

Appendix

Quantifying Random Drift in an Multi-level Selection Model

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1 Expected number of offspring

1.1 Expected number of offspring

In order to be able to quantify random drift in our model, we need to assign the expected number of offspring to all individuals for every time step. Comparing this expected value to the corresponding actual number of offspring then hints at the effect of random drift on the system.

We start by considering the expected number of offspring for individual i in group j , E_{ij} , and the actual number of offspring of individual i in group j , O_{ij} . E_{ij} is then determined by considering the probabilities of individual i in group j having 0 offspring $\Pr(O_{ij} = 0)$, having 1 offspring $\Pr(O_{ij} = 1)$ and having 2 offspring $\Pr(O_{ij} = 2)$ in the next time step. Note that for the number of offspring in the next time step, the individual itself counts as well. Meaning that when an individual reproduces and also survives into the next time step, this is considered as 2 offspring. Recognising this, let

$$\begin{aligned} E_{ij} &= 0 \cdot \Pr(O_{ij} = 0) + 1 \cdot \Pr(O_{ij} = 1) + 2 \cdot \Pr(O_{ij} = 2), \\ &= \Pr(O_{ij} = 1) + 2 \cdot \Pr(O_{ij} = 2), \end{aligned} \quad (1)$$

be the expected value of offspring for individual i in group j .

Although the calculation of E_{ij} is quite a simple equation, the probabilities itself are more complex calculations. Specifically, for calculating the probabilities of having a certain number of offspring, we need to consider all possible scenarios for a single time step. This can become quite tedious and therefore it can be made more comprehensible by making a decision tree which shows all possible outcomes for an individual (figure S1). In figure S1 two decision trees are shown: one considering all possible outcomes if group j is full (figure S1a) and one considering all possible outcomes if group j is not full (figure S1b). Whether group j is full or not, drastically changes the possible scenarios for a single time step.

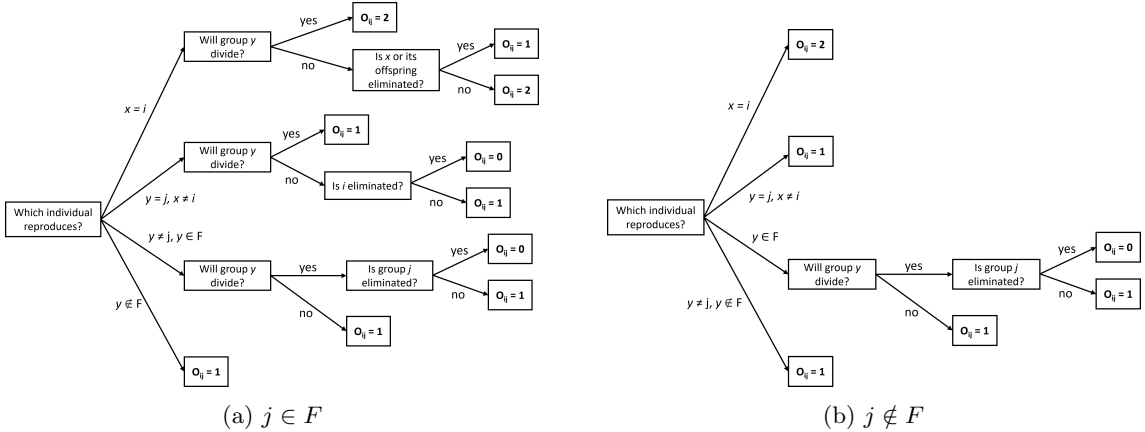


Figure S1: S1a is a decision tree for individual i in group j when group j is full, showing all possible scenarios for individual i in a single time step. Similarly, S1b is a decision tree for individual i in group j when group j is not full, showing all possible scenarios for individual i in a single time step. In these decision trees, individual x in group y is chosen to replicate. Finally, F is the collection for groups that are full.

1.2 Probability of getting 0 offspring

First, we calculate the probability of individual i in group j having 0 offspring, $\Pr(O_{ij} = 0)$. For calculating this probability, we need to consider all scenarios for individual i in group j having 0 offspring in the next time step. An individual having 0 offspring in our model is equivalent to this individual not reproducing and the individual itself getting eliminated. First we consider the scenario where group j has a size lower than n and is therefore not full. In this case, there is only one possibility for an individual to get 0 offspring. This is when group j gets eliminated following the division of another group. Considering F as the collection of groups that are full, the probability of individual i getting 0 offspring when group j is not full, $\Pr(O_{ij} = 0 \mid j \notin F)$, then

becomes

$$\begin{aligned}
\Pr(O_{ij} = 0 \mid j \notin F) &= \Pr(y \in F, y \text{ divides}, j \text{ eliminated} \mid j \notin F), \\
&= \Pr(y \in F \mid j \notin F) \Pr(y \text{ divides} \mid j \notin F, y \in F) \\
&\quad \Pr(j \text{ eliminated} \mid j \notin F, y \in F, y \text{ divides}), \\
&= \Pr(y \in F \mid j \notin F) \Pr(y \text{ divides} \mid y \in F) \\
&\quad \Pr(j \text{ eliminated} \mid y \text{ divides}),
\end{aligned} \tag{2}$$

where individual x in group y is chosen to replicate.

The resulting three probabilities in eq. 2 can be determined following the behaviour and parameters of the system. The probability that an individual from any full group reproduces, can be annotated as the sum of the fitness of all full groups, divided by the sum of the fitness of all groups. Fitness in this case is defined as the resulting value of calculations based on a pay-off matrix, which in our model determines the probability of reproduction for all individuals. Thus,

$$\Pr(y \in F \mid j \notin F) = \frac{\sum_{j \in F} \sum_{i=1}^{n_j} f_{ij}}{\sum_{k=1}^m \sum_{l=1}^{n_k} f_{lk}}, \tag{3}$$

where m is the number of groups in the system, n_j is the size of group j and f_{ij} stands for the fitness of an individual i in group j . Again, f_{ij} here represents a value resulting from calculations based on a pay-off matrix. Substituting eq. 3 in eq. 2 in addition to filling in the other probabilities, leads to

$$\Pr(O_{ij} = 0 \mid j \notin F) = \frac{\sum_{j \in F} \sum_{i=1}^{n_j} f_{ij}}{\sum_{k=1}^m \sum_{l=1}^{n_k} f_{lk}} \cdot q \cdot \frac{1}{m-1}. \tag{4}$$

In this equation, q is the parameter of the model giving the probability of a full group dividing.

Now we consider the scenarios for individual i getting 0 offspring when group j is full. In this case, the scenario described above is still applicable since when group j is full, it is still possible for another full group to divide and eradicate group j . Additionally, there is now also a scenario an individual other than individual i in group j divides, possibly resulting in the elimination of individual i . Thus the probability of getting 0 offspring when group j is full $\Pr(O_{ij} = 0 \mid j \in F)$ becomes

$$\begin{aligned}
\Pr(O_{ij} = 0 \mid j \in F) &= \Pr(y \neq j, y \in F, y \text{ divides}, j \text{ eliminated} \mid j \in F) + \\
&\quad \Pr(y = j, x \neq i, \neg y \text{ divides}, i \text{ eliminated} \mid j \in F) \\
&= \Pr(y \neq j, y \in F \mid j \in F) \Pr(y \text{ divides} \mid y \neq j, y \in F, j \in F) \\
&\quad \Pr(j \text{ eliminated} \mid y \neq j, j \in F, y \in F, y \text{ divides}) + \\
&\quad \Pr(y = j, x \neq i \mid j \in F) \Pr(\neg(y \text{ divides}) \mid j \in F, y = j, x \neq i) \\
&\quad \Pr(i \text{ eliminated} \mid y = j, j \in F, \neg(y \text{ divides}), x \neq i) \\
&= \Pr(y \neq j, y \in F) \Pr(y \text{ divides} \mid y \in F) \\
&\quad \Pr(j \text{ eliminated} \mid y \neq j, y \text{ divides}) + \\
&\quad \Pr(y = j, x \neq i) \Pr(\neg(y \text{ divides}) \mid y \in F) \\
&\quad \Pr(i \text{ eliminated} \mid y = j, j \in F, \neg(y \text{ divides}), x \neq i).
\end{aligned} \tag{5}$$

These probabilities can also be solved by considering the behaviour and the parameters of our model. This results in

$$\begin{aligned}
\Pr(O_{ij} = 0 \mid j \in F) &= \frac{\left(\sum_{j \in F} \sum_{i=1}^{n_j} f_{ij}\right) - \sum_{i=1}^{n_j} f_{ij}}{\sum_{k=1}^m \sum_{l=1}^{n_k} f_{lk}} \cdot q \cdot \frac{1}{m-1} + \\
&\quad \frac{\left(\sum_{i=1}^{n_j} f_{ij}\right) - f_{ij}}{\sum_{k=1}^m \sum_{l=1}^{n_k} f_{lk}} \cdot (1-q) \cdot \frac{1}{n+1}.
\end{aligned} \tag{6}$$

