

1 **Founder effects drive the genetic structure of passively**  
2 **dispersed aquatic invertebrates**

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18 Running title (45 characters):

19 Founder effects and local adaptation

20

## 21 **Abstract**

22 Populations of passively dispersed organisms in continental aquatic habitats typically show  
23 high levels of neutral genetic differentiation, despite their high dispersal capabilities. Several  
24 evolutionary factors, including founder events and local adaptation, and life cycle features  
25 such as high population growth rates and the presence of propagule banks, have been  
26 proposed to be responsible for this paradox. Here, we have modeled the colonization  
27 process in these organisms to assess the impact of migration rate, growth rate, population  
28 size, local adaptation and life-cycle features on their population genetic structure. Our  
29 simulation results show that the strongest effect on population structure is caused by  
30 persistent founder effects, resulting from the interaction of a few population founders, high  
31 population growth rates, large population sizes and the presence of diapausing egg banks. In  
32 contrast, the role of local adaptation, genetic hitchhiking and migration is limited to small  
33 populations in these organisms. Our results indicate that local adaptation could have  
34 different impact on genetic structure in different groups of zooplankters.

35

36 Keywords: migration, local adaptation, genetic differentiation, zooplankton, Monopolization  
37 Hypothesis, Rotifera, Cladocera.

38

39

## 40 Introduction

41 Successful dispersal and colonization are essential for the establishment and persistence of  
42 species, and an understanding of these processes is crucial in the face of changing climate ,  
43 habitat destruction, and biological invasions, which are rapidly affecting the abundance and  
44 distribution patterns of many species (Parmesan & Yohe, 2003; Chen et al., 2011; Blackburn,  
45 Lockwood & Cassey, 2015). The evolutionary outcome of dispersal and colonization results  
46 from a potentially complex interplay of neutral and selective factors, including local  
47 adaptation, founder effects or bottlenecks causing genetic drift during the first stages of  
48 colonization, inbreeding depression, or high levels of gene flow that could erode local  
49 adaptation (Lenormand, 2002; Kliber & Eckert, 2005; Rosenblum, Hickerson & Moritz, 2007;  
50 Keller & Taylor, 2008; Verhoeven et al., 2011). In addition, life-cycle features and  
51 demographic characteristics may act as modulators and lead to different evolutionary  
52 outcomes (Burton, Phillips & Travis, 2010). For example, species with high population growth  
53 rates after a bottleneck are more likely to maintain their genetic variability (“founder-flush”  
54 model) (Carson, 1968; Templeton, 2008), and populations of organisms with resistant life  
55 stages (e.g. diapausing eggs) are more likely to be connected by migration even at long  
56 distances (Frisch, Green & Figuerola, 2007). Predicting the outcome of these factors is a  
57 major question in evolutionary and conservation ecology, and requires an understanding of  
58 the effect of each factor and their interactions.

59 Populations of passively dispersing aquatic invertebrates (e.g., freshwater bryozoans,  
60 rotifers, cladocerans, copepods, anostracans, notostracans) and macrophytes inhabiting  
61 lentic habitats typically present a high level of neutral genetic differentiation (Freeland et al.

62 2000; Zierold et al. 2007; Mills et al. 2007; Muñoz et al. 2008; Makino and Tanabe 2009; Xu  
63 et al. 2009; Escudero et al. 2010), despite their high dispersal capabilities through diapausing  
64 propagules (Allen, 2007; Frisch, Green & Figuerola, 2007; Vanschoenwinkel et al., 2011). This  
65 has been termed the “migration-gene flow paradox”. Regardless of their taxonomic  
66 disparity, these organisms share biological features promoting a rapid monopolization of  
67 resources in the new environment: high population growth rates, large population sizes and  
68 the production of resistant stages in their life cycle. The latter can accumulate in sediments  
69 and form diapausing propagule banks (Hairston, 1996; Brendonck & De Meester, 2003) and  
70 constitute the dispersal stage. As a result, once a habitat becomes available and is colonized,  
71 the population can grow very quickly creating a numerical advantage that dilutes the genetic  
72 impact of further immigrants (Waters, Fraser & Hewitt, 2013), resulting in a persistent  
73 founder effect (Boileau, Hebert & Schwartz, 1992). This explanation was expanded by (De  
74 Meester et al., 2002) into the so called “Monopolization Hypothesis” (MH hereafter) to  
75 include local adaptation as an important force contributing to reduce effective gene flow  
76 and therefore maintaining the genetic structure of passively dispersed aquatic organisms.  
77 The MH postulates that the migration-gene flow paradox could be explained by a  
78 combination of three factors: (1) persistent founder effects, (2) selection against immigrants  
79 due to local adaptation and (3) buildup of linkage disequilibrium between neutral markers  
80 and genes under selection.

81       Local adaptation is an important and rapid process in many zooplanktonic organisms  
82 (Meester 1996; Cousyn et al. 2001; Decaestecker et al. 2007; Costanzo and Taylor 2010). The  
83 impact of local adaptation on population genetic structure is diverse as it is dependent on  
84 the impact of other evolutionary forces, not only selection (Kawecki & Ebert, 2004). For

85 instance, it can promote genetic differentiation, ‘isolation-by-adaptation’ sensu (Nosil, 2007)  
86 or reinforce the existing genetic differentiation by reducing effective gene flow (Orsini et al.,  
87 2013). Irrespective of local adaptation, populations recently founded by a small number of  
88 propagules can be highly inbred and show inbreeding depression (De Meester, 1993;  
89 Tortajada, Carmona & Serra, 2009). This could give migrants a fitness advantage and favor  
90 gene flow into the population (Ebert et al., 2002; Haag et al., 2006). The accumulation of  
91 large numbers of resistant stages as seed or diapausing egg banks (i.e. propagule banks) in  
92 sediments is also a characteristic of many aquatic species inhabiting temporary habitats.  
93 These propagule banks have an important role in ecological (Chesson 1983; Cáceres 1997)  
94 and evolutionary processes (Brendonck & De Meester, 2003). They increase the effective  
95 population size due to postponed reproduction in the bank, and thus reduce genetic drift  
96 (Kaj, Krone & Lascoux, 2001). However, this effect may be indirect, as gene flow is also  
97 postponed in the bank (Kaj, Krone & Lascoux, 2001; Berg, 2005).

98         The relative importance of and the interactions between the demographic, neutral and  
99 selective processes acting during colonization has remained poorly understood. Therefore,  
100 an explicit analysis of the effects of local adaptation, persistent founder effects, and their  
101 interplay on the differentiation of populations of aquatic organisms is due, especially during  
102 the first stages of colonization when populations are still small and, thus, more sensitive to  
103 stochastic effects.

104         Here, we have modeled the colonization process of zooplanktonic organisms to clarify  
105 how migration rate, growth rate, population size, local adaptation and the existence of a  
106 propagule bank shape the population genetic structure during the first stages of  
107 colonization. Our primary interest is to gain insights into the relative importance of (1)

108 persistent founder effects, (2) selection against immigrants as a consequence of local  
109 adaptation, and (3) random associations between neutral genes and genes under selection  
110 (linkage disequilibrium).

111

## 112 **Materials and Methods**

113 We developed a genetic and demographic model to analyze the effects of population growth  
114 rate, population size, presence of a diapausing egg bank and local adaptation on the  
115 population genetic structure of aquatic organisms. We assumed a geographic scenario with  
116 two habitats, with local populations connected through reciprocal migration. These local  
117 populations are founded simultaneously after a single event of migration from a source  
118 population.

119 The model was based on the life cycle of rotifers and cladocerans (i.e. cyclical  
120 parthenogenesis), which are major taxonomic groups in the zooplankton. Cyclical  
121 parthenogenesis combines parthenogenesis with episodic sexual reproduction and typically  
122 consists of several asexual generations followed by a sexual generation, generally associated  
123 with habitat degradation. The sexual generation produces diapausing eggs that hatch into  
124 asexual individuals once the habitat becomes suitable again. As not all eggs hatch from one  
125 growth period to the next, they may accumulate in the sediment and form extensive  
126 diapausing egg banks (Brendonck & De Meester, 2003).

127 The demographic submodel is outlined in Fig. 1. Briefly, it consists in six steps:

128 step 1. Hatching of diapausing eggs (resident and immigrant)

129 step 2. Asexual proliferation

130 step 3. Sexual reproduction and production of diapausing eggs

131 step 4. Diapausing eggs survival in the sediment

132 step 5. Migration of diapausing eggs

133 step 6. Back to step 1

134 Note that this demography implies two time scales: (1) a within-planktonic growth  
135 period (often within-year; index,  $t$ ), and (2) an among-sexual generations scale (often  
136 among-years; index,  $y$ ).

