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An empiricist's guide to modern coexistence theory for competitive communities

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<p>Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.</p>	
Empiricist's Guide Supplemental Computer Code.nb	

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 quantifying 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 six 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’ resource use 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.

Introduction

Throughout most of the history of community ecology, it has been assumed that niche differentiation among species is the primary biological mechanism that can offset the negative impacts of interspecific competition on species coexistence (Chase and Leibold 2003, Gause 1934, Leibold 1995, Tilman 1982). 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 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 (MacArthur 1970, MacArthur and Levins 1967, Rescigno and Richardson 1965, Tilman 1977). 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 hypothesized that niche differences are not required for coexistence (Hubbell 2001). Instead, he argued that 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 neutral 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 will only coexist for long time periods 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.

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 variation in biological traits such as potential growth rates or resistance to consumers (Barabás et al. 2018, Chesson 2018). 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. competition for a limiting resource) (Barabás et al. 2018, Ellner et al. 2019, Miller and

Klausmeier 2017). Thus, Chesson's framework provides a general framework for predicting species coexistence.

Since the development of Chesson's theory, much attention in ecology has turned towards the empirical estimation of ND and RFD in order to determine how these forces contribute to coexistence in real communities. Empiricists have proposed several different approaches to quantify ND and RFD in specific study systems. The various methods for quantifying ND and RFD were derived from different models of species interactions, make different assumptions, and use different experimental designs. Therefore, it remains unclear which method(s) are best suited for a given study, whether the methods give comparable estimates of ND and RFD, and whether the methods actually make the same prediction regarding coexistence. If Chesson's theory is to become widely implemented in empirical studies and in applied contexts, we need a 'users guide' to help ecologists decide among these empirical approaches and identify potential shortcomings and pitfalls for each method.

Here we provide a summary and comparison of five methods that have been proposed to measure ND and RFD empirically, and a sixth method that does not give estimates of ND and RFD but has been used to predict coexistence based on Chesson's theory. In Part 1, we explain the theoretical basis of each method, illustrate how it can be implemented empirically, and ask whether the methods yield the same estimates of ND and RFD. In Part 2 we provide a list of decision steps to guide empiricists in selecting the most appropriate method(s) for their study system and aims. In Part 3, we discuss the main advantages and disadvantages of the methods and make suggestions for future empirical work on coexistence theory.

Part 1. Summary of Empirical Methods for Implementing Chesson's Theory

In this part of the paper we briefly summarize Chesson's theory, then summarize each of five empirical methods for measuring ND and RFD by explaining how the methods relate to Chesson's theory, how they can be implemented empirically, and highlight critical limitations and assumptions.

1.1. 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, Chesson's criterion for mutual invasibility can be expressed as an inequality involving both ND and RFD (Equation 1, following (Carroll et al. 2011, Narwani et al. 2013)).

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

In this inequality, the term $1 - ND$ represents the degree of niche overlap (ρ in Chesson (1990, 2018)), 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 ($\frac{k}{k_i}$ 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.

Chesson showed how ND and RFD can be derived from the classic Lotka-Volterra competition model (Chesson 2000). 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 α_{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 α_{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 (Chesson 2018):

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

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

ND and RFD estimates from Equations (3) and (4) can then be used in Equation 1 to predict coexistence. The focus of this review is to provide empiricists with a practical guide to selecting and implementing empirical methods for modern coexistence theory. Other recent papers provide a more detailed exploration of the mechanics of modern coexistence theory and its extension to other aspects of ecology (Barabás et al. 2018, Broekman et al. 2019, Chesson 2018, Ellner et al. 2019, Hart et al. 2018).

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 five different empirical approaches for estimating ND and RFD.

1.2 Method based on the Lotka-Volterra model for continuous reproduction

Since Chesson originally used the Lotka-Volterra model to explain his criterion for coexistence (Section 1.1), the most direct empirical approach for estimating ND and RFD is to parameterize the Lotka-Volterra competition model for continuous reproduction (Equation 2) using data collected from experiments or time-series observations from natural ecosystems.

1.2.1 Empirical approaches. While numerous studies have parameterized the Lotka-Volterra model for continuous reproduction, relatively few empirical studies have parameterized the model in order to calculate ND and RFD (Armitage and Jones 2019). Empiricists have two options for estimating the per capita intraspecific (α_{ii} and α_{jj}) and interspecific competition coefficients (α_{ij} and α_{ji}) needed to calculate ND and RFD using Equations 3 and 4. The first option is to measure the population density of each species over time, using plots or microcosms containing each species grown as a monoculture and, separately, one co-culture of the two species (Figure 1). From these time series, the empiricist would fit Equation 2 for each pair of species using maximum likelihood, Bayesian, or least-squares methods (for details see (Armitage and Jones 2019, Geijzenborffer et al. 2011, Pascual and Kareiva 1996)) and obtain the four interaction terms used in Equations 3 and 4.

An alternative option is to avoid fitting the Lotka Volterra model directly to the timeseries and, instead, use simplifications to derive inter- and intraspecific interaction coefficients from the carrying capacities and short-term growth rates observed in experiments (Figure 1). From each monoculture timeseries, the empiricist could 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). The

intraspecific interaction coefficients could be estimated as the slope of each species' per capita growth rate as a function of its own population density (Figure 1, right), although this slope can be non-linear in practice (see Limitations, below). Alternatively, an empiricist can assume that intraspecific interaction coefficients are equal to the inverse of the carrying capacity for each species in monoculture ($\alpha_{ii}=1/K_i$). Next, the empiricist can substitute parameter estimates from the monocultures and use linear regression to estimate the interspecific interaction coefficients (α_{ij} and α_{ji}) in Equation 2 from growth rates observed near equilibrium. We illustrate these steps in the Supplemental Computer Code. Finally, the empiricist can use all four interaction coefficients to compute ND and RFD using Equations 3 and 4.

1.2.2 Limitations. A critical assumption of this approach is that the intra- and inter-specific competition coefficients of the Lotka Volterra model are fixed with respect to population sizes of either species. In other words, the first individual and the last individual added to a population are assumed to have the same per capita effect on the growth rates of its own species or that of its competitor. This assumption is not always met in real biological communities where intra- and inter-specific competition coefficients can depend on species' densities (Abrams 1980, Chesson 2018, Smith-Gill and Gill 1978). Appendix A in the Supporting Information shows that, when applied to numerical simulations based on a well-known consumer resource model, intraspecific coefficients measured in monoculture near 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 approach can be used to estimate ND and RFD.

1.3 Annual plant model for discrete reproduction

Although the Lotka-Volterra method for continuous reproduction is seldom used to estimate ND and RFD, there is extensive empirical work using similar models where reproduction occurs at discrete intervals. The annual plant model for discrete reproduction (Adler et al. 2007, Chesson 2008) is used most frequently to estimate ND and RFD (Bimler et al. 2018, Broekman et al. 2019, Godoy and Levine 2014, Godoy et al. 2017, Lanuza et al. 2018, Levine and HilleRisLambers 2009, Matías et al. 2018), but the closely related Ricker (Chu and Adler 2015, Hart and Marshall 2013) and Beverton-Holt (Cushing et al. 2004, Fujiwara et al. 2011, Germain et al. 2016, Hart et al. 2018) models could also be employed using a similar approach.

1.3.1 Empirical approaches. Unlike the Lotka-Volterra model for continuous reproduction, which requires long timeseries for parameterization, the methods for discrete growth can be parameterized based on a single generation. To do this, an empiricist would grow each focal species at multiple different population densities of its own species and that of its competitor (Godoy and Levine 2014). At the end of the growing season, the number and viability of seeds produced by each individual plant in the absence of competition is used to calculate the proportion of seeds lost prior to the next growing season (η_i) and a fecundity term (λ) used in Equation 5:

$$N_{i,t+1} = \frac{\lambda_i N_{i,t}}{1 + \alpha_{ii} N_{i,t} + \alpha_{ij} N_{j,t}} \quad (5)$$

In this model, $N_{i,t}$ is the density of species i at time t and the interaction coefficients (α) are equivalent to those in the Lotka-Volterra model but describe effects of competition on fecundity instead of growth rate. Using the density and fecundity of each focal species and its competitor, an empiricist can use maximum likelihood, least squares, or Bayesian methods to fit the

interaction coefficients needed to calculate ND following Equation 2 and RFD following Equation 6 (Bimler et al. 2018, Godoy and Levine 2014, Lanuza et al. 2018, Matías et al. 2018):

$$RFD = \frac{\eta_i - 1\sqrt{\alpha_{ji}\alpha_{jj}}}{\eta_j - 1\sqrt{\alpha_{ij}\alpha_{ii}}} \quad (6)$$

Levine and HilleRisLambers (2009) demonstrated how the annual plant model can be implemented experimentally to estimate niche differences. In their study with 10 species of grassland plants, they manipulated the density of each focal species by varying the number of seeds belonging to the focal species versus all other species. At the end of the growing season, they quantified ND as described above. Then, using their estimates of ND from this method, they experimentally removed the impact of those ND to illustrate that ND was partially responsible for coexistence.