1.3 Probability of getting 2 offspring

Now we will calculate the probability of individual i in group j getting 2 offspring in the next time step. For calculating this probability, we will need to consider all scenarios where individual i gets 2 offspring in the next time step. Individual i having 2 offspring is equivalent to individual i reproducing and both individual i and its offspring surviving into the next time step. First we

will consider all scenarios When group j is not full. In this case, there is only one possibility for i getting 2 offspring. This is the scenario where i reproduces. The equation is relatively simple:

$$\begin{aligned}\Pr(O_{ij} = 2 \mid j \notin F) &= \Pr(y = j, x = i \mid j \notin F) \\ &= \frac{f_{ij}}{\sum_{k=1}^m \sum_{l=1}^{n_k} f_{lk}}.\end{aligned}\tag{7}$$

When we consider the case where group j is full, there are two scenarios of individual i getting 2 offspring. For both cases i reproduces, then either group j divides or it does not. When it does not divide, an individual in group j gets eliminated and when this is not individual i or its offspring, the offspring over the next time step is 2. When group j does divide, individual will have 2 offspring regardless of which other group is eliminated. Describing this probability $\Pr(O_{ij} = 2 \mid j \in F)$ in an equation results in

$$\begin{aligned}\Pr(O_{ij} = 2 \mid j \in F) &= \Pr(y = j, x = i, y \text{ divides} \mid j \in F) + \\ &\quad \Pr(y = j, x = i, \neg(y \text{ divides}), \neg(O_{ij} \text{ eliminated})), \\ &= \Pr(y = j, x = i \mid j \in F) \Pr(y \text{ divides} \mid y = j, x = i, j \in F) + \\ &\quad \Pr(y = j, x = i \mid j \in F) \Pr(\neg(y \text{ divides}) \mid y = j, x = i, j \in F) \\ &\quad \Pr(\neg(O_{ij} \text{ eliminated}) \mid y = j, x = i, \neg(y \text{ divides}), j \in F), \\ &= \Pr(y = j, x = i \mid j \in F) (\Pr(y \text{ divides} \mid j \in F) + \\ &\quad \Pr(\neg(y \text{ divides}) \mid j \in F) \Pr(\neg(O_{ij} \text{ eliminated}) \mid y = j, x = i, \neg(y \text{ divides}), j \in F)).\end{aligned}\tag{8}$$

Considering the behaviour and parameters of our models results in the following equation:

$$\Pr(O_{ij} = 2 \mid j \in F) = \frac{f_{ij}}{\sum_{k=1}^m \sum_{l=1}^{n_k} f_{lk}} \left(q + (1 - q) \cdot \left(1 - \left(\frac{2}{n + 1} \right) \right) \right)\tag{9}$$

1.4 Probability of getting 1 offspring

Finally, most scenarios for individual i in our model, lead to individual i having 1 offspring in the next time step. Either by not reproducing and not getting eliminated, or by individual i reproducing but itself or their offspring getting eliminated. This second scenario however, is only possible when group j is full. Regardless of group j being full or not, the easiest way to calculate $\Pr(O_{ij} = 1 \mid j \in F)$ and $\Pr(O_{ij} = 1 \mid j \notin F)$ is by subtracting $\Pr(O_{ij} = 0)$ and $\Pr(O_{ij} = 2)$ from 1. This leads to the following equations:

$$\Pr(O_{ij} = 1 \mid j \in F) = 1 - \Pr(O_{ij} = 0 \mid j \in F) - \Pr(O_{ij} = 2 \mid j \in F)\tag{10}$$

and

$$\Pr(O_{ij} = 1 \mid j \notin F) = 1 - \Pr(O_{ij} = 0 \mid j \notin F) - \Pr(O_{ij} = 2 \mid j \notin F)\tag{11}$$

2 Quantifying evolution

2.1 Price's equation

For our study, we use Price's equation and expand on it. Therefore we need to understand Price's equation.

In 1972, George Price proposed a simple equation describing evolution of a certain phenotypic character in a population from one generation to another (Price, 1972). This equation is now known as Price's equation and looks as follows

$$\bar{w} \Delta \bar{\phi} = \text{Cov}(w_i, \phi_i) + \overline{w_i \Delta \phi_i}\tag{12}$$

In Price's equation, \bar{w} denotes the average number of offspring of all N individuals of the parent population and thus $\bar{w} = \frac{1}{N} \sum_i^N w_i$ with w_i being the number of offspring of the i th individual. $\Delta \bar{\phi}$ then denotes the difference in average phenotypic character ϕ between the parent and the offspring population. Naturally, ϕ_i denotes the value of phenotypic character ϕ for the i th individual. The first term on the right hand side of the equation describes the change in $\Delta \bar{\phi}$ due to natural selection. The covariance of w_i and ϕ_i is larger than 0 when individuals with higher ϕ tend to have a higher number of offspring. Logically, a covariance lower than 0 means that individuals with

a higher ϕ tend to have a lower number of offspring. In these cases natural selection affects the change in average ϕ .

The second term on the right hand side of the equation describes change in $\bar{\phi}$ due to transmission bias; the case where offspring deviates from their parent with respect to ϕ . $\Delta\phi_i$ then is the difference between the character value of the i th individual and the average of its offspring. $\overline{\Delta\phi_i}$ is then the average transmission bias in the whole population, thus $\overline{\Delta\phi_i} = \frac{1}{N} \sum_1^N \Delta\phi_i$.

2.2 Adding random drift

Price's equation itself, does not yet contain any stochastic factors and thus does not describe random drift. However, based on work by Grafen (2000) we are able to quantify random drift as well. To include random drift, w_i is still defined as the realised number of offspring, but now we also consider an expected number of offspring w_i^* . Now, we can define

$$w_i = w_i^* + \delta_i, \quad (13)$$

where δ_i is the deviation of the realised number of offspring from the expected number of offspring. Adding random drift to Price's equation, given there is no transmission bias ($\overline{w_i \Delta\phi_i} = 0$) results in the following equation:

$$\overline{w \Delta\phi} = \underbrace{\text{Cov}(w_i^*, \phi_i)}_{\text{Selection}} + \underbrace{\text{Cov}(\delta_i, \phi_i)}_{\text{Random Drift}}. \quad (14)$$

In this equation, the first term on the right hand side, represents change due to natural selection, and the second term, represents change due to random drift.

2.3 Calculating the drift term

Now we need to know how we can calculate the effect of random drift on the change in average ϕ , $\text{Cov}(\delta_i, \phi_i)$, in our model. For all N individuals in our model,

$$\begin{aligned} \text{Cov}(\delta_i, \phi_i) &= \frac{1}{N} \sum_{i=1}^N (\phi_i - \bar{\phi})(\delta_i - \bar{\delta}), \\ &= \frac{1}{N} \sum_{i=1}^N \phi_i(\delta_i - \bar{\delta}). \end{aligned} \quad (15)$$

for the i th individual. In this equation, $-\bar{\phi}$ can be removed, making the equation simpler. Going through all individuals of the entire population is the same as going through all individuals for every groups. And since our model is based on groups, it is easier to express the equation in this way. Additionally, it is easier to consider cooperators and defectors independently, since all cooperators and all defectors in a group have the same expected number of offspring. Letting Ω_{C_j} be all cooperators in a group j and Ω_{D_j} be all defectors in a group j , results in

$$\begin{aligned} \text{Cov}(\delta_i, \phi_i) &= \frac{1}{N} \sum_{j=1}^m \left(\sum_{i \in \Omega_{C_j}} \phi_i(\delta_i - \bar{\delta}) + \sum_{i \in \Omega_{D_j}} \phi_i(\delta_i - \bar{\delta}) \right), \\ &= \frac{1}{N} \sum_{j=1}^m \sum_{i \in \Omega_{C_j}} \delta_i - \bar{\delta}, \\ &= \frac{1}{N} \sum_{j=1}^m \left(\left(\sum_{i \in \Omega_{C_j}} \delta_i \right) - f_{C_j} \bar{\delta} \right). \end{aligned} \quad (16)$$

The phenotypic character ϕ in our model is the trait of being cooperator or defector. Since for cooperators $\phi = 1$ and for defectors $\phi = 0$, the equation can be simplified. Furthermore, f_{C_j} and f_{D_j} are the absolute frequencies of cooperators and defectors respectively in group j . Since $\bar{\delta}$ is a constant that gets summed for the amount of individuals in the subgroup are present, $\sum_{i \in \Omega_{C_j}} \bar{\delta} = f_{C_j} \bar{\delta}$.

The deviation of realised fitness to expected fitness can also be described for group j without summing for all individuals: $\sum_{i \in \Omega_{C_j}} \delta_i = f'_{C_j} - f_{C_j} \cdot E_{C_j}$, where f'_{C_j} is the absolute frequency of

offspring for the cooperators in group j and E_{C_j} is the expected number of offspring for a single cooperator in group j . Furthermore, $\bar{\delta} = \bar{w} - \bar{w}^*$ (see eq. 13) and thus the equation becomes

$$\begin{aligned}\text{Cov}(\delta_i, \phi_i) &= \frac{1}{N} \sum_{j=1}^m f'_{C_j} - f_{C_j} E_{C_j} - f_{C_j} (\bar{w} - \bar{w}^*), \\ &= \frac{1}{N} \sum_{j=1}^m f'_{C_j} - f_{C_j} (E_{C_j} + \bar{w} - \bar{w}^*)\end{aligned}\tag{17}$$

This final equation is understandable. In every group, it is checked whether the number of offspring in the group is significantly different from the number of offspring in other groups given the expected number of offspring and the drift that is present in the system.