137 Migration, either from the source population or between habitats, is assumed to occur  
138 via diapausing eggs, which are passively transferred between habitats, and their hatching  
139 time is assumed to be the same as for locally produced diapausing eggs. As migration rates  
140 are low relative to the size of diapausing egg bank, emigration is assumed to have negligible  
141 effects on the source bank.

142

#### 143 *Genetic submodel*

144 All individuals are considered to have  $n$  neutral loci and  $n$  loci under selection. All loci are  
145 biallelic and no mutation is assumed. Absence of linkage is assumed among neutral loci and  
146 among loci under selection. Contrarily, the model accounts for physical linkage between  
147 each neutral locus and a corresponding selected locus. Several recombination levels,  
148 including absence of linkage, were assumed. Loci under selection act additively on growth  
149 rate. Consequently, no dominance and no epistatic effects are assumed. Local adaptation  
150 requires a genotype-environment interaction on fitness. This is modeled through  $\delta_{i,j,l}$ , which  
151 is the effect on the intrinsic growth rate (see below) of allele  $i$  ( $i: 1, 2$ ) at locus  $j$  ( $j: 1, \dots, n$ ) in

152 locality  $l$  ( $l: 1, 2$ ). The assumptions are (1)  $\delta_{1,j,1} = \delta_{2,j,2}$ , and (2)  $\delta_{i,j,l} = -\delta_{j \neq i,j,l}$ ; so, homozygotes  
 153 will experience an increase or decrease of their growth rate by  $|2\delta|$  depending on the  
 154 locality, whereas heterozygotes do not. Hence, the growth rate for each genotype  $g$  in each  
 155 locality  $l$  ( $r_{g,l}$ ) can be decomposed into  $r$  (basal growth rate) and  $\theta$  (deviation of each  
 156 genotype), so that

$$157 \quad r_{g,l} = r + \theta_{g,l}$$

158 where  $g$  is the genotype,  $l$  is the locality, and  $\theta_{g,l}$  is the summation of the fitness components  
 159 ( $\delta$ ) in locality  $l$  of the alleles carried by a genotype  $g$  in the  $n$  loci under selection. Thus, in any  
 160 given locality, the growth rate during the asexual reproduction will vary between the limits  $r$   
 161  $\pm 2n\delta$ .

162 Sexual reproduction is assumed to be panmictic and, for simplicity, is considered to be  
 163 synchronic and at the end of the growing season ( $t = \tau$ ). As linkage disequilibrium can occur  
 164 due to selection and genetic drift, gametic frequencies are computed. Gametes are then  
 165 drawn to produce the diapausing eggs.

166 Genetic distance between populations was estimated based on neutral loci as

$$167 \quad F_{ST} = \frac{\overline{H}_T - \overline{H}_S}{\overline{H}_T},$$

168 where  $\overline{H}_T$  is the average expected heterozygosity for the two populations considered as a  
 169 single one for the neutral loci, and  $\overline{H}_S$  the average of the mean expected heterozygosity  
 170 within each populations for the neutral loci (Hedrick, 2011). Allelic frequencies for each locus  
 171 were computed using the total number of alleles. For the loci under selection, genetic  
 172 distance ( $F_{STQ}$ ) was computed analogously to the neutral loci (Le Corre & Kremer, 2012).  $F_{ST}$   
 173 and  $F_{STQ}$  values were obtained just after hatching of diapausing eggs.

174



175 *Population growth*

176 The asexual phase spans from time  $t = 0$  to  $\tau$ , which is the moment when sexual  
177 reproduction takes place. During the asexual phase the population grows deterministically  
178 according to a logistic growth model:

$$179 \quad \frac{dN_{i,g}}{dt} = N_{i,g} r_{i,g} \left[ 1 - \frac{\sum_g N_{i,g}}{K} \right]$$

180 where  $N_{i,g}$  is the density of the genotype  $g$  in the locality  $i$ ,  $r_{i,g}$  is its intrinsic population  
181 growth rate during the asexual phase, and  $K$  the carrying capacity. Note that  $K$  is the same  
182 regardless of genotype. At the onset of each asexual growth season ( $t = 0$ ),  $N_{i,g}$  is the sum of  
183 the hatched diapausing eggs, a fraction of them having been locally produced  $H_{i,g}$ , and the  
184 rest being immigrants  $M_{i,g}$ .

185 At  $t = \tau$  of the sexual generation  $y$ , the number of diapausing eggs produced  $P_{i,g}(y)$  is  
186 stochastically computed from  $N_{i,g}(\tau, y)$  assuming a sexual proportion  $m$  (fraction of the  
187 females that becomes sexual), a sex ratio  $sr$  and an effective fecundity  $e$  (number of  
188 diapausing eggs produced per sexual female).

189 Mortality of diapausing eggs in the sediment with egg bank was assumed to be age-  
190 independent (annual survival rate  $\gamma$ ). Empirical information supporting this assumption for  
191 field populations is not available. Notice however that absence of egg bank can be due to  
192 fast senescence. When a new planktonic growing season starts ( $t = 0$ ) a fraction  $\lambda$  of the  
193 diapausing eggs in the sediment hatches.

194

195 *Source population and local population founding*

196 The two populations are founded at time  $y = t = 0$  by  $F$  diapausing eggs randomly drawn  
197 from a single source population. The source population is assumed to be in Hardy-Weinberg  
198 equilibrium and of infinite size, so that extraction of migrants does not change genotype  
199 frequencies. All loci are considered neutral in the source population, so no preadaptation to  
200 any of the populations exists.

201

202 *Model implementation*

203 The impact of carrying capacity ( $K$ ), growth rate ( $r$ ), migration ( $M$ ), selection pressure ( $\delta$ ) and  
204 recombination rate on  $F_{ST}$ 's were analyzed by exploring a range of realistic values for  
205 zooplanktonic organisms.  $K$  was varied from  $2 \cdot 10^2$  to  $2 \cdot 10^7$  individuals, which is equivalent to  
206 densities from 0.001 to 100 individuals/L in a small pond of 200 m<sup>2</sup> and 1 m depth, in good  
207 agreement with reported average densities of cladocerans and rotifers (Carmona, Gómez &  
208 Serra, 1995; Ortells, Gómez & Serra, 2003; Tavernini, 2008).  $r$  was explored from 0.05 to 1  
209 days<sup>-1</sup>. Cladocerans show maximum  $r$  of 0.2-0.6 days<sup>-1</sup> and rotifers 0.2-1.5 days<sup>-1</sup> (Allan,  
210 1976). The number of population founders ( $F$ ) was set to 1 diapausing egg across most  
211 simulations, that is, foundation is considered a rare event. Note that as the model assumes  
212 cyclical parthenogenesis, a single diapausing egg is enough for population foundations. The  
213 effect of numbers of founders ( $F$ ) was also explored (1, 2, 5, 50 diapausing eggs). Other  
214 parameter values used in the simulations are shown in Table 1.

215 Simulations considered two scenarios regarding diapausing egg banks: (1) an annual,  
216 age-independent, diapausing egg survival rate on the sediment ( $\gamma = 0.763$ ) (i.e., existence of  
217 a diapausing egg bank); and (2)  $\gamma = 0.763$  for eggs of age = 1 and a  $\gamma = 0$  for older eggs (i.e.,  
218 absence of diapausing egg bank). Parameters for the diapausing egg bank ( $\gamma$  and  $\lambda$ , the  
219 annual hatching rate) were estimated from rotifer diapausing egg banks (García-Roger,  
220 Carmona & Serra, 2006c) by adjusting them to the model described by García-Roger *et al.*  
221 (García-Roger, Carmona & Serra, 2006a).

222 The simulation model was implemented in C++ and based on Monte-Carlo procedures  
223 (code available at [github.com/monpau/founder\\_effects](https://github.com/monpau/founder_effects)). The Mersenne twister algorithm  
224 (Matsumoto & Nishimura, 1998) was used as random number generator. The logistic model  
225 was iterated numerically. 50 replicates for each parameter combination (but 100 for values  
226 of  $\delta$  and recombination rate) were performed. For each replicate, a source population was  
227 randomly created by drawing from a uniform distribution the allelic frequencies of the  $n$  and  
228  $s$  loci. After foundation of the two populations, 1000 sexual generations (4000 generations  
229 for some scenarios) were simulated.

