Appendixes

Online Appendix A: Model Description and Non-dimensionalization

Our model tracks the dynamics of a one way cross-feeding interaction between two populations: a producer, $A$, of a metabolic by-product, $E$, and a cross-feeder (non-producer), $B$. Building on the competitive Lotka-Volterra model, our model explicitly captures the dynamics of the two strategists as well as the cross-feeding by-product and is defined by the following system of ordinary differential equations:

\[
\begin{align*}
\frac{da}{dt} &= (r_a(1 - (a + \beta b)/k_a) - fe)a \\
\frac{db}{dt} &= (r_b(1 - (\gamma a + b)/k_b) + ghe)b \\
\frac{de}{dt} &= ya - heb - ue
\end{align*}
\]

(A1)

The above system can be rewritten in non-dimensional form (see Table A1 for a full description of the non-dimensional quantities) (Segel 1972, Murray 2002), and the non-dimensional system becomes:

\[
\begin{align*}
\frac{dA}{dt} &= (r(1 - \alpha A - \beta B) - fE) A \\
\frac{dB}{dt} &= ((1 - \gamma A - B) + ghE) B \\
\frac{dE}{dt} &= yA - heb - uE
\end{align*}
\]

(A2)

The densities of producer ($A$) and cross-feeder ($B$) are scaled to the carrying capacity of $B$ ($k_b$), and the individual intrinsic growth rates are scaled to the intrinsic growth
rate of $B (r_h)$. We assume that the by-product enhances the cross-feeder’s growth, and this (indirect) benefit is described by $gh$, where $h$ represents the by-product consumption rate by the cross-feeder and $g$ is a conversion constant, which can be viewed as the cross-feeder’s uptake efficiency of the by-product. In contrast, the by-product inhibits the producer’s growth at a constant rate $f$. $u$ represents the by-product decay rate, and $y$ represents the rate of the by-product production by the producer. $\alpha$ is the producer’s intraspecific competition coefficient, and measures the degree of competition among the population of producers relative to the competition among the population of cross-feeders ($\alpha = k_d/k_u$, see Table A1). $\beta$ is the cross-feeder’s interspecific competition coefficients on the producer, and $\gamma$ is the producer’s interspecific competition coefficients on the cross-feeder, thus $\beta$ and $\gamma$ measure the competitive effect of $B$ on $A$ and $A$ on $B$, respectively. Note that when $f = g = h = y = u = 0$, we recover the classic competitive Lotka-Volterra equations.
Table A1. Parameters description and respective dimensionless parameters

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Dimension</th>
<th>Dimensionless parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>Producer</td>
<td>Mass</td>
<td>$A = a/k_a$</td>
</tr>
<tr>
<td>$b$</td>
<td>Cross-feeder and non-producer</td>
<td>Mass</td>
<td>$B = b/k_b$</td>
</tr>
<tr>
<td>$e$</td>
<td>Metabolic by-product</td>
<td>Mass</td>
<td>$E = e/k_b$</td>
</tr>
<tr>
<td>$r_a, r_b$</td>
<td>Intrinsic growth rate of A and B, respectively</td>
<td>Time$^{-1}$</td>
<td>$r = r_a/r_b$</td>
</tr>
<tr>
<td>$k_a, k_b$</td>
<td>Carrying capacity of A and B, respectively</td>
<td>Mass</td>
<td>$\alpha = k_b/k_a$</td>
</tr>
<tr>
<td>$\beta, \gamma$</td>
<td>Interspecific competition coefficients of A and B, respectively</td>
<td>-</td>
<td>$\beta = \beta k_b/k_a$</td>
</tr>
<tr>
<td>$f$</td>
<td>By-product toxicity rate</td>
<td>mass$^{-1}.time^{-1}$</td>
<td>$f = f k_b/r_b$</td>
</tr>
<tr>
<td>$h$</td>
<td>Consumption rate of by-product</td>
<td>mass$^{-1}.time^{-1}$</td>
<td>$h = h k_b/r_b$</td>
</tr>
<tr>
<td>$y$</td>
<td>By-product production rate</td>
<td>time$^{-1}$</td>
<td>$y = y/r_b$</td>
</tr>
<tr>
<td>$g$</td>
<td>Cross-feeder uptake efficiency (of by-product)</td>
<td>constant</td>
<td>-</td>
</tr>
<tr>
<td>$u$</td>
<td>By-product decay rate</td>
<td>time$^{-1}$</td>
<td>$u = u/r_b$</td>
</tr>
<tr>
<td>$t$</td>
<td>Time</td>
<td>time</td>
<td>$t = t r_b$</td>
</tr>
</tbody>
</table>
Appendix B: Model Equilibria and Stability Analysis