2.4 Calculating the selection term

As seen in equation 14, the selection term is given as the covariance of the expected number of offspring with the phenotypic character, $\text{Cov}(w_i^*, \phi_i)$. We want to calculate this for our model and thus for all individuals N in our model,

$$\begin{aligned}\text{Cov}(w_i^*, \phi_i) &= \frac{1}{N} \sum_{i=1}^N (\phi_i - \bar{\phi})(w_i^* - \bar{w}^*), \\ &= \frac{1}{N} \sum_{i=1}^N \phi_i (w_i^* - \bar{w}^*).\end{aligned}\tag{18}$$

We are again able to remove $\bar{\phi}$ from the equation. Then, we consider not just all individuals, but we consider them per group and per phenotype:

$$\begin{aligned}\text{Cov}(w_i^*, \phi_i) &= \frac{1}{N} \sum_{i=1}^N \phi_i (w_i^* - \bar{w}^*), \\ &= \frac{1}{N} \sum_{j=1}^m \left(\sum_{i \in \Omega_{C_j}} \phi_i (w_i^* - \bar{w}^*) + \sum_{i \in \Omega_{D_j}} \phi_i (w_i^* - \bar{w}^*) \right), \\ &= \frac{1}{N} \sum_{j=1}^m \sum_{i \in \Omega_{C_j}} w_i^* - \bar{w}^*, \\ &= \frac{1}{N} \sum_{j=1}^m f_{C_j} (w_{C_j}^* - \bar{w}^*), \\ &= \sum_{j=1}^m p_{C_j} (w_{C_j}^* - \bar{w}^*).\end{aligned}\tag{19}$$

Since for the defectors $\phi_i = 0$ and for the cooperators $\phi_i = 1$, the formula becomes much simpler when considering the individuals per group and per phenotype since now only the cooperators are considered in the formula. For every cooperator in group j the expected number of offspring is the same. Additionally, the average expected number of offspring is determined for every group. Therefore, the difference in expected fitness of an cooperator and the population average, can be simply multiplied by the number of cooperators in that group j , f_{C_j} . Finally, $p_{C_j} = \frac{f_{C_j}}{N}$ for group j .

3 Dividing Drift and Selection

In order to get full understanding of the model and the terms affecting selection, we want to distinguish a within-group and an among-group term of both selection and drift. Considering the selection term, following the Law of Total Covariance, results in the following equation:

$$\text{Cov}(w_i^*, \phi_i) = \underbrace{\text{Cov}_a(\{w_i^*\}_w, \{\phi_i\}_w)}_{\text{Among-group Selection}} + \underbrace{\langle \text{Cov}_w(w_i^*, \phi_i; j) \rangle_a}_{\text{Within-group Selection}}.\tag{20}$$

Similarly, the drift term can be divided into a within-group and an among-group term.

$$\text{Cov}(\delta_i, \phi_i) = \underbrace{\text{Cov}_a(\{\delta_i\}_w, \{\phi_i\}_w)}_{\text{Among-group Drift}} + \underbrace{\langle \text{Cov}_w(\delta_i, \phi_i; j) \rangle_a}_{\text{Within-group Drift}}. \quad (21)$$

3.1 Among-group selection

The among-group selection term can be calculated for our model as follows:

$$\begin{aligned} \text{Cov}_a(\{w_i^*\}_w, \{\phi_i\}_w) &= \frac{1}{N} \sum_{j=1}^m (\{\phi\}_w - \langle \{\phi\}_w \rangle_a) (\{w^*\}_w - \langle \{w^*\} \rangle_a) n_j \\ &= \frac{1}{N} \sum_{j=1}^m (\{\phi\}_w - \bar{\phi}) (\{w^*\}_w - \bar{w}^*) n_j \\ &= \frac{1}{N} \sum_{j=1}^m (\{w^*\}_w - \bar{w}^*) \{\phi\}_w n_j \\ &= \frac{1}{N} \sum_{j=1}^m (\{w^*\}_w - \bar{w}^*) f_{C_j} \\ &= \frac{1}{N} \sum_j \{w^*\}_w f_{C_j} - \bar{w}^* f_{C_j} \\ &= -\frac{1}{N} N_C \bar{w}^* + \frac{1}{N} \sum_{j=1}^m \{w^*\}_w f_{C_j} \\ &= -p_C \bar{w}^* + \sum_{j=1}^m \{w^*\}_w p_{C_j} \end{aligned} \quad (22)$$

In the final equation, $p_C = \frac{N_C}{N}$ and $p_{C_j} = \frac{f_{C_j}}{N}$. The equation shows that the effect of among-group selection depends on the sum of the mean expected fitness per group (weighted by group size), minus the population average of the expected fitness (multiplied by the proportion of cooperators).

3.2 Within-group selection

The within-group selection term can be calculated in our model as follows:

$$\begin{aligned} \langle \text{Cov}_w(\phi_i, w_i^*; j) \rangle_a &= \frac{1}{N} \sum_{j=1}^m \text{Cov}(\phi_{ij}, w_{ij}^*) n_j \\ &= \frac{1}{N} \sum_{j=1}^m \left(\frac{1}{n_j} \sum_{i=1}^{n_j} (\phi_{ij} - \{\phi\}_w) (w_{ij}^* - \{w^*\}_w) \right) n_j \\ &= \frac{1}{N} \sum_{j=1}^m \sum_{i=1}^{n_j} (w_{ij}^* - \{w^*\}_w) \phi_{ij} \\ &= \frac{1}{N} \sum_{j=1}^m \left(\sum_{i \in \Omega_{C_j}} (w_{iC_j}^* - \{w^*\}_w) \phi_{iC_j} + \sum_{i \in \Omega_{D_j}} (w_{iC_j}^*) - \{w^*\}_w \phi_{iD_j} \right) \\ &= \frac{1}{N} \sum_{j=1}^m \sum_{i \in \Omega_{C_j}} w_{iC_j}^* - \{w^*\}_w \\ &= \frac{1}{N} \sum_{j=1}^m f_{C_j} (w_{iC_j}^* - \{w^*\}_w) \end{aligned} \quad (23)$$

Because $\phi_{iD_j} = 0$ and $\phi_{iC_j} = 1$, the final equation only considers cooperators. It shows that the within-group selection is based on every group's covariance of expected fitness with phenotypic character ϕ , weighed by group size.

3.3 Among-group drift

The among-group drift term can be calculated for our model as follows:

$$\begin{aligned}
\text{Cov}_a(\{\phi_{ij}\}_w, \{\delta_{ij}\}_w) &= \frac{1}{N} \sum_{j=1}^m (\{\phi_{ij}\}_w - \langle \{\phi_{ij}\}_w \rangle_a) (\{\delta_{ij}\}_w - \langle \{\delta_{ij}\}_w \rangle_a) n_j \\
&= \frac{1}{N} \sum_{j=1}^m (\{\phi_{ij}\}_w - \bar{\phi}) (\{\delta_{ij}\}_w - \bar{\delta}) n_j \\
&= \frac{1}{N} \sum_{j=1}^m (\{\delta_{ij}\}_w - \bar{\delta}) \{\phi\}_w n_j \\
&= \frac{1}{N} \sum_{j=1}^m (\{\delta_{ij}\}_w - \bar{\delta}) f_{C_j} \\
&= \frac{1}{N} \sum_{j=1}^m \{\delta_{ij}\}_w f_{C_j} - \bar{\delta} f_{C_j} \\
&= -p_C \bar{\delta} + \frac{1}{N} \sum_{j=1}^m \{\delta_{ij}\}_w f_{C_j} \\
&= -p_C \bar{\delta} + \frac{1}{N} \sum_{j=1}^m (\{w\}_w - \{w^*\}_w) f_{C_j} \\
&= -p_C \bar{\delta} + \sum_{j=1}^m (\{w\}_w - \{w^*\}_w) p_{C_j}
\end{aligned} \tag{24}$$

In the final equation, $p_C = \frac{N_C}{N}$ and $p_{C_j} = \frac{f_{C_j}}{N}$. The among group drift is thus determined by the deviation in expected and realised number of offspring per group and the population average of this deviation.

3.4 Within-group drift

The within-group drift term can be calculated in our model as follows:

$$\begin{aligned}
\langle \text{Cov}_w(\phi_i, \delta_i; j) \rangle_a &= \frac{1}{N} \sum_{j=1}^m \text{Cov}(\phi_{ij}, \delta_{ij}) n_j \\
&= \frac{1}{N} \sum_{j=1}^m \left(\frac{1}{n_j} \sum_i^{n_j} (\phi_{ij} - \{\phi\}_w) (\delta_{ij} - \{\delta\}_w) \right) n_j \\
&= \frac{1}{N} \sum_{j=1}^m \sum_i^{n_j} (\delta_{ij} - \{\delta\}_w) \phi_{ij} \\
&= \frac{1}{N} \sum_{j=1}^m \left(\sum_{i \in \Omega_{C_j}} (\delta_{ij} - \{\delta\}_w) \phi_{i_{C_j}} + \sum_{i \in \Omega_{D_j}} (\delta_{ij} - \{\delta\}_w) \phi_{i_{D_j}} \right) \\
&= \frac{1}{N} \sum_{j=1}^m \sum_{i \in \Omega_{C_j}} \delta_{i_{C_j}} - \{\delta\}_w \\
&= \frac{1}{N} \sum_{j=1}^m -f_{C_j} \{\delta\}_w + \sum_{i \in \Omega_{C_j}} \delta_{i_{C_j}} \\
&= \frac{1}{N} \sum_{j=1}^m -f_{C_j} (\{w\}_w - \{w^*\}_w) + \sum_{i \in \Omega_{C_j}} w_{ij} - w_{ij}^* \\
&= \frac{1}{N} \sum_{j=1}^m -f_{C_j} (\{w\}_w - \{w^*\}_w) - f_{C_j} w_{i_{C_j}}^* + \sum_{i \in \Omega_{C_j}} w_{ij}
\end{aligned} \tag{25}$$

The final equation consists of parts that are relatively easy to determine within our simulation.

