

# Document for USRA

October 16, 2017

## 1 Methods

### 1.1 Model

We model obligate sexual hosts competing with obligate asexual hosts based on the model introduced by Lively (2010). Whereas most mathematical models used in the context of evolution of sex study population in a theoretical setting, Lively (2010) explicitly models epidemiological and ecological structure, making it a suitable candidate for modeling a natural population Ashby and King (2015). We further extend the model by adding a spatial structure and stochasticity.

All hosts are assumed to be diploids with two biallelic loci, and parasites are assumed to be haploids. For convenience, we use indices 1 – 4 to refer to following haplotypes (Agrawal and Otto, 2006). For example, an individual with genotype 12 has haplotypes  $AB$  and  $Ab$  and an arbitrary genotype is denoted as  $ij$ .

Let  $S_{ij}^k(t)$  and  $A_{ij}^k(t)$  be the number of sexual and asexual hosts with genotype  $ij$  in site  $k$  at generation  $t$ . For simplicity, we drop the superscript representing sites and write  $S_{ij}(t)$  and  $A_{ij}(t)$ , unless denoted otherwise. Following Lively (2010), the expected number of sexual offsprings (without recombination or outcrossing) produced in the next generation by hosts from a single site is given by

$$S'_{ij} = (1 - s) (W_U S_{ij,U}(t) + W_I S_{ij,I}(t)), \quad (1)$$

where  $s$  is the proportion of males produced.  $S_{ij,U}$  and  $S_{ij,I}$  represent the number of uninfected and infected sexual hosts in site  $k$ , respectively and  $W_U$  and  $W_I$  are their corresponding fitnesses.

Let  $g_i$  be the expected number of gametes with haplotype  $i$  passed on to the

next generation by sexual hosts from a single site:

$$\begin{aligned}
g_1 &= \sum_{j=1}^4 \delta_{1j} S'_{1j} - r S'_{14} + r S'_{23}, \\
g_2 &= \sum_{j=1}^4 \delta_{2j} S'_{2j} - r S'_{23} + r S'_{14}, \\
g_3 &= \sum_{j=1}^4 \delta_{3j} S'_{3j} - r S'_{23} + r S'_{14}, \\
g_4 &= \sum_{j=1}^4 \delta_{4j} S'_{4j} - r S'_{14} + r S'_{23},
\end{aligned} \tag{2}$$

where  $r$  is the recombination probability. After recombination and outcrossing, the expected number of sexual offsprings with genotype  $ij$  produced in the next generation by hosts from a single site can be written as

$$S''_{ij} = \frac{(1 - \delta_{ij}) g_i g_j}{2 \sum_k g_k}, \tag{3}$$

where  $\delta_{ij}$  is the Kronecker-delta.

We assume that a population distribution  $\epsilon \cdot 100\%$  of its offsprings to other sites evenly. Then, the expected number of sexual offspring with genotype  $ij$  in the next generation (accounting for contributions from all sites) is given by

$$E(S_{ij}^k(t+1)) = (1 - \epsilon_{\text{site}}) (S_{ij}^k)'' + \frac{\epsilon_{\text{site}}}{n_{\text{site}} - 1} \sum_{l \neq k} (S_{ij}^l)'' . \tag{4}$$

We then take a poisson random variable to simulate process error and allow for stochastic migration to avoid fixation:

$$S_{ij}^k(t+1) \sim \text{Poisson}(\lambda = E(S_{ij}^k(t+1))) + \text{Bernoulli}(p = p_{\text{sex}}), \tag{5}$$

where  $p_{\text{sex}}$  is the probability that a sexual host enters the population.

Asexual hosts are assumed to be strictly clonal. Then, the expected number of asexual offsprings with genotype  $ij$  produced in the next generation by hosts from a single site is given by

$$A'_{ij} = W_U A_{ij,U}(t) + W_I A_{ij,I}(t). \tag{6}$$

Accounting for contributions from all sites, we get

$$E(A_{ij}^k(t+1)) = (1 - \epsilon_{\text{site}}) (A_{ij}^k)' + \frac{\epsilon_{\text{site}}}{n_{\text{site}} - 1} \sum_{l \neq k} (A_{ij}^l)' . \tag{7}$$

Finally, we take a poisson random variable to obtain the number of asexual offsprings in the next generation and allow for migration:

$$A_{ij}^k(t+1) \sim \text{Poisson}(\lambda = E(A_{ij}^k(t+1))) + \text{Bernoulli}(p = p_{\text{asex}}), \tag{8}$$

where  $p_{\text{asex}}$  is the probability that an asexual host enters the population.

