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

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- National Science Foundation
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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

Lotka-Volterra

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

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

Lotka-Volterra

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

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

Schreiber, Bürger, and Bolnick

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

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

Schreiber, Bürger, and Bolnick

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

Variables

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

Parameters

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

Our Extension

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

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

Our Extension

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

Our Extension

Average Attack Rate

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

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

Our Extension

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

Our Extension

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

Our Extension

Ecological Component of the Model

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

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

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

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

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Start Date: March 2014 - - Today's Date: March 3, 2015

Let $M_i(t)$ be the density of the i^{th} predator species, and let $N_j(t)$ be the density of the j^{th} prey species. Let $\overline{m_i}(t)$ be the mean of a single quantitative trait in the i^{th} predator species, and let $\overline{n_j}(t)$ be the mean of a single quantitative trait in the j^{th} prey species. Suppose the traits are normally distributed, with σ_i^2 as the constant variance of the i^{th} predator species, and with β_j^2 as the constant variance of the j^{th} prey species.

$$p(m_i, \overline{m_i}) = \frac{1}{\sqrt{2\pi\sigma_i^2}} \exp\left[-\frac{(m_i - \overline{m_i})^2}{2\sigma_i^2}\right]$$
$$p(n_j, \overline{n_j}) = \frac{1}{\sqrt{2\pi\beta_j^2}} \exp\left[-\frac{(n_j - \overline{n_j})^2}{2\beta_j^2}\right]$$

All of the species' phenotypic variances have a genetic and environment component,

$$\sigma_i^2 = \sigma_{Gi}^2 + \sigma_{Ei}^2$$
$$\beta_j^2 = \beta_{Gj}^2 + \beta_{Ej}^2$$

Let $a_{ij}(m_i, n_j)$ be the attack rate of an individual predator from species i on an individual prey from species j. Supposing the attack rate is optimal at α_{ij} when the predator's trait and prey's trait are at an optimal difference θ_{ij}, and decreases in a Gaussian manner as the trait's diverge from that difference, then

$$a_{ij}(m_i, n_j) = \alpha_{ij} \exp\left[-\frac{(m_i - n_j - \theta_{ij})^2}{2\tau_{ij}^2}\right]$$

where τ_{ij} determines how phenotypically specialized a predator individual of species i must be to use a prey individual of species j. Let $\overline{a_{ij}}(\overline{m_i}, \overline{n_j})$ be the mean attack rate of predator species i on prey species j. Thus,

$$\begin{aligned}\overline{a_{ij}}(\overline{m_i}, \overline{n_j}) &= \int_{-\infty}^{\infty} \int_{\infty}^{\infty} a_{ij}(m_i, n_j) \cdot p(m_i, \overline{m_i}) \cdot p(n_j, \overline{n_j}) dm_i dn_j \\ &= \frac{\alpha_{ij}\tau_{ij}}{\sqrt{\sigma_i^2 + \beta_j^2 + \tau_{ij}^2}} \exp\left[-\frac{(\overline{m_i} - \overline{n_j} - \theta_{ij})^2}{2(\sigma_i^2 + \beta_j^2 + \tau_{ij}^2)}\right]\end{aligned}$$

Let u be the number of predator species, and let v be the number of prey species. If predators have a linear functional response, convert the consumed prey into offspring with efficiencies e_{ij}, and experience a per-capita mortality rate d_i, then the fitness of a predator with phenotype m_i is

$$W_i(m_i, [N]_1^v, [n]_1^v) = \sum_{j=1}^{v} (e_{ij} a_{ij}(m_i, n_j) N_j) - d_i$$

and thus the mean fitness of the i^{th} predator population is

$$
\begin{aligned}
\overline{W_i}(\overline{m_i}, [N]_1^v, [\overline{n}]_1^v) &= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} W_i(m_i, [N]_1^v, [n]_1^v) p(m_i, \overline{m_i}) p(n_j, \overline{n_j}) dm_i dn_j \\
&= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \left(\sum_{j=1}^{v} (e_{ij} a_{ij}(m_i, n_j) N_j) - d_i \right) p(m_i, \overline{m_i}) p(n_j, \overline{n_j}) dm_i d \\
&= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \sum_{j=1}^{v} e_{ij} a_{ij}(m_i, n_j) N_j p(m_i, \overline{m_i}) p(n_j, \overline{n_j}) dm_i dn_j \\
&\qquad - \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} d_i \; p(m_i, \overline{m_i}) p(n_j, \overline{n_j}) dm_i dn_j \\
&= \sum_{j=1}^{v} (e_{ij} \overline{a_{ij}}(\overline{m_i}, \overline{n_j}) N_j) - d_i
\end{aligned}
$$

