Symbiosis mediated by sanctions and recognition

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

Terms

This creates a stand-alone model of symbiosis mediated both by host recognition of symbiont signalling and by host sanctions against non-cooperating symbionts.

Assume infinite populations of interacting, haploid, hosts and symbionts. A host's ability to sanction a non-cooperative symbiont is determined by its genotype at a single locus; hosts carrying the allele H at this locus are able to sanction, while those carrying the h allele are not. A haploid symbiont is cooperative if it carries the M allele, but not if it carries the m allele. Hosts and symbionts encounter each other at random and initiate symbiosis without respect to their genotypes. Whether a diploid host intiates 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.

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 C_S. Hosts interacting with non-mutualist symbionts (m genotype) pay the cost without gaining the benefit. unless they are able to sanction (H genotype). The effectiveness of sanctions, ω, determines how much of the cost of symbiosis a host can avoid when interacting with a non-cooperative symbiont; greater values of ω mean that sanctions do more to reduce the cost of hosting non-cooperators.

Symbiosis outcomes and fitness expressions

First, a host payoff matrix describes the outcomes of encounters between host genotypes HR, Hr, hR, and hr (rows); and symbiotes MS, Ms, mS, and ms (colums). Payoffs are multiplied by a convenience term ϵ, which is used in the approximation employed at later stages of the analysis.

```
In[1]:= pmH = ϵ {{ B_H - C_H, 0, - (1 - ω) C_H, 0},
        {0, B_H - C_H, 0, - (1 - ω) C_H},
        { B_H - C_H, 0, -C_H, 0},
        {0, B_H - C_H, 0, -C_H}};
    MatrixForm[pmH]
```

Out[2]//MatrixForm=

$$\begin{pmatrix} \epsilon\ (B_H - C_H) & 0 & \epsilon\ (-1 + \omega)\ C_H & 0 \\ 0 & \epsilon\ (B_H - C_H) & 0 & \epsilon\ (-1 + \omega)\ C_H \\ \epsilon\ (B_H - C_H) & 0 & -\epsilon\ C_H & 0 \\ 0 & \epsilon\ (B_H - C_H) & 0 & -\epsilon\ C_H \end{pmatrix}$$

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

```
In[3]:= pmS = ε {{ BS - CS, 0, (1 - ω) BS, 0},
          {0, BS - CS, 0, (1 - ω) BS},
          { BS - CS, 0, BS, 0},
          {0, BS - CS, 0, BS}};
       MatrixForm[pmS]
```

Out[4]//MatrixForm=

$$
\begin{pmatrix}
\epsilon\,(B_S - C_S) & 0 & \epsilon\,(1 - \omega)\,B_S & 0 \\
0 & \epsilon\,(B_S - C_S) & 0 & \epsilon\,(1 - \omega)\,B_S \\
\epsilon\,(B_S - C_S) & 0 & \epsilon\,B_S & 0 \\
0 & \epsilon\,(B_S - C_S) & 0 & \epsilon\,B_S
\end{pmatrix}
$$

Fitness expressions

Host fitness

```
In[19]:= wHR = 1 + PMS pmH[[1, 1]] + PMs pmH[[1, 2]] + PmS pmH[[1, 3]] + Pms pmH[[1, 4]];
       wHr = 1 + PMS pmH[[2, 1]] + PMs pmH[[2, 2]] + PmS pmH[[2, 3]] + Pms pmH[[2, 4]];
       whR = 1 + PMS pmH[[3, 1]] + PMs pmH[[3, 2]] + PmS pmH[[3, 3]] + Pms pmH[[3, 4]];
       whr = 1 + PMS pmH[[4, 1]] + PMs pmH[[4, 2]] + PmS pmH[[4, 3]] + Pms pmH[[4, 4]];
       wbarH = PHR wHR + PHr wHr + PhR whR + Phr whr;
```

Symbiont fitnesses

```
In[24]:= wMS = 1 + PHR pmS[[1, 1]] + PHr pmS[[2, 1]] + PhR pmS[[3, 1]] + Phr pmS[[4, 1]];
       wMs = 1 + PHR pmS[[1, 2]] + PHr pmS[[2, 2]] + PhR pmS[[3, 2]] + Phr pmS[[4, 1]];
       wmS = 1 + PHR pmS[[1, 3]] + PHr pmS[[2, 3]] + PhR pmS[[3, 3]] + Phr pmS[[4, 1]];
       wms = 1 + PHR pmS[[1, 3]] + PHr pmS[[2, 3]] + PhR pmS[[3, 3]] + Phr pmS[[4, 1]];
       wbarS = PMS wMS + PMs wMs + PmS wmS + Pms wms;
```

