

The Introduction to Godwin et al. does a very nice job of motivating this paper. The growing understanding and appreciation of Chesson's approach to coexistence theory, especially since his 2000 ARES paper and the subsequent "popular expositions" by others, has blossomed into a thriving empirical research enterprise aimed at quantifying the niche differences (ND) and relative fitness differences (RFD) among competing species. From such results, we might finally learn just how important ND are for the maintenance of species richness, a longstanding goal in community ecology with heightened recent attention sparked by the Neutral Theory. A stumbling block, however, is that multiple ways of quantifying ND and RFD have been proposed. It is not clear how they relate to each other, and whether or not it's legitimate to compare estimates from different methods. This paper aims to clear the air by giving a unified presentation of the methods, examining closely how they relate to each other. The unfortunate conclusion is that the differences are too substantial to allow direct cross-system comparisons among estimates obtained by the different methods. That's bad news, but it's bad news that community ecologists need to hear.

It is the reviewer's job to be critical, but the authors make it hard for me to do a lot of that. The paper as a whole is well structured. The Introduction is effective without being overly long. Paragraphs flow logically into the next paragraph, sentences make sense the first time you read them, conclusions are supported by the evidence, figures are easy to understand and genuinely helpful. The suggested future directions contained no surprises, but that's because I'm in full agreement with the authors. I wish it was always this easy.

Nonetheless, there are a couple of issues that I think need to be addressed.

First, I think the authors need to confront the question of whether ND and RFD actually exist, or to what extent they exist. Are they a property of a community (the species present, and how they interact) or are they only properties of some particular models? Two things in this paper raise this issue. First, neither these authors, nor anybody else previously, present ND and RFD by giving a general definition that is then applied to various models. Instead, we see a series of examples in which quantities named ND and RFD can be defined, such that coexistence is predicted (at least pairwise) when ND is sufficient to overwhelm RFD.<sup>1</sup> Second, the authors write (line 632, correcting a typo): "ND and RFD are not terms that can be quantified directly from experiments or observations". If they are undefined, and unmeasurable even in principle, how can we say that they actually exist as properties of a real community? I think we need a discussion of this issue first, and then the details.

The second is much more straightforward. Some of what the authors say about Chesson (1990) seems to be wrong. My guess is that this is more appearance than reality, and the reality is that a lot of details and definitions have been left out about how their notation relates to Chesson's, and about the extent to which

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<sup>1</sup>Chesson's recent attempt to alleviate this situation by defining average fitnesses based on a 'reference model where no coexistence is possible' (J. Ecology 106: 1773) is no better. He presents two examples of reference models and declares the problem solved, but it isn't solved without a general prescription for constructing the reference model.

they use the fact that  $a_{ij} = a_{ji}$  in Chesson (1990) to make his 1990 formulas look more like later formulas that refer to an alternative way of specifying the Lotka-Volterra model (their equation (2) versus equation (3) in Chesson 1990).

1. Equation (1), in Box 1, does not actually appear in Chesson (1990). The closest thing is his equation (13)

$$\theta\rho < \frac{k_i}{k_j} < \frac{\theta}{\rho} \quad (1)$$

which does not have the same form as equation (1) in Box 1 (i.e., the two outermost expressions are not inverses of each other). Lower down in Box 1 the authors say that the RFD in their equation (1) is given by “ $\frac{f_j}{f_i}$  in Chesson (1990)” but  $f_i, f_j$  do not appear anywhere in Chesson (1990). It’s not clear what the authors are trying to say with regard to Chesson (1990), and taken at face value what they do say is wrong.

2. I’m similarly confused by equations (10) and (11). Referring to equation (4) in Chesson (1990), equation (10) in the present manuscript says that  $ND = 1 - a_{ij}$ . Referring to equation (5) in Chesson (1990), equation (11) says that  $RFD = \frac{k_j}{k_i}$ . Below (10) and (11) the manuscript says that the coexistence condition can be found by substituting these into the equation from Box 1,

$$1 - ND < RFD < \frac{1}{1 - ND}. \quad (2)$$

Making that substitution, the resulting coexistence condition is

$$a_{ij} < \frac{k_j}{k_i} < \frac{1}{a_{ij}}. \quad (3)$$

However, that’s not the actual coexistence condition in Chesson (1990) (equation (13) in that paper, eqn. (1) in this review).

So as the manuscript stands, I think that anyone who looks back from this paper to Chesson (1990) is liable to get very confused. The point of online SI is that you can show all the details and all the steps. I would like the authors to include all the details and all the steps needed to clear up my points of confusion and support all their assertions about Chesson (1990).

#### Minor points:

1.  $\frac{1}{\alpha_{ii}}$  in equation (B2) should be  $\frac{1}{\alpha_{jj}}$
2. The right panel in Figure 1, Box B should be switched to species 2. Also, the crucial distinction between bold and regular typeface is not very clear until the PDF is enlarged to about 200% of real size. I suggest supplementing bold/regular with color, e.g. in each box unknown parameters are in regular typeface and some color other than red or blue.

3. For the sake of completeness, I think it would be useful to expand Fig. 3 to depict experiments and data that could be used to estimate  $w_{il}$ .
4. I think Supporting Information C goes off-track at equation (1). The Lotka-Volterra competition model can't actually be written in that form without re-defining the  $\alpha_{ij}$ , and that would have the unfortunate result that the  $\alpha_{ij}$  in equations (C2) and (C3) are not the same as the ones in the rest of the paper. I think it would be better to say: Consider what happens when we try to apply the NFD method to the Lotka-Volterra model. In order for population growth rates to be frequency dependent, the total density  $N_1 + N_2$  must be held constant at some value  $B$ . If  $f_i$  denotes the frequency of species  $i$ , then we have  $N_i = f_i B$  and the Lotka-Volterra model can be re-written as

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i(1 - \alpha_{ii}f_iB - \alpha_{ij}(1 - f_iB)) \quad (4)$$

The right hand side, as a function of  $f_i$ , has intercept  $r_i(1 - \alpha_{ij}B)$  and slope  $r_iB(\alpha_{i2} - \alpha_{i1})$ , and so on (these aren't directly related to the actual  $ND$  and  $RFD$  for the Lotka-Volterra model, etc.).