

Comparing empirical methods measuring intra- and inter-specific competition coefficients

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Introduction

1 The classic Lotka-Volterra model

In the classic Lotka-Volterra model, the *pre capita* growth rate of species i can be described by the following equation.

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i (1 - \alpha_{ii} N_i - \sum_{j \neq i} \alpha_{ij} N_j) \quad (1)$$

In the above equation, N_i and r_i are the density and the intrinsic growth rate of species i respectively. The α_{ii} is the intra-specific competition coefficient, which describes the *per capita* effect of species i on the *per capita* growth rate of species i . The α_{ij} is the inter-specific competition coefficient, which describes the *per capita* effect of species j on the *per capita* growth rate of species i . For any two species (e.g. i and j) to stably coexist, the mutual invasibility is the criteria must be met, which means the two species need to be able to invade the other one from rare, i.e. both species need to have positive invasion growth rate. For the two species to have positive invasion growth rate, the intra-specific competition coefficient must be greater than the inter-specific competition coefficient, i.e. $\alpha_{ii} > \alpha_{ij}$ and $\alpha_{jj} > \alpha_{ji}$.

To use the Lotka-Volterra model to predict coexistence for species i and j , one must first estimate six different parameters that are used in the Lotka-Volterra model: intrinsic growth rate of each species (r_i and r_j), intra-specific competition coefficients (α_{ii} and α_{jj}), and inter-specific competition coefficients (α_{ij} and α_{ji}). In theory, this could be accomplished using maximum likelihood method from a single co-culture time-series dataset, where both species are introduced at low density and allowed to grow to steady-state. However, in practice, it is difficult to parameterize all six variables from a single time-series. An alternative would be to use three independent dataset for each species pair: each species as a monoculture and one co-culture of the two species (Fig. 1). In addition, to have precise estimate of these coefficients, the time series would need to be clean

enough.

The Lotka-Volterra model assumes constant intra- and inter-specific competition coefficient with respect to population sizes and time - the first individual and the last individual have the same per-capita effect on the growth rates. While this assumption may not be realistic for all study systems, these parameters are exactly the same as used in Chesson's seminal paper and require no further assumptions before they can be used for compute niche difference (ND) and relative fitness difference (RFD).

2 Sensitivity method

Sensitivity method is another method proposed to measure niche difference (ND) and relative fitness difference (RFD) without specifically estimating the inter-specific competition coefficients ([7]). Instead, sensitivity method relies on the effect of inter-specific competition on the population dynamics. Sensitivity method is also based on the idea of mutual invasibility that species need to be able to invade its competitor(s) from rare in order to coexist. When invading its competitor(s), if a species has low invasion growth rate, this species is more affected by its competitor(s) so that this species' niche should overlap with its competitor(s) more. To quantify the effect of competitor(s) on the focal species i , sensitivity metric (S_i) compares the focal species i 's *per capita* growth rate when invading its competitor(s) versus the focal species i 's *per capita* growth rate when growing alone. The difference between the two growth rates is then the proxy of the effect of competitor(s) on the focal species i . Specifically, according to Carroll *et al.* 2011, sensitivity metric (S_i) is calculated by the following formula.

$$S_i \equiv \frac{\mu_i - \mu_{ij}}{\mu_i} \quad (2)$$

In equation 2, μ_i is the *per capita* growth rate of species i when growing alone and μ_{ij} is the *per capita* growth rate of species i when its competitor(s) (species j) is at its carrying capacity. To use sensitivity (S_i) to calculate niche difference (ND) and relative fitness difference (RFD) and predict coexistence, Carroll *et al.* argued that ND can be defined as the geometric mean of sensitivity metrics and RFD can be defined as the geometric standard deviation of sensitivity metrics.

However, although sensitivity method is a general procedure and is not restricted to a specific competition model, it only intuitively connects species competition and population dynamics. Moreover, there is no rigorous proof of why ND and RFD can be defined as the geometric mean

and standard deviation of sensitivity metrics (S_i). Here we argue that sensitivity metric is not just an intuitive connection but actually describes the impact of entire competitor(s) population on the focal species i . In addition, defining ND and RFD as the geometric mean and standard deviation of sensitivity metrics is valid theoretically.

