Multiple friends with benefits: An optimal mutualist management strategy?

Supplementary Material

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List of Appendices:

Appendix A: Model Analysis

Analytical Model Verification

To verify that the model follows biological intuition, we consider a one-tree, one-fungus equilibrium. Imagine that environmental conditions are constant (i.e., N = total nutrients = $N_S + N_T$; $N_S = N - N_T$). From dN_T/dT we find:

$$\begin{aligned}
\frac{dN_T}{dT} &= 0 = (N - N_T)\, e_1 F_1 - m_N N_T && \text{(A1)}\\
N_T\,(m_N + e_1 F_1) &= N e_1 F_1 && \text{(A2)}\\
N_T^* &= \frac{N e_1 F_1}{m_N + e_1 F_1}. && \text{(A3)}
\end{aligned}$$

As fungal efficiency, e_1, and fungal abundance, F_1, increase, N_T^* approaches N.

At equilibrium, F_T, the total number of tree root tips, is constant. When there is only one fungal species occupying tips of type F_1, we have $F_T = F_0 + F_1$, so $F_0 = F_T - F_1$. From dF_1/dT we have:

$$\begin{aligned}
\frac{dF_1}{dT} &= 0 = \frac{F_T - F_1}{F_T} r_1 F_1 - m_1 F_1 && \text{(A4)}\\
r_1\,(F_T - F_1) &= m_1 F_T && \text{(A5)}\\
F_1^* &= F_T \frac{(r_1 - m_1)}{r_1} = F_T \left(1 - \frac{m_1}{r_1}\right), && \text{(A6)}
\end{aligned}$$

so the proportion of colonized tips, F_1/F_T, approaches 1 as fungal mortality, m_1, decreases, and as fungal reproductive rate, r_1, increases.

Substituting for r_1:

$$F_1^* = F_T \left[1 - \frac{m_1}{b_1\left(\frac{\eta_1 H}{k_1 + H} + 1\right)}\right] = F_T \left[1 - \frac{m_1\,(k_1 + H)}{b_1\,(\eta_1 H + k_1 + H)}\right] \qquad \text{(A7)}$$

we see that for a positive equilibrium fungal abundance, we must have

$$b_1(\eta_1 H + k_1 + H) > m_1 k_1 + m_1 H \tag{A8}$$

$$H > k_1\left(\frac{m_1 - b_1}{b_1\eta_1 + b_1 - m_1}\right), \tag{A9}$$

which gives a lower bound for one of the tree's controls, H.

Because at equilibrium the total number of root tips, F_T, is constant, the rate of root tip production, G, must equal the rate of tip mortality, $m_1 F_1$. Thus, there is a direct relationship between the tree control on root tip production, and fungal tip colonization: $G = m_1 F_1$. We can substitute this relationship for G, and our equilibrium value for N_T^*, into dB/dT to obtain:

$$\frac{dB}{dT} = 0 = p\frac{Ne_1F_1}{m_N + e_1F_1} - m_B B - (w_1 + H)F_1 - c_1 m_1 F_1 \tag{A10}$$

$$m_B B = p\frac{Ne_1F_1}{m_N + e_1F_1} - (w_1 + H)F_1 - c_1 m_1 F_1 \tag{A11}$$

$$B^* = F_1\left[\frac{pNe_1 - (w_1 + H + c_1 m_1)(m_N + e_1F_1)}{m_B(m_N + e_1F_1)}\right]. \tag{A12}$$

Note that: (1) B^* increases with increasing photosynthetic rate, p, and decreases with increasing tree respiration rate, m_B, and increasing cost terms (c_1, H, and w_1); (2) When $F_1 = 0$, $B^* = 0$, so that the tree cannot survive without a fungal partner to provide nutrients; and (3) Because the expression for B^* is quadratic in F_1, it is quadratic in the control G, and there will be some optimal value $\hat{G}$ at which B is maximized.

Optimization Approach

To maximize the objective function, we employ Pontryagin's Maximum Principle, which tells us that the allocation of tree carbon to root tip growth (g) and fungal rewards (h_i) that maximizes the objective function also maximizes the Hamiltonian:

$$H = be^{-\delta t} + \lambda_b\frac{db}{dt} + \lambda_0\frac{df_0}{dt} + \sum_i \lambda_i\frac{df_i}{dt} + \lambda_T\frac{dn_T}{dt} + \lambda_S\frac{dn_S}{dt} \tag{A13}$$

at every time t.

