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Autopolyploid establishment depends on life history strategy and the mating outcomes of clonal architecture

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35 **ABSTRACT**

36 Polyploidy is a significant component in the evolution of many taxa, particularly plant groups.
37 However, the mechanisms promoting or preventing initial polyploid establishment in natural
38 populations are often unclear. We develop spatially explicit agent-based simulation models to
39 explore how perennial life history and clonal propagation influence the early stages of polyploid
40 establishment. Our models show that polyploid establishment is unlikely among short-lived
41 plants. Polyploids have increased establishment probability when both diploid and polyploid
42 lifespans are long, especially when unreduced gamete production is non-zero. Further, polyploids
43 that combine sexual and clonal reproduction can establish across a wide range of life history
44 strategies. Polyploid genets containing many, far spreading ramets are most successful, but
45 genets with tightly clumped ramets have similar establishment probability when pollen dispersal
46 is local and rates of self-fertilization are high. Clonal architecture has a substantial impact on the
47 spatial structure of the mixed cytotype population during establishment; altering patterns of
48 mating within or between cytotypes, the mechanisms through which polyploid establishment
49 proceeds, and the final composition of the polyploid population after successful establishment.
50 Overall, our findings provide insight into the complex relationship between polyploidy,
51 perenniality, and clonal reproduction, and offer testable predictions for future empirical work.

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53

54

55 INTRODUCTION

56 Polyploidy has played a key role in the evolutionary history and diversification of plants (Wood
57 et al. 2009; Husband et al. 2013), and there is growing evidence that it is also common within
58 many animal clades (Otto and Whitton 2000). Polyploids arise through whole-genome
59 duplication (WGD) events resulting in more than two complete chromosome sets in an
60 individual, which may occur through the hybridization of two species (allopolyploidy) or within
61 a single species (autopolyploidy). Because a WGD event can result in instant reproductive
62 isolation and drastic phenotypic change between a polyploid and its progenitors (Baack et al.
63 2015), polyploidy is often viewed as one of the quintessential examples of sympatric speciation.
64 Indeed, approximately 15% and 30% of speciation events in angiosperms and ferns respectively
65 have been attributed to polyploidization (Wood et al. 2009). Though polyploidy is prevalent
66 throughout plants and the wider tree of life, many of the ecological and evolutionary mechanisms
67 leading to the establishment success or failure of newly formed polyploids in natural populations
68 are poorly understood (Husband 2000; Ramsey and Ramsey 2014; Soltis et al. 2016*b*).

69 The rate of polyploid formation surely exceeds the rate of successful establishment (Ramsey
70 and Schemske 2002), because rare polyploids experience significant fitness disadvantages when
71 they first arise in populations dominated by their lower-ploid parents (Husband 2000; Ramsey
72 and Schemske 2002). Here, the majority of the polyploid mating opportunities are intercytotype,
73 resulting in inviable odd-ploidy offspring and low fitness, and ultimately polyploid exclusion
74 from the population (Levin 1975). This process of Minority Cytotype Exclusion (MCE) is
75 expected to be a significant barrier to polyploid evolution (Thompson and Lumaret 1992;
76 Husband 2000; Fowler and Levin 2016), and in many ways is analogous to the challenges faced
77 by a mutant genotype invading a resident population with a lack of compatible mates, or as

78 individuals colonize new habitat (Baack 2005; Pannell et al. 2015). In general, polyploid
79 establishment is more probable when the effects of MCE are mitigated (Stebbins 1950), which
80 may occur through: 1) a shift in the balance of intra- vs. intercytotype mating, 2) a reduced
81 reliance on sexual reproduction, 3) high rates of polyploid formation, or 4) increased persistence
82 time.

83 The process of polyploid establishment and MCE are challenging to study empirically (e.g.,
84 Husband 2000; Sutherland et al. 2020), but previous theoretical treatments largely confirm that
85 polyploid establishment is facilitated by factors contributing to the four MCE-reducing processes
86 listed above. Studies have identified important roles for self-fertilization (Levin 1975; Rodríguez
87 1996; Rausch and Morgan 2005), local dispersal (Baack 2005), asexuality (Nakayama et al.
88 2002; Yamauchi et al. 2004; Spoelhof et al. 2020), elevated unreduced gamete (UG) production
89 (Felber and Bever 1997; Burton and Husband 2001; Husband 2004), and iteroparity (Rodríguez
90 1996). Most of these studies have explicitly represented plant systems and autopolyploidy (but
91 see Fowler and Levin 2016), but even within this framework there remain significant gaps in our
92 knowledge of the critical early period immediately following polyploid formation (Spoelhof et
93 al. 2017).

94 A perennial life history strategy and asexual reproduction through clonal propagation have
95 long been hypothesized to increase polyploid establishment success (Gustafsson 1948; Stebbins
96 1950; Rodríguez 1996; Chrtek et al. 2017), and both have the potential to reduce MCE via one or
97 more mechanisms. Perenniality (coupled with iteroparity) increases the persistence of a new
98 polyploid over several generations and the number of reproductive bouts during an individual's
99 lifetime, and should increase the likelihood of viable intracytotype mating via self-fertilization
100 (Gustafsson 1948; Otto and Whitton 2000; Rice et al. 2019). Additionally, perenniality and

101 longer polyploid lifespans may influence the probability that neopolyploid individuals
102 originating from different WGD events will overlap in time, increasing opportunities for
103 successful polyploid outcrossing.

104 Unlike perenniality, clonal reproduction directly contributes to polyploid fitness through the
105 production of clonal offspring. Clonal propagation decreases the probability of complete
106 polyploid exclusion, and increases the probability of intracytotype mating through
107 geitonogamous self-fertilization between shoots within a genetic clone (i.e., a genet, comprised
108 of numerous genetically-identical ramets; Vallejo-Marín et al. 2010). Since mating in plants
109 generally occurs between near neighbours, the placement and arrangement of ramets can
110 dramatically alter the sexual fitness of clonal plants by affecting pollen transport within and
111 between genets (Handel 1985; Vandepitte et al. 2013; Van Drunen et al. 2015). The potential for
112 geitonogamy to benefit an establishing polyploid is then inherently dependent on both population
113 spatial structure and clonal architecture. Dense genets with closely packed ramets (i.e., phalanx
114 architecture; Charpentier 2002; Vallejo-Marín et al. 2010) exhibit high rates of geitonogamous
115 self-fertilization and little outcrossing. If the costs of inbreeding are low (Husband et al. 2008), a
116 polyploid with a phalanx strategy can create its own local pocket of same-cytotype mates (Li et
117 al. 2004; Baack 2005). In contrast, sparse genets with widely dispersed ramets (i.e., guerrilla
118 architecture Charpentier 2002) should promote intermingling between different genets and
119 mating via outcrossing. A guerrilla architecture and a high capacity for lateral growth could
120 promote the spread of polyploids throughout a population (Van Drunen et al. 2015; Herben et al.
121 2017), and may be a better strategy if inbreeding depression is high. Thus, though either type of
122 clonal architecture could promote polyploid establishment, the pathway to establishment could
123 be fundamentally different between strategies. However, only a handful of polyploid

124 establishment models include spatial or population structure (Li et al. 2004; Baack 2005;
125 Spoelhof et al. 2020; Griswold 2021), and none have considered the effects of geitonogamy or
126 clonal architecture.

127 Evaluating the influence that perenniality or clonality have on polyploid establishment is
128 complicated by the correlations amongst these traits. At a broad scale, phylogenetic and
129 biogeographical studies have demonstrated a positive evolutionary association between
130 polyploidy and perenniality or clonality (Gustafsson 1948; Herben et al. 2017; Rice et al. 2019;
131 Van Drunen and Husband 2019), but these relationships may be confounded by the fact that all
132 clonal plants are perennial, and that the perennating organs of many plants are themselves clonal
133 modules (e.g., tillering grasses; Klimeš et al. 1997). Thus, the relative importance of perenniality
134 and clonality, and their potential interactions, during the initial stages of polyploid evolution are
135 not well-defined.

136 Successful polyploid establishment generally requires some difference between cytotypes
137 that conveys a benefit to the polyploids (Levin 1975), an idea corroborated by classic two-
138 species coexistence theory (reviewed in Barabás et al. 2018). Many models incorporate this
139 through niche shifts reducing competition between cytotypes (e.g., Rodríguez 1996), or by
140 directly setting polyploid fitness higher than that of diploids (e.g., Baack 2005). Relatively few
141 explicitly explore other phenotypic differences between cytotypes (but see Rausch and Morgan
142 2005; Chrtek et al. 2017; Griswold 2021), though in practice WGD can result in sweeping
143 changes to gene expression (Levin 2002; Soltis et al. 2016a), physiology (Maherali et al. 2009;
144 Anneberg and Segraves 2020), or morphology in new polyploids (Husband et al. 2016). WGD is
145 expected to produce bigger cells with long cell cycles, which should slow development, delay
146 maturity, and potentially increase lifespan (Bennett 1972; Levin 2002; Beaulieu et al. 2008;

147 Blomme et al. 2014), resulting in polyploids that are more perennial than diploids. The
148 immediate effects of WGD on clonal reproduction are less predictable. Newly synthesized
149 polyploids can be more or less clonal than diploids (Van Drunen and Husband 2018a, 2018b;
150 Walczyk and Hersch-Green 2019), and established polyploids also show a similarly variable
151 relationship with clonality (e.g., Hroudová and Zákřavský 1993; Keeler 2004; Baldwin and
152 Husband 2013). In any case, we may hypothesize that an increase in clonal reproduction will aid
153 polyploid establishment, while a decrease will almost certainly ensure failure for a polyploid
154 among highly clonal diploids.

