

Analytically solving resource flows for a fully connected web: comparing MERA with or without interactions

Jade, Sep 25

Assuming all species are connected to one another in a fully connected web, the steady state abundances of all species can be analytically expressed, from which the amount of resource transferred between any two species 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 (θ) of the two species connected by the link. In this new framework the previous ambiguity of generalization cost and immigration sequence is completely avoided. A more general interpretation of link between species (general interspecific interaction) 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 :

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

Therefore the steady state resource content R_i can be expressed as

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

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

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

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 $1 - S_0$:

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

τ_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 τ_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 ($i = 1, 2, \dots, S_0$), we get S_0 equations:

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

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

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

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

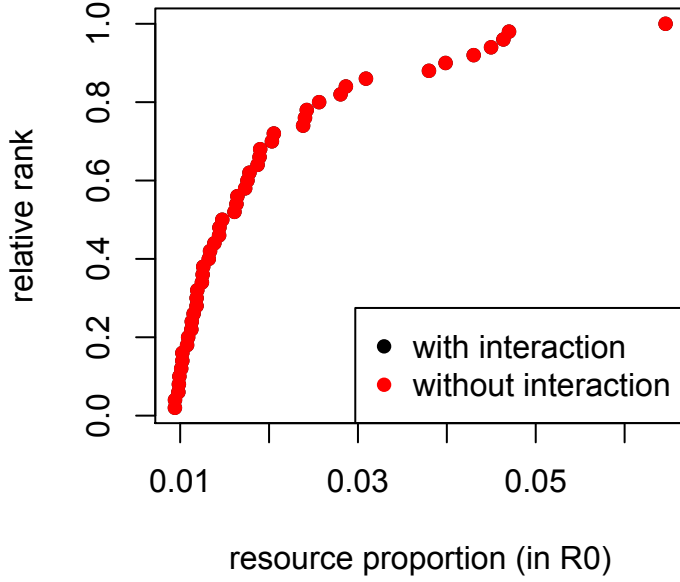
Where R_0 is a known constant (the constant input rate of the fundamental resource). Combining Eqs. 5 and 6, we have $S_0 + 1$ equations (which I will call balance equations throughout) with $S_0 + 1$ unknown values (C_i for $i = 0, 1, 2, \dots, S_0$), from which we can solve for C_i for all i and in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

2 Special case: 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} :

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

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 (allowing for additional interactions other than pure exploitative competition) or not (pure exploitative competition, as in the fundamental model of MERA).



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

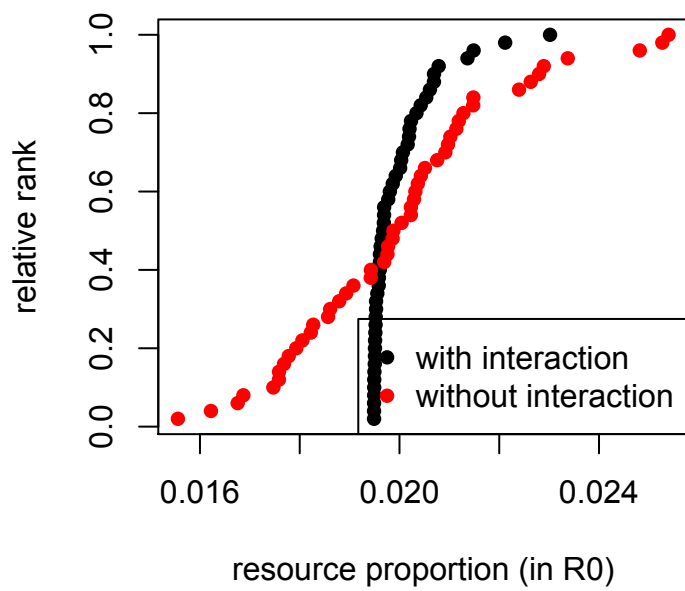
From Fig. 1 we can see that the resource distributions among species with or without interaction completely overlap. Only $D_r = 0.5$ is shown here but this is the case for other D_r values too (in appendix). However, when D_r is not the same for all species, resource flows are not symmetrical any more. In the next section I will show that the resource distribution can be more even or dispersed with interactions compared to without interactions under certain conditions.

