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Appendix D. Selection in simple theoretical models.

Here we examine net and fluctuating selection in several simple theoretical community models. We show that different models make contrasting predictions about how net and fluctuating selection will vary among species and along gradients of resource enrichment and environmental variability. These results indicate that empirically-observed patterns of variation in fluctuating selection can be useful for testing alternative hypotheses about the underlying mechanisms governing species dynamics and coexistence.

We first consider three different discrete time versions of the Lotka-Volterra competition model incorporating environmental stochasticity. These models can be regarded as simple phenomenological descriptions of species that compete less strongly interspecifically than intraspecifically, so that rare species have a frequency-dependent advantage over common ones. Environmental stochasticity generates fluctuating selection in these models because species are sometimes perturbed to high relative abundance and subsequently decline, and are sometimes perturbed to low relative abundance and subsequently increase.

The model of Ives et al. (1999) is

$$N_{i,t+1} = N_{i,t} \exp\left[r_i \left(1 - \frac{N_{i,t} + \sum_{j \neq i} \alpha_{ij} N_{j,t}}{K_i} \right) \right] \exp\left[e_{i,t}(0,\sigma) \right], \tag{D.1}$$

where $N_{i,t}$ is the abundance of species i at time t, $N_{j,t}$ is the abundance of species $j \neq i$, species i is characterized by maximum per-capita growth rate r_i and carrying capacity K_i, α_{ij} gives the per-capita competitive effect of species j on i, and $e_{i,t}(0,\sigma)$ is a normally distributed random variable with mean 0 and standard deviation σ chosen independently for each species at each timestep. Equation D.1 assumes that environmental noise acts as a multiplicative perturbation to per-capita growth rate. The model of Lehman and Tilman (2000) is

$$N_{i,t+1} = N_{i,t} + r_i N_{i,t} \left(1 - \frac{N_{i,t} + \sum_{j \neq i} \alpha_{ij} N_{j,t}}{K_i + e_{i,t}(0,\sigma)} \right), \tag{D.2}$$

where all terms are defined as in Eq. D.1. Equation D.2 assumes that environmental noise acts as an additive perturbation to carrying capacity K_i. The model of Hughes and Roughgarden (2000) is

$$N_{i,t+1} = N_{i,t} + r_i N_{i,t} \left(1 - \frac{N_{i,t} + \sum_{j \neq i} \alpha_{ij} N_{j,t}}{K_i} \right) + e_{i,t}(0,\sigma). \tag{D.3}$$

Equation D.3 assumes that environmental noise acts as an additive perturbation to total population growth rate.

We did not attempt to exhaustively explore parameter space, and instead present illustrative results. For each model, we consider $s = 10$ species with $\alpha_{ij} = 0.5$, $r_i = r$, and $K_i = K$ (results are qualitatively similar if K, r, and α are allowed to vary among species). We simulate each model for 100 timesteps starting each species at initial density $N_i = K/4$, drop the first 10 timesteps to remove transients, and then calculate net and fluctuating selection from the remaining 90 timesteps. Because species abundances are known without error, we calculated net and fluctuating selection directly from the simulated dynamics rather than by first fitting a statistical model to the dynamics.

In all models, mean fluctuating selection increases approximately linearly with increasing environmental noise σ (Fig. D1a). Increasing noise generates larger perturbations to species abundances, leading to stronger fluctuating selection because species exhibit a frequency-dependent response to perturbations. All three models therefore predict that increasingly-variable environmental conditions should be associated with increasingly strong fluctuating selection, all else being equal. This prediction is not supported by our empirical results.

Increasing noise also slightly increases net selection in all three models (Fig. D1a), but for trivial reasons. With increasing noise there is an increasing probability that any given species will exhibit a substantially higher or lower relative abundance at the end of the simulation than the beginning. Increasing noise does not actually generate long-term directional trends in species' relative abundances.

If carrying capacity K is taken as a measure of enrichment, these models can be used to predict how net and fluctuating selection will vary along enrichment gradients. The model of

Lehman and Tilman (2000) predicts that fluctuating selection will decline with increasing enrichment, while the other two models predict that fluctuating selection is independent of enrichment (Fig. D1b). The models of Lehman and Tilman (2000) and Hughes and Roughgarden (2000) predict that net selection declines with increasing enrichment, while the model of Ives et al. (1999) predicts that net selection is independent of enrichment (Fig. D1b). None of these predictions regarding the effects of enrichment on selection is supported by our empirical results. Failure of a range of stochastic competition models to reproduce observed patterns of net and fluctuating selection along gradients of environmental variability and enrichment suggests that observed patterns of selection do not arise solely from the combination of frequency dependence and environmental stochasticity.

