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

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

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

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

$$
\begin{aligned}
X_{a0} \propto{}& \hat{n}_0 B(x_{t0}, X_{t0})\, D[1](p)(x_{a0}, X_{a0}) - \hat{n}_0 C_t(X_{t0})\, D[1](p)(x_{a0}, X_{a0}) \\
&- \hat{n}_0 D[0](C_a)(X_{a0}) - D[0](C_g)(X_{a0}) + D[0](R)(X_{a0}, X_{t0}) \\
X_{t0} \propto{}& \hat{n}_0 p(x_{a0}, X_{a0})\, D[1](B)(x_{t0}, X_{t0}) \\
&- \hat{n}_0 p(x_{a0}, X_{a0})\, D[0](C_t)(X_{t0}) + D[1](R)(X_{a0}, X_{t0}) \\
x_{a0} \propto{}& \hat{N}_0 b(x_{t0}, X_{t0})\, D[0](p)(x_{a0}, X_{a0}) - \hat{N}_0 c_t(x_{t0})\, D[0](p)(x_{a0}, X_{a0}) \\
&- \hat{N}_0 D[0](c_a)(x_{a0}) - D[0](c_g)(x_{a0}) + D[0](r)(x_{a0}, x_{t0}) \\
x_{t0} \propto{}& \hat{N}_0 p(x_{a0}, X_{a0})\, D[0](b)(x_{t0}, X_{t0}) \\
&- \hat{N}_0 p(x_{a0}, X_{a0})\, D[0](c_t)(x_{t0}) + D[1](r)(x_{a0}, x_{t0})
\end{aligned}
$$

The base model without symbiosis dynamics

For the base dynamics without symbiosis, we set

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

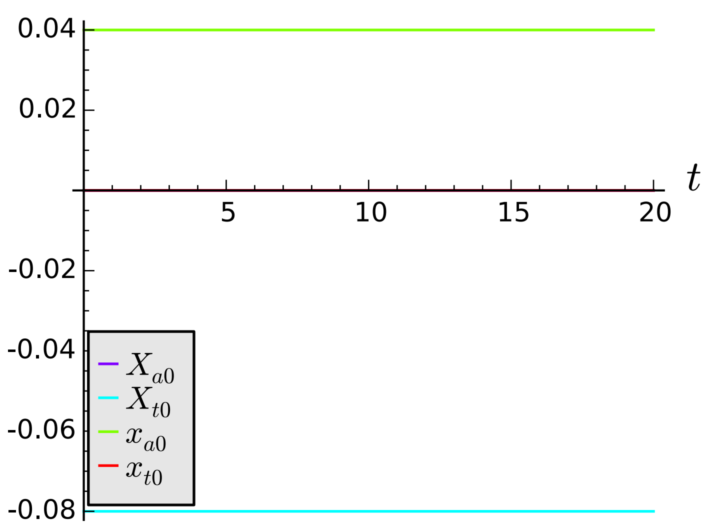
$$C_a(x) \to 0$$
$$p(x, y) \to 0$$
$$c_a(x) \to 0$$
$$C_g(x) \to 0$$
$$c_g(x) \to 0$$

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

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

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

$$
\begin{aligned}
\frac{dX_{a0}}{dt} &= -(\hat{n}_0 D[0]\left(C_a\right)\left(X_{a0}\right) - \hat{n}_0 D[1]\left(p\right)\left(x_{a0}, X_{a0}\right))\hat{N}_0 \\
\frac{dX_{t0}}{dt} &= 0 \\
\frac{dx_{a0}}{dt} &= -\left(\hat{N}_0 D[0]\left(c_a\right)\left(x_{a0}\right) - \hat{N}_0 D[0]\left(p\right)\left(x_{a0}, X_{a0}\right)\right)\hat{n}_0 \\
\frac{dx_{t0}}{dt} &= 0
\end{aligned}
$$

