

Comparing empirical methods measuring inter- and inter-specific interaction coefficient

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Introduction

Contemporary coexistence theory is established on Chesson's key insight toward the mutual invasibility criterion of the classic Lotka-Volterra competition model [3, 4, 5, 6, 1].

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{21} N_2) \quad (1)$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{12} N_1 - \alpha_{22} N_2) \quad (2)$$

In the classic Lotka-Volterra competition model, species are guaranteed to coexist when intra-specific interaction is greater than inter-specific interaction, i.e. $\alpha_{11} > \alpha_{12}$ and $\alpha_{22} > \alpha_{21}$. Chesson showed that this mutual invasibility criterion can be defined in terms that quantify the degree of niche overlap, ρ between species and their difference between their average fitness, $\frac{f_2}{f_1}$ (f_i is the same as the k_i in Chesson's original paper). Chesson defines niche overlap (ρ) as $\sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}}$. The relative fitness difference (RDF; $\frac{f_2}{f_1}$) is defined as $\frac{\alpha_{12}}{\alpha_{22}} \frac{1}{\rho}$; therefore $\frac{f_2}{f_1} = \sqrt{\frac{\alpha_{12}\alpha_{11}}{\alpha_{21}\alpha_{22}}}$.

From the above definition and deduction, the ratio of inter- specific to intra- specific competition coefficients is equal to the product of a niche overlap term (ρ) and a fitness ratio term ($\frac{f_2}{f_1}$)

$$\frac{\alpha_{12}}{\alpha_{22}} = \frac{f_2}{f_1} \rho \quad (3)$$

From the mutual invasibility criterion, we know that the right hand side of Eq. 2 must be < 1 for species 1 to be able to invade a population of species 2 at equilibrium. This is the same as saying $f_2/f_1 < 1/\rho$. By the same logic, for species 2 to be able to invade a population of species 1, $f_1/f_2 < 1/\rho$. Therefore, satisfaction of the mutual invasibility criterion, i.e., stable coexistence, requires

$$\rho < \frac{f_2}{f_1} < \frac{1}{\rho}. \quad (4)$$

Since both niche overlap term (ρ) and a fitness ratio term ($\frac{f_2}{f_1}$) depend on inter- and intra-specific interaction coefficient (α_{ii} and α_{ij}), estimation of α s is critical in assessing species coexistence. Conceptually, α_{ij} captures the *per capita* impact of species j on species i . Four empirical methods so far are proposed to estimate α_{ij} . These four methods include (1) Letten et al.'s method [9], (2) sensitivity method [2, 11], (3) negative frequency dependency (NFD) method [10, 8], and (4) calculating α by fitting growth curves to population dynamics. In this article I discuss if these four methods are actually estimating α s in the following generic Lotka-Volterra competition model.

1 Letten *et al.* 2017's method

Letten *et al.* 2017 reorganize the mechanistic consumer-resource model ([12]; equation 5 to 8) to a phenological Lotka-Volterra form so that one can decipher the parameters impacting species' *per capita* growth rate.

$$\frac{dN_1}{dt} = r_1 \frac{R_2}{R_2 + K_{12}} - DN_1 \quad (5)$$

$$\frac{dN_2}{dt} = r_2 \frac{R_1}{R_1 + K_{21}} - DN_2 \quad (6)$$

$$\frac{dR_1}{dt} = D(S_1 - R_1) - r_1 \frac{R_1}{(R_1 + K_{11})y_1 1} N_1 - r_2 \frac{R_1}{(R_1 + K_{21})y_2 1} N_2 \quad (7)$$

$$\frac{dR_2}{dt} = D(S_2 - R_2) - r_1 \frac{R_2}{(R_2 + K_{12})y_1 2} N_1 - r_2 \frac{R_2}{(R_2 + K_{22})y_2 2} N_2 \quad (8)$$

According to Letten *et al.* the inter- and intra-specific interaction coefficients can be expressed as following,

$$\alpha_{11} = \frac{C_{12}}{y_{21}D(S_2 - R_2^*)} \quad (9)$$

$$\alpha_{12} = \frac{C_{22}}{y_{22}D(S_2 - R_2^*)} \quad (10)$$

$$\alpha_{22} = \frac{C_{21}}{y_{12}D(S_1 - R_1^*)} \quad (11)$$

$$\alpha_{21} = \frac{C_{11}}{y_{11}D(S_1 - R_1^*)} \quad (12)$$

In the above equations, C_{ij} is the consumption of species i on resource j , D is the dilution rate, y_{ij} is the yield of species i per resource j , S_i is the supply rate of resource i , and R_i^* is the resource density at the equilibrium.

