Quantifying the effects of parasites on the maintenance of sex

Sang Woo Park

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Evolution of sex

- **Two-fold cost of sex**: (1) cost of producing males and (2) cost of meiosis
- the two-fold cost of cost of sex asumes that **all else is equal**
- only 0.01% eukaryotes conform to purely asexual reproduction. How?

Red Queen Hypothesis

- sexual reproduction creates rare genotypes that can escape infection (**negative frequncy dependence**)
- snail population in New Zealand (host for sterilizing trematode infection) is believed to support the hypothesis [1]
- prevalence of sex should be **positively correlated** with prevalence of infection [2]
- unable to detect any correlation in a similar snail-trematode system. Why? [3]

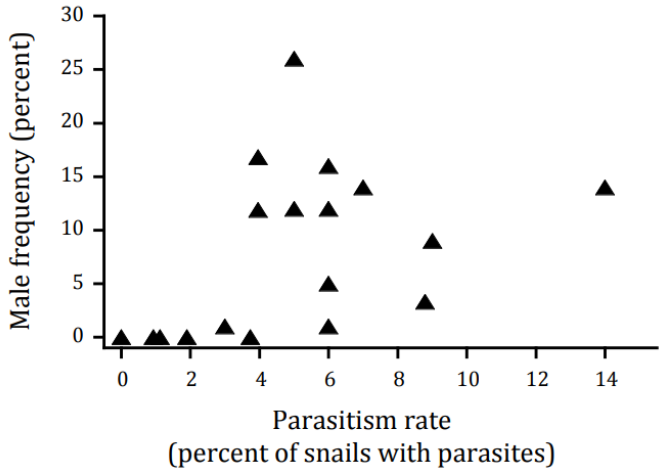

Figure: Prevalence of infection is positively correlated with male frequency [4].

Mathematical model

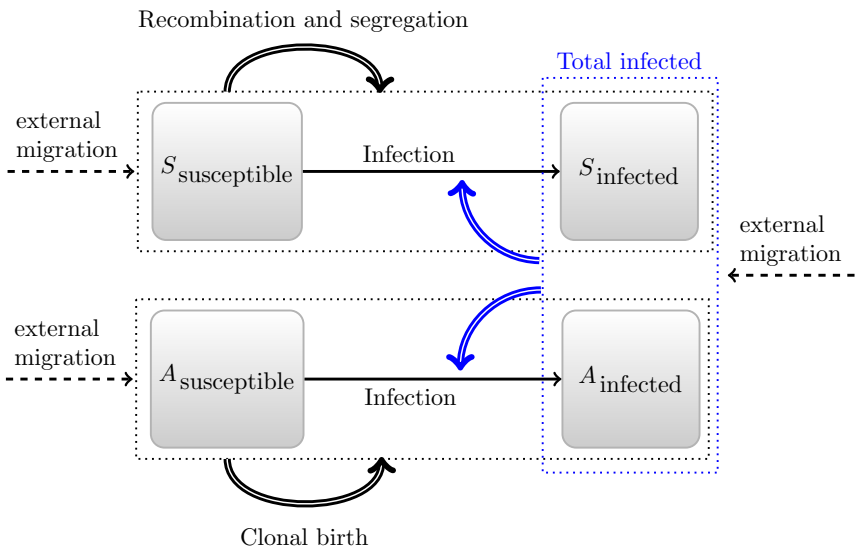

Figure: Graphical representation of the model. Double lined arrows represent dynamics that are affected by mixing betwee habitats.

- competition of obligate sexual v.s. obligate asexual hosts under parasite selection. Hosts are assumed to be diploids and parasites are assumed to be haploids [5]

- offsrpings produced by hosts from a site:

$$\begin{cases} S'_{ij} = c_b(1-s)\left(W_U S_{ij,U}(t) + W_I S_{ij,I}(t)\right) \\ A'_{ij} = W_U A_{ij,U}(t) + W_I A_{ij,I}(t) \end{cases}$$

  S'_{ij} then goes through recombination and segregation after. Virulence is defined as $V = 1 - W_I/W_U$.

