Does hybridization between divergent progenitors drive whole-genome duplication?

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1   OPINION

2

3   **Does hybridization between divergent progenitors drive whole-**

4   **genome duplication?**

5

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24

25 **Abstract**

26

27 Hybridization and whole-genome duplication are both potential mechanisms of rapid

28 speciation which sometimes act in concert. Recent surveys, showing that homoploid

29 hybrid species tend to be derived from parents that are less evolutionarily divergent than

30 parents of polyploid hybrid species (allopolyploids), have been interpreted as supporting

31 a hypothesis that high divergence between hybridizing species drives whole-genome

32 duplication. Here we argue that such conclusions stem from problems in sampling

33 (especially the omission of autopolyploids) and null model selection, and underestimate

34 the importance of selection. The data simply demonstrate that hybridization between

35 divergent parents has a higher probability of successfully producing a species if followed

36 by polyploidization.

37

38 **Introduction**

39

40 Hybrid speciation occurs when two existing species cross and produce phenotypically

41 distinct offspring (or later-generation progeny) which then become reproductively

42 isolated from their parents. This mode of speciation was once regarded as unimportant

43 (Darwin 1859; Mayr 1963) but is now seen as a significant evolutionary process in both

44 plants (Rieseberg & Willis 2007; Soltis & Soltis 2009) and animals (Jesús Mavárez &

45 Linares 2008; Mallet 2007). This new view of hybrid speciation has developed through

46 both the discovery of numerous hybrid species, and an increased understanding of

47 processes which allow the obstacles to hybrid speciation to be overcome (Mallet 2007;

48 Rieseberg 1997).

49

50 Several obstacles stand in the way of successful hybrid speciation (reviewed in Grant

51 1981; Mallet 2007; Rieseberg 1997; Soltis & Soltis 2009). Geographic separation or

52 reproductive differences may prevent crossing between two potential parent species. If

53 hybridization does occur, the progeny may abort or have low fitness due either to genetic

54 incompatibilities between the parental genomes, or the generation of maladaptive

55 phenotypes. Even if the hybrid has high fitness, it may never achieve reproductive

56 isolation and will backcross with its parents, leading to introgression. Successful hybrid

57 speciation is therefore a comparatively rare event that occurs under a limited range of

58 conditions.

59

60   One process involved in the success of hybrid species is transgressive segregation: the

61   expression of trait values that exceed the range between the parental means (McDade

62   1990; Rieseberg *et al.* 2003). Transgressive segregation raises the likelihood of speciation

63   as the hybrids have new phenotypes not found in the parental species and may therefore

64   occupy an underused fitness peak on the local adaptive landscape (Mallet 2007). Under a

65   scenario involving transgressive segregation, ecological differentiation will occur rapidly

66   following hybridization, conferring a degree of reproductive isolation which may then be

67   reinforced with pre-zygotic isolation.

68

69   Another process frequently allowing success of hybrids is whole-genome duplication,

70   which is commonly found in plants and more rarely in animals (Mable 2004; Otto &

71   Whitton 2000; Rieseberg & Willis 2007). After genome doubling, backcrosses with

72   parental diploid species will generate progeny with an odd number of genome sets and

73   typically low fitness, providing post-zygotic reproductive isolation (Ramsey & Schemske

74   1998). Parental genomic incompatibilities may be overcome because genome doubling

75   causes every chromosome to have an identical homologue – thus pairing between

76   divergent parental chromosomes at meiosis is not necessary for successful gamete

77   formation. Whole-genome duplication can occasionally confer phenotypic changes such

78   as increased size or a change in sexual system, which may also contribute to speciation

79   (Otto & Whitton 2000).

80

81   **The role of genetic divergence**

82

83   The extent to which genetic divergence between parental species affects hybrid

84   speciation processes is currently under debate. The probability of ecological

85   differentiation following hybridization would seem to increase with the level of

86   divergence between the hybridizing parental species, as increased divergence would

87   likely expand the range of possible intermediate phenotypes. Recent evidence also

88   suggests that transgressive segregation in hybrids increases with genetic distance between

89   parental species (Stelkens & Seehausen 2009). Wide hybrids may therefore have more

90   evolutionary potential than hybrids between closely related species.