1.3.2 Limitations. An obvious limitation of the annual plant model is that it can only be applied to species and communities that follow discrete reproduction. This makes the method attractive for studying plant communities, but it could be impractical for other communities which are better suited to the Lotka-Volterra method for continuous reproduction or one of the other methods summarized here. Also, similar to the Lotka-Volterra model for continuous reproduction, this method assumes that the inter- and intraspecific interaction coefficients are independent of species' densities. To verify that this assumption is met, an empiricist would need to grow each species and combination at several different densities in their experiment to check for approximate linearity. Another limitation of the annual plant model, and also the Lotka-Volterra model for continuous reproduction, is when species engage in direct facilitation (Rohr et al. 2014). Specifically, facilitation can make one or more interaction coefficients negative, which is problematic for the calculation of ND and RFD following Equations 3 and 4. Bimler et al (2018) demonstrate a solution that can be employed when species exhibit facilitation.

226

227 *1.4 Sensitivity method*

228 The third method for estimating ND and RFD, the sensitivity method, is similar to the
 229 Lotka-Volterra method in that it requires information from direct competition experiments. The
 230 sensitivity method quantifies the proportional reduction in a species' growth rate when invading
 231 a steady-state population of its competitor (Carroll et al. 2011, Narwani et al. 2013). In this
 232 method, the maximum growth rate of each species in monoculture (μ_i) and when invading a
 233 steady-state population of the competitor species (μ_{ij}) are used to calculate each species'
 234 sensitivity to interspecific competition (S_i) using Equation 7:

$$235 \quad S_i \equiv \frac{\mu_i - \mu_{ij}}{\mu_i} \quad (7)$$

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

$$238 \quad ND = 1 - \sqrt{S_i S_j} \quad (8)$$

$$239 \quad RFD = \sqrt{\frac{S_i}{S_j}} \quad (9)$$

240 A species' sensitivity to competition is jointly determined by ND and RFD (Carroll et al.
 241 2011, Narwani et al. 2013). Specifically, greater ND between the two species reduces the impact
 242 of interspecific competition so that S_i will approach zero. Greater RFD, on the other hand, causes
 243 species to be asymmetrically affected by competition such that one species' sensitivity increases
 244 while the other's decreases. While Carroll and others (2011) verbally argued that this method is
 245 compatible with Chesson's theory, in Appendix B we show explicitly how this method relates to
 246 Chesson's theory and prove that it is identical to Equations 3 and 4 when evaluated at the steady-
 247 state population density of the resident species.

248 1.4.1 Empirical approaches. The experiment by Narwani et al. (2013) provides an
249 example for how to implement the sensitivity method empirically (see also (Gallego et al. 2019,
250 Grainger et al. 2019, Li et al. 2019)). Their experimental system involved species of freshwater
251 green algae growing under controlled conditions in the laboratory. They grew each species as a
252 monoculture, starting from low densities and allowing the populations to reach their carrying
253 capacity. From these time series, they quantified the per capita maximum growth rate of each
254 species as a monoculture (μ_i and μ_j), which occurs when the focal species is at low density. After
255 each species reached its carrying capacity, they introduced the other species from low density
256 (e.g. 0.01% of K) and quantified the per capita growth rate of each species when invading the
257 other (μ_{ij} and μ_{ji}). Finally, for each pair of species, they used these growth rates to calculate the
258 sensitivity metrics (S_i and S_j) using Equation 7 and used those sensitivity metrics to calculate ND
259 and RFD using Equations 8 and 9.

260 1.4.2 Limitations. Despite its simple design and straightforward parameterization, the
261 sensitivity method has several limitations. First, the method is only practical for organisms that
262 can be grown as monocultures and whose population growth rates can be measured over
263 tractable periods of time. Second, this method requires that the resident species is maintained at a
264 steady-state population density, which could be difficult to achieve outside a chemostat system.
265 Third, it is important to note that the invasion growth rates (μ_{ij} and μ_{ji}) must be measured when
266 the invader population density is low. If the growth rate of the invader species were measured at
267 greater density of the invader species or lower density of the resident species (i.e. long after
268 invasion), then the S_i would be affected by both intra- and inter specific competition and the
269 resulting prediction regarding coexistence could be incorrect. Finally, the sensitivity method can
270 only be applied to competitive interactions. When species engage in facilitation, invasion growth

rates could be higher than when grown in monoculture ($S_i < 0$), making Equations 8 and 9 inappropriate.

1.5 Parameterizing MacArthur's consumer resource model

The fourth method to estimate ND and RFD from empirical data is to parameterize MacArthur's consumer-resource model (MacArthur 1970) then use these parameters to calculate ND and RFD (Carroll et al. 2011, Chesson 1990, Chesson 2000). This method is different from the Lotka-Volterra, annual plant model, and sensitivity methods because it does not rely on experiments where the species are grown together in order to quantify how the species influence each other's growth rates. Instead, this method works by parameterizing a mechanistic model that describes how species consume, and thus compete for, two or more prey resources (MacArthur 1970), then reorganizing those parameters following an analytical solution to estimate ND and RFD for assessing Chesson's inequality.

MacArthur's CRM is composed of differential equations representing the growth of each consumer species as a function of resource densities (Equation 10) and a differential equation (or set) that describes the population dynamics of each prey resource and their mortality due to consumption by the consumers (Equation 11).

$$\frac{1}{X_i} \frac{dX_i}{dt} = b_i \left(\sum_{l=1}^m c_{il} w_{il} R_l - m_i \right) \quad (10)$$

$$\frac{1}{R_l} \frac{dR_l}{dt} = r_l \left(1 - \frac{R_l}{K_l} \right) - \sum_{i=1}^n c_{il} X_i \quad (11)$$

In this model X_i is population density of the consumer species i and R_l is population density of the prey resource l . The term b_i represents the effect of prey consumption on the growth rate of the consumer, r_l is the maximum per-capita growth rate of prey resource l , K_l is the carrying capacity for the prey species l , w_{il} represents the increase in consumer population density for

each unit of prey resource l consumed. The term c_{il} is the resource capture rate by consumer i on resource l and m_i is the density-independent mortality for consumer species i . By implementing a time-scale separation technique (Chesson 1990), parameters in MacArthur's consumer resource model can be used to calculate ND and RFD using Equations 12 and 13 (Carroll et al. 2011):

$$ND = 1 - \sum_l c_{il} c_{jl} \frac{w_{il} K_l}{r_l} \quad (12)$$

$$RFD = \frac{\sum_l c_{jl} w_{il} K_l - m_j}{\sum_l c_{il} w_{jl} K_l - m_i} \quad (13)$$

The estimates of ND and RFD from this method can then be used to evaluate Chesson's inequality and predict coexistence.

1.5.1 Empirical approaches. Because we are not aware of any empirical studies that have parameterized the MacArthur model for the purpose of estimating ND and RFD, we describe the experimental approach that would be required (Figure 3). First, the empiricist would identify or define the prey resources that are available to the consumer species. Each prey resource would be inoculated or planted at low density into an environment free of other prey resources and consumers (see Lotka Volterra model for continuous reproduction), then the population density would be measured over time in order to estimate the per capita maximum growth rate of the prey (r_l , which occurs as the prey population density approaches zero) and its carrying capacity (K_l , which occurs when the prey growth rate approaches zero). Next, the experimentalist would introduce each consumer species into several different densities of each prey resource growing as a monoculture. Under those different prey resource densities, the experimentalist would measure the per capita consumption rate of prey resource by the consumer species (c_{il} , by linear regression of consumption versus prey density) and the yield of consumer density or biomass per unit prey resource consumed (w_{il}). These parameters can then be used in Equations 12 and 13 to

obtain ND and RFD, which can subsequently be used directly in Equation 1 to predict coexistence.

1.5.2 Limitations. The method based on MacArthur's model requires as many consumption experiments as there are resources, and each of these experiments involves 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.

1.6 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). While Tilman's R^* model was extended to include biotic resources (Tilman 1982), there is not presently an analytical translation of that model to obtain ND and RFD. 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 resources (Equation 14) and another set of equations describes the dynamics of abiotic resources and their depletion due to uptake by the consumer and dilution (Equation 15).

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \min \left[\frac{S_i}{S_i + k_{ii}}, \frac{S_j}{S_j + k_{ij}} \right] - D \quad (14)$$

$$\frac{1}{R_i} \frac{dS_i}{dt} = D(S_{i0} - S_i) - \sum_{i=1}^n \frac{N_i}{y_{ii}} r_i \min \left[\frac{S_i}{S_i + k_{ii}}, \frac{S_j}{S_j + k_{ij}} \right] \quad (15)$$

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 16 and 17 can be used to estimate ND and RFD:

$$ND = 1 - \sqrt{\frac{y_{12}y_{21}}{y_{11}y_{22}}} \quad (16)$$

$$RFD = \frac{\sqrt{\left(\frac{D k_{21}}{D - r_2} + S_1 \right)^2 y_{11}y_{21}}}{\sqrt{\left(\frac{D k_{12}}{D - r_1} + S_2 \right)^2 y_{12}y_{22}}} \quad (17)$$

1.6.1 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.

