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# Chesson's coexistence theory: Comment

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Recently, Barabas et al (2018) tried to explain some of my contributions to species coexistence theory. They include many laudatory comments, and it might seem churlish to complain, but unfortunately, I found many mistakes in their account. I was not shown a copy of Barabas et al (2018) before it was accepted and appeared online, precluding my commenting before publication. Fortunately, my recent publication (Chesson 2018) provides detailed discussions of many of my concerns. Here, I focus on a key part of Barabas et al (2018) that receives scant attention in Chesson (2018), namely, the development of multispecies coexistence theory in Chesson (1994), which has been the foundation of much other work. I first briefly explain the key developments as I see them. I show also how my approach extends beyond the quadratic approximations of Chesson (1994) to exact results not

available from Barabas et al (2018). I then briefly point out how my account differs from Barabas et al (2018), finally mentioning other shortcomings of Barabas et al (2018) that are covered in Chesson (2018).

### *Multispecies coexistence in a temporally varying environment*

Chesson (1994) asks, What are the general properties of coexistence mechanisms in a temporally varying environment, how can these mechanisms be defined and measured, and how do multiple mechanisms of coexistence combine?  Coexistence in a variable environment has long been understood as arising from nonlinear dependence of per capita population growth on the varying environmental factors and population densities (Levins 1979, Armstrong and McGehee 1980, Chesson and Warner 1981). Nonlinearities include interactions between variables that may reflect life-history properties and population structure (Chesson 1990).

To gain a general understanding of how different kinds of nonlinearities can influence species coexistence in a variable environment, Chesson (1994) considered a general model in which population growth of any given species $j$ in a guild of $n$ competing species depends on two basic variables, $E_j(t)$, the environmental response, and $C_j(t)$, the competitive response, with $E_j(t)$ commonly representing a life-history parameter that varies over time, $t$, as a function of the physical environment, and $C_j(t)$ defining how growth is constrained by competition, both within and between species. These two variables are combined according to the biology of the species by a function $g_j$, so that the per capita growth rate of species $j$ takes the form

$$r_j(t) = g_j(E_j(t), C_j(t)), \tag{1}$$

which is assumed to increase with $E_j(t)$, while decreasing with $C_j(t)$. Table 1 gives simple examples of the function $g_j$ for specific models, and Fig 1 graphs some of them. Chesson (1994) focuses on discrete time and defines $r_j(t)$ as $\ln N_j(t+1) - \ln N_j(t)$, justified extensively elsewhere, e.g. Chesson (2018). Although the key ideas apply also to continuous-time models, with $r_j(t) = (dN_j/dt)/N_j)$, e.g. by Li and Chesson (2016), more powerful results are available for discrete-time models.

A basic level of understanding is achieved by considering deviations from an equilibrium condition ($r_j(t) = 0$) defined by specific values, $E_j^*$ and $C_j^*$ of $E_j(t)$ and $C_j(t)$, for which

$$g_j(E_j^*, C_j^*) = 0 . \tag{2}$$

Appropriately set up, $E_j(t)$ and $C_j(t)$ fluctuate about these equilibrial values. In analysis of variance parlance, deviations of $E_j(t)$ from $E_j^*$ give the main effect of the environment on population growth as

$$\mathsf{E}_j(t) = g_j(E_j(t), C_j^*) . \tag{3}$$

Similarly, deviations of $C_j(t)$ from $C_j^*$ give the main effect of competition as

$$\mathsf{C}_j(t) = -g_j(E_j^*, C_j(t)) , \tag{4}$$

where the negative sign in (4) is to make $r_i(t)$ decrease with $\mathsf{C}_j(t)$ as it does with $C_j(t)$. These variables $\mathsf{E}_j$ and $\mathsf{C}_j$ are transformations of the variables $E_j$ and $C_j$ into units of $r_j$ (standard units), and so have the same meanings in all models, despite the various meanings that $E_j$ and $C_j$ have in different models (Table 1), allowing a unified treatment. Because $\mathsf{E}_j$ and $\mathsf{C}_j$ are 0 respectively for $E_j = E_j^*$ and $C_j = C_j^*$ their equilibrial values, $\mathsf{E}_j^*$ and $\mathsf{C}_j^*$, are both 0.

