Notes 2

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Let's try to think about this more generally. We want to design and experiment for red queen hypothesis and perform power analysis.

1 Empirical studies

What I should be looking at:

- From Auld et al. (2016): "heritable component, rapid parasite evolution, and temporally shifting parasite-mediate selection"

1.1 Not Red queen?

- Michiels et al. (2001) says that their system does not match requirements of the red queen hypothesis (weak infection fitness cost). They think that there might be other factors involved.

2 Model

2.1 Notes

Michiels et al. (2001): heterozygote triploids are hard to distinguish so di-allelic representation is used

Lively (2001) suggests that prevalence is actually not a good measure. Risk of infection (probability of exposure to ifective parasite propagules) is a better measure. Near the *switch point*, asexuals can have higher prevalence but this range is fairly narrow.

Hakoyama and Iwasa (2004) tried to model Japanese crucian carp and showed that parasitism may explain the evolution of sex. They also show that coexistence of parthnogenetic complex is more likely than that of gynogenetic complex. Read this paper later to see how we want to analyze our model!

Neiman et al. (2017) emphasizes importance of a pluralist approach and suggests directions. It's worth noting that many of pluralist studies include red queen dynamics. We are being a pluralist because we're adding ecological feedback in the model. I don't think we have to test for power yet as there aren't many appropriate systems but it might still be important and interesting to compare power for pluralist idea vs. red queen alone. See Meirmans and Neiman (2006) for testing interactive effects.

Agrawal and Lively (2002) says that dynamical qualities of matching alleles model can be observed across other continuum. We can just stick with MA for now.

Agrawal (2009) says GFG model failed to show selection for sex or recombination in diploid model. In MA and IMA models, recombination was often more favored than sex. However, they also saw cases where sex was favored but recombination was not. Using a haploid model can be misleading.

2.2 Deterministic model

We simulate red queen dynamics based on matching alleles (MA) model using diploid hosts and haploid parasites. Instead of using modifier genes, we model obligate asexual and sexual population explicitly. Assuming there are two biallelic loci, there are four types of gametes that can be produced: AB, Ab, aB, ab. We will be using indices $1 - 4$ for simplicity to refer to these gametes (Agrawal and Otto, 2006).

Let A_{ij} and S_{ij} represent density of total asexual and sexual population with genotype ij. Following Lively (2010), we can write

$$S'_{ii} = (1-s)S_0(g_i^2)[W_I P_{ij} + W_U(1-P_{ij})],$$
$$S'_{ij} = (1-s)S_0(2g_i g_j)[W_I P_{ij} + W_U(1-P_{ij})],$$
$$A'_{ij} = A_{ij}[W_I P_{ij} + W_U(1-P_{ij})],$$

where s is the proportion of male offspring produced, S_0 is the total density of the sexual population, g_i is the frequency of gamete i before recombination and P_{ij} is the probability of infection. W_I and W_U are modeled in the same way as Lively (2010). After recombination, μ individuals enter all sexual genotypes.

Let λ_i be the mean number of poisson mean number of exposures for hosts with genotype ij by parasite with haplotype i, we can write

$$P_{ij} = 1 - \exp(-(\lambda_i + \lambda_j)/2).$$

By doing so, we are assuming that effects of dominance do not exist. Then, we get

$$\lambda_i = \beta \left(\sum_p 2_{ip}^{\delta}(S_{ip,i,I} + A_{ip,i,I}) + \kappa \right)$$

To avoid fixation, we assume that new parasites enter the population at a constant rate.

Here, density of genotype ip infected with haplotype i – $S_{ij,i,I}$ and $A_{ij,i,I}$ – is given by

$$S_{ij,i,I} = \frac{\lambda_i(t-1)}{\lambda_i(t-1) + \lambda_j(t-1)} S_{ij,I}, ...$$

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Study	Host	Parasite	Experiment	Notes
Michiels et al. (2001) - Lab	Flatworm *Schmidtea poly-chroa* - obligate sexual diploid and parthenogenetic triploid	Amoeboid proto-zoan (Asexual)	Compare propor-tion of infected in-dividuals in mixed samples with LRT; rate of infection	Highly hetero-geneous spatial distribution; need longer study
Kumpulainen et al. (2004) - Field	psychid moth	hymenopteran par-asitoids	test prevalence of parasitoids and prevalence of sex-ual reproduction	demonstrates cost of sex; no evi-dence for different reproduction mode preferring different space
Ben-Ami and Heller (2005) - Field	snails	trematodes	correlation for males and fre-quency of infection	Male frequencies decreased bu infection levels increased
Bruvo et al. (2007) - Field	Planarian flat-worm *Schmidtea polychroa* - diploid sexuals and (mostly) triploid parthenogens	only look at asex-ual; test for infec-tion rates among the clonal lineage; relate parasite load and fertility		
Verhoeven and Biere (2013) - Field	Dandelions - diploid sexual and triploid obligate apomicts	Microbial commu-nities, fungus, and weevil	Experiment + testing infection prevalence in nature	See geographic parthenogenesis; they address that they might have a power problem
Šimková et al. (2013)	Gibel carp - sexual diploid and gyno-genetic triploid	metazoan para-sites	Comparison of MHC genes: do sexual individu-als have higher variability + do asexual invidiauls suffer from higher parasite load	"Coexistence may be maintained by male mate choice or spatial and tem-poral extinction and recoloniza-tion"; need longer study
Auld et al. (2016) - Lab	Daphnia - partly sexual and asexual	*Pasteuria ramosa*	Time shift ex-periment (testing for proportion of infected and spores per host) with MCMCglmm	Unrealistic setting in nature; their study looks at within-host factors
Slowinski et al. (2016)	*Caenorhabditis elegans* - hermaphrodite and obligate sexual	*Serratia marcescens*	Introduction of mixed mating into outcrossing population and exposing different types of parasites - test selfing rates using ANOVA	parasite has to be coevolving