



## An Empiricist's Guide to Modern Coexistence Theory for Competitive Communities

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**1 An Empiricist’s Guide to Modern Coexistence Theory for Competitive Communities**

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## Abstract

While most ecological theories have historically invoked niche differences as the primary mechanism allowing species coexistence, we now know that coexistence in competitive communities depends on the balance of two opposing forces: niche differences (ND) that determine how species limit their own growth rate versus that of their competitor, and relative fitness differences (RFD) that establish competitive hierarchies among species. Several different empirical methods have been proposed for measuring ND and RFD in order to make predictions about coexistence of species, yet it remains unclear which method(s) are appropriate for a given empirical study and whether or not those methods yield the same information. Here we compare five different empirical methods and provide a practical guide to help empiricists determine which method(s) are best for their study system. We show that there are important tradeoffs between mechanistic methods, which require detailed understanding of species niches and physiology but are more tractable experimentally, and phenomenological methods which do not require this detailed information but can be impractical for some study designs. Finally, we show that the methods do not always yield the same values and therefore we caution against future syntheses that compile these estimates from different empirical studies.

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**Introduction**

Throughout most of the history of community ecology, it has been assumed that niche differentiation among species is primary biological mechanism that can offset the negative impacts of interspecific competition on species coexistence (Gause 1934; Tilman 1982; Leibold 1995; Chase & Leibold 2003). This idea originated when Volterra (1931) introduced a dynamic model of competition that became the foundation for the competitive exclusion principle, which states that if two species have identical niche requirements then one of them will inevitably become locally extinct (Gause 1934). The competitive exclusion principle led to two conclusions about coexistence in competitive communities: 1) species will coexist only if they are limited by different resources (or consumers) at the same location and time, or if they partition resources (or consumers) in space or time and, as a result, 2) ecosystems should contain only as many species as there are limiting resources (or consumers) (Rescigno & Richardson 1965; MacArthur & Levins 1967; MacArthur 1970; Tilman 1977; Leibold 1995). Nearly all subsequent hypotheses to explain coexistence have argued that biodiversity exists because of such niche differences among species.

But starting in 2000, theories of species coexistence began to undergo a major revision. In 2001, Hubbell published The Unified Neutral Theory of Biodiversity (Hubbell 2001), which argued that patterns of biodiversity in nature can be explained by a simple model that does not invoke niche differences among species. According to Hubbell’s theory, species coexist because their demographic parameters are identical, or nearly so, such that the consequences of their interactions are essentially equal among all species. Based on this theory, Hubbell argued that the biodiversity observed in nature can be explained by a series of stochastic events that cause some populations to become dominant while others become extinct.

Even as Hubbell was developing his neutral theory, Chesson (2000) was completing a ground-breaking theory of coexistence that would provide a framework for integrating the niche and neutral perspectives on biodiversity. Chesson's coexistence framework was built on his insight into the invasibility criterion: a pair of species can coexist only if each species is capable of invading a steady-state population of its competitor. Chesson showed how a species' growth rate when invading a resident species can be decomposed into two general terms, which he called stabilizing and equalizing forces (Box 1). Stabilizing forces cause species to limit their own growth rate more than they limit the growth rate of other species (intra > interspecific competition). These stabilizing forces, also known as niche differences (ND), occur when species partition limiting resources in space or time, or when they experience differential consumption by consumers. In contrast, equalizing forces minimize differences in competitive abilities among species. Equalizing forces, which have also been called relative fitness differences (RFD), are the result of inherent variation in biological traits such as minimum requirements for shared resources or consumers, differential resistance to consumers, or differences in potential growth rates (Levine & HilleRisLambers 2009; HilleRisLambers *et al.* 2012). As summarized in Box 1, Chesson showed it is the balance of ND and RFD that ultimately determines whether species maintain non-negative long-term growth rates in competitive communities (Chesson 2000).

It has subsequently been shown that Hubbell's neutral theory represents a specific, limiting case of Chesson's coexistence theory where NDs and RFDs are both zero, causing the outcome of competition to be approximated by a random walk toward extinction (Adler *et al.* 2007). Stabilizing and equalizing forces have been identified in both fluctuation-dependent mechanisms (e.g. storage effects) and fluctuation-independent mechanisms of coexistence (e.g.

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3 88 competition for a limiting resource) (Miller & Klausmeier 2017; Barabas *et al.* 2018; Ellner *et al.*  
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5 89 2019). Thus, Chesson’s inequality provides a general framework for predicting species  
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8 90 coexistence.

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10 91 Since the development of Chesson’s theory, much attention in ecology has turned  
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12 92 towards the empirical estimation of ND and RFD in order to determine how these forces  
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14 93 contribute to coexistence in real communities. Empiricists have proposed several different  
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16 94 approaches to quantify ND and RFD in specific study systems. The various methods for  
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18 95 quantifying ND and RFD were derived from different models of species interactions, make  
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20 96 different assumptions, and use different experimental designs. Therefore, it remains unclear  
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22 97 which method(s) are best suited for a given study, whether the methods give comparable  
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24 98 estimates of ND and RFD, and whether the methods actually make the same prediction regarding  
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26 99 coexistence. If Chesson’s theory is to become widely implemented in empirical studies and in  
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30 100 applied contexts, we need a ‘users guide’ to help ecologists determine which of these empirical  
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33 101 approaches meets their needs.

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35 102 Here we provide a summary and comparison of four methods that have been proposed to  
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37 103 measure ND and RFD empirically, and a fifth method that does not give estimates of ND and  
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39 104 RFD but has been used to predict coexistence based on Chesson’s theory. In Part 1, we explain  
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41 105 the theoretical basis of each method, illustrate how it can be implemented empirically, and ask  
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43 106 whether the methods yield the same estimates of ND and RFD. In Part 2 we provide a list of  
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45 107 decision steps to guide empiricists in selecting the most appropriate method(s) for their study  
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47 108 system and aims. In Part 3, we discuss the main advantages and disadvantages of the methods  
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49 109 and make suggestions for future empirical work on coexistence theory.  
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## Part 1. Summary of Five Empirical Methods for Implementing Chesson's Theory

In this part of the paper we summarize each of five empirical methods for measuring ND and RFD by explaining how the method relates to Chesson's theory (Box 1), showing how the method can be implemented empirically, and highlighting the method's key limitations and assumptions.

### *1.2 Method based on the parameterized Lotka-Volterra model*

Since Chesson originally used the Lotka-Volterra model to explain his criterion for coexistence (Box 1), the most obvious empirical approach for estimating ND and RFD is to parameterize the Lotka-Volterra competition model (Equation 2) using data collected from experiments or time-series observations from natural ecosystems.

1.2.1 Empirical approaches. Using the Lotka-Volterra model requires estimating six different parameters used in Equation 2: intrinsic per capita growth rate of each species ( $r_i$  and  $r_j$ ), per capita intra-specific competition coefficients ( $\alpha_{ii}$  and  $\alpha_{jj}$ ), and per capita inter-specific competition coefficients ( $\alpha_{ij}$  and  $\alpha_{ji}$ ). The simplest way to parameterize the Lotka-Volterra model from experiments would be to measure the population density of each species over time, using plots or microcosms containing each species grown alone as a monoculture and, separately, one co-culture of the two species (Figure 1). From each monoculture time series, the empiricist would estimate the maximum per capita growth rate of each species ( $r_i$ ), which occurs as the species' density approaches zero, and the steady-state population size of each species in monoculture (carrying capacity,  $K_i$ ).

Empiricists have two options for estimating the intraspecific competition coefficients ( $\alpha_{ii}$ ). The first option is to estimate these interaction coefficients using the slope of each species'

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3 134 relative growth rate (scaled on its maximum growth rate  $r_i$ ) versus its population density in  
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5 135 monoculture (Figure 1A and 1B, right). This slope has the opposite sign of the intraspecific  
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7 136 interaction coefficient  $\alpha_{ii}$ . However, in practice this slope is unlikely to be fixed across all  
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10 137 population densities (see Limitations, below). The alternative option is to assume that  
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12 138 intraspecific competition coefficients ( $\alpha_{ii}$ ) are equal to  $1/K_i$ , which comes directly from the  
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14 139 Lotka-Volterra model in Equation 2. This approach yields estimates of  $\alpha_{ii}$  that cannot, say, be  
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17 140 used in Equation 2 to re-create transient dynamics observed in time series, but can be used to  
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19 141 estimate ND and RFD and predict coexistence using Chesson's inequality (Box 1).  
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22 142 Next, from the co-culture time series (Figure 1C), the empiricist would use non-linear  
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24 143 regression to parameterize the interspecific interaction coefficients ( $\alpha_{ij}$  and  $\alpha_{ji}$ ) by substituting  
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26 144 the parameter estimates from the monocultures into Equation 2. Finally, the empiricist can use all  
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28 145 four interaction coefficients to compute ND and RFD using Equations 3 and 4 (Box 1).  
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31 146 1.2.2 Limitations. A key assumption of this approach is that the intra- and inter-specific  
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33 147 competition coefficients are fixed with respect to population sizes of either species. In other  
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35 148 words, the first individual and the last individual added to a population have the same per capita  
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37 149 effect on the growth rates of its own species or that of its competitor. This assumption is not  
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40 150 always met in real biological communities where intra- and inter-specific competition  
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42 151 coefficients can depend on species' densities (Smith-Gill & Gill 1978; Abrams 1980). The  
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44 152 assumption also does not apply when the mechanisms leading to competition are driven by non-  
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47 153 linear dependence on resources. Examples include functional responses of consumers to prey  
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49 154 density and non-linear dependence of growth rates on abiotic resource availability. Figure A1 in  
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51 155 the Supporting Information shows that, when applied to numerical simulations based on a well-  
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54 156 known consumer resource model, intraspecific coefficients measured in monoculture near  
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equilibrium lead to inaccurate predictions regarding coexistence. However, when the intraspecific interaction terms are replaced by  $1/K_i$  the method yields accurate predictions. Therefore, in those situations where competition coefficients are fixed with respect to population size, or can be measured at low population densities of each species, this empirical approach can be used to estimate ND and RFD.

### 1.3 Sensitivity method

The second method for estimating ND and RFD, the sensitivity method, is similar to the Lotka-Volterra method in that it is phenomenological and requires information from direct competition experiments. The sensitivity method quantifies the proportional reduction in a species' growth rate when invading a steady-state population of its competitor (Carroll *et al.* 2011; Narwani *et al.* 2013). In this method, the maximum growth rate of each species in monoculture ( $\mu_i$ ) and when invading a steady-state population of the competitor species ( $\mu_{ij}$ ) are used to calculate each species sensitivity to interspecific competition ( $S_i$ ) using Equation 5:

$$S_i \equiv \frac{\mu_i - \mu_{ij}}{\mu_i} \quad (5)$$

Carroll and others (2011) and others have shown that ND is proportional to the geometric mean of these sensitivity measures, whereas RFD represent variation around the mean:

$$ND = 1 - \sqrt{S_i S_j} \quad (6)$$

$$RFD = \sqrt{\frac{S_i}{S_j}} \quad (7)$$

A species' sensitivity to competition is jointly determined by ND and RFD (Carroll *et al.* 2011; Narwani *et al.* 2013). Specifically, greater ND between the two species reduces the impact of interspecific competition so that  $S_i$  will approach zero. Greater RFD, on the other hand, causes species to be asymmetrically affected by competition such that one species' sensitivity increases

while the other's decreases. While Carroll and others (2011) verbally argued that this method is compatible with Chesson's theory, in Appendix A we show explicitly how this method relates to Chesson's theory and prove that it is identical to Equations 3 and 4 when evaluated at the steady-state population density of the resident species.