230 Sampling effects were taken into account for hatching and survival of diapausing eggs  
231 if the total number of eggs in the population was lower than 1000. Selection of immigrants  
232 and gametes for mating were performed randomly regardless of the number of  
233 eggs/individuals involved.

234 The assessment of statistical differences between  $F_{ST}$ 's values under a neutral scenario  
235 and scenarios with selective pressure and different recombination rates was performed with  
236 an ANOVA and *a priori* contrasts. Correlations between  $F_{ST}$  and  $F_{STQ}$  at different  
237 combinations of population size, recombination rates and selective pressure were also

238 tested using Kendall's Tau and Spearman's Rho. All statistical analyses were performed using  
239 SPSS v. 17 (SPSS Inc., Chicago, USA)

## 240 **Results**

241 The population dynamics of a newly founded population, using the parameters shown in  
242 Table 1, with  $\tau = 60$  days and  $r = 0.3 \text{ days}^{-1}$  – which are realistic values for both the length of  
243 the growth season (Tavernini, 2008) and the intrinsic growth rate of many aquatic  
244 invertebrates (Allan, 1976) – show that carrying capacity ( $K$ ) is reached in less than two  
245 sexual generations, even in the case of the highest  $K$  (i.e.  $K = 2 \cdot 10^7$  individuals). Thus,  $K$  is a  
246 good proxy of population size and we will use both terms interchangeably hereafter.

### 247 *Effect of migration*

248 The effect of the number of immigrants on genetic differentiation strongly depends on  $K$  (i.e.  
249 population size; Fig. 2). In both the small and the large populations,  $F_{ST}$  decreases with  
250 increasing migration rates, as expected under a neutral scenario (Wright, 1931). For the  
251 lowest carrying capacity tested ( $K=2 \cdot 10^2$  individuals; Fig. 2.A),  $F_{ST}$  decreased rapidly down to  
252 very low levels with increasing migration. By contrast, for the highest  $K$  tested ( $K = 2 \cdot 10^7$   
253 individuals; Fig. 2.B),  $F_{ST}$  was rather insensitive to the effect of migration, and populations  
254 remained highly differentiated ( $F_{ST} > 0.2$ ) even at high levels of migration. The number of  
255 migrants needed to cause a considerable decrease of genetic differentiation is in the order of  
256 100 and 1000 individuals/sexual generation for the situation without and with diapausing  
257 eggs respectively.

258 *Effect of population size*

259 Carrying capacity (i.e population size) had strong effects on  $F_{ST}$  (Fig. 3). In small populations  
260 (i.e. low  $K$ ) populations did not differ genetically, while in large populations,  $F_{ST}$  remained as  
261 high as the values observed just after population foundation. This pattern suggests  
262 importance of migration and persistent founder effects respectively. At intermediate values  
263 of  $K$ , genetic differentiation peaked, probably due to higher drift effects. In other words, the  
264 highest  $F_{ST}$  values are found at intermediate population sizes. The pattern is qualitatively  
265 similar with and without diapausing egg bank, but the maximum genetic differentiation  
266 occurred in large populations without egg bank, and maximum  $F_{ST}$  is higher with diapausing  
267 egg bank. These results are robust to changes in the maximum number of sexual generations  
268 explored (results for maximum  $y = 100, 500, 2000$  and  $4000$  generations, data not shown).  
269 However, at 100 and to a lesser extent 500 sexual generations, the peak of  $F_{ST}$  at  
270 intermediate population sizes was less pronounced than at later sexual generations.

271 The dynamics and net increment of  $F_{ST}$  was explored from the 1<sup>st</sup> to the 4000<sup>th</sup> sexual  
272 generation (Figure 4). In the absence of a diapausing egg bank (Fig. 4 A),  $F_{ST}$  decreases with  
273 time at low population size, and this situation is reversed when  $K$  increases, to finally  
274 become virtually constant at the largest population size explored ( $K = 2 \cdot 10^7$ ). A similar  
275 qualitative pattern is found when a diapausing egg bank is present (Fig. 4 B), although the  
276 shift to an increasing  $F_{ST}$  time course occurs at lower population sizes, and also  $F_{ST}$  constancy  
277 is achieved at lower  $K$ . Note that the small negative change found at  $K = 2 \cdot 10^2$  with and  
278 without bank is associated to the very low initial  $F_{ST}$  values (Fig. 4 C, D). Also note that  $F_{ST}$   
279 values are calculated after hatching of residents and immigrants; for instance, at  $y = 1$ ,  $F_{ST}$   
280 value is not the value after foundation but after migration. In summary, population size and

281 presence or absence of a diapausing egg bank are key to predict the main force shaping the  
282 genetic structure. Decreasing  $F_{ST}$  indicates that migration is the dominant factor, while  
283 increasing values show that drift becomes dominant. The time-constant  $F_{ST}$  indicates the  
284 importance of persistent founder effects on the shaping of the genetic structure of  
285 populations.

286 Population growth rate interacts with population size in determining the level of  
287 genetic differentiation (Fig. 5). Low growth rates result in low genetic differentiation,  
288 regardless of population size, indicating a high impact of migration. However, for population  
289 growth rates above  $0.1 \text{ d}^{-1}$ , which are common for zooplanktonic organisms, genetic  
290 differentiation becomes sensitive to variations in population size.

#### 291 *Effects of the number of founders*

292 Increasing the number of population founders  $F$  results in a dramatic decrease of  $F_{ST}$  values  
293 just after foundation (Fig. 6); for instance, if compared to  $F = 1$ ,  $F_{ST}$  is reduced by half for  $F =$   
294 2, and approaches 0 for  $F = 50$ . After 4000 sexual generations, the level of population  
295 differentiation still shows a negative relationship with the number of founders. Given this  
296 strong effect, we explored in further simulations how  $F$  affects the relationships between  
297 population differentiation and other factors. Our results suggest that the patterns outlined  
298 above are qualitatively maintained for  $F > 1$  (data not shown).

#### 299 *Effect of local adaptation*

300 The effect of local adaptation was explored at two levels of  $K$  ( $2 \cdot 10^4$  and  $2 \cdot 10^7$  individuals),  
301 which are realistic values for cladocerans and rotifers respectively. Two different selection  
302 scenarios ( $\delta = 10^{-4} \text{ days}^{-1}$ , weak selection, and  $10^{-2} \text{ days}^{-1}$ , strong selection) in the

303 presence/absence of diapausing egg bank, and six recombination rates – from complete  
304 linkage to unlinked genes – were tested (Fig. 7 summarizes the results for the scenario with  
305 diapausing egg bank; see Fig. S1, for the equivalent scenario without diapausing egg bank).

306 With strong selection,  $F_{STQ}$  reaches almost maximum values – i.e., populations are  
307 almost fixed for the locally adapted alleles – regardless of  $K$  (Fig. 7). In the case of  
308 populations with  $K=2\cdot 10^4$ , all  $F_{ST}$  values are statistically different from those obtained  
309 without selection (p-values < 0.05 except at 0.5 recombination rate; p-value = 0.057).  
310 However,  $F_{ST}$  values are similar irrespective of the recombination rate. In contrast, for high  $K$ ,  
311 only those values of  $F_{ST}$  with complete linkage (recombination rate = 0) are statistically  
312 different of those found without selection. This indicates that genetic hitchhiking in large  
313 populations acts only on neutral loci tightly linked to those under selection. Otherwise,  
314 linkage to the genes under selection does not reduce the persistence of founder effects.

315 As expected,  $F_{STQ}$  indicates that local adaptation becomes less important with weak  
316 selection. In large populations ( $K = 2\cdot 10^7$ ),  $F_{ST}$  values do not statistically differ from the  
317 neutral scenario, showing the higher importance of founder effects. Moreover,  $F_{STQ}$  values  
318 also appear to be affected by persistent founder effects. In contrast to the situation with  
319 strong selection, genetic linkage does not alter differentiation at neutral loci. However, in  
320 small populations ( $K = 2\cdot 10^4$ ), local adaptation does play a role. Mean  $F_{ST}$  values statistically  
321 differ from the neutral scenario at all recombination rates (from 0.0 to 0.5), and the variance  
322 of the distribution of  $F_{ST}$  values is decreased (see Fig. 3 for comparison). Note that drift is the  
323 dominant factor in relatively small ( $K = 2\cdot 10^4$ ) populations with diapausing egg bank.

