

Symbiosis mediated by recognition

Supplement to Yoder and Tiffin, "Sanctions, recognition, and variation in mutualistic symbiosis"

Terms

This creates a stand-alone model of symbiosis mediated only by host recognition of signals produced by symbionts.

Assume infinite populations of interacting, haploid, hosts and symbionts. Whether a diploid host initiates symbiosis with a symbiont is determined by the host's genotype at the R/r locus and the symbiont's at the S/s locus; hosts with the R allele will initiate symbiosis with symbionts carrying the S allele, and hosts with r will initiate symbiosis with symbionts carrying s. When symbiosis is initiated, symbionts cooperate if they carry the M allele at a second locus, or do not cooperate if they carry the m allele (as in the model of symbiosis mediated by sanctions).

In successful interaction, the host pays a cost C_H and receives a benefit B_H ; the symbionts pay a cost C_S and receive benefit B_S . Hosts interacting with non-mutualist symbionts (m genotype) pay the cost without gaining the benefit.

Symbiosis outcomes and fitness

First, a host payoff matrix describes the outcomes of encounters between host genotypes R or r (rows) and symbiont genotypes MS, Ms, mS, and ms (columns). Payoffs are multiplied by a convenience term ϵ , which is used in the approximation employed at later stages of the analysis.

```
In[1]:= pmH =  $\epsilon$  { {  $B_H - C_H$ , 0, -  $C_H$ , 0 },  
                { 0,  $B_H - C_H$ , 0, -  $C_H$  } };  
MatrixForm[pmH]
```

```
Out[2]//MatrixForm=  

$$\begin{pmatrix} \epsilon (B_H - C_H) & 0 & -\epsilon C_H & 0 \\ 0 & \epsilon (B_H - C_H) & 0 & -\epsilon C_H \end{pmatrix}$$

```

Then, the symbiont payoff matrix (same orientation, for convenience).

```
In[3]:= pmS =  $\epsilon$  { {  $B_S - C_S$ , 0,  $B_S$ , 0 },  
                { 0,  $B_S - C_S$ , 0,  $B_S$  } };  
MatrixForm[pmS]
```

```
Out[4]//MatrixForm=  

$$\begin{pmatrix} \epsilon (B_S - C_S) & 0 & \epsilon B_S & 0 \\ 0 & \epsilon (B_S - C_S) & 0 & \epsilon B_S \end{pmatrix}$$

```

Fitness expressions

From the payout matrices, we can derive fitness statements for each host and symbiont genotype. For each species, fitness is determined as $1 + P$, where P is the payout from the symbiosis, determined by the frequencies of the other species' genotypes.

Host fitness

```
In[8]:= wR = 1 + PMS pmH[[1, 1]] + PMS pmH[[1, 2]] + PMS pmH[[1, 3]] + PMS pmH[[1, 4]];
wr = 1 + PMS pmH[[2, 1]] + PMS pmH[[2, 2]] + PMS pmH[[2, 3]] + PMS pmH[[2, 4]];
wbarH = pR wR + (1 - pR) wr;
```

Symbiont fitnesses

```
In[18]:= wMS = 1 + pR pms[[1, 1]] + (1 - pR) pms[[2, 1]];
wMs = 1 + pR pms[[1, 2]] + (1 - pR) pms[[2, 2]];
wmS = 1 + pR pms[[1, 3]] + (1 - pR) pms[[2, 3]];
wms = 1 + pR pms[[1, 4]] + (1 - pR) pms[[2, 4]];
wbarS = PMS wMS + PMs wMs + PmS wmS + Pms wms;
```

Allele frequency dynamics

To convert between symbiote haplotype frequencies and allele frequencies, we create a set of substitutions relating haplotype frequencies to allele frequencies and linkage disequilibrium, δ_S . As above, we multiply δ by the convenience term ϵ to facilitate the approximations we perform at later stages.

```
In[23]:= ChangeVars = {PMS → pM pS +  $\epsilon \delta_S$ , PMs → pM (1 - pS) -  $\epsilon \delta_S$ ,
  PmS → (1 - pM) pS -  $\epsilon \delta_S$ , Pms → (1 - pM) (1 - pS) +  $\epsilon \delta_S$ };
```

With these substitutions and the fitness expressions, we can calculate the per-generation rate of change in allele frequency for each host and symbiont locus. To produce expressions that are tractable for stability analysis, we perform a Taylor series approximation, assuming that the costs and benefits of symbiosis are small and of order ϵ (i.e., selection arising from the symbiosis is weak) and the symbiont loci are in quasi linkage equilibrium (δ is small and of order ϵ). This QLE approximation is valid if the symbiont loci are not strongly epistatic, which is consistent with the assumption that selection is weak.