1.6.2 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.

1.7 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 (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 and HilleRisLambers 2009, Schreiber et al. 2019).

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 and 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 steady-state monoculture at its carrying capacity and any increase in the population density of one species will be offset by a decrease in population density of another species. Under this assumption, increasing species i 's frequency means that individuals of species i will compete more with individuals of its own kind than with individuals of other species, and will thus experience stronger intraspecific competition than interspecific competition. Therefore, if intraspecific competition is greater than inter-specific competition, the species affects its own growth rate more than it affects the growth rate of other species, and the NFD slope should be negative. As discussed below, this relationship is not always linear and its slope can be positive under some conditions (Godoy and Levine 2014, Levine and HilleRisLambers 2009).

The NFD method is most often used as a graphical approach for understanding the impact of ND (Figure 5). Adler et al. (2007) argue that a more negative NFD slope represents a stronger stabilizing force, which is proportional to the ND in Chesson's inequality. Similarly, they argue that the difference between species' growth rate in the absence of stabilizing forces is the equalizing force, proportional to RFD. Although they did not use the NFD method to estimate ND and RFD, Adler and others showed how both the slope and elevation of the NFD plot are needed to accurately predict whether each species has a positive growth rate at a frequency

approaching 0. If this condition is met, the species are mutually invisable and should coexist based on Chesson's criterion. However, this is not the exclusive condition for coexistence. Recent work has shown that if species exhibit non-linear frequency dependence -positive slopes at some frequencies and negative slopes at other frequencies - they can potentially coexist at intermediate frequencies (Schreiber et al. 2019). However, unless both species have positive growth rates when rare, such scenarios are only locally stable and environmental fluctuations are likely to drive one species extinct. In the next section we discuss how deviations from linearity and/or positive frequency dependence impact empirical application of this approach.

1.7.1 Empirical approaches. The NFD method could be implemented using either experiments or observations from natural ecosystems (Figure 5A). Using the experimental approach, an empiricist would need to ensure that total community density or biomass was saturated such that any decrease in the resident's population density is replaced with 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 different habitat patches or along ecological gradients in natural ecosystems (Adler et al. 2010). 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 determine whether both species exhibit a positive growth rate when their frequency approaches zero (Figure 5B), which is necessary to meet the mutual invasibility criterion for stable long-term coexistence.

Numerous studies have used the NFD approach to illustrate the effects of ND and RFD in both models and real biological communities (Armitage and Jones 2019, Godoy and Levine

2014, Levine and HilleRisLambers 2009, Yenni et al. 2012, Yenni et al. 2017). For example, Levine and HilleRisLambers (2009) 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 regressing the growth rate of each species against its frequency in the initial community. Their experiment showed that 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.

1.7.2 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 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 or demonstrate the impact of ND and RFD. Second, the NFD method assumes that the community density is saturated across the range of species' frequencies observed, but it may not be possible to verify this condition in observational studies based on natural ecosystems. If this assumption were not met, both species could exhibit positive growth rates across all frequencies, which would lead to inaccurate predictions for long-term coexistence.

The third limitation of the NFD method is that the relationship between a species' frequency and growth rate can be nonlinear (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. In Appendix C, we show the NFD method using linear extrapolation can lead to incorrect predictions about species coexistence when applied to systems

with nonlinear relationships between species' growth rates and densities. If the relationship between each species' frequency and its growth rate is nonlinear or locally positive (Schreiber et al. 2019), 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).

1.8 Do the methods give the same prediction regarding coexistence?

Although each of the six 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. Similarly, we could not apply methods based on discrete versus continuous reproduction to the same simulations. 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 for continuous reproduction (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 A2; 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).

1.9 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 not guaranteed 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 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 studies 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). 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 five 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.

Question 2 asks whether the empiricist knows which specific resources the species are competing for and can mechanistically model competition for those resources. This question separates the five methods for estimating ND and RFD into two separate groups. The phenomenological methods (Lotka-Volterra for continuous reproduction, annual plant model, and the sensitivity method, highlighted in green) are those that are informed by directly quantifying species interactions based on experiments or time series, but cannot be used to make *a priori* predictions about coexistence based solely on physiology or population dynamics in monoculture. In contrast, the mechanistic methods (MacArthur's CRM or Tilman's CRM, highlighted in blue) assume that species interact only by competing for specific shared resources and require that the empiricist can parameterize a model describing intra- and interspecific density dependence according to those resources. While some have shown that phenomenological methods such as the annual plant model can be used to quantify the effects of resources or environment on coexistence (Hart and Marshall 2013, Lanuza et al. 2018, Matías et al. 2018), those effects can only be quantified after observing species interactions. In certain cases, it will not be possible for an empiricist to answer 'yes' to Question 2, because the resources required for species to grow are either not known or have not been parameterized. When one cannot answer 'yes' to Question 2, then the phenomenological methods may be appropriate. Because Question 2 is so consequential, the remaining steps are particular to either the phenomenological or mechanistic methods.

Deciding among the Lotka-Volterra method for continuous reproduction, the annual plant model, and the sensitivity method (phenomenological methods, highlighted in green), depends

on the answers to Questions 3 through 6. If the empiricist is unable to grow each species in monoculture (Question 3) then only the annual plant model is available (but see (Lanuza et al. 2018)). Next, an empiricist working with long-lived species or in protected habitats would likely answer ‘observational’ to Question 4, eliminating the sensitivity method. Similarly, if the empiricist is unable to maintain one species at steady-state near its carrying capacity (Question 5), the sensitivity method cannot be used. 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. Finally, Question 6 separates the three phenomenological methods according to whether they can be applied to discrete and/or continuous reproduction.

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 2, see section 1.6).

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 studies needed to quantify ND and RFD using each method. The most

important difference 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 three phenomenological methods require each pair of species to be grown together in at least one co-culture, but the mechanistic methods do not require any co-cultures. This distinction means that only the mechanistic methods can be used to make predictions about coexistence of species without performing pairwise competition experiments or analyzing time series from co-cultures.

Another practical difference among the methods is that, depending on the study design, experiments using the phenomenological methods can require more experimental treatments to predict pairwise coexistence among a pool of species than the mechanistic methods do. For the phenomenological methods, the number of experimental treatments required for all pairwise combinations of species increases exponentially with each additional species being considered. In contrast, for the mechanistic methods the total number of experimental treatments required increases linearly with the number of species being considered. As a result, the relative efficiency of the phenomenological versus mechanistic methods depends upon both the number of species being considered and also the number of resources. When the number of species being considered is small and the number of limiting resources is few, the difference in experimental effort can be modest. If the mechanistic methods require parameterizing four or more limiting resources, then the phenomenological methods may be more efficient for a pool of four species. However, for larger pools of species the difference can be substantial. Obtaining pairwise estimates of ND 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 each method. In the case of the

NFD, annual plant model, and sensitivity methods, these time series may be short in duration (i.e. at least one generation). However, the Lotka-Volterra method for continuous reproduction requires long time series in order to parameterize both the interaction coefficients and carrying capacities, which could be prohibitive except for quickly-growing species like microbes.

Part 3. Tradeoffs Among Methods and Suggested Future Directions

Having explained how to select and implement the different 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.

3.1 Tradeoffs between phenomenological and mechanistic methods

It is 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. NFD, Lotka-Volterra for continuous reproduction, annual plant model, and sensitivity methods) require no assumptions about the resources that species compete for. This could be beneficial for empiricists who can still measure ND and RFD even if they lack a parameterized mechanistic model of resource use and competition. But the trade-off for this simplicity and generality is the need for pairwise experiments to directly quantify interaction coefficients, which causes the total effort to increase exponentially as more species are considered. However, recent papers have shown how the annual plant model can be

parameterized from multispecies communities without pairwise experiments (Lanuza et al. 2018, Matías et al. 2018, Zepeda and Martorell 2019).

Second, the results of phenomenological experiments are specific to each pair of species tested and cannot be generalized to interactions beyond that pair. An empiricist who is able to answer ‘yes’ to Question 2 in Table 1 could use a mechanistic method to predict coexistence (or not) for not only the species pair of interest, but any and all species pairs of interest based solely on experiments that are performed with each species grown in monoculture. Third, the predictions from the phenomenological methods are specific to the exact environmental conditions, like resource density or resource supply rates, used in that experiment and typically cannot be generalized outside of those same conditions (but see (Hart and Marshall 2013, Lanuza et al. 2018)). However, the mechanistic methods offer the capability to make predictions about species coexistence under different environmental conditions (e.g. nutrient conditions (Ellner et al. 2019, Letten et al. 2017)). This capability of the mechanistic methods to handle some changes to environmental context, while limited, could be useful for predicting how anthropogenic stressors (e.g. nutrient pollution) are likely to affect species coexistence.

