



Founder effects drive the genetic structure of passively dispersed aquatic invertebrates

Journal:	<i>Journal of Evolutionary Biology</i>
Manuscript ID:	JEB-2012-00023
Manuscript Type:	Research Papers
Date Submitted by the Author:	10-Jan-2012
Complete List of Authors:	Montero-Pau, Javier; Univeristat de València, Institut Cavanilles de Biodiversitat i Biologia Evolutiva Gomez, Africa; University of Hull, Biological Sciences Serra, Manuel; Universitat de València, Institut Cavanilles de Biodiversitat i Biologia Evolutiva
Keywords:	migration, local adaptation, genetic differentiation, zooplankton, Monopolization Hypothesis, Rotifera, Cladocera

Founder effects drive the genetic structure of passively dispersed aquatic invertebrates

Javier Montero-Pau^{1,2,#}, Africa Gómez² and Manuel Serra¹

¹ *Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, A.O.22085, 46071, Valencia, Spain*

² *Department of Biological Sciences, University of Hull, Hull, HU6 7RX, UK*

[#]Corresponding author:

Javier Montero-Pau, Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, A.O.22085, 46071, Valencia (Spain)

Phone: (+34) 963543664

Fax: (+34) 963543 670

javier.montero@uv.es

Running title (45 characters):

Founder effects and local adaptation

Abstract

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

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

Introduction

Successful dispersal and colonization are essential for the establishment and persistence of species, and an understanding of these processes is crucial on the face of changing climate and habitat destruction, which is rapidly affecting the abundance and distribution patterns of many species (Parmesan & Yohe, 2003; Chen *et al.*, 2011). The evolutionary outcome of dispersal and colonization results from a complex interplay of neutral and selective factors, including local adaptation, founder effects or bottlenecks causing genetic drift during the first stages of colonization, inbreeding depression, or high gene flow that could erode local adaptation, etc (Lenormand 2002; Kliber & Eckert, 2005; Rosenblum *et al.*, 2007; Keller & Taylor, 2008; Verhoeven *et al.*, 2011). These factors shape the genetic structure of populations and the evolutionary history of species. In addition, life-cycle features and demographic characteristics are also needed to understand dispersion and colonization (Burton *et al.*, 2010). For example, species with high population growth rates after a bottleneck are more likely to increase their genetic variability (“founder-flush” model) (Carson, 1968; Templeton, 2008), and populations of organisms with resistant life stages are more likely to be connected by migration even at long distances (Frisch *et al.*, 2007). Predicting the outcome of all these factors is a major question in evolutionary and conservation ecology, which requires an understanding of the effect of each factor and their interactions.

Populations of passively dispersing aquatic invertebrates (e.g., freshwater bryozoans, rotifers, cladocerans, copepods, anostracans, notostracans) and macrophytes inhabiting lentic habitats often present a high level of neutral genetic differentiation (e.g., Freeland *et al.*, 2000; Zierold *et al.*, 2007; Muñoz *et al.*, 2008; Xu *et al.*, 2009; Makino & Tanabe, 2009; Escudero *et al.*, 2010; Xiang *et al.*, 2011), despite their high dispersal capabilities through

diapausing propagules (Frisch *et al.*, 2007; Allen, 2007; Vanschoenwinkel *et al.*, 2011). This has been termed the “migration-gene flow paradox”. Regardless of their taxonomic disparity, these organisms share biological features promoting a rapid monopolization of resources in the new environment: high population growth rates, large population sizes and the production of resistant stages in their life cycle, which can accumulate in sediments forming diapausing propagule banks (Hairston, 1996; Brendonck & De Meester, 2003) and constitute the dispersal stage. As a result, once a habitat becomes available and is colonized, the population can grow very quickly creating a numerical advantage that dilutes the genetic impact of further immigrants (“high-density blocking”) (Hewitt, 1993), resulting in a persistent founder effect (Boileau *et al.*, 1992). This explanation was expanded by De Meester *et al.* (2002) into the so called “Monopolization Hypothesis” (MH hereafter) to include local adaptation as an important force contributing to reduce effective gene flow and therefore to maintain the genetic structure of passively dispersed aquatic organisms. The MH postulates that the migration-gene flow paradox could be explained by a combination of three factors: (1) persistent founder effects, (2) selection against immigrants due to local adaptation and (3) associations arising randomly between neutral markers and genes under selection.

Local adaptation is an important and rapid process in many zooplanktonic organisms (e.g., Cousyn *et al.*, 2001; Decaestecker *et al.*, 2007; Costanzo & Taylor, 2010). The impact of local adaptation on population genetic structure is diverse as it is dependent on the impact of other evolutionary forces, not only selection (Kawecki & Ebert, 2004). For instance, it can promote genetic differentiation (“isolation-by-adaptation”) (Nosil *et al.*, 2007) or reinforce the existing genetic differentiation (De Meester *et al.*, 2002) by reducing gene flow. Irrespective of being locally adapted, populations recently founded by a small number of

propagules can be highly inbred and show inbreeding depression (De Meester, 1993; Tortajada *et al.*, 2009). This could give migrants a fitness advantage and favor gene flow into the population (Ebert *et al.*, 2002; Haag *et al.*, 2006). The accumulation of large numbers of resistant stages as seed or diapausing egg banks (i.e. propagule banks) in sediments is also a characteristic of many aquatic species inhabiting temporary habitats. These propagule banks have an important role in ecological (Chesson, 1983; Cáceres, 1997) and evolutionary processes (Brendonck & De Meester, 2003). They increase the effective population size due to postponed reproduction in the bank, and thus reduce genetic drift (Kaj *et al.*, 2001). However, this effect could not be direct, as gene flow is also postponed in the bank (Kaj *et al.*, 2001; Berg, 2005).

The relative importance and interactions between the demographic, neutral and selective processes acting during colonization has remained poorly understood. Therefore, an explicit theoretical analysis of the effects of local adaptation, persistent founder effects, and their interplay on the differentiation of populations of aquatic organisms is timely, specially, during the first stages of colonization when populations are still small and, thus, more sensitive to the outcome of this interplay.

Here we have modeled the colonization process of zooplanktonic organisms with the aim of clarifying how migration rate, growth rate, population size, local adaptation, and life-cycle features like the existence of propagule banks shape the population genetic structure during the first stages of colonization, and how these factors interplay with genetic and selective processes. Of primary interest in our analysis is gaining insights into the relative importance of (1) persistent founder effects, (2) selection against immigrants as a consequence of local adaptation, and (3) random associations between neutral genes and genes under selection.

109

110 Materials and Methods

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

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

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

- 125 step 1. Hatching of diapausing eggs (resident and immigrant)
- 126 step 2. Asexual proliferation
- 127 step 3. Sexual reproduction and production of diapausing eggs
- 128 step 4. Diapausing eggs survival in the sediment
- 129 step 5. Migration of diapausing eggs
- 130 step 6. Back to step 1

Note that this demographic dynamics implies two different time scales: (1) a within-planktonic growing period (often within-year; index, t), and (2) an among-sexual generations scale (often among-years; index, y).

Migration, either from the source population or between habitats, is assumed to occur via diapausing eggs, which are passively transferred between habitats, and their hatching time is assumed to be the same as for locally produced diapausing eggs.

Genetic submodel

All individuals are considered to have n neutral loci and s loci under selection. All loci are biallelic and no mutation is assumed. The model accounts for physical linkage between selected and neutral loci with a variable recombination level. Loci under selection act additively on growth rate. Consequently, no dominance and no epistatic effects are assumed. For simplicity, every allele is considered to contribute with an equal value, δ , to the growth rate. Local adaptation requires a genotype-environment interaction on fitness. This is modeled through $\delta_{i,j,l}$, which is the effect on the intrinsic growth rate (see below) of allele i ($i: 1, 2$) at locus j ($j: 1, \dots, s$) in 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 will experience an increase or decrease of their growth rate depending on the locality, whereas heterozygotes do not. Hence, the growth rate for each genotype g in each locality l ($r_{g,l}$) can be decomposed in r (basal growth rate) and θ (deviation of each genotype), so that

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

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

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

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

$$F_{St} = \frac{\overline{Ht} - \overline{Hs}}{\overline{Ht}}$$

where \overline{Ht} is the average expected heterozygosity for the two populations considered as a single one for the neutral loci, and \overline{Hs} the average of the mean expected heterozygosity within each populations for the neutral loci. Allelic frequencies for each locus were computed using the total number of alleles. For the loci under selection, Q_{st} values were computed analogously to F_{st} values. F_{st} and Q_{st} values were obtained just after hatching of diapausing eggs.