An equilibria analysis of model A2 (Otto and Day 2007) reveals that the system has six equilibria (denoted by \( A^* \), \( B^* \), \( C^* \)). Two equilibria are biologically invalid (note that we assume that all parameters are positive),

\[
A^* = 0, B^* = 0, C^* = 0, \text{ and } A^* = 0, B^* = -u/h, C^* = -(h + u)/gh^2.
\]

Four equilibria are biologically valid. The producer only equilibrium is

\[
A^* = ru/(aru + fy), E^* = ry/(aru + fy), B^* = 0.
\]

The cross-feeder only equilibrium is

\[
B^* = 1, A^* = 0, E^* = 0,
\]

Coexistence equilibria 1 and 2 that we denote by \( A_1^* \), \( B_1^* \),\( E_1^* \) and \( A_2^* \), \( B_2^* \), \( E_2^* \) take the form:

\[
A_{1,2}^* = (A' - z\sqrt{C}) / (2hr (\alpha - \beta\gamma) (f\gamma + argh))
\]

\[
B_{1,2}^* = (A' - \sqrt{C}) / (2hr (\alpha - \beta\gamma)) \quad (B1)
\]

\[
E_{1,2}^* = (A - \sqrt{C}) / (2h (f\gamma + argh))
\]

and,

\[
A_{2,2}^* = (A' - z\sqrt{C}) / (2hr (\alpha - \beta\gamma) (f\gamma + argh))
\]

\[
B_{2,2}^* = (A' + \sqrt{C}) / (2hr (\alpha - \beta\gamma)) \quad (B2)
\]

\[
E_{2,2}^* = (A + \sqrt{C}) / (2h (f\gamma + argh))
\]
where
\[ C = -4rhy(β-1)(fγ + argh) + [ru(α - βγ) + rh(α - γ) + (f + rghβ)y]², \]
\[ z = (f + rghβ), \]
\[ A = rh(γ - α) + ru(βγ - α) - y(f + rghβ), \]
\[ A' = A - 2rh(γ - α), \]
\[ A'' = fγ + ghr² (2haα - haβ + uαβ + ghyβ² - β(h + uβ) γ) + rf(h(α + 2gyβ + γ - 2βγ) + u(α - βγ)) \]
(B3)

From the expressions for the coexistence equilibria we can note that if \( α = γβ \) the equilibria no longer exist rather than being inaccessible. This suggests that there is no coexistence if the product of intraspecific competition is equal to the product of interspecific competition. Also, it should be noted that there is a small parameter space where equilibrium 1 \( (A_1^*, B_1^*, E_1^*) \) and equilibrium 2 \( (A_2^*, B_2^*, E_2^*) \) are both accessible (results not shown).

The stability analysis of Model A2 reveals that the producer alone equilibrium is locally stable when \( u > y(f + rgh)/(r(γ - α)) \) (i.e. \( u \) threshold for pure \( A^* \) stability) and \( α < γ \). The cross-feeder alone equilibrium is locally stable when \( β > 1 \). Thus for sufficiently high interspecific competition of the cross-feeder on the producer, a rare population of producers cannot invade a resident population of cross-feeders. The stability analysis of the coexistence equilibria is difficult to perform analytically, so we investigated their stability using numerical simulations. In sum, our analytical and numerical analyses (fig. B1) suggest that the model is mostly defined by four main regions: i) Pure producer is locally stable, thus a rare population of cross-feeder
cannot invade a resident population of producers. This region is defined by $\beta < 1$ and $u >$ threshold for pure $A^*$ stability. None of the coexistence equilibria are accessible. (Figure B1A, B); ii) Pure cross-feeder is locally stable, thus a rare population of producer cannot invade a resident population of cross-feeder. This region is defined by $\beta > 1$ and $u <$ threshold for pure $A^*$ stability. Both coexistence equilibria 1 and 2 may be accessible for some parameter space, but they are unstable. Any small perturbation of the initial conditions moves the system to the pure cross-feeder equilibrium. (Figure B1A, C); iii) Stable coexistence. $\beta < 1$ and $u <$ threshold for pure $A^*$ stability, where coexistence equilibrium 2 is accessible and stable, while coexistence equilibrium 1 is non-accessible (Figure B1A, D); iv) Bistability region. This region is defined by $\beta > 1$ and $u >$ threshold for $A$ stability. Coexistence equilibrium 1 is attainable but unstable (i.e. a repellor), and is associated with a separatrix that passes through it, and this separatrix subdivides the phase plane space into the two basins of attraction associated with the two attractors (i.e. locally stable pure $A^*$ and locally stable pure $B^*$ equilibria). Whether the system approaches a pure producer or pure cross-feeder equilibrium will depend on initial conditions. Any small perturbation of the initial conditions moves the system to either the pure producer or pure cross-feeder equilibrium (Figure B1A, E, F). While not discussed here, it should be noted that limit cycles (populations oscillations) are also a possible outcome. Numerical simulations suggest that limit cycles may occur when the parameters that govern the by-product dynamics are significantly lower than the effect of competition (e.g. there is a stable limit cycle under the following parameter values, $r = 1$, $\alpha = 0.8$, $\gamma = 1$, $g = 1$, $f = 0.1$, $y = 0.03$, $h = 0.01$, $\beta = 0.9$ and $u = 0.002$). However, this
limit cycle is stable (results not shown), and this means that the equilibrium is also stable, therefore, our results would not be affected by the presence of this limit cycle.