In the absence of the predators, each prey experience logistic growth with intrinsic growth rates r_j and carrying capacities K_j. Thus the fitness of a prey with phenotype n_j is

$$
Y_j(N_j, n_j, [M]_1^u, [m]_1^u) = r_j \left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} (a_{ij}(m_i, n_j) M_i)
$$

and thus the mean fitness of the j^{th} prey population is

$$\overline{Y_j}(N_j, \overline{n_j}, [M]_1^u, [\overline{m}]_1^u) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} Y_j(N_j, n_j, [M]_1^u, [m]_1^u) p(m_i, \overline{m_i}) p(n_j, \overline{n_j}) dm_i dn_j$$

$$= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \left(r_j \left(1 - \frac{N_j}{K_j}\right) - \sum_{i=1}^{u} \left(a_{ij}(m_i, n_j) M_i\right) \right) p(m_i, \overline{m_i}) p$$

$$= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} r_j \left(1 - \frac{N_j}{K_j}\right) p(m_i, \overline{m_i}) p(n_j, \overline{n_j}) dm_i dn_j$$

$$- \sum_{i=1}^{u} M_i \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} a_{ij}(m_i, n_j) p(m_i, \overline{m_i}) p(n_j, \overline{n_j})$$

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

So the ecological dynamics of the model (population densities) are given by

$$\begin{cases} \dfrac{dM_i}{dt} & = M_i \overline{W_i}(\overline{m_i}, [N]_1^v, [\overline{n}]_1^v) \\ \dfrac{dN_j}{dt} & = N_j \overline{Y_j}(N_j, \overline{n_j}, [M]_1^u, [\overline{m}]_1^u) \end{cases} \quad (1)$$

We assume the distribution of phenotypes remains Gaussian. Thus the evolutionary dynamics are given by

$$\begin{cases} \dfrac{d\overline{m_i}}{dt} &= \sigma_{Gi}^2 \, \dfrac{\partial \overline{W_i}}{\partial \overline{m_i}} \\ \dfrac{d\overline{n_j}}{dt} &= \beta_{Gj}^2 \, \dfrac{\partial \overline{Y_j}}{\partial \overline{n_j}} \end{cases} \tag{2}$$

where

$$\frac{\partial \overline{W_i}}{\partial \overline{m_i}} = \sum_{j=1}^{v} \frac{e_{ij}\alpha_{ij}\tau_{ij}N_j(\theta_{ij} + \overline{n_j} - \overline{m_i})}{(\sigma_i^2 + \beta_j^2 + \tau_{ij}^2)^{3/2}} \exp\left[-\frac{(\overline{m_i} - \overline{n_j} - \theta_{ij})^2}{2(\sigma_i^2 + \beta_j^2 + \tau_{ij}^2)}\right], \quad \text{and}$$

$$\frac{\partial \overline{Y_j}}{\partial \overline{n_j}} = \sum_{i=1}^{u} \frac{\alpha_{ij}\tau_{ij}M_i(\theta_{ij} + \overline{n_j} - \overline{m_i})}{(\sigma_i^2 + \beta_j^2 + \tau_{ij}^2)^{3/2}} \exp\left[-\frac{(\overline{m_i} - \overline{n_j} - \theta_{ij})^2}{2(\sigma_i^2 + \beta_j^2 + \tau_{ij}^2)}\right]$$