3 Numerically solving the balance equations when $D_{r,i}$ is normally distributed

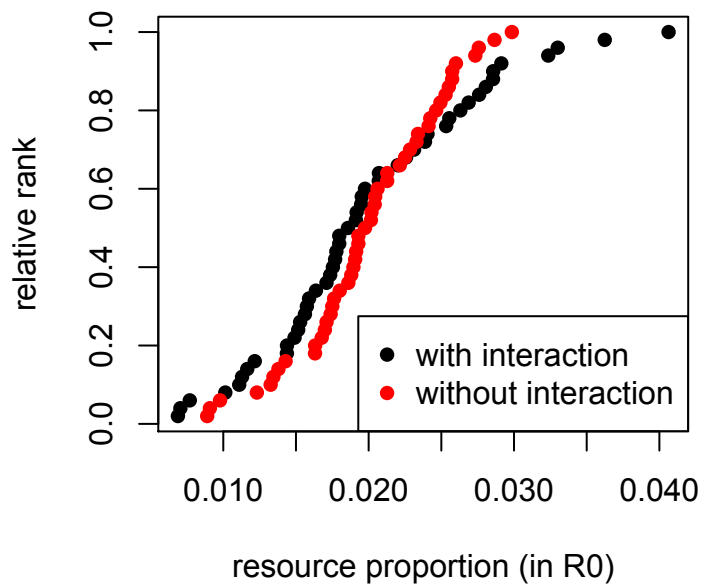
In this section I am going to assume that D_r follows a normal distribution with a mean of 0.5 and a standard deviation of 0.1. Three scenarios will be compared: 1) θ is a positive function of D_r ($\theta_i = D_{r,i}$ or $\theta_i = 10D_{r,i}$); 2) θ is a negative function of D_r ($\theta_i = D_{r,i}^{-1}$ or $\theta_i = 10D_{r,i}^{-1}$); 3) θ is independent from D_r (draw from a uniform distribution with a mean of 1 or 10). For each scenario the resource distributions predicted by MERA with or without interactions are plotted on the same graph as follows:

3.1 When θ is a positive function of D_r

a)



b)

