

# An Empiricist's Guide To Modern Coexistence Theory (MCT)

July 31, 2018

## 1 Introduction

[Brad, please help fill-in this section]

1. Big-picture of why MCT is the best tool we have for evaluating coexistence of species.
2. Multiple methods have been proposed for evaluating the potential for coexistence among species using empirical data. Although each of these methods is designed to evaluate Chesson's inequality criterion, it remains unclear 1) whether these methods are functionally equivalent and 2) which methods are most appropriate for a given study system.
3. We compare five different methods that have been proposed for evaluating

## 2 Summary of Methods For Empirically Evaluating MCT

### 2.1 The classic Lotka-Volterra model

In the classic Lotka-Volterra model, the *per 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  $\alpha_{ii}$  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  $\alpha_{ij}$  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 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 empirically 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 ( $\alpha_{ii}$  and  $\alpha_{jj}$ ), and inter-specific competition coefficients ( $\alpha_{ij}$  and  $\alpha_{ji}$ ). 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

datasets for each species pair: each species as a monoculture and one co-culture of the two species (Fig. 1). An important consideration is that, 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.

## 2.2 Sensitivity method

Sensitivity method is another method proposed to measure niche difference (ND) and relative fitness difference (RFD) without explicitly estimating the inter-specific competition coefficients [8]. 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 from rare in order to coexist. When invading its competitor, if a species has low invasion growth rate, this species is more affected by its competitor so that this species' niche should overlap with its competitor more. To quantify the effect of the competitor on the focal species  $i$ , the sensitivity metric ( $S_i$ ) compares the focal species  $i$ 's *per capita* growth rate when invading its competitor versus the focal species  $i$ 's *per capita* growth rate when growing alone from rare. The difference between the two growth rates is then the proxy of the effect of competitor 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,  $\mu_i$  is the *per capita* growth rate of species  $i$  when growing alone from rare and  $\mu_{ij}$  is the *per capita* growth rate of species  $i$  when its competitor (species  $j$ ) is at its carrying capacity. If either species has a growth rate less than or equal to zero when invading, this means that there will not be coexistence (mutual invasion criterion). The mutual invasion experiment can not only

be used to directly testing for mutual invasibility, but also to empirically estimate ND and RFD [8]. Specifically, to use sensitivity ( $S_i$ ) to calculate niche difference (ND) and relative fitness difference (RFD) and predict coexistence, Carroll *et al.* 2011 argued that ND can be defined as the geometric mean of sensitivity metrics and RDF can be defined as the geometric standard deviation of the sensitivity metrics.

The sensitivity method has been argued to be a general procedure that is not restricted to a specific competition model, and intuitively connects species competition and population dynamics [8]. However, here we show that the sensitivity metric is not just an intuitive connection but actually describes the impact of the entire competitor population on the focal species  $i$ . Specifically, 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 ( $\mu_{ij}$ ) 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  $\mu_i$  is therefore  $r_i$  and  $\mu_{ij}$  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 ( $\alpha_{ij}$ ). 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 ( $\alpha_{ij}$ ).

Moreover, there is only verbal argument stating why ND and RFD can be defined as the

geometric mean and standard deviation of sensitivity metrics ( $S_i$ ). Here we argue that defining ND and RFD as the geometric mean and standard deviation of sensitivity metrics is theoretically valid. 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 ( $\rho$ ) 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 ( $\alpha_{ii}$ ) must be greater than the inter-specific competition ( $\alpha_{ij}$ ) 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. In brief, the sensitivity metric ( $S_i$ ) is not equivalent to the competition coefficient ( $\alpha_{ij}$  in the Lotka-Volterra model, but due to its methmatic attributes, it can be used to calculate ND and RFD directly.

### 2.3 Negative Frequency dependency (NFD) method

The negative frequency dependency (NFD) method [6, 7, 9, 10]. The NFD method 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 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 greater than the inter-specific competition coefficient, i.e. the focal species  $i$  limits itself more than it limits its competitor, 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, we argue that negative frequency is to be expected when the focal species  $i$  limits itself more than it limits its competitor, i.e. intra-specific competition coefficient is greater than inter-specific competition coefficient. Therefore, negative frequency should guarantee stable coexistence. However, we also argue that the magnitude of negative frequency dependency (the slope) is not equivalent to either intra- or inter-specific competition coefficients [6]. When calculating negative frequency dependency (NFD), 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. Here we show that the NFD is therefore not equivalent but related to the competition coefficients in the Lotka-Volterra model.