Local 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. As above, we multiply δ by the convenience term ϵ to facilitate the approximations we perform at later stages.

```
In[28]:= ChangeVars = {PHR → pH pR + ε δH, PHr → pH (1 - pR) - ε δH,
         PhR → (1 - pH) pR - ε δH, Phr → (1 - pH) (1 - pR) + ε δH, PMS → pM pS + ε δS,
         PMs → pM (1 - pS) - ε δS, PmS → (1 - pM) pS - ε δS, Pms → (1 - pM) (1 - pS) + ε δS};
```

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 benenfits 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 (each δ_i 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

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

In[29]:= `P_HR ' = P_HR wHR / wbarH;`
`P_Hr ' = P_Hr wHr / wbarH;`
`P_hR ' = P_hR whR / wbarH;`
`P_hr ' = P_hr whr / wbarH;`

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

In[33]:= `P_HR '' = P_HR ' P_HR ' (1) + P_HR ' P_Hr ' (1 / 2) + P_HR ' P_hR ' (1 / 2) +`
`    P_HR ' P_hr ' (1 / 4) + P_Hr ' P_HR ' (1 / 2) + P_Hr ' P_Hr ' (0) + P_Hr ' P_hR ' (1 / 4) +`
`    P_Hr ' P_hr ' (0) + P_hR ' P_HR ' (1 / 2) + P_hR ' P_Hr ' (1 / 4) + P_hR ' P_hR ' (0) +`
`    P_hR ' P_hr ' (0) + P_hr ' P_HR ' (1 / 4) + P_hr ' P_Hr ' (0) + P_hr ' P_hR ' (0) + P_hr ' P_hr ' (0);`
`P_Hr '' = P_HR ' P_HR ' (0) + P_HR ' P_Hr ' (1 / 2) + P_HR ' P_hR ' (0) + P_HR ' P_hr ' (1 / 4) +`
`    P_Hr ' P_HR ' (1 / 2) + P_Hr ' P_Hr ' (1) + P_Hr ' P_hR ' (1 / 4) + P_Hr ' P_hr ' (1 / 2) +`
`    P_hR ' P_HR ' (0) + P_hR ' P_Hr ' (1 / 4) + P_hR ' P_hR ' (0) + P_hR ' P_hr ' (0) +`
`    P_hr ' P_HR ' (1 / 4) + P_hr ' P_Hr ' (1 / 2) + P_hr ' P_hR ' (0) + P_hr ' P_hr ' (0);`
`P_hR '' = P_HR ' P_HR ' (0) + P_HR ' P_Hr ' (0) + P_HR ' P_hR ' (1 / 2) + P_HR ' P_hr ' (1 / 4) +`
`    P_Hr ' P_HR ' (0) + P_Hr ' P_Hr ' (0) + P_Hr ' P_hR ' (1 / 4) + P_Hr ' P_hr ' (0) +`
`    P_hR ' P_HR ' (1 / 2) + P_hR ' P_Hr ' (1 / 4) + P_hR ' P_hR ' (1) + P_hR ' P_hr ' (1 / 2) +`
`    P_hr ' P_HR ' (1 / 4) + P_hr ' P_Hr ' (0) + P_hr ' P_hR ' (1 / 2) + P_hr ' P_hr ' (0);`
`P_hr '' = P_HR ' P_HR ' (0) + P_HR ' P_Hr ' (0) + P_HR ' P_hR ' (0) + P_HR ' P_hr ' (1 / 4) +`
`    P_Hr ' P_HR ' (0) + P_Hr ' P_Hr ' (0) + P_Hr ' P_hR ' (1 / 4) + P_Hr ' P_hr ' (1 / 2) +`
`    P_hR ' P_HR ' (0) + P_hR ' P_Hr ' (1 / 4) + P_hR ' P_hR ' (0) + P_hR ' P_hr ' (1 / 2) +`
`    P_hr ' P_HR ' (1 / 4) + P_hr ' P_Hr ' (1 / 2) + P_hr ' P_hR ' (1 / 2) + P_hr ' P_hr ' (1);`