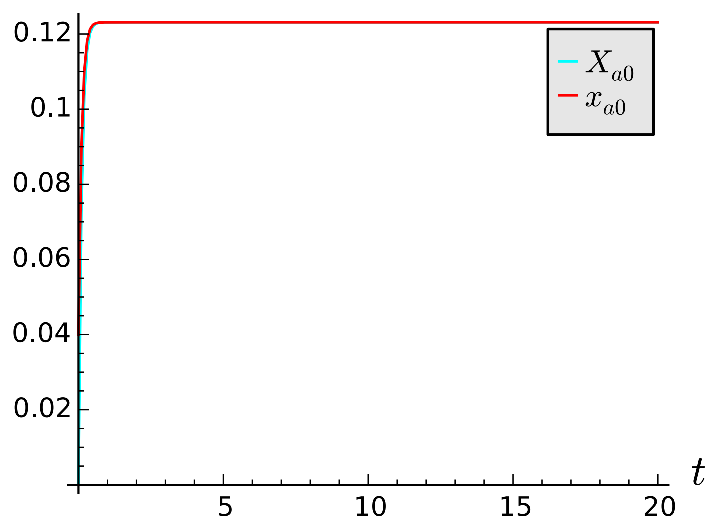
Or

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

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

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

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



So here we see that both invest positively in association.

The selective pressures on investment are

$$X_{a0} \to -\hat{n}_0 D[0]\,(C_a)\,(X_{a0}) + \hat{n}_0 D[1]\,(p)\,(x_{a0}, X_{a0})$$

$$x_{a0} \to -\hat{N}_0 D[0]\,(c_a)\,(x_{a0}) + \hat{N}_0 D[0]\,(p)\,(x_{a0}, X_{a0})$$

So the condition for increase in guest investment is

$$-\hat{N}_0 D[0]\,(c_a)\,(x_{a0}) + \hat{N}_0 D[0]\,(p)\,(x_{a0}, X_{a0}) > 0$$

And for increase in host investment

$$-\hat{n}_0 D[0]\,(C_a)\,(X_{a0}) + \hat{n}_0 D[1]\,(p)\,(x_{a0}, X_{a0}) > 0$$

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.

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

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

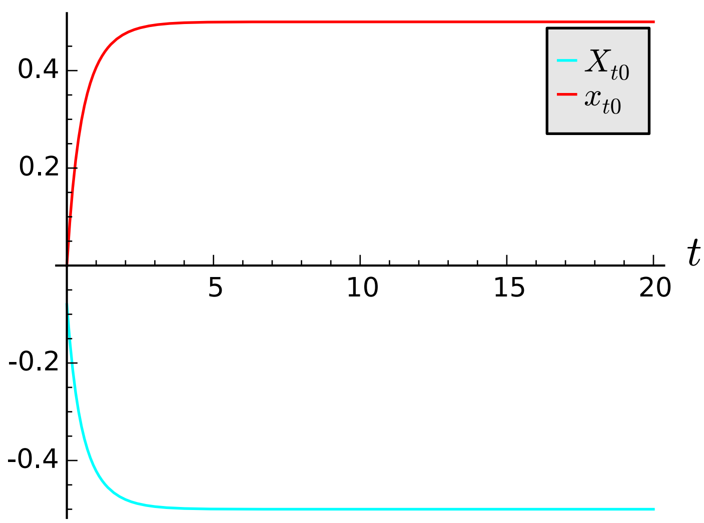
And its adaptive dynamics is

$$\frac{dX_{a0}}{dt} = 0$$
$$\frac{dX_{t0}}{dt} = (\hat{n}_0 p D[1]\,(B)\,(x_{t0}, X_{t0}) - \hat{n}_0 p D[0]\,(C_t)\,(X_{t0}))\hat{N}_0$$
$$\frac{dx_{a0}}{dt} = 0$$
$$\frac{dx_{t0}}{dt} = \left(\hat{N}_0 p D[0]\,(b)\,(x_{t0}, X_{t0}) - \hat{N}_0 p D[0]\,(c_t)\,(x_{t0})\right)\hat{n}_0$$

Or

$$\frac{dX_{a0}}{dt} = 0$$
$$\frac{dX_{t0}}{dt} = -(2\,X_{t0}\hat{n}_0 p + \hat{n}_0 p)\hat{N}_0$$
$$\frac{dx_{a0}}{dt} = 0$$
$$\frac{dx_{t0}}{dt} = -\left(2\,\hat{N}_0 p x_{t0} - \hat{N}_0 p\right)\hat{n}_0$$

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



The selective pressures on investment are

$$X_{t0} \to \hat{n}_0 pD[1]\,(B)\,(x_{t0}, X_{t0}) - \hat{n}_0 pD[0]\,(C_t)\,(X_{t0})$$
$$x_{t0} \to \hat{N}_0 pD[0]\,(b)\,(x_{t0}, X_{t0}) - \hat{N}_0 pD[0]\,(c_t)\,(x_{t0})$$