As students of analysis of variance understand, the joint effect of two variables comes from their main effects plus their interaction, giving here

$$r_j(t) = \mathsf{E}_j - \mathsf{C}_j + \mathsf{I}_j , \tag{5}$$

where the dependence of $E_j(t)$, $C_j(t)$, and $I_j(t)$ on $t$ has been omitted for notational simplicity. The interaction, $I_j$, is key to the storage effect coexistence mechanism. It can be defined precisely as $I_j = r_j(t) - E_j + C_j$, which makes equation (5) trivially true, but an informative approximation is given as $I_j \approx \gamma_j E_j C_j$ where

$$\gamma_j = \frac{\partial^2 r_j}{\partial E_j \partial C_j}. \tag{6}$$

It follows that

$$r_j(t) \approx E_j - C_j + \gamma_j E_j C_j. \tag{7}$$

Equation (7) is a simple generic form applying to the whole class of models defined by equation (1). It shows that $r_j(t)$ is approximately linear in each standard variable separately, with the other held constant, but with the slopes of these linear relationships varying with the value of the other variable. These features are shown in Fig 1(c) for $r_j(t)$ plotted against $C_j$ for the case $\gamma_j < 0$, which means that when the environment is less favorable (i.e., $E_j$ is lower), $r_j(t)$ is less sensitive to competition, $C_j$. This is "buffered population growth," key to the storage effect (Li and Chesson 2016). Note also that $r_j(t)$ is exactly linear in $C_j$, indeed equal to $-C_j$ by definition when $E_j = 0$ ($E_j = E_j^*$), and exactly equal to $E_j$, and therefore linear in $E_j$, when $C_j = 0$ ($C_j = C_j^*$). Expression (7) is in fact the second order Taylor expansion of $r_j(t)$ in $E_j$ and $C_j$ about zero. Because the transformations, $E_j \to E_j$ and $C_j \to C_j$, make $r_j(t)$ linear separately in $E_j$ and $C_j$, the Taylor expansion (7) has no squared terms in $E_j$ and $C_j$. The sole quadratic term is the bilinear form, $\gamma_j E_j C_j$.

Equation (7) immediately reveals how environmental fluctuations can affect long-term population growth, which is determined by the time average, $\bar{r}_j$, of $r_j(t)$, because, according to the assumptions in Chesson (1994), the time average, $\overline{E_j C_j}$, of the product of $E_j$ and $C_j$ is approximately equal to their temporal covariance. Hence

$$\overline{r}_j \approx \overline{E_j} - \overline{C_j} + \gamma_j \, \mathrm{cov}(E_j, C_j) \,. \tag{8}$$

The covariance can only be nonzero when both the environment and competition fluctuate

over time and are temporally correlated, which can reflect such factors as the timing of

resource consumption and the timescale of resource depletion (Kuang and Chesson 2009, Li

and Chesson 2016). Moreover, its presence in $\overline{r}_j$ requires $\gamma_j$ to be nonzero, which in Fig 1(a)-

(c) is due to the nonparallelism of the curves, and can reflect life-histories and population

structure (Chesson 1990). Although the specific representation of the interaction as

$I_j \approx \gamma_j \overline{E_j C_j}$ is valuable for insights about the biological mechanisms, its numerical accuracy

can be limited (Kuang and Chesson 2009, Appendix E). For accuracy, expression (5) gives an

exact representation of long-term population growth as

$$\overline{r}_j = \overline{E_j} - \overline{C_j} + \overline{I}_j \,, \tag{9}$$

which would often be calculated numerically, for example, by simulation.

While the interaction term in these expressions leads to the storage effect, further

effects of temporal fluctuations on long-term growth are hidden in the time average, $\overline{C_j}$, of $C_j$

because it can be nonlinear in competitive factors that it shares with other species. The

general assumption of Chesson (1994) is that $C_j$ can be written as a function of $p$ competitive

factors, $(F_1, ..., F_p) = \mathbf{F}$, which can be specific resources, natural enemies (to include apparent

competition), species densities, densities at a particular life-history stage, or surrogates for

any of these. Thus, there is assumed to be a nonlinear function $\phi_j$ defining $C_j$ in terms of these

factors: $C_j = \phi_j(F_1, F_2, ..., F_p) = \phi_j(\mathbf{F})$,

(10)

which in Chesson (1994) is presented in two steps: $C_j = \phi'_j(\mathbf{F})$ for some function $\phi'_j$ and then

