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

Sam Fleischer, Pablo Chavarria

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

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Lotka-Volterra Schreiber, Bürger,

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Preliminary Results

 $1 \times 2$ 



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

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$$\frac{dN}{dt} = N(b - aM)$$
$$\frac{dM}{dt} = M(eaN - d)$$

- ► *N* ≡ Prey Density
- $ightharpoonup M \equiv \mathsf{Predator} \; \mathsf{Density}$

#### **Parameters**

- $ightharpoonup a \equiv Attack rate$
- $ightharpoonup b \equiv Prey birth rate$
- $ightharpoonup e \equiv \text{Efficiency}$
- $ightharpoonup d \equiv \mathsf{Predator} \; \mathsf{death} \; \mathsf{rate}$

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$$\frac{dM}{dt} = M(eaN - d)$$

- ► *N* ≡ Prey Density
- $ightharpoonup M \equiv \mathsf{Predator} \; \mathsf{Density}$

### **Parameters**

- ▶  $a \equiv$  Attack rate  $\leftarrow$  No variation!
- $b \equiv Prey birth rate$
- $ightharpoonup e \equiv \text{Efficiency}$
- $ightharpoonup d \equiv Predator death rate$

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

- ► *N* ≡ Prey Density
- $ightharpoonup M \equiv \mathsf{Predator} \; \mathsf{Density}$
- $m \equiv Predator Character (Trait Value)$

#### **Parameters**

- ho  $\alpha$   $\equiv$  Maximum attack rate
- $\bullet$   $\theta \equiv$  Optimal trait value
- $ightharpoonup au \equiv Specialization Constant$

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

- $ightharpoonup N \equiv \text{Prey Density}$
- $ightharpoonup M \equiv \mathsf{Predator} \; \mathsf{Density}$
- $m \equiv Predator Character (Trait Value)$

#### **Parameters**

- ho  $\alpha$   $\equiv$  Maximum attack rate
- $\bullet$   $\theta \equiv$  Optimal trait difference
- $ightharpoonup au \equiv Specialization Constant$

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

$$(m - \overline{m})^2$$

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

- ► *N* ≡ Prey Density
- $ightharpoonup \overline{n} \equiv \text{Mean Prey Character}$
- ▶ M ≡ Predator Density
- $ightharpoonup \overline{m} \equiv \text{Mean Predator Character}$

#### **Parameters**

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

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# Average Attack Rate

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

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

## **Variables**

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

#### **Parameters**

- $ightharpoonup \beta^2 \equiv \text{Prey Trait Variance}$
- $ightharpoonup \sigma^2 \equiv \text{Predator Trait Variance}$
- ho  $\alpha$   $\equiv$  Maximum attack rate
- ho  $\theta \equiv Optimal trait difference$
- $ightharpoonup au \equiv \mathsf{Specialization}$  Constant

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## **Fitness Assumptions**

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

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

## **Variables**

- N ≡ Prey Density
- $ightharpoonup n \equiv \mathsf{Prey} \; \mathsf{Character}$
- $ightharpoonup M \equiv \mathsf{Predator} \; \mathsf{Density}$
- $ightharpoonup m \equiv Predator Character$

#### **Parameters**

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

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## **Average Fitness**

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

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

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

$$= e N \overline{a}(\overline{m}, \overline{n}) - d$$

### **Variables**

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

#### **Parameters**

- $ightharpoonup r \equiv$  Intrinsic Prey Growth Rate
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# **Ecological Components**

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

### **Variables**

- N ≡ Prey Density
- $ightharpoonup \overline{n} \equiv \mathsf{Mean} \; \mathsf{Prey} \; \mathsf{Character}$
- $ightharpoonup M \equiv \mathsf{Predator} \; \mathsf{Density}$
- $ightharpoonup \overline{m} \equiv \text{Mean Predator Character}$

#### **Parameters**

- $ightharpoonup r \equiv$  Intrinsic Prey Growth Rate
- $ightharpoonup K \equiv$  Prey Carrying Capacity
- $ightharpoonup d \equiv \mathsf{Predator} \; \mathsf{Death} \; \mathsf{Rate}$
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$$\frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}}$$
$$\frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

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

#### **Parameters**

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

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

# **Ecological Components**

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

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

## **Evolutionary Components**

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

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

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# **Prey Fitness**

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

## Predator Fitness

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

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# **Prey Fitness**

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

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

## **Predator Fitness**

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

## Notation

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

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# **Prey Fitness**

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

$$\downarrow$$

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

### **Predator Fitness**

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

$$\downarrow$$

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

#### Notation

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

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## **Average Fitness**

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

$$\begin{split} \overline{W}_{i}(\overline{m}_{i}, [\overline{n}_{j}]_{j=1}^{v}, [N_{j}]_{j=1}^{v}) \\ &= \int\limits_{\mathbb{R}^{u+1}} W_{i} \cdot p_{i}(m_{i}, \overline{m_{i}}) \cdot \prod_{j=1}^{v} \left[ p(n_{j}, \overline{n}_{j}) \right] dm_{i} \prod_{j=1}^{v} \left[ dn_{j} \right] \\ &= \sum_{i=1}^{v} \left[ e_{ij} N_{j} \overline{a}_{ij} (\overline{m}_{i}, \overline{n}_{j}) \right] - d_{i} \end{split}$$