155 Theory is a valuable tool in exploring the elusive early steps in polyploid evolution, and for
156 understanding how the traits implicated in these high-level patterns might causally influence key
157 individual- and population-level processes. Here, we explore the effects of perenniality and
158 clonal reproduction on the early stages of autopolyploid establishment using spatially explicit,
159 agent-based simulation models incorporating the complex dynamics between reproductive
160 strategy, perenniality, and population spatial structure. Specifically, we ask: 1) Does a perennial
161 life history increase polyploid establishment? 2) Does clonal reproduction increase polyploid
162 establishment? 3) How is polyploid establishment influenced by genet size and architecture? and
163 4) Do differences in life history or reproductive strategy between polyploids and diploids further
164 influence these processes?

165

166 **METHODS**

167 *MODEL OVERVIEW:*

168 Models were written in R v3.6.2 (R Development Core Team 2019), the full code is available
169 online (<https://github.com/wevandrunen/autopolyploid-establishment-lifecycles>-

170 [clonalarchitecture](#)). Simulations take place on a square population lattice measuring $D \times D$ units.
171 The population lattice exhibits periodic boundary conditions, such that pollen, seed, or clonal
172 ramets that disperse beyond the grid limits in one direction re-enter the population on the
173 opposite edge (i.e., the grid is toroidal). Individuals occupy all cells in the lattice, and population
174 size ($N = D \times D$) is constant over each generation. Models are initialized with $N - 1$ diploid
175 individuals, and a single tetraploid individual at a random location. The population then
176 undergoes a series of biological processes over a set number of time-steps, equivalent to growing
177 seasons or generations. For each generation, the sequence of events is: sexual and clonal
178 reproduction, survival, and offspring recruitment (fig. 1).

179 We make several assumptions about the equivalency of diploid vs. tetraploid individuals.
180 Cytotypes are equal competitors and occupy the same ecological niche, and diploids and
181 tetraploids have equal seed germination and ramet establishment probability. Finally, individual
182 fecundity and survival are not age related; individuals reproduce sexually and asexually
183 immediately upon recruitment into the population, have a fixed reproductive output per
184 generation, and have a constant probability of survival to the next generation over their lifetime.

185

186 *STEP 1 – REPRODUCTION:*

187 The first step in each generation is pollen dispersal and ovule fertilization (fig. 1). All individuals
188 are hermaphroditic and produce ov ovules per generation (fig. 1). Pollen production is unlimited
189 and no ovule is left unfertilized, but not all fertilizations will result in viable seed (see below).
190 Ovule fertilization proceeds by first determining the pollen density from each individual in the
191 population at the location of the ovule source, including pollen produced by the ovule source
192 itself. Pollen dispersal is described by Gamma distribution $P(x)$ (eq. [1]) with shape parameter β

193 set to 1, corresponding to leptokurtic pollen distribution (fig. S1A; figs. S1–S12 and table S1 are
194 available online) where pollen density is highest at the pollen source ($x = 0$).

$$195 \quad P(x), S(x) = \alpha^\beta x^{\beta-1} \frac{e^{-\alpha x}}{\Gamma(\beta)} \quad (1)$$

196 The rate parameter α is calculated as β/d_p , where d_p is the average pollen dispersal distance
197 (fig. 1). Due to the toroidal shape of the population grid, pollen from an individual could arrive at
198 a location through multiple routes, and we calculate pollen densities using the shortest distance
199 between the pollen donor and ovule source. The selected pollen donor for each ovule is chosen
200 by the weighted pollen probability density at the ovule location. All pollen is assumed to be
201 equally able to fertilize an ovule: there is no pollen precedence, female mate choice, or
202 performance differences between reduced (1n) and unreduced (2n) pollen.

203 The outcome of each mating event, and seed viability, is determined by the identity of the
204 gamete sources. A mating event may result in one of 22 cross-types, that fall into four categories
205 per cytotype: within shoot self-fertilization (autogamy), between ramet self-fertilization
206 (geitonogamy), intercytotype outcrossing, and intracytotype outcrossing (table S1). Rates of self-
207 fertilization vs. outcrossing are therefore emergent properties of the model, determined
208 intrinsically through pollen donor selection. Self-fertilized seeds are inviable with probability k_2
209 or k_4 and viable with probability $(1 - k_2)$ or $(1 - k_4)$, for diploids and tetraploids respectively
210 (table S1, fig. 1), which may be interpreted as early acting inbreeding depression. Diploids
211 produce unreduced gametes (2n) with probability ug , and reduced gametes (1n) with probability
212 $(1 - ug)$ (table S1, fig. 1). Tetraploids make only reduced gametes (2n), and the formation of
213 ploidy levels higher than tetraploid cannot occur. Intercytotype crosses, or intracytotype crosses
214 involving unreduced gametes, are viable only when the offspring is tetraploid, and triploidy is
215 assumed to be lethal (table S1). All seeds produced via intracytotype outcrossing with reduced

216 gametes are viable. After fertilization, all viable seeds are stored in a common pool for
217 recruitment into the next generation.

218 Individuals can produce a number of clonal ramets in each generation, c_2 for diploids, and c_4
219 for tetraploids (fig. 1). The c_2 and c_4 parameters are constant throughout a single model run,
220 though they may differ from each other. For some scenarios, c_2 and/or c_4 are zero, meaning no
221 ramets are produced by individuals of that cytotype and reproduction is entirely sexual. Ramets
222 are stored in the same offspring pool as the seeds for the recruitment step.

223

224 *STEP 2 – SURVIVAL:*

225 Diploid and tetraploid individuals within the population survive between generations with
226 probability sv_2 or sv_4 (fig. 1). For annual life histories these probabilities are zero. For perennials
227 an average of sv_2 diploid and sv_4 tetraploid individuals survive between generations, and the
228 remainder of the population, up to N , is supplemented by new recruits from the available
229 offspring pool.

230

231 *STEP 3 – RECRUITMENT:*

232 Offspring are recruited onto the sites newly vacated by deceased individuals, and may be either
233 sexually produced seedlings or clonal ramets. The recruitment process is similar to ovule
234 fertilization, where the probability of a recruit colonizing a vacant site is calculated as the seed or
235 ramet density at the site, dispersed from their source locations. Seed probabilities follow the
236 Gamma function $S(x)$ (eq. [1]), where β is set to 1 and the rate parameter α is β/d_s , where d_s is
237 the average seed dispersal distance (fig. 1). In contrast, ramet dispersal $C(x)$ is assumed to
238 conform to a bell-shaped Gaussian distribution (eq. [2], variance $\sigma^2 = 0.15$; fig. S1B) such that

239 peak probability density occurs at the mean ramet dispersal distance from the parental source
240 (d_{C2} or d_{C4} , fig. 1).

$$241 \quad C(x) = \frac{e^{-(x-d_c)^2/(2\sigma^2)}}{\sqrt{2\pi\sigma^2}} \quad (2)$$

242 Recruitment sites are filled in random order, and offspring are removed from the common
243 pool following successful recruitment. Since ramet probability density is formulated to be high
244 relative to seed density at $x \approx d_c$ from a source plant (fig. S1), clonal recruitment will occur much
245 more frequently at these distances than seed colonization, mirroring a biologically realistic
246 scenario where the competitive and establishment ability of ramets is higher than that of
247 seedlings (Vallejo-Marín et al. 2010). Centering ramet colonization at d_c results in higher ramet
248 density at a “spacer distance” away from the primary shoot and imposes strong spatial structure
249 on clonal genets (e.g., Winkler and Stöcklin 2002). After recruitment, seedlings are assigned new
250 unique genet IDs, while ramets retain the ID of their parent. Data on the survivors and new
251 cohort of individuals is passed to the next generation, and the reproduction step begins again.

252

253 *PARAMETERIZATION:*

254 There are 15 adjustable parameters in the model (fig. 1). Except where noted, simulations take
255 place on a square lattice with dimension $D = 30$ and a population of $N = 900$, which remains
256 constant across generations. Simulations begin with only one polyploid individual ($t = 1$). The
257 number of ovules produced per individual (ov) is five for both diploids and tetraploids, resulting
258 in 4500 seeds per generation for a population of $N = 900$. Under the most restrictive
259 circumstances for sexual reproduction (i.e., high selfed-seed inviability, limited pollen dispersal,
260 no unreduced gamete production, and similar cytotype frequencies), trials showed that at least
261 2000 viable seeds were produced per generation; enough to minimize the possibility of

262 anomalous long-distance dispersal events. Diploid individuals may produce unreduced gametes
263 (UGs) at frequency ug , and reduced gametes at frequency $1 - ug$ (table S1).

264 Two parameters affect the realized amount of self-fertilization: pollen dispersal distance (d_p)
265 alters the probability of self-pollination (autogamous or geitonogamous), and selfed-seed
266 inviability (k) alters the probability that self-fertilized offspring are included in the pool of viable
267 recruits (fig. 1, table S1). We focus on these two parameters because they are expected to be
268 influential on sexual fitness in clonal plants (Eckert 2000; Van Drunen et al. 2015), where
269 dispersal distance determines pollen kernel density (fig. S1), and regulates whether pollen is
270 likely to remain within a ramet, encounter other ramets in the same genet, or encounter ramets
271 from different genets. We test the effects of nine combinations of d_p and k (3×3) across different
272 model scenarios, hereafter referred to as the core dispersal-inviability parameter set. The three
273 core value for average pollen dispersal distance (d_p) were 0.5 grid units (pollen rarely exits the
274 source cell), 2 (local dispersal), and 5 (far dispersal) (figs. 1, S1). For simplicity, average seed
275 dispersal distances were assumed to mirror those of pollen ($d_p = d_s$), and are equal between
276 cytotypes for all simulations. The probability of selfed-seed inviability for diploids (k_2) and
277 tetraploids (k_4) took the values 0.1, 0.5, or 0.9 (fig. 1) and were equal in most scenarios, where
278 larger values indicate stronger inviability or inbreeding depression.

279 The remaining six parameters differentiate the life history and reproductive strategies of
280 diploid or tetraploid individuals: per generation survival (sv_2 and sv_4), clonal ramet production
281 (c_2 and c_4), and average ramet dispersal distance (d_{C2} and d_{C4}) (fig. 1). These parameters are
282 described in more detail in the following sections.