So the condition for increase in guest investment is

$$\hat{N}_0 pD[0]\,(b)\,(x_{t0}, X_{t0}) - \hat{N}_0 pD[0]\,(c_t)\,(x_{t0}) > 0$$

And for increase in host investment

$$\hat{n}_0 pD[1]\,(B)\,(x_{t0}, X_{t0}) - \hat{n}_0 pD[0]\,(C_t)\,(X_{t0}) > 0$$

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

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

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

And its adaptive dynamics is

$$\frac{dX_{a0}}{dt} = (\hat{n}_0 B(x_{t0}, X_{t0}) D[1](p)(x_{a0}, X_{a0}) - \hat{n}_0 C_t(X_{t0}) D[1](p)(x_{a0}, X_{a0}) - \hat{n}_0 D[0](C_a)(X_{a0}) - D[0](C_g)(X_{a0}))\hat{N}_0$$

$$\frac{dX_{t0}}{dt} = (\hat{n}_0 p(x_{a0}, X_{a0}) D[1](B)(x_{t0}, X_{t0}) - \hat{n}_0 p(x_{a0}, X_{a0}) D[0](C_t)(X_{t0}))\hat{N}_0$$

$$\frac{dx_{a0}}{dt} = \left(\hat{N}_0 b(x_{t0}, X_{t0}) D[0](p)(x_{a0}, X_{a0}) - \hat{N}_0 c_t(x_{t0}) D[0](p)(x_{a0}, X_{a0}) - \hat{N}_0 D[0](c_a)(x_{a0}) - D[0](c_g)(x_{a0})\right)\hat{n}_0$$

$$\frac{dx_{t0}}{dt} = \left(\hat{N}_0 p(x_{a0}, X_{a0}) D[0](b)(x_{t0}, X_{t0}) - \hat{N}_0 p(x_{a0}, X_{a0}) D[0](c_t)(x_{t0})\right)\hat{n}_0$$

Or

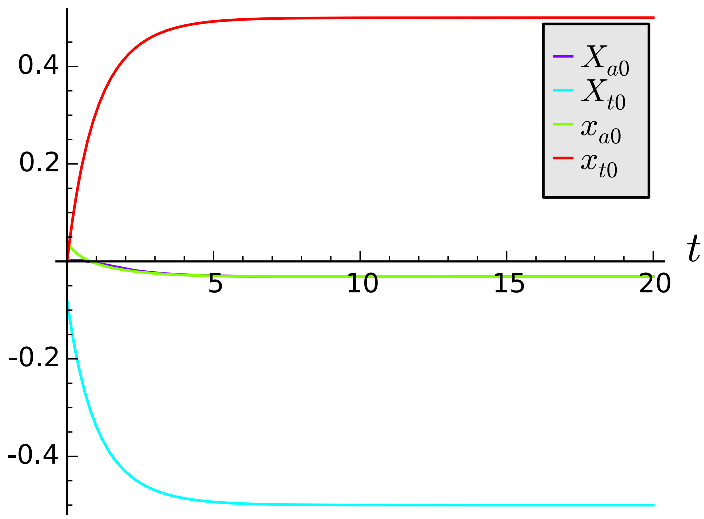
$$\frac{dX_{a0}}{dt} = -\left(2X_{a0}\hat{n}_0 + \frac{X_{t0}^2 \hat{n}_0 e^{(-X_{a0} - x_{a0})}}{\left(e^{(-X_{a0} - x_{a0})} + 1\right)^2} + \frac{(X_{t0} + x_{t0})\hat{n}_0 e^{(-X_{a0} - x_{a0})}}{\left(e^{(-X_{a0} - x_{a0})} + 1\right)^2}\right)\hat{N}_0$$