Assuming there is only one predator species and one prey species, all subscripts are dropped, and the $(4uv)$-dimensional system becomes a 4 dimensional system:

$$
\begin{cases}
f_1 = \dfrac{dM}{dt} & = M\overline{W}(\overline{m}, N, \overline{n}) \\
f_2 = \dfrac{dN}{dt} & = N\overline{Y}(N, \overline{n}, M, \overline{m}) \\
f_3 = \dfrac{d\overline{m}}{dt} & = \sigma_G^2 \, \dfrac{\partial \overline{W}}{\partial \overline{m}} \\
f_4 = \dfrac{d\overline{n}}{dt} & = \beta_G^2 \, \dfrac{\partial \overline{Y}}{\partial \overline{n}}
\end{cases}
\tag{3}
$$

where

$$
\begin{aligned}
\overline{W}(\overline{m}, N, \overline{n}) &= e\overline{a}(\overline{m}, \overline{n})N - d \\
\overline{Y}(N, \overline{n}, M, \overline{m}) &= r\left(1 - \frac{N}{K}\right) - \overline{a}(\overline{m}, \overline{n})M \\
\frac{\partial \overline{W}}{\partial \overline{m}} &= \frac{e\alpha\tau N(\theta + \overline{n} - \overline{m})}{(\sigma^2 + \beta^2 + \tau^2)^{3/2}} \exp\left[-\frac{(\overline{m} - \overline{n} - \theta)^2}{2(\sigma^2 + \beta^2 + \tau^2)}\right] \\
\frac{\partial \overline{Y}}{\partial \overline{n}} &= \frac{\alpha\tau M(\theta + \overline{n} - \overline{m})}{(\sigma^2 + \beta^2 + \tau^2)^{3/2}} \exp\left[-\frac{(\overline{m} - \overline{n} - \theta)^2}{2(\sigma^2 + \beta^2 + \tau^2)}\right]
\end{aligned}
$$

$$f_3 = 0 \implies \overline{m} - \overline{n} = \theta \ \text{ or } \ N = 0 \quad (4)$$

$$f_4 = 0 \implies \overline{m} - \overline{n} = \theta \ \text{ or } \ M = 0 \quad (5)$$

$$f_1 = 0 \implies M = 0 \ \text{ or } \ N = \frac{d\sqrt{\sigma^2 + \beta^2 + \tau^2}}{e\alpha\tau} \exp\left[\frac{(\overline{m} - \overline{n} - \theta)^2}{2(\sigma^2 + \beta^2 + \tau^2)}\right] \quad (6)$$

$$f_2 = 0 \implies N = 0 \ \text{ or } \ M = \frac{r\sqrt{\sigma^2 + \beta^2 + \tau^2}}{\alpha\tau}\left(1 - \frac{N}{K}\right) \exp\left[\frac{(\overline{m} - \overline{n} - \theta)^2}{2(\sigma^2 + \beta^2 + \tau^2)}\right] \quad (7)$$

Clearly, $M = N = 0$ satisfies the equilibrium conditions. (7) is satisfied by $N = 0$, which, by (6), implies $M = 0$. This is intuitive because the predator can only survive if there is prey.
On the other hand, (6) is satisfied by $M = 0$, which, by (7), implies either $N = 0$ or $N = K$. This is intuitive because the prey can reach equilibrium at its carrying capacity.
For coexistence equilibria (represented by M^* and N^*), let

$\overline{m} - \overline{n} = \theta$. Then

$$\begin{cases} N^* = \dfrac{d\sqrt{\sigma^2 + \beta^2 + \tau^2}}{e\alpha\tau} \\ M^* = \dfrac{r\sqrt{\sigma^2 + \beta^2 + \tau^2}}{\alpha\tau}\left(1 - \dfrac{N^*}{K}\right) \end{cases}$$

Thus coexistence equilibria can be reached with the above values of N^* and M^* and any values $\overline{m}$ and $\overline{n}$ so long as $\overline{m} - \overline{n} = \theta$.

