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1 Methods

1.1 Model

To study the effect of parasite on the evolution of sex and perform a power analysis, we developed a discrete time stochastic model that can be applied to various systems. We model discrete generations to test for robustness of experimental designs to systems that have different generation lengths. Using a continuous time model would require us to adjust parameters to a proper time scale.

Here, we model diploid hosts and haploid parasites where the hosts are divided into obligate sexuals and obligate asexuals. Although natural systems that have been studied under the context of the Red Queen Hypothesis often contains polyploid asexuals (Dybdahl and Lively, 1995; Michiels et al., 2001; Ben-Ami and Heller, 2005; Bruvo et al., 2007; Verhoeven and Biere, 2013; Šimková et al., 2013), we do not consider polyploidy for simplicity. Assuming there are two biallelic loci, there are four types of haplotypes: AB, Ab, aB, ab. We will be using indices $1-4$ herefafter to refer to these gametes (Agrawal and Otto, 2006). For example, a genotype 12 has haplotypes AB and Ab.

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 all dynamics apply to each site independently unless noted otherwise. Following Lively (2010), we can write the expected number of sexual individuals in the next generation without recombination or outcrossing as follows:

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

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. S'_{ij} can be thought of as genotype contribution to the next generation.

Let G_i be the expected number of haplotype i passed on to the next gener-

ation in site k. Then, we have

$$\begin{aligned} G_1 &= \sum_{j=1}^{4} \delta_{1j} S'_{1j} - rS'_{14} + rS_{23}, \\ G_2 &= \sum_{j=1}^{4} \delta_{2j} S'_{2j} - rS'_{23} + rS_{14}, \\ G_3 &= \sum_{j=1}^{4} \delta_{3j} S'_{3j} - rS'_{23} + rS_{14}, \\ G_4 &= \sum_{j=1}^{4} \delta_{4j} S'_{4j} - rS'_{14} + rS_{23}, \end{aligned} \tag{2}$$

where r is the recombination probability. Following outcrossing, the expected the number of genotypes in the next generation is

$$S''_{ij} = \frac{(1 - \delta_{ij}) G_i G_j}{2 \sum_k G_k}, \tag{3}$$

where δ_{ij} is the Kronecker-delta. Finally, the number of sexual hosts with genotype ij in the next generation follows a poisson distribution:

$$S_{ij}(t+1) \sim \text{Poisson}(\lambda = S''_{ij})$$

As recombination and outcrossing do not occur in the asexual population, the expected number of asexual individuals in the next generation is given by

$$A'_{ij} = W_U A_{ij,U}(t) + W_I A_{ij,I}(t). \tag{4}$$

Then, the number of asexual hosts with genotype ij in the next generation is given by

$$A_{ij}(t+1) \sim \text{Poisson}(\lambda = A'_{ij}). \tag{5}$$

To model infection, we combine the approaches by Lively (2010) and Ashby and King (2015) Given the number of infected individuals at a site, we can compute the expected number of individuals infected with haplotype i at generation t:

$$I_i(t) = \sum_p 2^{\delta_{ij}} \left(S_{ip,i,I}(t) + A_{ip,i,I}(t) \right), \tag{6}$$

Here, $S_{ip,i,I}$ and $A_{ip,i,I}$ are the expected number of sexual and asexual individuals infected with haplotype i. Following Ashby and King (2015), we assume that mutation can occur in one locus with probability ϵ. Then, we find the

expected number of haplotypes within a population after mutation:

$$\begin{aligned} I_1' &= (1-\epsilon)I_1 + \frac{\epsilon}{2}(I_2 + I_3), \\ I_2' &= (1-\epsilon)I_2 + \frac{\epsilon}{2}(I_1 + I_4), \\ I_3' &= (1-\epsilon)I_3 + \frac{\epsilon}{2}(I_1 + I_4), \\ I_4' &= (1-\epsilon)I_4 + \frac{\epsilon}{2}(I_2 + I_3). \end{aligned} \tag{7}$$

Let λ_i^k be the poisson mean number of exposures caused by parasite with haplotype i from site k in the next generation Lively (2010):

$$\lambda_i^k = \frac{\beta^k}{2N^k(t+1)} I_i'. \tag{8}$$

Here, we are assuming that effects of dominance do not exist Ashby and King (2015). Then, a host with genotype ij in site k experience the following force of infection caused by haplotype i:

$$\mathrm{FOI}_i^k = (1-\epsilon_{\mathrm{site}})\lambda_i^k + \frac{\epsilon_{\mathrm{site}}}{n-1}\sum_{s\neq k}\lambda_i^s$$

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

$$P_{ij}^k(t+1) = 1 - \exp\left(\mathrm{FOI}_i^k + \mathrm{FOI}_j^k\right). \tag{9}$$

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

$$\begin{aligned} S_{ij,I}^k(t+1) &\sim \mathrm{Binom}(S_{ij}^k(t+1), P_{ij}^k) \\ A_{ij,I}^k(t+1) &\sim \mathrm{Binom}(A_{ij}^k(t+1), P_{ij}^k) \end{aligned} \tag{10}$$

Expected number of individuals infected with haplotype i is given by a ratio based on the orce of infection:

$$\begin{aligned} S_{ij,i,I}^k(t+1) &= \frac{\mathrm{FOI}_i^k}{\mathrm{FOI}_i^k + \mathrm{FOI}_j^k} S_{ij,I}^k(t+1) \\ A_{ij,i,I}^k(t+1) &= \frac{\mathrm{FOI}_i^k}{\mathrm{FOI}_i^k + \mathrm{FOI}_j^k} A_{ij,I}^k(t+1) \end{aligned} \tag{11}$$

- I might want to add genetic drift using binomial distribution.
- I'm going to add migration as well but I don't know how I should order the dynamics. 'Migration - Drift - Selection' seems reasonable. This way, an aseuxal individual can enter the population and die off from the drift.

1.2

References

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