nature ecology & evolution

SUPPLEMENTARY INFORMATION

https://doi.org/10.1038/s41559-018-0679-z

In the format provided by the authors and unedited.

Coexistence theory and the frequency-dependence of priority effects

Po-Ju Ke[1,4*] **and Andrew D. Letten**[1,2,3,4*]

[1]Department of Biology, Stanford University, Stanford, CA, USA. [2]Centre for Integrative Ecology, University of Canterbury, Christchurch, New Zealand. [3]Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland. [4]These authors contributed equally: Po-Ju Ke,
Andrew D. Letten. *e-mail: pojuke@stanford.edu; andrew.letten@usys.ethz.ch

Supplementary Information:
Coexistence theory and the frequency-dependence of priority effects

Po-Ju Ke[1] and Andrew D. Letten[1,2,3]

[1]Department of Biology, Stanford University, Stanford, California, 94305-5020, USA
[2]Centre for Integrative Ecology, University of Canterbury, Christchurch, New Zealand
[3]Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zürich, 8092 Zürich, Switzerland

Positive frequency dependence in an equilibrium system

In Figure 1 in the main text we provided an example of PFD emerging from resource competition in an equilibrium system. To produce Figure 1 we used the approach implemented in Letten *et al.* (2017) [1] to translate changes in the parameters of Tilman's consumer-resource model [2] into changes to the stabilization potential and fitness ratio of coexistence theory (but see [3] and [4] for an alternative approach). In this part of the supplementary methods we explain the underlying mathematical treatment.

The key to the approach in [1] is to solve the coexistence equilibrium of a consumer resource model and rearrange it algebraically to a form that is comparable to the equilibrium of a two species Lotka-Volterra competition model. To better understand the procedure, consider a Lotka-Volterra competition model for two consumer species (i.e. N_1 and N_2):

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - a_{11} N_1 - a_{12} N_2\right), \tag{S1.1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - a_{21} N_1 - a_{22} N_2\right). \tag{S1.2}$$

This simple model has two monoculture fixed point of either species, i.e., $N_i = \frac{1}{\alpha_{ii}}$, as well as a coexistence fixed point that simultaneously fulfills $N_1^* = \frac{1}{a_{11}} - \frac{a_{12}}{a_{11}} N_2^*$ and $N_2^* = \frac{1}{a_{22}} - \frac{a_{21}}{a_{22}} N_1^*$. In panel c of the figure in Box 1, we demonstrate that the coexistence fixed point is the only stable equilibrium with the following parameters: $r_1 = r_2 = 0.1$, $\alpha_{12} = 0.96$, $\alpha_{21} = 0.8$, and $\alpha_{11} = \alpha_{22} = 1.4$. In panel a of the figure in Box 1, alternative stable states, such that the competition outcome is one of the two monoculture fixed point depending on species' initial density, can emerge when $\alpha_{11} = \alpha_{22} = 0.64$. To demonstrate alternative stable states, we started trajectories from either higher density of N_1 (upper panels: $N_{1(0)} = 1$, $N_{2(0)} = 0.2$) or N_2 (lower panels: $N_{1(0)} = 0.2$, $N_{2(0)} = 1$).

For Figure 1, we take Tilman's model [2, p. 270] where two consumers (i.e. N_1 and N_2) are competing for two perfectly substitutable resources, R_1 and R_2, and solve for its coexistence equilibrium. The dynamics of this system can be described as

follows:

$$\frac{dN_1}{dt} = r_1 N_1 \left[\frac{w_{11}R_1 + w_{12}R_2 - T_1}{k_1 + w_{11}R_1 + w_{12}R_2 - T_1} \right] - DN_1, \tag{S2.1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[\frac{w_{21}R_1 + w_{22}R_2 - T_2}{k_2 + w_{21}R_1 + w_{22}R_2 - T_2} \right] - DN_2, \tag{S2.2}$$

$$\frac{dR_1}{dt} = D\left(S_1 - R_1\right) - c_{11}N_1 - c_{21}N_2, \tag{S2.3}$$

$$\frac{dR_2}{dt} = D\left(S_2 - R_2\right) - c_{12}N_1 - c_{22}N_2. \tag{S2.4}$$