1.3.1 Empirical approaches. The experiment by Narwani et al. (2013) provides an example for how to implement the sensitivity method empirically. Their experimental system involved species of freshwater green algae growing under controlled conditions in the laboratory. They grew each species as a monoculture, starting from low densities and allowing the populations to reach their carrying capacity. From these time series, they quantified the per capita maximum growth rate of each species as a monoculture ( $\mu_i$  and  $\mu_j$ ), which occurs when the focal species is at low density. After each species reached its carrying capacity, they introduced the other species from low density (e.g. 0.01% of  $K$ ) and quantified the per capita growth rate of each species when invading the other ( $\mu_{ij}$  and  $\mu_{ji}$ ). Finally, for each pair of species, they used these growth rates to calculate the sensitivity metrics ( $S_i$  and  $S_j$ ) using Equation 5 and used those sensitivity metrics to calculate ND and RFD using Equations 6 and 7.

1.3.2 Limitations. The sensitivity methods is only practical for organisms that can be grown as monocultures and whose population growth rates can be measured over tractable periods of time. Also, it is important to note that the invasion growth rates ( $\mu_{ij}$  and  $\mu_{ji}$ ) must be measured when the invader population density is low. If the growth rate of the invader species were measured at greater density of the invader species or lower density of the resident species (i.e. long after invasion), then the  $S_i$  would be affected by both intra- and inter specific competition. The resulting predicting regarding species coexistence could be incorrect.

#### 203 1.4 Parameterizing MacArthur's consumer resource model

204 The third method to estimate ND and RFD from empirical data is to parameterize  
 205 MacArthur's consumer-resource model (MacArthur 1970) then use these parameters to calculate  
 206 ND and RFD using Chesson's original derivation (Chesson 1990, 2000). This method is different  
 207 from both the Lotka-Volterra and sensitivity methods because it does not rely on experiments  
 208 where the species are grown together in order to quantify how the species influence each other's  
 209 growth rates. Instead, this method works by parameterizing a mechanistic model that describes  
 210 how species consume, and thus compete for, two or more prey resources (MacArthur 1970), then  
 211 reorganizing those parameters following an analytical solution to estimate ND and RFD for  
 212 assessing Chesson's inequality (Box 1).

213 MacArthur's CRM is composed of differential equations representing the growth of each  
 214 consumer species as a function of resource densities (Equation 8) and a differential equation (or  
 215 set) that describes the population dynamics of each prey resource and their mortality due to  
 216 consumption by the consumers (Equation 9).

$$217 \quad \frac{1}{X_i} \frac{dX_i}{dt} = b_i \left( \sum_{l=1}^m c_{il} w_{il} R_l - m_i \right) \quad (8)$$

$$218 \quad \frac{1}{R_l} \frac{dR_l}{dt} = r_l \left( 1 - \frac{R_l}{K_l} \right) - \sum_{i=1}^n c_{il} X_i \quad (9)$$

219 In this model  $X_i$  is population density of the consumer species  $i$  and  $R_l$  is population density of  
 220 the prey resource  $l$ . The term  $b_i$  represents the effect of prey consumption on the growth rate of  
 221 the consumer,  $r_l$  is the maximum per-capita growth rate of prey resource  $l$ ,  $K_l$  is the carrying  
 222 capacity for the prey species  $l$ ,  $w_{il}$  represents the increase in consumer population density for  
 223 each unit of prey resource  $l$  consumed. The term  $c_{il}$  is the resource capture rate by consumer  $i$  on  
 224 resource  $l$  and  $m_i$  is the density-independent mortality for consumer species  $i$ . Chesson showed  
 225 that, by implementing a time-scale separation technique, parameters in MacArthur's consumer

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3 226 resource model can be used to calculate ND and RFD using Equations 10 and 11 (Chesson 1990,  
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5 227 2000):

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8 228  $ND = 1 - \sum_l c_{ij} c_{jl} \frac{w_{il} K_l}{r_l}$  (10)

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11 229  $RFD = \frac{\sum_l c_{jl} w_{il} K_l - m_j}{\sum_l c_{il} w_{il} K_l - m_i}$  (11)

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14 230 The estimates of ND and RFD from this method can then be used to evaluate Chesson's  
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16 231 inequality and predict coexistence (Box 1).

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18 232 1.4.1 Empirical approaches. Because we are not aware of any empirical studies that have  
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20 233 parameterized the MacArthur model for the purpose of estimating ND and RFD, we describe the  
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22 234 experimental approach that would be required (Figure 3). First, the empiricist would identify or  
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24 235 define the prey resources that are available to the consumer species. Each prey resource would be  
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26 236 inoculated or planted at low density into an environment free of other prey resources and  
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28 237 consumers, then the population density would be measured over time in order to estimate the per  
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30 238 capita maximum growth rate of the prey ( $r_l$ , which occurs as the prey population density  
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32 239 approaches zero) and its carrying capacity ( $K_l$ , which occurs when the prey growth rate  
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34 240 approaches zero). Next, the experimentalist would introduce each consumer species into several  
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36 241 different densities of each prey resource growing as a monoculture. Under those different prey  
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38 242 resource densities, the experimentalist would measure the per capita consumption rate of prey  
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40 243 resource by the consumer species ( $c_{il}$ ) and the yield of consumer density or biomass per unit prey  
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42 244 resource consumed ( $w_{il}$ ). These parameters can then be used in Equations 10 and 11 to obtain ND  
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44 245 and RFD, which can subsequently be used in Equation 1 to predict coexistence.

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46 246 1.4.2 Limitations. The method based on MacArthur's model requires as many  
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48 247 consumption experiments as there are resources, and each of these experiments involves  
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50 248 measuring consumption rates at a range of resource species densities (Figure 3 B and C). The

precise number of parameters to be estimated depends on the number of prey resources considered by the model. For example, for two consumer species and three prey resources (Figure 3), the hypothetical experiment requires 18 parameters to be quantified: 3 different maximum per capita growth rates and 3 carrying capacities of the prey resources ( $r_l$  and  $K_l$ ,  $l = 1$  to 3), 6 per capita consumption rates ( $c_{il}$ ;  $i = 1$  and 2,  $l = 1$  to 3), and 6 yields ( $w_{il}$ ;  $i = 1$  and 2,  $l = 1$  to 3). While this constraint does not impact the ability of the method to predict coexistence under defined conditions, it could limit the extent to which those predictions can be applied to natural environments where the number of potential prey species is large.

### 1.5 Parameterizing Tilman's consumer resource model

Like the method based on MacArthur's CRM, the method based on Tilman's CRM does not require species to be grown together in a competition experiment. However, unlike the method based on MacArthur's CRM, the method based on Tilman's CRM is specific to abiotic resources that are controlled by a constant rate of supply and do not have their own intrinsic growth rate (i.e. a chemostat). Letten and others (2017) showed how Tilman's consumer resource model (Tilman 1977) can be reorganized to a Lotka-Volterra form in order to estimate ND and RFD. In this model, one set of differential equations describes the growth of each consumer species as a function of the availability of two essential and non-substitutable resources (Equation 12) and another set of equations describes the dynamics of abiotic resources and their depletion due to uptake by the consumer and dilution (Equation 13).

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \min \left[ \frac{S_i}{S_i + k_{ii}}, \frac{S_j}{S_j + k_{ij}} \right] - D \quad (12)$$

$$\frac{1}{R_i} \frac{dS_i}{dt} = D(S_{i0} - S_i) - \sum_{i=1}^n \frac{N_i}{Y_{ii}} r_i \min \left[ \frac{S_i}{S_i + k_{ii}}, \frac{S_j}{S_j + k_{ij}} \right] \quad (13)$$

In this model,  $N_i$  is the population density of species  $i$ ,  $r_i$  is the maximum per capita growth rate of species  $i$ ,  $y_{ii}$  is the yield of species  $i$  on resource  $i$ , and  $k_{ii}$  is the half saturation constant for growth of species  $i$  on resource  $i$ . The term  $S_{i0}$  is the external supply concentration for resource  $i$ ,  $S_i$  is the concentration of resource  $i$  in the environment, and  $D$  is equal to both the supply rate of resources and the density-independent loss rate for both species.

To use this method to calculate ND and RFD an empiricist must first determine which species is limited by each resource by comparing the supply ratio for the two resources against the  $R^*$ s for each species at the pre-determined dilution rate. (e.g., using Resource-Ratio theory (Tilman 1982)). Under conditions where species 1 is limited by resource 2 and species 2 is limited by resource 1, equations 14 and 15 can be used to estimate ND and RFD:

$$ND = 1 - \sqrt{\frac{y_{12}y_{21}}{y_{11}y_{22}}} \quad (14)$$

$$RFD = \frac{\sqrt{\left(\frac{D k_{21}}{D - r_2} + S_1\right)^2 y_{11}y_{21}}}{\sqrt{\left(\frac{D k_{12}}{D - r_1} + S_2\right)^2 y_{12}y_{22}}} \quad (15)$$

#### 1.5.1 Empirical approaches. To illustrate how this method could be implemented

empirically, we describe the approach that Tilman first used to parameterize his model (Tilman 1977). First, he inoculated each species as a monoculture into growth medium containing a range of concentrations of the limiting resource (either silicate or phosphate) with all other resources in excess. By calculating the exponential growth rate at each level of the limiting resource he fitted estimates of half saturation constants ( $k_{ij}$ ) for each resource and a single maximum per capita growth rate for both resources ( $r_i$ ) (Figure 4). Next, Tilman quantified the yields ( $y_{ij}$ ) of each species on each resource by measuring the elemental content of a known number of cells. As

shown by Letten et al. (2017), the parameters described above can be used to predict coexistence under different resource supply ratios and dilution rates in a chemostat.

1.5.2 Limitations. The method using Tilman's CRM requires an empiricist to know precisely which resources the species compete for, which limits its applicability to many real scenarios and ecosystems where the identity of limiting resources and the supply rates may not be known. Additionally, the resource supply concentrations must be fixed and the supply rates must be equal to the density-independent loss rate, which can only be achieved in certain experimental settings like chemostats.

#### *1.6 Negative frequency dependence (NFD) method*

The final method that we summarize, the negative frequency dependence method (NFD), has not been proposed as a means of obtaining estimates of ND and RFD that are directly compatible with Chesson's inequality (Box 1, Equation 1). In fact, in Supporting Information C, we explicitly show that the NFD method cannot be used to derive estimates of ND and RFD that are consistent with Chesson's theory. However, the NFD method can be used to predict coexistence using the criterion of mutual invasibility and has been used to illustrate the impacts of ND and RFD in manipulative experiments (Adler *et al.* 2007; Levine & HilleRisLambers 2009).