Note that the above consumption term (C_{ij}) is a function of resource density in the generic consumer-resource model, e.g. $C_{12} = \frac{r_1 R_2}{R_2 + K_{12}}$. However, if the consumption term is resource density dependent, this linkage would not hold. The linkage between consumer-resource model and Lotka-Volterra model only exist when all the consumption of species i on resource j are resource density independent. For example, Letten *et al.*'s predicted coexistence region will only match simulation results with empirical parameter values when letting C_{ij} equals to $\frac{D}{y_{ij}}$. That is to say, Letten *et al.*'s method only works in a special case of consumer-resource model.

2 Sensitivity method

The idea of using sensitivity is to estimate α_{ij} , i.e. the *per capita* impact of one species (j) on the other species (i), as the reduction of species i 's growth rate due to species j . The sensitivity is therefore defined as the proportional reduction in invading species' growth rate due to inter-specific competition [2]. Specifically, it is calculated by dividing the difference between *per capita* growth rate of species i when growing alone (μ_i) in monoculture and when invading species j (μ_{ij}) by the *per capita* growth rate of species i when growing alone i [2, 11]. The following equation is the definition of sensitivity of species i when invading species j .

$$S_{ij} \equiv \frac{\mu_i - \mu_{ij}}{\mu_i} \quad (13)$$

From the classic Lotka-Volterra competition model (equation 1 and 2), $\mu_i = r_i$ and $\mu_{ij} = r_i(1 - \alpha_{ij}N_j^*)$. Consequently,

$$S_{ij} \equiv \frac{\mu_i - \mu_{ij}}{\mu_i} = \frac{r_i - r_i(1 - \alpha_{ij}N_j^*)}{r_i} = \alpha_{ij}N_j^* \quad (14)$$

From equation 14, we see that sensitivity (S_{ij}) measures the overall population effect of species j on focal species i but not the "per capita" effect of species j . Small tweak should be implemented when using sensitivity method to estimate α .

In addition, when Carroll *et. al* 2011 used the sensitivity to predict coexistence, they defined the ND as the geometric mean of S_{ij} and RDF as the geometric standard deviation of S_{ij} . This makes intuitive sense because when species overlap their niche more, the larger the sensitivity (S_{ij}) should be. In addition, since geometric mean is more sensitive to changes near 0 than changes closer to 1, using geometric mean makes the ND more sensitive to species that are less responsive to competition (i.e. species has lower S_{ij}) so gives more weight to these species. However,

this definition does not have direct linkage to the Lotka-Volterra model. Surprisingly, defining ND and RFD as the geometric mean and standard deviation of sensitivity (S_{ij}) accurately predict the species coexistence.

3 Negative frequency dependency (NFD) method

This method is to investigate how the *per capita* growth rate of a focal species i would depend on the frequency (%) of focal species i in a community [1, 10, 8, 7]. The logic of this negative frequency dependency (NFD) method is to use the frequency of focal species (i), or one minus the frequency of competing species (j), to proxy the impact of the competing species (j). Lower frequency of the focal species (i) means the higher frequency and thus stronger impact of the competing species is. Accordingly, the dependency of focal species i 's *per capita* growth rate on the frequency is actually the "per %" impact of competing species j in the community on the *per capita* growth rate of a focal species i . The NFD is therefore not a proper measure of *per capita* impact of competing species on the *per capita* growth rate of focal species i .

Mathematically, the negative frequency dependency (NFD) cannot be readily derived from the Lotka-Volterra model without making any assumptions. In the Lotka-Volterra model, there is no term describing the frequency. The only way to make the *per capita* growth rate a function of the frequency of species i is to assume a one-to-one conversion between focal species i and the competing species j and a constant community density. By doing so, the Lotka-Volterra competition model can be rewritten as followed.

$$\frac{dN_i}{dt} = r_i N_i (1 - \alpha_{ii} N_i - \alpha_{ij} (1 - N_i)) \quad (15)$$

In equation 15, N_i becomes the frequency, not the density, of species i . To calculate the negative frequency dependency (NFD), we take derivative of equation 15 in terms of N_i .

$$NFD \equiv \frac{\partial \frac{dN_i}{dt}}{\partial N_i} = r_i (\alpha_{ij} - \alpha_{ii}) \quad (16)$$

From equation 16, the change of *per capita* growth rate of focal species i with respect to species i 's

frequency should be $r_i(\alpha_{ij} - \alpha_{ii})$ but not α_{ij} . In addition, this is the "per %", not the "*per capita*" impact of competing species j on the *per capita* growth rate of focal species i . Accordingly, NFD is not a proper measurement of α_{ij} . What is ever worse is that this derivation is founded on a strong assumption that the one individual increase of competing species j leads to one individual decrease of the focal species i and the community density is constant.

4 Fitting growth curve to the population dynamics

This method is probably the most straightforward. However, the caveat is that one must have a clean time series of species in mono-culture as well as in bi-culture. The efforts to obtain such time series is not trivial. Moreover, different species might need different growth curve model specification to fit the growth curve.

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