Chesson's coexistence theory

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Abstract

We give a comprehensive review of Chesson's coexistence theory, summarizing, for the first time, all its fundamental details in one single document. Our goal is for both theoretical and empirical ecologists to be able to use the theory to interpret their findings, and to get a precise sense of the limits of its applicability. To this end, we introduce an explicit handling of limiting factors, and a new way of defining the scaling factors which partition invasion growth rates into the different mechanisms contributing to coexistence. We explain terminology such as relative nonlinearity, storage effect, and growth-density covariance, both in a formal setting and through their biological interpretation. We review the theory's applications and contributions to our current understanding of species coexistence. While the theory is very general, it is not well suited to all problems, so we carefully point out its limitations. Finally, we critique the paradigm of decomposing invasion growth rates into stabilizing and equalizing components: we argue that these concepts are useful when used judiciously, but have often been employed in an overly simplified way to justify false claims.

Keywords: average fitness differences, community ecology, competitive advantage, equalizing effect, growth-density covariance, relative nonlinearity, stabilization, storage effect, theoretical ecology, variable environment theory

1 Introduction

The theory of species coexistence developed by Peter Chesson and colleagues, often referred to simply as "modern coexistence theory" (Mayfield and Levine 2010, HilleRisLambers et al. 2012, Letten et al. 2017, Saavedra et al. 2017), is one of today's leading frameworks in community ecology. From its initial focus on two species coexisting via the storage effect (Chesson and Warner 1981), it has grown to encompass multispecies competition in temporally (Chesson 1994) and spatially (Chesson 2000a) variable environments, with important extensions concerning coexistence in general (Chesson 2000b, 2003). It dispels mistaken ideas about coexistence in variable environments (Chesson and Huntly 1997, Fox 2013), and replaces them with rigorous theory. It identifies a handful of mechanisms with the capacity to promote coexistence, and provides a starting point for measuring them empirically (Chesson 1994, 2000a). Furthermore, it provides a straightforward interpretation of coexistence as resulting from a balance between stabilization and differences in species' overall competitive abilities (Chesson 2000b, 2003). This in turn has contributed to the resurgence and revision of the niche concept (Chesson 1991, Leibold 1995, Chase and Leibold 2003, Meszéna et al. 2006, Letten et al. 2017), and a vast wealth of empirical applications (Angert et al. 2009, Adler et al. 2010, Narwani et al. 2013, Chesson et al. 2013, Godoy et al. 2014, Chu and Adler 2015, Kraft et al. 2015, Usinowicz et al. 2017, and many others). It has introduced a new benchmark for the generality and logical coherence of any comprehensive

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theory in community ecology. As such, it behooves community ecologists to understand its methods, accomplishments, and limitations.

While Chesson's coexistence theory is widely recognized, its methods and scope are often not well understood. References to the storage effect and relative nonlinearity are very common in the literature; by comparison, quantitative treatments are relatively rare. For example, Chesson (2000a), which proposed the spatial storage effect, has been cited over 350 times according to Scopus, and many of these citations come from empirical studies—yet we are only aware of one published work that empirically measures the spatial storage effect using the methods that article proposes (Sears and Chesson 2007). As a consequence, misuses of these terms are frequent in practice. The disconnect between the formal theory and verbal formulations of it is well illustrated by the fact that most studies using terms such as "stabilization" and "equalization" cite Chesson (2000b), even though these concepts have since undergone an important revision (Chesson 2003). The theory's scope is also commonly misrepresented: it is often referred to as simply the stabilizing/equalizing framework, neglecting its arguably more relevant contributions to understanding coexistence in variable environments. Most problematic of all, Chesson's formalism is sometimes co-opted to justify conclusions which either require great care of interpretation, or are simply not supported by the theory. One such claim is that stabilization is always increased by reducing the ratio of inter- to intraspecific competition; another is that Chesson's theory proves the possibility of the stable coexistence of arbitrarily similar species.

Part of the reason for the aforementioned problems is that learning the theory from scratch is a daunting task. First, it is scattered across articles and book chapters. The general theory of coexistence in temporally variable environments is found in Chesson (1994); its generalization to spatial variation in Chesson (2000a). The concept of a stabilizing mechanism is treated separately in Chesson (2000b) and Chesson (2003). In a parallel development, Chesson (1990), Chesson and Kuang (2008), Chesson (2011), and Chesson (2013) develop a very similar concept but in a different context. In addition, the theory has changed over time. For example, in Chesson (2000b), stabilization was introduced as a species-level concept; in Chesson (2003), it was framed as a property of entire communities. Existing reviews cover aspects of the theory, but they either do not derive any of the technical details (e.g., Chesson 2008), or cover only parts of the theory (Chesson et al. 2005, Adler et al. 2007, Chesson 2009). On top of this, the sources are difficult reading, and some aspects are either never explained in sufficient detail to make applications easy, or else their limitations are not clearly outlined. For example, the scaling factors which partition invasion growth rates into resident and invader contributions have managed to confound even those familiar with the theory (personal communications). Furthermore, while the theory is very general, it is not omnipotent. In some cases, especially when species compete for a large number of resources, Chesson's theory is less useful than other methods. In other cases, it simply does not apply: complex dynamics and communities with a large number of species are usually outside of its grasp. Existing literature does not discuss these limitations in detail, which makes it difficult for newcomers to see what the theory can and cannot do.

Given that the theory is at the same time influential and arcane, difficult to understand and easy to misunderstand, and fragmented across time and space, we believe it is in need of a review accessible to a wide audience. Here we present a self-contained account of the current theory, with emphasis on the insights it provides while pointing out its limitations and misuses. The review is structured as follows. Section 2 presents the technical machinery of the theory, with an explicit focus on limiting factors and an improved way of handling the scaling factors which partition invasion growth rates into various coexistence-affecting contributions. Section 3 gives the biological interpretation of these

basic mechanisms. Section 4 reviews the theoretical and empirical advances the theory has facilitated. Section 5 covers current challenges, limitations, and open questions for the body of theory itself. Section 6 discusses the merits and problems of decomposing invasion growth rates into stabilization and competitive advantage terms. Finally, Section 7 summarizes our outlook on the theory's place in community ecology.

2 A technical summary of Chesson's coexistence theory

Chesson's theory has an arcane reputation to it, which is undoubtedly one reason why it is not more widely used. Despite appearances, the fundamental ideas behind the theory are rather simple. Starting from the assumption that environmental fluctuations are small, the theory simplifies ecological models via quadratic expansions of species growth rates around equilibrium. Next, it averages these growth rates over the environmental fluctuations; this introduces means, variances, and covariances between different quantities, which are interpreted as different mechanisms that may promote coexistence. The theory then examines the growth rate of each species when at low abundance while the other species are at their resident states, to determine whether all are able to rebound from rarity and therefore coexist.

While the discussion will inevitably be filled with occasionally rather long equations, it involves no *deep* mathematics. The mathematically deep part of the theory is mostly concerned with making sure that the approximations made by the theory are internally consistent, which is covered in e.g. Chesson (1994) and Chesson (2000a). Here we take this self-consistency for granted and appeal to intuition in performing the approximations. We include a summary of the basic mathematical tools needed in Appendix S1.

Below we show step-by-step how Chesson's framework can be applied to any model designed for studying the effect of small environmental fluctuations in stationary environments. We first assume that the community is spatially well-mixed, and extend the theory to spatially variable environments only in Section 2.6.

2.1 The quadratic approximation of the growth rates

The starting point for the analysis is an ecological community model of the form

$$\frac{\mathrm{d}n_j}{\mathrm{d}t} = n_j r_j(E_j, C_j) \qquad (j = 1, 2, \ldots, S), \tag{1}$$

where n_j is the abundance (density) of species j, t is time, S is the number of species, and r_j is species j's per capita growth rate. This, in turn, is written as a function of density-independent environmental parameters E_j and density-dependent interaction parameters C_j (Chesson 1994). The E_j may only contain environmental effects which influence the dynamics but are uninfluenced by it in turn. In contrast, the C_j depend either directly on the abundances n_j, or on limiting (regulating) factors which are influenced by the abundances. By definition, all density- and frequency-dependent feedback loops must be exclusively mediated by the C_j.[1]

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[1] In Chesson's works, the interaction parameters are called competitive factors, because they are assumed, by default, to measure the degree of competition in the system (i.e., increasing C_j causes a reduction in r_j). Though the interaction parameters indeed often measure competitive effects, this is not in any way a requirement: since all species interactions must be mediated via the C_j, they may include both positive and negative effects. We therefore do not make the default assumption of competition in this work.

Though generalizations are possible (Angert et al. 2009, Kuang and Chesson 2010, Chesson and Kuang 2010, Stump and Chesson 2015, 2017), for simplicity, in this article we follow the convention that there is only one E_j and C_j parameter per species. These are therefore not atomic model parameters, but combinations of model parameters and exogenous variables. To give an example, we consider a simple linear resource consumption model with per capita growth rates given by $r_j = b_j F - m_j$, where F is some limiting resource, b_j is the amount of growth species j achieves on one unit of resource, and m_j is a mortality rate. Here one cannot identify E_j with the density-independent parameters b_j and m_j separately. Instead, one may designate $E_j = -m_j$ and $C_j = b_j F$, leading to $r_j = E_j + C_j$. Alternatively, one could also choose $E_j = 0$ and $C_j = b_j F - m_j$, or $E_j = b_j$ and $C_j = b_j(F-1) - m_j$ (both also leading to $r_j = E_j + C_j$). However, one may not choose $E_j = b_j F$ and $C_j = -m_j$ because, although their sum is still equal to r_j, the E_j must not depend on the density-dependent limiting resource F. As seen, the choice of E_j and C_j is generally not unique (Chesson 1994)—however, while certain choices may make calculations easier than others, this ambiguity does not influence the final results (Section 2.8).

A key idea behind Chesson's coexistence theory is to reduce the complexity of the (arbitrarily complicated) system Eq. 1 by approximating the per capita growth rate, r_j, as a quadratic function of E_j and C_j. This is done using a standard Taylor series expansion (Appendix S1). For some models, the quadratic expansion is exact (see, e.g., Section 2.5 or Appendix S4), but for more complicated ones, this allows one to capture much of the model's interesting aspects while keeping them sufficiently simple to be manageable. It is difficult to overstate how fruitful Chesson's quadratic expansion has proven both in elucidating when fluctuations are important for coexistence in general, and uncovering the role of environmental fluctuations in particular empirical systems—we shall see examples of both kinds throughout this article.

To perform the Taylor series expansion, one has to know which values of the variables E_j and C_j we are approximating around. Any species stably present in its environment has an average long-term per capita growth rate of zero. Thus, equilibrium growth is a good baseline for the approximation. We designate "equilibrium" values for the environmental and interaction parameters, E_j^* and C_j^*, such that $r_j(E_j^*, C_j^*) = 0$. Their values will generally not be unique. For instance, if $r_j = E_j + C_j$, then any $E_j^* = -C_j^*$ leads to $r_j(E_j^*, C_j^*) = 0$. That is, there are infinitely many E_j^*, C_j^* combinations leading to zero per capita growth—however, choosing a value for one will fix the value of the other (Chesson 1994). Since the goal is to expand the growth rates around E_j^* and C_j^* assuming small fluctuations, the strategy is to choose E_j^* to fall near the mean value of E_j. Importantly, with Chesson's (1994) assumptions, this guarantees that C_j^* will fall near the mean of the C_j as well. In general, the closer E_j^* and C_j^* are to the true mean values, the more accurate the approximation will be.

Let us now perform the expansion of the growth rates around E_j^* and C_j^*. The detailed, mathematically rigorous discussion of when and how this can be done can be found in Chesson (1994) and Chesson (2000a). The quick-and-dirty summary of these results is that as long as fluctuations are assumed to be small, and E_j^* and C_j^* fall near the means of E_j and C_j, then terms whose joint order in $(E_j - E_j^*)$ and $(C_j - C_j^*)$ is larger than quadratic may be neglected. The quadratic expansion, using Eq. S1.1, thus reads

$$r_j(E_j, C_j) \approx \alpha_j(E_j - E_j^*) + \frac{1}{2}\alpha_j^{(2)}(E_j - E_j^*)^2 + \beta_j(C_j - C_j^*) + \frac{1}{2}\beta_j^{(2)}(C_j - C_j^*)^2$$
$$+ \zeta_j(E_j - E_j^*)(C_j - C_j^*)$$

(2)

(the 0th-order term was $r_j(E_j^*, C_j^*) = 0$), where the Taylor coefficients

$$\alpha_j = \frac{\partial r_j}{\partial E_j}, \quad \alpha_j^{(2)} = \frac{\partial^2 r_j}{\partial E_j^2}, \quad \beta_j = \frac{\partial r_j}{\partial C_j}, \quad \beta_j^{(2)} = \frac{\partial^2 r_j}{\partial C_j^2}, \quad \zeta_j = \frac{\partial^2 r_j}{\partial E_j \partial C_j} \tag{3}$$

are evaluated[2] at $E_j = E_j^*$ and $C_j = C_j^*$. To write Eq. 2 in a simpler form, let us introduce the new variables

$$\mathscr{E}_j = \alpha_j(E_j - E_j^*) + \frac{1}{2}\alpha_j^{(2)}(E_j - E_j^*)^2, \tag{4}$$

$$\mathscr{C}_j = \beta_j(C_j - C_j^*) + \frac{1}{2}\beta_j^{(2)}(C_j - C_j^*)^2, \tag{5}$$

called the standardized environmental and interaction parameters (Chesson 1994, 2000a). Eq. 2 may now be written $r_j \approx \mathscr{E}_j + \mathscr{C}_j + \zeta_j(E_j - E_j^*)(C_j - C_j^*)$, which is simpler than before but problematic because r_j should be expressed as a function of $\mathscr{E}_j$ and $\mathscr{C}_j$ only. This, however, can be done by examining the product $\mathscr{E}_j\mathscr{C}_j$:

$$\begin{aligned}\mathscr{E}_j\mathscr{C}_j &= \left(\alpha_j(E_j - E_j^*) + \frac{1}{2}\alpha_j^{(2)}(E_j - E_j^*)^2\right)\left(\beta_j(C_j - C_j^*) + \frac{1}{2}\beta_j^{(2)}(C_j - C_j^*)^2\right)\\ &\approx \alpha_j\beta_j(E_j - E_j^*)(C_j - C_j^*),\end{aligned} \tag{6}$$

because all further terms are of higher joint order in $(E_j - E_j^*)$ and $(C_j - C_j^*)$ than quadratic and so can be neglected (Chesson 1994). Therefore, after introducing $\gamma_j = \zeta_j/(\alpha_j\beta_j)$, Eq. 2 can be written

$$r_j \approx \mathscr{E}_j + \mathscr{C}_j + \gamma_j\mathscr{E}_j\mathscr{C}_j, \tag{7}$$

the standard form of the quadratic approximation found in the works of Chesson.[3]

The parameter γ_j measures the strength of interaction between environmental effects and species interactions (Chesson 1994). If it is equal to zero, then improving the environment by X units (increasing $\mathscr{E}_j$ by X) and making species interactions more beneficial by Y units (increasing $\mathscr{C}_j$ by Y) will result in the per capita growth rates increasing by $X + Y$ units in Eq. 7. So γ_j measures the deviation from this baseline additive expectation: a positive (negative) γ_j means the growth benefit of species j will be greater (smaller) than expected. See Section 3 for a biological interpretation of γ_j.

Most existing discussions of Chesson's general formalism conclude the quadratic approximation with Eq. 7. In fact, there is another important step to be done, one which is discussed in Chesson (1994) for specific types of models, and handled on a model-to-model basis in subsequent works. Here we make this step fully general. By definition, the $\mathscr{C}_j$ are density-dependent, inheriting the dependence from C_j via Eq. 5. They are therefore functions of limiting factors $F_1, F_2, \ldots, F_L$, which themselves

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[2] Chesson defines the Taylor coefficients β_j and $\beta_j^{(2)}$ with negative signs to conform to the usual interpretation of the interaction parameters measuring competition. While this is perfectly reasonable, it has two downsides: first, the C_j may measure positive interactions as well; second, the juggling of extra negative signs makes calculation errors easier (we speak from experience). We therefore do not follow Chesson's sign conventions here, and define everything with positive signs. Naturally, the final results are insensitive to the sign convention used.

[3] An alternative derivation proceeds by first defining $\mathscr{E}_j = r_j(E_j, C_j^*)$ and $\mathscr{C}_j = r_j(E_j^*, C_j)$, and then performing the expansion in these new variables—this will also lead to Eq. 7 (Chesson 1994, 2000a). Eqs. 4 and 5 may then be thought of as quadratic approximations to $\mathscr{E}_j = r_j(E_j, C_j^*)$ and $\mathscr{C}_j = r_j(E_j^*, C_j)$.

depend on the species' abundances. We use the term "limiting factor" to refer to any density- or frequency-dependent variable affecting population growth. Limiting factors can include resources, predators, refuges, or the species' abundances themselves. In Chesson's framework, the interaction parameters are also expanded to quadratic order in the limiting factors. To do so, we first define "equilibrium" values for the limiting factors, such that C_j as a function of these factor levels is equal to C_j^*:

$$C_j(F_1^{*j}, F_2^{*j}, \ldots, F_L^{*j}) = C_j^*, \tag{8}$$

where F_k^{*j} is the level of the kth limiting factor that makes the jth interaction parameter "equilibrial" (Chesson 1994). After finding the F_k^{*j}, we expand $\mathscr{C}_j$ around them (Eq. S1.1):

$$\mathscr{C}_j \approx \sum_{k=1}^{L} \phi_{jk}(F_k - F_k^{*j}) + \frac{1}{2}\sum_{k=1}^{L}\sum_{l=1}^{L} \psi_{jkl}(F_k - F_k^{*j})(F_l - F_l^{*j}), \tag{9}$$

where the 0th-order term $\mathscr{C}_j(F_1^{*j}, F_2^{*j}, \ldots, F_L^{*j})$ vanished due to Eqs. 5 and 8, and the Taylor coefficients

$$\phi_{jk} = \frac{\partial \mathscr{C}_j}{\partial F_k}, \quad \psi_{jkl} = \frac{\partial^2 \mathscr{C}_j}{\partial F_k \partial F_l} \tag{10}$$

are evaluated at $F_k = F_k^{*j}$. They may be functions of time, since they are not evaluated at $E_j = E_j^*$. This concludes the approximation procedure for an arbitrary model.

In models with a single limiting factor F, one can simply solve Eq. 8 for F^{*j}, and then perform the quadratic expansion around that value—see Appendix S2 for an example. When there is more than one limiting factor however, Eq. 8 does not have a unique solution for the F_k^{*j}. Rather, as with E_j^* and C_j^*, the choice of F_k^{*j} is arbitrary, as long as Eq. 8 holds and F_k^{*j} is close to the mean of F_k. They then have to be determined another way—for instance, using a set of equations governing the dynamics of the F_k; or, if the theory is used to describe an experiment or observation, from measured data on equilibrial levels of the limiting factors. This difficulty foreshadows a recurring theme in Chesson's theory: namely, that it is more useful when there is only one single limiting factor. Subsequently, we will see further examples for this.

2.2   Time averaging

In averaging temporally, one must assume that fluctuations are *stationary*—their statistical properties are constant in time (Turchin 2003). It is also assumed that the characteristic time scale of the fluctuations is not so short as to make it irrelevant for population dynamics, nor so long as to slide into other, nonstationary processes (such as Milankovitch cycles), rendering the assumption of stationarity untenable. With these caveats, the time average of Eq. 7 for any species j reads

$$\begin{aligned}
\overline{r}_j &\approx \overline{\mathscr{E}}_j + \overline{\mathscr{C}}_j + \gamma_j \overline{\mathscr{E}_j \mathscr{C}_j} \\
&= \overline{\mathscr{E}}_j + \overline{\mathscr{C}}_j + \gamma_j \overline{\mathscr{E}}_j \overline{\mathscr{C}}_j + \gamma_j \mathrm{cov}(\mathscr{E}_j, \mathscr{C}_j)
\end{aligned} \tag{11}$$

(Chesson 1994), where the overbar denotes time averaging, $\mathrm{cov}(\cdot, \cdot)$ denotes covariance, and we used Eq. S1.2 to write the average of a product. An important technical result (Chesson 2000a, Appendix III) establishes that if the variance of E_j is small, then the variance of C_j will be of the same order of

magnitude. From Eqs. 4 and 5, $\overline{\mathscr{E}}_j$ and $\overline{\mathscr{C}}_j$ are both proportional to this variance. Their product is then proportional to this small variance squared, which can be neglected. We therefore can write

$$\overline{r}_j \approx \overline{\mathscr{E}}_j + \overline{\mathscr{C}}_j + \gamma_j \text{cov}(\mathscr{E}_j, \mathscr{C}_j). \tag{12}$$

Substituting $\mathscr{C}_j$ from Eq. 9 into Eq. 12, we get

$$\overline{r}_j \approx \overline{\mathscr{E}}_j + \sum_{k=1}^{L} \overline{\phi_{jk}(F_k - F_k^{*j})} + \frac{1}{2} \sum_{k=1}^{L} \sum_{l=1}^{L} \overline{\psi_{jkl}(F_k - F_k^{*j})(F_l - F_l^{*j})} + \gamma_j \text{cov}(\mathscr{E}_j, \mathscr{C}_j). \tag{13}$$

Using Eq. S1.2 again:

$$
\begin{aligned}
\overline{r}_j \approx{} & \overline{\mathscr{E}}_j + \sum_{k=1}^{L} \overline{\phi}_{jk}(\overline{F}_k - F_k^{*j}) + \frac{1}{2} \sum_{k=1}^{L} \sum_{l=1}^{L} \overline{\psi}_{jkl} \overline{(F_k - F_k^{*j})(F_l - F_l^{*j})} \\
& + \gamma_j \text{cov}(\mathscr{E}_j, \mathscr{C}_j) + \sum_{k=1}^{L} \text{cov}(\phi_{jk}, F_k) + \frac{1}{2} \sum_{k=1}^{L} \sum_{l=1}^{L} \text{cov}\Big(\psi_{jkl}, (F_k - F_k^{*j})(F_l - F_l^{*j})\Big),
\end{aligned}
\tag{14}
$$

where we replaced $\text{cov}(\phi_{jk}, F_k - F_k^{*j})$ with $\text{cov}(\phi_{jk}, F_k)$, which can be done since F_k^{*j} is a constant (Eq. S1.3). The mean of the standardized environmental parameters $\overline{\mathscr{E}}_j$ may be written, using Eq. 4, as $\overline{\mathscr{E}}_j = \alpha_j \overline{(E_j - E_j^*)} + \alpha_j^{(2)} \overline{(E_j - E_j^*)^2}/2$, which simplifies to $\overline{\mathscr{E}}_j = \alpha_j^{(2)} \text{var}(E_j)/2$ if E_j^* was chosen to be equal to $\overline{E}_j$.

