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

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## Observations

- 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

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

## Variables

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

## Parameters

- $a \equiv$ Attack rate
- $b \equiv$ Prey birth rate
- $e \equiv$ Efficiency
- $d \equiv$ Predator death rate

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

**Variables**

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

**Parameters**

- $a \equiv$ Attack rate $\longleftarrow$ *No variation!*
- $b \equiv$ Prey birth rate
- $e \equiv$ Efficiency
- $d \equiv$ Predator death rate

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

**Variables**

- $N \equiv$ Prey Density
- $M \equiv$ Predator Density
- $m \equiv$ Predator Character (Trait Value)

**Parameters**

- $\alpha \equiv$ Maximum attack rate
- $\theta \equiv$ Optimal trait value
- $\tau \equiv$ Specialization Constant

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

**Variables**

- $N \equiv$ Prey Density
- $M \equiv$ Predator Density
- $m \equiv$ Predator Character (Trait Value)

**Parameters**

- $\alpha \equiv$ Maximum attack rate
- $\theta \equiv$ Optimal trait value $\longleftarrow$ *No variation!*
- $\tau \equiv$ Specialization Constant

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

**Variables**

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

**Parameters**

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

## Distribution Assumptions

- Trait values are **normally distributed** over the populations

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

## Variables

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

## Parameters

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

## Average Attack Rate

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

## Variables

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

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

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

## Variables

- $N \equiv$ Prey Density
- $n \equiv$ Prey Character
- $M \equiv$ Predator Density
- $m \equiv$ Predator Character

## Parameters

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

## Average Fitness

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

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

## 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

## 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

- $N \equiv$ 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 character is always in the direction which increases the mean fitness in the population.

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

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

## Variables

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

## Parameters

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

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

**Ecological Components**

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

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

**Evolutionary Components**

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

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

## Prey Fitness

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

## Predator Fitness

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

## 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

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

## 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

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

$$\downarrow$$

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

## Notation

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

## Average Fitness

$$\overline{Y}_j([\overline{m}_i]_{i=1}^u, \overline{n}_j, [M_i]_{i=1}^u, N_j)$$

$$= \int_{\mathbb{R}^{u+1}} Y_j \cdot \prod_{i=1}^{u} \left[ p_i(m_i, \overline{m_i}) \right] \cdot p(n, \overline{n}) \prod_{i=1}^{u} \left[ dm_i \right] dn_j$$

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

$$\overline{W}_i(\overline{m}_i, [\overline{n}_j]_{j=1}^v, [N_j]_{j=1}^v)$$

$$= \int_{\mathbb{R}^{u+1}} W_i \cdot p_i(m_i, \overline{m_i}) \cdot \prod_{j=1}^{v} \left[ p(n_j, \overline{n}_j) \right] dm_i \prod_{j=1}^{v} \left[ dn_j \right]$$

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

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

**Ecological Components**

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

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

**Evolutionary Components**

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

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

# Equilibria

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

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

**Extinction**

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

**Exclusion**

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

# Equilibria

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

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**Extinction** $\boxed{\textit{Unstable}}$

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

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

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**Extinction** $\boxed{\textit{Unstable}}$

