

Supplementary Material for  
**On the consequences of the interdependence of stabilizing and  
equalizing mechanisms**  
in *The American Naturalist*

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## 1 The coexistence condition of the 2-species framework

The coexistence criterion in the 2-species framework

$$\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho} \quad (\text{S1})$$

is derived from 2-species Lotka-Volterra dynamics (Chesson 2018). Eqn. S1 is a reformation of  $a_{11} > a_{21}$  and  $a_{22} > a_{12}$  (Vandermeer 1975), which is equivalent to invasibility or global stability of the feasible equilibrium in 2-species Lotka-Volterra dynamics (Goh 1976). Note that the equivalence between invasibility and persistence is a particular feature of 2-species Lotka-Volterra dynamics (Goh 1977). Barabás et al. (2018) have shown that invasibility criteria does not guarantee stable coexistence for many 2-species population dynamics.

Eqn. S1 has been extended to a large class of two-species dynamics based on invasibility (Hart et al. 2018). As the models are different, often the definitions of niche overlap and fitness ratio have to be redefined to yield the expression in Eqn. S1. Here we take the annual plant model (Watkinson 1980) as an example, which has been widely applied in empirical tests of MCT (Levine and HilleRisLambers 2009, Godoy and Levine 2014, Godoy et al. 2014, Siefert et al. 2019). The annual plant model reads

$$\frac{N'_i}{N_i} = (1 - g_i)s_i + \frac{g_i\lambda_i}{1 + \alpha_{ii}g_iN_i + \alpha_{ij}g_jN_j} \quad (\text{S2})$$

(Watkinson 1980), where  $N_i$  ( $N'_i$ ) is the seed abundance in the seedbank in the current (next) year,  $g_i$  is the per-year germination probability,  $s_i$  the annual survival probability in the seedbank,  $\lambda_i$  the annual fecundity, and  $\alpha_{ij}$  competition coefficients. Godoy and Levine (2014) have shown that the invasibility criterion in the annual plant model is equivalent to

$$\tilde{\alpha}_{jj} > \tilde{\alpha}_{ij} \quad (\text{S3})$$

where

$$\tilde{\alpha}_{ij} = \frac{g_j\alpha_{ij}}{\frac{\lambda_i g_i}{1 - (1 - g_i)s_i} - 1} \quad (\text{S4})$$

We recover Eqn. S1 by defining niche overlap and the fitness ratio through Eqns. 6-7 with  $\tilde{\alpha}_{jj}$ . Here invasibility also guarantees the feasibility of the system, as the equilibrium abundances are

$$N_1^* = \frac{\tilde{\alpha}_{22} - \tilde{\alpha}_{12}}{\tilde{\alpha}_{11}\tilde{\alpha}_{22} - \tilde{\alpha}_{12}\tilde{\alpha}_{21}} \quad (\text{S5})$$

$$N_2^* = \frac{\tilde{\alpha}_{11} - \tilde{\alpha}_{21}}{\tilde{\alpha}_{11}\tilde{\alpha}_{22} - \tilde{\alpha}_{12}\tilde{\alpha}_{21}} \quad (\text{S6})$$

Therefore the arguments in the main text apply to the annual plant model.

## 2 Deriving the parameters in MacArthur's consumer-resource model

We evaluate  $r_i$  and  $\beta_{ij}$  in Eqn. 13 with the parameterization  $v_k = 1$ ,  $m_k = 0$ , and  $c_{ik}$  and  $R_k^0$  given by Eqns. 16 and 17, respectively. Keeping in mind that the number of resources is so large and their gradation so fine that the sums can be well approximated by integrals, we can write

$$\begin{aligned}
 r_i &= \sum_{k=1}^L c_{ik} v_k R_k^0 - m_i \\
 &= \sum_{k=1}^L c_{ik} R_k^0 \\
 &= \sum_{k=1}^L \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} \frac{e^{-\frac{x_k^2}{2\omega^2}}}{\sqrt{2\pi\omega^2}} \\
 &\approx \int_{-\infty}^{\infty} \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} \frac{e^{-\frac{x_k^2}{2\omega^2}}}{\sqrt{2\pi\omega^2}} dx_k \\
 &= \frac{e^{-\frac{\mu_i^2}{2(\sigma^2 + \omega^2)}}}{\sqrt{2\pi(\sigma^2 + \omega^2)}}
 \end{aligned} \tag{S7}$$

Here we used the fact that the convolution of two normal distributions is yet another normal distribution with the summed means and variances. Similarly,

$$\begin{aligned}
 \beta_{ij} &= \sum_{k=1}^L c_{ik} c_{jk} v_k \\
 &= \sum_{k=1}^L c_{ik} c_{jk} \\
 &= \sum_{i=1}^L \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} \frac{e^{-\frac{(x_k - \mu_j)^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} \\
 &\approx \int_{-\infty}^{\infty} \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} \frac{e^{-\frac{(x_k - \mu_j)^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} dx_k \\
 &= \frac{e^{-\frac{(\mu_i - \mu_j)^2}{4\sigma^2}}}{\sqrt{4\pi\sigma^2}}.
 \end{aligned} \tag{S8}$$

Since  $a_{ij} = \beta_{ij}/r_i$ , we get

$$a_{ij} = \sqrt{\frac{\omega^2 + \sigma^2}{2\sigma^2}} e^{-\frac{(\mu_i - \mu_j)^2}{4\sigma^2} + \frac{\mu_i^2}{2(\sigma^2 + \omega^2)}} \tag{S9}$$

The niche overlap and fitness ratio have been determined in full generality in Eqns. 14-15. In this particular parameterization, where  $r_i$  is given by Eqn. S7 and  $a_{ij}$  by Eqn. S9, substituting these expressions into Eqns. 6-7 yields the simplified

$$\rho = e^{-\frac{(\mu_1 - \mu_2)^2}{4\sigma^2}} \tag{S10}$$

$$\frac{\kappa_1}{\kappa_2} = \frac{e^{-\frac{\mu_2^2 - \mu_1^2}{2(\sigma^2 + \omega^2)}}}{e^{-\frac{\mu_2^2 - \mu_1^2}{2(\sigma^2 + \omega^2)}}} \tag{S11}$$

### 3 Interdependence in the asymmetric MacArthur consumer-resource model

MacArthur's consumer-resource model makes the assumption that a species' consumption of a resource is proportional to the gain in growth it gets from that resource. The consequence is that interspecific consumer-consumer competition is symmetric. However, species may also eat resources they gain disproportionately little growth from. The biological consequence is that consumption may not necessarily lead to the same proportional consumer gain in population growth for different species.