To show that negative frequency dependency (NFD) metrics can not be used directly to measure competition coefficients ( $\alpha_{ij}$ ), we attempt to derive the NFD metrics from the Lotka-Volterra model again. We found that, the NFD metrics cannot be readily derived from the Lotka-Volterra model without making further assumptions. In fact, only when the community density is fixed, frequency dependency is equivalent to density dependency, which is modeled by  $\alpha_{ij}$  in the Lotka-Volterra model [6]. 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. Moreover, since the competition coefficients ( $\alpha_{ij}$ ) describe the *per capita* effect, we should further assume an 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 negative frequency dependency (NFD) metrics, we take derivative of equation 6 in terms of  $N_i/B$ .

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

This equation 7 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 7 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. From this equation, we first see that NFD is negative as long as the intra-specific competition ( $\alpha_{ii}$ ) is greater than the inter-specific competition ( $\alpha_{ij}$ ). 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 (Fig. 3). Most importantly, although NFD metrics has been used to estimate species coexistence empirically for annual plant communities (e.g. Godoy *et al.* 2014), NFD should be interpreted with caution as it is related but not equivalent to the competition coefficients ( $\alpha_{ij}$ )

and thus should not be directly used to calculate ND and RFD, and to predict species coexistence.

## 2.4 MacArthur's consumer resource model

In 1970, MacArthur proposed a consumer resource model to describe how species compete for different prey resources [1, 2]. This model can be reorganized into Lotka-Volterra form to more closely understand the rather phonological competition coefficients ( $\alpha_{ij}$ ) between competing species [4, 5]. After the reorganization shown in [4], the following equation represent the linkage between the Lotka-Volterra model and the parameters of MacArthur's consumer resource model.

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

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

Left hand side of equation 8 and 9 consists of parameters in the Lotka-Volterra model, while the right hand side consists of parameters from MacArthur's consumer resource model. On the left hand side,  $\alpha_{ij}$  is the competition coefficient and  $f_i$  is *per capita* growth rates of the species  $i$  in the absence of resource limitation, which determines the winner of the competition [5]. On the right hand side,  $c_{il}$  and  $c_{jl}$  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, and  $r_l$  and  $K_l$  are the *per capita* growth rate and carrying capacity of resource  $l$ . Through this linkage, empirically measured parameters in MacArthur's consumer resource model can be translated into parameters in Lotka-Volterra model and thus be used to calculate niche difference (ND) and relative fitness difference (RFD).



The contemporary coexistence theory is 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 ( $\rho$ ) 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, i.e. the similarity between  $c_{il}$  and  $c_{jl}$  (Fig. 4). The niche difference (ND) is thus  $1 - \rho$ . Second, Chesson defined relative fitness difference (RFD;  $\frac{f_j}{f_i}$ , 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  $\rho$  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.

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

## 2.5 Tilman's resource ratio consumer resource model

Similar to MacArthur's consumer resource model, Tilman's resource ratio consumer resource model [3] can also be translated to a Lotka-Volterra form [11]. Letten *et al.* 2017 reorganize Tilman's two-species consumer resource model for two essential resources to the following Lotka-Volterra form (equation 11 to 14), so that one can decipher the parameters impacting species' *per capita* growth rate. According to Letten *et al.* the inter- and intra-specific competition coefficients can be expressed as following,

$$\alpha_{ii} = \frac{c_{ij}}{D(S_j - R_{ij}^*)} \quad (11)$$

$$\alpha_{ij} = \frac{c_{jj}}{D(S_j - R_{ij}^*)} \quad (12)$$

$$\alpha_{jj} = \frac{c_{ji}}{D(S_i - R_{ji}^*)} \quad (13)$$

$$\alpha_{ji} = \frac{c_{ii}}{D(S_i - R_{ji}^*)} \quad (14)$$

In the above equations,  $c_{ij}$  is the consumption term of consumer species  $i$  on resource  $j$ , so it contains a parameter  $y_{ij}$  that representt the yield of consumer species  $i$  per resource  $j$ .  $D$  is the dilution rate,  $S_i$  is the supply rate of resource  $i$ , and  $R_{ij}^*$  is the minimum resource density of resource  $j$  that still allows the species  $i$  to have positive *per capita* growth rate.

