Quantitative predictions from competition theory with an incomplete knowledge of model parameters tested against experiments across diverse taxa

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ABSTRACT

The capacity of community ecology for making quantitative predictions is often limited by incomplete empirical information which precludes obtaining reasonable estimates of model parameters. This is particularly the case for communities with large species richness S since it is practically impossible to perform the S monoculture experiments (to obtain the species carrying capacities) plus the $S \times (S-1)/2$ pairwise experiments (required to estimate the entire set of interspecific interaction coefficients of the interaction or community matrix). However quantitative predictive tools are vital for understanding the fate of ecological communities.

Here we derive an analytical approximation for predicting the relative yield total (or equivalently the mean relative yield) as a function of the mean intensity of the interspecific competition and the species richness. The rationale is that with incomplete information on model parameters it seems more reasonable to attempt to predict "macroscopic" or mean quantities, defined for the whole community of competing species, rather than making detailed "microscopic" predictions, like species abundances.

This method, with only a fraction of the model parameters (carrying capacities and competition coefficients), is able to predict accurately empirical measurements covering a wide variety of taxa —algae, plants, protozoa, etc.

Our aim with this approach is to contribute in making community ecology a more quantitative and predictive science. We argue that such parsimonious modeling is preferable than more realistic/complex theories involving additional parameters which can be very difficult to measure.

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1. Introduction

Competition plays a key role in structuring ecological communities (Morin, 2011; May 1973). The classical theoretical framework for competition is the Lotka-Volterra competition theory (LVCT)(Lotka, 1925; Volterra, 1926). The Lotka-Volterra equations of competition describe the population dynamics of S species competing for some common resource in a community as:

$$\frac{1}{Y_i}\frac{dY_i}{dt} = r_i \left(1 - \frac{\sum_{j=1}^{S} \alpha_{ij} Y_j}{K_i} \right) \qquad i = 1, ..., S \qquad (1)$$

where Y_i is the yield of species i (either its population density, biomass density, biovol, etc.), r_i is its maximum per capita growth rate, K_i is the carrying capacity of species i (the asymptotic value the yield reaches when the species is isolated from the other competing species) and α_{ij} is the coefficient of competition of species j over species i(the intraspecific competition coefficients of a species with itself, α_{ii}, are customarily taken equal to 1). The LVCT can be thought as the first order or linear approximation in a Taylor series expansion of the per-capita growth rates of species about the equilibrium points of a more complex and general theory of competition (Volterra, 1926; Volterra, 1931).

For large values of S the focus of Lotka-Volterra competition theory has been almost exclusively on community stability and species coexistence, not on making quantitative predictions to be tested against experimental data, like relative species abundance in equilibrium (Hubbel, 2002). A main difficulty for quantitative analysis of the equilibrium state is how to obtain the set of parameters $\{K_i; \alpha_{ij}\}$ of Eq. (1) which are relevant at equilibrium. A straightfor-

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ward procedure is to perform a) the S single species or monoculture experiments, and from each of them to estimate K_i as the asymptotic biomass density of species i; and b) the $S \times (S-1)/2$ pairwise experiments and for each of them, from the pair of the biculture yields, B_i and B_j, infer α_{ij} and α_{ji} (see below). Among several practical limitations of this approach, the principal one is that it is feasible provided S is not too large since the number of required experiments grows as S^2. Thus, for large values of S, only a fraction of these experiments is commonly carried out and consequently we have an incomplete knowledge of model parameters.

Here we test the Lotka-Volterra competition theory as a quantitatively predictive tool for equilibrium with an incomplete knowledge of the S^2 model parameters, as it usually happens in real life. Therefore we do not attempt of making detailed "microscopic" predictions for each species in a community, like the species yields $\{Y_i\}$, that require the full set of model parameters. Rather our goal is to predict aggregate or average productivity metrics. Thus, we focus on global or "macroscopic" quantities, for the whole community of competing species. In order to have a robust description, independent of how the yield is measured in different communities (population density, biomass density, biovol, etc.) and capable of making comparisons among widely different taxa, these macroscopic quantities are built from relative yields $y_i = Y_i/K_i$ (i.e. the species yield in mixture normalized by its yield in monoculture).