Population growth

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

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

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

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

Mortality of diapausing eggs in the sediment is assumed to be age-independent (annual survival rate γ). When a new planktonic growing season starts ($t = 0$) a fraction λ of the diapausing eggs in the sediment hatches.

Source population and local population founding

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

Model implementation

The impact of carrying capacity (K), growth rate (r), migration (M), selection pressure (δ) and recombination rate on F_{st} 's were analyzed by exploring a range of realistic values for zooplanktonic organisms. K was tested from $2 \cdot 10^2$ to $2 \cdot 10^7$ individuals, which would be the equivalent to densities from 0.001 to 100 individuals/L in a small pond of 200 m² and 1 m depth, equivalent to reported average densities of cladocerans and rotifers (Carmona *et al.*, 1995; Ortells *et al.*, 2003; Tavernini, 2008). r was explored from 0.05 to 1 days⁻¹. Cladocerans show maximum r of 0.2-0.6 days⁻¹ and rotifers 0.2-1.5 days⁻¹ (Allan, 1976). The number of population founders (F) was set to 1 diapausing egg across most simulations, that is, foundation is considered a rare event. Note that as the model assumes cyclical parthenogenesis, a single diapausing egg is enough for population foundations. The effect of

199 numbers of founders (F) was also explored (1, 2, 5, 50 diapausing eggs). Other parameter
200 values used in the simulations are shown in Table 1.

201 Simulations considered two scenarios regarding diapausing egg banks: (1) an annual,
202 age independent, diapausing egg survival rate on the sediment ($\gamma = 0.763$) (i.e., existence of
203 a diapausing egg bank); and (2) $\gamma = 0.763$ for eggs of age = 1 and a $\gamma = 0$ for older eggs (i.e.,
204 absence of diapausing egg bank). Parameters for the diapausing egg bank (γ and λ , the
205 annual hatching rate) were estimated from rotifer diapausing egg banks (García-Roger *et al.*,
206 2006b) by adjusting them to the model described by García-Roger *et al.* (2006a).

207 The simulation model was implemented in C++ and based on Monte-Carlo
208 procedures. The Mersenne twister algorithm (Matsumoto & Nishimura, 1998) was used as
209 random number generator. 50 replicates for each parameter combination (but 100 for
210 values of δ and recombination rate) were performed. For each replicate, a source population
211 was randomly created by drawing from a uniform distribution the allelic frequencies of the n
212 and s loci. After foundation of the two populations, 1000 sexual generations (4000
213 generations for some scenarios) were simulated.

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

218 The assessment of statistical differences between F_{st} 's values under a neutral
219 scenario and scenarios with selective pressure and different recombination rates was
220 performed with an ANOVA and *a priori* contrasts. Correlations between F_{st} and Q_{st} at
221 different conditions of population size, recombination rates and selective pressure were also

tested using Kendall's Tau and Sperman's Rho. All statistical analyses were performed using SPSS Inc.

Results

Overview

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

Effect of migration

Our model results show that the effect of migration on the genetic differentiation is strongly dependent on K (i.e. population size) (Fig. 2). In both the small and the large populations F_{st} decreases with increasing migration rates, as expected under a neutral scenario. In the lowest carrying capacity tested ($K=2 \cdot 10^2$ individuals; Fig. 2.A), F_{st} decreased rapidly down to very low levels with increasing migration. By contrast, at the highest K tested ($K = 2 \cdot 10^7$ individuals; Fig. 2.B), F_{st} was rather insensitive to the effect of migration, and populations remained highly differentiated ($F_{st} > 0.2$) even at high levels of migration. The number of migrants needed to cause a striking decrease of genetic differentiation is in the order of 100 and 1000 individuals/sexual generation for the situation without and with diapausing eggs respectively.

Effect of population size

Carrying capacity (i.e population size) had strong effects on F_{st} (Fig. 3). At low population sizes (i.e. low K) populations did not differ genetically, while at high population sizes, F_{st} remained as high as the values observed just after population foundation. This pattern suggests importance of migration and persistent founder effects respectively. At intermediate values, genetic differentiation peaked, probably as a result of higher drift effects. As a result the highest F_{st} values are found at intermediate population sizes. The pattern is qualitatively similar regardless the existence or not of a diapausing egg bank, but the maximum genetic differentiation occurred at higher population sizes if no egg bank was assumed. These results are robust regarding the maximum number of sexual generations explored (results for maximum $y = 100, 500, 2000$ and 4000 generations, data not shown). However, at 100 and to a lesser extent 500 sexual generations the peak of F_{st} at intermediate population sizes was less pronounced than at later sexual generations.

The dynamics and net increment of F_{st} was explored from the 1st to the 4000th sexual generation (Figure 4). In the absence of a diapausing egg bank (Fig. 4 A), F_{st} decreases with time at low population size, and this situation is reversed when K increases, to finally become virtually constant at the largest population size explored ($K = 2 \cdot 10^7$). A similar qualitative pattern is found when a diapausing egg bank is present (Fig. 4 B), although the shift to an increasing F_{st} time course occurs at lower population sizes, and also F_{st} constancy is achieved at lower K . Note that the small negative change found at $K = 2 \cdot 10^2$ with and without bank is associated to the very low initial F_{st} values (Fig. 4 C, D). Also note that F_{st} values are calculated after hatching of residents and immigrants; for instance, at $y = 1$, F_{st} value is not the value after foundation but after migration. In summary, population size and presence or absence of a diapausing egg bank are key to predict the main force shaping the genetic structure. Decreasing F_{st} indicates that migration is the dominant factor, while

increasing values show that drift becomes dominant. The time-constant F_{st} indicates the importance of persistent founder effects on the shaping of the genetic structure of populations.

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

Effects of the number of founders

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

Effect of local adaptation

The effect of local adaptation was explored at two levels of K ($2 \cdot 10^4$ and $2 \cdot 10^7$ individuals), which are realistic values for cladocerans and rotifers respectively. Two different selection scenarios ($\delta = 10^{-4} \text{ days}^{-1}$, weak selection, and $10^{-2} \text{ days}^{-1}$, strong selection) in the presence/absence of diapausing egg bank, and six recombination rates -from complete linkage to unlinked genes- were also tested (Fig. 7 summarizes the results for the scenario with diapausing egg bank; see Fig. S1, for the equivalent scenario without diapausing egg bank).

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

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

The scenario without diapausing egg bank (see Supplementary Fig. S1) is similar to that with diapausing egg bank in the case of strong selection. However, some differences can be highlighted. If compared to the strong selection scenario, in weak selection conditions: (1) at $K = 2\cdot 10^7$ genes under selection are less affected by persistent founder effects and populations show a trend to be locally adapted; (2) at $K = 2\cdot 10^4$, F_{st} values at recombination

rates 0.0 and 0.1 are statistically different from the neutral scenario –unlike at higher recombination rates–, which indicates that genetic hitchhiking could be of some importance; (3) at $K = 2 \cdot 10^4$ F_{st} and Q_{st} had higher variance at all recombination rates.

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

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

Discussion

The understanding of the evolutionary factors responsible for the strong population structure of passively dispersed aquatic organisms in the face of potentially high gene flow has attracted considerable attention in the last decade (De Meester *et al.*, 2002; Mills *et al.*, 2007; Campillo *et al.*, 2009). The model presented here explores formally, in a powerful and extended way, the effects of different evolutionary forces on population structure. Our simulation results show that the strongest effect was caused by persistent founder effects, resulting largely from the distinctive life history traits of these organisms, including the interaction of the following factors: few population founders, high rates of population growth, large population sizes and the presence of diapausing egg banks. These results are in agreement with those of Boileau *et al.* (1992), who proposed that persistent founder effects

are an important force shaping the genetic structure of passively dispersed aquatic organisms, although he did not explore the importance of selection or genetic linkage. The most remarkable and novel result of our simulations is that the role of local adaptation and genetic hitchhiking on shaping genetic structure of these organisms is not significant in large populations, although it plays a significant role in small populations.