The NFD method quantifies the change in per capita growth rate of a species as a function of its frequency in a community (Adler *et al.* 2007; Levine & HilleRisLambers 2009). Here the frequency of a species refers to the proportion of total biomass or individuals in a community belonging to that species. This method makes the key assumption that the community is saturated with respect to total species densities. Thus, a frequency of 1 represents a

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3 315 steady-state monoculture at its carrying capacity and any increase in the population density of  
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5 316 one species will be offset by a decrease in population density of another species. Under this  
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7 317 assumption, the slope of the NFD relationship reflects the difference between intra- versus inter-  
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9 318 specific competition (Adler *et al.* 2007). Increasing species *i*'s frequency means that individuals  
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11 319 of species *i* will compete more with individuals of its own kind than with individuals of other  
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13 320 species, and will thus experience stronger intraspecific competition than interspecific  
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15 321 competition. Therefore, if intra-specific competition is greater than inter-specific competition,  
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17 322 the species affects its own growth rate more than it affects the growth rate of other species, and  
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19 323 the NFD slope should be negative.  
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24 324 The NFD method is most often used as a graphical approach for understanding the  
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26 325 balance of ND and RFD (Figure 5). Adler *et al.* (2007) argue that a more negative NFD slope  
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28 326 represents a stronger stabilizing force, which is proportional to the ND in Chesson's inequality.  
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30 327 Similarly, they argue that the difference between species' growth rate in the absence of  
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32 328 stabilizing forces is the equalizing force, proportional to RFD. Although they did not used the  
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34 329 NFD method to estimate ND and RFD, Adler and others showed how both the slope and  
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36 330 elevation of the NFD plot are needed to accurately predict whether each species has a positive  
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38 331 growth rate at a frequency approaching 0. If this condition is met, the species are mutually  
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40 332 invisable and should coexist based on Chesson's criterion (Box 1).  
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44 333 1.6.1 Empirical approaches. The NFD method could be implemented using either  
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46 334 experiments or observations from natural ecosystems (Figure 5A). Using the experimental  
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48 335 approach, an empiricist could growth both species together and measure their densities over  
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50 336 time. To do this, the empiricist would need to ensure that total community density or biomass  
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53 337 was saturated such that any decrease in the resident's population density is met with an increase  
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in the density of the invader. Next, the empiricist could use the time series for each species' density to calculate the per capita growth rate and frequency of each species at each time point. Alternatively, the NFD method could be implemented using observational data from natural ecosystems (Adler *et al.* 2010) by pairing estimates of per capita growth rate and the relative frequency of the species in different habitat patches or along ecological gradients. This approach could allow an empiricist to estimate frequency dependence for species that are not easily manipulated (e.g. trees). Using pairs of growth rate and frequency from either experiments or observational studies, the empiricist can estimate the growth rate when each species approaches frequency of zero (Figure 5B). If either of the two species does not have a positive growth rate when rare, then the pair will not coexist.

Levine *et al.* (2009) demonstrated how the NFD method can be implemented experimentally. In their study with 10 species of grassland plants, they manipulated the relative frequency of each focal species by varying the proportion of seeds belonging to the focal species versus all other species. The authors experimentally removed the effect of niche differences on growth rates by maintaining each species' density at a constant, non-equilibrium level that was not subject to competition from other species. They then quantified the slope of NFD by plotting the growth rate of each species against its frequency in the initial community. Their experiment showed that effectively removing niche differences among species (even without measuring them) led to dominance by the species with the highest per capita growth rates. In other words, in the absence of ND the outcome of competition was determined by RFD. Similarly, other studies have measured the slope of NFD as evidence for the importance of stabilizing forces, but did not directly interpret the slope as ND or the intercepts as RFD (Yenni *et al.* 2017).

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1.6.2 Limitations. Despite some of the desirable aspects of the NFD method in terms of

empirical approaches (above), it has three key limitations. First, unlike the other four methods summarized in this paper, the NFD method does not yield estimates of ND and RFD. This may not be a concern if the purpose of the study is simply to predict species coexistence. Second, the NFD method assumes that the community density is saturated across the range of species' frequencies observed. Meeting this assumption in experiments would require long time series to show that total biomass of a community is fixed. In observational studies based on natural ecosystems, it might not be possible to ensure that total biomass is saturated.

The third limitation of the NFD method is that the relationship between a species' frequency and growth rate is often non-linear (Figure 5). As long as the relationship between a species' frequency and its growth rate is linear, the NFD slope and elevation can theoretically be used to predict whether both species will have positive growth rates when rare, thus meeting the mutual invasibility criterion. If the NFD relationship is not linear, which can occur in systems where species interactions are governed by simple linear terms (Supporting Information Figure C1), then the NFD method can give inaccurate predictions. In Appendix C, we show the NFD method can lead to incorrect predictions about species coexistence when applied to systems with non-linear relationships between species' growth rates and densities. If the slope and elevation of the NFD plot are evaluated over a narrow range of species frequencies, and those data are used to predict growth rate as frequency approaches zero, then the method could make inaccurate predictions about mutual invasibility and coexistence. If the relationship between each species' frequency and its growth rate is not linear, then an empiricist would need to either 1) measure the growth rate of each species across the full range of frequencies to establish that the growth rate of each species is linearly related to its frequency or 2) evaluate the growth rate of each species

when rare (i.e. directly demonstrate mutual invasibility). Both of these options would increase the effort required but may be necessary in systems where only observational studies are possible.

### *1.7 Do the methods give the same prediction regarding coexistence?*

Although each of the five methods can be used to predict coexistence, the experimental approaches required for those methods are different, and it is not clear that the methods would yield the same predictions (or values of ND and RFD) if applied to the same study system. Here we use numerical simulations to investigate whether four of those methods, when implemented as shown in Figures 1, 2, 3, and 5, lead to the same prediction regarding coexistence and give the same estimates of ND and RFD. We could not include both the method based on MacArthur's CRM and the method based on Tilman's CRM since these mechanistic models have incompatible assumptions – the resources in MacArthur's CRM have their own population dynamics while the resources in Tilman's CRM are abiotic and governed by a constant rate of supply. We chose to use numerical simulation for this demonstration since we are unaware of any empirical dataset that has been, or could be, analyzed using more than two of the methods. The numerical simulations were based on Tilman's consumer-resource model (Tilman 1977) with two species of phytoplankton competing for two essential resources (See Supporting Information A). For each set of resource conditions, we performed numerical simulations that represent four distinct methods: 1) fitting the Lotka-Volterra model (Figure 1), 2) the sensitivity method (Figure 2), 3) the method using Tilman's CRM (Figure 4), and 4) the NFD method (Figure 5).

Figure 6 shows that under specific limiting assumptions, all four methods made the same prediction about coexistence and these predictions matched the outcome based on the simulations. However, this agreement among the methods was conditional on how the Lotka-Volterra and NFD methods were implemented. The Lotka-Volterra method only matched the predictions for coexistence from the other methods when we assumed that intraspecific competition coefficients were equal to the inverse of the carrying capacity (Supporting Information Figure A1; Section 1.2). Similarly, the NFD method only matched the predictions for coexistence from the other methods when we 1) evaluated the slope of NFD when species' frequencies were approaching zero and 2) used both the slope and the intercept to predict the growth rate when frequency approaches zero (Supporting Information Figure A1).

*1.8 Do the methods yield the same values of ND and RFD?*

Although the methods gave the same predictions regarding coexistence, Figure 6 (F and G) shows that the methods do not yield the same values of ND and RFD, even when applied to the same simulated study system. The Lotka-Volterra method (using the simplification that  $\alpha_{ii}=1/K_i$ ) and the sensitivity method gave identical estimates of ND and RFD across the range of resource conditions used, but these estimates differed from the method based on Tilman's consumer resource model. This disparity can be explained by the fact that the Lotka-Volterra and sensitivity methods assume that per capita inter- and intraspecific interaction coefficients are independent of species' densities. In contrast, the method based on Tilman's consumer resource model does not assume that interaction coefficients are independent of species densities, but instead quantifies both inter- and intraspecific interaction coefficients only at the steady-state densities predicted for monocultures that undergo invasion. This means that the interaction

coefficients, and thus ND and RFD, measured according to either of the phenomenological methods (Figures 1 and 2) are unlikely to match the values predicted from a mechanistic method, even though both can correctly predict mutual invasibility.

## **Part 2. An Empiricist's Guide to Selecting a Method to Estimate ND and RFD**

Having described and compared the foundation of each empirical method, here in Part 2 of the paper we offer practical guidance to help empiricists determine 1) which method(s) are most appropriate for their study system and 2) how much experimental effort is required for each method. To aid our discussion, we have summarized the methods in Table 1, which is organized into three sections. The section labeled 'Decision Steps' is a decision tree that allows an empiricist to identify the most appropriate method for their study system. The section labeled 'Method' directs the empiricist to the key literature needed to implement the approach. Last, the section of the table labeled 'Experimental Requirements' outlines key aspects of the experiments that are required to use the method.

### *2.1 Decision Steps - deciding which method to use*

The first decision step in Table 1 asks whether the method must yield estimates of ND and RFD that can be directly related back to Chesson's inequality (Equation 1, Box 1). Thus, Question 1 isolates the NFD method from all others. This distinction is important since the outputs from the NFD method cannot be compared to the other four methods. However, the NFD method can accurately predict coexistence based on mutual invasibility and, depending on the answers to the remaining questions, it could be the most appropriate method for certain study systems. In particular, the NFD method is the only option that does not require an empiricist to

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3 451 grow each species alone as a monoculture (Question 2). This could be an advantage for study  
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8 453 The next decision step asks whether the empiricist knows which specific resources the  
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10 454 species are competing for and can quantify the dependence of each species' population dynamics  
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12 455 on those resources (Question 3). This question separates the four methods for estimating ND and  
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14 456 RFD into two separate groups. The phenomenological methods (Lotka-Volterra and sensitivity  
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16 457 method) are those that are informed by directly quantifying species interactions, but which make  
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18 458 no assumptions about the resources that species are competing for (highlighted in green). The  
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20 459 mechanistic methods based on MacArthur's CRM or Tilman's CRM assume that species interact  
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22 460 only by competing for shared resources (highlighted in blue). In certain cases, it will not be  
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24 461 possible for an empiricist to answer 'yes' to Question 3, because the resources required for  
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26 462 species to grow are either not known or cannot be readily quantified. When one cannot answer  
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28 463 yes to Question 3, then the Lotka-Volterra and sensitivity methods may be appropriate. Because  
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30 464 Question 3 is so consequential, the remaining steps are particular to either the phenomenological  
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32 465 or mechanistic methods.  
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37 466 Deciding between the Lotka-Volterra method and the sensitivity method  
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39 467 (phenomenological methods, highlighted in green), depends on whether the method must work  
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41 468 for observational datasets (Question 4), whether it is necessary to experimentally grow each  
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43 469 species at its carrying capacity (Question 5), and whether the method can be used to predict  
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45 470 coexistence among 3 or more species simultaneously (Question 7). An empiricist working with  
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47 471 long-lived species or in protected habitats would likely answer 'observational' to Question 4,  
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49 472 eliminating the sensitivity method. In this case, the empiricist would need to decide whether it is  
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51 473 essential to obtain values of ND and RFD compatible with the other four methods (requiring the  
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Lotka Volterra method) or whether the NFD method could be employed to predict mutual invasibility and thus coexistence. Question 5 could be particularly important for studies performed using slow-growing species where it is possible to estimate the carrying capacity term from a time series of species densities, but it would take too long for the species to approach the carrying capacity to justify beginning an invasion by the other species. Lastly, only the sensitivity method can be used beyond pairwise species interactions (Carroll *et al.* 2011); however, doing so is limited to situations where all non-focal species can be considered in aggregate (e.g. species  $i$  invading a community of  $j + k + l$ ). Deciding between the MacArthur and Tilman CRM methods (mechanistic methods, highlighted in blue), is straightforward and depends on whether the resources that the species compete for are abiotic and governed by a constant rate of supply (e.g. inorganic nutrients consumed by plants) or biotic with their own population dynamics (Question 6).

Depending upon the study system or experimental constraints, an empiricist may have multiple options for which method to use. In these cases, it can be useful to consider the experimental requirements of each method (below) and the tradeoffs among the methods discussed in Part 3.