The first macroscopic quantity we consider is the sum of the S relative yields, or relative yield total, RYT:

$$RYT = \sum_{i=1}^{S} y_i. \tag{2}$$

This index allows comparing community productivity on a relative basis. Agricultural science is an example of an area where it is widely used to determine productivity in crop mixtures (de Wit, 1970). A $RYT > 1$ denotes species complementarity leading thus to increased total resource use (Loreau and Hector, 2001). This, in turn, implies that the yield performance will be better in polyculture than in monoculture, a phenomenon termed as *overyielding* (Vandermeer, 1989). There is a large ecological literature on the subject (Vandermeer, 1989; Donald, 1963; Trenbath, 1974; Tilman, 1999). Experiments with plants have shown that overyielding varied greatly depending on the functional characteristics of the species involved (Huston, 2000; Fridley, 2003) and the biotic and abiotic environment (Fridley, 2003; Fridley, 2001). However, many experimental studies found a significant increase of community biomass with increasing biodiversity, as reviewed in (Schmid et al., 2002). Moreover, there is consensus that at least some minimum number of species is essential for ecosystem functioning and that a larger number of species is probably required for maintaining the stability of ecosystem processes in changing environments (Loreau et al., 2001). The RYT divided by S is equal to the mean relative yield MRY, another measure of community productivity, which can be used to assess the impact of biodiversity loss on the ability of ecosystems to provide ecological services.

Another macroscopic quantity is the mean intensity of interspecific competition, a. To mathematically define it we rewrite the equilibrium solutions of (1) in terms of relative yields, y_i, as:

$$\sum_{j=1}^{S} a_{ij} y_j = 1, \qquad i = 1, ..., S, \tag{3}$$

where $a_{ij} = \alpha_{ij} K_j/K_i$. (Notice that the diagonal terms of the interaction matrix **A**, corresponding to intra-specific competition, remain equal to 1 since $a_{ii} = \alpha_{ii} K_i/K_i = \alpha_{ii} = 1$). Thus a is defined as the mean over the off-diagonal elements of **A**:

$$a = \overline{a_{i \neq j}}. \tag{4}$$

We derive an analytical approximate expression for the RYT as a function of the mean competition intensity a and the species richness S. We show that this formula, with and incomplete knowledge of Lotka-Volterra competition parameters, reproduces quite accurately the empirical RYT and MRY obtained from experiments across diverse taxa. Hence, this approach becomes particularly useful to predict aggregate/average productivity metrics for ecological communities involving many coexisting species in which, at best, only a fraction of these model parameters can be experimentally obtained.

We end by discussing possible applications of this framework that should be regarded as a step in a parsimonious modelling strategy aiming at making community ecology quantitative and predictive science, in terms of quantities that can be measured experimentally.

2. Methods and materials

Solving Eq. (3) for a competition matrix which has all its off-diagonal terms equal to a (and the diagonal ones equal to 1),[1] we obtain:

$$y = \frac{1}{1 + (S-1)a}. \tag{5}$$

An estimation of a can be obtained either from the statistical sampling of pairwise experiments or from knowing the intensity of resource overlap among different species in a community competing for this (these) resource(s) (MacArthur and Levins, 1967). Therefore, we obtain an approximate expression for the relative yield total produced by the simplified competition matrix as a function of a and S:

$$RYT(a, S) \simeq \frac{S}{1 + (S-1)a}. \tag{6}$$

To test the approximated formula (6) for the RYT we searched for experiments that for a given community of S species, besides measuring the yields of

i) these S species in competition, Y_i (one treatment), also measured the yields of:
ii) species in isolation or monocultures K_i (in all or at least some of the S treatments) and of
iii) species in bicultures, B_i (in all or at least some of the S(S-1)/2 treatments).

i) & ii) serve to compute the relative yields y_i and from them, using (2), the RYT. From i) & iii) we compute the $b_i = B_i/K_i$ and, inverting (3) for $S = 2$, we can extract the competition coefficients for the pair of species i-j as

$$a_{ij} = (1 - b_i)/b_j, \quad a_{ji} = (1 - b_j)/b_i, \tag{7}$$

and then by taken their mean obtain a. There are lots of published experimental studies that measured all these quantities for $S = 2$, but the number decreases quickly as S grows. In fact, for $S > 8$ we couldn't find an experiment in which the totality of the $S(S+1)/2$ treatments was carried out but only a percentage f_e of the them (see Table 1). The proposed method aims at providing RYT precisely for cases in which $f_e < 100\%$, and thus we have incomplete information on model parameters. Therefore we took the mean $\overline{a_{i \neq j}}$ over the subset of pairwise experiments that were carried out (see next section).

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[1] That is, a kind of m̈ean fieldäpproximation −in the space of interaction parameters− for the competition matrix, *i.e.* all the off-diagonal interspecific interaction coefficients replaced by their mean value a.