

# fdcoexist equation only

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## Basic Equation

This document resumes the equation used in our model and details the different processes. Our coexistence model is developed following this equation (Beverton-Holt equation):

$$N_{t+1,i,x} = \frac{R_{i,x} \times N_{t,i,x}}{1 + A \times \alpha_i} \quad (1)$$

with

$$\alpha_i = \sum_{j=1, j \neq i}^S N_{t,j,x} \times (1 - \delta_{ij}) \quad (2)$$

$$R_{i,x} = k \times \exp\left(-\frac{(\text{trait}_i - \text{env}_x)^2}{2 \times \text{width}^2}\right) \quad (3)$$

If we replace  $\alpha_i$  and  $R_{i,x}$  in the first equation it gives:

$$N_{t+1,i,x} = \frac{k \times \exp\left(-\frac{(\text{trait}_i - \text{env}_x)^2}{2 \times \text{width}^2}\right) \times N_{t,i,x}}{1 + A \times \sum_{j=1, j \neq i}^S N_{t,j,x} \times (1 - \delta_{ij})} \quad (4)$$

## Detailing the computation of $\delta_{ij}$

$\delta_{ij}$  is the functional dissimilarity coefficient between species  $i$  and species  $j$ . It reflects the fact that the more two species are dissimilar the less competition they experience from each other.

First we can compute  $\delta_{ij}$  as the euclidean distance between species using multiple traits:

$$\delta_{ij} = \sqrt{\sum_{c=1}^{T_c} (\text{trait}_{i,c} - \text{trait}_{j,c})^2}, \quad (5)$$

with  $T_c$  the number of traits contributing to competition,  $\text{trait}_{i,c}$  trait  $c$  of species  $i$  and  $\text{trait}_{j,c}$  trait  $c$  of species  $j$ . If want to take the contribution of traits to competition we have to modify the trait values as follow:

$$\delta_{ij} = \sqrt{\sum_{c=1}^{T_c} [\sqrt{w_c}(\text{trait}_{i,c} - \text{trait}_{j,c})]^2} \quad (6)$$

$$\delta_{ij} = \sqrt{\sum_{c=1}^{T_c} w_c \times (\text{trait}_{i,c} - \text{trait}_{j,c})^2}, \quad (7)$$

with  $w_c$  the contribution of trait  $c$  in limiting similarity.

However, we here consider linear dissimilarity, the influence of species is directly proportional to their distance. There are some evidence in the literature that closer species have disproportionately more impact that species further way. This suggest an exponential shape of the competition as follow:

$$\delta'_{ij} = \exp \left[ \left( \frac{\delta_{ij} - \min(\delta_{ij})}{\max(\delta_{ij}) - \min(\delta_{ij})} \right)^d \right], \quad (8)$$

with  $d$  the power to which we should scale the exponential relationship

## Adding intra-specific competition

The equation above only considers inter-specific competition when  $j \neq i$  in the sum. We can however add intra-specific competition when  $j = i$ . Each site has a species-specific carrying capacity  $K$  as the number of individuals approaches this carrying capacity the intra-specific competition increases:

$$\alpha_{ii} = B \times N_{t,i,x} \quad (9)$$

Thus the equation becomes:

$$N_{t+1,i,x} = \frac{k \times \exp \left( -\frac{(\text{trait}_i - \text{env}_x)^2}{2 \times \text{width}^2} \right) \times N_{t,i,x}}{1 + A \left( \sum_{j=1, j \neq i}^S N_{t,j,x} (1 - \delta_{ij}) + \frac{B}{A} \times N_{t,i,x} \right)} \quad (10)$$

with  $A$  the coefficient scaling inter-specific competition and  $B$  the one for intra-specific competition.

## Multi-trait growth term

Because several traits participate to the growth term depending on their contribution we can rewrite the growth term as:

$$R_{i,x} = \sum_{g=1}^T w_g \times k \times \exp \left( -\frac{(\text{trait}_{g,i} - \text{env}_x)^2}{2 \times \text{width}^2} \right) \quad (11)$$

with  $g$  the trait number,  $0 \leq w_g \leq 1$  the contribution of this trait to growth (and  $\sum_{g=1}^T w_g = 1$ ),  $\text{trait}_{g,i}$  the trait number  $g$  of species  $i$ .

## Adding Hierarchical competition

If we add hierarchical competition, the species with the largest trait has an increased growth. We can include this as a “bonus” term in the computation of the growth term  $R_{i,x}$  such as:

$$R_{i,x} = R_{i,x,\text{env}} + R_{i,x,\text{hierarch.}} \quad (12)$$

$$R_{i,x,\text{hierarch.}} = \sum_{c=1}^{T_c} w_c \times H \times \frac{t_i}{\max(t_i)} \quad (13)$$

$$R_{i,x} = k \left[ \sum_{g=1}^T w_g \times \exp \left( -\frac{(\text{trait}_{g,i} - \text{env}_x)^2}{2 \times \text{width}^2} \right) + \frac{H}{k} \sum_{c=1}^{T_c} w_c \frac{\text{trait}_i}{\max(\text{trait}_i)} \right], \quad (14)$$

with  $w_g$  the weight of traits contributing to growth,  $w_c$  the weight of traits contributing to competition (as many as  $T_c$ ).

So the final equation looks like the following:

$$N_{t+1,i,x} = \frac{k \left[ \sum_{g=1}^T w_g \times \exp \left( -\frac{(\text{trait}_{i,g} - \text{env}_x)^2}{2 \times \text{width}^2} \right) + \frac{H}{k} \sum_{c=1}^{T_c} w_c \frac{\text{trait}_{i,c}}{\max(\text{trait}_{i,c})} \right] \times N_{t,i,x}}{1 + A \left( \sum_{j=1, j \neq i}^S N_{t,j,x} (1 - \delta_{ij}) + \frac{B}{A} \times N_{t,i,x} \right)} \quad (15)$$

If we consider that traits contributing to limiting similarity may not contribute to hierarchical competition we can develop the total equation as follow:

$$N_{t+1,i,x} = \frac{k \left[ \sum_{g=1}^{T_g} w_g \times \exp \left( -\frac{(\text{trait}_{i,g} - \text{env}_x)^2}{2 \times \text{width}^2} \right) + \frac{H}{k} \sum_{h=1}^{T_h} w_h \frac{\text{trait}_{i,h}}{\max(\text{trait}_{i,h})} \right] \times N_{t,i,x}}{1 + A \left[ \sum_{j=1, j \neq i}^S N_{t,j,x} \left( 1 - \sqrt{\sum_{c=1}^{T_c} w_c \times (\text{trait}_{i,c} - \text{trait}_{j,c})^2} \right) + \frac{B}{A} \times N_{t,i,x} \right]}, \quad (16)$$

with  $w_g$ ,  $w_h$  and  $w_c$ , the contribution respectively of trait to growth, hierarchical competition and limiting similarity with  $T_g$ ,  $T_h$  and  $T_c$  the number of traits respectively contributing to growth, hierarchical competition and limiting similarity.