283

284 *LIFE HISTORY STRATEGY SCENARIOS:*

285 We first examine the effect of perenniality on polyploid establishment in the absence of clonal
286 reproduction ($c_2 = c_4 = 0$). Diploid and tetraploid individuals may have the same probability of
287 survival between generations ($sv_2 = sv_4$), or survival probabilities may differ ($sv_2 \neq sv_4$). For
288 equal strategies, sv_2 and sv_4 ranged from 0 (a short-lived annual strategy with zero survival
289 probability between generations) to 0.9 (a long-lived perennial strategy with a 90% survival
290 probability) in increments of 0.1 (fig. 1). For the core dispersal-inviability parameter set, there
291 were 90 unique scenarios where diploids and polyploids have equal life-histories.

292 Because genome duplication is expected to slow growth rates and increase lifespans, we
293 only consider tetraploid survival probability exceeding that of diploids, defining a “Tetraploid
294 Survival Advantage” as $sv_4 - sv_2$. Diploid survival probability per generation ranged from 0 to
295 0.8, while tetraploid survival could take any larger value (e.g., for $sv_2 = 0$, sv_4 can be 0.1 – 0.9).
296 This results in 45 pairs of sv_2 and sv_4 , and a total of 405 parameter combinations.

297 We ran several additional simulations to determine how alternate model formulations could
298 influence the effect of life history on tetraploid establishment. For these models, we consider:

299 1) *Low population density* – Imposing a fully occupied grid may misrepresent the population
300 structure of some plants; more closely resembling a population of long-lived trees than patchy
301 herbaceous species. Less local competition for recruitment sites may increase polyploid
302 establishment potential. We reran the full set of 495 life history simulations on a larger
303 population lattice of $D = 40$ units with population size constant at $N = 900$ randomly distributed
304 individuals, for a ~45% decrease in plant density.

305 2) *Unequal selfed-seed inviability* – Because inbreeding depression is expected to be weaker
306 in polyploids (Husband and Schemske 1997; Husband et al. 2008), we tested scenarios where the
307 probability of selfed-seed inviability for diploids was $k_2 = 0.9$, and for tetraploids k_4 took lower

308 values in increments of 0.2 (minimum 0.1). For these 4 k_2 - k_4 pairs, we reran the equal and
309 unequal life history scenarios described above with pollen-seed dispersal $d_p = d_s = 0.5$ only (220
310 total parameter combinations).

311 3) *Non-zero UG production* – We consider values of unreduced gamete production (ug) by
312 diploids of 0.01, 0.05, 0.1, 0.15, and 0.2 (fig. 1). Simulations for equal and unequal life histories
313 were rerun for a subset of the core dispersal-inviability parameters ($d_p = d_s = 0.5$, and $k_2 = k_4 =$
314 0.1), for 275 total parameter combinations.

315

316 *CLONAL REPRODUCTION SCENARIOS:*

317 Here, we allow diploid and tetraploid ramet production to be non-zero; reproduction occurs both
318 sexually and clonally. In the equal clonality scenario, both diploids and tetraploids are perennial
319 ($sv_2 > 0$, $sv_4 > 0$), and produce an equal number of clonal ramets per generation ($c_2 = c_4 > 0$) at
320 some average distance away from the parent plant ($d_{c2} = d_{c4} > 0$). For both ramet production and
321 dispersal we consider two values: small vs. large genets ($c_2 = c_4 = 1$ or 5 ramets produced per
322 generation) and clumped vs. dispersed clonal architecture ($d_{c2} = d_{c4} = 0.5$ or 5 mean grid units).
323 All four combinations of clonal parameters were examined, hereafter referred to as clonal
324 strategies. For each strategy we include equal and unequal life history strategies, resulting in
325 1620 parameter combinations over the core dispersal-inviability set.

326 We vary ramet production and clonal architecture separately to determine how differences in
327 clonality between cytotypes alters polyploid establishment, concentrating on equal life history
328 strategies only. Keeping ramet dispersal distance (i.e., clonal architecture) equal between
329 cytotypes ($d_{c2} = d_{c4} = 0.5$ or 5), there are six combinations of c_2 and c_4 , including $c_2 = 0$ or $c_4 = 0$,
330 for a total of 108 scenarios for the core dispersal-inviability parameter set. Similarly, keeping

331 ramet production equal between cytotypes ($c_2 = c_4 = 1$ or 5) while varying ramet dispersal results
332 in 18 additional combinations.

333 To test alternate model formulations for the clonal scenarios, we also consider:

334 1) *Exponential ramet dispersal* – Our model implicitly includes a competitive advantage to
335 clonal ramets over seedling recruits by assuming a normal Gaussian distribution for ramet
336 dispersal probability (eq. [2]; fig. S1B). We compared our main results with a model where
337 ramet dispersal follows an exponential density function (eq. [1]; fig. S1A), so that the
338 recruitment probability at a site x grid units away from the parent plant is the same for both
339 sexual and clonal offspring. We reran the full set of equal clonality scenarios (1620 parameter
340 combinations).

341 2) *Unequal selfed-seed inviability* – We set the probability of selfed-seed inviability for
342 diploids at $k_2 = 0.9$, while for tetraploids k_4 took lower values in increments of 0.2 (minimum
343 0.1). For these 4 k_2 - k_4 pairs, we reran the equal clonality and equal life history scenarios
344 described above, for ramet dispersal with either a Gaussian (432 parameter combinations) or
345 exponential probability function (432 parameter combinations).

346

347 *MODEL OUTPUT:*

348 Simulations were replicated 20 times for each of the 5175 unique sets of parameters we
349 investigated, for a total of 103 500 model runs. A replicate could result in three possible
350 outcomes: exclusion of diploids (fixation of tetraploids), exclusion of tetraploids (fixation of
351 diploids), or a stable equilibrium that includes both cytotypes. Exclusion of diploids occurs once
352 tetraploids have replaced all diploids—because tetraploids cannot produce double-reduced
353 gametes, there is no way for diploids to re-enter the population. Complete exclusion of

354 tetraploids can only occur when UG production is zero; otherwise a low equilibrium frequency
355 of tetraploids is expected as new tetraploid individuals are occasionally formed via UGs. In this
356 case, the stability of cytotype coexistence was assessed by examining average tetraploid
357 frequency over the last 100 generations of the simulation, and deviations of less than 10
358 individuals per generation over this period were deemed stable. One of the three final states was
359 generally reached within 100 generations, but we continued simulations for a maximum of 500
360 generations when unreduced gamete (UG) production was non-zero, to capture rare or delayed
361 events. To determine the probability of polyploid fixation for a particular parameter set, we
362 calculated the proportion of replicates that end in each state, and average the number of
363 generations needed to reach them.

364 For each simulation run, we tracked several demographic and reproductive metrics per
365 generation, including diploid and tetraploid survivorship, number and average size of diploid and
366 tetraploid individuals and genets, average local neighbourhood composition (defined as an
367 extended Moore neighbourhood 2 grid units in each dimension; total 24 surrounding cells not
368 including the focal cell), local neighbourhood vacancy (total 25 cells including the focal cell), the
369 total number of offspring of each sexual cross-type produced (table S1), the number of clonal
370 ramets produced, as well as the number of each offspring type successfully recruited into the
371 population.

372

373 **RESULTS**

374 *LIFE HISTORY:*

375 In models with equal survivorship ($sv_2 = sv_4$) between cytotypes and no clonal reproduction,
376 there was no successful establishment of tetraploids, unless other conditions were also met (e.g.,

377 $ug \neq 0$). Under unequal survivorship ($sv_2 \neq sv_4$), tetraploid establishment only occurred under
378 short pollen and seed dispersal distances ($d_p = d_s = 0.5$, high autogamy). Establishment
379 probability increased when both diploids and tetraploids had high survival, and when tetraploids
380 had significant survival advantages over diploids (fig. 2A). When selfed-seed inviability was
381 high ($k_2 = k_4 = 0.9$), tetraploids needed a large survivorship advantage and a survival probability
382 of at least 0.8 to establish, regardless of diploid survival (fig. 2A). When selfed-seed inviability
383 was low ($k_2 = k_4 = 0.1$), tetraploids needed a minimum survival advantage of 0.4 when among
384 annual diploids ($sv_2 = 0$), but only 0.2 when diploids had higher survival probabilities (fig. 2A).
385 Time to tetraploid fixation was more rapid with larger tetraploid survival advantages, but was not
386 affected by diploid survival probability; whereas tetraploid exclusion was significantly slower
387 when tetraploid survival advantage was large and when diploid survival was high (fig. S2).

388 Lower population densities expanded the parameter space that allowed successful tetraploid
389 establishment (fig. S3A), but tetraploid fixation or exclusion times were longer (figs. S3B, C).
390 Reducing the inviability of selfed-seed in tetraploids relative to diploids significantly increased
391 establishment probability (fig. 2B), even when cytotype survival was equal. Times to exclusion
392 were similar to the equal self-seed inviability simulations, but fixation times were significantly
393 faster (figs. S4A, B).