In[37]:= `p_H ' = Simplify[P_HR '' + P_Hr '' /. ChangeVars];`

In[38]:= `p_R ' = Simplify[P_HR '' + P_hR '' /. ChangeVars];`

In[39]:= `δ_H ' = Simplify[ (P_HR '' P_hr '' - P_Hr '' P_hR '') /. ChangeVars];`

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

In[40]:= `AΔp_H = Simplify[Normal[Series[p_H ' - p_H, {ε, 0, 1}]]] /. ε → 1`

Out[40]= $\omega\, C_H\, (-1 + p_H)\, p_H\, (-1 + p_M)\, (1 - p_S + p_R\, (-1 + 2\, p_S))$

In[42]:= `AΔp_R = FullSimplify[Normal[Series[p_R ' - p_R, {ε, 0, 1}]]] /. ε → 1`

Out[42]= $(C_H\, (1 + \omega\, p_H\, (-1 + p_M)) - B_H\, p_M)\, (-1 + p_R)\, p_R\, (-1 + 2\, p_S)$

In[43]:= `AΔδ_H = FullSimplify[Normal[Series[δ_H ' - δ_H, {ε, 0, 1}]]] /. ε → 1`

Out[43]= $\frac{1}{2}\, (-\omega\, C_H\, (-1 + p_H)\, p_H\, (-1 + p_M)\, (-1 + p_R)\, p_R\, (-1 + 2\, p_S) - \delta_H)$

Symbiote

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

In[44]:= `P_MS ' = P_MS wMS / wbarS;`
`P_Ms ' = P_Ms wMs / wbarS;`
`P_mS ' = P_mS wmS / wbarS;`
`P_ms ' = P_ms wms / wbarS;`

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

In[48]:= `P`$_{MS}$`'' = P`$_{MS}$`' P`$_{MS}$`' (1) + P`$_{MS}$`' P`$_{Ms}$`' (1 / 2) + P`$_{MS}$`' P`$_{mS}$`' (1 / 2) +`
`P`$_{MS}$`' P`$_{ms}$`' (1 / 4) + P`$_{Ms}$`' P`$_{MS}$`' (1 / 2) + P`$_{Ms}$`' P`$_{Ms}$`' (0) + P`$_{Ms}$`' P`$_{mS}$`' (1 / 4) +`
`P`$_{Ms}$`' P`$_{ms}$`' (0) + P`$_{mS}$`' P`$_{MS}$`' (1 / 2) + P`$_{mS}$`' P`$_{Ms}$`' (1 / 4) + P`$_{mS}$`' P`$_{mS}$`' (0) +`
`P`$_{mS}$`' P`$_{ms}$`' (0) + P`$_{ms}$`' P`$_{MS}$`' (1 / 4) + P`$_{ms}$`' P`$_{Ms}$`' (0) + P`$_{ms}$`' P`$_{mS}$`' (0) + P`$_{ms}$`' P`$_{ms}$`' (0);`
`P`$_{Ms}$`'' = P`$_{MS}$`' P`$_{MS}$`' (0) + P`$_{MS}$`' P`$_{Ms}$`' (1 / 2) + P`$_{MS}$`' P`$_{mS}$`' (0) + P`$_{MS}$`' P`$_{ms}$`' (1 / 4) +`
`P`$_{Ms}$`' P`$_{MS}$`' (1 / 2) + P`$_{Ms}$`' P`$_{Ms}$`' (1) + P`$_{Ms}$`' P`$_{mS}$`' (1 / 4) + P`$_{Ms}$`' P`$_{ms}$`' (1 / 2) +`
`P`$_{mS}$`' P`$_{MS}$`' (0) + P`$_{mS}$`' P`$_{Ms}$`' (1 / 4) + P`$_{mS}$`' P`$_{mS}$`' (0) + P`$_{mS}$`' P`$_{ms}$`' (0) +`
`P`$_{ms}$`' P`$_{MS}$`' (1 / 4) + P`$_{ms}$`' P`$_{Ms}$`' (1 / 2) + P`$_{ms}$`' P`$_{mS}$`' (0) + P`$_{ms}$`' P`$_{ms}$`' (0);`
`P`$_{mS}$`'' = P`$_{MS}$`' P`$_{MS}$`' (0) + P`$_{MS}$`' P`$_{Ms}$`' (0) + P`$_{MS}$`' P`$_{mS}$`' (1 / 2) + P`$_{MS}$`' P`$_{ms}$`' (1 / 4) +`
`P`$_{Ms}$`' P`$_{MS}$`' (0) + P`$_{Ms}$`' P`$_{Ms}$`' (0) + P`$_{Ms}$`' P`$_{mS}$`' (1 / 4) + P`$_{Ms}$`' P`$_{ms}$`' (0) +`
`P`$_{mS}$`' P`$_{MS}$`' (1 / 2) + P`$_{mS}$`' P`$_{Ms}$`' (1 / 4) + P`$_{mS}$`' P`$_{mS}$`' (1) + P`$_{mS}$`' P`$_{ms}$`' (1 / 2) +`
`P`$_{ms}$`' P`$_{MS}$`' (1 / 4) + P`$_{ms}$`' P`$_{Ms}$`' (0) + P`$_{ms}$`' P`$_{mS}$`' (1 / 2) + P`$_{ms}$`' P`$_{ms}$`' (0);`
`P`$_{ms}$`'' = P`$_{MS}$`' P`$_{MS}$`' (0) + P`$_{MS}$`' P`$_{Ms}$`' (0) + P`$_{MS}$`' P`$_{mS}$`' (0) + P`$_{MS}$`' P`$_{ms}$`' (1 / 4) +`
`P`$_{Ms}$`' P`$_{MS}$`' (0) + P`$_{Ms}$`' P`$_{Ms}$`' (0) + P`$_{Ms}$`' P`$_{mS}$`' (1 / 4) + P`$_{Ms}$`' P`$_{ms}$`' (1 / 2) +`
`P`$_{mS}$`' P`$_{MS}$`' (0) + P`$_{mS}$`' P`$_{Ms}$`' (1 / 4) + P`$_{mS}$`' P`$_{mS}$`' (0) + P`$_{mS}$`' P`$_{ms}$`' (1 / 2) +`
`P`$_{ms}$`' P`$_{MS}$`' (1 / 4) + P`$_{ms}$`' P`$_{Ms}$`' (1 / 2) + P`$_{ms}$`' P`$_{mS}$`' (1 / 2) + P`$_{ms}$`' P`$_{ms}$`' (1);`

