and their established counterpart. Natural polyploid lineages are intermediate, and have a higher
84 amount of ID than synthetic neopolyploids, and a smaller amount than diploids.

85

86

87 **Material & Methods:**

88

89 *Dataset compilation*

90

91 For this study, we were interested in the amount of ID in polyploids (auto- and
92 allopolyploids, and of synthetic and natural genomic origins) compared to their diploid
93 progenitors. As the studies comparing diploid and polyploid populations of the same species in
94 the same article were rare, we extended the research to articles estimating the level of ID in
95 polyploid populations, even without diploid controls.

96 We used Google Scholar, Web of Science, PubMed and Agricola databases in order to
97 perform our literature survey. We used the keywords (“neopolyploid*” or “synthetic
98 polyploid*” or “polyploid*”) and (“inbreeding”, “inbreeding depression”, “fitness”), and
99 “plant*”. To be incorporated in the data collection, the selected study had to (1) define clearly
100 the type (allo- or autopolyploidy) and level of ploidy of the population under study, (2) give the
101 level of ID in the populations under study, or at least give the fitness of outbred and inbred
102 progenies, such that we were able to infer ID ourselves, and (3) that ID equals $\delta = 1 - (W_s/W_o)$
103 when $W_s < W_o$ and $\delta = (W_o/W_s) - 1$ when $W_s > W_o$, where W_s and W_o are respectively the fitness
104 of selfed and outcrossed progenies [12]. Most of the time, the studies reported the numerical
105 values in tables, but we sometimes had to extract the data directly from the figures, by using
106 Plot Digitizer [26]. In the following part of the manuscript, we assumed that estimates found in
107 synthetic polyploids (called neopolyploids in the following parts of the manuscript) will be our
108 proxies for the short-term consequences of polyploidization on ID, while estimates from natural
109 populations will be our proxies for the long-term consequences, even if the time since
110 polyploidization is generally unknown and can greatly differ between species. A summary of
111 the sampled species and articles can be found in Table 1.

112

113 *Considering phylogenetic non-independence*

114

115 We tested if there was a potential phylogenetic correlation of our estimates in our
116 analyses. To do so, we used the divergence times found in the TimeTree’s database [27], in
117 order to reconstruct the phylogeny of our selected species. We then used the MEGA-X software
118 [28] to transform the obtained matrix of distance into NEWICK format, with an UPGMA
119 method. During this process, seven species were not found. We used the TimeTree database to
120 find closely related species used for replacement of the missing ones (see Figure S1 and
121 associated text to have the list of species). To test for a potential phylogenetic non-
122 independence, we used the obtained phylogeny and ran linear mixed effect models by using the
123 ‘metafor’ R package [29], and more precisely the rma.mv function that allows integrating
124 phylogenetic correlation matrix into linear models. We tested if the amount of ID differed
125 among diploid, neo- and natural polyploids using nested models. A first one in which a random-
126 effect ‘Species’ is specified, and a second in which we included the phylogenetic correlation
127 matrix as an additional random effect. The significance of the phylogenetic matrix was tested
128 by performing a Likelihood Ratio Test (LRT) between the two abovementioned models.

129

130 ***Inbreeding depression***

131

132 We chose to perform a Bayesian meta-analysis, by using the MCMCglmm package [30].

133 We wrote the following model:

134

$$135 \delta_{ij} = \mu + \text{ploidy}_i + \text{species}_j + \varepsilon_{ij} \quad (1)$$

136

137 where δ_{ij} is the level of ID, μ is the mean value, and ploidy_i is the effect of the ploidy i (diploid,
138 neo-polyploid [synthetic polyploid], and established tetraploid). As mentioned before, we only

139 included a single random effect: species j is the effect of the j th species, and ε_{ij} is the residual
140 error. We assumed that the residual error followed a Gaussian distribution. We performed these
141 models with two different datasets. The first one in which restricted to studies in which ID is
142 estimated in diploid and/or neo- and natural polyploids simultaneously (called relatedness-
143 controlled analysis after). In this dataset, we subtracted the ID level of diploids from the values
144 of polyploids ($\Delta\delta = \delta_{\text{poly}} - \delta_{\text{diplo}}$). If $\Delta\delta < 0$ (respectively > 0), it means that δ is smaller
145 (respectively higher) in polyploids compared to diploids. In a second analysis, we included all
146 studies and compared untransformed values of δ for diploids and polyploids (called complete
147 analysis after). This analysis is potentially less robust, because we are comparing unrelated
148 diploid and polyploid species, that can differ for other life-history traits potentially affecting ID
149 levels.