### 324 *Effects of diapausing egg banks*

325 The scenario without diapausing egg bank (see Supplementary Fig. S1) is similar to that with  
326 diapausing egg bank in the case of strong selection. However, some differences can be  
327 highlighted. If compared to the strong selection scenario, in weak selection conditions: (1) at  
328  $K = 2 \cdot 10^7$  genes under selection are less affected by persistent founder effects and  
329 populations show a trend to be locally adapted; (2) at  $K = 2 \cdot 10^4$ ,  $F_{ST}$  values at recombination  
330 rates 0.0 and 0.1 are statistically different from the neutral scenario – unlike at higher  
331 recombination rates –, which indicates that genetic hitchhiking could be of some  
332 importance; (3) at  $K = 2 \cdot 10^4$   $F_{ST}$  and  $F_{STQ}$  had higher variance at all recombination rates.

333 In the absence of a diapausing egg bank, populations reach maximum  $F_{STQ}$  values in  
334 about 40-50 sexual generations regardless of population size (data not shown). However,  
335 when a diapausing egg bank exists, advantageous alleles need a longer time to reach fixation  
336 (about 150 sexual generations for  $K = 2 \cdot 10^4$ , and about 300 generations for  $K = 2 \cdot 10^7$ ).

337 We computed  $F_{STQ}$  vs.  $F_{ST}$  correlations within each tested parameter combination.  
338 Significant correlations were found only in the case of the low  $K$  ( $2 \cdot 10^4$ ) without diapausing  
339 egg bank. Correlation coefficient is always positive, and the ranges are: Kendall's tau = 0.66-  
340 0.53 and Spearman's rho = 0.73-0.56 for strong selection; Kendall's tau = 0.68-0.32 and  
341 Spearman's rho = 0.80-0.38 for weak selection.

## 342 **Discussion**

343 The understanding of the evolutionary factors responsible for the strong population  
344 structure of passively dispersed aquatic organisms in the face of potentially high gene flow  
345 has attracted considerable attention in the last decade (De Meester et al., 2002; Mills, Lunt



346 & Gómez, 2007; Campillo et al., 2009). We have presented a specific model and, by  
347 simulation, explored the effects of genetic drift (founder effects), gene flow via migration  
348 and local adaptation on genetic differentiation. Our results show that the strongest effect  
349 was caused by persistent founder effects, resulting largely from the distinctive life history  
350 traits of these organisms: few population founders, high rates of population growth, large  
351 population sizes and the presence of diapausing egg banks. These results are in agreement  
352 with those of Boileau *et al.* (Boileau, Hebert & Schwartz, 1992), who proposed that  
353 persistent founder effects are an important force shaping the genetic structure of passively  
354 dispersed aquatic organisms, although he did not explore the importance of selection or  
355 genetic linkage. The most remarkable and novel result of our simulations is that the role of  
356 local adaptation and genetic hitchhiking on shaping genetic structure of these organisms is  
357 not significant in large populations, although it plays a significant role in small populations.

358 In agreement with (Boileau, Hebert & Schwartz, 1992), migration has a very limited  
359 effect on the population structure of passively dispersed aquatic organisms. For instance, a  
360 migration rate of 1000 individuals per sexual generation is needed to cause a noticeable  
361 effect on  $F_{ST}$  in a large population. Although direct estimates of the number of dispersing  
362 stages are unavailable, this extremely large value appears unlikely to occur between non-  
363 connected ponds (Cáceres & Soluk, 2002; Allen, 2007; Frisch, Green & Figuerola, 2007), and  
364 is inconsistent with estimates of the number of founders in populations, which are expected  
365 to be correlated with regular immigration rates (Louette et al., 2007) Badosa *personal*  
366 *communication*). However, in small populations, our model recovers the expected pattern  
367 for the combined effect of migration and drift under neutral genetic differentiation.

368           Among the factors studied in our model, population size has been shown to be largely  
369 responsible for establishing the levels of genetic differentiation observed in natural  
370 populations of aquatic organisms. In addition, this effect is strongly reinforced when a  
371 diapausing egg bank is established. Although egg banks could increase gene flow by  
372 postponing migration in the bank (Kaj, Krone & Lascoux, 2001; Berg, 2005), they act mainly  
373 buffering the effects of migration and reducing genetic drift, which favors the establishment  
374 of persistent founder effects. In our model, we assumed a parameter range in agreement  
375 with values reported for many aquatic organisms. Nevertheless, due to computational  
376 limitations the values used for population sizes and egg bank densities had to be limited, and  
377 could underestimate those attained in many natural populations. Some estimated  
378 population sizes and diapausing egg bank densities in rotifers are one or two orders of  
379 magnitude higher than the maximum values considered here (Carmona, Gómez & Serra,  
380 1995; Ortells, Gómez & Serra, 2003). Diapausing egg bank densities for zooplanktonic  
381 organisms are in the order of  $10^3$ - $10^7$  eggs/m<sup>2</sup> (Hairston, 1996), although densities in the  
382 sediment layers that could provide recruits are uncertain. However, modeling larger  
383 population sizes is unlikely to change our results qualitatively; if anything, they would  
384 increase the relative impact of persistent founder effects.

385           Local adaptation seems to be common and has been well documented in cladocerans  
386 (Cousyn et al., 2001; De Meester et al., 2002; Decaestecker et al., 2007) but, seems to be  
387 rarer in rotifers – though study effort in rotifers is much lower and restricted to rather  
388 generalist species – ([Campillo et al. 2010](#)). However, the effect of local adaptation on  
389 genetic structure does not seem to be general, as it is weakened by neutral and  
390 demographic factors. A limited role for local adaptation in continental aquatic invertebrates

391 has been recently suggested (Campillo et al., 2009; Allen, Thum & Cáceres, 2010). Our  
392 results indicate that although local adaptation does occur, its effects are only apparent on  
393 population structure when population sizes and diapausing egg banks are relatively small.  
394 Given that rotifers tend to have larger population sizes than cladocerans, this would mean  
395 that the effects of local adaptation on population structure could differ between these  
396 organisms. According to our results, genetic hitchhiking appears to be of limited importance  
397 in shaping neutral genetic differentiation. We have only detected signs of its effect at (1)  
398 completely linked genes with high population size and strong selection, and at (2)  
399 intermediate population size without egg bank and weak selection. The lack of observed  
400 impact does not mean that genetic hitchhiking has no importance, but that other processes  
401 are dominating the outcome. We must stress that our main question is not whether local  
402 adaptation occurs or not, but if this adaptation affects genetic differentiation in neutral  
403 markers. We acknowledge that, due to computational limitations, our model simplifies the  
404 selective scenarios acting on continental aquatic invertebrates. As selection in natural  
405 populations of aquatic invertebrates is likely to be multifactorial, and fluctuating, this  
406 scenarios should be further explored.

407 Genetic analyses in recently established populations indicate that the number of  
408 founders is small (Haag et al., 2005; Louette et al., 2007; Ortells, Olmo & Armengol,  
409 2011)Badosa personal communication), and accordingly a single founder was assumed in  
410 most simulations. By assuming a single founder, the studied scenario corresponds, for  
411 instance, to a situation where a new region consisting of several lakes is open to colonization  
412 – e.g. after glaciation –, with few founders of any single lake, but with varying migration

413 rates among lakes. When we relaxed the assumption of a single founder, the only  
414 remarkable observed effect was a reduction on the final value of  $F_{ST}$ .

415 Globally, our results show that population genetic structure in these organisms is  
416 driven by persistent founder effects, genetic drift or local adaptation, with population size  
417 and the egg bank having a strong control on the dominance of each of these factors. In turn,  
418 these demographic variables can be linked to ecological features. If so, a habitat  
419 classification linking ecological factors, demographic features, and mechanisms acting on  
420 genetic structure could be possible. Therefore, in populations inhabiting permanent ponds  
421 and lakes where a low investment in diapause is generally found – as reflected in small  
422 diapausing egg banks in comparison to temporary or ephemeral ponds (Hebert 1974; Hebert  
423 1974; García-Roger et al. 2006; Campillo et al. 2010) –, an increased effect of local  
424 adaptation and genetic drift is expected. In contrast, in environmental conditions limiting  
425 population sizes, such as small rock pools or nutrient-poor lakes, migration can attain higher  
426 importance. If despite this, high genetic differentiation is detected, an effect of selective  
427 forces can be hypothesized. For instance, genetic hitchhiking has been suggested for a  
428 *Daphnia* metapopulation inhabiting temporal rock pools (Haag et al., 2006). Besides  
429 ecological features, our results suggest that differences can be expected between taxa  
430 differing in body size and so in their typical population sizes, and therefore differences  
431 between the smaller rotifers and the larger cladocerans are expected. As far as our results  
432 identify a restricted number of factors driving the genetic structure, they provide insights  
433 beyond the life cycle assumed (i.e., cyclical parthenogenesis), and could be extended to  
434 organisms with similar demographic features (i.e. high growth rates, high population  
435 densities or presence of seed or egg banks). For example, populations of sexual species with

436 high growth rates (i.e. *r* strategists) like crustaceans such *Artemia* or copepods, which  
437 produce egg banks, are also likely to benefit from a numerical advantage that will reduce the  
438 impact of migration on the genetic structure of their populations (Boileau, Hebert &  
439 Schwartz, 1992).