- expected offsprings in site k in next generation accounting for mixing between sites:

$$\mathrm{E}\left(X^k_{ij}(t+1)\right) = (1-\epsilon_{\text{site}})X^k_{ij} + \frac{\epsilon_{\text{site}}}{n_{\text{site}}-1}\sum_{l\neq k} X^l_{ij},$$

  where X can be replaced with either A or S.

- number of offsprings is taken as a poisson random variable

s: frequency of males, W_U and W_I: fitness of uninfected and infected hosts, c_b scaling factor for cost of sex, ϵ_{site}: mixing between sites

- poisson mean number of exposures caused by parasites i:

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

where I_i' is the number of hosts infected by parasite i after accounting for recombination.

- accounting for mixing between sites:

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

- force of infection: $\text{FOI}_{ij}^k = \lambda_{i,\text{total}}^k + \lambda_{j,\text{total}}^k$.
- infection is modeled using a binomial random variable with $P_{ij}^k(t+1) = 1 - \exp\left(\text{FOI}_{ij}^k\right)$.

β^k: the transmission rate at each site.

Simulation

- transmission rate is randomly drawn from a lognormal distribution with parameters $\beta_{\text{meanlog}}, \beta_{\text{sdlog}}$
- number of asexual genotypes present in the system is fixed to G_{asex}
- sexual hosts are allowed to mix under parasite selection without asexual hosts for 500 generations; then, asexual hosts are introduced and the simulation runs for 600 generations

Approximate Bayesian Computation

- fitted to two spatial data [3, 4] and one spatio temporal data [1]
- prior distribution on $\beta_{\text{meanlog}}, \beta_{\text{sdlog}}, c_b, \epsilon_{\text{site}}, V, G_{\text{asex}}$. Rest are fixed.
- almost uninformative priors for all except c_b; it was scaled to approximately match the 95% CI for cost of sex reported by [6]
- considered absolute difference in summary statistics: mean prevalence of sex and infection and CV in mean prevalence of sex and infection across generations/sites

Parameters	Dagan *et al.* [3]	McKone *et al.* [4]	Vergara *et al.* [1]
β_{meanlog}	$\text{Cauchy}(\text{location} = 0, \text{scale} = 2)$		$\text{Cauchy}(\text{location} = 2, \text{scale} = 1)$
β_{sdlog}	$\text{Lognormal}(\text{meanlog} = 0, \text{sdlog} = 2)$		
c_b	$\text{Lognormal}(\text{meanlog} = -0.1, \text{sdlog} = 0.1)$		
ϵ_{site}	$\text{Beta}(\text{shape1} = 1, \text{shape2} = 9)$	$\text{Beta}(\text{shape1} = 2, \text{shape2} = 8)$	$\text{Beta}(\text{shape1} = 1, \text{shape2} = 9)$
V	$\text{Beta}(\text{shape1} = 6, \text{shape2} = 2)$		
G_{asex}	$\text{BetaBinom}(\text{size} = 9, \text{prob} = 5/9, \text{theta} = 5) + 1$	$\text{BetaBinom}(\text{size} = 9, \text{prob} = 3/9, \text{theta} = 5) + 1$	

Sequential Monte Carlo

- way to approximate the posterior more efficiently
- perform ABC with high tolerance; perform ABC again but draw a weighted sample from the accepted values instead and "jump"
- modified Population Monte Carlo suggested by [7]. Parameters were transformed to an unconstrained scale (possible for all except G_{asex}) and jump through gaussian kernel independently for each parameter:

$$q(\cdot|\theta_i^*) \sim \text{Normal}(\mu = \theta_i^*, \sigma^2 = 2\text{Var}(\theta_{i,t-1})),$$

  where θ_i^* is the i-th parameter of a transformed accepted parameter sample, θ^*, from the last run (a sample we're jumping from) and θ_{t-1} is the marginal set of accepted i-th parameters from the last run,
- binomial jump for G_{asex} but prevent it from fixing:

$$q(\cdot|G_{\text{asex}}^*) \sim \text{Binomial}(\text{size} = 9, p = (G_{\text{asex}}^* - 0.5)/10)) + 1$$