For local stability around the various equilibria

$E^* = (M^*, N^*, \overline{m}^*, \overline{n}^*)$, we find the Jacobian matrix:

$$J^* = J\Big|_{E^*} = \begin{pmatrix} \frac{\partial f_1}{\partial M}\Big|_{E^*} & \frac{\partial f_1}{\partial N}\Big|_{E^*} & \frac{\partial f_1}{\partial \overline{m}}\Big|_{E^*} & \frac{\partial f_1}{\partial \overline{m}}\Big|_{E^*} \\ \frac{\partial f_2}{\partial M}\Big|_{E^*} & \frac{\partial f_2}{\partial N}\Big|_{E^*} & \frac{\partial f_2}{\partial \overline{m}}\Big|_{E^*} & \frac{\partial f_2}{\partial \overline{m}}\Big|_{E^*} \\ \frac{\partial f_3}{\partial M}\Big|_{E^*} & \frac{\partial f_3}{\partial N}\Big|_{E^*} & \frac{\partial f_3}{\partial \overline{m}}\Big|_{E^*} & \frac{\partial f_3}{\partial \overline{m}}\Big|_{E^*} \\ \frac{\partial f_4}{\partial M}\Big|_{E^*} & \frac{\partial f_4}{\partial N}\Big|_{E^*} & \frac{\partial f_4}{\partial \overline{m}}\Big|_{E^*} & \frac{\partial f_4}{\partial \overline{m}}\Big|_{E^*} \end{pmatrix}$$

The conditions for stability of E^* are equivalent to the conditions by which all roots of the characteristic polynomial of J^* have non-positive real parts (i.e. the Routh-Hurwitz criterion). First, we must calculate the partial derivatives.

$$\frac{\partial f_1}{\partial M} = \overline{W}(\overline{m}, N, \overline{n})$$

$$\frac{\partial f_1}{\partial N} = e\overline{a}(\overline{m}, \overline{n}) \cdot M$$

$$\frac{\partial f_1}{\partial \overline{m}} = \frac{e\overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot M \cdot N \cdot (\theta + \overline{n} - \overline{m})$$

$$\frac{\partial f_1}{\partial \overline{n}} = \frac{e\overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot M \cdot N \cdot (\overline{m} - \overline{n} - \theta)$$

$$\frac{\partial f_2}{\partial M} = -\overline{a}(\overline{m}, \overline{n}) \cdot N$$

$$\frac{\partial f_2}{\partial N} = \overline{Y}(N, \overline{n}, M, \overline{m}) - \frac{Nr}{K}$$

$$\frac{\partial f_2}{\partial \overline{m}} = \frac{\overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot M \cdot N \cdot (\overline{m} - \overline{n} - \theta)$$

$$\frac{\partial f_2}{\partial \overline{n}} = \frac{\overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot M \cdot N \cdot (\theta + \overline{n} - \overline{m})$$

$$\frac{\partial f_3}{\partial M} = 0$$

$$\frac{\partial f_3}{\partial N} = \frac{\sigma_G^2 e\overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot (\theta + \overline{n} - \overline{m})$$

$$\frac{\partial f_3}{\partial \overline{m}} = \frac{\sigma_G^2 e\overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot N \left(\frac{(\overline{m} - \overline{n} - \theta)^2}{\sigma^2 + \beta^2 + \tau^2} - 1 \right)$$

$$\frac{\partial f_3}{\partial \overline{n}} = \frac{\sigma_G^2 e\overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot N \left(1 - \frac{(\overline{m} - \overline{n} - \theta)^2}{\sigma^2 + \beta^2 + \tau^2} \right)$$

$$\frac{\partial f_4}{\partial M} = \frac{\beta_G^2 \overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot (\overline{n} - \overline{m})$$

$$\frac{\partial f_4}{\partial N} = 0$$

$$\frac{\partial f_4}{\partial \overline{m}} = \frac{\beta_G^2 \overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot M \left(\frac{(\overline{m} - \overline{n} - \theta)^2}{\sigma^2 + \beta^2 + \tau^2} - 1 \right)$$

$$\frac{\partial f_4}{\partial \overline{n}} = \frac{\beta_G^2 \overline{a}(\overline{m}, \overline{n})}{\sigma^2 + \beta^2 + \tau^2} \cdot M \left(1 - \frac{(\overline{m} - \overline{n} - \theta)^2}{\sigma^2 + \beta^2 + \tau^2} \right)$$

$E^* = (0, 0, \overline{m}^*, \overline{n}^*)$ where $\overline{m}^*$ and $\overline{n}^*$ are arbitrary values. Then

$$J^* = J\big|_{E^*} = \begin{pmatrix} -d & 0 & 0 \\ 0 & r & 0 \\ 0 & \dfrac{\sigma_G^2 e\overline{a}(\overline{m}^*, \overline{n}^*)}{\sigma^2 + \beta^2 + \tau^2} \cdot (\theta + \overline{n}^* - \overline{m}^*) & 0 \\ \dfrac{\beta_G^2 \overline{a}(\overline{m}^*, \overline{n}^*)}{\sigma^2 + \beta^2 + \tau^2} \cdot (\theta + \overline{n}^* - \overline{m}^*) & 0 & 0 \end{pmatrix}$$

Since J^* is a lower-triangular matrix, its eigenvalues are its diagonal entries: $-d$, r, 0, and 0. Since r is positive, this equilibrium is locally unstable.

