1 The role of hybrid seed inviability in angiosperm speciation

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44 *Abstract*
45 Understanding which reproductive barriers contribute to speciation is essential to

46 understanding the diversity of life on earth. Several contemporary examples of strong hybrid

47 seed inviability (HSI) between recently diverged species suggest that HSI may play a

48 fundamental role in plant speciation. Yet, a broader synthesis of HSI is needed to clarify its

49 role in diversification. Here, I review the incidence and evolution of HSI. HSI is common and

50 evolves rapidly, suggesting that it may play an important role early in speciation. The

51 developmental mechanisms that underlie HSI involve similar developmental trajectories in

52 endosperm, even between evolutionarily deeply diverged incidents of HSI. HSI is often

53 accompanied by whole-scale gene misexpression in hybrid endosperm, including

54 misexpression of imprinted genes which have a key role in endosperm development. I explore

55 how an evolutionary perspective can clarify the repeated and rapid evolution of HSI. In

56 particular, I evaluate the evidence for conflict between maternal and paternal interests in

57 resource allocation to offspring (i.e. parental conflict). I highlight that parental conflict theory

58 generates explicit predictions regarding the expected hybrid phenotypes and genes responsible

59 for HSI. While much phenotypic evidence supports a role of parental conflict in the evolution

60 of HSI, an understanding of the underlying molecular mechanisms of this barrier is essential to

61 test parental conflict theory. Lastly, I explore what factors may influence the strength of

62 parental conflict in natural plant populations as an explanation for why rates of HSI may differ

63 between plant groups and the consequences of strong HSI in secondary contact.

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Introduction

Evaluating which reproductive barriers contribute to the origin and maintenance of species is foundational to speciation research. The exceptional floral diversity and prevalence of local adaptation in angiosperms has inspired plant biologists to argue for a primary role of extrinsic prezygotic barriers such as immigrant inviability or pollinator isolation (Ramsey et al., 2003; Lowry et al., 2008; Kay and Sargent, 2009; Sobel, 2014; Todesco et al., 2020; Wessinger, 2021; Christie et al., 2022). Undoubtedly, these barriers played a crucial role in the diversification of the ~300,000 extant angiosperms (Christenhusz and Byng, 2016). Yet, other angiosperm key innovations likely contributed to their diversity (Sanderson and Donoghue, 1994). Here, I argue that the evolution of the endosperm has contributed to angiosperm diversification via its contribution to a common, rapidly evolving, and strong intrinsic postzygotic reproductive barrier− hybrid seed inviability (HSI).

Endosperm is a nutritive tissue essential for embryo development unique to angiosperms (Baroux et al., 2002). Endosperm is initiated after fertilisation of the central cell and usually has a composition of 2:1 maternal:paternal genomes (though see (Williams and Friedman, 2002)). This 2:1 ratio is crucial for endosperm development, as many genes expressed therein are imprinted (i.e. their expression is parent of origin biased). The balance of maternally- and paternally-expressed genes (i.e. MEGs and PEGs) mediates typical endosperm development (Spillane et al., 2000; Köhler et al., 2003a; b, 2005; Tiwari et al., 2010; Batista et al., 2019). In interploidy crosses, an excess of maternal or paternal expression results in canonical parent of origin specific developmental abnormalities (Lin, 1984; Ehlenfeldt and Ortiz, 1995; Scott et al., 1998). Typical development can be restored by modifying imprinted gene expression (Erilova et al., 2009; Jullien and Berger, 2010; Kradolfer et al., 2013; Wolff et al., 2015), highlighting the importance of imprinting in endosperm development.

96   The endosperm's role as a nutritive conduit makes it a prime target for conflict between

97   ovule- and pollen-parents over resource allocation to offspring (Haig and Westoby, 1989;

98   Moore and Haig, 1991). Parental conflict arises in non-monogamous systems because pollen

99   parents are not equally related to all of the offspring produced, thereby favouring the evolution

100   of paternally-derived alleles that preferentially solicit maternal resources (Trivers, 1974;

101   Charnov, 1979; Queller, 1983; Haig and Westoby, 1989). In response, maternally-derived

102   alleles that restrict resource allocation to offspring can evolve, and a co-evolutionary arms race

103   between paternally-excessive and maternally-repressive alleles can ensue. Within populations,

104   ovule- and pollen-parents should be well matched, but populations can differentially

105   experience this arms race (Haig, 1997; Wilkins and Haig, 2001; Van Cleve and Feldman, 2007;

106   Brandvain, 2010; Brandvain and Haig, 2018). Crosses between populations with different

107   histories of conflict can reveal such mismatches, resulting in parent of origin growth effects

108   (Lloyd, 1968; House et al., 2010; Willi, 2013; Cailleau et al., 2018; Raunsgard et al., 2018).