An alternative possibility is that fluctuating selection arises from internally-generated fluctuations in relative abundance arising from species interactions, as opposed to externally-generated fluctuations arising from abiotic perturbations. A classic model non-equilibrium, fluctuation-dependent competitive coexistence is the consumer-resource model of Armstrong and McGehee (1980), the dynamics of which have been well-studied (e.g., Abrams et al. 2003). The model assumes a single resource R that grows logistically, and is consumed by competing consumers with Type II or Type I functional responses. The consumers (C_i, where $I = 1,\ldots,k$) have a birth rate that is proportional to the amount of ingested resources, and a constant per capita mortality rate. The model is give be the following system of equations

$$\begin{aligned} \frac{dR}{dt} &= rR\left(1-\frac{R}{K}\right)-\sum_{i=1}^{k}\frac{C_i m_i R}{1+h_i m_i R} \\ \frac{dC_i}{dt} &= C_i\left(\frac{\varepsilon_i m_i R}{1+h_i m_i R}-\delta_i\right) \end{aligned}, \qquad \text{(D.4a-b)}$$

where r and K are the maximum per-capita growth rate and carrying capacity respectively for logistic growth in the resource, m_i is attack rate of consumer i, h_i is its handling time, ε_i is its conversion efficiency of ingested resources to new consumers, and δ_i is its per-capita mortality rate. If $h_i>0$, the consumer has a type II functional response, but if $h_i=0$ the consumer has a Type I functional response.

Using a representative set of parameters, we find that fluctuating selection increases with increasing enrichment (Fig. D2). While we did not explore parameter space exhaustively, we found this qualitative relationship to hold for a number of parameter combinations. Because Eq. D.4 is deterministic, it makes no prediction regarding the effects of abiotic environmental variability on selection, but it could be extended to incorporate environmental variability (e.g., Vasseur and Fox 2007).

