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

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Introduction

We five fluctuation independent methods proposed to evaluate whether species can coexist.

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.

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

In the model, N_i is the density of species i, r_i is the intrinsic growth rate. 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 the two species to stably coexist, the intra-specific competition coefficient must be greater than the inter-specific competition coefficient, i.e. $\alpha_{ii} > \alpha_{ij}$.

To use this model to predict species coexistence, one must have a clean enough time series of population density to estimate the competition coefficients (Fig. 1). The effort to obtain such time series is not trivial. In addition, fitting parameters is also not easy.

2 Sensitivity method

Following the same logic that intra-specific competition coefficient must be greater than the inter-specific one to guarantee stable coexistence, the sensitivity method is proposed [7]. The idea of sensitivity method is to estimate the reduction of species i's *per capita* growth rate due to the existence of the other species (Fig. 2). This reduction is the impact of the other species on species i's *per capita* growth rate, which is the meaning of inter-specific competition coefficient (α_{ij}). Specifically, according to Carroll *et al.* 2011, sensitivity is calculated by the following formula.

$$S_{ij} \equiv \frac{\mu_i - \mu_{ij}}{\mu_i} \tag{2}$$

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 the other species j is at its carrying capacity. Since μ_{ij} is measured when the other species j is at the carrying capacity, 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. Accordingly, the sensitivity measures the "population" impact of species j, but not the *per capita* impact of species j.

To show that sensitivity is actually the population level, not the *per capita*, impact, we derive the sensitivity (S_{ij}) from the classic Lotka-Volterra competition model (equation 1). The μ_i is then r_i and μ_{ij} is $r_i(1 - \alpha_{ij}N_j^*)$. Consequently,

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

From equation 3, we see clearly 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 the sensitivity method to estimate αs.

However, sensitivity (S_{ij}) is not being used as αs directly. When Carroll *et. al* used the sensitivity (S_{ij}) to calculated niche difference (ND), relative fitness difference (RDF) and eventually predict species 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 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. This definition does not have direct linkage to the Lotka-Volterra model or any mathematical deduction. 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

The negative frequency dependency (NFD) method [5] 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 NFD is thus to measure how the *per capita* growth rate of a focal species i would reduce with the increase of the frequency (%) of the other species (j) in a community. This reduction is the impact of the other competing species j on the *per capita* growth rate of species i. However, when calculating the NFD, increase of the other species j' frequency is being represented by the decrease of focal species i's own frequency [5, 6, 8, 9]. Lower frequency of the focal species (i) means the higher frequency and thus stronger impact of the competing species j. Accordingly, the dependency of focal species i's *per capita* growth rate on its 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.

Again, to show that NFD is not a proper measurement of inter-specific competition coefficient, we attempt to derive the NFD from the Lotka-Volterra model again. We found that, the negative frequency dependency (NFD) cannot be readily derived from the Lotka-Volterra model without making further assumptions. 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 Lokta-Volterra competition model can be rewritten as followed.

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i(1 - \alpha_{ii}N_i - \sum_{j\neq i}\alpha_{ij}(B - N_i)) \tag{4}$$

In equation 4, 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 negative frequency dependency (NFD), we take derivative of equation 4 in terms of N_i/B.

$$NFD \equiv \frac{\partial \frac{1}{N_i} \frac{dN_i}{dt}}{\partial \frac{N_i}{B}} = \frac{\partial \frac{1}{N_i} \frac{dN_i}{dt}}{\frac{1}{B} \partial N_i} = B \frac{\partial \frac{1}{N_i} \frac{dN_i}{dt}}{\partial N_i} = B r_i (\alpha_{ij} - \alpha_{ii}) \tag{5}$$

This equation 5 describe the change of species i's *per capita* growth rate with respective to the change of its own frequency in a community (Fig. 3). From equation 5 or figure 3, the NFD 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. This means 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. In addition, NFD cannot readily be used to calculate ND and RFD and predict species coexistence. What is even worse is that negative frequency dependency method 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 that the community density is fixed at some arbitrary level.