In case $\mathscr{C}_j$ does not have any explicit time dependence, the coefficients of Eq. 10 will also be time-independent. Then, after introducing the simplifying notation $V_{jkl} = \overline{(F_k - F_k^{*j})(F_l - F_l^{*j})}$ for the covariance matrix of the limiting factors, we have the simplified formula

$$\overline{r}_j \approx \left(\overline{\mathscr{E}}_j - \sum_{k=1}^{L} \phi_{jk} F_k^{*j}\right) + \sum_{k=1}^{L} \phi_{jk} \overline{F}_k + \frac{1}{2} \sum_{k=1}^{L} \sum_{l=1}^{L} \psi_{jkl} V_{jkl} + \gamma_j \text{cov}(\mathscr{E}_j, \mathscr{C}_j). \tag{15}$$

We have also rearranged the equation slightly: now the first term contains only constants, the second is linear and the third quadratic in the limiting factors, and the last one is a covariance term.

For simplicity of bookkeeping, from now on we will use this equation instead of Eq. 14. However, the more general case can always be recovered simply by replacing ϕ_{jk} and ψ_{jkl} with their time averages, and $\gamma_j \text{cov}(\mathscr{E}_j, \mathscr{C}_j)$ with the sum of all three covariance terms of Eq. 14 if needed. As will be seen, this way of writing the growth rates conveniently separates the contributions of different mechanisms to coexistence.

2.3   Resident and invader growth rates

Chesson's coexistence theory is based on invasion analysis. Invasion analysis was introduced in ecology by Turelli (1978), with important subsequent advances in the theory of invasion processes in general (Schreiber 2000, Hofbauer and Schreiber 2010, Schreiber et al. 2011). When performing invasion analysis, one species out of the S-species community (the invader) is assumed to be at low density, such that it is affected by the other species, but it has no effect on its surroundings. This means that its population dynamics are especially simple: the invader is undergoing density-independent growth. Moreover, since we have assumed a stationary environment, the invader grows with a constant average

long-term growth rate. If this long-term growth rate, called the *invasion growth rate*, is negative or zero, the species cannot invade: coexistence is lost (Schreiber et al. 2011). However, for positive invasion growth rates, the species is able to recover from low density with nonzero probability (Turelli 1980). If we also assume that "low" density means something much smaller than resident densities but still large enough so that demographic stochasticity plays no significant role, then a positive invasion rate ensures that the invader can establish itself in the community. If all S species have positive invasion growth rates, the species can mutually invade each other when they drop to low abundance, and therefore they are able to coexist. However, if even a single species has a nonpositive invasion growth rate, it cannot rebound from low density, and coexistence is lost.

Invasion analysis assumes that the resident community, composed of the $S - 1$ species in the absence of the invader, eventually settles down to some stationary state after the invader is removed. This means that all resident species can persist at equilibrium, in a limit cycle, or a stochastic steady state, but that they must have an average growth rate of zero. It is this stationary state against which the invader's long-term low-density growth rate is evaluated. Without this assumption, invaders' environments would not be stationary and invasion growth rates would not be well-defined. Although in principle possible, the theory does not consider what happens when two or more species are simultaneously perturbed down to the invader state. Though this has ramifications for the theory (Section 5.2), the simplest assumption is that of a single invader at a time.

With these preliminaries, we write the long-term per capita growth rate of the species assuming species i is the invader. This proceeds by writing Eq. 15 with the assumption that all quantities are evaluated when species i is absent and the remaining $S - 1$ species have assumed their stationary states. The standardized environmental parameters $\mathscr{E}_j$ are insensitive to this distinction, as these are by definition density- and frequency-independent. However, the limiting factors F_k, and by extension the standardized interaction parameters $\mathscr{C}_j$, will differ depending on the identity of the invader (e.g., if two species compete for soil nitrate, the nitrate levels will be different depending on which species is resident unless they have precisely identical nitrate usage). One way to express this in notation is to add a superscript "$-i$" to quantities which are evaluated in the absence of the invading species i:

$$\overline{r}_j^{-i} \approx \left(\overline{\mathscr{E}}_j - \sum_{k=1}^{L} \phi_{jk} F_k^{*j} \right) + \sum_{k=1}^{L} \phi_{jk} \overline{F}_k^{-i} + \frac{1}{2} \sum_{k=1}^{L} \sum_{l=1}^{L} \psi_{jkl} V_{jkl}^{-i} + \gamma_j \text{cov}(\mathscr{E}_j, \mathscr{C}_j^{-i}). \tag{16}$$

Keeping track of the "$-i$" superscripts encumbers notation, so from here on we will omit them unless they are necessary for avoiding ambiguity. Instead, it should be understood that the limiting factors and standardized interaction parameters will generally depend on the identity of the invading species. Note that the Taylor coefficients ϕ_{jk}, ψ_{jkl}, and γ_j are evaluated using the (invader-independent) E_j^*, C_j^*, and F_k^{*j}, so they do not depend on invader identity.

Importantly, the accuracy of the quadratic approximation will generally depend on $\overline{F}_k^{-i}$ falling near the F_k^{*j}. The reason one should keep this in mind is that the F_k^{*j} are calculated to satisfy the resident equilibrium condition $r_j(E_j^*, C_j^*(F_k^{j*})) = 0$; however, putting a species into its invasion state constitutes a large perturbation, which may therefore have a substantial effect on $\overline{F}_k^{-i}$, potentially making it quite different from F_k^{*j}. Whether the approximation is ultimately acceptable for the purposes of the model in question must be ascertained on a case-by-case basis—though see Chesson (1994, Appendix II) for general guidelines.

If $\overline{r}_i > 0$ for all S species in the role of the invader i, the species can mutually invade and we have coexistence.

2.4   Partitioning the sum of invader and resident growth rates

One might think Eq. 16 spells the end of the theoretical part of the framework: we simply evaluate the invasion growth rates for all species as invaders, and check whether they all turn out positive. However, further gains are made by considering not only the value of each term in Eq. 16, but also how they differ between species. For example, knowing that a particular term affects all species equally shows that it has no impact on coexistence (since no species benefits relative to its competitors), and knowing that a term is always greater for invaders means it promotes coexistence, since that term gives all species an advantage when they are rare. To make such comparisons, Chesson (1994, 2000a) considers a weighted sum of the invader and resident growth rates. Let us introduce constants d_j^{-i}, to be determined later, and form

$$\overline{r}_i^{-i} = \frac{1}{d_i^{-i}} \sum_{j=1}^{S} d_j^{-i} \overline{r}_j^{-i}. \tag{17}$$

As long as $d_i^{-i} \neq 0$, the sum is equal to $\overline{r}_i$ because all resident rates are zero. This expression is further expanded using Eq. 16 (in keeping with our notational shorthand, from here onward we omit the "$-i$" superscripts):

$$\overline{r}_i \approx \frac{1}{d_i} \sum_{j=1}^{S} d_j \left[\left(\overline{\mathscr{E}}_j - \sum_{k=1}^{L} \phi_{jk} F_k^{*j} \right) + \sum_{k=1}^{L} \phi_{jk} \overline{F}_k + \frac{1}{2} \sum_{k=1}^{L} \sum_{l=1}^{L} \psi_{jkl} V_{jkl} + \gamma_j \mathrm{cov}(\mathscr{E}_j, \mathscr{C}_j) \right]. \tag{18}$$

Breaking up the sum over all species j into the contribution from the invader i and residents $s \neq i$, we can equivalently write

$$\overline{r}_i \approx \underbrace{\left[\left(\overline{\mathscr{E}}_i - \sum_{k=1}^{L} \phi_{ik} F_k^{*i} \right) + \sum_{s \neq i} \frac{d_s}{d_i} \left(\overline{\mathscr{E}}_s - \sum_{k=1}^{L} \phi_{sk} F_k^{*s} \right) \right]}_{\text{constant terms, } r_i'} + \underbrace{\left[\sum_{k=1}^{L} \phi_{ik} \overline{F}_k + \sum_{s \neq i} \sum_{k=1}^{L} \frac{d_s}{d_i} \phi_{sk} \overline{F}_k \right]}_{\text{linear terms, } \Delta \rho_i}$$
$$+ \underbrace{\left[\sum_{k=1}^{L} \sum_{l=1}^{L} \psi_{ikl} V_{ikl} + \sum_{s \neq i} \sum_{k=1}^{L} \sum_{l=1}^{L} \frac{d_s}{d_i} \psi_{skl} V_{skl} \right]}_{\text{quadratic terms, } \Delta N_i} + \underbrace{\left[\gamma_i \mathrm{cov}(\mathscr{E}_i, \mathscr{C}_i) + \sum_{s \neq i} \frac{d_s}{d_i} \gamma_s \mathrm{cov}(\mathscr{E}_s, \mathscr{C}_s) \right]}_{\text{covariance terms, } \Delta I_i}, \tag{19}$$

where each of the collected terms is a sum of invader and resident contributions:

$$\overline{r}_i = r_i' + \Delta \rho_i + \Delta N_i + \Delta I_i. \tag{20}$$

Here r_i' is the invasion growth rate of species i in the absence of any frequency-dependent effects; $\Delta \rho_i$ summarizes fluctuation-independent frequency dependence such as those stemming from resource partitioning or species-specific predation pressures; ΔN_i is *relative nonlinearity*; and ΔI_i is the *storage effect* (more on these in Section 3).

We now determine the constants d_j. Our goal is to choose them so that we can eliminate the linear term $\Delta \rho_i$. As we will see, this provides a major simplification to Eq 19 which confers the theory much of its utility. For this purpose, assume for the moment that there are more species than limiting factors (i.e., $S > L$). If that is the case, then ϕ_{jk}, which is an $S \times L$ matrix, has more rows than columns. Treating its rows as separate vectors, with ϕ_{jk} being the kth component of the jth vector, we use the result that having more vectors than components means these vectors are necessarily linearly

dependent (Appendix S1). This means we can conveniently choose nonzero numbers d_j such that they are solutions to the system of L linear equations

$$\sum_{j=1}^{S} d_j \phi_{jk} = 0 \qquad (k = 1, 2, \ldots, L). \tag{21}$$

While the linear dependence of the ϕ_{jk} ensures that some of the d_j will be nonzero, Eq. 17 still breaks down if $d_i = 0$, so this procedure can only be performed if d_i in particular can be chosen to be nonzero. We will assume this for now; the case when this is not possible, along with the ensuing ramifications, are discussed in Section 5.3. However, even when $d_i \neq 0$, the choice of the d_j will not be unique (Appendix S1). For now, let us assume any one valid choice has been made and move on.

By virtue of Eq. 21, choosing the scaling factors d_j this way will cancel the linear terms in $\overline{F}_k$ from Eq. 18. Consequently, the $\Delta \rho_i$ term will then be absent from Eq. 19. Since calculating the $\overline{F}_k$ would entail determining the levels of the limiting factors with species i being the invader, one would in principle require an extra set of equations governing the dynamics of F_k. By eliminating the linear terms, one does not need to do this anymore. The V_{jkl} and covariance terms still depend on the F_k; however, we will see that sometimes these quantities can be calculated without a detailed knowledge of the dynamics of the limiting factors (for an example, see Appendix S4). After canceling the linear terms, $\Delta \rho_i$ vanishes from Eq. 19, so Eq. 20 reduces to $\bar{r}_i = r'_i + \Delta N_i + \Delta I_i$.

In the special case of a single limiting factor F, the matrix ϕ_{jk} reduces to the vector ϕ_j, and ψ_{jkl} to ψ_j. The scaling factors may then be chosen as follows (Chesson 1994):

$$d_i^{-i} = \frac{1}{\phi_i}, \qquad d_{s \neq i}^{-i} = -\frac{1}{(S-1)\phi_s}, \tag{22}$$

satisfying Eq. 21 for any species as invader. Eq. 19 then reads

$$\bar{r}_i \approx \left[(\overline{\mathscr{E}}_i - \phi_i F^{*i}) - \frac{1}{S-1} \sum_{s \neq i}^{S} \frac{\phi_i}{\phi_s} (\overline{\mathscr{E}}_s - \phi_s F^{*s}) \right]$$
$$+ \left[\psi_i V_i - \frac{1}{S-1} \sum_{s \neq i}^{S} \frac{\phi_i}{\phi_s} \psi_s V_s \right] + \left[\gamma_i \text{cov}(\mathscr{E}_i, \mathscr{C}_i) - \frac{1}{S-1} \sum_{s \neq i}^{S} \frac{\phi_i}{\phi_s} \gamma_s \text{cov}(\mathscr{E}_s, \mathscr{C}_s) \right], \tag{23}$$

where each bracketed term is now the difference between the invader and the arithmetic average of the scaled resident values. This transparent partitioning of the invasion growth rates opens up the possibility for a straightforward interpretation of its terms (Section 3).

As stated before, canceling the linear terms in the limiting factors is only possible if there are more species than factors. Otherwise this cannot be done, because then the only solution to Eq. 21 is $d_j = 0$ for all species, leading to division by zero in Eq. 17. The d_j may still be used to eliminate a set of $S-1$ limiting factors. This choice will affect our definition of $\Delta \rho_i$. For example, if we choose to eliminate the first $S-1$ factors, this reduces $\Delta \rho_i$ in Eq. 19 to

$$\Delta \rho_i = \sum_{k=S}^{L} \phi_{ik} \overline{F}_k + \sum_{s \neq i}^{S} \sum_{k=S}^{L} \frac{d_s}{d_i} \phi_{sk} \overline{F}_k. \tag{24}$$

This means that only the last $L - S + 1$ factors contribute to $\Delta \rho_i$. Alternatively, one may eliminate any $S - 1$ independent linear combinations of the limiting factors. In either case, since the linear terms in

$\overline{F}_k$ are not actually eliminated, the utility of using the scaling factors in the first place is compromised. We discuss this problem in more detail in Section 5.4.

As a remark, we note that Chesson (1994, 2000a) used both a different definition and a different notation for the scaling factors. He introduced $q_{is} = -\partial \mathscr{C}_i / \partial \mathscr{C}_s$ evaluated at $\mathscr{C}_s = 0$, which replaces d_s/d_i in Eq. 19. The negative sign is supposed to emphasize that the terms in Eq. 20 are differences between invader and scaled resident values. While this notation is suggestive, it would only represent a true difference if all d_s/d_i values could be chosen negative. This can be achieved for a single limiting factor F (Eqs. 22 and 23), but in general not for multiple ones—hence we have chosen to abandon the original sign convention. More problematically, the derivative $\partial \mathscr{C}_i / \partial \mathscr{C}_s$ is purely formal and does not have a definite value in general, because even when $\mathscr{C}_i$ can be expressed as a function of $\mathscr{C}_s$, the mapping is usually not unique (Chesson 1994). We believe the reason for the use of this derivative anyway is that original formulations of Chesson's theory do not explicitly account for the limiting factors, which are necessary for our approach. Our method using the d_j via Eq. 21 (which has been inspired by Chesson and Huntly 1997, Appendix C) acknowledges the non-uniqueness of the scaling factors from the get-go, yields the same result as $\partial \mathscr{C}_i / \partial \mathscr{C}_s$ when the derivative is well-defined, and works even when it is not.

2.5   Why should one partition the invasion growth rates like this?

One may reasonably ask why we add the scaled resident growth rates to the invasion rate in Eq. 17, when those are zero by definition. Could we not simply write the invasion growth rate for each species separately via Eq. 16 and not worry about the d_j? One could in fact do that; however, the above partitioning can yield real insight into coexistence, as we hope to demonstrate with the examples below.

Consider the following minimal model of competition for nest sites: two species have birth rates b_j and mortalities m_j, and each of J nest sites may be occupied by one single individual. Then the probability of an offspring being able to find a nest site for itself is proportional to the fraction F of empty sites: $F = 1 - (n_1 + n_2)/J$, where n_j is the number of sites species j's individuals already occupy. The per capita growth rates may then be written as

$$r_j = b_j F - m_j. \tag{25}$$

If b_j, m_j, and J are all constant, the model outcome can be determined using the R^*-rule (Hsu et al. 1977, Tilman 1982): whichever species can tolerate the lower fraction of empty sites F at equilibrium wins. What happens though when F is allowed to fluctuate, perhaps due to regular disturbance of the available sites J or population abundances n_j?

For a long time, it was argued that such fluctuations slow down or eliminate the process of competitive exclusion (Hutchinson 1961, Connell 1971, Huston 1979). This argument is incorrect however, as can be seen in multiple ways. One is to apply the R^*-rule to the time-averaged model $\overline{r}_j = b_j \overline{F} - m_j$, demonstrating that the winner will be whoever tolerates the lowest number of empty sites on average (e.g., Fox 2013). Alternatively, following Chesson and Huntly (1997), one may introduce the quantity $H = \log(n_1)/b_1 - \log(n_2)/b_2$, a scaled difference of the log-densities of the two species. Using the fact that the time derivative of the log-density is the per capita growth rate, we have $dH/dt = r_1/b_1 - r_2/b_2$, the difference of the scaled growth rates. dH/dt being always positive (negative) means H, and therefore the density of species 1 relative to 2 (2 relative to 1) is always increasing. Since we assume no abundance can get arbitrarily large (population regulation would kick

in), this can only happen if species 2 (1) is going extinct. Thus, dH/dt can be thought of as the scaled rate of competitive exclusion. Substituting in the growth rates from Eq. 25 yields

$$\frac{dH}{dt} = \frac{r_1}{b_1} - \frac{r_2}{b_2} = F - \frac{m_1}{b_1} - F + \frac{m_2}{b_2} = \frac{m_2}{b_2} - \frac{m_1}{b_1}, \tag{26}$$

from which F has canceled, so dH/dt is literally the difference of the two species' R^*-values.

The fact that dH/dt is constant in this model means that the speed of competitive exclusion proceeds at the exact same pace at all times, regardless of the value and fluctuations of F. Putting it differently: in this model, despite appearances, *fluctuations actually play no role in coexistence whatsoever*, with both the identity of the winning species and the rate of competitive exclusion being determined by the four constant parameters b_1, b_2, m_1, and m_2.

The two scaling factors $1/b_1$ and $-1/b_2$ used in dH/dt are exactly what Eq. 21 would give for d_1 and d_2 in this model, and amount to the same effect of canceling F. The advantage of using the scaling factors compared to applying R^*-criteria to time-averaged models is twofold. First, they tell us not only the identity of the winning species, but the entire timeframe of exclusion. Second, they can be applied even when there are multiple limiting factors.

To illustrate how to use the scaling factors when working with Chesson's theory, we now analyze Eq. 25 using Chesson's method. This also provides the simplest possible working example showcasing how the framework as a whole can be applied. Let us proceed step by step.

Step 1: Choose the environmental and interaction parameters E_j and C_j. They are not unique, but one very natural choice is $E_j = -m_j$ and $C_j = b_j F$. The per capita growth rates then read

$$r_j(E_j, C_j) = \underbrace{b_j F}_{C_j} - \underbrace{m_j}_{E_j} = E_j + C_j. \tag{27}$$

We now determine the "equilibrium" values E_j^* and C_j^*. We can choose E_j^* to be the mean of $E_j = -m_j$; since the m_j are not fluctuating, $E_j^* = -m_j$. By definition, $r_j(E_j^*, C_j^*) = 0$, therefore $E_j^* = -m_j$ fixes $C_j^* = m_j$. The F^{*j} is defined to satisfy $C_j(F^{*j}) = C_j^*$ (Eq. 8); this equation reads $b_j F^{*j} = m_j$ for this model, from which $F^{*j} = m_j/b_j$. That is, F^{*j} is equal to species j's R^*-value on that resource.

An alternative way of choosing the parameters is $E_j = b_j$ and $C_j = F$ with $E_j^* = b_j$, $C_j^* = F^{*j} = m_j/b_j$. See Appendix S4 for the model analysis using this parameterization. (Note that in the Appendix, b_j is no longer constant, but a function of time—which means that in addition to the results here, an extra term for the storage effect also appears. Setting the b_j to be constant recovers the result in this section.)

Step 2: Determine the standardized environmental and interaction parameters $\mathscr{E}_j$ and $\mathscr{C}_j$. We first need to calculate the Taylor coefficients of Eq. 3 for Eq. 27:

$$\alpha_j = \frac{\partial r_j}{\partial E_j} = 1, \ \ \alpha_j^{(2)} = \frac{\partial^2 r_j}{\partial E_j^2} = 0, \ \ \beta_j = \frac{\partial r_j}{\partial C_j} = 1, \ \ \beta_j^{(2)} = \frac{\partial^2 r_j}{\partial C_j^2} = 0, \ \ \zeta_j = \frac{\partial^2 r_j}{\partial E_j \partial C_j} = 0. \tag{28}$$

We now evaluate Eqs. 4 and 5:

$$\mathscr{E}_j = \alpha_j(E_j - E_j^*) + \frac{1}{2}\alpha_j^{(2)}(E_j - E_j^*)^2 = 1 \times (-m_j + m_j) + 0 = 0, \tag{29}$$

$$\mathscr{C}_j = \beta_j(C_j - C_j^*) + \frac{1}{2}\beta_j^{(2)}(C_j - C_j^*)^2 = 1 \times (b_j F - m_j) + 0 = b_j F - m_j. \tag{30}$$

The $\mathscr{C}_j$ may also be written in the form of Eq. 9. From Eq. 10, we get $\phi_j = b_j$ and $\psi_j = 0$. We therefore have $\mathscr{C}_j = b_j F - m_j = \phi_j(F - F^{*j})$.

Step 3: Calculate the time-averaged growth rates. The time-averaged growth rates read

$$\bar{r}_j = \overline{\mathscr{E}}_j + \overline{\mathscr{C}}_j = b_j\overline{F} - m_i = \phi_j(\overline{F} - F^{*j}). \tag{31}$$

The covariance term $\gamma_i \mathrm{cov}(\mathscr{E}_j, \mathscr{C}_j)$ is absent because ζ_j is zero (Eq. 28), and therefore so is $\gamma_j = \zeta_j/(\alpha_j\beta_j)$.

Step 4: Calculate the invasion growth rates $\bar{r}_i$. This will still be given by Eq. 31, but it is understood that $\overline{F}$ is evaluated at the level determined by whichever species is resident. This level cannot be computed without an extra equation determining the dynamics of F, but as we will see, this is not needed here.

Step 5: Form weighted sum of invader and resident growth rates. The scaling factors d_j are solutions to the system of linear equations Eq. 21. For this model, there is a single equation with two unknowns, reading $d_i\phi_i + d_s\phi_s = 0$. The choice $d_i = 1/\phi_i$ and $d_s = -1/\phi_s$ satisfies the equation (and is exactly what Eq. 22 recommends). Eq. 17 then reads, for two species, as

$$\bar{r}_i = \frac{1}{d_i}(d_i\bar{r}_i + d_s\bar{r}_s) = \phi_i\left(\frac{\bar{r}_i}{\phi_i} - \frac{\bar{r}_s}{\phi_s}\right), \tag{32}$$

where $\bar{r}_s = 0$. Using Eq. 31, we get

$$\bar{r}_i = \phi_i\left(\frac{\bar{r}_i}{\phi_i} - \frac{\bar{r}_s}{\phi_s}\right) = \phi_i\left(\frac{\phi_i(\overline{F} - F^{*i})}{\phi_i} - \frac{\phi_s(\overline{F} - F^{*s})}{\phi_s}\right) = \phi_i(F^{*s} - F^{*i}). \tag{33}$$

After substituting in $\phi_j = b_j$ and $F^{*j} = m_j/b_j$, the final form of the invasion growth rates reads

$$\bar{r}_i = b_i\left(\frac{m_s}{b_s} - \frac{m_i}{b_i}\right), \tag{34}$$

recovering the result that only the species with the lower m_j/b_j (R^*-value) will be able to invade and persist.

