
Plant pollinator behavior RI model

My goal is to understand the relationship between pollinator behavior (which is often measured in the field and lab) and plant reproductive isolation. I want to 1. Mathematically formalize the relationship between the behavior of pollinators and the RI it causes in plants. 2. Understand how multiple pollinators showing different behavior cause RI in plants. 3. determine how variation in frequency of pollinators and frequency of plants effects plant RI.

Reproduction isolation

We are going to quantify reproductive isolation as inverse to the proportion of heterospecific matings (H) predicted by the behavior.

Pollinator behavior

There are two aspects of pollinator behavior we are interested in - preference and constancy. Preference is when a pollinator over visits one type of plant relative to what is expected by chance. Proportion of visits (ψ) is a function of the preference (ρ) and the frequency of plants (f). Preference comes from Smith and Macnair 1996 and Greenwood and Elton 1979 but has been modified to go from -1 to 1 to match constancy.

Smith Macnair:

$$\psi_{old} = (\rho * f) / (\rho * f + (1-f))$$

modified: so that $\rho_{old} = \left(\frac{-1-\rho}{-1+\rho} \right)$

$$\psi = \frac{f(1+\rho)}{1+(-1+2f)\rho}$$

Constancy (κ) is the tendency of a pollinator to move more frequently between like plants than unlike plants. It is a function of proportion of heterospecific visits (H) and proportion of visits to a plant (ψ). Constancy comes from Gegear and Thomson (2004 CI).

$$\kappa = ((1-H)-\psi) / ((1-H) + \psi - 2\psi(1-H))$$

Variables

H	Proportion of heterospecific matings
f	Frequency of plant
ϕ	Frequency of pollinator
ψ	Proportion of visits by pollinator made to a particular plant
V	Proportion of visits to a plant made by a particular pollinator

Parameters

ρ	Preference
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κ Constancy

Linking RI and behavior

My first goal is to determine the relationship between pollinator behavior and plant RI so we need to figure out how constancy and preference effect H - heterospecific matings. The constancy formula above includes both H and proportion of visits (which is a function of preference) so I can solve that formula for H in terms of constancy (κ) and proportion of visits (ψ). Then simplify:

$$\text{In}[*]:= \kappa[H_ , \psi_] := \left((1 - H) - \psi \right) / \left((1 - H) + \psi - 2 \psi (1 - H) \right)$$

$$\text{Solve}[\kappa == \left((1 - H) - \psi \right) / \left((1 - H) + \psi - 2 \psi (1 - H) \right), H]$$

$$\left\{ \left\{ H \rightarrow \frac{(-1 + \kappa) (-1 + \psi)}{1 - \kappa + 2 \kappa \psi} \right\} \right\}$$

$$\text{Solve}[\psi == \frac{f (1 + \rho)}{1 + (-1 + 2 f) \rho}, \rho]$$

$$\left\{ \left\{ \rho \rightarrow \frac{f - \psi}{-f - \psi + 2 f \psi} \right\} \right\}$$

$$\text{In}[*]:= \text{Simplify} \left[\frac{(-1 + \kappa) \left(-1 + \left(\frac{f (1 + \rho)}{1 + (-1 + 2 f) \rho} \right) \right)}{1 - \kappa + 2 \kappa * \left(\frac{f (1 + \rho)}{1 + (-1 + 2 f) \rho} \right)} \right]$$

$$\text{Out}[*]:= - \frac{(-1 + f) (-1 + \kappa) (-1 + \rho)}{1 + (-1 + 2 f) \rho + \kappa (-1 + 2 f + \rho)}$$

The formula to calculate H across plant frequency for any preference or constancy:

$$\text{In}[*]:= H[f_ , \rho_ , \kappa_] := - \frac{(-1 + f) (-1 + \kappa) (-1 + \rho)}{1 + (-1 + 2 f) \rho + \kappa (-1 + 2 f + \rho)};$$

The formula for RI is 1-2H and thus:

$$\text{Simplify} \left[1 - 2 * \left(- \frac{(-1 + f) (-1 + \kappa) (-1 + \rho)}{1 + (-1 + 2 f) \rho + \kappa (-1 + 2 f + \rho)} \right) \right]$$

$$1 + \frac{2 (-1 + f) (-1 + \kappa) (-1 + \rho)}{1 + (-1 + 2 f) \rho + \kappa (-1 + 2 f + \rho)}$$

$$\text{In}[*]:= \text{RI}[f_ , \rho_ , \kappa_] := 1 + \frac{2 (-1 + f) (-1 + \kappa) (-1 + \rho)}{1 + (-1 + 2 f) \rho + \kappa (-1 + 2 f + \rho)}$$

Multiple pollinators

Many plants have multiple pollinators. These pollinators may have different strengths of constancy and preference. How does frequency of pollinators with different behavior change RI (heterospecific matings?)