Our simulations also show that, in agreement with Boileau *et al.* (1992), migration has a very limited effect on the population structure of passively dispersed aquatic organisms. For instance, a migration rate of 1000 individuals per sexual generation is needed to cause a noticeable effect on F_{st} in a large population. Although direct estimates of the number of dispersing stages are unavailable, this seems an extremely large value unlikely to occur between non-connected ponds (Cáceres & Soluk, 2002; Frisch *et al.*, 2007; Allen, 2007), and inconsistent with estimates of the number of founders in populations, which are expected to be correlated with regular immigration rates (Louette *et al.*, 2007, Badosa *personal communication*). However, in small populations, our model recovers the expected pattern for the combined effect of migration and drift under neutral genetic differentiation.

Among the factors studied in our model, population size has been shown to be largely responsible for establishing the levels of genetic differentiation observed in natural populations of aquatic organisms. In addition, this effect is strongly reinforced when a diapausing egg bank is established. Although egg banks could increase gene flow by postponing migration in the bank (Kaj *et al.*, 2001; Berg, 2005), they act mainly buffering the effects of migration and reducing genetic drift, which favors the establishment of persistent founder effects. In our model, we assumed a parameter range in agreement with values reported for many aquatic organisms. Nevertheless, due to computational limitations the values used for population sizes and egg bank densities had to be limited, and could

underestimate those attained in many natural populations. Some estimated population sizes and diapausing egg bank densities in rotifers are 1 or 2 orders of magnitude higher than the maximum values considered here (Carmona *et al.*, 1995; Ortells *et al.*, 2003). Diapausing egg bank densities for zooplanktonic organisms are in the order of 10^3 - 10^7 eggs/m² (review in Hairston, 1996 for different zooplanktonic taxa), although densities in the sediment layers that could provide recruits are uncertain. However, modeling larger population sizes is unlikely to change our results qualitatively; if anything, they would make the relative impact of persistent founder effects stronger.

Local adaptation seems to be common and has been well documented in cladocerans (e.g., De Meester, 1996; Cousyn *et al.*, 2001; Decaestecker *et al.*, 2007) but seems to be rarer in rotifers -though study effort in rotifers is much lower and restricted to rather generalist species- (Campillo *et al.*, 2011). However, the effect of local adaptation on the genetic structure does not seem to be general, as its effect is weakened by neutral and demographic factors. A limited role for local adaptation in continental aquatic invertebrates has been recently suggested (Campillo *et al.*, 2009; Allen *et al.*, 2010). Our results indicate that local adaptation does occur, but it only has a noticeable effect on population structure when population sizes and diapausing egg banks are relatively small. Given that rotifers tend to have larger population sizes than cladocerans, this would mean that the effects of local adaptation on population structure could differ between these organisms. According to our results, the role of genetic hitchhiking of neutral genes linked to genes under selection appears to be of limited importance on genetic differentiation. We have only detected signs of its effect at (1) completely linked genes with high population size and strong selection, and at (2) intermediate population size without egg bank and weak selection. The lack of observed impact does not mean that genetic hitchhiking has no importance, but that other

processes are dominating the outcome. We must stress that our main question is not whether local adaptation occurs or not, but if this adaptation affects genetic differentiation in neutral markers. We acknowledge that, due to computational limitations, our model simplifies the selective scenarios acting on continental aquatic invertebrates. As selection in natural populations of aquatic invertebrates is likely to be multifactorial, and fluctuating, this scenarios should be further explored.

Genetic analyses in recently established populations indicate that the number of founders is small (Haag *et al.*, 2005; Louette *et al.*, 2007; Ortells *et al.*, 2011; Badosa *personal communication*), and consistently a single founder was assumed in most simulations. By assuming a single founder in most simulations, the studied scenario corresponds, for instance, to a situation where a new region consisting of several lakes is open to colonization –e.g. after glaciation–, with few founders of any single lake, but with varying migration rates among lakes. When we relaxed the assumption of a single founder, the only remarkable observed effect was a negative one on the final value of F_{st} .

Globally, our results show that population genetic structure in these organisms is driven by persistent founder effects, genetic drift or local adaptation, with population size and the egg bank having a strong control on the dominance of each of these factors. In turn, these demographic variables can be linked to ecological features. If so, a habitat classification linking ecological factors, demographic features, and mechanisms acting on genetic structure could be possible. Therefore, in populations inhabiting permanent ponds and lakes where a low investment in diapause is generally found –as reflected in small diapausing egg banks in comparison to temporary or ephemeral ponds (Hebert, 1974a; Hebert, 1974b; García-Roger *et al.*, 2006b; Campillo *et al.*, 2011)–, an increased effect of local adaptation and genetic drift is expected. In contrast, in environmental conditions limiting

population sizes, such as small rock pools or nutrient-poor lakes, migration can attain higher importance. If even so, high genetic differentiation is detected, an effect of selective forces can be hypothesized. For instance, genetic hitchhiking has been suggested for a *Daphnia* metapopulation inhabiting temporal rock pools (Haag *et al.*, 2006). Besides ecological features, our results suggest that differences can be expected between taxa differing in body size and so in their typical population sizes, and therefore differences between the smaller rotifers and the larger cladocerans are expected. As far as our results identify a restricted number of factors driving the genetic structure, they provide insights beyond the life cycle assumed (i.e., cyclical parthenogenesis), and could be extended to organisms with similar demographic features (i.e. high growth rates, high population densities or presence of seed or egg banks). For example, populations of sexual species with high growth rates (i.e. *r* strategists) like crustaceans such *Artemia* or copepods, which produce egg banks, are also likely to benefit from a numerical advantage that will reduce the impact of migration on the genetic structure of their populations (Boileau *et al.*, 1992).

As we have shown, the rapid growth rate of colonists acts as a barrier against new migrants, and this is reinforced by the formation of diapausing stage banks and in some cases, by local adaptation. This process leads to a persistent founder effect, and consequently, to a deviation from the migration-drift equilibrium. This has repercussions when interpreting phylogeographic signals (Gómez *et al.*, 2002; Waters, 2011). For instance patterns of “isolation-by-distance” found in several aquatic organisms, regardless of their reproductive mode, have been suggested to be due to a process of sequential colonizations (Gómez *et al.* 2007; Gouws & Stewart, 2007; Mills *et al.*, 2007; Muñoz *et al.*, 2008). Our results are consistent with these proposals and suggest that caution should be applied when inferring a migration-drift mechanism of ‘isolation by distance’ from such patterns (i.e.,

correlation between genetic and geographical distances). Also, the establishment of persistent founder effects and competitive exclusion of closely related species can explain the phylogenetic overdispersion in communities, given a phylogenetic limiting similarity between species (Violle *et al.*, 2011).

During the time window from the arrival of first colonizers to the establishment of the founder effects, the genetic structure of the population is still sensitive to migration or drift. Our results point out that this period is short, as a result of the high population growth rates of most aquatic organisms. Nevertheless, we found that with relatively low population growth rates, the numerical advantage is delayed and genetic differentiation is relatively low. In a similar way, inbreeding depression could act favoring gene flow (Tortajada *et al.*, 2009; Tortajada *et al.*, 2010). Although this factor has not been explicitly modeled here, it will act in a similar way of reducing the growth rate, which will favor gene flow. However, severe inbreeding could also reduce the effective population size, and increase genetic drift, which will increase genetic differentiation. A more detailed exploration of this scenario will be needed and it will depend on the magnitude of the purging and migration.

Other factors not implemented in our model but likely to occur in the wild could also counteract the high genetic differentiation. For example, processes able to reduce population size during asexual growth phase (e.g., perturbations or environmental fluctuations) could increase the impact of gene flow. In addition, it will be of interest to test the strength of persistent founder effects buffering migrants with a higher fitness than locally adapted residents. These factors -inbreeding depression, environmental fluctuations, and preadapted immigrants- were not invoked in the initial formulation of the Monopolization Hypothesis and should be investigated in future analyses. An additional prospective is to include the effect of metapopulation structure. Recently, Walser & Haag

(2012) have shown that population turnover, which is expected to have high rate in small populations, could also explain the high genetic population differentiation.