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

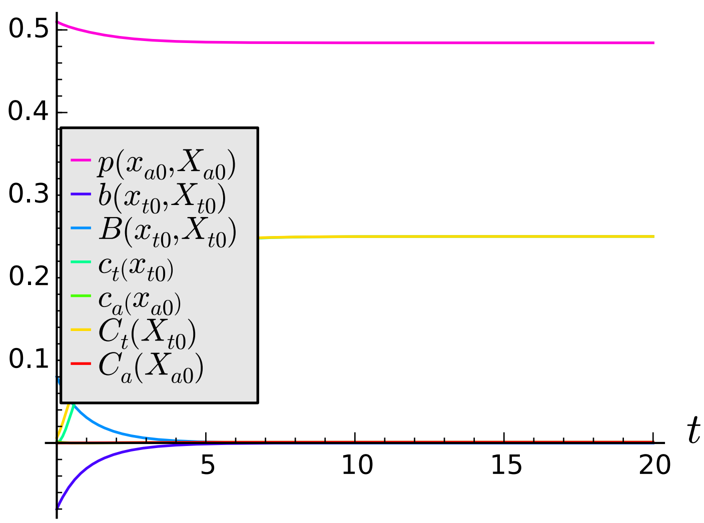
$$\frac{dx_{a0}}{dt} = -\left(2\hat{N}_0 x_{a0} + \frac{\hat{N}_0 x_{t0}^2 e^{(-X_{a0} - x_{a0})}}{\left(e^{(-X_{a0} - x_{a0})} + 1\right)^2} - \frac{\hat{N}_0(X_{t0} + x_{t0})e^{(-X_{a0} - x_{a0})}}{\left(e^{(-X_{a0} - x_{a0})} + 1\right)^2}\right)\hat{n}_0$$

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

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.

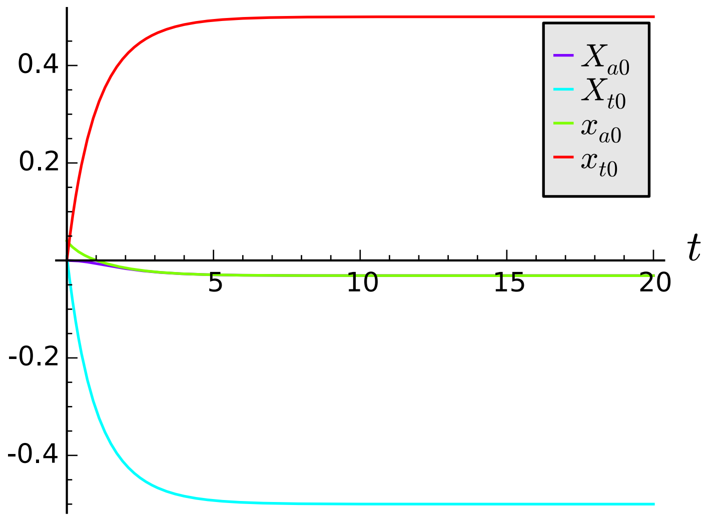


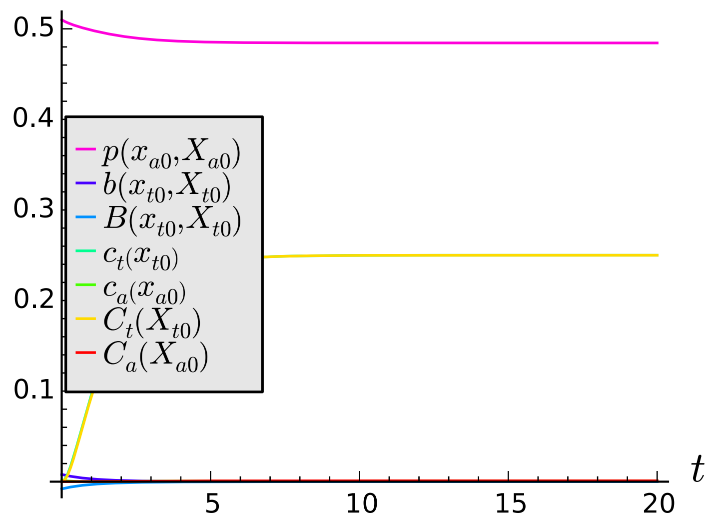
So here both guest and host become anti-association, while their contributions to transfer diverge to strong opposite values. Why is that?