In[52]:= `p`$_M$`' = Simplify[P`$_{MS}$`'' + P`$_{Ms}$`'' /. ChangeVars];`

In[53]:= `p`$_S$`' = Simplify[P`$_{MS}$`'' + P`$_{mS}$`'' /. ChangeVars];`

In[54]:= δ_S`' = Simplify[`$\left(P_{MS}'' \, P_{ms}'' - P_{Ms}'' \, P_{mS}''\right)$` /. ChangeVars];`

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

In[55]:= `AΔp`$_M$` = Simplify[Normal[Series[p`$_M$`' - p`$_M$`, {ϵ, 0, 1}]]] /. ϵ → 1`

Out[55]= $- (-1 + p_M) \, p_M$
$(-C_S \, (p_H \, (-1 + p_R) \, (-1 + p_S) + p_R \, p_S) + B_S \, (p_R \, (-1 + p_S) + p_H \, (1 - p_S + p_R \, (-1 + \omega + p_S))))$

In[57]:= `AΔp`$_S$` = Simplify[Normal[Series[p`$_S$`' - p`$_S$`, {ϵ, 0, 1}]]] /. ϵ → 1`

Out[57]= $- (B_S - C_S) \, p_M \, (p_H \, (-1 + p_R) + p_R) \, (-1 + p_S) \, p_S$

In[58]:= `AΔ`δ_S` = FullSimplify[Normal[Series[`δ_S`' - `δ_S`, {ϵ, 0, 1}]]] /. ϵ → 1`

Out[58]= $\dfrac{1}{2} \, ((B_S - C_S) \, (-1 + p_M) \, p_M \, (p_H \, (-1 + p_R) + p_R) \, (-1 + p_S) \, p_S - \delta_S)$

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[62]:= **Eqs = Simplify[Solve[AΔp_H == 0 && AΔp_R == 0 && AΔp_M == 0 &&**
   AΔp_S == 0 && AΔδ_H == 0 && AΔδ_S == 0, {p_H, p_R, p_M, p_S, δ_H, δ_S}]];

MatrixForm[
 Eqs]