109   Mismatches can also lead to dysfunctional endosperm and inviability. Given this rapid

110   evolution, HSI may play an important role early in speciation (Zeh and Zeh, 2000; Gutierrez-

111   Marcos et al., 2003).

112   Differences in the extent of parental conflict between taxa have been conceptualised

113   with endosperm balance numbers (i.e. effective ploidy; (Johnston and Hanneman, 1980, 1982;

114   Lin, 1984)). Inspired by the observation that interploidy and interspecific HSI exhibit similar

115   phenotypes, endosperm balance number is a relative ranking of taxa based on crossing

116   outcomes when each taxon acts as an ovule- or pollen-parent, where higher effective ploidy

117   taxa mimic higher ploidy taxa (Johnston and Hanneman, 1980, 1982; Lin, 1984; Städler et al.,

118   2021). Despite phenotypic parallels, the underlying genetic basis of inviability likely differs

119   between interploidy and interspecific HSI, as HSI is instantaneous with polyploidization and

120   requires no allelic evolution (Scott et al., 1998). Conversely, interspecific HSI must be caused

121   by divergence of genes with parent of origin effects. Thus, while both types of HSI can

122   elucidate if/how parental conflict manifests in seeds, interspecific HSI can reveal if/how

123   parental conflict shapes allelic evolution. Yet, much less is known about the incidence, pace,

124   and mechanisms underlying interspecific HSI.

125   Here I review HSI among diploid taxa and assess its commonality and evolutionary

126   rate. I synthesise current knowledge of the genetic and developmental bases of interspecific

127   HSI, and discuss whether they support a role of parental conflict. Lastly, I consider why HSI

128   might evolve more readily in some plant groups, and its implications for secondary contact.

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130   *HSI is a significant reproductive barrier*

131   HSI arises when heterospecific pollen fertilises an ovule of another species, but the hybrid seed

132   does not reach maturation, usually due to defective endosperm. Many incidences of HSI were

133   described in both crops and natural systems in the twentieth century (Table 1). Often,

134   reproductive isolation was complete in at least one cross direction. While these classic studies

135   highlight the commonality of HSI, only more recently have we begun to understand its

136   evolutionary pace.

137   At the most extreme end, incomplete HSI between *Clarkia xantiana* subspecies has

138   evolved in 65KYA (Briscoe Runquist et al., 2014) and strong, asymmetric HSI between selfing

139   and outcrossing populations of *A. lyrata* evolved in 35KYA (İltaş et al., 2021). In many cases,

140   strong HSI evolves in hundreds of thousands of years to ~1-2MYA (Table 1). This is much

141   faster than hybrid inviability in organisms like *Drosophila,* frogs, *Lepidoptera,* birds, and fish

142   which often take >>1MYA (Coyne and Orr, 1997; Sasa et al., 1998; Presgraves, 2002; Price

143   and Bouvier, 2002; Bolnick and Near, 2005). Similarly, in orchids, which lack endosperm, HSI

144   evolves later than hybrid sterility or necrosis (Scopece et al., 2007, 2008). Despite these

145   intriguing patterns, formal comparisons between endosperm-bearing angiosperms and other

146   lineages are needed.

147   Work in *Mimulus, Streptanthus,* and Solanaceae indicate that HSI can evolve rapidly,

148   and in some cases faster than postmating-prezygotic isolation (Fig. 1; (Vickery, 1964; Jewell

149   et al., 2012; Garner et al., 2016; Oneal et al., 2016; Kostyun and Moyle, 2017; Christie and

150   Strauss, 2018; Roth et al., 2018a; Coughlan et al., 2020; Sandstedt et al., 2020)). In *Mimulus*

151   nearly complete HSI has been found between lineages of *M. decorus*, which diverged

152   ~150KYA, and within the *M. tilingii* complex, which diverged ~400KYA (Sandstedt et al.,

153   2020), but, no incidence of complete postmating-prezygotic isolation is reported for this group.

154   In *Streptanthus* and *Jaltomata*, the earliest complete HSI is found at ~2.5MYA and 1.1MYA,

155   respectively (Fig. 1). For *Streptanthus*, the earliest incidence of complete postmating-

156   prezygotic isolation is similar to that of complete HSI, but HSI is generally a stronger barrier

157   (mean fruit set RI=0.43, mean HSI RI=0.81 (Christie and Strauss, 2018)). Within the

158   Solanaceae, seed set evolves more slowly than HSI (*Jaltomata* (Kostyun and Moyle, 2017),

159   *Nolana* (Jewell et al., 2012), and three pairwise crosses within *Solanum* (Roth et al., 2018a)).

160   However, other incidences of strong postmating-prezygotic isolation occur in *Solanum* (Baek

161   et al., 2015, 2016)), and many species pairs within *Jaltomata* and *Nolana* are unable to form

162   fruits due to pollen-pistil incompatibilities (Jewell et al., 2012; Kostyun and Moyle, 2017),

163   suggesting that postmating-prezygotic barriers evolve rapidly in the Solanaceae. In total, HSI

164   is common, evolves rapidly, and can confer significant reproductive isolation. Given that HSI

165   manifests in the first generation of hybridization, it may serve as a formidable reproductive

166   barrier.