The total proportion of heterospecific matings (H) is the sum of the product of each pollinator heterospecific matings (h) and the proportion of visits to a plant by a particular pollinator .

$$H = \sum V_i * h_i$$

Where V is the proportion of all the visits to a plant that are by a given pollinator (i). And h is the proportion of heterospecific matings that pollinator makes.

$$V_i = \frac{\phi_i * \psi_i}{\sum_{j=1}^n \phi_j * \psi_j}$$

The proportion of visits to a plant by a pollinator (V) is a function of the pollinator's frequency (ϕ) and the proportion of visits the pollinator makes to the plant (ψ). Remember that ψ is a function of preference and plant frequency.

$$\text{In}[] := \text{Htot}[f_ , \phi_ , \rho1_ , \kappa1_ , \rho2_ , \kappa2_] := \left(\begin{array}{l} V := \frac{\left(\phi * \left(\frac{f (1+\rho1)}{1+(-1+2 f) \rho1} \right) \right)}{\phi * \left(\frac{f (1+\rho1)}{1+(-1+2 f) \rho1} \right) + (1-\phi) * \left(\frac{f (1+\rho2)}{1+(-1+2 f) \rho2} \right)} ; \\ H[fq_ , \rho_ , \kappa_] := - \frac{(-1+f q) (-1+\kappa) (-1+\rho)}{1+(-1+2 f q) \rho + \kappa (-1+2 f q + \rho)} ; \\ Ht := V * H[f, \rho1, \kappa1] + (1-V) * (H[f, \rho2, \kappa2]) ; \\ Ht \end{array} \right) ;$$

Simplify[

$$\left(\frac{\left(\phi * \left(\frac{f (1+\rho1)}{1+(-1+2 f) \rho1} \right) \right)}{\phi * \left(\frac{f (1+\rho1)}{1+(-1+2 f) \rho1} \right) + (1-\phi) * \left(\frac{f (1+\rho2)}{1+(-1+2 f) \rho2} \right)} \right) * \left(- \frac{(-1+f) (-1+\kappa1) (-1+\rho1)}{1+(-1+2 f) \rho1 + \kappa1 (-1+2 f + \rho1)} \right) + \\ \left(1 - \left(\frac{\left(\phi * \left(\frac{f (1+\rho1)}{1+(-1+2 f) \rho1} \right) \right)}{\phi * \left(\frac{f (1+\rho1)}{1+(-1+2 f) \rho1} \right) + (1-\phi) * \left(\frac{f (1+\rho2)}{1+(-1+2 f) \rho2} \right)} \right) \right) * \left(- \frac{(-1+f) (-1+\kappa2) (-1+\rho2)}{1+(-1+2 f) \rho2 + \kappa2 (-1+2 f + \rho2)} \right)] \\ \frac{(-1+f) \left(\frac{(-1+\kappa2) (1+(-1+2 f) \rho1) (-1+\rho2) (1+\rho2) (-1+\phi)}{1+(-1+2 f) \rho2 + \kappa2 (-1+2 f + \rho2)} - \frac{(-1+\kappa1) (-1+\rho1) (1+\rho1) (1+(-1+2 f) \rho2) \phi}{1+(-1+2 f) \rho1 + \kappa1 (-1+2 f + \rho1)} \right)}{1+\rho2-2\rho2\phi+2f\rho2\phi+\rho1(-1-\rho2+2f(1+\rho2-\phi)+2\phi)}$$

In[] := Htotal[f_ , \phi_ , \rho1_ , \kappa1_ , \rho2_ , \kappa2_] :=

$$\frac{(-1+f) \left(\frac{(-1+\kappa2) (1+(-1+2 f) \rho1) (-1+\rho2) (1+\rho2) (-1+\phi)}{1+(-1+2 f) \rho2 + \kappa2 (-1+2 f + \rho2)} - \frac{(-1+\kappa1) (-1+\rho1) (1+\rho1) (1+(-1+2 f) \rho2) \phi}{1+(-1+2 f) \rho1 + \kappa1 (-1+2 f + \rho1)} \right)}{1+\rho2-2\rho2\phi+2f\rho2\phi+\rho1(-1-\rho2+2f(1+\rho2-\phi)+2\phi)} ;$$

