

Reply

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Chesson's coexistence theory: reply

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Chesson's (2019) comment on our review of modern coexistence theory (Barabás et al. 2018) focuses on perceived mistakes and provides a re-derivation of key results from his own perspective. The criticisms concern three main issues: the definition of standardized environmental and interaction parameters; the definition of comparison quotients and the meaning of their non-uniqueness; and the status of the theory when there are at least as many limiting factors as species in the system. He makes many important observations, and the provision of his own derivation of the theory gives a unique perspective on what elements of the theory are deemed important and why. Additionally, Chesson (2019) mentions in passing several elements of our review that he believes are not handled well. However, we argue that the differences between Chesson's (2019) account of the theory and ours are overstated, turning out to be differences of emphasis and interpretation, rather than fundamental mistakes. We therefore take this opportunity to clarify our point of view, and to synthesize Chesson's perspective with ours for an improved outlook on the theory.

DEFINITIONS OF THE STANDARDIZED ENVIRONMENTAL AND INTERACTION PARAMETERS

After choosing environmental and interaction parameters E_j and C_j (both may depend on time), the theory starts by writing the per capita growth rates r_j as their function: $r_j = g_j(E_j, C_j)$. Based on this parameterization of the growth rates, Chesson (1994, 2019) defines the

standardized environmental and interaction parameters \mathcal{E}_j and \mathcal{C}_j via

$$\mathcal{E}_j = r_j(E_j, C_j^*), \quad \mathcal{C}_j = r_j(E_j^*, C_j), \quad (1)$$

where E_j^* and C_j^* are "equilibrium" values such that $r_j(E_j^*, C_j^*) = 0$ (Chesson defines \mathcal{C}_j with an extra negative sign, conforming to the situation where C_j measures a competitive reduction in growth rates). In our review, we did mention these definitions, though only as a reference. Instead, we defined the standardized parameters as quadratic approximations to these formulas (Barabás et al. 2018:279):

$$\begin{aligned} \mathcal{E}_j &= \alpha_j (E_j - E_j^*) + \frac{1}{2} \alpha_j^{(2)} (E_j - E_j^*)^2, \\ \mathcal{C}_j &= \beta_j (C_j - C_j^*) + \frac{1}{2} \beta_j^{(2)} (C_j - C_j^*)^2 \end{aligned} \quad (2)$$

where the α s and β s are Taylor coefficients. Chesson (2019) mentions two problems with our definitions. First, they are less accurate than those of Eq. 1. Second, they do not yield critical understanding of the underlying theory.

Eq. 1 is indeed more accurate than Eq. 2, as the latter is a quadratic approximation to the former. Fig. 1 of Chesson (2019) presents a model example, showing that, for large environmental variation, the difference in accuracy is especially pronounced in favor of Eq. 1. While this is true, one must keep in mind that the theory as a whole is based on a small fluctuation approximation. This assumption pervades the development of the theory; e.g., the quadratic approximation of the standardized interaction parameters \mathcal{C}_j in the limiting factors rests on this (Eq. 11 in Chesson [2019]; Eq. 9 in Barabás et al. [2018]), as does the approximation $\overline{\mathcal{E}_j \mathcal{C}_j} \approx \text{cov}(\mathcal{E}_j, \mathcal{C}_j)$, which neglects the $\mathcal{E}_j \mathcal{C}_j$ term. For small environmental variability, the difference between Eqs. 1 and 2 diminishes. From the point of view of deriving the equations of the theory or applying them to particular ecological models, and making sure that they are accurate to quadratic order, it therefore does not matter which set of definitions one uses, and the difference in accuracy between Eqs. 1 and 2 is beside the point. To go beyond small fluctuation approximations, one way to go is to estimate model quantities via simulations in the first place (Ellner et al. 2016, 2019, Chesson 2019).

