MERA without the resource constraint — growth function in a non-zero-sum scenario

Jade, Oct 5

Previously MERA describes a zero-sum scenario where there is a resource constraint that has to be satisfied at all times (the sum of resource use over all species equals a constant R_0, i.e. the amount of resource available from the environment). This framework is useful in describing the steady state but does not help reveal the dynamics when the community is far from being saturated, e.g. dynamics the exponential growth function describes. Here I try to solve the MERA maximization equations without the resource constraint, corresponding to a non-zero-sum scenario, where the total resource use of the community does not stay at one level but can potentially grow from near-zero to a steady state where the resource utilized does not change through time (this value depends on the number of species and species attributes).

Equations in this write-up are based on the generalized MERA. Please refer to the June 8 write-up for the original derivations.

1 Resource distribution without resource constraint

In MERA the total number of allocation microstates W_{total} is given by:

$$W_{total} = W_{grouping} \times W_{across} \times \prod_{i}^{S_0} W_{within,i}^{D_{r,i}} \tag{1}$$

In the June 8 write-up I have proved that when there is no upper limit to the amount of resource acquired by an individual, $W_{grouping}$ is a constant (given the abundances for all species):

$$W_{grouping} = \prod_{i}^{S_0} \frac{N_i!}{1!1!...} = \prod_{i}^{S_0} N_i! = C \tag{2}$$

The expression for W_{across} is similar except that now we have an extra group, i.e. the redundant resource that is not utilized by any species. The amount of resource in the redundant group is annotated by R^r:

$$W_{across} = \frac{R_0!}{R^r! \prod_i^{S_0} R_i!} \tag{3}$$

$W_{within,i}$ is the same as before:

$$W_{within,i} = \frac{R_i!}{\prod_j^{N_i} r_{i,j}!} \tag{4}$$

R_i is the total resource amount allocated to species i and $r_{i,j}$ is the amount allocated to individual j of the species. For each species i, $W_{within,i}$ is maximized when each individual gets the same amount of resource $r_{i,j} = \frac{R_i}{N_i}$:

$$\max\ \log(W_{within,i}) = \max(R_i \log R_i - \sum_{j}^{N_j} r_{i,j} \log r_{i,j}) = R_i \log\ N_i \tag{5}$$

Combining Eqs. 1-4 and log-transform:

$$\log\, W_{total} = \log\, C - R_0(\sum_i^{S_0} P_i \log\, P_i + P^r \log\, P^r) + \sum_i^{S_0} D_{r,i} R_i \log\, N_i \tag{6}$$

Where $P_i = R_i/R_0$ is the relative resource abundance of species i in the community ($P^r = R^r/R_0$ corresponds to the redundant group) and $p_{ij} = r_j/R_i$ is the relative resource abundance of individual j in species i. With the normalization rule ($\sum_i^{S_0} P_i + P^r = 1$) as the only constraint, to maximize W_{total} I define the objective function S as:

$$\begin{aligned} S(W,\lambda) &= \log\, W_{total} - \lambda(1 - \sum_i^{S_0} P_i - P^r) \\ &= \log\, C - R_0 \sum_i^{S_0} P_i(\log\, P_i - D_{r,i} \log\, N_i) + \lambda \sum_i^{S_0} P_i - R_0 P^r \log\, P^r + \lambda P^r - \lambda \end{aligned} \tag{7}$$

Taking the derivative of $S(W,\lambda)$ over P_i:

$$\frac{\partial S(W,\lambda)}{\partial P_i} = -R_0(1 + \log\, P_i - D_{r,i} \log\, N_i) + \lambda = 0 \tag{8}$$

For P^r:

$$\frac{\partial S(W,\lambda)}{\partial P^r} = -R_0(1 + \log\, P^r) + \lambda = 0 \tag{9}$$

Setting these derivatives to zero we get the P_i and P_r that maximize W_{total} under the normalization constraint:

$$P_i = e^{\frac{\lambda}{R_0} - 1} N^{D_{r,i}} \tag{10}$$

and

$$P^r = e^{\frac{\lambda}{R_0}-1} \tag{11}$$

Substituting into the constraint we can get that:

$$\begin{aligned} \sum_i^{S_0} P_i + P^r = e^{\frac{\lambda}{R_0}-1}(\sum_i^{S_0} N_i^{D_{r,i}} + 1) = 1 \\ => e^{\frac{\lambda}{R_0}-1} = \frac{1}{\sum_i^{S_0} N^{D_{r,i}} + 1} \end{aligned} \tag{12}$$

Therefore

$$P_i = \frac{N_i^{D_{r,i}}}{\sum_i^{S_0} N_i^{D_{r,i}} + 1} \tag{13}$$

and

$$P^r = \frac{1}{\sum_i^{S_0} N^{D_{r,i}} + 1} \tag{14}$$

From Eqs 13-14 we can see that, when resource is not constrained to be fully consumed, there is always some portion of the total resource that is not consumed by any species (P^r is always bigger than 0). More specifically, the more individuals there are and the higher D_r of all species, the lower the proportion of the redundant resource. This makes intuitive sense: when the community is comparatively empty and homogeneous, the resource use efficiency is low; when the community gets more saturated and diverse, the resource can be more thoroughly exploited. When $\sum_i^{S_0} N^{D_{r,i}} >> 1$, there is practically no redundant resource ($P^r --> 0$), suggesting that nearly all resources are allocated to individuals.

2 From resource distribution to growth function

To get to growth function, we have to re-introduce the per capita resource requirement θ as follows: at any time, the number of individuals maintained by the species is the resource it acquired in the last allocation period divided by its per capita resource requirement, or $N_{i,t+1} = R_{i,t}/\theta_i$. Notice that this is a more relaxed definition than the previous one assuming θ units for survival and 2θ for reproduction. Basically this new definition does not assume any particular demographic process to be associated with resource acquisition (e.g. birth or death) but simply states that the amount of resource is proportional to the number of individuals present in the population by a species specific coefficient that is relatively stable through time. In other words, we are only interested in the net growth of the population, e.g. plus 1, and don't care whether it is due to 1 death and 2 births or 99 deaths and 100 births. Please refer to the June 8 write-up for more discussions.

Given the definition of θ_i, we can derive the net growth rate of species i given the current abundance and its species attributes:

$$N_{i,t+1} = (1 + g_{i,t})N_{i,t} = \frac{R_{i,t}}{\theta_i} = \frac{R_0 P_{i,t+1}}{\theta_i} \tag{15}$$

Substituting Eq. 13 into 15 we get

$$
\begin{aligned}
(1+g_{i,t})N_{i,t} &= \frac{R_0 N_{i,t}^{D_{r,i}}}{\theta_i(\sum_i^{S_0} N_{i,t}^{D_{r,i}}+1)} \\
=> g_{i,t} &= \frac{R_0 N_{i,t}^{D_{r,i}-1}}{\theta_i(\sum_i^{S_0} N_{i,t}^{D_{r,i}}+1)} - 1
\end{aligned}
\tag{16}
$$

It is easy to prove that the steady state abundance is the same expression as with resource constraint (by setting $g_i = 0$ for all i):

$$SSN_i = (C\theta_i)^{\frac{1}{D_{r,i}-1}} \tag{17}$$

Just that with the resource constraint, the constant C is bigger and SSN_is are smaller for all species.

plot out growth function result for g no bigger than r_i.

2.1 Special case: when there is only one species

Previously when there is resource constraint, the one-species case of MERA is very uninteresting: the species simply has to consume all resource and stays at that state forever. However, under the unconstrained framework, the one-species scenario is much more complicated. Particularly, if this species has