# Analytically solving trophic links for a fully connected food web

Jade, Sep 21

Add in the fundamental resource!!!

Assuming all species are connected to one another in a fully connected food web, the steady state abundances of all species can be analytically expressed, from which the amount of resource transferred between any two species, i.e. the width of any trophic link, can be numerically determined without any simulation procedure. Specifically when all species share the same relative individual distinguishability $D_r$, each link can be analytically solved as a simple function of the product of resource requirements ($\theta$) of the two species connected by the link. Interpretations and applications of this new framework will be discussed.

# 1 Expressing the steady state abundances in a fully connected web

First let's recall the steady state abundance expression when there is only one resource :

$$N_i = C\theta_i^{\frac{1}{D_{r,i}-1}} \tag{1}$$

Therefore the steady state resource content $R_i$ can be expressed as

$$R_i = \theta_i \times N_i = C^{\frac{1}{D_{r,i}-1}} \times \theta_i^{\frac{D_{r,i}}{D_{r,i}-1}} \tag{2}$$

Given this, the amount of resource transferred from species $i$ to species $j$ $R_{ij}$ can be expressed as

$$R_{ij} = C_i^{\frac{1}{D_{r,j}-1}} \times \theta_j^{\frac{D_{r,j}}{D_{r,j}-1}} \qquad (i \text{ in } 0,1,..., S_0,\ j \text{ in } 1,2,..., S_0) \tag{3}$$

Where $C_i$ is a constant for species $i$ determined by its resource content (given $R_i$, $C_i$ can be solved by $\sum_j^{S_0} R_{ij} = R_i$). Notice that Eq. 3 also applies to flows from the fundamental resource (denoted by $R_0$) to each species, i.e. $i$ can be 0 and $R_{0j}$ denotes the flow from the fundamental resource to species $j$.

When each of the species can prey on all species (including itself) and the fundamental resource and meanwhile be preyed on by all species, its steady state resource content can be expressed in two ways, 1) as the sum of in-flows, or resources obtained from all species and 2) as the sum of out-flows, or resources given by the species to all species. Of course the trophic efficiency has to be considered in these expressions. This relationship put into equations is as follows:

for all $i$ in 1 - $S_0$:

$$\begin{aligned} R_i = \tau_u \times \sum_{j=0}^{S_0} R_{ji} &= \tau_u \sum_{j=0}^{S_0} C_j^{\frac{1}{D_{r,i}-1}} \theta_i^{\frac{D_{r,i}}{D_{r,i}-1}} && \text{(in-flows)} \\ = \sum_{j=1}^{S_0} R_{ij} &= \sum_{j=1}^{S_0} C_i^{\frac{1}{D_{r,j}-1}} \theta_j^{\frac{D_{r,j}}{D_{r,j}-1}} && \text{(out-flows)} \end{aligned} \tag{4}$$

$\tau_u$ is the trophic efficiency quantifying the proportion of flow-in resources transferred into biomass of the species. The prey distinguishability does not affect steady state abundance of the predator (for derivations see previous Write-up on May 8: A more complete model for the multiple resource scenario of MERA).

Also please notice that in Eq. 4 I have assumed that all resource of the species can be given out to its predators while previously I have assumed the maximal predation ratio to be 0.5 (in other words, $\sum_j^{S_0} R_{ij} = R_i/2$). This assumption is modified because 1) previously this 0.5 maximal predation ratio was imposed so that a species can recover within one generation time to its pre-predation steady state abundance. This was based on the implicit assumption that all species have the same generation time, which is apparently not realistic. In other words, removing the 0.5 maximal predation ratio recognizes the possibility of a species being pushed below half of its pre-predation steady abundance, but it can take time ($> 1$ generation time) to recover its abundance since the predator can have a longer generation time. An alternative justification for this is that the intrinsic growth rates for all species are assumed to be much higher than what can be realized in this model that all species can recover to its steady state abundance before predation happens again. But of course predation cannot completely wipe out a species, which means the maximal predation ratio should always be smaller than 1. But in Eq. 4 this effect can be fully captured by the value of $\tau_u$ (e.g. when maximal predation ratio is 0.5 and $\tau_u = 0.1$ as previously assumed, it is equivalent to $\tau_u = 0.05$ in Eq. 4).