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Instead, the goal of our alternate approach in Barabás et al. (2018) was to offer a new angle to view the structure of the theory. This takes us to the other criticism of Eq. 2 by Chesson (2019), that it does not yield the same insight into the theory as Eq. 1. Clearly, different ways of arriving at a result emphasize different aspects of the same underlying concepts. Ours emphasizes how a straightforward quadratic expansion recovers all salient quantities of the theory. In the end, we would argue that having both developments is better than having just one or the other. Out of a pool of possible parameterizations, it is best to use the one that yields the most insight into the problem at hand. Standard parameterizations facilitate the comparison of different models and results. That said, we see no reason to rely on a single one exclusively.

THE COMPARISON QUOTIENTS

In relation to the comparison quotients q_{is} that are used in invader-resident comparisons (denoted $d_j d_i$ in Barabás et al. 2018:283), Chesson (2019) objects that we have confused them with the conceptually different scaling factors (which are used, among other things, to decompose invasion rates into stabilizing and equalizing contributions), and takes issue with our claim that using partial derivatives does not properly define the q_{is} , whose non-uniqueness we seemingly deemed a flaw of the theory.

We have not in fact confused comparison quotients with scaling factors, but this is obfuscated by conflicting terminology in the literature. Historically, the q_{is} had not been assigned a particular name until Ellner et al. (2016) called them scaling factors. It was only in Chesson (2019) that the term “comparison quotient” was offered, to differentiate them from another set of quantities called “scaling factors,” which were independently introduced by Chesson and Huntly (1997). Their purpose was to cancel linear terms in the limiting factors (Chesson and Huntly 1997: Appendix C), and they therefore closely correspond to our d_j in Barabás et al. (2018); in fact, as we pointed out in our review, our inspiration for these factors was Chesson and Huntly (1997) in the first place. Without being explicitly named, scaling factors underwent further evolution (e.g., Chesson 2003, 2008, Yuan and Chesson 2015) and became a tool for nondimensionalizing invasion growth rates and decomposing them into stabilizing and equalizing contributions. Finally, Chesson (2018) gave scaling factors their official name, notation (as b_i), and a general definition.

In Barabás et al. (2018), we consistently denote what Chesson would call the comparison quotients q_{is} by $d_j d_i$, and call the individual d_i scaling factors (in line with Chesson and Huntly 1997). In turn, the b_i of Chesson (2018), which he calls scaling factors, we denote by ϕ_i and do not give them any particular name. In no place do we refer to one as if it was the other, either in

notation or in terminology. We of course did not use the terms “comparison quotient” and “scaling factor” as suggested by Chesson (2018, 2019), as our review was published prior to these works. That said, we have nothing against adopting Chesson’s suggested terminology as described above. During review, it was suggested that the d_i should then also receive their own name. We suggest calling the d_i the “(linear) cancellation coefficients,” to emphasize their role in eliminating the linear terms in the limiting factors from the invader-resident comparison.

Apart from terminology, another possible reason for the impression that we have conflated comparison quotients and scaling factors is the fact that the scaling factors happen to be the same as the “canonical” choice of invader comparison quotients in the presence of a single limiting factor, because then $d_i = 1/\phi_i$ for any invader species i (Barabás et al. 2018: Eq. 22). That scaling factors and comparison quotients are related in this way is itself a noteworthy result. It is an open question whether this should be treated as an opportunity to unify the concepts of scaling factors and comparison quotients, or if it is better for future developments of the theory to still treat them as separate entities, despite the fact that they are related.

Chesson (2019) also points out that we unduly criticized the definition of comparison quotients in terms of the partial derivative $\partial \mathcal{C}_i / \partial \mathcal{C}_s$ evaluated at $\mathcal{C}_s = 0$ (Chesson 1994, Chesson 2019: Eq. 4). This was not our intention, though we do see that it was possible to read our text that way (last paragraph of *Partitioning the sum of invader and resident growth rates*). We regret if we were interpreted by readers as claiming that this definition is faulty, and so we would like to emphasize here that this is not the case. As pointed out by Chesson (2019), the derivative works just as well as our method, as long as the invader’s \mathcal{C}_i is expressible as a function of resident \mathcal{C}_s values, which is another way of saying that the number of independent limiting factors should be lower than the number of species competing for them. The derivative will not be unique unless the number of limiting factors is one less than the number of species (in which case, the d_i are unique up to a common multiplicative constant that cancels from $q_{is} = d_j d_i$). Otherwise, the invader \mathcal{C}_i can be expressed as a function of the resident \mathcal{C}_s in multiple ways; Chesson (2019) explains very clearly why this is a natural consequence of the theory. In the end, both our method and that of Chesson (1994, 2019) yield the same results, and both can be non-unique for the exact same reason.