Result - ABC

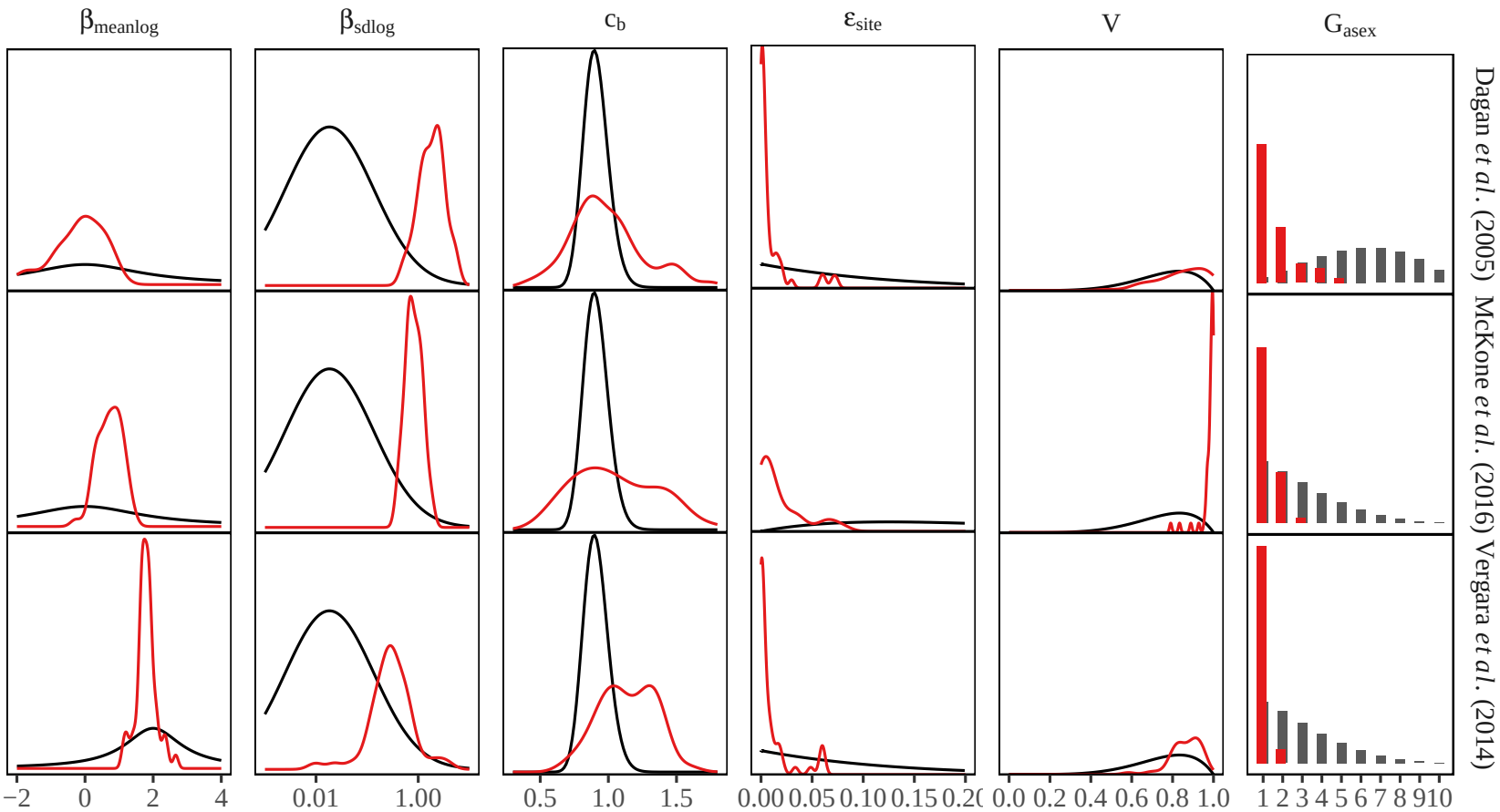

Figure: (black) prior distributions where parameters sampled from and (red) posterior distributions obtained from ABC