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

Let's try different initial conditions



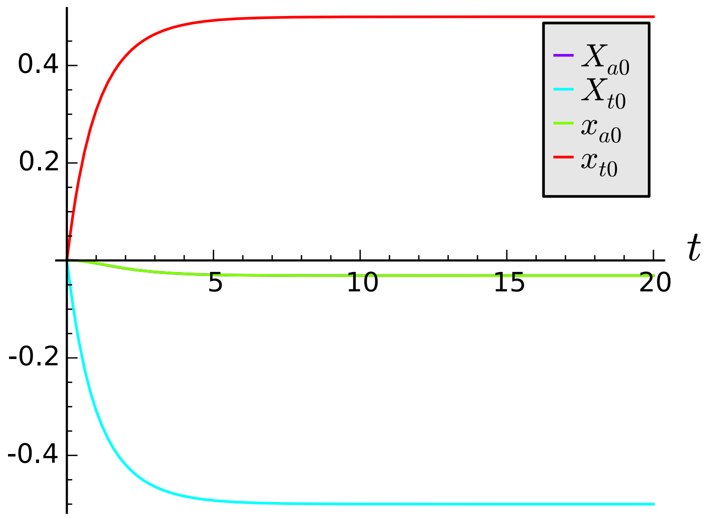


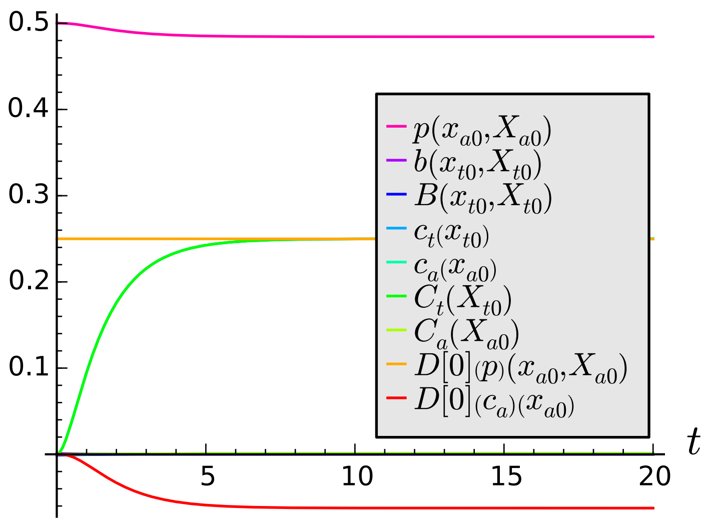
I am puzzled why x_{a_0} goes downward. Given that it's

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

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

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

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

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

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

Equilibrium conditions are

$$
\begin{aligned}
W &= 2\,X_t \\
Vx_t &= X_t^2 - WX_t + 8\,X_a \\
&= -X_t^2 + 8\,X_a \\
v &= 2\,x_t \\
wX_t &= x_t^2 - vx_t + 8\,x_a \\
&= -x_t^2 + 8\,x_a
\end{aligned}
$$

