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A Framework for Stochastic, Size-structured Neutral Model for Community

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Introduction

Let's consider trees in a forest. Forests are an important part of global carbon cycle, which plays a critical role in climate change, a serious problem facing human society.

- **main question** What is the basic mechanism allowing all of the tree species to coexist?
- **niche difference** A species' niche is all of the resources and environmental conditions it requires for living. Niche differences are the classical mechanism that ecologists hypothesize to explain competitive coexistence.
- **neutral biodiversity theory (NBT)** An alternative (and simpler) hypothesis is that all of the tree species in a forest coexist because they have same niche. Neutral biodiversity theory describes such a community, in which the stochastic events like birth, mortality, growth and speciation will dominate in shaping community-level characteristics. Deviations of observations from NBT's predictions could indicate when mechanisms other than chance are important.
- **size-structured biodiversity neutral theory** The original NBT ignored potential variation within species in birth and death rates. Size-structured NBT aims to improve upon NBT by considering size variation among individuals and associated variation in birth and death rates.
- **improving model of speciation and incorporating size variation in births** Prior work[1] began to develop size-structured NBT, but approximated speciation to be like immigration, and ignored size variation in birth rates. We are working to overcome these limitations to develop an accurate and complete size-structured NBT.

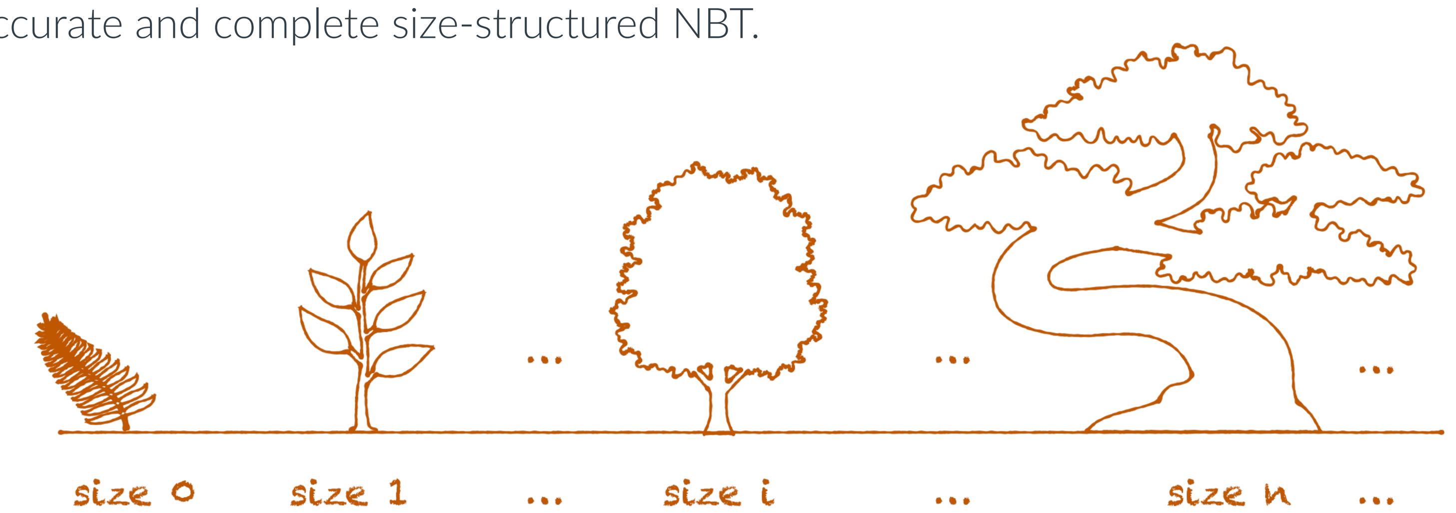

Figure 1. Size-structured NBT justifies individuals by size instead of species, because they all have same niche

Methods

- **our spark for the original model**:

  birth rate = b, death rate= d, speciation rate = ν and growth rate = g

$$\frac{\partial S(n,t)}{\partial t} = \nu\delta_{n,1} + b(n-1)S(n-1,t) + d(n+1)S(n+1,t) - (b+d)nS(n,t), \quad \delta_{n,1} = \begin{cases} 0 & n \neq 0 \\ 1 & n = 0 \end{cases}$$