394 The rate of unreduced gamete (UG) production was positively associated with tetraploid
395 fixation probability, with the critical value being between $ug = 0.15$ and $ug = 0.2$ when cytotype
396 life history strategies were equal and pollen-seed dispersal distance was moderate to far ($d_p = d_s$
397 $= 2$ or 5), and this threshold was reduced to $ug = 0.1$ when $d_p = d_s = 0.5$ and selfed-seed
398 inviability was low ($k_2 = k_4 = 0.1$; data not shown). When cytotypes varied in life history
399 strategy, tetraploids were always successful when $ug \geq 0.1$ (fig. S5A), unless diploid and

400 tetraploid survival were both very high ($sv_2 = sv_4 = 0.9$), where 500 generations was just shy of
401 enough time for complete fixation (fig. S6A). When $ug = 0.05$, a tetraploid survival advantage of
402 0.2 resulted in tetraploid establishment across all diploid survival probabilities (fig. 2C), and
403 when tetraploid advantage was 0.1 establishment success was positively correlated with diploid
404 survival; low diploid survival resulted in tetraploid establishment only rarely, intermediate
405 survivals ($sv_2 = 0.3-0.4$) showed a trend towards eventual tetraploid establishment (fig. S6A),
406 and $sv_2 \geq 0.5$ always ended in tetraploid fixation in less than 500 generations (fig. 2C). Further
407 reducing UG production to $ug = 0.01$ revealed a similar pattern (fig. 2C, Figure 6A). For
408 simulations that did not proceed towards tetraploid fixation, both cytotypes coexisted with low
409 tetraploid frequencies of ~ 10 tetraploids per generation (1% of the population) for $ug = 0.05$, and
410 ~ 2 (0.2%) when $ug = 0.01$ (figs. S6A, B). In general, mean time to tetraploid fixation was slower
411 for more perennial populations, and when tetraploid survival advantage was small, but these
412 relationships were dependent on ug value (fig. S5B).

413

414 *CLONAL REPRODUCTION:*

415 *Clonality and Life History Strategy:*

416 Tetraploid establishment probability was higher when individuals were able to reproduce both
417 sexually and clonally (fig. 3), but the effects of clonality were strongly dependent on genet size
418 and architecture (small vs. large genets, clumped vs. dispersed ramets). As in the nonclonal
419 scenarios, establishment increased with both diploid survival and tetraploid survival advantage,
420 but still no establishment occurred when cytotypes had equal life histories (figs. 3, S7). Large
421 dispersed clonal strategies had the highest establishment probabilities across parameter space
422 (fig. 3). Differences between clonal strategies were weaker when pollen and seed dispersal

423 distances were short ($d_p = d_s = 0.5$, high autogamy, low geitonogamy), but when pollen and seed
424 dispersal was far ($d_p = d_s = 5$, low autogamy and high geitonogamy) small and clumped genets
425 were substantially less successful than large and dispersed genets (fig. 3). Selfed-seed inviability
426 did not influence clonal tetraploid establishment probability (fig. S7), nor did lowering selfed-
427 seed inviability for tetraploids relative to diploids (fig. S8). Mean time to tetraploid fixation was
428 faster for all clonal strategies compared to the nonclonal, but there were no consistent differences
429 in exclusion time (fig. S9). The effects of life history strategy on establishment under the
430 alternate exponential formulation for ramet dispersal were nearly identical to the nonclonal
431 scenarios, but with faster time to fixation (fig. S10). Unlike under Gaussian ramet dispersal,
432 reducing tetraploid selfed-seed inviability compared to diploids increased establishment
433 probability (fig. S8).

434

435 *Divergent Clonal Strategies:*

436 Tetraploids with fewer ramets than diploids had no establishment success (fig. 4). When
437 tetraploid ramet production was higher, tetraploid establishment depended on clonal architecture,
438 pollen and seed dispersal distance, and life history strategy (fig. 4). Increasing pollen and seed
439 dispersal distances decreased establishment probability, particularly for clumped genets (fig. 4).
440 Tetraploids with greater survivorship tended to have lower establishment success when the
441 difference in genet size between cytotypes was large ($c_2 = 0$, $c_4 = 5$; fig. 4), but establishment
442 was positively correlated with survival when differences were small ($c_2 = 0$, $c_4 = 1$) and genets
443 were dispersed (fig. 4). Selfed-seed inviability did not affect tetraploid establishment (results not
444 shown).

445 Tetraploids with clumped clonal architecture could not establish among dispersed diploids,
446 but dispersed tetraploid genets generally had high establishment success among clumped
447 diploids (fig. S11). In the latter scenario, tetraploids with large genets were little affected by
448 pollen and seed dispersal distance, and establishment decreased with survival (fig. S11).
449 Conversely, for small genets establishment success decreased with increasing pollen and seed
450 dispersal distance (fig. S11). Here, increasing survival lowered establishment probability when
451 pollen and seed dispersal was restricted ($d_p = d_s = 0.5$), but enhanced it when pollen and seed
452 dispersal was far ($d_p = d_s = 2$ or 5 , fig. S11). Selfed-seed inviability did not affect tetraploid
453 establishment when clonal architecture differed between cytotypes (results not shown).

454

455 *The Mating and Demographic Consequences of Clonal Reproduction:*

456 To illustrate the effects of different clonal strategies on patterns of tetraploid establishment, we
457 focus on the set of models where $sv_2 = 0.5$, $sv_4 = 0.9$, $d_p = d_s = 0.5$ or 5 , $k_2 = k_4 = 0.1$, and $ug = 0$,
458 as this combination led to successful establishment in the majority of simulations. Diploids and
459 tetraploids have equal clonal strategies ($c_2 = c_4$, $dc_2 = dc_4$).

460 Reproductive and clonal strategies substantially influenced the spatial structure of tetraploid
461 populations, even when overall establishment probabilities were similar (fig. 5A). In the
462 nonclonal scenarios, tetraploids spread into the diploid population in a tight circle, and at 30
463 generations only occupied 3-5% of the population (fig. 5B). In comparison, clonal tetraploids
464 established quicker, with clumped architectures expanded from localized points, and dispersed
465 architectures quickly establishing across the entire population lattice (fig. 5B). Low ramet
466 production promoted the establishment of many distinct tetraploid genets, but populations with
467 high ramet production were often dominated by a few very large genets (fig. 5B).

468 Structural differences between clonal strategies affected patterns of within- vs. between-
469 cytotype mating during the establishment process, and the timing and location of recruitment of
470 sexual vs. clonal offspring. For nonclonal tetraploids, when simulations began most ovules were
471 involved in self-fertilized autogamous or inviable intercytotype matings, and nearly all viable
472 offspring and recruits were autogamously produced (fig. 6A). As the simulations progressed and
473 tetraploids increased in number, intracytotype matings and recruits became more common (fig.
474 6A).

475 All clonal tetraploids experienced early increases in geitonogamous mating (fig. 6B) and
476 geitonogamous seed production (fig. 6C). When pollen and seed dispersal were restricted ($d_p = d_s$
477 = 0.5) autogamy was prevalent, though geitonogamy remained high for large and dispersed
478 strategies until tetraploid fixation, whereas outcrossed mating was more frequent in small and
479 clumped genets (fig. 6B). In contrast, when pollen and seed dispersal distances were far ($d_p = d_s$
480 = 5) geitonogamous mating was dominant early during establishment, but intercytotype mating
481 overtook geitonogamy before fixation for all but the large dispersed clonal strategy (fig. 6B).
482 Sexual offspring were rarely recruited in the clonal scenarios, even when they were more
483 abundant than ramets (figs. 6C, D). Seedling recruitment frequencies mirrored those of the viable
484 seedlings available (fig. 6C), and was more common late during the establishment process, under
485 far pollen and seed dispersal distances ($d_p = d_s = 5$), and for small and clumped clonal
486 architectures (fig. 6D).

487 Under the alternate exponential formulation for ramet dispersal, tetraploid establishment was
488 nearly identical to the nonclonal scenario; sexual offspring recruited were mainly the result of
489 autogamy, and geitonogamy played little to no role (fig. S12). However, clonal ramet

490 recruitment spiked early in establishment, particularly for large and dispersed strategies, but then
491 remained at a low frequency until tetraploid fixation (fig. S12).

492

493 **DISCUSSION**

494 Our results indicate that a perennial life history strategy and clonal reproduction can increase
495 polyploid establishment potential. However, we find that this is only the case when polyploids
496 have some advantage over diploids (e.g., higher per generation survival), or when unreduced
497 gamete production is high, suggesting that the ability to perennate or to produce clonal ramets
498 may not be enough to overcome Minority Cytotype Exclusion (MCE) in some circumstances. By
499 investigating how various clonal and life history strategies affects the spatial structure,
500 demography, and mating patterns within a mixed-ploidy population, we identify mechanisms
501 that can influence the spread of polyploids into a diploid population. Our model is the first to
502 incorporate the spatial attributes of clonal architecture and within-genet geitonogamous self-
503 fertilization, and we find that clonal strategy has a significant effect on the polyploid
504 establishment process, and major consequences for polyploid population structure.

505

506 *PERENNIALITY PROMOTES POLYPLOIDY:*

507 Perennial polyploids should experience weaker Minority Cytotype Exclusion (MCE) pressure
508 than annual polyploids because lengthening lifespan increases the chances of reproductive
509 success via self-fertilization, and reduces stochastic loss of all polyploids from the population.
510 Our model supports these hypotheses and provides mechanistic links behind the broad-scale
511 associations between polyploids and perenniality (Rice et al. 2019; Van Drunen and Husband
512 2019), which highlight the importance of spatial structure, temporal dynamics, and chance
513 during the first few generations after a neopolyploid arises.

514 We find that polyploids are more likely to succeed among longer-lived diploid species,
515 especially if perennial diploids give rise to polyploids with slightly longer lifespans. Notably, the
516 polyploid survival advantage needed for consistently successful establishment decreased with
517 increasing diploid perenniality (fig. 2A). This pattern was driven by the demographic
518 consequences of 1) competition for space in the population, and 2) drawn-out polyploid
519 persistence when polyploids, or both cytotypes, were long-lived. When diploids are short-lived,
520 recruitment sites open up close to the rapidly-cycling diploids, which precludes the initial
521 recruitment of polyploid offspring and increases the likelihood of stochastic loss of all polyploids
522 unless they have very high relative survivorship. In contrast, when diploids and polyploids are
523 both long-lived there is significantly slower population turnover, longer polyploid persistence,
524 and more potential for polyploid offspring recruitment. However, when population density is low
525 the conditions under which polyploids can establish are greater (fig. S3). This suggests that in
526 less competitive environments, polyploid success may be less dependent on the life history
527 strategy of diploids, in line with previous models showing that ecological niche (Fowler and
528 Levin 1984; Rodríguez 1996) and physical (Griswold 2021) segregation can facilitate polyploid
529 establishment, even when individuals have an annual life history strategy.