## 2.2 Experimental requirements

In addition to the 'Decision Steps' outlined in Table 1, there are important practical differences for the experimental or observational studies needed to quantify ND and RFD using each method. The most important difference in study design among these methods is whether or not they require the species to be grown together in order to make a prediction about coexistence. The NFD method and the two phenomenological methods require each pair of species to be

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3 497 grown together in at least one co-culture, but the mechanistic methods do not require these co-  
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5 498 cultures. This distinction means that only the mechanistic methods can be used to make  
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7 499 predictions about coexistence of species without performing pairwise competition experiments or  
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10 500 analyzing time series from co-cultures.  
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12 501 Another practical difference among the methods is that, depending on the study design,  
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14 502 experiments using the phenomenological methods can require more experimental treatments to  
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17 503 predict pairwise coexistence among a pool of species than the mechanistic methods do. For the  
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19 504 phenomenological methods, the number of experimental treatments required for all pairwise  
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21 505 combinations of species increases exponentially with each additional species being considered.  
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24 506 In contrast, for the mechanistic methods the total number of experimental treatments required  
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31 509 of species being considered and also the number of resources. When the number of species being  
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33 510 considered is small and the number of limiting resources is few, the difference in experimental  
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35 511 effort can be modest. For example, to predict pairwise coexistence among a pool of four species,  
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37 512 using the sensitivity method requires 16 experimental treatments (time series): 4 monocultures to  
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39 513 parameterize both maximum growth rate and carrying capacity and 12 invasions to parameterize  
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41 514 sensitivity (A invading B, B invading A, etc.). In contrast, using either of the consumer resource  
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44 515 models (two limiting resources) would require two experiments per species for a total of 8  
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46 516 experiments. If the mechanistic methods require parameterizing four or more limiting resources,  
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48 517 then the phenomenological methods may be more efficient for a pool of four species. However,  
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51 518 for larger pools of species the difference can be substantial. Obtaining pairwise estimates of ND  
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and RFD for a pool of 10 species requires between 55 and 180 treatments for the phenomenological methods but as few as 20 treatments for mechanistic methods.

In addition to the number of experimental treatments required for each method, it is important to consider the amount of effort and time required for phenomenological methods. In the case of the NFD and sensitivity methods, these time series may be short in duration (i.e. at least one generation) and focused only on population dynamics when species densities are very low or near the steady-state density of monocultures. However, the Lotka-Volterra method requires longer time series in order to parameterize both the interaction coefficients and carrying capacities. Longer time series in monoculture and co-culture are more easily attainable for quickly-growing species like microbes, but even short time series could be prohibitively arduous for slowly growing species like trees.

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### 531 **Part 3. Tradeoffs Among Methods and Suggested Future Directions**

Having explained how to select and implement the five methods, we offer some advice for empiricists about navigating tradeoffs among the methods, how to compare and synthesize measurements of ND and RFD from different methods, and lastly, key future directions for implementing modern coexistence theory empirically.

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#### 537 *3.1 Tradeoffs between phenomenological and mechanistic methods*

It is highly likely that empiricists will face tradeoffs when selecting a particular method for their study system. The most obvious and important tradeoffs occur between the phenomenological methods and the mechanistic methods, which differ in two important ways. First, the phenomenological methods (i.e. the NFD, Lotka-Volterra, and sensitivity methods)

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3 542 make no assumptions about the resources that species compete for. This could be beneficial for  
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5 543 empiricists who can still measure ND and RFD even if they lack detailed information about the  
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8 544 biological resources that species compete for. But the trade-off for this lack of knowledge is the  
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10 545 need for pairwise experiments to directly quantify ND and RFD, which causes the total effort to  
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12 546 increase exponentially as more species are considered. Second, the results of phenomenological  
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14 547 experiments are specific to each pair of species tested and cannot be generalized to interactions  
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17 548 beyond that pair. An empiricist who is able to answer ‘yes’ to Question 3 in Table 1 could use a  
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19 549 mechanistic method to predict coexistence (or not) for not only the species pair of interest, but  
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21 550 any and all species pairs of interest based solely on experiments that are performed with each  
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23 551 species grown alone in monoculture. Third, the predictions from the phenomenological methods  
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27 553 used in that experiment and cannot be generalized outside of those same conditions. However,  
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30 554 the mechanistic methods also offer the capability to make predictions about species coexistence  
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32 555 under different environmental conditions (e.g. nutrient conditions (Letten *et al.* 2017)). This  
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34 556 capability of the mechanistic methods to handle some changes to environmental context, while  
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44 560 *3.2 Comparing and synthesizing measurements of ND and RFD*

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47 561 To date, only three of the four methods proposed for measuring niche and relative fitness  
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49 562 differences have been used empirically. Furthermore, we are unaware of any study that has  
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51 563 applied more than one method to the same empirical study system. As such, we have no way to  
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53 564 compare the performance of the methods empirically. Therefore, we believe an important avenue  
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for future research is to measure ND and RFD using different methods within the same study system to demonstrate equivalence or non-equivalence of these methods.

Even as we call for more comparative studies, we caution against the inevitable urge to synthesize ND and RFD through an informal data synthesis or more formal meta-analysis. Although all five methods can correctly predict the qualitative outcome of coexistence, the methods are by no means mathematically or practically equivalent. As we have shown, the methods will not always yield the same ND and RFD, even when applied to the same species and environmental conditions. Indeed, given the differences in how the methods are implemented (Figures 1-5), there is no reason to expect, *a priori*, that the methods are directly comparable. Therefore, measurements produced using different methods should not be mixed-and-matched to produce some synthesized estimate of the niche or fitness difference for, say, grassland plants.

### *3.3 Future directions for implementing modern coexistence theory*

In our view, there are at least two important new directions that work on species coexistence must go if Chesson's modern coexistence theory is to become widely implemented and more practical. First, each of the empirical methods described in this review are focused on fluctuation-independent mechanisms. It is well-known that environmental fluctuations mediate species coexistence in some empirical systems (Caceres 1997; Jiang & Morin 2007) and any modern theory of coexistence is incomplete without them. There have been limited empirical studies that explicitly quantify the fluctuation dependent mechanisms, i.e. relative nonlinearities and storage effects (but see (Angert *et al.* 2009; Letten *et al.* 2018)). Ellner *et al.* (2019) recently showed how fluctuation-dependent and fluctuation-independent mechanisms can be quantified through numerical simulation of mechanistic models (as opposed to the analytical solutions used

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in the methods based on Tilman’s and MacArthur’s CRM). This approach is not focused on estimating ND and RFD, but can be used to predict coexistence based on the mutual invasibility criterion and can decompose invasion growth rates to understand the impacts of environmental fluctuations and even species’ traits. Importantly, the approach by Ellner et al. can accommodate non-competitive interactions such as facilitation, which are not compatible with Chesson’s original derivation using the Lotka-Volterra model (but see (Bimler *et al.* 2018)). However, despite this versatility, the approach used by Ellner et al requires a parameterized model of intraspecific and interspecific interactions, so it has the same limitations as the mechanistic methods described here. To also include fluctuation-dependent mechanisms of coexistence in Chesson’s framework, we need to expand the scope of the five methods reviewed here or even develop new empirical methods.

Second, empirical studies on coexistence need to move beyond prediction of pairwise species interactions. Several authors have recently emphasized that modern coexistence theory is under-developed for multi-species systems (Carroll *et al.* 2011; Levine *et al.* 2017; Ellner *et al.* 2019). In theory, the pairwise competitive hierarchy between species *i* versus *j* and *j* versus *k* might not directly translate to species *i* and *k*, particularly when these species are engaged in intransitive competition or higher-order interactions (Levine *et al.* 2017). In fact, none of the three phenomenological methods (the NFD, Lotka-Volterra and sensitivity methods) can deal with intransitive competition or higher-order interactions. Importantly, the emphasis to date on pairwise interactions and experimentation means that intransitive competitive interactions and higher-order interactions, if present, are unaccounted for in our understanding. Chesson’s coexistence framework has been a major advance for understanding coexistence among pairs of

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3 610 species, and how to expand this framework to multi-species systems should be a priority for the  
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For Review Only

### Box 1. Brief review of Chesson's theory

When Chesson first introduced his theory for coexistence, he did not prescribe a specific empirical approach or experiment that should be used to estimate ND and RFD in real biological communities. Instead, he used a phenomenological model of competition to show how the mutual invasibility criterion, a prerequisite for coexistence, depends on how each species limits their own growth rate versus that of their competitor (Chesson 1990). For a pair of species to coexist, ND must be sufficiently large to offset and stabilize the competitive hierarchies generated by RFDs. Specifically, he showed that the criterion for mutual invasibility can be expressed as an inequality involving both ND and RFD (Equation 1).

$$1 - ND < RFD < \frac{1}{1 - ND} \quad (1)$$

In this inequality, the term  $1 - ND$  represents the degree of niche overlap ( $\rho$  in Chesson (1990)), which ranges from zero when species do not share any resources to one when the resource requirements of species are identical. RFD represents the ratio of competition-free fitness among the two species ( $\frac{f_j}{f_i}$  in Chesson (1990)). When two species exhibit identical niches (ND equals 0), their RFD alone determines the competitive hierarchy and which species will become extinct. If this inequality is not satisfied, then one of the species is unable to maintain long-term, positive growth rates and will go locally extinct.

Because ND and RFD are not terms that cannot be quantified directly from experiments or observations, Chesson showed how these forces can be derived from the classic Lotka-Volterra competition model. In this model, the *per capita* growth rate of species  $i$  is a function of both intraspecific and interspecific competition as described by Equation 2:

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \left( 1 - \alpha_{ii} N_i - \sum_{j \neq i} \alpha_{ij} N_j \right) \quad (2)$$

In Equation 2,  $N_i$  is the density of species  $i$ , and  $r_i$  is the intrinsic per capita growth rate of species  $i$ . The intra-specific competition coefficient  $\alpha_{ii}$  describes the *per capita* effect of species  $i$  on the *per capita* relative growth rate of species  $i$  and is equal to the inverse of the carrying capacity ( $K_i$ ) for species  $i$ . The inter-specific competition coefficient  $\alpha_{ij}$  describes the *per capita* effect of species  $j$  on the *per capita* relative growth rate of species  $i$ . Equations 3 and 4 relate the inter- and intra-specific interaction coefficients from the Lotka-Volterra model to ND and RFD:

$$ND = 1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} \quad (3)$$

$$RFD = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}} \quad (4)$$

ND and RFD from Equations (3) and (4) can then be used in Equation 1 to predict coexistence. Because Chesson derived ND, RFD and the inequality for mutual invasibility based on the Lotka-Volterra competition model, we use the same approach to explain four of the empirical approaches described below and show that a fifth approach is ultimately not compatible with Chesson's derivation.

## Supporting Information

In the supporting information section, we provide: (A) Numerical Simulation of Experiments to Measure ND and RFD and Predict Coexistence, (B) Relating the Sensitivity Method to Chesson's Definition of ND and RFD Using the Lotka Volterra Model, and (C) Relating the Negative Frequency Dependence Method to Chesson's ND and RFD. A Wolfram Mathematica notebook used for the simulations is provided as a separate file.

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Decision Steps:	1: Must the method yield estimates of ND and RFD (i.e. Chesson's inequality)?	No	Yes	Yes	Yes	Yes
	2: Can you grow each species as a monoculture?	Yes or No	Yes	Yes	Yes	Yes
	3: Do you know the resources the species are competing for?	No	No	No	Yes	Yes
	4: What type of study will be used to parameterize the model?	Experimental or Observational	Experimental or Observational	Experimental	Experimental	Experimental
	5: Does the method require $\geq 1$ species at steady-state near its carrying capacity?	No	No	Yes	No	No
	6: Is the resource abiotic (non-dynamic), biotic (dynamic), or undefined?	Undefined	Undefined or biotic (dynamic)	Undefined	Biotic (dynamic)	Abiotic* (non-dynamic)
	7: Can the method predict coexistence among 3 or more species simultaneously?	Yes	No	Yes	Yes	No
Method		Negative frequency dependence	Lotka-Volterra	Sensitivity	MacArthur's CRM	Tilman's CRM
	Foundational paper for model	Rees and Westoby 1997	Volterra 1928	MacArthur 1970	MacArthur 1970	Tilman 1977
	Theoretical paper linking model to MCT	Adler et al 2007	Chesson 2000	Carrol et al 2011	Chesson 1990	Letten 2017
	Empirical paper using model for MCT	Yenni et al 2017	Godoy and Levine 2014	Narwani et al 2013	none	Letten 2017
Experimental Requirements	Does the method require the species to be grown together?	Yes	Yes	Yes	No	No
	How many experimental treatments required to measure ND and RFD for all pairs of n species?	$m \cdot n \cdot (n-1)$ , where $m \geq 2$	$n + [n(n-1)/2]$	$n^2$	$m \cdot n$ , where m= number of resources	$m \cdot n$ , where m= number of resources
	Are time-series of species densities required?	Yes, $\geq 1$ generation	Yes, enough generations to approach k	Yes, $\geq 1$ generation	No	No

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722 Table 1. A practical guide to help empiricists determine which method(s) are most appropriate for a given study system and question.

