

# Appendix S1

## Fixed-sized versus fluctuating-size Lotka-Volterra dynamics

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In the main text we noted the similarity between our lottery model and the better-known Lotka-Volterra competition model, which was famously used by MacArthur and Levins (1967) to derive coexistence conditions along a niche axis. Here we expand on that comment and show numerical results indicating the similarity between the two models.

The Lotka-Volterra model reads

$$\frac{dN_i}{dt} = N_i \left( r_i - \sum_j A_{ij} N_j \right) \quad (\text{S1})$$

where  $N_i$  is species  $i$ 's abundance,  $r_i$  its maximal growth rate (intrinsic fitness), and the competition coefficient  $A_{ij}$  quantifies the competitive impact on species  $i$  caused by species  $j$ .

Our stochastic simulation is a Moran-like process in that it assumes the community size is fixed and that the dynamics involve death events followed by immediate replacement by a recruited individual. In our Moran-like process, the probability that a death event befalls species  $i$  is  $\sum_j A_{ij} N_i N_j / \sum_{kl} A_{kl} N_k N_l$ . The new recruit can either be an immigrant with probability  $m$  or a local birth event with probability  $1 - m$ . If it is a local birth, the probability that species  $i$  is chosen at this stage is  $r_i N_i / \sum_j r_j N_j$ , and if it is an immigration event, the probability is simply its relative abundance in the regional pool  $p_i$ , where  $\sum_i p_i = 1$ .

In general, if death and replacement events alternate, and the probabilities of death and recruitment of an individual of species  $i$  are  $d_i(\{N\}) N_i / \sum_j d_j(\{N\}) N_j$  and  $b_i(\{N\}) N_i / \sum_j b_j(\{N\}) N_j$  respectively, then the expected change in abundance of species  $i$  over the interval  $\Delta t$  given its current abundance  $N_i(t) = N_i$  is

$$\begin{aligned} \mathbb{E}[N_i(t + \Delta t) - N_i(t) | N(t) = N_i] &= \left( 1 - \frac{d_i(\{N_i\}) N_i}{\sum_j d_j(\{N_i\}) N_j} \right) \frac{b_i(\{N_i\}) N_i}{\sum_j b_j(\{N_i\}) N_j} \Delta t \\ &\quad - \frac{d_i(\{N_i\}) N_i}{\sum_j d_j(\{N_i\}) N_j} \left( 1 - \frac{b_i(\{N_i\}) N_i}{\sum_j b_j(\{N_i\}) N_j} \right) \Delta t \\ &= \left( \frac{b_i(\{N_i\}) N_i}{\sum_j b_j(\{N_i\}) N_j} - \frac{d_i(\{N_i\}) N_i}{\sum_j d_j(\{N_i\}) N_j} \right) \Delta t \end{aligned} \quad (\text{S2})$$

This is a probabilistic model where the expected change per event is the weighted sum of possible gains and losses, weighted by the probability of their occurrence. For simplicity we are scaling time so that the event rate per unit time is 1. The corresponding deterministic model is  $N_i(t + \Delta t) - N_i(t) =$

$\mathbb{E}[N_i(t + \Delta t) - N_i(t)|N(t) = N_i]$ , and the affiliated differential equation is

$$\frac{dN_i}{dt} \approx \frac{N_i(t + \Delta t) - N_i(t)}{\Delta t} = \frac{b_i(\{N_i\})N_i}{\sum_j b_j(\{N_i\})N_j} - \frac{d_i(\{N_i\})N_i}{\sum_j d_j(\{N_i\})N_j} \quad (\text{S3})$$

In our stochastic simulation,  $d_i(\{N_i\}) = \sum_j A_{ij}N_j$  and  $b_i(\{N_i\}) = r_i$ . Substituting these leads to

$$\frac{dN_i}{dt} = N_i \left( \frac{r_i}{\sum_k r_k N_k} - \frac{\sum_j A_{ij}N_j}{\sum_{kl} A_{kl}N_k N_l} \right) \quad (\text{S4})$$

Although this differential equation differs from the Lotka-Volterra model in Eq. S1, numerical simulations using the Euler method produce virtually identical dynamics for the parameter values tested (results not shown as they are visually indistinguishable). We note that there is a time scale conversion between the fixed size and fluctuating size models (Eqs. S4 and S1), namely  $t_{\text{Eq.4}}/t_{\text{Eq.1}} = \sum_k r_k N_k(0)$ . Also note that in the main text we measured time in terms of events (death immediately followed by replacement); if time is measured in terms of days or years etc, there will be an exponential distribution of intervals between consecutive events (assuming deaths follow a Poisson process). Since we are approximating the event rate as fixed, the expected value of the relative persistence times measured in days will be the same as the relative persistence times measured in events.

