

Effects of Structured Interaction Matrices on Spatial Multispecies Communities

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Modeling multispecies communities is a challenge of modern theoretical ecology. Although highly interacting, species-rich ecosystems abound in nature, attempts to find stable theoretical solutions of such systems has been difficult. We employ a recently suggested algorithm to create structured interaction matrices for such communities, and simulate the resulting populations on a spatial grid with nearest-neighbor interactions and randomly located migration events. We find that communities generated by the structured matrices are more stable over time than ones that emerge from unstructured interactions. We also examine phylogenetic distance between individuals and conclude that these stable communities are locally more homogeneous than might have been expected.

I. INTRODUCTION

In naturally occurring ecosystems, data that describes the structure of the community is easily collected, but the underlying dynamics are harder to determine. Accordingly, ecologists seek tools that connect structure to dynamics.

Some of these tools include models such as Lotka-Volterra, and rules like Taylor’s power law [6]. In this study, we use models inspired by Lotka-Volterra and variations of Taylor’s power law to measure the stability of multispecies communities.

In the next section, we give background information on the models. The following section describes our implementation of them as a spatial simulation. Subsequently, we describe our results, before framing them within existing theory in the final section.

II. LOTKA-VOLTERRA MODEL

The classical model of Lotka (1932) and Volterra (1926) assumes that species diminish each other’s growth rates by direct interference: a relative increase of one species (x_j) causes another species (x_i) to decrease:

$$\frac{dx_i}{dt} = r_i x_i \left(\frac{K_i - x_i - \sum_{j=1}^n \alpha_{ij} x_j}{K_i} \right) \quad (1)$$

The model has been criticized for its simplicity and emphasis on competition over all other types interactions [1]. Yet it remains a useful tool that is often used to model inter- and intraspecies dynamics.

The condition for coexistence of two species can be reduced to the values of the interspecific competition coefficients. Assuming carrying capacities K and single-species growth rates r equal unity, stable coexistence results if $\alpha_{ij}, \alpha_{ji} < 1$.

Higher numbers of species can stably coexist, but the necessary conditions are more difficult to find. As shown by Robert May in 1972 [2], even small amounts of niche overlap between species causes the system to transition

to an unstable state. This means that stable coexistence requires most of the competition coefficients to be near or equal to zero (or that the interaction matrix has a low connectivity [3]). Such an assumption is unrealistic, because all members of a multispecies ecosystem must compete to some degree for shared resources.

A. Interaction Matrix Algorithms

In order to study the stability of large, highly interacting multispecies communities, we make use of two algorithms that address May’s conundrum. The first [4], which we will call the structured algorithm, generates structured interaction matrices. It assumes the Darwinian concept of higher niche overlap between more closely related species. The second [3], to be referred to as the unstructured algorithm, uses unstructured interaction matrices. It mirrors May’s instability transition by showing that varying the connectivity of an interaction matrix changes the probability distribution of the multispecies population.

1. The Structured Algorithm

Shtilerman et. al. claim to solve May’s coexistence problem with the following algorithm:

- 1: A “daughter” species evolves from a randomly chosen (but weighted by fitness) “mother” species.
- 2: The daughter species inherits slightly modified versions of the mother’s competition coefficients:

$$\alpha_{daughter,j} = \alpha_{mother,j}(1 - \gamma) + \gamma\epsilon \quad (2)$$

where $\gamma \ll 1$ and ϵ is drawn from a Gamma distribution of mean 1 and variance 1.

- 3: The daughter and mother species are connected by significant niche overlap:

$$\alpha_{\text{mother,daughter}} = h(1 - \gamma) + \gamma\epsilon \quad (3)$$

where again, ϵ is a random variable and $h \leq 1$ but should be high enough to reflect the strong overlap (≈ 0.9).

The process repeats itself until an interaction matrix is complete. The structure of the matrix is block-diagonal, as seen in Figure 1, with strongly interacting “sub-communities” that are weakly connected to each other.

2. The Unstructured Algorithm

The connectivity, C , of the interaction matrix is the only given quantity in this algorithm, from which all else follows. The matrix is composed of numbers randomly distributed between 0 and 1. If $\alpha_{ij} > 0$, species i is connected to species j , and $\alpha_{ji} > 0$ as well, although the two numbers do not have to be close. At each time step, the following occurs:

- 1: With probability μ , a randomly chosen site in the ecosystem, occupied by a species B , is replaced by a species A randomly chosen from the species pool.
- 2: With probability $1 - \mu$, two randomly chosen individuals, A and B , interact. If $\alpha_{AB} > \alpha_{BA}$, A spreads, replacing B . If $\alpha_{AB} = \alpha_{BA}$, nothing happens.

For small values of μ (≈ 0.001) and $\frac{S}{N}$ (number of species divided by number of individuals), the probability distribution transitions from Gaussian to log-normal to power law as C increases.