3.2 Comparing and synthesizing measurements of ND and RFD

To date, only five of the six methods proposed for measuring niche and relative fitness differences have been used empirically and the far majority of those empirical studies have used the annual plant model or similar models. Furthermore, we are unaware of any study that has applied more than one method to estimate ND and RFD in the same empirical study system. As such, we have no way to compare the performance of the methods empirically. Therefore, we believe an important avenue for future research is to measure ND and RFD using different

634 methods within the same study system to demonstrate equivalence or non-equivalence of these
635 methods.

636 Even as we call for more comparative studies, we caution against the inevitable urge to
637 synthesize ND and RFD through an informal data synthesis or more formal meta-analysis.
638 Although all of the methods can, in principle, correctly predict the qualitative outcome of
639 coexistence, the methods are by no means mathematically or practically equivalent. As we have
640 shown, the methods will not always yield the same ND and RFD, even when applied to the same
641 species and environmental conditions. Any differences in environmental conditions (e.g.
642 resources or temperature) would affect the measured ND and RFD such that comparisons should
643 not be attempted (Bimler et al. 2018, Chesson 2017, Chesson 2018). Indeed, given the
644 differences in how the methods are implemented (Figures 1-5), there is no reason to expect, *a*
645 *priori*, that the methods are directly comparable. Therefore, measurements produced using
646 different methods should not be mixed-and-matched to produce some synthesized estimate of the
647 niche or fitness difference for, say, grassland plants (studied exclusively using the annual plant
648 model) and phytoplankton studied with different methods.

649 3.3 Future directions for implementing modern coexistence theory

651 In our view, there are at least two important new directions that work on species
652 coexistence must go if Chesson's modern coexistence theory is to become widely implemented.
653 First, each of the empirical methods described in this review are focused on fluctuation-
654 independent mechanisms. It is well-known that environmental fluctuations mediate species
655 coexistence in some empirical systems (Caceres 1997, Jiang and Morin 2007) and any modern
656 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, Stouffer et al. 2018)). To also include fluctuation-dependent mechanisms of coexistence in Chesson's framework, we need to expand the scope of the six methods reviewed here or even develop new empirical methods. 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 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 difficult to reconcile with Chesson's original derivation using the Lotka-Volterra model (but see (Bimler et al. 2018)). However, despite its versatility compared to the other two mechanistic methods, the approach used by Ellner et al requires a parameterized mechanistic model of intraspecific and interspecific interactions, so it has the same limitations as the mechanistic methods described here.

Second, empirical studies on coexistence need to move beyond prediction of pairwise species interactions. Until recently, empirical implementation of modern coexistence theory for multi-species systems lagged behind theoretical developments. For example, multiple papers have shown how ND and RFD could theoretically be calculated for one species versus a community during invasion (Carroll et al. 2011, Chesson 2008) yet very few empirical studies have attempted this approach (Godoy and Levine 2014). Moreover, the pairwise competitive interactions among species may be altered, or even reversed, when those species are engaged in intransitive competition (Barabas et al. 2016, Chesson 2015, Gallien et al. 2017), which is known

to occur in plant communities (Soliveres and Allan 2018, Soliveres et al. 2015, Ulrich et al. 2018). Recent papers have shown how intransitive interactions in the annual plant model can be quantified for multispecies communities and how this affects pairwise estimates of ND and RFD (Godoy 2019, Godoy et al. 2017, Matías et al. 2018, Stouffer et al. 2018). While that approach can be used to quantify the impact of intransitive interactions on pairwise ND and RFD, other recent theoretical work has shown how calculation of ND and RFD can be expanded to describe entire multispecies communities (Saavedra et al. 2017). In contrast, higher-order interactions are known to occur in plant communities (Mayfield and Stouffer 2017) and are predicted to alter the outcome of pairwise competition (Letten and Stouffer 2019, Levine et al. 2017, Saavedra et al. 2017), yet we lack empirical studies illustrating how those higher-order interactions impact ND and RFD or our predictions for coexistence. Chesson’s coexistence framework has been a major advance for understanding coexistence among pairs of species, and further application of this framework to multi-species systems should be a priority for the field.

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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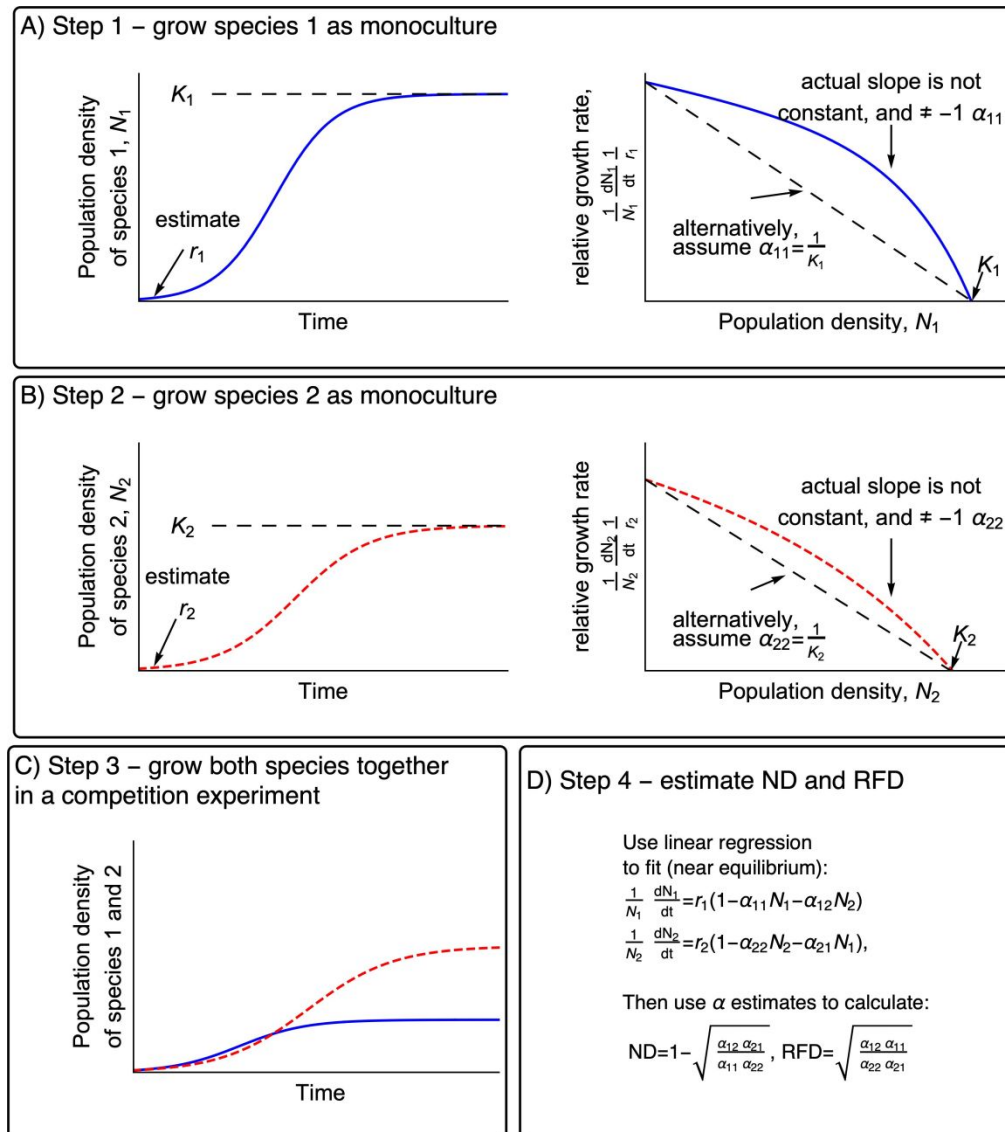
Decision Steps:	1: Must the method yield estimates of ND and RFD (i.e. Chesson's inequality)?	No	Yes	Yes	Yes	Yes	Yes
	2: Can you mechanistically model resource competition among species?	No	No	No	No	Yes, biotic (dynamic)	Yes, abiotic (non-dynamic)
	3: Can you grow each species as a monoculture?	Yes or No	Yes	Yes or No	Yes	Yes	Yes
	4: What type of study will be used to parameterize the method?	Experimental or Observational	Experimental or Observational	Experimental or Observational	Experimental	Experimental	Experimental
	5: Can you maintain ≥ 1 species at steady-state near its carrying capacity?	Yes, for total biomass	Yes or No	Yes or No	Yes	No	No
	6: Is reproduction discrete or continuous?	Continuous or discrete	Continuous	Discrete	Continuous or discrete	Continuous	Continuous
Method		Negative frequency dependence	Lotka-Volterra for continuous reproduction	Annual plant model	Sensitivity	MacArthur's CRM	Tilman's CRM
	Theoretical paper linking model to MCT	Adler et al 2007	Chesson 2000	Adler et al 2007; Adler et al 2010	Carrol et al 2011	Chesson 1990	Letten 2017
	Empirical paper using model for MCT	Yenni et al 2017	Armitage and Jones 2019	Godoy and Levine 2014; Chu and Adler 2015	Narwani et al 2013	none	Letten 2017
Experimental Requirements	Does the method require the species to be grown together?	Yes	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 $m \geq 2$ mixtures	$n + [n(n-1)/2]$	$[m^2 \cdot n \cdot (n-1)]/2$, where $m \geq 2$ mixtures	n^2	$r \cdot n$, where r = number of resources	$r \cdot n$, where r = number of resources
	Are time-series of species densities required?	Yes, ≥ 1 generation	Yes, enough generations to approach k	Yes, ≥ 1 generation	Yes, ≥ 1 generation	No	No

847

848 Table 1. A practical guide to help empiricists determine which method(s) are most appropriate for a given study system and question.
849 See Part 2 for a step-by-step explanation of this guide. The citations given for each method are selected examples, see the text for
850 additional references that explain each method and its implementation.