167

168   *HSI is borne in the endosperm*

169 Like interploidy crosses, interspecific HSI is conferred by parent of origin specific endosperm

170 defects (Ishikawa et al., 2011; Rebernig et al., 2015; Baek et al., 2016; Oneal et al., 2016;

171 Lafon-Placette et al., 2017; Roth et al., 2018a; Coughlan et al., 2020; İltaş et al., 2021;

172 Sandstedt and Sweigart, 2022). A causal link between inappropriate endosperm development

173 and inviability is evidenced by embryo rescue experiments, where dissected embryos are plated

174 on a nutritive medium akin to a synthetic endosperm. Often, dissected embryos develop into

175 healthy plants, suggesting that incompatibilities in the endosperm, rather than embryo, cause

176 HSI (Sukno et al., 1999; Rodrangboon et al., 2002; Rebernig et al., 2015; Lafon-Placette et al.,

177 2017, 2018; Sandstedt and Sweigart, 2022).

178   Parent of origin specific endosperm defects are remarkably similar across incidences of

179 HSI, even between highly diverged taxa with different endosperm developmental programs. In

180 one direction of the cross seeds are larger, though flat or disc-like. In these crosses, endosperm

181 fails to cellularize in taxa with nuclear-type endosperm (Ishikawa et al., 2011; Rebernig et al.,

182 2015; Lafon-Placette et al., 2017, 2018; İltaş et al., 2021), or cells become overly large and fail

183 to divide in taxa with cellular-type endosperm (Roth et al., 2018a; Coughlan et al., 2020;

184 Sandstedt and Sweigart, 2022). This delayed development results in diffuse endosperm,

185 arrested embryos, and seed collapse, reminiscent of paternal-excess interploidy crosses. The

186 reciprocal cross resembles maternal-excess interploidy crosses; seeds are smaller, narrower

187 and/or shrivelled (Ishikawa et al., 2011; Rebernig et al., 2015; Lafon-Placette et al., 2017, 2018;

188 Roth et al., 2018a; Coughlan et al., 2020; İltaş et al., 2021; Sandstedt and Sweigart, 2022).

189 Endosperm proliferation is precocious; for taxa with nuclear-type endosperm, endosperm

190 cellularizes prematurely (Rebernig et al., 2015; Lafon-Placette et al., 2017). For taxa with

191 cellular-type endosperm, development is accelerated (Roth et al., 2018a; Coughlan et al., 2020;

192 Sandstedt and Sweigart, 2022). The resultant endosperm is smaller, with fewer cells than pure-

193 species crosses in both cases. These parallel developmental phenotypes among divergent

194   incidences of HSI and developmental systems hint at a shared evolutionary explanation, and

195   the parent of origin effects that mimic excess paternal or maternal expression support parental

196   conflict.

197   Finer scale patterns of endosperm dysregulation offer unique insights into the

198   mechanistic causes and evolutionary drivers of HSI. Successful seed development requires

199   coordination of endosperm, embryo, and maternal integuments, facilitated by a dynamic

200   exchange of nutrients, hormones, and other signals (Doll and Ingram, 2022; Povilus and

201   Gehring, 2022). Endosperm itself is a complex tissue, with many specialised components.

202   Under parental conflict, tissues that mediate nutrient exchange should exhibit paternal-excess

203   or maternal-repression phenotypes. In the endosperm, chalazal haustoria directly facilitate

204   nutrient exchange between maternal tissues and embryos (Povilus and Gehring, 2022). The

205   chalazal haustorium is also involved in regulating cellularization in taxa with nuclear-type

206   endosperm via *TERMINAL FLOWER 1* (*TF1*) expression (Zhang et al., 2020). Cellularization

207   signals a transition from a phase of endosperm growth and sucrose deposition by the maternal

208   plant to one of endosperm consumption by the embryo (Doll and Ingram, 2022). Lastly, the

209   chalazal haustorium is a hotspot for imprinted gene expression (Walia et al., 2009; Picard et

210   al., 2021), and genes that are uniquely expressed therein show elevated rates of adaptive

211   evolution (Geist et al., 2019). Together, this makes it an ideal target for parental conflict. In

212   *Mimulus,* chalazal haustoria persist later in development in paternal-excess hybrids than pure

213   species or maternal-excess hybrids (Sandstedt and Sweigart, 2022). Similar abnormalities have

214   been described in other systems (Brink and Cooper, 1947). Although it's well established that

215   HSI is borne in the endosperm, a mechanistic understanding of embryo-endosperm-maternal

216   integument communication during development is required to understand how these

217   relationships fail in HSI.

218

219 *Genetic of HSI*

220 Parental conflict predicts that lineages with different effective ploidies have diverged in

221 imprinted loci involved in resource partitioning and subsequent mismatches of these MEGs

222 and PEGs leads to parent of origin endosperm abnormalities and inviability. It follows that if

223 parental conflict were driving the evolution of HSI 1) taxa with different effective ploidies

224 should exhibit signals of adaptive divergence in imprinting, 2) hybrids should exhibit abnormal

225 expression of loci that are imprinted in at least one parental species, and 3) the loci that cause

226 HSI should correspond to a subset of the loci in 1 and 2. However, many particulars of this

227 model remain unanswered, and an integration of expression surveys, population genetics, and

228 genetic mapping is required.