91

92   However, genetic differentiation between parental species is likely to be positively

93   correlated with some of the obstacles to hybridization. Under a general model of

94   allopatric speciation, geographic separation is likely to be more pronounced between

95   distantly related species, reducing the incidence of hybridization between distant

96   relatives. In addition, genetic incompatibilities due to, for example, chromosomal

97   rearrangements, Dobzhansky-Muller incompatibilities, or differential loss of duplicated

98   genes, are also likely to increase with genetic divergence, leading to hybrid inviability

99   (Lynch 1991; Orr 1995). Thus, wide hybrids (i.e., hybrids between divergent parents) are

100   less likely to form than those between close relatives, and may have lower fitness.

101

102   As some of the negative effects of genetic divergence between parental species can be

103   overcome by whole-genome duplication, we would expect formation of hybrid polyploid

104   species to be successful over a greater range of parental divergences than homoploid

105   hybrid species. At high parental divergences, allopolyploids may benefit from effects of

106 transgressive phenotypes, while homoploid hybrids between highly divergent parents,

107 which are likely to be sterile, may not similarly benefit. Thus, we might expect the

108 average divergence between parents of allopolyploids to be higher than that of homoploid

109 hybrid species, simply because polyploidy enables wide hybrids to be viable.

110

111 Several researchers have made the intriguing suggestion that rather than being a random

112 mutation that fortuitously confers viability to a wide hybrid, successful polyploidy is

113 determined by wide hybridization: genomic differentiation between parental species in

114 fact drives successful whole-genome duplication in their hybrids. Winge (1917) first

115 suggested that "occasional hybridization might be the cause" (p. 13) of polyploidy. He

116 developed "a scheme showing the different degrees of physiogenetic likeness between

117 gametes – and thus also between their chromosomes – endeavouring at the same time to

118 ascertain what results we can expect in each case from the fusion of gametes" (p. 196). In

119 this scheme a hybrid in which the chromosomes from parental species were unable to pair

120 would have to undergo chromosome doubling in the zygote to have "any possibility at all

121 of propagating" (p. 199). Subsequent workers proposed that this doubling would occur

122 through unreduced gamete formation. Darlington (1937) suggested that gametic doubling

123 occurs in hybrids because meiosis has proved unworkable. Similarly, Grant (1981)

124 considered that reduced chromosome pairing in hybrids between parents whose

125 chromosomes had different structures would "set the stage" for unreduced gamete

126 formation. Ramsey and Schemske (1998) found unreduced gametes to occur at a

127 frequency of 28% in hybrids but only 0.6% in non-hybrids. This could suggest that

128 unreduced gamete formation is actually triggered in hybrids.

129

130   Darlington (1937) also suggested another level at which this drive could occur. He

131   proposed an inverse relationship between the fertility of a diploid hybrid and that of a

132   tetraploid to which it gives rise. He reasoned that at low parental divergences, homoploid

133   hybrids will be fertile because chromosomes will be able to pair at meiosis, but

134   allopolyploids will be of low fertility because pairing will occur between both duplicated

135   chromosomes and homeologous chromosomes from each parent, causing uneven

136   segregation. In contrast, at high parental divergences, homoploid hybrids will be sterile

137   due to failure of chromosome pairing, but allopolyploids will be fertile due to consistent

138   bivalent formation at meiosis. This has sometimes been called "Darlington's rule" (not to

139   be confused with Darlington's rule in biogeography which states that with every ten-fold

140   increase in area, the number of species doubles). A literature survey by Clausen, Keck

141   and Hiesey (1945) seemed to support this rule by showing that the success and constancy

142   of allopolyploids is "linked with the degree of relationship found between their parents"

143   (p. 2). They argued that the "parent species…should be closely enough related to produce

144   a vigorous F_1 hybrid, but remotely enough so that the balance between their combined

145   genomes can be perpetuated" (p. 68-69). Stebbins (1950) agreed with this conclusion.

