Symbiosis in the Sea

This model for symbiotic guest-host interaction in the sea is based on Roughgarden's 1975 paper, which considers selection on the guest only.

Here we add fairly arbitrary functional forms to include the host dynamics in the model, which retaining the Lotka-Volterra form which lets us looks at adaptive motion in the plane of interaction coefficients.

The guest dynamics:

$$\frac{dn}{ndt} = r_g + a_{gH}N + a_{gg}n$$

.

The host strategy/phenotype is

- X_a: investment for/against (+/−) association ("colonization" in the original) by guest
- X_t: investment for/against transfer of resources ("exploitation") by guest (given association).

$$\frac{dN}{Ndt} = r_H + a_{Hg}n + a_{HH}N$$

let a_{gg} and a_{HH} be constant, uninteresting to adaptation.

Investment has cost so r_H is at maximum at $X_a = X_t = 0$.

I propose

- $p(x_a, X_a)$: probability of association per pair of individuals

on host side:

- $C_g(X_a)$: general (density independent) cost of investment re association

- $C_a(X_a)$: per-guest cost of investment re association
- $C_t(X_t)$: cost of investment re transfer
- (and add density-independent investment re transfer?)
- $B(x_t, X_t)$: benefit $(+/-)$ to individual host of transfer with individual guest. Not including C_t.
- K: density dependence among hosts

on guest side:

- $c_g(x_a)$: search cost
- $c_a(x_a)$: cost of association after host is found
- $c_t(x_t)$: cost of investment in transfer
- $b(x_t, X_t)$: benefit to guest of transfer
- k: density dependence among guests (does this make sense?)

So we then have

$$\frac{dn}{ndt} = r_0 - c_g(x_a) + (p(x_a, X_a)(b(x_t, X_t) - c_t(x_t)) - c_a(x_a))N - kn$$
$$\frac{dN}{Ndt} = R_0 - C_g(X_a) + (p(x_a, X_a)(B(x_t, X_t) - C_t(X_t)) - C_a(X_a))n - KN$$

This is oddly symmetric - maybe I abstracted it too much. But one asymmetry is that the benefit to the host can be positive or negative, while it's assumed positive for the guest. Thus the host might want to invest in defense against guests, while guests will always want to associate and transfer.

The dynamics:

$$\frac{dN_0}{dt} = -(K_0 N_0 - ((B_{00} - C_{t0})p_{00} - C_{a0})n_0 + C_{g0} - R_0)N_0$$
$$\frac{dn_0}{dt} = (((b_{00} - c_{t0})p_{00} - c_{a0})N_0 - k_0 n_0 - c_{g0} + r_0)n_0$$

Whence the selective pressure on the ecological quantities is

$$R_0 \to 1$$
$$C_{g0} \to -1$$
$$C_{a0} \to -\hat{n}_0$$
$$C_{t0} \to -\hat{n}_0 p_{00}$$
$$B_{00} \to \hat{n}_0 p_{00}$$

$$
\begin{aligned}
p_{00} &\to \hat{N}_0 b_{00} - \hat{N}_0 c_{t0} + B_{00}\hat{n}_0 - C_{t0}\hat{n}_0 \\
r_0 &\to 1 \\
c_{g0} &\to -1 \\
c_{a0} &\to -\hat{N}_0 \\
c_{t0} &\to -\hat{N}_0 p_{00} \\
b_{00} &\to \hat{N}_0 p_{00}
\end{aligned}
$$

Dynamics with constraints:

$$
\frac{dN_0}{dt} = -(KN_0 - ((B(x_{t0}, X_{t0}) - C_t(X_{t0}))p(x_{a0}, X_{a0}) - C_a(X_{a0}))n_0 + C_g(X_{a0}) - R(X_{a0}, X_{t0}))N_0
$$

$$
\frac{dn_0}{dt} = (((b(x_{t0}, X_{t0}) - c_t(x_{t0}))p(x_{a0}, X_{a0}) - c_a(x_{a0}))N_0 - kn_0 - c_g(x_{a0}) + r(x_{a0}, x_{t0}))n_0
$$

And selective pressure on constraining characters is

$$
\begin{aligned}
\dot{X}_{a0} \propto\ & \hat{n}_0 \partial_1 p(x_{a0}, X_{a0}) B(x_{t0}, X_{t0}) - \hat{n}_0 \partial_1 p(x_{a0}, X_{a0}) C_t(X_{t0}) \\
& - {C_a}'(X_{a0})\hat{n}_0 - {C_g}'(X_{a0}) + \partial_0 R(X_{a0}, X_{t0})
\end{aligned}
$$

$$
\dot{X}_{t0} \propto -{C_t}'(X_{t0})\hat{n}_0 p(x_{a0}, X_{a0}) + \hat{n}_0 \partial_1 B(x_{t0}, X_{t0}) p(x_{a0}, X_{a0}) + \partial_1 R(X_{a0}, X_{t0})
$$

$$
\begin{aligned}
\dot{x}_{a0} \propto\ & \hat{N}_0 \partial_0 p(x_{a0}, X_{a0}) b(x_{t0}, X_{t0}) - \hat{N}_0 \partial_0 p(x_{a0}, X_{a0}) c_t(x_{t0}) \\
& - \hat{N}_0 {c_a}'(x_{a0}) - {c_g}'(x_{a0}) + \partial_0 r(x_{a0}, x_{t0})
\end{aligned}
$$

$$
\dot{x}_{t0} \propto -\hat{N}_0 {c_t}'(x_{t0}) p(x_{a0}, X_{a0}) + \hat{N}_0 \partial_0 b(x_{t0}, X_{t0}) p(x_{a0}, X_{a0}) + \partial_1 r(x_{a0}, x_{t0})
$$

The base model without symbiosis dynamics

For the base dynamics without symbiosis, we set

$$
\begin{aligned}
k &\to 1 \\
K &\to 1 \\
r(x, y) &\to 1 \\
R(x, y) &\to 1
\end{aligned}
$$

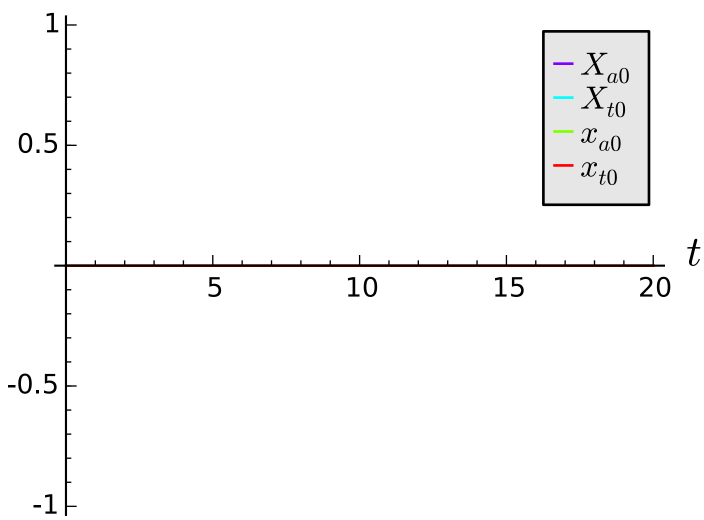
$$C_a(x) \to 0$$
$$p(x,y) \to 0$$
$$c_a(x) \to 0$$
$$C_g(x) \to 0$$
$$c_g(x) \to 0$$

Dynamics with no symbiosis:

$$\frac{dN_0}{dt} = -(N_0 - 1)N_0$$
$$\frac{dn_0}{dt} = -(n_0 - 1)n_0$$

And its adaptive dynamics is

$$\frac{dX_{a0}}{dt} = 0$$
$$\frac{dX_{t0}}{dt} = 0$$
$$\frac{dx_{a0}}{dt} = 0$$
$$\frac{dx_{t0}}{dt} = 0$$



Since here we've declared that there is no association, and hence no transfer, and no cost or benefit whatsoever to investment in either, investment remains fixed at its initial value of zero.