In addition, the state and adjoint variables satisfy the adjoint equations:

$$\frac{\partial \lambda_b}{\partial t} = -\frac{\partial H}{\partial b} \tag{A14}$$

$$\frac{\partial \lambda_0}{\partial t} = -\frac{\partial H}{\partial f_0} \tag{A15}$$

$$\frac{\partial \lambda_i}{\partial t} = -\frac{\partial H}{\partial f_i} \tag{A16}$$

$$\frac{\partial \lambda_T}{\partial t} = -\frac{\partial H}{\partial n_T} \tag{A17}$$

$$\frac{\partial \lambda_S}{\partial t} = -\frac{\partial H}{\partial N_S} \tag{A18}$$

These adjoint equations represent the shadow values (i.e., the values associated with the preservation) of photosynthetic biomass, the root tip pools, and the nutrient stocks, respectively. At the end of the timeframe of analytical interest (i.e., when $t = t_{end}$), these shadow values are therefore zero, giving the transversality condition $\lambda_b(t_{end}) = \lambda_0(t_{end}) = \lambda_i(t_{end}) = \lambda_T(t_{end}) = \lambda_S(t_{end}) = 0$. The other boundary conditions (the initial conditions for the state variables b, f_0, f_i, n_T and n_S) are assigned at the beginning of the analysis.

Furthermore, by setting $\partial H/\partial g = 0$ and $\partial H/\partial h_i = 0$, we can determine the positive values of the controls which maximize the Hamiltonian and, therefore, the objective function. In the two-fungus case (Main Text Equations 9-15), the tree has three optimal controls, $g(t)$, $h_1(t)$, and $h_2(t)$, which it can vary in time to maximize the objective function. The Hamiltonian and adjoint equations, respectively, are:

$$
\begin{aligned}
H &= be^{-\delta t} + \lambda_b \left[n_T - b - \left[\omega_1 + h_1(t)\right] f_1 - \left[\omega_2 + h_2(t)\right] f_2 - g(t)\left[1 + \phi g(t)\right]\right] \\
&\quad + \lambda_0 \left[-\frac{f_0}{f_0 + f_1 + f_2} \left(\rho_1(t) f_1 + \rho_2(t) f_2\right) + g(t) - \mu_0 f_0 \right] \\
&\quad + \lambda_1 \left[\frac{f_0}{f_0 + f_1 + f_2} \rho_1(t) f_1 - \mu_1 f_1 \right] + \lambda_2 \left[\frac{f_0}{f_0 + f_1 + f_2} \rho_2(t) f_2 - \mu_2 f_2 \right] \\
&\quad + \lambda_T \left[n_S \left(\epsilon_1 f_1 + \epsilon_2 f_2\right) - \mu_N n_T\right] + \lambda_S \left[\alpha \cos\left(\frac{2\pi}{t_{end}} \nu t \right) - \frac{dn_T}{dt} \right] \qquad \text{(A19)}
\end{aligned}
$$

$$
\frac{d\lambda_b}{dt} = -\frac{\partial H}{\partial b} = \lambda_b - e^{-\delta t} \qquad \text{(A20)}
$$

$$
\frac{d\lambda_0}{dt} = -\frac{\partial H}{\partial f_0} = \frac{f_1 + f_2}{\left(f_0 + f_1 + f_2\right)^2} \left[\lambda_0 \left(\rho_1 f_1 + \rho_2 f_2\right) - \lambda_1 \rho_1 f_1 - \lambda_2 \rho_2 f_2\right] + \mu_0 \lambda_0 \qquad \text{(A21)}
$$

$$
\begin{aligned}
\frac{d\lambda_1}{dt} &= -\frac{\partial H}{\partial f_1} = \left(\lambda_0 - \lambda_1\right) \left[\frac{f_0 \left(f_0 + f_2\right)}{\left(f_0 + f_1 + f_2\right)^2} \rho_1 \right] + \left(\lambda_2 - \lambda_0\right) \left[\frac{f_0 f_2 \rho_2}{\left(f_0 + f_1 + f_2\right)^2} \right] \\
&\quad + \lambda_1 \mu_1 + \left(\lambda_S - \lambda_T\right) n_S \epsilon_1 + \lambda_b \left(\omega_1 + h_1\right) \qquad \text{(A22)}
\end{aligned}
$$

$$
\begin{aligned}
\frac{d\lambda_2}{dt} &= -\frac{\partial H}{\partial f_2} = \left(\lambda_0 - \lambda_2\right) \left[\frac{f_0 \left(f_0 + f_1\right)}{\left(f_0 + f_1 + f_2\right)^2} \rho_2 \right] + \left(\lambda_1 - \lambda_0\right) \left[\frac{f_0 f_1 \rho_1}{\left(f_0 + f_1 + f_2\right)^2} \right] \\
&\quad + \lambda_2 \mu_2 + \left(\lambda_S - \lambda_T\right) n_S \epsilon_2 + \lambda_b \left(\omega_2 + h_2\right) \qquad \text{(A23)}
\end{aligned}
$$

$$
\frac{d\lambda_T}{dt} = -\frac{\partial H}{\partial n_T} = \left(\lambda_T - \lambda_S\right) \mu_N - \lambda_b \qquad \text{(A24)}
$$

$$
\frac{d\lambda_S}{dt} = -\frac{\partial H}{\partial n_S} = \left(\lambda_S - \lambda_T\right) \left(\epsilon_1 f_1 + \epsilon_2 f_2\right) \qquad \text{(A25)}
$$