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

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

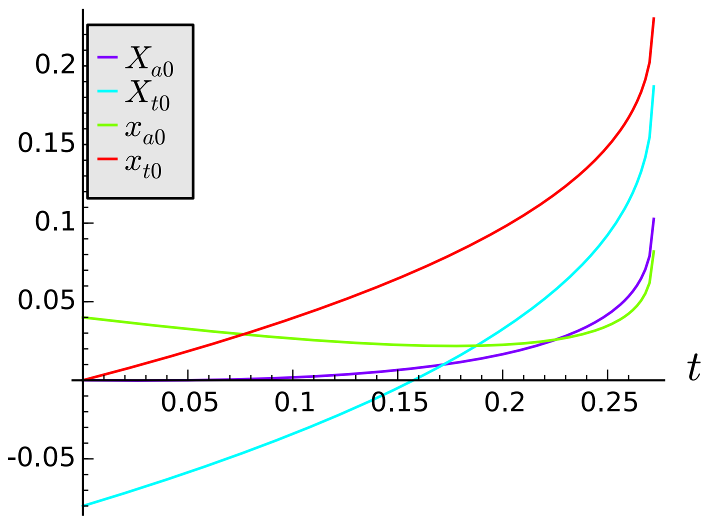
for

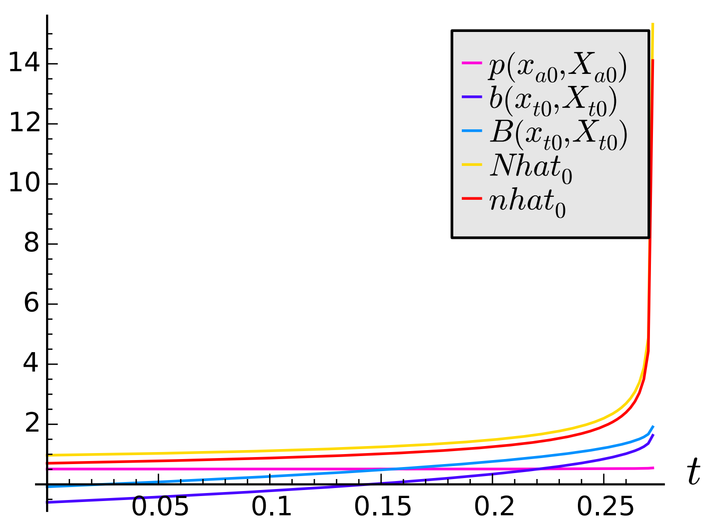
$$\frac{dX_{a0}}{dt} = -\frac{1}{8}\left(2\,X_{t0}^2\hat{n}_0 + 16\,X_{a0}\hat{n}_0 - (2\,X_{t0} + 15\,x_{t0})\hat{n}_0\right)\hat{N}_0$$

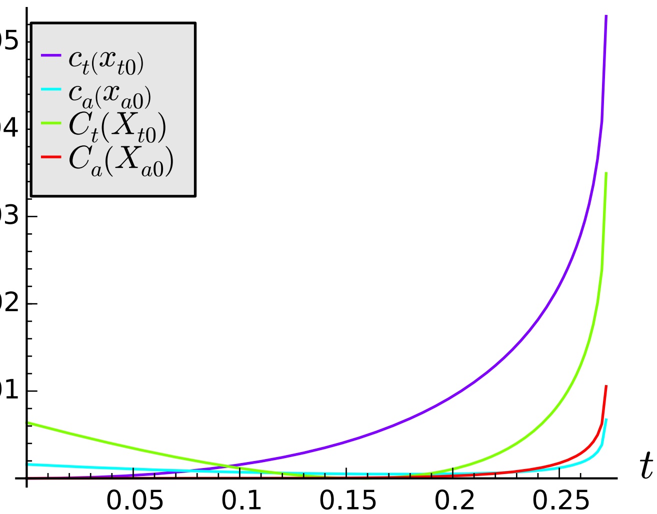
$$\frac{dX_{t0}}{dt} = -\frac{1}{4}\left(2\,(X_{a0} + x_{a0} + 2)X_{t0}\hat{n}_0 - (X_{a0} + x_{a0} + 2)\hat{n}_0\right)\hat{N}_0$$

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

$$\frac{dx_{t0}}{dt} = -\frac{1}{4}\left(2\,\hat{N}_0(X_{a0} + x_{a0} + 2)x_{t0} - \hat{N}_0(X_{a0} + x_{a0} + 2)\right)\hat{n}_0$$