Translating this into mathematical language, if consumption is  $c_{ik}$ , then growth is given by  $w_{ik}c_{ik}$ . The symmetric MacArthur's consumer-resource model is a special case where  $w_{ik} = v_k$  for all species. Following the notations in the main text,

$$\frac{1}{N_i} \frac{dN_i}{dt} = \sum_{k=1}^L w_{ik}c_{ik}R_k - m_i \quad (i = 1, \dots, S), \quad (\text{S12})$$

$$R_k = R_k^0 - \sum_{j=1}^S c_{jk}N_j \quad (k = 1, \dots, L) \quad (\text{S13})$$

where  $N_i$  and  $m_i$  are species  $i$ 's density and mortality rate, respectively;  $R_k$  is the concentration of resource  $k$ ;  $w_{ik}$  is the efficiency of species  $i$  transforming the consumption of resource  $k$  (i.e., the value of resource  $k$  for species  $i$ );  $c_{ik}$  is species  $i$ 's rate of consumption of resource  $k$ ;  $S$  is the number of consumer species;  $L$  is the number of distinct resources; and  $R_k^0$  is the maximum (saturation) level of resource  $k$  in the absence of consumption.

These yield the basic consumer-resource dynamics,

$$\frac{1}{N_i} \frac{dN_i}{dt} = \underbrace{\left( \sum_{k=1}^L w_{ik}c_{ik}R_k^0 - m_i \right)}_{r_i} - \sum_{j=1}^S \underbrace{\left( \sum_{k=1}^L w_{ik}c_{ik}c_{jk} \right)}_{\beta_{ij}} N_j \quad (\text{S14})$$

For two species, the equations read as

$$\frac{1}{N_1} \frac{dN_1}{dt} = \underbrace{\left( \sum_{k=1}^L w_{1k}c_{1k}R_k^0 - m_1 \right)}_{r_1} - \underbrace{\left( \sum_{k=1}^L w_{1k}c_{1k}^2 \right)}_{\beta_{11}} N_1 - \underbrace{\left( \sum_{k=1}^L w_{1k}c_{1k}c_{2k} \right)}_{\beta_{12}} N_2 \quad (\text{S15})$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = \underbrace{\left( \sum_{k=1}^L w_{2k}c_{2k}R_k^0 - m_2 \right)}_{r_2} - \underbrace{\left( \sum_{k=1}^L w_{2k}c_{2k}c_{1k} \right)}_{\beta_{21}} N_1 - \underbrace{\left( \sum_{k=1}^L w_{2k}c_{2k}^2 \right)}_{\beta_{22}} N_2 \quad (\text{S16})$$

The niche overlap and fitness ratio can be expressed via Eqns. 6-7, taking into account the definition  $a_{ij} = \beta_{ij}/r_i$ :

$$\rho = \frac{\sqrt{(\sum_k w_{1k}c_{1k}c_{2k})(\sum_k w_{2k}c_{1k}c_{2k})}}{\sqrt{(\sum_k w_{1k}c_{1k}^2)(\sum_k w_{2k}c_{2k}^2)}} \quad (\text{S17})$$

$$\frac{\kappa_1}{\kappa_2} = \left( \frac{\sum_k w_{1k}c_{1k}R_k^0 - m_1}{\sum_k w_{2k}c_{2k}R_k^0 - m_2} \right) \sqrt{\frac{(\sum_k w_{2k}c_{2k}^2)(\sum_k w_{2k}c_{2k}c_{1k})}{(\sum_k w_{1k}c_{1k}^2)(\sum_k w_{1k}c_{1k}c_{2k})}} \quad (\text{S18})$$

As in the main text, we also consider a simpler parameterization of the model. We set  $m_i = 0$  and assume that resources form a one-dimensional continuum. The consumption rates  $c_{ik}$  is

$$c_{ik} = \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} \quad (\text{S19})$$

where  $x_k$  is the quality of resource  $k$ . The saturation resource concentrations  $R_k^0$  also follow a normal curve:

$$R_k^0 = \frac{e^{-\frac{x_k^2}{2\omega^2}}}{\sqrt{2\pi\omega^2}} \quad (\text{S20})$$

where  $\omega$  is the width of the resource spectrum. The transformation efficiencies  $w_{ik}$  are

$$w_{ik} = \frac{e^{-\frac{(x_k - \mu_i)^2}{2\tau_i^2}}}{\sqrt{2\pi\tau_i^2}} \quad (\text{S21})$$

With the assumptions above, one can obtain  $\beta_{ij}$  and  $r_i$  from Eqn. S14, by approximating the sums over the one-dimensional resource continuum with integrals:

$$\beta_{ij} = \sum_{k=1}^L w_{ik} c_{ik} c_{jk} \approx \int_{-\infty}^{\infty} w_{ik} c_{ik} c_{jk} dx_k = \frac{\exp\left(-\frac{(\mu_i - \mu_j)^2 (\sigma^2 + \tau_i^2)}{2\sigma^2 (\sigma^2 + 2\tau_i^2)}\right)}{2\pi\sigma\sqrt{\sigma^2 + 2\tau_i^2}} \quad (\text{S22})$$

$$r_i = \sum_{k=1}^L w_{ik} c_{ik} R_k^0 \approx \int_{-\infty}^{\infty} w_{ik} c_{ik} R_k^0 dx_k = \frac{\exp\left(-\frac{\mu_i^2 (\sigma^2 + \tau_i^2)}{2(\sigma^2 (\tau_i^2 + \omega^2) + \tau_i^2 \omega^2)}\right)}{2\pi\sigma\tau_i\omega\sqrt{\frac{1}{\sigma^2} + \frac{1}{\tau_i^2} + \frac{1}{\omega^2}}} \quad (\text{S23})$$