$E^* = (0, K, \overline{m}^*, \overline{n}^*)$ where $\overline{m}^*$ and $\overline{n}^*$ are arbitrary values. Then

$$J^* = J\big|_{E^*} = \begin{pmatrix} e\overline{a}(\overline{m}^*, \overline{n}^*)K - d & 0 & 0 & 0 \\ 0 & -r & 0 & 0 \\ 0 & j_{32} & j_{33} & j_{34} \\ j_{41} & 0 & 0 & 0 \end{pmatrix}$$

where

$$j_{32} = \frac{\sigma_G^2 e\overline{a}(\overline{m}^*, \overline{n}^*)}{\sigma^2 + \beta^2 + \tau^2} \cdot (\theta + \overline{n}^* - \overline{m}^*)$$

$$j_{33} = \frac{\sigma_G^2 e\overline{a}(\overline{m}^*, \overline{n}^*)}{\sigma^2 + \beta^2 + \tau^2} \cdot K \left(\frac{(\overline{m}^* - \overline{n}^* - \theta)^2}{\sigma^2 + \beta^2 + \tau^2} - 1 \right)$$

$$j_{34} = \frac{\sigma_G^2 e\overline{a}(\overline{m}^*, \overline{n}^*)}{\sigma^2 + \beta^2 + \tau^2} \cdot K \left(1 - \frac{(\overline{m}^* - \overline{n}^* - \theta)^2}{\sigma^2 + \beta^2 + \tau^2} \right)$$

$$j_{41} = \frac{\beta_G^2 \overline{a}(\overline{m}^*, \overline{n}^*)}{\sigma^2 + \beta^2 + \tau^2} \cdot (\theta + \overline{n}^* - \overline{m}^*)$$

By reordering the variables $E^{**} = (M^*, N^*, \overline{n}^*, \overline{m}^*)$, we can force J^* to be a lower-triangular matrix, and hence it's eigenvalues are its diagonal entries:

$$J^{**} = J\Big|_{E^{**}} = \begin{pmatrix} e\overline{a}(\overline{m}^*, \overline{n}^*)K - d & 0 & 0 & 0 \\ 0 & -r & 0 & 0 \\ j_{41} & 0 & 0 & 0 \\ 0 & j_{32} & j_{34} & j_{33} \end{pmatrix}$$

Thus the eigenvalues are $e\overline{a}(\overline{m},\overline{n})K - d$, $-r$, 0, and j_{33}. Thus E^* is stable if the following hold:

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

E^* is unstable if either of the above fails.

$E^* = (M^*, N^*, \mu^*, \mu^*)$ where μ^* is an arbitrary value. Then

$$J^* = J\Big|_{E^*} = \begin{pmatrix} 0 & er\left(1-\dfrac{N^*}{K}\right) & 0 & 0 \\ -\dfrac{d}{e} & -\dfrac{rN^*}{K} & 0 & 0 \\ 0 & 0 & -\dfrac{d\sigma_G^2}{\sigma^2+\beta^2+\tau^2} & \dfrac{d\sigma_G^2}{\sigma^2+\beta^2+\tau^2} \\ 0 & 0 & -\dfrac{r\beta_G^2\left(1-\dfrac{N^*}{K}\right)}{\sigma^2+\beta^2+\tau^2} & \dfrac{r\beta_G^2\left(1-\dfrac{N^*}{K}\right)}{\sigma^2+\beta^2+\tau^2} \end{pmatrix}$$