As mentioned before, a useful aspect of the scaling factor approach is that it applies in the presence of multiple limiting factors. For instance, generalizing Eq. 25 to three species competing for two resources, we have

$$r_j = \sum_{k=1}^{2} b_{jk}F_k - m_j \qquad (j = 1, 2, 3). \tag{35}$$

Applying Eq. 21, the d_j are solutions to the linear system of equations

$$b_{11}d_1 + b_{21}d_2 + b_{31}d_3 = 0, \tag{36}$$

$$b_{12}d_1 + b_{22}d_2 + b_{32}d_3 = 0, \tag{37}$$

whose general solution is

$$d_j = \begin{pmatrix} b_{22}b_{31} - b_{21}b_{32} \\ b_{11}b_{32} - b_{12}b_{31} \\ b_{12}b_{21} - b_{11}b_{22} \end{pmatrix} c \tag{38}$$

where c is an arbitrary constant. Partitioning the invader growth rates using Eq. 17, we get

$$\bar{r}_i = \frac{1}{d_i}\sum_{j=1}^{3} d_j \bar{r}_j = \frac{1}{d_i}\sum_{j=1}^{3} d_j \left(\sum_{k=1}^{2} b_{jk}\overline{F}_k - m_j\right) = \frac{1}{d_i}\sum_{k=1}^{2}\underbrace{\sum_{j=1}^{3} d_j b_{jk}\overline{F}_k}_{0,\text{ by Eq. 21}} - \sum_{j=1}^{3}\frac{d_j}{d_i}m_j = -\sum_{j=1}^{3}\frac{d_j}{d_i}m_j, \quad (39)$$

which is independent of the resources $\overline{F}_k$, demonstrating yet again that fluctuations in resource levels have no impact on coexistence. Those species which end up with a positive $\bar{r}_i$ will coexist, with the other(s) going extinct. For example, if

$$b_{jk} = \begin{pmatrix} 1 & 2 \\ 3 & 4 \\ 5 & 7 \end{pmatrix}, \qquad m_j = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}, \qquad (40)$$

then we get $d_j = (1, 3, -2)\,c$, and substitution into Eq. 39 yields $\bar{r}_1 = 6$, $\bar{r}_2 = 2$, and $\bar{r}_3 = -3$, predicting the extinction of species 3. Note that one can only use this result if, when moving any of the species into the invader state, the other two can coexist—otherwise the resident average growth rates will not be zero, rendering Eq. 17 inapplicable. This has to be ascertained independently. The problems stemming from the nonexistence of an $(S-1)$-species resident stationary state are discussed in detail in Section 5.2.

2.6 Spatial variation

Up to this point we have looked at community models where space plays no role. Let us now assume that there are several local populations, their locations indexed by the variable $x = 1, 2, \ldots, Q$. Each local population has per capita growth rate $r_j(x)$, with the environmental and interaction parameters $E_j(x)$ and $C_j(x)$ also potentially depending on location. To highlight the effects of spatial structure on coexistence, we assume no temporal fluctuations in this section.

The growth of each species is still given by Eq. 1, but now the total population abundances n_j are made up of the contributions from each location ($n_j(x)$ for location x), i.e., $n_j = \sum_{x=1}^{Q} n_j(x)$. The landscape-level growth rate can then be written as

$$r_j(E_j, C_j) = \frac{1}{n_j}\frac{\mathrm{d}n_j}{\mathrm{d}t} = \frac{1}{\sum_{y=1}^{Q} n_j(y)}\frac{\mathrm{d}\left(\sum_{x=1}^{Q} n_j(x)\right)}{\mathrm{d}t} = \frac{1}{\sum_{y=1}^{Q} n_j(y)}\sum_{x=1}^{Q}\frac{\mathrm{d}n_j(x)}{\mathrm{d}t}. \qquad (41)$$

The term $\mathrm{d}n_j(x)/\mathrm{d}t$ quantifies the change in population density in any location. It can be written as the change due to births and deaths $n_j(x)r_j(x)$, plus immigration $c_j(x)$, minus emigration $e_j(x)$. Thus, the above formula can be written as

$$\begin{aligned}
r_j(E_j, C_j) &= \frac{1}{\sum_{y=1}^{Q} n_j(y)}\sum_{x=1}^{Q}\frac{\mathrm{d}n_j(x)}{\mathrm{d}t} \\
&= \frac{1}{\sum_{y=1}^{Q} n_j(y)}\sum_{x=1}^{Q}\left(n_j(x)r_j(x) + c_j(x) - e_j(x)\right) \\
&= \frac{1}{Q}\sum_{x=1}^{Q}\left(\frac{n_j(x)}{\frac{1}{Q}\sum_{y=1}^{Q} n_j(y)}\right)r_j(x) + \frac{1}{\sum_{y=1}^{Q} n_j(y)}\sum_{x=1}^{Q}\left(c_j(x) - e_j(x)\right).
\end{aligned} \qquad (42)$$

The last term contains the net effect of immigration and emigration across the community. If we assume that our community is closed, then this term will vanish, since every immigrant in one patch must have emigrated from another patch. Thus, the landscape-level growth rate is simply the mean of $r_j(x)$ weighted by the relative density of species j at each location. Denoting this relative density by $v_j(x) = n_j(x)/(Q^{-1}\sum_{y=1}^{Q} n_j(y))$, we have

$$r_j(E_j, C_j) = \frac{1}{Q}\sum_{x=1}^{Q} v_j(x)r_j(x) = \overline{v_j(x)r_j(x)}, \tag{43}$$

where the overbar now denotes spatial averaging (Chesson 2000a). Noting that $\overline{v_j(x)} = 1$, we expand the average using Eq. S1.2 as $\overline{v_j(x)r_j(x)} = \overline{r_j(x)} + \mathrm{cov}(v_j(x), r_j(x))$, where we have a spatial covariance. The landscape-level growth rates therefore read

$$r_j(E_j, C_j) = \overline{r_j(x)} + \mathrm{cov}(v_j(x), r_j(x)). \tag{44}$$

The first term in Eq. 44 is the spatial average of the local growth rates (Chesson 2000a). Its evaluation proceeds in a way that is exactly analogous to the purely temporal case. The environmental and interaction parameters $E_j(x)$ and $C_j(x)$ now have spatial dependence, as do the $F_k^{*j}(x)$. The Taylor coefficients of Eqs. 3 and 10 are evaluated using these spatially equilibrial values of the limiting factors. Like in the temporal case, it is assumed that higher-order terms in the (spatial) variance of $E_j(x)$ and $C_j(x)$ are negligible. Therefore, in the case of pure spatial variation, the form of the invasion growth rate for the invader i corresponds to Eq. 20:

$$\overline{r_i(x)} = r_i' + \Delta\rho_i + \Delta N_i + \Delta I_i, \tag{45}$$

where it is understood that each term represents a spatial average. The coexistence mechanisms of the temporal case thus have spatial analogues: ΔN_i is the spatial relative nonlinearity, and ΔI_i is the spatial storage effect (Chesson 2000a).

The covariance term of Eq. 44, on the other hand, is something that has no temporal analogue. This *growth-density covariance* (also called a *fitness-density covariance*; Chesson 2000a, Melbourne et al. 2007, Shoemaker and Melbourne 2016) contributes positively to the invasion growth rate if the relative abundance of the invader is larger in locations where it can (locally) grow faster. Analogous to $\Delta\rho_i$, ΔN_i, and ΔI_i, its contribution to invasion growth rates can be written

$$\Delta\kappa_i = \mathrm{cov}(v_i(x), r_i(x)) + \sum_{s\neq i}^{S} \frac{d_s}{d_i}\mathrm{cov}(v_s(x), r_s(x)). \tag{46}$$

Thus, the full form of the invasion growth rate reads

$$\overline{r}_i = r_i' + \Delta\rho_i + \Delta N_i + \Delta I_i + \Delta\kappa_i. \tag{47}$$

2.7   Community-level stabilization and competitive advantages

For a single limiting factor and no spatiotemporal variation, we expect that one species will outcompete all others (Armstrong and McGehee 1980, Meszéna et al. 2006, Pásztor et al. 2016 chapter 7). In Chesson's theory, this is expressed by Eqs. 20 and 47 reducing to $\overline{r}_i = r_i'$ (given by the first bracketed

term of Eq. 23). As all quantities encoded in r'_i are hard constants which do not change their values depending on the identity of the invading species, only the one species with the largest r'_i can persist: coexistence is impossible unless some other mechanisms contribute to the invasion growth rates of the species that would otherwise be excluded (Chesson 2000b). These "other mechanisms", both fluctuation-dependent and -independent, are encoded in the $\Delta\rho_i$, ΔN_i, ΔI_i, and $\Delta\kappa_i$ terms. For species to coexist, these terms must be large enough to overcome the r'_i-disadvantage of all losing species in the absence of the mechanisms.

To give a precise meaning to this line of intuitive reasoning, a weighted average A of the invasion rates is defined,

$$A = \frac{1}{S}\sum_{i=1}^{S}\frac{\overline{r}_i^{-i}}{\phi_i}, \tag{48}$$

where it is important to stress that the summation goes over all species *as invaders* (Chesson 2003). The ϕ_i are given by Eq. 10 as usual, taking into account that there is only one limiting factor (in the absence of coexistence-enhancing mechanisms), so the matrix ϕ_{ik} reduces to the vector ϕ_i. As long as all ϕ_i are positive (and they can be made so if the single limiting factor is a resource or predator shared by all the focal species), a negative A indicates that stable coexistence is impossible, because it means that at least one species has a negative invasion growth rate. On the other hand, for $A > 0$, it is possible to have coexistence, though of course there is no guarantee: if two species have $\overline{r}_1/\phi_1 = 3$ and $\overline{r}_2/\phi_2 = -1$, then $A = (3-1)/2 = 1$ but the second species still cannot invade. The quantity A therefore, while not a foolproof measure, is still at least an indicator of how strongly stabilized coexistence is in the community as a whole.

Substituting Eq. 47 into Eq. 48, we get

$$A = \frac{1}{S}\sum_{i=1}^{S}\frac{1}{\phi_i}\left(r'_i + \Delta\rho_i + \Delta N_i + \Delta I_i + \Delta\kappa_i\right) = \widetilde{r'} + \widetilde{\Delta\rho} + \widetilde{\Delta N} + \widetilde{\Delta I} + \widetilde{\Delta\kappa}, \tag{49}$$

where tildes denote weighted averages over all S species as invaders ($\widetilde{r'} = S^{-1}\sum_{i=1}^{S}r'_i/\phi_i$ and so on). We now clarify the rationale behind the factors $1/\phi_i$ in Eq. 48. With their use, the community average $\widetilde{r'}$ is equal to zero as long as the scaling factors d_i have been chosen according to Eq. 22. Substituting r'_i from the first bracketed term of Eq. 23 and using the simplifying notations $w_j = (\overline{\mathscr{E}}_j - \phi_j F^{*j})/\phi_j$ and $W = \sum_{j=1}^{S}w_j$, we can write

$$\widetilde{r'} = \frac{1}{S}\sum_{i=1}^{S}\frac{r'_i}{\phi_i} = \frac{1}{S}\sum_{i=1}^{S}\left[\underbrace{\left(\frac{\overline{\mathscr{E}}_i - \phi_i F^{*i}}{\phi_i}\right)}_{w_i} - \frac{1}{S-1}\sum_{s\neq i}\underbrace{\left(\frac{\overline{\mathscr{E}}_s - \phi_s F^{*s}}{\phi_s}\right)}_{w_s}\right]$$

$$= \frac{1}{S}\left[\sum_{i=1}^{S}w_i - \frac{1}{S-1}\sum_{i=1}^{S}\sum_{s\neq i}w_s\right] = \frac{1}{S}\left[\sum_{i=1}^{S}w_i - \frac{1}{S-1}\sum_{i=1}^{S}\left(\sum_{s=1}^{S}w_s - w_i\right)\right] \tag{50}$$

$$= \frac{1}{S}\left[\underbrace{\sum_{i=1}^{S}w_i}_{W} - \frac{1}{S-1}\sum_{i=1}^{S}\underbrace{\sum_{s=1}^{S}w_s}_{W} + \frac{1}{S-1}\underbrace{\sum_{i=1}^{S}w_i}_{W}\right] = \frac{1}{S}\left[W - \frac{S}{S-1}W + \frac{1}{S-1}W\right] = 0,$$

which is indeed zero. Eq. 49 therefore simplifies to

$$A = \widetilde{\Delta\rho} + \widetilde{\Delta N} + \widetilde{\Delta I} + \widetilde{\Delta\kappa}, \tag{51}$$

containing the sum of the weighted averages of only those terms which can potentially contribute to coexistence (Chesson 2003): fluctuation-independent mechanisms ($\widetilde{\Delta\rho}$), relative nonlinearities ($\widetilde{\Delta N}$), storage effects ($\widetilde{\Delta I}$), and growth-density covariances ($\widetilde{\Delta\kappa}$). It is important that the r_i' cancel from any notion of stabilization. The r_i' terms contain all density- and frequency-independent factors; for instance, imposing an extra mortality rate on a species will sometimes only affect its r_i'. Such an extra mortality should never show up in a stabilization term, which is supposed to measure all those effects acting to overcome the extra mortalities to promote coexistence.

Having defined the stabilization term A as the average of the scaled invasion growth rates, one may express the invasion rates in terms of their difference from this community average. In mathematical terms, $\bar{r}_i/\phi_i = f_i + A$, where f_i is the difference from the average for species i:

$$f_i = \frac{\bar{r}_i}{\phi_i} - A = r_i' + (\Delta\rho_i - \widetilde{\Delta\rho}) + (\Delta N_i - \widetilde{\Delta N}) + (\Delta I_i - \widetilde{\Delta I}) + (\Delta\kappa_i - \widetilde{\Delta\kappa}). \tag{52}$$

The f_i being the difference from the average A means that the f_i always sum to zero.

Chesson called f_i the *average fitness difference* term (Chesson 2003, Yuan and Chesson 2015). It has since been called "relative fitness" and "relative fitness difference" (Carroll et al. 2011), "competitive ability difference" (Mayfield and Levine 2010), and simply "fitness" (Cadotte 2007, Adler et al. 2010). An effect or process bringing the f_i closer to zero was coined an *equalizing mechanism* (Chesson 2000b, 2003) or an *equalizing effect* (Loreau et al. 2012; see their analysis for why this term is actually more appropriate than calling it a mechanism).

The above concept of "fitness" should not be confused with the word's established evolutionary meaning. In evolutionary biology, the general definition for the fitness of a species i is its long-term average growth rate, $\bar{r}_i$ (Metz et al. 1992); or, in case $\bar{r}_i$ is evaluated with species i in its invasion state, it corresponds to species i's invasion fitness (Geritz et al. 1998). We believe it is important to distinguish evolutionary fitness from the concept defined in Eq. 52. Methods of evolutionary analysis such as adaptive dynamics (Geritz et al. 1998, Meszéna 2005) are based on invasion analysis just like Chesson's theory. The two frameworks may thus fruitfully combine, whereby Chesson's theory is used to describe ecological scenarios and adaptive dynamics to predict their evolutionary trajectories. But then the two conflicting concepts of "fitness" are bound to cause confusion.

For this reason, we will call f_i the *single-factor competitive advantage* (*competitive advantage*, or just *advantage*, for short) of species i. The "single-factor" in the name is a reminder that f_i is evaluated with a single focal limiting factor in mind; "competitive" expresses the fact that in the absence of coexistence-affecting mechanisms ($\Delta\rho_i = \Delta N_i = \Delta I_i = \Delta\kappa_i = 0$) only the species with the largest f_i can persist; and "advantage" makes it explicit that the concept is community- and context-dependent (i.e., having an advantage is always relative to who the other competitors are—see Section 6.2 for a discussion of this point).

Using the f_i, the role of A as the community-level stabilization becomes more clear. Since $\bar{r}_i/\phi_i = f_i + A$, a species has positive invasion growth rate if its competitive (dis)advantage boosted by the stabilization term A is positive. In the community context: if A is large enough so that $\min(f_i) + A > 0$, then all invasion growth rates are positive and we have coexistence. In words, coexistence requires that the stabilization A is able to overcome the competitive disadvantage of the species with the most negative f_i (Yuan and Chesson 2015). In this way, the quantities A and f_i provide one possible mathematical realization of the intuitive line of reasoning stated at the beginning of this section.

As a historical remark, it should be noted that there has been an evolution in the concepts of stabilization and competitive advantages. Chesson (2000b) originally identified the advantage term with r'_i/ϕ_i and stabilization with all the rest of the terms in Eqs. 20 and 47 scaled by $1/\phi_i$. Stabilization was therefore a species-level as opposed to community-level metric. This was later updated (Chesson 2003, Yuan and Chesson 2015) to the formalism described above, where stabilization is defined at the level of the community. To add to the confusion, there is yet another way of defining these terms, inspired by MacArthur's consumer-resource model (Chesson 1990, Chesson and Kuang 2008, Chesson 2011, 2013). This model can be cast in the Lotka–Volterra form

$$r_j = b_j - \sum_{k=1}^{S} a_{jk}n_k, \tag{53}$$

where n_j and b_j are species j's density and intrinsic growth rate, and a_{jk} is the reduction in species j's per capita growth rate caused by one unit of density of species k. The competitive advantage ratio f_j/f_k and stabilization A are then given by

$$\frac{f_j}{f_k} = \frac{b_j}{b_k}\sqrt{\frac{a_{kk}a_{kj}}{a_{jj}a_{jk}}}, \qquad 1-A = \sqrt{\frac{a_{jk}a_{kj}}{a_{jj}a_{kk}}} \tag{54}$$

($1-A$ is also known as the "niche overlap index"; Pianka 1973, Chesson 2011, Pásztor et al. 2016 p. 211). Eq. 54 only applies to Lotka–Volterra and some related models however, such as the annual plant model (Godoy and Levine 2014, Saavedra et al. 2017). Worse, it can only be used to evaluate coexistence between two species. This two-species coexistence condition reads $1-A < f_j/f_k < 1/(1-A)$, a relation that has been known for a long time (Vandermeer 1975, Chesson 1990, Godoy and Levine 2014). Carroll et al. (2011) did propose a generalization of Eq. 54 to several species, but showing that their method produces consistent results is ongoing work.

Despite the conceptual evolution of A and f_i in the literature, most studies still cite Chesson (2000b) when referring to stabilization and competitive advantages: to-date, it has received more than 2200 citations according to Scopus. In contrast, Chesson (2003), which presents the currently most up-to-date version of the decomposition, has only about 50 citations. Also, for some reason, even though Chesson (2000b) is the most cited method, the most commonly used one is the method based on the Lotka–Volterra equations—even by those articles which cite Chesson (2000b) when introducing the concepts of stabilization and competitive advantages. Here we will rely on the most recent definition (Chesson 2003) given by Eqs. 48 and 52, with community-level stabilization and applicability to an arbitrary number of species.

2.8   Parameter ambiguities

Having covered all salient technical details of Chesson's theory, one may justifiably worry that it is fraught with seemingly arbitrary parameter choices. The choice of the environmental and interaction parameters E_j and C_j is not unique. Once they are chosen, one still needs to pick a suitable E_j^* and C_j^*, which are also not unique. Designating the limiting factors is not unique. Next, the equilibrial levels of the limiting factors, F_k^{*j} (the level of factor k for species j), have to be determined via Eq. 8—but this equation only has a unique solution if there is just a single limiting factor. Finally, the scaling factors d_j are solutions to the system of linear equations Eq. 21, and since the system can only be usefully applied if it is underdetermined (more unknowns than equations), the solution is again not going to be unique. Let us comment on each of these ambiguities in turn.

The non-uniqueness of E_j and C_j is not particularly problematic. Though the form of the quadratic expansion in Eq. 2 might change, what is really important is the dependence on the limiting factors, governed by Eq. 9—but then any intermediate ambiguities stemming from different choices of the C_j will ultimately cancel due to the chain rule. However, some terms in the quadratic approximation may be interpreted differently depending on this choice. For example, a crude but readily available parameterization for any model is $E_j = 0$ and $C_j = r_j$. With this extreme choice, $\mathrm{cov}(\mathscr{E}_j, \mathscr{C}_j)$ will always be zero (no storage effect!), but the covariances do not, of course, disappear: they will instead be mediated by the other covariance terms in Eq. 14. The final results will be exactly the same, though their verbal descriptions may differ depending on parameterization.

Second, in choosing E_j^* and C_j^*, one should keep in mind that the closer these quantities are to the actual mean values $\overline{E}_j$ and $\overline{C}_j$, the more accurate the quadratic approximation will be. We therefore give the explicit recommendation to always choose $E_j^* = \overline{E}_j$ (which is easily calculable, since E_j is by definition density- and frequency-independent), and then calculate the corresponding C_j^* by solving $r_j(E_j^*, C_j^*) = 0$, eliminating this ambiguity altogether.

Third, there is ambiguity in defining the limiting factors F_k. This is inevitable. For instance, if species are limited by a resource, one may designate the limiting factor both as the amount of resource itself or, alternatively, as the degree of depletion of the resource. The final results will be insensitive to the choice made—however, some choices may be mathematically more convenient than others. One should therefore strive to make the problem as simple as possible (see Barabás et al. 2014 for an in-depth discussion).

Next, the F_k^{*j} are fully determined by Eq. 8 only if there is one single limiting factor in the system. Otherwise, one cannot say much above and beyond what we stated in Section 2.1: one may use the equations governing the limiting factors, or measure their values. This ambiguity is a true weakness that must be addressed on a problem-to-problem basis.

Finally, in choosing the d_j, one should keep in mind that their purpose is to cancel the linear terms in the limiting factors. For a single limiting factor, we recommend using the standard Eq. 22 (Chesson 1994), once again eliminating any ambiguity. For multiple factors, as long as there is just one more species than factors ($L = S - 1$), the solution to Eq. 21 will be unique up to a multiplicative constant, and since Eq. 19 depends only on the ratios of the factors, this constant will cancel. For multiple factors but with $1 < L < S - 1$, no such quasi-uniqueness holds for the solution of Eq. 21—but for the purposes of eliminating the $\Delta \rho_i$ term, any choice with nonzero d_i^{-i} will work. By Eq. 17, the actual invasion growth rates themselves are insensitive to the values of the d_j, so the final results are unaffected by this ambiguity. However, the interpretation of Eq. 19 may of course be sensitive to the particular choice made—see Section 5.4 for subtleties.

In summary: despite appearances, the theory is not nearly as ridden with arbitrary choices as it may first appear. With proper care, the ambiguities of parameterization are either eliminated, or else are irrelevant to the final results. The one exception is F_k^{*j} for multiple limiting factors, which usually cannot be chosen without the governing equations for the F_k. This makes the theory considerably less convenient for analyzing models with multiple limiting factors.

