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On the Consequences of the Interdependence of Stabilizing and Equalizing Mechanisms

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ABSTRACT: We present an overlooked but important property of modern coexistence theory (MCT), along with two key new results and their consequences. The overlooked property is that stabilizing mechanisms (increasing species' niche differences) and equalizing mechanisms (reducing species' fitness differences) have two distinct sets of meanings within MCT: one in a two-species context and another in a general multispecies context. We demonstrate that the two-species framework is not a special case of the multispecies one, and therefore these two parallel frameworks must be studied independently. Our first result is that, using the two-species framework and mechanistic consumer-resource models, stabilizing and equalizing mechanisms exhibit complex interdependence, such that changing one will simultaneously change the other. Furthermore, the nature and direction of this simultaneous change sensitively depend on model parameters. The second result states that while MCT is often seen as bridging niche and neutral modes of coexistence by building a niche-neutrality continuum, the interdependence between stabilizing and equalizing mechanisms acts to break this continuum under almost any biologically relevant circumstance. We conclude that the complex entanglement of stabilizing and equalizing terms makes their impact on coexistence difficult to understand, but by seeing them as aggregated effects (rather than underlying causes) of coexistence, we may increase our understanding of ecological dynamics.

Keywords: competition, fitness difference, modern coexistence theory, niche overlap, nonorthogonality, niche-neutrality continuum.

Introduction

Modern coexistence theory (MCT; Chesson 2018) is a leading theoretical framework for studying the coexistence of competing species. It has proposed two classes of ecological mechanisms for coexistence (Chesson 2000, 2003): stabilizing

mechanisms (increasing species' niche differences) and equalizing mechanisms (reducing species' fitness differences). This framework has been widely used to study the conditions leading to coexistence, both in theoretical (HilleRisLambers et al. 2012; Fukami et al. 2016; Turcotte and Levine 2016; Vellend 2016; Letten et al. 2017; Hart et al. 2018; Ke and Letten 2018; Usinowicz and Levine 2018) and in empirical (Adler et al. 2013; Narwani et al. 2013; Godoy and Levine 2014; Godoy et al. 2014; Chu and Adler 2015; Kraft et al. 2015; Usinowicz et al. 2017; Germain et al. 2018; Letten et al. 2018; Hart et al. 2019; Li et al. 2019) contexts. Yet the ecological interpretation and consequences of these mechanisms continue to be a matter of debate (Letten et al. 2017; Saavedra et al. 2017; Barabás et al. 2018; Chesson 2018).

The concepts of MCT are highly general, applying to a wide range of systems. The main question is therefore not whether stabilizing and equalizing mechanisms can be identified in specific empirical or theoretical scenarios but whether and how doing so will advance our understanding of coexistence. In fact, MCT holds two key premises that, when true, greatly simplify analysis. The first is that stabilizing and equalizing mechanisms are two fundamentally different, high-level ecological processes (Adler et al. 2007; Vellend 2016). The second states that one can disentangle the relative roles of the two mechanisms in shaping species coexistence (Letten et al. 2017; Bartomeus and Godoy 2018). These premises are often visualized and quantified by taking the two mechanisms as orthogonal axes of variation with a continuum region of coexistence (fig. 1; Adler et al. 2007; Chesson and Kuang 2008; Mayfield and Levine 2010; Narwani et al. 2013; Kraft et al. 2015; Bartomeus and Godoy 2018). They also have some immediate, striking consequences, such as bridging niche and neutral modes of coexistence. Figure 1 shows that, starting from the point of neutrality, a small fitness inequality can be compensated by a very small amount of stabilization (leading to quasi neutrality), and from there, one can continuously move to

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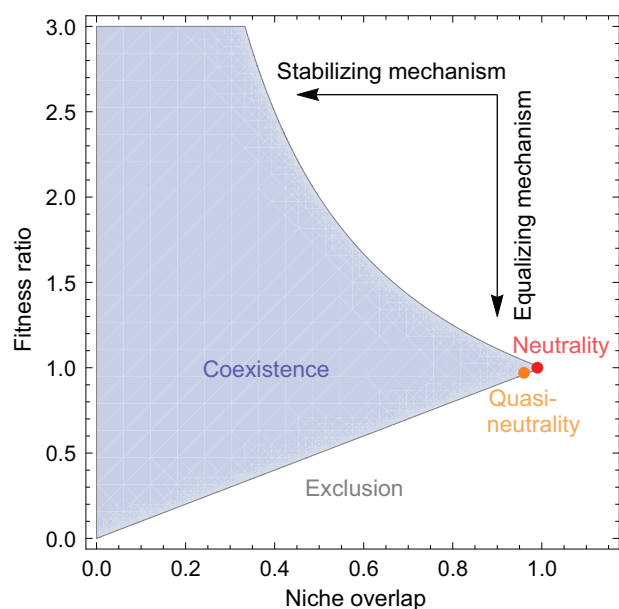


Figure 1: Premises of modern coexistence theory. Following the directions of the arrows, stabilizing mechanisms reduce niche overlap, while equalizing mechanisms bring the fitness ratio closer to 1. The two mechanisms are represented as orthogonal to each other. The blue region denotes the combinations of niche overlap and fitness ratio compatible with coexistence. The red point denotes neutrality, whereas the orange point is simply a representation of quasi neutrality (i.e., a small fitness inequality).

the region with small niche overlap and small fitness inequality. However, it has remained unclear whether the two premises hold in general, especially given the potential interdependence (nonorthogonality) between the two mechanism types (Chesson 2000; Loreau et al. 2012; Adler et al. 2013; Kraft et al. 2015; Letten et al. 2017).

Importantly, there are two parallel subframeworks within MCT for studying coexistence (see “Mathematical Formalisms”). One considers coexistence as a function of niche overlap between species. While this approach is in principle extensible to more complicated scenarios, it has mostly been used in a two-species Lotka-Volterra (LV) competition setting (Chesson 1990, 2000, 2018; Chesson and Kuang 2008). We will thus call it here the two-species framework. In turn, there is also a multispecies framework, which is more clearly applicable to a larger set of models and an arbitrary number of species (Chesson 2000, 2003, 2018; Yuan and Chesson 2015). Recent theoretical work has shown that within the multispecies framework, the stabilizing and equalizing mechanisms are not independent given that one is defined as a function of the other one, potentially changing the ecological interpretation and consequences of these mechanisms (Barabás et al. 2018). However, most studies investigating these mechanisms theoretically and experimentally are based on the two-species framework (Levine and HilleRisLambers

2009; Narwani et al. 2013; Godoy et al. 2014; Chu and Adler 2015; Kraft et al. 2015; Mordecai et al. 2015; Germain et al. 2016; Letten et al. 2017; Bimler et al. 2018; Cardinaux et al. 2018; Germain et al. 2018; Petry et al. 2018). Within the two-species framework, it is still an open question whether stabilizing and equalizing mechanisms are independent and opposing forces and whether the premises of MCT hold.