723 See Part 2 for a step-by-step explanation of this guide. \* While consumer-resource models that include a second trophic level (e.g.

724 predators, P\*) have been developed and used empirically, these approaches have not been linked to ND and RFD.

## Figures

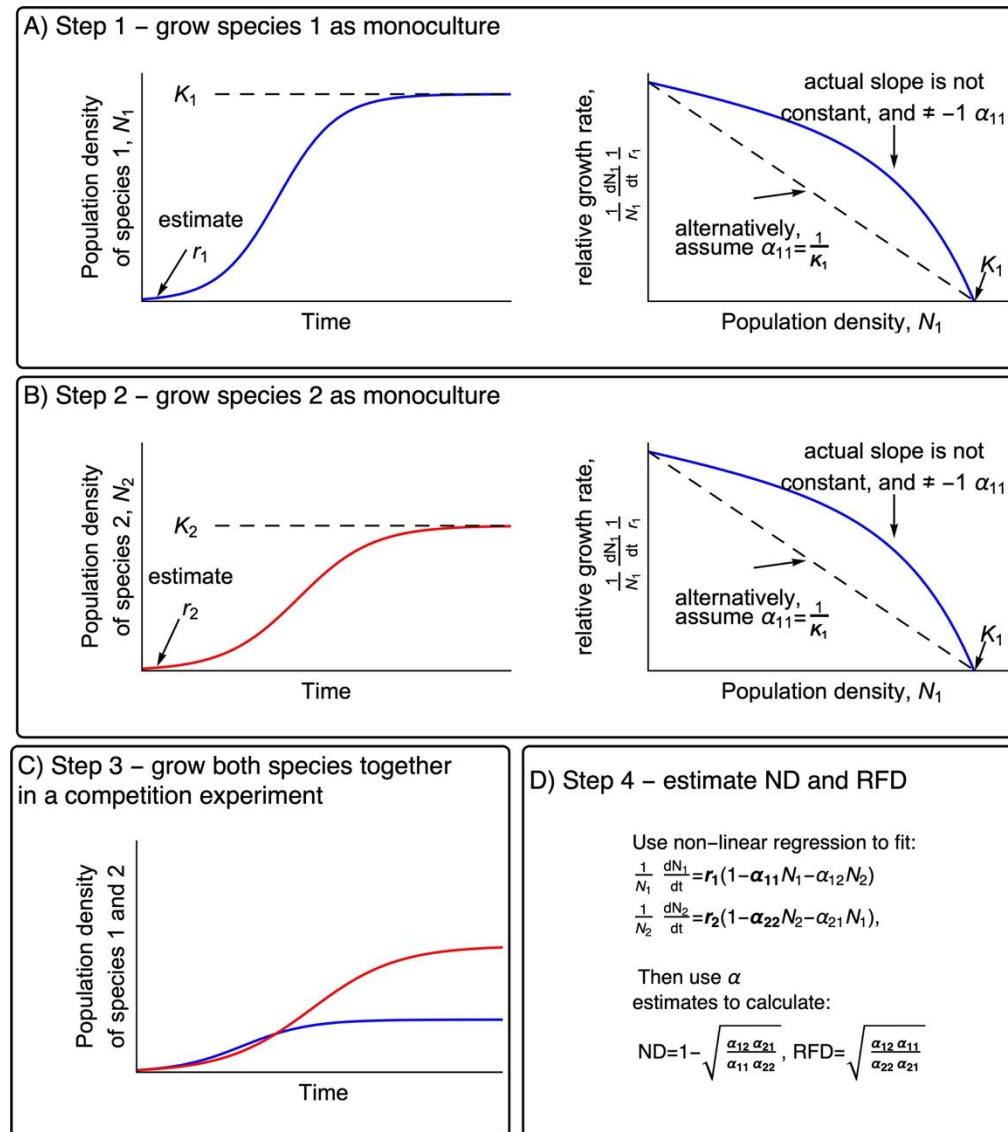


Figure 1. Conceptual plots illustrating how to use the Lotka-Volterra method to estimate ND and RFD for use in Chesson's inequality (Equation 1). In each panel, unknown parameters are displayed in regular typeface and previously-estimated parameters are listed in bold typeface. In panels A and B, the left-hand plots show the time course of the experiment and the right-hand plots show the relative growth rate as a function of population density – the slope of this relationship is equal to the intraspecific competition coefficient (sign reversed).

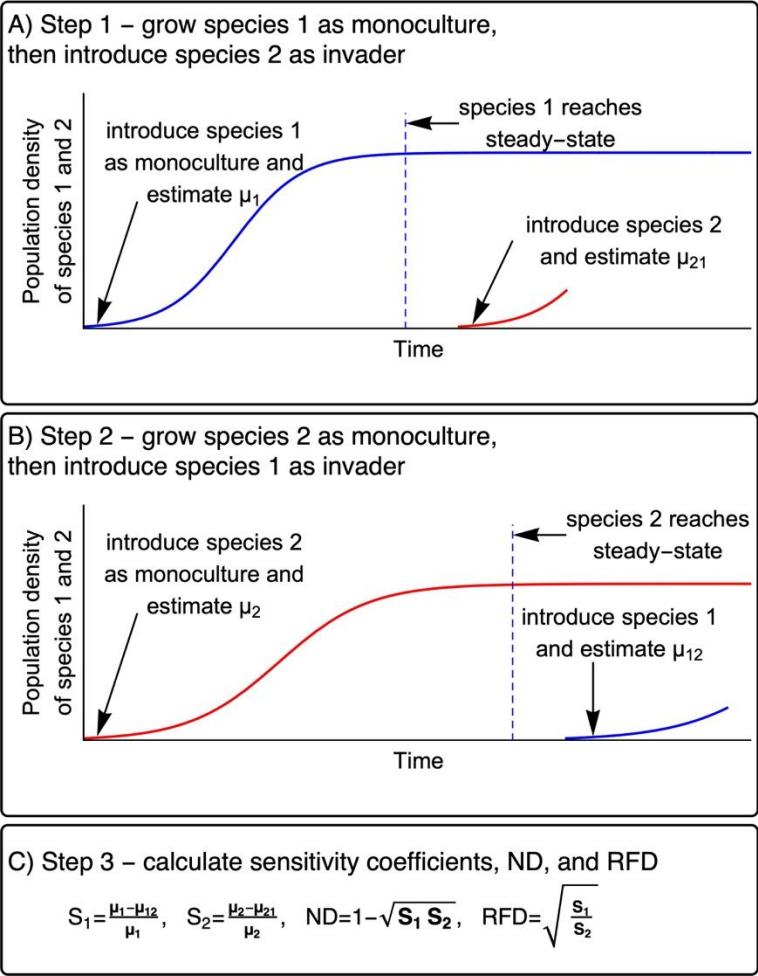


Figure 2. Conceptual plot depicting how to implement the sensitivity method in an experiment.

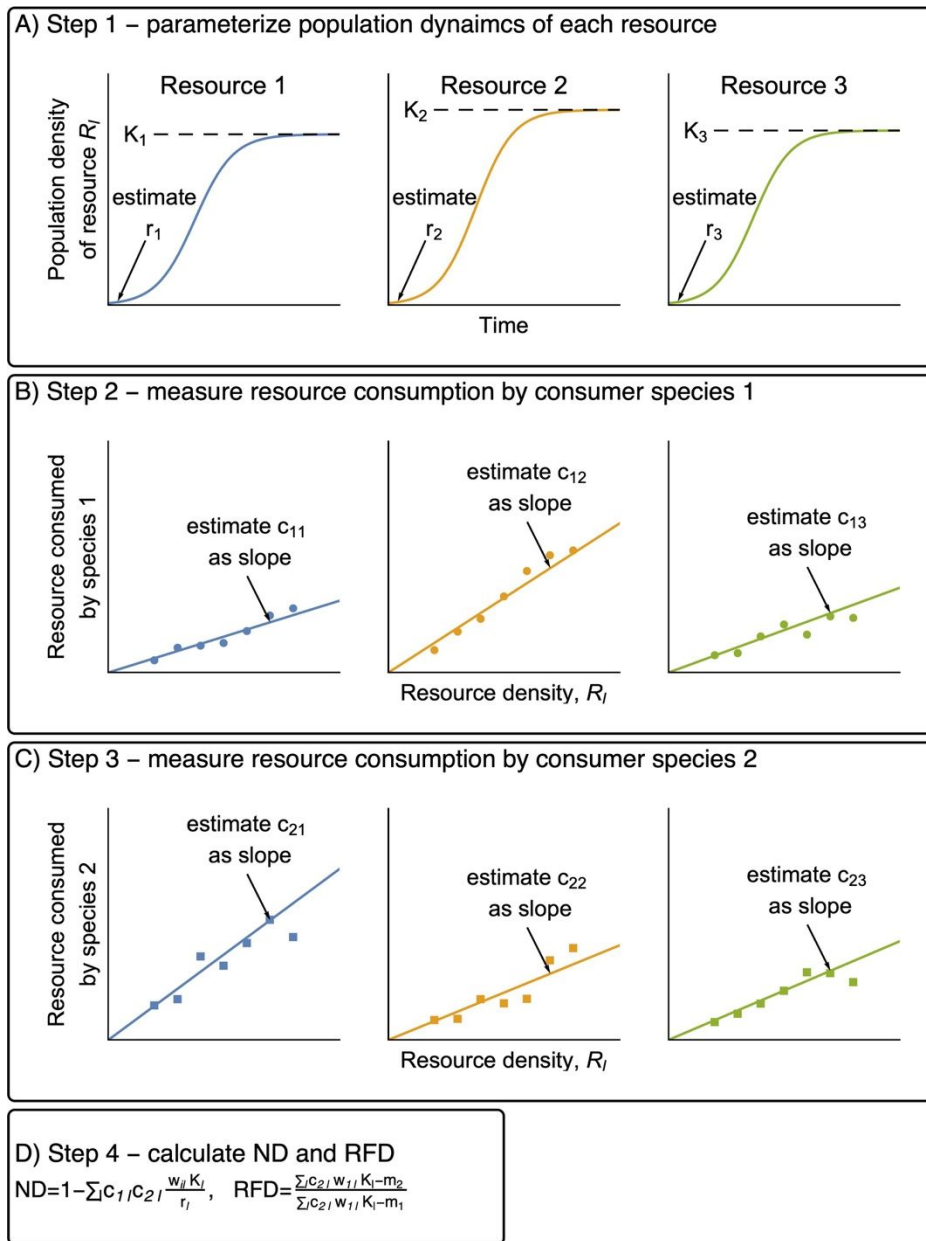


Figure 3. Conceptual plots depicting how the method based on Mac Arthur's CRM could be implemented. The yield term ( $w_{il}$ , increase in consumer units per unit prey resource consumed), can be estimated by measuring these changes for each combination of consumer and resource.