530 Interactions between the spatial and demographic effects of divergent life history strategies
531 in mixed-cytotype populations offers a reason why polyploidy is more common in perennial
532 species – the $\geq 40\%$ increase in survivorship needed to establish among short-lived diploids in
533 our model (fig. 2A) may be an unfeasibly large shift in neopolyploids, whereas a survival
534 probability increase of 20% among long-lived diploids may be more tenable. There are numerous
535 examples of naturally occurring polyploids that exhibit a life history shift compared to their
536 diploid relatives. For example, in the mixed-ploidy species *Centaurea stoebe* tetraploids are

537 iteroparous short-lived perennials while diploids are predominantly semelparous annuals (Mráz
538 et al. 2012), and tetraploid cultivars of *Nasturtium officinale* perennate more easily than diploid
539 lines (Manton 1935). But few studies have addressed life history changes in perenniality in
540 neopolyploids (but see Müntzing 1936), limiting our understanding of the strength of the
541 immediate effects of WGD and phenotypic differences between diploids and polyploids, and the
542 consequences for polyploid establishment in natural populations. Indeed, here we demonstrate
543 that autopolyploids are unable to establish among diploids with equal life history strategies
544 unless they have additional advantages (e.g., significantly lower inbreeding depression), a result
545 corroborated by previous models (Rodríguez 1996; Chrtek et al. 2017; Spoelhof et al. 2020).

546 Polyploid persistence time was prolonged when diploids and polyploids were highly
547 perennial, considerably slowing model dynamics by decreasing polyploid death and recruitment
548 rates (see also Chrtek et al. 2017; Spoelhof et al. 2020). Surveys in natural populations have
549 found that cytotype frequencies in annual species can fluctuate wildly between growing seasons,
550 sometimes leading to the complete loss of diploids or polyploids within a population (Čertner et
551 al. 2017), whereas cytotype coexistence in perennial species may be maintained over many
552 generations (Lumaret et al. 1987; Keeler 2004; Kao and Parker 2010). Thus, perenniality has
553 been invoked as a non-adaptive factor promoting cytotype coexistence in nature (Duchoslav et
554 al. 2010; Hanzl et al. 2014; Hanušová et al. 2019), though it is often unknown whether mixed-
555 ploidy populations are in stable states, or represent only short snapshots of ongoing competition
556 and exclusion (Kolář et al. 2017). Our results suggest that perenniality may contribute to an
557 illusion of stable coexistence for a much longer timeframe than field studies typically encompass
558 (e.g., (e.g., Čertner et al. 2017; but see Buggs and Pannell 2006). For some perennial scenarios
559 both cytotypes coexisted for more than 300 generations while moving steadily towards polyploid

560 fixation or exclusion (fig. S2), whereas annual polyploids were typically excluded in 1 or 2
561 generations. Either end of this temporal spectrum presents challenges for studying neopolyploid
562 establishment in natural populations, emphasizing the utility of theory in understanding this
563 process.

564 An extended period of close interaction between perennial diploids and polyploids may have
565 significant consequences for polyploid evolution during and after establishment. For example,
566 ongoing intercytotype reproductive events could result in selection for assortative mating,
567 driving divergence in floral morphology or phenology between diploids and polyploids (Oswald
568 and Nuismer 2011; Husband et al. 2016). Prolonged intercytotype mating will also promote
569 polyploid establishment when diploid unreduced gamete (UG) production is nonzero, because
570 the probability of two UGs giving rise to a viable polyploid offspring in a diploid-diploid cross is
571 ug^2 , but the probability of one UG being involved in a diploid-polyploid cross is ug (table S1).
572 Our model is the first to incorporate UG production and perenniality, and we find that a UG
573 production rate of 1-5% is sufficient to ensure polyploid success when diploids and polyploids
574 are perennial, providing polyploids also have a small survival advantage (fig. 2C). This is similar
575 to estimates of UG frequencies in natural populations (0.05-2%; Ramsey and Schemske 1998;
576 Kreiner et al. 2017), and is substantially lower than the UG production rate of ~17% required for
577 non-selfing annuals with random mating (Felber 1991; Husband 2004), or 10% for annuals with
578 self-fertilization and low inbreeding depression (Rausch and Morgan 2005). UG production may
579 then be less of a limiting step for polyploid formation among perennials where reproductive
580 events are spread over multiple generations.

581
582 *CLONALITY INFLUENCES THE ESTABLISHMENT PROCESS:*

583 When all else is equal between cytotypes, simply being clonal is not enough to ensure
584 establishment success under any scenario we investigated – some small advantage over diploids
585 is needed (e.g., higher ramet production). In our model, increased clonality confers high
586 establishment success, as in mixed diploid-tetraploid *Chamerion angustifolium* (fireweed), where
587 neotetraploids exhibit immediate increases in clonal rootbud production (Van Drunen and
588 Husband 2018*b*). Conversely, decreased clonal investment in polyploids results in no
589 establishment (fig. 4), a pattern consistent with the lack of natural cytotype variation in *Fragaria*
590 *vesca* (woodland strawberry), where artificial neotetraploids have lower stolon production (Van
591 Drunen and Husband 2018*a*). These remain the only species in which neopolyploid investment
592 in clonal reproduction has been measured, but if this pattern applies more generally, it would
593 suggest that the production of clonal ramets is an important factor in polyploid establishment
594 (Spoelhof et al. 2017).

595 Perenniality and clonal reproduction have both been implicated in polyploid success in
596 natural populations (Rice et al. 2019; Van Drunen and Husband 2019), but few studies have
597 contrasted their importance in the early stages of polyploid evolution. Here, we show that
598 polyploids with a combination of perenniality and clonal reproduction generally have greater
599 establishment success than polyploids that are strictly sexual. In some scenarios, perenniality
600 alone was enough to ensure polyploid establishment (e.g., when autogamy was high). While
601 clonal reproduction did not affect final establishment probability in these simulations, it still
602 significantly altered the establishment process. For instance, polyploids were able to spread into
603 the diploid population faster when clonal, even when seedlings and ramets were equal
604 competitors (fig. S10), but this effect was heavily moderated by clonal strategy. Spoelhof et al.
605 (2020) speculated that rapid clonal expansion may increase establishment probability, but result

606 in genetically homogeneous polyploid populations. We confirm this outcome, particularly for
607 clonal strategies that produce many ramets with high lateral spread (fig. 5B). Here, it is possible
608 that polyploids may enjoy short-term success, but may not survive in the long-term if the lack of
609 genetic variability in the polyploid population leads to reduced evolutionary potential (Muller
610 1932; Pan and Price 2002; Barrett 2015; Herben et al. 2016). According to our results, polyploids
611 conforming to a large-clumped clonal architecture may be the most successful if they spread
612 quickly while maintaining higher genet diversity than polyploids with more dispersible ramets
613 (fig. 5B). Nonetheless, spreading architectures may perform well in environments with high
614 temporal variability or frequent disturbance where slower expansion could result in the stochastic
615 loss of all polyploids (Čertner et al. 2017), especially if genetic uniformity is counteracted by
616 recurrent polyploid formation, immigration, or high rates of vegetative somatic mutation
617 between ramets (Yu et al. 2020).

618 Our model demonstrates that spatial clonal architecture has a large effect on the polyploid
619 establishment process, but that no single clonal strategy is superior under all circumstances.
620 Similarly, phylogenetic comparative studies have found mixed support for associations between
621 particular clonal strategies and polyploid occurrence, depending on the group of species being
622 studied (Herben et al. 2017; Van Drunen and Husband 2019). Overall, given the wide diversity,
623 evolutionary lability, and multi-functional nature of clonal modes across the angiosperms
624 (Herben and Klimešová 2020), it seems unlikely that there is a one-size-fits-all hypothesis
625 describing the relationship between clonal reproduction and polyploidy. For example, bulbs or
626 corms (generally “clumped” clonal architectures) are involved in resource storage (Klimeš et al.
627 1997), which may affect over-winter survival or the timing and extent of sexual reproduction in
628 the next growing season. Thus, polyploid establishment may indeed be successful due to

629 clonality in species with these strategies, but for significantly different reasons than explored in
630 our current model.

631

632 *CLONAL ARCHITECTURE & MATING:*

633 Clonal reproduction may enhance polyploid establishment by creating local polyploid majorities
634 (Baack 2005; Spoelhof et al. 2020), but previous models have overlooked one of the key aspects
635 of this polyploidy-promoting mechanism: geitonogamous self-fertilization. Geitonogamous self-
636 fertilization between different flowers on the same plant, or between clonal ramets, is often
637 regarded as a negative and non-adaptive side-effect of outcrossing (Lloyd 1992; Eckert 2000).
638 Geitonogamy generally involves mating costs, as it requires the same pollination process as
639 would occur with outcrossing, but it reduces outcross siring success and results in pollen (Harder
640 and Barrett 1995; Lau et al. 2008) and seed discounting (Lloyd 1992) when there is any
641 inbreeding depression. But geitonogamy is rarely considered in the complete absence of
642 compatible mates, where self-fertilization may be the only recourse for producing viable sexual
643 offspring. Our model shows that geitonogamous self-fertilization between clonal ramets can
644 confer a significant fitness advantage to establishing polyploids by enabling them to acquire
645 same-cytotype mates, revealing a situation where geitonogamy might be adaptive. Here, when a
646 new polyploid is instantly reproductively isolated from its progenitors, the costs typically
647 associated with pollen and seed discounting via geitonogamy instead apply to intercytotype
648 outcrossing that does not produce viable recruits.