Here we move from a phenomenological to a mechanistic approach to investigate the interdependence between stabilizing and equalizing mechanisms within the two-species framework, as well as the dynamical consequences derived from that potential interdependence. In the literature, MCT is often framed in phenomenological terms (Adler et al. 2007; Mayfield and Levine 2010; Kraft et al. 2015), meaning that stabilizing and equalizing mechanisms are defined in terms of competition coefficients that represent only the outcome of a mechanism, not the mechanism itself. Previous theoretical work has translated the phenomenological side of MCT into a mechanistic view and investigated the particular conditions and mathematical constraints leading to the independence between the stabilizing and equalizing mechanisms (Letten et al. 2017; Chesson 2018). In contrast, here we focus on how general the independence between the mechanisms is and its consequences for species coexistence.

We first present a brief summary of the multispecies and two-species frameworks, demonstrating that the two-species framework is not a special case of the multispecies one. Next, drawing on general mechanistic consumer-resource models (with MacArthur’s [1970] consumer-resource model as an example in the main text), we present a mechanistic understanding of the stabilizing and equalizing mechanisms. We then show that stabilizing and equalizing mechanisms are almost always interdependent, with the relationship exhibiting complex patterns. Next, we show that the interdependence can easily reverse the positive effect of these mechanisms on species coexistence, and separating the role of each term is impossible without a knowledge of the mechanistic governing dynamics. We then show how the interdependence always works to break the niche-neutrality continuum. Finally, we discuss how a different interpretation of the existence and relationship between these two mechanisms can shed new light on the conditions leading to species coexistence.

The Multispecies and Two-Species Frameworks

Mathematical Formalisms

Here we briefly summarize the mathematical formulations derived for the multispecies and two-species frameworks following recent reviews (Barabás et al. 2018; Chesson 2018). We focus exclusively on the canonical formalisms of these two frameworks (Chesson 2018; Spaak and DeLaender 2018).

In the multispecies framework defined by MCT, the dynamics of S interacting species read

$$\frac{1}{N_i} \frac{dN_i}{dt} = f_i(E_i, C_i) \quad (i = 1, \dots, S) \quad (1)$$

(eq. [1] in both Barabás et al. [2018] and Chesson [2018]), where the per capita growth rate f_i of species i is a function of the environmental parameters E_i and density-dependent interaction parameters C_i . The invasion growth rate \mathcal{R}_i of species i is defined as the per capita growth rate f_i when species i is absent and all other species are at their stationary state under the absence of the invader. As usual in studies of invasibility, “absence” means that the invader abundance is so small that it does not influence residents at all, and so it is treated as being formally zero.

Species differ in how sensitively they respond to competition, that is, how much reduction of their per capita growth rate they suffer from a unit increase in the strength of competition they experience. Standardizing growth rates by scaling them with this sensitivity makes them more naturally comparable. If species i has sensitivity ϕ_i , then the quantity \mathcal{R}_i/ϕ_i is called the scaled invasion rate. Community average stabilization, A , is defined as the arithmetic average of the scaled invasion rates, whereas the average fitness difference ξ_i of a species i is the difference between the community average stabilization and its own scaled invasion rate (Barabás et al. 2018; Chesson 2018). Mathematically,

$$A = \frac{1}{S} \sum_{i=1}^S \frac{\mathcal{R}_i}{\phi_i}, \quad (2)$$

$$\xi_i = \frac{\mathcal{R}_i}{\phi_i} - A \quad (3)$$

(eqq. [48] and [52] in Barabás et al. [2018] or eqq. [31] and [32] in Chesson [2018]). Since the sum of the stabilization and fitness difference is equal to the scaled invasion rate, coexistence in the multispecies framework requires that the stabilization A overcomes all ξ_i to turn them positive:

$$\xi_i + A > 0 \quad \text{for all } i. \quad (4)$$

Importantly, the dependence between the two terms is immediately seen from equations (2) and (3), where ξ_i is a function of A . While the definitions in equations (2) and (3) may seem abstract and far away from the biology of real communities, they can have theoretical utility, offering insights into coexistence that would otherwise not be easily available. For instance, if some mechanism has a negligible effect on A but has strong influence over the ξ_i , then without any further investigation we know that this mechanism will not promote coexistence but rather influence the winner of competition. This is precisely what was found when decomposing the impact of a competition-predation trade-off via equations (2) and (3) (Stump and Chesson 2017).

In turn, the two-species framework in MCT is based on the two-species LV model

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \left(1 - \sum_{j=1}^2 a_{ij} N_j \right) \quad (i = 1, 2) \quad (5)$$

(Chesson 2000, 2012, 2018), where N_i is the abundance of species i , r_i is its intrinsic growth rate, and a_{ij} is the relative reduction in species i 's intrinsic growth caused by one unit of abundance of species j . Two quantities, the niche difference $1 - \rho$ and fitness ratio κ_1/κ_2 , are respectively defined as

$$1 - \rho = 1 - \sqrt{\frac{a_{12}a_{21}}{a_{11}a_{22}}}, \quad (6)$$

$$\frac{\kappa_1}{\kappa_2} = \sqrt{\frac{a_{21}a_{22}}{a_{12}a_{11}}} \quad (7)$$

(eq. [54] in Barabás et al. [2018] or eqq. [39] and [40] in Chesson [2018]). Species coexistence requires that

$$\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho} \quad (8)$$

(p. 287 in Barabás et al. [2018] or eq. [23] in Chesson [2018]), which implies that the fitness ratio has to be constrained between ρ and its reciprocal. The derivation of equation (8), with slightly different parameterization, can be found in Vandermeer (1975; his a_{ij} are our $r_i a_{ij}$) or Chesson and Huntly (1997), for example. Note that this coexistence criterion applies to some other population dynamics, such as the annual plant model (Levine and HilleRisLambers 2009; Godoy et al. 2014; Siefert et al. 2019) and the Law-Watkinson competition model (Hart et al. 2018, 2019), after reparameterization (supplemental material, sec. 1).

The Two-Species Framework Is Not a Special Case of the Multispecies One

Generally speaking, stabilizing mechanisms increase A (in the multispecies framework) or $1 - \rho$ (two-species framework), while equalizing mechanisms reduce the difference between the ξ_i (multispecies case) or the κ_i (two-species case). Also, the LV model (eq. [5]) is a special case of the general population dynamics in equation (1). Hence, it may be natural to assume that stabilization and equalization in the two-species framework are, in a sense, a particular case of stabilization and equalization in the multispecies framework. However, while equations (4) and (8) do predict coexistence identically, the meanings of stabilization and equalization are distinct, because it is not the case that $A = 1 - \rho$ and $\xi_i = \kappa_i$. In fact, one can move back and forth between the (A, ξ_i) and (ρ, κ_i) parameterizations using the formulas $A = (1 - \rho)(\kappa_1 + \kappa_2)/2$ and $\xi_1 = -\xi_2 = (\kappa_1 - \kappa_2)(1 + \rho)/2$, their inverses (Chesson 2018, eq. [A51]). Below we show that these relationships mean that $A = 1 - \rho$ and $\xi_1 = \kappa_1$ can never be achieved simultaneously.