146   However, a recent survey of neopolyploids (Ramsey & Schemske 2002) did not show

147   significantly lower fertility in autopolyploids than allopolyploids, and we now know that

148   many allopolyploids do not show consistent bivalent formation and that non-homologous

149   transposition can occur between parental genomes (Leitch & Leitch 2008). These

150   findings suggest that although Darlington's rule may describe the average fertility of

151 hybrids and allopolyploids, selection may subsequently play a large role in preserving

152 fertile autopolyploids, as well as allopolyploids that formed from closely related parents.

153

154 **New evidence**

155

156 Three recent studies have re-visited the hypothesis that high divergence between

157 hybridizing species drives whole-genome duplication, using molecular methods to assess

158 divergence between the progenitor species of natural polyploid species, assuming as

159 Darlington (1937) did that genetic differentiation will correlate with structural

160 differentiation of chromosomes: Chapman and Burke (2007), Buggs *et al.* (2008) and

161 Paun *et al.* (2009). Chapman and Burke (2007) provided the first study that directly

162 compares the genetic distance between the parental species of homoploid and polyploid

163 hybrid species. They calculated Kimura's two-parameter (K2P) genetic distance between

164 DNA sequences from the internal transcribed spacer (ITS) region of nuclear ribosomal

165 RNA genes of 12 species pairs that have given rise to homoploid hybrid species and 26

166 species pairs that have given rise to allopolyploid species. They compared all hybrid

167 versus allopolyploid parental pairs and found a significantly larger divergence between

168 the parents of allopolyploids. They concluded that "the extent of evolutionary divergence

169 between hybridizing taxa plays an important role in determining the outcome of hybrid

170 speciation" (p. 1778).

171

172 Buggs *et al.* (2008) tested the hypothesis that closely related parents are less likely to

173 form a successful polyploid than more divergent parents. They examined molecular

174 phylogenies of eight genera that contain polyploids, using node-based and clade-based

175 methods of calculating the phylogenetic distance between parental pairs. They compared

176 these with expected divergences based on the null hypothesis that hybridization would

177 occur successfully at random between all species of a genus. They found that the

178 phylogenetic divergence between parents of polyploids was not significantly different

179 from the divergence expected under the null hypothesis. The same analysis on homoploid

180 hybrids in the same genera found a lower divergence between the parents of homoploid

181 hybrids than the null expectation, even when unstable hybrids were included. They

182 concluded that "contrasting patterns of divergence between the parents of polyploids and

183 homoploid hybrids are…determined by the restriction of homoploid hybrid formation to

184 low parental divergence, rather than the restriction of polyploid formation to high

185 parental divergence" (p. 87).

186

187 Paun *et al.* (2009) conducted an additional analysis that combined and improved some of

188 the approaches of Chapman and Burke (2007) and Buggs *et al.* (2008). For 16 homoploid

189 hybrids and 32 allopolyploids, they calculated uncorrected p-distances and K2P distances

190 between parental pairs using nuclear and/or chloroplast sequences. They converted each

191 of these distances to a genetic divergence index (GDI) by dividing parental divergence by

192 the average genetic distance between all pairs in each genus based on the same molecular

193 markers. The GDI gave very similar results for both distance measures, and parents of

194 polyploids were found to be significantly more divergent than parents of hybrids (Figure

195 1). Fitting a heuristic model to their data, Paun *et al.* (2009) suggested that at a GDI of

196 around 0.75, there is an equal probability of a hybrid being homoploid or allopolyploid,

197   but above this point, allopolyploidy is more likely, and below this, homoploidy is more

198   likely. They concluded that "parental divergence drives ploidy".