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851 Figures



852

853 Figure 1. Conceptual plots illustrating how to use the Lotka-Volterra model for continuous

854 reproduction to estimate ND and RFD for use in Chesson's inequality (Equation 1). In each

855 panel, unknown parameters are displayed in regular typeface and previously-estimated

856 parameters are listed in bold typeface. In panels A and B, the left-hand plots show the time

857 course of the experiment and the right-hand plots show the relative growth rate as a function of

858 population density – the slope of this relationship is equal to the intraspecific competition

859 coefficient (sign reversed).

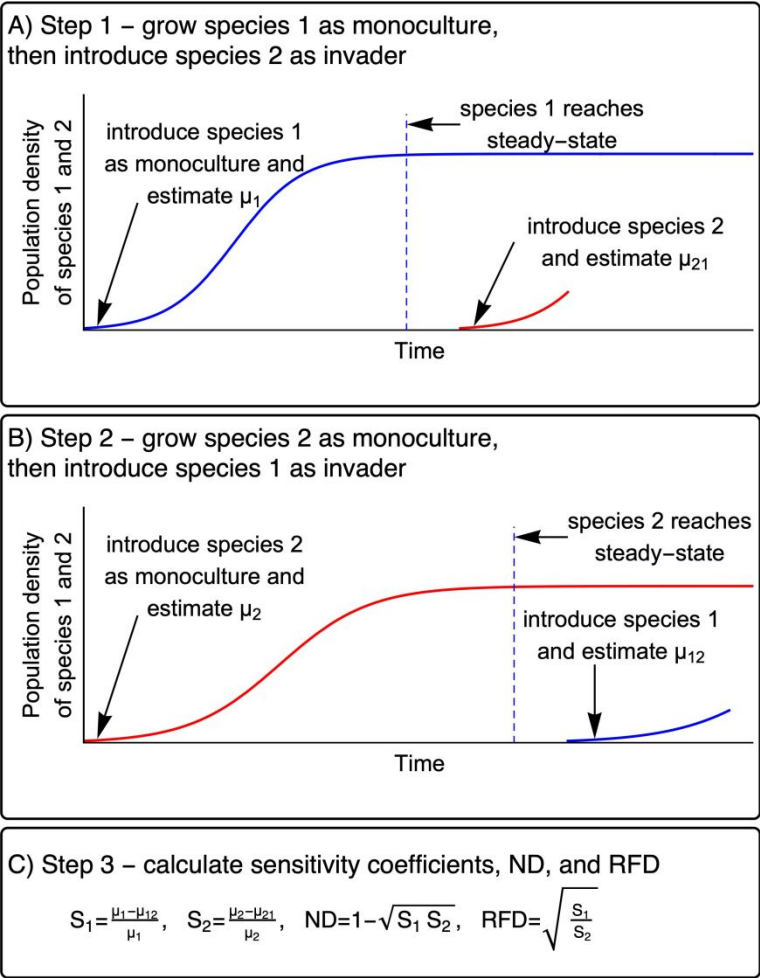
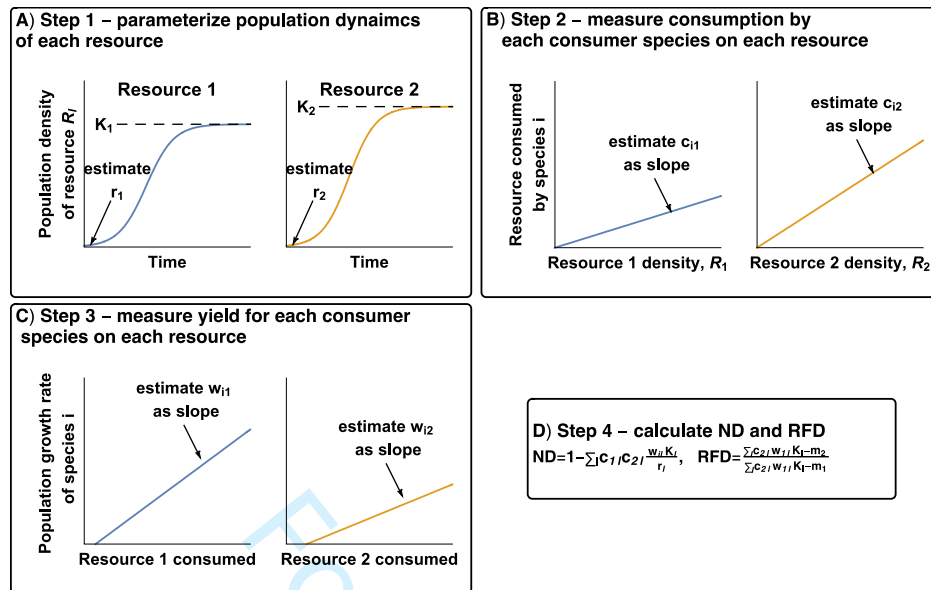


Figure 2. Conceptual plot depicting how to implement the sensitivity method in an experiment.



864

865 Figure 3. Conceptual plots depicting how the method based on Mac Arthur's CRM could be

866 implemented.

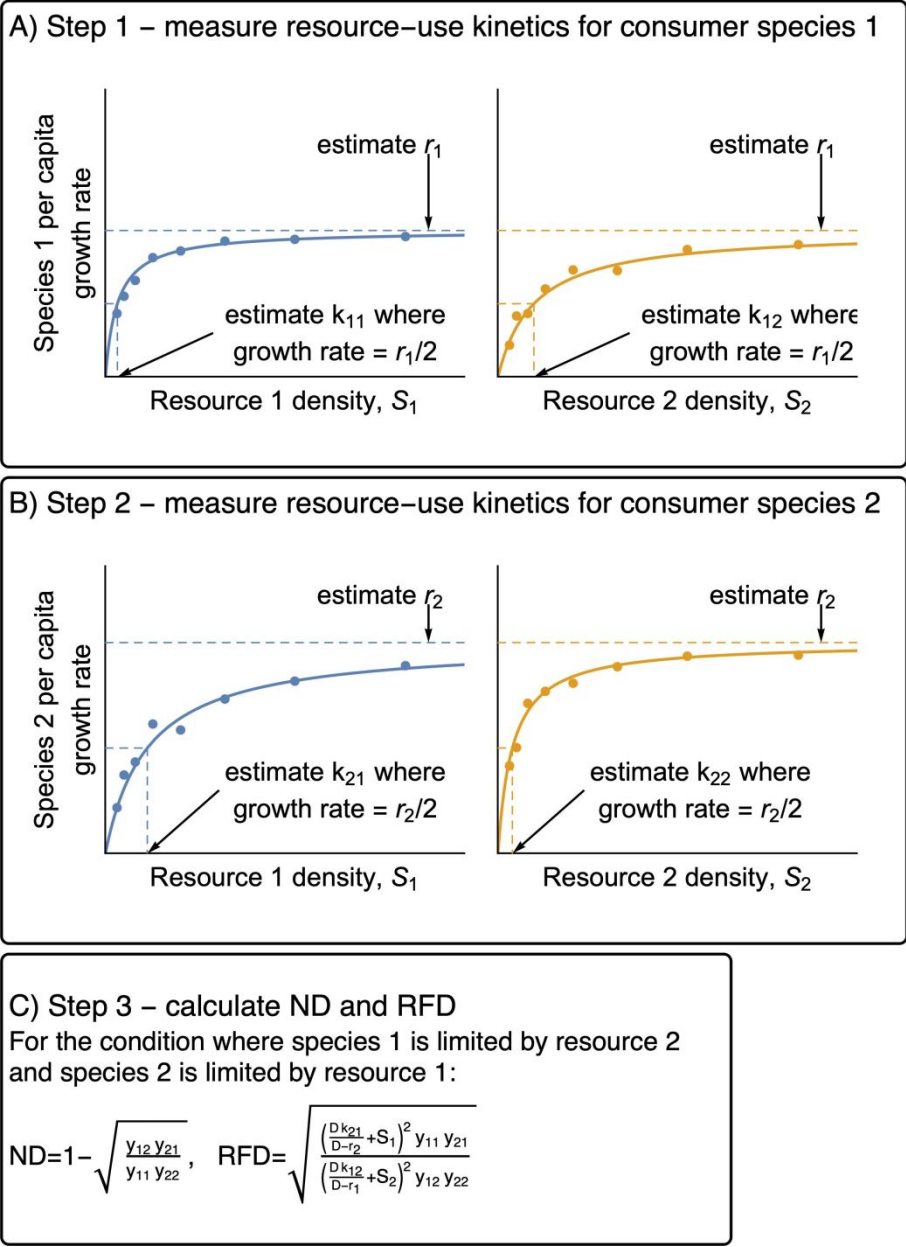


Figure 4. Conceptual plot depicting how to use the method based on Tilman’s consumer resource model. Panels A and B show the experiments needed to parameterize the maximum growth rates and Monod half-saturation constants for growth on each resource, separately for each species. The yield of each species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