To verify the equivalence of the coexistence conditions, we determine the invasion growth rates \mathcal{R}_i . In monoculture, the

equilibrium density of one species (say, species 2) in the absence of the other, from equation (5), is simply $N_2^* = 1/a_{22}$. The invading species 1 then has an invasion rate of $\mathcal{R}_1 = r_1(1 - a_{12}/a_{22})$, where 0 was substituted for the invader and $1/a_{22}$ for the resident density. By a similar argument, $\mathcal{R}_2 = r_2(1 - a_{21}/a_{11})$. Coexistence is obtained if equation (4) holds: $\xi_i + A = \mathcal{R}_i/\phi_i > 0$. Since ϕ_i is positive, this translates to $\mathcal{R}_i > 0$ for both species, which in turn holds whenever $a_{12} < a_{22}$ and $a_{21} < a_{11}$ are fulfilled simultaneously (Chesson 2000). But this is exactly the criterion of equation (8), after multiplying through by $\sqrt{a_{12}a_{11}/(a_{21}a_{22})}$.

Despite this equivalence, the concepts of stabilization and equalization in the two frameworks do not map onto one another: the two-species framework is not a reparameterized special case of the multispecies one. This is not surprising in light of the fact that the coexistence criteria (eqq. [4], [8]) are different. Indeed, it is clear from these equations that in the multispecies framework, coexistence is promoted by a large A and ξ_i 's close to 0 whereas in the two-species case, coexistence requires a large $1 - \rho$ and κ_i 's close to 1. Here we show that there is no choice of parameters for which the two frameworks are equivalent. This can be proven by attempting to equate A with $1 - \rho$ and ξ_i with κ_i . Using equations (2) and (3) and equations (6) and (7),

$$1 - \sqrt{\frac{a_{12}a_{21}}{a_{11}a_{22}}} = \frac{1}{2} \left(\frac{\mathcal{R}_1}{\phi_1} + \frac{\mathcal{R}_2}{\phi_2} \right), \tag{9}$$

$$\sqrt{\frac{a_{12}a_{11}}{a_{21}a_{22}}} = \frac{\mathcal{R}_2/\phi_2 - A}{\mathcal{R}_1/\phi_1 - A}, \tag{10}$$

where $\mathcal{R}_1 = r_1(1 - a_{12}/a_{22})$ and $\mathcal{R}_2 = r_2(1 - a_{21}/a_{11})$. Thus, ignoring other constraints on the scaling factors ϕ_1 and ϕ_2 , one could ask whether there is any combination of their values that satisfies these equations. Because A is the average of \mathcal{R}_1/ϕ_1 and \mathcal{R}_2/ϕ_2 and ξ_i measures the difference

between \mathcal{R}_i/ϕ_i and A , it follows that $\xi_2/\xi_1 = -1$, regardless of model parameters (for visualization, see fig. 2). Therefore, equation (10) does not have a real solution: one can never find positive ϕ_1, ϕ_2 values to force $A = 1 - \rho$ and $\xi_i = \kappa_i$, making the definitions equivalent across the two-species and multispecies frameworks. This incompatibility implies that, despite the identical nomenclature, the words “stabilization” and “equalization” are distinct mathematical entities in the two frameworks.

In light of this, it is natural to ask whether equation (8) can be generalized to an arbitrary number of competing species. Strictly speaking, the generalization is probably either impossible to give in the form of a combination of simple invasion criteria, or else the condition would have to be so restrictive that it must be derived on a case-by-case basis (e.g., eq. [4] in Chesson 2000). This is because even simple LV systems exhibit complex behavior, which renders any invasibility-based condition insufficient for determining coexistence. For example, species may stably coexist even if they cannot invade the resident communities corresponding to their absence (due either to priority effects or to locally but not globally stable equilibria), and conversely, all species being able to invade does not necessarily mean that they will coexist because of potential coextinctions following those invasions (Chesson 2003, 2018; Allesina and Levine 2011; Soliveres et al. 2015; Barabás et al. 2016, 2018; Gallien et al. 2017; Levine et al. 2017; Saavedra et al. 2017). A multispecies generalization of equation (8) was derived by Chesson (2018, eq. [44]). This, however, is an invasion and not a coexistence condition. As such, while being useful as an invasion condition, it is strictly speaking neither necessary nor sufficient for coexistence, due to the reasons above. In light of this, combining invasion analyses with other approaches such as permanence criteria (Schreiber et al. 2011; Chesson 2018; Hening and Nguyen 2018) may be more fruitful avenues for studying multispecies coexistence.

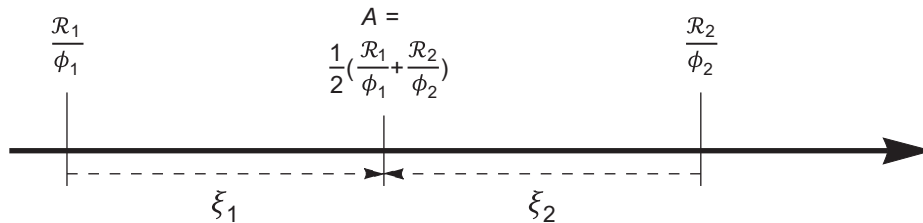


Figure 2: Proof of the incompatibility between the concepts of stabilizing and equalizing mechanisms in the two-species and multispecies frameworks. The axis represents the scaled invasion growth rate \mathcal{R}/ϕ . Following the multispecies framework, the community average stabilization A is defined as the mean of the scaled invasion rates, $(\mathcal{R}_1/\phi_1 + \mathcal{R}_2/\phi_2)/2$, while the fitness ξ_i is defined as the difference between the scaled invasion growth rate \mathcal{R}_i/ϕ_i and A . It can be geometrically observed that the fitness ratio ξ_1/ξ_2 is always equal to -1 in the multispecies framework. However, κ_1/κ_2 in the two-species framework must be nonnegative. Since stabilizing effects increase A (or $1 - \rho$), while equalizing ones reduce the difference between the ξ_i (or κ_i), but these can never be equal, this proves that stabilizing and equalizing mechanisms are incompatible across the two theoretical frameworks in modern coexistence theory.

From a Phenomenological to a Mechanistic Interpretation

The previous section confirmed that we need to study the relationship between stabilizing and equalizing mechanisms in the two-species framework independently from the multi-species one. Because the parameters of the two-species LV model (eq. [5]) are phenomenological (representing the outcome of some mechanism instead of the actual mechanism itself), we first focus on the phenomenological interpretation of the stabilizing and equalizing mechanisms. Stabilizing mechanisms require decreasing the niche overlap ρ (eq. [6]). Decreasing niche overlap is equivalent to decreasing the relative strength of interspecific interactions relative to self-regulation. Similarly, achieving greater fitness equalization requires reducing the fitness difference between species, bringing the fitness ratio κ_1/κ_2 closer to 1 (eq. [7]). Decreasing fitness difference is achieved by bringing the effect that species 1 has on itself relative to its effect on species 2 (a_{21}/a_{11}) closer to the effect that species 2 has on species 1 relative to its effect on itself (a_{22}/a_{12}).