$C_j = \phi_j(\mathbf{F}) = -g_j(E_j^*, \phi'_j(\mathbf{F}))$. To ensure consistency in the procedures, an equilibrial value

$\mathbf{F}^* = (F_1^*,...,F_p^*)$ would normally be chosen first, then $C_j^* = \phi_j'(\mathbf{F}^*)$, with $E_j^*$ solved from

equation (2). Expression (10) can be expanded to quadratic order and averaged over time to

give the form

$$\overline{\mathsf{C}_j} \approx \phi_j(\mathbf{F}^*) + \sum_{l=1}^{p} \phi_{jl}^{(1)} \overline{(F_l - F_l^*)} + \frac{1}{2} \sum_{l=1}^{p} \sum_{m=1}^{p} \phi_{jlm}^{(2)} \overline{(F_l - F_l^*)(F_m - F_m^*)},$$

(11)

where $\phi_{jl}^{(1)}$ is the first partial derivative of $\phi_j$ in $F_l$, and $\phi_{jlm}^{(2)}$ is the second partial derivative in $F_l$

and $F_m$, all evaluated at equilibrial values. The effects of temporal fluctuations emerge in the

quadratic terms of equation (11), which under the assumptions in Chesson (1994), reduce to a

linear combination of temporal variances and covariances.

To understand what these long-term growth rates mean for species coexistence, we

need to understand how they vary with the circumstances. The basic idea is to see if a species

that has fallen to low density has a natural tendency to recover (has $\overline{r} > 0$), and thus avoid

extinction. That means evaluating $\overline{r}$ at low density, and in general this means in the limit as

the density goes to zero. At this point, the species is referred to as an invader, designated as

"species $i$," and other species, not perturbed to low density, as residents. The superscript $\{-i\}$

indicates a measurement with species $i$ in the invader state. Thus, $\mathsf{C}_s^{\{-i\}}$ is $\mathsf{C}_s$ for resident

species $s$ with $i$ as invader, while $\mathsf{C}_i^{\{-i\}}$ is the corresponding invader $\mathsf{C}$. A critical assumption

of the analysis, and an important restriction on it, is that $\mathsf{C}_i^{\{-i\}}$ can be expressed as a function

of the $\mathsf{C}_s^{\{-i\}}$, the idea being that resident species are responsible for the competition that the

invader experiences, which should be related to the competition the residents experience. In

terms of competitive factors, $F$, it means that the factors that an invader depends on should be

able to be solved for in terms of the $\mathsf{C}_s^{\{-i\}}$ from equation (10) by putting $j = s$, $\mathsf{C}_j = \mathsf{C}_s^{\{-i\}}$ and

solving (10) simultaneously for all resident species. Note that the competitive factors of

relevance can depend on which species is the invader, and if they have not otherwise been specified, they can always be chosen as $F_s = C_s^{\{-i\}}$, $s \neq i$, under the assumption that $C_i^{\{-i\}}$ is a function of them.

The analysis also requires that the residents form a *stable community*, which means that they fluctuate in a stationary manner over time with all species densities remaining positive (Chesson 1994, Chesson 2018). The invader species $i$ will have $\bar{r}_i > 0$ if it is advantaged over residents, which necessarily have $\bar{r}_s = 0$ because they have no long-term trends in population growth. Although residents have 0 long-term growth, the components, $\bar{E}_s, \bar{C}_s$ and $\bar{I}_s$ are not in general zero. These quantities can then be compared with the corresponding quantities for invaders to see where advantage to invaders accrue. The tricky part is knowing how to make the comparison, and for this we need constants, $q_{is}$, which might be called "comparison quotients," not to be confused with scaling factors (Chesson 2018). Then the 0 value $\sum_s q_{is} \bar{r}_s$ is subtracted from $\bar{r}_i$ to give,

$$
\begin{aligned}
\bar{r}_i &= \bar{r}_i - \sum_s q_{is} \bar{r}_s \\
&\approx \left[ \bar{E}_i - \sum_s q_{is} \bar{E}_s \right] - \left[ \bar{C}_i - \sum_s q_{is} \bar{C}_s \right] + \left[ \gamma_i \operatorname{cov}(E_j, C_j) - \sum_s q_{is} \gamma_s \operatorname{cov}(E_s, C_s) \right]. \\
&= \quad\quad \Delta E \quad\quad - \quad\quad \Delta C \quad\quad + \quad\quad\quad \Delta I
\end{aligned}
$$