In equation 2, the reduction of species i 's *per capita* growth rate, i.e. the nominator, is actually caused by the entire population of the other species j because the invasion growth rate (μ_{ij}) is measured when the other species j is at the carrying capacity. Accordingly, the sensitivity (S_i) measures the "population" impact of species j , but not the *per capita* impact of species j on the focal species i . To show that sensitivity is actually the population level impacts, not the *per capita* level, we derive the sensitivity (S_i) from the classic Lotka-Volterra competition model (equation 1). The μ_i is therefore r_i and μ_{ij} is $r_i(1 - \alpha_{ij}N_j^*)$. Accordingly,

$$S_i \equiv \frac{\mu_i - \mu_{ij}}{\mu_i} = \frac{r_i - r_i(1 - \alpha_{ij}N_j^*)}{r_i} = \alpha_{ij}N_j^* \quad (3)$$

From equation 3, we see that sensitivity (S_i) is the equilibrium density of species j (N_j^*) times the *per capita* competition coefficient (α_{ij}). The sensitivity thus is a measurement of 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 the sensitivity method to estimate *per capita* inter-specific competition coefficients (α_{ij}).

Secondly, we show that geometric mean and standard deviation of sensitivity metrics are theoretical valid definitions of niche difference (ND) and relative fitness difference (RFD). In the Lotka-Volterra model, species' density at the equilibrium (N_i^*) is actually $\frac{1}{\alpha_{ii}}$. Therefore, sensitivity (S_i) can be expressed as $\frac{\alpha_{ij}}{\alpha_{jj}}$, which represents the inter-specific competition scaled on intra-specific competition coefficient. According to Chesson (1990), niche overlap (ρ) is defined as $\sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}}$. $\sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}}$ can then be expressed as $\sqrt{S_i S_j}$, which is the geometric mean of sensitivity $S - i$ and S_j .

The niche difference (ND) is therefore $1 - \rho = 1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} = 1 - \sqrt{S_i S_j}$. In addition, $\sqrt{\frac{S_i}{S_j}} = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}}$, and $\sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}}$ is the definition of the inverse of relative fitness difference of species j over species i (RFD; $\frac{k_j}{k_i}$ in Chesson 1990).

With the above derivation, we can also derive a coexistence criteria using the sensitivity metric. From the Lotka-Volterra model model, intra-specific competition (α_{ii}) must be greater than the inter-specific competition (α_{ij}) to guarantee stable coexistence. Therefore we can have the following deduction.

$$\frac{\alpha_{ij}}{\alpha_{jj}} = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}} \times \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} = \sqrt{\frac{S_i}{S_j}} \times \rho < 1, \text{ so } \sqrt{\frac{S_i}{S_j}} < \frac{1}{\rho} \quad (4)$$

$$\frac{\alpha_{ii}}{\alpha_{ji}} = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}} \times \sqrt{\frac{\alpha_{ii}\alpha_{jj}}{\alpha_{ij}\alpha_{ji}}} = \sqrt{\frac{S_i}{S_j}} \times \rho < 1, \text{ so } \sqrt{\frac{S_i}{S_j}} > \rho \quad (5)$$

Combining equation 4 and 5, we have an inequality for coexistence expressed with sensitivity metrics, $\rho < \sqrt{\frac{S_i}{S_j}} < \frac{1}{\rho}$, which is in the same form as in Chesson's coexistence framework.

3 Frequency dependency (FD) method

The frequency dependency (FD) method [5, 6, 8, 9] is also derived from the same logic that intra-specific competition coefficient must be greater than the inter-specific competition coefficient for stable coexistence. The rationale of FD is to measure how the *per capita* growth rate of a focal species i would be affected by the increase of its own the frequency (%) in a community. If the intra-specific competition coefficient is not greater than the inter-specific competition coefficient, i.e. the focal species i is more limited by its competitor(s) than by itself, increasing relative frequency of focal species i release itself from the stronger impacts form its competitor(s). In this case, no or even positive frequency dependency would be observed because *per capita* growth rate of the focal species i does not negatively depends on its own frequency. On the other hand, if the intra-specific competition coefficient is greater than the inter-specific competition coefficient, i.e. the focal species i limits itself more than it limits its competitor(s), increasing relative frequency of the focal species i will decrease its own *per capita* growth rate. In this case, frequency dependency is negative because *per capita* growth rate of a focal species i negatively depends on its own frequency. Given this rationale, as long as a species limits itself more than it limits its competitor(s), negative frequency dependency can be expected but the magnitude of the dependency (the slope) is not equivalent to either intra- or inter-specific competition coefficients [5]. When calculating frequency dependency (FD), the *per capita* growth rate is being plotted against the frequency of the focal species, so it is actually the "per %" impact on the *per capita* growth rate. The NFD is therefore not equivalent but related to the competition coefficients in the Lotka-Volterra model.

