**Part 3.**

In Part 1 of this paper, we explained how each of five models/methods can be used to quantify niche differences (ND) and relative fitness differences (RFD), which can then be used to predict coexistence among pairs of species. We further showed that while the methods are not mathematically identical, nor do they always give comparable values of ND and RFD, they all qualitative predict the outcome of species interactions, and correctly predict whether or not species coexist. Then, in Part 2 of the paper we offered a decision-making framework that can be used by empiricists to select the most appropriate model/method for their particular study system, specific aims, and experimental capabilities. Now, in Part 3, we end the paper by offering some advice for empiricists about how to navigate tradeoffs among the models/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

Given the substantial differences in experimental design requirements and effort that is needed to execute the five methods described in Part 1 of the paper, it is highly likely that empiricists will face choices that require tradeoffs in selection of a particular model or method for their study system. The most obvious and important tradeoffs occur among the phenomenological methods and the mechanistic methods, which differ in three important ways: First, the phenomenological methods (LIST HERE) make 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 detailed information about the biological resources that species compete for. But the trade-off for this lack of knowledge is the experiments that need to be performed to quantify ND and RFD are more elaborate and cumbersome. Indeed, a key disadvantage of all three phenomenological methods is that they require each pair of species to be grown together in competition, which causes the total effort to increase exponentially as more species are considered. In addition, the results of phenomenological experiments are specific to each pair of species tested, and cannot be generalized to interactions beyond that pair. They are also specific to the particular environmental conditions (resources and resource densities/supply rates) used in that experiment, and cannot be generalized.

But for those who can identify the biological resources species compete for, use of the mechanistic models allows for simpler, less complex experiments that are more easily generalized to predict coexistence among all species in the focal species pool. Indeed, an empiricist who is able to answer ‘yes’ to Question 3 in Table 1 could use a mechanistic model to predict coexistence (or not) not just of a single species pair of interest, but of any and all species pairs of interest based solely on experiments that take measurements from each species grown alone in monoculture. Importantly, the mechanistic experiments also offer the ability to make predictions about species coexistence under different environmental conditions. For example, Letten et al. (Letten et al. 2017) showed that the Tilman consumer resource model can be used to predict the ND and RFD at different nutrient supply rates or dilution rates. The ability 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.

The ability to make predictions about combinations of species without the need to perform all pairwise competition experiments has already been touted as a benefit of the mechanistic models [Tilman 1982], and it could be useful for addressing certain ecological questions that don’t always lend themselves well to manipulative experiments (e.g. invasions by introduced species, coexistence of rare or endangered species). The key point here is that there is a trade-off between the simplicity and generality of results, and how much one knows about the focal species and what they compete for.

3.2 Comparing and synthesizing measurements of ND and RFD

To date, only three of the five models/methods described for measuring niche and relative fitness differences have been used empirically. No one, to our knowledge has used the MacArthur Resource Model or Tilman’s Consumer Resource Model to quantify ND and RFD in any real system, despite publications showing these can be used to do so. That means that most of our inferences about ND and RFD that have been measured empirically stem from phenomenological models of coexistence. Furthermore, we are unaware of any empirical study that has applied more than one of model/method to the same empirical study system. As such, we have no way to compare the performance of the methods/models empirically. Therefore, we believe an important avenue for future research is to focus on measuring ND and RFD using more mechanistic models, and for studies that measure ND and RFD using different methods in the same study system so that we can compare results and attempt to demonstrate equivalence of these methods.

Even as we call for more mechanistic experiments and comparative studies, we caution against the urge that will eventually rise to synthesize measures of ND and RFD in an informal data synthesis or more form meta-analysis. Although we have shown that all five existing models/methods should correctly predict the qualitative outcome of coexistence, the methods are by no means mathematically equivalent. There is no reason to expect, a prior, that the quantitative values of ND (or RFD) measured for a particular group of organisms for one method will produce quantitatively similar values of ND (or RFD) for that same group of organisms using a different method. As such, the methods are not directly comparable, and the measurements they produce should not be mixed-and-matched to produce some synthesized estimate of the niche or fitness difference for, say, grassland plants.

3.2 Future directions for implementing modern coexistence theory

In our view, there are at least three important new directions that work on species coexistence must go if Chesson’s modern theory of coexistence is to become more general and practical. First, it needs to move beyond prediction of pair-wise species interactions. Several authors have recently emphasized that modern coexistence theory is under-developed for multi-species systems (Carroll et al 2011, ADD RECENT LEVINE ET AL. PAPER). In theory, competitive hierarchy between species *i* versus *j* and *j* versus *k* might not directly translate to species *i* and *k*, when these species are engaged in intransitive competition or higher-order interaction (Levine et al. 2017). In fact, none of the three phenomenological methods (NFD, LV, and Sensitivity) 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. Chesson’s coexistence framework is an informative synthesis so far, and how to expand this framework to multi-species system is a direction worth pursuing.

Second, we need to expand consideration of the five models/methods reviewed in this paper to also include fluctuation dependent mechanisms of coexistence like relative nonlinearities and storage effects. To our knowledge, ND and RFD have not been explicitly defined for fluctuation dependent mechanisms of coexistence, much less have empiricists actually measured ND and RFD using these models as a template. Even so, it is well-known that environmental fluctuations mediate species coexistence in some empirical systems where environmental fluctuations cannot be negligible (Jiang andMorin 2007, Angert et al. 2009), and any modern theory of coexistence is incomplete without them.

Lastly, we think a fruitful avenue for future work is to focus on the application of modern coexistence theory to key environmental problems. Here we need to describe applications to IAS and Ecosystem Services.