Based purely on such phenomenological considerations, it has been claimed that the fitness ratio “fundamentally measures the overall relative degrees of adaptedness of the species to their common environment,” while niche overlap “is independent of how well the species are adapted to the environment” (Chesson 2012, p. 10068). However, phenomenological parameters represent infinitely many possibilities for the underlying mechanisms (O’Dwyer 2018; Letten and Stouffer 2019). As such, no general claim on their mechanistic meaning (such as their relationship to adaptation) could ever be falsified. Therefore, without translating these terms into a mechanistic interpretation, we cannot take for granted that the niche overlap and fitness ratio are not simply different manifestations of the same cause. In this particular case, we speculate whether niche overlap and fitness ratio (different manifestations) are dependent on the same mechanistic adaptation process (same cause), such as changes in niche width or preference.

MacArthur’s Consumer-Resource Model

While previous work has identified scenarios in which a similar mechanism may or may not influence both niche overlap and fitness ratio (Letten et al. 2017), we need to investigate the generality of mechanisms leading to this potential interdependence. Indeed, the definitions of niche overlap ρ and the fitness ratio κ_1/κ_2 in the two-species framework (Chesson 1990, 2000, 2012) are motivated by MacArthur’s (1970) influential consumer-resource model. This model serves as the prototype for a large class of consumer-resource models (May and MacArthur 1972; Tilman 1982; Chase and Leibold 2003; Koffel et al. 2016; Rohr et al. 2016; Rael et al. 2018). Here, for this reason, we translate the stabilizing and equalizing mech-

anisms into their mechanistic meanings using MacArthur’s model. Because this model is a special case of resource competition, we have also explored other models that allow for more complex interactions: the asymmetric MacArthur model (supplemental material, sec. 3) and Tilman’s model (supplemental material, sec. 4; Tilman 1982; Chase and Leibold 2003; Letten et al. 2017).

MacArthur’s consumer-resource model can be cast in the form of equation (5), but the intrinsic growth rates r_i and competition coefficients a_{ij} are expressed in terms of lower-level parameters. The basic equations (MacArthur 1970) read

$$\frac{1}{N_i} \frac{dN_i}{dt} = \sum_{k=1}^L c_{ik} v_k R_k - m_i \quad (i = 1, \dots, S), \quad (11)$$

where N_i and m_i are species i ’s density and mortality rate, respectively; R_k and v_k are the concentration and unit value of resource k ; c_{ik} is species i ’s rate of consumption of resource k ; S is the number of consumer species; and L is the number of distinct resources. Assuming fast resource dynamics as in MacArthur (1970), resource concentrations can be expressed directly as

$$R_k = R_k^0 - \sum_{j=1}^S c_{jk} N_j \quad (k = 1, \dots, L), \quad (12)$$

where the first term, R_k^0 , is the maximum (saturation) level of resource k in the absence of consumption and the second term is the amount of resource k locked up in the biomass of consumers. Substituting equation (12) back into equation (11) and rearranging, we get

$$\frac{1}{N_i} \frac{dN_i}{dt} = \underbrace{\left(\sum_{k=1}^L c_{ik} v_k R_k^0 - m_i \right)}_{r_i} - \sum_{j=1}^S \underbrace{\left(\sum_{k=1}^L c_{ik} c_{jk} v_k \right)}_{\beta_{ij}} N_j. \quad (13)$$

Using the definition $a_{ij} = \beta_{ij}/r_i$ ($i, j = 1, 2$), and for $S = 2$ species, we recover the LV model of equation (5). The niche overlap and fitness ratio can now be written using equations (6) and (7) (these expressions were already obtained, with slightly different parameterizations, by Chesson and Kuang [2008] and Chesson [2011]):

$$\rho = \frac{\sum_k c_{1k} c_{2k} v_k}{\sqrt{(\sum_k c_{1k}^2 v_k)(\sum_k c_{2k}^2 v_k)}}, \quad (14)$$

$$\frac{\kappa_1}{\kappa_2} = \left(\frac{\sum_k c_{1k} v_k R_k^0 - m_1}{\sum_k c_{2k} v_k R_k^0 - m_2} \right) \sqrt{\frac{\sum_k c_{2k}^2 v_k}{\sum_k c_{1k}^2 v_k}}. \quad (15)$$

It is clear that R_k^0 and m_i affect only the fitness ratio, while c_{ik} and v_k are involved in the niche overlap as well. This means that, generally speaking, niche overlap cannot be adjusted independently from the fitness ratio, and for the fitness ratio to

be independently adjustable, R_k^0 and m_i must not depend on the consumption vectors c_{ik} and resource values v_k .

To make this point more specific, let us consider one particularly simple parameterization of the model. We set $v_k = 1$ and $m_i = 0$ (i.e., there is only competition-induced mortality) and assume that resources form a one-dimensional continuum, mimicking resource quality or location. Denoting species i 's niche center (preference) by μ_i and niche width by σ , one commonly used choice for c_{ik} is

$$c_{ik} = \frac{\exp\left(-\frac{(x_k - \mu_i)^2}{2\sigma^2}\right)}{\sqrt{2\pi\sigma^2}} \quad (16)$$

(MacArthur and Levins 1967; MacArthur 1970), where x_k is the quality of resource k . This expression assumes equal niche widths across the two species—an assumption that we relax in section 5 of the supplemental material. In turn, let the saturation resource concentrations R_k^0 also follow a normal curve:

$$R_k^0 = \frac{\exp\left(-\frac{x_k^2}{2\omega^2}\right)}{\sqrt{2\pi\omega^2}}, \quad (17)$$

where ω is the width of the resource spectrum. The niche overlap and fitness ratio now read, in this particular parameterization, as

$$\rho = \exp\left(-\frac{(\mu_1 - \mu_2)^2}{4\sigma^2}\right), \quad (18)$$

$$\frac{\kappa_1}{\kappa_2} = \exp\left(-\frac{\mu_1^2 - \mu_2^2}{2(\sigma^2 + \omega^2)}\right) \quad (19)$$

(supplemental material, sec. 2). Both ρ (eq. [18]) and κ_1/κ_2 (eq. [19]) depend on the same parameters, except for ω , which appears only in the fitness ratio. That is, changing either the niche centers μ_i or niche width σ will affect both terms simultaneously. Importantly, this confounding of the two expressions cast doubt on the interpretation that the two mechanisms are ecologically different (Chesson 2012). In particular, as both the niche centers μ_i and the niche width σ are widely regarded as fingerprints of species adaptation (Sexton et al. 2017; Batstone et al. 2018), it questions the claim that niche overlap, as defined in the two-species framework, is independent of species adaptation.

Generality and Complexity of the Interdependence

When Are Stabilizing and Equalizing Mechanisms Independent?