Host

```
In[27]:= pR' = pR wR / wbarH;
AΔpR = FullSimplify[Normal[Series[(pR' - pR) /. ChangeVars, { $\epsilon$ , 0, 1}]] /.  $\epsilon \rightarrow 1$ 
Out[28]:= (CH - BH pM) (-1 + pR) pR (-1 + 2 pS)
```

Symbiote

First, we calculate new symbiont haplotype frequencies as a result of selection

```
In[29]:= PMS' = PMS wMS / wbarS;
PMs' = PMs wMs / wbarS;
PmS' = PmS wmS / wbarS;
Pms' = Pms wms / wbarS;
```

Then, we account for recombination, assuming complete recombination between loci.

```

In[33]:= PMS'' = PMS' PMS' (1) + PMS' PMS' (1/2) + PMS' PMS' (1/2) +
PMS' PMS' (1/4) + PMS' PMS' (1/2) + PMS' PMS' (0) + PMS' PMS' (1/4) +
PMS' PMS' (0) + PMS' PMS' (1/2) + PMS' PMS' (1/4) + PMS' PMS' (0) +
PMS' PMS' (0) + PMS' PMS' (1/4) + PMS' PMS' (0) + PMS' PMS' (0) + PMS' PMS' (0);
PMS'' = PMS' PMS' (0) + PMS' PMS' (1/2) + PMS' PMS' (0) + PMS' PMS' (1/4) +
PMS' PMS' (1/2) + PMS' PMS' (1) + PMS' PMS' (1/4) + PMS' PMS' (1/2) +
PMS' PMS' (0) + PMS' PMS' (1/4) + PMS' PMS' (0) + PMS' PMS' (0) +
PMS' PMS' (1/4) + PMS' PMS' (1/2) + PMS' PMS' (0) + PMS' PMS' (0);
PMS'' = PMS' PMS' (0) + PMS' PMS' (0) + PMS' PMS' (1/2) + PMS' PMS' (1/4) +
PMS' PMS' (0) + PMS' PMS' (0) + PMS' PMS' (1/4) + PMS' PMS' (0) +
PMS' PMS' (1/2) + PMS' PMS' (1/4) + PMS' PMS' (1) + PMS' PMS' (1/2) +
PMS' PMS' (1/4) + PMS' PMS' (0) + PMS' PMS' (1/2) + PMS' PMS' (0);
PMS'' = PMS' PMS' (0) + PMS' PMS' (0) + PMS' PMS' (0) + PMS' PMS' (1/4) +
PMS' PMS' (0) + PMS' PMS' (0) + PMS' PMS' (1/4) + PMS' PMS' (1/2) +
PMS' PMS' (0) + PMS' PMS' (1/4) + PMS' PMS' (0) + PMS' PMS' (1/2) +
PMS' PMS' (1/4) + PMS' PMS' (1/2) + PMS' PMS' (1/2) + PMS' PMS' (1);

```

```

In[37]:= pM' = Simplify[PMS'' + PMS'' /. ChangeVars];

```

```

In[38]:= ps' = Simplify[PMS'' + PMS'' /. ChangeVars];

```

```

In[39]:= deltaS' = Simplify[(PMS'' PMS'' - PMS'' PMS'') /. ChangeVars];

```

We can then approximate per-generation change in allele frequencies and LD.

```

In[40]:= ADeltaP_M = Simplify[Normal[Series[pM' - p_M, {epsilon, 0, 1}]]] /. epsilon -> 1

```

```

Out[40]= C_S (-1 + p_M) p_M (-1 + p_S + p_R (-1 + 2 p_S))

```

```

In[41]:= ADeltaP_S = Simplify[Normal[Series[ps' - p_S, {epsilon, 0, 1}]]] /. epsilon -> 1

```

```

Out[41]= -(B_S - C_S p_M) (-1 + 2 p_R) (-1 + p_S) p_S

```

```

In[42]:= ADeltaD_S = FullSimplify[Normal[Series[deltaS' - delta_S, {epsilon, 0, 1}]]] /. epsilon -> 1