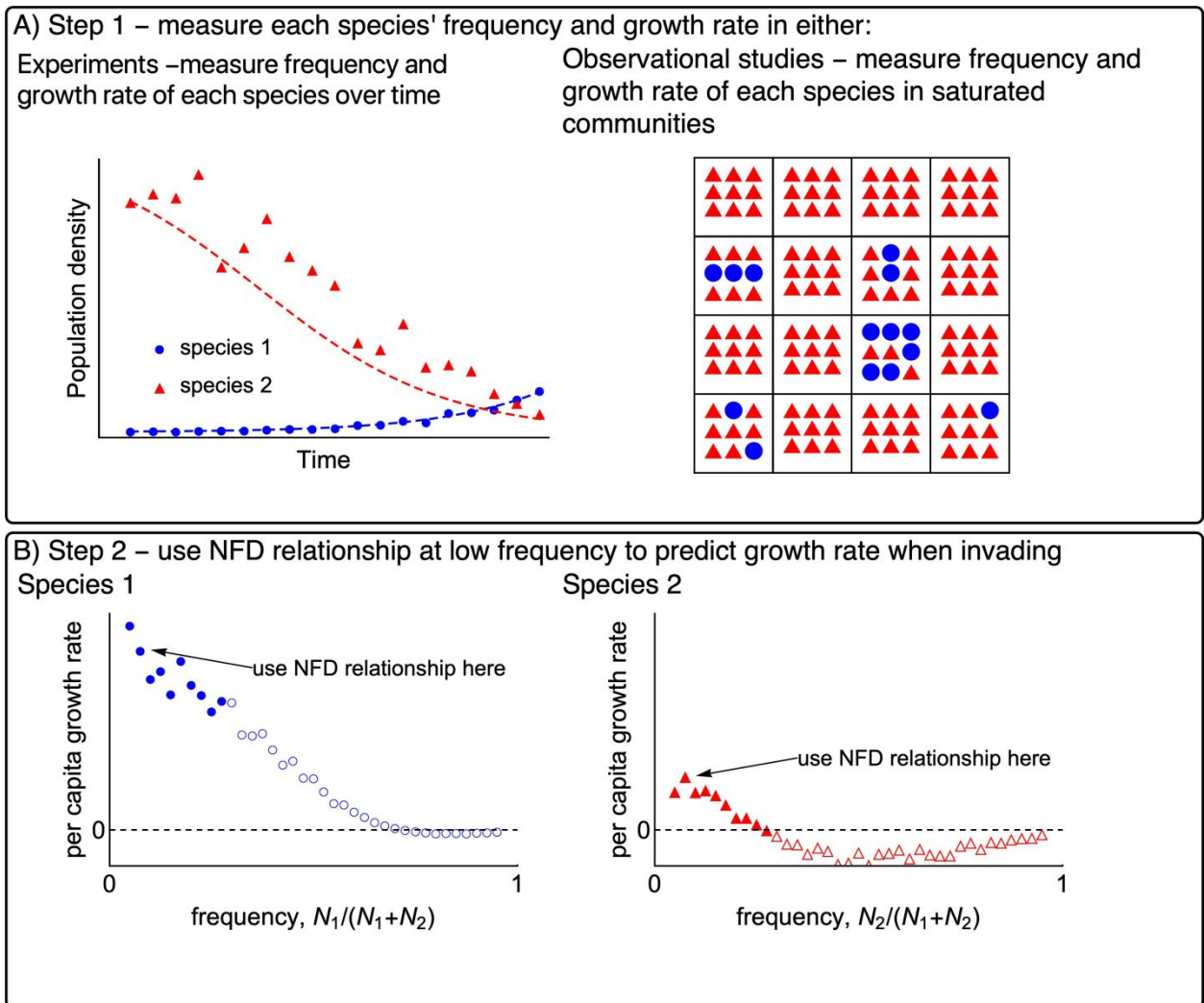


Figure 5. Conceptual diagram depicting how the NFD method could be implemented, either through an experiment or using observational data from different communities. Panel A shows two options for obtaining pairs of each species' frequency and its growth rate in a saturated community. The first option 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.

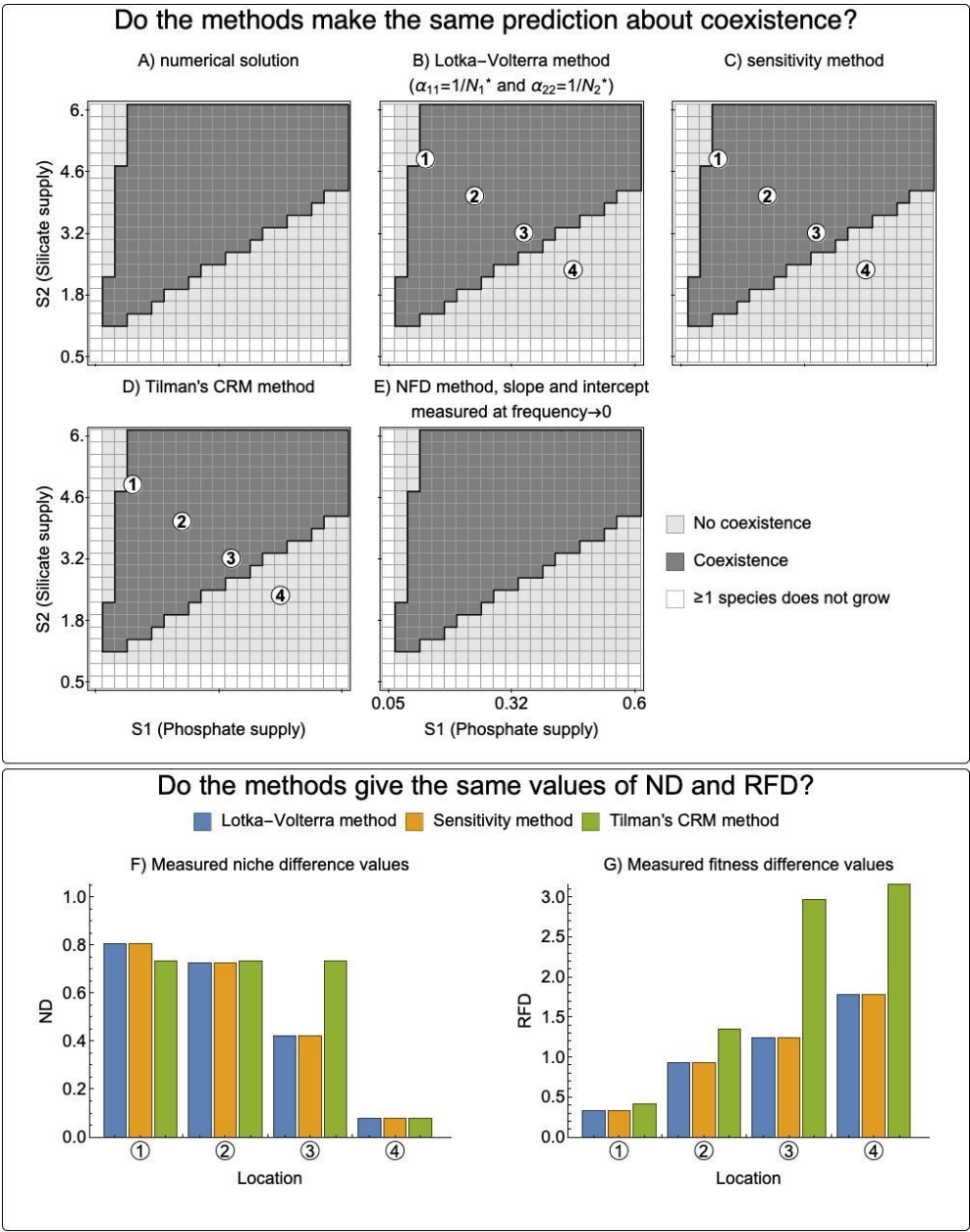


Figure 6. Comparison of four methods for predicting coexistence and estimating ND and RFD.