The niche overlap and fitness ratio now read, in this particular parameterization, as

$$\rho = e^{-\frac{(\mu_1 - \mu_2)^2 (2\sigma^4 + 3\sigma^2\tau_2^2 + 3\sigma^2\tau_1^2 + 4\tau_1^2\tau_2^2)}{4\sigma^2(\sigma^2 + 2\tau_1^2)(\sigma^2 + 2\tau_2^2)}} \quad (\text{S24})$$

$$\frac{\kappa_1}{\kappa_2} = e^{\frac{1}{2} \left( \frac{\mu_2^2 (\sigma^2 + \tau_2^2)}{\tau_2^2 (\sigma^2 + \omega^2) + \sigma^2 \omega^2} - \frac{\mu_1^2 (\sigma^2 + \tau_1^2)}{\tau_1^2 (\sigma^2 + \omega^2) + \sigma^2 \omega^2} \right)} \sqrt{\frac{(\tau_2^2 (\sigma^2 + \omega^2) + \sigma^2 \omega^2) \exp\left(-\frac{(\mu_1 - \mu_2)^2 (\sigma^2 + \tau_2^2)}{2\sigma^2 (\sigma^2 + 2\tau_2^2)}\right)}{\sigma^2 + 2\tau_2^2}}{\frac{(\tau_1^2 (\sigma^2 + \omega^2) + \sigma^2 \omega^2) \exp\left(-\frac{(\mu_1 - \mu_2)^2 (\sigma^2 + \tau_1^2)}{2\sigma^2 (\sigma^2 + 2\tau_1^2)}\right)}{\sigma^2 + 2\tau_1^2}}} \quad (\text{S25})$$

(obtained from Eqns. 6-7 and  $a_{ij} = \beta_{ij}/r_i$ ). Considering the interdependence of the two terms in this model, we find a similar pattern to what we see for the symmetric MacArthur model (Figure S1).

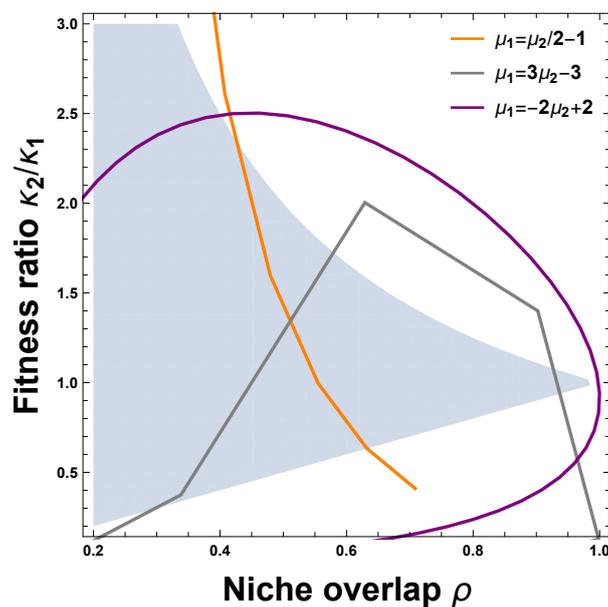


Figure S1: **Interdependence of stabilizing and equalizing mechanisms in the 2-species asymmetric MacArthur consumer-resource model.** The solid lines show how three different hypothesized relationships between mechanistic parameters generate qualitatively different relationships between niche overlap and the fitness ratio. The blue region denotes combinations of fitness ratio and niche overlap compatible with coexistence, based on Eqn. 8. Parameters:  $\sigma = 1$ ,  $\omega = 1/2$ ,  $\tau_1 = 0.4$ ,  $\tau_2 = 10$ .

## 4 Interdependence in Tilman's consumer-resource model

Here we consider the model of two consumers competing for two substitutable resources (Tilman 1982),

$$\frac{dN_1}{dt} = r_1 N_1 \left[ \frac{w_{11}R_1 + w_{12}R_2 - T_1}{k_1 + w_{11}R_1 + w_{12}R_2 - T_1} \right] - DN_1 \quad (\text{S26})$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[ \frac{w_{21}R_1 + w_{22}R_2 - T_2}{k_2 + w_{21}R_1 + w_{22}R_2 - T_2} \right] - DN_2 \quad (\text{S27})$$

$$\frac{dR_1}{dt} = D(S_1 - R_1) - c_{11}N_1 - c_{21}N_2 \quad (\text{S28})$$

$$\frac{dR_2}{dt} = D(S_2 - R_2) - c_{12}N_1 - c_{22}N_2 \quad (\text{S29})$$

The niche overlap and fitness ratio are (see derivation in Letten et al. (2017), Ke and Letten (2018)):

$$\rho = \frac{\sqrt{(c_{21}\omega_1 + c_{22})(c_{11}\omega_2 + c_{12})}}{\sqrt{(c_{11}\omega_1 + c_{12})(c_{21}\omega_2 + c_{22})}} \quad (\text{S30})$$

$$\frac{\kappa_1}{\kappa_2} = A \frac{\sqrt{(c_{11}\omega_1 + c_{12})(c_{21}\omega_1 + c_{22})}}{\sqrt{(c_{21}\omega_2 + c_{22})(c_{11}\omega_2 + c_{12})}} \quad (\text{S31})$$

where  $\omega_1 = w_{11}/w_{12}$ ,  $\omega_2 = w_{21}/w_{22}$  and  $A = \frac{\left( S_2 + \frac{w_{21}}{w_{22}} S_1 - \left[ \frac{D(k_2 - T_2) + r_2 T_2}{w_{22}(r_2 - D)} \right] \right)}{\left( S_2 + \frac{w_{11}}{w_{12}} S_1 - \left[ \frac{D(k_1 - T_1) + r_1 T_1}{w_{12}(r_1 - D)} \right] \right)}$ . Interdependence patterns are shown in Figure S2.