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 Lokta-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 Lottka-Volterra model and the parameters of MacArthur's consumer resource model.

$$\alpha_{ij} = \sum_l c_{il} c_{jl} \frac{w_l K_l}{r_l} \tag{6}$$

$$f_i = \sum_l c_{il} w_l K_l - m_i \tag{7}$$

In equation 6 to 7, 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. Chesson defined the similarity of species's consumption rates on each resource as the niche closeness of the two species (ρ; Fig. 4), so that niche difference (ND) is $1 - \rho$. Chesson then showed that ρ can be expressed as $\sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}}$. Accordingly, $\frac{f_j}{f_i}$ can be expressed as $\frac{\alpha_{ij}}{\alpha_{jj}}\frac{1}{\rho} = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{ji}\alpha_{jj}}}$ and is defined as the relative fitness difference (RDF). f_i here is the same as the k_i in Chesson 1990. Because species can stable coexist if and only if intra-specific competition (α_{ii}) is greater than the inter-specific competition (α_{ij}), we can derive the following coexistence criterion.

$$\rho < \frac{f_2}{f_1} < \frac{1}{\rho}. \tag{8}$$

5 Tilman's resource ratio consumer resource model

Letten *et al.* 2017 reorganize Tilman's consumer resource model ([3]) to the following Lokta-Volterra form (equation 9 to 12), so that one can decipher the parameters impacting species' *per capita* growth rate.

$$\frac{dN_1}{dt} = r_1 \frac{R_2}{R_2 + K_{12}} - DN_1 \tag{9}$$

$$\frac{dN_2}{dt} = r_2 \frac{R_1}{R_1 + K_{21}} - DN_2 \tag{10}$$

$$\frac{dR_1}{dt} = D(S_1 - R_1) - r_1 \frac{R_1}{(R_1 + K_{11})y_11} N_1 - r_2 \frac{R_1}{(R_1 + K_{21})y_21} N_2 \tag{11}$$

$$\frac{dR_2}{dt} = D(S_2 - R_2) - r_1 \frac{R_2}{(R_2 + K_{12})y_12} N_1 - r_2 \frac{R_2}{(R_2 + K_{22})y_22} N_2 \tag{12}$$

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

$$\alpha_{11} = \frac{c_{12}}{y_{21}D(S_2 - R_2^*)} \tag{13}$$

$$\alpha_{12} = \frac{c_{22}}{y_{22}D(S_2 - R_2^*)} \tag{14}$$

$$\alpha_{22} = \frac{c_{21}}{y_{12}D(S_1 - R_1^*)} \tag{15}$$

$$\alpha_{21} = \frac{c_{11}}{y_{11}D(S_1 - R_1^*)} \tag{16}$$

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. $c_{12} = \frac{r_1 R_2}{R_2 + K_{12}}$ in Tilman's 1977 deduction. However, if the consumption term is resource density dependent, competition coefficients (α_{ij}) becomes resource dependent as well. In such generic case, the linkage between Tilman's consumer resource model and Lotka-Volterra model made by Letten *et al.* 2017 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 evaluated at the equilibrium where resource density is fixed. For example, when at equilibrium, consumer's consumption (C_{ij}) should be equal to the dilution rate (D) divided by the yield of consumer (C_{ij}). Figure 5 shows the zero growth isocline of consumption rate of the two competing species and their consumption rate (dashed lines) on two essential resources. In this case, coexistence region predicted by Letten *et al.* 2017 will match the simulated results with empirical parameter values. Letten *et al.*'s method only works in the equilibrium of Tilman's consumer resource model. Consequently, when using parameters from Tilman's consumer resource model to calculate competition coefficients (α_{ij}) and make coexistence prediction, one will need to make an assumption that the system is at the equilibrium.