Result - simulated data v.s. observed data

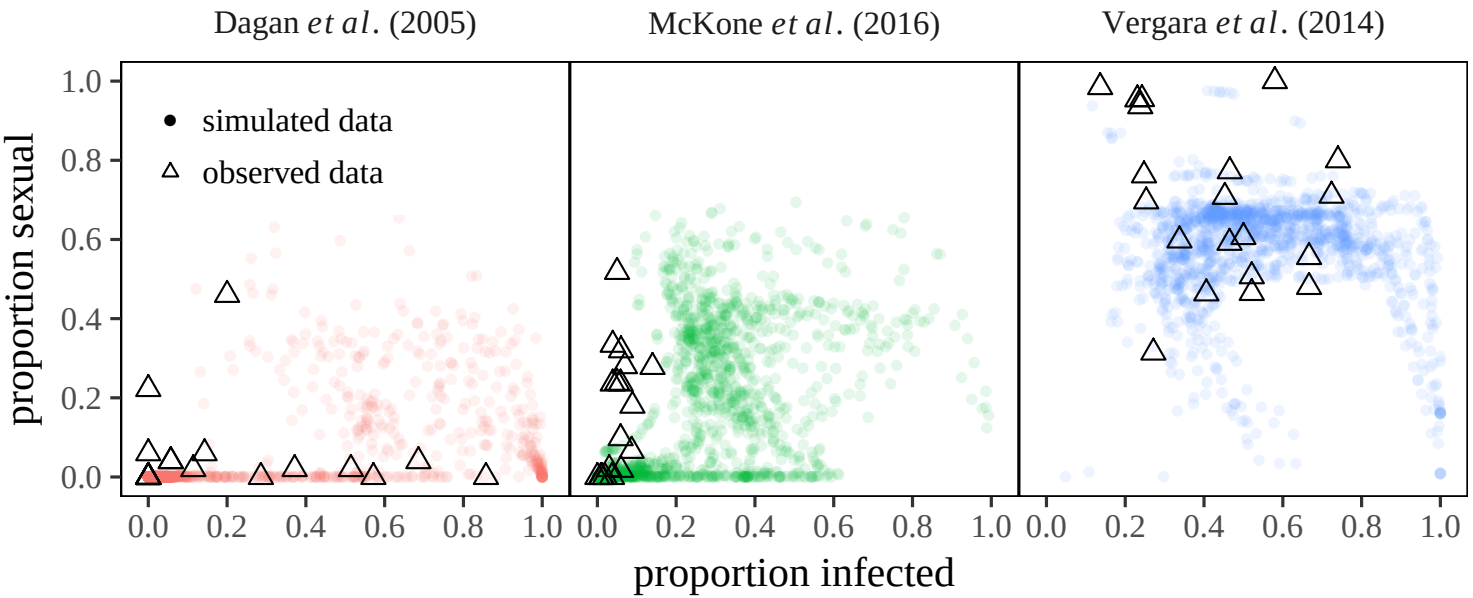

Figure: Simulated data v.s. observed data. Each point for simulated data represents mean proportion infected and sexual at each site.

- overestimates proportion infected when fitted to McKone *et al.* [4]
- spatial structure allows high level of infection to be maintained even at high virulence (middle panel)
- initially increasing prevalence of sexual reproduction pulls back infection (consistent with [2]) and causes prevalence of infection to decrease; quadratic overall?