Applying Eq. 4 to all species ($i = 1, 2, ..., S_0$), we get $S_0$ equations:

(for all $i$ in 1 - $S_0$:)

$$\tau_u \sum_{j=0}^{S_0} C_j^{\frac{1}{D_{r,i}-1}} \theta_i^{\frac{D_{r,i}}{D_{r,i}-1}} = \sum_{j=1}^{S_0} C_i^{\frac{1}{D_{r,j}-1}} \theta_j^{\frac{D_{r,j}}{D_{r,j}-1}} \tag{5}$$

Finally we have an equation for the balance of the fundamental resource:

$$R_0 = \sum_{j=1}^{S_0} C_0^{\frac{1}{D_{r,j}-1}} \theta_j^{\frac{D_{r,j}}{D_{r,j}-1}} \tag{6}$$

Where $R_0$ is a known constant (the constant input rate of the fundamental resource). Combining Eqs. 5 and 6, we have $S_0 + 1$ equations (which I will call balance equations throughout) with $S_0 + 1$ unknown values ($C_i$ for $i =$ 0, 1, 2,... $S_0$), from which we can solve for $C_i$ for all $i$ and in turn the flows $R_{ij}$ from any $i$ node (species or resource) to any $j$ species.

# 2 Solving the balance equations: when $D_r$ is the same for all species

Assuming $D_r$ is the same for all species, from the balance equations (Eqs. 5-6) it is easy to get (derivation is in appendix, please double check) the analytical solution for $R_ij$:

$$R_{ij} \propto (\theta_i \theta_j)^{\frac{D_r}{D_r - 1}} \qquad (i \text{ and } j \text{ both in } 1,2,...,S_0) \tag{7}$$

The proportional coefficient (see derivations in appendix) is shared among all $i$ and $j$. Eq. 7 suggests that the amount of resource flow between two species is a simple (negative) function of the product between their resource requirements, so that the bigger this product, the smaller the resource flow between the species. It also suggests that the flow is symmetrical, i.e. the amount of resource from $i$ to $j$ is always equal to the amount from $j$ to $i$. In other words, the net exchange of resource among species is zero. Therefore, when $D_r$ is the same for all species, it does not matter whether species can get resource from one another (additional interactions other than pure competition) or not (pure competition, as in the fundamental model of MERA).

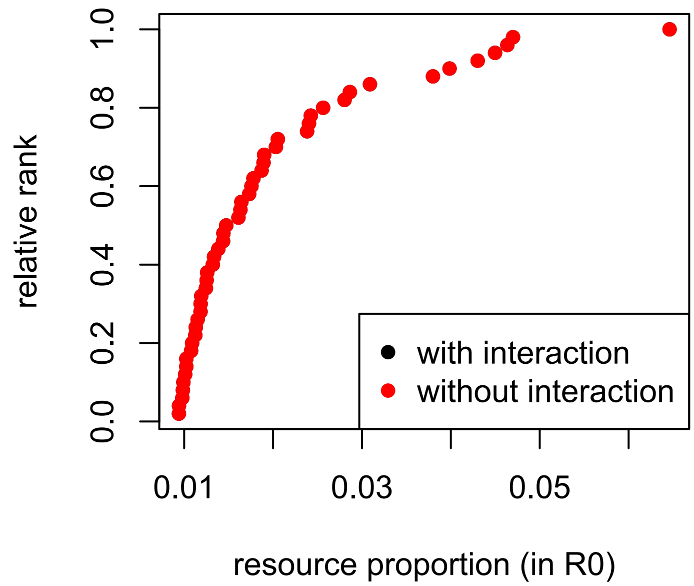


**Fig. 1 Species resource relative rank distribution when $D_r = 0.5$ for all species**

Derivation for Eq. 7