# The Effects of Intraspecific Genetic Variation on the Dynamics of Predator-Prey Ecological Communities

Sam Fleischer, Pablo Chavarria

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### Preparing Undergraduates through Mentoring for PhDs (PUMP) Research Symposium

Advisor: Dr. Jing Li, Mathematics, CSU Northridge Consultant: Dr. Casey terHorst, Biology, CSU Northridge Supported By: Pacific Math Alliance, PUMP, CSU Northridge

### Overview

- Motivation
  - Observations in Nature
  - Previous Models
- Our Expansions
  - Gaussian Attack Rate under Coevolution
  - Introduce Stabilizing Selection
  - General Ditrophic Expansion
- Discussion

### Observations in Nature

- Predator/Prey interactions are prevalent in nature
  - Crab vs. gastropod [Saloniemi, 1993]
  - Classical Lotka-Volterra model
    - Genetic adaptation is insignificant

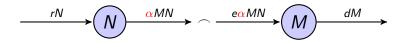


### Observations in Nature

- Predator/Prey interactions are prevalent in nature
  - Crab vs. gastropod [Saloniemi, 1993]
  - Classical Lotka-Volterra model
    - Genetic adaptation is insignificant
- There is trait variation within species, which causes variation in fundametal model parameters
  - Relative strength of crab claw vs. gastropod shell [Saloniemi, 1993]
  - Incorporating trait variation provides richer dynamics than classical
     Lotka-Volterra models



### Classical Lotka-Volterra Model

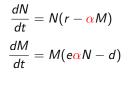


### **Variables**

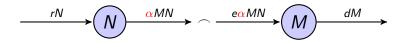
• 
$$N \equiv \text{Prey Density}$$

• 
$$M \equiv \text{Predator Density}$$

- $\alpha \equiv$  Attack rate
- $r \equiv \text{Prey birth rate}$
- $e \equiv \text{Efficiency}$
- $d \equiv \text{Predator death rate}$



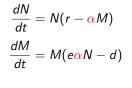
### Classical Lotka-Volterra Model



### **Variables**

- $N \equiv \text{Prey Density}$
- $M \equiv \text{Predator Density}$

- $\alpha \equiv$  Attack rate  $\leftarrow$  No variation!
- $r \equiv \text{Prey birth rate}$
- $e \equiv \text{Efficiency}$
- d = Predator death rate





### Schreiber, Bürger, and Bolnick's Expansion

Assume the Predator Species has a normally distributed trait value.

$$p(m, \overline{m}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(m - \overline{m})^2}{2\sigma^2}\right]$$

### **Parameters**

**Variables** 

•  $m \equiv \text{Predator Trait Value}$ 

• 
$$\sigma^2 \equiv \text{Predator Trait Variance}$$

### Schreiber, Bürger, and Bolnick's Expansion

Assume the Predator Species has a normally distributed trait value.

$$p(m, \overline{m}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(m - \overline{m})^2}{2\sigma^2}\right]$$

Attack Rate is a Function of the Predator's Trait Value

$$a(m) = \alpha \exp \left[ -\frac{(m-\theta)^2}{2\tau^2} \right]$$

#### **Parameters**

#### **Variables**

•  $m \equiv \text{Predator Trait Value}$ 

- $\sigma^2 \equiv \text{Predator Trait Variance}$
- $\alpha \equiv Maximum attack rate$
- $\tau \equiv$  Specialization Constant
- $\theta \equiv \text{Optimal trait value}$



### Schreiber, Bürger, and Bolnick's Expansion

Assume the Predator Species has a normally distributed trait value.

$$p(\mathbf{m}, \overline{\mathbf{m}}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(\mathbf{m} - \overline{\mathbf{m}})^2}{2\sigma^2}\right]$$

Attack Rate is a Function of the Predator's Trait Value

$$a(m) = \alpha \exp \left[ -\frac{(m-\theta)^2}{2\tau^2} \right]$$

#### **Parameters**

#### **Variables**

- $m \equiv \text{Predator Trait Value}$
- (((No Prey Trait Value)))

- $\sigma^2 \equiv \text{Predator Trait Variance}$
- $\alpha \equiv Maximum attack rate$
- $\tau \equiv$  Specialization Constant
- $\theta \equiv \text{Optimal trait value}$ † **No variation!**



### Normally Distributed Trait Values

Assume Prey and Predator have normally distributed trait values.