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 ( $\alpha_{ij}$ ) becomes resource dependent as well. Although the competition coefficients ( $\alpha_{ij}$ ) are not fixed values as in the Lotka-Volterra model, Letten *et al.*'s derivation can still be used to predict coexistence based on the mutual *per capita* effects of each species on the other at 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  $\alpha_{ij}$  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 methods 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.

### **3 When, why, and how each method should be used (narrative for the table)**

#### **3.1**

Having summarized each method and its principles of operation, an empiricist is left to determine which method(s) are most appropriate for their study system, experimental approach, and goals. The upper section of Table 1 is a decision tree that divides the five methods with respect to several sequential bifurcations.

#### **3.2**

The first bifurcation is whether or the empiricist knows the factors that influence population dynamics in their study system.

1. This question divides the five methods into two completely separate groups: phenomenological methods that are informed by quantifying species interactions but make no assumptions about mechanisms, and two methods based on consumer resource models in which species interact only through specific mechanisms.

2. As shown in section 2, both of the consumer resource models can be used to estimate interaction coefficients and obtain estimates of ND and RFD. However, none of the phenomenological methods can be used to predict the mechanisms by which species interact in consumer-resource models.

**3.2.0.1** Due to the completely divergent properties of these two classes of models, several of the remaining decision steps are specific within either the the consumer-resource models or the phenomenological methods.

### 3.3

3. Among the phenomenological methods highlighted in red, the negative frequency dependence method is distinct because it does not require monocultures. The Lotka-Volterra and Sensitivity methods are further distinguished by the need for each species to be grown at steady state as monocultures. Another important difference among the phenomenological methods is that the Lotka-Volterra and negative frequency dependence methods can be applied to observational datasets or study systems where manipulation is not feasible. These two methods are also particularly well-suited for long-lived organisms where manipulative experiments are not feasible.

### 3.4

The consumer-resource models are differentiated primarily based on whether the resource is abiotic (e.g. inorganic nutrients consumed by plants) or biotic and has its own population dynamics.

### 3.5

Having considered the questions under the section ‘Information About Study System’, an empiricist should be able to identify the method that is most appropriate. In the section ‘Method’ we direct the reader to 1) the foundational paper that describes the underlying model for population dynamics, 2) the theoretical paper that relates the model to Modern Coexistence Theory and Chesson’s Inequality, and 3) an example of an empirical study that employed the method in the context of modern coexistence theory.

### 3.6

Using the first half of the table as a guide will should result in one preferred method, or in some cases a choice between two (e.g. LV and sensitivity) that can be further informed by the inputs/outputs

section of the table (see below).

### 3.7

These five methods differ in terms of the information that would be required as ‘inputs’ in order to estimate ND and RFD. 1. For instance, the phenomenological methods differ in terms of the number, length, and types of time series required. As a result, the number of new experiments required increases linearly or exponentially with each additional species. In contrast, the consumer-resource models require only as many additional experiments as the number of resources.

2. While all of the the phenomenological methods require at least one co-culture of each species pair in order to quantify the strength of their interaction. The direct Lotka-Volterra method requires a minimum of one co-culture, but the sensitivity and NFD methods require two or more co-cultures. In contrast, the methods based on consumer-resource models do not require any co-culture in order to predict interaction strength.

3. The number of experiments required grows more quickly for some methods (esp phenomenological ones)

4. Due to the need for long time-series, some of the methods would not be tractable for long-lived species (e.g. the all-in-one LV parameterization that Oscar demonstrated). However, the NFD method can work for long-lived species using a space for time substitution.

### 3.8

We showed how each of these methods, with the notable exception of negative frequency dependence, can be used to obtain estimates of ND and RFD. While the methods differ in terms of their experimental design and assumptions about population dynamics, we expect these methods to give the same prediction regarding coexistence when applied to the same species and environmental

conditions. In terms of model output then, the key differences are between phenomenological and consumer-resource methods.

1. Only the consumer resource models are able to predict the potential for coexistence among combinations of species without growing those species together simultaneously.

2. None of the phenomenological methods can be used to make predictions about novel combinations of species or different environmental contexts. However, consumer resource models can be used to predict ND and RFD under limited sets of different environmental conditions. For instance, Letten et al show that the Tilman  $R^*$  model can be used to predict the ND and RFD at different resource supply ratios or dilution rates [Letten et al 2017], but if for example, temperature were changed, the model offers no prediction.

## 4 Cautions and future directions

### 4.1 Caution 1: Empirical tests of these methods are rare

Although a few of the ‘linking’ papers use empirical data (e.g. Letten et al), I am unaware of any that applied more than one of these methods to the same dataset.

