

The Ecological Effects of Trait Variation in a u -Predator, v -Prey System

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

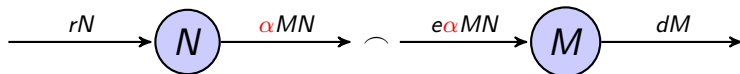
- Motivation / Observations in Nature
- Model Formulation
 - Classical Lotka-Volterra Predator-Prey Model
 - Schreiber, Bürger, and Bolnick's Extension
 - Our Extension
- Preliminary Results
- Future Work

Motivation / Observations in Nature

- Predator/Prey interactions are prevalent in nature
 - Crab vs. gastropod [Saloniemi, 1993]
 - Protist vs. bacteria [terHorst]
- There is trait variation within species
 - Thickness of plant cuticula [Saloniemi, 1993]
 - Strength of gastropod shell [Saloniemi, 1993]
- Incorporating trait variation provides **richer dynamics** than classical Lotka-Volterra models



Classical Lotka-Volterra Model



Variables

- $N \equiv$ Prey Density
- $M \equiv$ Predator Density

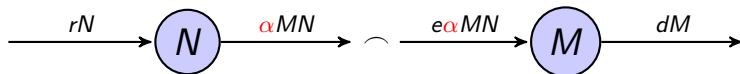
Parameters

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

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

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

Classical Lotka-Volterra Model



Variables

- $N \equiv$ Prey Density
- $M \equiv$ Predator Density

Parameters

- $\alpha \equiv$ Attack rate \leftarrow **No variation!**
- $r \equiv$ Prey birth rate
- $e \equiv$ Efficiency
- $d \equiv$ Predator death rate

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

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

Schreiber, Bürger, and Bolnick's Extension

Assume the **Predator Species** has a normally distributed trait value.

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

Parameters

- $\sigma^2 \equiv$ Predator Trait Variance

Variables

- $m \equiv$ Predator Trait Value

Schreiber, Bürger, and Bolnick's Extension

Assume the **Predator Species** has a normally distributed trait value.

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

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

- $m \equiv$ Predator Trait Value

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

Schreiber, Bürger, and Bolnick's Extension

Assume the **Predator Species** has a normally distributed trait value.

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

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

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

Variables

- $m \equiv$ **Predator Trait Value**
- (((No Prey Trait Value)))

Parameters

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

Our Extension

Assume **Prey** and **Predator** have normally distributed trait values.

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

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

Variables

- $n \equiv$ Prey Trait Value
- $m \equiv$ Predator Trait Value

Parameters

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

Our Extension

Assume **Prey** and **Predator** have normally distributed trait values.

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

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

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

Variables

- $n \equiv$ Prey Trait Value
- $m \equiv$ Predator Trait Value

Parameters

- $\beta^2 \equiv$ Prey Trait Variance
- $\sigma^2 \equiv$ Predator Trait Variance
- $\alpha \equiv$ Maximum attack rate
- $\theta \equiv$ Optimal trait difference
- $\tau \equiv$ Specialization Constant

Average Attack Rate

$$\begin{aligned}\bar{a}(\bar{n}, \bar{m}) &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} a(n, m) \cdot p(n, \bar{n}) \cdot p(m, \bar{m}) \, dn \, dm \\ &= \frac{\alpha \tau}{\sqrt{\sigma^2 + \beta^2 + \tau^2}} \exp \left[-\frac{((\bar{m} - \bar{n}) - \theta)^2}{2(\sigma^2 + \beta^2 + \tau^2)} \right]\end{aligned}$$

Variables

- $\bar{n} \equiv$ Mean Prey Character
- $\bar{m} \equiv$ Mean Predator Character

Parameters

- $\beta^2 \equiv$ Prey Trait Variance
- $\sigma^2 \equiv$ Predator Trait Variance
- $\alpha \equiv$ Maximum attack rate
- $\theta \equiv$ Optimal trait difference
- $\tau \equiv$ Specialization Constant

Fitness Assumptions

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

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

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

Variables

- $N \equiv$ Prey Density
- $n \equiv$ Prey Trait Value
- $M \equiv$ Predator Density
- $m \equiv$ Predator Trait Value

Parameters

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

Average Fitness

$$\begin{aligned}\overline{Y}(\overline{m}, \overline{n}, M, N) &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} Y(m, n, M, N) \cdot p(m, \overline{m}) \cdot p(n, \overline{n}) \, dmdn \\ &= r \left(1 - \frac{N}{K} \right) - M\overline{a}(\overline{n}, \overline{m})\end{aligned}$$