By setting $\partial H / \partial g = 0$, we obtain:

$$
g^* = \frac{\lambda_0 - \lambda_b}{2\phi \lambda_b} \qquad \text{(A26)}
$$

Because g^* can take on only positive values, and because based on the transversality condition and adjoint equations we know that $\lambda_b \geq 0$ for $0 \leq t \leq t_{end}$, we have the relation:

$$
g^* = \begin{cases} 0, & \text{if } \lambda_0 \leq 0 \\ \max\left(0, \frac{\lambda_0 - \lambda_b}{2\phi \lambda_b}\right), & \text{if } \lambda_0 > 0 \end{cases}
$$

For the second optimal control, setting $\partial H/\partial h_i = 0$ gives:

$$h_i^* = \pm\sqrt{\frac{(\lambda_i - \lambda_0)\, f_0 f_i \beta_i \kappa_i \eta_i}{(f_0 + f_i)\, \lambda_b f_i}} - \kappa_i \tag{A27}$$

Because h_i^* can take on only positive values and $\lambda_b \geq 0$, we have the relation:

$$h_i^* = \begin{cases} \max\left(0, \sqrt{\dfrac{(\lambda_i - \lambda_0)\, f_0 f_i \beta_i \kappa_i \eta_i}{(f_0 + f_i)\, \lambda_b f_i}} - \kappa_i\right), & \text{if } \lambda_i > \lambda_0 \\ 0, & \text{if } \lambda_0 \geq \lambda_i \end{cases}$$

Thus, the tree's decision to provide supplemental carbon to fungus i depends upon the relative shadow values of colonized and uncolonized root tips. Rewards are allocated only when the future benefits of colonized root tips (i.e., λ_i) exceed the future value of uncolonized roots (i.e., λ_0) by a margin that satisfies the above condition (for an example, see Figure B7).

Because of the complexity of our model, we used numerical methods to solve these equations for constant and variable environmental conditions, to determine the host tree's optimal investment strategy in its fungal partners.

Appendix B: Supplemental Figures

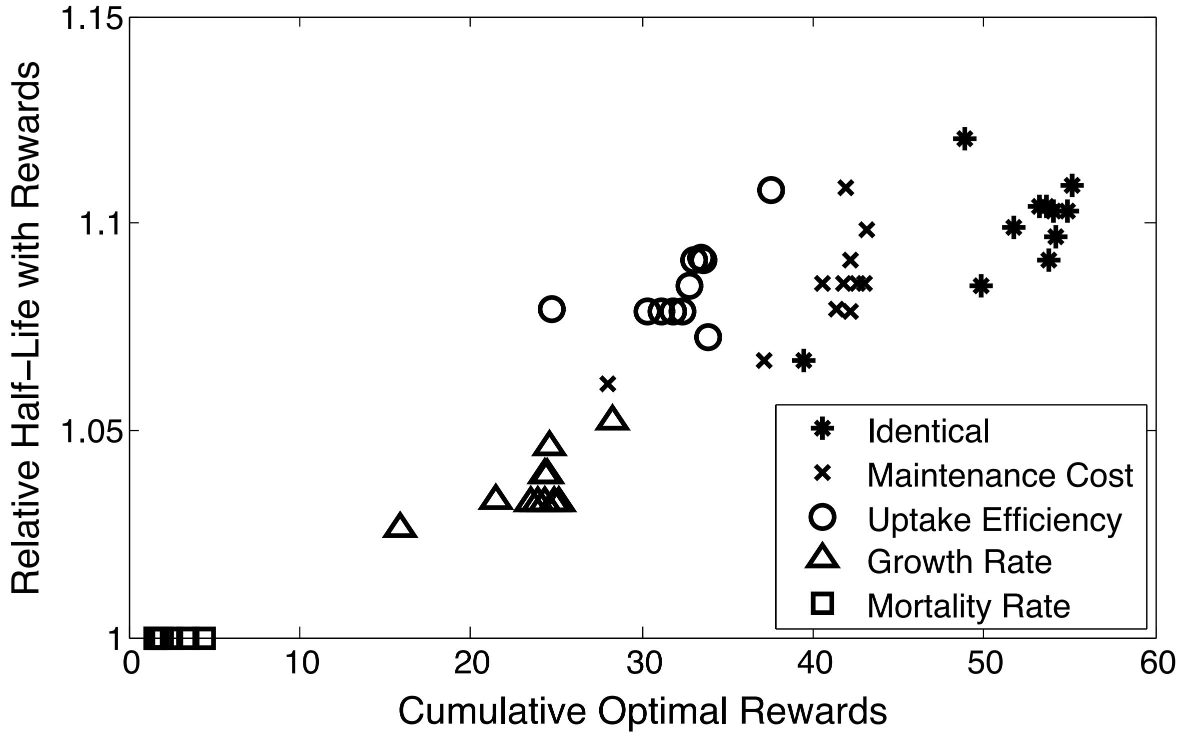

Figure B1: Half-life of Fungus 2 with rewards (i.e., optimal solution) relative to its half-life without rewards (i.e., $h_2(t) = 0$ for all t), as a function of the total amount of tree rewards provided in the optimal case. The greater the amount of tree rewards, the greater Fungus 2's relative persistence. Point shape indicates the parameter by which Fungus 2 differs from Fungus 1; parameter choices correspond to black stars in Main Text Figure 3. Each of the 11 replicate points in a shape set represents one of eleven environmental conditions where $\alpha = 5$ and $\nu = \{0, 1, 2, ..., 10\}$.