3   Interpreting the terms of the partitioned growth rate

As seen in Eqs. 20 and 47, Chesson's coexistence theory partitions the invasion growth rates into four or five distinct terms: a combination of fluctuation-independent terms r_i' and $\Delta\rho_i$, relative nonlinear-

ities ΔN_i, storage effects ΔI_i, and (in spatial models) growth-density covariances $\Delta \kappa_i$. While such a classification scheme may at first appear scholastic and contrived, this is in fact not so: each term is a direct consequence of the quadratic approximation scheme of Eqs. 7 and 9. Therefore, to this quadratic approximation, all contributions to the invasion rates are cleanly partitioned into only these five terms accounting for all possible mechanisms. Here we review the standard interpretations of these terms, and how they may contribute to maintaining coexistence. An important caveat is that these interpretations all rely on Eq. 23—which only holds when all but a single limiting factor are amalgamated into the $\Delta \rho_i$ term. We therefore make this assumption here, and will consider the complications caused by multiple explicitly handled limiting factors in Section 5.4.

The two variation-independent terms r_i' and $\Delta \rho_i$ describe any mechanism in which an invader experiences less density dependence on average than residents (Chesson 1994). The r_i' quantify differences in performance without frequency dependence: if one species is more adapted to the environment than another (i.e., $\overline{\mathscr{E}}_i > \overline{\mathscr{E}}_s$ for most residents), then those terms will be positive. In turn, $\Delta \rho_i$ measures effects that can help all invaders. It encodes the effect of classical coexistence mechanisms which do not depend on spatiotemporal fluctuations. Such stabilizing effects typically occur because species are regulated by different limiting factors. Examples include coexistence via partitioning of resources (as in standard consumer-resource models such as the MacArthur consumer-resource model or the Tilman model; MacArthur 1970, Tilman 1982), and via differential predator pressures leading to reduced apparent competition (Holt 1977). Unlike the other mechanisms, those contributing to r_i' and $\Delta \rho_i$ operate within a particular time and place, and do not require multiple observations across many time points (McPeek and Gomulkiewicz 2005).

In Chesson's works, $\Delta \rho_i$ is generally not discussed (but see Kuang and Chesson 2010, Chesson and Kuang 2010, Stump and Chesson 2015, 2017). The reason is that most of Chesson's works assume that there is just one single limiting factor, in which case the scaling factors d_j are chosen to eliminate $\Delta \rho_i$. Chesson's theory was originally designed to answer the question: what is the role of fluctuations in maintaining coexistence (Chesson and Warner 1981, Chesson 1994)? Since a large number of limiting factors allow for coexistence via well-understood classical mechanisms, the simplest and most critical test of a theory of coexistence in variable environments concerns the case when there is just one limiting factor—i.e., when classical mechanisms would not allow for diversity. While this is a perfectly valid point, in some cases a combination of many distinct limiting factors and also temporal fluctuations contribute to invasion growth rates. For this reason, it is important to retain the $\Delta \rho_i$ term when discussing coexistence in general.

Relative nonlinearities, ΔN_i, occur through differential responses to the variance of the limiting factors. As seen in Eq. 23, ΔN_i is proportional to the difference in resident and invader ψ_j, which describe how the standardized interaction parameters depend on a single limiting factor F in a nonlinear way (cf. Eq. 9). As such, they are equal to zero whenever the $\mathscr{C}_j$ are linear functions of F, making ΔN_i zero as well. Under purely temporal variation (whose analysis originally gave the mechanism its name), the same happens if the resident and invader $\mathscr{C}_j$ have the exact same nonlinear dependence on F, making ψ_j equal between the two. Therefore, ΔN_i is nonzero only if the interaction parameters of the species are not just nonlinear functions, but differently shaped nonlinear functions of the limiting factor. This explains the etymology behind the perhaps otherwise puzzling nomenclature "relative nonlinearity." Examples of biological mechanisms leading to such an effect include predators with different handling times being affected differently by fluctuations in prey densities (Armstrong and McGehee 1980), and

long-lived species being less harmed by a year of poor recruitment than shorter-lived ones (Chesson 2003). See Appendix S3 for a simple model of relative nonlinearity.

For relative nonlinearities to affect coexistence, the variance in density dependence must differ depending upon which species is the invader (Chesson 1994, 2009). If it did not, then variation would simply help one species and hurt the other, without promoting coexistence overall. Levins (1979) referred to this effect as "consuming the variance", because for it to promote coexistence, the species who benefits from variation in the limiting factor must decrease this variance, as resident, more than its competitors—which could occur if the predator with the fastest handling times also dampens predator-prey fluctuations (Armstrong and McGehee 1980).

Storage effects, ΔI_i, depend on the covariance between species' environmental and interaction parameters, $\text{cov}(\mathscr{E}_j, \mathscr{C}_j)$, and the interaction coefficient γ_j (Eq. 23). It will be nonzero if periods of beneficial environmental conditions (high $\mathscr{E}_j$) coincide with periods of beneficial interactions (high $\mathscr{C}_j$), such as increased benefit from mutualists or reduced pressure from competitors. One way to achieve this for all species simultaneously is for them to partition *time* as a "resource" axis. Suppose two bird species compete over nest sites. Without temporal fluctuations, whichever species is better on average at acquiring nest sites will outcompete the other. However, if the environment is seasonal with wet and dry seasons, and one species is a wet-season specialist and the other a dry-season specialist, then both of them will experience good environments exactly when the other species is unable to perform well—that is, good environments coincide with reduced competition, creating a storage effect (Barabás et al. 2012a). Real-world examples include annual plants having different germination rates that depend on precipitation (Angert et al. 2009, Holt and Chesson 2014), phytoplankton with different growth rates depending on temperature (Eppley 1972), and seedling recruitment depending in part on temperature (Grubb 1977)—each of which have been shown to produce storage effects (Chesson 1994, Miller and Klausmeier 2017). Appendix S4 presents a simple example for a model of coexistence via the storage effect.

For the storage effect to enhance coexistence, one of two other conditions must be true (Chesson and Warner 1981, Chesson 1994): *either* the invader's γ_i should be positive and $\text{cov}(\mathscr{E}_j, \mathscr{C}_j)$ be greater for the invader than the residents; *or* the other way round—the invader's γ_i should be negative and residents should have a larger covariance term than the invader. Let us discuss the first of these scenarios (but see Chesson 1994 for an example of the latter). Imagine that $\mathscr{C}_j$ is determined by the availability of resources, and $\mathscr{E}_j$ represents an organism's ability to take up resources. In this case, $\text{cov}(\mathscr{E}_j, \mathscr{C}_j)$ will usually be negative for residents, because there will be resource shortages when they are most able to capture resources (Miller and Klausmeier 2017). For example, if many plants germinate, free space and water will be scarce; if plankton grow rapidly, they will likely consume the available nitrogen, or block the light. Because the invader is too rare to directly affect the resources, $\text{cov}(\mathscr{E}_j, \mathscr{C}_j)$ will be less negative for the invader.[4] In turn, γ_j will be positive if there is some way to "store" the effects of good times, to get organisms through bad ones (Chesson 1994; note that since Chesson's sign convention differs from ours, his γ_j is negative whenever ours is positive). Many bet-hedging strategies will produce this effect. They typically occur if organisms have a long-lived adult stage or a dormant stage that is relatively unaffected by both competitive and environmental conditions (Chesson 1994, 2000a). For example, seedling survival in tropical trees is highly sensitive to environmental conditions

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[4]In most former cases (e.g., Chesson 1994, 2000a, Kuang and Chesson 2010, Miller and Chesson 2009), $\mathscr{C}_j$ is a measure of the level of competition, so that increasing $\mathscr{C}_j$ reduces $\bar{r}_j$. As such, the interpretation is reversed: If many plants germinate, competition will increase, and thus $\text{cov}(\mathscr{E}_j, \mathscr{C}_j)$ will be positive for residents and less positive for invaders.

and neighbor density, but adult tree survival is not; thus, a high bout of recruitment will be "stored" in the adult population for decades—expressed mathematically by the species having a positive γ_j. When these two factors occur together, invaders are more likely to experience low competition during their best times (e.g., nutrients are more plentiful when temperatures are ideal for growth), and they can store the benefits of good times to get through times of high competition (e.g., low nutrients) and poor environmental conditions (e.g., extreme temperatures).

Spatial relative nonlinearities and spatial storage effects are mathematically identical to their temporal counterparts. However, differences between space and time cause them to operate slightly differently. For example, living longer does not alter the impact of spatial variation in competition (Chesson 2000a). Thus, lifespan differences will not produce spatial relative nonlinearities, even though they can produce temporal ones. Instead, spatial relative nonlinearities may be generated by differences in dispersal (Snyder and Chesson 2004) or the handling time of prey (Wilson and Abrams 2005). In a spatial storage effect, space itself is often the bet-hedging strategy that generates storage (γ_j)—thus, annual plants with seed dormancy can "store" the benefits of good habitat, though they could not store good years (Chesson 2000a). However, despite these small differences, the mechanisms work basically the same way: spatial relative nonlinearities promote coexistence if the species who benefits from spatial variation reduces it, and spatial storage effects promote coexistence if $\mathscr{E}_j$ and $\mathscr{C}_j$ covary spatially in a way that benefits the invader. For instance, if an environment has dry and wet patches, with a dry- and a wet-adapted species competing over the landscape, then the invader will find that competition is weaker (higher $\mathscr{C}_j$) exactly where its preferred patches are (higher $\mathscr{E}_j$), since its competitor is more concentrated in the other patch type.

Growth-density covariances, $\Delta\kappa_i$, quantify how spatial variation in population density affects coexistence (Chesson 2000a). The invasion rate of individuals in a given area will vary across the landscape. If a population is concentrated in favorable locations, then it will grow faster than if it were spread uniformly across the landscape. A recent study (Stump and Chesson 2015) has also examined growth-density covariances in more depth, by partitioning them into a covariance between species interactions and density, $\text{cov}(\nu_j(x), C_j(x))$, and the covariance between environmental conditions and density, $\text{cov}(\nu_j(x), E_j(x))$. A simple model of purely growth-density covariance-mediated coexistence is presented in Appendix S5.

For growth-density covariances to promote coexistence, invaders must be more concentrated in favorable locations than residents; i.e., $\text{cov}(\nu_j(x), r_j(x))$ must be greater for invaders compared to residents. One way this can occur is if species are distributed differently across the landscape, such as insect species laying eggs on different ephemeral resources (Chesson 2000a). A very rare species can be relatively abundant in a given location even if it is rare in absolute terms; the same cannot be said for a common species. Thus, if the species are segregated, competition will be low where the rare species is relatively abundant, and will be high where the common species is relatively abundant. Additionally, if conditions are stable over time, then rare species will often build up where conditions are most favorable, thus leading to a higher growth-density covariance for the invader (Chesson 2000a).

4   How Chesson's coexistence theory has contributed to ecology

Chesson's coexistence theory is a framework theory. Similar to the theory of structured populations in population ecology (Caswell 2001) or the Price equation of evolutionary biology (Frank 2012), it is tautological in the sense that its results hold for any dynamical system that can be parameterized

via Eq. 1 and approximated quadratically as in Section 2.1. Its utility, just like in the other two cases, should not be judged by its "truth" (which is guaranteed by its logical structure alone), but whether the perspective it offers leads to a fruitful research program. In fact, Chesson's theory has proven useful for many problems in community ecology, both for clarifying theoretical questions and for interpreting empirical research. Here we summarize these advances.

4.1   Theoretical analysis of particular coexistence mechanisms

Chesson's coexistence theory has allowed in-depth study of how particular interactions affect coexistence. Temporal and spatial (habitat) partitioning have been thoroughly examined, as they are the very mechanisms the theory was originally developed to understand. For example, a temporal storage effect can happen if annual plants partition the timing of their germination (Chesson 1994) and/or growth (Angert et al. 2009), if coral reef fish partition their spawning times (Chesson and Warner 1981), if phytoplankton temporally partition their resource uptake (Miller and Klausmeier 2017), if plants partition their responses to temporally varying disturbances (Miller and Chesson 2009, Miller et al. 2012), or if trees temporally partition their seedlings' competitive ability (Chesson 2003). In each case, the temporally varying effect generates the standard environmental parameters $\mathscr{E}_j$, and species can coexist if residents generate less competition when conditions for the invader are most favorable. Similarly, a spatial storage effect and growth-density covariance can be generated if trees spatially partition their regeneration niche (Chesson 2000a, Stump and Chesson 2015), or if annual plants spatially partition their germination rates (Chesson 2000a, Snyder and Chesson 2003). In each case, habitat generates the spatially-dependent environmental parameter, which affects coexistence if it covaries with competition (for a storage effect) or population density (for a growth-density covariance).

Predation has also been thoroughly studied using Chesson's theory. Earlier work had generally concluded that generalist predators tend to undermine coexistence (Holt 1977), while specialized predators tend to promote it (Grover 1994). Since then, studies have shown that predators are capable of generating a diverse set of mechanisms. In essence, predators are a limiting factor (i.e., an F_k, contributing to $\mathscr{C}_j$), and thus can produce any mechanism. If predators have specialized behavior, they will generate a variation-independent mechanism contributing to $\Delta\rho_i$ (Chesson and Kuang 2008, Stump and Chesson 2015). However, specialist predators have a much weaker effect on stability if they can always be found near adults of their preferred prey (Stump and Chesson 2015), a phenomenon often called distance-responsive predation or the Janzen-Connell effect (Janzen 1970, Connell 1971, Comita et al. 2014). In a variable environment, generalist predators can generate a storage effect if they have a rapid behavioral (Chesson and Kuang 2010) or numerical (Mordecai 2014) response to their prey; i.e., if their effect covaries with $\mathscr{E}_j$. However, if they respond slowly to their prey, then there will be little or no correlation between environmental conditions and predation (leading to $\text{cov}(\mathscr{E}_j, \mathscr{C}_j) \approx 0$), and thus no storage effect (Kuang and Chesson 2009). Also, if the residents can satiate their predators in a good year, but invaders cannot, then this can create a negative storage effect, undermining coexistence (Stump and Chesson 2017). Additionally, predator-prey cycles (i.e., variation in F_j) are capable of promoting coexistence via relative nonlinearity (Chesson 1994, Chesson and Kuang 2008). Finally, competition-predation tradeoffs are likely to affect both $\Delta\rho_i$ (Kuang and Chesson 2008) and r'_i (Stump and Chesson 2017).

The theory has also been used to better understand the impact of temporal disturbances on coexistence. Many once believed that disturbances promote diversity by removing biomass, thereby reducing competition between species (Hutchinson 1961, Connell 1971, Huston 1979). One of the

theory's major accomplishments has been disproving this claim (Fox 2013), as we discussed in Section 2.5. Rather, disturbances can only promote diversity if they create opportunities for temporal niche differentiation (Chesson and Huntly 1997, Barabás et al. 2012a), manifesting either as relative nonlinearity or a storage effect. For example, if disturbances affect species differently, then those (density-independent) disturbances are encoded in the $\mathscr{E}_j$, needed to produce a storage effect (Miller and Chesson 2009, Miller et al. 2012). Disturbances may also have nonlinear effects on population growth, and can help generate the variation needed to generate relative nonlinearity (Roxburgh et al. 2004, Miller et al. 2012). Finally, disturbances can also generate growth-density covariances, as shown by Snyder (2008) and Shoemaker and Melbourne (2016).

4.2   Aiding our thinking about community processes

The ideas of Chesson's coexistence theory have been used to understand how broader patterns in ecology may operate, even in the absence of specific models. This may be typified by the verbal model in Butler and Chesson (1990), which describes how sessile marine animals could coexist on reefs, and suggests what would need to be measured to test these ideas. For example, they suggest that species may coexist if recruitment varies over time. To test this, ecologists would need to measure which recruitment parameters vary over time ($\mathrm{var}(\mathscr{E}_j)$), how much those parameters differ between species ($\mathrm{cov}(\mathscr{E}_j, \mathscr{E}_k)$), the link between those parameters and competition ($\mathrm{cov}(\mathscr{E}_j, \mathscr{C}_j)$), and what factors could lead to a nonzero γ_j.

Such a qualitative approach to testing was performed by Sears and Chesson (2007), who examined whether two Chihuahuan annual plants could coexist via a spatial storage effect. They used a neighbor-removal experiment to quantify $\mathrm{cov}(\mathscr{E}_j(x,t), \mathscr{C}_j(x,t))$. They found that this covariance reduced flower production in the numerically dominant species by about 20%, but had no effect on a species that recently became rare. This 20% does not directly translate into a spatial storage effect—that would require quantifying γ_j, and the relationship between flower production and $\bar{r}_j$—however, it suggests that habitat partitioning in this system is less important than temporal partitioning, which would give invaders a 40% boost under pairwise interactions (Chesson et al. 2013).

Another important example concerns the clarification of ideas related to phyloecology. Closely related species are sometimes ecologically similar (Violle et al. 2011, Novotny et al. 2006; but see Narwani et al. 2017 for counterexamples). Because of this, many have claimed that more closely related species are less likely to coexist (Webb et al. 2002, Violle et al. 2011). However, Mayfield and Levine (2010) pointed out that ecologically similar species have both low stabilization and a similar competitive advantage—thus, knowing whether two species are related will not tell one whether those species will coexist. If relatives are ecologically similar, this could have two effects at the community level (Stump 2017). First, it will likely have an advantage-equalizing effect (i.e., f_i values will be closer to zero), since strong competitors will experience heavy competition if their close relatives are also strong competitors. Second, it will make the community less stabilized overall (A will be lower), because a species that becomes rare will be replaced by its closest relatives, making it more difficult for the species to recover. Interestingly, this means that while phylogenetic signal is uninformative about two-species interactions, it is informative about multispecies ones at the community level (Stump 2017).

Qualitative insight from the theory has also been used to understand how functional traits affect coexistence (Violle et al. 2011, D'Andrea and Ostling 2016). Adler et al. (2013) examined whether commonly measured traits are likely to generate any of the mechanisms summarized by the terms in

Eqs. 20 and 47. They pointed out that many studies have shown traits varying along gradients (e.g., specific leaf area is often correlated with nutrient abundance), suggesting that spatial storage effect and growth-density covariance are occurring. However, they also point out that no study has specifically linked traits to organismal performance (i.e., specific leaf area has not been strongly connected to $\mathscr{E}_j$); without this link, a spatial storage effect will not be possible.

4.3   Empirical tests of the strength of coexistence

A major advantage of Chesson's coexistence theory is its ability to quantify how strongly particular mechanisms contribute to coexistence. A great illustration of this is found in two studies which examined how differences in germination lead to coexistence between desert annual plants. In the Chihuahuan (Chesson et al. 2013) and the Sonoran (Angert et al. 2009) deserts, yearly differences in germination were found to produce a storage effect whereby each species' invasion growth rate is increased by approximately $\bar{r}_i \approx 0.06$ and $\bar{r}_i \approx 0.05$ per year, respectively.

Usinowicz et al. (2012, 2017) measured the storage effect in several forests using parameterized models. Trees vary their seed production from year to year, and these studies suggested that such variation produces a storage effect. The storage effect was measured using a novel method that is not exactly comparable to those in Angert et al. (2009) and Chesson et al. (2013). With that caveat, they found that the storage effect had a pairwise stabilizing effect ranging from about 50% (Bonanza, Alaska) to about 65% (Barro Colorado Island, Panama). Their model assumed that seedlings experience strong interspecific competition in their first year of life—an assumption for which there is mixed evidence (e.g., Johnson et al. 2012). Our own preliminary simulations suggest that removing this assumption weakens the storage effect by about half. However, the qualitative results are the same and still surprising even if the effect sizes are weakened, because they suggest that the storage effect is nearly as strong in tropical forests (where it has mostly been ignored) as it is in desert annual plants, where it is seen as a dominant mechanism.

Adler et al. (2010) applied Chesson's methods to perennial plant species in Idaho, USA. They found that invasion growth rates were large and positive for all species. Moreover, when the stabilizing mechanisms were "switched off" (which cannot be done in nature but is easily done with the empirically fitted model), the growth rates were all small and some were negative. They concluded that stabilizing forces in this system are very strong—much stronger than necessary to ensure coexistence.

Many additional studies have examined the outcome of pairwise competition, based on the Lotka–Volterra formalism mentioned at the end of Section 2.7 (Eq. 54). These studies produce results that are not directly comparable to the ones above, and have the drawback that they can only examine pairwise coexistence (Barabás et al. 2016, Saavedra et al. 2017). But they can show whether pairs of species coexist, and if so, how strongly their coexistence is stabilized.

Godoy et al. (2014) and Kraft et al. (2015) used the Lotka–Volterra methods to study whether annual plants can coexist in California serpentine soils. Their results suggested that most pairs of species should be unable to coexist. This seems extreme, but may be explained in part by their methodology. First, these studies estimated competitive effects at a single time and place; thus, they could accurately capture variation-independent mechanisms, but not mechanisms that rely on spatial or temporal variation in the environment (Kraft et al. 2015). In other words, only contributions to $\Delta\rho_i$ were measured, but not to ΔN_i, ΔI_i, or $\Delta\kappa_i$. Second, they were based on pairwise comparisons instead of studying the community as a whole, since the Lotka–Volterra methods only allow for those. Saavedra et al. (2017) later showed that analyzing the entire community substantially altered the conclusions.

The Lotka–Volterra methods were also used to study phytoplankton competing in a chemostat. Narwani et al. (2013) found that species were competitively very similar with $f_j/f_k < 1.3$ for all but one outlier, but also that stability was weak, with the niche overlap index $1 - A$ between 0.65 and 1.1. They found that about half the species should coexist, though this conclusion is again based on pairwise comparisons which may or may not be indicative of coexistence in the community as a whole. Their findings do suggest that these phytoplankton may be ecologically similar—though that could also be because the chemostat environment leaves little room for ecological differentiation (Chu and Adler 2015).

Finally, the Lotka–Volterra methods were used to study coexistence between long-lived plants in five grassland systems in western North America (Chu and Adler 2015). They used mapping data to track individuals over a period of 13 to 40 years, in between 26 and 178 quadrats. These systems were overstabilized, with an average competitive advantage ratio of 1.5 and an average niche overlap index of 0.29 (with this value of $1 - A$, communities could coexist with an advantage ratio of up to 4.76). The authors argue that these communities were so strongly stabilized because they examined a large range of spatial and temporal conditions, and because the study focused on only the most dominant plants.

4.4   Testing particular hypotheses

The quantification techniques of Chesson's coexistence theory can also be applied to test specific hypotheses. For example, Godoy et al. (2014) recently tested whether unrelated species were more likely to coexist than related species. They found that in their system of California annual plants, this was not the case; rather, related species were more likely to coexist because they were competitively similar. In the same system, Kraft et al. (2015) tested the hypothesis that trait differences promote coexistence. They found that no single trait contributed to stabilization, but that most single traits produced competitive advantages. Complex combinations of traits were able to produce stabilization; however, the authors point out that most studies of trait-based coexistence are based on single trait axes. Again, these results are limited by the fact that they measured competition in a single time and place. For instance, it has been shown in the Sonoran Desert that a high specific leaf area is helpful in wet years but not dry years (Angert et al. 2009), so differences in specific leaf area may lead to a temporal storage effect which would have remained undetected by Kraft et al. (2015).

Also, Usinowicz et al. (2017) used their data to test the hypothesis that the tropics are more species-rich because stabilizing mechanisms are stronger there. They measured the storage effect in 10 forests across 65 degrees of latitude, and found that the storage effect was one and a half times as strong in tropical forests as it was in boreal forests. Their results were measured using pairwise comparisons however, and as usual, one should be circumspect when generalizing the results of pairwise tests to entire communities (Barabás et al. 2016, Saavedra et al. 2017, Levine et al. 2017).