To show that FD can not be used directly to measure of competition coefficients, we attempt to derive the FD from the Lotka-Volterra model again. We found that, the frequency dependency (FD) cannot be readily derived from the Lotka-Volterra model without making further assumptions. In fact, in Adler (et al.) already pointed out that frequency dependency and density dependency,

which is modeled by α in the Lotka-Volterra model, are interchangeable only when the community density is fixed. In the Lotka-Volterra model, there is no term describing the frequency of species. The only way to make the *per capita* growth rate a function of the frequency of species i is to assume a fixed total community density and one-to-one conversion between the focal species i and the competing species j . By doing so, the Lotka-Volterra competition model can be rewritten as followed.

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i (1 - \alpha_{ii} N_i - \sum_{j \neq i} \alpha_{ij} (B - N_i)) \quad (6)$$

In equation 6, B is the fixed community density and one unit decrease of N_i will lead to one unit increase of N_j . Note that this B is an arbitrarily defined constant describing a fixed community density and has nothing do to with the equilibrium of any of the species. To calculate the frequency dependency (FD), we take derivative of equation 6 in terms of N_i/B .

$$FD \equiv \frac{\partial \frac{1}{N_i} \frac{dN_i}{dt}}{\partial \frac{N_i}{B}} = \frac{\partial \frac{1}{N_i} \frac{dN_i}{dt}}{\frac{1}{B} \partial N_i} = B \frac{\partial \frac{1}{N_i} \frac{dN_i}{dt}}{\partial N_i} = Br_i (\alpha_{ij} - \alpha_{ii}) \quad (7)$$

This equation 7 describe the change of species i 's *per capita* growth rate with respect to the change of its own frequency in a community (Fig. 3). From equation 7 or figure 3, the FD depends on a combination of *per capita* growth rate (r_i) and the fixed community density (B) in addition to the intra- and inter-specific competition coefficients. From this equation, we first see that FD is negative as long as the intra-specific competition (α_{ii}) is greater than the inter-specific competition (α_{ij}). Additionally, higher *per capita* growth rate of a species and higher community density (e.g. in the later more mature stage of the community) would lead one to estimate stronger frequency dependency. Most importantly, FD cannot readily be used to calculate competition coefficients and then the ND and RFD to predict species coexistence.

4 MacArthur's consumer resource model

In 1970, MacArthur proposed a consumer resource model to describe how species compete for different resources ([2]). This model has been reorganized into Lotka-Volterra form many times to understand the rather phonological competition coefficients (α_{ij}) more closely ([1, 2, 4, 7]). After the reorganization shown in [4], the following equation represent the linkage between α_{ij} in the Lotka-Volterra model and the parameters of MacArthur's consumer resource model.

$$\alpha_{ij} = \sum_l c_{il} c_{jl} \frac{w_l K_l}{r_l} \quad (8)$$

$$f_i = \sum_l c_{il} w_l K_l - m_i \quad (9)$$

In equation 8 to 9, c_{ij} and c_{ij} are the consumption of species i and j on resource l respectively; m_i is the mortality of species i ; w_i is the value of one unit of resource l to the species; r_l and K_l are the per capita growth rate and carrying capacity of resource l . The contemporary coexistence framework (the idea of niche difference and relative fitness difference) developed by Chesson is founded on this linkage between MacArthur's consumer resource model and Lotka-Volterra model.

The modern coexistence theory is established on Chesson's key insight toward the mutual invasibility criteria for stable coexistence in the classic Lotka-Volterra competition model ([4]). Chesson showed that the mutual invasibility criteria i.e. $\alpha_{ii} > \alpha_{ij}$ and $\alpha_{jj} > \alpha_{ji}$, can be expressed in a different fashion. First, Chesson defined the niche overlap (ρ) as $\sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}}$ to describe how similar the two competing species are in terms of using resources (Fig. 4). The niche difference (ND) is thus $1 - \rho$. Second, Chesson defined relative fitness difference (RDF; $\frac{f_j}{f_i}$, the f_i is the same as the k_i in Chesson 1990) as $\frac{\alpha_{ij}}{\alpha_{jj}} \frac{1}{\rho} = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}}$ to describe which species should exclude the other one if they completely overlap their resource use. Accordingly, the product of ρ and RFD is the ratio of inter-