Evolution of association investment

To study the incentive structure for association, we set

$$
\begin{aligned}
k &\to 1 \\
K &\to 1 \\
r(x,y) &\to 1 \\
R(x,y) &\to 1
\end{aligned}
$$

$$
\begin{aligned}
c_a(x) &\to x^2 \\
p(x,y) &\to \frac{1}{e^{(-x-y)}+1} \\
C_a(x) &\to x^2 \\
C_g(x) &\to 0 \\
c_g(x) &\to 0
\end{aligned}
$$

$$
\begin{aligned}
B(x,y) &\to 1 \\
b(x,y) &\to 1 \\
C_t(x) &\to 0 \\
c_t(x) &\to 0
\end{aligned}
$$

Dynamics with association only:

$$
\begin{aligned}
\frac{dN_0}{dt} &= -(n_0(C_a\left(X_{a0}\right) - p\left(x_{a0}, X_{a0}\right)) + N_0 - 1)N_0 \\
\frac{dn_0}{dt} &= -(N_0(c_a\left(x_{a0}\right) - p\left(x_{a0}, X_{a0}\right)) + n_0 - 1)n_0
\end{aligned}
$$

Or

$$
\begin{aligned}
\frac{dN_0}{dt} &= -\left(\left(X_{a0}^2 - \frac{1}{e^{(-X_{a0}-x_{a0})}+1}\right)n_0 + N_0 - 1\right)N_0 \\
\frac{dn_0}{dt} &= -\left(\left(x_{a0}^2 - \frac{1}{e^{(-X_{a0}-x_{a0})}+1}\right)N_0 + n_0 - 1\right)n_0
\end{aligned}
$$

And its adaptive dynamics is

$$
\begin{aligned}
\dot{X}_{a0} &= -\big({C_a}'(X_{a0})\hat{n}_0 - \hat{n}_0\partial_1 p(x_{a0}, X_{a0})\big)\hat{N}_0 \\
\dot{X}_{t0} &= 0 \\
\dot{x}_{a0} &= -\Big(\hat{N}_0{c_a}'(x_{a0}) - \hat{N}_0\partial_0 p(x_{a0}, X_{a0})\Big)\hat{n}_0 \\
\dot{x}_{t0} &= 0
\end{aligned}
$$

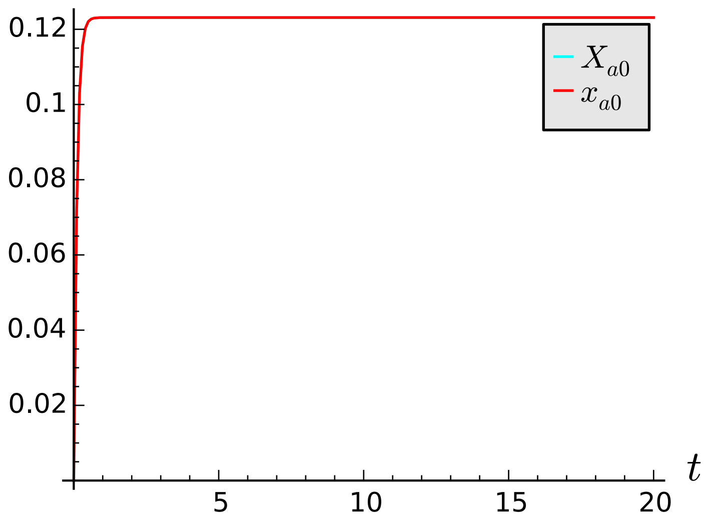
Or

$$\frac{dX_{a0}}{dt} = -\left(2\,X_{a0}\hat{n}_0 - \frac{\hat{n}_0 e^{(-X_{a0}-x_{a0})}}{\left(e^{(-X_{a0}-x_{a0})}+1\right)^2}\right)\hat{N}_0$$

$$\frac{dX_{t0}}{dt} = 0$$

$$\frac{dx_{a0}}{dt} = -\left(2\,\hat{N}_0 x_{a0} - \frac{\hat{N}_0 e^{(-X_{a0}-x_{a0})}}{\left(e^{(-X_{a0}-x_{a0})}+1\right)^2}\right)\hat{n}_0$$

$$\frac{dx_{t0}}{dt} = 0$$



So here we see that both invest positively in association.

The selective pressures on investment are

$$X_{a0} \to -C_a{}'(X_{a0})\hat{n}_0 + \hat{n}_0\partial_1 p(x_{a0}, X_{a0})$$

$$x_{a0} \to -\hat{N}_0 c_a{}'(x_{a0}) + \hat{N}_0\partial_0 p(x_{a0}, X_{a0})$$

So the condition for increase in guest investment is

$$-\hat{N}_0 c_a{}'(x_{a0}) + \hat{N}_0\partial_0 p(x_{a0}, X_{a0}) > 0$$

And for increase in host investment

$$-C_a{}'(X_{a0})\hat{n}_0 + \hat{n}_0\partial_1 p(x_{a0}, X_{a0}) > 0$$

I.e. marginal increase in benefit exceeds marginal increase in cost. Marginal because cost and benefit are balanced at each population equilibrium. Due to the factor of $\hat{N}$ or $\hat{n}$, I wonder if the net balance of cost/benefit could decrease rather than increase.

So either investment in association will rise provided benefit rises faster than cost, and stop when the derivatives become equal.

We have assumed functional forms such that benefit increases more quickly than cost near zero investment, so investment rises from zero until the marginal benefit no longer exceeds marginal cost.

Analysis of association-only model

Let's go through this simpler model, because this may be enough for the paper.

Ecological quantities

In the above the ecological quantities subject to variation and selection are c_a, C_a, the costs of each population's investment in association, and p, the net probability of associating. The other quantities are being held fixed, and in particular, in the above we have $b = B = 1$, meaning that transfer is beneficial to both guest and host. Let's keep b and B variable to make their role visible.

With that we have

$$\dot{x}_a = \hat{N}(b\partial_0 p - \partial_0 c_a)$$
$$\dot{X}_a = \hat{n}(B\partial_1 p - \partial_0 C_a).$$

It seems clear that one could make these go either way. We assume $b > 0$ (guest benefits from transfer), and $\partial_0 p > 0$, $\partial_1 p > 0$ as investment in association makes it more probable. Also assume c_a and C_a increase with the magnitude of investment, so the sign of their derivative matches the sign of the argument, and is zero at 0.

It follows that at the neutral point $(x_a, X_a) = (0, 0)$, selection is positive on x_a, and selection on X_a matches the sign of B. In many cases, depending on the functional forms of p, c_a, and C_a, there will be an equilibrium at which these differences come to zero, and in cases where there is not, it is possible for investment to diverge away from zero.

Interactions

Under these assumptions, in which r, R aren't affected by investment in association, all selection is via the interaction terms a_{gH}, a_{Hg}.

The guest is selected to raise a_{gH} by adjusting x_a, which changes p and c_a. Specifically, it raises x_a, which raises

$$a_{gH} = b\,p(x_a, X_a) - c_a(x_a)$$

by increasing bp more than it increases c_a, and stops when increase in c_a becomes as large as the increase in benefit.