Comment: Even if we do use some empirically-derived parameter values to perform two or more of these methods, this is still an ad hoc test. Because the experiments for each method are designed differently, such back-calculations have limited utility.

What would be much more useful is a study that uses two of these experimental approaches for the same set of species and environmental conditions. For example, one use mono- and co-cultures to obtain both LV model alphas and also the sensitivities to invasion. Then use the alphas, which are obtained under some specified range of population densities, to get ND and RFD.

### 4.2 Caution 2: Intransitive interactions and environmental context

Some of these methods have been shown to work for  $\geq 2$  species at a time, both theoretically and experimentally [Reference Carroll et al 2011; OTHERS].

Although it seems obvious, employing one of the methods based on consumer-resource models requires that the empiricist knows the environmental factors that determine the outcome of competition, and specifically, that those factors are resources. While this has certain advantages, these consumer-resource models can only be applied in a limited subset of cases where this assumption is justified.



### **4.3 Need to compare these methods experimentally**

Narwani et al 2013 Ecology Letters - Used sensitivity method and coupled this with co-occurrence analyses from real lakes

We presently lack any (?) studies that have parameterized a CRM and then separately applied any of the phenomenological methods

## References

- [1] Robert MacArthur. “Species packing, and what competition minimizes.” In: *Proceedings of the National Academy of Sciences of the United States of America* 64.4 (Dec. 1969), pp. 1369–71. ISSN: 0027-8424. DOI: 10.1073/PNAS.64.4.1369. URL: <http://www.ncbi.nlm.nih.gov/pubmed/16591810><http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC223294>.
- [2] Robert MacArthur. “Species packing and competitive equilibrium for many species”. In: *Theoretical Population Biology* 1.1 (May 1970), pp. 1–11. ISSN: 0040-5809. DOI: 10.1016/0040-5809(70)90039-0. URL: <https://www.sciencedirect.com/science/article/pii/0040580970900390>.
- [3] David Tilman. “Resource competition between plankton algae: An experimental and theoretical approach”. In: *Ecology* 58.2 (1977), pp. 338–348.
- [4] Peter Chesson. “MacArthur’s consumer-resource model”. In: *Theoretical Population Biology* 37.1 (1990), pp. 26–38. ISSN: 10960325. DOI: 10.1016/0040-5809(90)90025-Q.
- [5] Peter Chesson. “Mechanisms of maintenance of species diversity”. In: *Annual Review of Ecology and Systematics* 31 (2000), pp. 343–66. ISSN: 0066-4162. DOI: 10.1146/annurev.ecolsys.31.1.343.
- [6] Peter B. Adler, Janneke HilleRisLambers, and Jonathan M. Levine. “A niche for neutrality”. In: *Ecology Letters* 10.2 (2007), pp. 95–104. ISSN: 1461023X. DOI: 10.1111/j.1461-0248.2006.00996.x.

- [7] Jonathan M Levine and Janneke HilleRisLambers. “The importance of niches for the maintenance of species diversity.” In: *Nature* 461.7261 (2009), pp. 254–7. ISSN: 1476-4687. DOI: 10.1038/nature08251. URL: <http://www.ncbi.nlm.nih.gov/pubmed/19675568>.
- [8] Ian T Carroll, Bradley J Cardinale, and Roger M Nisbet. “Niche and fitness differences relate the maintenance of diversity to ecosystem function of diversity relate the maintenance differences Niche and fitness to ecosystem function”. In: *Ecology* 92.5 (2011), pp. 1157–1165. ISSN: 0012-9658. DOI: 10.1890/10-0302.1. arXiv: arXiv:1011.1669v3. URL: <http://www.esajournals.org/doi/abs/10.1890/10-0302.1>.
- [9] J Hillerislambers et al. “Rethinking Community Assembly through the Lens of Coexistence Theory”. In: *Annu. Rev. Ecol. Evol. Syst* 43 (2012), pp. 227–48. ISSN: 1543-592X. DOI: 10.1146/annurev-ecolsys-110411-160411.
- [10] Oscar Godoy, Nathan J B Kraft, and Jonathan M. Levine. “Phylogenetic relatedness and the determinants of competitive outcomes”. In: *Ecology Letters* 17.7 (2014), pp. 836–844. ISSN: 14610248. DOI: 10.1111/ele.12289. arXiv: 2072.
- [11] Andrew D. Letten, Po Ju Ke, and Tadashi Fukami. “Linking modern coexistence theory and contemporary niche theory”. In: *Ecological Monographs* 87.2 (2017), pp. 161–177. ISSN: 15577015. DOI: 10.1002/ecm.1242. arXiv: 1106.4388.