To model infection, we combine the approaches by Lively (2010) and Ashby and King (2015). The expected number of infected hosts that carry parasite with genotype  $i$  at generation  $t$  is given by:

$$I_i(t) = \sum_p 2^{\delta_{ij}} (S_{ip,i,I}(t) + A_{ip,i,I}(t)), \quad (9)$$

where  $S_{ip,i,I}$  and  $A_{ip,i,I}$  are the expected number of sexual and asexual hosts infected with genotype  $i$  parasite. Following Ashby and King (2015), we assume that mutation can occur in one locus with probability  $\epsilon$ . We also allow for migration with probability  $p_{\text{parasite}}$  to avoid fixation. Then, the number of infected individuals carrying parasite with genotype  $i$  after mutation is given by:

$$\begin{aligned} I'_1 &= (1 - \epsilon)I_1 + \frac{\epsilon}{2} (I_2 + I_3) + \text{Bernoulli}(p = p_{\text{parasite}}), \\ I'_2 &= (1 - \epsilon)I_2 + \frac{\epsilon}{2} (I_1 + I_4) + \text{Bernoulli}(p = p_{\text{parasite}}), \\ I'_3 &= (1 - \epsilon)I_3 + \frac{\epsilon}{2} (I_1 + I_4) + \text{Bernoulli}(p = p_{\text{parasite}}), \\ I'_4 &= (1 - \epsilon)I_4 + \frac{\epsilon}{2} (I_2 + I_3) + \text{Bernoulli}(p = p_{\text{parasite}}). \end{aligned} \quad (10)$$

Let  $\lambda_i^k$  be the poisson mean number of exposures caused by parasites with genotype  $i$  from site  $k$  in the next generation Lively (2010):

$$\lambda_i^k = \frac{\beta^k}{2N^k(t+1)} I'_i, \quad (11)$$

where  $\beta^k$  represents parasite fecundity at site  $k$  Lively (2010). Assuming that infected hosts can also mix with hosts in other sites, the mean number of exposures to parasites with genotype  $i$  that a susceptible host in site  $k$  receives is

$$\lambda_{i,\text{total}}^k = (1 - \epsilon_{\text{site}})\lambda_i^k + \frac{\epsilon_{\text{site}}}{n_{\text{site}} - 1} \sum_{l \neq k} \lambda_i^l. \quad (12)$$

Then, a force of infection from parasite  $i$  that a susceptible host with genotype  $ij$  in site  $k$  experiences is

$$\text{FOI}_{ij}^k = \lambda_{i,\text{total}}^k + \lambda_{j,\text{total}}^k. \quad (13)$$

The probability of infection for a host with genotype  $ij$  at site  $k$  in the next generation is

$$P_{ij}^k(t+1) = 1 - \exp(-\text{FOI}_{ij}^k). \quad (14)$$

Finally, the number of infected individuals in the next generation follows a binomial distribution:

$$\begin{aligned} S_{ij,I}^k(t+1) &\sim \text{Binom}(S_{ij}^k(t+1), P_{ij}^k), \\ A_{ij,I}^k(t+1) &\sim \text{Binom}(A_{ij}^k(t+1), P_{ij}^k). \end{aligned} \quad (15)$$

Expected number of individuals infected with haplotype  $i$  in the next generation is given by a ratio of  $\lambda$ :

$$\begin{aligned} S_{ij,i,I}^k(t+1) &= \frac{\lambda_{i,\text{total}}^k}{\lambda_{i,\text{total}}^k + \lambda_{j,\text{total}}^k} S_{ij,I}^k(t+1) \\ A_{ij,i,I}^k(t+1) &= \frac{\lambda_{i,\text{total}}^k}{\lambda_{i,\text{total}}^k + \lambda_{j,\text{total}}^k} A_{ij,I}^k(t+1) \end{aligned} \quad (16)$$