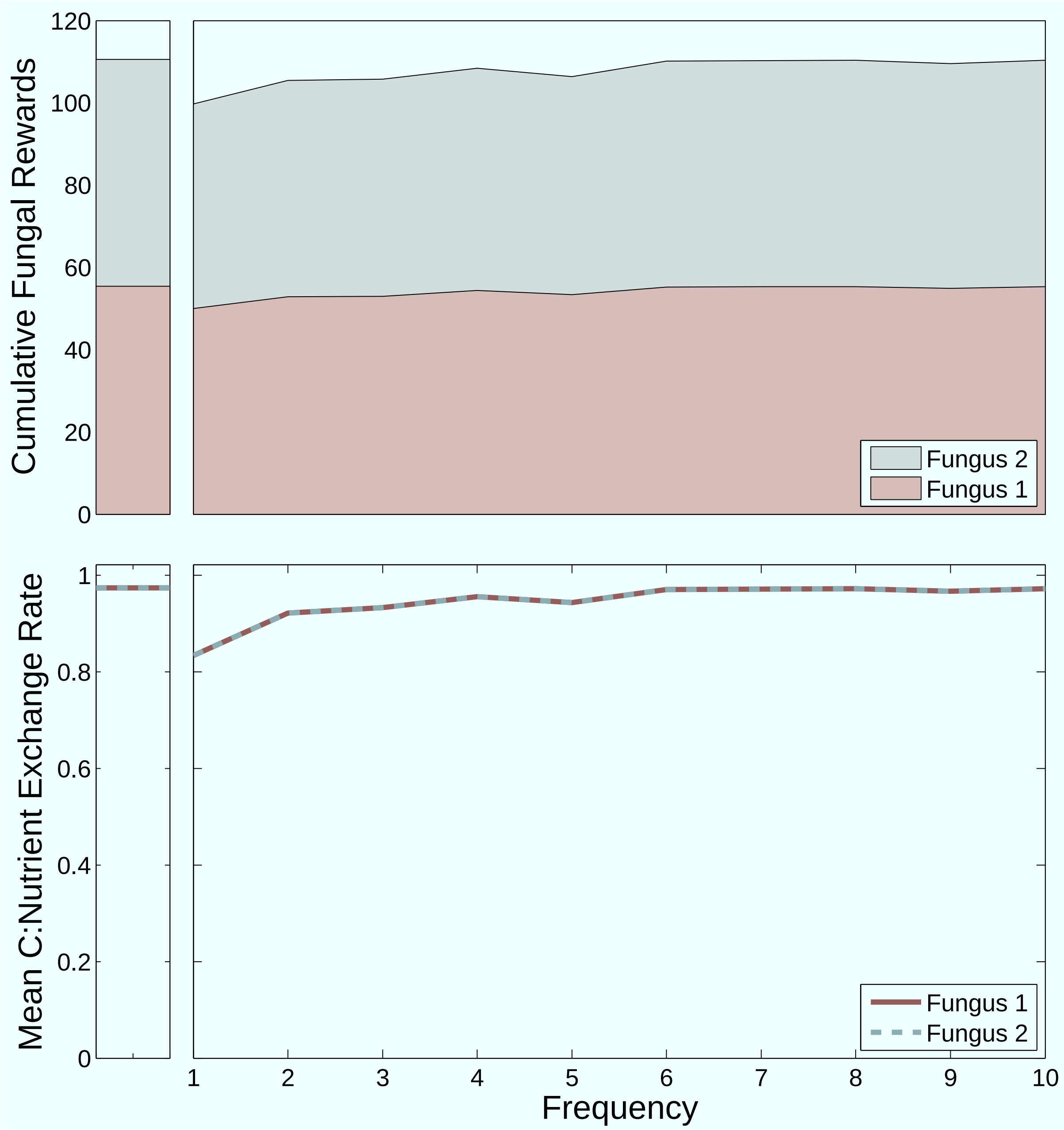

Figure B2: Total carbon rewards to Fungus 1 and Fungus 2 (as stacked area plots; top panels) and mean C:Nutrient exchange rate. In this case, Fungus 1 and Fungus 2 are identical, and $\alpha = 1$.