Concluding remarks

Molecular screening of natural population has uncovered an unexpectedly high genetic diversity in taxa with high dispersal potential. These findings challenged classical views of the evolutionary processes in small multicellular organisms, and when focused on aquatic invertebrates, brought to postulate a combination of processes as causal factors for that genetic differentiation, the Monopolization Hypothesis (De Meester, 2002). Our analysis shows that a quantitative elaboration of this multifactorial hypothesis is able to dissect the relative weights of the different factors, and their interactions. Specifically, we found that founder effects drive the genetic structure of passively dispersed aquatic organisms. We conclude that although selective factors and migration have a role in explaining genetic structure of continental aquatic invertebrates, demographic processes are dominant. By studying which factors are important in what circumstances, our analysis can help understanding relevant differences among the genetic structure of different species.

Acknowledgements

We thank Guillermo García Franco and José Gargallo Tuzón for their invaluable help with some parts of the code and programming support. We also would like to thank Luc De Meester, Raquel Ortells and M^a José Carmona for helpful comments on previous versions of this manuscript. This work was funded by a grant from the Spanish Ministerio de Ciencia e Innovación (CGL2009-07364) to MS. AG was supported by a National Environment Research

Council (NERC) Advanced Fellowship (NE/B501298/1) and JM-P by a fellowship by the Spanish Ministerio de Ciencia y Tecnología (BES2004-5248).

References

- Allan, J. D. 1976. Life history patterns in zooplankton. *Am. Nat.* 110: 165-180.
- Allen, M. R. 2007. Measuring and modeling dispersal of adult zooplankton. *Oecologia* 153: 135-143.
- Allen, M. R., Thum, R. A. & Cáceres, C. E. 2010. Does local adaptation to resources explain genetic differentiation among *Daphnia* populations? *Mol. Ecol.* 19: 3076-3087.
- Alver, M. O. & Hagiwara, A. 2007. An individual-based population model for the prediction of rotifer population dynamics and resting egg production. *Hydrobiologia* 593: 19-26.
- Aparici, E., Carmona, M. J., & Serra, M. 1998. Sex allocation in haplodiploid cyclical parthenogens with density-dependent proportion of males. *Am. Nat.* 152: 652-657.
- Berg, L. M. 2005. Fluctuating selection, egg banks and population genetic structure in cyclically parthenogenetic species. *Hydrobiologia* 549: 287-295.
- Berg, L. M. & Lascoux, M. 2000. Neutral genetic differentiation un an island model with cyclical parthenogenesis. *J. Evol. Biol.* 13: 488-494.
- Boileau, M. G., Hebert, P. D. N. & Schwartz, S. 1992. Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. *J. Evol. Biol.* 5: 25-39.
- Brendonck, L. & De Meester, L. 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia* 491: 65-84.
- Burton, O. J., Phillips, B. L. & Travis, J. M. J. 2010. Trade-offs and the evolution of life-histories during range expansion. *Ecol. Lett.* 13: 1210-1220.

- 507 Cáceres, C. E. & Soluk, D. A. 2002. Blowing in the wind: a field test of overland dispersal and
508 colonization by aquatic invertebrates. *Oecologia* 131: 402-408.
- 509 Cáceres, C. E. 1997. Temporal variation, dormancy, and coexistence: a field test of the
510 storage effect. *Proc. Natl. Acad. Sci.* 94: 9171-9175.
- 511 Campillo, S., García-Roger, E. M., Carmona, M. J., Gómez, A. & Serra, M. 2009. Selection on
512 life-history traits and genetic population divergence in rotifers. *J. Evol. Biol.* 22: 2542-2553.
- 513 Campillo, S., García-Roger, E. M., Carmona, M. J., & Serra, M. 2011. Local adaptation in
514 rotifer populations. *Evol. Ecol.* 25: 933-947.
- 515 Carmona, M. J., Gómez, A., & Serra, M. 1995. Mictic patterns of the rotifer *Brachionus*
516 *plicatilis* Müller in small ponds. *Hydrobiologia* 313: 365–371.
- 517 Carson, H. L. 1968. The population flush and its genetic consequences in Lewontin, R. C. (ed)
518 *Population biology and evolution*. Syracuse University Press, Syracuse, USA.
- 519 Chen, I.-C., Hill, J. K., Ohlemüller, R., Boy, D. B. & Thomas, C. D. 2011. Rapid range shifts of
520 species associated with high levels of climate warming. *Science* 333: 1024-1026.
- 521 Chesson, P. 1983. Coexistence of competitors in a stochastic environment: the storage
522 effect. *Lect. Notes Biomath.*, 52: 188-198.
- 523 Costanzo, K. S. & Taylor, D. J. 2010. Rapid ecological isolation and intermediate genetic
524 divergence in lacustrine cyclic parthenogens. *BMC Evol. Biol.* 10: 166.
- 525 Cousyn, C., De Meester, L., Colbourne, J. K., Brendonck, L., Verschuren, D. & Volckaert, F.
526 2001. Rapid, local adaptation of zooplankton behavior to changes in predation pressure in
527 the absence of neutral genetic changes. *Proc. Natl. Acad. Sci.* 98: 6256-6260.
- 528 De Meester, L. 1996. Local genetic differentiation and adaptation in freshwater zooplankton
529 populations: Patterns and processes. *Ecoscience* 3: 385-399.

- 530 De Meester, L., Gómez, A., Okamura, B. & Schwenk, K. 2002. The Monopolization
531 Hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecol.* 23: 121-
532 135.
- 533 De Meester, L. 1993. Inbreeding and outbreeding depression in *Daphnia*. *Oecologia* 96: 80-
534 84.
- 535 Decaestecker, E., Gaba, S., Raeymaekers, J. A. M., Stoks, R., Van Kerckhoven, L., Ebert, D. *et*
536 *al.* 2007. Host-parasite 'Red Queen' dynamics archived in pond sediment. *Nature* 450: 870-
537 873.
- 538 Ebert, D., Haag, C., Kirkpatrick, M., Riek, M., Hottinger, J. W. & Pajunen, V. I. 2002. A
539 selective advantage to immigrant genes in a *Daphnia* metapopulation. *Science* 295: 485-488.
- 540 Escudero, M., Vargas, P., Arens, P., Ouborg, N. J. & Luceño, M. 2010. The east-west-north
541 colonization history of the Mediterranean and Europe by the coastal plant *Carex extensa*
542 (Cyperaceae). *Mol. Ecol.* 19: 352-370.
- 543 Freeland, J. R., Romualdi, C. & Okamura, B. 2000. Gene flow and genetic diversity: a
544 comparison of freshwater bryozoan populations in Europe and North America. *Heredity* 85:
545 498-508.
- 546 Frisch, D., Green, A. J., & Figuerola, J. 2007. High dispersal capacity of a broad spectrum of
547 aquatic invertebrates via waterbirds. *Aquat. Sci.* 69: 568-574.
- 548 García-Roger, E. M., Carmona, M. J. & Serra, M. 2006a. A simple model relating habitat
549 features to a diapause egg bank. *Limnol. Oceanogr.* 51: 1542-1547.
- 550 García-Roger, E. M., Carmona, M. J. & Serra, M. 2006b. Patterns in rotifer diapausing egg
551 banks: Density and viability. *J. Exp. Mar. Biol. Ecol.* 336: 198-210.