$$p(n, \overline{n}) = \frac{1}{\sqrt{2\pi\beta^2}} \exp\left[-\frac{(n-\overline{n})^2}{2\beta^2}\right]$$

$$p(m, \overline{m}) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(m - \overline{m})^2}{2\sigma^2}\right]$$

#### **Variables**

- $n \equiv \text{Prey Trait Value}$
- $\overline{n} \equiv$  Average Prey Trait Value
- $m \equiv \text{Predator Trait Value}$
- $\overline{m} \equiv$  **Average** Predator Trait Value

- $\beta^2 \equiv \text{Prey Trait Variance}$
- $\sigma^2 \equiv \text{Predator Trait Variance}$

### Attack Rate

### Attack Rate is a Gaussian Function of the Prey's Trait Value and the Predator's Trait Value

$$a(n, \mathbf{m}) = \alpha \exp \left[ -\frac{((\mathbf{m} - \mathbf{n}) - \theta)^2}{2\tau^2} \right]$$

#### **Variables**

- $n \equiv \text{Prey Trait Value}$
- $\overline{n} \equiv$  **Average** Prey Trait Value
- $m \equiv \text{Predator Trait Value}$
- $\overline{m} \equiv$  **Average** Predator Trait Value

- $\alpha \equiv \text{Maximum attack rate}$
- $m{\Theta} \equiv \mbox{Optimal trait difference}$
- $\tau^2 \equiv \text{Specialization Constant}$

### Attack Rate

### Attack Rate is a Gaussian Function of the Prey's Trait Value and the Predator's Trait Value

$$a(n, \mathbf{m}) = \alpha \exp \left[ -\frac{((\mathbf{m} - \mathbf{n}) - \theta)^2}{2\tau^2} \right]$$

### Average Attack Rate

$$\overline{a}(\overline{n}, \overline{m}) = \int_{-\infty}^{\infty} \int_{\infty}^{\infty} a(n, m) \cdot p(n, \overline{n}) \cdot p(m, \overline{m}) \, dn dm$$

$$= \frac{\alpha \tau}{\sqrt{\sigma^2 + \beta^2 + \tau^2}} \exp \left[ -\frac{((\overline{m} - \overline{n}) - \theta)^2}{2(\sigma^2 + \beta^2 + \tau^2)} \right]$$

#### **Variables**

- $n \equiv \text{Prey Trait Value}$
- $\overline{n} \equiv$  **Average** Prey Trait Value
- $m \equiv \text{Predator Trait Value}$
- $\overline{m} \equiv$  Average Predator Trait Value

- ullet  $\alpha \equiv {\sf Maximum}$  attack rate
- ullet  $\theta \equiv \text{Optimal trait difference}$
- $\tau^2 \equiv \text{Specialization Constant}$
- ullet  $eta^2 \equiv$  Prey Trait Variance
- $\sigma^2 \equiv \text{Predator Trait Variance}$



### Fitness Assumptions

- Prey experiences logistic growth in absence of predator
- Predator experiences exponential decay in absence of prey

$$Y(N, n, M, m) = r\left(1 - \frac{N}{K}\right) - Ma(n, m)$$

$$W(N, n, M, m) = eNa(n, m) - d$$

#### **Variables**

- N ≡ Prev Density
- $n \equiv \text{Prey Trait Value}$
- $M \equiv \text{Predator Density}$
- m ≡ Predator Trait Value

- $r \equiv$  Intrinsic Prey Growth Rate
- $K \equiv \text{Prey Carrying Capacity}$
- $d \equiv \text{Predator Death Rate}$
- $e \equiv$  Efficiency



### Average Fitness

$$\overline{Y}(N, \overline{n}, M, \overline{m}) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} Y(N, n, M, m) \cdot p(m, \overline{m}) \cdot p(n, \overline{n}) dmdn$$

$$= r \left( 1 - \frac{N}{K} \right) - M\overline{a}(\overline{n}, \overline{m})$$

$$\overline{W}(N,\overline{n},M,\overline{m}) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} W(N,n,M,m) \cdot p(m,\overline{m}) \cdot p(n,\overline{n}) \ dmdn$$
$$= eN\overline{a}(\overline{n},\overline{m}) - d$$

#### **Variables**

- $N \equiv \text{Prey Density}$
- $\overline{n} \equiv$  **Average** Prey Trait Value
- $M \equiv \text{Predator Density}$
- $\overline{m} \equiv$  Average Predator Trait Value