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Figures
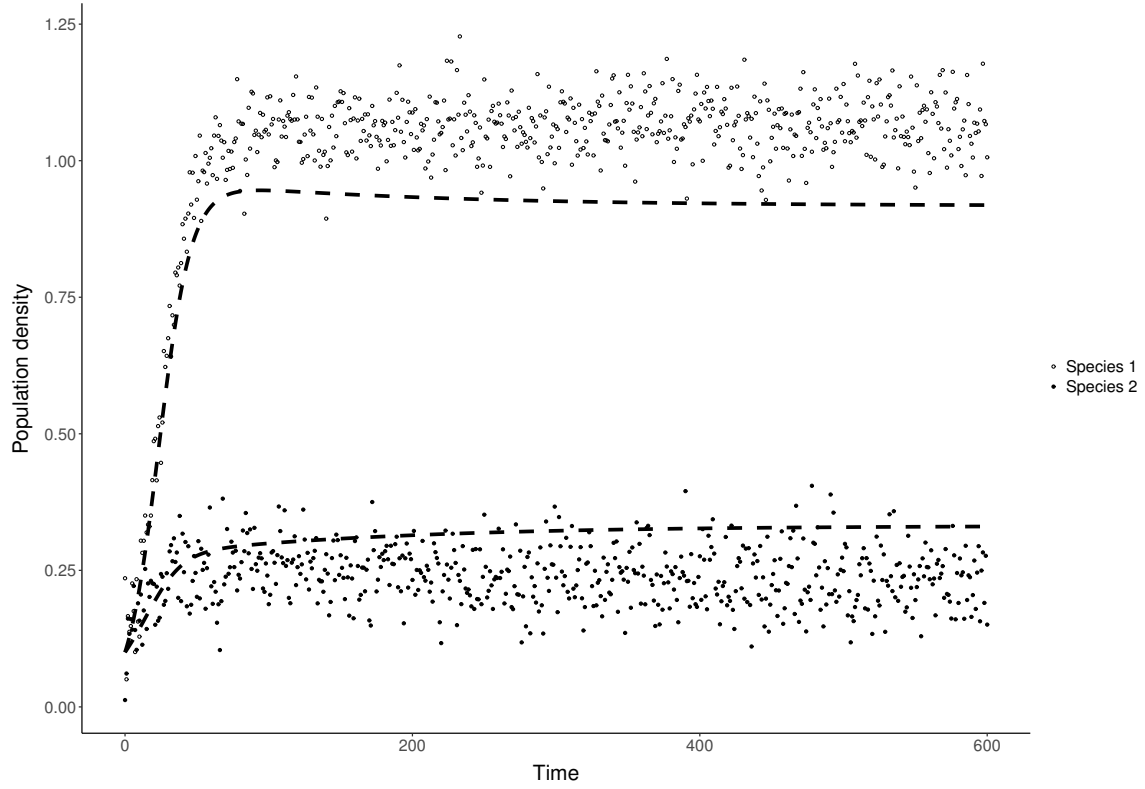
Figure 1: An example plot showing the estimation of α_{ij} from fitting Lotka-Volterra model to time series. The points represent the density of species i (open circles) and j (solid dots) respectively. The dashed lines are the two fitted growth curve. The species densities were generated by a Lotka-Volterra model and added some random noise. The parameters used in the Lotka-Volterra model are that $r_1 = 0.1$, $r_1 = 0.05$, $\alpha_{11} = 0.8$, $\alpha_{12} = \alpha_{21} = 0.6$, $\alpha_{22} = 1.5$. 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 $r_1 = 0.099$, $r_1 = 0.043$, $\alpha_{11} = 0.808$, $\alpha_{12} = 0.577$, $\alpha_{21} = 0.720$, $\alpha_{22} = 0.974$.
