Integrated MERA: combining MERA I, II, and III

Jade, Nov 6

Here I will merge 1) resource allocation among species and individuals as is described by MERA I & II and 2) resource acquisition by all species from the environment as is described by MERA III, and develop an integrated model of MERA. In the solution we can see that some of the properties of I, II and III are retained but there are also new properties emerging: not only θ and D_r, the intrinsic growth rate r of the species also affects its steady state abundance.

1 Quick recap of MERA II

First let's recall the generalized W_{total} derived from MERA II (June 8 write up):

$$\begin{aligned} \log W_{total} &= \log W_{across} + \sum_{i}^{S_0} D_{r,i} \log W_{within,i} \\ &= -R_0 \sum_{i}^{S_0} P_i \log P_i - \sum_{i}^{S_0} D_{r,i} R_i \sum_{j}^{N_i} p_{ij} \log p_{ij} \end{aligned} \tag{1}$$

Where $P_i = R_i/R_0$ is the relative resource abundance of species i in the community and $p_{ij} = r_j/R_i$ is the relative resource abundance of individual j in species i. Also $W_{grouping}$ is left out since the definition of demographic group is trivial here (in MERA II an individual can get any amount of resource). For each species i maximizing $\sum_j^{N_i} p_{ij}\log\, p_{ij}$ yields a uniform distribution for p_{ij}:

$$p_{ij} = \frac{1}{N_i} \tag{2}$$

Substituting Eq. 2 into Eq. 1 we get

$$\log\, W_{total} = -R_0 \sum_i^{S_0} P_i(\log\, P_i + D_{r,i}\log\, N_i) \tag{3}$$

Then $\log\, W_{total}$ is maximized respect to P_i subject to the normalization constraint ($\sum_i^{S_0} P_i = 1$), which gives

$$\begin{aligned} P_i &\propto N_i^{D_{r,i}} \\ => R_i &= R_0 \frac{N_i^{D_{r,i}}}{\sum_j^{S_0} N_j^{D_{r,j}}} \end{aligned} \tag{4}$$

A problem of this solution is that, there is no upper limit to how many resources a species can get. Specifically, if R_0 is big enough, R_i can be big even if N_i is small, generating unrealistically huge growth. Below I will show how MERA III helps solve this problem.

2 Combine II and III: allocation with upper limits for species boxes

In MERA III, we have introduced a resource acquisition procedure where resource in the environment are randomly allocated to resource acquisition activities of the species, the magnitude of which is regulated by the species current abundance N and intrinsic growth rate r (from here on I will call this value the resource capacity of the species, given its r and N at the time). The allocation stopped at the community level, not considering distribution of the resource among or within species. Here I will introduce an integrated procedure to allocate resources in the environment 1) to species resource capacity boxes (regulated by N and r), then 2) within each species to individuals.

*My original thought was to use MERA III to determine the resource constraint for the whole community, then apply MERA I or II to get species and individual level distributions. This turns out not to work as expected since although it can make sure the total resource capacity for the community is not surpassed, it does not guarantee for every single species not to surpass its resource capacity. Therefore the resource capacity boxes cannot be lumped and species level allocation has to happen simultaneously with acquisition. Under this framework, the concept for community-level resource constraint is not necessary any more. *

graph demo

C_i is the resource capacity for species i:

$$C_i = (r_i + 1)N_i\theta_i \tag{5}$$

R_i is the actual amount of resources allocated to species i.

The total number of microstates for a given species-level resource distribution R_i (i in 1, ..., S_0) is

$$W_{total}(R_{1,...,S_0}) = \prod_i^{S_0} W_{acquisition,i} \times W_{across} \times \prod_i^{S_0} W_{within,i}^{D_{r,i}} \tag{6}$$

Where $W_{acquisition,i}$ is the number of ways to select R_i out of C_i empty spots in the species capacity pool to be filled each with a unit of resource.

$$W_{acquisition,i} = \frac{C_i!}{R_i!(C_i - R_i)!} \tag{7}$$

A spot in C_i can be taken as a resource acquisition activity which can acquire one unit of resource if successful, or zero resource if failed. Therefore R_i/C_i can be taken as the success rate in resource acquisition.