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

Variables

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

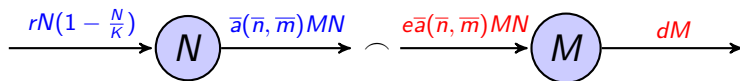
Parameters

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

Ecological Components

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

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



Variables

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

Parameters

- $r \equiv$ Intrinsic Prey Growth Rate
- $K \equiv$ Prey Carrying Capacity
- $d \equiv$ 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]

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

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

Variables

- $N \equiv$ Prey Density
- $\bar{n} \equiv$ Mean Prey Character
- $M \equiv$ Predator Density
- $\bar{m} \equiv$ Mean Predator Character

Parameters

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

The Complete 1×1 Model (One Predator Species, One Prey Species)

Ecological Components

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

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

Evolutionary Components

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

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

Equilibria - 1 × 1

$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N)$$

$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N)$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction

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

Exclusion

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

Equilibria - 1 × 1

$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N)$$

$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N)$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction *Unstable*

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

Exclusion

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

| | |
|-------------------|-----------------|
| Extinction | <i>Unstable</i> |
|-------------------|-----------------|

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

| | |
|------------------|--|
| Exclusion | <i>Stable under certain conditions</i> |
|------------------|--|

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

Necessary Conditions for Stable Exclusion:

- $d > e\bar{a}(\bar{m}^*, \bar{n}^*)K$
- $(\bar{m}^* - \bar{n}^* - \theta)^2 < \sigma^2 + \beta^2 + \tau^2$

Equilibria - 1 × 1

$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N)$$

$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N)$$

$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

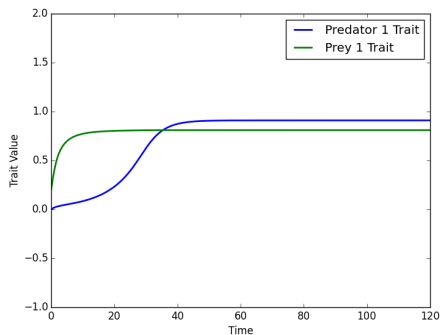
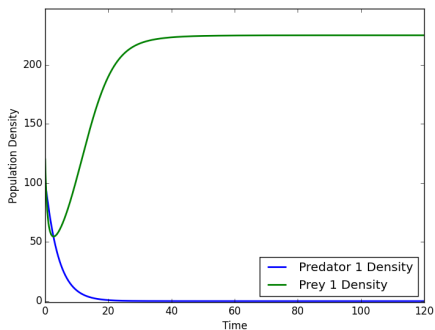
Coexistence

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

where $A = \sigma^2 + \beta^2 + \tau^2$ and μ^* is an arbitrary value.

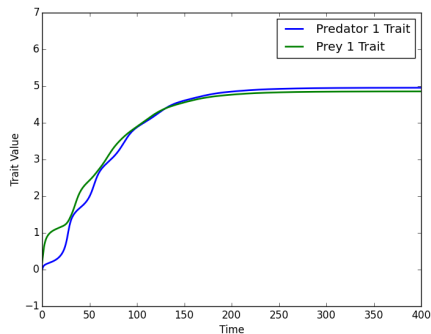
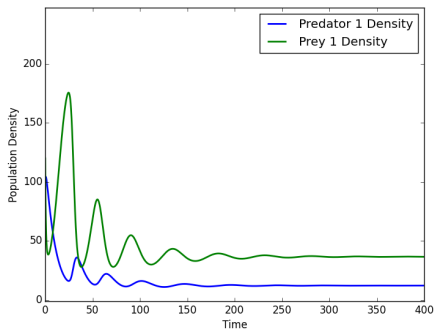
Figures - 1×1

Exclusion



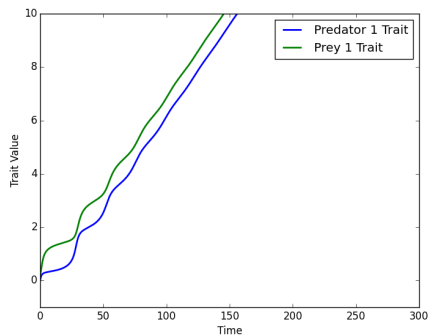
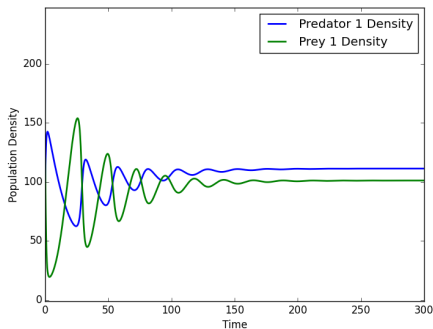
Figures - 1×1

Stable Coexistence



Figures - 1×1

Unstable Coexistence



Ask us about our
preliminary 1 × 2 results!