The host is selected to raise

$$a_{Hg} = B\,p(x_a, X_a) - C_a(X_a).$$

If B is negative, this is done by reducing p, via reducing X_a below zero, even though this raises the cost C_a. This proceeds until the cost increases are too much.

If B is positive, the host raises p by raising X_a until the cost becomes limiting.

Thus the direct effect of guest selection on the interaction pair is to raise a_{gH}, and of host selection is to raise a_{Hg}.

Guest selection impacts a_{Hg} indirectly via p: if B is positive the indirect effect is positive, and if B is negative it is negative. Likewise host selection affects a_{gH} indirectly, positively if B is positive and negatively if B is negative.

Thus the guest and host have matching incentives when both b and B are positive, and will construct a mutualism, and have conflicting incentives when $B < 0 < b$, and will pull in opposite directions, with the outcome depending on which has more influence over the changing interaction.

Under the assumption that p, c_a, and C_a are nonnegative, a_{gH} can be any sign, and a_{Hg} can be any sign if B is positive and can only be negative if B is negative. In the latter, conflicting case, an equilibrium level of p will be reached that depends on the details. If it is small, a_{gH} will be negative and a_{Hg} will be negative but small; if p is large at equilibrium, a_{gH} will be positive and a_{Hg} will be large and negative.

Thus the outcome is mutualistic when incentives are aligned, and either competitive or parasitic when incentives are in conflict.

[@@ todo: verify these conclusions numerically. Is the competitive outcome realistic? Why wouldn't the guest abandon association in that case?]

Calculations

Using functional forms

$$c_a(x_a) = \gamma x_a^2$$

$$C_a(X_a) = \Gamma X_a^2$$
$$p(x_a, X_a) = \frac{1}{2} + x_a + X_a$$

and restricting to the region where these forms work, $-\frac{1}{2} \leq x_a + X_a \leq \frac{1}{2}$, the equations for adaptive equilibrium are

$$b - 2\gamma x_a = 0$$
$$B - 2\Gamma X_a = 0$$

Combining:

$$X_a = \frac{B}{2\Gamma}$$
$$x_a = \frac{b}{2\gamma}$$
$$X_a = \frac{\gamma B}{\Gamma b} x_a$$

Thus x_a is positive and X_a has the sign of B.

If $B > 0$, then both x variables are positive, $p > \frac{1}{2}$,

$$\begin{aligned}
a_{gH} &= bp - \gamma x_a^2 \\
&= b\left(\frac{1}{2} + x_a + X_a\right) - \gamma x_a^2 \\
&= bX_a + \frac{1}{2}b + bx_a - \gamma x_a^2 \\
&= \frac{Bb}{2\Gamma} + \frac{b}{2} + \frac{b^2}{2\gamma} - \frac{b^2}{4\gamma} \\
&> 0
\end{aligned}$$

and

$$\begin{aligned}
a_{Hg} &= Bp - \Gamma X_a^2 \\
&= B\left(\frac{1}{2} + x_a + \frac{B}{2\Gamma}\right) - \frac{B^2}{4\Gamma} \\
&> 0.
\end{aligned}$$

If $B < 0$, then $X_a < 0$, and

$$\begin{aligned} a_{gH} &= \frac{b}{2}\left(\frac{B}{\Gamma} + 1 + \frac{b}{2\gamma}\right) \\ &> 0 \end{aligned}$$

if $-\frac{B}{\Gamma} < 1 + \frac{b}{2\gamma}$;

$$\begin{aligned} a_{Hg} &= \frac{B}{2}\left(\frac{b}{\gamma} + 1 + \frac{B}{2\Gamma}\right) \\ &> 0 \end{aligned}$$

if $-\frac{B}{\Gamma} > 1 + \frac{b}{\gamma}$.

In this case there are three generic cases:

$$\begin{cases} -\dfrac{B}{\Gamma} < 1 + \dfrac{b}{2\gamma} & a_{Hg} < 0 < a_{gH} \\ 1 + \dfrac{b}{2\gamma} < -\dfrac{B}{\Gamma} < 1 + \dfrac{b}{\gamma} & a_{Hg} < 0, a_{gH} < 0 \\ 1 + \dfrac{b}{\gamma} < -\dfrac{B}{\Gamma} & a_{gH} < 0 < a_{Hg}. \end{cases}$$

Interestingly, mutualism is only possible in the $B > 0$ case, in which case it is necessary.

END OF USEFUL PART, MAYBE

The following more complex model treatments might be overkill, and not worth bothering with.

Evolution of transfer

Maybe transfer, when association is held fixed, will behave similarly.

To study the incentive structure for transfer, we set

$$\begin{aligned} c_t(x) &\to x^2 \\ b(x, y) &\to x + y \\ C_t(x) &\to x^2 \\ B(x, y) &\to -x - y \end{aligned}$$

$$
\begin{aligned}
C_a(x) &\to 0 \\
p(x,y) &\to p \\
c_a(x) &\to 0 \\
C_g(x) &\to 0 \\
c_g(x) &\to 0
\end{aligned}
$$

Dynamics with transfer only:

$$
\begin{aligned}
\frac{dN_0}{dt} &= (n_0 p(B\left(x_{t0}, X_{t0}\right) - C_t\left(X_{t0}\right)) - N_0 + 1)N_0 \\
\frac{dn_0}{dt} &= (N_0 p(b\left(x_{t0}, X_{t0}\right) - c_t\left(x_{t0}\right)) - n_0 + 1)n_0
\end{aligned}
$$

Or

$$
\begin{aligned}
\frac{dN_0}{dt} &= -\big(\big(X_{t0}^2 + X_{t0} + x_{t0}\big)n_0 p + N_0 - 1\big)N_0 \\
\frac{dn_0}{dt} &= -\big(\big(x_{t0}^2 - X_{t0} - x_{t0}\big)N_0 p + n_0 - 1\big)n_0
\end{aligned}
$$

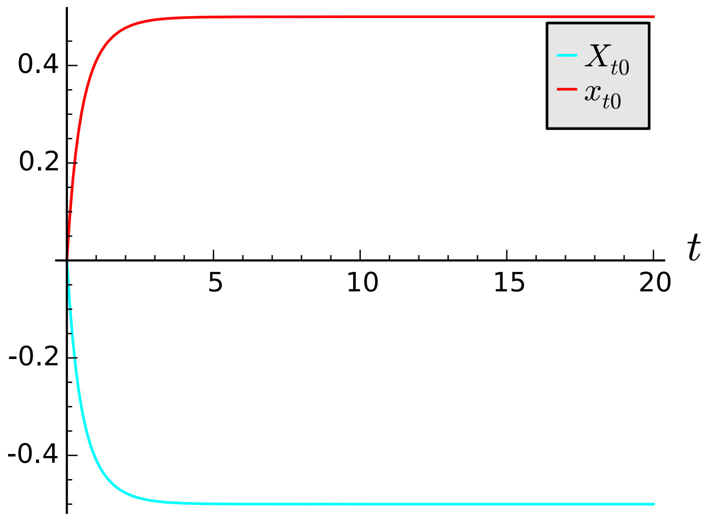
And its adaptive dynamics is

$$
\begin{aligned}
\dot{X}_{a0} &= 0 \\
\dot{X}_{t0} &= -\big(C_t{}'(X_{t0})\hat{n}_0 p - \hat{n}_0 p \partial_1 B(x_{t0}, X_{t0})\big)\hat{N}_0 \\
\dot{x}_{a0} &= 0 \\
\dot{x}_{t0} &= -\Big(\hat{N}_0 c_t{}'(x_{t0})p - \hat{N}_0 p \partial_0 b(x_{t0}, X_{t0})\Big)\hat{n}_0
\end{aligned}
$$

Or

$$
\begin{aligned}
\frac{dX_{a0}}{dt} &= 0 \\
\frac{dX_{t0}}{dt} &= -(2\,X_{t0}\hat{n}_0 p + \hat{n}_0 p)\hat{N}_0 \\
\frac{dx_{a0}}{dt} &= 0 \\
\frac{dx_{t0}}{dt} &= -\Big(2\,\hat{N}_0 p x_{t0} - \hat{N}_0 p\Big)\hat{n}_0
\end{aligned}
$$

To evaluate the dynamics we use $p = 1$.