150 For all analyses, we used the weakly informative, default priors proposed in
151 MCMCglmm [30]. For fixed effects, the prior is a normal distribution with mean being equal
152 to zero and a variance of 10^{10} . For random effects, inverse-Wishart priors are implemented,
153 with the degree of belief parameter being equal to zero and the expected variance being equal
154 to 1. For all models, we used a burn period of 1.000.000 iterations, with a thinning interval of
155 50, and the MCMC chains were run for 6.000.000 iterations in total. The parameter models and
156 associated 95% credible intervals were thus inferred from the sampling of the posterior
157 distribution 100.000 times. We did a visual examination of the convergence, posterior traces
158 and autocorrelation values of our models, as suggested in [30]. The trace of the sampled
159 posterior, and posterior distributions for both models are available in supplementary materials
160 (Figures S2 and S3).

161

162 **Results:**

163

164 The dataset was composed of 33 articles published between 1940 and 2020. These
165 articles covered 25 species divided into 15 families of angiosperms. The relatedness-controlled
166 analysis was based on 99 diploid-polyploids estimates of ID (70 in natural polyploid
167 populations, 29 in synthetic polyploids). The complete analysis compiled 225 estimates of ID
168 (195 in natural polyploid populations, 30 in synthetic polyploids). Most of the estimates have
169 been estimated for autopolyploid species (187 in auto- and 23 in allopolyploid species). A
170 summary can be found in Table 2.

171 We found that the phylogenetic matrix did not improve the model ($\chi^2 = 0.171$, d.f. = 1,
172 $p = 0.680$), so we decided to only keep the random effect 'Species'. We found no differences
173 between allo- and autopolyploid species (Tables S1, S2 & S3).

174 On average, polyploidy tended to decrease the amount of ID (Figure 1), with synthetic
175 polyploids having the smallest mean ID level, and natural polyploids being intermediate
176 between synthetic polyploids and diploids (Figure 1). In the relatedness-controlled analysis,
177 synthetic polyploids had a significantly smaller level of ID than their diploid relatives (Figure
178 1A), but natural polyploids had an intermediate level, not significantly different from synthetic
179 polyploids or diploids (Figure 1A). In the complete analysis, the amount of ID found in our
180 restricted set of diploid estimates was in line with what was found in bigger studies (0.42 in
181 [31], 0.38 [95% credible interval 0.27-0.60] in this study), confirming that we can use this value
182 for comparisons. We found that all cytotypes had significantly different amounts of ID (Figure
183 1B). The synthetic polyploids had the lowest amount (Figure 1B, with a decrease of 69.0%
184 compared to diploids), while natural polyploids were intermediate between the two other
185 cytotypes (Figure 1B, with a decrease of 30.7% compared to diploids and an increase of 126.8%
186 compared to synthetic polyploids).

187

188 **Discussion:**

189

190 *Inbreeding depression and establishment of new polyploid lineages*

191

192 In this study, we found that ID decreases in polyploid populations compared to diploids.
193 This result increases our understanding of how neopolyploid lineages can establish. Our meta-
194 analysis confirmed theoretical expectations that due to an initial bottleneck [16], the masking
195 of deleterious mutations that are in comparable frequencies as in diploids [18,32], and/or a
196 slower increase in homozygosity during selfing events [17], new polyploid lineages benefit
197 from a strong decrease in ID. Indeed, the small average amount of ID ($\delta = 0.119$) found in
198 synthetic polyploids suggests that potential bi-parental inbreeding should have a minor effect
199 on the establishment probability of neopolyploids [10,11]. In the long-term, however, the
200 amount of ID increases again in natural polyploids, as expected due to the increase in frequency
201 of recessive deleterious mutations because of their better masking in polyploids compared to
202 diploids[16,20]. Nevertheless, our results cannot conclude if natural polyploids have an
203 intermediate or similar amount of ID to their diploid progenitors.

