

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

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# Overview

- Motivation / Observations in Nature
- Model Formulation
- 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



# Normally Distributed Trait Values

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

## Parameters

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

# Attack Rate as a function of Normally Distributed Trait Values

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
- $\bar{n} \equiv$  Average Prey Trait Value
- $m \equiv$  Predator Trait Value
- $\bar{m} \equiv$  Average Predator Trait Value

## Parameters

- $\alpha \equiv$  Maximum attack rate
- $\theta \equiv$  Optimal trait difference
- $\tau^2 \equiv$  Specialization Constant

# Attack Rate as a function of Normally Distributed Trait Values

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

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

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

- $n \equiv$  Prey Trait Value
- $\bar{n} \equiv$  Average Prey Trait Value
- $m \equiv$  Predator Trait Value
- $\bar{m} \equiv$  Average Predator Trait Value

## Parameters

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

## Intrinsic Growth Rate as a function of the Normally Distributed Trait Value

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

- $n \equiv$  Prey Trait Value
- $\bar{n} \equiv$  Average Prey Trait Value

### Parameters

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

# Intrinsic Growth Rate as a function of the Normally Distributed Trait Value

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

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

Average Growth Rate

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

## Variables

- $n \equiv$  Prey Trait Value
- $\bar{n} \equiv$  Average Prey Trait Value

## Parameters

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

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

## Parameters

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

# Average Fitness

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

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

## Variables

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

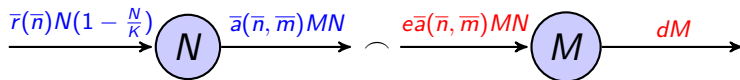
## Parameters

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

# Ecological Components

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

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



## Variables

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

## Parameters

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

# Evolutionary Components

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

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

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

## Variables

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

## Parameters

- $\phi \equiv$  Prey Optimum Trait Value
- $\gamma^2 \equiv$  Stabilizing Selection Constant
- $\bar{r} \equiv$  Average Intrinsic Prey Growth Rate Function
- $\beta_G^2 \equiv$  Prey genetic variance
- $\sigma_G^2 \equiv$  Predator genetic variance

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

## Ecological Components

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

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

## Evolutionary Components

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

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

# Equilibria - $1 \times 1$

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

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

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

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

## Extinction

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

## Exclusion

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









# Equilibria - 1 × 1

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

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

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

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

## Coexistence

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

$$\text{where } A = \sigma^2 + \beta^2 + \tau^2 \text{ and } B = \beta^2 + \gamma^2$$



## Equilibria - $1 \times 1$

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

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

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

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

<b>Coexistence</b>	<i>Locally stable under certain conditions</i>
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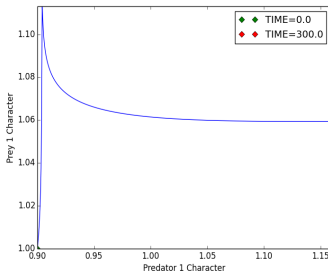
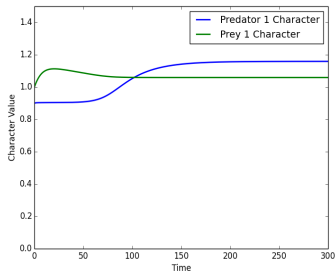
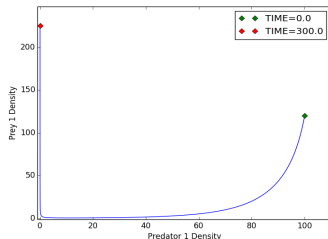
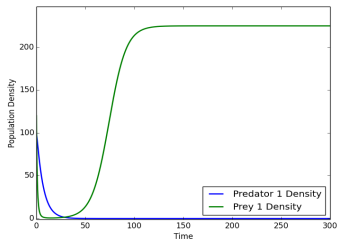
$$(N^*, M^*, \bar{n}^*, \bar{m}^*) = \left( \frac{d\sqrt{A}}{e\alpha\tau}, \frac{\rho\gamma\sqrt{A}}{\alpha\tau\sqrt{B}} \left( 1 - \frac{d\sqrt{A}}{Ke\alpha\tau} \right), \theta, \theta + \phi \right)$$

where  $A = \sigma^2 + \beta^2 + \tau^2$  and  $B = \beta^2 + \gamma^2$

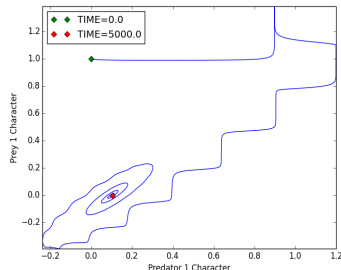
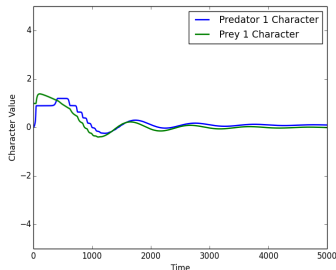
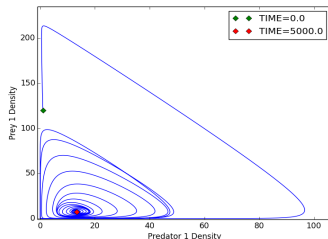
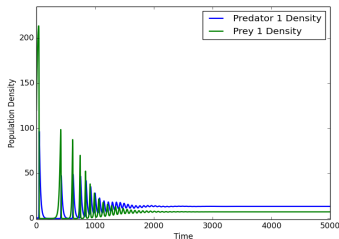
### Necessary Condition for Locally Stable Coexistence:

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

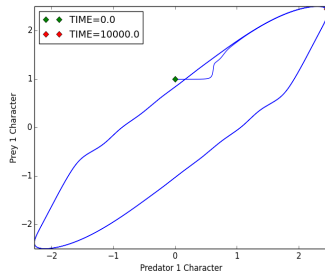
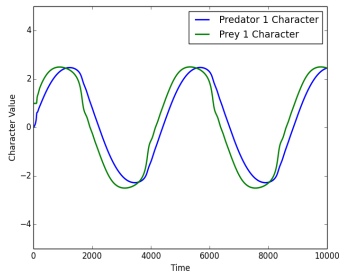
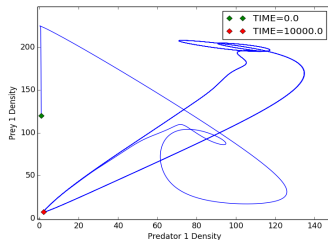
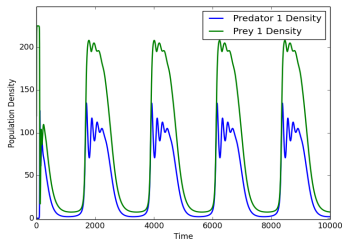
# Figures - $1 \times 1$ - Stable Exclusion



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



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



## Prey Fitness

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

## Predator Fitness

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



## Prey Fitness

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

↓

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

## Predator Fitness

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

## Notation

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

## Prey Fitness

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

↓

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

## Predator Fitness

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

↓

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

## Notation

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

# Average Fitness

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

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

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

## Ecological Components

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

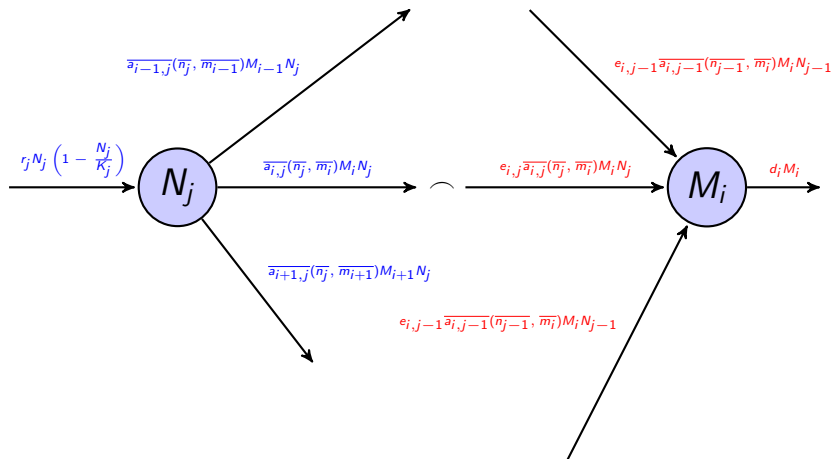
$$\frac{dM_i}{dt} = M_i \left[ \sum_{j=1}^v \left[ e_{ij} N_j \bar{a}_{ij}(\bar{m}_i, \bar{n}_j) \right] - d_i \right]$$

## Evolutionary Components

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

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

# 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!

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- 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 $\times$ 2

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

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

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

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

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

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

## 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 - $1 \times 2$

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

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

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

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

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

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

<b>Extinction</b>	<i>Unstable</i>
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$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*) = (0, 0, 0, \_, \_, \_)$$

## Exclusion

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

## Equilibria - $1 \times 2$

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

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

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

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

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

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

<b>Extinction</b>	<i>Unstable</i>
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$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*) = (0, 0, 0, \_, \_, \_)$$

### 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  $A_1 = \sigma^2 + \beta_1^2 + \tau_1^2$ ,  $\mu_1^*$  is an arbitrary value, and  $\mu_2^*$  is sufficiently far from  $\mu_1^* - \theta_1$ .

# 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** *Stable under certain conditions???*

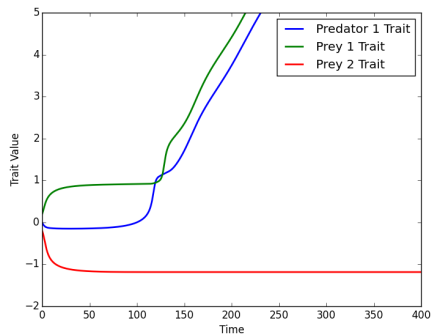
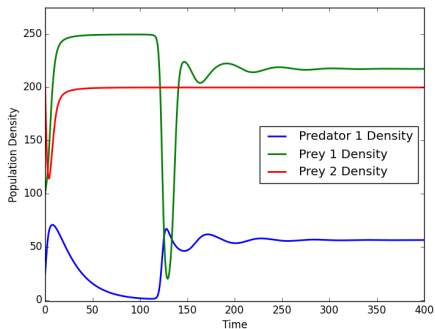
$$(N_1^*, N_2^*, M^*, \bar{n}_1^*, \bar{n}_2^*, \bar{m}^*)$$

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

where  $A_1 = \sigma^2 + \beta_1^2 + \tau_1^2$ ,  $\mu_1^*$  is an arbitrary value, and  $\mu_2^*$  is sufficiently far from  $\mu_1^* - \theta_1$ .

# Figures - $1 \times 2$

## Generalist Becomes Specialist





# Figures - 1 $\times$ 2

## Unstable Coexistence