specific to intra-specific competition coefficients, i.e. $\frac{\alpha_{ij}}{\alpha_{jj}} = \frac{f_j}{f_i} \rho$. When intra-specific competition of species j is greater than inter-specific competition of species i ($\alpha_{jj} > \alpha_{ji}$), $\frac{\alpha_{ij}}{\alpha_{jj}} = \frac{f_j}{f_i} \rho < 1$ so that $\frac{f_j}{f_i} < \frac{1}{\rho}$. By the same logic, when intra-specific competition of species i is greater than inter-specific competition of species j ($\alpha_{ii} > \alpha_{ij}$), $\frac{f_i}{f_j} < \frac{1}{\rho}$. Consequently, the mutual invasibility criteria for stable coexistence can be rewritten as the following inequality.

$$\rho < \frac{f_2}{f_1} < \frac{1}{\rho}. \quad (10)$$

5 Tilman's resource ratio consumer resource model

Letten *et al.* 2017 reorganize Tilman's consumer resource model ([3]) to the following Lotka-Volterra form (equation 11 to 14), so that one can decipher the parameters impacting species' *per capita* growth rate.

$$\frac{dN_1}{dt} = r_1 \frac{R_2}{R_2 + K_{12}} - DN_1 \quad (11)$$

$$\frac{dN_2}{dt} = r_2 \frac{R_1}{R_1 + K_{21}} - DN_2 \quad (12)$$

$$\frac{dR_1}{dt} = D(S_1 - R_1) - r_1 \frac{R_1}{(R_1 + K_{11})y_1 1} N_1 - r_2 \frac{R_1}{(R_1 + K_{21})y_2 1} N_2 \quad (13)$$

$$\frac{dR_2}{dt} = D(S_2 - R_2) - r_1 \frac{R_2}{(R_2 + K_{12})y_1 2} N_1 - r_2 \frac{R_2}{(R_2 + K_{22})y_2 2} N_2 \quad (14)$$

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

$$\alpha_{11} = \frac{c_{12}}{D(S_2 - R_2^*)} \quad (15)$$

$$\alpha_{12} = \frac{c_{22}}{D(S_2 - R_2^*)} \quad (16)$$

$$\alpha_{22} = \frac{c_{21}}{D(S_1 - R_1^*)} \quad (17)$$

$$\alpha_{21} = \frac{c_{11}}{D(S_1 - R_1^*)} \quad (18)$$

In the above equations, c_{ij} is the consumption of consumer species i on resource j , D is the dilution rate, y_{ij} is the yield of consumer 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, in the generic consumer resource model, the above consumption term (c_{ij}) is a function of resource density, e.g. $c_{12} = \frac{r_1 R_2}{y_{21}(R_2 + K_{12})}$ in Tilman's 1977 deduction. However, if the consumption term is resource density dependent, competition coefficients (α_{ij}) becomes resource dependent as well. Although the competition coefficients (α_{ij}) are not fixed values as in the Lotka-Volterra model, Letten *et al.*'s derivation can still be used to predict coexistence at the equilibrium. To use equation 11 to 14 to calculate competition coefficients for predicting coexistence at the equilibrium, one would have to assume that the consumption of species i on resource j is evaluated at the equilibrium. For example, when at equilibrium, consumer's consumption (C_{ij}) should be equal to the dilution rate (D) divided by the yield of consumer (y_{ij}). In another words, the α_{ij} describes impact of species j on the *per capita* growth rate of species i when the resource that limits species j is at the equilibrium, i.e. at the R^* level. This assumption is the same as the sensitivity method since both method are based on the mutual invasibility criteria for stable coexistence. This assumption is also valid because the mutual invasibility criteria is the logical basis for coexistence.