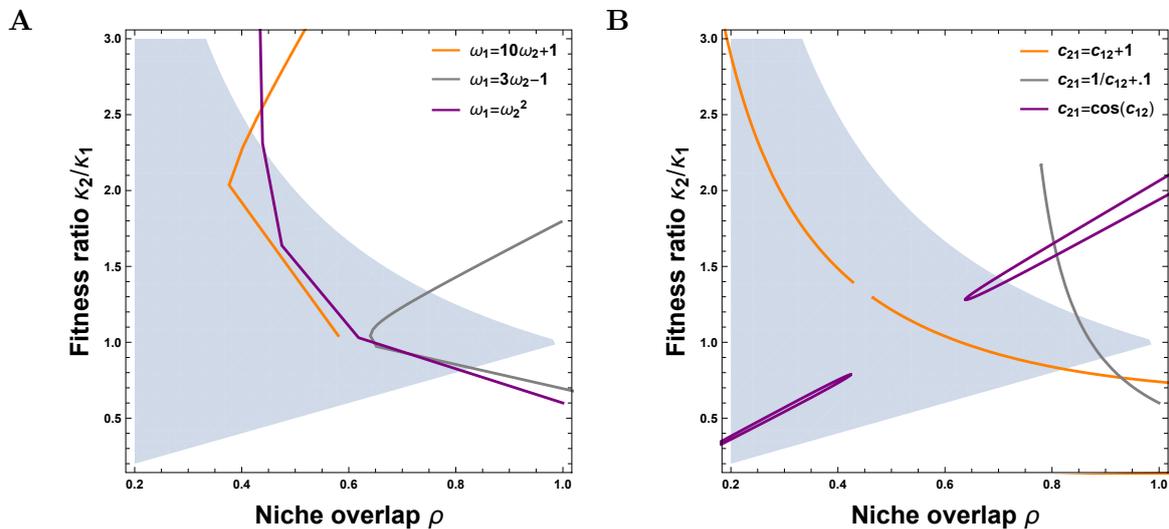


Figure S2: **Interdependence of stabilizing and equalizing mechanisms in the 2-species Tilman model.** The solid lines show how three different hypothesized relationships between mechanistic parameters generate qualitatively different relationships between niche overlap and fitness difference. The blue region shows combinations of the fitness ratio and niche overlap compatible with coexistence, based on Eqn. 8. Note how the system may even behave discontinuously (panel B, orange line). Parameters:  $D = 0.7$ ,  $k_1 = k_2 = 0.4$ ,  $r_1 = r_2 = 1$ ,  $T_1 = T_2 = 0.1$ .

## 5 Interdependence of mechanisms in MacArthur's consumer-resource model with unequal niche widths

We have focused our analysis on equal niche widths  $\sigma$  in the main text. Here we study the effect of species-specific niche widths.

### 5.1 Model setup

The model and its parameterization is the same as in Supplement 2, except that consumption is now given by

$$c_{ik} = \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma_i^2}}}{\sqrt{2\pi\sigma_i^2}} \quad (\text{S32})$$

with the niche width being potentially species-dependent (Fig. S3). The derivation for  $r_i$  and  $a_{ij}$  in Supplement 2 must now be repeated assuming distinct niche widths:

$$\begin{aligned} r_i &= \sum_{k=1}^L c_{ik} v_k R_k^0 - m_i \\ &= \sum_{k=1}^L c_{ik} R_k^0 \\ &= \sum_{k=1}^L \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma_i^2}}}{\sqrt{2\pi\sigma_i^2}} \frac{e^{-\frac{x_k^2}{2\omega^2}}}{\sqrt{2\pi\omega^2}} \\ &\approx \int_{-\infty}^{\infty} \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma_i^2}}}{\sqrt{2\pi\sigma_i^2}} \frac{e^{-\frac{x_k^2}{2\omega^2}}}{\sqrt{2\pi\omega^2}} dx_k \\ &= \frac{e^{-\frac{\mu_i^2}{2(\sigma_i^2 + \omega^2)}}}{\sqrt{2\pi(\sigma_i^2 + \omega^2)}} \end{aligned} \quad (\text{S33})$$

and

$$\begin{aligned} \beta_{ij} &= \sum_{k=1}^L c_{ik} c_{jk} v_k \\ &= \sum_{k=1}^L c_{ik} c_{jk} \\ &= \sum_{i=1}^L \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma_i^2}}}{\sqrt{2\pi\sigma_i^2}} \frac{e^{-\frac{(x_k - \mu_j)^2}{2\sigma_j^2}}}{\sqrt{2\pi\sigma_j^2}} \\ &\approx \int_{-\infty}^{\infty} \frac{e^{-\frac{(x_k - \mu_i)^2}{2\sigma_i^2}}}{\sqrt{2\pi\sigma_i^2}} \frac{e^{-\frac{(x_k - \mu_j)^2}{2\sigma_j^2}}}{\sqrt{2\pi\sigma_j^2}} dx_k \\ &= \frac{e^{-\frac{(\mu_i - \mu_j)^2}{2(\sigma_i^2 + \sigma_j^2)}}}{\sqrt{2\pi(\sigma_i^2 + \sigma_j^2)}} \end{aligned} \quad (\text{S34})$$

From these,  $a_{ij} = \beta_{ij}/r_i$  reads

$$a_{ij} = \sqrt{\frac{\sigma_i^2 + \omega^2}{\sigma_i^2 + \sigma_j^2}} e^{\frac{\mu_i^2}{2(\sigma_i^2 + \omega^2)} - \frac{(\mu_i - \mu_j)^2}{2(\sigma_i^2 + \sigma_j^2)}} \quad (\text{S35})$$

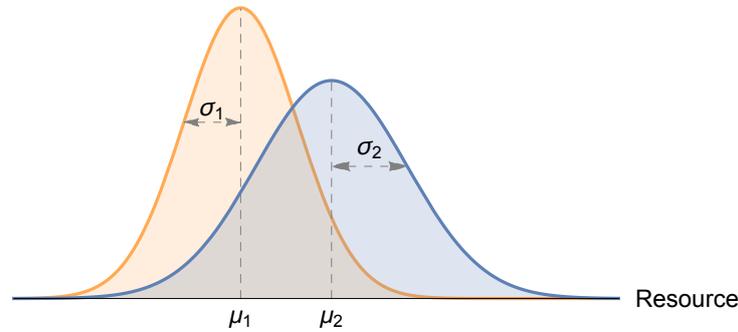


Figure S3: **Illustration of MacArthur's consumer-resource model with unequal niche widths.** The figure shows the resource consumption curves  $c_{1k}$  and  $c_{2k}$  of two competing species. Each species's curve maximizes consumption at some preferred niche position  $\mu$  and decays with a characteristic length  $\sigma$ . The resource overlap between the two species (shaded area) is proportional to the strength of interspecific competition (Eqn. 13).