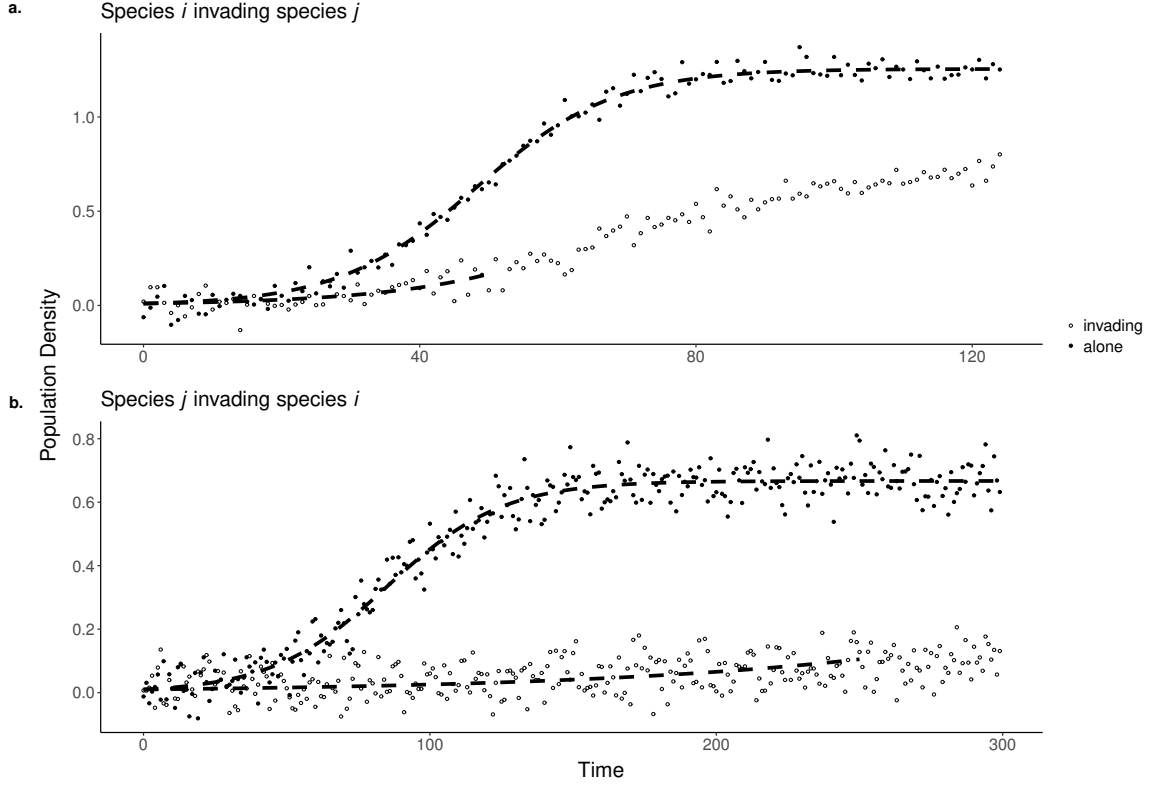
Figure 2: An example plot showing the estimation of sensitivity (S_{ij}) of species i invading species j (panel a.) or the reverse (panel b.). In both panels, solid dots are the growth curve species when growing alone and the open circles are the growth curve of species when invading the carrying capacity 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. s 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 $(\alpha_{12} = \alpha_{21} = 0.6)$.
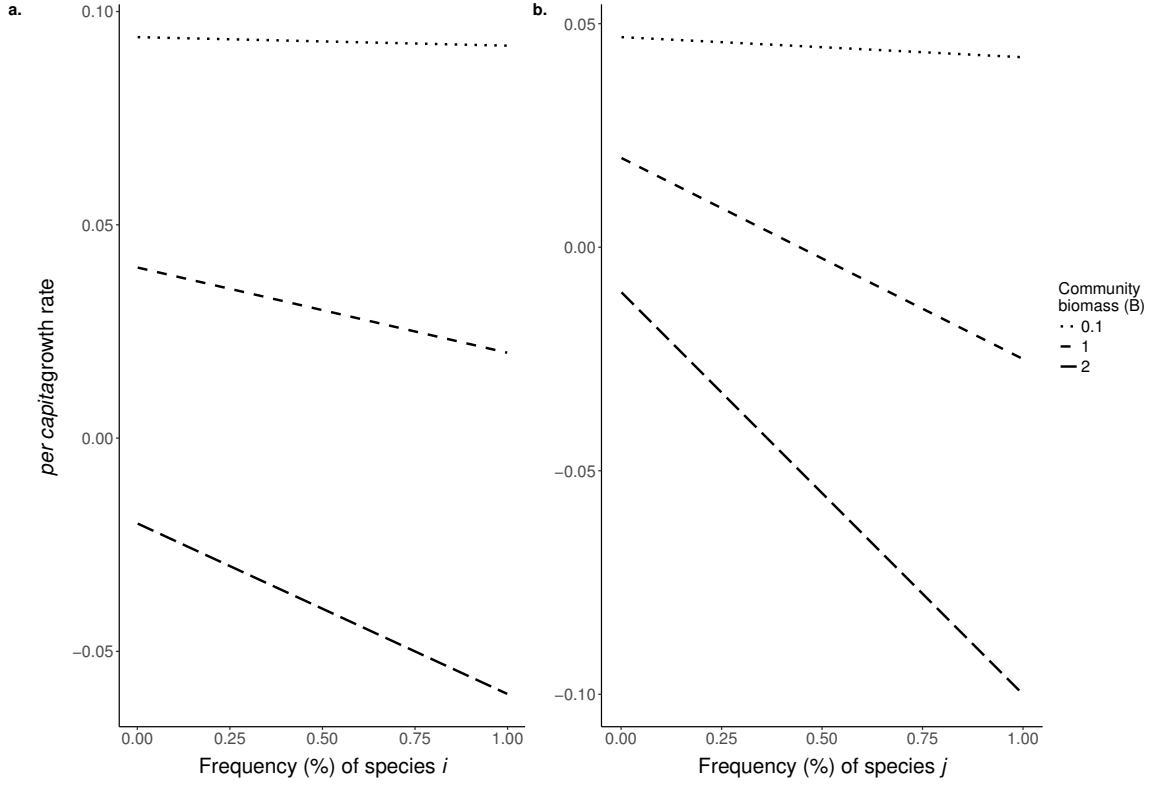