## Table

## Figures

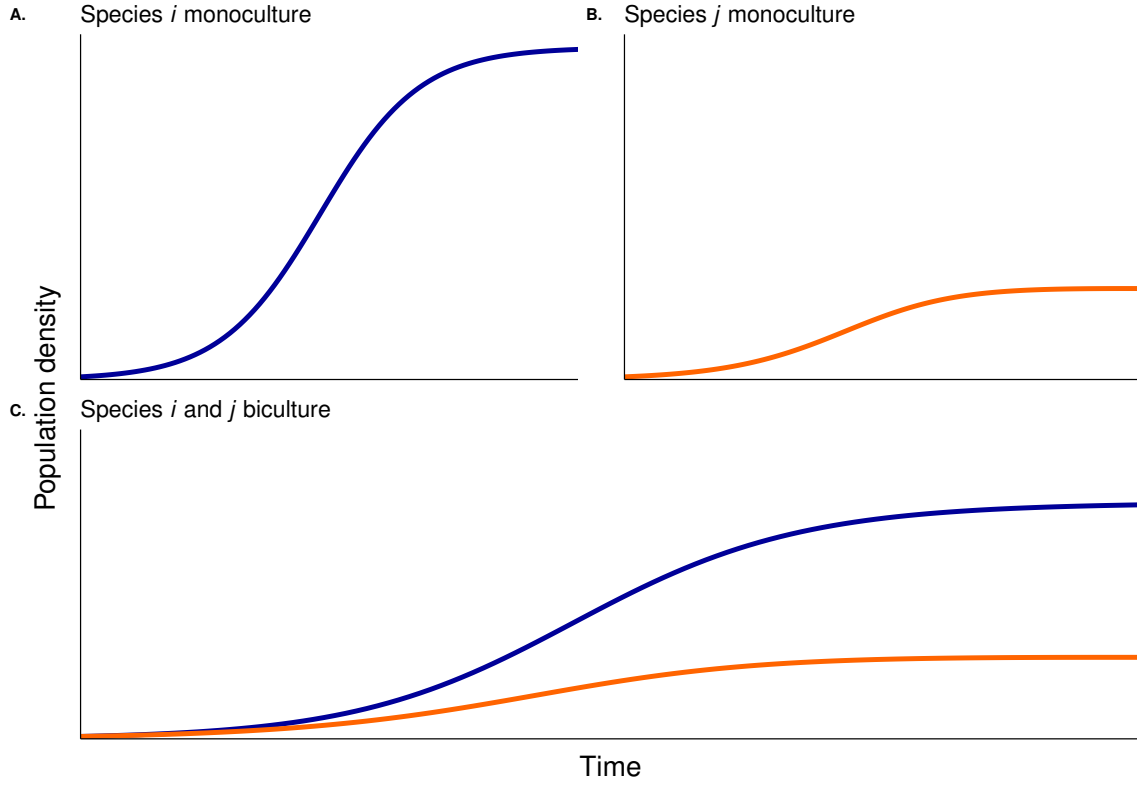


Figure 1: An example plot showing the estimation of  $\alpha_{ij}$  from fitting Lotka-Volterra model to time series. The points represent the density of species  $i$  (open circles) and  $j$  (solid dots) respectively. The dashed lines are the two fitted growth curve. The species densities were generated 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  $r_1 = 0.099$ ,  $r_2 = 0.043$ ,  $\alpha_{11} = 0.808$ ,  $\alpha_{12} = 0.577$ ,  $\alpha_{21} = 0.720$ ,  $\alpha_{22} = 0.974$ .