The selective pressures on investment are

$$X_{t0} \to -C_t{}'(X_{t0})\hat{n}_0 p + \hat{n}_0 p \partial_1 B(x_{t0}, X_{t0})$$
$$x_{t0} \to -\hat{N}_0 c_t{}'(x_{t0}) p + \hat{N}_0 p \partial_0 b(x_{t0}, X_{t0})$$

So the condition for increase in guest investment is

$$-\hat{N}_0 c_t{}'(x_{t0}) p + \hat{N}_0 p \partial_0 b(x_{t0}, X_{t0}) > 0$$

And for increase in host investment

$$-C_t{}'(X_{t0})\hat{n}_0 p + \hat{n}_0 p \partial_1 B(x_{t0}, X_{t0}) > 0$$

So yes, it's very similar. Investment in transfer increases when the marginal increase in benefit exceeds the marginal increase in cost.

The functions we chose have benefit changing more rapidly than cost near zero, so both players respond by shifting away from zero investment. Since we've made transfer benefit guests at the expense of hosts, guest invest in it and hosts invest in stopping it. The race quits when the cost of investment becomes equally marginally significant.

Adaptation in the full model

And when both association and transfer are up for adaptation?

To study the incentive structure for transfer, we set

$$\begin{aligned} c_a(x) &\to x^2 \\ p(x,y) &\to \frac{1}{e^{(-x-y)}+1} \\ C_a(x) &\to x^2 \\ C_g(x) &\to 0 \\ c_g(x) &\to 0 \end{aligned}$$

$$\begin{aligned} c_t(x) &\to x^2 \\ b(x,y) &\to x+y \\ C_t(x) &\to x^2 \\ B(x,y) &\to -x-y \end{aligned}$$

Dynamics:

$$\frac{dN_0}{dt} = (((B(x_{t0}, X_{t0}) - C_t(X_{t0}))p(x_{a0}, X_{a0}) - C_a(X_{a0}))n_0 - N_0 - C_g(X_{a0}) + 1)N_0$$

$$\frac{dn_0}{dt} = (((b(x_{t0}, X_{t0}) - c_t(x_{t0}))p(x_{a0}, X_{a0}) - c_a(x_{a0}))N_0 - n_0 - c_g(x_{a0}) + 1)n_0$$

Or

$$\begin{aligned} \frac{dN_0}{dt} &= -\left(\left(X_{a0}^2 + \frac{X_{t0}^2 + X_{t0} + x_{t0}}{e^{(-X_{a0}-x_{a0})}+1}\right)n_0 + N_0 - 1\right)N_0 \\ \frac{dn_0}{dt} &= -\left(\left(x_{a0}^2 + \frac{x_{t0}^2 - X_{t0} - x_{t0}}{e^{(-X_{a0}-x_{a0})}+1}\right)N_0 + n_0 - 1\right)n_0 \end{aligned}$$

And its adaptive dynamics is

$$\dot{X}_{a0} = \left(\hat{n}_0\partial_1 p(x_{a0}, X_{a0})B(x_{t0}, X_{t0}) - \hat{n}_0\partial_1 p(x_{a0}, X_{a0})C_t(X_{t0}) - {C_a}'(X_{a0})\hat{n}_0 - {C_g}'(X_{a0})\right)\hat{N}_0$$

$$\dot{X}_{t0} = -\left({C_t}'(X_{t0})\hat{n}_0 p(x_{a0}, X_{a0}) - \hat{n}_0\partial_1 B(x_{t0}, X_{t0})p(x_{a0}, X_{a0})\right)\hat{N}_0$$

$$\dot{x}_{a0} = \left(\hat{N}_0\partial_0 p(x_{a0}, X_{a0})b(x_{t0}, X_{t0}) - \hat{N}_0\partial_0 p(x_{a0}, X_{a0})c_t(x_{t0}) - \hat{N}_0{c_a}'(x_{a0}) - {c_g}'(x_{a0})\right)\hat{n}_0$$

$$\dot{x}_{t0} = -\left(\hat{N}_0{c_t}'(x_{t0})p(x_{a0}, X_{a0}) - \hat{N}_0\partial_0 b(x_{t0}, X_{t0})p(x_{a0}, X_{a0})\right)\hat{n}_0$$

Or

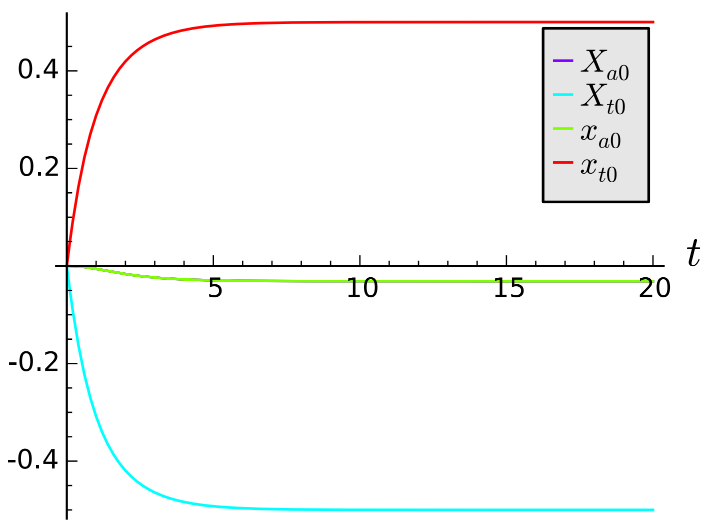
$$\frac{dX_{a0}}{dt} = -\left(2\,X_{a0}\hat{n}_0 + \frac{X_{t0}^2\hat{n}_0e^{(-X_{a0}-x_{a0})}}{\left(e^{(-X_{a0}-x_{a0})}+1\right)^2} + \frac{(X_{t0}+x_{t0})\hat{n}_0e^{(-X_{a0}-x_{a0})}}{\left(e^{(-X_{a0}-x_{a0})}+1\right)^2}\right)\hat{N}_0$$

$$\frac{dX_{t0}}{dt} = -\hat{N}_0\left(\frac{2\,X_{t0}\hat{n}_0}{e^{(-X_{a0}-x_{a0})}+1} + \frac{\hat{n}_0}{e^{(-X_{a0}-x_{a0})}+1}\right)$$