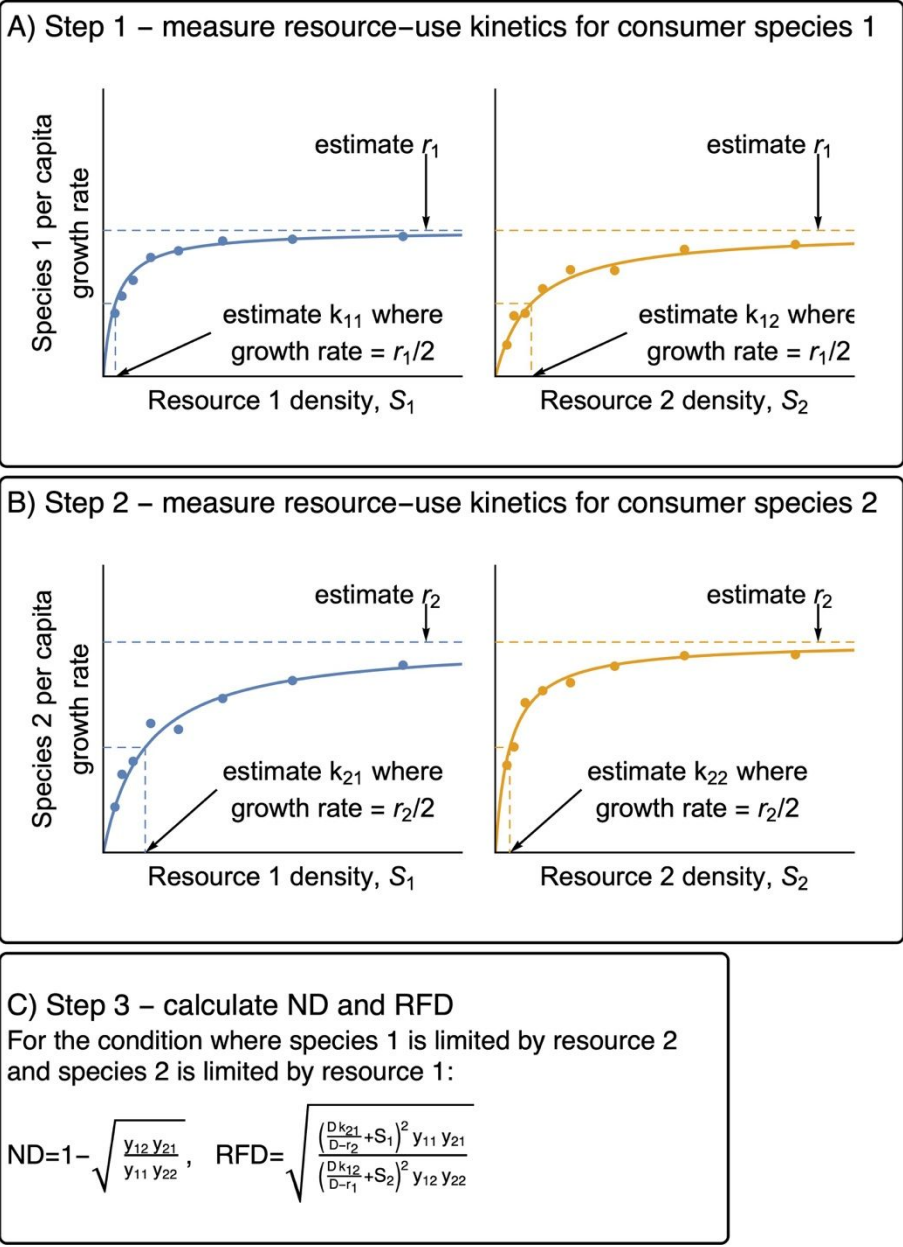


Figure 4. Conceptual plot depicting how to parameterize the method based on Tilman’s consumer resource model. Panels A and B show the experiments needed to parameterize the maximum growth rates and Monod half-saturation constants for growth on each resource, separately for each species. The yield of each species on each resource ( $y_{ii}$ ) can be estimated by measuring the amount of resource consumed by a known number of individuals.



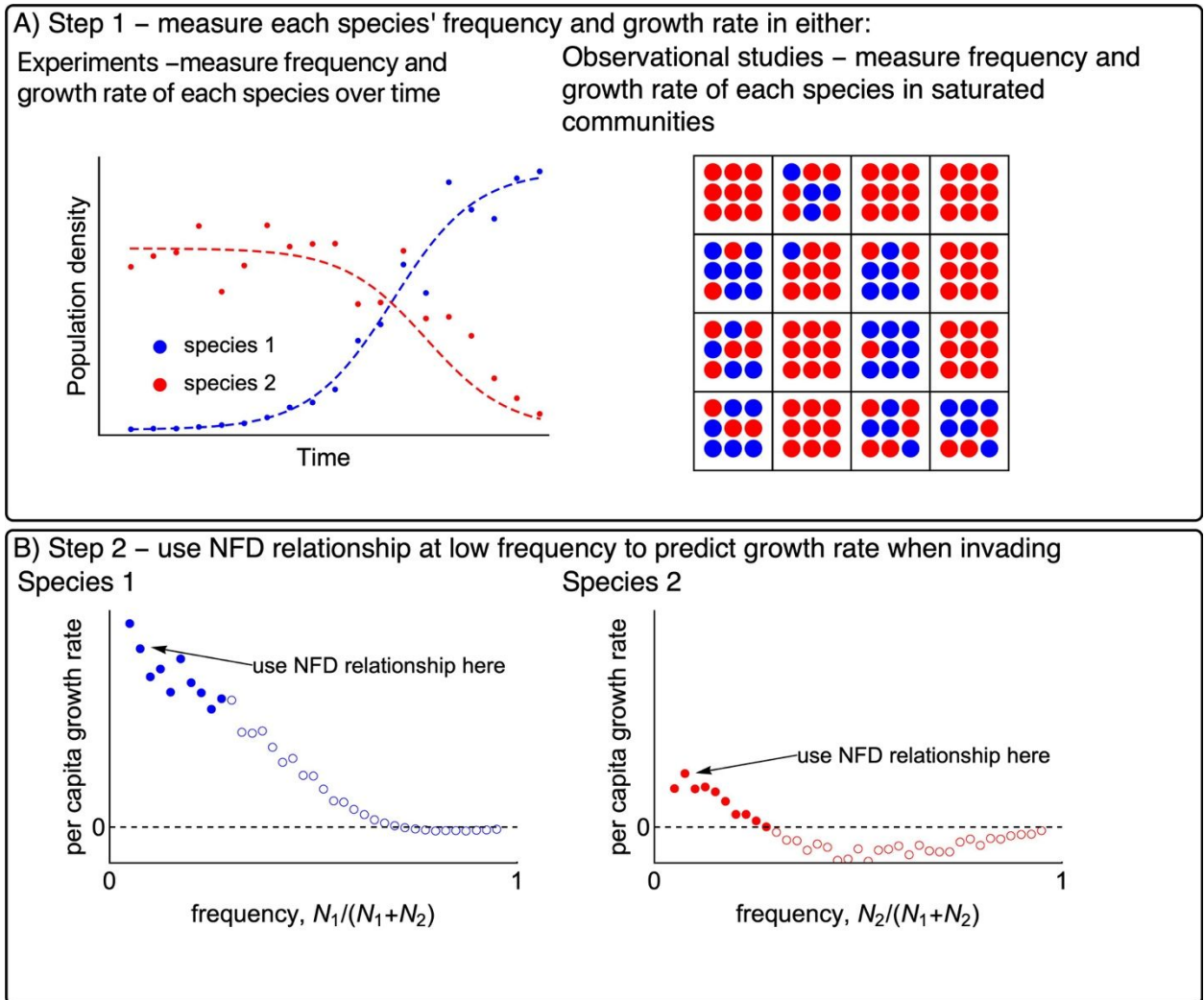


Figure 5. Conceptual diagram depicting how the NFD method could be implemented, either through an experiment or using observational data from different communities. Panel A shows two options for obtaining pairs of each species' frequency and its growth rate in a saturated community. The first option is to track population densities over time in one or more competition experiments. The second option is to obtain pairs of frequency and growth rate from different communities or habitat patches in a natural ecosystem. Panel B depicts how the data from either experiments or observational studies would be used to estimate the growth rate when frequency approaches zero.

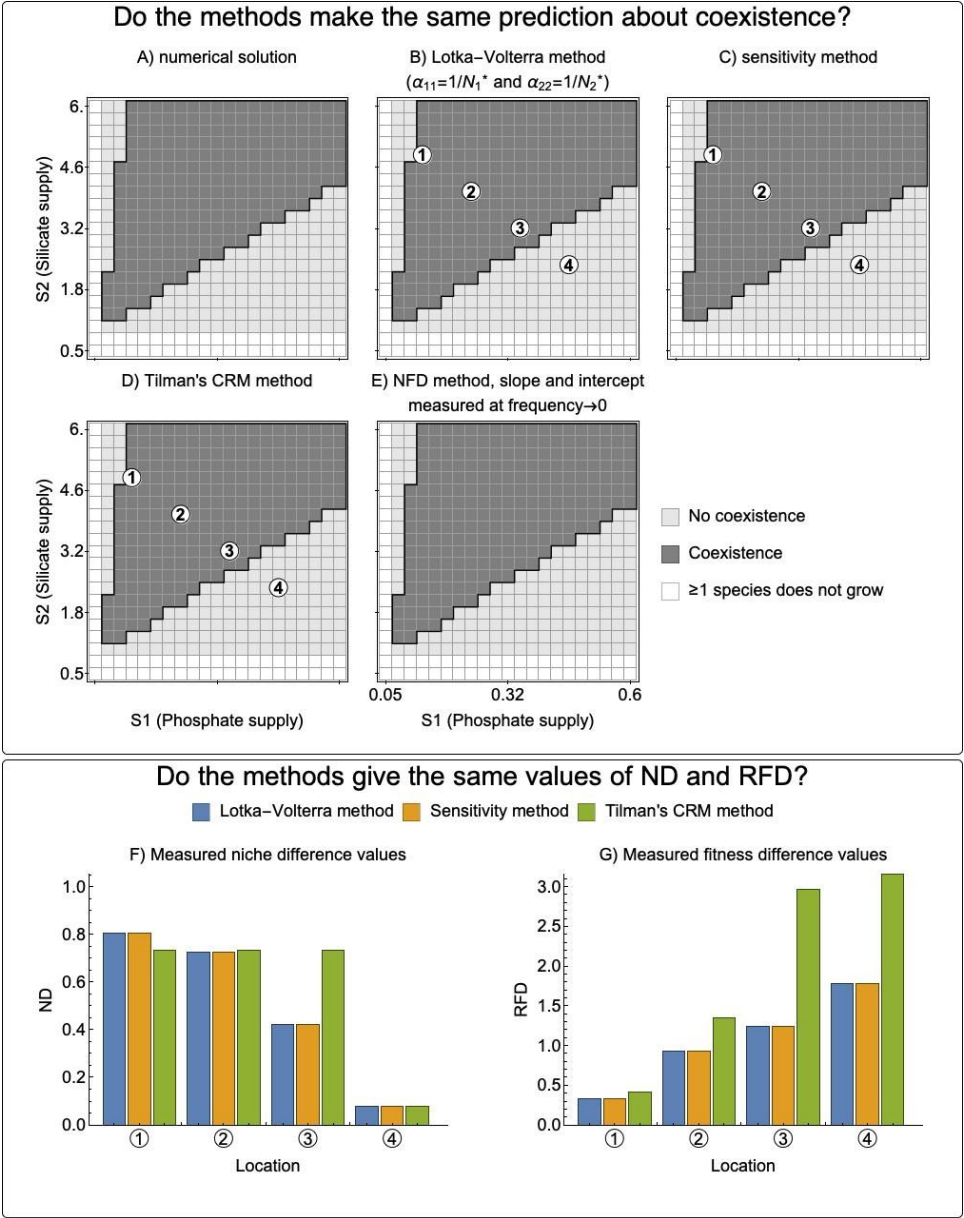


Figure 6. Comparison of four methods for predicting coexistence and estimating ND and RFD.