The possibility that the two mechanisms may depend on each other has already been pointed out in previous studies (Ches-

son 2000; Loreau et al. 2012; Adler et al. 2013; Kraft et al. 2015; Letten et al. 2017). However, the meaning of interdependence can be ambiguous. It is widely acknowledged that the niche overlap and fitness ratio are likely to share some mechanistic parameters (Chesson 2000, 2018; Letten et al. 2017). For example, both terms in MacArthur's consumer-resource model depend on the niche width σ and niche centers μ_i (eqq. [18], [19]). Yet sharing parameters is often not how interdependence is interpreted in the literature. In fact, studies have shown that it is possible to find mathematical constraints leading to the independence between the two mechanisms, despite sharing parameters (Letten et al. 2017; Chesson 2018). Instead, the commonly used concept of independence is "the principle that the ρ 's and κ 's can be varied independently" (Chesson 2018, p. 15 in supporting information). Correlation is often used along the same lines of this definition in empirical work (Kraft et al. 2015). Formally, suppose that $\{x_i\}_{i=1,\dots,n}$ are the mechanistic model parameters. Then we can call the two mechanisms independent if there exists some combination $c(x_1, \dots, x_n) = 0$ such that $\rho(c(x_1, \dots, x_n))$ remains constant while $\kappa_1(x_1, \dots, x_n)/\kappa_2(x_1, \dots, x_n)$ can vary freely, and vice versa. We use this definition of independence throughout the text.

Independence Is the Exception Rather than the Norm

To investigate the generality of interdependence between stabilizing and equalizing mechanisms in the two-species framework, we draw on the definitions of niche overlap and fitness ratio derived from MacArthur's consumer-resource model. Specifically, we study how the parameters need to be constrained to make ρ and κ_1/κ_2 independent of each other. We found that while independence can happen, it is extremely difficult to achieve and requires stringent mathematical constraints that may not be ecologically meaningful. These conditions are the following (a proof can be found in supplemental material, sec. 6): first, assume that the niche centers μ_i are fixed; then we have that (i) the fitness ratio changes independently of the stabilizing term only if σ is fixed while ω changes and (ii) the stabilizing term changes independently of the fitness ratio only if $\sigma^2 + \omega^2$ is fixed while σ changes; second, if the niche centers are allowed to change, then (i) the fitness ratio changes independently of the stabilizing term only if $|\mu_1 - \mu_2|$ is fixed while $\log(\kappa_1/\kappa_2) \propto (\mu_1 + \mu_2) \text{sign}(\mu_1 - \mu_2)$ and (ii) the stabilizing term changes independently of the fitness ratio only if $\mu_2^2 - \mu_1^2$ is fixed as a constant c while $\log \rho \propto (\sqrt{\mu_2^2 + c} \pm \mu_2)/(\sqrt{\mu_2^2 + c} \mp \mu_2)$.

Because these are highly unique conditions and it is likely that all parameters change simultaneously in nature in response to environmental variation (which would bring a more complicated set of constraints), it is fair to conclude that the stabilizing and equalizing mechanisms are almost inevitably dependent on one another. This result is consistent with

empirical findings that niche overlap and fitness ratio have weak correlations, because a null correlation can result from strong positive or negative interdependence (see detailed discussion in supplemental material, sec. 7).

The Interdependence Pattern Is Complex

Given the generality of interdependence, a natural question is whether some simple (and single) pattern of interdependence exists. Figure 3 shows three simple examples with different parameterizations of the niche center (preference) μ_1 and μ_2 to illustrate the effects of the interdependence on species coexistence. While the relationships of μ_1 and μ_2 are linear in all three examples, the qualitative behavior of the interdependence is entirely different in each case (monotonic decrease, piecewise linear, and smooth asymmetric). Under the first condition (orange line, $\mu_1 = \mu_2/2 - 1$), the stabilizing mechanism first introduces a positive effect on coexistence and then a negative effect. Under the second condition (gray line, $\mu_1 = 3\mu_2 - 3$), the stabilizing mechanism can promote coexistence

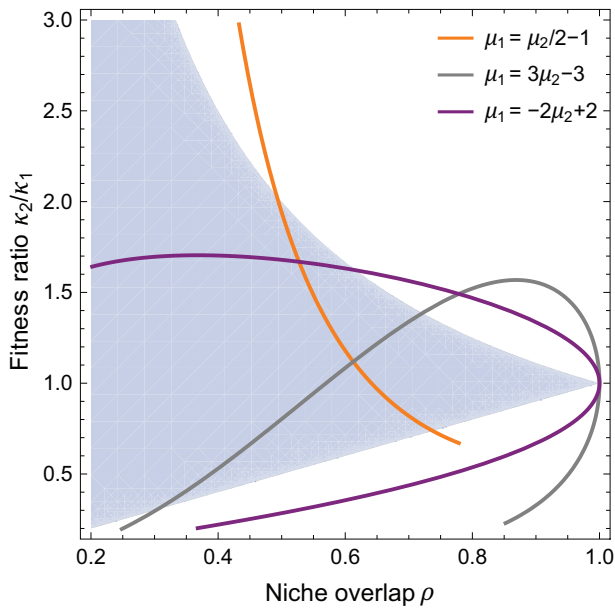


Figure 3: Interdependence of stabilizing and equalizing mechanisms in the two-species framework. The solid lines show how three different hypothesized relationships between species’ niche centers μ_1 and μ_2 generate qualitatively different relationships between niche overlap and fitness difference: monotonic decrease (orange), piecewise linear (gray), and smooth asymmetric (purple). Further examples are found in section 8 of the supplemental material. The blue region denotes combinations of fitness ratio and niche overlap compatible with coexistence, based on equation (8). This shows that the interdependence between the two mechanisms exhibits complex patterns. Parameters: $\sigma = 1$; $\omega = 1/2$.

as long as the fitness ratio is above some critical level. Under the third condition (purple line, $\mu_1 = -2\mu_2 + 2$), the stabilizing mechanism may either quickly or never achieve coexistence, based on whether the fitness ratio is larger than 1. Section 8 of the supplemental material has more examples showing the sensitivity of the sign and magnitude of these effects to changes in model parameters. That is, the niche overlap and fitness differences between two species can be transformed simply by changing the niche preferences of species. Importantly, these changes do not have a consistent impact on competition but depend on the niche width of species and the resource spectrum. This reveals that there is no simple (and single) pattern of the effects of these two mechanisms on species coexistence. This problem is also present in other mechanistic models (see supplemental material, secs. 3–5).

Consequences of the Interdependence

Aggregated Effects Instead of Ecological Mechanisms

One of the central claims of MCT is that species coexistence is the consequence of the stabilizing and equalizing mechanisms (Chesson 2012). This interpretation of MCT is rooted in the tacit assumption that coexistence is a linear combination of these two mechanisms (fig. 4A). However, as shown in figure 3, species coexistence is a nonlinear combination of the two mechanisms due to their interdependence (fig. 4B). Given the generality and complexity of this interdependence, the relative contribution of the two mechanisms to coexistence is extremely difficult to disentangle. In empirical work, a common practice is to consider the niche overlap and fitness ratio (computed by the inferred phenomenological interaction coefficients) as the contribution to coexistence by stabilizing and equalizing mechanisms, respectively (Levine and HilleRisLambers 2009; Adler et al. 2010; Chu and Adler 2015; Kraft et al. 2015). The question is whether this will actually reveal anything about coexistence that one did not already know from only the raw interaction coefficients themselves. We find that the complex, context-dependent entanglement of the two terms (see “Generality and Complexity of the Interdependence” and supplemental material, secs. 3–5) means that the relative contribution of each mechanism is not necessarily indicative of how the two species coexist, unless we know the governing mechanistic model. This suggests that these mechanisms are more appropriately seen as aggregated phenomenological effects, rather than the mechanistic causes, of species coexistence. For example, in the MacArthur model, the extra stabilization conferred by a change in trait is not what is causing coexistence. Instead, increased stabilization is the effect of the trait change, and the actual cause is related to how the trait change allows the species to be more independently regulated.