4 Fixation probability

For the next section, we consider a single mutant with a fitness advantage in a population of wildtypes. We are able to represent this by setting $b = 0$ and $c > 0$ in our model.

For the fixation probability, we use the formula proposed by Traulsen and Nowak (2006). They consider a very low q , a very low probability of group division, allowing them to separate the fixation into two parts. Firstly, an individual has to fix in their own group. Secondly, then, that group has to fix in the population of groups, in order for the mutant to fix in the entire population. Furthermore, Traulsen and Nowak (2006) consider cooperators and defectors, where we consider wildtypes and mutants. Therefore, the calculations for the fixation probability below, are in terms of cooperator and defector. Note that our interest of the fixation of a mutant is similar to Traulsen and Nowak (2006) considering a defector fixing in a population of cooperators.

The probability that a defector or cooperator, respectively, fixes in its group for $w \ll 1$ is defined as follows:

$$\phi_D = \frac{1}{n} \left(1 + \frac{w}{6} \delta_D \right) \quad (26)$$

$$\phi_C = \frac{1}{n} \left(1 - \frac{w}{6} \delta_C \right) \quad (27)$$

In these equations, n is the group size. Furthermore, in these equations

$$\delta_D = (2T - 2R + P - S)n - (T - 4R + 2P + S) \quad (28)$$

and

$$\delta_C = (T - R + 2P - 2S)n + (T + 2R - 4P + S), \quad (29)$$

based on the pay-off matrix proposed by Traulsen and Nowak (2006).

In addition to the fixation probability of an individual in their group, there is also a fixation probability of a single defector or cooperator group fixing in a population of groups. For $w \ll 1$, this results in:

$$\Phi_D \approx \frac{1}{m} \left(1 - \frac{w}{2} (m-1)(R-P) \right) \quad (30)$$

$$\Phi_C \approx \frac{1}{m} \left(1 + \frac{w}{2} (m-1)(R-P) \right) \quad (31)$$

Considering that an individual first has to fix in their own group and then that group has to fix in the population of groups, the fixation probabilities of a defector ρ_D and cooperator ρ_C are

$$\rho_D = \phi_D \Phi_D \quad (32)$$

$$\rho_C = \phi_C \Phi_C \quad (33)$$

This results in the following two equations:

$$\rho_D = \frac{1}{N} \left(1 + w \left(\frac{\delta_D}{6} - \frac{m-1}{2} (R-P) \right) \right) \quad (34)$$

$$\rho_C = \frac{1}{N} \left(1 + w \left(-\frac{\delta_C}{6} + \frac{m-1}{2} (R-P) \right) \right) \quad (35)$$

Knowing the equation for the fixation probability, we can consider the formula for the case where a single defector has to fix with $b = 0$ and $c > 1$. Important to note is that our goal is to gain some insight in how fixation probability depends on how the population is divided in groups. In other words, how ρ_D changes as function of m , where N is fixed. This allows for setting $n = \frac{N}{m}$. The equation for δ_D then becomes

$$\delta_D = 3c \frac{N - m}{m} \quad (36)$$

If we substitute eq. 36 into eq. 34, we get

$$\begin{aligned}
\rho_D &= \frac{1}{N} \left(1 + w \left(\frac{3c \frac{N-m}{m}}{6} - \frac{m-1}{2} \cdot -c \right) \right) \\
&= \frac{1}{N} \left(1 + w \left(\frac{c \frac{N-m}{m}}{2} + \frac{c(m-1)}{2} \right) \right) \\
&= \frac{1}{N} \left(1 + w \frac{c \left(\frac{N-m}{m} + m - 1 \right)}{2} \right) \\
&= \frac{1}{N} \left(1 + w \frac{c}{2} \left(\frac{N-m+m^2-m}{m} \right) \right) \\
&= \frac{1}{N} \left(1 + w \frac{c}{2} \left(\frac{m^2-2m+N}{m} \right) \right) \\
&= \frac{1}{N} + \frac{wc}{2N} \cdot \frac{m^2-2m+N}{m}
\end{aligned} \tag{37}$$

The equation shows that the fixation probability of an individual with a fitness advantage (in this case the defector) equals the term $\frac{1}{N}$, the fixation probability in a neutral setting, plus a second term $\frac{wc}{2N} \cdot \frac{m^2-2m+N}{m}$. This equation shows a convex function with a single minimum for the domain $m = 1$ to $m = N$.

Now we want to find for which m there is a minimum. First we take the derivative of the function.

$$\begin{aligned}
\rho'_D(m) &= \frac{wc}{2N} \frac{m(2m-2) - (m^2-2m+N) \cdot 1}{m^2}, \\
&= \frac{wc}{2N} \frac{2m^2-2m-m^2+2m-N}{m^2}, \\
&= \frac{wc}{2N} \frac{m^2-N}{m^2},
\end{aligned} \tag{38}$$

Finding for which value of m there is a minimum demands us to set the derivative equal to zero, which leads to

$$\begin{aligned}
\frac{wc}{2N} \frac{m^2-N}{m^2} &= 0 \\
\frac{m^2-N}{m^2} &= 0 \\
N &= m^2 \\
m &= \sqrt{N}
\end{aligned}$$

Thus, in the domain of $m = 1$ to $m = N$, $m_{min} = \sqrt{N}$, which means that the fixation probability of an individual with a fitness advantage is lowest when the total population is perfectly divided (when $m = n$). $m = \sqrt{N}$ gives

$$\begin{aligned}
\rho_D(\sqrt{N}) &= \frac{1}{N} + \frac{wc}{2N} \frac{(\sqrt{N})^2 - 2\sqrt{N} + N}{\sqrt{N}} \\
&= \frac{1}{N} + \frac{wc}{2N} (2\sqrt{N} - 2) \\
&= \frac{1}{N} + \frac{wc(\sqrt{N}-1)}{N}
\end{aligned}$$

Thus $\rho_{Dmin} = \frac{1}{N} + \frac{wc(\sqrt{N}-1)}{N}$ in the domain of $m = 1$ to $m = N$. This shows that the fixation probability at its lowest point is still higher than the neutral fixation probability $\frac{1}{N}$.

Finally, looking at the function, it becomes apparent that there is a certain symmetry around

this minimum, where m and $\frac{N}{m}$ give the same fixation probability. Filling in $\frac{N}{m}$ for m results in

$$\begin{aligned}
\frac{1}{N} + \frac{wc}{2N} \frac{(\frac{N}{m})^2 - 2\frac{N}{m} + N}{\frac{N}{m}} &= \frac{1}{N} + \frac{wc}{2N} \frac{\frac{N^2}{m^2} - s\frac{N}{m} + N}{\frac{N}{m}} \\
&= \frac{1}{N} + \frac{wc}{2N} \frac{\frac{N^2}{m} - 2N + Nm}{N} \\
&= \frac{1}{N} + \frac{wc}{2N} (\frac{N}{m} - 2 + m) \\
&= \frac{1}{N} + \frac{wc}{2N} (\frac{N}{m} - 2 + m) \frac{m}{m} \\
&= \frac{1}{N} + \frac{wc}{2N} \frac{N - 2m + m^2}{m}
\end{aligned}$$

which of course is the same as the original equation. This proves that it does not make a difference whether a population is divided into 4 groups of 25 individuals or 25 groups of 4 individuals, in terms of fixation probability.