## 5.2 Derivation of the niche overlap and the fitness ratio

The niche overlap and fitness ratio (Eqns. 6-7) are computed using Eqn. S35 as

$$\rho = \frac{\sqrt{2}}{\sqrt{\frac{\sigma_1}{\sigma_2} + \frac{\sigma_2}{\sigma_1}}} e^{-\frac{(\mu_1 - \mu_2)^2}{2(\sigma_1^2 + \sigma_2^2)}} \quad (\text{S36})$$

$$\frac{\kappa_1}{\kappa_2} = \sqrt{\frac{\sigma_1(\sigma_2^2 + \omega^2)}{\sigma_2(\sigma_1^2 + \omega^2)}} e^{\frac{\mu_2^2}{2(\sigma_2^2 + \omega^2)} - \frac{\mu_1^2}{2(\sigma_1^2 + \omega^2)}} \quad (\text{S37})$$

To simplify the problem further, here we look at the limit where the saturation concentration  $R_k^0$  of each resource is equal. This will happen when  $\omega \rightarrow \infty$  (Eqn. 17). Eqn. S37 then reduces to the simple

$$\frac{\kappa_1}{\kappa_2} = \sqrt{\frac{\sigma_1}{\sigma_2}} \quad (\text{S38})$$

In this limit therefore, species fitness can be identified with  $\sqrt{\sigma_i}$ . That is, the niche width is the only fundamental parameter determining  $\kappa_i$ , so it can be understood as an intrinsic property of species  $i$ . In contrast, the niche overlap  $\rho$  (Eqn. S36) is a function of both the niche centers  $\mu_i$  and niche widths  $\sigma_i$ . Note that  $\rho$  is smaller when the  $\sigma$ 's decrease (species are more specialized) or when  $|\mu_1 - \mu_2|$  is larger (species' diets are more different).

In this model and parameterization, we found that fitness defined in MCT is an intrinsic property of species, which is different from the common definition of fitness that is fundamentally dependent on other species (Vellend 2016). We have also found that niche overlap  $\rho$  is dependent on niche width  $\sigma$ , which does not agree with the statement that " $\rho$  is independent of how well the species are adapted to the environment." (Chesson 2012) as the evolution of niche width  $\sigma$  is widely taken as a sign of adaptation (Sexton et al. 2017).

### 5.3 The interdependence of niche overlap and fitness ratio

To investigate the potential relationship between stabilizing and equalizing mechanisms, we can recall that in MacArthur's niche model, species' niche widths ( $\sigma_1$ ,  $\sigma_2$ ) are key determinants for both niche overlap  $\rho$  (Eqn. S36) and fitness ratio  $\kappa_1/\kappa_2$  (Eqn. S38). Therefore, the only situation under which the stabilizing mechanism can act independently from the equalizing mechanism is when  $\kappa_1/\kappa_2$  remains fixed, which implies that species could only change their difference between preferred niches relative to a species' niche width, i.e.,  $|\mu_1 - \mu_2|/\sigma_2$  (note that  $\sigma_1/\sigma_2$  also needs to remain fixed). Similarly, the only situation under which the equalizing mechanism can act independently from the stabilizing mechanism is when the difference in preferred niches  $|\mu_1 - \mu_2|$  relative to a species' niche width has exactly the value given by the nonlinear pattern (see Section 5.4)

$$\frac{|\mu_1 - \mu_2|}{\sigma_2} = \left(\frac{\kappa_1}{\kappa_2}\right)^2 \frac{|\mu_1 - \mu_2|}{\sigma_1} = \sqrt{\left(1 + \left(\frac{\kappa_1}{\kappa_2}\right)^4\right) \left[\log\left(\frac{2}{\rho^2}\right) - \log\left(\frac{1 + (\kappa_1/\kappa_2)^4}{(\kappa_1/\kappa_2)^2}\right)\right]} \quad (\text{S39})$$

This pattern can be quite complex depending on the fixed value of niche overlap  $\rho$  (see Fig. S4). Therefore, it is highly unlikely that these two mechanisms are independent.

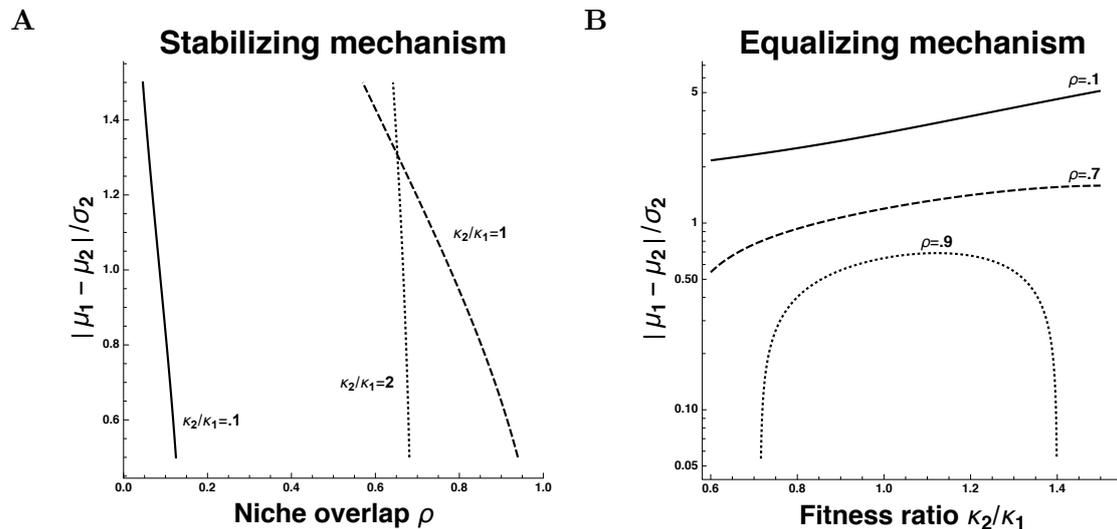


Figure S4: **Condition for independence between stabilizing and equalizing mechanisms.** In order for one mechanism to act independently from the other mechanism, the quantity  $|\mu_2 - \mu_1|/\sigma_2$  (the difference in preferred niche relative to a species' niche width) has to follow a complex pattern depending on the fixed fitness ratio  $\kappa_1/\kappa_2$  (Panel A) or niche overlap  $\rho$  (Panel B). This shows that the dependence of the two mechanisms would emerge under all but the most restrictive assumptions.