- $r \equiv$  Intrinsic Prey Growth Rate
- $K \equiv \text{Prey Carrying Capacity}$
- $d \equiv \text{Predator Death Rate}$
- $e \equiv \text{Efficiency}$



### **Ecological Components**

$$\begin{split} \frac{dN}{dt} &= N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) = N \bigg[ r \left( 1 - \frac{N}{K} \right) - M \overline{a}(\overline{n}, \overline{m}) \bigg] \\ \frac{dM}{dt} &= M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) = M [eN \overline{a}(\overline{n}, \overline{m}) - d] \end{split}$$

$$\xrightarrow{rN\left(1-\frac{N}{K}\right)} N \xrightarrow{\overline{a}(\overline{n},\overline{m})MN} 
\xrightarrow{e\overline{a}(\overline{n},\overline{m})MN} 
\xrightarrow{dM}$$

#### **Variables**

- N ≡ Prey Density
- $\overline{n} \equiv$  **Average** Prey Trait Value
- $M \equiv \text{Predator Density}$
- $\overline{m} \equiv$  Average Predator Trait Value

- $r \equiv$  Intrinsic Prey Growth Rate
- ullet  $K \equiv$  Prey Carrying Capacity
- $\bullet$   $d \equiv$  Predator Death Rate
- $e \equiv$  Efficiency



### **Evolutionary Components**

 The evolution of the mean trait value is always in the direction which increases the mean fitness in the population. [Lande, 1976]

$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2 \frac{M(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{n}, \overline{m})$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} = \sigma_G^2 \frac{eN(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{n}, \overline{m})$$

#### **Variables**

- N ≡ Prey Density
- ullet  $\overline{n} \equiv$  Mean Prey Character
- $M \equiv \text{Predator Density}$
- $\bullet$   $\overline{m} \equiv$  Mean Predator Character

- $\beta_G^2 \equiv \text{Prey genetic variance}$
- $\sigma_G^2 \equiv$  Predator genetic variance

# The Complete $1 \times 1$ Model (One Prey Species, One Predator Species)

### **Ecological Components**

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) = N \left[ r \left( 1 - \frac{N}{K} \right) - M \overline{a}(\overline{m}, \overline{n}) \right]$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) = M [eN \overline{a}(\overline{m}, \overline{n}) - d]$$

### **Evolutionary Components**

$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2 \frac{M(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{n}, \overline{m})$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} = \sigma_G^2 \frac{eN(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{n}, \overline{m})$$

#### **Extinction**

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

**Extinction** *Unstable* 

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#### **Exclusion**

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \mu^*, \mu^* + \theta)$$

where  $\mu^*$  is arbitrary

### **Extinction** *Unstable*

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

#### **Exclusion**

$$(N^*, \underline{M}^*, \overline{n}^*, \overline{m}^*) = (K, 0, \mu^*, \mu^* + \theta)$$

where  $\mu^*$  is arbitrary

Necessary Condition for Asymptotically Stable Exclusion:

$$d > \frac{Ke\alpha\tau}{\sqrt{A}}$$
 where  $A = \sigma^2 + \beta^2 + \tau^2$ 

#### Coexistence

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (\frac{d\sqrt{A}}{e\alpha\tau}, \frac{r\sqrt{A}}{\alpha\tau} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \mu^*, \mu^* + \theta)$$

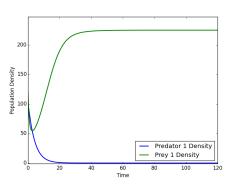
#### Coexistence

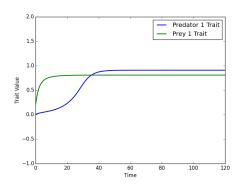
$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (\frac{d\sqrt{A}}{e\alpha\tau}, \frac{r\sqrt{A}}{\alpha\tau} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \mu^*, \mu^* + \theta)$$

Necessary Condition for Asymptotically Stable Coexistence:

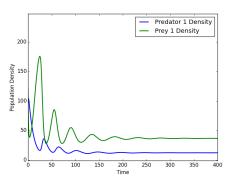
$$\frac{\sigma_G^2}{\beta_G^2} > \frac{r}{d} \left( 1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right)$$