204

205 *The joint evolution of polyploidy, range expansion and mating system*

206

207 Our results also give insights into why polyploidization can also lead to the evolution of
208 other life-history traits. It has been observed that polyploid lineages can lead to the expansion
209 of geographic [33] and climatic niches [34,35]. A theoretical argument is that a reduction in ID
210 may favor such expansions, as biparental inbreeding, expected during the process due to

211 bottleneck events [14], should have a minor effect in (neo)polyploids compared to diploids [11].
212 Our results support the theoretical prediction.

213 Finally, our results indicate that polyploidization could favor the transition from
214 predominantly outcrossing to predominantly selfing mating systems. If an association between
215 polyploidy and higher selfing rates has been found [36], it has been shown that this effect
216 depends on the kind of ploidy. Husband *et al.* [21] showed that autopolyploid species generally
217 self-fertilize less than diploid ones, while allopolyploids showed the opposite pattern [21,37].
218 Since our dataset is mainly composed of autopolyploid species (Table 1), our finding seems to
219 be counterintuitive. Nevertheless, recent theoretical advances showed selfing only promotes
220 autopolyploidization when neopolyploid lineages are at least as fit as their diploid counterparts
221 [38], which is generally not the case [8,39].

222 Our results however suggest that geographic expansion and/or the evolution of selfing
223 are more likely to occur in the very first generations following genome doubling, as ID is
224 smaller in synthetic polyploids than in natural ones.

225

226 *Potential limitations*

227

228 Even if informative, our study could suffer from potential bias. The first one is that
229 synthetically produced polyploids could not be representative of natural young polyploid
230 lineages. Nevertheless, the chemical treatments used to generate synthetic polyploids
231 generally lead to a high to moderate death rate of treated diploids (see for example [40]),
232 mimicking the expected bottleneck of genetic diversity that occurs during polyploidization
233 events [16]. A second bias could be that the sampled diploid and natural polyploid lineages

234 could differ in their selfing rate, which could be problematic if polyploids are more often
235 predominantly selfers compared to diploids, as the observed decrease in ID could be due to an
236 increased selfing rate that purges more efficiently deleterious mutations in natural polyploids
237 compared to diploids [20]. Nevertheless, quick comparisons of the selfing rate found in our
238 diploid and natural polyploid species suggest no differences (Table S4), and our dataset is
239 mainly composed of autopolyploid species, that tend to have a smaller selfing rate than their
240 diploid progenitors on average [21]. These results suggest that our analysis is conservative, and
241 that the observed decrease in ID is due to the consequences of polyploidization *per se*. Finally,
242 it is generally assumed that ID will affect the survival probability of polyploid populations, but
243 such an association remains to be tested empirically.

244

245 **Conclusions:**

246

247 Our results are of primary importance for the understanding of polyploid establishment,
248 and for the joint evolution of polyploidy with other life-history traits such as mating systems.
249 However, our results remain preliminary, and further studies are needed to confirm the patterns
250 described. Especially, theoretical and empirical studies in allopolyploid species would be of
251 primary importance since there are few.

252

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255

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259

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425 **Table 1.** Summary of the sampled species, their ploidy levels, their genomic origin (auto- or
 426 allopolyploid), if they are natural or synthetic polyploids.

Species	Ploidy levels	Genomic origin	Natural / synthetic	References
<i>Acacia auriculiformis</i>	2x, 4x	autopolyploid	synthetic	[41]
<i>Agropyron cristatum</i>	2x, 4x	autopolyploid	natural & synthetic	[24,42]
<i>Amsinckia gloriosa</i>	2x, 4x	autopolyploid	natural	[43]
<i>Anthericum liliago</i>	2x, 4x	allopolyploid	natural	[44]
<i>Aster kantoensis</i>	4x	autopolyploid	natural	[45]
<i>Beta vulgaris</i>	4x	autopolyploid	natural	[46]
<i>Campanula americana</i>	4x	autopolyploid	natural	[47,48]
<i>Centaurea stoebe</i>	2x, 4x	allopolyploid	natural	[14]
<i>Chamerion angustifolium</i>	2x, 4x	autopolyploid	natural & synthetic	[21,49–51]
<i>Clarkia davyi</i>	2x, 4x	allopolyploid	natural	[52]
<i>Clarkia gracilis</i>	2x, 4x	allopolyploid	natural	[52]
<i>Digitalis purpurea</i>	4x	autopolyploid	natural	[53]
<i>Fragaria vesca</i>	2x, 4x	autopolyploid	synthetic	[54]
<i>Iris versicolor</i>	4x	allopolyploid	natural	[55]
<i>Jasione maritima</i>	2x, 4x	autopolyploid	synthetic	[22]
<i>Knautia arvensis</i>	4x	autopolyploid	natural	[56]
<i>Medicago sativa</i>	4x	autopolyploid	natural	[23,57,58]
<i>Mercurialis annua</i>	6x	autopolyploid	natural	[59,60]
<i>Pyrus communis</i>	4x	autopolyploid	natural	[61]
<i>Scalesia affinis</i>	4x	autopolyploid	natural	[62]
<i>Silene virginica</i>	4x	autopolyploid	natural	[63]
<i>Spartina alterniflora</i>	4x	allopolyploid	natural	[64]
<i>Trifolium hybridum</i>	4x	autopolyploid	synthetic	[65]
<i>Vaccinium corymbosum</i>	2x, 4x	autopolyploid	natural	[66]