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

## **Ecological Components**

$$\frac{dN_{j}}{dt} = N_{j}\overline{Y}_{j} = N_{j} \left[ r_{j} \left( 1 - \frac{N_{j}}{K_{j}} \right) - \sum_{i=1}^{u} M_{i}\overline{a}_{ij}(\overline{m}_{i}, \overline{n}_{j}) \right]$$

$$\frac{dM_{i}}{dt} = M_{i}\overline{W}_{i} = M_{i} \left[ \sum_{j=1}^{v} \left[ e_{ij}N_{j}\overline{a}_{ij}(\overline{m}_{i}, \overline{n}_{j}) \right] - d_{i} \right]$$

## **Evolutionary Components**

$$\begin{split} \frac{d\overline{n}_{j}}{dt} &= \beta_{jG}^{2} \frac{\partial \overline{Y}_{j}}{\partial \overline{n}_{j}} = \beta_{jG}^{2} \sum_{i=1}^{u} \left[ \frac{M_{i}(\theta_{ij} + \overline{n_{j}} - \overline{m_{i}})}{\sigma_{i}^{2} + \beta_{j}^{2} + \tau_{ij}^{2}} \overline{a}_{ij}(\overline{m_{i}}, \overline{n_{j}}) \right] \\ \frac{d\overline{m}_{i}}{dt} &= \sigma_{iG}^{2} \frac{\partial \overline{W}_{i}}{\partial \overline{m}_{i}} = \sigma_{iG}^{2} \sum_{i=1}^{v} \left[ \frac{e_{ij} N_{j}(\theta_{ij} + \overline{n_{j}} - \overline{m_{i}})}{\sigma_{i}^{2} + \beta_{i}^{2} + \tau_{ii}^{2}} \overline{a}_{ij}(\overline{m_{i}}, \overline{n_{j}}) \right] \end{split}$$

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$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N) \qquad \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

### Extinction

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

## **Exclusion**

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

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$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N) \qquad \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{n}}$$

# **Extinction** *Unstable*

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

### **Exclusion**

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

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$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N) \qquad \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Extinction** *Unstable* 

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

**Exclusion** Stable under certain conditions

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

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$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N) \qquad \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Extinction** *Unstable* 

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (0, 0, \underline{\hspace{1em}}, \underline{\hspace{1em}})$$

**Exclusion** Stable under certain conditions

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

# **Necessary Conditions for Stable Exclusion:**

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

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$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N) \qquad \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

### Coexistence

$$(N^*, M^*, \overline{n}^*, \overline{m}^*) = (\frac{d\sqrt{A}}{e\alpha\tau}, \frac{r\sqrt{A}}{\alpha\tau} \left(1 - \frac{d\sqrt{A}}{Ke\alpha\tau}\right), \mu^*, \mu^* - \theta)$$
  
where  $A = \sigma^2 + \beta^2 + \tau^2$  and  $\mu^*$  is an arbitrary value.

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$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N) \qquad \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Coexistence** Stable under certain conditions

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

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

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$$\frac{dN}{dt} = N \cdot \overline{Y}(\overline{m}, \overline{n}, M, N) \qquad \frac{d\overline{n}}{dt} = \beta_G^2 \frac{\partial \overline{Y}}{\partial \overline{n}} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}, N) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Coexistence** Stable under certain conditions

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

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

# **Necessary Condition for Stable Coexistence:**

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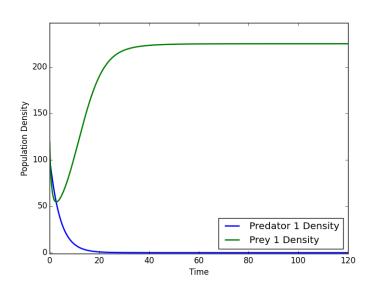
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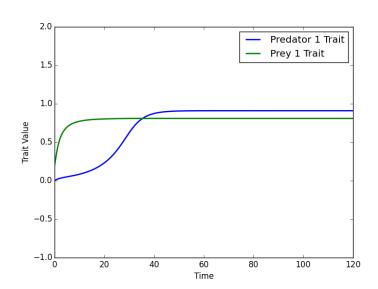
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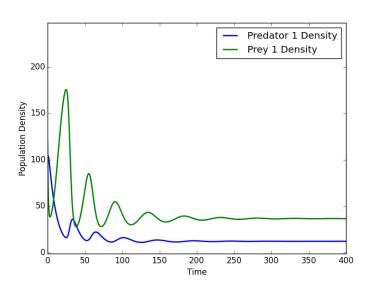
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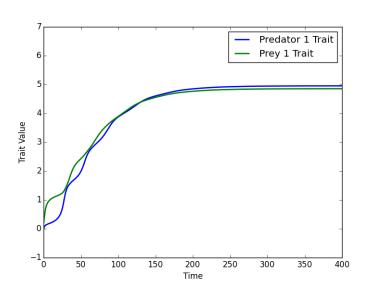
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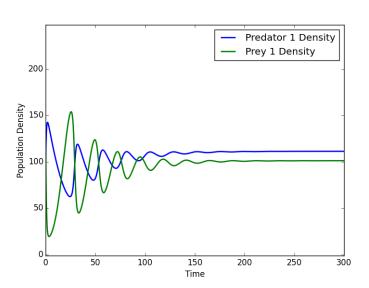
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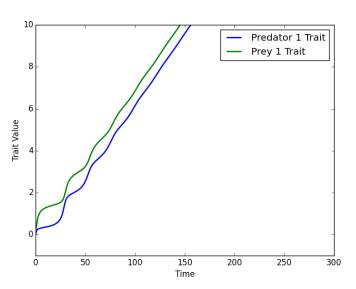
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$$\begin{split} \frac{dN_1}{dt} &= N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) & \frac{d\overline{n}_1}{dt} &= \beta_{1,G}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\ \frac{dN_2}{dt} &= N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) & \frac{d\overline{n}_2}{dt} &= \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\ \frac{dM}{dt} &= M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) & \frac{d\overline{m}}{dt} &= \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}} \end{split}$$