199

200   Although Paun *et al.* (2009) calculated the average divergence between all species pairs

201   in each genus, they did not use this as a null hypothesis for the expected divergence

202   between parents of allopolyploids as in Buggs *et al.* (2008). If we carry out a two-tailed

203   paired *t*-test on the genetic distances between parental pairs and the average genetic

204   distance between all species pairs in their respective genera, using the data from Table S1

205   of Paun *et al.* (2009), we find a significant difference between these values for homoploid

206   hybrids ($t = 3.427$, d.f. $= 15$, $P < 0.01$), but no significant difference for allopolyploids (t

207    $= 1.533$, d.f. $= 31$, $P > 0.1$). A Wilcoxon matched-pairs signed-ranks test gives similar P

208   values. Significantly, this result agrees with that of Buggs *et al.* (2008): homoploid hybrid

209   formation occurs at low parental divergence, but polyploid formation fits a model of

210   random hybridization.

211

212   **Null models and sampling issues**

213

214   The three studies summarized above therefore provide the same general pattern of results,

215   despite differences in methodology and sampling. They allow us to predict that wide

216   hybridization has a higher probability of producing a successful species if followed by

217   genome doubling. The authors of the three studies disagree over whether or not the

218   results constitute good evidence for high parental divergence driving ploidy. This

219   difference is partly due to the use of different null hypotheses. By basing their

220   conclusions on comparisons between homoploid hybrids and allopolyploids, Chapman

221   and Burke (2007) and Paun *et al.* (2009) seem to view the parental divergence of

222   homoploid hybrids as a null hypothesis of the distribution expected of allopolyploids

223   without the action of drive. This is problematic for two reasons. First, homoploid hybrids

224   are likely to be restricted in the parental divergences under which they can form. Second,

225   polyploid and hybrid species may not be comparable: while polyploid species typically

226   have post-zygotic reproductive isolation from their parents, homoploid hybrids are likely

227   to be more interfertile with their parents than the parents are with each other. Most

228   homoploid hybrid species, such as *Helianthus anomalus, H. deserticola, and H.*

229   *paradoxus* (Rieseberg 2003), are introgressed ecological forms that survive in habitats

230   unused by the parental species and are not clearly able to coexist with their parents due to

231   a lack of post-zygotic isolation (Rieseberg 1997).

232

233   Buggs *et al.* (2008) view random hybridization as a better null model than homoploid

234   hybrid species formation as the former assumes that parental divergence has no *a priori*

235   influence on the probability of allopolyploidization. This random hybrid formation model

236   is likely to be overly simplistic, as acknowledged by Buggs *et al.* (2008), but fits the data

237   well. Sang *et al.* (2004) suggested a model for the origin of tetraploids as a function of

238   genomic divergence between diploid progenitors, but as they suggest, this needs to be

239   made more mathematically rigorous, with better natural population estimates of the rates

240   of hybridization, unreduced gamete formation, and establishment of the resulting

241   lineages. It seems, for example, that wide hybridization may increase rates of unreduced

242   gamete formation (see above) but, as Ramsey and Schemske (1998) argue, this rise in

243 mutation rate is likely to be at least cancelled out by low hybridization rates and may

244 therefore not increase the frequency of allopolyploids at high parental divergences.

245

246 Our ability to draw firm conclusions is also restricted by sampling limitations. Chapman

247 and Burke (2007), Buggs *et al.* (2008) and Paun *et al.* (2009) agree that improved

248 sampling is needed of homoploid hybrids, which are very difficult to detect and may in

249 fact be quite rare in nature. We suggest that the lack of allopolyploids between closely

250 related species (Figure 1) may also be due to sampling bias as these may also be hard to

251 detect (Rieseberg & Willis 2007); for example, a recently discovered allotetraploid

252 formed by interspecific hybridization between *Mimulus nasutus* and *M. guttatus* was

253 identified as the former species until it gave anomalous results in a crossing experiment

254 (Sweigart *et al.* 2008). There is an urgent need for thorough molecular analysis of many

255 additional hybridizing plant groups, particularly those genera containing hybrids as well

256 as polyploids, such as the genera *Crepis, Clarkia*, *Betula*, and *Gilia*.