5 Additional figures

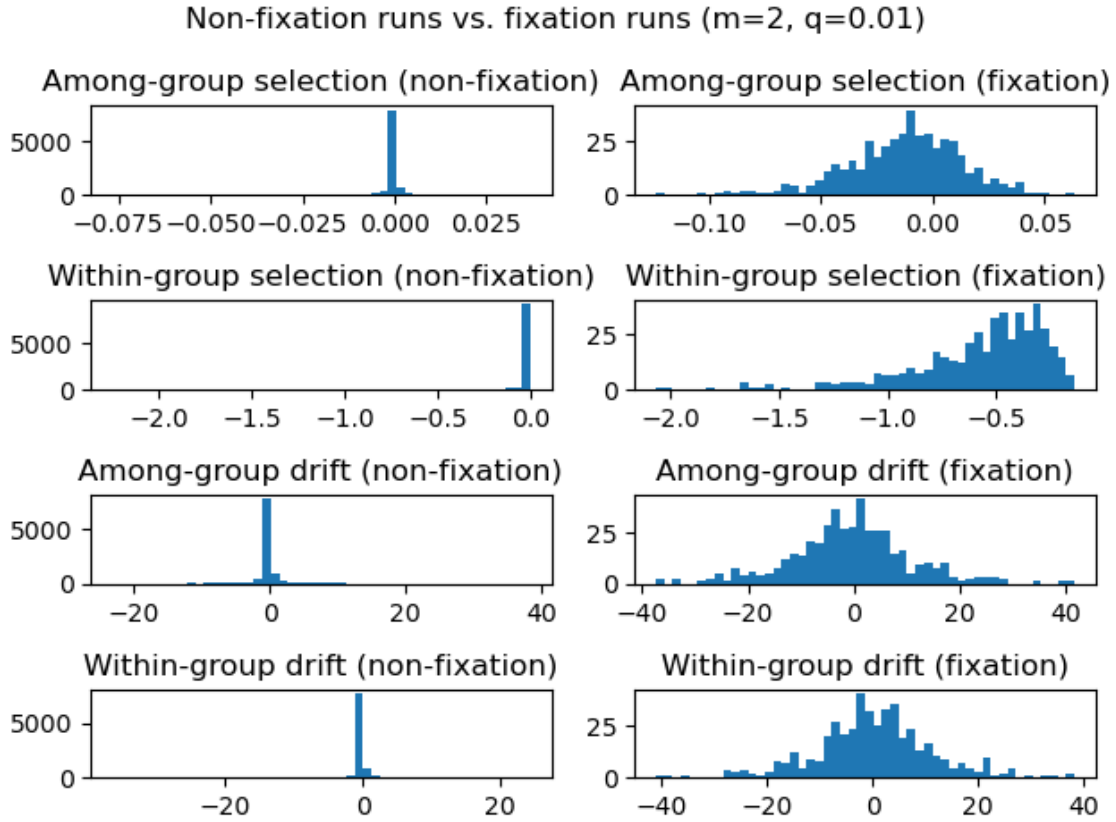


Figure S2: The figure shows multiple histograms of the values for the among-group and within-group selection and drift terms for runs where the mutant reached fixation as well as runs where it did not for $m = 2$. For these simulations, $q = 0.01$, $w = 0.01$, $N = 100$, $b = 0$ and $c = 10$.

Non-fixation runs vs. fixation runs ($m=4, q=0.01$)

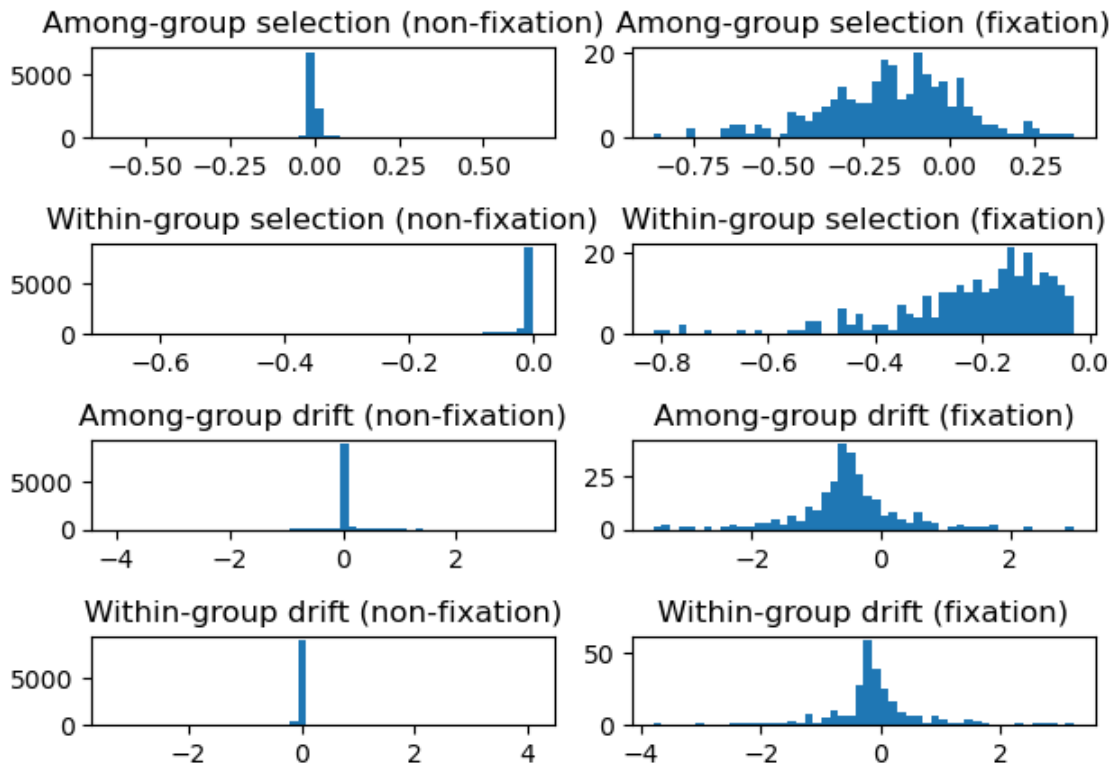


Figure S3: This figure shows similar histograms as figure S2, however, for the runs in this figure $m = 4$

Non-fixation runs vs. fixation runs ($m=5, q=0.01$)

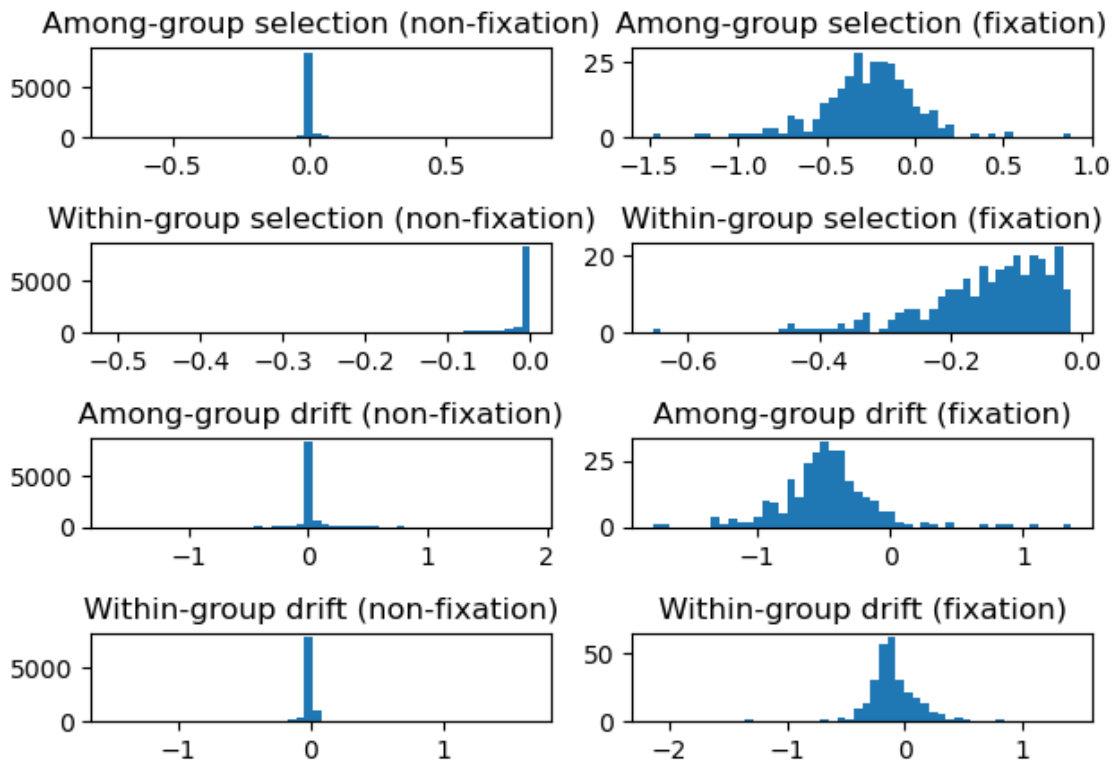


Figure S4: This figure shows similar histograms as figure S2, however, for the runs in this figure $m = 5$

Non-fixation runs vs. fixation runs ($m=10, q=0.01$)