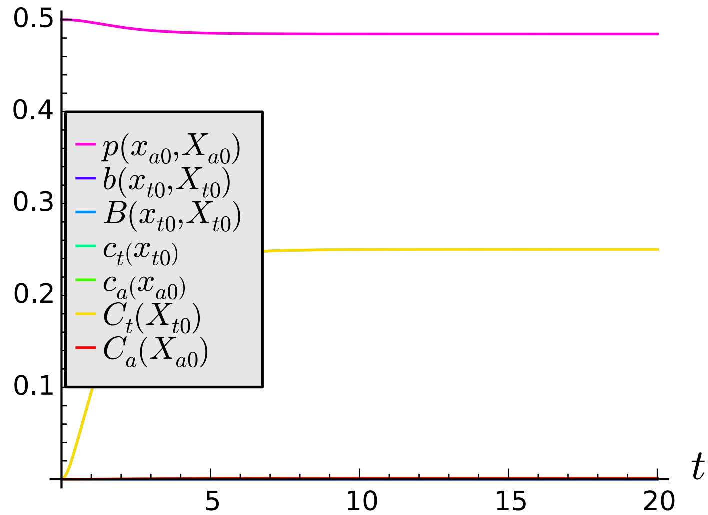
$$\frac{dx_{a0}}{dt} = -\left(2\,\hat{N}_0x_{a0} + \frac{\hat{N}_0x_{t0}^2e^{(-X_{a0}-x_{a0})}}{\left(e^{(-X_{a0}-x_{a0})}+1\right)^2} - \frac{\hat{N}_0(X_{t0}+x_{t0})e^{(-X_{a0}-x_{a0})}}{\left(e^{(-X_{a0}-x_{a0})}+1\right)^2}\right)\hat{n}_0$$

$$\frac{dx_{t0}}{dt} = -\hat{n}_0\left(\frac{2\,\hat{N}_0x_{t0}}{e^{(-X_{a0}-x_{a0})}+1} - \frac{\hat{N}_0}{e^{(-X_{a0}-x_{a0})}+1}\right)$$

This is as above, except that in investment in association, the impact of the probability of association is modulated by the consequences of transfer, which can be positive or negative. Previously that consequence was fixed at a constant positive value.

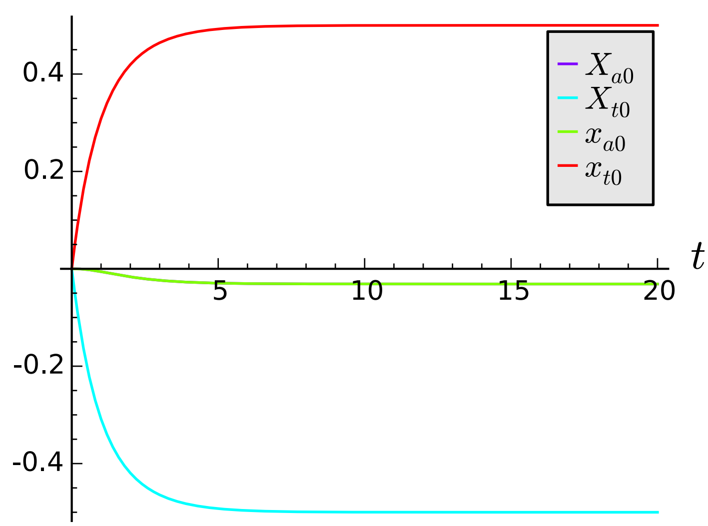


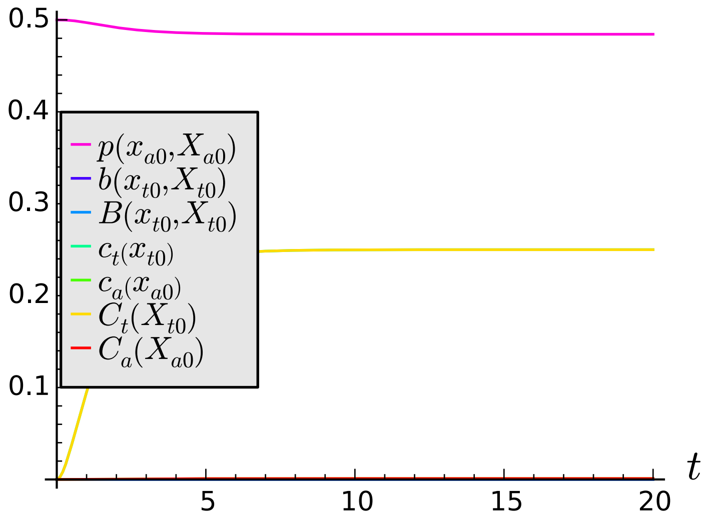
So here both guest and host become anti-association, while their contributions to transfer diverge to strong opposite values. Why is that?



Could it be bistable, and the guest, who is getting hurt initially by the transfer, drives the polarization?

Let's try different initial conditions



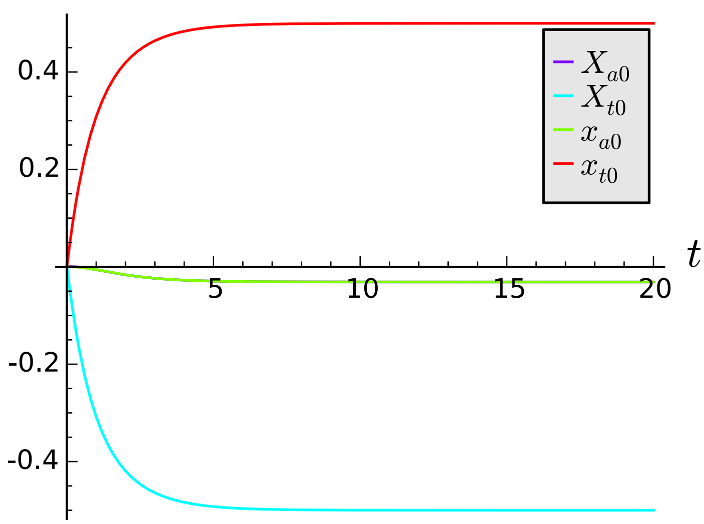


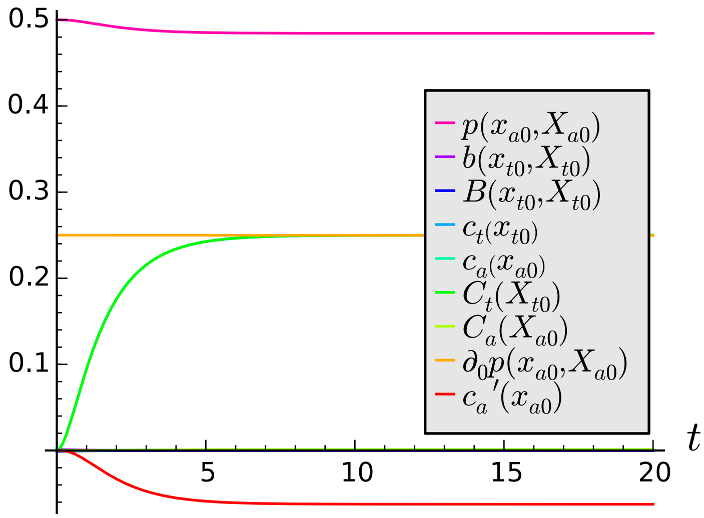
I am puzzled why x_{a_0} goes downward. Given that it's

$$\dot{x}_{a0} = \left[\hat{N}_0(b(x_{t0}, X_{t0}) - c_t(x_{t0}))\partial_1 p(x_{a0}, X_{a0}) - \hat{N}_0 \partial_1 c_a(x_{a0}) - \partial_1 c_g(x_{a0})\right] \hat{n}_0$$

with $b - c_t = 0.008 > 0$, $\partial_1 p = 0.25 > 0$, $\partial_1 c_a = 0.02$, and $\partial_1 c_g = 0$, it looks like the situation is that the p part is being dominated by the cost c_a.

So how about this:





A cooperative example?

