

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:

$$W_{total} = W_{grouping} \times W_{across} \times \prod_i^{S_0} W_{within,i}^{D_{r,i}} \quad (1)$$

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):

$$W_{grouping} = \prod_i^{S_0} \frac{N_i!}{1!1!...} = \prod_i^{S_0} N_i! = C \quad (2)$$

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 :

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

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

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

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 $r_{i,j} = \frac{R_i}{N_i}$:

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

Combining Eqs. 1-4 and log-transform:

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

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:

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

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

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

For P^r :

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

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

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

and

$$P^r = e^{\frac{\lambda}{R_0}-1} \quad (11)$$

Substituting into the constraint we can get that:

$$\begin{aligned} \sum_i^{S_0} P_i + P^r &= e^{\frac{\lambda}{R_0}-1} \left(\sum_i^{S_0} N_i^{D_{r,i}} + 1 \right) = 1 \\ \Rightarrow e^{\frac{\lambda}{R_0}-1} &= \frac{1}{\sum_i^{S_0} N_i^{D_{r,i}} + 1} \end{aligned} \quad (12)$$

Therefore

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

and

$$P^r = \frac{1}{\sum_i^{S_0} N_i^{D_{r,i}} + 1} \quad (14)$$

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 $\sum_i^{S_0} N_i^{D_{r,i}} \gg 1$, there is practically no redundant resource ($P^r \rightarrow 0$), 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:

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

Substituting Eq. 13 into 15 we get

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

2.1 Steady state

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):

$$N_i(\text{steady state}) = (C\theta_i)^{\frac{1}{D_{r,i}-1}} \tag{17}$$

For the steady state resource, substituting Eq. 17 into Eq. 13 we get:

$$P_i(\text{steady state}) = \frac{(C\theta_i)^{\frac{D_{r,i}}{D_{r,i}-1}}}{\sum_i^{S_0} (C\theta_i)^{\frac{D_{r,i}}{D_{r,i}-1}} + 1} \tag{18}$$

For the redundant resource,

$$P^r(\text{steady state}) = \frac{1}{\sum_i^{S_0} (C\theta_i)^{\frac{D_{r,i}}{D_{r,i}-1}} + 1} \tag{19}$$

C can be determined by the equivalence equation:

$$\begin{aligned}
\sum_i^{S_0} R_i &= \sum_i^{S_0} N_i \times \theta_i = \sum_i^{S_0} C^{\frac{1}{D_{r,i}-1}} \theta_i^{\frac{D_{r,i}}{D_{r,i}-1}} \\
&= \sum_i^{S_0} R_0 P_i = \frac{R_0 \sum_i^{S_0} (C\theta_i)^{\frac{D_{r,i}}{D_{r,i}-1}}}{\sum_i^{S_0} (C\theta_i)^{\frac{D_{r,i}}{D_{r,i}-1}} + 1}
\end{aligned} \tag{20}$$

From Eqs. 18-20 we can see that the proportion of resource consumed by species at steady state is determined by both the species attributes (θ and

D_r) and the constant C , which is related to the total resource available R_0 .

In the next section I will look at some special cases to further reveal the implications of these equations.

3 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. From Eqs. 13, 14 and 16 we can get the equations for one species:

$$P_1 = \frac{N_1^{D_{r,1}}}{N_1^{D_{r,1}} + 1} \quad (21)$$

$$P^r = \frac{1}{N_1^{D_{r,1}} + 1} \quad (22)$$

$$g_1 = \frac{R_0 N_1^{D_{r,1}-1}}{\theta(N_1^{D_{r,1}} + 1)} - 1 \quad (23)$$

Next let's look at some more specific cases. First if $D_{r,1} = 0$ the equations reduce to:

$$P_1 = P^r = 0.5 \quad (24)$$

$$g_1 = \frac{R_0}{2\theta_1 N_1} - 1 \quad (25)$$

Therefore when there is only one species, and the species has $D_r = 0$, it always gets half of the total resource regardless of its abundance, i.e. from any initial state through to the steady state. At the other extreme when $D_{r,1} = 1$:

$$P_1 = \frac{N_1}{N_1 + 1} \quad (26)$$

$$P^r = \frac{1}{N_1 + 1} \quad (27)$$

$$g_1 = \frac{R_0}{\theta_1(N_1 + 1)} - 1 \quad (28)$$

In this case the resource consumed by the species increases with the number of individuals it has (the rich gets richer?). By setting $g_1 = 0$ we can solve for resource distribution at steady state to be $P_1 = (R_0 - \theta_1)/R_0$ and $P^r = \theta_1/R_0$. Therefore when there is only one species with $D_r = 1$, the smaller its resource requirement θ , the more resource it can obtain eventually.