440 As we have shown, the rapid growth rate of colonists acts as a barrier against new  
441 migrants, and this is reinforced by the formation of diapausing stage banks and, in some  
442 cases, by local adaptation. This process leads to a persistent founder effect, and  
443 consequently, to a deviation from the migration-drift equilibrium. This has repercussions  
444 when interpreting phylogeographic signals (Gómez, Carvalho & Lunt, 2000; Waters, 2011).  
445 For instance patterns of “isolation-by-distance” found in several aquatic organisms,  
446 regardless of their reproductive mode, have been suggested to be due to a process of  
447 sequential colonizations (Gouws & Stewart, 2007; Gómez et al., 2007; Mills, Lunt & Gómez,  
448 2007; Muñoz et al., 2008). Our results are consistent with these proposals and suggest that  
449 caution should be applied when inferring a migration-drift mechanism of ‘isolation by  
450 distance’ from such patterns (i.e., correlation between genetic and geographical distances).  
451 Also, the establishment of persistent founder effects and competitive exclusion of closely  
452 related species can explain the phylogenetic overdispersion in communities, given a  
453 phylogenetic limiting similarity between species (Violle et al., 2011).

454 During the time window from the arrival of first colonizers to the establishment of the  
455 founder effects, the genetic structure of the population is still sensitive to migration or drift.  
456 Our results point out that this period is short, as a result of the high population growth rates  
457 of most aquatic organisms. Nevertheless, we found that with relatively low population  
458 growth rates, the numerical advantage is delayed and genetic differentiation is relatively

459 low. Inbreeding depression is expected to be larger in small populations (Lohr and Haag  
460 2015), and it could act favoring gene flow (Haag et al., 2002; Tortajada, Carmona & Serra,  
461 2009, 2010). Although this factor has not been explicitly modeled here, it will act in a similar  
462 way of reducing the growth rate, which will favor effective gene flow. However, severe  
463 inbreeding could also reduce the effective population size, and increase genetic drift, which  
464 will increase genetic differentiation. A more detailed exploration of this scenario will be  
465 needed and it will depend on the relative magnitude of the purging and migration.

466 Other factors not implemented in our model, but likely to occur in the wild, could also  
467 counteract the high genetic differentiation. For example, processes able to reduce  
468 population size during asexual growth phase (e.g., perturbations or environmental  
469 fluctuations) could increase the impact of gene flow. In addition, it will be of interest to test  
470 the strength of persistent founder effects buffering migrants with a higher fitness than  
471 locally adapted residents. These factors – inbreeding depression, environmental  
472 fluctuations, and preadapted immigrants – were not invoked in the initial formulation of the  
473 Monopolization Hypothesis and should be investigated in future analyses. An additional  
474 prospective is to include the effect of metapopulation structure. Recently, (Walser & Haag,  
475 2012) have shown that population turnover, which is expected to have high rate in small  
476 populations, could also explain the high genetic population differentiation.

477

#### 478 *Concluding remarks*

479 Molecular screening of natural population has uncovered an unexpectedly high genetic  
480 diversity in taxa with high dispersal potential. These findings challenged classical views of the  
481 evolutionary processes in small multicellular organisms, and when focused on aquatic

482 invertebrates, brought to postulate a combination of processes as causal factors for that  
483 genetic differentiation, the Monopolization Hypothesis (De Meester et al., 2002). Our  
484 analysis shows that a quantitative elaboration of this multifactorial hypothesis is able to  
485 dissect the relative weights of the different factors, and their interactions. Specifically, we  
486 found that founder effects drive the genetic structure of passively dispersed aquatic  
487 organisms. We conclude that although selective factors and migration have a role in  
488 explaining genetic structure of continental aquatic invertebrates, demographic processes are  
489 dominant. By studying which factors are important in what circumstances, our analysis can  
490 help understanding relevant differences among the genetic structure of different species.

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669

670

## 671 **Figure legends**

672 Figure 1. Demographic submodel.

673 Figure 2. Population differentiation ( $F_{ST}$ ) after 1000 sexual generations plotted against  
674 migration ( $M$ ) with and without a diapausing egg bank for (A)  $K = 2 \cdot 10^2$ , and (B)  $K = 2 \cdot 10^7$   
675 individuals. The rest of parameters were  $r = 0.3 \text{ d}^{-1}$ ,  $n = 5$ ,  $s = 0$  and  $F = 1$ . Box plots are based  
676 on 50 replicate simulations. Boxes represent 25<sup>th</sup> /75<sup>th</sup> percentile and black dots the 5<sup>th</sup>/95<sup>th</sup>  
677 percentile. Thin black lines and thick gray lines in each bar represent the median and the  
678 mean, respectively. Dashed, horizontal lines show the initial value of  $F_{ST}$  after foundation.

679 Figure 3. Population differentiation ( $F_{ST}$ ) after 1000 sexual generations plotted against  
680 carrying capacity ( $K$ ) with and without a diapausing egg bank. Simulation values for other  
681 parameters were  $r = 0.3 \text{ d}^{-1}$ ,  $n = 5$ ,  $s = 0$ ,  $F = 1$  and  $M = 2$ . Data is based on 50 replicate  
682 simulations. Boxes represent 25<sup>th</sup> /75<sup>th</sup> percentile and black dots the 5<sup>th</sup>/95<sup>th</sup> percentile. Thin  
683 black lines and thick gray lines in each bar represent the median and the mean, respectively.  
684 Dashed line shows the initial value of  $F_{ST}$  after foundation.

685 Figure 4. Effect of different carrying capacities ( $K$ ) on the trajectory of  $F_{ST}$  along 4000 sexual  
686 generations. (A, B) Box plot of the increment of  $F_{ST}$  ( $\Delta F_{ST}$ ) after 4000 sexual generations (A)  
687 without and (B) with diapausing egg bank is shown. (C, D) Time course of the average  $F_{ST}$   
688 values along 4000 generations (C) without and (D) with diapausing egg bank. Simulation  
689 conditions were  $r = 0.3 \text{ d}^{-1}$ ,  $n = 5$ ,  $s = 0$ ,  $F = 1$  individual and  $M = 2$  individuals. Data is based on  
690 50 replicates. Boxes represent 25<sup>th</sup> /75<sup>th</sup> percentile and black dots the 5<sup>th</sup>/95<sup>th</sup> percentile.



691 Thin black lines and thick gray lines in each bar represent the median and the mean,  
692 respectively. Dotted lines show the initial value of  $F_{ST}$  after foundation.

693 Figure 5. Contour plot showing  $F_{ST}$  values after 1000 sexual generations at different  
694 combinations to population growth rates and carrying capacity (A) without and (B) with  
695 diapausing egg bank. Simulation conditions were  $n = 5$ ,  $s = 0$ ,  $F = 1$  and  $M = 2$ . Data is based  
696 on 50 replicates.

697 Figure 6. Time course of the average  $F_{ST}$  value along 4000 generations for different number  
698 of founders ( $F = 1, 2, 5$  and  $50$ ), for  $K = 2 \cdot 10^4$  (A) and  $K = 2 \cdot 10^7$  (B) and  $M = 2$ . Solid lines:  
699 without diapausing egg bank, dotted lines: with diapausing egg bank. Average  $F_{ST}$  values  
700 obtained from 50 replicates.