How to make this model select for mutualism.

To study the incentive structure for transfer, we set

$$k \to 20$$
$$K \to 20$$

$$c_a(x) \to x^2$$
$$p(x, y) \to \frac{1}{4}x + \frac{1}{4}y + \frac{1}{2}$$
$$C_a(x) \to x^2$$
$$C_g(x) \to 0$$
$$c_g(x) \to 0$$

$$c_t(x) \to x^2$$
$$b(x, y) \to vx + wy$$
$$C_t(x) \to x^2$$
$$B(x, y) \to Vx + Wy$$

$$
\begin{aligned}
\frac{dX_{a0}}{dt} &= -\frac{1}{4}\left(X_{t0}^2\hat{n}_0 - (W X_{t0} + V x_{t0})\hat{n}_0 + 8\,X_{a0}\hat{n}_0\right)\hat{N}_0 \\
\frac{dX_{t0}}{dt} &= \frac{1}{4}\left(W(X_{a0} + x_{a0} + 2)\hat{n}_0 - 2\,(X_{a0} + x_{a0} + 2)X_{t0}\hat{n}_0\right)\hat{N}_0 \\
\frac{dx_{a0}}{dt} &= -\frac{1}{4}\left(\hat{N}_0 x_{t0}^2 - (X_{t0} w + v x_{t0})\hat{N}_0 + 8\,\hat{N}_0 x_{a0}\right)\hat{n}_0 \\
\frac{dx_{t0}}{dt} &= \frac{1}{4}\left(\hat{N}_0(X_{a0} + x_{a0} + 2)v - 2\,\hat{N}_0(X_{a0} + x_{a0} + 2)x_{t0}\right)\hat{n}_0
\end{aligned}
$$

Equilibrium conditions are

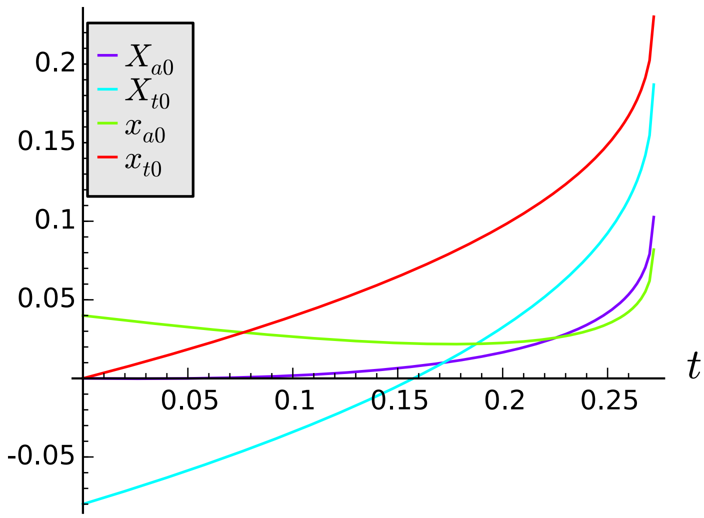
$$
\begin{aligned}
W &= 2\,X_t \\
V x_t &= X_t^2 - W X_t + 8\,X_a \\
&= -X_t^2 + 8\,X_a \\
v &= 2\,x_t \\
w X_t &= x_t^2 - v x_t + 8\,x_a \\
&= -x_t^2 + 8\,x_a
\end{aligned}
$$

So to have all x values equal to $1/2$, we set

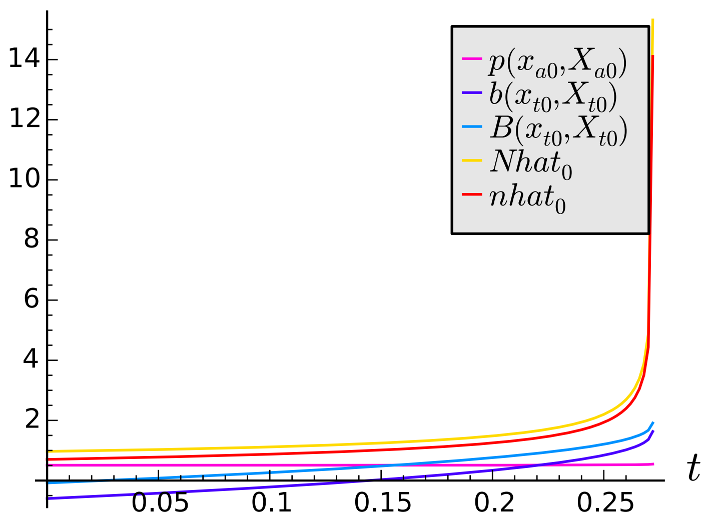
$$
\begin{aligned}
V &\to \frac{15}{2} \\
w &\to \frac{15}{2} \\
v &\to 1 \\
W &\to 1
\end{aligned}
$$

for

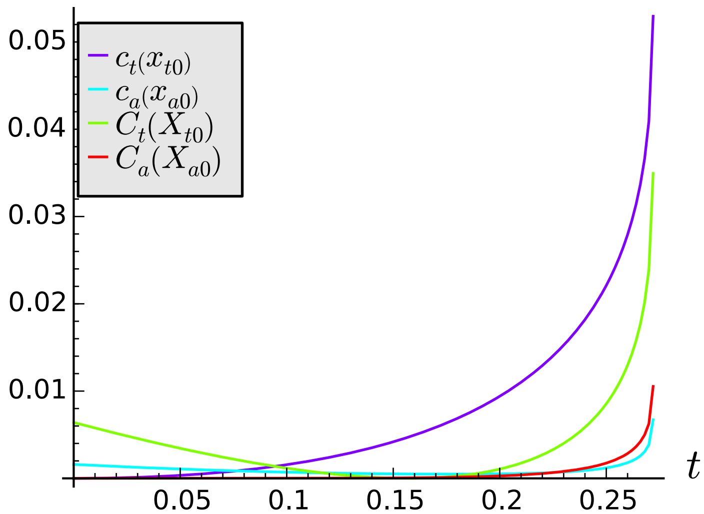
$$
\begin{aligned}
\frac{dX_{a0}}{dt} &= -\frac{1}{8}\left(2\,X_{t0}^2\hat{n}_0 + 16\,X_{a0}\hat{n}_0 - (2\,X_{t0} + 15\,x_{t0})\hat{n}_0\right)\hat{N}_0 \\
\frac{dX_{t0}}{dt} &= -\frac{1}{4}\left(2\,(X_{a0} + x_{a0} + 2)X_{t0}\hat{n}_0 - (X_{a0} + x_{a0} + 2)\hat{n}_0\right)\hat{N}_0 \\
\frac{dx_{a0}}{dt} &= -\frac{1}{8}\left(2\,\hat{N}_0 x_{t0}^2 - \hat{N}_0(15\,X_{t0} + 2\,x_{t0}) + 16\,\hat{N}_0 x_{a0}\right)\hat{n}_0 \\
\frac{dx_{t0}}{dt} &= -\frac{1}{4}\left(2\,\hat{N}_0(X_{a0} + x_{a0} + 2)x_{t0} - \hat{N}_0(X_{a0} + x_{a0} + 2)\right)\hat{n}_0
\end{aligned}
$$



X_{a0}
X_{t0}
x_{a0}
x_{t0}
0.2
0.15
0.1
0.05
-0.05
0.05
0.1
0.15
0.2
0.25
t



$p(x_{a0},X_{a0})$
$b(x_{t0},X_{t0})$
$B(x_{t0},X_{t0})$
$Nhat_0$
$nhat_0$
14
12
10
8
6
4
2
0.05
0.1
0.15
0.2
0.25
t



Why does it stop? Because the population equilibrium stops being viable, it looks like. Loss of B-stability. I'll probably want to look into the B-stability criteria, try to avoid this explosion. At first, I'll leave it as it is, since initial increase in mutualism is enough for my purposes.