649 Rates of geitonogamy are expected to vary with clonal architecture (Charpentier 2002;
650 Matsuo et al. 2014; Van Drunen et al. 2015). We can clearly see this in our model, where the
651 long reach of dispersed polyploid genets enables ramet recruitment over a wide area, leading to

652 large genets and high rates of geitonogamy. In contrast, seedlings are equal or better dispersers
653 than ramets when clonal architecture is clumped (fig. S1), resulting in smaller genets, more
654 sexual recruits, and more frequent intracytotype outcrossing than geitonogamous self-
655 fertilization (fig. 6). These mating differences contribute to establishment speed and overall
656 establishment probability, especially when pollen and seed dispersal distances are long and
657 sexual reproduction is not dominated by autogamy. Across all clonal strategies, however,
658 geitonogamy substantially reduced ovule waste to intercytotype mating early in the
659 establishment process (fig. 6).

660 We might then predict that neopolyploids will experience strong selection on traits that
661 increase geitonogamy, such as ramet production (Hu et al. 2015), clonal architecture (Van
662 Drunen and Husband 2018a), or floral display size (Vamosi et al. 2007). But as polyploids
663 spread throughout the population and intracytotype outcrossing becomes more probably,
664 selection may reverse and instead favour outcross sexual reproduction. There is some evidence
665 for this occurring in autotetraploid *Chamerion angustifolium*, where initial WGD-driven
666 increases in synthetic neotetraploid rootbud production is significantly reduced in naturally-
667 occurring tetraploids (Van Drunen and Husband 2018b; Walczyk and Hersch-Green 2019). In
668 our model we saw a shift towards recruiting outcrossed seedlings as polyploids became common
669 (fig. 6), but we could not evaluate selection on reproductive strategy directly because we did not
670 include phenotypic trait evolution. Future work that allows for heritable variation in reproductive
671 strategy and sex allocation, and resource-based trade-offs between reproductive modes could
672 therefore be particularly insightful.

673 Clonal reproduction and geitonogamous self-fertilization may be less likely to facilitate
674 polyploid success when pollen is limited and pollen discounting is high (Yamauchi 2006), or

675 when ramet recruitment into the population is low. In our model, we assumed that clonal ramets
676 were better competitors than seedlings, and so polyploid ramets were recruited much more often
677 than sexual offspring, even when they were less common in the recruitment pool (fig. 6). In
678 contrast, when ramets and seedlings were equal competitors in the exponential ramet dispersal
679 scenarios there were no differences in establishment probability between clonal and nonclonal
680 polyploids, though fixation times were still substantially shorter (figs. S8, S10). Ramet
681 competitive superiority is realistic for most clonal species, where ramet recruits tend to be more
682 common than seedlings within populations (Eriksson 1993; Vallejo-Marín et al. 2010;
683 Vandepitte et al. 2010; Johnson et al. 2020), but the validity of this assumption may vary for
684 different taxa, and ecological or demographic conditions. For instance, considering only within-
685 population processes ignores the role of seedlings in long-distance colonisation events and meta-
686 populations dynamics (Winkler and Fischer 2001; Griswold 2021; but see Scherrer et al. 2017),
687 and thus polyploids arising from diploids that occur in patchy habitats might benefit from more
688 dispersible sexual offspring than locally-restricted clonal propagules.

689

690 *CONCLUSIONS:*

691 Whether perenniality and clonal reproduction promote polyploid establishment depends on
692 multiple factors, including the phenotypic effects of WGD, local habitat availability, clonal
693 strategy, mating patterns and pollination system, inbreeding depression, and more. Ultimately,
694 determining whether the processes in our model occur in natural populations will require fine-
695 scale genetic data and extensive sampling, and may not be possible in polyploid systems that are
696 long established. Further models exploring a variety of situations (e.g., clonal vs. sexual
697 reproduction and polyploid establishment in patchy habitats), and experimental studies involving

698 synthetic neopolyploids or very young natural neopolyploids (e.g., tetraploid *Mimulus guttatus* in
699 the Shetland Isles; Simón-Porcar et al. 2017) will be key to unraveling the individual and
700 interactive roles of perenniality and clonality in early polyploid evolution.

701

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706

707 **DATA AND CODE AVAILABILITY**

708 All of the code needed to run the simulation model in this article is available online at:
709 <https://github.com/wevandrunen/autoployploid-establishment-lifecycle-clonalarchitecture>.

710

711 **AUTHOR CONTRIBUTION STATEMENT**

712 W.E.V. and J.F. conceived of the study. W.E.V. developed the model, and analyzed the output.
713 W.E.V. wrote the manuscript with input from J.F.

714

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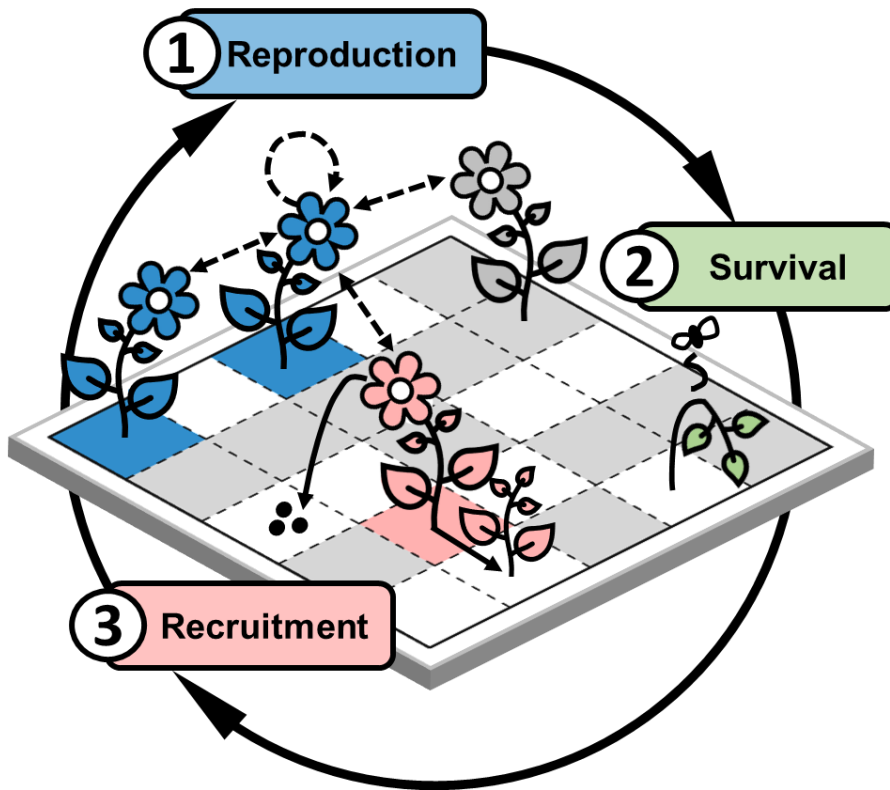
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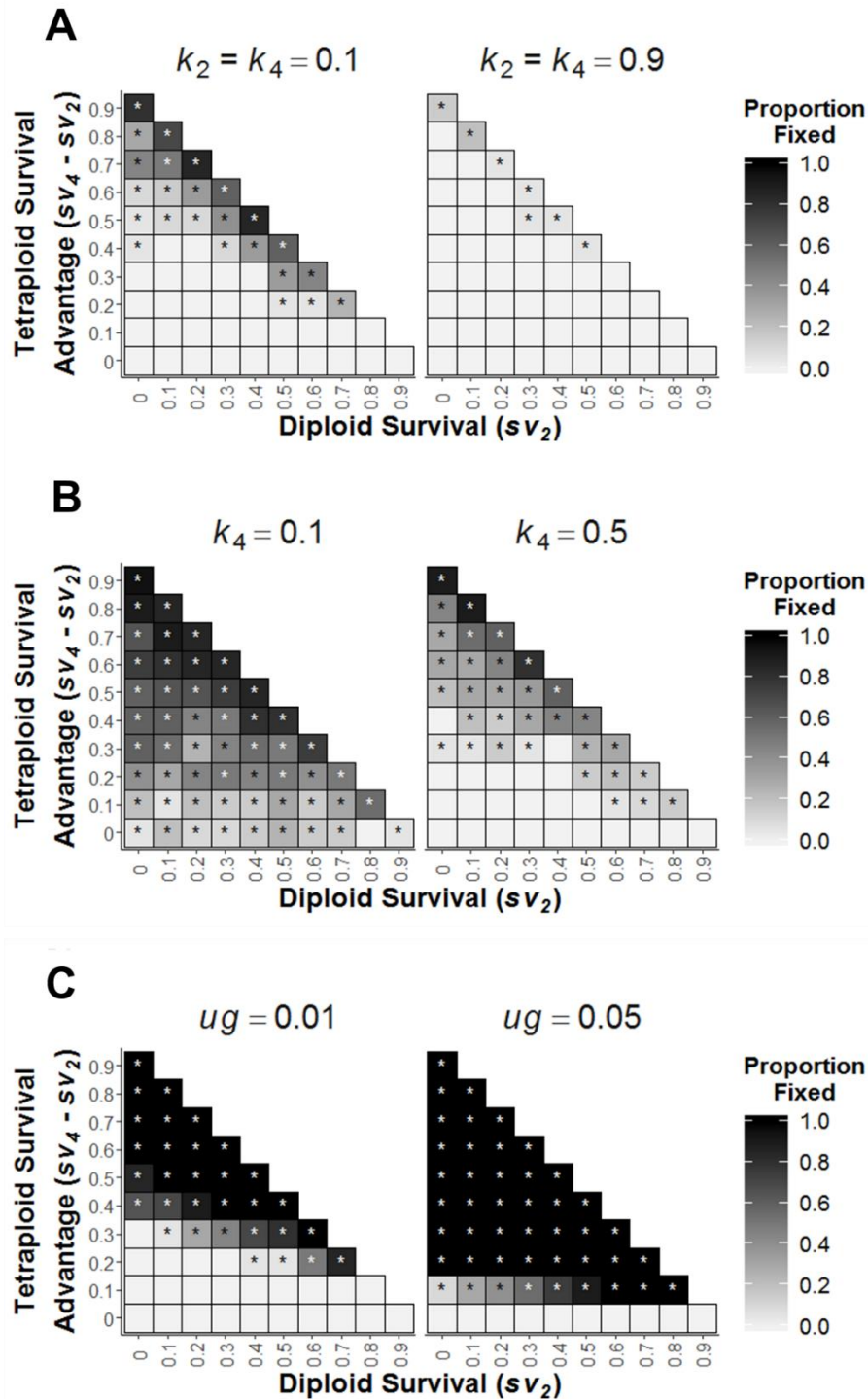
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938 **FIGURES**
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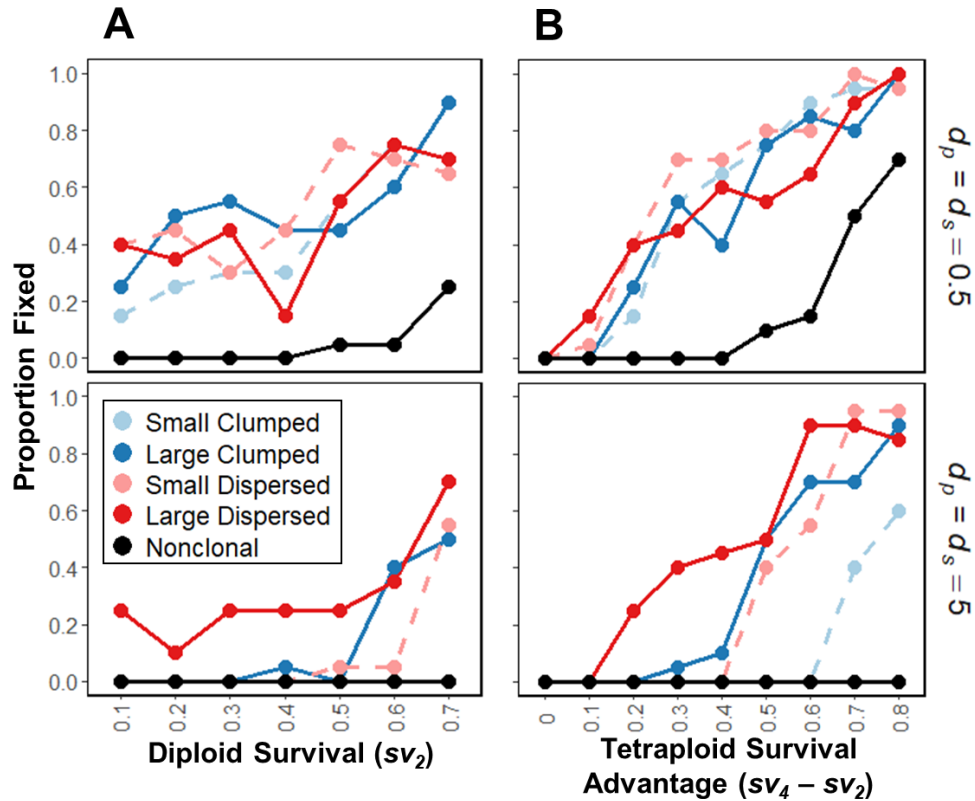
Parameter	Description	Values
D	Lattice dimensions	30
N	Population size	900
t	Initial number of polyploids	1
ov	Ovule number	5
d_p	Average pollen dispersal	0.5, 2, 5
ug	Unreduced gametes	0 – 0.2
k_2	2x selfed-seed inviability	0.1, 0.5, 0.9
k_4	4x selfed-seed inviability	0.1, 0.5, 0.9
c_2	2x per generation ramet production	0, 1, 5
c_4	4x per generation ramet production	0, 1, 5
sv_2	2x per generation survival	0 - 0.9
sv_4	4x per generation survival	0 - 0.9
d_s	Average seed dispersal	0.5, 2, 5
d_{c2}	2x average ramet dispersal	0.5, 5
d_{c4}	4x average ramet dispersal	0.5, 5