Figure 3: An example plot showing the negative frequency dependency (NFD) of species i (panel a.) and species j (panel b.). To calculate NFD, we first determined an arbitrary community biomass (B) and gradually increased the frequency of the focal species (species i in panel a. and species j in panel 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 5. For example, when communiby 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 αs (α_{12}=0.8, $\alpha_{12} = \alpha_{21} = 0.6$, and $\alpha_{22} = 1.5$).
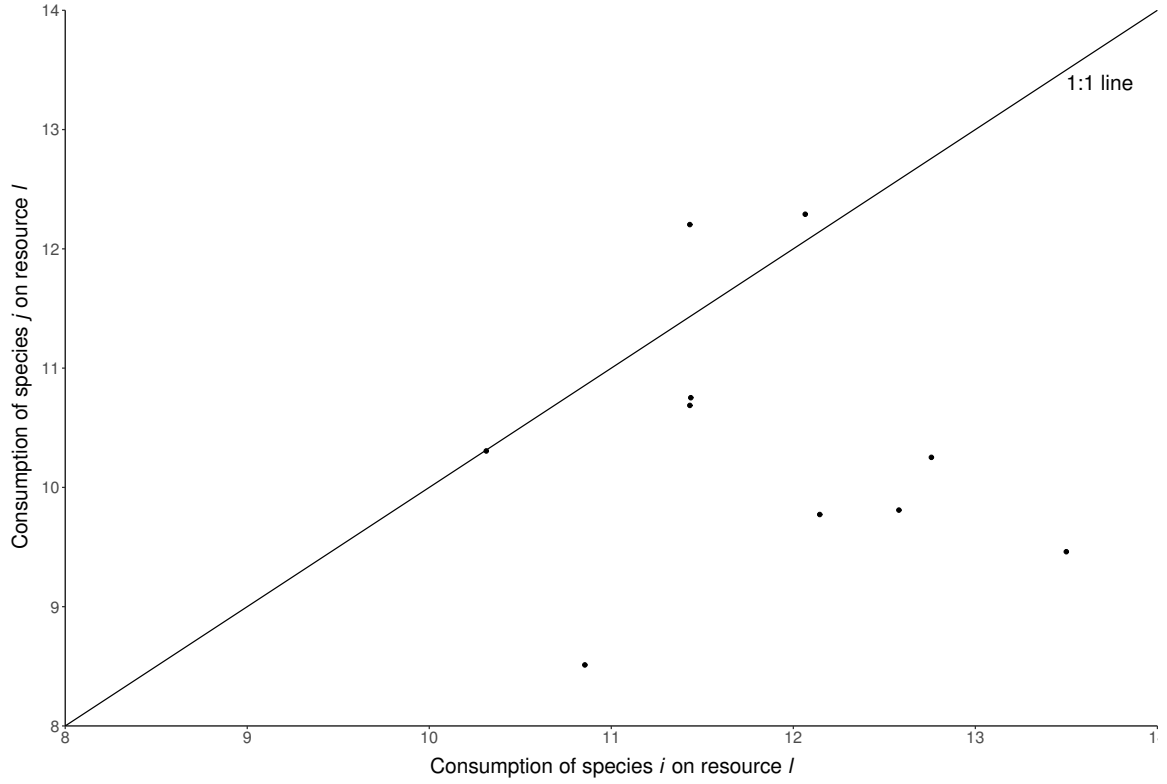
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Figure 4: An example plot demonstrating the idea of niche difference (ND; ρ) in MacArthur's consumer resource model. Consumption