229 Imprinting can evolve rapidly. Conservation of imprinted loci is generally low,

230 suggesting rapid turnover (Zhang et al., 2011; Waters et al., 2013; Hatorangan et al., 2016;

231 Klosinska et al., 2016; Chen et al., 2018; Flores-Vergara et al., 2020; Picard and Gehring,

232 2020). In *Capsella,* species generally exhibit more PEGs than MEGs, with the number of PEGs

233 and the expression of MEGs scaling with effective ploidy, suggests that compensatory

234 expression of MEGs may effectively balance PEG expression (Fig. 2; (Lafon-Placette et al.,

235 2018)). In *Solanum*, species exhibit more MEGs than PEGs, and the number of each scales

236 with effective ploidy (Florez-Rueda et al., 2016; Roth et al., 2018b, 2019). Lastly, imprinted

237 genes, particularly PEGs, show some signs of adaptive evolution (Hatorangan et al., 2016;

238 Tuteja et al., 2019).

239 Of the few studies that have quantified expression in hybrid endosperm, misexpression

240 is rampant. In *Capsella,* hybrid endosperm misexpression resembles interploidy crosses for

241 both paternal- and maternal-excess crosses (Rebernig et al., 2015). In *Solanum*, inviable

242 hybrids show extensive expression differences from intraspecific crosses (Florez-Rueda et al.,

243 2016, 2021a; Roth et al., 2019). While all hybrids exhibit maternally biassed expression

244 (Florez-Rueda et al., 2016), MEGs and PEGs tend to be overexpressed in maternal- and

245 paternal-excess crosses, respectively (Roth et al., 2019). In both *Capsella* and *Solanum*

246 paternal-excess crosses overexpress several PEGs, including AGAMOUS-LIKE Type1

247 MADS-box (AGL) genes whose overexpression is implicated in both interploidy and

248 interspecific HSI in *Arabidopsis (Rebernig et al., 2015; Roth et al., 2019)*. Hybrids also exhibit

249 complex patterns of misexpression. In *Solanum*, reciprocal F1s show a deficit of sRNA

250 expression, which contributes to greater gene expression in hybrid than intraspecific

251 endosperm (Florez-Rueda et al., 2021a). In *Capsella*, paternal-excess hybrids show reduced

252 chromatin condensation and methylation, which may cause dysregulated gene expression,

253 particularly of *PHERES1* (*PHE1*) targets (Dziasek et al., 2021). *PHE1* is a master regulator of

254 PEGs (Batista et al., 2019). How much of endosperm misexpression is a cause versus

255 consequence of inviability remains unknown, but a fundamental role of overexpression of some

256 MEGs and PEGs is evidenced by the fact that induced polyploidization of the lower effective

257 ploidy taxa can restore seed viability (Lafon-Placette et al., 2017, 2018; Tonosaki et al., 2018;

258 Sandstedt and Sweigart, 2022).

259 Although much remains unknown about the genetic basis of HSI, genetic mapping and

260 inheritance patterns suggest that HSI is caused by many moderate-to-large, parent of origin

261 effect loci ((Rebernig et al., 2015; Garner et al., 2016; Lafon-Placette et al., 2017; Dziasek et

262 al., 2021); i.e. 18 QTL control HSI between *M. guttatus* and *M. tilingii,* each of which decreases

263 viability by 20-60% (Garner et al., 2016)). Explicit links between imprinted genes and HSI

264 have been made in *A. thaliana* and *A. arenosa,* wherein loss of function *PHE1*, *AGL90,* and

265 *AGL62* mutants partially restores seed viability (Josefsson et al., 2006; Walia et al., 2009).

266 Although not uniquely supportive of parental conflict, parental conflict does predict a

267 polygenic basis of HSI. This is because paternal-excess alleles instigate the arms race, while

268 the evolution of maternal-repressive alleles are compensatory. However, in most incidences of

269   asymmetric HSI, paternal-excess crosses are more lethal. Without multiple rounds of allelic

270   replacement, paternal-excess hybrids have the same genotype as the genotype formed with the

271   initial evolution of a paternal-excess allele (Fig. 2), presenting a similar evolutionary

272   conundrum as is faced by single locus underdominance. Other aspects of the genetic basis of

273   HSI remain unknown. For example, whether HSI is governed by derived-ancestral or derived-

274   derived incompatibilities can elucidate the evolutionary pace of lower effective ploidy taxa

275   (Fig. 2). Whether HSI is caused by recurrent evolution of new MEGs/ PEGs or compensatory

276   MEG/PEG expression can inform how these arms races function at a molecular level.

277

278   *Parental conflict and effective ploidy; WISO and beyond*

279   Why should taxa differ in effective ploidy? Parental conflict suggests that variance in paternity

280   creates competition among siblings for limited maternal resources, and thus paternally-derived

281   resource acquiring alleles can evolve (Queller, 1983; Haig and Westoby, 1989). This

282   observation has sparked the WISO (weaker-inbreeder/stronger-outbreeder) hypothesis, which

283   predicts that parental conflict should be stronger in outbreeding taxa than selfing ones.