We opted for our approach because it reduces the problem of finding the comparison quotients to the solution of a system of linear algebraic equations. This felt more direct than computing $\partial \mathcal{C}_i / \partial \mathcal{C}_s$, which requires the implicit function theorem to even interpret correctly, and potentially obscure methods such as generalized

inverses to actually evaluate. As an added benefit, the fact that a set of linear equations may have a non-unique solution is well known, and we hope this helps shed new light on the origins of the non-uniqueness of the comparison quotients (this is why, despite the criticisms, Chesson (2019) acknowledges that our method has merit). We reiterate that the purpose of our approach is not to dismiss that of Chesson (1994, 2019). Both are equally adequate and lead to the same result, and it is up to the user to decide which formulation they prefer.

THE NUMBER OF LIMITING FACTORS REACHING OR EXCEEDING THE NUMBER OF SPECIES

Chesson (2019) argues that we underestimate the utility of the theory when there are at least as many limiting factors L as species S . This is in response to our claim that the theory “does not offer any advantages, and may even work worse than other methods, if there are as many or more limiting factors as species” (Barabás et al. 2018:300). To be fair, we did follow that sentence up by saying that this limitation, along with others, may not be fundamental to the theory and could be amended by future work. In light of this, it is especially helpful that Chesson (2019) cites example applications with as many or more limiting factors than species, with a worked-out example in an Appendix.

The example of Chesson’s Appendix has two species in a MacArthur-style consumer–resource model (MacArthur 1970, Chesson 1990). In this case, due to the assumption of a timescale separation between resources and consumers (the former are much faster than the latter), the limiting factors become the species’ population densities themselves, and the competitive factors are weighted sums of them: $C_j = \sum_{k=1}^S \sigma_{jk} E_k N_k$, where S is the number of species, σ_{jk} is the interaction coefficient between species k and j based on the degree of overlap in their resource use, E_k is the k th environmental parameter, and N_k is the density of species k . Then, one can indeed obtain the comparison quotients using $\partial \mathcal{C}_i / \partial \mathcal{C}_s$ evaluated at $\mathcal{C}_s = 0$ (Chesson 2019: Eq. 14). The reason this works is that the invader species is absent from the community: $N_i^{-i} = 0$, which also means that the corresponding limiting factor is absent. In the two-species case for instance, letting i be the invader and s the resident, we have $C_i^{-i} = \sigma_{is} E_s N_s$ and $C_i^{-i} = \sigma_{ss} E_s N_s$, where N_s is the monoculture equilibrium density of the resident. We can therefore write $C_i^{-i} = \sigma_{is} E_s N_s = \sigma_{ss} E_s N_s \sigma_{is} / \sigma_{ss} = C_s^{-i} \sigma_{is} / \sigma_{ss}$, which is now explicitly a function of C_s^{-i} . Taking the derivative with respect to this variable yields the comparison quotients: $q_{is} = \partial C_i^{-i} / \partial C_s^{-i} = \sigma_{is} / \sigma_{ss}$.

More generally, in any S -species community with limiting factors proportional to the population densities, putting species i in the invader state will also set the i th factor to zero. This factor therefore disappears without

having to cancel it out, so the number of limiting factors to be eliminated is reduced from S to $S - 1$. This is now less than the number of species, so either the method of Chesson (2019: Eq. 14) or our method of the cancellation coefficients d_j (Barabás et al. 2018, Eq. 21) may be applied to cancel the remaining $S - 1$ factors. All in all, here indeed comparison quotients can be obtained even though there are as many limiting factors as species. On the downside, this method requires a separation of time scales which may not always hold. Relaxing this requirement to obtain comparison quotients when $L < S$ is still avenue for future research (Barabás et al. 2018: 295–296).