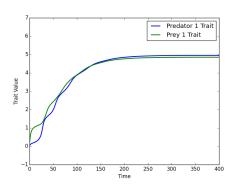
Our Expansions



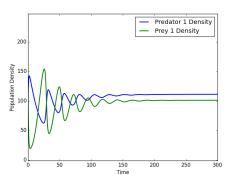


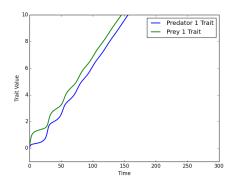
### Figures - $1 \times 1$ - Stable Coexistence





### Figures - $1 \times 1$ - "Arms Race" Coexistence





### Avoiding an "Arms Race" with Stabilizing Selection

### Assume Prey Growth Rate is a Function of the Prey's Trait Value

$$r(n) = \rho \exp \left[ -\frac{(n-\phi)^2}{2\gamma^2} \right]$$

#### **Variables**

- $n \equiv \text{Prey Trait Value}$
- $\overline{n} \equiv$  Average Prey Trait Value

- $\rho \equiv Maximum Growth Rate$
- $\bullet$   $\phi \equiv$  Prey Optimum Trait Value
- $\gamma^2 \equiv$  Stabilizing Selection Constant



### Avoiding an "Arms Race" with Stabilizing Selection

### Assume Prey Growth Rate is a Function of the Prey's Trait Value

$$r(n) = \rho \exp \left[ -\frac{(n-\phi)^2}{2\gamma^2} \right]$$

#### **Averge Growth Rate**

$$\overline{r}(\overline{n}) = \int_{-\infty}^{\infty} r(n) \cdot p(n, \overline{n}) dn$$
$$= \frac{\rho \gamma}{\sqrt{\beta^2 + \gamma^2}} \exp\left[-\frac{(n - \phi)^2}{2\gamma^2}\right]$$

### **Variables**

- $n \equiv \text{Prey Trait Value}$
- $\overline{n} \equiv$  **Average** Prey Trait Value

- $\rho \equiv Maximum Growth Rate$
- $\bullet$   $\phi \equiv \text{Prey Optimum Trait Value}$
- $\gamma^2 \equiv$  Stabilizing Selection Constant
- $\beta^2 \equiv \text{Prey Trait Variance}$

### Fitness Assumptions

- Prey experiences logistic growth in absence of predator
- Predator experiences exponential decay in absence of prey

$$Y(N, n, M, m) = r(n) \left(1 - \frac{N}{K}\right) - Ma(n, m)$$

$$W(N, n, M, m) = eNa(n, m) - d$$

#### **Variables**

- N ≡ Prey Density
- $n \equiv \text{Prey Trait Value}$
- $M \equiv \text{Predator Density}$
- $m \equiv \text{Predator Trait Value}$

- $r \equiv$  Intrinsic Prey Growth Rate Function
- $K \equiv \text{Prey Carrying Capacity}$
- $d \equiv Predator Death Rate$
- $e \equiv$  Efficiency



# The Complete $1 \times 1$ Model (One Prey Species, One Predator Species)

### **Ecological Components**

$$\frac{dN}{dt} = N \cdot \overline{Y}(N, \overline{n}, M, \overline{m}) = N \left[ \overline{r}(\overline{n}) \left( 1 - \frac{N}{K} \right) - M \overline{a}(\overline{n}, \overline{m}) \right]$$

$$\frac{dM}{dt} = M \cdot \overline{W}(N, \overline{n}, M, \overline{m}) = M [eN \overline{a}(\overline{n}, \overline{m}) - d]$$

### **Evolutionary Components**

$$\begin{split} \frac{d\overline{n}}{dt} &= \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2 \left[ \overline{r}(\overline{n}) \left( 1 - \frac{N}{K} \right) \frac{(\phi - \overline{n})}{\beta^2 + \gamma^2} + \frac{M(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{m}, \overline{n}) \right] \\ \frac{d\overline{m}}{dt} &= \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} = \sigma_G^2 \frac{eN(\theta - (\overline{m} - \overline{n}))}{\sigma^2 + \beta^2 + \tau^2} \overline{a}(\overline{n}, \overline{m}) \end{split}$$

#### **Extinction**

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

**Extinction** *Unstable* 

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

### **Extinction** *Unstable*

$$(N^*, \underline{M}^*, \overline{n}^*, \overline{m}^*) = (0, \underline{0}, \underline{\phantom{0}}, \underline{\phantom{0}})$$

#### **Exclusion**

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \mu^*, \mu^* + \theta)$$
 where  $\mu^*$  is arbitrary