Here, r_i represents the maximum population growth rate for species i ($i = 1$ or 2) and D represents the constant mortality of the consumers and turnover rate of resources. Per capita resource consumption rate of consumer N_i on resource R_j ($j = 1$ or 2) is represented by c_{ij}, whereas w_{ij} represents a weighting factor that converts availability of R_j into its value for consumer N_i. Following a Monod growth model, k_i is the half-saturation constant for N_i resource consumption, and T_i is the minimum amount of total resource required for N_i to grow. Finally, S_1 and S_2 represent the resource supply concentrations for R_1 and R_2, respectively. Certain assumptions of this Monod growth model, such as constant supply of resource and strong recipient control of consumption rate, may not be applicable to many systems. However, this should not affect the results qualitatively [4].

The coexistence equilibrium of the model in Eqns. (S2.1) to (S2.4) was solved in [2, p. 270]. In brief, we obtained the consumer's zero net growth isolines (ZNGIs), which represent resource combinations of R_1 and R_2 that cause each consumer's growth to equal its mortality, by setting consumer dynamics to zero:

$$R_2 = -\frac{w_{11}}{w_{12}} R_1 + B_1, \tag{S3.1}$$

$$R_2 = -\frac{w_{21}}{w_{22}} R_1 + B_2. \tag{S3.2}$$

where $B_1 = \left[\frac{D(k_1 - T_1) + r_1 T_1}{w_{12}(r_1 - D)}\right]$, and $B_2 = \left[\frac{D(k_2 - T_2) + r_2 T_2}{w_{21}(r_2 - D)}\right]\left(\frac{w_{21}}{w_{22}}\right)$. The equilibrium resource densities, R_1^* and R_2^*, were solved as the crossing point of the two ZNGIs. By substituting the solution into Eqns. (S2.3) and (S2.4), we obtained the equilibrium consumer densities, N_1^* and N_2^*. More importantly, we rearranged N_1^* and N_2^* in a form comparable to that of the Lotka-Volterra model. For N_1, the specific relationship of its equilibrium density can be derived by Eqn.(S2.3)$\times\frac{w_{11}}{w_{12}}$+Eqn.(S2.4), whereas that for N_2 can be derived by Eqn.(S2.3)$\times\frac{w_{21}}{w_{22}}$+Eqn.(S2.4):

$$N_1^* = \left[\frac{D\left(S_2 + \frac{w_{11}}{w_{12}} S_1 - B_1\right)}{c_{12} + c_{11}\frac{w_{11}}{w_{12}}}\right] - \left[\frac{c_{22} + c_{21}\frac{w_{11}}{w_{12}}}{c_{12} + c_{11}\frac{w_{11}}{w_{12}}}\right] N_2^*, \tag{S4.1}$$

$$N_2^* = \left[\frac{D\left(S_2 + \frac{w_{21}}{w_{22}} S_1 - B_2\right)}{c_{22} + c_{21}\frac{w_{21}}{w_{22}}}\right] - \left[\frac{c_{12} + c_{11}\frac{w_{21}}{w_{22}}}{c_{22} + c_{21}\frac{w_{21}}{w_{22}}}\right] N_1^*. \tag{S4.2}$$