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 943 **Figure 1:** Simulation model workflow, and the adjustable parameters associated with each of the three main steps per generation.
 944 Models are initiated on a $D \times D$ population lattice containing both tetraploids (t individuals, 4x, coloured cells) and diploids ($N - t$
 945 individuals, 2x, grey cells), where each lattice cell can hold one individual. In Step 1, pollen is dispersed (dashed lines) within shoot,
 946 between shoots in the same genet (blue tetraploid genet), between members of the same cytotype (blue and pink tetraploids), and
 947 between cytotypes (blue tetraploid and grey diploid). Seeds are fertilized, and clonal ramets are produced. Individuals die in Step 2
 948 according to their survival probability, leaving empty spaces in the population (white cells). In Step 3, empty cells are colonized by
 949 newly produced seeds or ramets. The surviving individuals and the new cohort of recruits then repeat this cycle, which continues for a
 950 specified number of generations. See the main text for more detail.

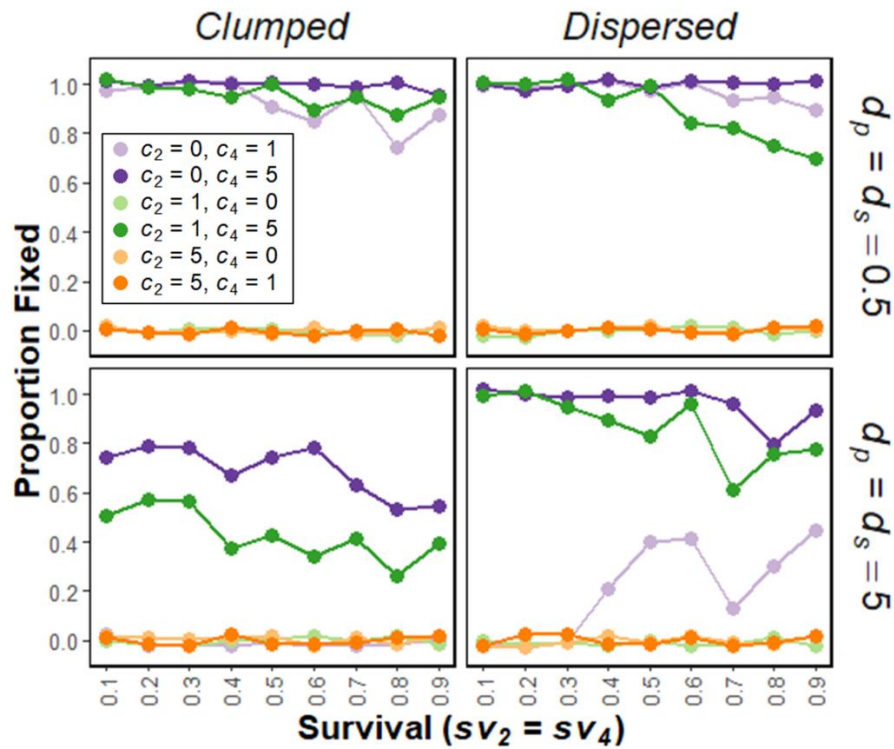


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953 **Figure 2:** Effect of life history strategy on polyploid establishment for a range of diploid and tetraploid
 954 survival probabilities (sv_2 , sv_4). Establishment success is measured as the proportion of simulation
 955 replicates in which tetraploids spread to fixation, and exclude diploids from the population. Panel A
 956 shows establishment under equal selfed seed inviability ($k_2 = k_4$), while in Panel B tetraploid selfed-
 957 seed inviability is lower than diploids ($k_2 = 0.9$, k_4 value above panels). There is no unreduced gamete
 958 production in Panels A and B ($ug = 0$). In Panel C, unreduced gamete production is non-zero, and
 959 selfed-seed inviability is $k_2 = k_4 = 0.1$. Asterisks denote parameter combinations where at least one
 960 simulation replicate resulted in tetraploid fixation. For all models $d_p = d_s = 0.5$.