This transition is equivalent to May’s instability transition, because in this well-mixed environment, highly connected interaction matrices will cause the strongest species to outcompete the rest of the population, given enough time. Species that are unconnected ($\alpha_{ij} = \alpha_{ji} = 0$) can coexist.

III. SIMULATIONS IN SPACE

The well-mixed nature of the unstructured algorithm is what allows for the probability density of the population to depend solely on the connectivity of the interaction matrix. Furthermore, above a certain level of connectivity, the algorithm makes no distinctions: all highly connected matrices yield power law distributions.

We were curious about the effects of a structured matrix, where the distribution might depend not only on the number of nonzero components, but also on their location. We needed more details about the population than its probability distribution, and thus decided to analyze the spatial distribution of the population.

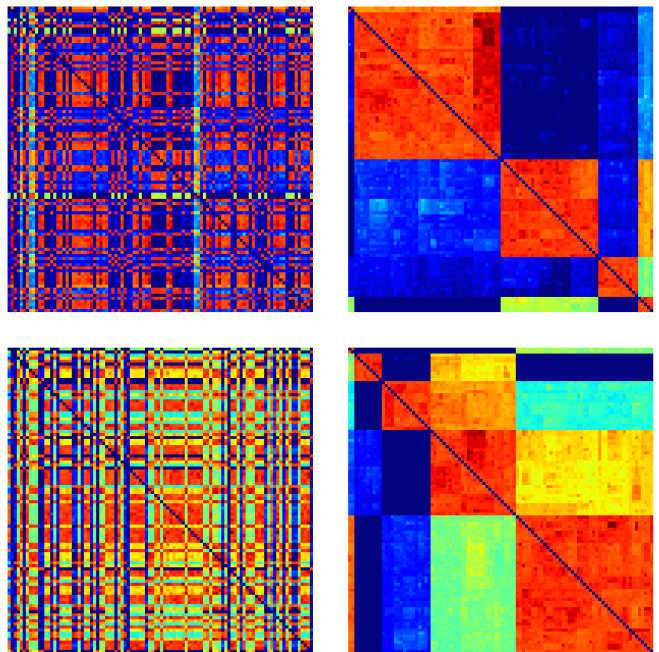


FIG. 1. Left: interaction matrices were generated using the structured algorithm. Right: by tracking phylogenetic distance during mother-daughter speciation events, we rearranged the matrices to reveal block-diagonal “sub-communities.”

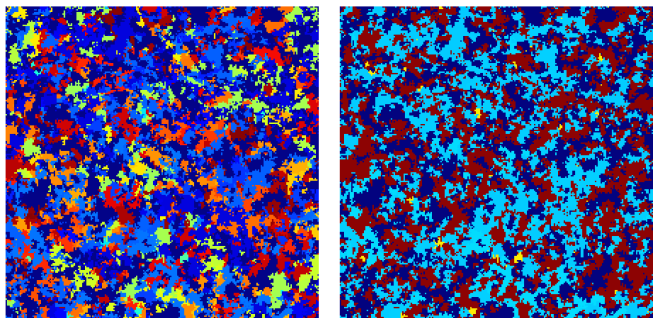


FIG. 2. A structured ecosystem after 10,000 generations. Left: ordered by species. Right: ordered by phylogenetic distance.

To create a spatial simulation, we first built matrices using the structured algorithm, and then modified the unstructured algorithm to include only nearest-neighbor interactions. The random migration events did not change.

Ecosystems were constructed using both structured and unstructured interactions. After 10,000 generations of simulation (N time steps per generation), we used a variation of Taylor’s power law to evaluate the spatial and temporal stability of these ecosystems, which we describe in the next section.

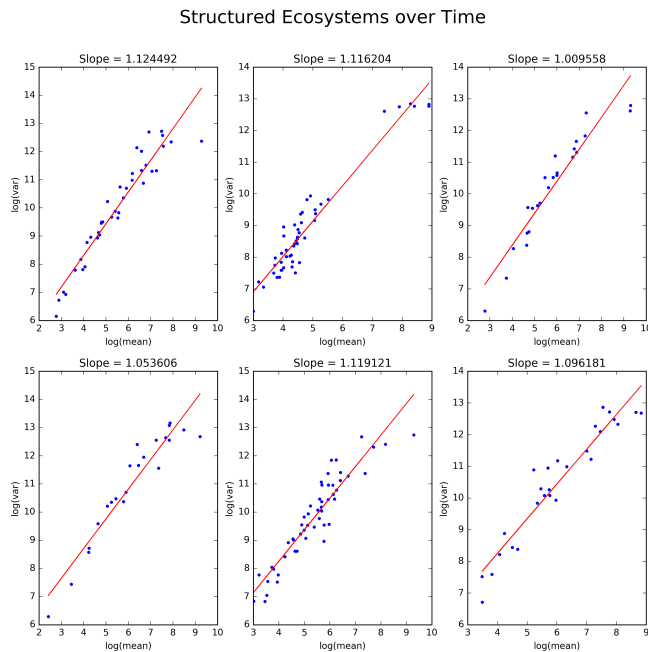


FIG. 3. We find a good fit with the multispecies temporal version of Taylor’s law. The mean slope is 1.087.