### **Extinction** *Unstable*

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \_, \_)$$

#### **Exclusion**

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \mu^*, \mu^* + \theta)$$
 where  $\mu^*$  is arbitrary

Necessary Condition for Asymptotically Stable Exclusion:

$$d > \frac{Ke\alpha\tau}{\sqrt{A}}$$
 where  $A = \sigma^2 + \beta^2 + \tau^2$ 

#### Coexistence

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau}, \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \phi, \theta + \phi\right)$$
where  $A = \sigma^2 + \beta^2 + \tau^2$  and  $B = \beta^2 + \gamma^2$ 

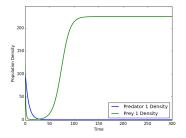
#### Coexistence

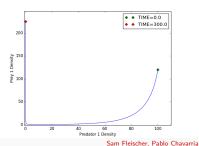
$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau}, \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \phi, \theta + \phi\right)$$
where  $A = \sigma^2 + \beta^2 + \tau^2$  and  $B = \beta^2 + \gamma^2$ 

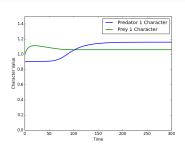
Necessary Condition for Asymptotically Stable Coexistence:

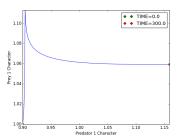
$$\frac{\sigma_G^2}{\beta_G^2} > \frac{\rho \gamma}{d\sqrt{B}} \left( 1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right) \left( 1 - \frac{A}{B} \right)$$

### Figures - $1 \times 1$ - Stable Exclusion



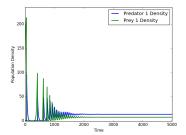


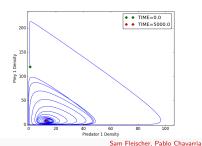


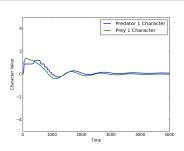


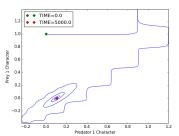


# Figures - $1 \times 1$ - Stable Coexistence



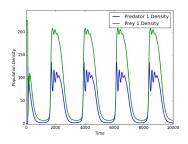


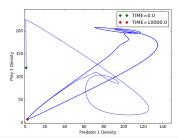


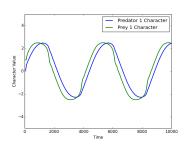


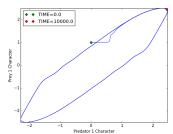


### Figures - $1 \times 1$ - Stable Cycles (Red Queen Dynamics)[Kindrik, Kondrashov, 1994]



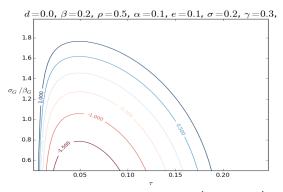








### Contour Plot - Coexistence Asymptotic Stability Criterion



$$f_{ ext{stable}}( ext{system parameters}) = rac{\sigma_{G}^{2}}{eta_{G}^{2}} - rac{
ho\gamma}{d\sqrt{B}} \left(1 - rac{d\sqrt{A}}{ ext{Ke}lpha au}
ight) \left(1 - rac{A}{B}
ight)$$

 $f_{\mathsf{stable}} > 0 \implies \mathsf{Coexistence} \ \mathsf{is} \ \mathit{stable}$ 

 $f_{\text{stable}} < 0 \implies \text{Coexistence is } \textit{unstable}$ 

 $f_{\text{stable}} = 0 \implies \text{Hopf Bifurcation}$ 

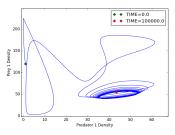


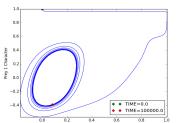
 $\tau = 0.05$ : Limit Cycle

VS.