284   Subsequently, HSI should be stronger between selfing and outcrossing lineages (Brandvain and

285   Haig, 2005). Much evidence supports WISO, including an excess of HSI between selfers and

286   outcrossers (Brandvain and Haig, 2005; Rebernig et al., 2015; Lafon-Placette and Köhler,

287   2016; İltaş et al., 2021), as well as stronger HSI between mating systems than within mating

288   systems for intraspecific crosses (i.e. (İltaş et al., 2021) versus (Willi, 2013; Hämälä et al.,

289   2017)). However, recent work has also highlighted that some taxonomic groups rapidly evolve

290   HSI with no corresponding mating system shift (Roth et al., 2018a; Coughlan et al., 2020).

291   Differences in demography or life history may influence the variance in paternity by

292   influencing levels of biparental inbreeding and relatedness within a fruit. Intuitively, these

293   differences may result in similar dynamics as those seen between selfers and outcrossers (i.e.

294   species with high levels of biparental inbreeding may behave similarly to selfers). However,

295   this hypothesis requires rigorous testing; including formal meta-analyses and theoretical

296   explorations.

297

298   *Conclusions and implications*

299   HSI may play a fundamental role in plant speciation. Yet, the importance of reproductive

300   barriers is measured by their primary role in the origin of species and their secondary role in

301   species maintenance. Despite the potentially potent role of HSI in species formation, its role in

302   species maintenance remains largely unexplored. Recent work in *Mimulus* suggests that

303   hybridization in the context of mixed paternity fruits (i.e. fruits containing both hybrids and

304   conspecific seeds), can mediate growth costs for conspecific seeds that develop alongside

305   hybrids with higher effective ploidy fathers (Coughlan, 2022), suggesting that HSI may confer

306   indirect costs in secondary contact. How these growth costs translate into selection coefficients

307   requires exploration. Secondly, much remains unknown about how introgression influences the

308   fate of HSI alleles. Whether these incompatibilities resist introgression and maintain species

309   boundaries, or whether one set of parental alleles will introgress into another (and if so, whether

310   this is determined by effective ploidy) remains unanswered. Lastly, earlier work proposed that

311   HSI may serve as a rare instance of reinforcement via a postzygotic barrier, particularly if it

312   prevented significant maternal investment (Grant, 1954; Coyne, 1974), but this idea is largely

313   untested. A growing appreciation for the generative role of HSI has revealed much about its

314   developmental and genetic bases and evolutionary drivers. Yet, much remains unknown about

315   this fruitful reproductive barrier.