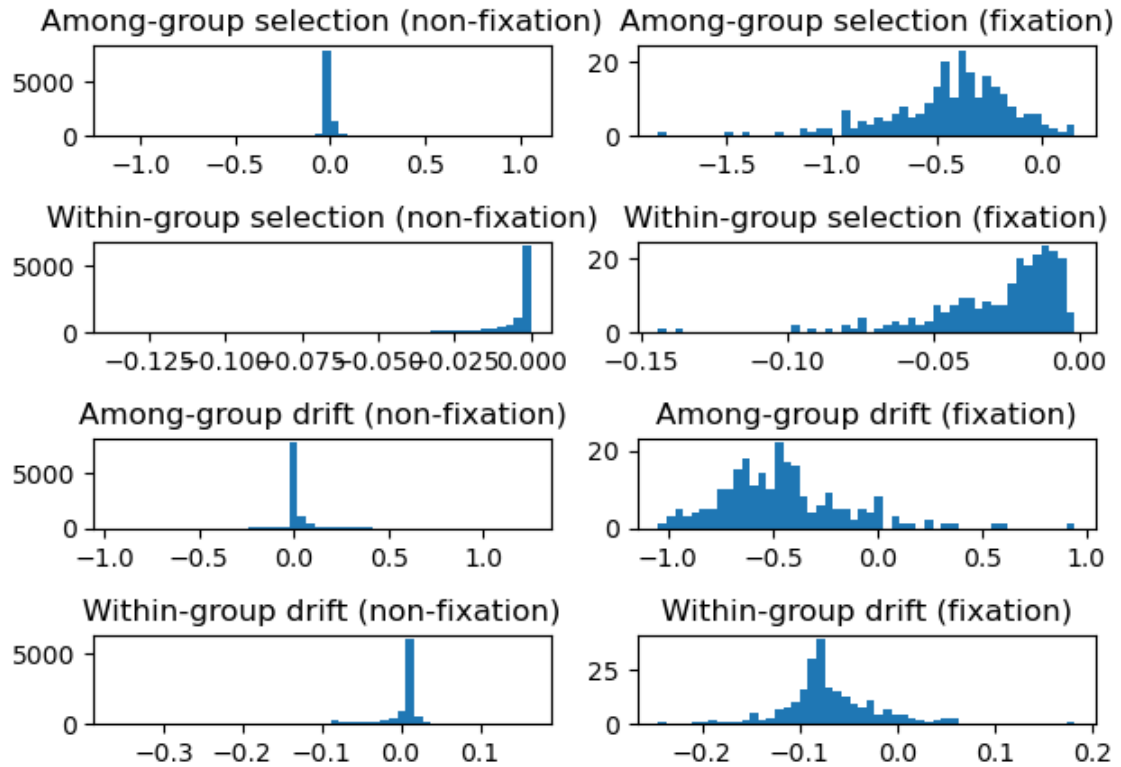


Figure S5: This figure shows similar histograms as figure S2, however, for the runs in this figure $m = 10$

Non-fixation runs vs. fixation runs ($m=20, q=0.01$)

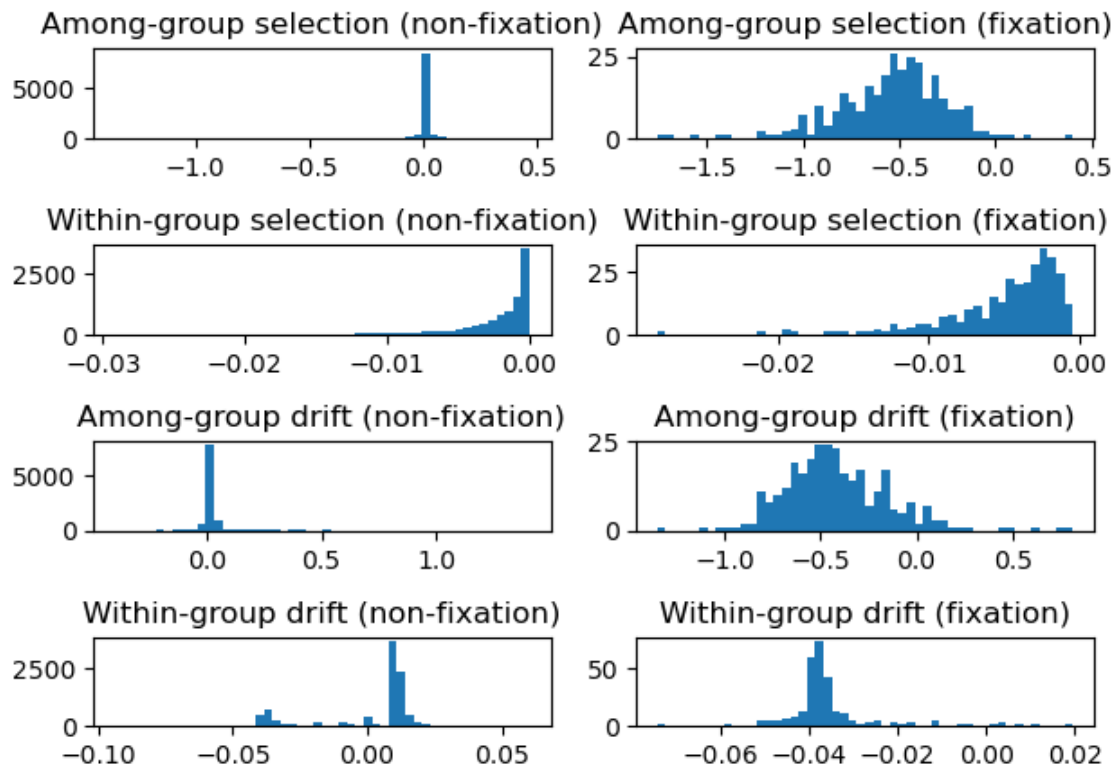


Figure S6: This figure shows similar histograms as figure S2, however, for the runs in this figure $m = 20$

Non-fixation runs vs. fixation runs ($m=25, q=0.01$)

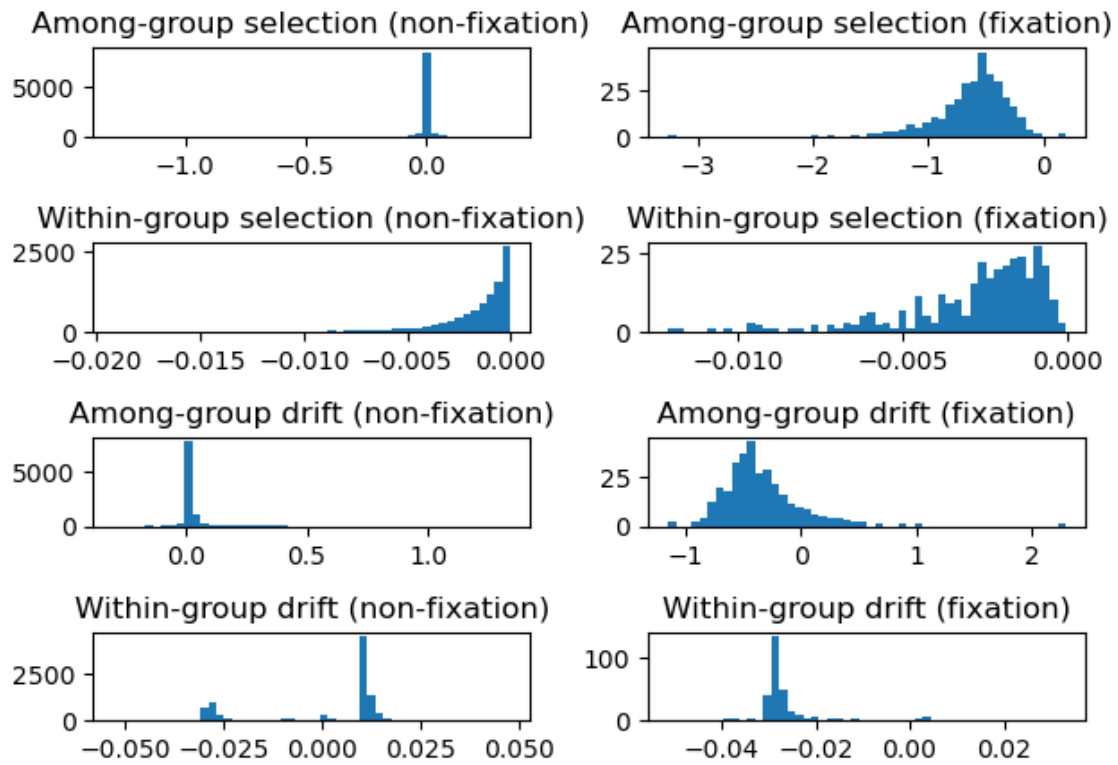


Figure S7: This figure shows similar histograms as figure S2, however, for the runs in this figure $m = 25$

Non-fixation runs vs. fixation runs ($m=2, q=1$)

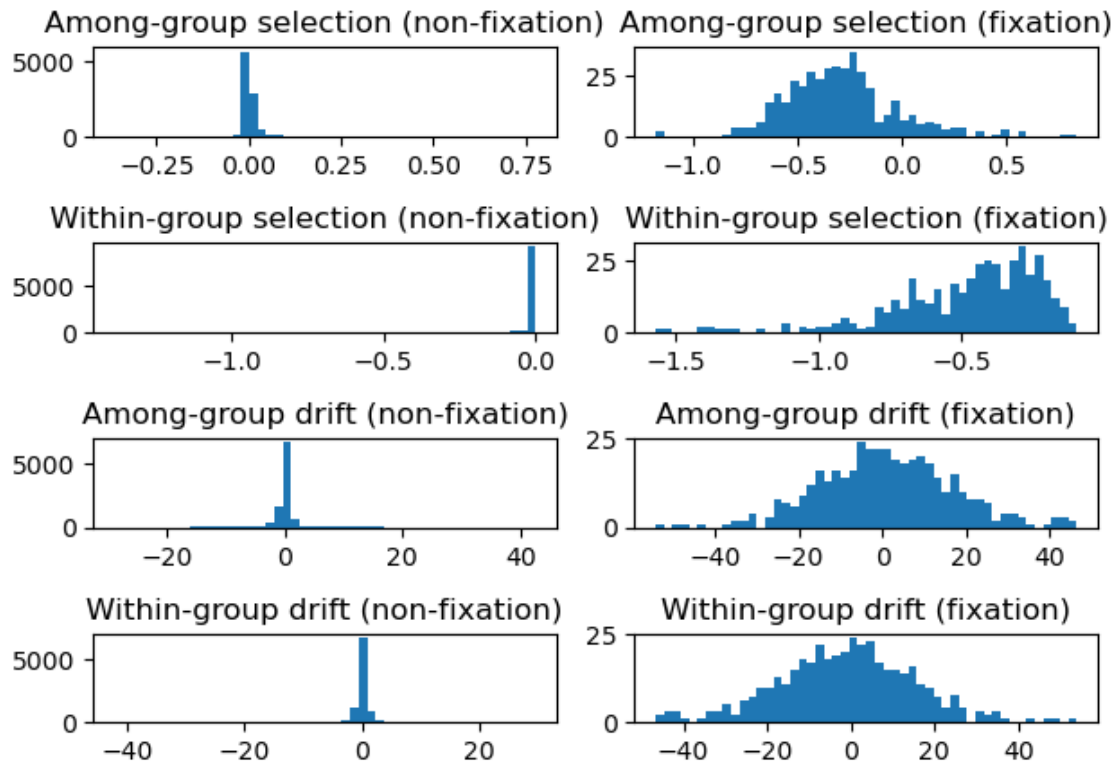


Figure S8: This figure shows similar histograms as figure S2, however, for the runs in this figure, $q = 1$.