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Figures

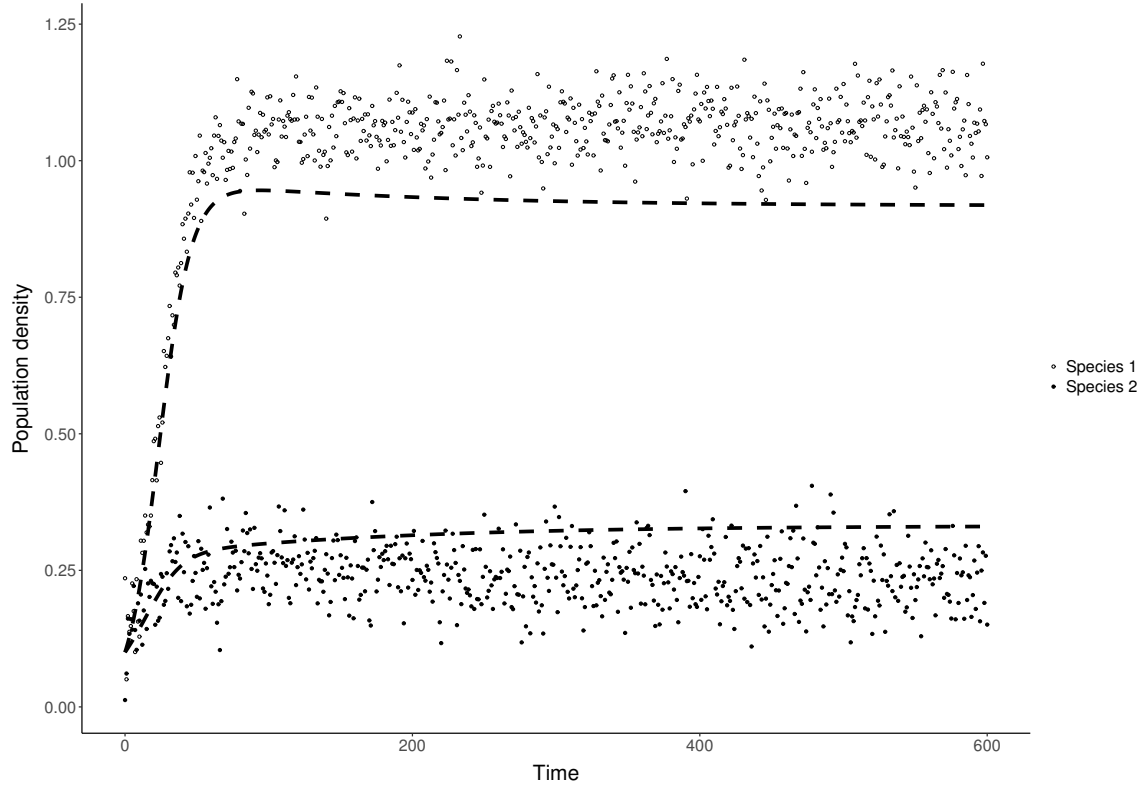


Figure 1: An example plot showing the estimation of α_{ij} from fitting Lotka-Volterra model to time series. The points represent the density of species i (open circles) and j (solid dots) respectively. The dashed lines are the two fitted growth curve. The species densities were generated by a Lotka-Volterra model and added some random noise. The parameters used in the Lotka-Volterra model are that $r_1 = 0.1$, $r_2 = 0.05$, $\alpha_{11} = 0.8$, $\alpha_{12} = \alpha_{21} = 0.6$, $\alpha_{22} = 1.5$. The random noise are from a normal distribution with mean equals to 0 and standard deviation equals to 0.05. The fitted parameters are that $r_1 = 0.099$, $r_2 = 0.043$, $\alpha_{11} = 0.808$, $\alpha_{12} = 0.577$, $\alpha_{21} = 0.720$, $\alpha_{22} = 0.974$.