4.5   Automating model analysis

Finally, tools are currently being developed to automate model analyses. Such tools are designed so that someone with an empirically parameterized model can quantify storage effects, relative nonlinearities, and other mechanisms in their system. These tools will be most useful for complex models, such as those with age structure, which cannot be analyzed simply (but see Dewi and Chesson 2003). They will not reveal how particular mechanisms work, but will be of great value in empirical tests of each mechanism. Currently, one such model exists for quantifying models with temporal variation

(Ellner et al. 2016). Additionally, an improved model for temporal dynamics (S. Ellner, personal communication) is near production.

5   Challenges and limitations

Despite its high level of generality and variety of applications, Chesson's theory has its drawbacks. Many of the limitations arise from the fact that the theory is founded on invasion analysis. A major advantage of invasion analysis is its treatment of spatiotemporally variable environments: instead of having to evaluate a stochastic stationary state and its stability, one simply looks at whether the long-term average growth rate of a species is positive when at low abundance. However, invasion analysis does have some limitations. First, we show that invasion analysis sometimes fails to predict if species coexist or are excluded. Next, we discuss a separate issue with the scaling factors d_j when species respond to groups of limiting factors in similar ways. Finally, we argue that much of Chesson's theory is based on the assumption of a single limiting factor, and show how relaxing this assumption can create problems.

5.1   Complex dynamics

One limitation of invasion analysis is that it may be uninformative or downright misleading in the presence of complex dynamics with alternative stable states. Counterexamples to the standard picture "species coexist when they can all invade" are possible both ways: species may be able to invade but still go extinct; and conversely, species may be unable to invade but still coexist.

An example of the former scenario is provided by a model of asymmetric Lotka–Volterra competition between a resident and a very similar mutant species, with an added Allee effect:

$$r_j = g_j \frac{\overline{n}}{1+\overline{n}} - m - n_j - \alpha_{jk} n_k \qquad (j = 1, 2; \ k \neq j), \tag{55}$$

where the n_j are population densities, $\overline{n} = n_1 + n_2$ is their sum, g_j are maximum rates of intrinsic growth, m is a baseline mortality rate, and α_{jk} is the competition coefficient of species k on j. Generally, species 1 has a monoculture equilibrium that is stable in the absence of species 2. When the mutant species 2 is introduced at a low density, it can initially grow and knock off species 1 from its attractor, driving it towards extinction. Under some circumstances however, species 2 cannot persist without 1, and therefore goes extinct as well ("evolutionary suicide", Gyllenberg and Parvinen 2001). So even though species 2 can invade, it still goes extinct *after* the invasion phase (Figure 1**a**). This example involves the coextinction of the species, but this is not a necessary outcome: in other models, following a successful invasion, the invader eventually goes extinct while the resident does not ("the resident strikes back", Geritz et al. 2002).

As an example of the second scenario, consider the case of two competitors both exhibiting an Allee effect. As a result, neither of them can grow from low density. Once over a threshold density, however, they can establish themselves and coexist. This model can be thought of as adding Allee effects to standard two-species Lotka–Volterra competition:

$$r_j = g_j \left(\frac{n_j}{A_j} - 1 \right) \left(1 - \frac{n_j}{K_j} \right) - \alpha_{jk} n_k \qquad (j = 1, 2; \ k \neq j), \tag{56}$$
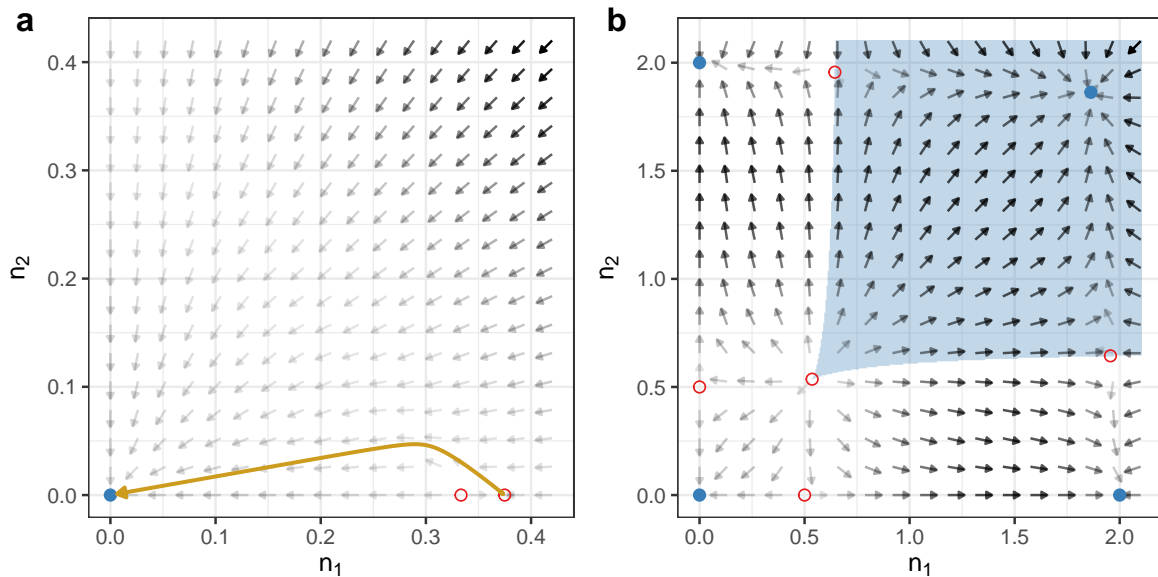
Figure 1: Phase planes of hypothetical two-species communities, with the axes representing the densities of species 1 and 2. Stable vs. unstable equilibria are marked by solid blue vs. open red circles. The arrows point in the direction of the local dynamical flow. The shade of the arrows represents the speed of the local flow, with darker hues corresponding to faster flows. **a.** A community of two very similar species, corresponding to Eq. 55, with parameters $g_1 = 1.833$, $g_2 = 1.821$, $m = 0.125$, $\alpha_{12} = 1.01$, and $\alpha_{21} = 0.99$. Species 2 can invade the monoculture equilibrium $n_1^* = 0.375$ of species 1 (which is stable as long as species 2 is absent), but is unable to persist. The yellow curve shows the dynamical trajectory of the invasion process, with species 1 starting from its equilibrium and species 2 from a small invasion density of 0.001. **b.** Two-species community corresponding to Eq. 56, with parameters $g_1 = g_2 = 2$, $A_1 = A_2 = 1/2$, $K_1 = K_2 = 2$, and $\alpha_{12} = \alpha_{21} = 1/5$. None of the five boundary equilibria allow invasion from low density. Despite this, coexistence is possible: there is a coexistence equilibrium with a basin of attraction (shaded area) which is substantially large, even though it does not extend to the boundaries.

where the A_j are Allee thresholds (such that in monoculture, the density n_j dropping below A_j means the extinction of species j), and the K_j are maximum monoculture equilibrium abundances ("carrying capacities"). Both species now have negative invasion growth rates, yet can coexist if they start at high density (Figure 1**b**).

5.2 Stability and feasibility of the resident community

Invasion analysis proceeds by checking whether each of the S species would be able to invade the $(S-1)$-species community of residents, assumed to be at some stationary state. If the $(S-1)$-species stationary state does not exist for *all* species as invaders, then invasion analysis fails. The problem is related to the previous one of complex dynamics and alternative stable states. However, here the source of the problem is the nonexistence of the resident community, which can happen even if the system's dynamical behavior is otherwise simple.

First, it is possible that a change in the resident community will lead to negative invasion growth rates, even though species can coexist. As an example, let us consider the Lotka–Volterra model

(Eq. 53) with three species and parameter values

$$b_j = \begin{pmatrix} 0.55 \\ 0.61 \\ 0.42 \end{pmatrix}, \qquad a_{jk} = \begin{pmatrix} 1 & 1.1 & 1.2 \\ 0.8 & 1 & 1.5 \\ 0.7 & 0.7 & 1 \end{pmatrix}. \tag{57}$$

It is easy to verify that there is a stable coexistence equilibrium: $(n_1^* = 0.05, n_2^* = 0.15, n_3^* = 0.28)$. However, it turns out that species 1 cannot invade from the stationary state corresponding to its absence. This is because species 2 and 3 cannot coexist alone, and species 1 cannot invade a monoculture of species 2. To show this, let species 1 be the invader. The subcommunity corresponding to its absence has parameters

$$b_j = \begin{pmatrix} 0.61 \\ 0.42 \end{pmatrix}, \qquad a_{jk} = \begin{pmatrix} 1 & 1.5 \\ 0.7 & 1 \end{pmatrix} \qquad (j,k = 2,3) \tag{58}$$

which leads to the unstable equilibrium $n_2^* = 0.2$, $n_3^* = 0.28$ and thus founder effects: the winner is determined by the initial conditions. Assuming initial conditions are such that species 2 wins, the final stable equilibrium is species 2 having a monoculture equilibrium density $b_2/a_{22} = 0.61$. Species 1, the invader, cannot invade this monoculture: the subsystem

$$b_j = \begin{pmatrix} 0.55 \\ 0.61 \end{pmatrix}, \qquad a_{jk} = \begin{pmatrix} 1 & 1.1 \\ 0.8 & 1 \end{pmatrix} \qquad (j,k = 1,2) \tag{59}$$

solidly predicts species 2 winning. Invasion analysis thus incorrectly predicts that coexistence in this system is impossible. In fact, species 1 ironically has no problem growing from an arbitrarily low abundance and coexisting with the other two, for quite a wide range of initial abundances $n_2(0)$ and $n_3(0)$, as long as $n_3(0)$ is not precisely zero.

It is also possible that species have positive invasion growth rates, but will not coexist due to changes in the resident community. A well-known example of this is intransitive competition (rock-paper-scissors dynamics; May and Leonard 1975, Allesina and Levine 2011). If the rock-species is brought into the invader state, the paper-species cannot coexist with the scissors-species: only the scissors-species remains. As a result, the rock-species can invade this monoculture. And yet, there is no guarantee that the three species together will coexist: the community may exhibit ever larger oscillations that drive each species closer and closer to extinction (May and Leonard 1975).

As seen, a blind application of invasion criteria without regards to whether all $(S-1)$-species communities are stable and feasible may quickly lead to nonsensical results. The problem of evaluating the $(S-1)$-species resident community gets especially difficult if the number of species is large. For example, a 99-species community is arguably just as intractable as a 100-species one. But if the $(S-1)$-species community is no easier to handle than S species, then nothing is gained by invasion analysis—in fact, for $S = 100$, analyzing the one hundred different 99-species resident communities is approximately 100 times more inconvenient than simply analyzing the full 100-species model in the first place. Furthermore, in species-rich systems the relegation of one species into the invader state is often followed by coextinctions (Case 1990). That is, the $(S-1)$-species resident stationary states usually do not exist. Then invasion criteria can no longer be used to assess coexistence in the first place.

Generally speaking, invasion criteria are most useful either when the number of species is very small, or if the structure of interactions between them is especially simple. One such simple structure is *diffuse competition*, where there is one common intra- and another common interspecific competition coefficient (Chesson 1994, 2000a,b, 2003). The $(S-1)$-species state is then simple to evaluate (Bastolla

et al. 2005), and the invasion criterion is easily applicable—at least in simple competition models such as the annual plant or Lotka–Volterra models. Chesson's works often make the assumption of diffuse competition; indeed, this is the reason why multispecies invasion growth rate formulas (such as Eq. 4 in Chesson 2000b) were possible to derive. If such a simple interaction structure is lacking, evaluation of multispecies stationary states becomes increasingly difficult, and quickly becomes unfeasible.

5.3   The conditioning of the scaling factors

If there are more species than limiting factors in the system, one can solve Eq. 21 for the scaling factors d_j, conveniently eliminating the linear terms in the limiting factors from the equations. Since there are fewer equations than unknowns, the solution will not be unique. Even though this gives some freedom in choosing the scaling factors, one must take $d_i^{-i} \neq 0$, otherwise there is division by zero in Eq. 17. A nonzero d_i^{-i}, however, simply cannot be achieved in certain cases. As an example, consider the model

$$r_j = \sum_{k=1}^{L} \phi_{jk} F_k - m_j \qquad (j = 1, 2, \dots, S) \tag{60}$$

with two limiting factors and three species, where ϕ_{jk} is given by the matrix

$$\phi_{jk} = \begin{pmatrix} 1 & 1 \\ 2 & 2 \\ 3 & 2 \end{pmatrix}. \tag{61}$$

Substitution into Eq. 21 yields a system of two linear equations for three unknowns:

$$d_1 + 2d_2 + 3d_3 = 0, \tag{62}$$
$$d_1 + 2d_2 + 2d_3 = 0. \tag{63}$$

The general solution is $d_j = (2, -1, 0) c$, where c is an arbitrary constant. As such, the only freedom in choosing the factors differently depending on invader identity is in choosing a different c. Unfortunately, regardless of its value, d_3 is necessarily zero. Therefore, for Eq. 61, the scaling factors cannot be used to partition the invasion growth rate of species 3 via Eq. 19. The crux of the problem is that the first and second rows of ϕ_{jk}, as two-dimensional vectors, lie along the exact same line, while the third does not (Figure 2**a**). It is therefore impossible to obtain the third vector as a linear combination of the first two (Appendix S1).

The same problem occurs in the following example with four species and three limiting factors:

$$\phi_{jk} = \begin{pmatrix} 1 & 2 & 3 \\ 1 & 1 & 2 \\ 2 & 1 & 3 \\ 2 & 2 & 1 \end{pmatrix}. \tag{64}$$

Solving Eq. 21 yields $d_j = (1, -3, 1, 0) c$, so the invasion rate of species 4 cannot be partitioned via Eq. 19. In this example the vectors formed by the first three rows are confined to a two-dimensional plane in the three-dimensional space spanned by the limiting factors (Figure 2**b**). The fourth vector lies outside this plane and so the corresponding scaling factor is zero. This example therefore suffers from
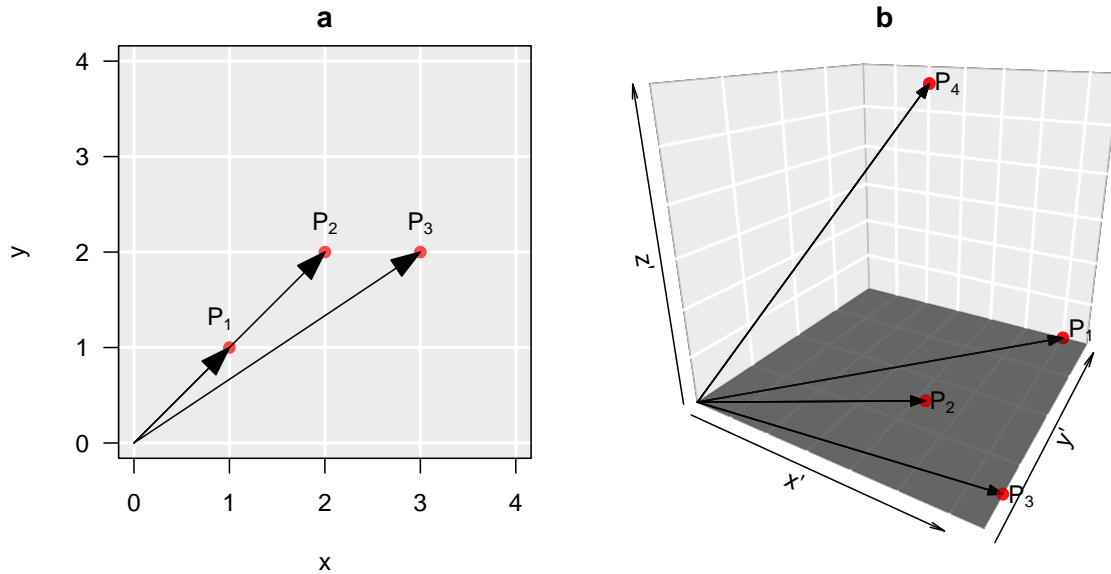
Figure 2: a. Vectors formed by the rows of matrix ϕ_{jk} in Eq. 61, plotted on the x-y plane, where x and y are respectively the coordinates of the points given by the two columns of ϕ_{jk}. The first and second species have colinear vectors, while the third is off the line. The third vector cannot be constructed as a linear combination of the first two. **b.** Vectors formed by the rows of matrix ϕ_{jk} in Eq. 64, plotted in the three-dimensional space defined by orthogonal axes $x' = 5x + 2y + 7z$, $y' = -3x + 4y + z$, and $z' = x + y - z$, where x, y, z are analogously defined as above. The first three species lie on the plane $z' = 0$, whereas the fourth does not. The fourth vector cannot be written as a linear combination of the first three.

the same problem as the first—but, unlike before, in this case there is no obvious way of telling so just by looking at the matrix ϕ_{jk}, because no two rows are exactly proportional to one another.

In general, whenever a subset of the species have an identical relationship between responses to different limiting factors while other species have different ones, at least one of the scaling factors will necessarily be zero. Mathematically, this situation translates as a subset of the vectors defined by the ϕ_{jk} living in a lower-dimensional subspace relative to the entire L-dimensional space determined by the L limiting factors (colinear vectors in the 2-dimensional example in Eq. 61; coplanar vectors in the 3-dimensional example in Eq. 64).

All such cases have the property that an arbitrarily small perturbation of the entries of ϕ_{jk} will in general resolve the degeneracy, and lead to a case where all scaling factors are nonzero. Geometrically, this is because the rows need to be precisely linearly dependent to lead to zero scaling factors. For instance, taking the first example in Eq. 61: if we replace ϕ_{11} by 1.001, the scaling factors become $d_j = (-2000, 998, 2)\,c$, with none of them being zero anymore. While this seems to suggest that the problem of zero scaling factors is merely of academic interest, it actually reveals a potential empirical problem. The ϕ_{jk} are often empirically measured quantities, and as such, come with inevitable measurement error. When a subset of the rows of the matrix are nearly linearly dependent, small errors of measurement will translate into large differences in the d_j. For example, an uptake rate of 1 will often be indistinguishable from an uptake rate of 1.001; however, changing the entry in a ϕ_{jk} matrix

from 1 to 1.001 can vastly change the d_j:

$$
\phi_{jk} = \begin{pmatrix} 1.001 & 1 \\ 2 & 2 \\ 3 & 2 \end{pmatrix} \Rightarrow d_j = \begin{pmatrix} -2000 \\ 998 \\ 2 \end{pmatrix} c, \qquad \phi_{jk} = \begin{pmatrix} 1 & 1.001 \\ 2 & 2 \\ 3 & 2 \end{pmatrix} \Rightarrow d_j = \begin{pmatrix} 2000 \\ -1003 \\ 2 \end{pmatrix} c, \quad (65)
$$

where c is an arbitrary constant. The different d_j values lead to wildly different calculations for the invasion growth rates. For instance, applying Eq. 17 to the model in Eq. 60 which has three species and two limiting factors, Eq. 39 yields the partitioned invasion growth rates. Calculating the third invasion rate for both scenarios in Eq. 65 and assuming $m_j = 1$ for all three species, we find that $\bar{r}_3 = 500$ in the first scenario and $\bar{r}_3 = -499.5$ in the second (empirically indistinguishable) one. That is, a tiny error in measurement translates into a huge difference of calculated invasion growth rates.

It is important to appreciate that the problem is not with any deficiency in measurement techniques or numerical methods. Rather, it is the model itself which is ill-conditioned, and therefore no method could ever resolve it (short of measurements of infinite precision). The problem is intrinsic to the formalism, and one must be aware of it when analyzing particular models.

5.4   The number of limiting factors

The scaling factors d_j were introduced to cancel the linear terms in the limiting factors F_k. However, the maximum number of limiting factors that can be canceled is $S-1$. This result immediately connects to classical coexistence theory: if there are more species than limiting factors, it is impossible for them to coexist at a stable equilibrium point. Stable equilibrium, in this context, means no spatiotemporal fluctuations. Therefore all coexistence mechanisms in Eqs. 20 and 47 that depend on such fluctuations (ΔN_i, ΔI_i, and $\Delta \kappa_i$) will be zero. But if there are more species than limiting factors, then the $\Delta \rho_i$ term will also be zero with an appropriate choice of the d_j. So the only term left will be r_i', and since some of these are necessarily negative, coexistence is precluded. This is nothing else but the principle of competitive exclusion in its classical form (Levin 1970). The scaling factors therefore offer more than mathematical convenience: by forcing $\Delta \rho_i$ to be zero, they make it explicit that coexistence is impossible in the absence of either as many limiting factors as species, or fluctuation-dependent mechanisms contributing to ΔN_i, ΔI_i, or $\Delta \kappa_i$.

That said, a number of problems arise in systems with as many or more limiting factors than species. In that case, not all linear terms in F_k can be canceled, and $\Delta \rho_i$ will no longer be zero. Unfortunately, to be able to actually evaluate $\Delta \rho_i$, one would have to know the equilibrium levels of the F_k, which cannot be obtained without additional equations governing the dynamics of the limiting factors. Even if these equations are available, solving the joint system may be difficult.

In some situations, the number of limiting factors is much larger than the number of species. In this case, it is unclear how one should choose the scaling factors d_j to lead to the simplest possible community description. In the special case where there is only one "major" limiting factor, F_1, and the effect of all the others is much weaker, one can choose $d_i = 1/\phi_{i1}$ and $d_{s \neq i} = -1/(\phi_{s1}(S-1))$ as in Eq. 22 (effectively proceeding as if this was the only limiting factor) which will be correct to a linear approximation—for technical details, see Kuang and Chesson (2010) and Stump and Chesson (2017). In other cases, there are formally an *infinite* number of resources, and none of them stand out as being overwhelmingly more important than any other. The classical example is species of different phenotypes partitioning a resource continuum—e.g., birds with different bill depths feeding on seeds of various sizes. When such an ecological situation is well-described by MacArthur's consumer-resource

model (MacArthur 1970, Chesson 1990), it can be cast in the Lotka–Volterra form of Eq. 53. For this case, Chesson (2011) suggests choosing $d_j = 1/\sqrt{a_{jj}}$. This choice, however, does not simplify invasion analysis in any way.

Additionally, there is an important caveat to the usual interpretation of the $\Delta\rho_i$, ΔN_i, ΔI_i, and $\Delta\kappa_i$ terms given in Section 3. Namely, these are generally only available when the number of limiting factors is one. In that case, each of these four terms can be chosen to be the difference between resident and average invader values (Eq. 23), which is the basis for all standard interpretations found in the literature. For more than one limiting factor however, this kind of partitioning may not be available, and with it the attending advantages in interpretation are lost as well. For example, in a system where $d_j = (1, -1, 1)$ and $\gamma_j = 1$, the storage effect for species 1 would be

$$\Delta I_1 = \text{cov}(\mathscr{E}_1, \mathscr{C}_1) - \text{cov}(\mathscr{E}_2, \mathscr{C}_2) + \text{cov}(\mathscr{E}_3, \mathscr{C}_3), \tag{66}$$

i.e., $\text{cov}(\mathscr{E}_2, \mathscr{C}_2)$ harms but $\text{cov}(\mathscr{E}_3, \mathscr{C}_3)$ helps the invader. In some cases these strange-looking weightings may be ecologically meaningful. For example, Stump and Klausmeier (2016) considered relative nonlinearity in a community where microbes exchanged resources, and found that the weighting terms were negative for species that competed for resources, but positive where species exchanged resources. However, even when such interpretations exist, they will often be slightly different from the usual one (Section 3). One way around this problem is to formally treat models as having only one limiting factor by choosing the d_j to eliminate one single F_k, absorbing the rest into the $\Delta\rho_i$ term. With this modification, Eqs. 22 and 23 still hold, and the interpretations below also hold for any number of limiting factors—at the cost of the arbitrariness of which limiting factor was treated as the "baseline".