Non-fixation runs vs. fixation runs ($m=4, q=1$)

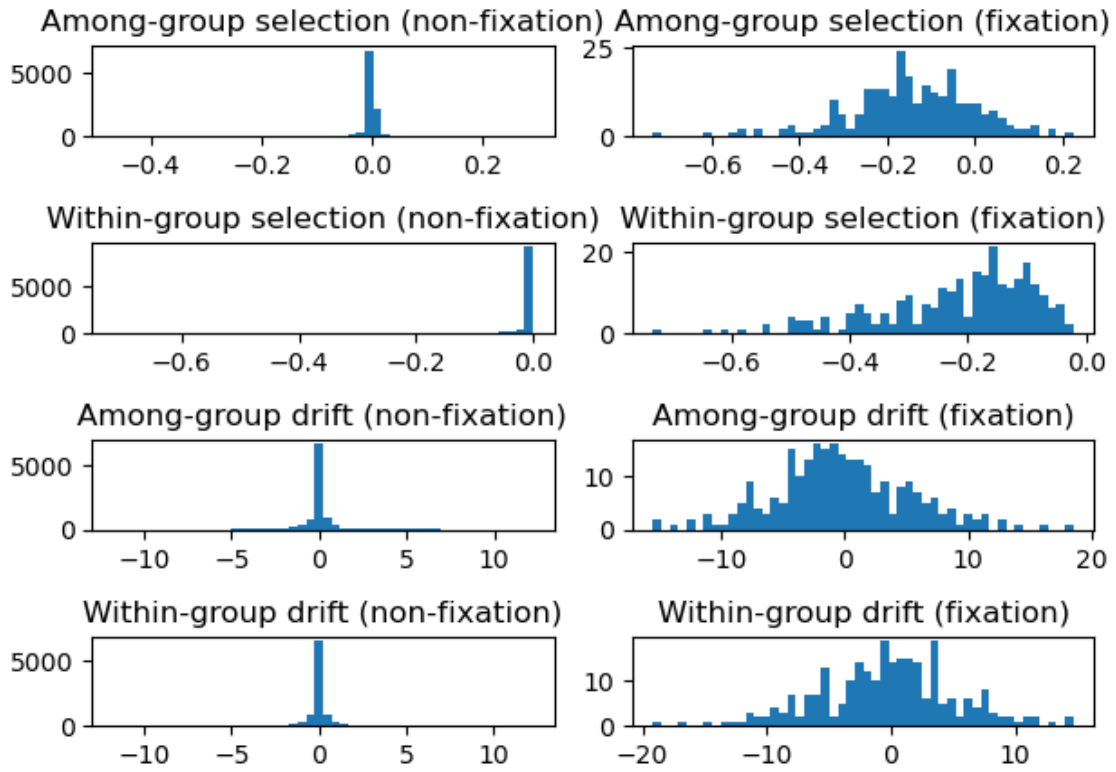


Figure S9: This figure shows similar histograms as figure S8, however, for the runs in this figure, $m = 4$.

Non-fixation runs vs. fixation runs ($m=5, q=1$)

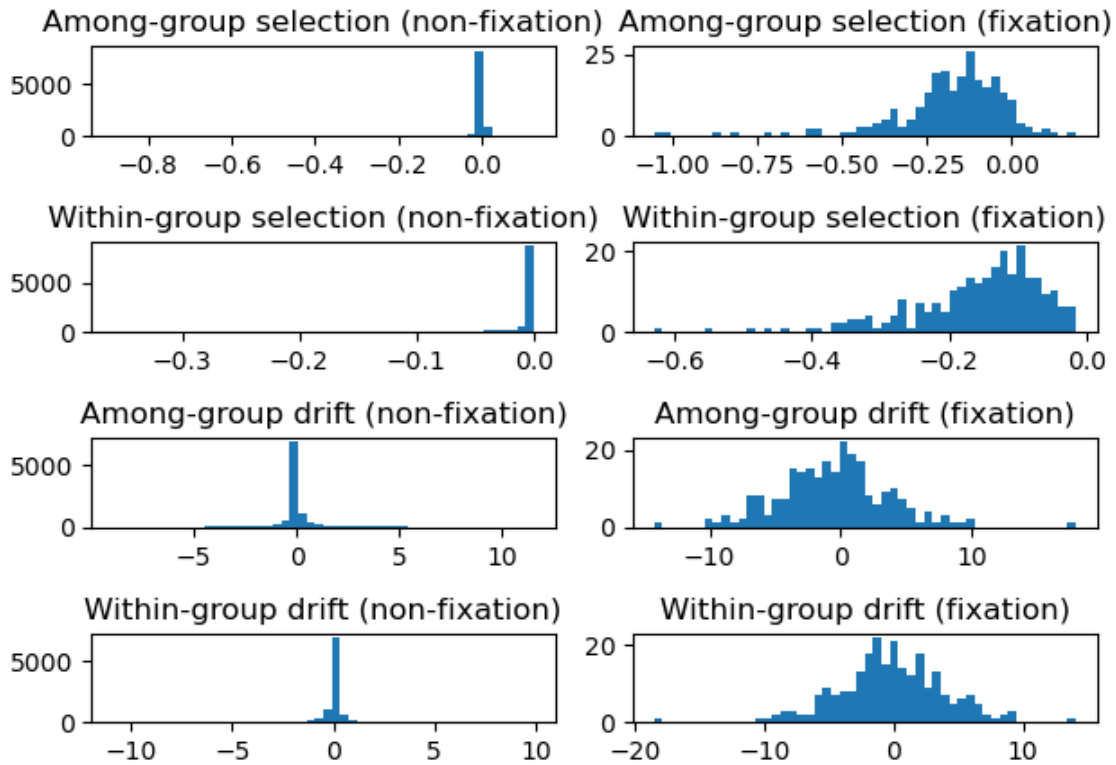


Figure S10: This figure shows similar histograms as figure S8, however, for the runs in this figure, $m = 5$.

Non-fixation runs vs. fixation runs ($m=10, q=1$)

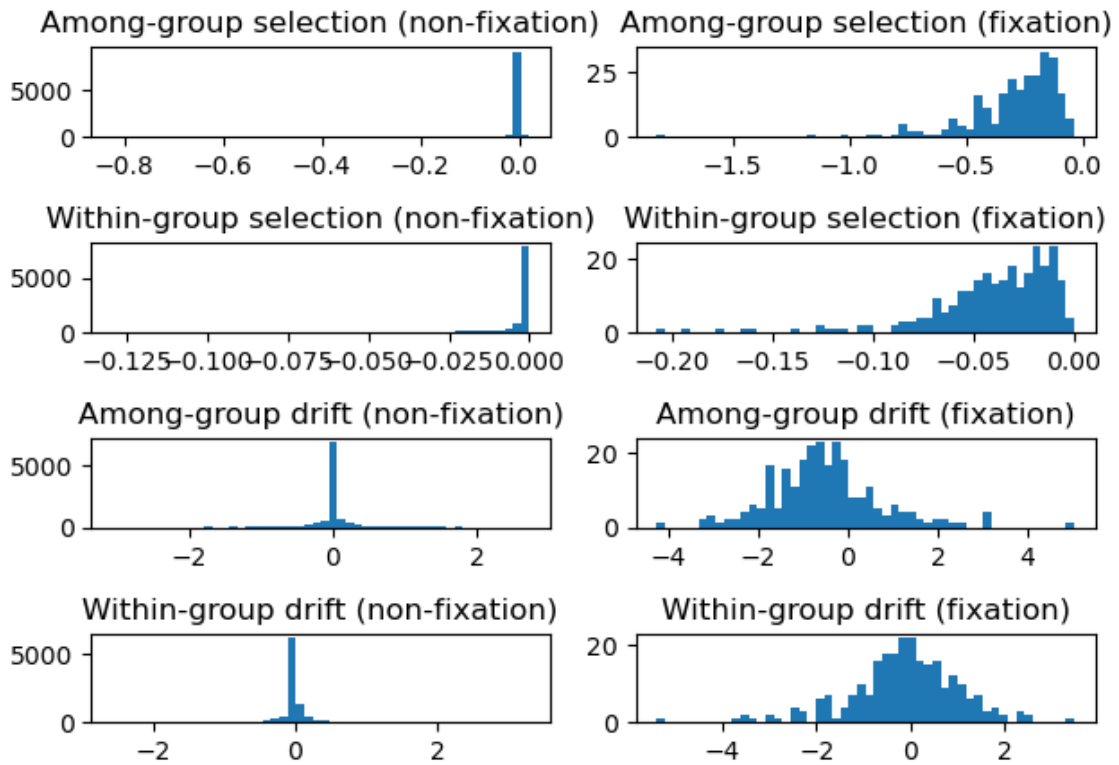


Figure S11: This figure shows similar histograms as figure S8, however, for the runs in this figure, $m = 10$.