- 552 Gómez, A., Montero-Pau, J., Lunt, D. H., Serra, M. & Campillo, S. 2007. Persistent genetic
553 signatures of colonization in *Brachionus manjavacas* rotifers in the Iberian Peninsula. *Mol.*
554 *Ecol.* 16: 3228-3240.
- 555 Gómez, A., Adcock, G. J., Lunt, D. H. & Carvalho, G. R. 2002. The interplay between
556 colonization history and gene flow in passively dispersing zooplankton: microsatellite
557 analysis of rotifer resting egg bank. *J. Evol. Biol.* 15: 158-171.
- 558 Gouws, G., & Stewart, B. A. 2007. From genetic structure to wetland conservation: a
559 freshwater isopod *Paramphisopus palustris* (Phreatoicidea: Amphisopidae) from the Swan
560 Coastal Plain, Western Australia. *Hydrobiologia* 589: 249-263.
- 561 Haag, C. R., Riek, M., Hottinger, J. W., Pajunen, V. I. & Ebert, D. 2005. Genetic diversity and
562 genetic differentiation in *Daphnia* metapopulations with subpopulations of known age.
563 *Genetics* 170: 1809-1820.
- 564 Haag, C. R., Riek, M., Hottinger, J. W., Pajunen, V. I. & Ebert, D. 2006. Founder events as
565 determinants of within-island and among-island genetic structure of *Daphnia*
566 metapopulations. *Heredity* 96: 150-158.
- 567 Hairston, N. G. 1996. Zooplankton egg banks as biotic reservoirs in changing environments.
568 *Limnol. Oceanogr.* 41: 1087-1092.
- 569 Hebert, P. D. 1974a. Enzyme variability in natural populations of *Daphnia magna*. II.
570 Genotypic frequencies in permanent populations. *Genetics* 77: 323-34.
- 571 Hebert, P. D. 1974b. Enzyme variability in natural populations of *Daphnia magna*. III.
572 Genotypic frequencies in intermittent populations. *Genetics* 77: 335-41.
- 573 Hewitt, G. 1993. Postglacial distribution and species substructure: lesson from pollen, insects
574 and hybrid zones. In *Evolutionary patterns and processes* (D.R. Lees & D. Edwards, eds.).
575 Academic Press, London, UK.

- 576 Kaj, I., Krone, S. M. & Lascoux, M. 2001. Coalescent theory for seed bank models. *J. Appl.*
577 *Probab.* 38: 285-300.
- 578 Kawecki, T. J. & Ebert, D. 2004. Conceptual issues in local adaptation. *Ecol. Lett.* 7: 1225-
579 1241.
- 580 Keller, S. R., & Taylor, D. R. 2008. History, chance and adaptation during biological invasion:
581 separating stochastic phenotypic evolution from response to selection. *Ecology Letters* 11:
582 852-66.
- 583 Kliber, A., & Eckert, C. G. 2005. Interaction between founder effect and selection during
584 biological invasion in an aquatic plant. *Evolution* 59: 1900-1913.
- 585 Knowlton, N. 1993. Sibling species in the sea. *Annu. Rev. Ecol. Syst.* 24: 189-216.
- 586 Lenormand, T. 2002. Gene flow and the limits to natural selection. *TREE* 17: 183-189.
- 587 Louette, G., Vanoverbeke, J., Ortells, R., & De Meester, L. 2007. The founding mothers: the
588 genetic structure of newly established *Daphnia* populations. *Oikos* 116: 728-741.
- 589 Makino, W. & Tanabe, A. S. 2009. Extreme population genetic differentiation and secondary
590 contac in the freshwater copepod *Acanthodiaptomus pacificus* in the Japanese Archipelago.
591 *Mol. Ecol.* 18: 3699-3713.
- 592 Matsumoto, M. & Nishimura, T. 1998. Mersenne twister: a 623-dimensionally
593 equidistributed uniform pseudo-random number generator. *ACM Trans. Model. Comput.*
594 *Simul.* 8: 3-30.
- 595 Mills, S., Lunt, D. H. & Gómez, A. 2007. Global isolation by distance despite strong regional
596 phylogeography in a small metazoan. *BMC Evol. Biol.* 7: 225.
- 597 Muñoz, J., Gómez, A., Green, A. J., Figuerola, J., Amat, F. & Rico, C. 2008. Phylogeography
598 and local endemism of the native Mediterranean brine shrimp *Artemia salina*
599 (Branchiopoda: Anostraca). *Mol. Ecol.* 17: 3160-3177.

- 600 Nosil, P., Egan, S. P. & Funk, D. J. 2007. Differentiation between walking-stick ecotypes:
601 "isolation by adaptation" and multiple roles for divergent selection. *Evolution* 62: 316-336.
- 602 Ortells, R., Gómez, A., & Serra, M. 2003. Coexistence of cryptic rotifer species: ecological and
603 genetic characterisation of *Brachionus plicatilis*. *Freshw. Biol.* 48: 2194-2202.
- 604 Ortells, R., Olmo, C. & Armengol, X. 2011. Colonization in action: genetic characteristics of
605 *Daphnia magna* Strauss (Crustacea, Anomopoda) in two recently restored ponds.
606 *Hydrobiologia* doi:10.1007/s10750-011-0741-1
- 607 Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts
608 across natural systems. *Nature* 421: 37-42.
- 609 Rosenblum, E. B., Hickerson, M. J. & Moritz, C. 2007. A multilocus perspective on
610 colonization accompanied by selection and gene flow. *Evolution* 61: 2971-2985.
- 611 Tavernini, S. 2008. Seasonal and inter-annual zooplankton dynamics in temporary pools with
612 different hydroperiods. *Limnologica* 38: 63-75.
- 613 Templeton, A. R. 2008. The reality and importance of founder speciation in evolution.
614 *BioEssays* 30: 470-479.
- 615 Tortajada, A. M., Carmona, M. J. & Serra, M. 2009. Does haplodiploidy purge inbreeding
616 depression in rotifer populations? *PLoS One* 4: e8195.
- 617 Tortajada, A. M., Carmona, M. J. & Serra, M. 2010. Effects of population outcrossing on
618 rotifer fitness. *BMC. Evol. Biol.* 10: 312.
- 619 Vanoverbeke, J. and De Meester, L. 2010. Clonal erosion and genetic drift in cyclical
620 parthenogens -the interplay between neutral and selective processes. *J. Evol. Biol* 23: 997-
621 1012.

- 622 Vanschoenwinkel, B., Waterkeyn, A., Nhiwatiwa, T., Pinceel, T., Spooren, E., Geerts, A. *et al.*
623 2011. Passive external transport of freshwater invertebrates by elephant and other mud-
624 wallowing mammals in an African savannah habitat. *Freshw. Biol.* 56: 1606-1619.
- 625 Verhoeven, K. J. F., Macel, M., Wolfe, L. M., & Biere, A. 2011. Population admixture,
626 biological invasions and the balance between local adaptation and inbreeding depression.
627 *Proc. R. Soc. B* 278: 2-8.
- 628 Violle, C., Nemergut, D. R., Pu, Z. & Jiang, L. 2011. Phylogenetic limiting similarity and
629 competitive exclusion. *Ecol. Lett.* 14: 782-787.
- 630 Walser, B. & Haag, C. R. 2012. Strong intraspecific variation in genetic diversity and genetic
631 differentiation in *Daphnia magna*: the effects of population turnover and population size.
632 *Mol. Ecol.* doi:10.1111/j.1365-294X.2011.05416.x
- 633 Waters, J. M. 2011. Competitive exclusion: phylogeography's "elephant in the room"? *Mol.*
634 *Ecol.* 20:4388-4394
- 635 Xiang, X.-L., Xi, Y.-L., Wen, X.-L., Zhang, G., Wang, J.-X. & Hu, K. 2011. Genetic differentiation
636 and phylogeographical structure of the *Brachionus calyciflorus* complex in eastern China.
637 *Mol. Ecol.* 20: 3027-3044.
- 638 Xu, S., Hebert, P. D. N., Kotov, A. A. & Cristesu, M. E. 2009. The noncosmopolitanism
639 paradigm of freshwater zooplankton: insights from the global phylogeography of the
640 predatory cladoceran *Polyphemus pediculus* (Linnaeus, 1761) (Crustracea, Onychopoda).
641 *Mol. Ecol.* 18: 5161-5179.
- 642 Zierold, T., Hanfling, B. & Gómez, A. 2007. Recent evolution of alternative reproductive
643 modes in the 'living fossil' *Triops cancriformis*. *BMC Evol. Biol.*, 7: 161.
- 644

Figure legends

Figure 1. Demographic submodel.

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

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

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

thick gray lines in each bar represent the median and the mean respectively. Dotted lines show initial value of F_{st} after foundation.