We conclude that Chesson's coexistence theory is most powerful when there is only a single limiting factor. In that case, there is a simple recipe for choosing the scaling factors (Eq. 22) leading to a partitioning of the invasion rates via Eq. 23 which has the simple interpretation of comparing invader quantities with average resident ones. Furthermore, $\Delta\rho_i$ is eliminated, so coexistence is maintained purely by fluctuation-dependent mechanisms. When the number of limiting factors is greater than one but smaller than the number of species, $\Delta\rho_i$ can still be eliminated but Eq. 23 and the interpretational advantages it comes with are no longer available. Finally, when the number of limiting factors is equal to or larger than the number of species, it is unclear how one should designate the scaling factors d_j to simplify the problem as much as possible. Finding strategies for doing so is avenue for future research.

6 The stabilization-competitive advantage paradigm: strengths and weaknesses

In addition to technical problems that are built into the mathematics of the framework, there are also issues with how these formal aspects have been interpreted. In particular, the concepts of stabilization A and competitive advantages f_i (Eqs. 48 and 52) may now have the dubious achievement of being even more universally confused than the concept of the "niche" was reputed to have been (Real and Levin 1991). As we argue below, these concepts are frequently invoked in discussions of coexistence without sufficient regard to their formal meaning. We first tackle the apparent limitation that A and f_i are only defined for a single limiting factor, and argue that this limitation is inherent to biology, not to the theory itself. Next, we discuss how the notion that these two terms are independent can lead to pitfalls and incorrect conclusions. We finish by discussing what A and f_i really are, and how they can be useful: as summary statistics of the scaled invasion growth rates.

6.1   Which limiting factor should be considered the baseline for evaluating stabilization and competitive advantages?

The definitions for stabilization and competitive advantages hold when there is a single limiting factor. They will also hold for an arbitrary number of limiting factors as long as all but one of them are amalgamated into the $\Delta\rho_i$ term of Eqs. 20 and 47. This brings up the question of which limiting factor, out of all possible ones, should be treated as the baseline—i.e., which one should be eliminated via a proper choice of the scaling factors d_j and thus excluded from $\Delta\rho_i$. Appendix S6 presents a particular example with two consumer species competing for two resources, with the first species specializing on resource 1 and the second species on resource 2. In this case, if we pick resource 1 as the baseline, we find that species 1 has a positive advantage and species 2 a negative one, which the stabilization term overcomes to allow for coexistence. In turn, picking resource 2 as the baseline means species 2 has the positive advantage, with stabilization preventing species 1 from being excluded. Does this introduce a fatal arbitrariness to the concepts of stabilization and competitive advantages? If not, which interpretation is the correct one?

Both interpretations are correct, and it does not matter which limiting factor (or linear combination thereof) one treats as the baseline. When choosing resource 1 as the baseline, our thought process is as follows: were we to eliminate the influence of resource 2, we would find that species 1 excludes species 2. This fact is expressed by species 1 having a positive advantage f_1, and species 2 a negative $f_2 = -f_1$. However, resource 2 creates an $A > 0$ that boosts f_2 to make the invasion rate of species 2 positive and coexistence possible. Choosing resource 2 as the baseline, the same interpretation holds with the species' roles reversed. The bottom line is that when two species coexist, they are equally fit from an evolutionary point of view, both having average long-term growth rates of zero. Judging which species is competitively superior only makes sense when coexistence is not possible, which requires the absence of all stabilizing mechanisms. Since in the presence of multiple resources there is no unique way of eliminating just one of them, it is meaningless to ask which resource is providing the stabilization—it is either and both. The ambiguity in the definitions of stabilization and competitive advantages stemming from the arbitrary choice of a baseline factor is therefore not a defect in the theory. Rather, it expresses a fundamental fact about what coexistence means.

This issue may seem to arise only when there are multiple limiting factors. In fact, the same ambiguity is present even when there is only one factor, though this fact is veiled by a thick layer of mathematical formalism. As an illuminating example, consider the following simple model of two species consuming a single resource: $r_1 = b_1 F - m_1$ and $r_2 = b_2(F - \overline{F})^2 - m_2$, where b_j and m_j are the consumption and mortality rates, and F is the resource which is fluctuating in time with mean $\overline{F}$. The time averages then read $\overline{r}_1 = b_1\overline{F} - m_1$ and $\overline{r}_2 = b_2 V - m_2$, where V is the variance of the resource. Quite literally, species 1 consumes the mean and species 2 the variance of the resource (Levins 1979, Kisdi and Meszéna 1993, Szilágyi and Meszéna 2010); formally, $F_1 = \overline{F}$ and $F_2 = V$ act as two separate limiting factors. As such, we have a choice to make: which one should we treat as the baseline? Chesson's formalism gives a fixed if arbitrary answer to this question: it is always $\overline{F}$ which is the baseline and V (or any other fluctuation-dependent quantity whose value would be zero in the absence of environmental variability) is the mechanism. The reason for this lies in the intellectual origins of what Chesson's theory was designed to illuminate: the role of fluctuations in maintaining coexistence. The baseline scenario is therefore always the one without fluctuations, in which case only the $\Delta\rho_i$ terms can maintain coexistence in Eqs. 20 and 47. Since, as mentioned before, this term is zero in most of Chesson's works due to there being only a single limiting factor, there is no longer any

ambiguity in defining A and f_i as long as we accept the rule that fluctuation-dependent limiting factors can never be the baseline. Nevertheless, we note that it is in principle possible to evaluate A and f_i on one of the effective, fluctuation-induced limiting factors such as the variance of a resource, even if this has never actually been done before.

In summary, while the ambiguity in the definitions of the stabilization and competitive advantage terms is real, this is not a failure of the theory but a biologically important necessity whenever species are actually coexisting as opposed to just having the survival of the best competitor.

6.2   Stabilization and competitive advantages are not independent

The decomposition of invasion growth rates into stabilization and competitive advantages appears to simplify the analysis of coexistence: we determine A and the f_i's, and figure out which is bigger. A simple but useful classification system suggests itself (Adler et al. 2007, Mayfield and Levine 2010), whereby a community is robust (small f_i, large A), dynamic (large f_i, large A), unstable (large f_i, small A), or quasi-neutral (small f_i, small A). The nature of the particular scenario could then inform management decisions by assessing whether the system is under threat of extinctions.

Alas, A and f_i are not independent quantities. Rather, any model parameter—e.g., the rate of resource uptake—will generally affect both terms simultaneously. In fact, the very definitions of A and f_i (the mean scaled invasion rate and the ith scaled rate minus this mean; Eqs. 48 and 52) reveal that this must be so. That A and f_i are interconnected has been pointed out in the literature before (Loreau et al. 2012, Adler et al. 2013, Letten et al. 2017). Despite this, both terms are commonly displayed and discussed in a way that suggests that they can vary independently. For example, many works display them as orthogonal axes of variation (Adler et al. 2007, Chesson and Kuang 2008, Narwani et al. 2013, Kraft et al. 2015), and some (e.g., Mayfield and Levine 2010) explicitly talk about scenarios where some trait influences either just one or the other term. Thinking of stabilization and competitive advantages as independent quantities may lead to overreaching conclusions about coexistence. Below we discuss some examples drawn from the literature or personal communications.

1. The quantity A measures how stabilized the community is. The statement is tautologically true, since in Chesson's theory stabilization is by definition the mean scaled invasion growth rate. However, this does not necessarily say much about coexistence, because the average of the $\bar{r}_i/\phi_i$ can be arbitrarily large without the species actually coexisting. Thus, A alone is insufficient to judge coexistence: the f_i are also needed. This is more obvious when we think in terms of the invasion rates. In a two-species community, $\bar{r}_1/\phi_1 = \bar{r}_2/\phi_2 = 10$ leads to $A = 10$, and so does $\bar{r}_1/\phi_1 = 21$ and $\bar{r}_2/\phi_2 = -1$; but the species coexist only in the first case. Similarly, a system with a high A and large differences in competitive advantages may in many ways be less stable than a community with a lower A and no advantage differences (Yenni et al. 2012).

2. A species' competitive advantage is a fundamental property of that organism. We have often heard people speak of "the" competitive advantage of an organism, much like they speak of its R^*-value: that it is a fundamental trait of an organism which could be measured outside of its competitive context. This sometimes holds under very stringent assumptions, such as those that would make the advantage terms equal to an R^*-comparison, like in the example of Section 2.5 (see also Stump and Klausmeier 2016). However, it will not be true generally. An organism's competitive advantage is no more a fundamental property than its invasion growth rate. Thus, any factor that changes an organism's growth rate—a change in abiotic conditions, or a different set of competitors, or the introduction of a predator—will change its f_i value. Indeed, this becomes obvious when one

considers a rock-paper-scissors community: a rock-species will have positive f_{rock} if competing against scissors, and negative f_{rock} if competing against paper, even though f_{paper} is negative in a community with scissors and paper. There is no way to rank the competitive hierarchy of these species without knowing who the other competitors are.

3. Stabilization measures the volume of parameter space compatible with coexistence (Chesson 2008, Yuan and Chesson 2015). This claim is based on the coexistence condition $\min(f_i) + A > 0$. Quoting from Yuan and Chesson (2015): "Hence if the f_i can be varied independently of A then we see that A determines the size of the coexistence region in terms of the [competitive advantages], f_i. A larger value of A gives a larger region of f_i values permitting coexistence." This is technically true—if certain model parameters affect only the f_i but not A, then for those parameters, a larger A means that a wider range of those parameters will be compatible with coexistence. As seen from Eq. 51, any quantity influencing only the r_i' term of Eqs. 20 and 47 will have this property. For instance, Yuan and Chesson (2015) present an example of a two-species lottery model where fecundity affects only the f_i. However, as they themselves point out, this property holds only for this parameter in this particular model, and even there it is lost for three or more species. As discussed earlier, the problem is that model parameters generally affect both A and f_i, making the premise of the argument invalid. While parameters influencing only the f_i are not inconceivable, they constitute a special case. Using A to measure the size of parameter space allowing coexistence is therefore of limited applicability.

4. Very similar species may stably coexist, because similar species must also have similar competitive advantages, and therefore require a very small amount of stabilization to overcome their inequalities (Adler et al. 2007). This argument seems true on the surface if one thinks of A and f_i as independently adjustable, but runs into trouble when one thinks in terms of model parameters potentially affecting both. While parameters which influence the f_i without changing A are at least conceivable, it is much more difficult to have a parameter affecting A but leaving all the f_i intact, as this would require the parameter to simultaneously influence all scaled invasion rates by the exact same amount (thus changing their mean without affecting any of the differences from that mean). In fact, classical ecological arguments and adaptive dynamics both demonstrate that the stable coexistence of similar species is highly unlikely (Geritz et al. 1998, Meszéna 2005, Gyllenberg and Meszéna 2005, Meszéna et al. 2006, Barabás et al. 2013a,b, 2014).

To show where the disconnect arises, we recast a classical problem of limiting similarity in terms of A and f_i (Appendix S7). We consider a general scenario where two very similar species compete. These species are identical except for a small difference δ in a single quantitative trait. We show that if the strength of competition decreases with increasing trait difference, then the competitive advantages are proportional to δ, which means they indeed approach zero with decreasing trait differences. Unfortunately however, stabilization turns out to be proportional to δ^2, which, for sufficiently small δ, decreases faster than the competitive advantages. Therefore, stabilization cannot overcome the competitive disadvantage of the losing species even though both approach zero with decreasing trait differences.

Just as before, the tacit assumption that A and f_i are independent misleads us into thinking that arbitrarily similar species may stably coexist. Once we account for their dependence on model parameters, A and f_i give the same result as classical arguments.

5. Stabilization stems from "any [species] differences that cause species to more strongly limit themselves than others". The above is a quote from HilleRisLambers et al. (2012), but see also Chesson (2000b), Adler et al. (2007), Levine and HilleRisLambers (2009), Mayfield and Levine (2010),

Adler et al. (2010), Chesson (2011), Narwani et al. (2013), Kraft et al. (2015), and others. The claim is based on the Lotka–Volterra definition of stabilization (Section 2.7), and is valid in systems with two species. When there are more than two species, however, it is no longer the case that species can coexist if every direct interspecific interaction is weaker than every direct intraspecific interaction (i.e., if $a_{jj} > a_{jk}$ for all j and k).

First, coexistence via intransitive competitive loops or certain types of complex dynamics makes it possible for species to coexist even if intraspecific effects are weaker than interspecific ones (Barabás et al. 2016, Saavedra et al. 2017, Levine et al. 2017; Sections 5.1 and 5.2). But even in the realm of standard symmetric competition where such complications are absent, it is simply not true that A strictly increases with a decreasing ratio of inter- to intraspecific competition. We illustrate this using an example in Appendix S8. We consider three species evenly spaced along a trait axis, with trait difference δ between adjacent species, and competition strictly decreasing with increasing trait difference. We set the intrinsic growth rates so that there are no competitive advantages: $f_1 = f_2 = f_3 = 0$. Because there are no advantages, and intraspecific competition is greater than interspecific competition for every species, one might think species should be guaranteed to coexist. However, this is not the case; rather, every species has a negative invasion growth rate (Figure 3), precluding coexistence. This occurs because the middle species can outcompete either of the other two by itself (and thus keep both invaders out), but cannot invade a community where species 1 and 3 are already established, due to too much competition from each. As a result, these simple competitive interactions can create a priority effect, leading to a negative A, over some range of trait differences (Figure 3).

The claim that reducing the ratio of inter- to intraspecific competition acts to increase A is based on an intuitively appealing but ultimately invalid generalization of a two-species result to the case of arbitrarily many species. Simply, in a multispecies community, any direct competitive effects are part of a larger web of interactions. As such, indirect effects can lead to a non-monotonic relationship between interspecific competition and A. Thus, the claim that species coexist when intraspecific competition is stronger than interspecific competition is only true when the entire web of interactions is taken into account. When it is not, then factors reducing a_{jk} relative to a_{jj} may act to decrease A instead of increasing it, hindering coexistence.

6.3 Stabilization and competitive advantages are summary statistics

In the end, stabilization and competitive advantages are no more and no less than what their definitions say: the mean scaled invasion growth rate, and departures from this mean (Eqs. 48 and 52). They do not possess any default biological meaning and, despite their evocative names, are not directly connected to any particular biological process or mechanism. It is important not to fall foul of a reification process—whereby the name given to a concept becomes the basis for its interpretation, instead of its actual definition. The terms "stabilization" and "competitive advantages" (not to mention the original "average fitness differences") might be so suggestive as to seem to lend meaning to A and f_i beyond what they actually measure. This can obscure the fact that A and the f_i actually contain exactly as much information as the invasion rates.

Stabilization and competitive advantages cannot be measured independently of the invasion rates: the only way to evaluate them is by obtaining the $\bar{r}_i/\phi_i$ first and then applying Eqs. 48 and 52. The epistemological status of A and f_i is therefore very different from that of seemingly similar theoretical concepts. Take the long-term geometric growth rate of a structured population as an example. The growth rate is given by the dominant eigenvalue λ_1 of the population projection matrix, which is a
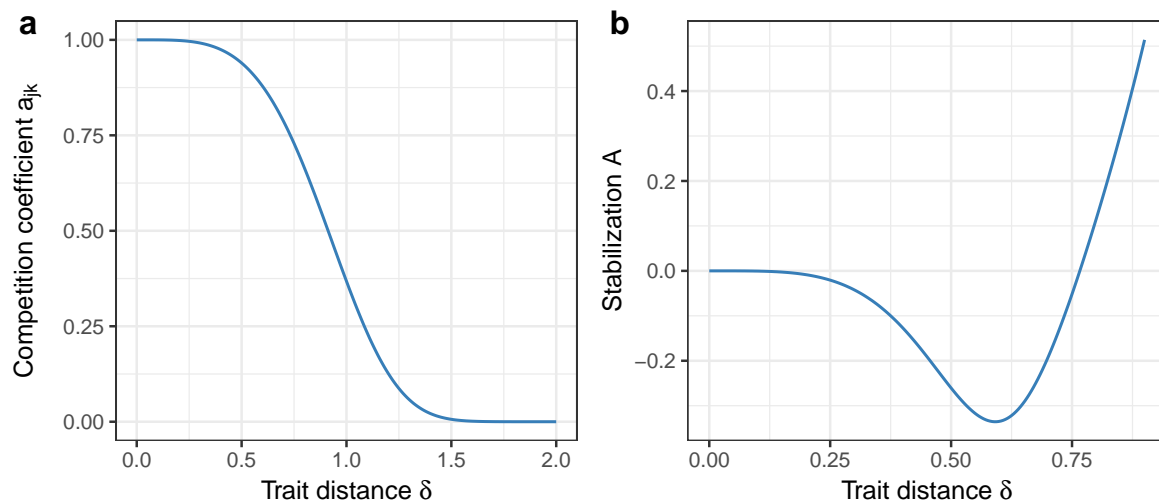
Figure 3: Species might not coexist even if intraspecific competition is stronger than interspecific competition and there are no competitive advantages. Three species are evenly spaced along a one-dimensional trait axis, such that there is a distance δ between species pairs 1-2 and 2-3, and 2δ between 1-3. They compete according to a Lotka-Volterra model with competition coefficients determined by trait distance alone. **a.** The competition coefficients a_{jk}, here given by $\exp(-\delta^4)$, are a decreasing function of the trait distance between species. Intrinsic growth rates are set such that there are no competitive advantages across species (Appendix S8). **b.** Stabilization A as a function of the trait distance δ between adjacent species. When all species are identical, $A = 0$, and species coexist neutrally. However, a small increase in trait distance leads to a decrease instead of an increase in A and competitive exclusion—despite the fact that interspecific competition is always reduced compared to intraspecific competition by increasing δ. For coexistence, positive stabilization is needed, requiring substantial trait differences.

function of the matrix entries. It is therefore a summary statistic (albeit a complicated nonlinear one) of the vital rates. Nevertheless, λ_1 is not *merely* this statistic: it can be measured independently by taking the ratios of the observed number of individuals from one year to the next, at least as long as the population is at its stable stage distribution. The same does not hold for A and f_i. These are purely abstract quantities which, once calculated, cannot be checked against independent evidence: it is not the case that there is some known measurable property of an ecosystem, its "stabilization", which we have discovered to be also obtainable via the statistic A. The statement that "sufficient stabilization to overcome all competitive disadvantages is the key to coexistence" would only express a deep truth if A and f_i would possess an existence independent of $\bar{r}_i/\phi_i = f_i + A$. Since they do not, the above statement says no more and no less than that "the key to coexistence is that all invasion growth rates are positive".

Stabilization and competitive advantages do, of course, have theoretical utility. When properly applied, they may help gain intuition about coexistence that would otherwise not be easily available. For example, in a recent study, Stump and Chesson (2017) split the impact of a competition-predation tradeoff into its stabilizing and competitive advantage components. They showed that this tradeoff mainly affects the f_i, and therefore the winner of competition, rather than creating advantages to being rare.

As summary statistics about invasion growth rates, stabilization and competitive advantages also have obvious empirical value, similar to how a country's gross domestic product and Gini coefficient summarize the distribution of wealth in the population. They could thus be used to make comparisons

across different communities, for instance by comparing their A values. We would argue, however, that since A and the f_i are summary statistics rather than fundamental properties, other summary statistics may often be more useful for describing a system. For example, the classification scheme mentioned at the beginning of Section 6.2 could categorize communities without loss of information using the invasion rates themselves, as follows: robust (all $\bar{r}_i$ are large), dynamic (some $\bar{r}_i$ are large, some are small), unstable (some $\bar{r}_i$ are negative), or quasi-neutral (all $\bar{r}_i$ are near zero). Similarly, for conservation problems, knowing the invasion growth rate of the rarest species may be more important than knowing the average across the community. Additionally, it may be more meaningful to ask how some model parameter change is expected to alter the relationship between A and f_i, and whether that would promote coexistence or not.

7   Conclusions

Chesson's coexistence theory has made many fundamental contributions to community ecology, perhaps most importantly, clarifying how spatiotemporal fluctuations can work to maintain diversity. However, it is not without its shortcomings. The theory applies supremely well when there is only a single limiting factor, and quite well even for multiple factors, as long as their number is smaller than the number of species. However, it does not offer any advantages, and may even work worse than other methods, if there are as many or more limiting factors as species. More critically, it is unable to analyze communities with complex dynamics. As such, it may not apply in species-rich communities unless strong simplifying assumptions are made, such as diffuse competition. It is possible that some of these limitations are not fundamental to the theory, and may be amended by future work. However, this can only proceed if, instead of thinking that Chesson's theory has "solved the problem of coexistence", we treat this body of work as a springboard for tackling the outstanding problems.

One of our goals with this review was to clearly show which parts of the theory can and cannot (currently) hold weight. The dominant way of looking at coexistence in the 1960s and 1970s rested on the foundation built to a large extent by Hutchinson, Levins, and MacArthur (Hutchinson 1957, 1959, 1978, MacArthur and Levins 1967, Levins 1968, MacArthur 1970). It subsequently underwent a backlash, where many questioned whether the theory could live up to the high expectations at the time, and some suggested that the whole approach was fundamentally flawed (Lewin 1983). However, as Peter Chesson himself argued somewhat later, "...failings [of classical coexistence theory] have more to do with overly ambitious expectations from distorted versions of the theory, than with any fundamental error in the theory itself" (Chesson 1990). The current expectations of Chesson's theory are very ambitious; for it to fulfill its potential and avoid undergoing a similar backlash in the future, it is important that distorted versions of the theory are not used to support incorrect claims. Our hope is that this review helps ecologists by making the theory more transparent and approachable, and sheds light on how the theory should and should not be used.

Appendix S1   Mathematical toolbox

Here we summarize the three basic mathematical tools Chesson's coexistence theory heavily relies on, in order of appearance when developing the theory in Section 2.

1. Second-order Taylor expansions of functions of multiple variables $X_1, X_2, \ldots, X_S$ (Otto and Day 2007, pp. 100-106, 303-305). Given some fixed values $X_1^*, X_2^*, \ldots, X_S^*$, a twice continuously differentiable function $f(X_1, X_2, \ldots, X_S)$ can be expanded around these to second order with the formula

$$f(X_1, X_2, \ldots, X_S) \approx f(X_1^*, X_2^*, \ldots, X_S^*) + \sum_{i=1}^{S} \frac{\partial f}{\partial X_i}(X_i - X_i^*) + \frac{1}{2}\sum_{i=1}^{S}\sum_{j=1}^{S} \frac{\partial^2 f}{\partial X_i \partial X_j}(X_i - X_i^*)(X_j - X_j^*),$$
(S1.1)

where the partial derivatives are evaluated at $X_i = X_i^*$. In general, the approximation is better the closer the X_i are to the X_i^*.