We can see that Eqns. (S4.1) and (S4.2) consists of a first component only with N_1- and N_2-related parameters, respectively, and a second heterospecific density-dependent component which decreases with the density of its competitor. By comparing Eqns. (S4.1) and (S4.2) to the expression for a two species Lotka-Volterra competition model (i.e. $N_1^* = \frac{1}{a_{11}} - \frac{a_{12}}{a_{11}} N_2^*$ and $N_2^* = \frac{1}{a_{22}} - \frac{a_{21}}{a_{22}} N_1^*$), one can find the algebraic equivalents for a_{ij} as follows:

$$a_{11} = \frac{c_{12} + c_{11}\frac{w_{11}}{w_{12}}}{D\left(S_2 + \frac{w_{11}}{w_{12}} S_1 - B_1\right)}, \tag{S5.1}$$

$$a_{12} = \frac{c_{22} + c_{21}\frac{w_{11}}{w_{12}}}{D\left(S_2 + \frac{w_{11}}{w_{12}} S_1 - B_1\right)}, \tag{S5.2}$$

$$a_{22} = \frac{c_{22} + c_{21}\frac{w_{21}}{w_{22}}}{D\left(S_2 + \frac{w_{21}}{w_{22}}S_1 - B_2\right)}, \tag{S5.3}$$

$$a_{21} = \frac{c_{12} + c_{11}\frac{w_{21}}{w_{22}}}{D\left(S_2 + \frac{w_{21}}{w_{22}}S_1 - B_2\right)}. \tag{S5.4}$$

To this point, we have successfully expressed the phenomenological competition coefficients in terms of mechanistic consumer resource parameters. More importantly, the specific algebraic treatment applied to obtain Eqn. (S4) resulted in biologically meaningful expressions of the competition coefficients. In particular, the intra-specific competition coefficients (i.e. Eqns. (S5.1) and (S5.3)) only consist of mechanistic parameters of the focal species whereas the inter-specific competition coefficients (i.e. Eqns. (S5.2) and (S5.4)) includes parameters of the competitor.

Once the consumer resource model was translated to a Lotka-Volterra form, we can proceed to our second step: quantify niche overlap and fitness ratio based on specific formulas [5, 6]. In particular, for the two species Lotka-Volterra competition model, Peter Chesson defines niche overlap as $\rho = \sqrt{\frac{a_{12}a_{21}}{a_{11}a_{22}}}$ and fitness ratio as $\frac{f_2}{f_1} = \sqrt{\frac{a_{11}a_{12}}{a_{22}a_{21}}}$ [7]. For our specific consumer resource model, we can express these two components of coexistence theory with mechanistic consumer resource parameters as follows:

$$\rho = \sqrt{\frac{a_{12}a_{21}}{a_{11}a_{22}}} = \sqrt{\frac{\left(c_{22} + c_{21}\frac{w_{11}}{w_{12}}\right)\left(c_{12} + c_{11}\frac{w_{21}}{w_{22}}\right)}{\left(c_{12} + c_{11}\frac{w_{11}}{w_{12}}\right)\left(c_{22} + c_{21}\frac{w_{21}}{w_{22}}\right)}}, \tag{S6.1}$$

$$\frac{f_2}{f_1} = \sqrt{\frac{a_{11}a_{12}}{a_{22}a_{21}}} = \frac{\left(S_2 + \frac{w_{21}}{w_{22}}S_1 - B_2\right)}{\left(S_2 + \frac{w_{11}}{w_{12}}S_1 - B_1\right)}\sqrt{\frac{\left(c_{12} + c_{11}\frac{w_{11}}{w_{12}}\right)\left(c_{22} + c_{21}\frac{w_{11}}{w_{12}}\right)}{\left(c_{22} + c_{21}\frac{w_{21}}{w_{22}}\right)\left(c_{12} + c_{11}\frac{w_{21}}{w_{22}}\right)}}. \tag{S6.2}$$

In Figure 1 in the main text we plotted the ZNGI (i.e. eqns. (S3.1) and (S3.2)), the consumption vectors (species 1 in red and species 2 in blue), and the supply point. The consumption vectors for consumer i on the two substitutable resources is a vector with elements (c_{i1}, c_{i2}), and the supply point can be expressed as a point with coordinates (S_1, S_2). To study the effects of changing consumer resource parameters on stabilization potential (defined as 1 - ρ in the main text) and fitness ratio, we varied species' per capita consumption rates, c_{ij}, and the supply point. To keep the position of the ZNGIs fixed, we set the following parameters as: $D = 0.7$, $k_1 = k_2 = 0.4$, $r_1 = r_2 = 1$, $T_1 = T_2 = 0.1$, $w_{11} = w_{22} = 2$, and $w_{12} = w_{21} = 4$.