of species j on resource l (c_{jl}) are plotted against consumption of species i on resource l (c_{il}). The closeness between c_{jl} and c_{jl} 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 $1 - \rho = 0$.
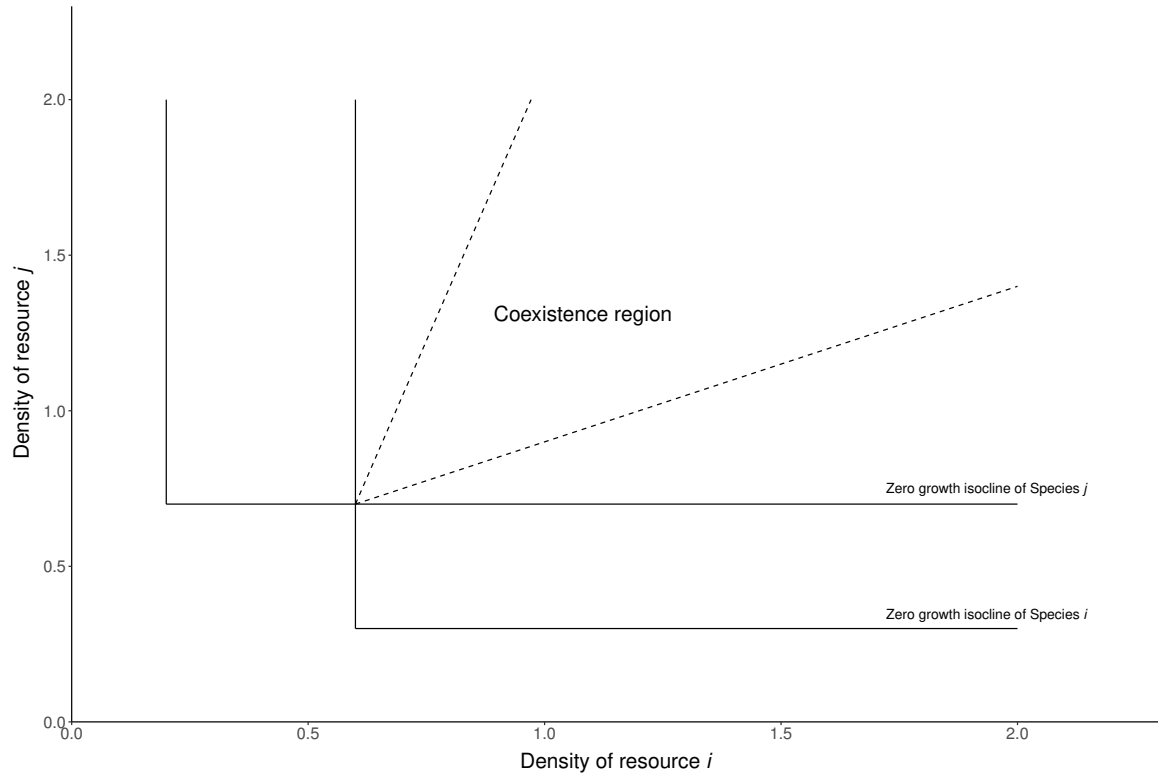
Figure 5: An classic example plot demonstrating the idea of Tilman's consumer resource model that founded the resource ratio theory. This plot shows the case of two essential resources case. The Two right angle lines are the zero growth isocline of species i and j. The two dashed lines are the consumption vector of the two species, so that the two species can only coexiste when resource supply rate are in this coexistence region.