In[]:=

$$\text{RI}[\text{f_}, \phi_, \rho1_, \kappa1_, \rho2_, \kappa2_] := \frac{(-1 + \text{f_}) \left(\frac{(-1 + \kappa2) (1 + (-1 + 2 \text{f_}) \rho1) (-1 + \rho2) (1 + \rho2) (-1 + \phi)}{1 + (-1 + 2 \text{f_}) \rho2 + \kappa2 (-1 + 2 \text{f_} + \rho2)} - \frac{(-1 + \kappa1) (-1 + \rho1) (1 + \rho1) (1 + (-1 + 2 \text{f_}) \rho2) \phi}{1 + (-1 + 2 \text{f_}) \rho1 + \kappa1 (-1 + 2 \text{f_} + \rho1)} \right)}{1 + \rho2 - 2 \rho2 \phi + 2 \text{f_} \rho2 \phi + \rho1 (-1 - \rho2 + 2 \text{f_} (1 + \rho2 - \phi) + 2 \phi)}$$

Frequency dependent selection

The pollinator preference function comes from Smith and Macnair. But their preference is from 0 to infinity.

$$\psi[\text{f_}, \rho_] := \frac{(\rho * \text{f_})}{(\rho * \text{f_}) + (1 - \text{f_})}$$

Preference 0-infinity with frequency dependent selection is below.

$$\psi[\text{f_}, \rho_, \text{b_}] := \frac{(\rho * \text{f_})^{\text{b_}}}{(\rho * \text{f_})^{\text{b_}} + (1 - \text{f_})^{\text{b_}}}$$

I want preference to be on the same scale as constancy and vary from -1 to 1. I therefore transformed the preference function.

$$\rho[\text{pscale_}] := \left(\frac{-1 - \text{pscale_}}{-1 + \text{pscale_}} \right)$$

scaled preference

$$\psi[\text{f_}, \rho_] := \frac{\text{f_} (1 + \rho)}{1 + \rho * (2 * \text{f_} - 1)}$$

scaled frequency dependent preference

$$\psi[\text{f_}, \rho\text{scale_}, \text{b_}] := \frac{\left(\left(\frac{-1 - \rho\text{scale_}}{-1 + \rho\text{scale_}} \right) * \text{f_} \right)^{\text{b_}}}{\left(\left(\frac{-1 - \rho\text{scale_}}{-1 + \rho\text{scale_}} \right) * \text{f_} \right)^{\text{b_}} + (1 - \text{f_})^{\text{b_}}}$$

Given that $\text{RI} = 1 - 2\text{H}$, and that $\text{H} = (\kappa - 1)(\psi - 1)/(1 - \kappa + 2\kappa\psi)$ then

$$\text{RI}[\text{f_}, \rho_, \kappa_, \text{b_}] :=$$

$$1 - 2 * \left((\kappa - 1) \left(\frac{\left(\left(\frac{-1 - \rho}{-1 + \rho} \right) * \text{f_} \right)^{\text{b_}}}{\left(\left(\frac{-1 - \rho}{-1 + \rho} \right) * \text{f_} \right)^{\text{b_}} + (1 - \text{f_})^{\text{b_}}} - 1 \right) / \left(1 - \kappa + 2\kappa \frac{\left(\left(\frac{-1 - \rho}{-1 + \rho} \right) * \text{f_} \right)^{\text{b_}}}{\left(\left(\frac{-1 - \rho}{-1 + \rho} \right) * \text{f_} \right)^{\text{b_}} + (1 - \text{f_})^{\text{b_}}} \right) \right)$$

$$\text{In[1]} := \text{Simplify} \left[1 - 2 (\kappa - 1) \left(\frac{\left(\left(\frac{-1 - \rho}{-1 + \rho} \right) * \text{f_} \right)^{\text{b_}}}{\left(\left(\frac{-1 - \rho}{-1 + \rho} \right) * \text{f_} \right)^{\text{b_}} + (1 - \text{f_})^{\text{b_}}} - 1 \right) / \left(1 - \kappa + 2\kappa \frac{\left(\left(\frac{-1 - \rho}{-1 + \rho} \right) * \text{f_} \right)^{\text{b_}}}{\left(\left(\frac{-1 - \rho}{-1 + \rho} \right) * \text{f_} \right)^{\text{b_}} + (1 - \text{f_})^{\text{b_}}} \right) \right]$$

$$\text{Out[1]} := 1 + \frac{2 (1 - \text{f_})^{\text{b_}} (-1 + \kappa)}{(1 - \text{f_})^{\text{b_}} + \left(-\frac{\text{f_} (1 + \rho)}{-1 + \rho} \right)^{\text{b_}} + \kappa \left(- (1 - \text{f_})^{\text{b_}} + \left(-\frac{\text{f_} (1 + \rho)}{-1 + \rho} \right)^{\text{b_}} \right)}$$

Considering TOTAL RI for a system with one pollinator and two plant species using different constancy formula!