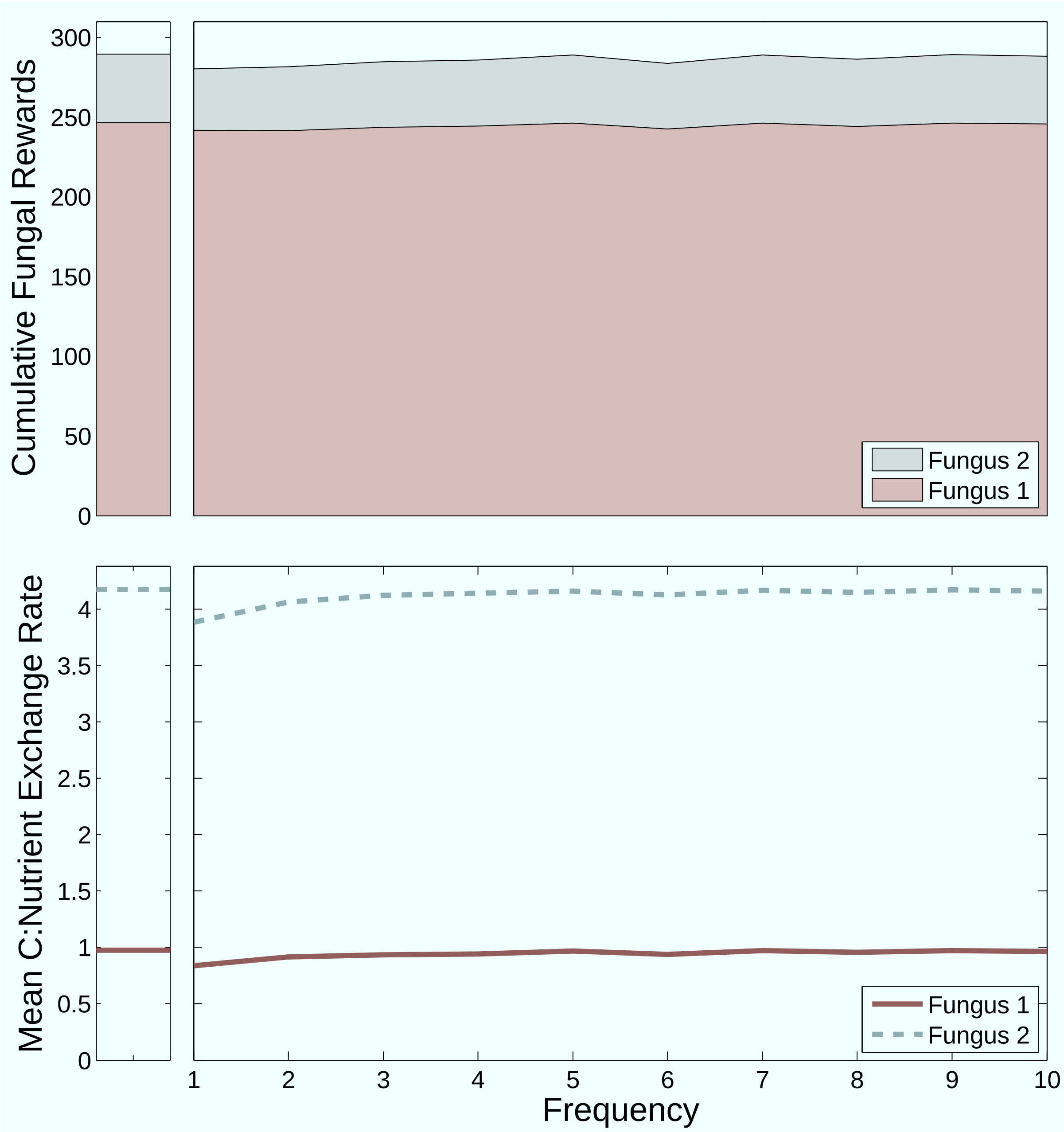

Figure B3: Total carbon rewards to Fungus 1 and Fungus 2 (as stacked area plots; top panels) and mean C:Nutrient exchange rate. In this case, Fungus 1 and Fungus 2 are identical except in maintenance costs ($\omega_2 = 1.53$), and $\alpha = 1$.