701 Figure 7. Box plot graph of  $F_{ST}$  and  $F_{STQ}$  values after 1000 sexual generations with different  
702 recombination rates for two different values of fitness components ( $\delta = 10^{-4}$  and  $10^{-2} \text{ d}^{-1}$ ) and  
703 with presence of a diapausing egg bank. For each of the fitness scenario, the left panel refers  
704 to  $K = 2 \cdot 10^4$  and the right panel to  $K = 2 \cdot 10^7$ . Other parameters were  $r = 0.3 \text{ d}^{-1}$ ,  $n = 5$ ,  $s = 5$ ,  $F$   
705  $= 1$  and  $M = 2$ . Data is based on 100 replicates. Boxes represent 25<sup>th</sup> /75<sup>th</sup> percentile and  
706 black dots the 5<sup>th</sup>/95<sup>th</sup> percentile. Thin black lines and thick gray lines in each bar represent  
707 the median and the mean, respectively. Dashed lines show the initial value of  $F_{ST}$  after  
708 foundation. Asterisks indicate  $F_{ST}$  statistically different from those without selection ( $\delta = 0$ )  
709 (\*\*,  $\alpha = 0.05$ ; \*,  $\alpha = 0.1$ ).

710

711

712 Table 1. Summary of model parameters and assumed values.

Parameter	Definition	Value
$F$	Number of founders (individuals)	1 - 50
$M$	Number of immigrants per sexual generation (individuals)	0 - $10^5$
$\gamma$	Annual survival proportion of eggs in the egg bank	0.763 *
$\lambda$	Annual hatching proportion of diapausing eggs	0.046 *
$y$	Sexual generations	1000/4000
$\tau$	Duration of the asexual growth period (days)	60
$r$	Clonal growth rate of each genotype ( $\text{days}^{-1}$ )	0.05 - 1.00
$K$	Carrying capacity (individuals)	$2 \cdot 10^2$ - $2 \cdot 10^7$
$m$	Sexual proportion	0.7 †
$sr$	Sex ratio	0.5 ‡
$e$	Diapausing egg production per sexual female	3
$n$	Number of neutral loci	5
$\delta$	Additive value on $r$ ( $\text{days}^{-1}$ )	$10^{-5}$ - $10^{-1}$

713 \* Calculated from (García-Roger, Carmona &amp; Serra, 2006b) † (Alver &amp; Hagiwara, 2007) ‡

714 (Aparici, Carmona &amp; Serra, 1998).

715

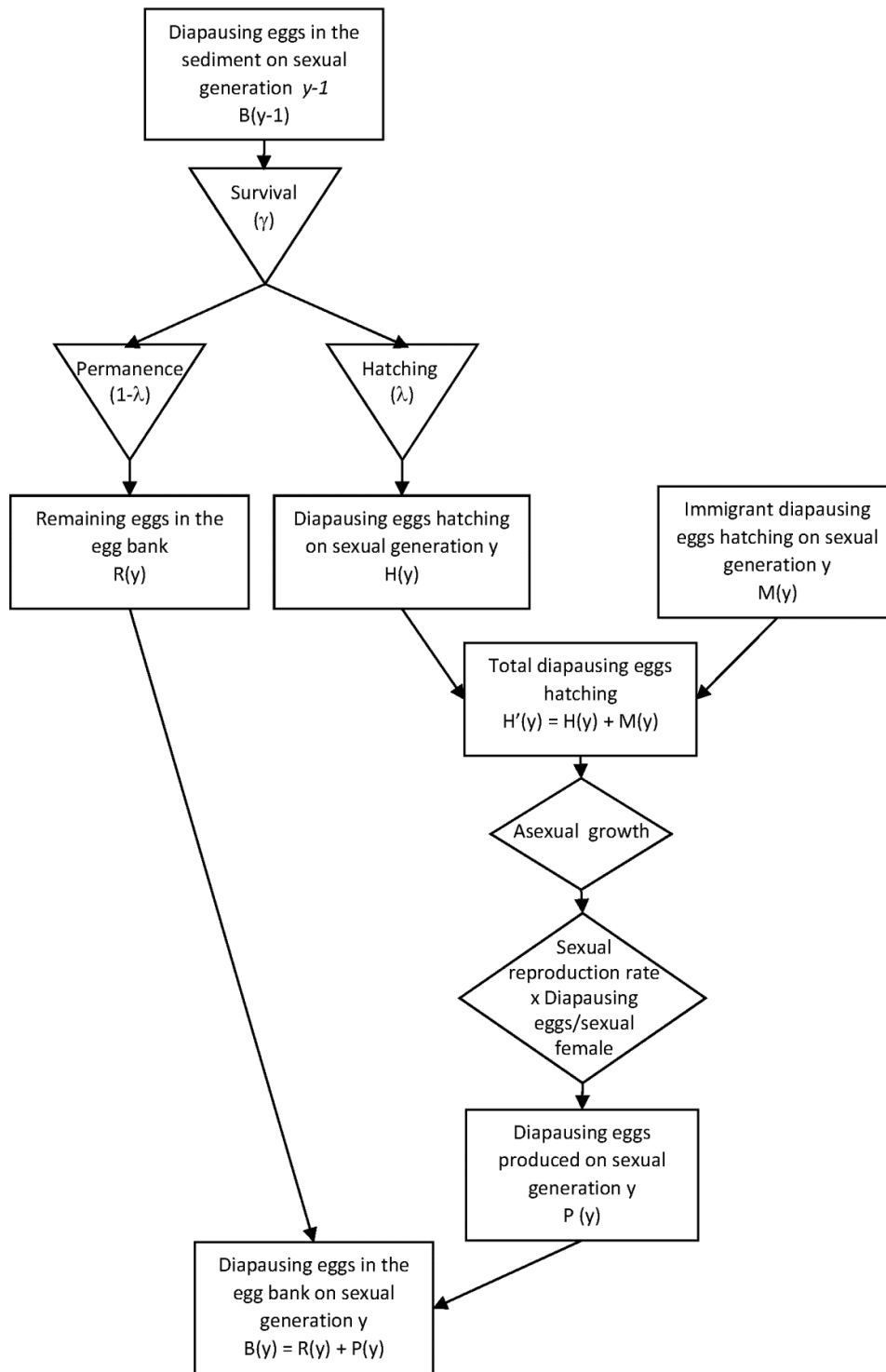


Figure 1.

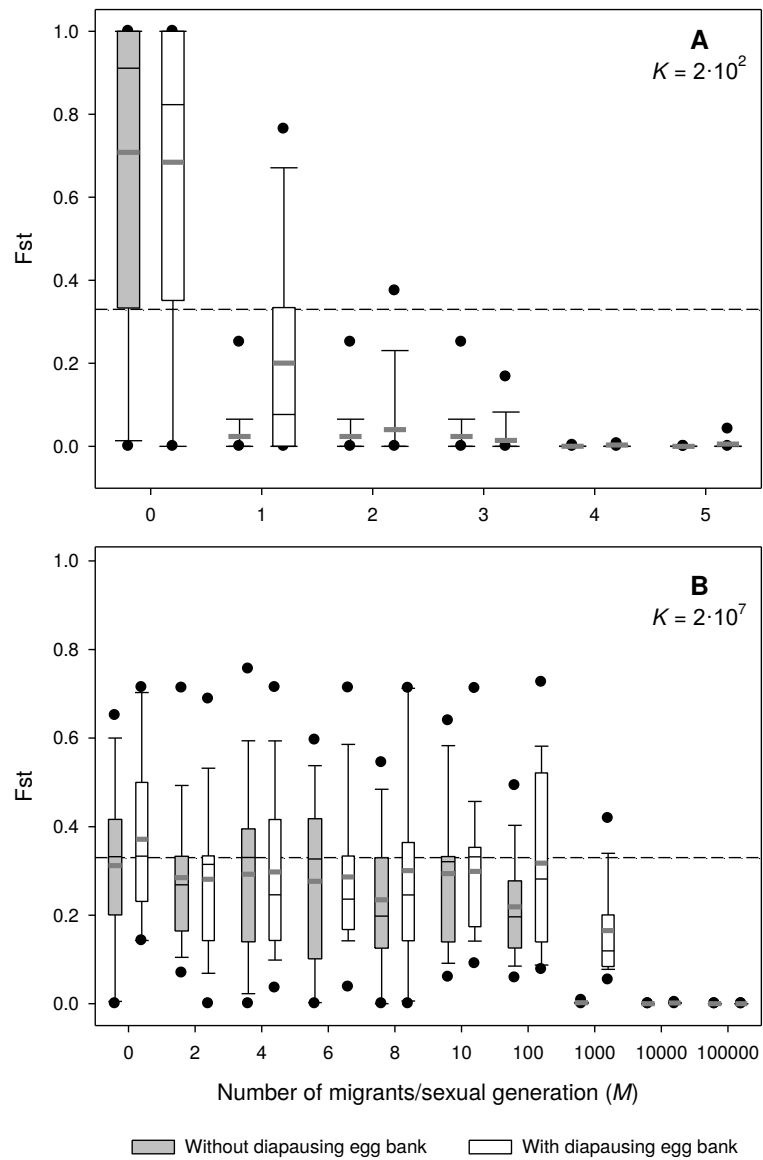


Figure 2.