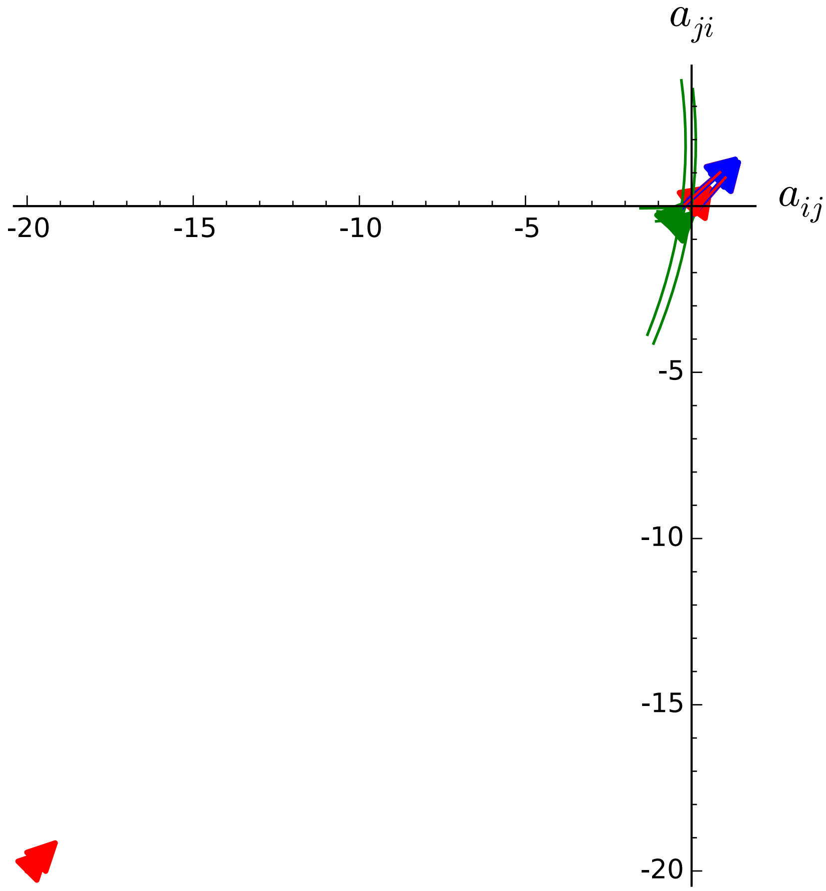






Why does it stop? Because the population equilibrium stops being viable, it looks like. Loss of B-stability. I'll probably want to look into the B-stability criteria, try to avoid this explosion. At first, I'll leave it as it is, since initial increase in mutualism is enough for my purposes.

The interactions



For a_{gH},

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

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

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

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

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

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:

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

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

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

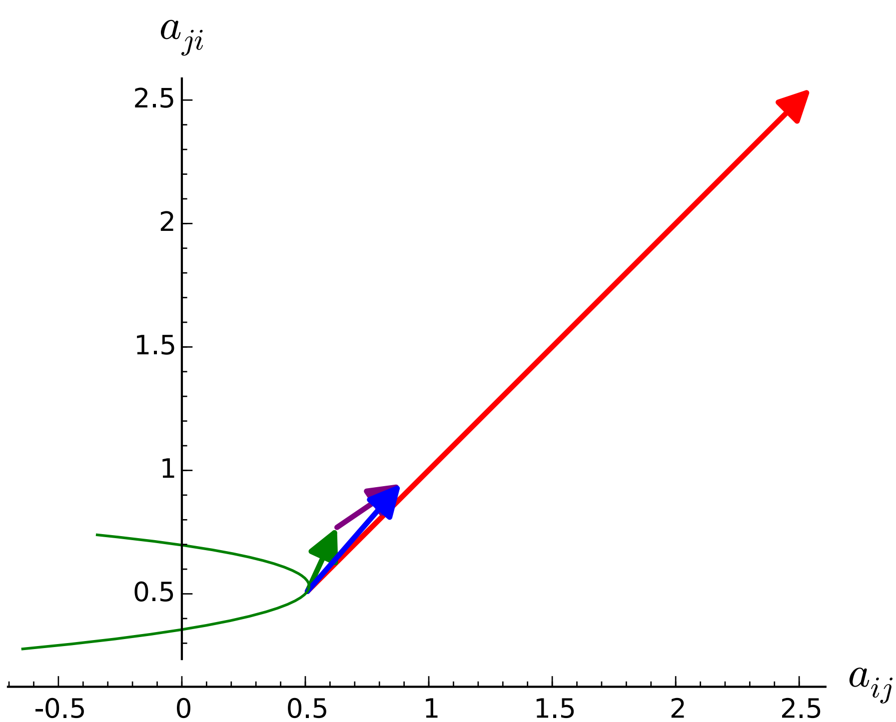
$$
\begin{aligned}
\frac{dA}{dt} &= \left({X_{a0}}'(t)\partial_1 p(x_{a0}\left(t\right), X_{a0}\left(t\right)) - ({c_a}'(x_{a0}\left(t\right)) - \partial_0 p(x_{a0}\left(t\right), X_{a0}\left(t\right))){x_{a0}}'(t),\right. \\
&\quad \left. -\left({C_a}'(X_{a0}\left(t\right)) - \partial_1 p(x_{a0}\left(t\right),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

The dynamics of the character variables are

$$X_{a0}{}'(t) = -\big(C_a{}'(X_{a0})\hat{n}_0 - \hat{n}_0\partial_1 p(x_{a0}, X_{a0})\big)\hat{N}_0$$
$$X_{t0}{}'(t) = 0$$
$$x_{a0}{}'(t) = -\Big(\hat{N}_0 c_a{}'(x_{a0}) - \hat{N}_0\partial_0 p(x_{a0}, X_{a0})\Big)\hat{n}_0$$
$$x_{t0}{}'(t) = 0$$

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 another situation where $2|dp/dx| < |c'|$ – in this latter case, the indirect effect is negative but too small to counter the direct effect.