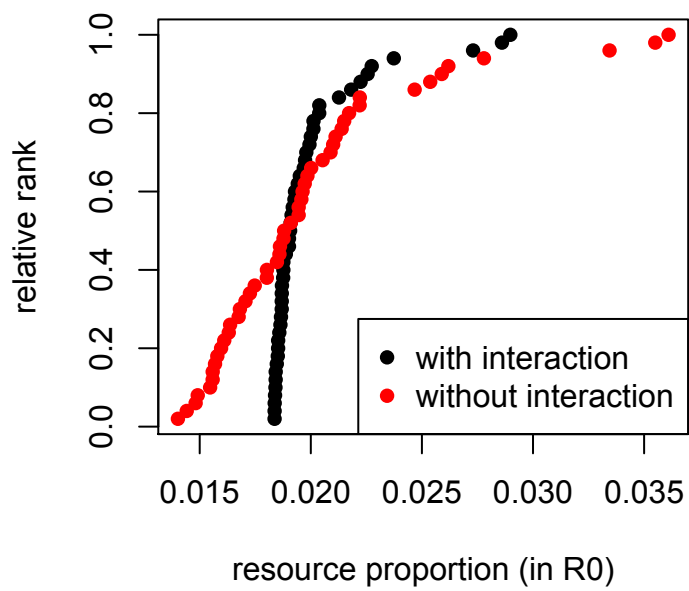


**Fig. 2 Species resource relative rank distribution when a) $\theta_i = D_{r,i}$
and b) $\theta_i = 10D_{r,i}$.**

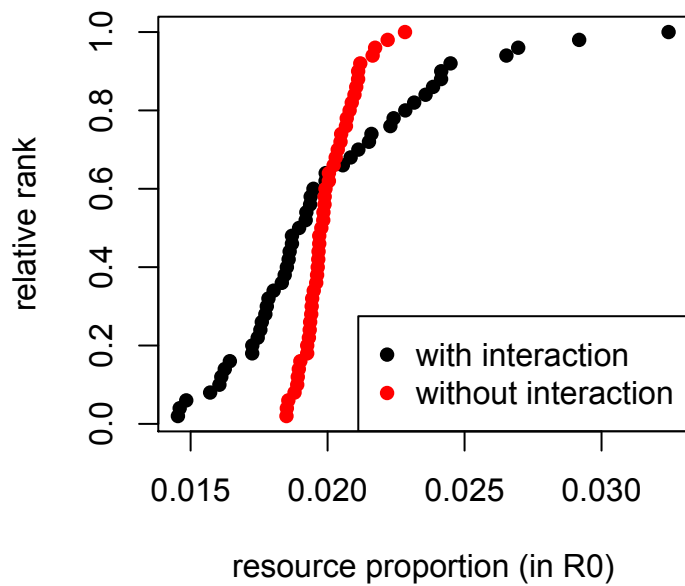
We can see that when $\theta_i = D_{r,i}$, allowing species to get resource from each other (i.e. with interaction) generates a more even resource distribution among species compared to the result from pure exploitative competition (i.e. without interaction). However, with total resource R_0 kept constant, if resource requirements of all species increase by 10 times, the effect of interaction is reversed: the resource distribution when species can get resource directly from each other is more dispersed than that when species can only indirectly interact through competing for the fundamental resource.

3.2 When θ is a negative function of D_r

a)



b)

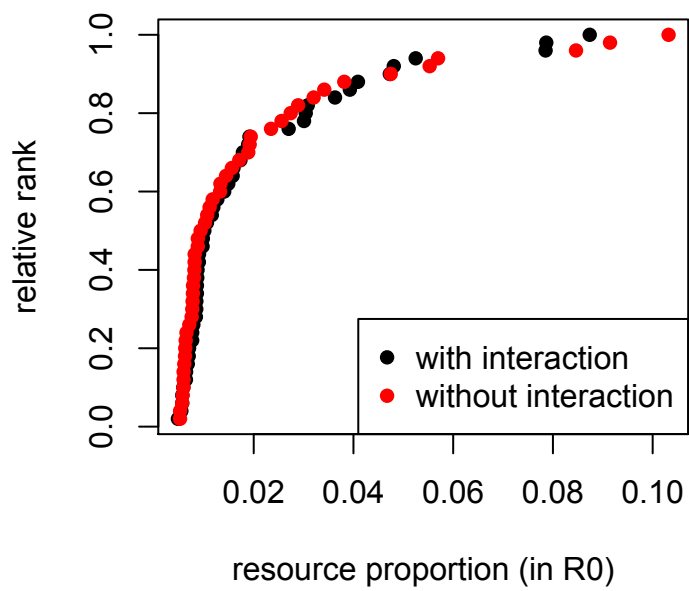


**Fig. 3 Species resource relative rank distribution when a) $\theta_i = D_{r,i}^{-1}$
and b) $\theta_i = 10D_{r,i}^{-1}$**

When θ and D_r are negatively related, although the shape of resource distribution is different from when they are positively related, the effect of interaction reverses in the similar way when the absolute values of θ increase: interaction only promotes the evenness of resource distribution when θ are comparatively small. When the magnitude of θ is big for all species, allowing interactions may increase the unevenness and therefore decrease the chance for coexistence.

3.3 When θ is independent of D_r

a)



b)

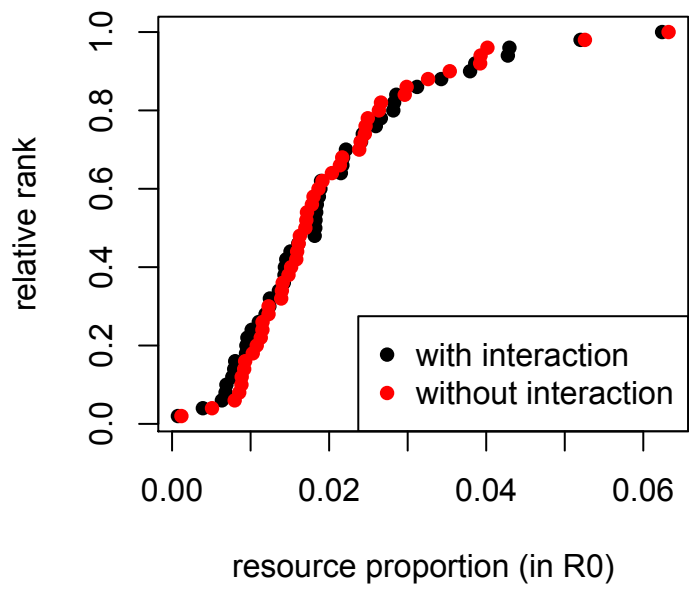


Fig. 4 Species resource relative rank distribution when θ_i follows a uniform distribution with a) mean = 1 and b) mean = 10

From Fig. 4 we can see that, apparently resource distributions are similar whether species are allowed to get resource from each other or not.