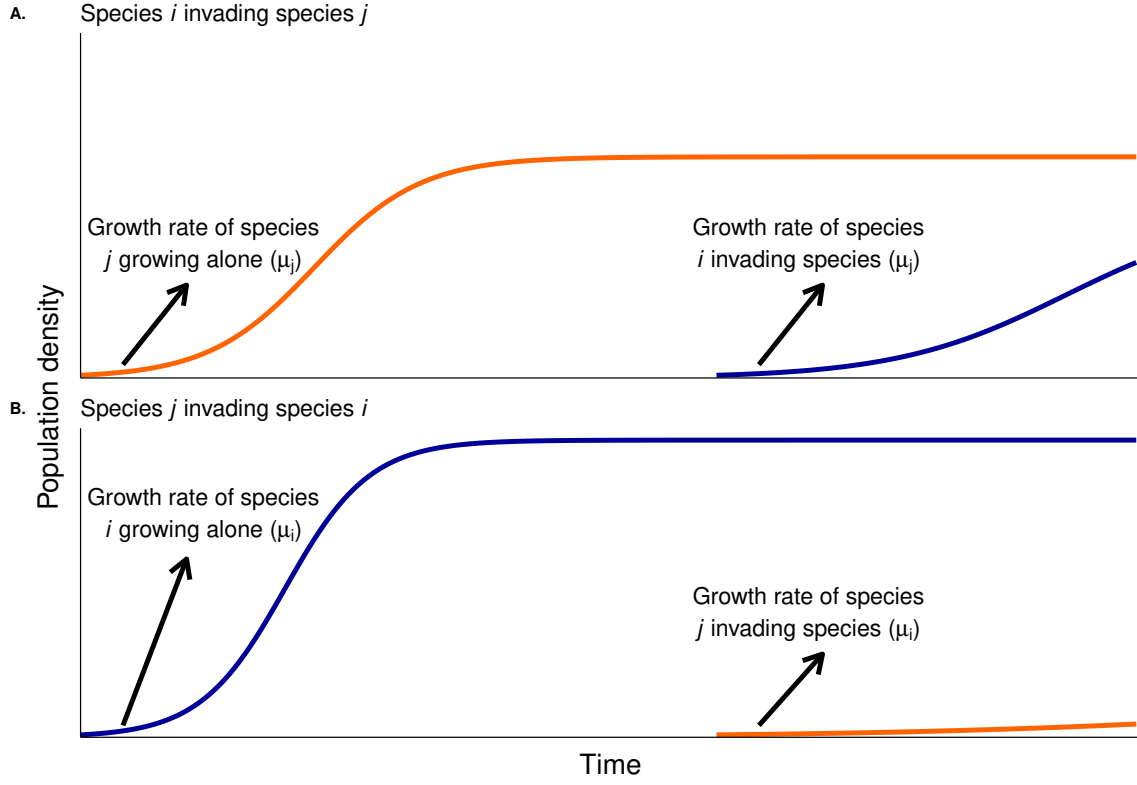


Figure 2: An example plot showing the estimation of sensitivity ( $S_{ij}$ ) of species  $i$  invading species  $j$  (panel a.) or the reverse (panel b.). In both panels, solid dots are the growth curve species when growing alone and the open circles are the growth curve of species when invading the 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  $\alpha_{12}$  is estimated to be 0.686 and  $\alpha_{21}$  is estimated to be 0.652, which is close to the predetermined inter-specific competition coefficients ( $\alpha_{12} = \alpha_{21} = 0.6$ ).