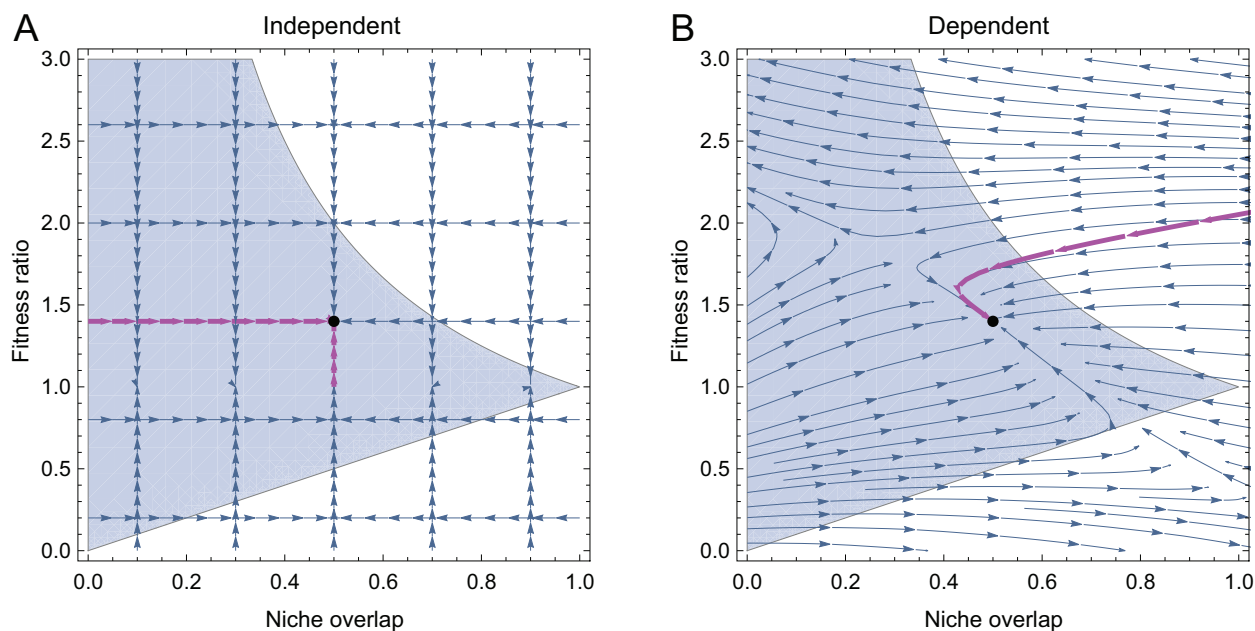


Figure 4: Difficulty in disentangling the contributions to coexistence. The black dots represent the system at equilibrium; arrows show which direction the niche overlap and fitness ratio can change. The purple highlighted segments represent the relative contribution of stabilizing and equalizing mechanisms to coexistence. Panel A shows a hypothetical example where coexistence can be disentangled into a linear combination of stabilizing and equalizing mechanisms if they are independent. In B, coexistence is a nonlinear combination of stabilizing and equalizing mechanisms and cannot be disentangled unless the governing mechanistic dynamics are known.

Breakdown of the Niche-Neutrality Continuum

To illustrate further consequences of the interdependence between stabilizing and equalizing mechanisms on the interpretation of ecological theory, we revisited the idea that the two mechanism types reconcile niche and neutral perspectives on coexistence. This idea takes various forms in the literature. One body of thought considers the relative importance of deterministic versus stochastic processes in generating larger-scale community patterns (Gravel et al. 2006; Haegeman and Loreau 2011; Rael et al. 2018). Another (which will be our focus here) argues that coexistence is best viewed from the angle of where communities lie in figure 1 (Adler et al. 2007; Mayfield and Levine 2010): communities with a fitness ratio close to 1 and small niche overlap are highly stable and driven by niche differentiation, communities with large fitness differences and large niche overlap are unstable and preclude coexistence, a fitness ratio of 1 and maximal niche overlap lead to neutral coexistence, and so on. By appropriately adjusting the niche overlap and fitness ratio, one can achieve anything between neutrality and 100% niche differentiation. Here neutrality is meant in the sense of identical parameter values across the species, leading to coexistence with neutral stability. By considering a demographically stochastic extension of the deterministic dynamics (as in Haegeman and Loreau 2011; Rael et al. 2018), one recovers the

model and dynamics behind the neutral theory of biodiversity (Hubbell 2001; Volkov et al. 2003; Azale et al. 2016), albeit without speciation or immigration.

One important consequence of this second idea would be the violation of the limiting similarity principle (MacArthur and Levins 1967; Tilman 1994; Meszena et al. 2006). Consider two species that are identical and so coexist at some neutrally stable equilibrium. We now assume that one species undergoes a trait change. If the effect of this change is to reduce niche overlap (and affect the fitness ratio so little that the coexistence condition, eq. [8], is maintained), then the two species will stably coexist, regardless of how small the trait change was. That is, even arbitrarily similar species do not necessarily exclude each other.

This conclusion, however, is contingent on the assumption that stabilizing and equalizing effects possess a fair degree of independence and therefore that communities are usefully viewed based on their position in figure 1. Seeing how complicated the interdependence between niche overlap and the fitness ratio can be, one is justified to be cautious with immediately accepting its conclusions. In fact, for sufficiently similar species, the interdependence is surprisingly always such as to prevent stable coexistence, regardless of the ecological scenario at hand.

This strange conspiracy between stabilizing and equalizing terms to prevent the coexistence of similar species can

be understood as follows. When some trait change occurs in two originally identical species, it will generally affect their fitness ratio of 1. By a Taylor expansion argument, a small $\Delta\mu$ trait change induces a fitness ratio change that is itself proportional to $\Delta\mu$: $\kappa_1/\kappa_2 \approx 1 + p\Delta\mu$. The same is not true of niche overlap, however, because identical species overlap maximally. When species are slightly altered to make them nonidentical, a small $\Delta\mu$ trait change will not induce a change in niche overlap that is itself proportional to $\Delta\mu$, because smooth functions do not change to first order around their maxima (note that biological realism requires this smoothness; Adler and Mosquera 2000; Barabás et al. 2013; D’Andrea et al. 2013). Instead, the reduction in niche overlap ρ will be proportional to $\Delta\mu^2$: $\rho \approx 1 - q\Delta\mu^2$. To a second-order approximation, therefore, equation (8) reads $1 - q\Delta\mu^2 \lesssim 1 + p\Delta\mu \lesssim 1 + q\Delta\mu^2$, imposing the lower limit $\Delta\mu \gtrsim p/q$ on species similarity.