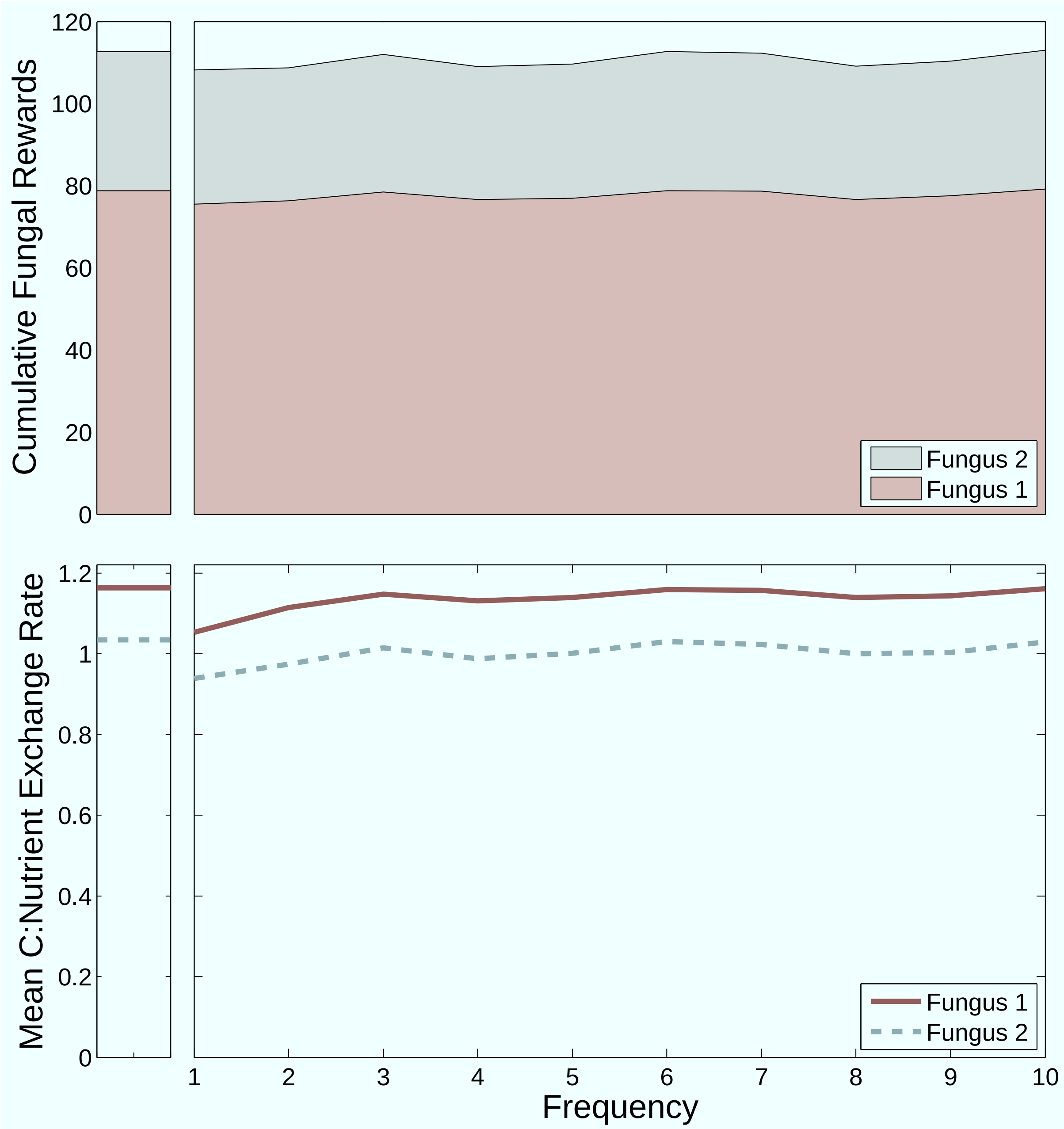

Figure B4: Total carbon rewards to Fungus 1 and Fungus 2 (as stacked area plots; top panels) and mean C:Nutrient exchange rate. In this case, Fungus 1 and Fungus 2 are identical except in nutrient uptake efficiency ($\epsilon_2 = 0.004$), and $\alpha = 1$.