(12)

The terms in [] identified as $\Delta E$, $\Delta C$, and $\Delta I$ indicate which processes contribute, and in what ways, to making $\bar{r}_i$ positive, allowing species $i$ to increase in density and avoid extinction. Note that an exact result is obtained by using equation (9) rather than (8), and defining

$$
\Delta I = \bar{I}_i - \sum_s q_{is} \bar{I}_s . \tag{13}
$$

How to choose the comparison quotients, $q_{is}$? The idea is that the comparison should eliminate common components of competition to highlight critical species differences. To do this Chesson (1994) considered how competition experienced by an invader changes when

competition experienced by a resident is perturbed, which gives

$$q_{is} = \frac{\partial \mathsf{C}_i^{\{-i\}}}{\partial \mathsf{C}_s^{\{-i\}}},$$ (14)

evaluated for the $\mathsf{C}_s^{\{-i\}} = 0$. This definition requires the restriction mentioned above that $\mathsf{C}_i^{\{-i\}}$

can be written as a function of the resident competitive responses, $(\mathsf{C}_1^{\{-i\}}, \dots, \mathsf{C}_n^{\{-i\}})$. The

comparison quotients defined by Eq. 14 eliminate linear terms in competitive factors (the first

sum in Eq.11 for $\overline{\mathsf{C}_j}$ ) in the specification of $\Delta C$, leaving just an equilibrial term and a

nonlinear term written as

$$\Delta C = \mathsf{C}_i^{\{-i\}*} + \Delta N,$$ (15)

where $\mathsf{C}_i^{\{-i\}*}$ is the competition the invader receives when the residents are at equilibrium ($C_s$

$= C_s^*$, $s \neq i$). The partition (15) thus quantifies equilibrium mechanisms in $\mathsf{C}_i^{\{-i\}*}$, and the

coexistence mechanism relative nonlinearity in $\Delta N$. This quantity is derived in Chesson

(1994, sec 4.2) in terms of the matrix $\boldsymbol{\Psi}$, with element $l$, $m$ defined as

$$\psi_{lm} = \tfrac{1}{2}\left(\phi_{ilm}^{(2)} - \sum_s q_{is}\phi_{slm}^{(2)}\right),$$ (16)

giving

$$\Delta N \approx \sum_{l,m} \psi_{lm} \,\mathrm{cov}(F_l, F_m).$$ (17)

Chesson (1994) writes this formula more compactly as $\Delta N \approx \mathrm{trace}\{\boldsymbol{\Psi}\,\mathrm{var}(\mathbf{F})\}$, where the

matrix var($\mathbf{F}$) has element $l$, $m$ equal to cov($F_l$, $F_m$). Note here that $\Delta N$ can also be defined

exactly as

$$\Delta N = \Delta C - \mathsf{C}_i^{\{-i\}*},$$ (18)

with $\Delta C$ defined as in equation (12), which therefore includes nonlinear terms beyond

quadratic. Thus, both approximate and exact approaches come from the same framework,

although the exact formulae would in general have to be evaluated numerically, for example

by simulation or numerical integration as used in Fig 1(d)-(f).

The long-term rate of increase from low density can now be written as

$$\overline{r}_i = \overline{r}_i' - \Delta N + \Delta I , \qquad (19)$$

where

$$\overline{r}_i' = \Delta E - \mathsf{C}_i^{\{-i\}*} , \qquad (20)$$

and is often described as the effect of equilibrium mechanisms, while $-\Delta N$ gives the effect of relative nonlinearity, and $\Delta I$ the storage effect. However, $\Delta E$ does reflect effects of fluctuations because in general the standard environmental responses $\mathsf{E}_j$ are nonlinear in the original responses, $E_j$, meaning that fluctuations will change $\overline{\mathsf{E}_j}$ , and in particular move it from 0 if $\overline{E}_j = E_j^*$, just as variance in the competitive factors causes $\Delta C$ to deviate from $\mathsf{C}_i^{\{-i\}*}$ by the amount $\Delta N$. Appendix S1 gives a simple model example of the calculations of the terms in equation (19).