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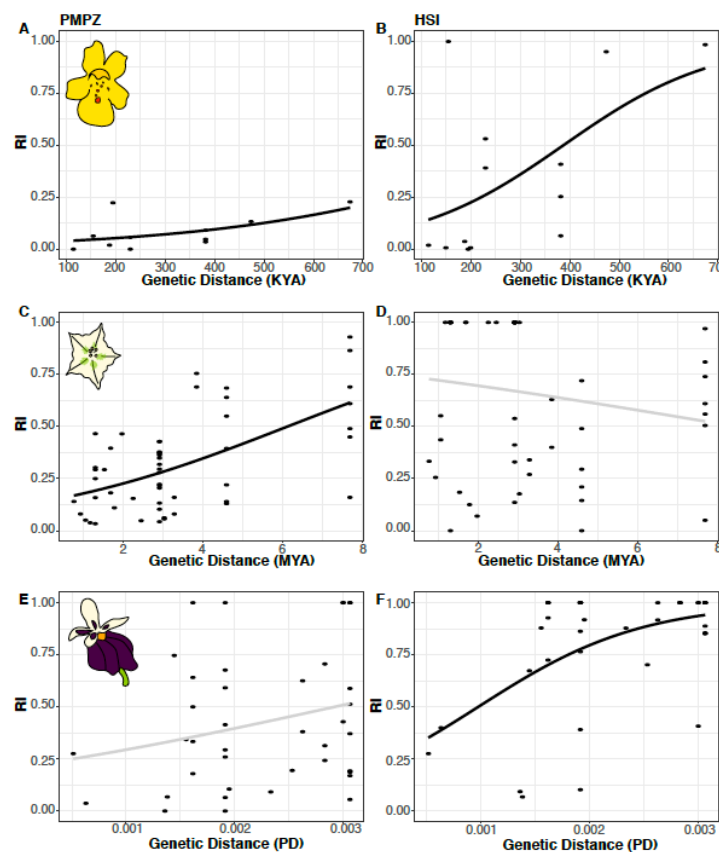
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787 ***Figure 1: Hybrid seed inviability can evolve rapidly.*** *The extent of premating-postzygotic*
788 *(PMPZ) isolation and hybrid seed inviability (HSI) as a function of divergence for three plant*
789 *groups; the* Mimulus guttatus *species complex, three genera within the Solanaceae, and the*
790 *genus* Streptanthus. *Data are fit with GLM with the following model: RI~Genetic Distance.*
791 *Significant relationships are indicated with a black line, while non-significant relationships*
792 *are indicated with grey. For* Mimulus *and the Solanaceae, PMPZ isolation is measured by*
793 *seed set per cross, for* Streptanthus *PMPZ is based on the ability to make a fruit. Data are*
794 *collated from:* Mimulus *crossing data: (Vickery, 1964; Garner et al., 2016; Oneal et al.,*
795 *2016; Coughlan et al., 2020; Sandstedt et al., 2020);* Mimulus *genetic data: (Brandvain et*
796 *al., 2014; Coughlan et al., 2020, 2021; Sandstedt et al., 2020), distances calculated using*
797 *(Brandvain et al., 2014); Solanaceae crossing data: (Jewell et al., 2012; Kostyun and Moyle,*
798 *2017; Roth et al., 2018a), Solanaceae divergence data: (Guerrero et al., 2013; Pease et al.,*
799 *2016; Wu et al., 2018); Streptanthus crossing and divergence data:(Christie and Strauss,*
800 *2018).*
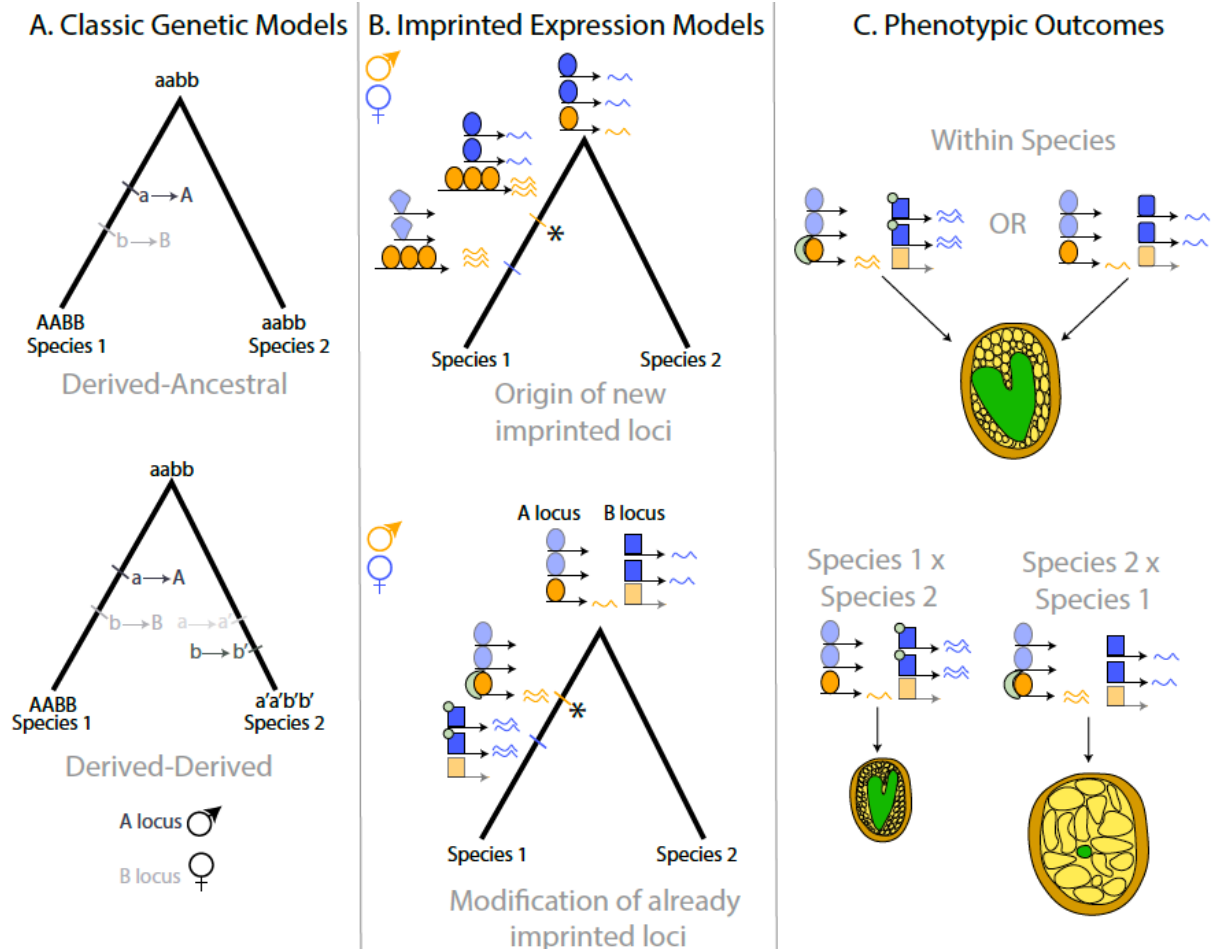
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802 *Figure 2: Genetic (A) and molecular models (B) underlying HSI highlight many*
803 *unanswered questions: (A) is HSI governed predominantly by substitutions in one or both*
804 *lineages (i.e. derived-ancestral vs derived-derived incompatibilities; top vs bottom panel*
805 *respectively)? (B) Does HSI evolve via recurrent evolution of new imprinted genes or*
806 *modified expression of pre-existing imprinted genes (or a combination)? The top panel*
807 *represents the evolution of a newly imprinted gene: increased expression of a paternally*
808 *derived allele (orange) selects for reduced maternal expression (blue) at a single locus,*
809 *resulting in a bi-parentally expressed gene becoming imprinted. The bottom panel depicts a*
810 *scenario where two genes are already imprinted. Increased expression of the PEG (orange)*
811 *selects for increased expression of a compensatory MEG (blue). Green shapes represent the*
812 *origin of new transcription factors or other molecular mechanisms of increasing gene*
813 *expression. While the (C) genotypes displayed in the phenotypic outcomes depict only a*
814 *single round of paternally-derived resource acquiring alleles and maternal-derived*
815 *compensatory alleles, multiple rounds of allelic substitution (either within one species, or in*
816 *both lineages) would have to occur for the Species 2 x Species 1 cross to be lethal, as the*
817 *genotype shown in the Species 2 x Species 1 cross is the same genotype that arises with the*
818 *origin of a paternally-derived, resource acquiring allele (denoted with a *).*