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

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

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

692 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
γ	Egg annual survival proportion in the bank egg	0.763 *
λ	Annual hatching proportion of diapausing eggs	0.046 *
y	Sexual generations	1000/4000
τ	Duration of the asexual growth period (days)	60
r	Clonal growth rate of each genotype (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
s	Number of loci under selection	5
δ	Additive value on r (days^{-1})	10^{-5} - 10^{-1}

693 * Calculated from García-Roger *et al.* (2006b) † (Alver & Hagiwara, 2007) ‡ (Aparici *et al.*,
694 1998)
695

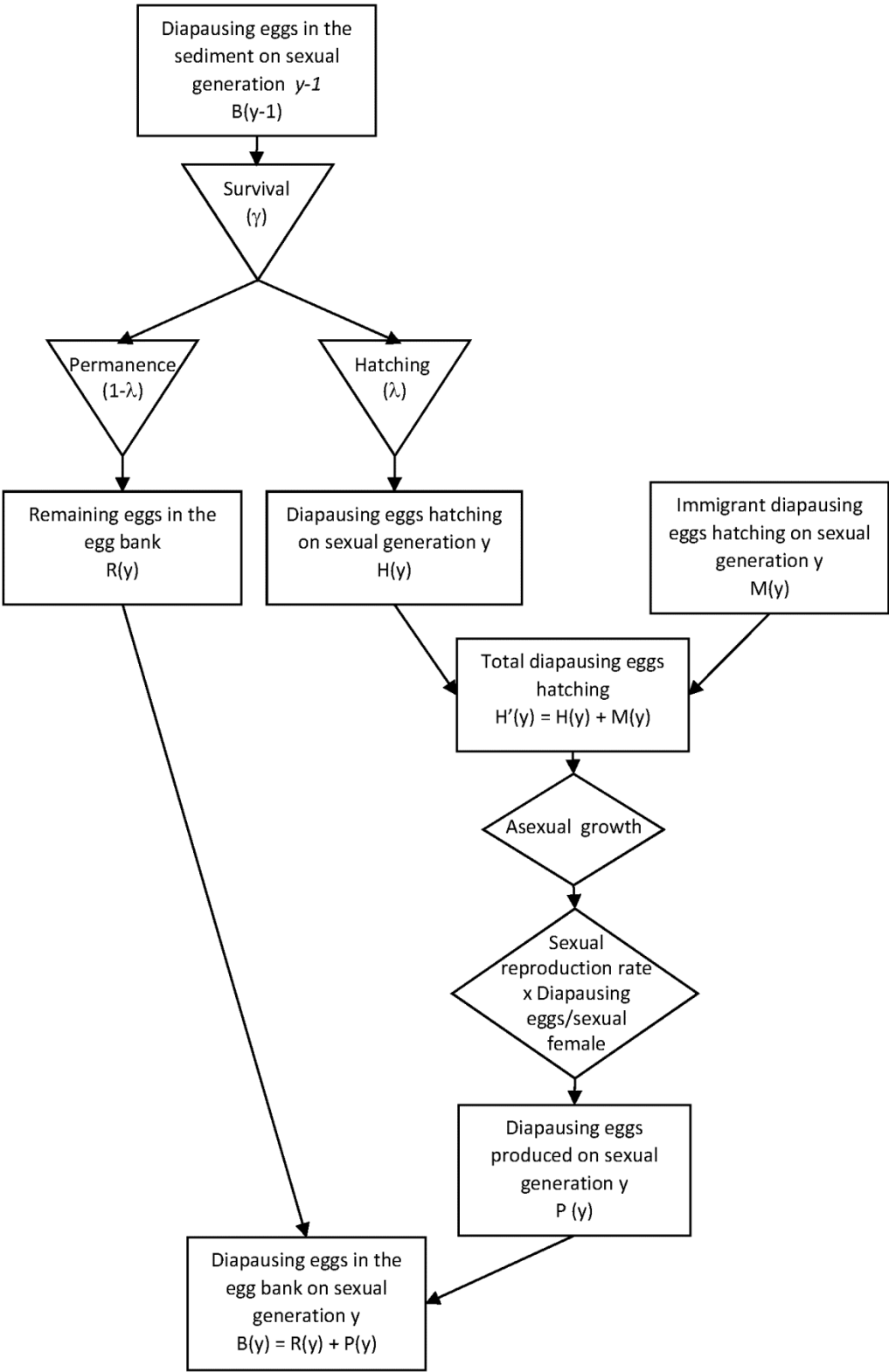
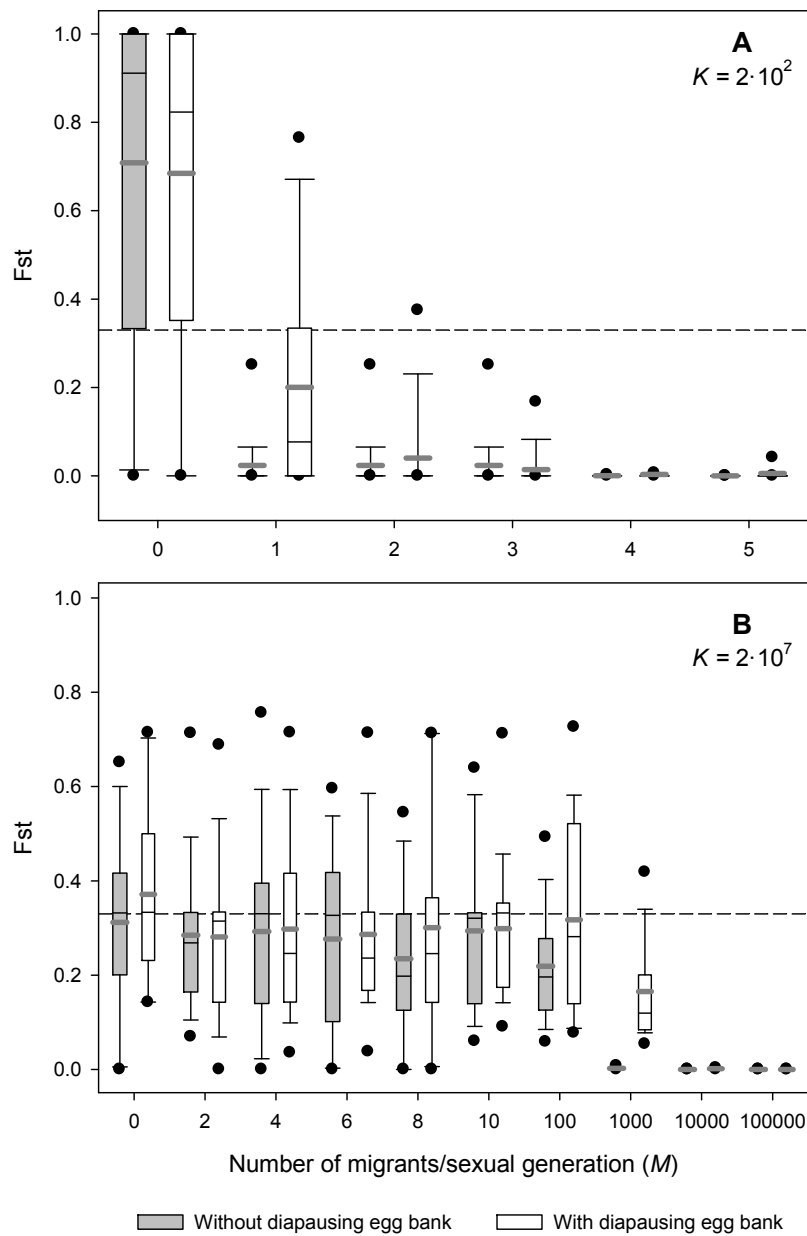


Figure 1.



699

700 Figure 2.

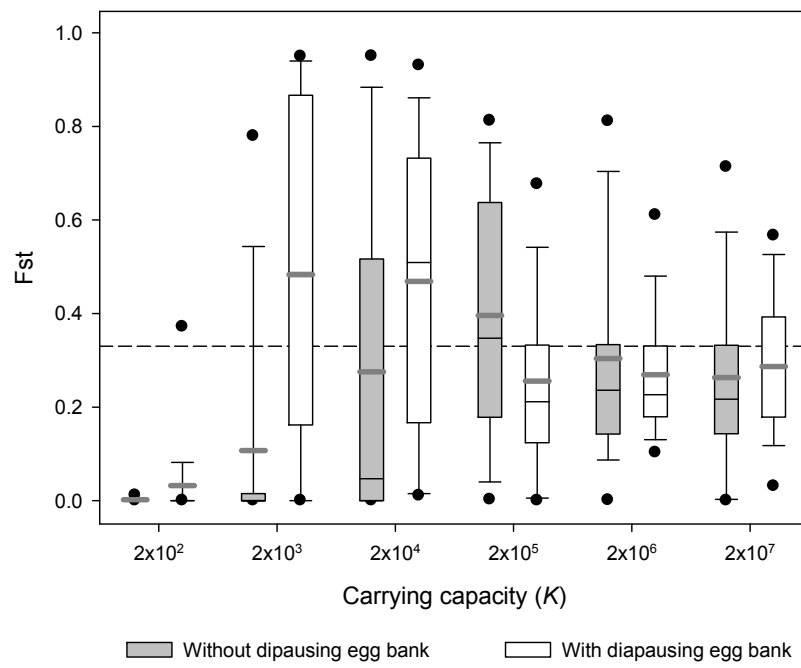


Figure 3.