Stochastic persistence theory (Schreiber et al. 2011), summarized in Chesson (2018), now shows how coexistence can be determined from the invasion rates, $\overline{r}_i$ . It is necessary to calculate $\overline{r}_i$ for every stable resident community that exists in the absence of species $i$, and this needs to be done for each species considered as the invader $i$ ($i$ = 1, …, $n$). When all these $\overline{r}_i$ values are positive, the full $n$-species community is stable, i.e. all $n$ species coexist, and have stationary fluctuations over time. As discussed in Chesson (2018), this specific condition justifies the conclusions on species coexistence for the specific examples in Chesson (1994). However, Schreiber et al 2011 show in fact that some $\overline{r}_i$ values can be negative for invasion into some specific subcommunities provided a weighted average of them, $\sum_i p_i \overline{r}_i$ , is positive in all cases for some fixed positive $p_i$'s. Stability of the $n$-species community then follows. Moreover, it is not necessary for all subsets of the full $n$-species to

form stable communities. For example, for rock-paper-scissors interactions with $n = 3$ (Schreiber et al 2011, Chesson 2018), two-species stable communities do not form, but stability of the three-species community can be established from the $\bar{r}_i$ for invasion into the three one-species communities, and the 0-species community.

### *Derivation of comparison quotients in terms of competitive factors*

Comparison quotients, $q_{is}$, defined by equation (14) as $\partial \mathsf{C}_i^{\{-i\}} / \partial \mathsf{C}_s^{\{-i\}}$, can be calculated from the dependence of the $\mathsf{C}_j$ on competitive factors (10). Note first of all that the $\phi_{jl}^{(1)}$, defined above as $\partial \mathsf{C}_i^{\{-i\}} / \partial F_l$, are connected to the $q_{is}$ by the relationship $\phi_{il}^{(1)} = \sum_s q_{is} \phi_{sl}^{(1)}$, which follows directly from the chain rule of differentiation, with all derivatives evaluated at $\mathbf{F} = \mathbf{F}^*$. Considering all $l$, gives a system of equations expressed in vector-matrix form as

$$\boldsymbol{\varphi}_i = \mathbf{q}_i \boldsymbol{\Phi}^{\{-i\}}. \tag{21}$$

Here $\mathbf{q}_i$ is the row vector ($q_{i1}$, ..., $q_{in}$) missing $q_{ii}$, $\boldsymbol{\Phi}$ is the matrix of derivatives, $\phi_{jl}^{(1)}$, $\boldsymbol{\Phi}^{\{-i\}}$ is this matrix missing the $i$th row, and $\boldsymbol{\varphi}_i$ as the $i$th row of $\boldsymbol{\Phi}$. Equation (21) can be solved for $\mathbf{q}_i$ using a generalized inverse, $(\boldsymbol{\Phi}^{\{-i\}})^-$, of the matrix $\boldsymbol{\Phi}^{\{-i\}}$ (Ben-Israel and Greville 2002), to give

$$\mathbf{q}_i = \boldsymbol{\varphi}_i \left( \boldsymbol{\Phi}^{\{-i\}} \right)^-. \tag{22}$$

Formula (22) is Eq. 34 of Chesson (1994), although a typesetting error dropped the "−" superscript. Note that in general $(\boldsymbol{\Phi}^{\{-i\}})^-$ is not the inverse of $\boldsymbol{\Phi}^{\{-i\}}$ because the usual matrix inverse need not exist, and cannot exist if the number of competitive factors is not equal to the number of resident species. However, generalized inverses are well-characterized (Ben-Israel and Greville 2002), and available in standard matrix computer packages (e.g. Gauss, Aptech Systems, Inc; Matlab, The MathWorks, Inc.; and R: (Friendly et al. 2019)). In general

they are not unique, which means that $\mathbf{q}_i$ is not unique in general, but there is a general

formula for all possible choices for $(\mathbf{\Phi}^{\{-i\}})^-$ (Ben-Israel and Greville 2002). Nonuniqueness

of $\mathbf{q}_i$ occurs when it is possible to express $\mathsf{C}_i^{\{-i\}}$ as a function of the $\mathsf{C}_s^{\{-i\}}$ in more than one

way, which is to be expected if there are fewer competitive factors than resident species. For

instance, in the simple case of a single competitive factor, $F$ ($\mathsf{C}_j = \phi_j(F)$,

