



# Community diversity and total abundance: Quantitative predictions from competition niche theory



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## ABSTRACT

Lotka–Volterra niche competition theory (LVNCT) is based on Lotka–Volterra competition equations with competition coefficients between pairs of species determined by the intensity of their niche overlap through the MacArthur–Levins niche overlap formula. Here I study analytically and numerically the predictions of LVNCT concerning total abundance and biodiversity, measured by the Shannon equitability index. Firstly, a set of simplifying assumptions that render the LVNCT amenable of analytical treatment are considered. In particular I derive an approximated formula for the total abundance, as the inverse of the mean value of the interspecific competition coefficients, which works pretty well both for the transient and steady regime and for a wide range of the typical niche width  $\sigma$ . Secondly, I analyze, by means of simulations, the effect of relaxing the above simplifying assumptions when considering more realistic conditions. It turns out that the approximated formula for the total abundance is quite robust and its potential implications for management are discussed. I also analyze the predicted relationship between community productivity and diversity.

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## 1. Introduction

The classical theory of community ecology is based largely on Lotka–Volterra competition (LVC) equations (Levins, 1968; Rose, 1987). Another central element of the classical framework is the concept of resource utilization niche (MacArthur and Levins, 1967; Schoener, 1989), which focuses on how species use consumable resources. In fact niche theory (NT) was essentially a group of theoretical models designed to address the problem of how many and how similar coexisting species could be within a given community (MacArthur and Levins, 1967; May and MacArthur, 1972). The relative utilization of resources along a resource spectrum or niche axis can be described as a frequency distribution. Species are thus characterized in terms of their similarity in resource use or their niche overlap. The basic idea is that there is a strong correspondence between the degree of niche overlap between two species and the intensity of their competition by shared resources (Morin, 2011). The combination of LVC and NT resulted in the Lotka–Volterra niche competition theory (LVNCT) (May, 1974; Pianka, 1976).

Just to fix ideas one may consider the niche axis as a gradient that is related to the size of organisms (but we should bear in mind that the niche concept is much general and does not necessarily implies the size of organisms). Each species is numbered by an index  $i$  and is represented by a normal distribution  $P_i(\xi) = \exp[-(\xi - \mu_i)^2 / (2\sigma_i^2)]$  centered at  $\mu_i$ , corresponding to its mean size (i.e. its position on this niche axis  $\xi$ ), and with a standard deviation  $\sigma_i$ , which measures the width of its niche. The competition for finite resources among the  $n$  species can be described by the Lotka–Volterra competition (LVC) equations:

$$\frac{dN_i}{dt} = r_i N_i \left( 1 - \frac{\sum_{j=1}^n \alpha_{ij} N_j}{K_i} \right) \quad i = 1, \dots, n, \quad (1)$$

where  $N_i$  is the population size of species  $i$ ,  $r_i$  is its maximum per capita growth rate,  $K_i$  is the carrying capacity of species  $i$  (the asymptotic population size it reaches when isolated from the other competing species) and the coefficient  $\alpha_{ij}$  is the coefficient of competition between species  $i$  and  $j$ . As mentioned measure of the intensity of this competition is provided by their niche overlap, i.e. the overlapping between  $P_i(\xi)$  and  $P_j(\xi)$ . Therefore the competition coefficients  $\alpha_{ij}$  can be computed by the MacArthur–Levins niche

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overlap (MLNO) formula (MacArthur and Levins, 1967):

$$\alpha_{ij} = \frac{\int_{-\infty}^{\infty} P_i(\xi)P_j(\xi)d\xi}{\int_{-\infty}^{\infty} P_i^2(\xi)d\xi} \quad (2)$$

The LVNCT resulting from (1) and (2) can be used as a predictive tool for the total abundance and biodiversity, two central metrics of community ecology (Berlow, 1999; Abrams, 2001; Morin, 2011), assuming the distribution of niches in resource space is known. Another important question is regarding the interrelation between total abundance and biodiversity. This relationship, besides being intimately connected with a recent debate among ecologists focused on mechanisms by which species diversity might affect net primary productivity (Loreau and Hector (2001)), is of paramount interest in more applied fields. For example, in agriculture where benefits of multi species mixtures include *overyielding*, i.e. production in mixtures that exceeds expectations based on monoculture yields (Trenbath, 1974). LVNCT can also serve as a baseline for analyzing more general mechanistic theories, taking into account other interactions than just mutual competition, to assess the effects on total abundance and biodiversity when including interspecific mutualism, facilitation or parasitism. For instance the effects of including a small dose of positive cooperative interactions among different competing populations in viral ecosystems were studied using LVNCT as a basis model (Arbiza et al., 2010).

Here I study, analytically and numerically, the predictions of LVNCT concerning total abundance and biodiversity (measured by the Shannon equitability index). In particular I focus on the dependence of these two quantities on the competition matrix  $\alpha$  which, in turn, depends on the typical niche width  $\sigma$ . I start in Section 2 by reviewing a series of simplifying assumptions that render the LVNCT amenable of analytical treatment and then I obtain analytical expressions for the total abundance and biodiversity, both for the transient and steady regime. In Section 3 I analyze, by means of simulations, the effect of relaxing the above simplifying assumptions and considering more realistic conditions. Predictions concerning the classical problem of the relationship between diversity and total abundance and productivity are also discussed Section 3.1. Section 4 is devoted to conclusions.