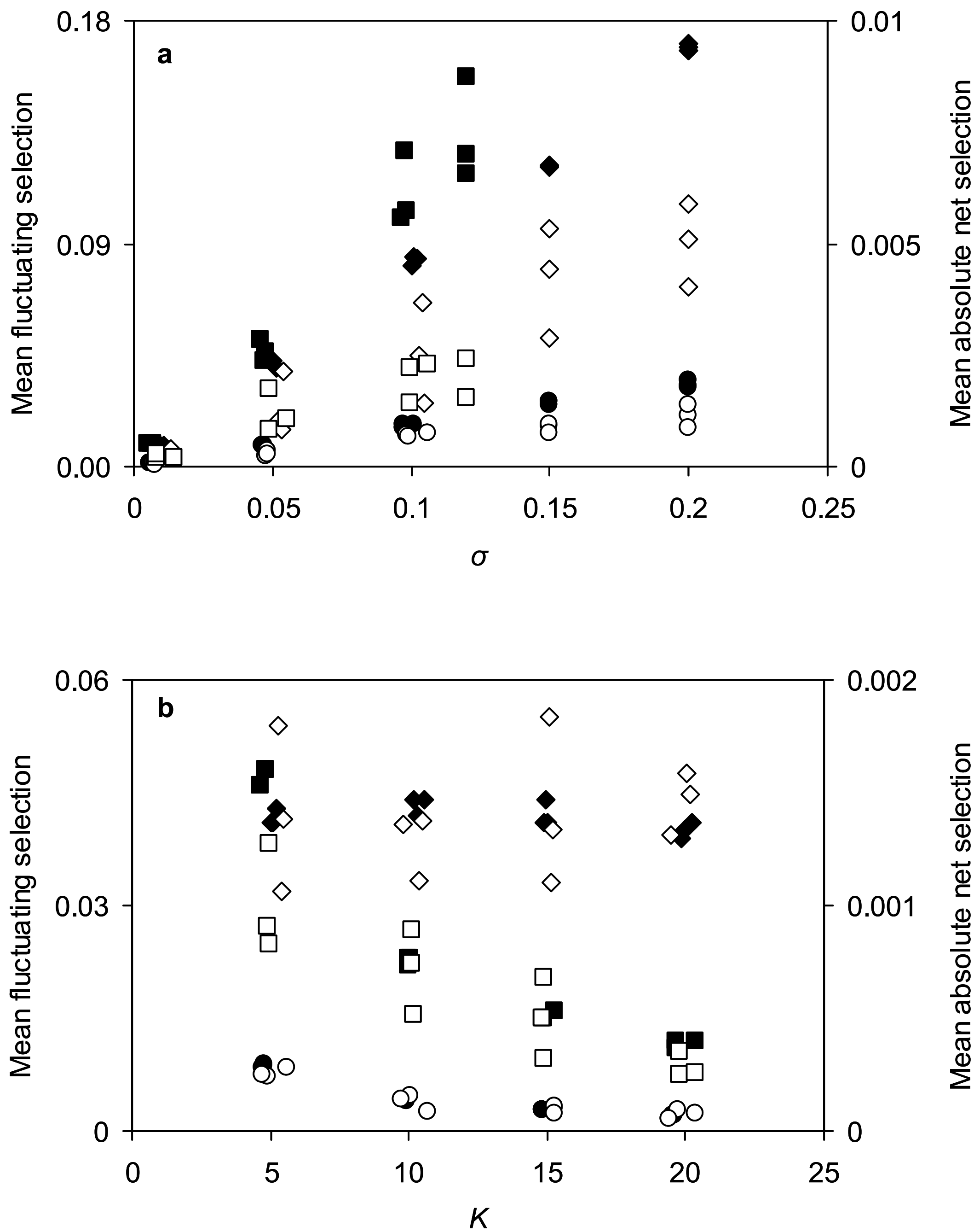

FIG. D1. Patterns of selection predicted by stochastic Lotka-Volterra competition models along gradients of (a) environmental noise strength σ and (b) enrichment K. Each point gives results from one simulation. Diamonds, Eq. D.1; circles, Eq. D.2; squares, Eq. D.3. Filled symbols, mean fluctuating selection; open symbols, mean absolute net selection. Some points are slightly jittered horizontally to improve visibility.

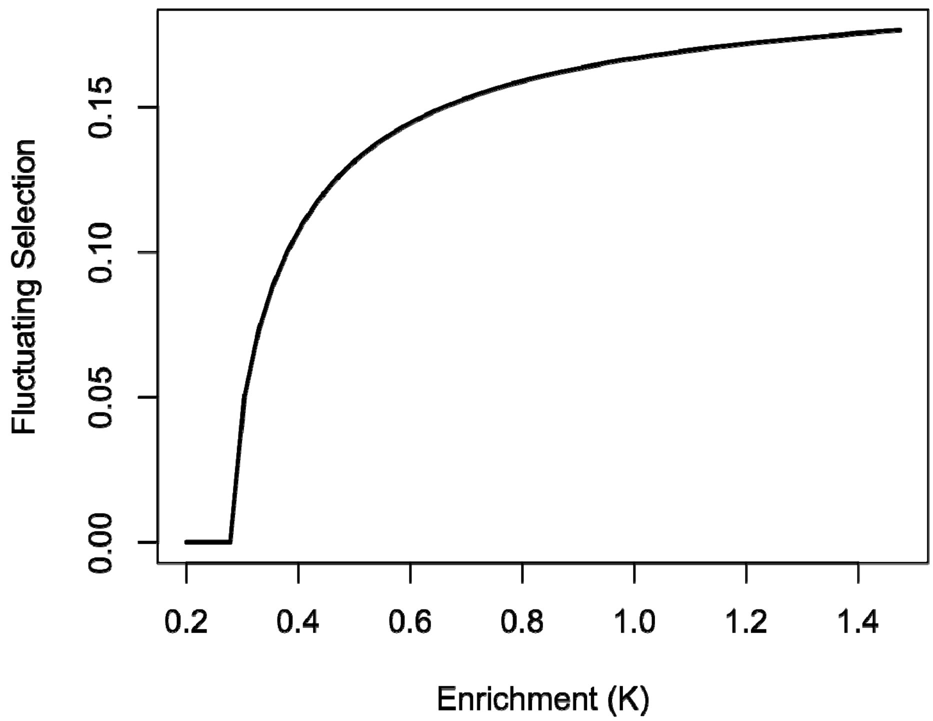

FIG. D2. Fluctuating selection as a function of enrichment in a consumer-resource model (Eq. D.4). Parameters are as follows: $r = 1$, $\varepsilon_1 = 0.6$, $\varepsilon_2 = 0.5$, $\delta_1 = 0.24$, $\delta_2 = 0.1067$, $h_1 = 0.67$, $h_2 = 1.25$, $m_1 = 9.15$, $m_2 = 4.88$.

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