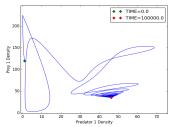
Node

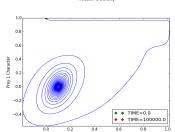
$$\frac{\sigma_{G}}{\beta_{C}} = 1.3 \implies f_{\mathsf{stable}} < 0$$





$$\frac{\sigma_G}{\beta_C} = 1.5 \implies f_{\text{stable}} > 0$$







# Summary of the $1 \times 1$ Model

- 4-dimensional system of ODEs
  - 2 ODEs describing the change in population size over time
  - 2 ODEs describing the change in **trait value** over time

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  - Exclusion (Stable under certain conditions)
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- Non-Equilibrium Dynamics
  - Constant Growth Rate
    - "Arms Race" Coexistence
  - Gaussian Growth Rate Function
    - Stable Limit Cycles

### **Expansion of Fitness Functions**

#### **Prey Fitness**

$$Y(N, n, M, m) = r(n) \left(1 - \frac{N}{K}\right) - Ma(n, m)$$

#### **Predator Fitness**

$$W(N, n, M, m) = eNa(n, m) - d$$

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#### **Predator Fitness**

$$W(N, n, M, m) = eNa(n, m) - d$$

$$\downarrow$$

$$W_i([N_j]_{j=1}^v, [n_j]_{j=1}^v, M_i, m_i) = \sum_{j=1}^v \left[ e_{ij} N_j a_{ij}(n_j, m_i) \right] - d_i$$

**Notation:** 
$$[x_i]_{i=1}^u = x_1, \dots, x_u$$

# Average Fitness Calculation

$$\overline{Y}_{j}(N_{j}, \overline{n_{j}}, [M_{i}]_{i=1}^{u}, [\overline{m_{i}}]_{i=1}^{u}) \\
= \int_{\mathbb{R}^{u+1}} Y_{j} \cdot \prod_{i=1}^{u} \left[ p_{i}(m_{i}, \overline{m_{i}}) \right] \cdot p(n, \overline{n}) \prod_{i=1}^{u} \left[ dm_{i} \right] dn_{j} \\
= \overline{r_{j}}(\overline{n_{j}}) \left( 1 - \frac{N_{j}}{K_{j}} \right) - \sum_{i=1}^{u} M_{i} \overline{a_{ij}}(\overline{n_{j}}, \overline{m_{i}})$$

$$\overline{W}_{i}(N_{j}, \overline{n_{j}}, [M_{i}]_{i=1}^{u}, [\overline{m_{i}}]_{i=1}^{u}) 
= \int_{\mathbb{R}^{u+1}} W_{i} \cdot p_{i}(m_{i}, \overline{m_{i}}) \cdot \prod_{j=1}^{v} \left[ p(n_{j}, \overline{n_{j}}) \right] dm_{i} \prod_{j=1}^{v} \left[ dn_{j} \right] 
= \sum_{i=1}^{v} \left[ e_{ij} N_{j} \overline{a_{ij}} (\overline{n_{j}}, \overline{m_{i}}) \right] - d_{i}$$

### The Complete $v \times u$ Model - (v Prey Species, u Predator Species)

### **Ecological Components**

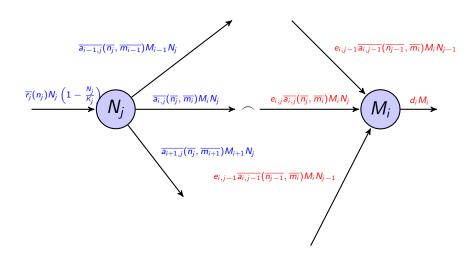
$$\frac{dN_{j}}{dt} = N_{j}\overline{Y_{j}} = N_{j}\left[\overline{r_{j}}(\overline{n_{j}})\left(1 - \frac{N_{j}}{K_{j}}\right) - \sum_{i=1}^{u} M_{i}\overline{a_{ij}}(\overline{n_{j}}, \overline{m_{i}})\right]$$

$$\frac{dM_{i}}{dt} = M_{i}\overline{W_{i}} = M_{i}\left[\sum_{j=1}^{v}\left[e_{ij}N_{j}\overline{a_{ij}}(\overline{n_{j}}, \overline{m_{i}})\right] - d_{i}\right]$$