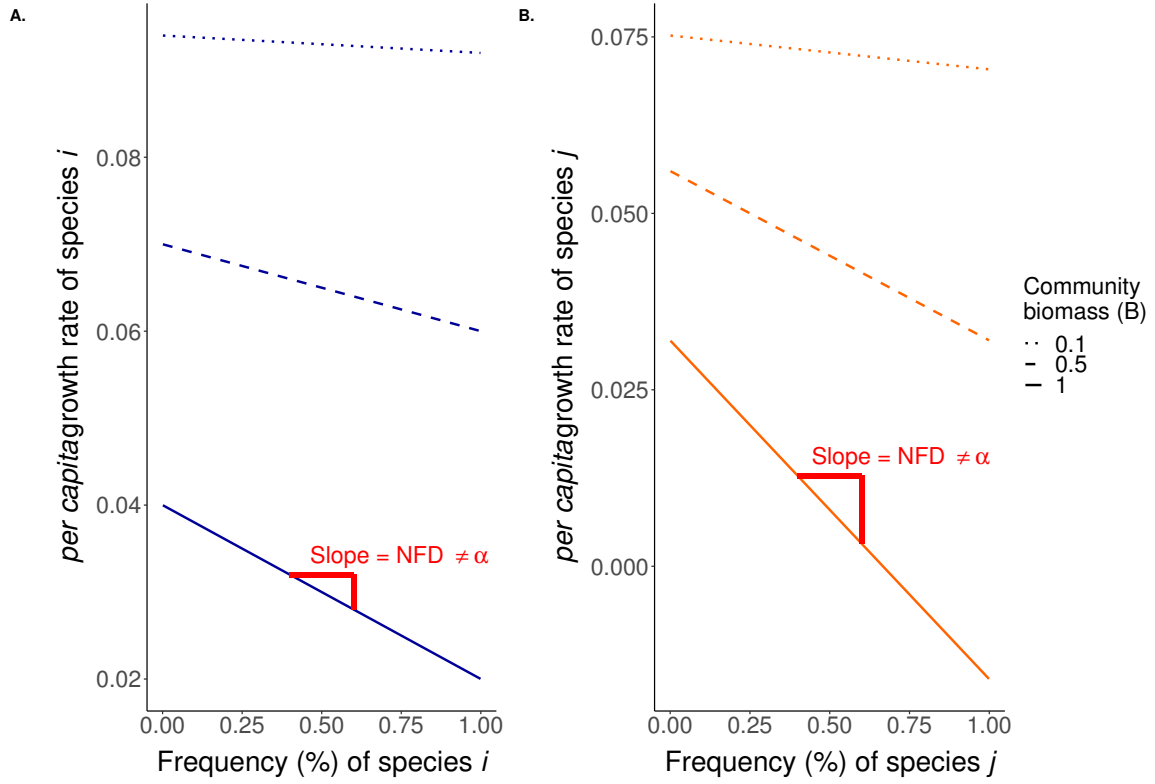


Figure 3: An example plot showing the negative frequency dependency (NFD) of species  $i$  (panel a.) and species  $j$  (panel b.). To calculate NFD, we first determined an arbitrary community biomass ( $B$ ) and gradually increased the frequency of the focal species (species  $i$  in panel a. and species  $j$  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  $\alpha$ s ( $\alpha_{12}=0.8$ ,  $\alpha_{12} = \alpha_{21} = 0.6$ , and  $\alpha_{22} = 1.5$ ).

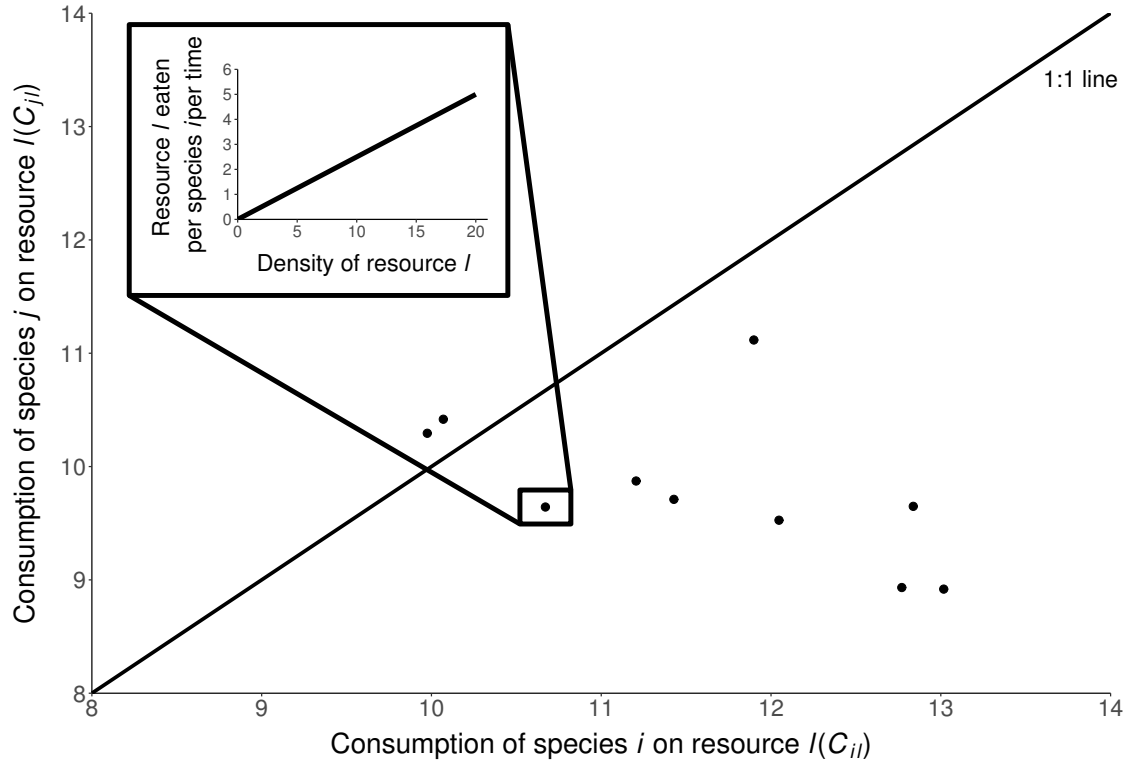


Figure 4: An example plot demonstrating the idea of niche difference (ND;  $\rho$ ) in MacArthur's consumer resource model. Consumption of species  $j$  on resource  $l$  ( $c_{jl}$ ) are plotted against consumption of species  $i$  on resource  $l$  ( $c_{il}$ ). The closeness between  $c_{jl}$  and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