Additionally, Fig. S5 shows that by simply varying the relationship between niche widths  $\sigma_1$  and  $\sigma_2$ , the stabilizing and equalizing mechanisms can exhibit either a positive, null, negative, or non-monotonic dependence. For example, the horizontal lines in the figure correspond to the relationships between  $\sigma_1$  and  $\sigma_2$ , where only the stabilizing mechanism operates to achieve coexistence. Instead in the relationship depicted by the red curve, by going from no coexistence to coexistence the system may need to first exhibit an anti-equalizing mechanism (and an anti-stabilizing mechanism) and then an equalizing mechanism (and a stabilizing mechanism). However, if the system is already inside the coexistence domain, the stabilizing and equalizing mechanisms cannot be performed simultaneously below a critical point (intersection of the curve line with the fitness equivalence line). Note that the relationship depicted by the orange curve is

similar to the red curve but in the opposite direction. Finally, in the relationship depicted by the black curve, depending on the direction over which the fitness difference deviates from 1 (rather than the magnitude only), the stabilizing mechanism can promote or hinder coexistence. While all these curves are theoretical, Fig. S5 shows that the dependence of the two mechanisms can significantly alter their effects on species coexistence.

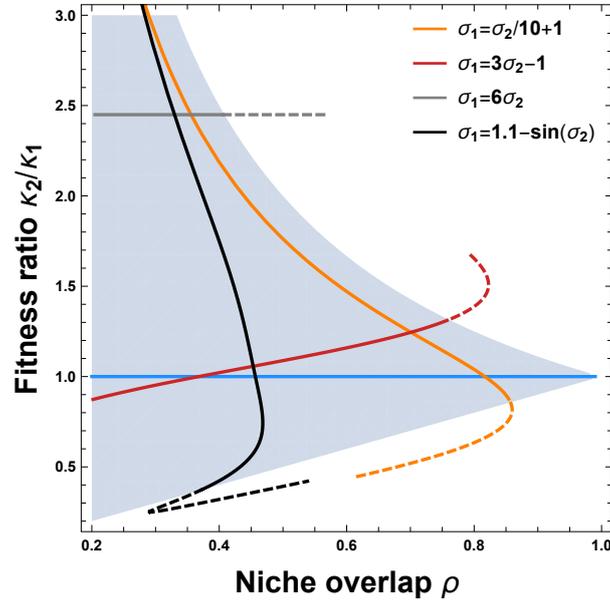


Figure S5: **Effect of the dependence between stabilizing and equalizing mechanisms on species coexistence.** The figure shows the niche overlap and fitness difference space, and their combinations under which two competing species can achieve coexistence (gray region). The blue horizontal line corresponds to the fitness equivalence. All the other lines in the figure show how four simple hypothetical relationships (legend) between species' niche widths ( $\sigma_1, \sigma_2$ ) can generate a null, positive, negative, or non-monotonic relationship between the stabilizing and equalizing mechanisms following MacArthur's consumer-resource model. Note that the effects of the mechanisms on species coexistence can be either in the same or opposite directions. This shows that the sign and magnitude of the effects are dictated by the type of dependence between the two mechanisms.

#### 5.4 Derivation of Eqn. S39

In order for the equalizing mechanism to act independently, the niche overlap  $\rho$  needs to be a specific constant. With the notation  $k = \kappa_1/\kappa_2$ , this constant is derived as

$$\rho = \frac{\sqrt{2}}{\sqrt{\frac{\sigma_1}{\sigma_2} + \frac{\sigma_2}{\sigma_1}}} e^{-\frac{(\mu_1 - \mu_2)^2}{2(\sigma_1^2 + \sigma_2^2)}} \quad (\text{S40})$$

$$\Rightarrow \log(\rho) = \log\left(\frac{\sqrt{2}}{\sqrt{k^2 + k^{-2}}}\right) - \frac{(\mu_1 - \mu_2)^2}{2\sigma_2^2(1 + k^4)} \quad (\text{S41})$$

$$\Rightarrow \frac{(\mu_1 - \mu_2)^2}{\sigma_2^2} = (1 + k^4) \left[ \log(2/\rho^2) - \log(k^2 + k^{-2}) \right] \quad (\text{S42})$$

## 6 Conditions for the independence of stabilizing and equalizing mechanisms in MacArthur's consumer-resource model

Here we show the unique conditions needed to make the stabilizing and equalizing contributions independent in MacArthur's consumer-resource model. The niche overlap and fitness ratio, in the parameterization of Supplement 2, read

$$\rho = e^{-\frac{(\mu_1 - \mu_2)^2}{4\sigma^2}} \quad (\text{S43})$$

$$\frac{\kappa_1}{\kappa_2} = e^{\frac{\mu_2^2 - \mu_1^2}{2(\sigma^2 + \omega^2)}} \quad (\text{S44})$$

Stabilizing mechanisms reduce the niche overlap  $\rho$ , while equalizing mechanisms reduce the fitness ratio  $\kappa_1/\kappa_2$ . If the two mechanisms are independent, then the niche overlap and fitness ratio can change independently. Because the niche centers  $\mu_i$ , niche width  $\sigma$ , and resource spectrum width  $\omega$  together determine their interdependence, we study the constraints on each parameter compatible with the independence of the two terms.