2. Nonlinear averaging, which revolves mostly around simple identities concerning the means of products and covariances (Rice 2007, pp. 138-140). The two most important identities are that, for variable quantities X and Y,

$$\overline{XY} = \overline{X}\,\overline{Y} + \mathrm{cov}(X,Y),$$
(S1.2)

$$\mathrm{cov}(aX + c, bY + d) = ab\,\mathrm{cov}(X,Y),$$
(S1.3)

where the overbar denotes averaging, $\mathrm{cov}(X,Y)$ is the covariance between X and Y, and a, b, c, and d are constants.

3. Linear combinations and linear dependence, used in determining the scaling factors when summing resident and invader growth rates (Otto and Day 2007, pp. 228-230). Consider a set of vectors $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_S$. Let us assume that each vector has L components; v_{jk} is the kth component of the jth vector. A *linear combination* of vectors is any sum $a_1\mathbf{v}_1 + a_2\mathbf{v}_2 + \cdots + a_S\mathbf{v}_S$ (compactly written $\sum_{j=1}^{S} a_j\mathbf{v}_j$), where the a_j are constant numbers. *Linear dependence* of a set of S vectors $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_S$ revolves around the question of what values of the constants a_j will lead to the linear combination of the vectors being zero:

$$\sum_{j=1}^{S} a_j\mathbf{v}_j = 0.$$
(S1.4)

The set of vectors is *linearly independent* if the only way to uphold this equation is for all a_j to be zero; otherwise the set is *linearly dependent*. A linear combination with all $a_j = 0$ is called *trivial*; therefore, a set of vectors is linearly dependent if there exists a nontrivial linear combination satisfying Eq. S1.4.

The meaning of linear dependence is that some of the vectors from the set can be expressed using the others (as a linear combination). In that sense, those vectors are superfluous because they could be eliminated without losing the ability to use them. Indeed, assuming one of the constants a_i is nonzero, Eq. S1.4 can be rearranged:

$$a_i\mathbf{v}_i + \sum_{j \neq i}^{S} a_j\mathbf{v}_j = 0 \qquad \Rightarrow \qquad \mathbf{v}_i = -\frac{1}{a_i}\sum_{j \neq i}^{S} a_j\mathbf{v}_j,$$
(S1.5)

showing that $\mathbf{v}_i$ is not actually necessary to keep in the original set of S vectors, since it can be expressed via the others.

A simple but important result is that if there are more vectors than the number of components in each vector (i.e., $S > L$), then the set $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_S$ is necessarily linearly dependent. Intuitively,

this means that there are no more than two independent directions in a plane; no more than three in physical space; and so on. For instance, any vector in a plane can be expressed as a linear combination of $\mathbf{v}_1 = (1, 0)$ and $\mathbf{v}_2 = (0, 1)$. Adding a third vector, say $\mathbf{v}_3 = (2, -1)$, will make the set linearly dependent, since $\mathbf{v}_3 = 2\mathbf{v}_1 - \mathbf{v}_2$; or, equivalently, $2\mathbf{v}_1 - \mathbf{v}_2 - \mathbf{v}_3 = 0$.

To actually obtain the a_j which satisfy Eq. S1.4, notice that this equation is a system of L linear equations: written in components, $\sum_{j=1}^{S} a_j v_{jk} = 0$, which is a separate equation for each $k = 1, 2, \ldots, L$. Solving this system yields the a_j. Note that for $S > L$, there are fewer equations than unknowns—which means that the solution will not be unique.

Appendix S2   Quadratic expansion of a model with a single limiting factor

Consider a group of predator species preying on a resource with a type II functional response. The per capita growth rates are

$$r_j = \frac{a_j F}{1 + a_j h_j F} - m_j, \tag{S2.1}$$

where F is prey density, a_j the attack rate, h_j the handling time, and m_j the mortality of predator j. We assume that a_j, h_j, and m_j are constant.

To perform a quadratic expansion of the model, we first designate the environmental and interaction parameters. The choice is not unique, but one natural set of parameters is $E_j = -m_j$ and $C_j = a_j F/(1 + a_j h_j F)$. Here C_j is a function of the single limiting factor F. Designating $E_j^* = -m_j$ (the "average" of the constant $E_j = -m_j$), it follows that, to achieve $r_j(E_j^*, C_j^*) = 0$, we must have $C_j^* = m_j$.

With the help of the environmental and interaction parameters, the per capita growth rates may now be cast as $r_j = E_j + C_j$. From this, we calculate the Taylor coefficients of Eq. 3:

$$\alpha_j = \frac{\partial r_j}{\partial E_j} = 1, \ \ \alpha_j^{(2)} = \frac{\partial^2 r_j}{\partial E_j^2} = 0, \ \ \beta_j = \frac{\partial r_j}{\partial C_j} = 1, \ \ \beta_j^{(2)} = \frac{\partial^2 r_j}{\partial C_j^2} = 0, \ \ \zeta_j = \frac{\partial^2 r_j}{\partial E_j \partial C_j} = 0. \tag{S2.2}$$

The standardized parameters, from Eqs. 4 and 5, then evaluate to

$$\mathscr{E}_j = \alpha_j(E_j - E_j^*) + \frac{1}{2}\alpha_j^{(2)}(E_j - E_j^*)^2 = 1 \times (-m_j + m_j) + 0 = 0, \tag{S2.3}$$

$$\mathscr{C}_j = \beta_j(C_j - C_j^*) + \frac{1}{2}\beta_j^{(2)}(C_j - C_j^*)^2 = 1 \times \left(\frac{a_j F}{1 + a_j h_j F} - m_j\right) + 0 = \frac{a_j F}{1 + a_j h_j F} - m_j. \tag{S2.4}$$

Since there is only a single limiting factor F, one can find its "equilibrial" value by solving Eq. 8 for F^{*j}. For a single factor, this equation reads $C_j(F^{*j}) = C_j^*$, or

$$\frac{a_j F^{*j}}{1 + a_j h_j F^{*j}} = m_j, \tag{S2.5}$$

whose solution is $F^{*j} = (m_j/a_j)/(1 - h_j m_j)$.

We now use Eq. 10 to calculate the coefficients of the quadratic expansion:

$$\phi_j = \frac{\partial \mathscr{C}_j}{\partial F}\bigg|_{F=F^{*j}} = \frac{\partial}{\partial F}\left(\frac{a_j F}{1 + a_j h_j F} - m_j\right)\bigg|_{F=F^{*j}} = \frac{a_j}{(1 + a_j h_j F^{*j})^2} = a_j(1 - h_j m_j)^2, \tag{S2.6}$$

$$\psi_j = \left.\frac{\partial^2 \mathscr{C}_j}{\partial F^2}\right|_{F=F^{*j}} = \left.\frac{\partial^2}{\partial F^2}\left(\frac{a_j F}{1+a_j h_j F} - m_j\right)\right|_{F=F^{*j}} = \frac{-2a_j^2 h_j}{(1+a_j h_j F^{*j})^3} = -2a_j^2 h_j (1-h_j m_j)^3.$$

(S2.7)

Substituting these into Eq. 9, the full quadratic expansion reads

$$\mathscr{C}_j \approx \underbrace{a_j(1-h_j m_j)^2}_{\phi_j}\left(F - \underbrace{\frac{m_j}{a_j(1-h_j m_j)}}_{F^{*j}}\right) + \frac{1}{2}\underbrace{\left(-2a_j^2 h_j(1-h_j m_j)^3\right)}_{\psi_j}\left(F - \underbrace{\frac{m_j}{a_j(1-h_j m_j)}}_{F^{*j}}\right)^2,$$

(S2.8)

and since here we happen to have $r_j = \mathscr{C}_j$, the same expansion holds for the model Eq. S2.1 as a whole.

Appendix S3   Relative nonlinearity: a simple example

One of the simplest examples of a model producing relative nonlinearity is when two species consume a single limiting resource F with nonlinear functional responses. The per capita growth rates are given by

$$r_j = \frac{a_j F}{1+a_j h_j F} - m_j \qquad (j=1,2),$$

(S3.1)

where a_j is the attack rate, h_j the handling time, and m_j the mortality of consumer j.

    The quadratic expansion of this model was already performed in Appendix S2 with the choices $E_j = -m_j$, $C_j = a_j F/(1+a_j h_j F)$, and $E_j^* = -C_j^* = -m_j$. We got $\mathscr{E}_j = 0$ and

$$\mathscr{C}_j \approx \phi_j(F - F^{*j}) + \frac{1}{2}\psi_j(F - F^{*j})^2$$

(S3.2)

with $F^{*j} = (m_j/a_j)/(1-h_j m_j)$, $\phi_j = a_j(1-h_j m_j)^2$, and $\psi_j = -2a_j^2 h_j(1-h_j m_j)^3$. Writing the long-term growth rate of species j assuming species i is invading, we now explicitly note the invader-dependence of quantities using the superscript "$-i$":

$$\bar{r}_j^{-i} \approx \phi_j\overline{(F^{-i} - F^{*j})} + \frac{1}{2}\psi_j\overline{(F^{-i} - F^{*j})^2}.$$

(S3.3)

The scaling factors can be chosen using Eq. 22: $d_i = 1/\phi_i = (a_i(1-h_i m_i)^2)^{-1}$ and $d_s = -1/\phi_s = -(a_s(1-h_s m_s)^2)^{-1}$. Using the notation $V_j^{-i} = \overline{(F^{-i} - F^{*j})^2}$, the sum of the scaled invader and resident growth rates reads

$$\bar{r}_i^{-i} = \frac{1}{d_i}\left(d_i\bar{r}_i^{-i} + d_s\bar{r}_s^{-i}\right) = \phi_i\left(\overline{F^{-i}} - F^{*i} + \frac{1}{2}\frac{\psi_i}{\phi_i}V_i^{-i} - \overline{F^{-i}} + F^{*s} - \frac{1}{2}\frac{\psi_s}{\phi_s}V_s^{-i}\right)$$

$$= \phi_i(F^{*s} - F^{*i}) + \frac{\phi_i}{2}\left(\frac{\psi_i}{\phi_i}V_i^{-i} - \frac{\psi_s}{\phi_s}V_s^{-i}\right) = \underbrace{a_i(1-h_i m_i)^2\left(\frac{m_s}{a_s(1-h_s m_s)} - \frac{m_i}{a_i(1-h_i m_i)}\right)}_{r_i'}$$

(S3.4)

$$+ \underbrace{\frac{a_i(1-h_i m_i)^2}{2}\left(2a_s h_s(1-h_s m_s)V_s^{-i} - 2a_i h_i(1-h_i m_i)V_i^{-i}\right)}_{\Delta N_i},$$

where the terms r_i' and ΔN_i above have been identified using Eq. 19. Under the simplifying assumption $V_s^{-i} = V_i^{-i}$ (so we can drop the subscript and write V^{-i}), this becomes

$$\frac{\bar{r}_i^{-i}}{a_i(1 - h_i m_i)^2} = \left(\frac{m_s}{a_s(1 - h_s m_s)} - \frac{m_i}{a_i(1 - h_i m_i)} \right) + V^{-i}(a_s h_s(1 - h_s m_s) - a_i h_i(1 - h_i m_i)). \quad \text{(S3.5)}$$

If V^{-i} did not depend on the identity of the invading species, then ΔN_i would be positive for one species but negative for the other, precluding coexistence. However, V^{-i} is a function of who is resident. Thus, it is possible that ΔN_i is greater for one species than the other. To see this, imagine an example where $V^{-1} = 0$. In this case, the requirement for coexistence via relative nonlinearity is simply that $r_1' > 0$ (i.e., species 1 is the better equilibrium competitor), and that V^{-2} is sufficiently large to make $\Delta N_2 > |r_2'|$, allowing species 2 to overcome its equilibrium disadvantage by making use of fluctuations in F.

Appendix S4   The storage effect: a simple example

Let us consider here a very simple modification to Eq. 25:

$$r_j = b_j F - m_j, \quad \text{(S4.1)}$$

where b_j is the amount of growth species j gains from a unit resource, m_j is species j's mortality rate, and F is a limiting resource. This model looks identical to Eq. 25 in Section 2.5, but we make the extra assumption that, apart from F, the b_j are also time-dependent. This turns out to make all the difference in model outcome (Chesson and Huntly 1997, Fox 2013, Miller and Klausmeier 2017).

As usual, assigning environmental and interaction parameters can be done in various ways. Here we pick $E_j = b_j$ and $C_j = F$, and choose $E_j^* = \bar{b}_j$. It then follows that $C_j^* = F^{*j} = m_j/\bar{b}_j$, since $r_j(E_j^*, C_j^*) = \bar{b}_j(m_j/\bar{b}_j) - m_j = 0$. The Taylor coefficients from Eq. 3 evaluate to

$$\alpha_j = \frac{\partial r_j}{\partial E_j} = \frac{m_j}{\bar{b}_j}, \ \ \alpha_j^{(2)} = \frac{\partial^2 r_j}{\partial E_j^2} = 0, \ \ \beta_j = \frac{\partial r_j}{\partial C_j} = \bar{b}_j, \ \ \beta_j^{(2)} = \frac{\partial^2 r_j}{\partial C_j^2} = 0, \ \ \zeta_j = \frac{\partial^2 r_j}{\partial E_j \partial C_j} = 1. \quad \text{(S4.2)}$$

The per capita growth rates can now be written in the form of Eq. 2: $r_j = (m_j/\bar{b}_j)(E_j - E_j^*) + \bar{b}_j(C_j - C_j^*) + (E_j - E_j^*)(C_j - C_j^*)$; moreover, this expression directly evaluates to $b_j F - m_j$, i.e., the quadratic approximation of the model in this case is exact. The standardized parameters, from Eqs. 4 and 5, are $\mathscr{E}_j = (m_j/\bar{b}_j)(b_j - \bar{b}_j)$ and $\mathscr{C}_j = \bar{b}_j(F - m_j/\bar{b}_j)$. The parameter $\gamma_j = \zeta_j/(\alpha_j \beta_j)$ evaluates to $1/m_j$. Writing the model in the standard form of Eq. 7, we have $r_j = \mathscr{E}_j + \mathscr{C}_j + \mathscr{E}_j \mathscr{C}_j/m_j$, still evaluating to $b_j F - m_j$ exactly.

Taking the time average using Eq. 12:

$$\bar{r}_j = \overline{\mathscr{E}}_j + \overline{\mathscr{C}}_j + \text{cov}(\mathscr{E}_j, \mathscr{C}_j)/m_j = \bar{b}_j\bar{F} - m_j + \text{cov}\big((m_j/\bar{b}_j)(b_j - \bar{b}_j), \bar{b}_j(F - m_j/\bar{b}_j)\big)/m_j. \quad \text{(S4.3)}$$

Simplifying the covariance term using Eq. S1.3, we get

$$\bar{r}_j = \bar{b}_j\bar{F} - m_j + \text{cov}(b_j, F). \quad \text{(S4.4)}$$

We can now sum the weighted resident and invader growth rates, choosing $d_i = 1/\overline{b}_i$ and $d_s = -1/\overline{b}_s$:

$$
\begin{aligned}
\overline{r}_i = \frac{1}{d_i}(d_i\overline{r}_i + d_s\overline{r}_s) &= \overline{b}_i\left(\overline{F} - \frac{m_i}{\overline{b}_i} + \frac{1}{\overline{b}_i}\text{cov}(b_i, F) - \overline{F} + \frac{m_s}{\overline{b}_s} - \frac{1}{\overline{b}_s}\text{cov}(b_s, F)\right) \\
&= \underbrace{\overline{b}_i\left(\frac{m_s}{\overline{b}_s} - \frac{m_i}{\overline{b}_i}\right)}_{r_i'} + \underbrace{\overline{b}_i\left(\frac{1}{\overline{b}_i}\text{cov}(b_i, F) - \frac{1}{\overline{b}_s}\text{cov}(b_s, F)\right)}_{\Delta I_i}.
\end{aligned}
\tag{S4.5}
$$

This expression cannot be evaluated without knowing the covariance structure of the b_j with F when species i invades. Conceptually however, it still reveals a lot about when coexistence is promoted by temporal fluctuations. One assumption that simplifies analysis is that F^{-i} is some function of the environmental parameter $E_s = b_s$ of the resident; i.e., we have $F^{-i} = F^{-i}(b_s)$. (Since species i is in the invader state, it cannot influence F, so species s is driving its fluctuations.) Then, Taylor expanding F to linear order when species i is invading, we get

$$
F^{-i} \approx F^{*i} - \eta_s(b_s - \overline{b}_s),
\tag{S4.6}
$$

where $\eta_s = -\partial F/\partial b_s$ is evaluated at $b_s = \overline{b}_s$. It measures the force with which F is being driven by the resident species s. The derivative $\partial F/\partial b_s$ will typically be a negative function of b_s, since resources will be more depleted when the resident is better able to take them up. Hence, our sign convention makes η_s positive. Using Eq. S4.6, $\text{cov}(b_j, F) \approx \text{cov}(b_j, F^{*i} - \eta_s b_s + \eta_s \overline{b}_s) = -\eta_s \text{cov}(b_j, b_s)$, where we used Eq. S1.3 in the last step.

The problem is now determining the covariance structure of the b_j's. This could be measured empirically, but here instead we use the simple working assumption that $\text{cov}(b_j, b_s) = \sigma^2$ when $j = s$ and $\tau\sigma^2$ when $j \neq s$ (e.g., Chesson 1994, Stump and Chesson 2015). Here σ^2 is the variance of the b_j's, assumed to be the same for each species; and τ is a common correlation coefficient, also assumed to be the same between any nonidentical pair of species. With these assumptions, Eq. S4.5 simplifies to

$$
\overline{r}_i = \overline{b}_i\left(\frac{m_s}{\overline{b}_s} - \frac{m_i}{\overline{b}_i}\right) + \overline{b}_i\eta_s\sigma^2\left(\frac{1}{\overline{b}_s} - \frac{1}{\overline{b}_i}\tau\right).
\tag{S4.7}
$$

It is possible that the second term could harm one species. However, it could in fact be positive for both when invading. This can be seen clearly in the special case $\eta_i = \eta_s = \eta$, $\overline{b}_i = \overline{b}_s$, and $\tau = 0$:

$$
\overline{r}_i = (m_s - m_i) + \eta\sigma^2,
\tag{S4.8}
$$

and so if $\eta\sigma^2$ is larger than $|m_s - m_i|$, we have coexistence via the storage effect.

Appendix S5   The growth-density covariance: a simple example

We consider the simple linear resource consumption model of Section 2.5 with the twist that now there are two habitat patches, and the same resource is independently available in both. Denoting the density of species j in patch x by $n_j(x)$, their rate of change is governed by

$$
\frac{dn_j(x)}{dt} = b_j F(x) n_j(x) - m_j n_j(x) + D_j(x, y) n_j(y) - D_j(y, x) n_j(x).
\tag{S5.1}
$$

Here b_j and m_j are the patch- and time-independent resource uptake and mortality rates of species j, $F(x)$ is the available resource in patch x, and $D_j(x,y)$ is the rate of migration of species j from patch y to patch x. From this equation, the effective per capita growth rates in patch x are obtained by dividing the equation with $n_j(x)$ (Eq. 1):

$$r_j(x) = \frac{1}{n_j(x)} \frac{dn_j(x)}{dt} = b_j F(x) - m_j + \left(D_j(x,y) \frac{n_j(y)}{n_j(x)} - D_j(y,x) \right). \tag{S5.2}$$

The immigration and emigration terms have been parenthesized, since those cancel after spatial averaging (Section 2.6).

The environmental and interaction parameters can be chosen analogously to Section 2.5: $E_j(x) = -m_j$ (with no actual spatial dependence since m_j is assumed to be equal across the two patches), and $C_j(x) = b_j F(x)$. With these choices, $r_j(x) = E_j(x) + C_j(x)$. We can choose E_j^* as the spatial "average" of $E_j(x)$; here this is simply $E_j^* = -m_j$. It then follows that $C_j^* = m_j$, because this leads to $r_j(E_j^*, C_j^*) = E_j^* + C_j^* = 0$. F^{*j} is determined from the condition $C_j(F^{*j}) = C_j^*$ (Eq. 8), resulting in $F^{*j} = m_j/b_j$. Since $r_j(x) = E_j(x) + C_j(x)$, the Taylor coefficients from Eq. 3 will be

$$\alpha_j = \frac{\partial r_j}{\partial E_j(x)} = 1, \; \alpha_j^{(2)} = \frac{\partial^2 r_j}{\partial E_j^2(x)} = 0, \; \beta_j = \frac{\partial r_j}{\partial C_j(x)} = 1, \; \beta_j^{(2)} = \frac{\partial^2 r_j}{\partial C_j^2(x)} = 0,$$

$$\zeta_j = \frac{\partial^2 r_j}{\partial E_j(x) \partial C_j(x)} = 0, \tag{S5.3}$$

all evaluated at $E_j(x) = E_j^*$ and $C_j(x) = C_j^*$. Using these and Eqs. 4 and 5, the standardized environmental and interaction parameters are $\mathscr{E}_j(x) = 0$ and $\mathscr{C}_j(x) = b_j F(x) - m_j$. Or, writing $\mathscr{C}_j(x)$ in the form of Eq. 9, $\mathscr{C}_j(x) = \phi_j(F(x) - F^{*j})$, where $\phi_j = b_j$. Eq. S5.2 may therefore be written as $r_j(x) = \mathscr{C}_j(x)$ plus immigration minus emigration.

Applying Eq. 44 to this per capita growth rate, we can immediately write

$$\overline{r_j(x)} = \overline{\mathscr{C}_j(x)} + \text{cov}(v_j(x), r_j(x))$$
$$= b_j \overline{F(x)} - m_j + \text{cov}(v_j(x), r_j(x)), \tag{S5.4}$$

where we have spatial averages and covariances, and

$$v_j(x) = \frac{n_j(x)}{\frac{1}{2}(n_j(x) + n_j(y))} \tag{S5.5}$$

is the relative density of species j in patch x (Section 2.6). Putting species i in the invader state, we can write

$$\overline{r_j^{-i}(x)} = b_j \overline{F^{-i}(x)} - m_j + \text{cov}\left(v_j^{-i}(x), r_j^{-i}(x) \right). \tag{S5.6}$$

Applying Eq. 21 to find the scaling factors leads to the equation $d_i \phi_i + d_s \phi_s = 0$, where we assume species i is the invader and s is the resident. The choice $d_i = 1/\phi_i = 1/b_i$, $d_s = -1/\phi_s = -1/b_s$ satisfies this equation. We can now compare invader and resident growth rates using Eq. 17:

$$\overline{r_i(x)} = \frac{1}{d_i}\left(d_i \overline{r_i(x)} + d_s \overline{r_s(x)} \right) = b_i \left(\frac{\overline{r_i(x)}}{b_i} - \frac{\overline{r_s(x)}}{b_s} \right)$$

$$= \underbrace{b_i \left(\frac{m_s}{b_s} - \frac{m_i}{b_i} \right)}_{r_i'} + \underbrace{b_i \left(\frac{1}{b_i} \text{cov}(v_i(x), r_i(x)) - \frac{1}{b_s} \text{cov}(v_s(x), r_s(x)) \right)}_{\Delta \kappa_i}, \tag{S5.7}$$

where we dropped the "$-i$" superscripts for convenience. This is as far as one can go without specifying the detailed dynamics of $F(x)$, without which one cannot obtain $n_j(x)$ and $r_j(x)$ to explicitly evaluate the covariance terms. But even without doing so, one can gain qualitative insight into what conditions would lead to the $\Delta\kappa_i$ term promoting coexistence.