#### **Evolutionary Components**

$$\begin{split} \frac{d\overline{n_{j}}}{dt} &= \beta_{Gj}^{2} \frac{\partial \overline{Y_{j}}}{\partial \overline{n_{j}}} = \beta_{Gj}^{2} \left[ \overline{r_{j}}(\overline{n_{j}}) \left( 1 - \frac{N_{j}}{K_{j}} \right) \frac{(\phi_{j} - \overline{n_{j}})}{\beta_{j}^{2} + \gamma_{j}^{2}} \right. \\ &+ \sum_{i=1}^{u} \left[ \frac{M_{i}(\theta_{ij} - (\overline{m_{i}} - \overline{n_{j}}))}{\sigma_{i}^{2} + \beta_{j}^{2} + \tau_{ij}^{2}} \overline{a_{ij}}(\overline{n_{j}}, \overline{m_{i}}) \right] \right] \\ \frac{d\overline{m_{i}}}{dt} &= \sigma_{Gi}^{2} \frac{\partial \overline{W_{i}}}{\partial \overline{m_{i}}} = \sigma_{Gi}^{2} \sum_{i=1}^{v} \left[ \frac{e_{ij} N_{j}(\theta_{ij} - (\overline{m_{i}} - \overline{n_{j}}))}{\sigma_{i}^{2} + \beta_{j}^{2} + \tau_{ij}^{2}} \overline{a_{ij}}(\overline{n_{j}}, \overline{m_{i}}) \right] \end{split}$$

# The Complete $v \times u$ Model - (v Prey Species, u Predator Species)



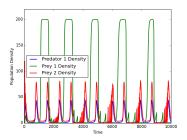
### The Complete $2 \times 1$ Model - (2 Prey Species, 1 Predator Species)

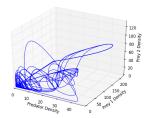
#### **Ecological Components**

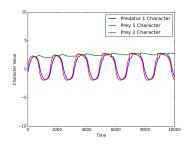
$$\begin{split} \frac{dN_1}{dt} &= N_1 \, \overline{Y_1} = N_1 \left[ \overline{r_1}(\overline{n_1}) \left( 1 - \frac{N_1}{K_1} \right) - M \overline{a_1}(\overline{n_1}, \overline{m}) \right] \\ \frac{dN_2}{dt} &= N_2 \, \overline{Y_2} = N_2 \left[ \overline{r_2}(\overline{n_2}) \left( 1 - \frac{N_2}{K_2} \right) - M \overline{a_2}(\overline{n_2}, \overline{m}) \right] \\ \frac{dM}{dt} &= M \, \overline{W} = M \left[ \sum_{j=1}^2 \left[ e_j \, N_j \, \overline{a_j}(\overline{n_j}, \overline{m}) \right] - d \right] \end{split}$$

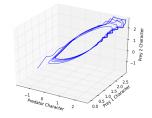
#### **Evolutionary Components**

$$\begin{split} \frac{d\overline{n_1}}{dt} &= \beta_{G1}^2 \frac{\partial \overline{Y_1}}{\partial \overline{n_1}} = \beta_{G1}^2 \bigg[ \overline{r_1}(\overline{n_1}) \left( 1 - \frac{N_1}{K_1} \right) \frac{(\phi_1 - \overline{n_1})}{\beta_1^2 + \gamma_1^2} + \frac{M(\theta_1 - (\overline{m} - \overline{n_1}))}{\sigma^2 + \beta_1^2 + \tau_1^2} \overline{a_1}(\overline{n_1}, \overline{m}) \bigg] \\ \frac{d\overline{n_2}}{dt} &= \beta_{G1}^2 \frac{\partial \overline{Y_2}}{\partial \overline{n_2}} = \beta_{G2}^2 \bigg[ \overline{r_2}(\overline{n_2}) \left( 1 - \frac{N_2}{K_2} \right) \frac{(\phi_2 - \overline{n_2})}{\beta_2^2 + \gamma_2^2} + \frac{M(\theta_2 - (\overline{m} - \overline{n_2}))}{\sigma^2 + \beta_2^2 + \tau_2^2} \overline{a_2}(\overline{n_2}, \overline{m}) \bigg] \\ \frac{d\overline{m}}{dt} &= \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} = \sigma_G^2 \sum_{i=1}^2 \bigg[ \frac{e_i N_i (\theta_i - (\overline{m} - \overline{n_i}))}{\sigma^2 + \beta_i^2 + \tau_i^2} \overline{a_j}(\overline{n_j}, \overline{m}) \bigg] \end{split}$$