Result - Power analysis

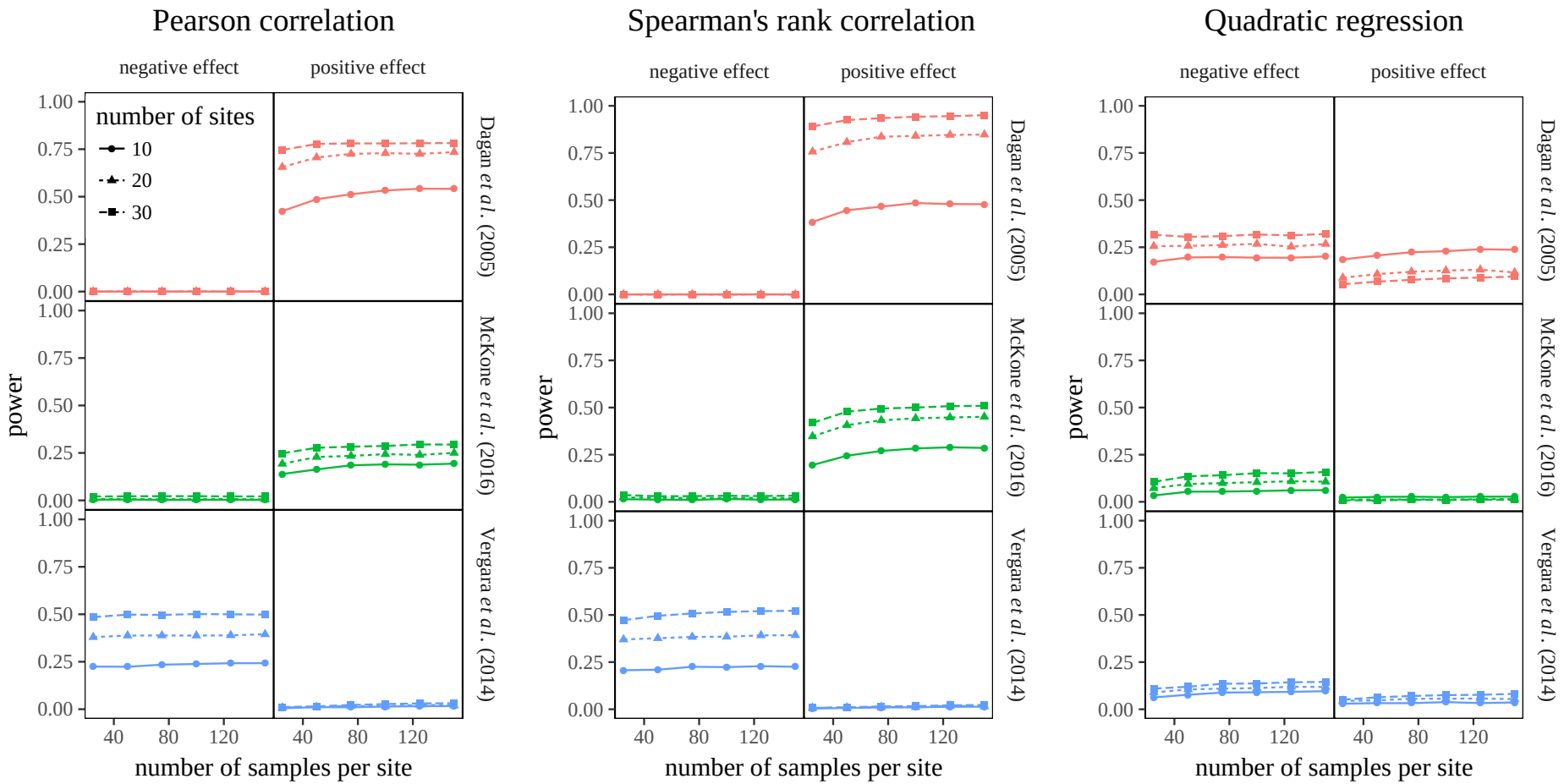

Figure: Power analysis for detecting a correlation and negative quadratic curvature.

Discussion - Why low power?