The interactions

`[WorkingWiki encountered errors: Error: <ww-make-failed: sea-up-a.pdf, /Selection_Gradients/sea-up-a.pdf.make.log> ]`

For a_{gH},

$$A = (b_{00}p_{00} - c_{t0}p_{00} - c_{a0},\, B_{00}p_{00} - C_{t0}p_{00} - C_{a0})$$

$$S = \left(\hat{N}_0,\, \hat{n}_0\right)$$

$$\begin{aligned}
D = \big(&p_{00}{}'(t)(b_{00}\,(t) - c_{t0}\,(t)) + b_{00}{}'(t)p_{00}\,(t) - c_{t0}{}'(t)p_{00}\,(t) \\
&- c_{a0}{}'(t),\, p_{00}{}'(t)(B_{00}\,(t) - C_{t0}\,(t)) + B_{00}{}'(t)p_{00}\,(t) - C_{t0}{}'(t)p_{00}\,(t) - C_{a0}{}'(t)\big) \\
= \Bigg(&-\frac{1}{8}\left(2\,x_{t0}\,(t)^2 - 15\,X_{t0}\,(t) + 16\,x_{a0}\,(t) - 2\,x_{t0}\,(t)\right)x_{a0}{}'(t) \\
&- \frac{1}{4}\,(2\,X_{a0}\,(t)\,x_{t0}\,(t) + 2\,x_{a0}\,(t)\,x_{t0}\,(t) - X_{a0}\,(t) - x_{a0}\,(t) + 4\,x_{t0}\,(t) - 2)x_{t0}{}'(t), \\
&\qquad -\frac{1}{8}\left(2\,X_{t0}\,(t)^2 + 16\,X_{a0}\,(t) - 2\,X_{t0}\,(t) - 15\,x_{t0}\,(t)\right)X_{a0}{}'(t) \\
&- \frac{1}{4}\,(2\,X_{a0}\,(t)\,X_{t0}\,(t) + 2\,X_{t0}\,(t)\,x_{a0}\,(t) - X_{a0}\,(t) + 4\,X_{t0}\,(t) - x_{a0}\,(t) - 2)X_{t0}{}'(t)\Bigg)
\end{aligned}$$

$$
\begin{aligned}
I &= (p_{00}{}'(t)(b_{00}(t) - c_{t0}(t)),\ p_{00}{}'(t)(B_{00}(t) - C_{t0}(t))) \\
&= \left(-\frac{1}{8}\left(2\,x_{t0}(t)^2 - 15\,X_{t0}(t) - 2\,x_{t0}(t)\right)X_{a0}{}'(t)\right. \\
&\qquad + \frac{15}{8}\,X_{t0}{}'(t)(X_{a0}(t) + x_{a0}(t) + 2), \\
&\qquad -\frac{1}{8}\left(2\,X_{t0}(t)^2 - 2\,X_{t0}(t) - 15\,x_{t0}(t)\right)x_{a0}{}'(t) \\
&\qquad \left. + \frac{15}{8}\,x_{t0}{}'(t)(X_{a0}(t) + x_{a0}(t) + 2)\right)
\end{aligned}
$$

$$
\begin{aligned}
\frac{dA}{dt} &= \big(2\,p_{00}{}'(t)(b_{00}(t) - c_{t0}(t)) + b_{00}{}'(t)p_{00}(t) - c_{t0}{}'(t)p_{00}(t) \\
&\quad - c_{a0}{}'(t),\ 2\,p_{00}{}'(t)(B_{00}(t) - C_{t0}(t)) + B_{00}{}'(t)p_{00}(t) - C_{t0}{}'(t)p_{00}(t) - C_{a0}{}'(t)\big) \\
= &\left(-\frac{1}{8}\left(2\,x_{t0}(t)^2 - 15\,X_{t0}(t) - 2\,x_{t0}(t)\right)X_{a0}{}'(t)\right. \\
&\qquad - \frac{1}{8}\left(2\,x_{t0}(t)^2 - 15\,X_{t0}(t) + 16\,x_{a0}(t) - 2\,x_{t0}(t)\right)x_{a0}{}'(t) \\
&\quad -\frac{1}{4}\left(2\,X_{a0}(t)\,x_{t0}(t) + 2\,x_{a0}(t)\,x_{t0}(t) - X_{a0}(t) - x_{a0}(t) + 4\,x_{t0}(t) - 2\right)x_{t0}{}'(t) \\
&\qquad + \frac{15}{8}\,X_{t0}{}'(t)(X_{a0}(t) + x_{a0}(t) + 2), \\
&\qquad -\frac{1}{8}\left(2\,X_{t0}(t)^2 + 16\,X_{a0}(t) - 2\,X_{t0}(t) - 15\,x_{t0}(t)\right)X_{a0}{}'(t) \\
&\quad -\frac{1}{4}\left(2\,X_{a0}(t)\,X_{t0}(t) + 2\,X_{t0}(t)\,x_{a0}(t) - X_{a0}(t) + 4\,X_{t0}(t) - x_{a0}(t) - 2\right)X_{t0}{}'(t) \\
&\qquad - \frac{1}{8}\left(2\,X_{t0}(t)^2 - 2\,X_{t0}(t) - 15\,x_{t0}(t)\right)x_{a0}{}'(t) \\
&\qquad \left. + \frac{15}{8}\,x_{t0}{}'(t)(X_{a0}(t) + x_{a0}(t) + 2)\right)
\end{aligned}
$$

Association-only interactions

That is complicated, so let's back off to study only changes in association, not in transfer.

In this case, for a_{gH},

The population dynamics of this version:

$$
\begin{aligned}
\frac{dN_0}{dt} &= -(n_0(C_a(X_{a0}) - p(x_{a0}, X_{a0})) + N_0 - 1)N_0 \\
\frac{dn_0}{dt} &= -(N_0(c_a(x_{a0}) - p(x_{a0}, X_{a0})) + n_0 - 1)n_0
\end{aligned}
$$

In this case, all the selection is on the a terms.

$$
\begin{aligned}
A &= \left(-c_a\left(x_{a0}\right) + p\left(x_{a0}, X_{a0}\right),\ -C_a\left(X_{a0}\right) + p\left(x_{a0}, X_{a0}\right)\right)\\
S &= \left(\hat{N}_0,\ \hat{n}_0\right)\\
D &= \big(-({c_a}'(x_{a0}\left(t\right)) - \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right))){x_{a0}}'(t),\\
&\qquad\qquad -\big({C_a}'(X_{a0}\left(t\right)) - \partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right))\big){X_{a0}}'(t)\big)\\
&= \left(\hat{N}_0({c_a}'(x_{a0}\left(t\right)) - \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right)))^2\gamma\hat{n}_0,\ \left({C_a}'(X_{a0}\left(t\right)) - \partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right))\right)^2\hat{N}_0\gamma\hat{n}_0\right)\\
I &= \big({X_{a0}}'(t)\partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right)),\ \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right)){x_{a0}}'(t)\big)\\
&= \Big(-\big({C_a}'(X_{a0}\left(t\right)) - \partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right))\big)\hat{N}_0\gamma\hat{n}_0\partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right)),\\
&\qquad -\hat{N}_0({c_a}'(x_{a0}\left(t\right)) - \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right)))\gamma\hat{n}_0\partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right))\Big)
\end{aligned}
$$

