# Modeling species fitness in competitive environments

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## ARTICLE INFO

## ABSTRACT

Using a model of resource acquisition, we studied species competition in a case where resources limit population growth. Our model is based on calculations of the distribution of individuals of single or multiple species over consumed resources. Calculations show that, as equilibrium is reached in purely resource competitive systems, the density of resources is lowered to the lowest sustainable level, directly leading to low levels of fitness among species. In the case of competition between species with different lowest sustainable levels, the density of the more successful must be limited by some cause other than the resource in question for all species to coexist. We explore two cases of such coexistence.

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## 1. Introduction

Competition for resources between subjects of the same species and between species is one of the most important factors in ecology and evolution. With competition, many evolutionary and ecological questions can be addressed. The ability of species to compete increases their chance of survival in the existing local ecosystems (Begon et al., 2005) and on the global scale influencing evolution directly (Darwin, 1859). Many numerical models are used for modeling the competition, such as the basic Lotka–Volterra equations (Volterra, 1931; Lotka, 1932) describing predation and competition, the Monod model (Monod, 1942, 1950; Herbert et al., 1956) used to describe different species competing for the same resources and Droop's model describing the growth of populations where nutrient quantities are growth limiting factors (Droop, 1974, 1975). All of these models have been widely used and improved for more realistic use in specific cases: for example, to study competition under multiple nutrient limitation (Tilman, 1982; Cherif and Loreau, 2010) and stability of ecological systems (Tilman, 1996; Huisman and Weissing, 1999; Lehman and Tilman, 2000; Mougi and Kondoh, 2012). The above models use the density of competing species and resources as observed/modeled variables and describe the dynamics of the system by coupled differential equations between them. Co-existence and biodiversity has been studied as a function of number of limiting resources (Tilman, 1982), temporal and spacial gradient of parameters (Tilman, 1999; Lehman and Tilman, 2000)

or as a consequence of chaotic behavior of the models for certain sets of parameters (Huisman and Weissing, 1999, 2002).

Alternatively there is a growing interest in individual-based models, where individuals are followed and their behavior is modeled depending on external parameters (DeAngelis and Mooij, 2005; Grimm et al., 2006; Railsback and Grimm, 2011; Martin et al., 2013). This is especially suitable for modelling small populations where we can follow individuals and their properties and consumption. Monte-Carlo methods are used to study system evolution under different circumstances and population survival probability can be studied.

In this article we propose a model that combines part of the benefits from both approaches. In this model we follow the temporal evolution not only of a population density but also the distribution of the population over successfully consumed resources. In this way, we can also take into account the fitness of the population. Information on fitness gives us further understanding of species competitiveness in the ecosystem and possible vulnerabilities to or advantages from ecosystem changes. We start by studying the temporal behavior of a simple one-species system and proceed to more complicated systems involving more species and resources.

## 2. Method

In presented model we follow the distribution of a population over resource consumption. Since sufficient consumption is needed for survival and even more for successful reproduction, this can be used as a measure of fitness (Begon et al., 2005). We take into account that only a limited amount of resources can be consumed and accumulated (Tilman and Kilham, 1976), although

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luxury intake is possible. Another important point is that consumed and accumulated resources are also used over time; therefore, only consumption during a certain relevant time window (RTW) is important for the current fitness of individuals. Throughout this article the most recent time window is used as RTW. RTW should be chosen long enough to account for the possibility of the fully fed individual to starve to death in case of lack of resources and on the other side to allow for the full starvation-recovery all the way to the excess accumulation. Although different parameters are defining fitness sufficient resource intake is crucial for specimen survival and reproduction ability and we use the amount of consumed resources over the RTW for a measure of fitness in this article.

We mark the amount of resources consumed by an individual over RTW with $K$. To describe the fitness of the entire population, we can use the density distribution of individuals over $K$ ($S = S(K)$). In the model, used population parameters are minimum resource consumption $K_s$ that still allows for survival of the individual, although the fitness in this case is too low for reproduction; $K_r$ is the minimum resource consumption needed for successful reproduction of the individual, and $K_{max}$ the estimated maximum possible consumption of resources over the RTW in case the resource is abundant. Reproduction rate and decay rate of the species are $K$ dependent, and we use reproduction rate $s_r$ to describe the reproduction of individuals with $K > K_r$, while the others do not reproduce. All the individuals with consumption below $K_s$ die, and we use $s_d$ to describe the death rate of the others caused by aging and external factors.