Our claim that Chesson’s framework loses its advantages compared to other methods when there are as many or more limiting factors than species was based on the fact that the theory is rooted in invasion analysis. What distinguishes it from “standard” textbook invasion analysis is the meaningful partitioning of invasion growth rates into the $\Delta \rho_i$, ΔN_i , ΔI_i , and $\Delta \kappa_i$ coexistence-affecting terms via the comparison quotients (Barabás et al. 2018: Eqs. 20 and 47). However, these quotients do not exist (or are all zero, if one uses our d_i) when $L \geq S$, unless we are in the realm of the example discussed above. Without the comparison quotients, the method effectively reduces to standard invasion analysis, and can do only as much. That said, there is more to the theory than the comparison quotients, and other aspects may still be useful for analysis, e.g., the quadratic expansion of growth rates. Furthermore, even when $L \geq S$, one can choose a subset of up to $S - 1$ limiting factors to eliminate explicitly, leaving the others as contributions to the $\Delta \rho_i$ term (Barabás et al. 2018:283). Though this leaves the $\Delta \rho_i$ term unevaluated, one still ends up with a meaningful partitioning of the invasion growth rates. Therefore, while the theory may not offer benefits over others in performing calculations, it still has strong heuristic power and can facilitate improved understanding even when $L \geq S$. We take it that this is what Chesson meant by pointing out that the theory is not primarily methodological, but a theory of coexistence in ecological communities: an important and valid point.

FURTHER POINTS

Chesson (2019) lists a number of additional issues that were “not handled well” by our review. As these were not expounded on, we do not respond to any specific criticisms here. Instead, we simply provide our own perspective on some of them, those about which we feel we have something relevant to say.

Species average fitness

In our review, we suggested replacing the term “average fitness difference” with “competitive advantage.” We

wish to emphasize that this was not because the original terminology cannot be justified (Chesson 2018). Rather, the problem is that subdisciplines such as adaptive dynamics (Geritz et al. 1998, Meszena 2005, Metz 2012) operate with a slightly different fitness concept. In adaptive dynamics, “fitness” corresponds to the realized per capita growth rate r_i of a rare invader in the environment defined by the resident species (Metz and Geritz 2016: *Invasion fitness and fitness proxies: a short review*). This differs from the “species average fitness” of Chesson (2018), which determines the identity of the competitively superior species in the absence of any coexistence-affecting mechanisms; and also from the “average fitness difference” (adjusted for the presence of such mechanisms) that was denoted by ξ_i in Chesson (2018) and by f_i in Barabas et al. (2018: Eq. 52). As we have stated in Barabas et al. (2018:286–287), we believe coexistence theory and adaptive dynamics combined could yield a method for studying evolution in variable environments. But then one may wish to avoid a potential terminological clash, where “fitness” means multiple, subtly different things. While the qualifier “species average” in front of “fitness” ought to clarify the distinction from the general fitness concept of adaptive dynamics, the term is often not used this way. As we have pointed out in Barabas et al. (2018:286), various aliases are in use, such as “relative fitness difference,” “fitness difference,” or just “fitness.” While we do not wish to insist on our own terminology, we hope this clarifies why we felt that there is a risk of a terminological clash, and opted for “competitive advantage” instead.

Community average stabilization and the size of the coexistence region

As long as the community average stabilization A and the average fitness differences f_i are independently adjustable, A will measure the size of the parameter region allowing for coexistence (Yuan and Chesson 2015). We have argued in Barabas et al. (2018:298) that, in general, A and f_i are not independent, thus limiting the use of A to measure the coexistence region. Since the publication of our review, there have been several new developments. Chesson (2018) proves a theorem stating that in models with sufficiently many parameters, one can always find some combination of them such that A and f_i are independently adjustable, at least for A sufficiently small. While this theorem shows that one can vary A and f_i independently in a broad class of models, it is silent on how likely this is to be the case in nature. Should field ecologists expect species differences in traits such as beak shape or flower color to contribute only to A , only to f_i , or both, confounding whether those differences promote coexistence by increasing stabilization or hinder it by increasing competitive advantages? We argue elsewhere that the independence of A and f_i is in fact highly