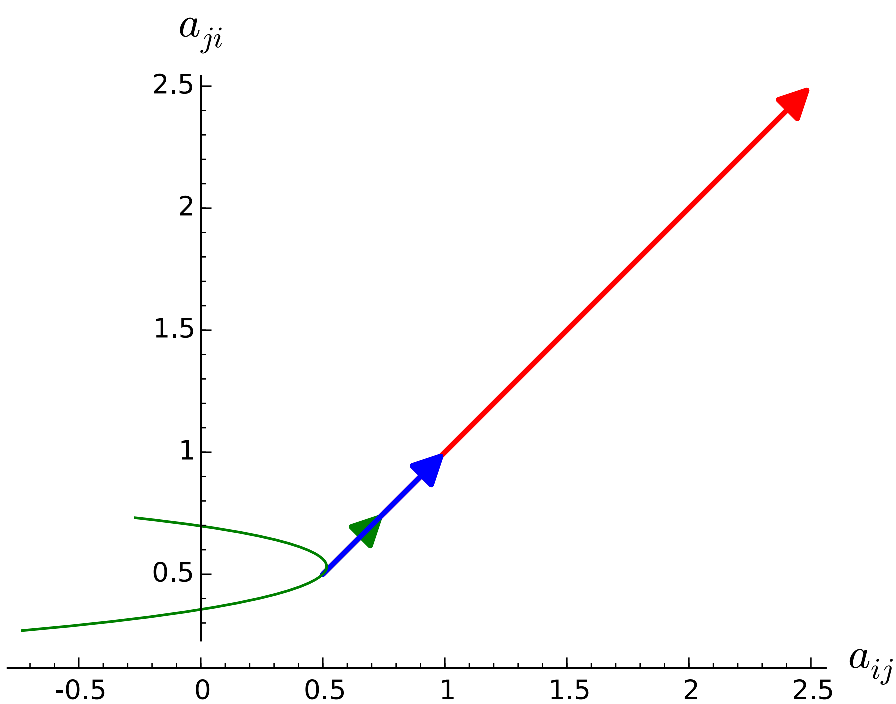
$$
\begin{aligned}
\frac{dA}{dt} &= \big({X_{a0}}'(t)\partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right)) - ({c_a}'(x_{a0}\left(t\right)) - \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right))){x_{a0}}'(t),\\
&\quad -\big({C_a}'(X_{a0}\left(t\right)) - \partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right))\big){X_{a0}}'(t) + \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right)){x_{a0}}'(t)\big)\\
&= \Big(\hat{N}_0({c_a}'(x_{a0}\left(t\right)) - \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right)))^2\gamma\hat{n}_0\\
&\quad -\big({C_a}'(X_{a0}\left(t\right)) - \partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right))\big)\hat{N}_0\gamma\hat{n}_0\partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right)),\ \big({C_a}'(X_{a0}\left(t\right)) - \partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right))\big)^2\hat{N}_0\\
&\qquad - \hat{N}_0({c_a}'(x_{a0}\left(t\right)) - \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right)))\gamma\hat{n}_0\partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right))\Big)\\
&= \left({x_{a0}}'(t)\left(\frac{e^{(-X_{a0}(t)-x_{a0}(t))}}{\left(e^{(-X_{a0}(t)-x_{a0}(t))}+1\right)^2} - 2\,x_{a0}\left(t\right)\right)\right.\\
&\qquad + \frac{{X_{a0}}'(t)e^{(-X_{a0}(t)-x_{a0}(t))}}{\left(e^{(-X_{a0}(t)-x_{a0}(t))}+1\right)^2},\ {X_{a0}}'(t)\left(\frac{e^{(-X_{a0}(t)-x_{a0}(t))}}{\left(e^{(-X_{a0}(t)-x_{a0}(t))}+1\right)^2} - 2\,X_{a0}\left(t\right)\right)\\
&\qquad\qquad \left. + \frac{{x_{a0}}'(t)e^{(-X_{a0}(t)-x_{a0}(t))}}{\left(e^{(-X_{a0}(t)-x_{a0}(t))}+1\right)^2}\right)
\end{aligned}
$$

The dynamics of the character variables are

$$
\begin{aligned}
{X_{a0}}'(t) &= -\big({C_a}'(X_{a0})\hat{n}_0 - \hat{n}_0\partial_1 p(x_{a0}, X_{a0})\big)\hat{N}_0\\
{X_{t0}}'(t) &= 0\\
{x_{a0}}'(t) &= -\left(\hat{N}_0{c_a}'(x_{a0}) - \hat{N}_0\partial_0 p(x_{a0}, X_{a0})\right)\hat{n}_0\\
{x_{t0}}'(t) &= 0
\end{aligned}
$$

So, all the selection is in the a terms between the host and guest. The guest's incentive is the probability of associating (with benefit 1) minus the cost of making it happen. The host's is the same (also with constant benefit 1 of associating).

The indirect effect is the effect of each one's change in p on the other, since both experience p in common. Since p is symmetric, the effect on the other is equal to that part of the direct effect on the self. This could be good or bad, depending on the parts p and c_a are playing in the incentive. In this case, with p and c increasing as we leave zero, the indirect impact is to increase each party's p a bit more, which is a positive exernality. It would be a negative externality if the incentive were to decrease both p and c.



Here I am using c to mean both c_a and C_a, casually. What are the conditions for incentive to increase a: it always increases:

$$(c'(x) - dp/dx)^2 > 0$$

For positive indirect effect:

$$(dp/dx)^2 - c'(x)dp/dx > 0$$

This requires c', dp/dx have opposite sign or $|c'| < |dp/dx|$. For actual increase in a, it's the direct effect plus the other party's indirect impact, which are composed from different values. They need the sum to be positive. I guess we could consider the sum of a terms? For that we get

$$
\begin{aligned}
\frac{d(a_{gH}+a_{Hg})}{dt} &= (dp/dx - c')^2 \\
&\quad + dp/dx(dp/dx - c') + (dp/dX - C')^2 + dp/dX(dp/dX - C') \\
&= (2dp/dx - c')(dp/dx - c') + (2dp/dX - C')(dp/dX - C')
\end{aligned}
$$

When is $(2dp/dx - c')(dp/dx - c')$ positive? I guess there are four cases:

- both positive: then a's increase if $dp/dx - c'$ positive or $2dp/dx - c$ negative, i.e. unless $dp/dx < c' < 2dp/dx$
- both negative: increase unless $2dp/dx < c' < dp/dx$
- $dp/dx < 0 < c'$: increase guaranteed
- $c' < 0 < dp/dx$: increase guaranteed

These conditions amount to either positive indirect effect, or a different condition where $2|dp/dx| < |c'|$ – in this latter case, the indirect effect is negative but too small to counter the direct effect. This is in a range where adaptation is driven by reducing the cost, rather than increasing association.

Maybe I should look at changing association directly - that's p, isn't it. The change in p is

$$dp/dt = dp/dx_a(dp/dx_a - c'(x_a)) + dp/dX_a(dp/dX_a - C'(x_a)).$$

If we imagine both players being roughly the same, this is what we were calling $dp/dx(dp/dx - c')$, which is the indirect effect. Since we have assumed association is positive for both, the indirect effect is the change in association.

Therefore, the conditions for increasing mutual benefit in the form of $a_{gH} + a_{Hg}$ are:

- association increases
- association decreases due to incentive to reduce cost, and cost reduction outweighs loss of association.