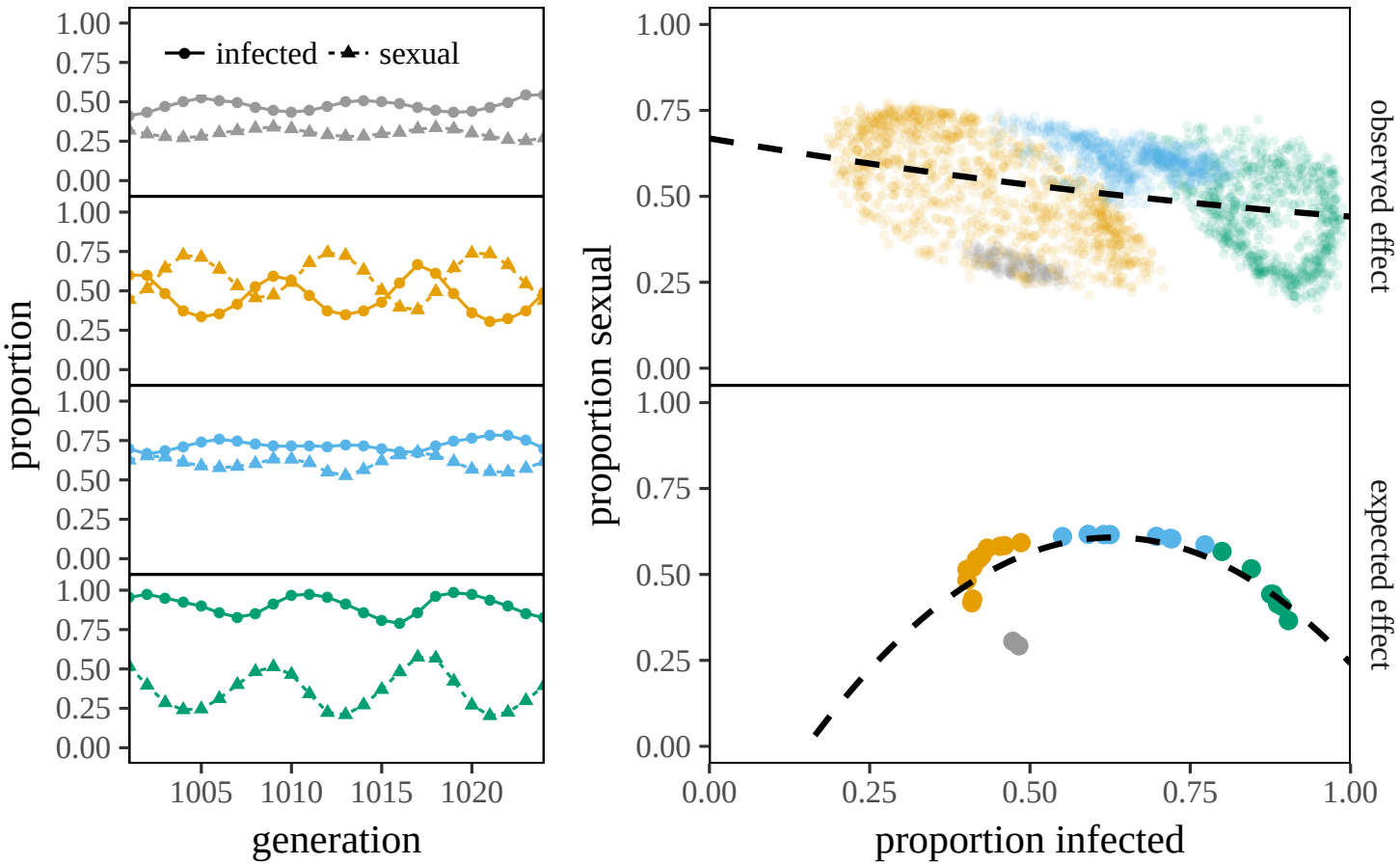

Figure: A sample data from a posterior sample. (left) type of cycles present in a simulated data (right) observed relationship v.s. expected relationship. (dashed line) quadratic regression.

Discussion - Why low power?