For example, applying this general idea to the MacArthur consumer-resource model but performing all calculations rigorously (supplemental material, sec. 9), it turns out that

stable coexistence requires the following lower bound to the similarity of the two species:

$$|\Delta\mu| > \frac{4|\mu_1|\sigma^2}{\sigma^2 + \omega^2}, \tag{20}$$

meaning that the degree of similarity, measured by $\Delta\mu = |\mu_1 - \mu_2|$, cannot be arbitrarily low unless $\mu_1 = 0$ exactly. The interdependence works to uphold the limiting similarity principle.

Thus, there are only two options for species coexistence within the context of deterministic community models encompassed by equations (1) and (5): either species are equivalent and therefore coexist with neutral stability or there is a substantially large trait difference between them. In between these two extremes, there is no coexistence. Figure 5A illustrates that the region of exclusion separates neutrality and the rest of the coexistence region. That is, the mechanistically disconnected coexistence region (eq. [20]; fig. 5A) is topologically different from the phenomenologically connected

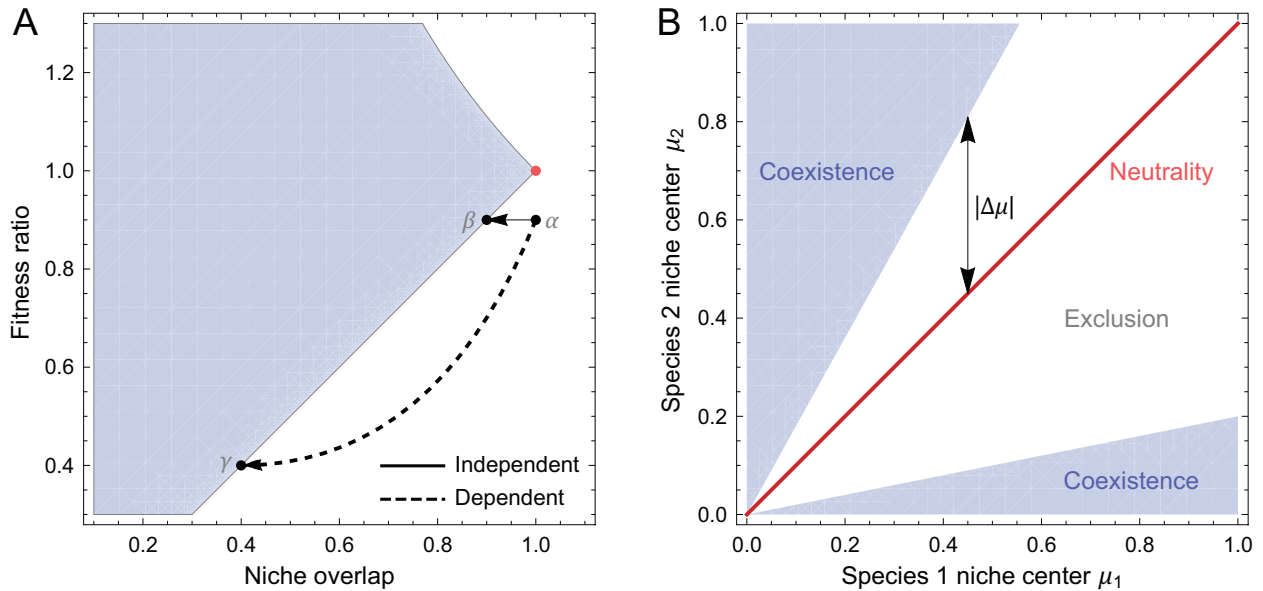


Figure 5: Breakdown of the niche-neutrality continuum and its origin. Panel A illustrates the generality of the niche-neutrality continuum’s breakdown. The dissimilarity of two species is measured by the difference between their niche centers μ_1 and μ_2 in MacArthur’s consumer-resource model. The red line denotes neutrality, where the species are identical. The two blue regions denote combinations of the two niche centers compatible with coexistence (the exact shape depends on the niche width σ and resource spectrum width ω ; here parameters are constrained so that $\sigma^2/(\sigma^2 + \omega^2) = 1/5$). The distance between the border of the coexistence region and the line of neutrality shows the minimal dissimilarity of the two species required for their coexistence (eq. [20]). This shows that a niche-neutrality continuum is not possible except under very restrictive assumptions. Panel B shows that the breakdown of the niche-neutrality continuum is caused by the discontinuous mapping from the phenomenological coexistence region in modern coexistence theory (eq. [8]; fig. 1) into the mechanistic coexistence region (eq. [20]). This discontinuity means that “small amount of extra stabilization required” does not translate to “small trait difference required.” Instead, a substantial amount of trait difference is needed to provide the necessary stabilization for coexistence. Species cannot coexist in system α , with identical niches and a fitness ratio slightly off of 1. If stabilizing and equalizing mechanisms are independent, species can coexist if the niche overlap is slightly reduced (system β). However, if the two mechanisms are interdependent, then reducing niche overlap may increase fitness differences, and species can coexist only if a large proportion of niche overlap is reduced (system γ).

coexistence region in MCT (eq. [8]; fig. 1). This discontinuous mapping from the phenomenological to the mechanistic space is caused by the interdependence of stabilizing and equalizing terms—in particular, by the inability of a small trait difference to provide sufficient stabilization for coexistence (see fig. 5B). In conclusion, the interpretation of stabilizing and equalizing terms as providing a continuum between niche and neutral coexistence modes will generally hold only under the tacit assumption that the two terms are independent under a mechanistic interpretation.

Discussion

Two Independent Frameworks

It is natural to assume that terminology such as stabilizing and equalizing mechanisms in MCT have a definite meaning. In fact, they currently have two independent definite meanings: one in the multispecies (eqq. [2], [3]) and one in the two-species (eqq. [6], [7]) framework. The existence of two parallel terminologies has rarely been mentioned and, to our knowledge, has so far never been emphasized. Chesson (2018) provides a useful discussion of how the two frameworks of equations (2) and (3) and equations (6) and (7) relate to each other but without stressing that “stabilizing mechanism” and “equalizing mechanism” have subtly different meanings depending on the approach considered. The reason for the difference is that the community average stabilization A of the multispecies framework is not equal to $1 - \rho$ in the two-species framework, and the same for ξ_i and κ_i . Even more is true: we have shown that there is no way to force $A = 1 - \rho$ and $\xi_i = \kappa_i$.

An important question arising from this incompatibility is how, then, one should interpret the foundational mechanisms in MCT leading to species coexistence: the stabilizing and equalizing mechanisms. It has already been shown that in the multispecies framework, the two mechanisms are not independent (Barabás et al. 2018). Yet in the two-species framework, these mechanisms are typically taken as independent and opposing forces (Chesson 2012; Bartomeus and Godoy 2018). Because the insights drawn from the multispecies framework cannot be directly applied to the two-species framework to verify this statement, it is then necessary to study the two-species framework independently. Furthermore, if these mechanisms are not independent in the two-species framework either, then it becomes necessary to understand how this interdependence affects the relationship of these mechanisms to species coexistence.