First, we assume that only the niche center  $\mu_i$  can change. Then the equalizing mechanism requires that  $|\mu_1 - \mu_2|$  is a constant while fitness difference changes as  $\log \frac{\kappa_1}{\kappa_2} \propto (\mu_1 + \mu_2) \text{sign}(\mu_1 - \mu_2)$ . The stabilizing mechanism requires that  $\mu_2^2 - \mu_1^2$  is a constant  $c$  while the niche overlap changes as  $\log \rho \propto \frac{\sqrt{\mu_2^2 + c - \mu_2}}{\sqrt{\mu_2^2 + c + \mu_2}}$  or  $\log \rho \propto \frac{\sqrt{\mu_2^2 + c + \mu_2}}{\sqrt{\mu_2^2 + c - \mu_2}}$ .

Second, we assume that only the niche width  $\sigma$  can change. Then, both equalizing and stabilizing mechanisms cannot be independent because fixing either  $\rho$  or  $\sigma$  requires fixing  $\sigma$  and automatically the other term is also fixed.

Third, we assume that only the resource spectrum width  $\omega$  can change. Then, the equalizing mechanism cannot be reduced given that  $\omega$  contributes only to  $\kappa_1/\kappa_2$ . Instead, the stabilizing mechanism can be reduced only at a fixed level of niche overlap.

From these three cases, it is evident that some mechanisms cannot happen under certain conditions, and even if they can, it is not easy to interpret these constraints in an ecologically meaningful way. Importantly, we have assumed that only one parameter is changing. If multiple parameters are allowed to change simultaneously, which is likely the case in nature, one would get even more complicated constraints.

## 7 Correlation between niche overlap and fitness ratio is not informative of the interdependence between stabilizing and equalizing mechanisms

Figure S6 shows that the correlation between niche overlap and fitness ratio does not reveal the level of interdependence between stabilizing and equalizing effects. In particular, regardless of the relationship between species' niche centers  $\mu_i$ , the resulting phenomenological correlation patterns are broad and non-indicative of the underlying process. The niche overlap and fitness ratio are written in the parameterization of Supplement 2:

$$\rho = e^{-\frac{(\mu_1 - \mu_2)^2}{4\sigma^2}} \quad (\text{S45})$$

$$\frac{\kappa_1}{\kappa_2} = \frac{\mu_2^2 - \mu_1^2}{e^{2(\sigma^2 + \omega^2)}} \quad (\text{S46})$$

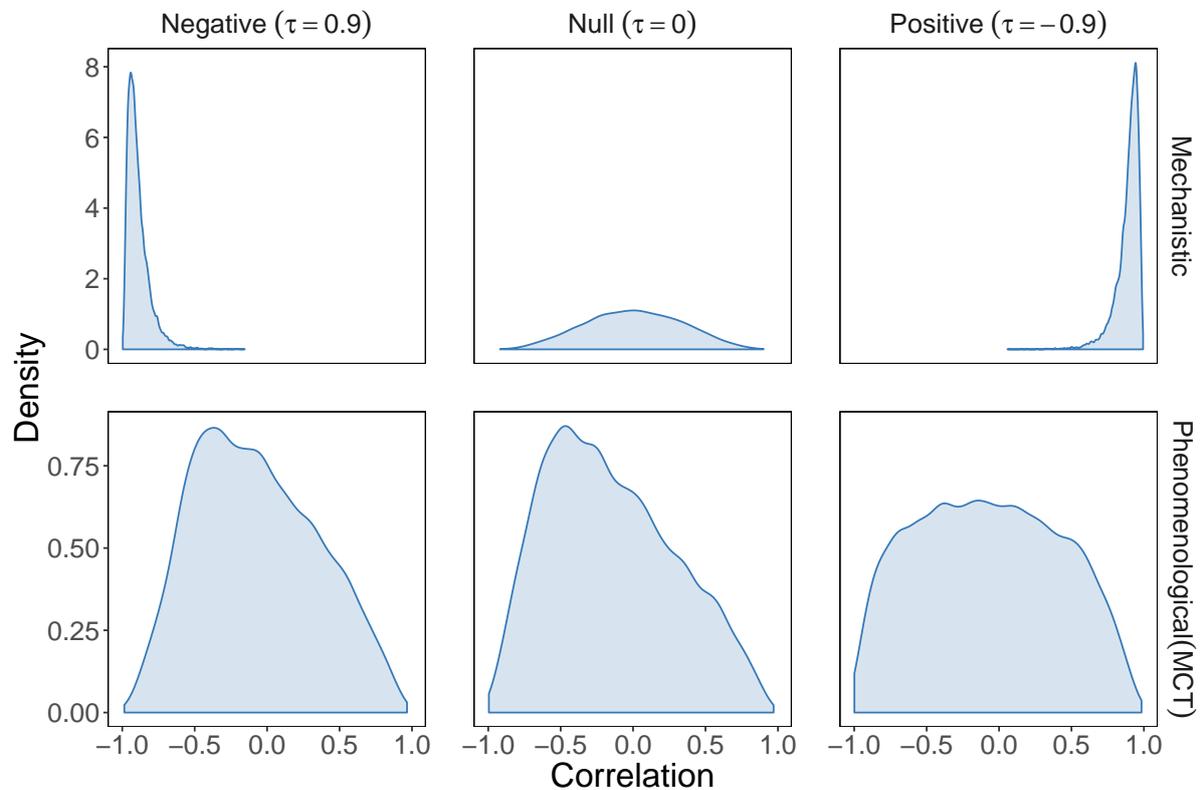


Figure S6: The distributions in the upper three panels show the relationship between the niche centers  $\mu_1$  and  $\mu_2$ , exhibiting negative (left), null (middle), and positive (right) interdependence. The distributions in the lower three panels show the corresponding correlations between the niche overlap  $\rho$  and fitness ratio  $\kappa_1/\kappa_2$ . Regardless of the relationship between the niche centers, the correlations always range from  $-1$  to  $1$ , with the signal of the original relationship completely washed out. Parameter values:  $\sigma = 1$ ,  $\omega = 1/2$ , and  $\mu_1$  and  $\mu_2$  are jointly sampled from a bivariate normal distribution with marginal means  $(0, 0)$ , marginal variances  $(1, 1)$ , and correlation  $\tau$  equal to  $-9/10$  (left),  $0$  (middle), or  $9/10$  (right).