4 Summary and discussion

A new framework based on the fundamental MERA resource allocation procedure is developed enabling resource transmission between species as well as between the fundamental resource and species. A set of balance equations describing steady state conditions for all nodes (resource and species) are established, from which the ultimate resource distribution among species can be derived.

From the result we can see there are two conditions for interaction to be neutral on resource distribution: 1) D_r is the same for all species in the community or 2) D_r and θ are independent from each other. Alternatively, if D_r and θ are somehow correlated (positively or negatively), allowing interactions among species increases evenness of resource distribution (and thus enhance species coexistence) when θ s are small but has the opposite effect when θ s are big.

One straightforward interpretation of the result is that smaller species coexist by interacting more while bigger species coexist by not interacting

too much. Also based on the fact that it is the relative magnitude between θ and total resource R_0 (which is kept constant for calculations above) that matters, increasing θ for all species is actually equivalent to decreasing R_0 . From this we can obtain a different perspective based on resource availability: when resource is abundant, interaction promotes species coexistence; when resource is scarce, interaction impedes species coexistence.

The interpretation of a fully connected web is tricky, since species in a community are not observed to be directly linked to each other anyhow. However, I think this treatment is worth exploring, especially if we think of the fundamental resource here to be an overall energy pool instead of any specific material, and the link predicted here to incorporate all kinds of species interaction (direct and indirect) through competition, facilitation, predation, etc., then all species in the community could be linked to each other one way or another. When links are symmetrical, large flows between species could suggest facilitation; when links are asymmetrical, net gain or loss between two species could suggest commensalism, herbivory or predation.

As for empirically testing of this new framework, we can take the number of trophic links of a food web L as known; assuming that trophic links (predation, herbivory and parasitism) are the strongest links among all interactions, take the strongest L links from a fully connected web and

compare the shape of the web connected by these links with an empirical food web. The parameters to be adjusted will be 1) θ and how it varies across species; 2) D_r and how it varies with θ . No additional parameters are needed.

5 Appendix

5.1 Derivation for Eq. 7

When D_r is the same for all species, Eq. 5 can be re-expressed as:

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

$$\frac{C_i^{\frac{1}{D_r-1}}}{\sum_{j=0}^{S_0} C_j^{\frac{1}{D_r-1}}} = \tau_u \frac{\theta_i^{\frac{D_r}{D_r-1}}}{\sum_{j=1}^{S_0} \theta_j^{\frac{D_r}{D_r-1}}} \quad (8)$$

Combining Eqs. 3 and 4 we can get:

$$\frac{R_{ij}}{\sum_i^{S_0} R_i} = \frac{C_i^{\frac{1}{D_r-1}}}{\sum_{i=1}^{S_0} C_i^{\frac{1}{D_r-1}}} \times \frac{\theta_j^{\frac{D_r}{D_r-1}}}{\sum_{j=1}^{S_0} \theta_j^{\frac{D_r}{D_r-1}}} \quad (9)$$

Plugging Eq. 8 into Eq. 9 we get:

$$\begin{aligned} \frac{R_{ij}}{\sum_i^{S_0} R_i} &= \tau_u \frac{\theta_i^{\frac{D_r}{D_r-1}}}{\sum_{j=1}^{S_0} \theta_j^{\frac{D_r}{D_r-1}}} \times \frac{\theta_j^{\frac{D_r}{D_r-1}}}{\sum_{j=1}^{S_0} \theta_j^{\frac{D_r}{D_r-1}}} \times \frac{\sum_{i=0}^{S_0} C_i^{\frac{1}{D_r-1}}}{\sum_{i=1}^{S_0} C_i^{\frac{1}{D_r-1}}} \\ &\Rightarrow R_{ij} = (\theta_i \theta_j)^{\frac{D_r}{D_r-1}} \times \frac{\sum_{i=0}^{S_0} C_i^{\frac{1}{D_r-1}} \sum_i^{S_0} R_i}{\sum_{i=1}^{S_0} C_i^{\frac{1}{D_r-1}} (\sum_{j=1}^{S_0} \theta_j^{\frac{D_r}{D_r-1}})^2} \end{aligned} \quad (10)$$

Notice that the second term of Eq. 10 is the same for all i and j .