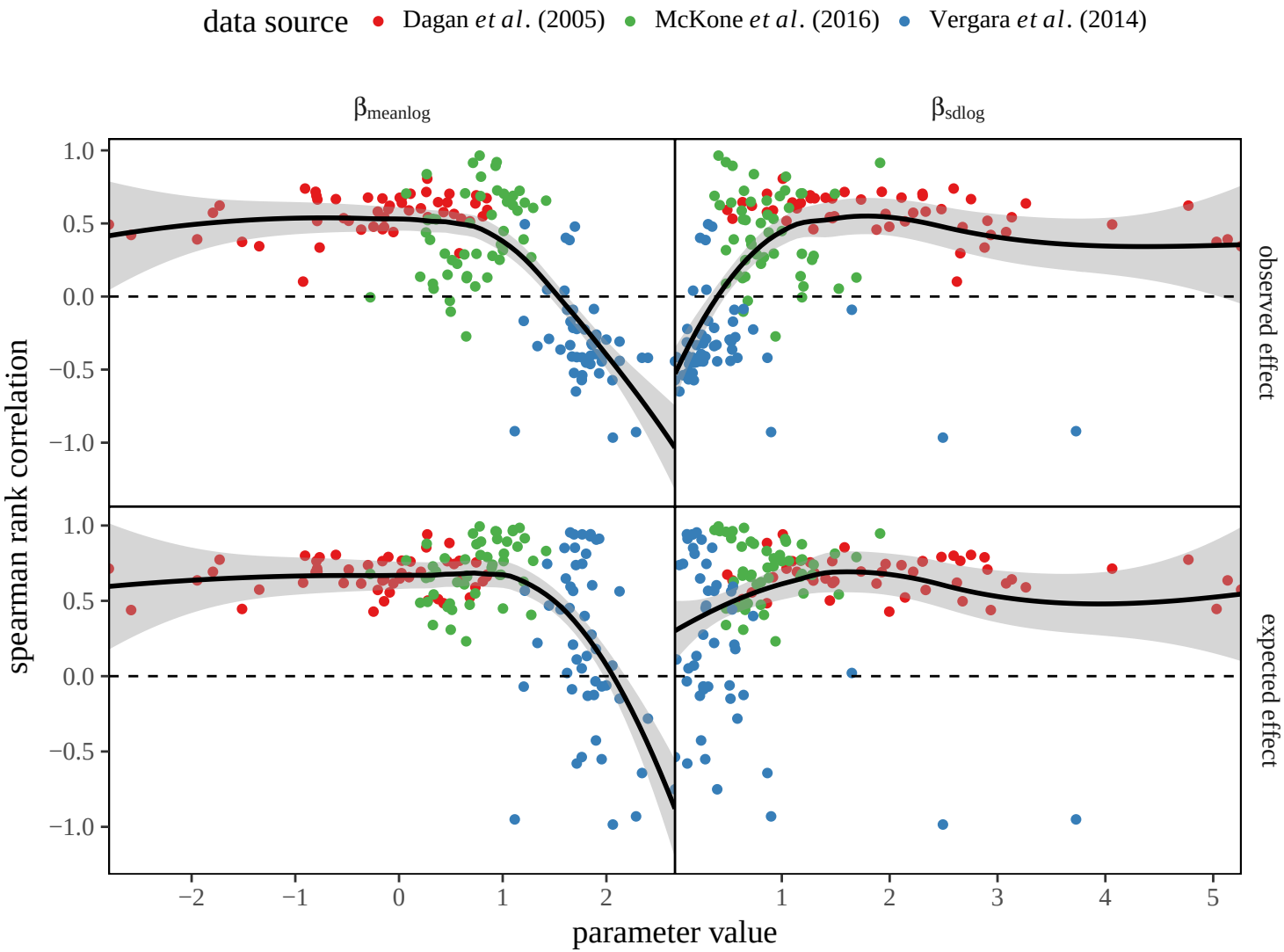

Figure: sensisivity plot of observed relationship v.s. expected relationship.

Conclusion/questions

- Red Queen hypothesis not appropriate for Dagan *et al.* data? (high asexual diversity, highly interconnected but diverse habitats, strong drift by seasonal flood [8])
- spatial data provides limited information; only Vergara *et al.* [1] had spatiotemporal data
- identify different cycles in nature?
- is there a way to detect the Red Queen cycles from a spatiotemporal data? or account for cycles in a spatial data?
- consider pluralistic approach (Red Queen hypothesis + other mechanisms for maintaining sex)?

Reference

[1] Daniela Vergara, Jukka Jokela, and Curtis M Lively. Infection dynamics in coexisting sexual and asexual host populations: support for the red queen hypothesis. *The American naturalist*, 184(S1):S22–S30, 2014.

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[4] Mark J McKone, Amanda K Gibson, Dan Cook, Laura A Freymiller, Darcy Mishkind, Anna Quinlan, Jocelyn M York, Curtis M Lively, and Maurine Neiman. Fine-scale association between parasites and sex in potamopyrgus antipodarum within a new zealand lake. *New Zealand Journal of Ecology*, 40(3):1, 2016.

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[7] Brandon M Turner and Trisha Van Zandt. A tutorial on approximate bayesian computation. *Journal of Mathematical Psychology*, 56(2):69–85, 2012.

[8] Frida Ben-Ami and Joseph Heller. Temporal patterns of geographic parthenogenesis in a freshwater snail. *Biological journal of the Linnean Society*, 91(4):711–718, 2007.