$\phi_j^{(1)} = d\phi_j(F)/dF\big|_{F=F^*}$) any resident $\mathsf{C}_s^{\{-i\}}$ determines $F$. Alone, each resident species $s$ gives

a $\mathbf{q}_i$ of the form $(0,..,\phi_i^{(1)}/\phi_s^{(1)},...0)$. The average of these, $\mathbf{q}_i = (\phi_i^{(1)}/\phi_1^{(1)},...,\phi_i^{(1)}/\phi_n^{(1)})/(n-1)$,

is also a solution of formula (22), which is the commonly used formula for the case of a

single competitive factor, and is justified as treating resident species equivalently. However,

each of these $\mathbf{q}_i$ possibilities has information to offer, as they each define a valid basis for

comparison. Although $\overline{r_i}$ must always be the same, its component parts, $\overline{r_i}'$, $\Delta N$, and $\Delta I$ would

differ for different $\mathbf{q}_i$, because the question being asked varies with $\mathbf{q}_i$. Using $\mathbf{q}_i =$

$(0,..,\phi_i^{(1)}/\phi_s^{(1)},...0)$, the question is in effect, in what way does species $i$ gain advantage at low

density relative to resident species $s$? In this way, a more detailed understanding of the

ability of a species to increase from low density is available than with the traditional

approach, which examines only the average over resident species.

  When there are more competitive factors than resident species, the requirement that

$\mathsf{C}_i^{\{-i\}}$ can be written as a function of resident $\mathsf{C}_s^{\{-i\}}$ becomes potentially more restrictive

because obtaining $\mathbf{F}$ from the resident $\mathsf{C}_s^{\{-i\}}$ involves more unknowns than equations.

Nevertheless, some such circumstances can be covered. For instance, explicit resource and

natural enemy models are discussed in Chesson (2018) with indeed more competitive factors

than resident species, including both resources and natural enemies as "competitive factors."

Typically, one assumes a fast timescale for these resources and natural enemies allowing

these competitive factors to come to equilibrium as a function of more slowly changing focal

species densities. It follows that the dimension of the competitive factors is reduced to the number of resident species, which in effect become the competitive factors, as in Appendix S1. Without a fast timescale assumption, one can proceed as if these timescale assumptions applied, and still obtain the correct result for an equilibrium invasion analysis (Chesson and Kuang 2008, supplementary information), potentially pointing to a more general way forward.

### *Critique*

Barabas et al (2018) has numerous interpretational errors, some of which lead them to cast serious doubt on the theory that they purport to be explaining. Key errors relating to Chesson (1994) are corrected here, including the correct definitions and meanings of $E$ and $C$, which are required for critical understanding, and for exact results to apply. Barabas et al (2018) define $E$ and $C$ as the quadratic approximations of Appendix S1, Eq. S3. Although these formulae are the basis of analysis of the model by quadratic approximation, they vary in accuracy depending on the scale on which $E$ and $C$ are defined (compare the ratio and ln scales for the lottery model, table 1, and Fig 1) as shown very clearly in Fig 1(d)-(f).

Barabas et al (2018) claim that formula (14) does not properly define the comparison quotients, $q_{is}$, but this ignores the key assumption that $C_i^{\{-i\}}$ is a function of the resident $C_s^{\{-i\}}$. Although some of their discussion of the $q_{is}$ has merit, they confuse them with scaling factors (explained in detail in Chesson 2018) and do not give the generalized-inverse formula (22), just an equation to be solved. A substantial body of theory characterizes generalized inverses. The fact that they are not in general unique is not a defect of theory, but, as explained here, an opportunity for richer understanding. Also not a defect is the fact that the vector $(C_1^*, ..., C_n^*)$ cannot be chosen arbitrarily when there are fewer competitive factors than species. It is

naturally constrained by the ecology of the situation to a lower dimensional space defined by the competitive factors, $F$, as explained above.

Barabas et al (2018) suggest that "other methods" would do a better job than Chesson (1994) when the number of competitive factors exceeds the number of resident species, without specifying what these methods are. Here, I have shown how this particular case can be at least partially resolved within the general framework of Chesson (1994). Moreover, Chesson (1994) is not primarily a methodological paper. It is theory, showing for a particular broad class of models, how coexistence can emerge in a variable environment, the broad characteristics of the mechanisms involved and how they can be jointly quantitative assessed. No other framework has successful combined these endeavors, approaches derived from it to reduce the pain of calculation, notwithstanding (Ellner et al. 2016, Ellner et al. 2019).