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$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{1,G}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} 
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

#### Extinction

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*) = (0, 0, 0, \underline{\phantom{m}}, \underline{\phantom{m}}, \underline{\phantom{m}})$$

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$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{1,G}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} 
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

Extinction Unstable

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

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$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{1,G}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Extinction** *Unstable* 

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

## **Exclusion**

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

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$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \qquad \frac{d\overline{n}_1}{dt} = \beta_{1,G}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} \\
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} \\
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Extinction** *Unstable* 

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

**Exclusion** Stable under certain conditions

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

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 $1 \times 1$  $1 \times 2$ 

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{1,G}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} 
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Extinction** *Unstable* 

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

**Exclusion** Stable under certain conditions

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

Generalist Becomes Specialist

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

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

$$\frac{dN_1}{dt} = N_1 \cdot \overline{Y}_1(\overline{m}, \overline{n}_1, M, N_1) \qquad \frac{d\overline{n}_1}{dt} = \beta_{1,G}^2 \frac{\partial \overline{Y}_1}{\partial \overline{n}_1} 
\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2} 
\frac{dM}{dt} = M \cdot \overline{W}(\overline{m}, \overline{n}_1, \overline{n}_2, N_1, N_2) \qquad \frac{d\overline{m}}{dt} = \sigma_G^2 \frac{\partial \overline{W}}{\partial \overline{m}}$$

**Extinction** *Unstable* 

$$(N_1^*, N_2^*, M^*, \overline{n}_1^*, \overline{n}_2^*, \overline{m}^*) = (0, 0, 0, \underline{\phantom{m}}, \underline{\phantom{m}}, \underline{\phantom{m}})$$

**Exclusion** Stable under certain conditions

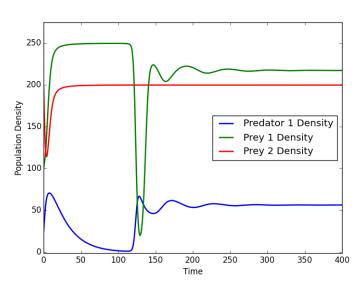
$$(\textit{N}_{1}^{*},\textit{N}_{2}^{*},\textit{M}^{*},\overline{\textit{n}}_{1}^{*},\overline{\textit{n}}_{2}^{*},\overline{\textit{m}}^{*})=(\textit{K}_{1},\textit{K}_{2},0,\_,\_,\_)$$

Generalist Becomes Specialist Stable under certain conditions

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

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

## **Generalist Becomes Specialist**



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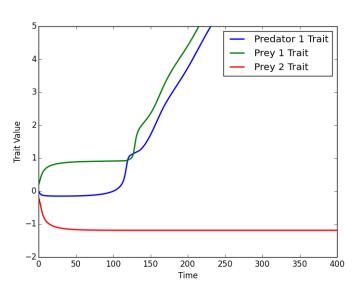
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## **Generalist Becomes Specialist**



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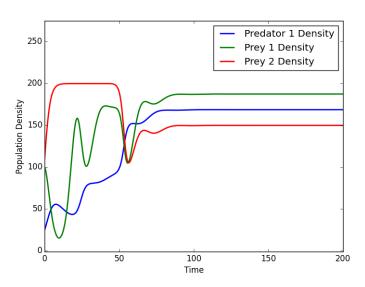
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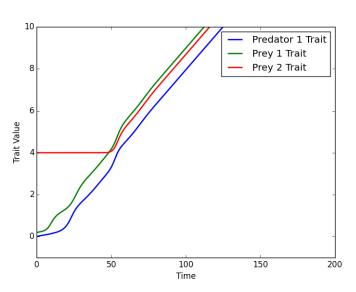
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