```

```

Out[42]= 1/2 (-C_S (-1 + p_M) p_M (-1 + 2 p_R) (-1 + p_S) p_S - delta_S)

```

Equilibrium/stability

We then solve for equilibria in the system (i.e., conditions under which host and symbiont allele frequencies, and LD between the symbiont loci, do not change).

```
In[48]:= LEqs = Simplify[Solve[AΔpR == 0 && AΔpM == 0 && AΔpS == 0 && AΔδS == 0, {pR, pM, pS, δS}]];
MatrixForm[LEqs]
```

Solve::svars : Equations may not give solutions for all "solve" variables. >>

Out[49]//MatrixForm=

$$\left(\begin{array}{l} \{p_R \rightarrow 1, p_S \rightarrow 0, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 0, p_S \rightarrow 1, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 0, p_M \rightarrow 0, p_S \rightarrow 0, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 1, p_M \rightarrow 0, p_S \rightarrow 0, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow \frac{1}{2}, p_M \rightarrow 0, p_S \rightarrow \frac{1}{2}, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 0, p_M \rightarrow 0, p_S \rightarrow 1, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 1, p_M \rightarrow 0, p_S \rightarrow 1, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 0, p_M \rightarrow 1, p_S \rightarrow 0, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 1, p_M \rightarrow 1, p_S \rightarrow 0, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow \frac{1}{2}, p_M \rightarrow 1, p_S \rightarrow \frac{1}{2}, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 0, p_M \rightarrow 1, p_S \rightarrow 1, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 1, p_M \rightarrow 1, p_S \rightarrow 1, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 1, p_M \rightarrow \frac{C_H}{B_H}, p_S \rightarrow 0, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 1, p_M \rightarrow \frac{B_S}{C_S}, p_S \rightarrow 0, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 0, p_M \rightarrow \frac{C_H}{B_H}, p_S \rightarrow 1, \delta_S \rightarrow 0\} \\ \{p_R \rightarrow 0, p_M \rightarrow \frac{B_S}{C_S}, p_S \rightarrow 1, \delta_S \rightarrow 0\} \end{array} \right)$$

Some of these are internal equilibria, an particularly internal equilibria with $0 < p_M < 1$, which implies variation for symbiont cooperation. However, the four equilibria for which this is the case also have hosts and symbionts fixed for incompatible recognition and signalling alleles — that is, hosts would never initiate symbiosis because there are no compatible symbionts present in the population.

Two other equilibria have $p_R = p_S = 1/2$, which maximizes variation in host-symbiont compatibility; these require $p_M = 1$ or $p_M = 0$. We will examine local stability at these.

```
In[51]:= Jac = FullSimplify[{D[AΔpR, pR], D[AΔpR, pM], D[AΔpR, pS], D[AΔpR, δ],
{D[AΔpM, pR], D[AΔpM, pM], D[AΔpM, pS], D[AΔpM, δ]}, {D[AΔpS, pR], D[AΔpS, pM],
D[AΔpS, pS], D[AΔpS, δ]}, {D[AΔδ, pR], D[AΔδ, pM], D[AΔδ, pS], D[AΔδ, δ]}];
```

```
In[52]:= FullSimplify[Eigenvalues[Jac /. LEqs[[5]]]]
```

```
Out[52]= {0, -\frac{1}{2} \pm \sqrt{B_S} \sqrt{C_H}, \frac{1}{2} \pm \sqrt{B_S} \sqrt{C_H}, -\frac{C_S}{2}}
```

Eigenvalues with imaginary components and zero real parts imply oscillation when

$$p_R \rightarrow \frac{1}{2}, p_M \rightarrow 0, p_S \rightarrow \frac{1}{2}, \delta \rightarrow 0.$$

```
In[53]:= FullSimplify[Eigenvalues[JacL /. LEqs[[10]]]]
```

```
Out[53]= {0, -\frac{1}{2} \sqrt{B_H - C_H} \sqrt{B_S - C_S}, \frac{1}{2} \sqrt{B_H - C_H} \sqrt{B_S - C_S}, \frac{C_S}{2}}
```

Eigenvalues greater than zero imply instability when $p_R \rightarrow \frac{1}{2}, p_M \rightarrow 1, p_S \rightarrow \frac{1}{2}, \delta \rightarrow 0$.