In panel (a) and (b), each species consumes more of its favored resource but with different degree of resource partitioning. The per capita consumption rates in panel (a) are $c_{11} = c_{22} = 2$ and $c_{21} = c_{12} = 4$, whereas that in panel (b) are $c_{11} = c_{22} = 2.843$ and $c_{21} = c_{12} = 3.452$. In panel (c) and (d), each species now consumes more of the resource favored by its competitor with $c_{11} = c_{22} = 3.552$ and $c_{21} = c_{12} = 2.718$. This potentially leads to priority effects depending on the fitness ratio between the two species, which can be altered by modifying the supply point from the black circle $(0.3, 0.38)$ to the black square $(0.248, 0.245)$.

Positive frequency dependence in an non-equilibrium system

In Figure 2 in the main text we provide an example of PFD emerging through the coexistence-affecting mechanism relative non-linearity. In this example two consumers compete for a single logistically-growing resource. One species has a type 3 functional response (blue in Fig. 2), given by:

$$\frac{dN_1}{dt} = N_1(\mu_{max_1}\frac{R^2}{Ks_1 + R^2} - d). \tag{S7.1}$$

The other species (red in Fig. 2) has a modified Monod (type 2) functional response with inhibition at high resource levels:

$$\frac{dN_2}{dt} = N_2(\mu_{max_2}\frac{R}{Ks_2 + R + \frac{R^2}{Ki}} - d). \tag{S7.2}$$

Here, N_i is the population density of consumer i ($i = 1$ or 2), μ_{max_i} is the maximum growth rate, Ks_i is the half saturation constant, R is the density/concentration of resource, d is the density independent mortality rate, and Ki is the inhibition term unique to the second species.

Resource dynamics are given by:

$$\frac{dR}{dt} = rR(1 - \frac{R}{K}) - \sum_{i=1}^{n} Q_i \frac{\mathrm{d}N_i}{\mathrm{d}t}, \qquad i = 1, 2, \tag{S7.3}$$

where r is the resource intrinsic rate of increase, K is the resource carrying capacity and Q_i is the resource quota of consumer i.

We used the following values for the parameters in Figure 2: $\mu_{max_1} = 0.029$, $\mu_{max_2} = 0.2$, $Ks_1 = 0.02$, $Ks_2 = 3$, $d = 0.01$, $Ki = 1$, $r = 0.5$, $K = 3$, $Q_1 = 0.01$ and $Q_2 = 0.01$. Simulations were run with the LSODA solver using the deSolve package v1.20 [8] in R v3.4.2. In Fig. 2b, the simulation was started with starting population sizes of 500 and 1 for blue and red respectively. In Fig 2c, the simulation was started with starting population sizes of 1 and 500 for blue and red respectively.

References

[1] Letten, A.D. *et al.* (2017) Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs* 87, 161–177

[2] Tilman, D. (1982) *Resource Competition and Community Structure. (Mpb-17).* Princeton University Press, Princeton, NJ, USA

[3] Meszéna, G. *et al.* (2006) Competitive exclusion and limiting similarity: a unified theory. *Theor. Popul. Biol.* 69, 68–87

[4] Kleinhesselink, A.R. and Adler, P.B. (2015) Indirect effects of environmental change in resource competition models. *Am. Nat.* 186, 766–776

[5] Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366

[6] Godoy, O. *et al.* (2014) Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.* 17, 836–844

[7] Chesson, P. (2013) Species Competition and Predation. In R. Leemans, ed., *Ecological Systems*. Springer New York, pp. 223–256

[8] Soetaert, K. *et al.* (2016) Package desolve