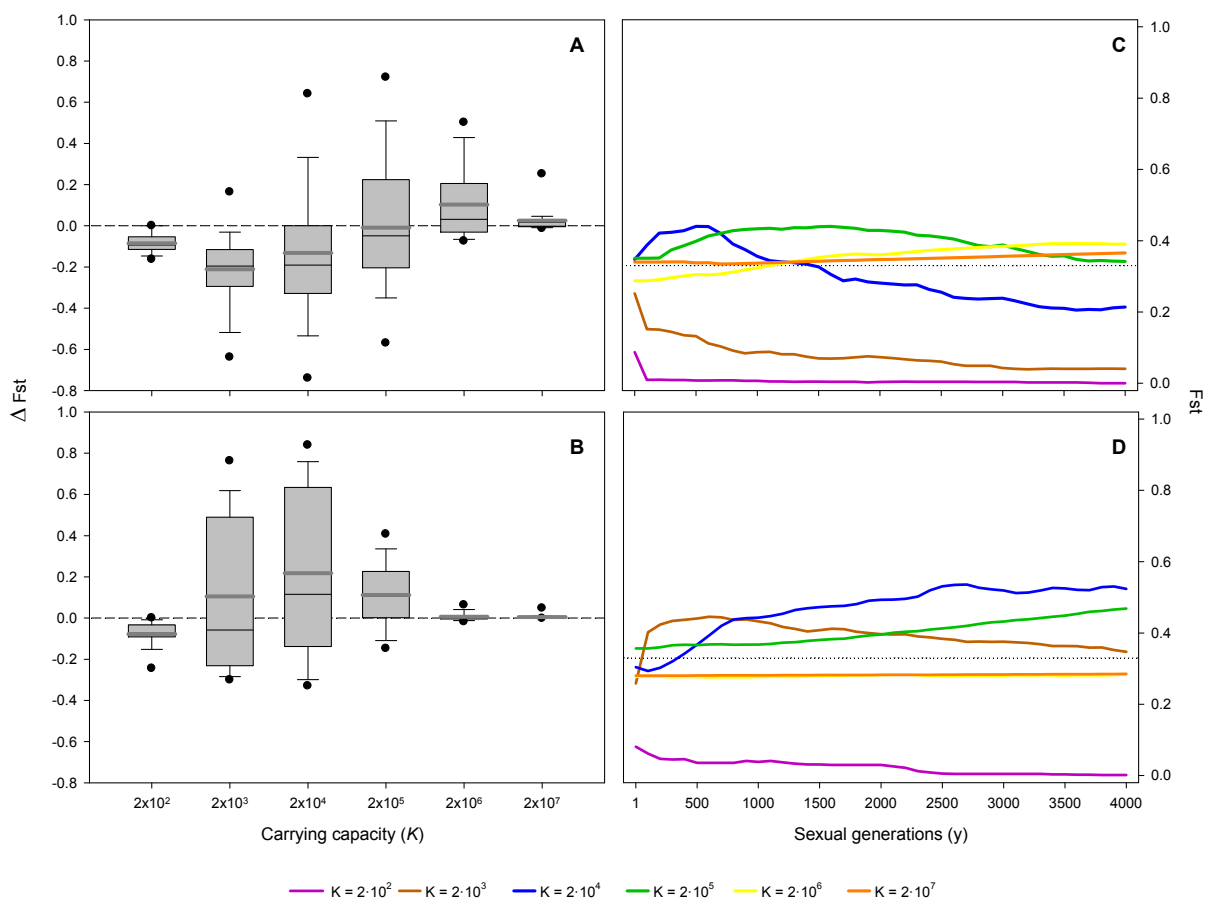


Figure 4.

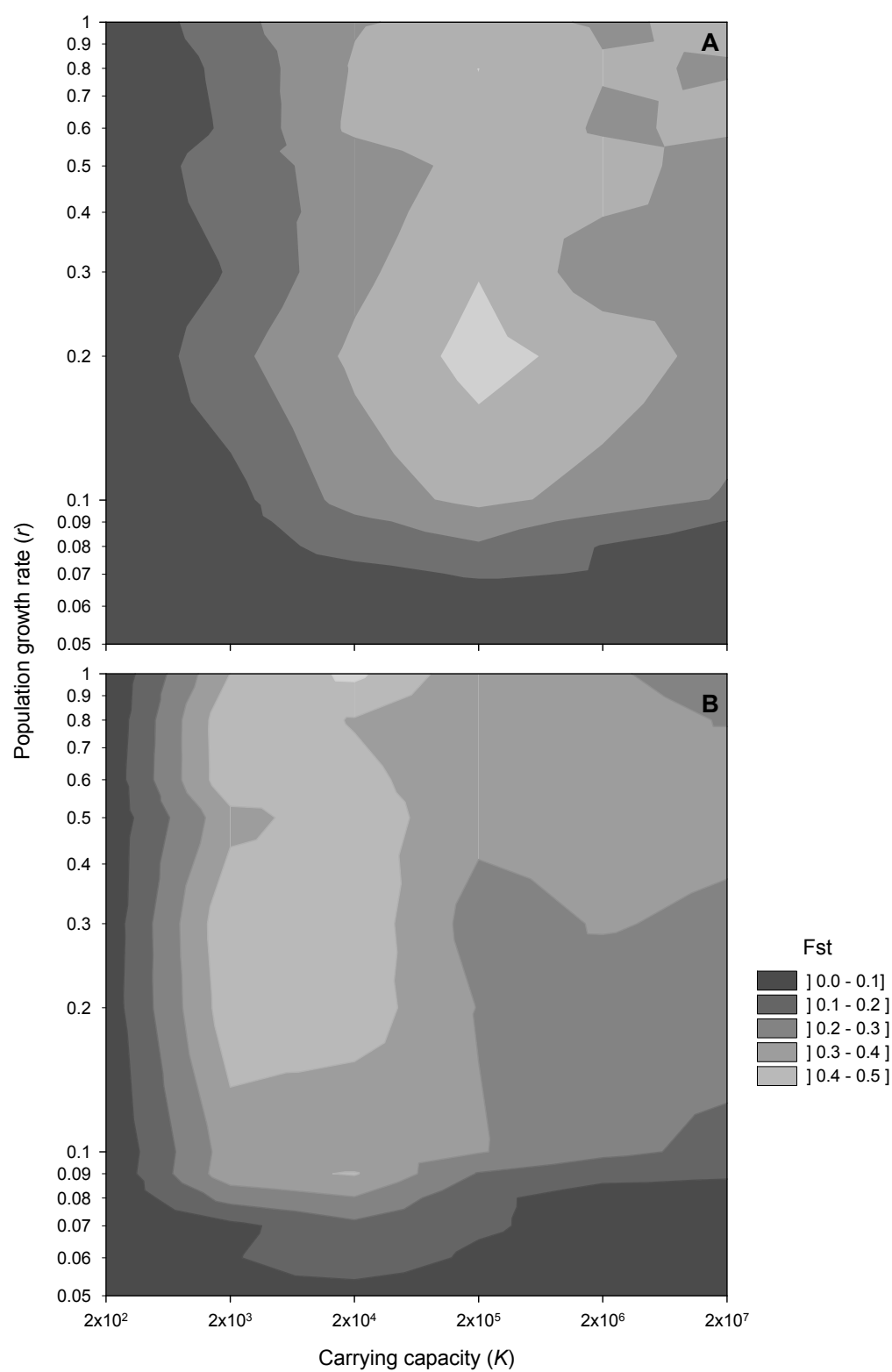


Figure 5.