If the species do not differentiate between the two habitat patches, then the resident will grow in density as much as it can in each patch. This means that $r_s(x)$ will be zero for both patches x, and so $\text{cov}(v_s(x), r_s(x)) = \overline{v_s(x)r_s(x)} - \overline{v_s(x)}\ \overline{r_s(x)} = 0$. In turn, the invader also does not differentiate between the patches; therefore, although its growth rate is not zero, it will grow equally well in both patches and so $\text{cov}(v_s(x), r_s(x))$ will again be zero. This leads to $\Delta\kappa_i = 0$ in Eq. S5.7 for both species as invaders, so only the r_i' term remains. This will be positive for the species with the lower m_j/b_j value and negative for the other. Coexistence is therefore precluded. In essence, the above assumptions describe what happens when the two patches are just an arbitrary subdivision of one single patch.

Now let us assume that species 1 prefers patch 1 and species 2 prefers patch 2, for instance because of visual or olfactory cues which attract them to those locations. We assume that their choice has no influence on their ecological performance though—in other words, only their migration rates are affected but not any of the vital rates. With species s resident, its relative density will be high in patch $s \neq i$. Due to its high abundance there however, its growth rate will be near zero. Conversely, in patch i where its relative density is low, there will be a surplus of unused resources, making its growth rate high. We thus expect $\text{cov}(v_s(x), r_s(x))$ to be negative and therefore help the invader in Eq. S5.7. In turn, $\text{cov}(v_i(x), r_i(x))$ will be positive: the invader's individuals will concentrate in patch i (note that in the covariance term it is the *relative* density that matters, which can be finite even if the invader's density is formally infinitesimally small), which is devoid of species s, resulting in a high local growth rate. And it will be rare in patch s where its growth rate is low since the resident is using most of the resources already. The effect of the two covariance terms is therefore to create a large positive $\Delta\kappa_i$. If this term is larger than r_i' for the disadvantaged species, we will have coexistence via the growth-density covariance.

Finally, note that in the above scenario we deliberately chose a trait unrelated to species performance to generate coexistence. This is because the example was designed to demonstrate how coexistence via pure growth-density covariance can arise. More interesting and/or realistic scenarios would also generate growth-density covariances, for instance if the two patches differed in temperature, and the two species were each adapted to tolerate one of the conditions better—however, this would also introduce a patch-dependence in $b_j(x)$, which in turn leads to a spatial storage effect.

Appendix S6   Stabilization and competitive advantages with two limiting factors

We start from a model of two consumer species competing for two limiting resources F_1 and F_2:

$$r_j = \phi_{j1}F_1 + \phi_{j2}F_2 - m_j \qquad (j = 1, 2), \tag{S6.1}$$

where the ϕ_{jk} are consumption rates and m_j the mortality of species j. Since there are two species and two limiting factors, one cannot eliminate both of them via any choice of the scaling factors d_j. However, we can eliminate one of the factors. Let that factor be F_1. Then, from Eq. 22, $d_i^{-i} = 1/\phi_{i1}$ and $d_s^{-i} = -1/\phi_{s1}$, where $s \neq i$ is the resident species. The long-term growth rates with species i invading

are therefore $r_j^{-i} = \phi_{j1}F_1^{-i} + \phi_{j2}F_2^{-i} - m_j$ (we assume no environmental fluctuations). We partition r_i^{-i} using Eq. 17:

$$r_i = \frac{1}{d_i}(d_i r_i + d_s r_s) = \phi_{i1}\left(\frac{r_i}{\phi_{i1}} - \frac{r_s}{\phi_{s1}}\right) = \phi_{i1}\left(-\frac{m_i}{\phi_{i1}} + \frac{\phi_{i2}}{\phi_{i1}}F_2^{-i} + \frac{m_s}{\phi_{s1}} - \frac{\phi_{s2}}{\phi_{s1}}F_2^{-i}\right), \tag{S6.2}$$

with F_1^{-i} having canceled, as it should. Rearranging, we get

$$\frac{r_i}{\phi_{i1}} = \underbrace{\left(\frac{m_s}{\phi_{s1}} - \frac{m_i}{\phi_{i1}}\right)}_{r_i'} + \underbrace{\left(\frac{\phi_{i2}}{\phi_{i1}} - \frac{\phi_{s2}}{\phi_{s1}}\right)F_2^{-i}}_{\Delta\rho_i}. \tag{S6.3}$$

We can now calculate A from Eq. 48 and the f_i from Eq. 52:

$$A = \frac{1}{2}\left(\frac{r_1}{\phi_{11}} + \frac{r_2}{\phi_{21}}\right) = \frac{1}{2}\left(\frac{\phi_{12}}{\phi_{11}} - \frac{\phi_{22}}{\phi_{21}}\right)(F_2^{-1} - F_2^{-2}), \tag{S6.4}$$

$$f_1 = \frac{r_1}{\phi_{11}} - A = \left(\frac{m_2}{\phi_{21}} - \frac{m_1}{\phi_{11}}\right) + \frac{1}{2}\left(\frac{\phi_{12}}{\phi_{11}} - \frac{\phi_{22}}{\phi_{21}}\right)(F_2^{-1} + F_2^{-2}), \tag{S6.5}$$

and $f_2 = -f_1$ since the sum of the f_i is always zero. To proceed, let us designate numerical values for the parameters:

$$m_j = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \qquad \phi_{jk} = \begin{pmatrix} 1 & 1/10 \\ 1/10 & 1 \end{pmatrix}, \qquad F_2^{-j} = \begin{pmatrix} 1/2 \\ 1 \end{pmatrix}, \tag{S6.6}$$

(the last one means that resource F_2 is $1/2$ when the first species is an invader, and 1 when the second). The matrix ϕ_{jk} implies species 1 is a specialist on resource 1 and species 2 on resource 2. Substituting these numbers into the expressions for A and f_i, we find $A = 2.475$ and $f_1 = -f_2 = 1.575$. Since $r_i/\phi_{i1} = f_i + A$ is greater than zero for both species as invaders, we have coexistence. Without the stabilization term A however, species 1 outcompetes species 2.

Suppose now that we do the exact same, but with treating F_2 as the baseline limiting factor instead. An analogous calculation then yields

$$A = \frac{1}{2}\left(\frac{\phi_{11}}{\phi_{12}} - \frac{\phi_{21}}{\phi_{22}}\right)(F_1^{-1} - F_1^{-2}), \tag{S6.7}$$

$$f_1 = \left(\frac{m_2}{\phi_{22}} - \frac{m_1}{\phi_{12}}\right) + \frac{1}{2}\left(\frac{\phi_{11}}{\phi_{12}} - \frac{\phi_{21}}{\phi_{22}}\right)(F_1^{-1} + F_1^{-2}) = -f_2, \tag{S6.8}$$

and after assigning $F_1^{-1} = 1$, $F_1^{-2} = 1/2$, we now get $f_2 = -f_1 = 1.575$, with $A = 2.475$ and both $r_i/\phi_{i1} = f_i + A$ positive. That is, now species 2 is the one outcompeting species 1 in the absence of the stabilization term A.

The difference in interpretation simply reflects the change in perspective when altering which limiting factor serves as the baseline. In the first scenario, resource 1 is the baseline, so stabilization is provided by resource 2. This can be seen from the expression for A: Eq. S6.4 is proportional to the difference of monoculture equilibrium levels of F_2 and does not depend on F_1 at all. In the second scenario, it is the other way round: resource 2 is the baseline and 1 provides stabilization, and species 2 is the better competitor for the baseline. Naturally, since the two descriptions refer to the one and same coexistence scenario, the final results for the invasion growth rates must be identical, regardless of how they are calculated.

Appendix S7   "Small stabilization required" does not translate to "small trait difference required"

Consider two species which are identical to one another except in a single quantitative trait. We make the following assumptions:

1. There is a long-term equilibrium state on which the system eventually settles.

2. Species only differ by a small amount δ in the quantitative trait of interest.

3. All species interactions depend only on the difference δ between traits, not on the individual trait values themselves.

4. The strength of interaction between species is a decreasing function of trait difference: more similar species interact more strongly. This decreasing function must be smooth to be biologically realistic (Adler and Mosquera 2000, D'Andrea et al. 2013, Barabás et al. 2013a), which we will assume here.

Otherwise, the dynamics may depend on the traits and densities n_j in an arbitrary way. Near the assumed equilibrium densities n_1^* and n_2^*, the per capita growth rates may be linearized:

$$r_j(n_1, n_2) \approx \underbrace{r_j(n_1^*, n_2^*)}_{0} + \sum_{k=1}^{2} \left. \frac{\partial r_j}{\partial n_k} \right|_{n_k = n_k^*} (n_k - n_k^*). \tag{S7.1}$$

Denoting the partial derivatives evaluated at the equilibrium by $-a_{jk}$, we have

$$r_j(n_1, n_2) \approx \underbrace{\sum_{k=1}^{2} a_{jk} n_k^*}_{b_j} - \sum_{k=1}^{2} a_{jk} n_k = b_j - \sum_{k=1}^{2} a_{jk} n_k, \tag{S7.2}$$

recovering the two-species Lotka–Volterra model with effective intrinsic growth rates b_j and interaction coefficients a_{jk}.

By the 3rd assumption, $a_{11} = a_{22}$ and $a_{12} = a_{21}$. Without loss of generality (e.g., by rescaling units), we can assume $a_{11} = a_{22} = 1$. By the 4th assumption, we then have $a_{12} = a_{21} = \alpha < 1$. We therefore write the model parameters as

$$b_j = \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}, \qquad a_{jk} = \begin{pmatrix} 1 & \alpha \\ \alpha & 1 \end{pmatrix}. \tag{S7.3}$$

With these parameters, when species i is invading, the equilibrium abundance of species $s \neq i$ is simply $n_s^{*-i} = b_s$. The invasion growth rate of species i is therefore $r_i = b_i - \alpha b_s$. The limiting factors in this model may be chosen to be the population densities n_1 and n_2 themselves (Chesson 1994). To decompose the scaled invasion growth rates as $r_i/\phi_i = f_i + A$, we first need to designate a baseline limiting factor. Here we choose this to be n_1 (but due to the symmetry of the matrix a_{ij}, the same result would be obtained by choosing n_2). The vector ϕ_j is now equal to a_{j1}; that is, $\phi_1 = 1$ and $\phi_2 = \alpha$. Using the invasion rates $r_i = b_i - \alpha b_s$, we first evaluate the stabilization term A from Eq. 48:

$$A = \frac{1}{2}\left(\frac{r_1}{\phi_1} + \frac{r_2}{\phi_2} \right) = \frac{1}{2}\left(r_1 + \frac{r_2}{\alpha} \right) = \frac{1}{2}\left(b_1 - \alpha b_2 + \frac{b_2 - \alpha b_1}{\alpha} \right) = \frac{1}{2}\left(\frac{1}{\alpha} - \alpha \right) b_2. \tag{S7.4}$$

In turn, we obtain the competitive advantage terms f_i from Eq. 52:

$$f_1 = \frac{r_1}{\phi_1} - A = b_1 - \alpha b_2 - A = b_1 - \alpha b_2 - \frac{1}{2}\left(\frac{1}{\alpha} - \alpha\right)b_2 = b_1 - \frac{1}{2}\left(\frac{1}{\alpha} + \alpha\right)b_2, \qquad (S7.5)$$

and $f_2 = -f_1$ since the sum of the f_i is always zero.

Because the species are very similar by hypothesis, we can approximate b_2 by Taylor expanding its value around b_1 (as a function of the trait): $b_2 \approx b_1 + p\delta$, where $p = \partial b_1 / \partial \delta$ is a Taylor coefficient. The same can be done with α, but there is a crucial difference: the interaction strengths have a maximum at $\delta = 0$ (by our 4th assumption). Therefore, the linear term in δ in the Taylor expansion is zero, and we must expand α to second order. The maximal strength of competition was scaled to 1, therefore $\alpha \approx 1 - q\delta^2$, where $q = -\partial^2\alpha/\partial\delta^2$ (the negative so that $q > 0$). Substituting these approximations into Eqs. S7.4 and S7.5, we get, to leading order,

$$A = \frac{1}{2}\left(\frac{1}{\alpha} - \alpha\right)b_2 \approx \frac{1}{2}\left(\frac{1}{1-q\delta^2} - 1 + q\delta^2\right)(b_1 + p\delta) \approx \frac{1}{2}\left(1 + q\delta^2 - 1 + q\delta^2\right)(b_1 + p\delta)$$
$$= q\delta^2(b_1 + p\delta) = b_1 q\delta^2 + pq\delta^3 \approx b_1 q\delta^2 \qquad (S7.6)$$

and

$$f_1 = -f_2 = b_1 - \frac{1}{2}\left(\frac{1}{\alpha} + \alpha\right)b_2 \approx b_1 - \frac{1}{2}\left(\frac{1}{1-q\delta^2} + 1 - q\delta^2\right)(b_1 + p\delta)$$
$$\approx b_1 - \frac{1}{2}\left(1 + q\delta^2 + 1 - q\delta^2\right)(b_1 + p\delta) = b_1 - (b_1 + p\delta) = -p\delta. \qquad (S7.7)$$

Eq. S7.7 tells us that stabilization must exceed $p\delta$ if both species are to have positive invasion growth rates. Using Eq. S7.6, this imposes a lower limit on the trait difference, $\delta_{\min} \approx p/(b_1 q)$. Notice that this limit occurs despite the fact that competitive advantage differences also decrease as δ decreases. Unfortunately for coexistence, stabilization decreases faster, proportional to δ^2 rather than δ. Therefore, an arbitrarily low stabilization requirement does not translate into an arbitrarily low trait difference requirement. We emphasize that this is not just a particular result from a particular model study: due to the generality of our basic assumptions, this is the expected outcome under most ecological scenarios.

Naturally, if $p = 0$ (meaning $b_1 = b_2$, and hence $f_1 = f_2 = 0$ due to Eq. S7.7), then $\delta_{\min} = 0$. In words, when there are no competitive advantages, then any nonzero trait difference suffices for coexistence. This is of course an exceptional case, as there is no reason for the effective intrinsic rates to be precisely equal. But even this seemingly natural result breaks down when we add another species, as our example in Appendix S8 shows.

Appendix S8   Substantial trait differences may be needed even with zero competitive advantages

Consider a three-species community with the assumptions of Appendix S7, plus the additional assumption that species 2 is exactly halfway between species 1 and 3: the trait distance between 1 and 2 (and 2 and 3) is δ, and the difference between 1 and 3 is 2δ. We then have the three-species effective Lotka–Volterra model

$$r_j = b_j - \sum_{k=1}^{3} a_{jk} n_k \qquad (S8.1)$$

with parameters

$$b_j = \begin{pmatrix} b_1 \\ b_2 \\ b_3 \end{pmatrix}, \qquad a_{jk} = \begin{pmatrix} 1 & \alpha & \beta \\ \alpha & 1 & \alpha \\ \beta & \alpha & 1 \end{pmatrix}, \tag{S8.2}$$

where $\beta < \alpha < 1$. To obtain the invasion growth rates, we first calculate the resident equilibrium abundances by setting the per capita growth rates and the abundance of the invading species in Eq. S8.1 to zero:

$$n_2^{*-1} = \frac{b_2 - \alpha b_3}{1 - \alpha^2}, \qquad n_1^{*-2} = \frac{b_1 - \beta b_3}{1 - \beta^2}, \qquad n_1^{*-3} = \frac{b_1 - \alpha b_2}{1 - \alpha^2},$$

$$n_3^{*-1} = \frac{b_3 - \alpha b_2}{1 - \alpha^2}, \qquad n_3^{*-2} = \frac{b_3 - \beta b_1}{1 - \beta^2}, \qquad n_2^{*-3} = \frac{b_2 - \alpha b_1}{1 - \alpha^2}. \tag{S8.3}$$

The invasion growth rates are

$$r_1 = b_1 - \alpha n_2^{*-1} - \beta n_3^{*-1}, \quad r_2 = b_2 - \alpha n_1^{*-2} - \alpha n_3^{*-2}, \quad r_3 = b_3 - \alpha n_2^{*-3} - \beta n_1^{*-3}. \tag{S8.4}$$

The three limiting factors in this model are the three densities. We choose n_2 as our baseline for decomposing the invasion rates into stabilization and competitive advantage terms, for reasons of symmetry (the same result is obtained by any other choice, though in a more complicated way). The ϕ_j are then given by a_{j2}, so $\phi_1 = \alpha$, $\phi_2 = 1$, and $\phi_3 = \alpha$.

    Our goal with this model is to show that species may not coexist even if there are no competitive advantages. Therefore, we decompose the scaled invasion growth rates as $r_i/\phi_i = f_i + A$ and focus on the special case where $f_1 = f_2 = f_3 = 0$. The requirement $f_1 = f_3$ translates to $r_1/\phi_1 = r_3/\phi_3$, which, due to $\phi_1 = \phi_3 = \alpha$, simplifies to $r_1 = r_3$. This can only hold for an arbitrary choice of α and β if $b_3 = b_1$, $n_2^{*-1} = n_2^{*-3}$, and $n_3^{*-1} = n_1^{*-3}$. Imposing these constraints on Eq. S8.3 and substituting the resulting equilibrium abundance expressions into Eq. S8.4, we obtain

$$r_1 = r_3 = \frac{1 - \beta}{1 - \alpha^2}(b_1 - \alpha b_2), \qquad r_2 = b_2 - \frac{2\alpha}{1 + \beta}b_1. \tag{S8.5}$$

Further requiring $f_1 = f_2$ means $r_2/\phi_2 = r_1/\phi_1$, or $r_2 = r_1/\alpha$. Using Eq. S8.5, this imposes the following relation between b_2 and $b_1 = b_3$:

$$b_2 = b_1 \frac{1 + 2\alpha^2 - 2\alpha^4 - \beta^2}{\alpha(1 + \beta)(2 - \alpha^2 - \beta)}. \tag{S8.6}$$

Intuitively, the reason the middle species needs a different (larger) intrinsic growth rate than the two edge species is that the middle species experiences more competition by being sandwiched between two other species which do not experience competition from one of their sides (central niche effect; Stump 2017). We now have $f_1 = f_2 = f_3 = 0$ and $r_1/\phi_1 = r_2/\phi_2 = r_3/\phi_3 = A$. Substituting Eq. S8.6 into Eq. S8.5 and simplifying, we find that each species has a scaled growth rate of

$$\frac{r_j}{\phi_j} = A = b_1 \frac{(1 - \beta)(1 + \beta - 2\alpha^2)}{\alpha(1 + \beta)(2 - \alpha^2 - \beta)}. \tag{S8.7}$$

    Because there are no competitive advantages, the requirement for coexistence is simply $A > 0$. But this can only happen for certain combinations of α and β, as we can see by studying the signs of

the different terms in Eq. S8.7. We can assume $b_1 > 0$, as otherwise coexistence would be trivially impossible. Of the remaining terms, the denominator is positive for any $\beta < \alpha < 1$, as is the factor $1 - \beta$ in the numerator. The sign of A must then be determined by the remaining factor, $1 + \beta - 2\alpha^2$. But this may clearly be negative for a wide range of parameterizations satisfying $\beta < \alpha < 1$, precluding coexistence.

To proceed further in connecting this result to traits, we must specify the map between trait differences and interaction strength. Here we assume $a_{ij} = \exp(-(\delta_{ij}/w)^\theta)$ for the interaction coefficient between species i and j (Figure S1**a**), where δ_{ij} is the trait distance between the two species, w is the characteristic scale of interaction—defining what constitutes small versus large trait differences—and θ is a shape parameter controlling how platykurtic ("boxy") the function is (Hernández-García et al. 2009, Pigolotti et al. 2010, Barabás et al. 2012b). As already pointed out in Appendix S7, biologically realistic interaction coefficients must be smooth functions of trait difference (Adler and Mosquera 2000, D'Andrea et al. 2013, Barabás et al. 2013a), imposing $\theta \geq 2$. With a trait difference δ between adjacent species, this gives us $\alpha = \exp(-(\delta/w)^\theta)$ and $\beta = \exp(-(2\delta/w)^\theta)$. The sign of A then reads

$$\text{sign}(A) = \text{sign}(1 + \beta - 2\alpha^2) = \text{sign}\left[1 + \exp(-(2\delta/w)^\theta) - 2\exp(-2(\delta/w)^\theta)\right]. \qquad (S8.8)$$

For the special case of $\theta = 2$, this is positive for any $\delta > 0$. However, for all $\theta > 2$, it imposes a minimum δ below which A is negative and coexistence is lost (Figure S1**b**). In the limit $\theta \to \infty$, where species with trait difference $\delta \leq w$ compete neutrally (all intra- and interspecific coefficients equal to one) and those with $\delta > w$ do not compete at all, the limit for coexistence naturally converges to $\delta/w = 1$ (Figure S1**c**).

In summary, coexistence is prevented here because, although by construction there are no competitive advantages, the stabilization A is negative for sufficiently small trait differences.
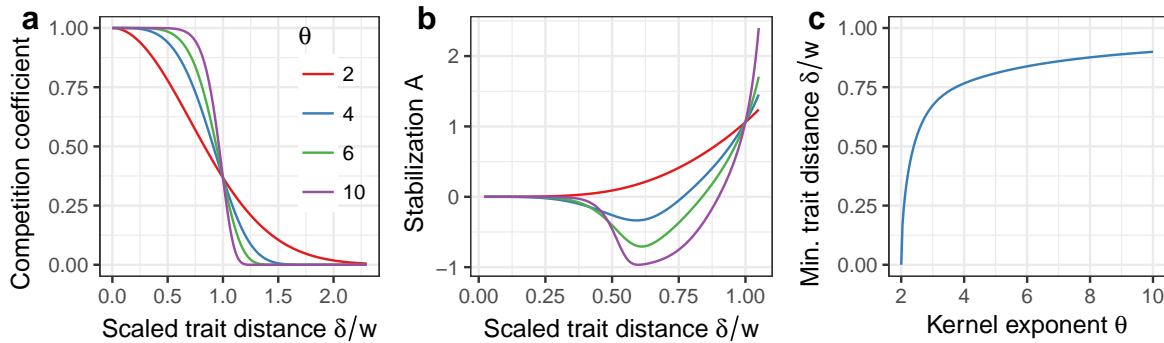

Figure S1: a. The form of the competition coefficient as a function of the scaled trait distance δ/w between two species, for various values of the kernel exponent θ. The qualitative shape of the function is unaffected, but the transition from strong to weak interactions gets more abrupt as θ increases. **b.** The stabilization term A for the three-species community, assuming no competitive advantages across the species. Stabilization is shown as a function of the nearest-neighbor scaled trait distance δ/w, for different values of θ. **c.** The minimum trait distance required for stable coexistence, as a function of θ. With the exception of $\theta = 2$, this is always a positive distance, imposing a limit to species similarity.

Acknowledgements

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