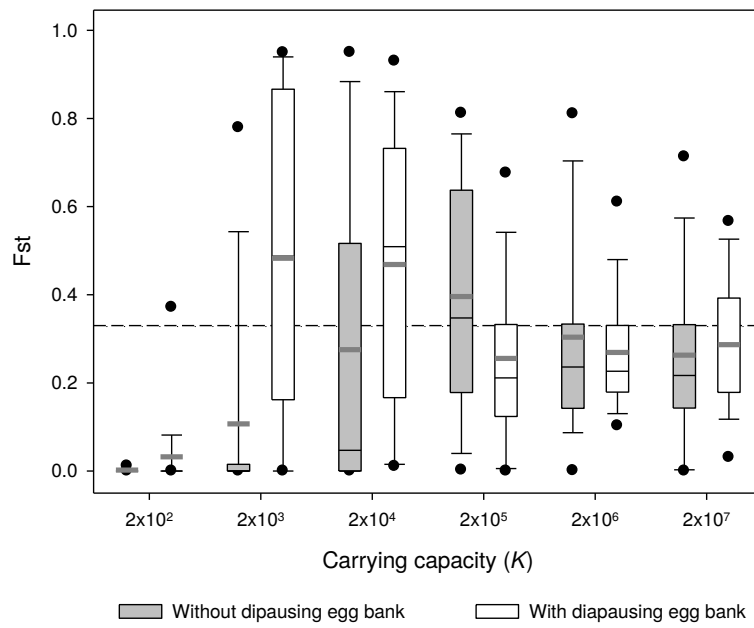


Figure 3.

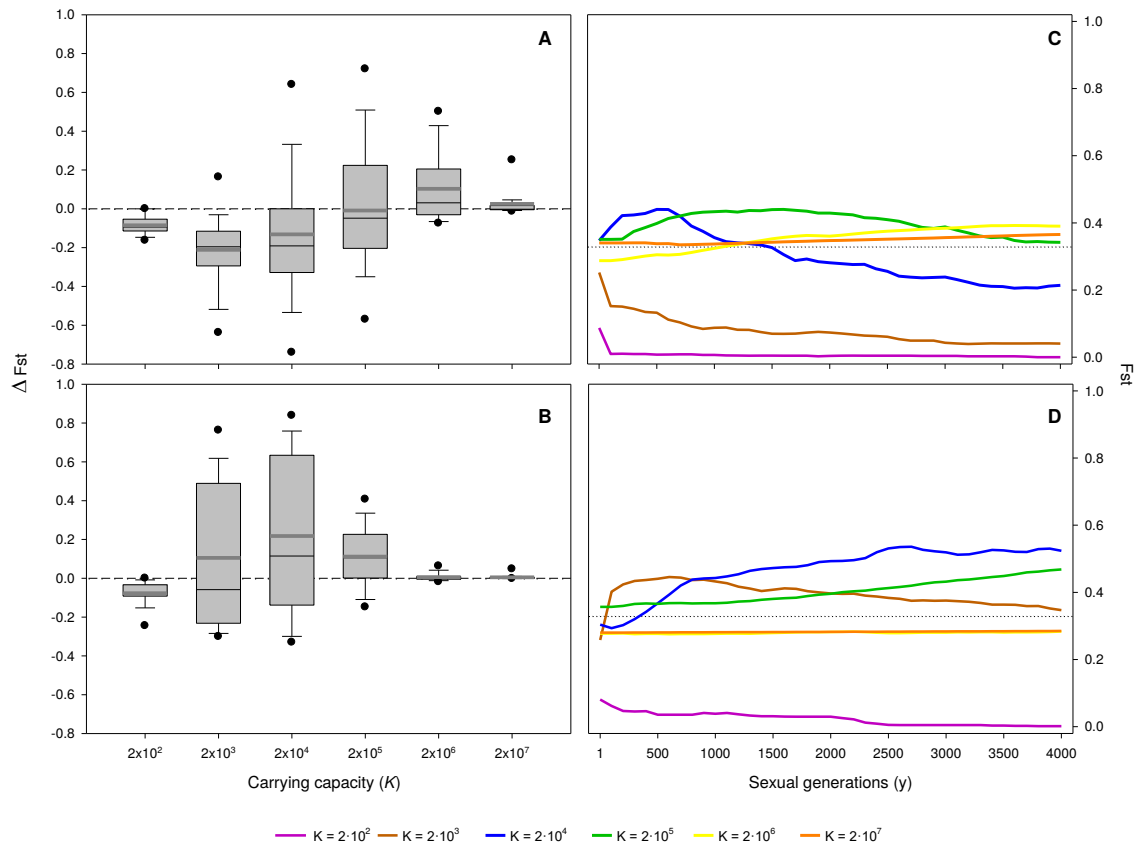


Figure 4.

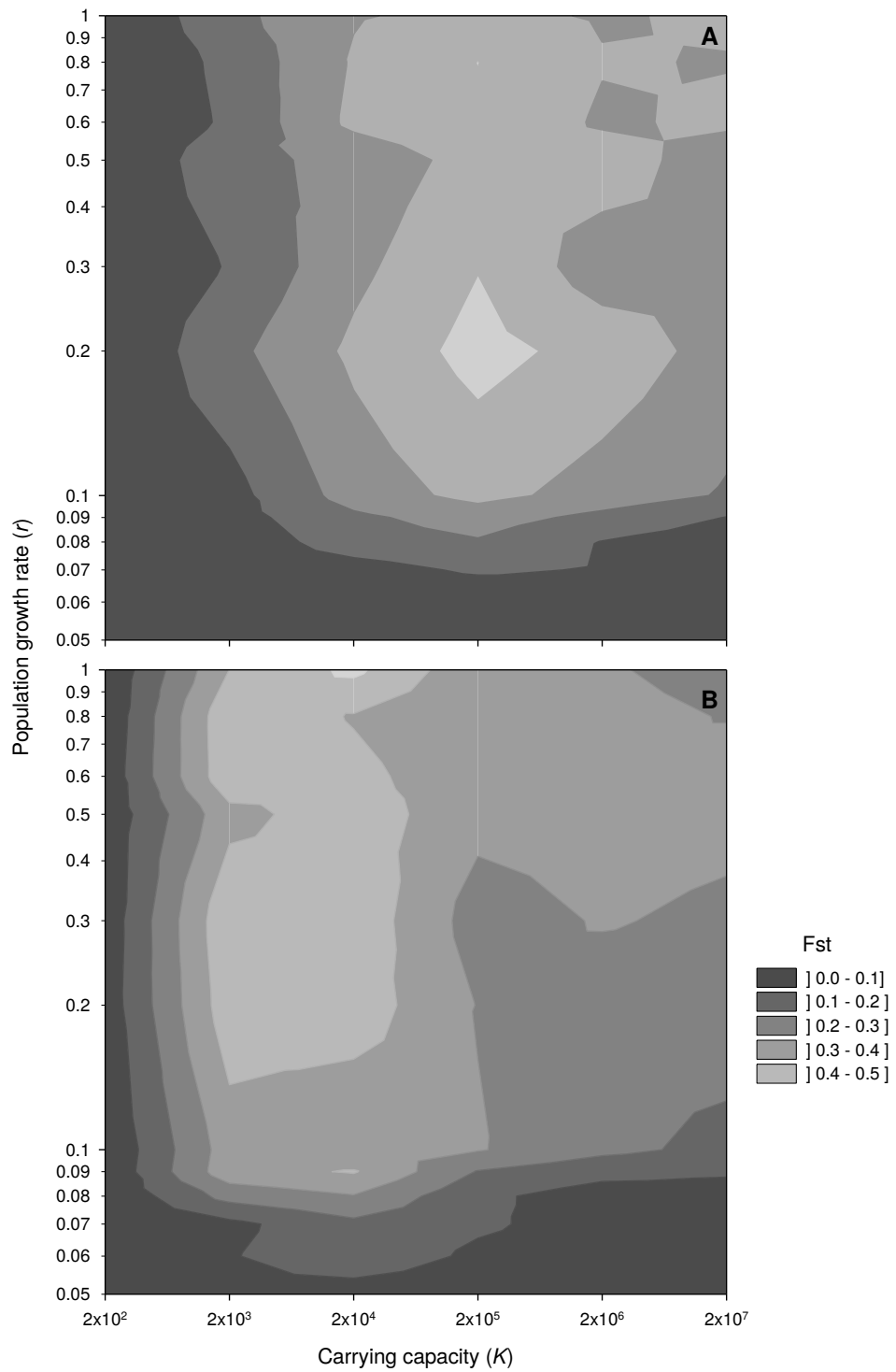


Figure 5.