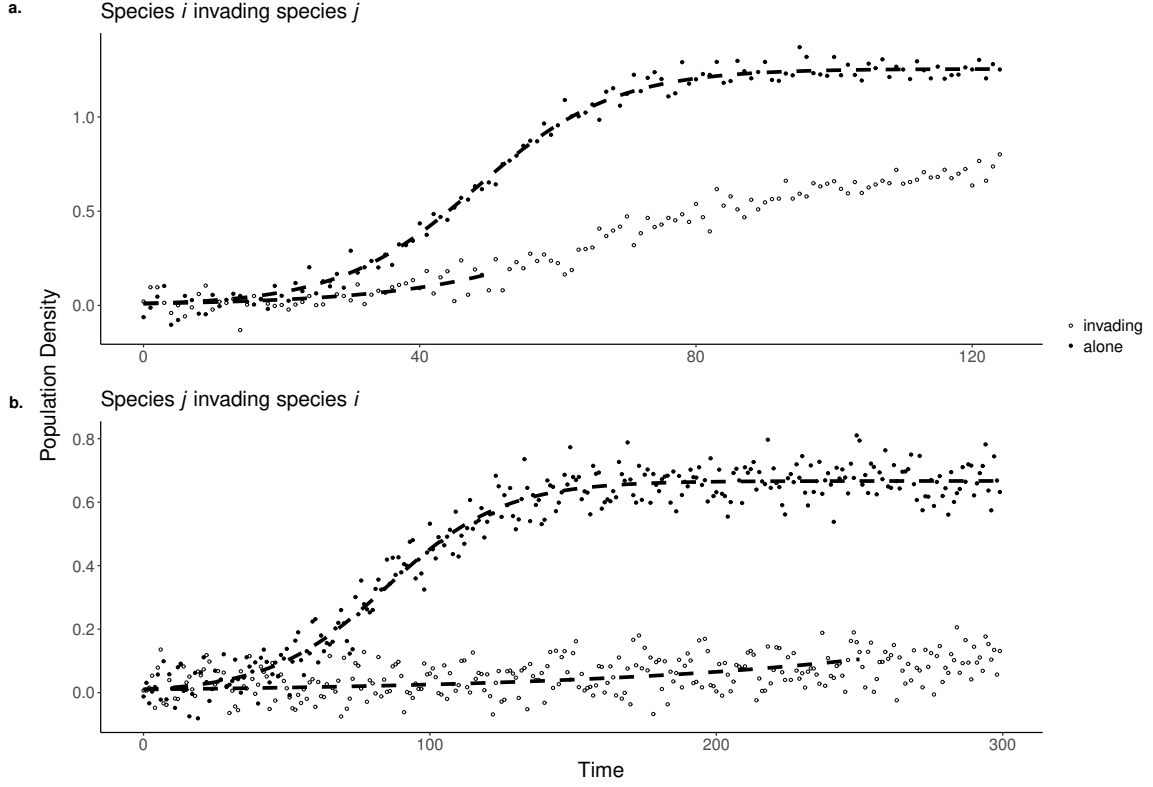


Figure 2: An example plot showing the estimation of sensitivity (S_{ij}) of species i invading species j (panel a.) or the reverse (panel b.). In both panels, solid dots are the growth curve species when growing alone and the open circles are the growth curve of species when invading the carrying capacity of the other species. These data is generated from the same Lotka-Volterra model as in figure 1. To estimate the sensitivity of the focal species (e.g. species i), the competing species (species j) is fixed at the equilibrium and invade the focus species to estimate the invading growth rate of the focal species. Using the sensitivity method, the α_{12} is estimated to be 0.686 and α_{21} is estimated to be 0.652, which is close to the predetermined inter-specific competition coefficients ($\alpha_{12} = \alpha_{21} = 0.6$).