**Figure B1.** Illustration of the stability conditions for the equilibria of the cross-feeding model. 

A, Diagram illustrating the four main regions of equilibria stability. Black region, pure producer is locally stable. White region, pure cross-feeder is locally stable. Stable coexistence region, coexistence equilibrium 2 is stable and attainable (the contour lines represent the proportion of producer \( p = A^* / (A^* + B^*) \) at coexistence equilibrium 2). Bistability region (i.e. either A or B invades), coexistence equilibrium 1 is accessible but unstable (the dashed lines represent the repellor value \( p^* = A^* / (A^* + B^*) \) at coexistence equilibrium 1). The grey horizontal
line represents the threshold of pure $B^*$ stability ($\beta = 1$), and the grey vertical line represents the value of $u$ threshold for pure $A^*$ stability ($u = y(f + rgh)/(r(\gamma - \alpha))$, see text for more details). B-F, Temporal dynamics of the densities of producer and cross-feeder for parameter values falling in B, the stable pure producer region ($\beta = 0.8, u = 9, A_0 = 0.9$ and $B_0 = 0.1$); C, the stable pure cross-feeder region ($\beta = 1.2, u = 6, A_0 = 0.1$ and $B_0 = 0.9$); D, the stable coexistence region ($\beta = 0.8, u = 6, A_0 = 0.5$ and $B_0 = 0.5$); and the bistability region ($\beta = 1.1$ and $u = 10$) when E, the producer invades ($A_0 = 0.85$ and $B_0 = 0.15$), and F, the cross-feeder invades ($A_0 = 0.80$ and $B_0 = 0.20$). Unless stated otherwise, the parameters used are $r = 1, \alpha = 0.9, \gamma = 1, g = 1, f = 0.01, y = 1$, and $h = 0.8, E_0 = 0.01$. 
Figure C1. Effect of the demographic, environmental, and metabolic parameters on mutualism. Each dashed and full line represents the threshold where $A_B^* = A_a^*$, and $B_A^* = B_a^*$, respectively, for a given set of parameter values. Mutualism is defined by the region below the dashed line and on the right of the filled line. When not otherwise specified the parameters used for the plots are $r = 1$, $\alpha = 0.9$, $\gamma = 1$, $g = 1$, $u$
= 0.1, f = 0.1, and y = 1.5. A, Mutualism is favoured by higher by-product production rate (higher y). Each line represents a different values of y such that y = [1.5, 2, 2.5, 3] from light to dark respectively; B, Mutualism is favoured by higher by-product toxicity (higher f). Each line represents a different values of f such that f = [0.01, 0.05, 0.1, 0.5] from light to dark respectively. Note that $B_A^* = B_a^*$ is independent on f (see text for more details); C, Mutualism is favoured by lower relative growth rate (lower r). Each line represents a different values of r such that r = [0.2, 0.5, 1, 1.5] from light to dark respectively. Note that $B_A^* = B_a^*$ is independent on r (see text for more details); D, Mutualism is favoured by a more durable by-product (lower u). Each line represents a different values of u such that u = [0.01, 0.05, 0.1, 0.2] from light to dark respectively.
Figure C2. Effect of by-product toxicity ($f$) on densities of producer when grown alone and in coculture with the cross-feeder ($A_a^*$ and $A_b^*$, respectively), and on densities of cross-feeder when grown alone and in coculture with the producer ($B_a^*$ and $B_a^*$, respectively). The grey line indicates the frontier between cross-feeder exploits producer and mutualism. The parameter values used are $r = 1$, $\alpha = 0.9$, $\beta = 0.2$, $\gamma = 1$, $g = 1$, $h = 0.8$, $u = 0.2$, and $y = 1.5$. 
Figure C3. Effect of relative growth rate ($r$) on densities of producer when grown alone and in coculture with the cross-feeder ($A_a^*$ and $A_b^*$, respectively), and on densities of cross-feeder when grown alone and coculture with the producer ($B_a^*$ and $B_A^*$, respectively). A, cross-feeder does not benefit from association ($h = 0.05$). The grey line indicates the frontier between competition and $A$ exploits $B$. B, cross-feeder benefits form association ($h = 0.3$). The grey line indicates the frontier between $B$ exploits $A$ and mutualism. The other parameter values used for the plots are $\alpha = 0.9$, $\beta = 0.2$, $\gamma = 1$, $g = 1$, $u = 0.1$, $f = 0.1$ and $y = 2$. 