unlikely (Song et al. 2019): unless one chooses very carefully which parameters to vary and exactly how, both quantities will simultaneously change in response to the change in parameters. That said, this is a rapidly developing area, and while perfect independence may be the exception, the same need not be true of quasi-independence, whereby some mechanism *mainly* affects either A or the f_i , leaving the other relatively intact. For instance, analysis of a competition-predation tradeoff revealed that it mostly affected only the f_i (Stump and Chesson 2017). Such quasi-independence is an intriguing possibility and an avenue for future work.

The significance of the ratio of intra- to interspecific competition

For two-species Lotka-Volterra competition, intraspecific competition must exceed interspecific competition for coexistence. This statement has strong heuristic power: coexistence requires that a species limits itself more than its competitor. Generalizations of this principle to multiple species and other models all emphasize that stable and robust coexistence requires that species’ growth rates are, to an extent, regulated by different factors (Levin 1970, Chesson 2000, Meszena et al. 2006, Pasztor et al. 2016), leading to the same effect.

Its heuristic power notwithstanding, a naive application of the “intra > inter” principle can lead to incorrect conclusions. We have shown an example in Barabas et al. (2018: Appendix S8) where increasing the ratio of intra- to interspecific competition coefficients does not necessarily move the system in the direction of stability. This is due to indirect effects that are absent in a two-species setting (Barabas et al. 2016). For instance, reducing intraspecific competition may allow two species to coexist that together are able to prevent a third from establishing, even though all three possible species pairs would form stable communities. In some situations it is even possible to increase the intraspecific competition strength of a single species and get a non-monotonic effect on community stability, with a stable configuration achieved only for intermediate strengths (Barabas et al. 2017).

Despite these examples (which Peter Chesson acknowledges; see Chesson 2018: Eq. 37 and surrounding text), one may justifiably argue that the heuristic is nevertheless important, as it usefully guides our thinking about what kinds of effects can promote coexistence. Naive applications notwithstanding, the general principle that species must be somewhat independently regulated for stable coexistence still stands. We therefore stress that our purpose is not to dispel the principle, but to warn against adopting an unquestioning acceptance of it, and using it where it does not apply. The examples in Barabas et al. (2016, 2018) are designed to bring attention to the non-intuitive role of indirect effects and

show how naive applications can run into trouble, rather than to question the heuristic itself.

Niche overlap and the ratio of species average fitnesses

While this was not explicitly mentioned by Chesson (2019), we bring it up here nevertheless, as it is a topic we have indeed not handled well. Unlike with the other issues where we see differences in emphasis but no outright error, this topic was treated far too superficially in Barabás et al. (2018:287), without explanation but with notation that could easily cause confusion. To remediate, we have included an Appendix S1 where we explain the origin of the often-used formulas

$$\rho = \sqrt{\frac{a_{jk}a_{kj}}{a_{jj}a_{kk}}}, \quad \frac{\kappa_j}{\kappa_k} = \frac{b_j}{b_k} \sqrt{\frac{a_{kj}a_{kk}}{a_{jj}a_{jk}}} \quad (3)$$

in detail, along with the meaning of ρ and the κ -ratio, and their connection to the community average stabilization A and average fitness differences f_i .

CONCLUSIONS

We have argued that the deviations of Barabás et al. (2018) from Chesson's formalism (Chesson 1994, 2018, 2019) are not errors but differences in terminology, emphasis, and perspective, which we believe can help clarify the theory's strengths and weaknesses. Regardless of which description one prefers, the theory has the potential to continue developing and contributing to our understanding of coexistence. Alongside many other possibilities, one untapped direction is its application to problems of adaptive dynamics in variable environments. While the adaptive dynamics of two species in cyclic environments has been explored before (Kremer and Klausmeier 2013), coexistence theory could help generalize these results to stationary nonperiodic fluctuations and an arbitrary number of species. Furthermore, the theory will continue to remain useful in guiding our thinking about coexistence in spatiotemporally variable environments.

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