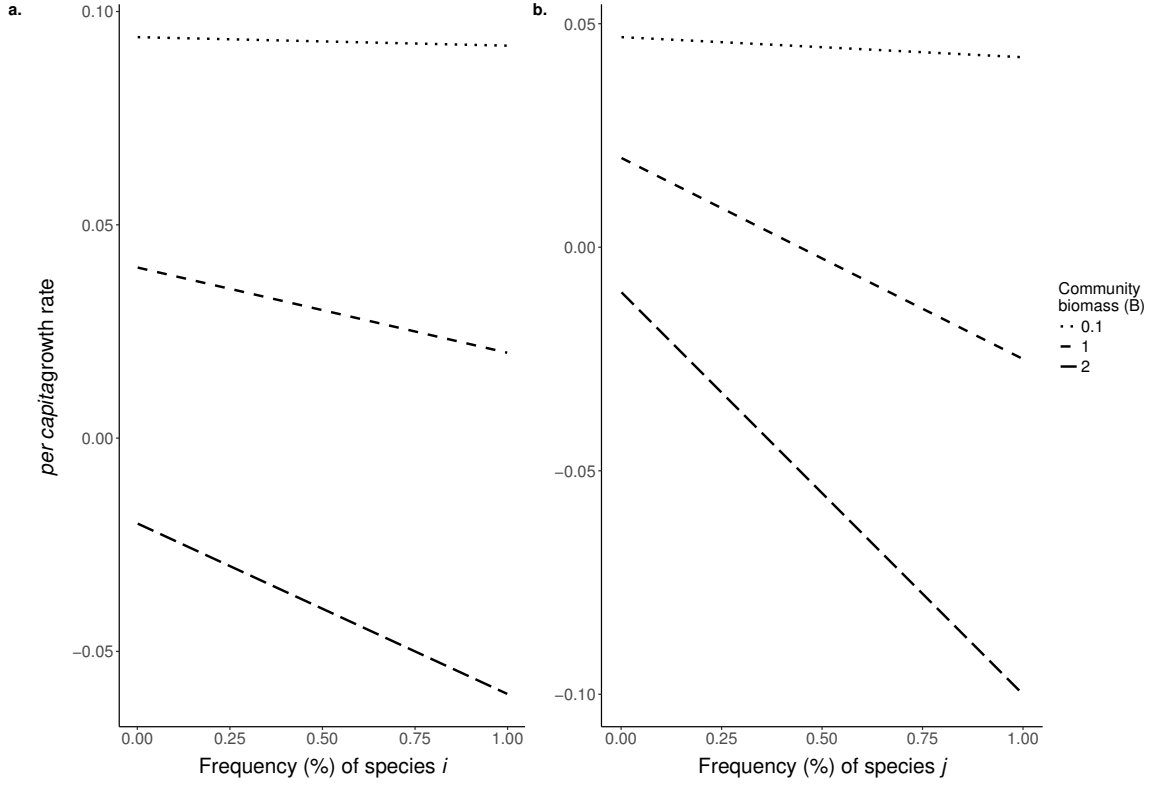


Figure 3: An example plot showing the negative frequency dependency (NFD) of species i (panel a.) and species j (panel b.). To calculate NFD, we first determined an arbitrary community biomass (B) and gradually increased the frequency of the focal species (species i in panel a. and species j in panel b.) to calculate the *per capita* growth rate of the focal species. Note that we directly calculated the *per capita* growth rate from equations of the Lotka-Volterra model not from numerical simulations. As the figure shows, the NFD depends on the arbitrarily community biomass (B). The resulting NFDs (slopes) match that are expected by equation 7. For example, when community biomass is 1 (dashed line in the middle), NFD of species i is -0.02 and NFD of species j is -0.045. This slope is far away from the predetermined α s ($\alpha_{12}=0.8$, $\alpha_{12} = \alpha_{21} = 0.6$, and $\alpha_{22} = 1.5$).