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

891 indicates that the model predicts coexistence. The raw RFD values from the sensitivity method
892 were converted to the same ordering as used in the other methods (species i in the denominator
893 rather than the species with the greater sensitivity). Because the NFD method cannot be used to
894 produce values of ND and RFD that are comparable with the other four methods, only the
895 predictions regarding coexistence are plotted.

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898 **Supporting Information A: Simulation of Experiments to Measure ND and RFD and** 899 **Predict Coexistence**

900 In this supplement, we present numerical simulations that compare the outcomes from
 901 three methods for measuring ND and RFD and also the NFD method for predicting coexistence.
 902 We used Tilman's parameterized consumer-resource model for two species of phytoplankton
 903 competing for essential resources (Tilman 1977). Annotated code for the simulations is provided
 904 in a supplemental file. Simulations were performed using the function NDSolve in Mathematica
 905 11.2 (Wolfram Research), employing a variable step size. For each set of resource supply
 906 concentrations, we performed four simulations: (1) species 1 as a monoculture, growing from
 907 rare to near its equilibrium density; (2) species 2 as a monoculture, growing from rare to near its
 908 equilibrium density; (3) species 1 at its equilibrium density, with species 2 invading from rare;
 909 (4) and species 2 at its equilibrium density, with species 1 invading from rare. Additionally, we
 910 performed numerical simulation where both species are introduced at low densities and asked
 911 whether they coexist at the equilibrium. For each set of simulations, we manipulated the supply
 912 concentration of the two resources in order to determine whether the methods consistently agree.

913 We implemented the Lotka-Volterra method using information from all four simulations
 914 described above. Simulations 1 and 2 were used to estimate r_i , K_i , and intraspecific interaction
 915 coefficients α_{ii} . We estimated the intraspecific interaction terms using two different approaches
 916 (Section 1.2). First, we estimated α_{ii} as the slope of the relative growth rate versus population
 917 density (sign reversed) as the monoculture simulations approach equilibrium (Figure 1).
 918 Alternatively, we used the assumption that $\alpha_{ii} = 1/K_i$. We then used the parameter values from the
 919 monocultures, along with simulations 3 and 4, to solve Equation 2 when each species is at low
 920 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 A1 (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 A1 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 rate as frequency approaches 0, but at the complementary frequency of species 2, the slope of

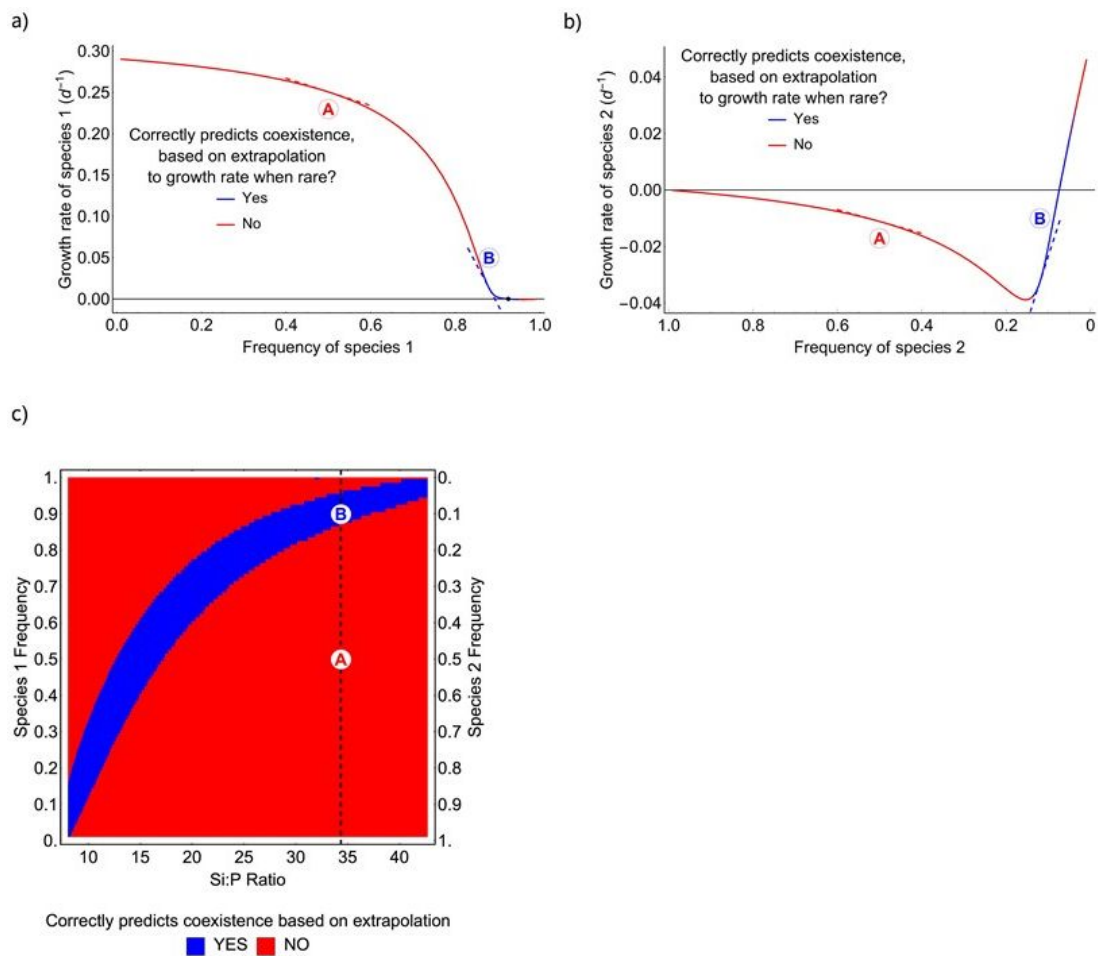
species 2's NFD predicts a negative growth rate when rare. However, based on the other 3 methods, numerical simulation, and Tilman's resource ratio theory, the species are predicted to coexist. Thus, measuring NFD under the red regions in Figure A1 will incorrectly predict exclusion even though the species will coexist. At the point labeled "B" in Figure A1, the slope and elevation of NFD for both species predicts a positive growth rate when rare. This region, depicted in blue, includes the equilibrium frequency for the two species. If an empiricist made their measurements between frequency of ~ 0.05 to ~ 0.85 for species 1, and used the slope of NFD, they would incorrectly predict that the species will not coexist. Since the frequency at which the species reach equilibrium depends on the resource supply ratio, there is no single frequency of the species that consistently leads to the correct predictions (Figure A1). While certain intermediate frequencies of the two species can be used to make accurate predictions, an empiricist would not know these frequencies without performing the competition experiments or examining frequency dependence across the entire range of frequencies. As a result, the only reliable way of implementing the NFD is to measure the slope and elevation for each species where its frequency approaches zero.

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

For the NFD method, accurate predictions required that the slope of NFD was evaluated approaching frequency of zero for each species (i.e. invasion conditions). In Figure A2 d-f, we show that evaluating the NFD slope at other frequencies leads to the wrong predictions. We used