Prey Fitness

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

Predator Fitness

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

Prey Fitness

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

↓

$$Y_j([m_i]_{i=1}^u, n_j, [M_i]_{i=1}^u, N_j) = r_j \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u M_i a_{ij}(n_j, m_i)$$

Predator Fitness

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

Notation

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

Prey Fitness

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

↓

$$Y_j([m_i]_{i=1}^u, n_j, [M_i]_{i=1}^u, N_j) = r_j \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u M_i a_{ij}(n_j, m_i)$$

Predator Fitness

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

↓

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

Notation

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

Average Fitness

$$\begin{aligned}
 \bar{Y}_j([\bar{m}_i]_{i=1}^u, \bar{n}_j, [M_i]_{i=1}^u, N_j) \\
 &= \int_{\mathbb{R}^{u+1}} Y_j \cdot \prod_{i=1}^u \left[p_i(m_i, \bar{m}_i) \right] \cdot p(n, \bar{n}) \prod_{i=1}^u [dm_i] dn_j \\
 &= r_j \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u M_i \bar{a}_{ij}(\bar{n}_j, \bar{m}_i)
 \end{aligned}$$

$$\begin{aligned}
 \bar{W}_i(\bar{m}_i, [\bar{n}_j]_{j=1}^v, [N_j]_{j=1}^v) \\
 &= \int_{\mathbb{R}^{u+1}} W_i \cdot p_i(m_i, \bar{m}_i) \cdot \prod_{j=1}^v \left[p(n_j, \bar{n}_j) \right] dm_i \prod_{j=1}^v [dn_j] \\
 &= \sum_{j=1}^v \left[e_{ij} N_j \bar{a}_{ij}(\bar{n}_j, \bar{m}_i) \right] - d_i
 \end{aligned}$$

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

Ecological Components

$$\frac{dN_j}{dt} = N_j \bar{Y}_j = N_j \left[r_j \left(1 - \frac{N_j}{K_j} \right) - \sum_{i=1}^u M_i \bar{a}_{ij}(\bar{m}_i, \bar{n}_j) \right]$$

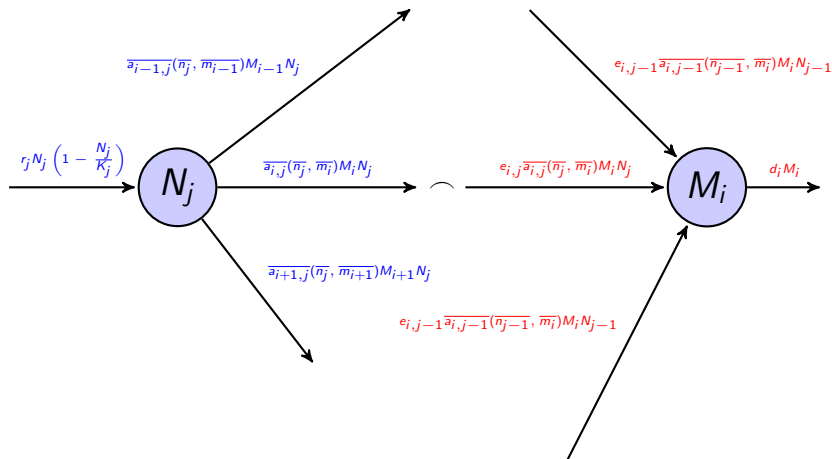
$$\frac{dM_i}{dt} = M_i \bar{W}_i = M_i \left[\sum_{j=1}^v \left[e_{ij} N_j \bar{a}_{ij}(\bar{m}_i, \bar{n}_j) \right] - d_i \right]$$

Evolutionary Components

$$\frac{d\bar{n}_j}{dt} = \beta_{Gj}^2 \frac{\partial \bar{Y}_j}{\partial \bar{n}_j} = \beta_{Gj}^2 \sum_{i=1}^u \left[\frac{M_i (\theta_{ij} + \bar{n}_j - \bar{m}_i)}{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2} \bar{a}_{ij}(\bar{m}_i, \bar{n}_j) \right]$$

$$\frac{d\bar{m}_i}{dt} = \sigma_{Gi}^2 \frac{\partial \bar{W}_i}{\partial \bar{m}_i} = \sigma_{Gi}^2 \sum_{j=1}^v \left[\frac{e_{ij} N_j (\theta_{ij} + \bar{n}_j - \bar{m}_i)}{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2} \bar{a}_{ij}(\bar{m}_i, \bar{n}_j) \right]$$