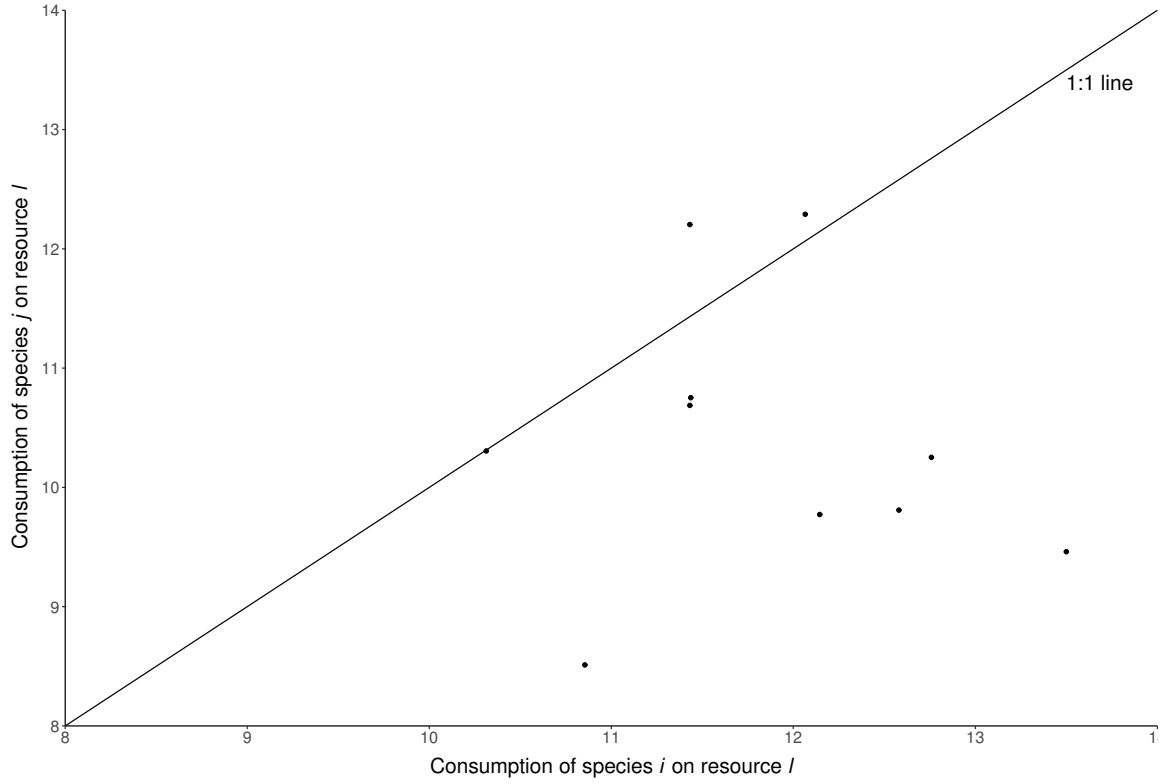


Figure 4: An example plot demonstrating the idea of niche difference (ND; ρ) in MacArthur's consumer resource model. Consumption of species j on resource l (c_{jl}) are plotted against consumption of species i on resource l (c_{il}). The closeness between c_{jl} and c_{il} are the closeness between these points to the 1:1 line and is expressed as ρ . For example, if all c_{jl} are equal to c_{il} , which means all points are on the 1:1 line, ρ is 1 and ND between species i and species j is $1 - \rho = 0$.

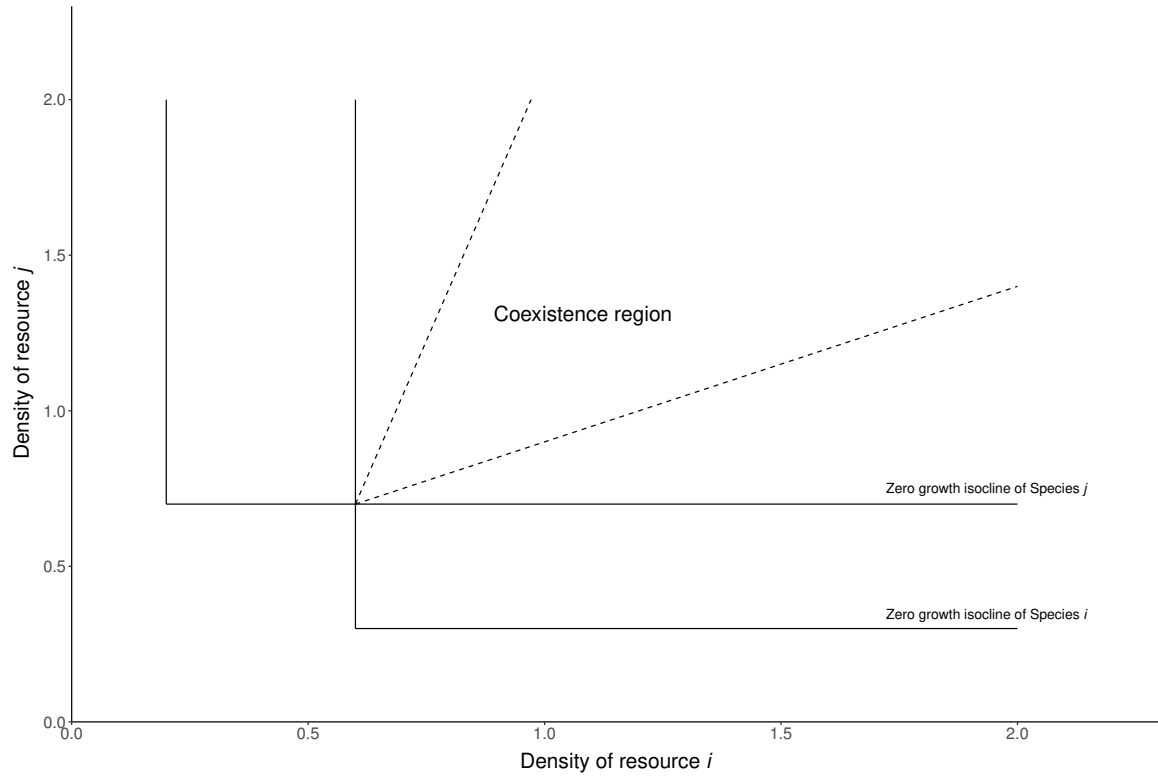


Figure 5: An classic example plot demonstrating the idea of Tilman's consumer resource model that founded the resource ratio theory. This plot shows the case of two essential resources case. The Two right angle lines are the zero growth isocline of species i and j . The two dashed lines are the consumption vector of the two species, so that the two species can only coexist when resource supply rate are in this coexistence region.