Non-fixation runs vs. fixation runs ($m=20, q=1$)

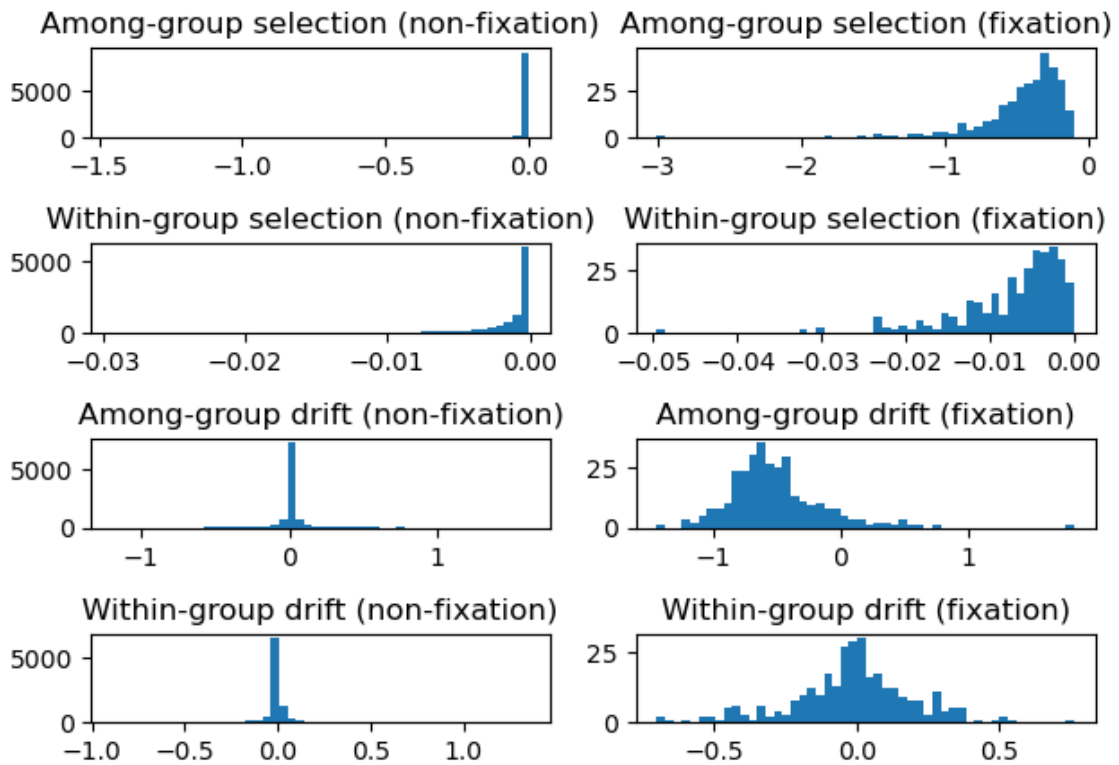


Figure S12: This figure shows similar histograms as figure S8, however, for the runs in this figure, $m = 20$.

Non-fixation runs vs. fixation runs ($m=25, q=1$)

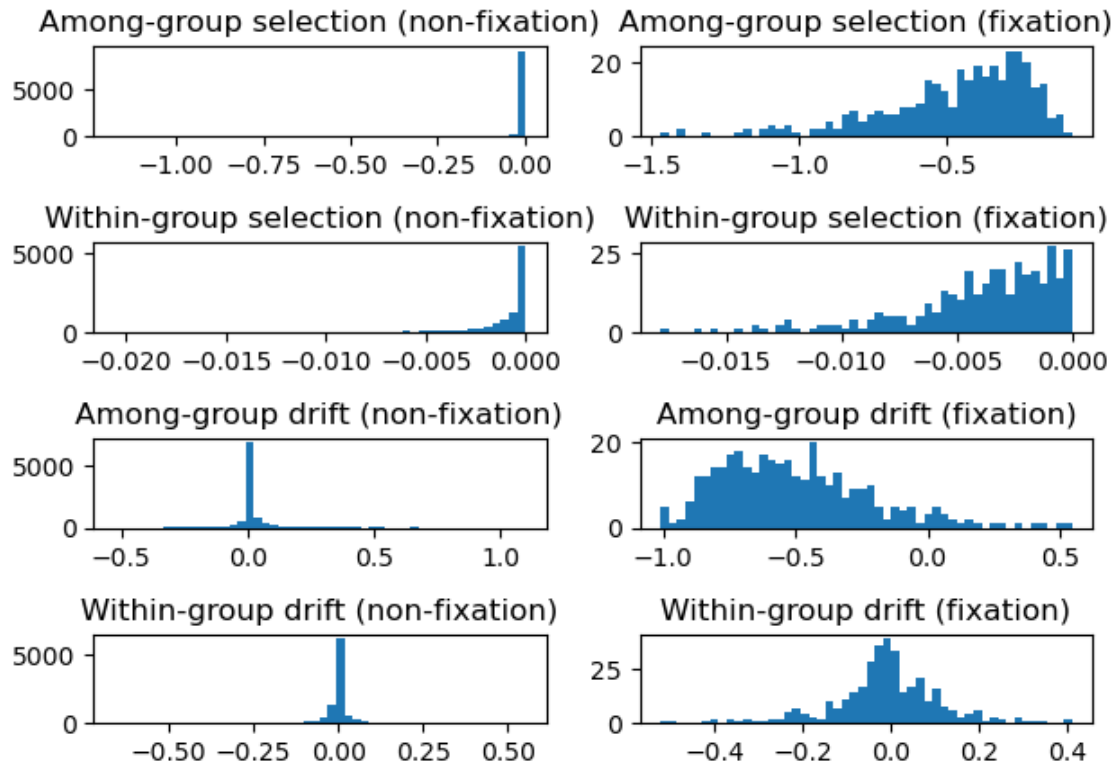


Figure S13: This figure shows similar histograms as figure S8, however, for the runs in this figure, $m = 25$.

Non-fixation runs vs. fixation runs ($m=50, q=1$)

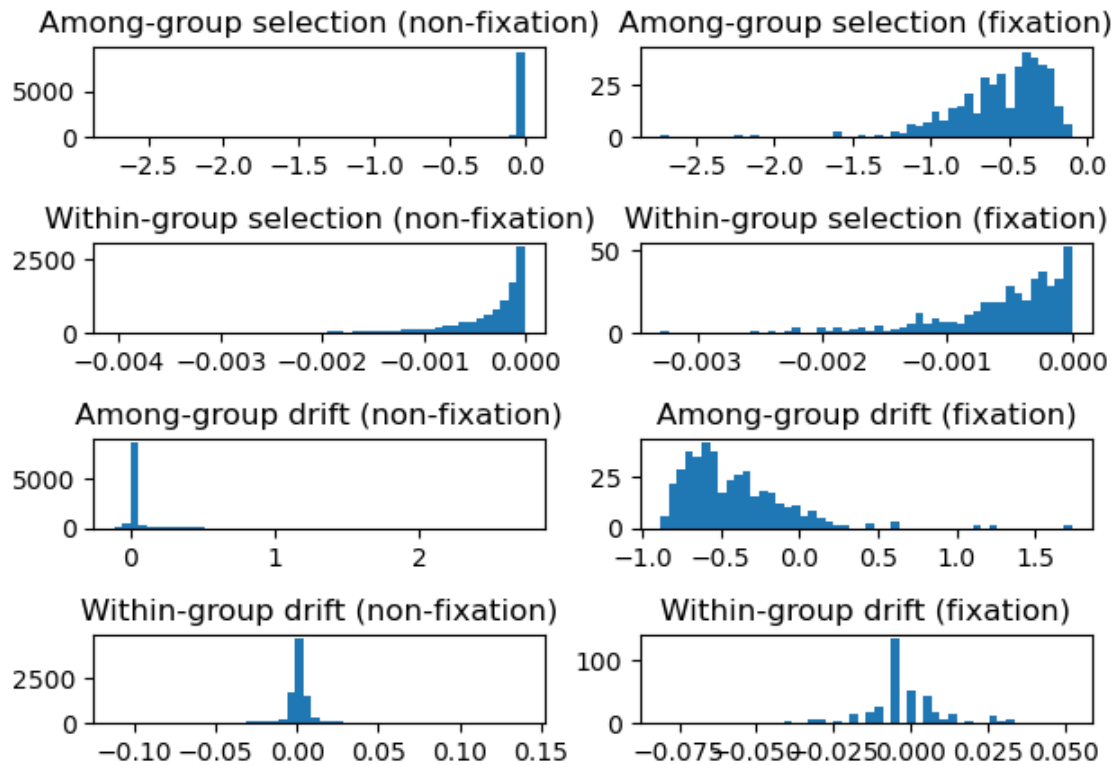


Figure S14: This figure shows similar histograms as figure S8, however, for the runs in this figure, $m = 50$.