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824 ***Table 1: incidences of HSI in agricultural and natural plant systems.*** *Group= taxonomic*
825 *group, Type= endosperm type (cellular or nuclear), Strength= qualitative assessment of HSI*
826 *(many older papers provide only qualitative assessments), divergence= estimate of divergence*
827 *times for the taxonomic group. In some cases, the actual species have been genotyped and*
828 *estimates made, but for others the crown age of the taxonomic group is given with some*
829 *description of the species crossed. Ploidy= interspecific among diploids ('IS'), interploidy*
830 *('IP'), or several crosses involving both intra-diploid and interspecific crosses ('both'). Ref=*
831 *reference for HSI and divergence times ('div')*
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Group	Type	Strength	Divergence	Ploidy	Ref
Solanum sect. *Petota*	celluar	several instances; often complete or strongly asymmetric	crown age ~5.9-8.5MY; incidences between species ~3-4MY diverged	Both	(Johnston and Hanneman, 1980, 1982; Dinu et al., 2005); Div: (Särkinen et al., 2013; Fumia, 2021; Tang et al., 2022)
Solanum sect. *Lycopersicon*	celluar	several instances; often complete or strongly asymmetric	crown age ~1.2-2.6MY, incidences in species pairs <1MY diverged	Both	(Rick, 1963; Ehlenfeldt and Hanneman, 1992; Ehlenfeldt and Ortiz, 1995; Baek et al., 2016; Roth et al., 2018a; Florez-Rueda et al., 2021b)Div:(Särkinen et al., 2013; Pease et al., 2016)
Brassica	nuclear	several instances; often strong	earliest incidences between species ~2MY diverged	Both	(Nishiyama et al., 1991); Div: (Li et al., 2017)
Nicotiana	celluar	several instances; often complete or strongly asymmetric	crown age ~10-13MYA; few crosses made between recently diverged species	Both	(McCray, 1932; East, 1935; Cooper and Brink, 1940); Div (Clarkson et al., 2017; Wang et al., 2022)
Triticum	nuclear	strong HSI between *T. boeoticum* and *T. urartu*	~1MY divergd	Both	(Gill and Waines, 1978); Div (Huynh et al., 2019)
Aegilops	nuclear	strong HSI between *Ae. tauschii* (*Ae. squarrosa*) and *Ae. speltoides*	~3-4MY diverged	IS	(Gill and Waines, 1978); Div (Huynh et al., 2019)
Avena	nuclear	several strong and/or asymmetric incidences	strong HSI between different clades ~7-11MY diverged, younger pairs not tested	Both	(Nishiyama and Yabuno, 1978)Nishiyama and Yabuno 1978; Div (Liu et al., 2017; Fu, 2018)
Hordeum	nuclear	some incidences within sections, stronger incidences between sections	"sections" not monophyletic; crown age of group(s) with HSI is ~1-2MYA	Both	(von Bothmer and Jacobsen, 1986); Div (Brassac and Blattner, 2015)
Oryza	nuclear	several strong instances; strongly asymmetric	earliest incidence from species <500KY diverged	IS	(Chu and Oka, 1970; Ishikawa et al., 2011); Div (Stein et al., 2018)
Phaseolus	nuclear	two incidences, both strong and asymmetric	2-4 MY diverged	IS	(Shii et al., 1982; Geerts et al., 2002); Div (Delgado-Salinas et al., 2006)