Interdependence of Stabilizing and Equalizing Effects

Focusing on the two-species framework, stabilizing and equalizing effects are often displayed as orthogonal axes of variation

(Adler et al. 2007; Chesson and Kuang 2008; Mayfield and Levine 2010; Narwani et al. 2013; Kraft et al. 2015; Bartomeus and Godoy 2018). While many studies have suggested that they may be neither independent nor opposing in both theoretical (Loreau et al. 2012; Adler et al. 2013; Letten et al. 2017; Barabás et al. 2018) and empirical (Cardinaux et al. 2018; Germain et al. 2018) contexts, the generality of this interdependence has been unclear given that there is no a priori expectation that can be derived from the phenomenological definitions of niche overlap and fitness difference (eqq. [6], [7]).

To formally study the interdependence of stabilizing and equalizing terms in the two-species framework, we have linked their mathematical structure to their mechanistic interpretation in MacArthur’s consumer-resource model. We have shown that interdependence emerges under all but the most restrictive assumptions. Furthermore, this dependence dictates the sign and magnitude of the effect of each individual mechanism (i.e., the mechanisms can have a positive, negative, or null effect) on species coexistence. These changes in sign and magnitude are highly sensitive to small alterations in model parameters (fig. 3; supplemental material, sec. 8), introducing a high uncertainty about the actual effect of these mechanisms. In sum, the mechanistic interdependence between stabilizing and equalizing mechanisms, together with the lack of a general effect on species coexistence, has revealed that the two mechanisms should be considered as aggregated effects rather than general ecological causes.

Rethinking Ecological Theory

Finally, the interdependence between stabilizing and equalizing mechanisms has an impact on how we interpret ecological theory. As an example, here we have revisited the idea of a niche-neutrality continuum. MCT is often considered as a reconciliation of niche theory and neutral theory (Adler et al. 2007; Chesson 2012) following the rationale that ecological processes can be decomposed into a continuum of stabilizing and equalizing mechanisms.

Based on the interdependence of the stabilizing and equalizing mechanisms, we argued that the niche-neutrality continuum is extremely unlikely to attain in the context of the community models specified by equations (1) and (5). To show this, first we demonstrated that the mechanistic meanings of niche overlap and fitness differences are not equivalent to niche- and neutrality-based concepts as their names might suggest (a similar idea has also been discussed by Letten et al. [2017] and Barabás et al. [2018]). Second, we have shown that the interdependence of the two mechanisms results in preventing the coexistence of overly similar species. That is, coexistence always requires either neutrality or a minimum level of dissimilarity between species. In between this minimum and neutrality there is no coexistence, breaking any continuum. Importantly, similar issues have also been

identified in the multispecies framework of MCT (Barabás et al. 2018), suggesting that changes in traits should not be directly interpreted as changes in stabilization. While this conclusion holds in the presented form in communities with large population sizes, sufficiently small selective advantages are overpowered by demographic stochasticity if effective population sizes are small (more precisely: a community with a selective advantage smaller than the reciprocal of the effective community size has dynamics practically indistinguishable from neutrality; e.g., Gillespie 2004, ch. 3.9). This means that combining a small nonzero fitness ratio with small population sizes may still lead to dynamics that are effectively neutral. The niche-neutrality continuum, in this sense, may be more defensible and is the topic of Gravel et al. (2006), Haegeman and Loreau (2011), and Rael et al. (2018), for example.

Ecologists have long been searching for the mechanisms leading to the coexistence of competing species. Knowing these mechanisms can equip one with a powerful understanding of how intrinsic and external perturbations can affect the biodiversity that we observe in nature. Because the stabilizing and equalizing mechanisms have been so influential in the ecological literature, we hope that this article helps to shed new light on their meaning and implications for a better understanding of species coexistence. Furthermore, these results reveal a potential necessity to establish a formalism that can account for and link processes between the two-species and multispecies frameworks. In this direction, two related linking formalisms have appeared, under the notions of structural stability (Saavedra et al. 2017; Cenci et al. 2018; Song et al. 2018) and community-wide sensitivity (Meszéna et al. 2006; Barabás et al. 2014); yet, regardless of the specific formalism, to have a predictive use, research needs to elucidate the consequences of the potential interdependence between the proposed processes.

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Statement of authorship: All authors designed the study, performed modeling work, and wrote the manuscript.

Data and Code Availability

The code in Mathematica and R supporting the results can be found in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.j27h930>; Song et al. 2019).

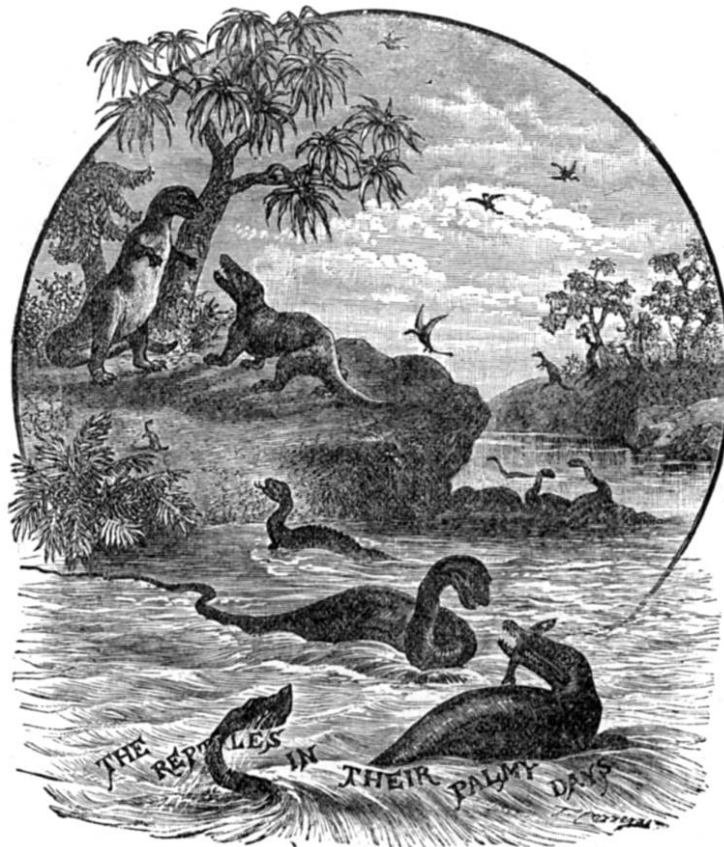
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“It is, moreover, a successful application of the principle of evolution, the theory forming the warp and woof of the work, and thus according with nature, while a wholesome and reverent tone pervades the pages. It is just the book to use in schools as a reader, or for collateral reading by classes in zoölogy.” Figured: “The Reptiles in Their Palmy Days.” From the review of Buckley’s *Winners in Life’s Race* (*The American Naturalist*, 1884, 18:47–50).