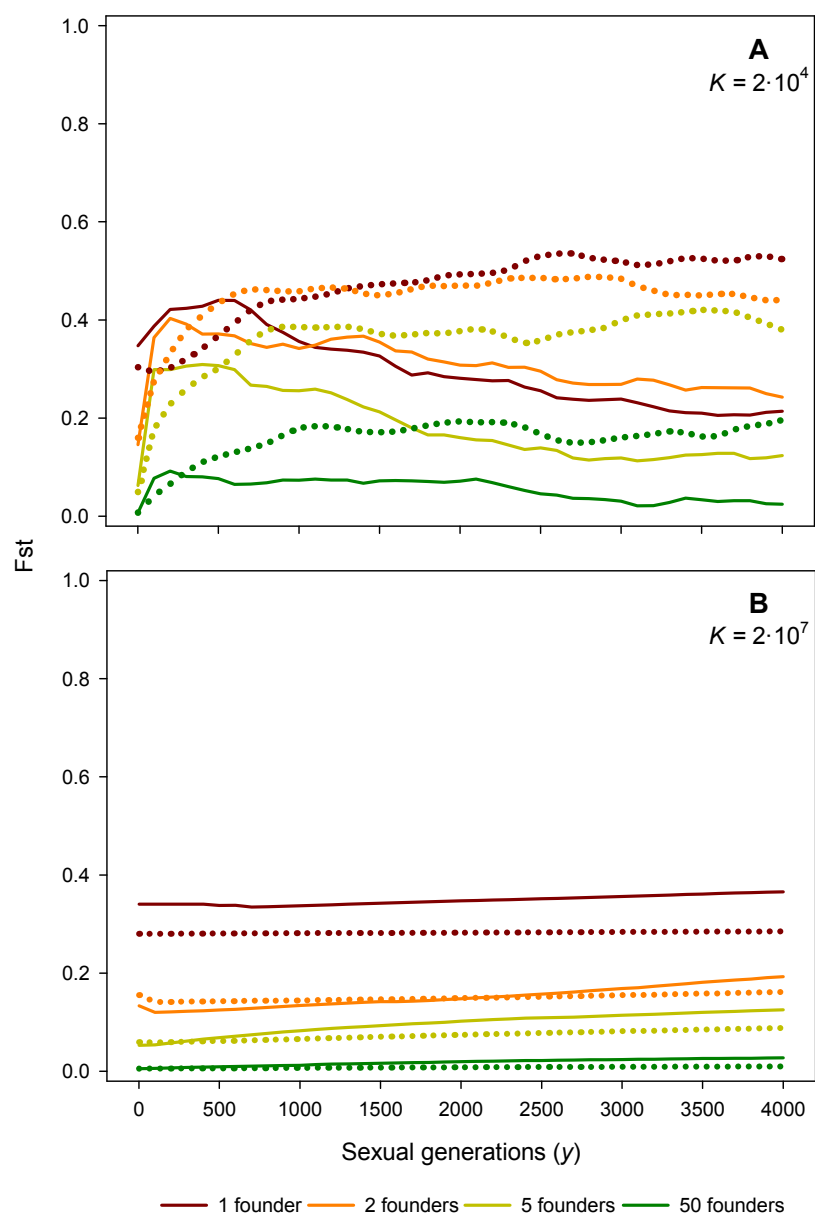


Figure 6.

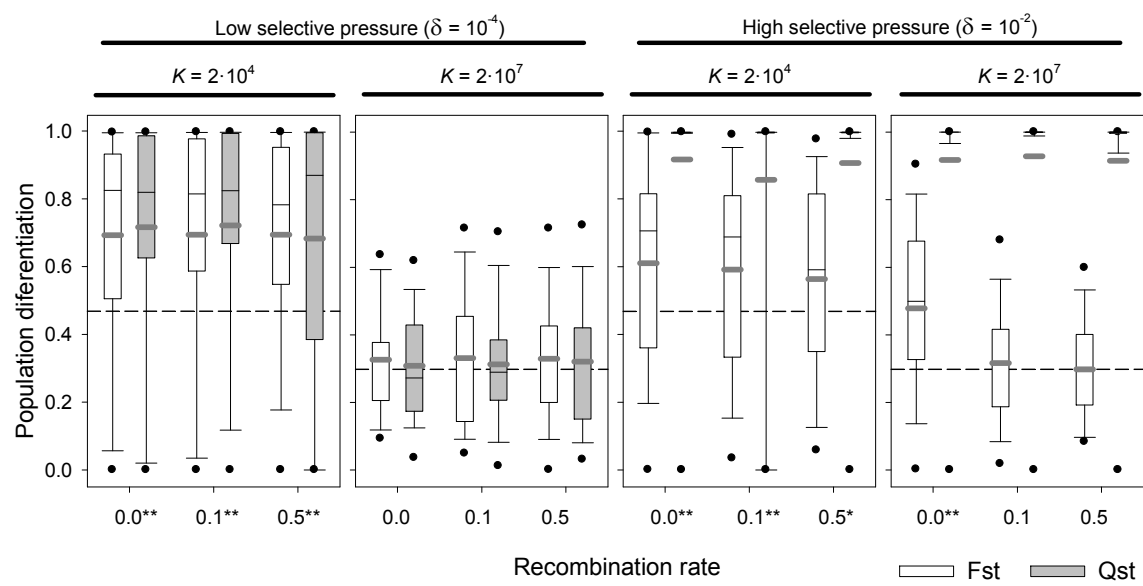


Figure 7.

Figure legends

Figure S1.- Box plot graph of Fst and Qst values after 1000 sexual generations with different recombination rates for two different values of fitness components ($\delta = 10^{-4}$ and 10^{-2} d^{-1}) and without presence of a diapausing egg bank. For each of the fitness scenario, the left panel refers to $K = 2 \cdot 10^4$ and the right panel, to $K = 2 \cdot 10^7$. The rest of parameters were $r = 0.3 \text{ d}^{-1}$, $n = 5$, $s = 5$, $F = 1$ and $M = 2$. Data is based on 100 replicates. Boxes represent 25th /75th percentile and black dots the 5th/95th percentile. Thin black lines and thick gray lines in each bar represent the median and the mean respectively. Dashed lines show the initial value of Fst after foundation. Asterisks indicate Fst statistically different from those without selection ($\delta = 0$) (**, $\alpha = 0.05$).

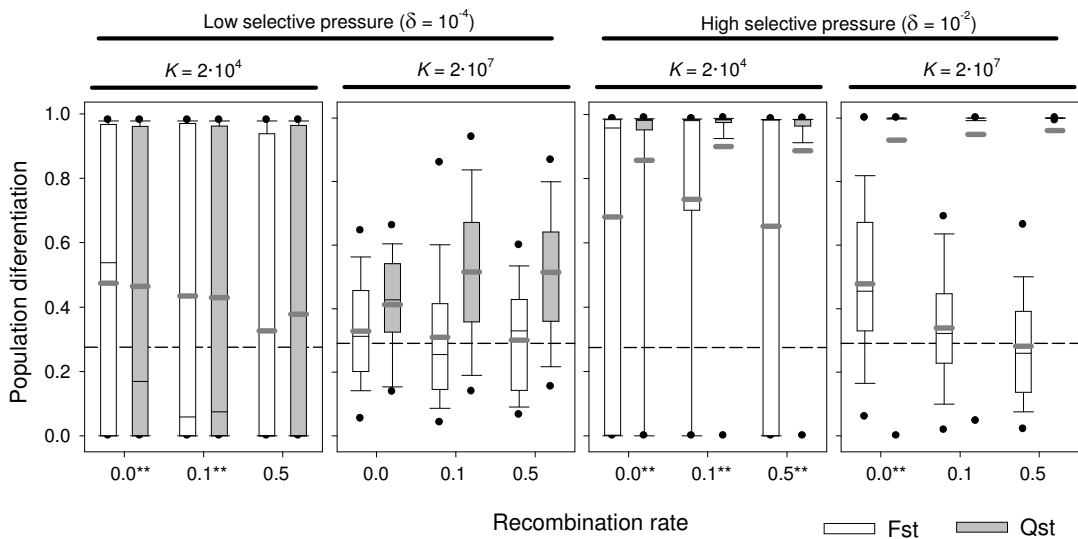


Figure S1.