To further make sure our stochastic niche model is compatible with the Lotka-Volterra model, we created a stochastic version of the latter by modeling death and birth events as Poisson processes, and simulated these stochastic dynamics using the Gillespie algorithm (Gillespie, 1977). More specifically, we modelled birth and death events as independent Poisson-distributed processes with probability per unit time  $N_i(1 - m)r_i + mp_i$  and  $N_i \sum_j A_{ij}N_j$  respectively for species  $i$ , where  $m$  is the immigration rate and  $p_i$  the regional abundance of species  $i$ . The Gillespie algorithm then implements these processes by choosing the amount of time between events according to a distribution determined by the total rate of all events, and deciding which event occurs according to its relative probability among all events. This simulation approach gives some quantitative differences in the persistence time distribution from our Moran process implementation of Eq. S4, but the shape of the distributions and the comparisons between neutral and partially stabilized communities were qualitatively the same. Namely, the niche case leads to many transient species with shorter persistence times than the neutral case (Fig. S1), and an inhomogeneous regional pool lessens the difference between niche and neutral persistence time distributions (Fig. S2).

We chose a lottery model (i) to be consistent with previous formulations and extensions of neutral theory (Hubbell, 2001; Jabot and Chave, 2011), and (ii) because it has the advantage that it does not require parameter-tuning to set the community size. The latter is convenient because community size affects stochastic dynamics irrespective of whether competition is neutral or niche-based. Had we not controlled for community size, we would need to tune parameters and average over a good number of runs to make community sizes comparable across our dynamic scenarios. This would make the project, and future study using the framework presented in this paper, much more computationally demanding. Our model provides a simulation approach for studying stochastic formulations of MacArthur and Levins' (1967) classical Lotka-Volterra niche-axis model, while disposing of the need to control for community size.

## References

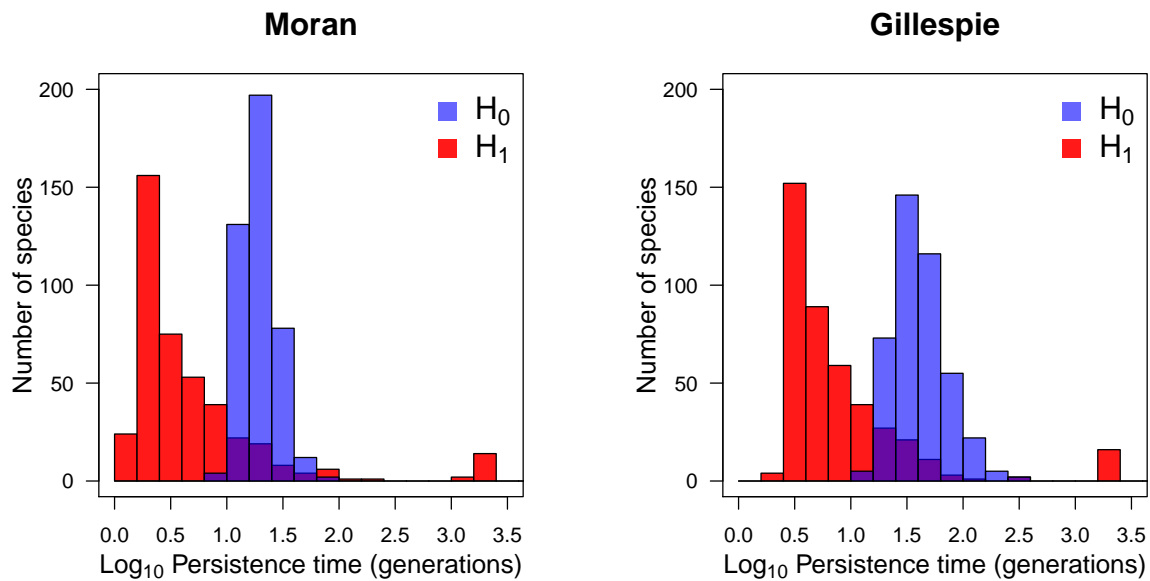
Gillespie, D. T. (1977). Exact Stochastic Simulation of couple chemical reactions. *The Journal of Physical Chemistry*, 81(25):2340–2361.

Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Jabot, F. and Chave, J. (2011). Analyzing tropical forest tree species abundance distributions using a nonneutral model and through approximate Bayesian inference. *The American naturalist*, 178(2):E37–47.

MacArthur, R. H. and Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist*, 101(921):377–385.

**Figure S1:** Persistence time distributions under a Moran process implementation of our fixed-size niche-axis model (left) and under a Gillespie algorithm implementation of the MacArthur-Levins model (right). Results shown for the baseline niche scenario. While non-resident species in both the niche and neutral communities tend to have somewhat longer persistence times with the Gillespie method, the difference between the niche and neutral distributions is essentially the same between the Moran and Gillespie methods. Plotted are the base-10 logarithms of the persistence times in units of community turnovers or generations. The Moran simulation results shown are equivalent to Fig. 1C in the main text, but here persistence time is plotted in absolute values instead of relative to the most persistent species in the simulation.



**Figure S2:** Effect of inhomogeneous regional abundances on the persistence time distribution in both the neutral and niche communities. Again the left graphs show the results of the Moran simulation method and the right the Gillespie method. The effects of a pool with logarithmically distributed random abundances (bright-colored bars) relative to the pool with identical regional abundances (light-colored bars) are the same across these two methods, although overall the transient species tend to have somewhat longer persistence times under the Gillespie method. Compare with Figs. 2A and 2E in the main text. (Again, here persistence is plotted in absolute rather than relative values.)