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

Out[63]//MatrixForm=

$$
\begin{pmatrix}
\{p_H \to 0, \; p_R \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to 0, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_M \to \frac{C_H}{B_H}, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_M \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 1, \; p_M \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 1, \; p_R \to 0, \; p_M \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 1, \; p_R \to 1, \; p_M \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to \frac{1}{\omega}, \; p_R \to \frac{-1+p_S}{-1+2\,p_S}, \; p_M \to 0, \; \delta_H \to \frac{(-1+\omega)\,C_H\,(-1+p_S)\,p_S}{\omega\,(-1+2\,p_S)}, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_M \to 0, \; p_S \to \frac{1}{2}, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 1, \; p_M \to 0, \; p_S \to \frac{1}{2}, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_M \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to 0, \; p_M \to 1, \; p_S \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to 1, \; p_M \to 1, \; p_S \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to \frac{p_H}{1+p_H}, \; p_M \to 1, \; p_S \to \frac{1}{2}, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to 0, \; p_M \to 1, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to 1, \; p_M \to 1, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_S \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to 1, \; p_M \to 0, \; p_S \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to \frac{1}{\omega}, \; p_R \to 1, \; p_S \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_S \to \frac{1}{2}, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 1, \; p_R \to 0, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to 0, \; p_M \to 0, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_R \to 0, \; p_M \to \frac{C_H\,(-1+\omega\,p_H)}{-B_H+\omega\,C_H\,p_H}, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_M \to \frac{C_H}{B_H}, \; p_S \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 1, \; p_R \to \frac{-B_S+C_S}{(-2+\omega)\,B_S+C_S}, \; p_M \to \frac{(-1+\omega)\,C_H}{-B_H+\omega\,C_H}, \; p_S \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to \frac{1}{\omega}, \; p_R \to 1, \; p_M \to 0, \; p_S \to 0, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 0, \; p_R \to 0, \; p_M \to \frac{C_H}{B_H}, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to 1, \; p_R \to 0, \; p_M \to \frac{(-1+\omega)\,C_H}{-B_H+\omega\,C_H}, \; p_S \to 1, \; \delta_H \to 0, \; \delta_S \to 0\} \\
\{p_H \to \frac{C_S}{\omega\,B_S}, \; p_R \to \frac{C_S}{\omega\,B_S+C_S}, \; p_M \to \frac{C_H\,(B_S-C_S)}{B_H\,B_S-C_H\,C_S}, \; p_S \to \frac{\omega\,B_S}{\omega\,B_S-C_S}, \; \delta_H \to \frac{(B_H-C_H)\,C_H\,C_S^2}{(\omega\,B_S+C_S)\,(B_H\,B_S-C_H\,C_S)}, \; \delta_S \to 0\}
\end{pmatrix}
$$

In[64]:= **Jac = FullSimplify[**
   {{D[AΔp_H, p_H], D[AΔp_H, p_R], D[AΔp_H, p_M], D[AΔp_H, p_S], D[AΔp_H, δ_H], D[AΔp_H, δ_S]},
    {D[AΔp_R, p_H], D[AΔp_R, p_R], D[AΔp_R, p_M], D[AΔp_R, p_S], D[AΔp_R, δ_H], D[AΔp_R, δ_S]},
    {D[AΔp_M, p_H], D[AΔp_M, p_R], D[AΔp_M, p_M], D[AΔp_M, p_S], D[AΔp_M, δ_H], D[AΔp_M, δ_S]},
    {D[AΔp_S, p_H], D[AΔp_S, p_R], D[AΔp_S, p_M], D[AΔp_S, p_S], D[AΔp_S, δ_H], D[AΔp_S, δ_S]},
    {D[AΔδ_H, p_H], D[AΔδ_H, p_R], D[AΔδ_H, p_M], D[AΔδ_H, p_S], D[AΔδ_H, δ_H], D[AΔδ_H, δ_S]},
    {D[AΔδ_S, p_H], D[AΔδ_S, p_R], D[AΔδ_S, p_M], D[AΔδ_S, p_S], D[AΔδ_S, δ_H], D[AΔδ_S, δ_S]}}];

We will evaluate the stability of equilibria that maintain some degree of host-symbiont compatibility, that are internal for allele frequencies at any locus, or that maintain non-zero LD in one species or the other. In the matrix above, those are rows 3, 8, 10, 14, 20, and 26, 27, and 31.

In[65]:= **FullSimplify[Eigenvalues[Jac /. Eqs[[3]]]]**

Out[65]= $\left\{ 0,\ 0,\ 0,\ -\frac{1}{2},\ -\frac{1}{2},\ -\frac{\omega\ (B_H - C_H)\ C_H\ (-1 + p_S)}{B_H} \right\}$

This will have one eigenvalue (the last) greater than zero for reasonable parmeter values, so it is not stable.

