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

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Preparing Undergraduates through Mentoring for PhDs (PUMP) Research Symposium

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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

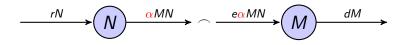


Observations in Nature

- 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



$$\frac{dN}{dt} = N(r - \frac{\alpha}{M})$$

$$\frac{dM}{dt} = M(e\alpha N - d)$$

- Prey Exponential Growth
- Predator Exponential Decay
- Linear Functional Response

Variables

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

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

Classical Lotka-Volterra Model

$$\xrightarrow{rN} \overbrace{N} \xrightarrow{\alpha MN} \frown \xrightarrow{e\alpha MN} \overbrace{M} \xrightarrow{dM}$$

$$\frac{dN}{dt} = N(r - \frac{\alpha}{\alpha}M)$$

$$\frac{dM}{dt} = M(e\alpha N - d)$$

- Prey Exponential Growth
- Predator Exponential Decay
- Linear Functional Response

Variables

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

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

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

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

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

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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.

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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.

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

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

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
- $M \equiv \text{Predator Density}$
- $\overline{m} \equiv$ Mean Predator Character

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

The Complete 1×1 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*

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

Extinction *Unstable*

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

Exclusion

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

where μ^* is arbitrary

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

Exclusion

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

where μ^* 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

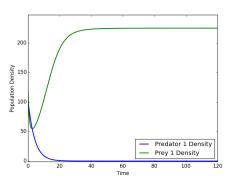
$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (\frac{d\sqrt{A}}{e\alpha\tau}, \frac{r\sqrt{A}}{\alpha\tau} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \mu^*, \mu^* + \theta)$$

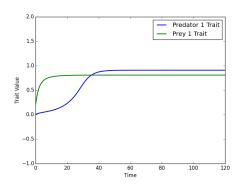
Necessary Condition for Asymptotically Stable Coexistence:

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

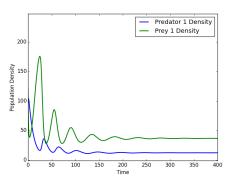
Our Expansions

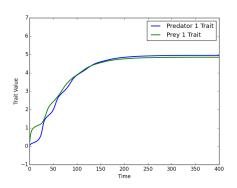
Figures - 1×1 - Stable Exclusion



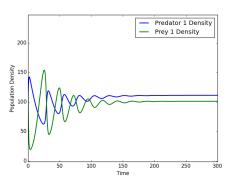


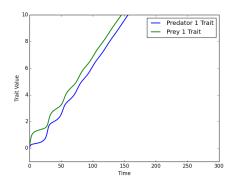
Figures - 1×1 - Stable Coexistence





Figures - 1×1 - "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

- $\rho \equiv Maximum Growth Rate$
- $\phi \equiv \text{Prey Optimum Trait Value}$
- $\gamma^2 \equiv$ 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 1×1 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

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

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

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Exclusion

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (K, 0, \mu^*, \mu^* + \theta)$$
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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 $B = \beta^2 + \gamma^2$

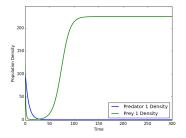
Coexistence

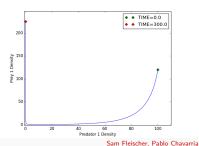
$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = \left(\frac{d\sqrt{A}}{e\alpha\tau}, \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}}\left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \phi, \theta + \phi\right)$$
where $A = \sigma^2 + \beta^2 + \tau^2$ and $B = \beta^2 + \gamma^2$

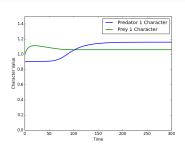
Necessary Condition for Asymptotically Stable Coexistence:

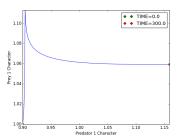
$$\frac{\sigma_G^2}{\beta_G^2} > \frac{\rho \gamma}{d\sqrt{B}} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right) \left(1 - \frac{A}{B} \right)$$

Figures - 1×1 - Stable Exclusion



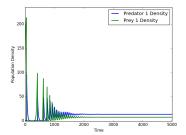


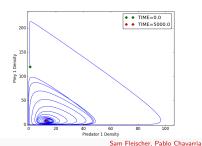


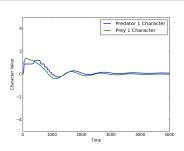


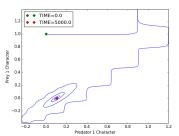


Figures - 1×1 - Stable Coexistence



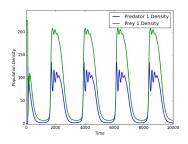


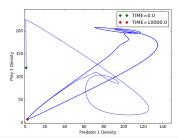


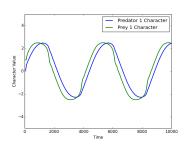


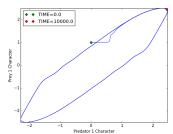


Figures - 1×1 - Stable Cycles (Red Queen Dynamics)[Kindrik, Kondrashov, 1994]



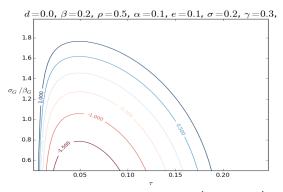








Contour Plot - Coexistence Asymptotic Stability Criterion



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

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

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

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

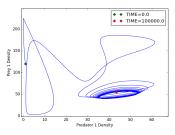


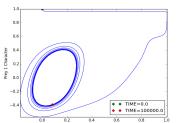
 $\tau = 0.05$: Limit Cycle

VS.