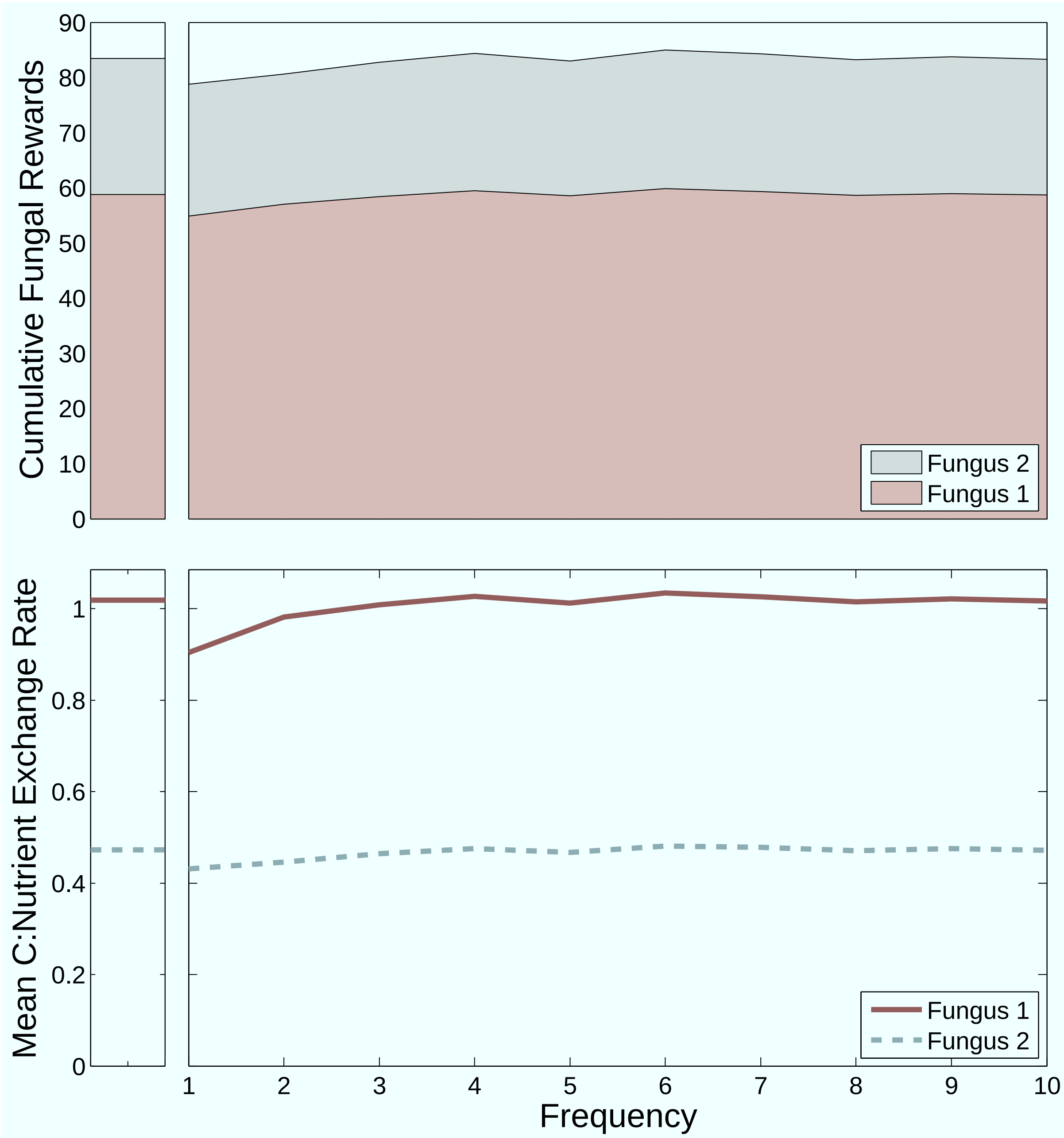

Figure B5: Total carbon rewards to Fungus 1 and Fungus 2 (as stacked area plots; top panels) and mean C:Nutrient exchange rate. In this case, Fungus 1 and Fungus 2 are identical except in basal reproductive rate ($\beta_2 = 0.006$), and $\alpha = 1$.