In[66]:= **FullSimplify[Eigenvalues[Jac /. Eqs[[8]]]]**

Out[66]= $\left\{ 0,\ -\frac{1}{2},\ -\frac{1}{2},\ -\frac{\sqrt{(-1 + \omega)\ \omega^2\ C_H^2\ (1 - 2\ p_S)^4\ (-1 + p_S)\ p_S}}{\omega\ (1 - 2\ p_S)^2},\right.$

$\left. \frac{\sqrt{(-1 + \omega)\ \omega^2\ C_H^2\ (1 - 2\ p_S)^4\ (-1 + p_S)\ p_S}}{\omega\ (1 - 2\ p_S)^2},\ \frac{(-1 + \omega)\ (B_S - C_S)\ (-1 + p_S)\ p_S}{\omega\ (-1 + 2\ p_S)} \right\}$

This will have at least one eigenvalue greater than zero for reasonable parameter values, so it is not locally stable.

In[85]:= **FullSimplify[Eigenvalues[Jac /. Eqs[[10]]]]**

Out[85]= $\left\{ -\frac{1}{2},\ -\frac{1}{2},\ 0,\ 0,\ -\frac{\omega\ C_H}{2},\ \frac{1}{2}\ (-C_S + B_S\ (1 + 2\ (-1 + \omega)\ p_R)) \right\}$

This will have at least one eigenvalue greater than zero for reasonable parameter values, so it is not locally stable.

In[90]:= **FullSimplify[Eigenvalues[Jac /. Eqs[[14]]]]**

Out[90]= $\left\{ 0,\ -\frac{\sqrt{B_H - C_H}\ \sqrt{B_S - C_S}\ \sqrt{\frac{p_H}{1 + p_H}}}{\sqrt{2}},\ \frac{\sqrt{B_H - C_H}\ \sqrt{B_S - C_S}\ \sqrt{\frac{p_H}{1 + p_H}}}{\sqrt{2}},\ -\frac{1}{2},\ -\frac{1}{2},\ \frac{p_H\ (C_S - \omega\ B_S\ p_H)}{1 + p_H} \right\}$

This will have at least one eigenvalue greater than zero for reasonable parameter values, so it is not locally stable.

In[72]:= **FullSimplify[Eigenvalues[Jac /. Eqs[[20]]]]**

Out[72]= $\left\{ -\frac{1}{2},\ -\frac{1}{2},\ 0,\ 0,\ 0,\ -\frac{1}{2}\ \omega\ C_H\ (-1 + p_M) \right\}$

This will have at least one eigenvalue greater than zero for reasonable parameter values, so it is not locally stable.

In[74]:= **FullSimplify[Eigenvalues[Jac /. Eqs[[26]]]]**

Out[74]= $\left\{ 0,\ 0,\ 0,\ -\frac{1}{2},\ -\frac{1}{2},\ \omega\ C_H\ \left(1 - \frac{C_H}{B_H}\right) \right\}$

This will have at least one eigenvalue greater than zero for reasonable parameter values, so it is not locally stable.

In[75]:= **FullSimplify[Eigenvalues[Jac /. Eqs[[27]]]]**

Out[75]= $\left\{ -\frac{1}{2}, \; -\frac{1}{2}, \; \frac{(-1+\omega) \; \omega \; B_S \; C_H \; (-B_H + C_H)}{(B_H - \omega \; C_H) \; ((-2+\omega) \; B_S + C_S)}, \; \frac{(-1+\omega) \; C_H \; (B_S - C_S) \; (\omega \; B_S - C_S)}{(B_H - \omega \; C_H) \; ((-2+\omega) \; B_S + C_S)}, \right.$

$-\frac{\sqrt{(-1+\omega)^2 \; B_S \; (B_H - C_H) \; C_H \; (-B_H + \omega \; C_H)^3 \; (B_S - C_S) \; ((-2+\omega) \; B_S + C_S)^3}}{(B_H - \omega \; C_H)^2 \; ((-2+\omega) \; B_S + C_S)^2},$

$\left. \frac{\sqrt{(-1+\omega)^2 \; B_S \; (B_H - C_H) \; C_H \; (-B_H + \omega \; C_H)^3 \; (B_S - C_S) \; ((-2+\omega) \; B_S + C_S)^3}}{(B_H - \omega \; C_H)^2 \; ((-2+\omega) \; B_S + C_S)^2} \right\}$

This will have at least one eigenvalue greater than zero for reasonable parameter values, so it is not locally stable.

In[95]:= **FullSimplify[Eigenvalues[Jac /. Eqs[[31]]]]**

Out[95]= $Aborted