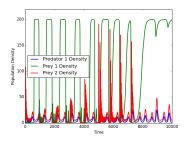


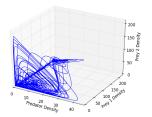


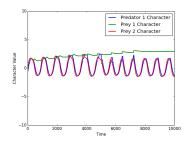


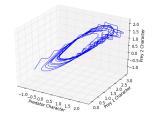




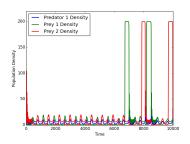


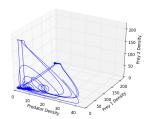


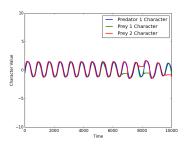


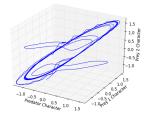




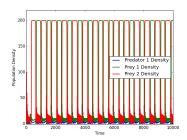


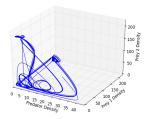


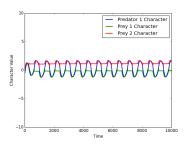


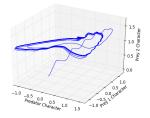














### The Complete $1 \times 2$ Model - (1 Prey Species, 2 Predator Species)

#### **Ecological Components**

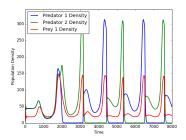
$$\frac{dN}{dt} = N\overline{Y} = N \left[ \overline{r}(\overline{n}) \left( 1 - \frac{N}{K} \right) - \sum_{i=1}^{2} M_{i} \overline{a_{i}}(\overline{n}, \overline{m_{i}}) \right]$$

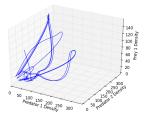
$$\frac{dM_{1}}{dt} = M_{1} \overline{W} = M_{1} \left[ e_{1} N \overline{a_{1}}(\overline{n}, \overline{m_{1}}) - d_{1} \right]$$

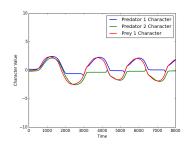
$$\frac{dM_{2}}{dt} = M_{2} \overline{W} = M_{2} \left[ e_{2} N \overline{a_{2}}(\overline{n}, \overline{m_{2}}) - d_{2} \right]$$

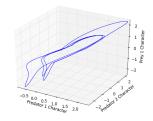
#### **Evolutionary Components**

$$\begin{split} \frac{d\overline{n}}{dt} &= \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} = \beta_G^2 \left[ \overline{r}(\overline{n}) \left( 1 - \frac{N}{K} \right) \frac{(\phi - \overline{n})}{\beta^2 + \gamma^2} + \sum_{i=1}^2 \left[ \frac{M_i (\theta_i - (\overline{m_i} - \overline{n}))}{\sigma_i^2 + \beta^2 + \tau_i^2} \overline{a_i} (\overline{n}, \overline{m_i}) \right] \right] \\ \frac{d\overline{m_1}}{dt} &= \sigma_{G1}^2 \frac{\partial \overline{W_1}}{\partial \overline{m_1}} = \sigma_{G1}^2 \left[ \frac{e_1 N (\theta_1 - (\overline{m_1} - \overline{n}))}{\sigma_1^2 + \beta^2 + \tau_1^2} \overline{a_1} (\overline{n}, \overline{m_1}) \right] \\ \frac{d\overline{m_2}}{dt} &= \sigma_{G1}^2 \frac{\partial \overline{W_2}}{\partial \overline{m_2}} = \sigma_{G1}^2 \left[ \frac{e_2 N (\theta_2 - (\overline{m_2} - \overline{n}))}{\sigma_2^2 + \beta^2 + \tau_2^2} \overline{a_2} (\overline{n}, \overline{m_2}) \right] \end{split}$$

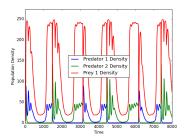


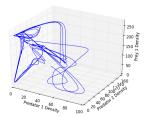


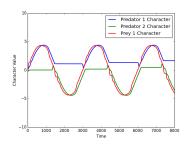


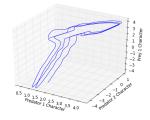














### Future Work

- $\bullet$  (1  $\times$  2) Two predator species in competition for one prey
- $(2 \times 1)$  Two prey species in apparent competition via one generalist predator
- $(2 \times 2)$  One specialist predator competing with one generalist predator for two prey
- (2 × 3) Two specialist predators competing with one generalist predator for two prey species
- $(u \times v)$  The General Ditrophic Expansion
- Intraguild Predation and General Multitrophic Expansion

### Thank You!

- PUMP (Preparing Undergraduates through Mentoring towards PhDs)
- The Pacific Math Alliance
- The National Math Alliance
- Dr. Helena Noronha, Dr. Ramin Vakilian, and all other PUMP organizers
- National Science Foundation
- California State University, Northridge
- Dr. Jing Li and Dr. Casey terHorst

# Questions?