257

258 The authors of the three studies disagree about the relevance of autopolyploids (defined

259 here as polyploids formed within a species) to the issue of parental divergence and

260 whole-genome duplication. We have long recognized that there is a continuum from true

261 autopolyploid to allopolyploid, with "hybrid autopolyploid" and "segmental

262 allopolyploid" as intermediate points in this continuum (Stebbins 1950). In a restriction

263 that appears to stem from the use of homoploid hybrids as a null model, Paun *et al.*

264 (2009) argue that autopolyploids should not be included in the analysis as they do not

265 directly correspond to hybrid speciation processes at the diploid level. In contrast, Buggs

266 *et al.* (2008) argue that the hypothesis that parental divergence drives polyploidy cannot

267 be tested fully without including divergences at or close to zero (e.g., autopolyploids).

268

269 These issues regarding the comparability of autopolyploids, allopolyploids and

270 homoploid hybrids are part of the broader problem of defining species. Classing two

271 groups as "species" seems to imply that they are comparable evolutionary units, but due

272 to the use of different species concepts and types of information, the classification of

273 certain groups as species is not standardized and somewhat arbitrary. Autopolyploids

274 seem to occur very frequently in nature (e.g. Ramsey & Schemske 1998; Soltis & Soltis

275 1993) but are rarely classified as separate species (Soltis *et al.* 2007), despite sometimes

276 strong reproductive isolation from their parents. Reliance upon named species as a unit of

277 comparison in surveys therefore introduces a strong bias against successful

278 autopolyploidization events, whose frequent occurrence in nature certainly contradicts the

279 idea that whole-genome duplication is less likely at low parental divergence. Likewise,

280 with homoploid hybrids, the division between a recurrent unstable hybrid and a hybrid

281 species is not straightforward.

282

283 If in our sampling of polyploids we were able to count all polyploidization events that

284 have led to an established population (whether classified by taxonomists as a species or

285 not), it is possible that the number of events would be highest for closely related parents

286 and actually decline with parental divergence. This distribution would directly contradict

287 the idea that parental divergence drives polyploidy, and would also contrast with the

288   random pattern of allopolyploid species formation in relation to parental divergence

289   noted by Buggs *et al.* (2008) in their survey and shown here in that of Paun *et al.* (2009).

290   Paun *et al.* (2009) make the interesting suggestion that inclusion of autopolyploids would

291   cause a bimodal distribution of polyploid frequency in relation to parental divergence,

292   indicating the presence of different phenomena. Whilst such a distribution could be an

293   artifact of the lack of detection of polyploids of intermediate parental divergence (i.e.

294   allopolyploids with closely related parents; see above), it might also be explained by

295   selection. For an unoccupied fitness peak that is close to an occupied peak to be filled by

296   a new variant, that variant must be reproductively isolated. Polyploidy typically confers

297   reproductive isolation from its parents at both low and high parental divergences; in

298   contrast, a homoploid hybrid is likely to occur and be reproductively isolated from its

299   parents only at intermediate parental divergences (i.e. low enough for the hybrids to be

300   viable but high enough for the hybrid to be isolated from both parents). Because

301   homoploid hybrids often come into existence before an allopolyploid forms (following

302   the Class 2 mode of allopolyploidization; Harlan & De Wet 1975), there will not be

303   strong selection for polyploidy at intermediate divergences, unless the new polyploid

304   would occupy a different adaptive peak from that of the extant homoploid hybrid.

305

306   **Conclusion**

307

308   In our view, the idea that parental divergence drives polyploidy is based on two factors.

309   The first is an over-emphasis on potential bias in mutational mechanisms (e.g., unreduced

310   gamete formation) without sufficient consideration of subsequent selection on the newly

311   formed hybrid or polyploid. The second is misinterpretation of survey data due to

312   problems in sampling (particularly the omission of autopolyploids) and null model

313   selection. The three recent studies reviewed here of the relationship between parental

314   divergence and hybrid speciation (Buggs *et al.* 2008; Chapman & Burke 2007; Paun *et al.*

315   2009) do not provide convincing evidence that polyploid species are less likely to form

316   successfully at lower parental divergences and therefore do not demonstrate that parental

317   divergence drives ecologically successful whole-genome duplication. Instead, they

318   simply allow us to predict that wide hybridization has a higher probability of producing a

319   successful species if followed by polyploidization.