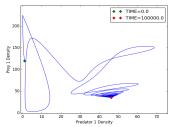
Node

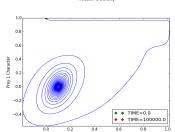
$$\frac{\sigma_{G}}{\beta_{C}} = 1.3 \implies f_{\mathsf{stable}} < 0$$





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







Summary of the 1×1 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

Summary of the 1×1 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
- 3 equilibrium points
 - Extinction (Unstable)
 - Exclusion (Stable under certain conditions)
 - Coexistence (Stable under certain conditions)

Summary of the 1×1 Model

- 4-dimensional system of ODEs
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- 3 equilibrium points
 - Extinction (Unstable)
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 - Coexistence (Stable under certain conditions)
- 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

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

Expansion of Fitness Functions

Prey Fitness

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

$$\downarrow$$

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

Predator Fitness

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

Expansion of Fitness Functions

Prey Fitness

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

$$\downarrow$$

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

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

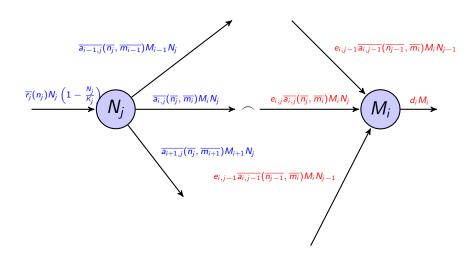
$$\frac{dN_{j}}{dt} = N_{j}\overline{Y_{j}} = N_{j}\left[\overline{r_{j}}(\overline{n_{j}})\left(1 - \frac{N_{j}}{K_{j}}\right) - \sum_{i=1}^{u} M_{i}\overline{a_{ij}}(\overline{n_{j}}, \overline{m_{i}})\right]$$

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

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)



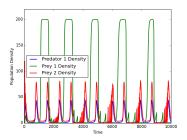
The Complete 2×1 Model - (2 Prey Species, 1 Predator Species)

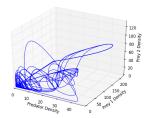
Ecological Components

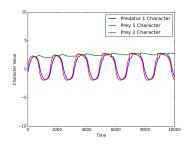
$$\begin{split} \frac{dN_1}{dt} &= N_1 \, \overline{Y_1} = N_1 \left[\overline{r_1}(\overline{n_1}) \left(1 - \frac{N_1}{K_1} \right) - M \overline{a_1}(\overline{n_1}, \overline{m}) \right] \\ \frac{dN_2}{dt} &= N_2 \, \overline{Y_2} = N_2 \left[\overline{r_2}(\overline{n_2}) \left(1 - \frac{N_2}{K_2}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

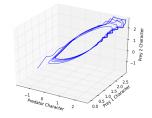
Evolutionary Components

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

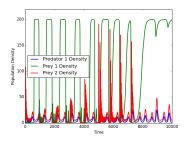


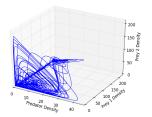


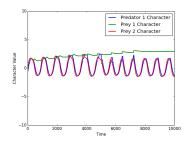


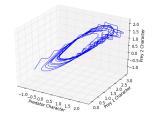




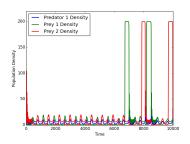


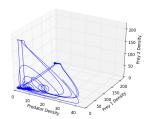


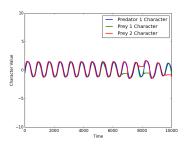


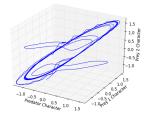




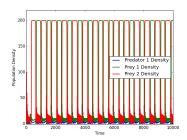


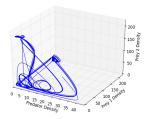


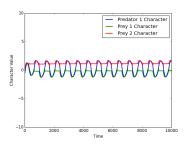


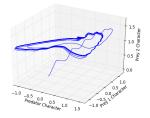














The Complete 1×2 Model - (1 Prey Species, 2 Predator Species)

Ecological Components

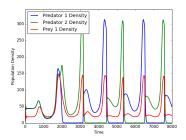
$$\frac{dN}{dt} = N\overline{Y} = N \left[\overline{r}(\overline{n}) \left(1 - \frac{N}{K} \right) - \sum_{i=1}^{2} M_{i} \overline{a_{i}}(\overline{n}, \overline{m_{i}}) \right]$$

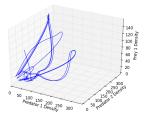
$$\frac{dM_{1}}{dt} = M_{1} \overline{W} = M_{1} \left[e_{1} N \overline{a_{1}}(\overline{n}, \overline{m_{1}}) - d_{1} \right]$$

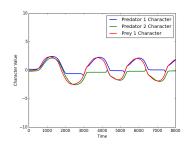
$$\frac{dM_{2}}{dt} = M_{2} \overline{W} = M_{2} \left[e_{2} N \overline{a_{2}}(\overline{n}, \overline{m_{2}}) - d_{2} \right]$$

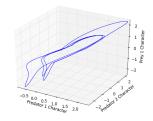
Evolutionary Components

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

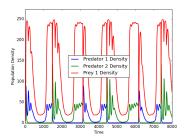


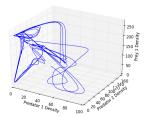


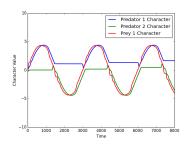


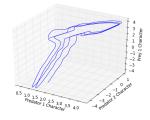














Future Work

- \bullet (1 \times 2) Two predator species in competition for one prey
- (2×1) Two prey species in apparent competition via one generalist predator
- (2×2) 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?