3.1 A modified model: adding a constraint on resource obtainable

From Eq. 23, 25 and 28 we can see that the net growth rate of the species is a negative function of the number of individuals it currently has. This means that when abundance is very low, growth rate can be very high: in the case of $D_r = 0$, when the steady state abundance $\frac{R_0}{2\theta_1} = 100$ and initial abundance $N_{1,t=0} = 1$, the initial growth rate is 99, which means the 1

individual needs to give birth to 99 individuals all at once. For the case $D_r = 1$, the population does not jump to its steady state in one step, but the net growth rate when N is low is still potentially high (actually in the former example if $D_r = 1$ the net growth rate when $N_{1,t=0} = 1$ is also 99). This clearly contradicts common sense. The reason why this is happening in the current model is that even without the resource constraint, we have assumed all resource to be potentially available to the species. However, we would naturally think that the amount of resource obtainable by the species is limited by its abundance. Particularly, if there are only a few individuals, they can only be efficiently exposed to a limited amount of resource out there; the more individuals there are, the more resource they can potentially acquire. With this as the baseline, I am going to modify the model trying to incorporate a constraint on resource available for the community as a function of its total abundance. For the one species case, I will simply assume that the resource available for the population is proportional to its current abundance until it reaches the total resource in the environment, or

$$R_{0,t} = \min\{r_1 N_{1,t}, R_0\} \quad (29)$$

Given this, the net growth function (suppressing t in the subscript) is:

$$\begin{aligned} g_1 &= \frac{r_1 N_1^{D_{r,1}}}{\theta_1(N_1^{D_{r,1}} + 1)} - 1 && \text{(when } N_1 < \frac{R_0}{r_1} \text{)} \\ &= \frac{R_0 N_1^{D_{r,1}-1}}{\theta_1(N_1^{D_{r,1}} + 1)} - 1 && \text{(when } N_1 \geq \frac{R_0}{r_1} \text{)} \end{aligned} \quad (30)$$

I have used r to denote the amount of resource an individual can contribute to the total resource availability for the community (only one species in this case). You can probably see some connections between this parameter and the classic definition of intrinsic growth rate (usually with the same annotation): they both describe how much net growth the population can reach when abundance is far from reaching its steady state level (carrying capacity). But you can also see that they are not exactly the same: while intrinsic growth rate directly specifies the maximal net growth rate of the population (the g here), the r parameter only specifies how much resource the population can get; the actual net growth rate is still derived from the MERA procedure. Their relationship is described by Eq. 30.

Now let's again look at the case $D_r = 0$. Eq. 30 reduces to :

$$\begin{aligned} g_1 &= \frac{r_1}{2\theta_1} - 1 && (\text{when } N_1 < \frac{R_0}{r_1}) \\ &= \frac{R_0}{2\theta_1 N_1} - 1 && (\text{when } N_1 \geq \frac{R_0}{r_1}) \end{aligned} \tag{31}$$

To see what exactly it looks like, g is plotted against N and different r values are compared:

Discuss the exponential growth when $D_r = 0$. Steeper than exponential growth when $D_r > 0$.

Net growth does not slow down until near steady state. (Optimal fishing level is higher than half). Maybe solve analytically for the optimal fishing level.

The abruptness of the growth turn. Shall we try to smooth it by modifying Eq. 29 (to be a smooth function of N)?

How about more complicated reliance of resource obtainable on N (e.g. $R_{0,t} = rN_t^2$)

A key problem is the unknown reliance of resource obtainable on N .

The possibility that more species add to smoothness.