## 8 Examples of the dependence between niche overlap and the fitness ratio in MacArthur's consumer-resource model

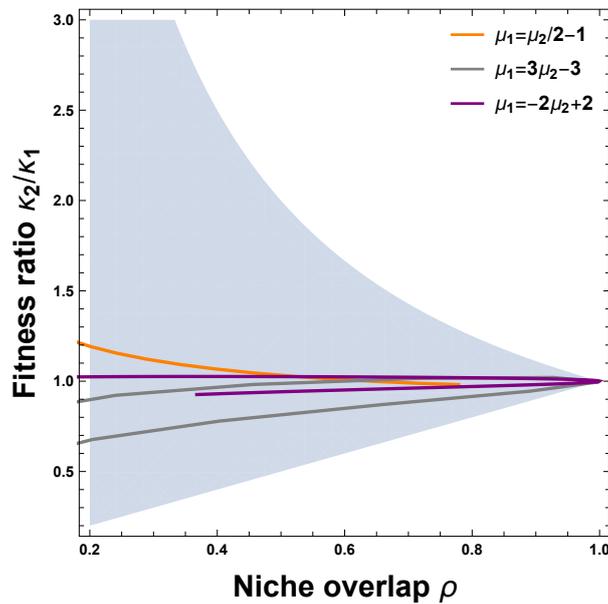


Figure S7: Same as Fig. 3 but with  $\sigma = 1$  and  $\omega = 5$ . Species almost always coexist under this condition.

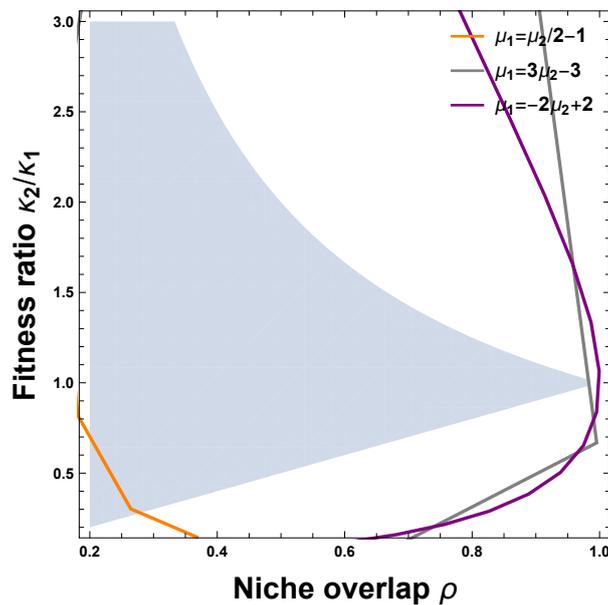


Figure S8: Same as Fig. 3 but with  $\sigma = 1/2$  and  $\omega = 1/10$ . Species almost never coexist under this condition.

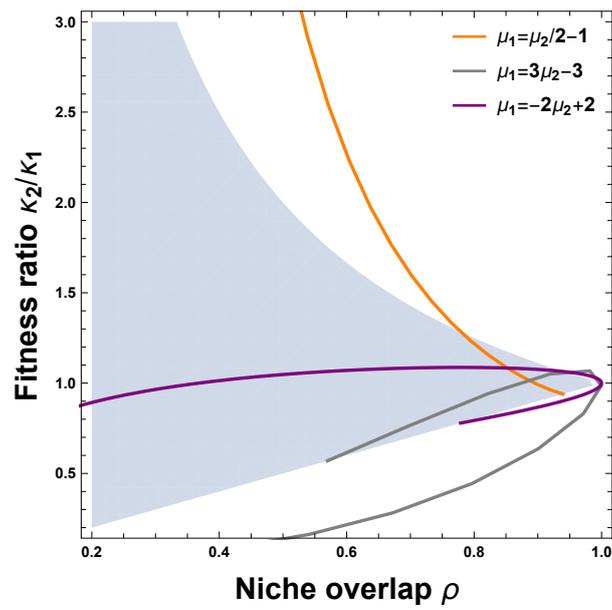


Figure S9: Same as Fig. 3 but with  $\sigma = 2$  and  $\omega = 2$ . Both coexistence and exclusion are possibilities under this condition.

## 9 Derivation of the lower bound of species similarity

Using Eqns. 18-19 and assuming similar species, we Taylor expand  $\rho$ ,  $1/\rho$ , and  $\kappa_1/\kappa_2$  in  $\mu_2$  around  $\mu_1$  to leading order:

$$\rho \approx 1 - \frac{\Delta\mu^2}{4\sigma^2} \quad (\text{S47})$$

$$\frac{1}{\rho} \approx 1 + \frac{\Delta\mu^2}{4\sigma^2} \quad (\text{S48})$$

$$\frac{\kappa_1}{\kappa_2} \approx 1 + \frac{\mu_1\Delta\mu}{\sigma^2 + \omega^2} \quad (\text{S49})$$

where  $\Delta\mu = \mu_2 - \mu_1$ . The coexistence condition Eqn. 8 then translates to

$$1 - \frac{\Delta\mu^2}{4\sigma^2} < 1 + \frac{\mu_1\Delta\mu}{\sigma^2 + \omega^2} < 1 + \frac{\Delta\mu^2}{4\sigma^2} \quad (\text{S50})$$

or

$$-\Delta\mu < \frac{4\mu_1\sigma^2}{\sigma^2 + \omega^2} < \Delta\mu \quad (\text{S51})$$

Compactly, this can be written as the single necessary condition

$$|\Delta\mu| > \frac{4|\mu_1|\sigma^2}{\sigma^2 + \omega^2} \quad (\text{S52})$$

The right hand side is a nonnegative constant which does not depend on  $\Delta\mu$ . It is equal to 0 if and only if  $\mu_1 = 0$ . In every other case, there is a minimum difference  $\Delta\mu$  between the two species' niche centers below which the inequality is violated and coexistence is lost.

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