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



Future Work

- Two Predators competing for One Prey
- One Specialist Predator Competing with One Generalist Predator for Two Prey Species
- Two Specialist Predators Competing with One Generalist Predator for Two Prey Species
- Further Analysis of the General $u \times v$ Model
- Intra-Guild Predation
- Adding Evolutionary Cost to Prey
- Adding Evolutionary Cost to Predator

Thank You!

- Pacific Coast Undergraduate Math Conference
- Dr. Alissa Crans, Dr. Karrolyne Fogel, Dr. Kendra Killpatrick, Dr. John Rock, and all other PCUMC Organizers
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- Dr. Helena Noronha
- Pacific Math Alliance PUMP Undergraduate Research Groups
- California State University, Northridge
- Dr. Jing Li and Dr. Casey terHorst

Questions?

Equilibria - 1 × 2

$$\frac{dN_1}{dt} = N_1 \cdot \bar{Y}_1(\bar{m}, \bar{n}_1, M, N_1)$$

$$\frac{dN_2}{dt} = N_2 \cdot \bar{Y}_2(\bar{m}, \bar{n}_2, M, N_2)$$

$$\frac{dM}{dt} = M \cdot \bar{W}(\bar{m}, \bar{n}_1, \bar{n}_2, N_1, N_2)$$

$$\frac{d\bar{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \bar{Y}_1}{\partial \bar{n}_1}$$

$$\frac{d\bar{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \bar{Y}_2}{\partial \bar{n}_2}$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Equilibria - 1 × 2

$$\frac{dN_1}{dt} = N_1 \cdot \bar{Y}_1(\bar{m}, \bar{n}_1, M, N_1)$$

$$\frac{d\bar{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \bar{Y}_1}{\partial \bar{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \bar{Y}_2(\bar{m}, \bar{n}_2, M, N_2)$$

$$\frac{d\bar{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \bar{Y}_2}{\partial \bar{n}_2}$$

$$\frac{dM}{dt} = M \cdot \bar{W}(\bar{m}, \bar{n}_1, \bar{n}_2, N_1, N_2)$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Extinction

$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*) = (0, 0, 0, _, _, _)$$

Equilibria - 1 × 2

$$\frac{dN_1}{dt} = N_1 \cdot \bar{Y}_1(\bar{m}, \bar{n}_1, M, N_1)$$

$$\frac{d\bar{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \bar{Y}_1}{\partial \bar{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \bar{Y}_2(\bar{m}, \bar{n}_2, M, N_2)$$

$$\frac{d\bar{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \bar{Y}_2}{\partial \bar{n}_2}$$

$$\frac{dM}{dt} = M \cdot \bar{W}(\bar{m}, \bar{n}_1, \bar{n}_2, N_1, N_2)$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Extinction Unstable

$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*) = (0, 0, 0, _, _, _)$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1)$$

$$\frac{d\bar{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \bar{Y}_1}{\partial \bar{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2)$$

$$\frac{d\bar{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \bar{Y}_2}{\partial \bar{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2)$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

| | |
|-------------------|-----------------|
| Extinction | <i>Unstable</i> |
|-------------------|-----------------|

$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*) = (0, 0, 0, _, _, _)$$

Exclusion

$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*) = (K_1, K_2, 0, _, _, _)$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \bar{Y}_1(\bar{m}, \bar{n}_1, M, N_1)$$

$$\frac{d\bar{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \bar{Y}_1}{\partial \bar{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \bar{Y}_2(\bar{m}, \bar{n}_2, M, N_2)$$

$$\frac{d\bar{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \bar{Y}_2}{\partial \bar{n}_2}$$

$$\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2)$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

| | |
|-------------------|-----------------|
| Extinction | <i>Unstable</i> |
|-------------------|-----------------|

$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*) = (0, 0, 0, _, _, _)$$

Exclusion *Stable under certain conditions*

$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*) = (K_1, K_2, 0, _, _, _)$$