967 the NFD plot to evaluate coexistence at three frequencies, including near 0% (panel c of Figure
968 A2) and 50% (panel e), and either with or without considering the elevation in addition to the
969 slope (panels d, f). We see that using the NFD slope evaluated at near 0% frequency will
970 consistently yield accurate predictions of species coexistence that match the those of the other
971 methods.
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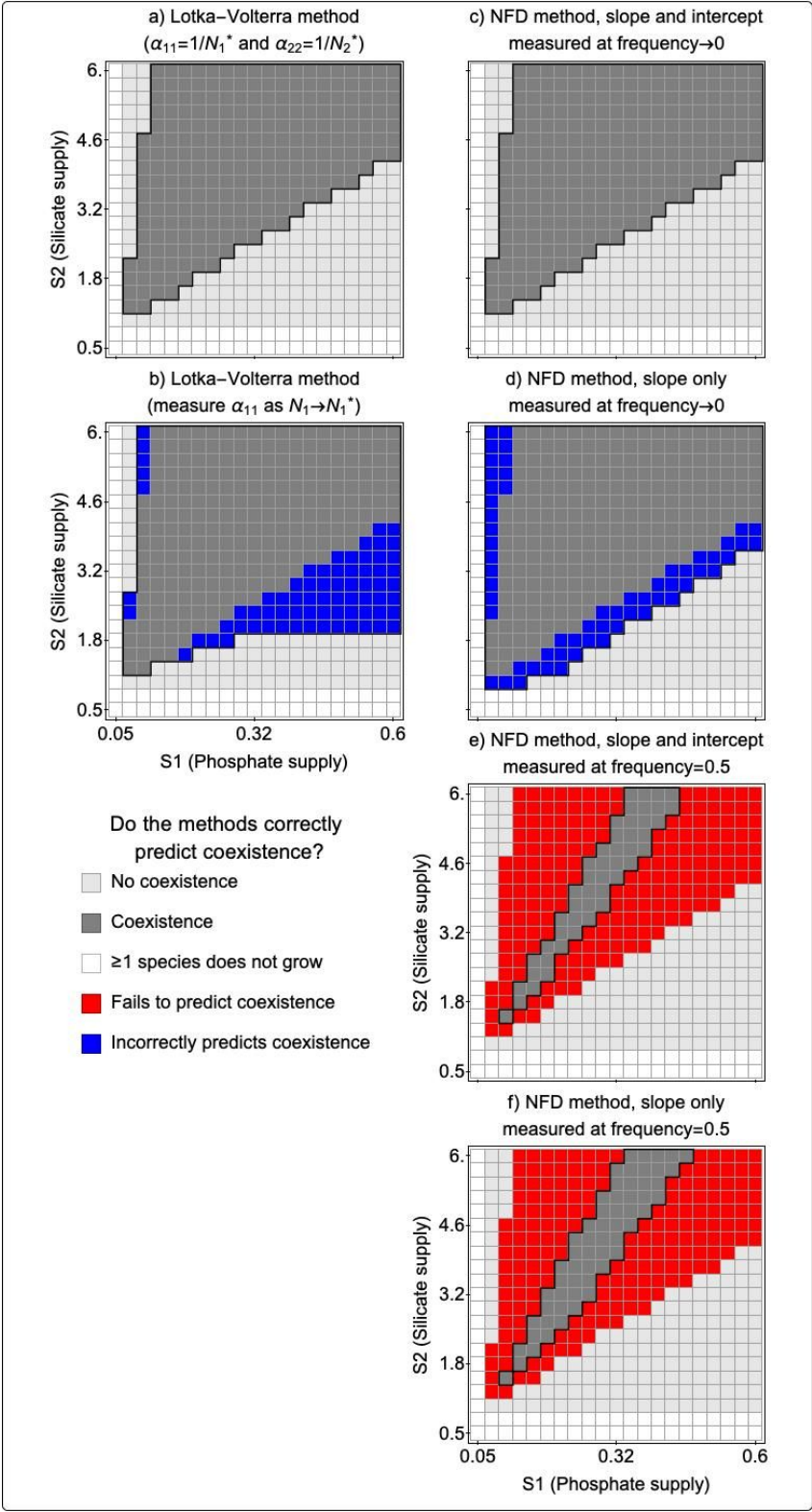
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Supporting Information Figure A1. Results of simulation experiments using the NFD method. Panels a and b show per capita growth rate versus the frequency of species 1 and 2. At any frequency of the two species, the NFD method requires that we use the 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

984 panels a and b. For all of the Si:P ratios shown in panel c, the species are mutually inviable and
985 will coexist. This plot indicates that using NFD will often predict that the species will not
986 coexist, when in fact they do coexist. This is important because without examining the full range
987 of species frequencies in an experiment, one would not know whether and where the relationship
988 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 μ_i in Equation 5 is the maximum per capita growth rate in monoculture, equal to r_i in Equation 2. The μ_{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 (α_{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).

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

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

Conceptually, when the per capita growth rate is being plotted against the frequency of the focal species, the NFD slope is actually the “per-frequency” impact on the per capita growth rate of each species. Because this slope is fundamentally different than the interaction coefficients in the Lotka Volterra model, 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 . Also note that the interaction coefficients used here 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, α_{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.

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

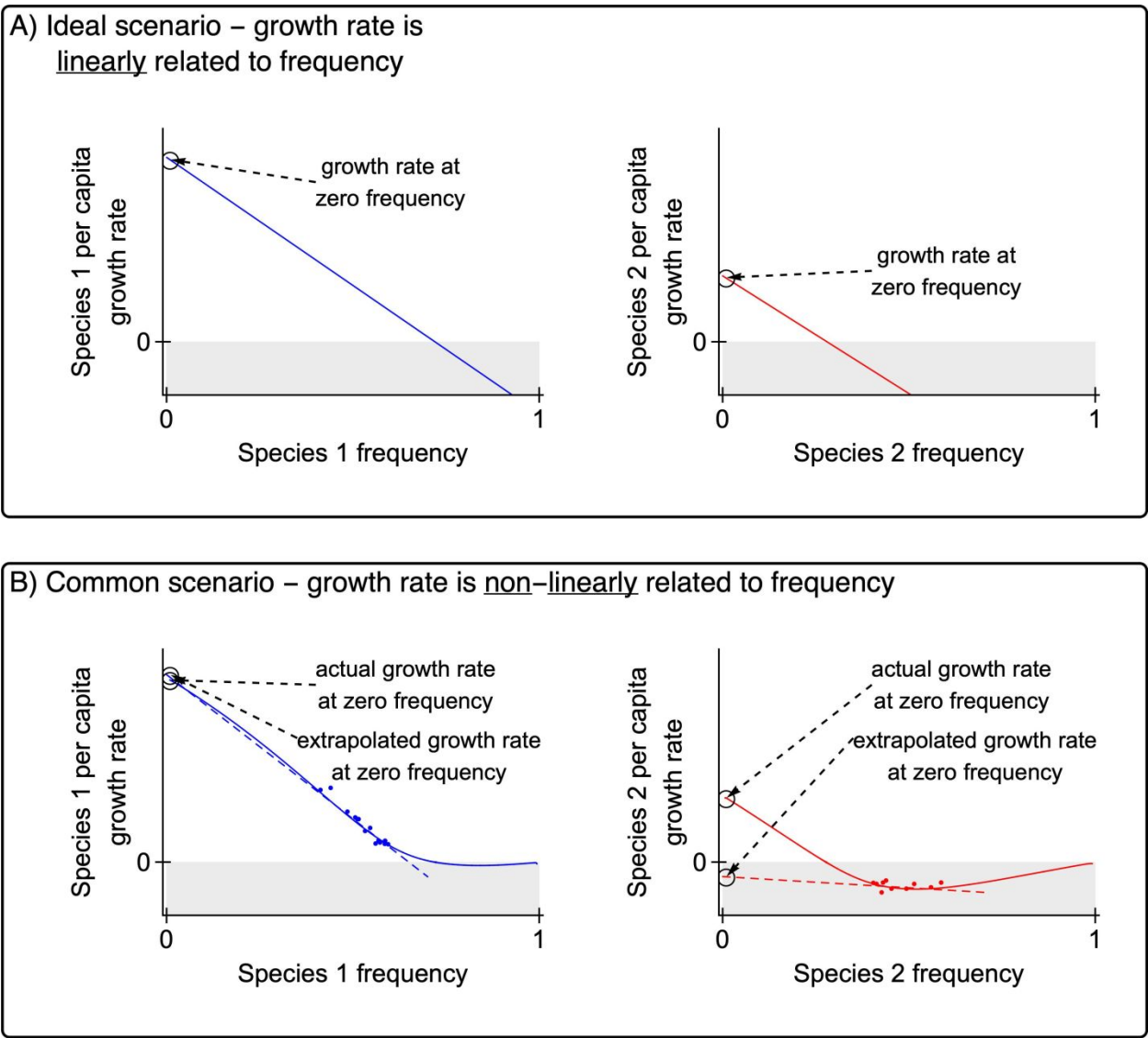
$$NFD \text{ intercept} \equiv r_i(1 - \alpha_{ij}) \quad (C3)$$

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 analogous form to Chesson's definition of ND and RFD. Thus, while the NFD method can correctly predict mutual invasibility, the NFD intercept and slope should not be interpreted as RFD and ND in order to evaluate Chesson's inequality.

The utility of the NFD method depends on its ability to correctly predict whether species have positive growth rates when their frequencies approach zero. If the relationship between a species frequency and its growth rate is non-linear, however, then the accuracy of the NFD method is critically dependent on the range of species frequencies used by an empiricist. In Figure C1 we show that the NFD relationship can be non-linear even when the underlying population dynamics are governed by the Lotka-Volterra model. The result of this non-linearity is that, depending on the range of species' frequencies used to estimate the NFD slope and intercept, this method can give inaccurate predictions.



1050

1051 Figure C1: Panel A shows a hypothetical situation where species frequencies are linearly

1052 to their growth rate and an empiricist can extrapolate to predict growth rates at frequency of zero

1053 and diagnose mutual invasibility. Panel B shows the more likely scenario in which growth rates

1054 are non-linearly dependent upon species frequencies. These plots were made using numerical

1055 simulation of the two-species Lotka Volterra Model, using parameter values that should allow

1056 for coexistence (at frequency of 0.72 for species 1). The points in Panel B represent

1057 measurements collected at intermediate frequency of both species. Using those measurements

1058 and extrapolating to zero frequency yields the incorrect prediction that the species will not
1059 coexist.

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