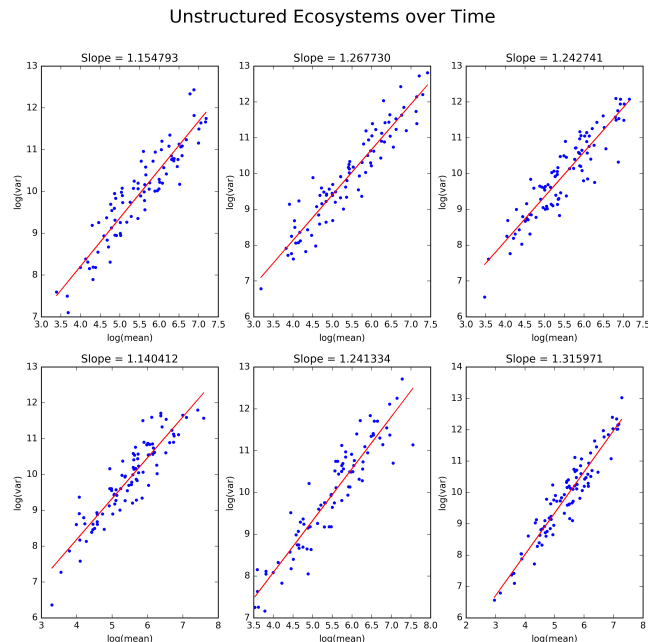


FIG. 4. The unstructured ecosystems also show a good fit, with a mean slope of 1.23,

IV. RESULTS

Taylor’s power law [6] relates the mean (m) and variance (V) of a species abundance as:

$$V = am^b \quad (4)$$

If $b = 1$, the population distribution is Poisson-like, and is distributed randomly. Values of b greater than 1 indicate aggregation, and are more commonly seen in nature. Values less than 1 indicate uniform distributions, and are very rare.

The rule is well established and widely used in ecology, with some believing it should be considered more fundamental than the model of logistic growth [5].

Many extensions of the rule have been developed, and we use one that was recently suggested for multispecies population densities over time [5]:

$$V_s = am_s^b \quad (5)$$

$$s = 1, 2, \dots, S$$

where m_s is the mean population abundance of one species over time, and S is the total number of species. In proposing this variation, its author [5] argued that the larger the value of b , the more temporally aggregated and less stable is the multispecies population. As b increases, variations in the aggregation increase, which could lead to extinction of some species. For $b \leq 1$, the community aggregation over time is essentially constant, or “temporally uniform.”

We applied this rule to our structured and unstructured ecosystems, as seen in Figures 3 and 4. We achieved a good fit with the model, with values of b greater than 1 in both cases.

Interestingly, the unstructured interactions yield a higher value of b than the structured interactions (a mean of 1.23 vs. 1.09), indicating that the latter is more temporally stable.

Values of b near 1 may also be interpreted as reflective of near-neutral interactions among species [5]. We might have expected this, because the block-diagonal “sub-communities” in the structured matrices, while highly interacting within, interact weakly among each other. This structure can be seen in Figure 2, which depicts an ecosystem ordered both by species and phylogenetic distance. The phylogenetic ordering exposes the sub-community clustering: each color corresponds to a sub-community, with some sub-communities inhabiting (dominating) more space than others.

V. DISCUSSION

The aforementioned niche-overlap hypothesis says that competition between more closely related species should be stronger. Continuing with this argument, some conclude that local communities should exhibit phylogenetic overdispersion, with species being less related on average than if drawn randomly from the global species pool.

Shtilerman et. al. conjecture that their model challenges this conclusion [4]. While members of the sub-communities do compete strongly with each other, the variance of their competition coefficients is smaller than

that of the entire matrix. Fitness differences are defined as the level of variance of these coefficients. Therefore, while competition may push members of a sub-community apart in space, their smaller fitness differences pull them back together.

Having access to our spatially simulated ecosystems allowed us to directly measure local versus global phylogenetic distance. We divided the ecosystems into 300 sub-populations and measured the averaged phylogenetic distance between many random pairs, and did the same

throughout the global population. The results across all ecosystems show that globally, individuals are about 20% more distantly related than locally, confirming the prediction of Shtilerman et. al.

Our findings show that the structured interactions proposed by Shtilerman et. al. lead to ecosystems that are temporally more stable than those generated by naive, unstructured interactions, and locally more homogeneous than expected. The structured algorithm gives rise to multispecies communities with a stable mechanism of interaction between balanced sub-communities.

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