The methods were compared using simulations based on Tilman's parameterized CRM (Supporting Information A). In panels A-E, the predictions for coexistence are compared against the coexistence outcome based on numerical simulation. White shading means that at least one species does not grow under that combination of resource supply concentrations, light gray shading indicates that the method predicts that the species will not coexist, and dark shading



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3 765 indicates that the model predicts coexistence. The raw RFD values from the sensitivity method  
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5 766 were converted to the same ordering as used in the other methods (species  $i$  in the denominator  
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7 767 rather than the species with the greater sensitivity). Because the NFD method cannot be used to  
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9 768 produce values of ND and RFD that are comparable with the other four methods, only the  
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11 769 predictions regarding coexistence are plotted.  
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**Supporting Information A: Simulation of Experiments to Measure ND and RFD and Predict Coexistence**

In this supplement, we present numerical simulations that compare the outcomes from three methods for measuring ND and RFD and also the NFD method for predicting coexistence. We used Tilman’s parameterized consumer-resource model for two species of phytoplankton competing for essential and non-substitutable resources (Tilman 1977). Annotated code for the simulations is provided in a supplemental file. Simulations were performed using the function NDSolve in Mathematica 11.2 (Wolfram Research), employing a variable step size. For each set of resource supply concentrations, we performed four simulations: (1) species 1 as a monoculture, growing from rare to near its equilibrium density; (2) species 2 as a monoculture, growing from rare to near its equilibrium density; (3) species 1 at its equilibrium density, with species 2 invading from rare; (4) and species 2 at its equilibrium density, with species 1 invading from rare. Additionally, we performed numerical simulation where both species are introduced at low densities and asked whether they coexist at the equilibrium. For each set of simulations, we manipulated the supply concentration of the two resources in order to determine whether the methods consistently agree.

We implemented the Lotka-Volterra method using information from all four simulations described above. Simulations 1 and 2 were used to estimate  $r_i$ ,  $K_i$ , and intraspecific interaction coefficients  $\alpha_{ii}$ . We estimated the intraspecific interaction terms using two different approaches (Section 1.2). First, we estimated  $\alpha_{ii}$  as the slope of the relative growth rate versus population density (sign reversed) as the monoculture simulations approach equilibrium (Figure 1). Alternatively, we used the assumption that  $\alpha_{ii}=1/K_i$ . We then used the parameter values from the monocultures, along with simulations 3 and 4, to solve Equation 2 when each species is at low

density and the other is near equilibrium. We used all four interaction coefficients to calculate ND and RFD using Equations 3 and 4. We implemented the sensitivity method following Equations 5 through 7, using output from all four simulations. The raw RFD values from the sensitivity method were converted to the same ordering as used in the other methods (species  $i$  in the denominator rather than the species with the greater sensitivity).

As described in Appendix C, the NFD method cannot be used to get ND and RFD estimates that are consistent with the other methods, but nonetheless this method can be used to predict coexistence based on the same criterion. However, as shown in Figure 5 (using the Lotka-Volterra model), accuracy of the NFD method depends on the range of frequencies used to get the slope and elevation. To illustrate how the non-constant NFD slope is problematic in predicting species coexistence, we used the simulations of mutual invasion (simulations 3 and 4), described above, to construct pairs of each species' frequency and their growth rate in a saturated community. For all of these simulations, we used only supply concentrations of the resources that are known to allow for coexistence. For each value of a species frequency between 0 and 1, we calculated the slope of growth rate versus frequency. Figure A1 shows that this slope is not constant and actually changes sign depending on the species' frequencies used. Thus, using only the slope of the NFD relationship is inadequate to predict coexistence.

Next, we used both the slope and elevation from the NFD method to extrapolate to frequency of 0 and predict whether the species is capable of invasion from rare (Figure A2 panels A and B). Figure A1 shows that for supply conditions known to allow coexistence, the accuracy of the predictions from the NFD method depends on the range of frequencies over which the slope of NFD was measured. We discuss two points (A and B in Figure A1) to explain this effect. At the point Labeled "A", the slope of NFD for species 1 predicts a positive growth

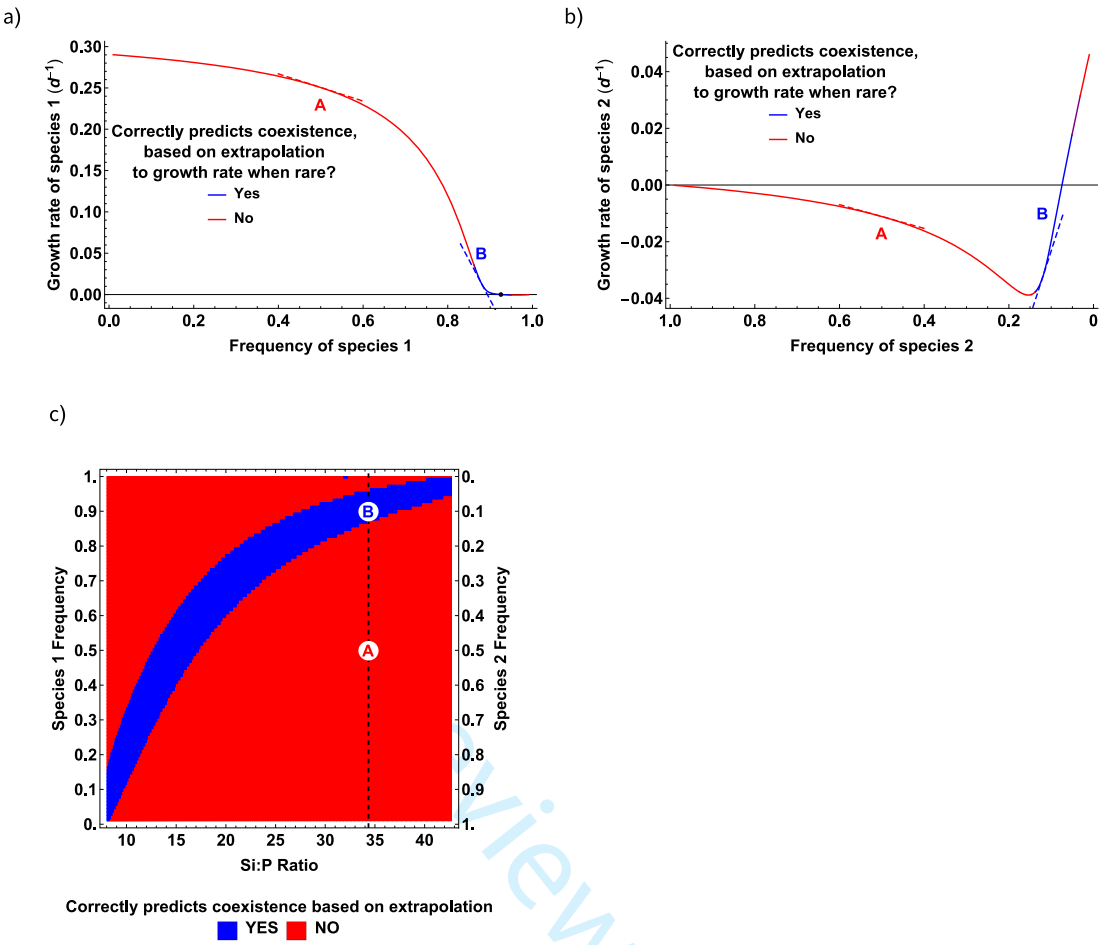
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3 818 rate as frequency approaches 0, but at the complementary frequency of species 2, the slope of  
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5 819 species 2's NFD predicts a negative growth rate when rare. However, based on the other 3  
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7 820 methods, numerical simulation, and Tilman's resource ratio theory, the species are predicted to  
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9 821 coexist. Thus, measuring NFD under the red regions in Figure A1 will incorrectly predict  
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11 822 exclusion even though the species will coexist. At the point labeled "B" in Figure A1, the slope  
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13 823 and elevation of NFD for both species predicts a positive growth rate when rare. This region,  
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15 824 depicted in blue, includes the equilibrium frequency for the two species. If an empiricist made  
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17 825 their measurements between frequency of ~0.05 to ~0.85 for species 1, and used the slope of  
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19 826 NFD, they would incorrectly predict that the species will not coexist. Since the frequency at  
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21 827 which the species reach equilibrium depends on the resource supply ratio, there is no single  
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23 828 frequency of the species that consistently leads to the correct predictions (Figure A1). While  
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25 829 certain intermediate frequencies of the two species can be used to make accurate predictions, an  
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27 830 empiricist would not know these frequencies without performing the competition experiments or  
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29 831 examining frequency dependence across the entire range of frequencies. As a result, the only  
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31 832 reliable way of implementing the NFD is to measure the slope and elevation for each species  
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33 833 where its frequency approaches zero.

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35 834       Next, we compared the four methods including the sensitivity method, the method based  
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37 835 on Tilman's CRM, the Lotka-Volterra method, and the NFD method using the numerical  
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39 836 simulations described above. Under specific assumptions, the methods gave the same prediction  
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41 837 regarding coexistence (Figure A2), though the methods did not produce consistent estimates of  
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43 838 ND and RFD (Figure 6).

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45 839       For the NFD method, accurate predictions required that the slope of NFD was evaluated  
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47 840 approaching frequency of zero for each species (i.e. invasion conditions). In Figure A2 d-f, we

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3 841 show that evaluating the NFD slope at other frequencies leads to the wrong predictions. We used  
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5 842 the NFD plot to evaluate coexistence at three frequencies, including near 0% (panel c of Figure  
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7 843 A2) and 50% (panel e), and either with or without considering the elevation in addition to the  
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9 844 slope (panels d, f). We see that using the NFD slope evaluated at near 0% frequency will  
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11 845 consistently yield accurate predictions of species coexistence that match the those of the other  
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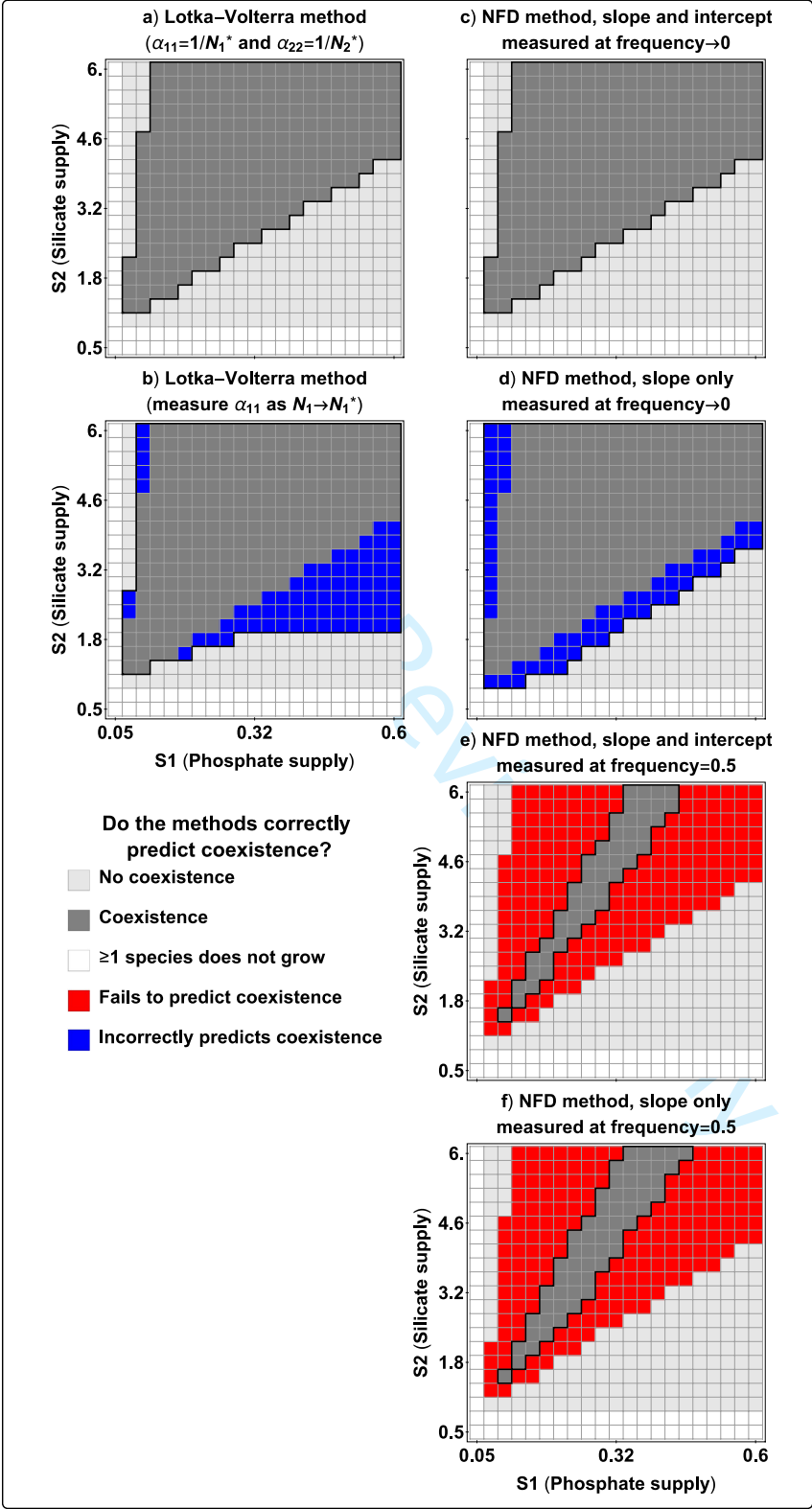


Supporting Information Figure A1. Results of simulation experiments using the NFD method.