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321

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391   **Figure Legend**

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393

394   **Figure 1.** Genetic divergence between parents of allopolyploid species versus

395   those of homoploid hybrid species, re-plotted from Paun *et al.* (2009). The

396   genetic divergence index on the horizontal axis is the uncorrected p-distance

397   between the two species, divided by the mean p-distance of all species pairs in

398   their genus. Two species pairs that give rise to both a homoploid hybrid species

399   and an allopolyploid species were included in both counts. A two-tailed paired *t*-

400   test on the genetic distances between parental pairs and the average genetic

401   distance between all species pairs in their respective genera, shows a significant

402   difference between these values for homoploid hybrids ($t = 3.427$, d.f. = 15, $P <$

403   0.01), but no significant difference for allopolyploids ($t = 1.533$, d.f. = 31, $P > 0.1$).

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405

406   **Figure 1**

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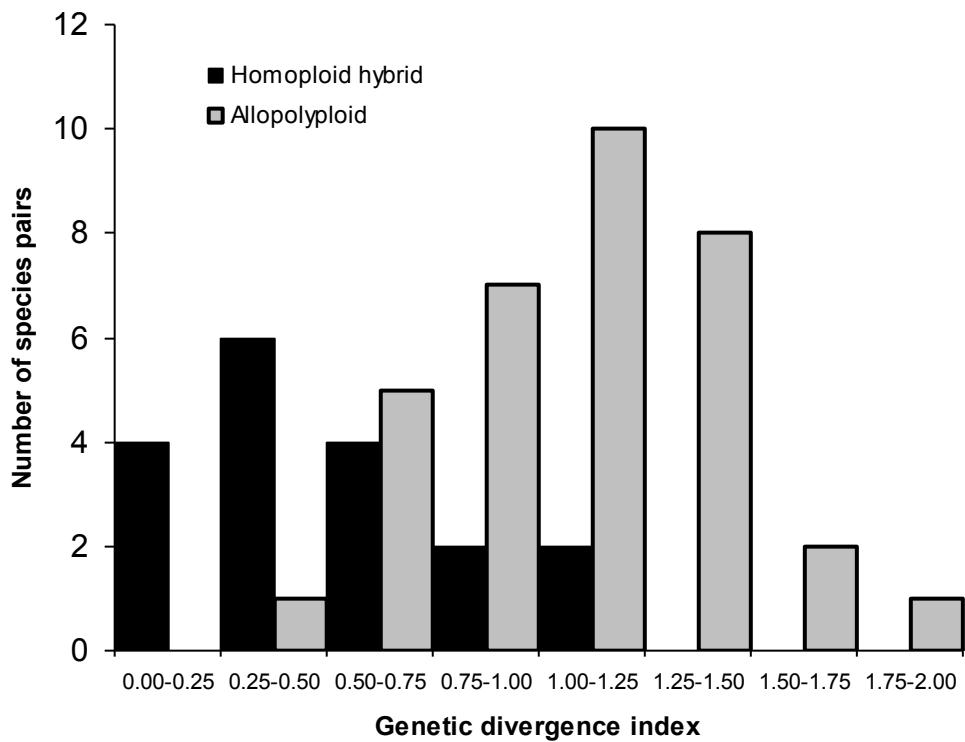
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417

Author descriptions

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Richard Buggs uses molecular genetic and bioinformatics approaches to study duplicate

gene evolution in recent *Tragopogon* allopolyploids.

Pamela Soltis' research interests include: plant phylogenetics, polyploidy, gene family

evolution, phylogeography and conservation genetics.

Doug Soltis is interested in angiosperm phylogeny, genome doubling, floral

developmental genetics, phylogeography and molecular cytogenetics.

426