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

**Exclusion** $\boxed{\textit{Stable under certain conditions}}$

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

**Necessary Conditions for Stable Exclusion:**

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

# Equilibria

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

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

**Coexistence**

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

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

# Equilibria

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

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

**Coexistence** $\boxed{\textit{Stable under certain conditions}}$

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

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

# Equilibria

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

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

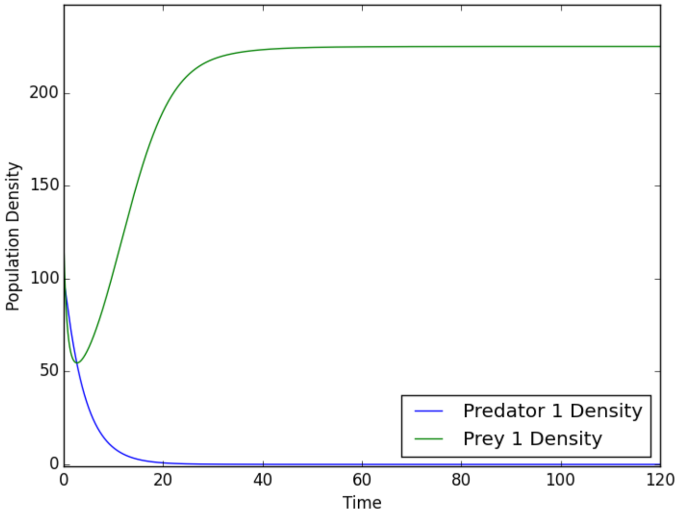
where $A = \sigma^2 + \beta^2 + \tau^2$ and $\mu^*$ is an arbitrary value.