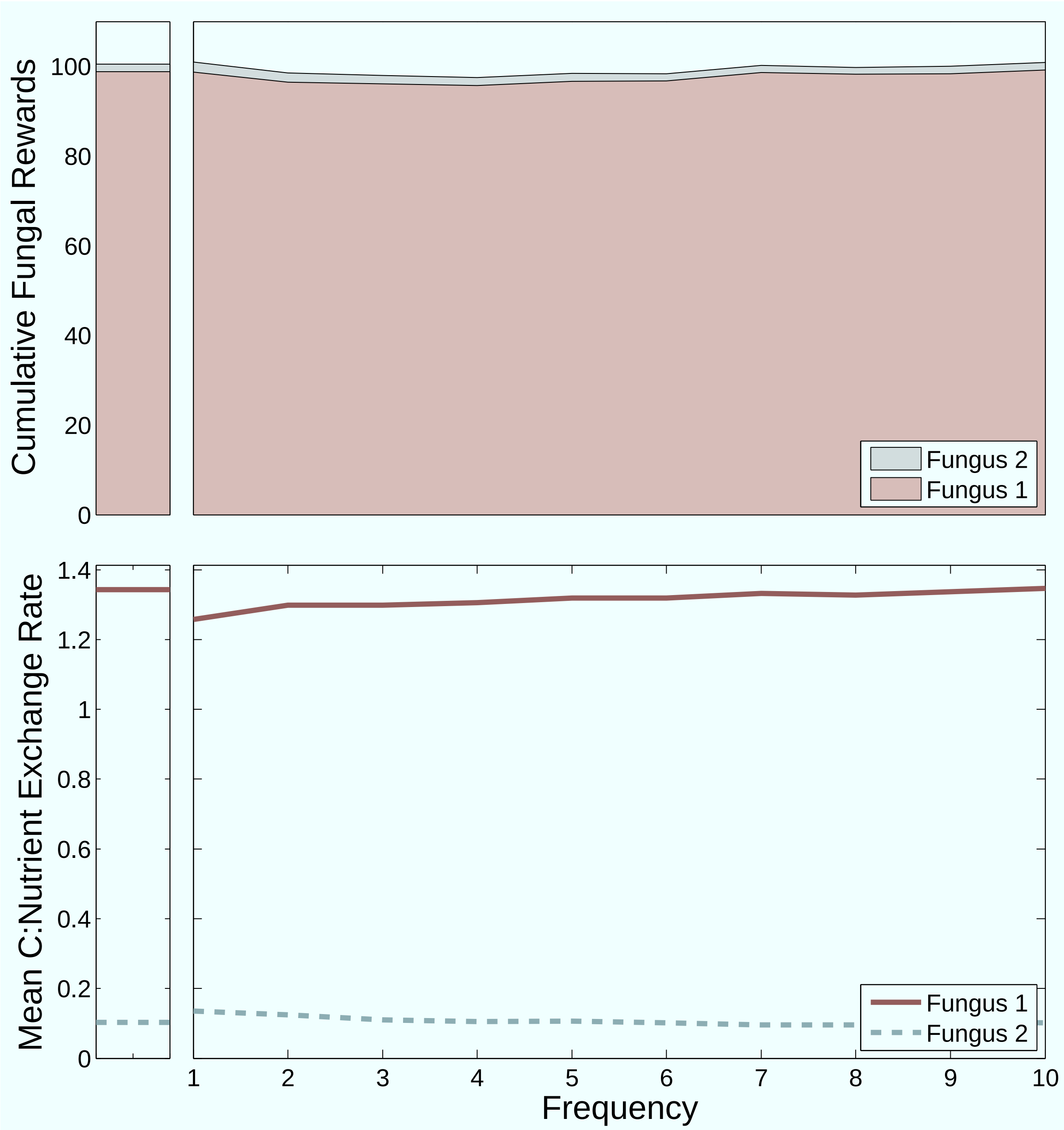

Figure B6: Total carbon rewards to Fungus 1 and Fungus 2 (as stacked area plots; top panels) and mean C:Nutrient exchange rate. In this case, Fungus 1 and Fungus 2 are identical except in mortality rate ($\mu_2 = 0.25$), and $\alpha = 1$.

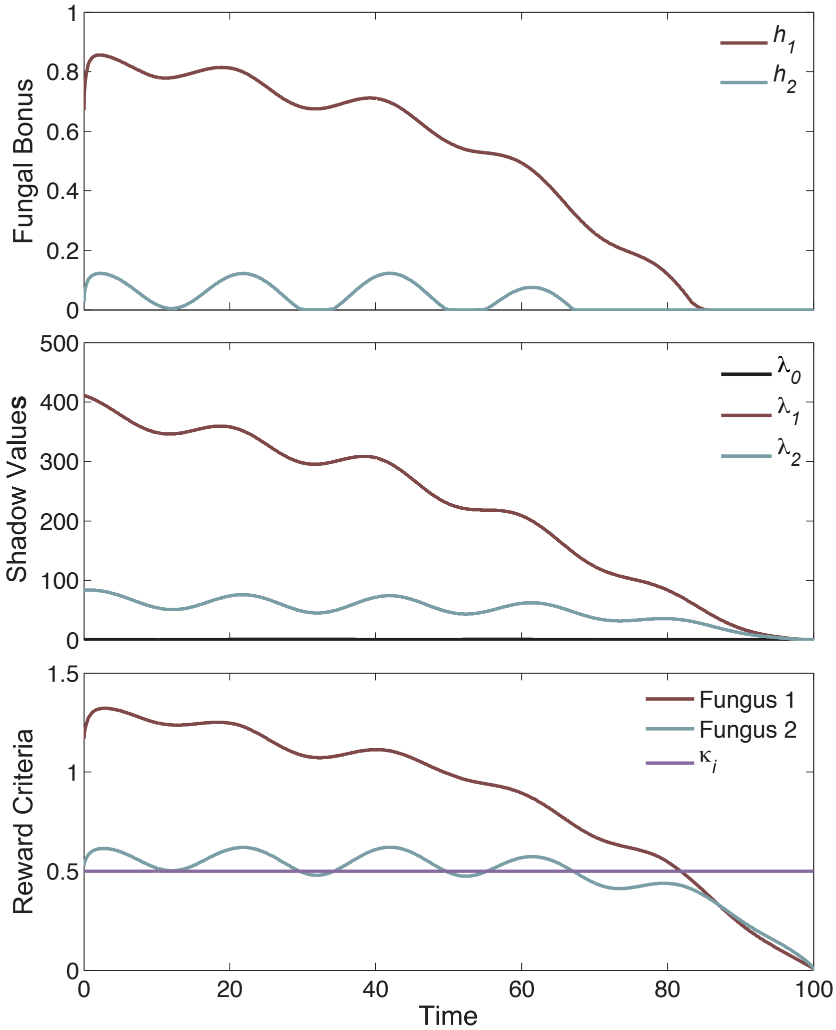

Figure B7: Optimal reward investment criteria. The top panel shows the optimal rewards h_1 and h_2 that the tree gives its fungal partners (note that these are the same conditions as in Main Text Fig. 2d-f). The middle panel shows the shadow values for the three categories of root tips (uncolonized, λ_0; colonized by Fungus 1, λ_1; and colonized by Fungus 2, λ_2. The bottom panel shows the intersection of the reward criteria given by equation A27. Red and blue lines correspond to $\{[(\lambda_i - \lambda_0)\, f_0 f_i \beta_i \kappa_i \eta_i] \,/\, [(f_0 + f_i)\, \lambda_b f_i]\}^{1/2}$ for $i = 1$ and 2, respectively. Here, $\kappa_1 = \kappa_2$ (purple line).