

Document for USRA

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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 δ_{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

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

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

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

where p_{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

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

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

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

where p_{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 ϵ . We also allow for migration with probability p_{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 λ_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 β^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 λ :

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

1.2 Simulations

1.3 Approximate Bayesian Computation

2 Results

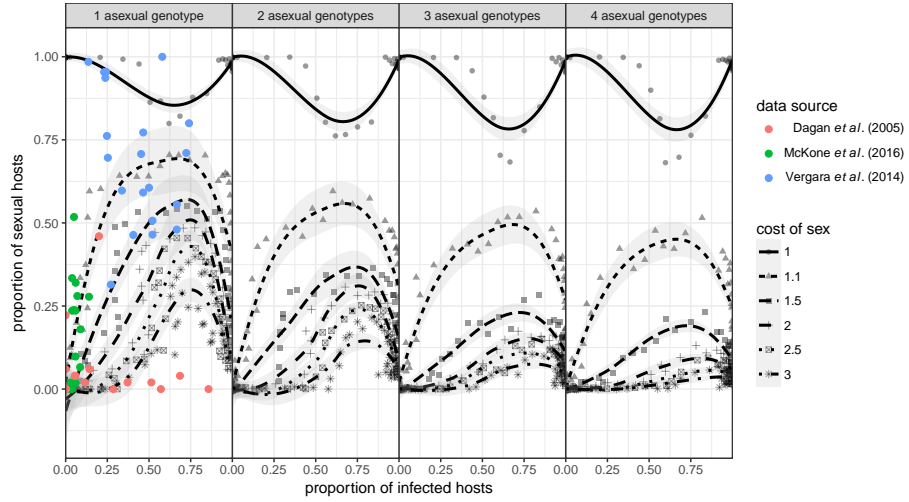


Figure 1: **Need caption.** Need caption

References

- Agrawal, A. F. and S. P. Otto (2006). Host-parasite coevolution and selection on sex through the effects of segregation. *The American Naturalist* 168(5), 617–629.
- 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. (2010). An epidemiological model of host–parasite coevolution and sex. *Journal of evolutionary biology* 23(7), 1490–1497.