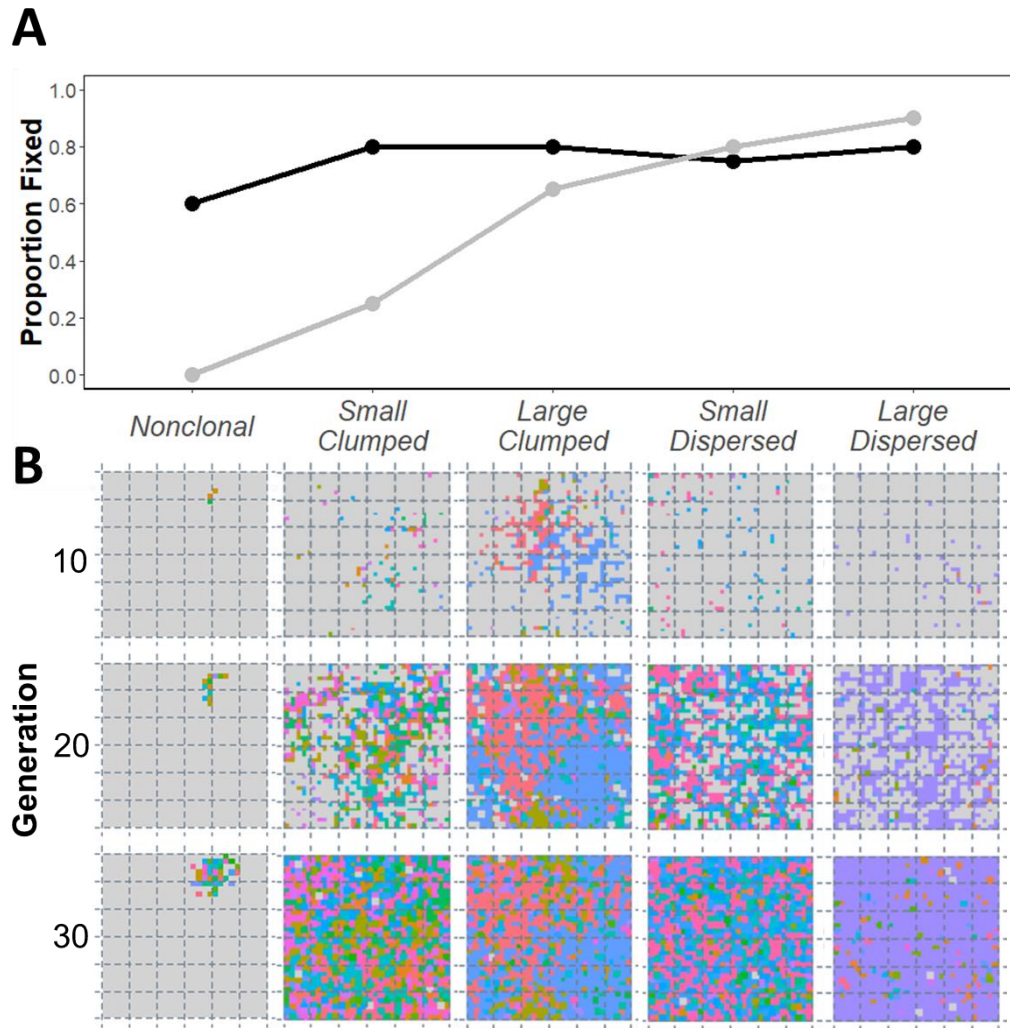


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 962 **Figure 3:** Influence of interactions between clonal strategy and life history on polyploid
 963 establishment, when cytotypes have identical clonal architectures (*Clumped* $d_{c2} = d_{c4} = 0.5$, blue;
 964 *Dispersed* $d_{c2} = d_{c4} = 5$, red), and equal ramet production (genets are *Small* $c_2 = c_4 = 1$, light
 965 dashed lines; or *Large* $c_2 = c_4 = 5$, dark solid lines). In Panel A diploid survival probability (sv_2)
 966 takes the values on the x-axis and tetraploid survival (sv_4) is 0.2 higher. In panel B diploid
 967 survival (sv_2) is held at 0.1, and tetraploids have a survival advantage ($sv_4 - sv_2$) according to the
 968 x-axis. Average pollen (d_p) and seed (d_s) dispersal distances vary between rows in each panel. For
 969 all models, selfed-seed inviability is equal between cytotypes ($k_2 = k_4 = 0.1$), and there is no
 970 unreduced gamete production ($ug = 0$).



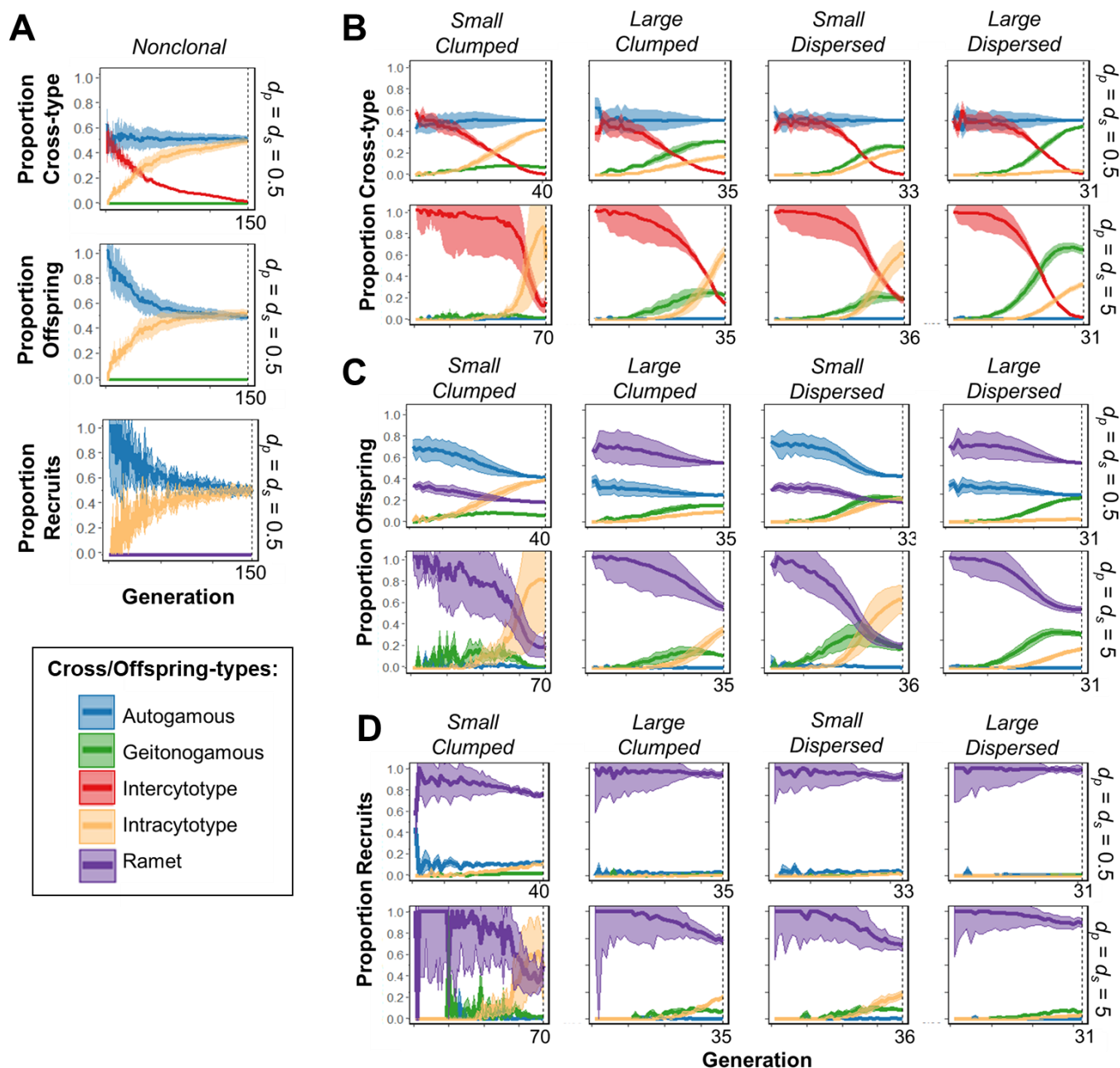
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Figure 4: Polyloid establishment probability when diploids and tetraploids have unequal ramet production (i.e., unequal genet size, $c_2 \neq c_4$). In comparison to diploids, tetraploids can produce a few more ramets ($c_2 = 0, c_4 = 1$; light purple lines), many more ramets ($c_2 = 0$ or $1, c_4 = 5$; dark purple and dark green lines), fewer ramets ($c_2 = 5, c_4 = 1$; dark orange lines), or no ramets ($c_2 = 1$ or $5, c_4 = 0$; light green and light orange lines). Clonal architecture is the same for both cytotypes, with the *Clumped* strategy in the left column ($d_{C2} = d_{C4} = 0.5$), and the *Dispersed* strategy in the right column ($d_{C2} = d_{C4} = 5$). Average pollen and seed dispersal distances ($d_p = d_s$) varies between rows. Life history strategies are equal between cytotypes ($sv_2 = sv_4$), as shown on the x-axis. For all models, selfed-seed inviability is equal between cytotypes ($k_2 = k_4 = 0.1$), and there is no unreduced gamete production ($ug = 0$). Points are slightly jittered vertically.



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987 **Figure 5:** Contrasting the spread and establishment probability of nonclonal tetraploids and each clonal
 988 strategy. Panel A shows the proportion of simulations with successful polyploid establishment between
 989 nonclonal and clonal strategies (black $d_p = d_s = 0.5$, grey $d_p = d_s = 5$). Cytotypes have identical
 990 architecture (*Clumped* $d_{C2} = d_{C4} = 0.5$; *Dispersed* $d_{C2} = d_{C4} = 5$), and equal ramet production (genets are
 991 *Small* $c_2 = c_4 = 1$; or *Large* $c_2 = c_4 = 5$). In Panel B, tetraploids (coloured cells) expand into the 2-
 992 dimensional population of diploids (grey cells), for $d_p = 0.5$ (black line in A). Each colour represents a
 993 different tetraploid genet. For all models, $sv_2 = 0.5$, $sv_4 = 0.9$, selfed-seed inviability is equal between
 994 cytotypes ($k_2 = k_4 = 0.1$), and there is no unreduced gamete production ($ug = 0$).
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Figure 6: Mating outcomes and offspring recruitment during polyploid establishment, averaged (\pm SE) across simulation replicates per generation. Tetraploid mating events in Panel A (nonclonal) and Panel B (clonal) can result in four cross-types: autogamous self-fertilization (blue, cross-types #16-17 in Table S1), geitonogamous self-fertilization (green, #18-19), intercytype mating (red, #20), or intracytype mating (yellow, #22). The recruitment pool in Panel A (nonclonal) and Panel C (clonal) contains any viable sexual offspring and clonal ramets (purple) produced, which may then be recruited into the population as shown in Panel A (nonclonal) and Panel D (clonal). In Panel A all scenarios have $d_p = 0.5$, as no establishment occurred when $d_p = 5$. In Panels B - D, clonal strategy varies across columns, and average pollen and seed dispersal distance ($d_p = d_s$) varies between rows. Cytotypes have identical architecture (*Clumped* $d_{C2} = d_{C4} = 0.5$; *Dispersed* $d_{C2} = d_{C4} = 5$), and equal ramet production (genets are *Small* $c_2 = c_4 = 1$; or *Large* $c_2 = c_4 = 5$). For all models, $sv_2 = 0.5$, $sv_4 = 0.9$, selfed-seed inviability is equal between cytotypes ($k_2 = k_4 = 0.1$), and there is no unreduced gamete production ($ug = 0$). Generations are truncated at the fastest tetraploid fixation time per parameter combination, indicated on the bottom right of each panel.