## 2. Method and results

### 2.1. The fully simplified model: analytical results on biodiversity and total abundance

It is possible to obtain analytic expressions for species relative abundances, in terms of the dominant eigenvector of  $\alpha$ , provided we consider a series of simplifications (Fort et al., 2009):

- S1. All species have the same per capita growth rate which we take equal to 1:  $r_i = 1 \forall i$ .
- S2. All species have the same carrying capacity:  $K_i = K \forall i$ .
- S3. All species have the same niche width:  $\sigma_i = \sigma \forall i$ .
- S4. To avoid border effects, the niche is defined as circular, i.e. periodic boundary conditions (PBC) are imposed. This is done by just taking the smallest of  $|\mu_i - \mu_j|$  and  $1 - |\mu_i - \mu_j|$  as the distance between the niche centers.

Conditions S1 to S4 define the *fully simplified model* (FSM thereafter). S1 to S3 are neutral assumptions (i.e. assume functional equivalence between species) and thus the fate of a species depends just on its position on the niche axis.

Under simplifying conditions S1 and S2 the system of Eq. (1) reduces to

$$\frac{dx_i}{dt} = x_i \left( 1 - \sum_{j=1}^n \alpha_{ij} x_j \right) \quad i = 1, \dots, n, \quad (3)$$

where  $x_i = N_i/K$ . Conditions S3 to S4 in turn allow to write the competition coefficients  $\alpha_{ij}$  as:

$$\alpha_{ij} = e^{-\frac{(|\mu_i - \mu_j|)^2}{4\sigma^2}}, \quad (4)$$

where  $|\mu_i - \mu_j| = \min\{|\mu_i - \mu_j|, 1 - |\mu_i - \mu_j|\}$  implements the circularity of the niche axis.

From (3) and (4) it is possible to predict the number of surviving species for asymptotic times,  $n_\infty$ , as a function of  $\sigma$  (Fort et al., 2009, 2010). For example, for  $\sigma = 0.1, 0.15$  and  $0.2$   $n_\infty$  becomes, respectively, equal to six, four and two species.

As a measure of the total abundance,  $X$ , I will use the sum of species abundance densities normalized by their carrying capacities, and as measure of biodiversity the Shannon's *equitability index*  $H$  (or normalized entropy).  $X$  and  $H$  are given respectively by

$$X = \sum_{i=1}^n \frac{N_i}{K_i} = \sum_{i=1}^n x_i, \quad (5a)$$

$$H = -\sum_{i=1}^n \frac{x_i}{X} \ln\left(\frac{x_i}{X}\right) / \ln(n). \quad (5b)$$

The possible values of  $H$  range from zero (when there is just one species) to 1 (when all the  $n$  species are equally represented).

The curves of the total abundance and the Shannon equitability as a function of time,  $X(t)$  and  $H(t)$  respectively, can be obtained by numerical integration of (3). As initial condition for the variables  $x_i$  I take species uniformly distributed along the niche axis, i.e.  $\mu_i = i/n$  ( $=1, 2, n$ ). In Fort et al. (2010) it was shown that no important differences are observed between the uniform and random distribution on the niche axis. Each  $x_i$  is a random number between 0 and  $x_{\max} \leq 1$  chosen from a uniform distribution ( $x_{\max} = 1$  would correspond to a maximum abundance equal to the carrying capacity, and varying  $x_{\max}$  from 0.01 to 1 does not introduce dramatic changes). Fig. 1 shows results for  $\sigma = 0.15$ . We can see that  $X(t)$  exhibits a sigmoidal behavior while  $H(t)$  is its mirror symmetric curve. Three different temporal scales are apparent for a wide set of initial conditions.<sup>1</sup> For a very short time  $\tilde{t}$  (typically  $\tilde{t} = 5$  to 10)  $X$  suffers a drastic variation quickly converging to a value  $\bar{X}$  and thereafter it exhibits a plateau.  $H$ , in turn, starts from a value close to its maximum,  $H = 1$ , and does not vary appreciably. At an intermediate time scale,  $t_i$ , the paces of change for both  $X$  and  $H$  increase. Finally, at a large asymptotic time scale,  $t_\infty$ ,  $X$  and  $H$  reach their equilibrium values  $X_\infty$  and  $H_\infty$ . Remarkably, the relative variation of  $X$  with  $t$  is much smaller than the relative variation of  $H$  with  $t$ . The above panels depict snapshots of species abundances vs. niche position  $\mu$  for four different times. The initial condition at  $t = 0$  consists in each  $x_i$  equal to a random number between 0 and 0.1 chosen from a uniform distribution. For  $t = 250$  a structure emerges and for  $t = 1000$  it transforms in a set of well defined lumps of species. For  $t = 3000$  we observe competitive exclusion: each lump is thinned out to a single species. The particular positions of the surviving species along the niche axis depend on the initial conditions.

<sup>1</sup> That includes random abundances, slightly perturbed uniform abundances, etc. However, for some particular initial conditions subtle transient additional structure can occur, for example the splitting of the middle phase into two slightly different values.

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