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428 **Table 2.** Summary of the number of estimates for the different categories of ploidy, for the
429 relatedness-controlled and complete analyses.

Dataset	Diploids	Neo-polyploids	Natural polyploids
Relatedness-controlled	84	29	70
Complete	84	30	195

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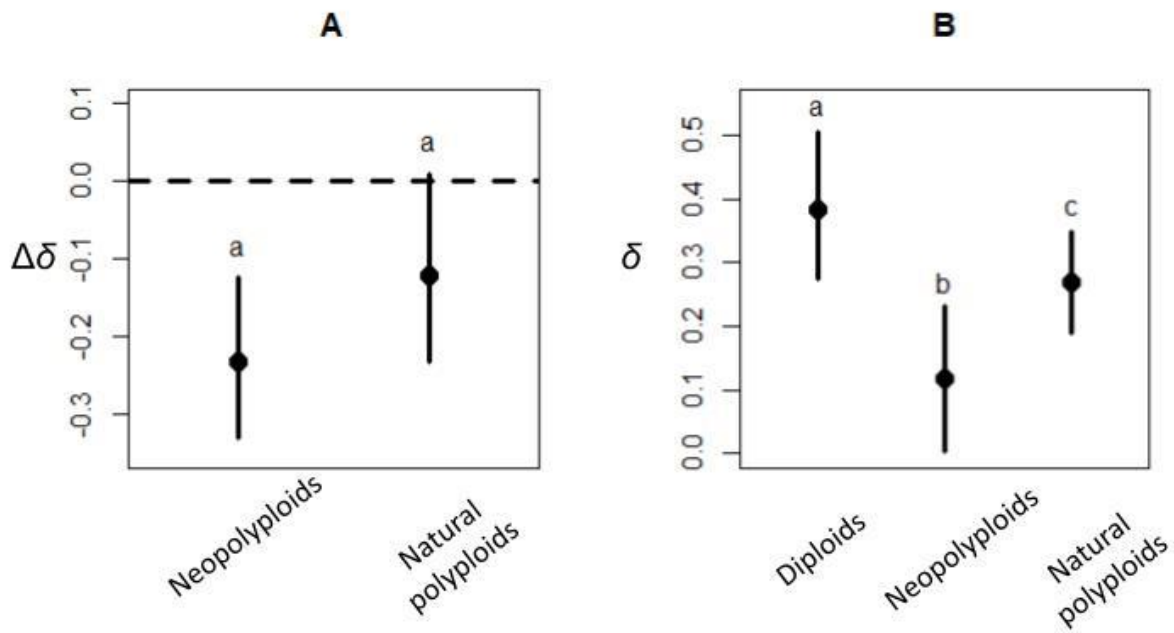
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440 **Figure 1.** The evolution of inbreeding depression in polyploids (neo- and natural polyploids)
 441 compared to their diploid progenitors. **A.** Relatedness-controlled analysis, with $\Delta\delta = \delta_{\text{poly}} -$
 442 δ_{diplo} , a negative value showing that inbreeding depression is smaller in polyploids compared to
 443 diploids. Here, $\Delta\delta$ is significantly different from zero for neopolyploids, but not for natural
 444 polyploids. **B.** Complete analysis. Different letters indicate significantly different mean values
 445 between ploidy levels. Error bars stand for the 95% credibility intervals.