Therefore the relative magnitude of R_{ij} is totally determined by $(\theta_i \theta_j)^{\frac{D_r}{D_r-1}}$.

5.2 More results for resource distribution when D_r is the same for all species (interaction neutral)

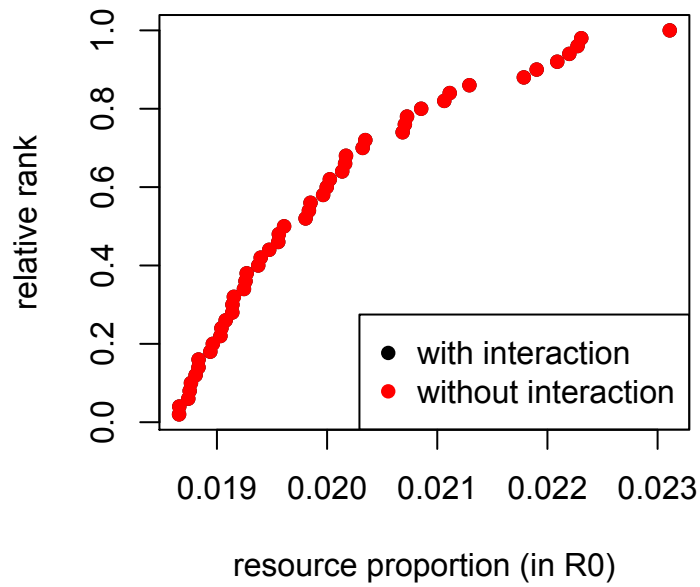


Fig. 1-2 Species resource relative rank distribution when $D_r = 0.1$ for all species

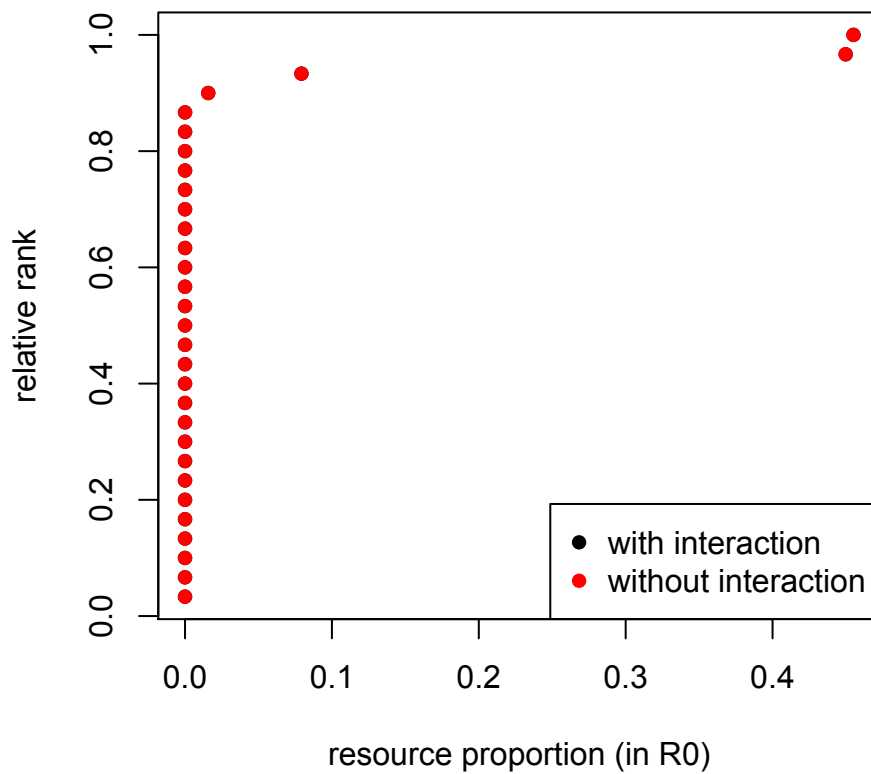


Fig. 1-3 Species resource relative rank distribution when $D_r = 0.8$
for all species