Cucumis	nuclear	several incidences; some strong, few asymmetric	most incidences between *C. melo* and species in Sect. Sagittani, which split ~9.5MYA	Both	(John R. Deakin et al., 1971); Div (Endl et al., 2018)
Glycine	nuclear	multiple incidences, several strong/complete	multiple incidences between species ~2-4MY diverged	Both	(Singh et al., 1988; Chung and Kim, 1990; Zhang and Palmer, 1990); Div (Egan and Doyle, 2010; Sherman-Broyles et al., 2014)
Medicago	nuclear	several incidences, often strong/complete	earliest incidences are between species ~2MY diverged; crown age is 6-16MYA	Both	(Oldemeyer, 1956; Fridriksson and Bolton, 1963; McCoy and Smith, 1986; Veronesi et al., 1986); Div (de Sousa et al., 2016)
Trifolium	nuclear	multiple strong/complete incidences,	crown age for Trifolium is ~11.8-16MYA, but many sister taxa exhibit HSI	Both	(Chou and Gibson, 1968; Williams and White, 1976; Parrott and Smith, 1986; Abberton, 2007); Div (Ellison et al., 2006; Yan et al., 2022)
Datura	celluar	several highly asymmetric incidences	crown age ~15MYA, few crosses between recently diverged species	Both	(Sansome et al., 1942; Satina et al., 1950); Div (Dupin and Smith, 2018)
Helianthus	nuclear	most annual-perennial crosses fail, but can be partially restored with embryo rescue	~1.5-3.3MY diverged	IS	(Seiler and Rieseberg, 2015); Div (Mason, 2018)
Impatiens	cellular	most stronger incidences are interploidy	-	Both	(Arisumi, 1973, 1982)
Primula	nuclear	multiple strong incidences	~2-3MYA	Both	(Valentine and Woodell, 1960, 1963); Div (Li et al., 2016)
Mimulus	cellular	several instances; sometimes complete, occasionally asymmetric	earliest incidence of complete HSI is ~150KYA	Both	(Vickery, 1964; Garner et al., 2016; Oneal et al., 2016; Coughlan et al., 2020; Sandstedt et al., 2020; Kinser et al., 2022); Fig.1
Gilia	nuclear	several instances; often complete, occasionally asymmetric	several instances in <2MYA	IS	(Grant, 1954; Grant and Grant, 1954); Div (Landis et al., 2018)
Clarkia	nuclear	modest HSI between C. xantiana subsp.	65KY diverged	IS	(Davis, 1970; Briscoe Runquist et al., 2014)
Collinsia	cellular	several instances; rarely complete, often asymmetric	strong HSI between species 900KY diverged	IS	(Ahloowalia and Garber, 1961; Bell and Garber, 1961); Div Randle (unpublished)
Capsella	nuclear	strong asymmetric HSI between *C. grandiflora* and *C. rubella*; complete between each and *C. orientalis*	earliest incidence ~100KYA, oldest incidence ~1MYA	IS	(Rebernig et al., 2015; Lafon-Placette et al., 2018)

		several incidences; complete between A. arenosa and both A. thaliana and A. lyrata; variable/asymmetric within A. lyrata	earliest incidence ~35KYA; latest is ~3.8-5.8MYA		
Arabidopsis	nuclear	several incidences; complete between A. arenosa and both A. thaliana and A. lyrata; variable/asymmetric within A. lyrata	earliest incidence ~35KYA; latest is ~3.8-5.8MYA	Both	(Josefsson et al., 2006; Hämälä et al., 2017; Lafon-Placette et al., 2017; İltaş et al., 2021)
Lilium	nuclear	several instance (~3% of crosses yield viable seed)	some instances as early as ~500KYA	IS	(Dowrick and Brandram, 1970; Van Tuyl et al., 1988); Div (Gao et al., 2015)
Eucalyptus	nuclear	variable: up ~35% of crosses yield no viable seed	probability of producing a hybrid is <5% by 7MY	IS	(Drake, 1975; Larcombe et al., 2015)
Silene	nuclear	several strong incidences	crown age for section Elisanthe ~1.3MYA	IS	(Prentice, 1978); Div (Moiloa et al., 2021)
Streptanthus	nuclear	common and typically strong	earliest complete incidence ~2.5MYA	IS	(Christie and Strauss, 2018).
Jaltomata	cellular	several incidences, often strong, commonly asymmetric	earliest complete incidence ~1.1MYA	IS	(Kostyun and Moyle, 2017); Div (Wu et al., 2018)
Nolana	cellular	several moderate, asymmetric incidences	earliest complete incidence ~2.2MYA	IS	(Jewell et al., 2012); Div (Guerrero et al., 2013)
Lolium	nuclear	multiple, strong incidences	~4.5MY diverged	IS	(Jenkin, 1935, 1954a; b; c); Div (Inda et al., 2014)

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