Gegeer and Thomson present a constancy formula based on the total heterospecific transitions in a community and not just in terms of a focal species. Because RI is usually calculated in terms of a focal species I modified this formula to be just heterospecific transitions for focal species. But, we can use the original constancy formula to calculate total RI for the whole two plant system as well.

First, the original constancy formula “e” is replaced by $(\psi^2 + (1 - \psi)^2)$

$$\text{In[*]} := \kappa t[\text{Ht_}, \psi_] := \frac{((1 - \text{Ht}) - (\psi^2 + (1 - \psi)^2))}{((1 - \text{Ht}) + (\psi^2 + (1 - \psi)^2) - 2 (\psi^2 + (1 - \psi)^2) (1 - \text{Ht}))}$$

Solve for Ht to get heterospecific matings

$$\text{In[*]} := \text{Solve}\left[\kappa t == \frac{((1 - \text{Ht}) - (\psi^2 + (1 - \psi)^2))}{((1 - \text{Ht}) + (\psi^2 + (1 - \psi)^2) - 2 (\psi^2 + (1 - \psi)^2) (1 - \text{Ht}))}, \text{Ht}\right]$$

$$\text{Out[*]} := \left\{ \left\{ \text{Ht} \rightarrow \frac{2 (-1 + \kappa t) (-\psi + \psi^2)}{1 + \kappa t - 4 \kappa t \psi + 4 \kappa t \psi^2} \right\} \right\}$$

$$\text{In[*]} := \text{Ht}[\text{f_}, \rho_ , \kappa t_] := \left(\begin{array}{l} \psi := \frac{\text{f} (1 + \rho)}{1 + (-1 + 2 \text{f}) \rho}; \\ \text{h} := \frac{2 (-1 + \kappa t) (-\psi + \psi^2)}{1 + \kappa t - 4 \kappa t \psi + 4 \kappa t \psi^2}; \\ \text{h} \\ \end{array} \right)$$

```

In[ ]:= RIt[f_, ρ_, κt_] := (
  ψ :=  $\frac{f (1 + \rho)}{1 + (-1 + 2 f) \rho}$ ;
  h :=  $\frac{2 (-1 + \kappa t) (-\psi + \psi^2)}{1 + \kappa t - 4 \kappa t \psi + 4 \kappa t \psi^2}$ ;
  ri := 1 - 2 h;
  ri
)

```

Now we can demonstrate that this works! and gives you the same RI for the system as calculating it for each species separately.

Consider an example, H1=4/8, H2=5/28, Ht=9/28, ψ1=8/28, ψ2=20/28, ρ=-0.428571 or 0.428571

```

In[ ]:= κ[4/8, 8/28]
κ[5/20, 20/28]
κt[9/28, 8/28]

```

```
Out[ ]:=  $\frac{3}{7}$ 
```

```
Out[ ]:=  $\frac{1}{11}$ 
```

```
Out[ ]:=  $\frac{119}{641}$ 
```

```

In[ ]:= H[0.5, -.428571, κ[4/8, 8/28]]
H[0.5, 0.428571, κ[5/20, 20/28]]
Ht[0.5, -.428571, κt[9/28, 8/28]]

```

```
Out[ ]:= 0.5
```

```
Out[ ]:= 0.25
```

```
Out[ ]:= 0.321429
```

```
In[ ]:= .5 * 8/28 + .25 * 20/28
```

```
Out[ ]:= 0.321429
```

try for ipomopsis in poverty gulch with hummingbird

```
In[ ]:=  $\kappa$ [0.04, 0.97435]
          $\kappa$ [0.75, 0.02564]
          $\kappa$ t[9/154, 0.97435]
```

```
Out[ ]:= -0.225636
```

```
Out[ ]:= 0.853664
```

```
Out[ ]:= -0.0824442
```

```
In[ ]:=  $\kappa$ t[9/154, 0.97435]
```

```
Out[ ]:= -0.0824442
```

```
In[ ]:= ag = RI[0.5, 0.9487179, -0.225806]
         tenu = RI[0.5, -0.9487179, 0.853658]
         RIt[0.5, 0.9487179,  $\kappa$ t[9/154, 0.97435]]
         tot == ag * 0.97435 + tenu * (1 - 0.97435)
```

```
Out[ ]:= 0.92
```

```
Out[ ]:= -0.500001
```

```
Out[ ]:= 0.883156
```

```
Out[ ]:= tot == 0.883577
```

```
In[ ]:= 0.90 * 0.974 + -0.45 * 0.026
```

```
Out[ ]:= 0.8649
```