- **discrete master equation model** describe the dynamics of the discrete community in NBT. n_i is the abundance in size class i. The expected number of species in a given state i at time t is $S(n_0,\cdots,n_i,\cdots,t)$:

$$\begin{aligned}\frac{\mathrm{d}S(n_0,\cdots,n_i,\cdots,t)}{\mathrm{d}t} &= \sum_{i=0} b_i(n_i-\delta_{i0})S(n_0-1,\cdots,n_i,\cdots,t) - \sum_{i=0} b_i n_i S(n_0,\cdots,n_i,\cdots,t) \\ &+ \nu\delta_{n_0 1}\prod_{i=1}\delta_{n_i,0} \\ &+ \sum_{i=0} d_i(n_i+1)S(n_0,\cdots,n_i+1,\cdots,t) - \sum_{i=0} d_i n_i S(n_0,\cdots,n_i,\cdots,t) \\ &+ \sum_{i=0} g_i(n_i+1)S(n_0,\cdots,n_i+1,n_{i+1}-1,\cdots,t) \\ &- \sum_{i=0} g_i n_i S(n_0,\cdots,n_i,n_{i+1},\cdots,t)\end{aligned} \quad (1)$$

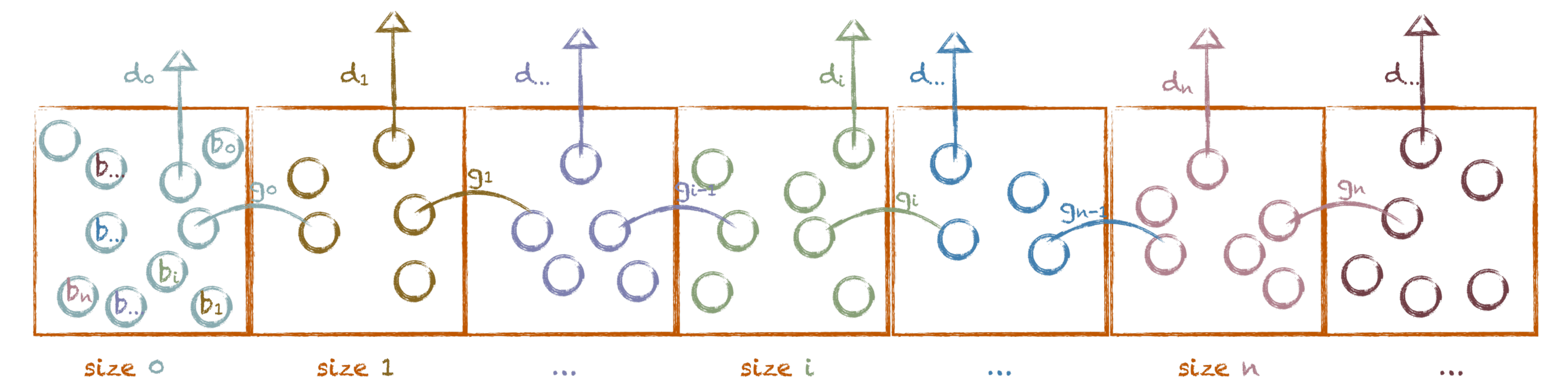

Figure 2. Each size state has stochastic birth, mortality and growth rate, the new individual will go to the size 0

- to take the biologically relevant limit of above equation in which discrete size classes become continuous, the above function in cast in terms of the mulvariate generating function as:

$$Z(h_0,\cdots,t) = \sum_{\{n_i\}} S(n_0,\cdots,t)e^{\sum_i h_i n_i} \quad (2)$$

where the sum is taken over all the possible combinations of abundances, and the generating function is defined so that derivatives of Z, taken at $h_i = 0$ are equal to moments of the distribution S.

- Further, we transform $\frac{dS}{dt}$ to $\frac{\partial Z}{\partial t}$ by multiplying $e^{\sum h_i n_i}$, using partition function's properties, and taking the limit of continuous size, as the separation between size classes, $\Delta m \longrightarrow 0$:

  Using dimensional analysis to assign the following scaling with Δm:

$$g_i = \frac{g(m_i)}{\Delta m} \qquad d_i = \frac{d_i}{d(m_i)} \qquad h_i = H(m_i)$$

$$\begin{aligned}\frac{\partial Z}{\partial t} &= \int_{m_0}^{\infty} \mathrm{d}m d(m)\frac{\delta Z}{\delta H(m)}\left(e^{-H(m)}-1\right) + \int_{m_0}^{\infty} \mathrm{d}m b(m)\frac{\delta Z}{\delta H(m)}\left(e^{H(m_0)}-1\right) \\ &+ \int_{m_0}^{\infty} \mathrm{d}m g(m)\frac{\delta Z}{\delta H(m)}\frac{\mathrm{d}H}{\mathrm{d}m} + \nu e^{H(m_0)}\end{aligned} \quad (3)$$

Results

- We found one possible solution to the equation above for the partition function:

$$Z = \int_{m_0}^{\infty} \mathrm{d}m f(m)\left(e^{H(m)}-1\right) \quad (4)$$

where $f(m)$ must satisfy the following conditions

$$\begin{cases} 0 = -\frac{\mathrm{d}(g(m)f(m))}{\mathrm{d}m} - d(m)f(m) + b(m)f(m)\left(e^{H(m_0)}-1\right) \\ f(m_0)g(m_0) = \nu\frac{e^{H(m_0)}}{e^{H(m_0)}-1} + \int_{m_0}^{\infty}\mathrm{d}m b(m)f(m)e^{H(m)} \end{cases}$$

- We next worked to derive the species abundance distribution (SAD) and the species biomass distribution (SBD) from this partition function by considering different forms for the function $H(m)$ appropriate to those distributions. For simplicity, we first consider a completely neutral community, whose growth rate, birth rate and mortality rates are independent of individual mass:

$$g(m) = g \qquad b(m) = b \qquad d(m) = d$$

for which we expect the SAD may be the same as the original NBT predictions.