Panels a and b show per capita growth rate versus the frequency of species 1 and 2. At any frequency of the two species, the NFD method requires that we use the slope to extrapolate and estimate the growth rate when frequency approaches zero (the extrapolated vertical intercept). For frequencies where this method predicts mutual invasibility for both species, i.e. species can coexist, the lines are blue. For frequencies of the two species where the method leads to the incorrect prediction, the lines are red. Both species have positive growth rates when their frequency approaches zero, indicating that they are mutually invisable. Panel c shows the accuracy of the NFD method as a function of the supply Si:P ratio and the frequency of the two species at which the method was applied. The vertical dashed line represents the slice depicted in

panels a and b. For all of the Si:P ratios shown in panel c, the species are mutually invisable and will coexist. This plot indicates that using NFD will often predict that the species will not coexist, when in fact they do coexist. This is important because without examining the full range of species frequencies in an experiment, one would not know whether and where the relationship between frequency and growth rate is non-linear.

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Supporting Information Figure A2. Results of simulation experiments comparing predictions from the Lotka-Volterra and NFD methods.



## Supporting Information B: Relating the Sensitivity Method to Chesson's Definition of ND and RFD Using the Lotka-Volterra Model

Here we show that sensitivity method is identical to the Lotka-Volterra method given the specific limiting assumptions of the sensitivity method. To do this, we derive the sensitivity metric ( $S_i$ ) from the Lotka-Volterra competition model (Equation 2). The  $\mu_i$  in Equation 5 is the maximum per capita growth rate in monoculture, equal to  $r_i$  in Equation 2. The  $\mu_{ij}$  is the invasion growth rate, so that we can replace  $N_j$  with species  $j$ 's carrying capacity,  $K_j$ , and replace  $N_i$  with 0, so that  $\mu_{ij} = r_i (1 - \alpha_{ij} K_j)$ . Using this substitution, we show in Equation B1 that the sensitivity metric ( $S_i$ ) is the equilibrium density of species  $j$  ( $K_j$ ) multiplied by the *per capita* competition coefficient ( $\alpha_{ij}$ ).

$$S_i \equiv \frac{\mu_i - \mu_{ij}}{\mu_i} = \frac{r_i - r_i(1 - \alpha_{ij} K_j)}{r_i} = \alpha_{ij} K_j \quad (\text{B1})$$

Since the intraspecific competition coefficients in the Lotka-Volterra model are equal to the inverse of the equilibrium population density for the monoculture ( $\alpha_{ii} = \frac{1}{K_i}$ ), the sensitivity metric can be shown to be equivalent to the ratio of interspecific to intraspecific interaction coefficients (Equation B2).

$$S_i = \alpha_{ij} K_j = \alpha_{ij} \frac{1}{\alpha_{ii}} = \frac{\alpha_{ij}}{\alpha_{ii}} \quad (\text{B2})$$

From this substitution, we can relate the sensitivity metric to Chesson's ND (Equation B3), RFD (Equation B4), and use these estimates to assess the conditions for coexistence (Equation 1)

$$\text{ND} = 1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} = 1 - \sqrt{S_i S_j} \quad (\text{B3})$$

$$\text{RFD} = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}} = \sqrt{\frac{S_i}{S_j}} \quad (\text{B4})$$

## Supporting Information C: Relating the Negative Frequency Dependence Method to Chesson's ND and RFD

Here we show that in order for the NFD slope to be constant, the community density must be both saturated and fixed across all frequencies of the species. To do so, we attempt to derive the NFD slope and intercept from the two species Lotka-Volterra competition model (Equation 1). Since there is no variable representing each species' frequency in the Lotka-Volterra model, we have to assume a fixed community density,  $B$ . This assumption also satisfies the assumption of the NFD method that the community density is always saturated. Fixing the community density makes the interspecific density dependence,  $\alpha_{ij}$ , equivalent to frequency dependence (Adler *et al.* 2007), and allows species' frequency to be represented by  $N_i/B$ . The two-species Lotka-Volterra competition model can then be rewritten as follows

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \left( 1 - \frac{\alpha_{ii}N_i + \alpha_{ij}(B - N_i)}{B} \right) \quad (C1)$$

, where  $B$  is the fixed community density and one unit decrease of  $N_i$  will lead to one unit increase of  $N_j$ . From Equation C1, we derive the NFD slope and intercept in the following equations.

$$NFD \text{ slope} \equiv \frac{\frac{1}{N_i} \frac{dN_i}{dt}}{\frac{N_i}{B}} = \frac{\frac{1}{N_i} \frac{dN_i}{dt}}{\frac{1}{B} \partial N_i} = B \frac{\frac{1}{N_i} \frac{dN_i}{dt}}{\partial N_i} = r_i(\alpha_{ij} - \alpha_{ii}) \quad (C2)$$

$$NFD \text{ intercept} \equiv r_i(1 - \alpha_{ij}) \quad (C3)$$

In Equation C2 the NFD slope becomes constant, which means that species' per capita growth rate linearly depends on its frequency.

In addition, from Equations C2 and C3, we argue that both NFD intercept and slope should be used with caution in evaluating Chesson's inequality. First, the NFD intercept represents whether species can successfully invade a steady-state population of its competitor at its carrying capacity, so it can be used to accurately assess mutual invasibility. However, neither the difference nor the ratio of two species' NFD intercepts (Equations C2 and C3) take an

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3 912 analogous form to Chesson's definition of ND and RFD. Thus, while the NFD method can  
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5 913 correctly predict mutual invasibility, the NFD intercept and slope should not be interpreted as  
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8 914 RFD and ND in order to evaluate Chesson's inequality.  
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10 915       The utility of the NFD method depends on its ability to correctly predict whether species  
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12 916 have positive growth rates when their frequencies approach zero. If the relationship between a  
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14 917 species frequency and its growth rate is non-linear, however, then the accuracy of the NFD  
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17 918 method is critically dependent on the range of species frequencies used by an empiricist. In  
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19 919 Figure C1 we show that the NFD relationship is non-linear even when the underlying population  
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21 920 dynamics are governed by the Lotka-Volterra model. The result of this non-linearity is that,  
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24 921 depending on the range of species' frequencies used to estimate the NFD slope and intercept, this  
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26 922 method can give inaccurate predictions.  
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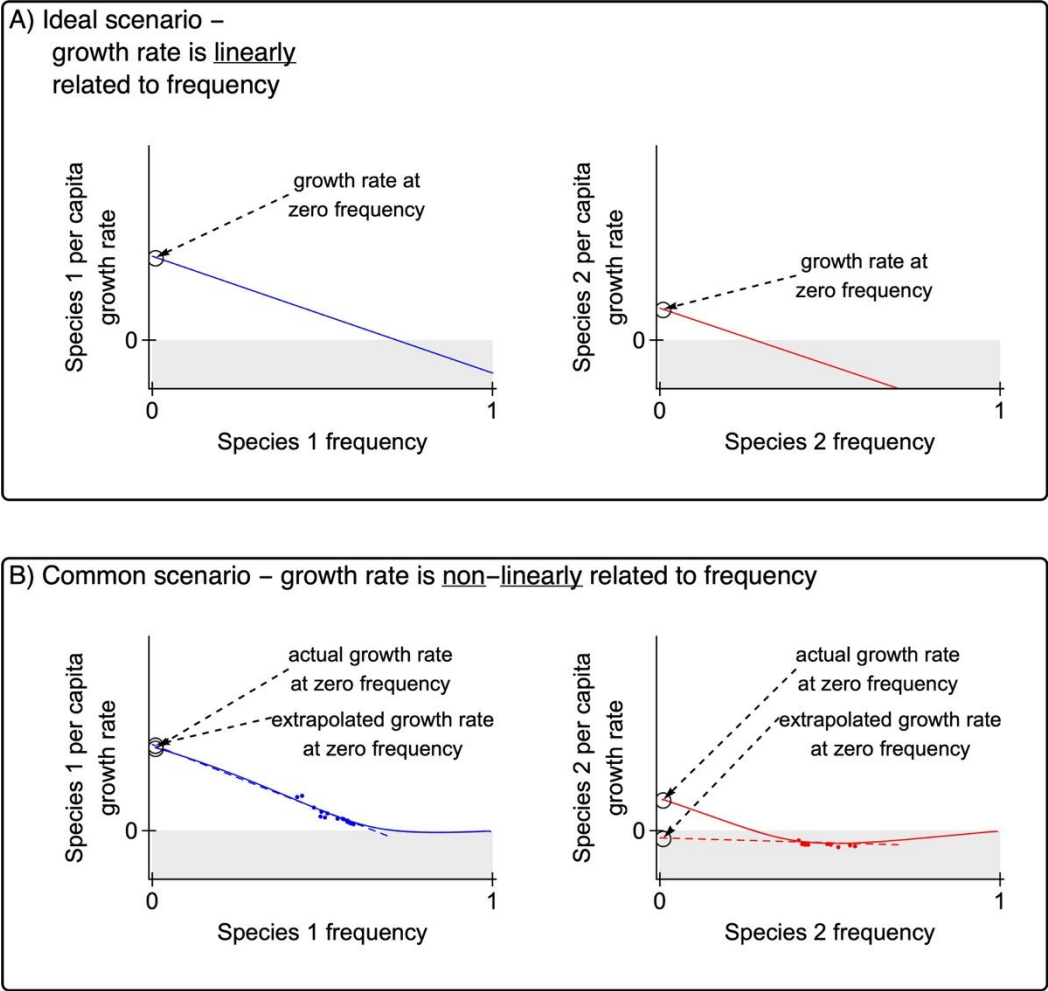


Figure C1: Panel A shows a hypothetical situation where species frequencies are linearly related to their growth rate and an empiricist can extrapolate to predict growth rates at frequency of zero and diagnose mutual invasibility. Panel B shows the more likely scenario in which growth rates are non-linearly dependent upon species frequencies. These plots were made using numerical simulation of the two-species Lotka Volterra Model, using parameter values that should allow for coexistence (at frequency of 0.72 for species 1). The points in Panel B represent measurements collected at intermediate frequency of both species. Using those measurements and extrapolating to zero frequency yields the incorrect prediction that the species will not coexist.

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