The characteristic polynomial is

$$P(\lambda) = |\lambda I - J^*| = \begin{vmatrix} \lambda & -er\left(1-\dfrac{N^*}{K}\right) & 0 & 0 \\ \dfrac{d}{e} & \lambda + \dfrac{rN^*}{K} & 0 & 0 \\ 0 & 0 & \lambda + \dfrac{d\sigma_G^2}{\sigma^2+\beta^2+\tau^2} & -\dfrac{d\sigma_G^2}{\sigma^2+\beta^2+\tau^2} \\ 0 & 0 & \dfrac{r\beta_G^2\left(1-\dfrac{N^*}{K}\right)}{\sigma^2+\beta^2+\tau^2} & \lambda - \dfrac{r\beta_G^2\left(1-\dfrac{N^*}{K}\right)}{\sigma^2+\beta^2+\tau^2} \end{vmatrix}$$

Thus,

$$P(\lambda) = \begin{vmatrix} \lambda & -er\left(1-\dfrac{N^*}{K}\right) \\ \dfrac{d}{e} & \lambda + \dfrac{rN^*}{K} \end{vmatrix} \cdot \begin{vmatrix} \lambda + \dfrac{d\sigma_G^2}{\sigma^2+\beta^2+\tau^2} & -\dfrac{d\sigma_G^2}{\sigma^2+\beta^2+\tau^2} \\ \dfrac{r\beta_G^2\left(1-\dfrac{N^*}{K}\right)}{\sigma^2+\beta^2+\tau^2} & \lambda - \dfrac{r\beta_G^2\left(1-\dfrac{N^*}{K}\right)}{\sigma^2+\beta^2+\tau^2} \end{vmatrix}$$

$$= P_1(\lambda) \cdot P_2(\lambda)$$

Thus the zeros of $P(\lambda)$ are the zeros of both $P_1(\lambda)$ and $P_2(\lambda)$.

$$P_1(\lambda) = \lambda^2 + \frac{rN^*}{K}\lambda + rd\left(1 - \frac{N^*}{K}\right) = 0$$
$$\implies \lambda_{1,2} = \frac{1}{2}\left[-\frac{rN^*}{K} \pm \sqrt{\Delta}\right]$$

Where $\Delta = \left(\frac{rN^*}{K}\right)^2 - 4rd\left(1 - \frac{N^*}{K}\right)$. Since $N^* < K$, $\sqrt{\Delta} < \left|\frac{rN^*}{K}\right|$. Thus $\mathrm{Re}(\lambda_{1,2}) < 0$.

$$P_2(\lambda) = \lambda^2 + \left(\frac{d\sigma_G^2 - r\beta^2\left(1 - \frac{N^*}{K}\right)}{\sigma^2 + \beta^2 + \tau^2}\right)\lambda + \left(\frac{rd\sigma_G^2\beta_G^2\left(1 - \frac{N^*}{K}\right)}{(\sigma^2 + \beta^2 + \tau^2)^2}\right) = 0$$
$$\implies \lambda_{3,4} = \frac{1}{2}\left[-\left(\frac{d\sigma_G^2 - r\beta^2\left(1 - \frac{N^*}{K}\right)}{\sigma^2 + \beta^2 + \tau^2}\right) \pm \sqrt{\Delta}\right]$$

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Special Case: $M^* = 0$, $N^* = K$

Where

$$\Delta = \left(\frac{d\sigma_G^2 - r\beta^2 \left(1 - \frac{N^*}{K}\right)}{\sigma^2 + \beta^2 + \tau^2} \right)^2 - \left(\frac{4rd\sigma_G^2\beta_G^2 \left(1 - \frac{N^*}{K}\right)}{(\sigma^2 + \beta^2 + \tau^2)^2} \right)$$

Again, since $N^* < K$, $\sqrt{\Delta} < \left| \left(\frac{d\sigma_G^2 - r\beta^2 \left(1 - \frac{N^*}{K}\right)}{\sigma^2 + \beta^2 + \tau^2} \right) \right|$. Thus $\mathrm{Re}(\lambda_{3,4}) < 0 \iff d\sigma_G^2 > r\beta_G^2 \left(1 - \frac{N^*}{K}\right)$. So the coexistence equilibrium is stable if

$$d\sigma_G^2 > r\beta_G^2 \left(1 - \frac{N^*}{K}\right)$$