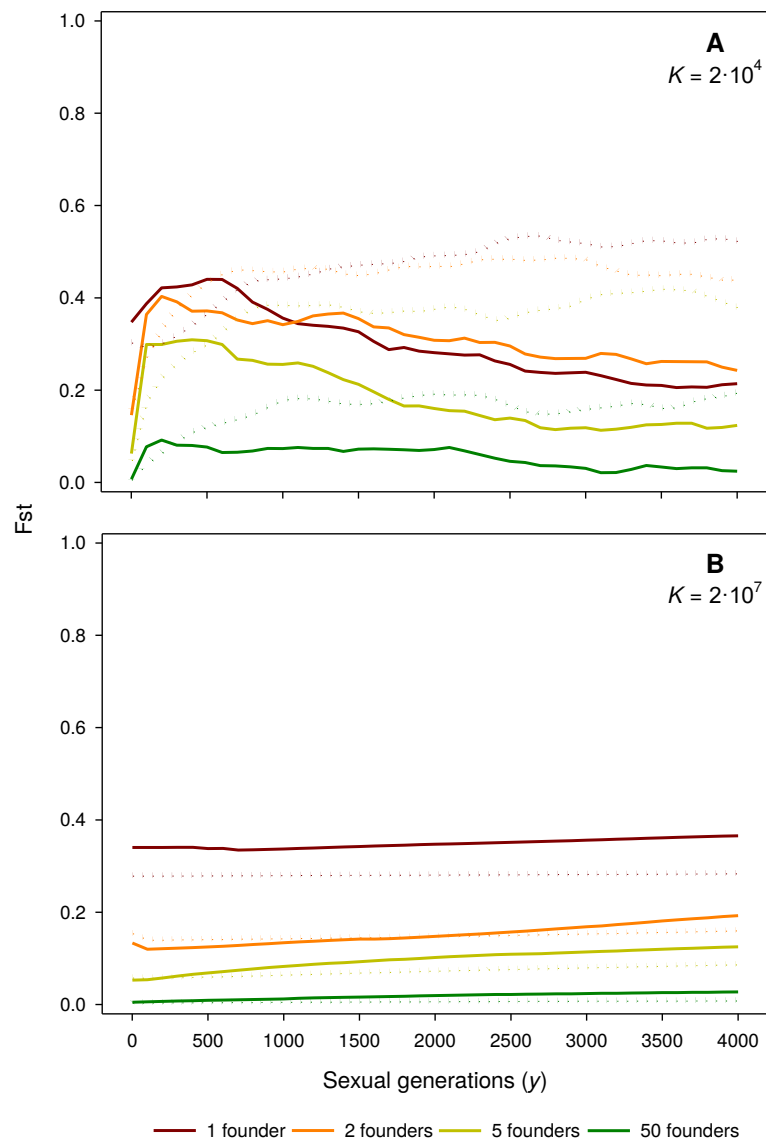


Figure 6.



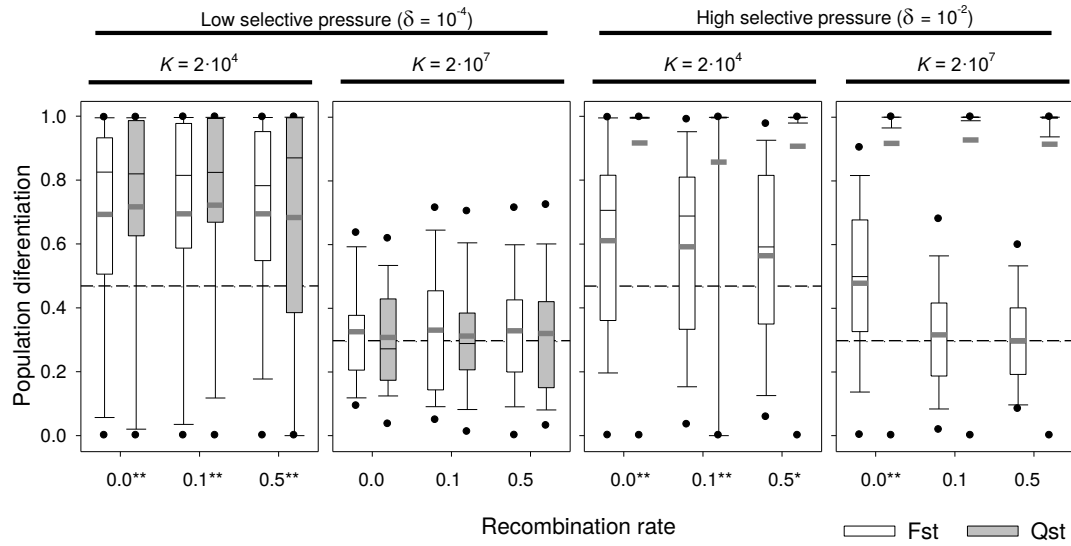


Figure 7.

1 **Figure legends**

2 Figure S1.- Box plot graph of  $F_{ST}$  and  $F_{STQ}$  values after 1000 sexual generations with different

3 recombination rates for two different values of fitness components ( $\delta = 10^{-4}$  and  $10^{-2} \text{ d}^{-1}$ ) and

4 without a diapausing egg bank. For each of the fitness scenario, the left panel refers to  $K =$

5  $2 \cdot 10^4$  and the right panel, to  $K = 2 \cdot 10^7$ . The rest of parameters were  $r = 0.3 \text{ d}^{-1}$ ,  $n = 5$ ,  $s = 5$ ,  $F$

6  $= 1$  and  $M = 2$ . Data is based on 100 replicates. Boxes represent 25<sup>th</sup> /75<sup>th</sup> percentile and

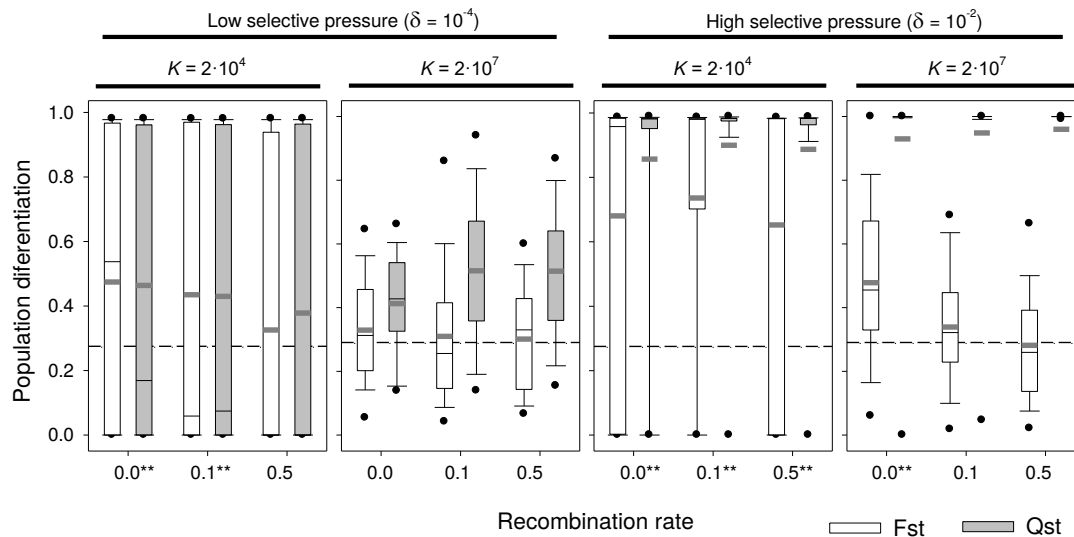
7 black dots the 5<sup>th</sup>/95<sup>th</sup> percentile. Thin black lines and thick gray lines in each bar represent

8 the median and the mean respectively. Dashed lines show the initial value of  $F_{ST}$  after

9 foundation. Asterisks indicate  $F_{ST}$  statistically different from those without selection ( $\delta = 0$ )

10 (\*\*,  $\alpha = 0.05$ ).

11



12

13 Figure S1.