When Barabas et al (2018) go beyond Chesson (1994) to later work, key issues are not handled well, including what scaling factors are, why "species average fitness" is an appropriate term, in what sense community average mechanism measures define the size of the coexistence region, how invasion rates, $\overline{r}_i$ , relate to coexistence, and the significance of the ratio of interspecific to intraspecific competition. Fortunately, all these issues are explained thoroughly and brought up to date in Chesson (2018), with further discussion in Chesson (2019).

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**Table 1 Models**

| Model | $r_j = g_j(E_j, C_j)$ | Meaning of $E_j$ | Meaning of $C_j$ | Other parameters |
|---|---|---|---|---|
| Lottery model, ratio-scale parameters, Chesson (1994) | $\ln\left\{1 - \delta_j + \dfrac{E_j}{C_j}\right\}$ | Per capita births | (Demand for space)/(supply of space) $\sum_{k=1}^{n} E_k N_k / \sum_{k=1}^{n} \delta_k N_k$ | $\delta_j$ adult death probability |
| Lottery model, ln scale parameters Chesson (1994) | $\ln\left\{1 - \delta_j + e^{E_j - C_j}\right\}$ | ln per capita births | ln (demand for space/supply of space) $\ln\left[\sum_{k=1}^{n} e^{E_k} N_k / \sum_{k=1}^{n} \delta_k N_k\right]$ | $\delta_j$ adult death probability |
| Seedbank model, Chesson (1990) | $\ln\left\{\begin{array}{l} s_j(1 - E_j) \\ + Y_j E_j / C_j \end{array}\right\}$ | Germination probability | Total seedling competition $1 + \sum_{k=1}^{n} \alpha_{jk} E_k N_k$ | $s_j$ seed survival probability; $\alpha_{jk}$ competition coefficient |
| MacArthur consumer-resource model, Li and Chesson (2016) | $E_j(H_j - C_j) - \mu_j$ | Resource uptake rate | Reduction in resource availability due to competition | $\mu_j$ maintenance requirement; $H_j$ maximum resource availability |

**Figure 1.** Lottery model per capita growth rate and invasion components for different competitive and environmental response scales. (a) – (c):  Each panel uses a different scale for the competitive and environmental responses in the lottery model (Table 1). The different curves in a panel are for different values of the environmental response. (a) Ratio scale, Table 1, row 1. (b) Natural log scale, Table 1, row 2.  (c) Standard scale responses, $E_j$ and $C_j$. Note that in (c) the line through the point $(C_j , r_j(t)) = (0,0)$ is straight, because it is the plot of $g_j(E_j^*, C_j)$ against $C_j$, i.e. $-C_j$ against $C_j$. Also, for $C_j = 0$, the spacing of the lines is even because then $r_j(t) = E_j$ and the spacing of the $E_j$ values is even. Straight lines, and even spacing of the curves, do not occur in the other panels despite even spacing of the $E_j$ values. Form (c) is an excellent approximation to the bilinear form Eq. 7 of the text. (d) – (f): The components, $\Delta E$ (d), $-\Delta N$ (e), and $\Delta I$ (f) of $\bar{r}_i$ for the lottery model with a common value of $C^*$ rendering $C_i^{\{-i\}^*} = 0$, and hence $\bar{r}_i = \Delta E - \Delta N + \Delta I$ . Solid lines: exact values (no approximations); short dashes: ratio scale quadratic approximation with variables as in (a); long dashes: ln scale quadratic approximation with variables as in (b).  The x-axis, var($E_s$), is variance of the resident ln scale environmental response. Invader variance, var($E_i$), = ½var($E_s$); $E_i$ and $E_s$ are independent, $E[E_i] – E[E_s] = –\tfrac{3}{8}$ var($E_s$), and $\delta_1 = 0.1$, $\delta_2 = 0.2$.  Note that in all cases, good quadratic approximations are found for var($E_s$) < 0.1, but the ratio scale approximations become poor at larger var($E_s$) values. In contrast, quadratic approximations remain good for the log scale variables.  Exact values are calculated using numerical integration.  The distributions of the environmental responses are normal on the ln scale.

**a**

$r_j(t)$

ratio scale $C_j$

**b**

$r_j(t)$

ln scale $C_j$

**c**

$r_j(t)$

$\mathscr{C}_j$

**d**

$\Delta E$

$\mathrm{var}(E_s)$

**e**

$-\Delta N$

$\mathrm{var}(E_s)$

**f**

$\Delta I$

$\mathrm{var}(E_s)$