Equilibria - 1 × 2

$$\frac{dN_1}{dt} = N_1 \cdot \bar{Y}_1(\bar{m}, \bar{n}_1, M, N_1)$$

$$\frac{dN_2}{dt} = N_2 \cdot \bar{Y}_2(\bar{m}, \bar{n}_2, M, N_2)$$

$$\frac{dM}{dt} = M \cdot \bar{W}(\bar{m}, \bar{n}_1, \bar{n}_2, N_1, N_2)$$

$$\frac{d\bar{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \bar{Y}_1}{\partial \bar{n}_1}$$

$$\frac{d\bar{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \bar{Y}_2}{\partial \bar{n}_2}$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Equilibria - 1×2

$$\frac{dN_1}{dt} = N_1 \cdot \bar{Y}_1(\bar{m}, \bar{n}_1, M, N_1)$$

$$\frac{d\bar{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \bar{Y}_1}{\partial \bar{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \bar{Y}_2(\bar{m}, \bar{n}_2, M, N_2)$$

$$\frac{d\bar{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \bar{Y}_2}{\partial \bar{n}_2}$$

$$\frac{dM}{dt} = M \cdot \bar{W}(\bar{m}, \bar{n}_1, \bar{n}_2, N_1, N_2)$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Generalist Becomes Specialist

$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*)$$

$$= \left(\frac{d\sqrt{A_1}}{e_1\alpha_1\tau_1}, K_2, \frac{r_1\sqrt{A_1}}{\alpha_1\tau_1} \left(1 - \frac{d\sqrt{A_1}}{K_1e_1\alpha_1\tau_1} \right), \mu_1^*, \mu_2^*, \mu_1^* - \theta_1 \right)$$

where $A_1 = \sigma^2 + \beta_1^2 + \tau_1^2$, μ_1^* is an arbitrary value, and μ_2^* is sufficiently far from $\mu_1^* - \theta_1$.

Equilibria - 1 \times 2

$$\frac{dN_1}{dt} = N_1 \cdot \bar{Y}_1(\bar{m}, \bar{n}_1, M, N_1)$$

$$\frac{d\bar{n}_1}{dt} = \beta_{G1}^2 \frac{\partial \bar{Y}_1}{\partial \bar{n}_1}$$

$$\frac{dN_2}{dt} = N_2 \cdot \bar{Y}_2(\bar{m}, \bar{n}_2, M, N_2)$$

$$\frac{d\bar{n}_2}{dt} = \beta_{G2}^2 \frac{\partial \bar{Y}_2}{\partial \bar{n}_2}$$

$$\frac{dM}{dt} = M \cdot \bar{W}(\bar{m}, \bar{n}_1, \bar{n}_2, N_1, N_2)$$

$$\frac{d\bar{m}}{dt} = \sigma_G^2 \frac{\partial \bar{W}}{\partial \bar{m}}$$

Generalist Becomes Specialist *Stable under certain conditions???*

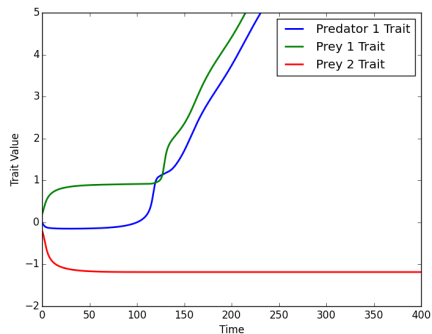
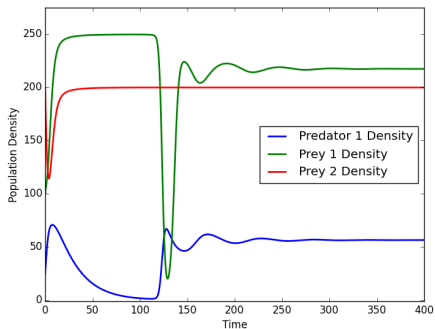
$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*)$$

$$= \left(\frac{d\sqrt{A_1}}{e_1\alpha_1\tau_1}, K_2, \frac{r_1\sqrt{A_1}}{\alpha_1\tau_1} \left(1 - \frac{d\sqrt{A_1}}{K_1e_1\alpha_1\tau_1} \right), \mu_1^*, \mu_2^*, \mu_1^* - \theta_1 \right)$$

where $A_1 = \sigma^2 + \beta_1^2 + \tau_1^2$, μ_1^* is an arbitrary value, and μ_2^* is sufficiently far from $\mu_1^* - \theta_1$.

Figures - 1×2

Generalist Becomes Specialist



Figures - 1 \times 2

Unstable Coexistence