**Necessary Condition for Stable Coexistence:**

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

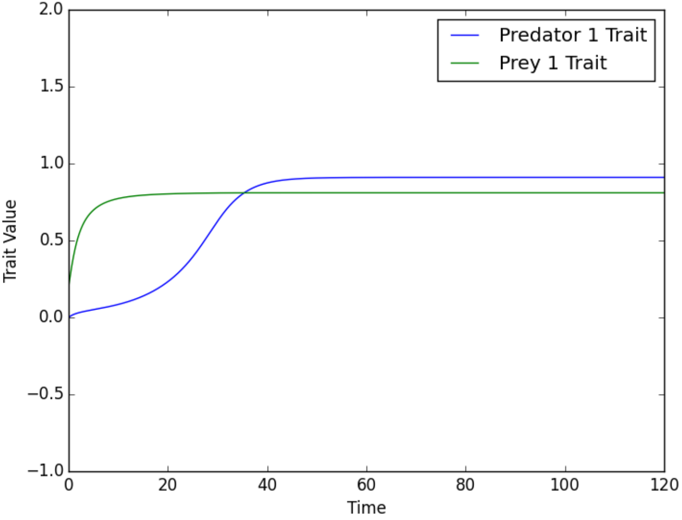
# Figures

**Exclusion**



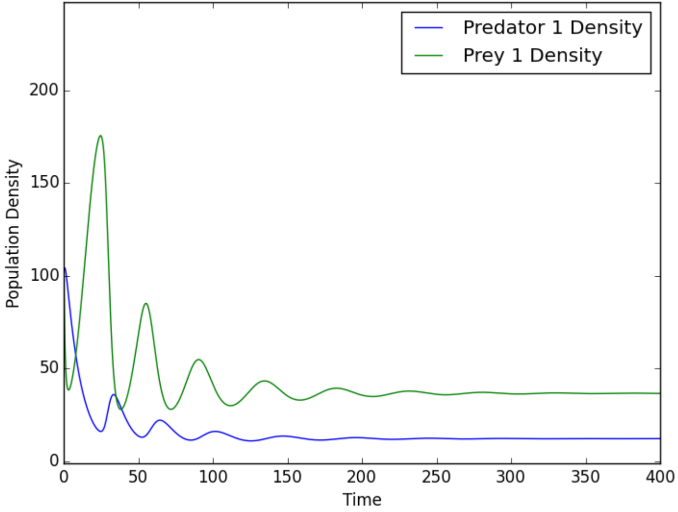
# Figures

## Exclusion



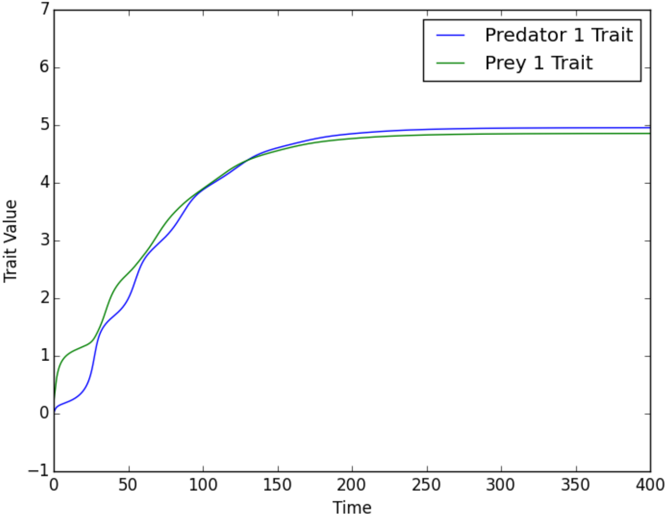
# Figures

## Stable Coexistence



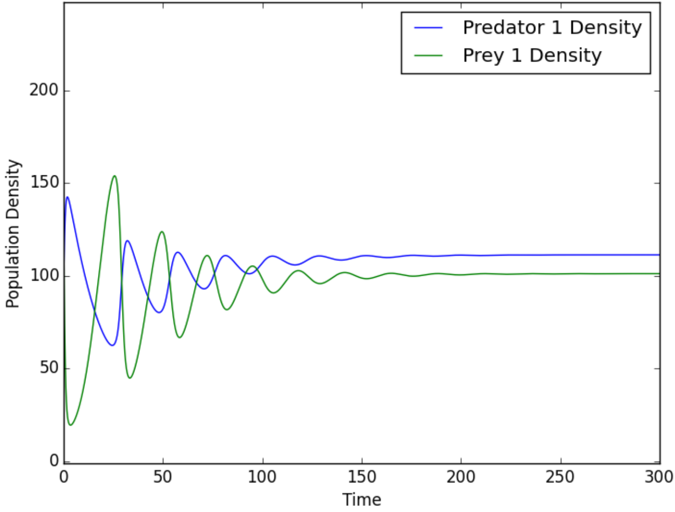
# Figures

## Stable Coexistence



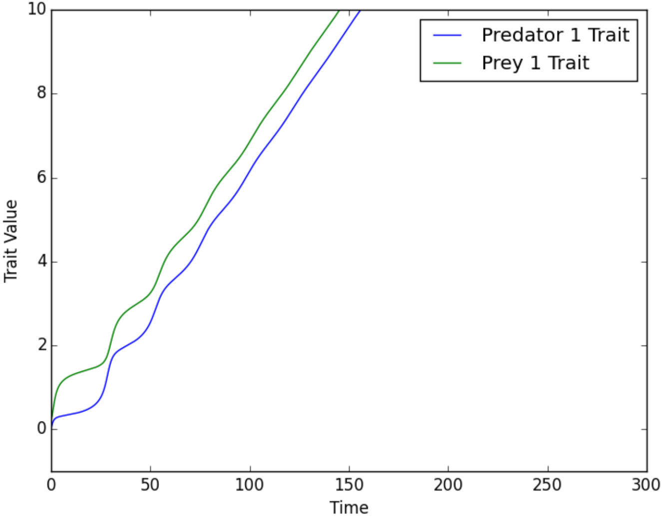
# Figures

## Unstable Coexistence



# Figures

## Unstable Coexistence



# Equilibria

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

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

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

# Equilibria

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

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**Extinction**

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

# Equilibria

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

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**Extinction** $\boxed{\textit{Unstable}}$

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**Extinction** $\boxed{\textit{Unstable}}$

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

**Exclusion**

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

# Equilibria

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

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

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

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# Equilibria

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

$$\frac{dN_2}{dt} = N_2 \cdot \overline{Y}_2(\overline{m}, \overline{n}_2, M, N_2) \qquad \frac{d\overline{n}_2}{dt} = \beta_{2,G}^2 \frac{\partial \overline{Y}_2}{\partial \overline{n}_2}$$

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

**Extinction** $\boxed{\textit{Unstable}}$

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

**Exclusion** $\boxed{\textit{Stable under certain conditions}}$

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

**Generalist Becomes Specialist**

$$\left(\frac{d\sqrt{A_1}}{e_1\alpha_1\tau_1}\ ,\ K_2\ ,\ \frac{r_1\sqrt{A_1}}{\alpha_1\tau_1}\left(1 - \frac{d\sqrt{A_1}}{K_1 e_1\alpha_1\tau_1}\right)\ ,\ \mu_1^*\ ,\ \mu_2^*\ ,\ \mu_1^* - \theta_1\right)$$

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

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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

**Exclusion**

# Figures

**Stable Coexistence**

# Figures

**Unstable Coexistence**