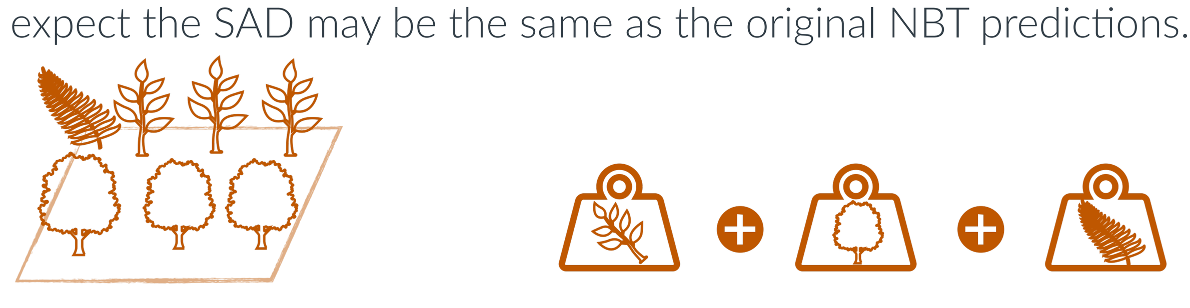

Figure 3. Species Abundance Distribution(SAD): The number of individuals in the community. Species Biomass Distribution(SBD): The mass of all individuals in the community

- Species Abundance Distribution (SAD)

  The total abundance of a community can be related to the partition function simply by choosing $H(m)$ to be a constant h (i.e. $h_i = h$ for all i). This can be seen by noting that the moment one would obtain by differentiating the partition function defined in Eq(3) with respect to h would be the average species abundance. We also assume for simplicity that new individuals are born with size zero (i.e. $m_0 = 0$):

  S(N)=the expected number of species with N total individuals across size classes

$$f_{\text{sad}}(m) = e^{(b(e^h-1)-d)m/g} \cdot \frac{\nu e^h}{g(e^h-1)(1-be^h(d-b(e^h-1)^{-1}))} \quad (5)$$

  $S(N)$ and $Z_{\text{sad}}[h]$ is related through

$$Z_{\text{sad}}[h] = \int S(N)e^{hN}\mathrm{d}m \quad (6)$$

  thus, using inverse Laplace transform we get

$$S(N) = \mathcal{L}^{-1}\left(Z_{\text{sad}}[-h]\right) \quad (7)$$

- Species Biomass Distribution (SBD)

  In SBD, we are interested in the distribution across the community of the total species biomass M, where $M = \sum_i m_i n_i$ or in the continuum limit $M = \int dm\, n(m)$. Similar to SAD, we can also choose a specific form of $H(m) = hm$ (i.e. $h_i = h \cdot m_i$). The partition function now is characterized by the expotential factor $e^{\int hmn(m)\mathrm{d}m} = e^{hM}$, whose derivative with respect to h (evaluated at $h = 0$) gives the average total biomass across species. Using the similar approach before, we first solve the biological realism condition equation, and find the bellowed solution:

  S(M) = the expected number of individuals with M total biomass

$$f_{\text{sbd}}(m) = \frac{\nu D}{(1+D)ge^{m_0 bD/g}}e^{mbD/g} \quad (8)$$

  Following the same procedure as SAD case, we can calculated the partition function $Z_{\text{sbd}}[h]$ and further resolve the distribution S(M) through inverse Laplace transform.

Discussion/conclusion

- We add biological realism that demographic rates in nature are correlated with size structure into neutral biodiversity theory to build a better model for comparison with real communities.
- We found the one possible time-independent solution to our key equation.
- We calculate the complete neutral case of SBD and SAD, and find an infinite series answer for SAD.

What we still need to do:

- We need to calculate the inverse Laplace transform for $Z_{\text{sad}}[h]$ and $Z_{\text{sbd}}[h]$ to get the $S(N)$ and $S(M)$
- We need to analysis the complete neutral case situation and stochastic size-structured situation for SBD and SAD based on our model.
- Once we solve for $S(N)$ and $S(M)$ we plan to compare these predictions to available data for forest communities.

References

[1] J.P.O'Dwyer, J.K.Lake, A.Ostling, V.M.Savage, and J.L.Green. An integrative framework for stochastic, size-structured community assembly. *Proceedings of the National Academy of Sciences*, 106:6170–6175, 2009.