W_{across} is the number of ways to allocate the total resource in the environment into species boxes (R_is) as well as the "unused" box (which contains all resources that are not utilized by any species).

$$W_{across} = \frac{R_0!}{\prod_i^{S_0} R_i! \times (R_0 - \sum_i^{S_0} R_i)!} \tag{8}$$

$W_{within,i}$ is the number of ways to allocate R_i resource units to N_i individuals:

$$W_{within,i} = \frac{R_i!}{\prod_j^{N_i} r_{ij}!} \tag{9}$$

Substituting Eqs. 7-9 into Eq. 6 and log-transform:

$$\begin{aligned}
\log W_{total} = \sum_i^{S_0} [C_i \log C_i - R_i \log R_i - (C_i - R_i) \log (C_i - R_i)] \\
+R_0 \log R_0 - \sum_i^{S_0} R_i \log R_i - (R_0 - \sum_i^{S_0} R_i) \log (R_0 - \sum_i^{S_0} R_i) \\
- \sum_i^{S_0} R_i D_{r,i} \log N_i \\
= R_0 \log R_0 + \sum_i^{S_0} C_i \log C_i \\
- \sum_i^{S_0} [2R_i \log R_i + (C_i - R_i) \log (C_i - R_i) + R_i D_{r,i} \log N_i] \\
-(R_0 - \sum_i^{S_0} R_i) \log (R_0 - \sum_i^{S_0} R_i)
\end{aligned} \tag{10}$$

Notice that in Eq. 10 $W_{within,i}$ is already maximized:

$$max(\log W_{within,i}) = R_i \log N_i \tag{11}$$

Maximizing $\log W_{total}$ (no constraint) yields

$$R_i^2 = (C_i - R_i)(R_0 - \sum_i^{S_0} R_i) N_i^{D_{r,i}} \tag{12}$$

Easy to see that the one species case with $D_{r,i} = 0$ (see discussion) gives exactly the same solution as the previous MERA III (write-up Oct 16). For an arbitrary set of N_is R_i has to numerically solved with S_0 simultaneous equations (Eq. 12 for all species). At steady state however, since the resource allocated to each species happen to provide for exactly the current abundance, or $\hat{R}_i = \theta_i \hat{N}_i$, we have

$$(\theta_i \hat{N}_i)^2 = \hat{R}_i^{\;2} = [(r_i + 1)\theta_i \hat{N}_i - \theta_i \hat{N}_i](R_0 - \sum_i^{S_0} \theta_i \hat{N}_i) \hat{N}_i^{\;D_{r,i}} = r_i \theta_i \hat{N}_i R_u \hat{N}_i^{\;D_{r,i}}$$
$$=> \hat{N}_i = (\frac{\theta_i}{r_i R_u})^{\frac{1}{D_{r,i}-1}} \tag{13}$$

where $R_u = R_0 - \sum_i^{S_0} \theta_i \hat{N}_i$ is the amount of unused resource at steady state. From Eq. 13 we can see that when all species have the same intrinsic growth rate r, the steady state solution is the same as MERA I and II ($\hat{N}_i \propto \theta_i^{\frac{1}{D_{r,i}-1}}$). However, when r_i varies from species to species, the steady state solution is different. Specifically, all else equal, a species with higher intrinsic growth rate will have higher steady state abundance and resource content. This reveals another condition for EER (energy equivalence rule) to hold: not only D_r but also r has to be the same for all species. This is possibly another reason why it is so hard to find patterns supporting the original steady state solution in data; we have been overlooking the species variation in intrinsic growth rate.

3 Result

For multiple competitors.

For multiple predators preying on one prey species.

4 Discussion

Although r_i plays a role in the steady state solution, as long as it scales with θ following a power-law relationship ($\log r \propto \log \theta$), $D_{r,i}$ can be estimated by regressing $\log N$ against $\log \theta$.

The space measurement can still be tested.

Why $D_{r,i} = 0$ or $D_{r,i} = 1$ for one species