Mathematically, the problem of density distribution with 'forgetfulness/use of accumulated resources' is not easy to solve; therefore, we use a distribution over $N$ discrete values of the amount of resource consumed ($K$) over the last RTW. In this way we use time steps of $\Delta t = RTW/N$, and in every time step an individual either consumes $\Delta K = K_{max}/N$ amount of resource or it does not. The probability ($P$) of an individual finding and consuming the resource depends on resource density $F(t)$ and on the space-covering speed of individual $v$ – a species – dependent parameter describing the amount of space (surface or volume) an individual can cover over the time. If we simply assume that finding a resource is sufficient for its consumption, the density of individuals that do not find the resource in $\Delta t$ can be calculated by integration of $d\underline{S} = -v\underline{S}(t)F(t)dt$ over $\Delta t$. Here we use $\underline{S}$ as the density of the individuals that have not yet consumed the resource. For those that have already consumed the resource we, assume that they digest for the rest of the $\Delta t$. Now the probability of finding and consuming $\Delta K$ in the time step can be calculated as:

$$P = \frac{[\underline{S}(t) - \underline{S}(t + \Delta t)]}{\underline{S}(t)}. \tag{1}$$

Resource density $F(t)$ depends on resource growth/inflow, resource decay/outflow and resource consumption by individuals. The temporal evolution of $F$ can be calculated by integration of $dF = [f_g - f_d F(t) - \Delta K v \underline{S}(t)F(t)]dt$. The growth term $f_g$ depends on the particular resource and can depend on density (reproduction, growth) or on other resources. Since we are interested in cases where competition takes place and most of the resources are in quasi-equilibrium, we simply take it as a constant. We use linear approximation $f_d F(t)$ for the decay/outflow term. This is useful because it also limits the growth of resources to the values below $F_{max} = f_g/f_d$. In our calculation most of the resource decrease is through consumption by the species being studied (the last term in the equation), and we can expect $f_d F(t)$ to be small. We can generalize our equations for multiple species and resources to coupled differential equations:

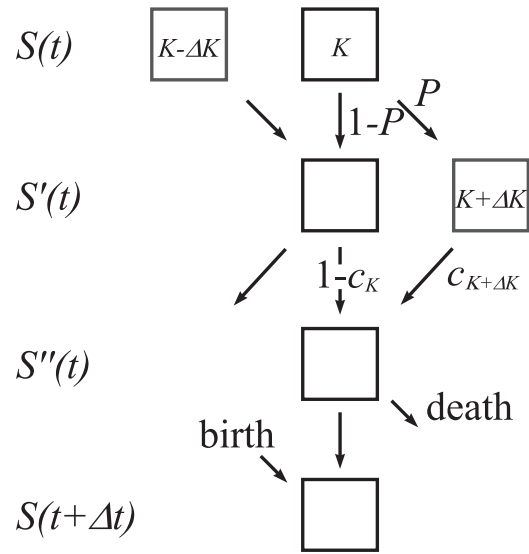$$dS_i^j = -v_{i,j} \underline{S}_i^j(t)F_j(t)dt \tag{2}$$



**Fig. 1.** Step diagram of species density calculation.

$$dF_j = \left( -\sum_i \Delta K_i^j v_i^j \underline{S}_{i=i}^j(t)F_j(t) + f_g^j(t) - f_d^j F_j(t) \right) dt \tag{3}$$

Here index $i$ indicates species and index $j$ resource. These equations can be integrated over a selected time unit $\Delta t$, and the probability for an individual to consume the resource can be calculated. Here we assumed $v$ to be $K$ independent and use $\underline{S}_i^j$ to be the full density of the species (initial $\underline{S}_i^j = \sum_K S_i(K)$), but the equations can also be expanded to use $\underline{S}$ for different $K$. Resource density $F$ is continuous function of time and is initialized to the final value from the previous step. The equations as stated above are for limiting resources. When two resources ($j', j''$) can be exchanged, single distribution $\underline{S}_i^{j'j''}$ should be used and will account for consumption of all exchangeable resources. Here we should point out that other models for the probability of resource consumption can be used with the rest of the calculation unchanged.

With probability calculated, we can calculate the next iteration of consumed resource distribution. This is performed in multiple steps, as shown in diagram in Fig. 1.

First, we calculate the density distribution for RTW + $\Delta t$ (time interval of $(N+1)\Delta t$):

$$S'(K, t) = PS(K - \Delta K, t) + (1 - P)S(K, t). \tag{4}$$

Now we must transform it back to distribution over RTW. For this we need to know for every $S(K)$ the part of it that consumed $\Delta K$ of resource RTW ago – $c(K)$. By subtraction of this part, we again have the distribution over the most recent RTW (last $N\Delta t$):

$$S''(K, t) = (1 - c(K))S'(K, t) + c(K + \Delta K)S'(K + \Delta K, t). \tag{5}$$

Finally, we account for those born and those that died:

$$S(K, t + \Delta t) = (1 - d(K))S''(K, t) + b(K, t). \tag{6}$$

The death rate here depends on $K$ (those with $K < K_s$ starve to death). In this paper we do not count the death rate due to external factors as $K$ dependent, but implementation of this would be straightforward. In the case of multiple resources, we assume no correlation between consumption of different resources and we calculate the deaths through lack of resources accordingly. The birth rate, on the other hand, depends on the subjects with $K > K_r$ giving us the full growth of $b = s_r \sum_{K > K_r} S''(K, t)$. Again, no correlation is assumed between different resource distributions, and in the case of multiple resources, we take into account that fitness