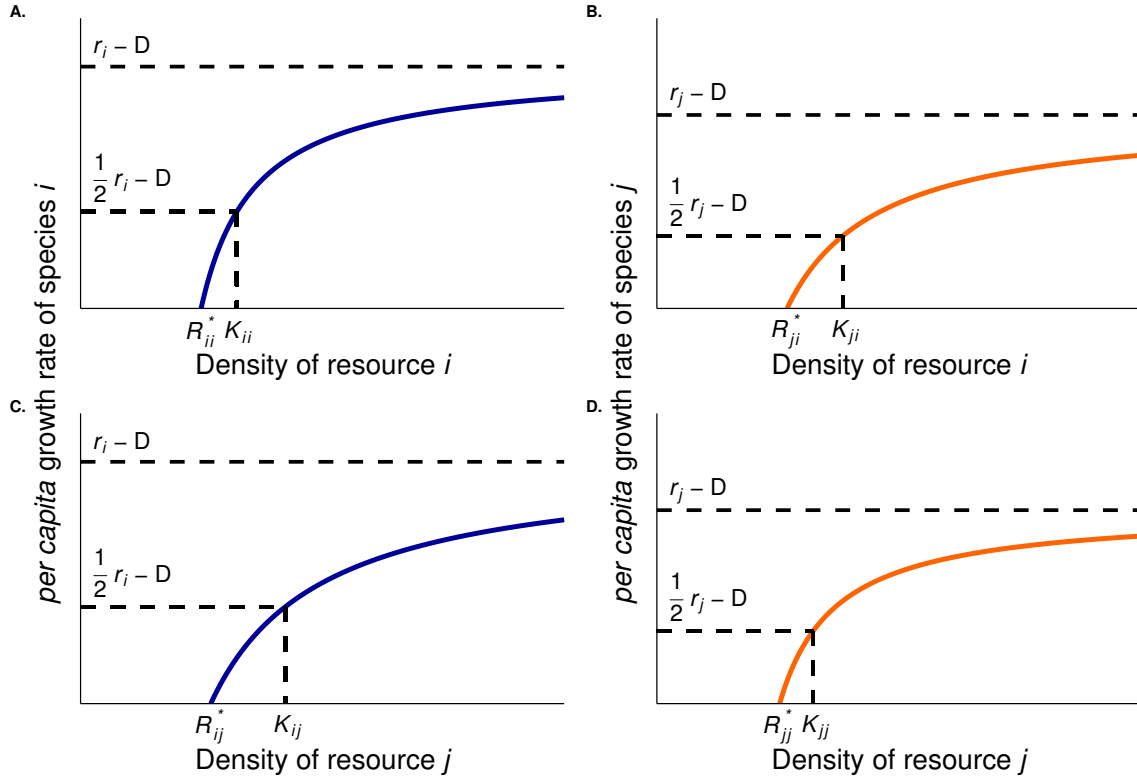


Figure 5: Example plots showing the empirical data required to estimate  $R^*$  in Tilman's consumer resource model for species  $i$  and  $j$  on resource  $i$  and  $j$ .  $R_{ij}^*$  means the minimum level of resource  $j$  that still allows species  $i$  to have positive *per capita* growth rate. In this example scenario, species  $i$  ( $j$ ) is limited by resource  $j$  ( $i$ ), so that the  $R_{ij}^*$  ( $R_{ji}^*$ ) is greater than  $R_{ii}^*$  ( $R_{jj}^*$ ). The  $R_{ij}^*$  ( $R_{ji}^*$ ) is the one being used to calculate  $\alpha_{ii}$  and  $\alpha_{ij}$  ( $\alpha_{jj}$  and  $\alpha_{ji}$ ) because it determine how sensitivity species  $i$  will be affected by the resource (resource  $j$ ) that limits the growth rate of species  $i$