## 1.2 Simulations

## 1.3 Approximate Bayesian Computation

## 2 Results

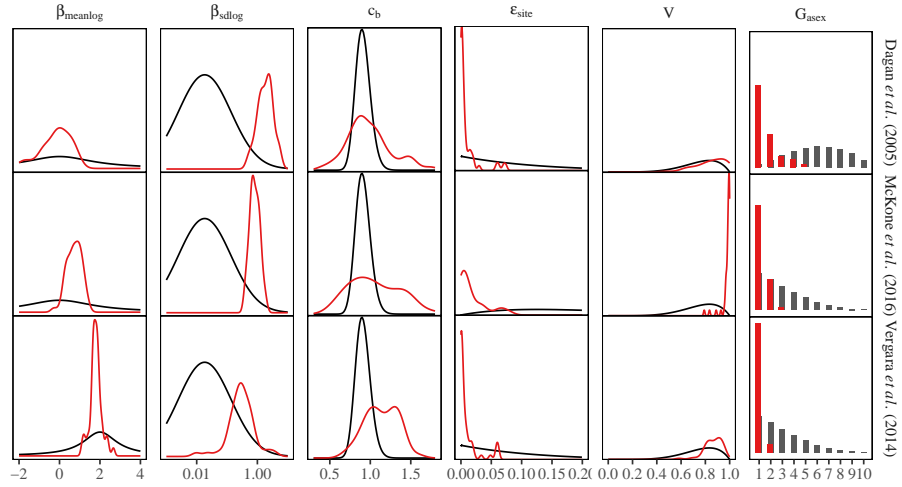


Figure 1: **Need caption.** Need caption

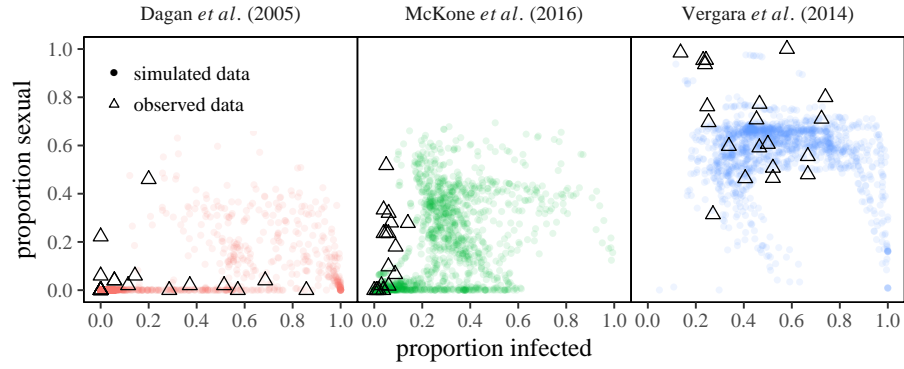


Figure 2: **Need caption.** Need caption

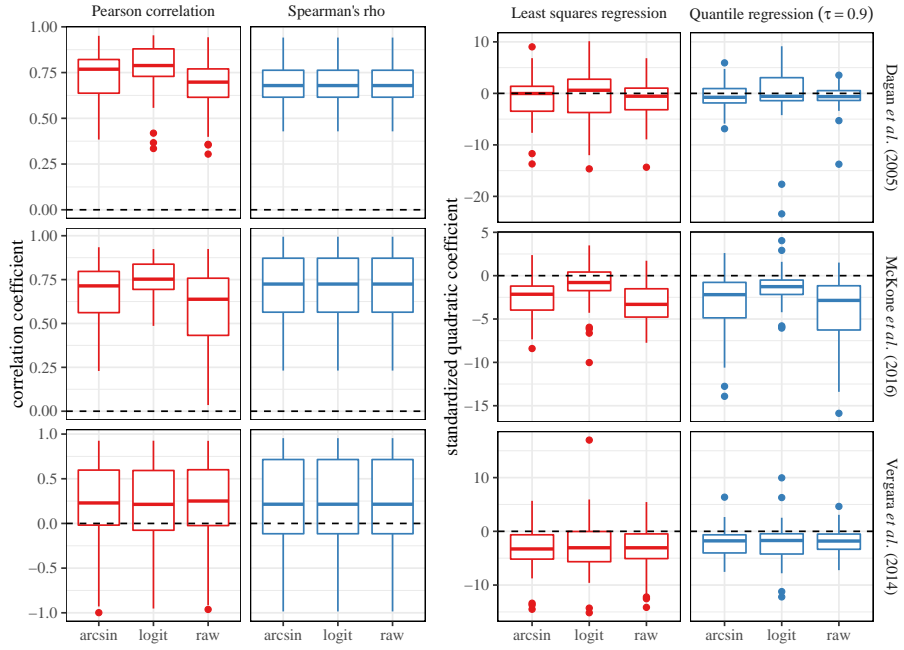


Figure 3: **Need caption.** Need caption

## References

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- Ashby, B. and K. C. King (2015). Diversity and the maintenance of sex by parasites. *Journal of evolutionary biology* 28(3), 511–520.
- Lively, C. M. (2010). An epidemiological model of host–parasite coevolution and sex. *Journal of evolutionary biology* 23(7), 1490–1497.